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(Continued on back cover)

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Fishery Bulletin

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Notes

EFFECTS OF TEMPERATURE AND SALINITY ON FERTILIZATION, EMBRYONIC DEVELOPMENT, AND HATCHING IN *BAIRDIELLA ICISTIA* (PISCES: SCIAENIDAE), AND THE EFFECT OF PARENTAL SALINITY ACCLIMATION ON EMBRYONIC AND LARVAL SALINITY TOLERANCE[1]

ROBERT C. MAY[2]

ABSTRACT

Eggs and larvae of the sciaenid fish bairdiella, *Bairdiella icistia*, were obtained from fish matured in the laboratory by photoperiod manipulation and induced to spawn by hormone injections. The effects of temperature and salinity on fertilization, embryonic development, hatching, and early larval survival were studied with the material thus obtained, and the effects on gametes of parental salinity acclimation were also investigated. Fertilization took place over a wide range of temperatures and salinities, but was completely blocked at salinities of 10‰ and below. A low level of spermatozoan activity may have accounted for the lack of fertilization at low salinities. Successful embryonic development occurred between temperatures of approximately 20° and 30°C, and salinities of 15 and 40‰. The production of viable larvae was estimated to be optimal at a temperature of 24.5°C and a salinity of 26.6‰. An interaction of the two factors was apparent, development at high salinities being most successful at low temperatures and development at high temperatures being most successful at low salinities. The stage of maturity of the spawning female had a great influence on the overall viability of the eggs produced, as well as on their response to temperature and salinity. Adult bairdiella matured sexually in dilute seawater with a salinity of 15‰, and the salinity tolerance of the eggs produced by these fish was unaltered.

The bairdiella, *Bairdiella icistia* (Jordan and Gilbert), is a sciaenid fish native to the Gulf of California. In 1950 the species was successfully introduced into the Salton Sea, a large saline lake in southern California (Whitney 1961). Salton Sea water has an ionic composition different from that of ocean water (Carpelan 1961; Young 1970), and its overall salinity, now approximately 38‰,[3] is rising at a rate of about 1‰ every 3 yr (U.S. Department of the Interior and the Resources Agency of California 1969). This rising salinity has caused concern that the present sport fishery in the Salton Sea (based on several fish species, including bairdiella) will fail when the upper salinity tolerances of the fishes are exceeded (Walker et al. 1961). Lasker et al. (1972) found that the survival of bairdiella eggs and early larvae was severely inhibited by Salton Sea water at a salinity of 40‰; thus, at the present rate of salinity increase, the bairdiella population may suffer a loss in recruitment within the next 10 yr.

The work reported in this paper was undertaken to provide more information on the salinity tolerance of bairdiella during early development, especially as influenced by temperature and by the acclimation of spawning parents to different salinities. Because of poor embryonic and larval survival in Salton Sea water (May 1972), these experiments were all conducted in seawater of ordinary ionic composition. The effects of Salton Sea water per se and their implications for the population of bairdiella in the Salton Sea will be discussed elsewhere (May in preparation).

Bairdiella normally spawn during April and May in the Salton Sea (Whitney 1961; Haydock 1971). However, thanks to the work of Haydock (1971), bairdiella can be induced to mature and spawn in the laboratory at any time of the year,

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[3]This value varies somewhat with season and location in the Salton Sea.

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making bairdiella eggs and larvae extremely favorable material for experimentation. In addition to providing a year-round supply of eggs, laboratory spawning techniques have permitted maintaining bairdiella at different salinities during maturation and spawning in order to test the effect of parental salinity acclimation on the salinity tolerance of the gametes, embryos, and larvae.

MATERIAL AND METHODS

Capture and Maintenance of Fish

Methods used for collecting and maintaining bairdiella were nearly identical to those described by Haydock (1971). Adult bairdiella were captured with a 60-m beach seine on the west coast of the Salton Sea, just north of the Salton Bay Yacht Club. Rectangular fiberglass tanks of 2,000-liter capacity were used to hold fish in the laboratory and were supplied with continuously flowing warm (22°C) seawater from the Southwest Fisheries Center system (Lasker and Vlymen 1969). Water was filtered through polypropylene GAF[4] snap-ring filter bags of 50-μm pore size (GAF Corp., Greenwich, Conn.). Mercury lamps provided illumination (Haydock 1971) and the photoperiod was controlled as desired by timers.

The fish were fed ad libitum twice each day with ground squid, supplemented by ground red crab, *Pleuroncodes planipes*, at a ratio of approximately 1 part of crab to 6 of squid (wet weight). The red crabs were intended as a source of carotenoids because some authors have indicated that parental carotenoid deficiency may affect the viability of offspring (Hubbs and Stavenhagen 1958).

Several outbreaks of the parasitic ciliate, *Cryptocaryon irritans* Brown, occurred (Wilkie and Gordin 1969) and were effectively controlled by adding copper sulfate at 0.2 ppm as Cu^{2+} in the morning and late afternoon, allowing the chemical to be diluted in the interim by the continuously flowing seawater. Whenever fish were handled, they were subsequently treated with Furacin antibiotic (Eaton Veterinary Laboratories, Norwich, N.Y.) at 130 ppm, which was gradually diluted in the open seawater system. This precaution effectively controlled bacterial infections and allowed repeated handling of fish without adverse consequences.

Induced Maturation and Spawning

Fish which had ripe gonads when captured were maintained in this condition for several months by exposing them to a photoperiod of 16 h light, 8 h darkness (16L:8D) at approximately 22°C (Haydock 1971). Prolonged exposure of female fish to long days resulted in eventual resorption of the ova. After a group of fish had been spawned out or had begun gonadal resorption, they were shifted to a short photoperiod (9L:15D) and colder water (15°C). After being held on short days for a few months, fish could then be brought to maturity by increasing the photoperiod at a rate of 30 min per day until 16L:8D was reached; after about 3 mo on 16L:8D at 22°C, the fish had developed mature ovaries and were ready to spawn. Successful spawning could be induced over a period of at least two or three more months before gonadal resorption began. Photoperiod manipulation was effective in inducing ovarian maturation regardless of the time of year, and the experiments described in this paper were conducted in the summer, fall, and winter instead of during the normal spring spawning period.

Bairdiella kept in the laboratory vary considerably in their ovarian development (Haydock 1971). In the present study the maturity of female fish was assessed from ovarian biopsies taken with a glass capillary tube (Stevens 1966). At first only the maximum oocyte diameters were recorded immediately after sampling, along with qualitative notes concerning the amount of ovarian stroma in the sample. When it became apparent that this was not a sufficiently sensitive measure of the state of maturity, the samples were preserved in 3% Formalin (in 50% seawater) and all oocyte diameters of 175 μm or greater were measured with an ocular micrometer a day or so later,[5] giving an oocyte size-frequency distribution based on measurements of approximately 100 oocytes. The fish which had been biopsied in this manner were marked individually on the lower jaw with injections of the dye, National Fast Blue 8GXM (= Fast Turquoise PT) (Kelley 1967; Haydock 1971).

Mature female fish weighing 100-150 g were injected in the epaxial musculature near the dorsal fin with 100 IU of gonadotropin from pregnant mare's serum (PMS; Sigma Chemical Co., St. Louis, Mo.) in a carrier of Ringer's solution, after

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]No measurable oocyte shrinkage occurred even after a week of preservation.

being anesthetized with MS-222 (tricaine methanesulfonate) at 150 ppm. Haydock (1971) found that salmon pituitary glands and PMS were both effective in inducing ovulation in bairdiella. PMS was used here because it had a standardized activity and was more readily available and easier to prepare than salmon pituitaries. The injected fish were checked for ovulation 30 h after injection and at hourly intervals thereafter until ovulation took place (Haydock 1971). In the vast majority of cases, ovulation occurred 30 or 31 h after the hormone injection. Spawning bairdiella of the size used in these experiments will yield 100,000 or more eggs (Haydock 1971). Male fish remained in a running ripe condition in the laboratory and did not require hormone injections. Bairdiella do not spawn spontaneously in captivity, whether injected or not, and gametes must be obtained by stripping. Haydock (1971) demonstrated that eggs must be fertilized 1 or 2 h after ovulation if maximal viability is to be retained.

Fertilization

Approximately 1,000 to 3,000 eggs were squeezed from an anesthetized, freshly ovulated female and added to a petri dish containing 75 ml of water of the desired temperature and salinity. When fertilizations under a number of conditions were to be made, eggs were added to all petri dishes before sperm was added. Sperm from a lightly anesthetized male fish was taken up in a pasteur pipette which was immediately filled and flushed with water from a petri dish containing eggs. Eggs and sperm were swirled in the dish for several seconds. This procedure was repeated for every dish, fresh sperm being obtained each time. After cleavage had begun, random samples (usually 100 to 300 eggs) were taken from each petri dish, preserved in 3% Formalin and later examined, and the number cleaving recorded. The percentage of eggs cleaving was taken as the percentage fertilized.

Spermatozoan activity was measured in various salinities by placing a drop of sperm under a cover slip, focusing on it with a compound microscope at 430× and adding seawater of the desired salinity. At frequent intervals after hydration, the activity of spermatozoa was rated on an arbitrary scale of 0 to 5, 0 being no activity and 5 being maximal activity. All such tests were conducted at approximately 25°C. More than 70 runs were made utilizing spermatozoa from nine fish, each run comprising between 4 and 15 observations, depending on the duration of activity.

Incubation

Developing eggs from the fertilization dishes were counted out by pipette under a dissecting microscope, rinsed with clean water of the test salinity to remove sperm, and transferred to incubators. The transfer of eggs was usually completed by the time the blastula stage had been reached, within 3 or 4 h after fertilization. One hundred developing eggs were placed in each incubator, and there were two replicate incubators for each experimental treatment. Each incubator (Figure 1) consisted of a 400-ml Pyrex beaker with an insert made from a truncated polypropylene beaker with its bottom covered by Nitex nylon mesh (350-μm mesh opening). Three hundred milliliters of water were added to each incubator. A slow stream of air bubbles in a centrally positioned glass tube created a flow of water such that eggs which rested on the bottom at low salinities were bathed by a continuous flow of aerated water (Figure 1).

One or two days before each experiment, seawater with a salinity of approximately 60‰ was made by adding artificial sea salts ("Instant Ocean"; Aquarium Systems, Inc., Wickliffe, Ohio) to HA Millipore-filtered seawater. This solution was filtered through paper (Whatman No. 1) to eliminate a residual cloudiness and then diluted with deionized water to the desired test salinities. Batches of seawater were aerated for several

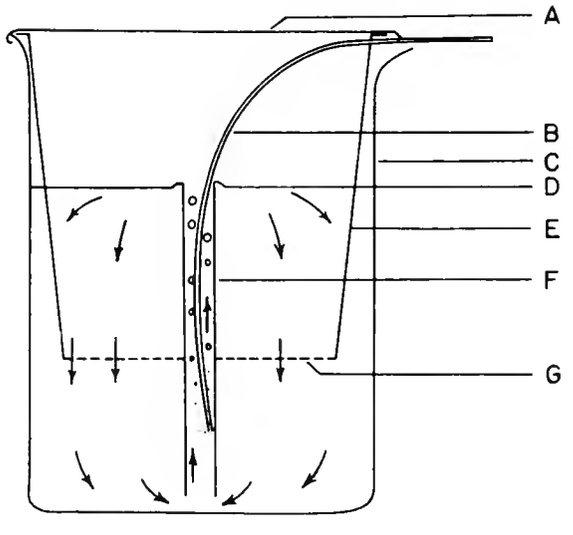


FIGURE 1.—Egg incubator. A) Parafilm cover; B) polyethylene air tube; C) 400-ml Pyrex beaker; D) water line; E) 250-ml polypropylene beaker, cut off at bottom; F) glass chimney; G) Nitex mesh. Arrows indicate direction of water flow.

hours before each experiment to stabilize oxygen tension and pH. Potassium penicillin G (50 IU/ml) and streptomycin sulfate (0.05 mg/ml) were added to the water just before it was placed in the incubators. Salinities were calculated by multiplying chlorinity values (Schales and Schales 1941) by 1.80655 (Johnston 1964) and remained within ±0.5‰ of the original salinity during an experiment. Temperatures were maintained within ±0.2°C of the desired value by immersing petri dishes and incubators in water baths equipped with cooling coils and thermostatically controlled heaters. The incubators were illuminated continuously from fluorescent room lamps which gave an intensity of from 320 to 480 lx at the water surface. Dissolved oxygen concentration in the incubators decreased with increasing temperature and salinity, and measured concentrations were within 2 or 3% of the saturation values given by Kinne and Kinne (1962). The highest oxygen content (at 18°C and 15‰) was 6.24 ml/liter, and the lowest (at 30°C and 55‰) was 4.05 ml/liter. The pH in the incubators increased with increasing salinity and decreasing temperature, varying between 8.08 and 8.27.

The percentage hatching and the condition of the larvae at hatching were recorded for each incubator. Supplementary containers (20-ml petri dishes) with 30 fertilized eggs each, were provided at each treatment to allow examination of eggs during development without disturbing the eggs in the incubators. Hatched larvae were not fed; some were kept in 400-ml beakers (without the polypropylene inserts used prior to hatching) and the pattern of mortality of the starved larvae recorded, and some were used in experiments on the temperature and salinity tolerance of yolk-sac larvae (May 1972).

During an early experiment, histological preparations were made of newly hatched larvae from different salinities at 25°C. Larvae were fixed in Bouin's solution, dehydrated in ethanol-normal butyl alcohol, embedded in paraffin, and sectioned transversely at 8 μm. Sections were stained with Mayer's hemalum and eosin.

Experimental Series

Two series of experiments on fertilization success, embryonic development, and hatching success were conducted, each series involving observations at 25 different combinations of temperature and salinity. Each series included two separate hormone-induced spawnings of fish held under identical conditions. The two spawnings in each series constituted a composite factorial array of treatments (a 3 × 5 plus a 2 × 5 factorial); this design, similar to those employed by Alderdice and his colleagues (Alderdice and Forrester 1967, 1971a, b; Alderdice and Velsen 1971), allowed coverage of a large factor space without utilizing all possible combinations of treatments. The ranges of temperature and salinity employed covered the viable ranges for bairdiella eggs, as determined in preliminary experiments. Table 1 indicates the temperatures and salinities in which eggs were fertilized and incubated in the two spawnings of each series.

The fish utilized for Series A were captured toward the end of the spawning season in the Salton Sea on 7 June 1971 and maintained on a 16L:8D photoperiod in 22°C water until the first hormone-induced spawning of the series on 23 August 1971 and the second on 1 September 1971. Ovarian biopsies indicated that the eggs were ready for spawning at this time, but only maximum oocyte diameters were measured and no oocyte size-frequency distributions were obtained. The tests were repeated in a second series of experiments, Series B. A group of fish captured in the Salton Sea on 20 May 1970 was shifted gradually

TABLE 1.—Dates and temperature-salinity conditions for experiments in Series A and B, 1971. There were two spawnings, performed at different dates, in each series; each spawning utilized eggs and sperm from different fish.

Temperature (°C)	Salinity (‰)	Series A		Series B	
		23 Aug.	1 Sept.	25 Nov.	3 Dec.
18	10	x		x	
	20	x		x	
	30	x		x	
	40	x		x	
	50	x		x	
21	15		x		x
	25		x		x
	35		x		x
	45		x		x
	55		x		x
24	10	x		x	
	20	x		x	
	30	x		x	
	40	x		x	
	50	x		x	
27	15		x		x
	25		x		x
	35		x		x
	45		x		x
	55		x		x
30	10	x		x	
	20	x		x	
	30	x		x	
	40	x		x	
	50	x		x	

from a short photoperiod to a 16L:8D photoperiod between 25 June and 10 July 1971. Half of these fish were transferred gradually to 15‰ and allowed to mature in that salinity as described below, while the other half were kept in seawater (approximately 33‰) and used to supply eggs for the Series B experiments. Prior to these spawnings, ovarian biopsies were taken and oocyte size-frequency distributions determined to assure that the fish were fully mature.

Acclimation of Spawning Fish to Low Salinity

These fish came from the same collection as those used to supply eggs in the Series B experiments and were brought to maturity simultaneously with them. The salinity was lowered to 15‰ over a period of 8 days by mixing seawater with an increasing proportion of fresh water. The day length was then increased from 9 to 16 h in 30-min increments, and the temperature was raised from 16° to 22°C over the same period (Figure 2). The tap water had been dechlorinated by passage through a commercial charcoal filter, and the mixed tap water and seawater flowed through the fish tank at 1,000 liters per hour (the same flow rate was maintained in the tank receiving straight seawater). Salinity was monitored daily in the seawater and low-salinity tanks. Variations were relatively slight during the period of gonadal maturation, monthly means ranging from 32.7 to 33.3‰ in the seawater tank and from 15.2 to 15.7‰ in the low-salinity tank.

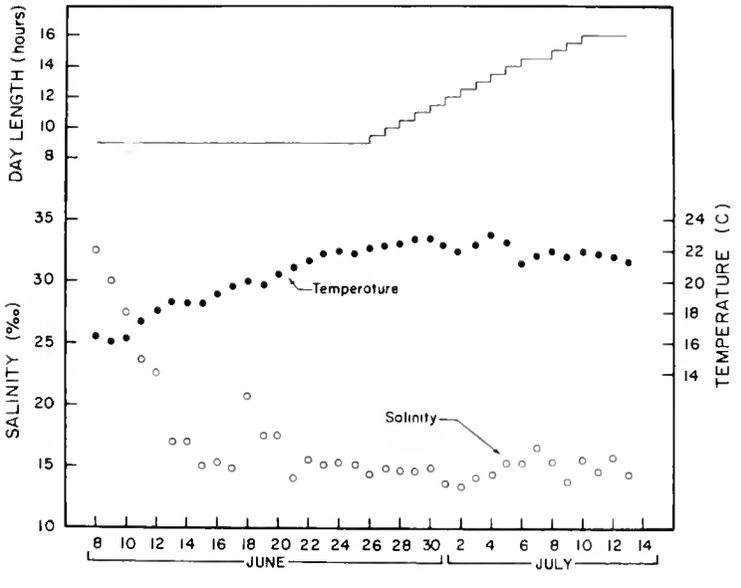


FIGURE 2.—Day length, temperature, and salinity during transition period, when fish were transferred to low-salinity water, warm temperatures, and long days.

Female fish living at 15‰ were injected with PMS on 25 October, 8 November, and 16 November 1971. Eggs were fertilized (with sperm from males also acclimated to 15‰) and incubated as described above, at salinities of 10, 15, 20, 30, 40, 45, and 50‰. The temperature was 24.0°±0.2°C in all experiments with eggs from fish acclimated to low salinity. Hatched larvae were kept in 400-ml beakers at their original salinity to determine the percentage surviving to yolk exhaustion. The activity of spermatozoa from fish acclimated to 15‰ was assessed at various salinities as described above.

RESULTS

Spermatozoan Activity

Bairdiella spermatozoa measured 40 μm in total length, the head being about 2.5 μm long. In distilled water and dechlorinated tap water, spermatozoa showed at most only slight movement, usually in the form of very slow undulations which lasted at least 10 min. After approximately 1 min, the heads of many of these spermatozoa seemed to acquire bright rings, which an oil-immersion lens revealed to be the tail curled around the head, still undulating slowly.

Bairdiella spermatozoa became activated immediately upon contact with seawater (Haydock 1971), and the intensity of activity varied with salinity and time after initial contact with water. Spermatozoa were most active at the higher salinities but remained active longest at the lower salinities. At 10 and 15‰, a small smount of activity remained even as long as 10 min after hydration, but at 10‰ spermatozoa seldom showed activity above level 3 and at 15‰ they only rarely and briefly attained level 5 (Figure 3). At 25‰ all activity ceased by 4 min after hydration, and at 35‰ no activity was usually seen after 3 min. At 45 and 55‰, activity had completely stopped by 1.5 min after hydration. On rare occasions, at salinities between 15 and 55‰, slow undulations of some spermatozoa were observed after other movements had ceased. No difference was noted between spermatozoan activity in seawater and in Salton Sea water, nor between the activity of spermatozoa from fish acclimated to a salinity of 15‰ and from those kept at 33‰. Spermatozoan activity in dilute suspensions of

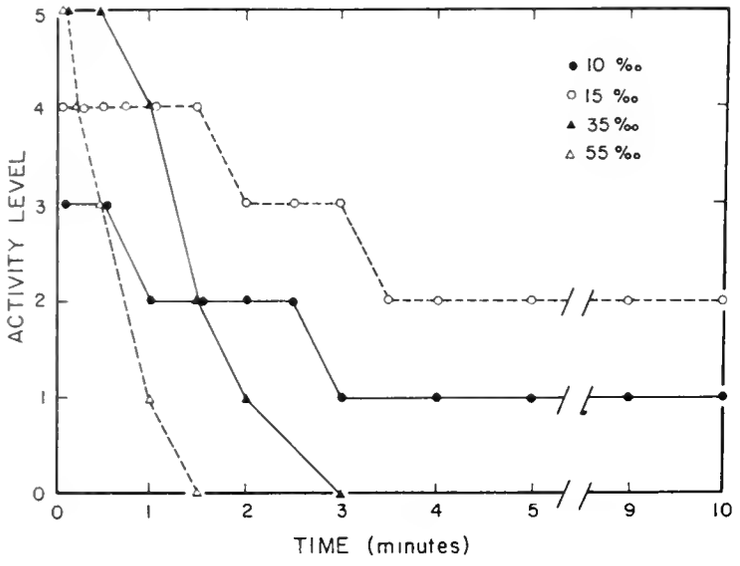


FIGURE 3.—Spermatozoan activity in four salinities as a function of time after hydration. The activity levels are described in the text.

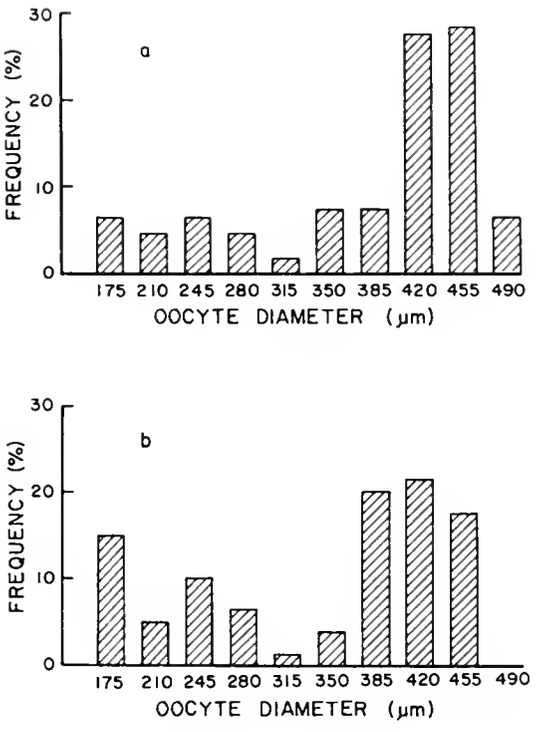


FIGURE 4.—Oocyte size-frequency distributions, based on ovarian biopsies, from fish used in Series B experiments. a) fish spawned on 25 November 1971, b) fish spawned on 3 December 1971.

sperm was the same as when hydration was carried out underneath a cover slip, indicating that the high concentration of spermatozoa in the latter case did not seriously affect the level or duration of their activity.

Maturity of Spawning Fish

Examination of many fish during this project showed that 500 μm was approximately the maximum diameter attained by oocytes in bairdiella before gonadal hydration. During hydration, which occurs in the laboratory only after an injection of gonadotropic hormone, the accession of water swells the eggs to 700 μm or more, the size at spawning. Ovarian biopsies showed that the two female fish used to supply eggs in the Series A experiments had oocytes as large as 500 μm before injection. The oocyte size-frequency distributions for the fish used in Series B (Figure 4) also showed maximum diameters of about 500 μm, and there were modes at 420 to 455 μm for the first fish and 385 to 455 μm for the second in Series B.

The much poorer fertilization and hatching success in Series A (see below) indicates that maximum oocyte diameter is not necessarily a good index of readiness for spawning. By this method it is impossible to tell whether there is a mode at the large end of the size-frequency distribution, as is characteristic of fish which are ready to spawn. The fish used to supply eggs in Series A were probably captured after the peak of spawning in the Salton Sea and their gonads at that time were probably either partly spent or beginning to be resorbed (see Haydock 1971). It was hoped that subsequent exposure to long days would induce ovarian recrudescence, but instead this treatment over a period of 2.5 mo apparently maintained the gonads at a suboptimal state of maturity or allowed them to regress even further (see Haydock 1971). A postspawning refractory period (Harrington 1959; Sehgal and Sundararaj 1970) may exist in bairdiella, but it cannot be very pronounced, since not only were eggs obtained from these fish after hormone injections in August and September, but at least 60% of the eggs could be fertilized under optimum conditions (see below). The fish used in Series B had completely regressed gonads when they were first exposed to long days in July 1971. By November 1971 or earlier they had developed ovaries capable of producing a large proportion of viable eggs, showing as much as 90% fertilization.

Fertilization

Although fertilization did take place at a salinity of 15‰, it was completely blocked at 10‰ (Table 2). In order to examine this phenomenon further, unfertilized eggs were placed in 10‰ water for various periods of time and then trans-

TABLE 2.—Percentage fertilization at various combinations of temperature and salinity in Series A and B.

Temperature (°C)	Salinity (‰)	Percentage fertilization	
		Series A	Series B
18	10	0	0
	20	14.5	28.9
	30	48.5	81.6
	40	24.4	87.5
	50	14.8	41.6
21	15	13.4	18.4
	25	43.5	69.9
	35	35.8	49.4
	45	38.8	59.9
	55	1.9	52.5
24	10	0	0
	20	63.1	62.3
	30	43.2	87.8
	40	7.4	81.3
	50	5.7	50.8
27	15	33.7	30.3
	25	52.6	77.2
	35	60.1	76.7
	45	16.8	82.0
	55	0	67.4
30	10	0	0
	20	48.7	74.6
	30	15.3	89.8
	40	2.7	68.7
	50	0	23.1

ferred to 20‰ and immediately exposed to sperm. The results (Table 3) showed that 10‰ water did not render the eggs infertile: even after 20 min at 10‰, a large proportion of the eggs could be fertilized at 20‰ and develop to hatching, although there was no fertilization in controls kept at 10‰. It was also found that eggs fertilized at 20‰ could be transferred to 10‰ and develop to hatching (Table 4). Thus the actual process of fertilization was somehow blocked at 10‰.

In Series A, fertilization was much more sensitive to high salinities and there seemed to be a greater temperature-salinity interaction than in Series B, with fertilization being more successful at high salinities when the temperature was low (Table 2). In Series B, at salinities above 10‰,

TABLE 3.—Effect of exposure to 10‰ water for various periods of time on fertilizability of bairdiella eggs at 20‰. At each time interval, between 200 and 400 eggs were transferred from 10 to 20‰, exposed to sperm, and later examined for fertilization. Thirty fertilized eggs from each group were followed until hatching.

Time at 10‰	Fertilized at 20‰ (%)	Hatching at 20‰ (%)
45 s	92.5	60.0
2 min	90.2	66.7
5 min	75.4	74.2
10 min	48.4	43.3
20 min	44.8	75.9

TABLE 4.—Survival and hatching of fertilized eggs transferred from 20‰ to 10‰ at various stages. Eggs were incubated in 20-ml petri dishes. The stages are described in Table 6.

Stage at transfer	Number of eggs transferred	Survival to stage VI (%)	Hatching (%)
IIe	30	96.7	63.3
IV	31	93.6	41.9
V	30	100	66.7
VII	29	—	62.1

fertilization was in nearly all cases over 50%, the few exceptions being at low temperature/low salinity and high temperature/high salinity combinations. A maximum of 89.8% fertilization was observed at 30°C-30‰ in Series B. The thermal limits for fertilization in Series B were evidently beyond the range tested (18°-30°C).

Normal Development

It will be helpful to outline the normal pattern of development of bairdiella eggs before discussing alterations in this pattern induced by various combinations of temperature and salinity. Newly spawned bairdiella eggs are approximately 725 μm in diameter and contain an oil globule with a diameter of about 18 μm. Occasionally there are two or three smaller oil globules instead of a single one. Like most pelagic eggs, bairdiella eggs float with the animal pole downward. The development of *Bairdiella icistia* eggs (Table 5, Figure 5) follows the pattern typical for small pelagic fish eggs and is not greatly different from that of *B. chrysura* as described by Kuntz (1915). Ahlstrom's numerical designation of developmental stages (Ahlstrom 1943) has been adopted here (Table 5), although some slight modifications of his scheme were necessary, and some of the stages have been broken down into substages. The times required to reach certain stages are listed (Table 5) for eggs at 33‰ at 25°C, based on observations made during a preliminary experiment in 1970. The newly hatched larvae are approximately 1.7 mm in length (snout to tip of notochord) and in ordinary seawater float upside down near the surface of the water.

Incubation Time

The time between fertilization and hatching varied with temperature and with salinity, and the patterns of hatching determined from the supplementary containers in Series B are shown in

TABLE 5.—Normal development of bairdiella eggs. Designation of stages in general follows Ahlstrom (1943), and times required to reach various stages are given for eggs in 33‰ water at 25°C.

Ahlstrom stage	Sub-stage	Approximate time after fertilization	Description
I	a	—	Unfertilized egg
	b	2 min	blastodisc
II	a	40 min	2 blastomeres
	b	50 min	4 blastomeres
	c	60 min	8 blastomeres
	d	2 h	Morula
	e	3 h	Blastula, periblast very apparent
III	a	6 h	Early gastrula, germ ring encircles as much as 1/3 of yolk, embryonic shield rudimentary
	b	7 h	Mid gastrula, embryonic shield expands, germ ring encircles as much as 2/3 of yolk
IV		8 h	Late gastrula, primitive streak forms
V		9 h	Blastopore closes, optic vesicles and Kupffer's vesicle form
VI	a	10 h	Somites begin to form; scattered melanophores appear, most dorsally behind optic vesicles, a few extending posteriad along notochord
	b	12 h	Lens and otic vesicles form, tip of tail reaches oil droplet
VII		15 h	Tail has moved beyond oil droplet and lifted off yolk; finfold apparent
VIII		17 h	Tail well beyond oil droplet; embryo twitches occasionally; heartbeat regular
—		20 h	Hatching

Figure 6. Series A showed similar patterns, but due to poorer survival the data are less complete and are not shown. In Figure 6 the cumulative percentage hatched has been plotted on a probability scale against time on an arithmetic scale; a straight line in this type of plot indicates a normal distribution (Sokal and Rohlf 1969), which is to be expected if differences in hatching time are due simply to random individual variation. At 30°C hatching was normally distributed for all salinities, but this was not true at the lower temperatures. At 27°C there was a plateau at 25‰, indicating that the hatching of certain eggs was delayed. At 24°C, hatching was distributed approximately in a normal fashion at 20, 40, and 50‰, but at 30‰ there was an inflection, the rate of hatching being slower after 23 h than before. At 21°C, hatching was distributed normally for 15, 35, and 45‰, but at 25‰ hatching took place in two phases separated by a 3-h period during which no hatching took place.

The time required for 50% of the larvae to hatch, estimated by graphical interpolation, decreased from 35.2 h at 21°C-25‰ to 16.0 h at 27°C-25‰. The estimated time at 50% hatching was slightly later at 30°C than at 27°C, although hatching began 2 h earlier in the former (see Figure 6). No clear-cut effect of salinity on median hatching times is discernible, but Figure 6 shows that hatching was completed more rapidly at the higher salinities (35‰ and above). The duration of hatching (the time between the appearance of the first and last hatched larvae) tended to be greater at the lower salinities and temperatures.

Embryonic Mortality

In certain treatments some surviving embryos failed to hatch but continued to develop within the chorion. Alderdice and Forrester (1971b) introduced the apt term, "postmature unhatched eggs" to describe such cases. Almost without exception, the postmature unhatched embryos were deformed in some way, usually bent and abnormally small. Often in such eggs part of the chorion was eventually digested away (Figure 7f), presumably by hatching enzymes, but the weak embryo was incapable of breaking completely free. Postmature unhatched eggs were most common at the low salinities, and the greatest proportion occurred at 30°C-20‰ (Table 6).

Eggs in Series A showed much higher mortality than those in Series B, especially at the higher temperatures and salinities (Table 7). The following description of embryonic mortality refers primarily to the eggs in Series B, which are considered more representative of normal, healthy eggs. The higher mortality in Series A usually showed up very early in embryonic development (prior to stage V); otherwise the two series showed similar trends.

No eggs hatched at 18°C and nearly all died during stage IIe (blastula). After the second cleavage at 18°C the blastomeres assumed a cloverleaf appearance which was not seen at higher temperatures (Figure 7; cf. Figure 5). Subsequent cleavages at 18°C were rather irregular, and during the blastula stage much of the cytoplasm gathered into isolated clumps, and the periblast became unusually large (Figure 7). Nearly all eggs stopped developing at this stage.

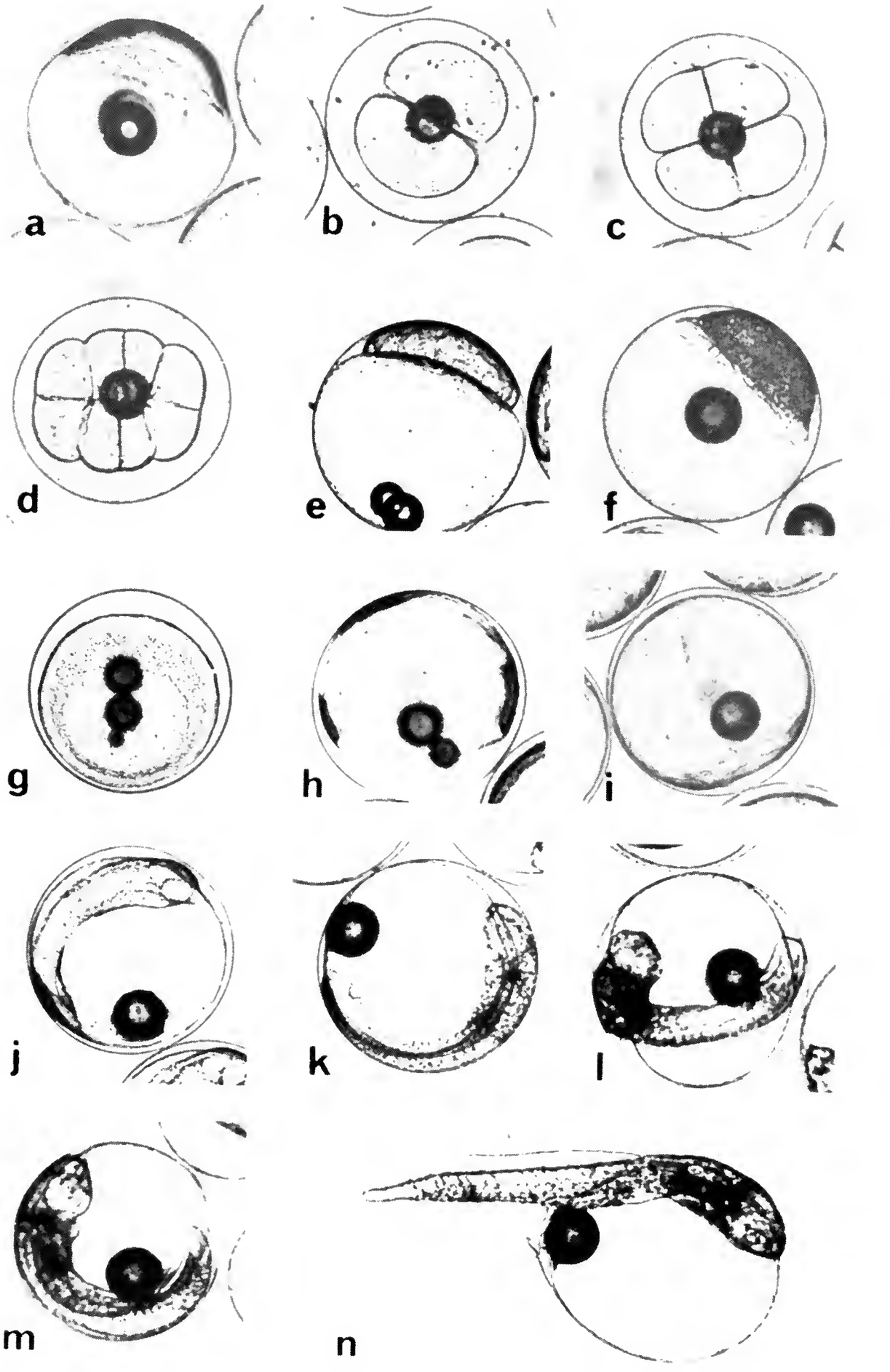


FIGURE 5.—Normal developmental stages of *Bairdiella icistia* at 25°C-33‰. a) stage Ib, 4 min after fertilization; b) stage IIa, 40 min; c) stage IIb, 50 min; d) stage IIc, 60 min; e) stage IId, 2 h; f) stage IIe, 3 h; g) stage IIIa, 6 h; h) stage IIIb, 7 h; i) stage IV, 8 h; j) stage V, 9 h; k) stage VI, 12 h; l) stage VII, 15 h; m) stage VIII, 17 h; n) newly hatched larva.

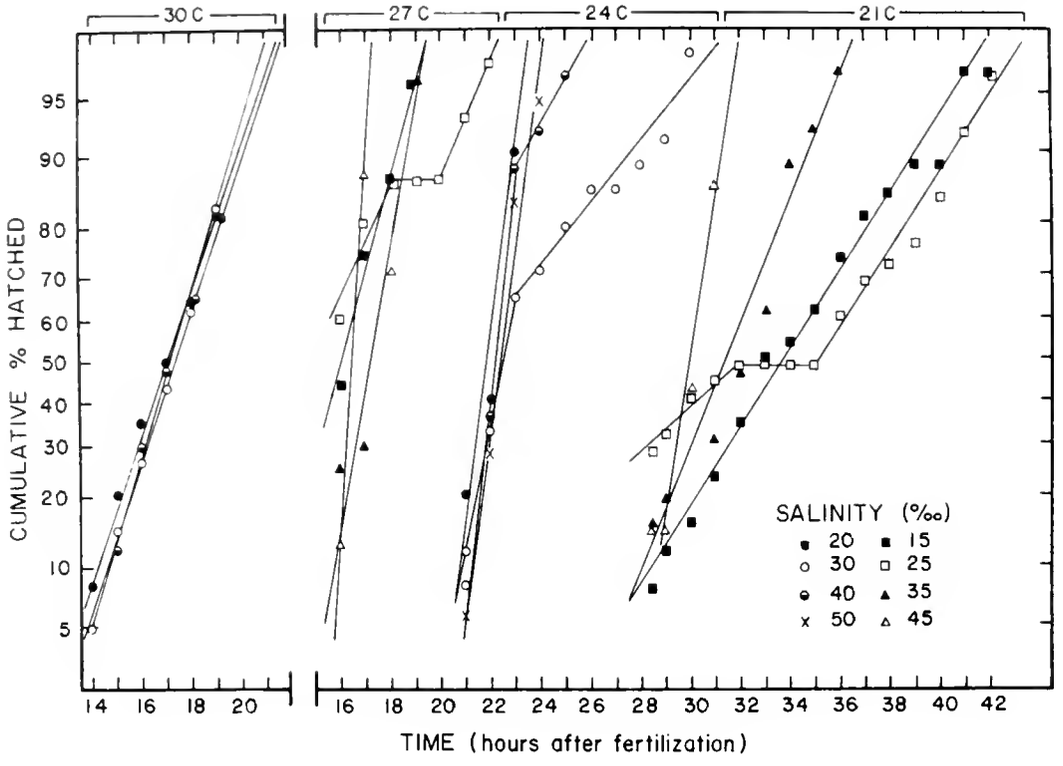


FIGURE 6.—Cumulative percentage of larvae hatching, as a function of time after fertilization, for the Series B experiments. Percentage hatching is plotted on a probability scale; lines were fitted by eye.

TABLE 6.—Percentage of postmature unhatched eggs at various combinations of temperature and salinity in Series B. There are two replicates at each treatment combination. Series A showed similar trends.

Salinity (‰)	Temperature (°C)			
	21	24	27	30
15	17.9		16.4	
	23.5		11.1	
20		19.2		43.4
		13.9		31.8
25	2.1		4.0	
	2.0		3.2	
30		7.8		6.7
		4.4		23.0
35	4.0		7.2	
	7.5		5.2	
40		0		3.1
		0		2.1
45	0		5.5	
	4.0		9.9	
50		0		0
		0.9		0
55	0		0	
	0		0	

TABLE 7.—Percentage total and viable hatch of fertilized eggs in various combinations of temperature and salinity in Series A and B. In each series there were two replicate groups of eggs (a and b) at each treatment combination.

Temperature (°C)	Salinity (‰)	Percentage total hatch				Percentage viable hatch			
		Series A		Series B		Series A		Series B	
		a	b	a	b	a	b	a	b
18	10	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0
	30	0	0	0	0	0	0	0	0
	40	0	0	0	0	0	0	0	0
	50	0	0	0	0	0	0	0	0
21	15	66.7	82.5	88.4	76.5	2.0	7.5	77.9	68.4
	25	25.0	40.4	94.7	92.9	20.0	29.3	77.9	59.7
	35	27.6	37.0	72.7	68.8	16.3	35.0	50.6	38.8
	45	1.9	7.1	72.8	47.5	0	2.0	18.1	11.9
	55	0	0	0	0	0	0	0	0
24	10	0	0	0	0	0	0	0	0
	20	62.6	39.8	96.0	96.0	33.3	23.5	70.0	80.2
	30	34.3	53.5	75.6	89.0	28.3	44.6	63.0	70.2
	40	24.2	51.4	66.3	80.0	10.1	38.3	34.6	53.8
	50	8.0	9.9	66.3	41.2	1.3	2.8	0	0
27	15	67.7	66.0	76.2	89.9	7.1	4.1	68.2	81.1
	25	22.6	34.1	79.8	88.4	22.6	30.6	70.8	81.0
	35	40.9	41.5	78.4	79.2	30.7	29.8	57.5	54.7
	45	11.9	4.5	42.9	31.9	0	1.5	0	0
	55	0	0	1.0	2.0	0	0	0	0
30	10	0	0	0	0	0	0	0	0
	20	12.0	14.4	85.9	73.8	7.0	3.1	38.2	28.6
	30	1.0	1.0	62.2	60.0	0	0	15.2	14.6
	40	0	0.9	4.1	6.2	0	0	0	0
	50	0	0	0	0	0	0	0	0

At 30°C, all eggs died at or before gastrulation at 50‰; at 40‰, a small proportion of the eggs survived the high early mortality but most of these failed to hatch, only 4-6% hatching successfully in Series B (Table 7). At 20 and 30‰ at 30°C, most embryonic mortality occurred after the embryos had developed pigmentation, although at 30‰ abnormal development was apparent in many eggs during cleavage and gastrulation

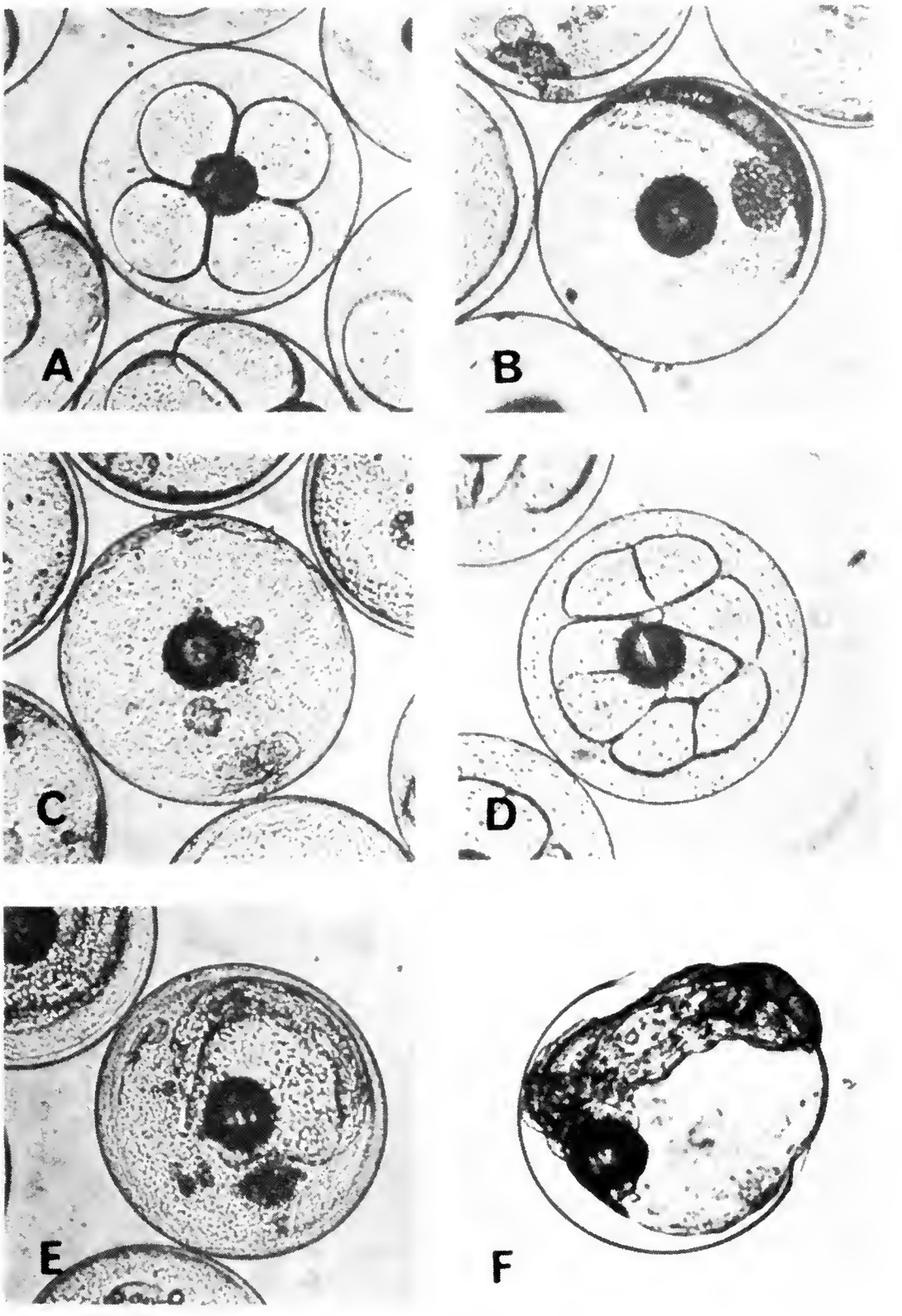


FIGURE 7.—Developmental abnormalities. A) stage IIb, at 18°C-30‰, showing unusual cloverleaf appearance of blastomeres; B) stage IIe, 18°C-30‰, showing enlarged periblast and clumped cytoplasm; C) stage IIe, 18°C-30‰, showing clumped cytoplasm; D) stage IIc, 30°C-30‰, showing irregular cleavage pattern; E) stage IIIa, 30°C-30‰, showing abnormal germ ring and clumping of cytoplasm; F) deformed embryo unable to free itself completely from the chorion, 24°C-20‰.

(Figure 7), and some eggs showed clumping of the cytoplasm similar to that observed at 18°C. Larvae hatching at 30°C were inactive. By following the development of individual eggs in the supplementary containers, it was noted that, no matter what the temperature or salinity, irregularly cleaving eggs usually died before completing gastrulation, and none ever hatched. At 21°, 24°, and 27°C, hatching was generally poorer at the higher salinities (Table 7). At 55‰ virtually no hatching

took place. A maximum of 96% hatching of fertilized eggs was observed at 24°C-20‰.

Deformed Larvae

Immediately after hatching, larvae often had curved bodies reflecting the curvature necessitated by confinement within the chorion (Figure 8), but such larvae soon straightened out. Some larvae, however, had sharply bent or kinked notochords at hatching, a deformity which was irreversible and which prevented normal swimming. These deformities were most common at high salinities (40‰ and above) and at 30°C. In Series A, salinities of 15 and 20‰ produced a high proportion of larvae with a strange deformation, in which the tail was recurved and fused to the trunk (Figure 8). Up to 78% of the larvae hatching at 27°C-15‰ showed this irreversible deformity in Series A, but the figure was only about 15% at 21°C-15‰ and less than 10% at 24°C-20‰; with one or two minor exceptions, other treatments in Series A did not produce this particular distortion, and it was not observed in any treatment in Series B. A greater proportion of late-hatching larvae in a given treatment displayed deformities than early-hatching larvae.

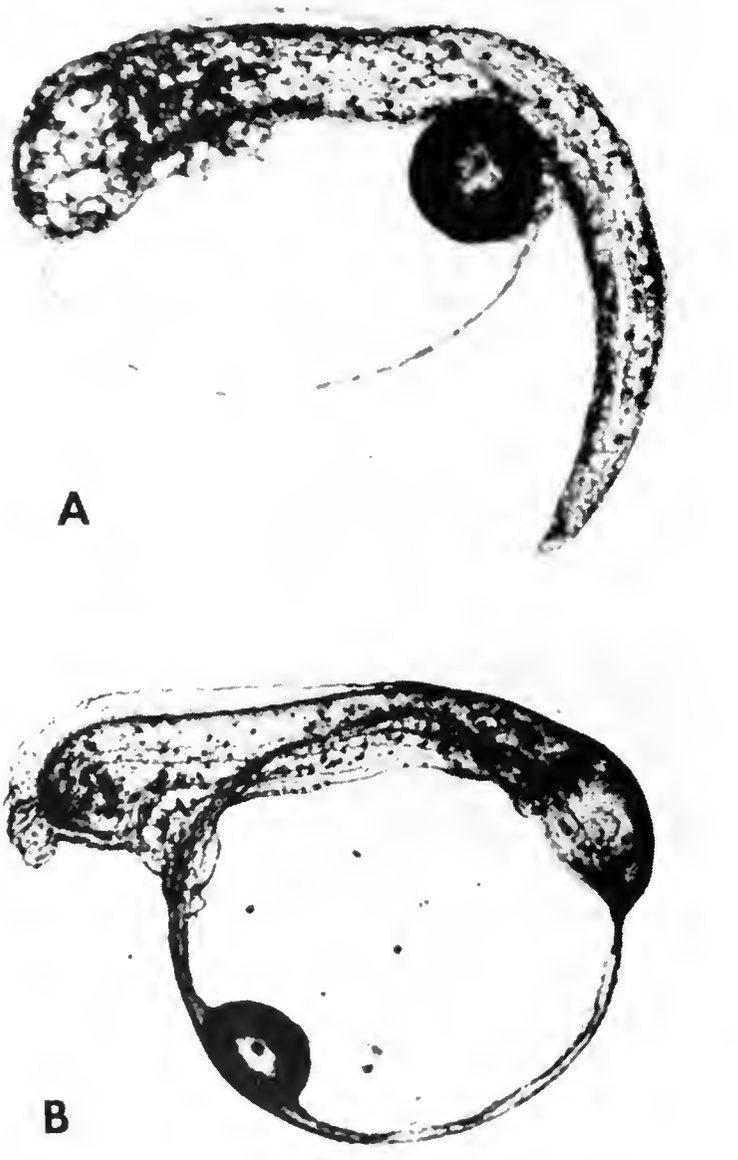


FIGURE 8.—Newly hatched larvae. A) ventral view of a normal larva, showing curvature often seen just after hatching, 24°C-30‰; B) lateral view of a larva with a recurved tail, 24°C-20‰, Series A.

Larvae hatching at 15 and 20‰ showed pronounced edema (Figure 9). Histological sections showed that the size of the subdermal space was inversely related to salinity (Figure 10), an osmotic phenomenon which Battle (1929) also observed in larvae of *Enchelyopus cimbrius*. The yolk sac of newly hatched bairdiella larvae was larger and contained more water at lower salinities (May 1972).

Survival of Starved Larvae

Besides showing deformities, at high temperatures and salinities many larvae died before exhausting their yolk supplies. At 45 and 50‰ all larvae in Series A were dead within 1 day after hatching, and the same was true of the few hatched larvae at 40‰ at 30°C (Figure 11). The time of major mortality and the maximum survival time of starved larvae were inversely proportional to temperature and salinity. Because some of the larvae from Series B were used in tests of temperature and salinity tolerance (May 1972), a complete set of survival curves is not available for them. However, estimates of the percentage of larvae surviving to yolk absorption were obtained from the remaining larvae and from larvae in the least stressful conditions in the tolerance experiments, and these estimates indicated better larval survival in Series B than in Series A. For example, the Series B curves for 27°C (Figure 12) did not show the high mortality before yolk exhaustion at 25 and 35‰ seen in Series A, and a similar difference between the two series occurred at 21°C. At 24°C-40‰, an estimated 70% of the larvae were alive at yolk exhaustion in Series B, compared with only about 20% in Series A. At the highest temperatures and salinities, however, Series B showed heavy early mortality similar to Series A.

Viable Hatch

The percentage hatching of viable larvae (Table

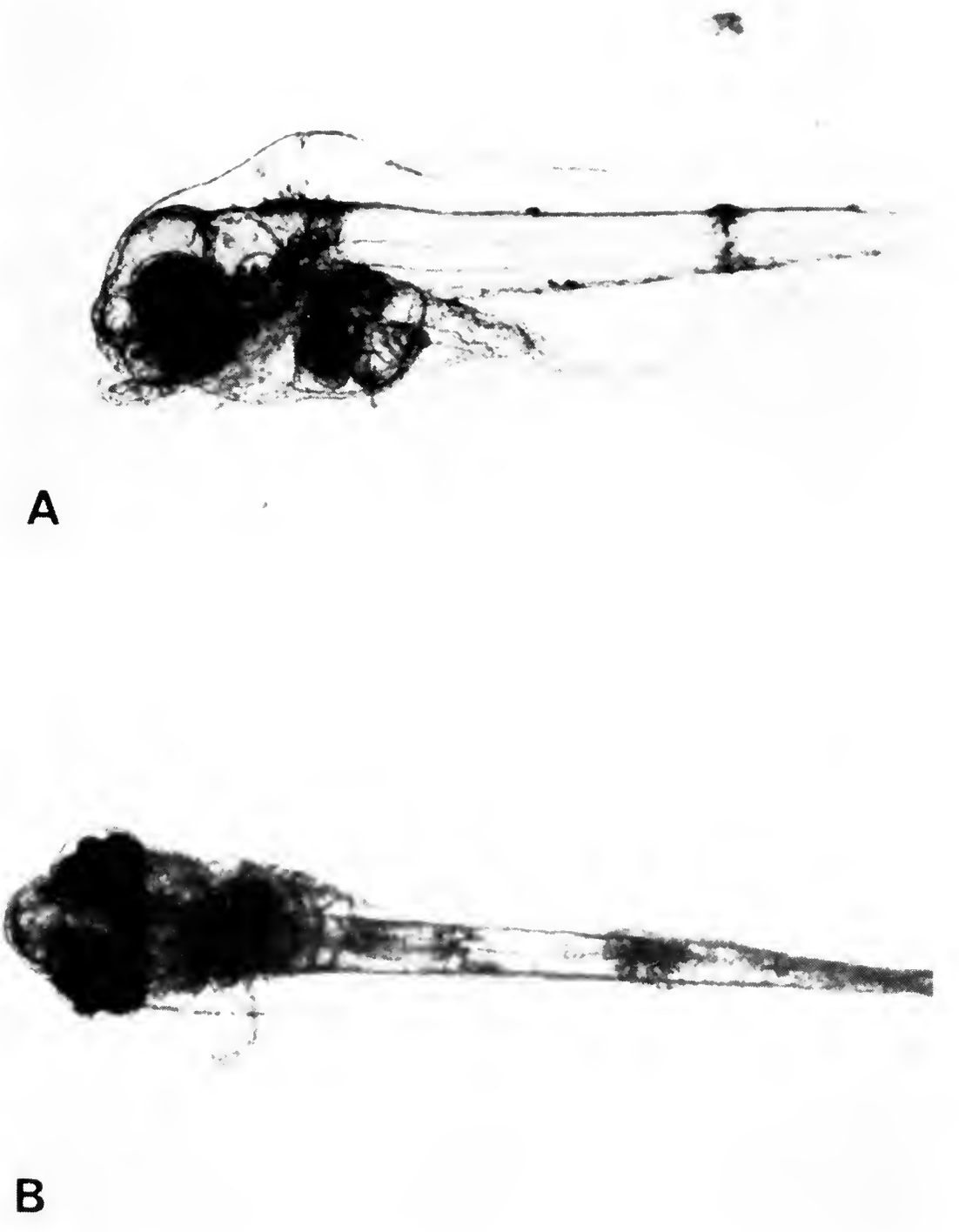
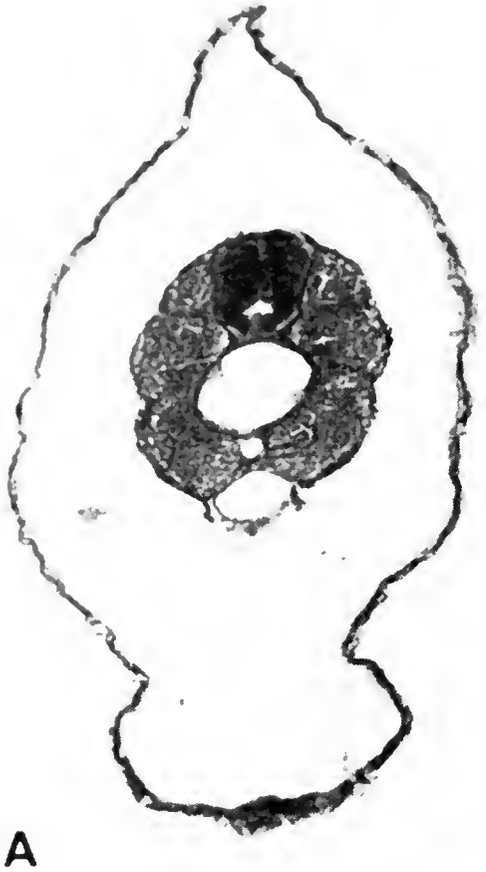


FIGURE 9.—Two-day-old larva, 24°C-20‰, with enlarged subdermal space. A) side view, B) dorsal view.

7), calculated from the preceding information, may be considered the ultimate criterion of successful development in these experiments. Viable larvae are defined here as morphologically normal larvae capable of surviving to yolk absorption, since all other larvae would not survive in nature. Series A showed a much lower viable hatch than Series B at very high and very low temperatures and salinities. Even for the best eggs, it is clear that salinities above 40‰ are detrimental to early survival, and that 30°C is extremely stressful. Survival at higher salinities was considerably better at low temperatures. The various observations on embryonic and larval survival in Series B are summarized (Figure 13) in the manner of Alderdice and Forrester (1967).

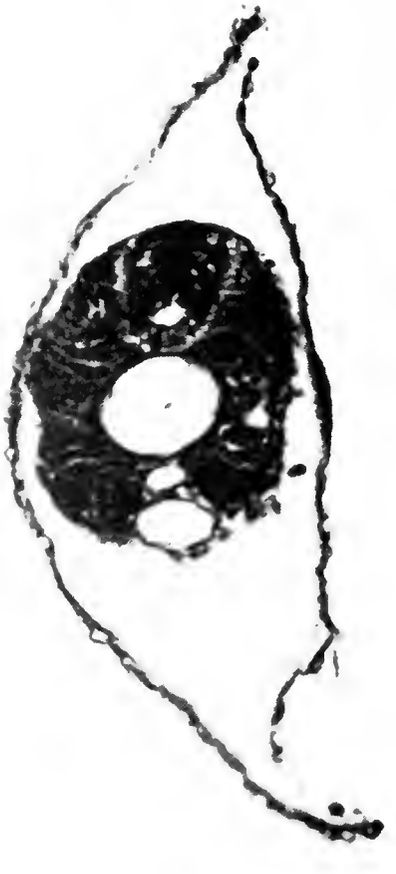
Response Surfaces

It has become customary to describe a biological



A

B



C

D

FIGURE 10.—Transverse sections of newly hatched larvae incubated in various salinities at 25°C. Serial sections were made of each larva, and the sections illustrated were located two sections posterior to the anus. A) 20‰, B) 33‰, C) 45‰, D) 50‰.

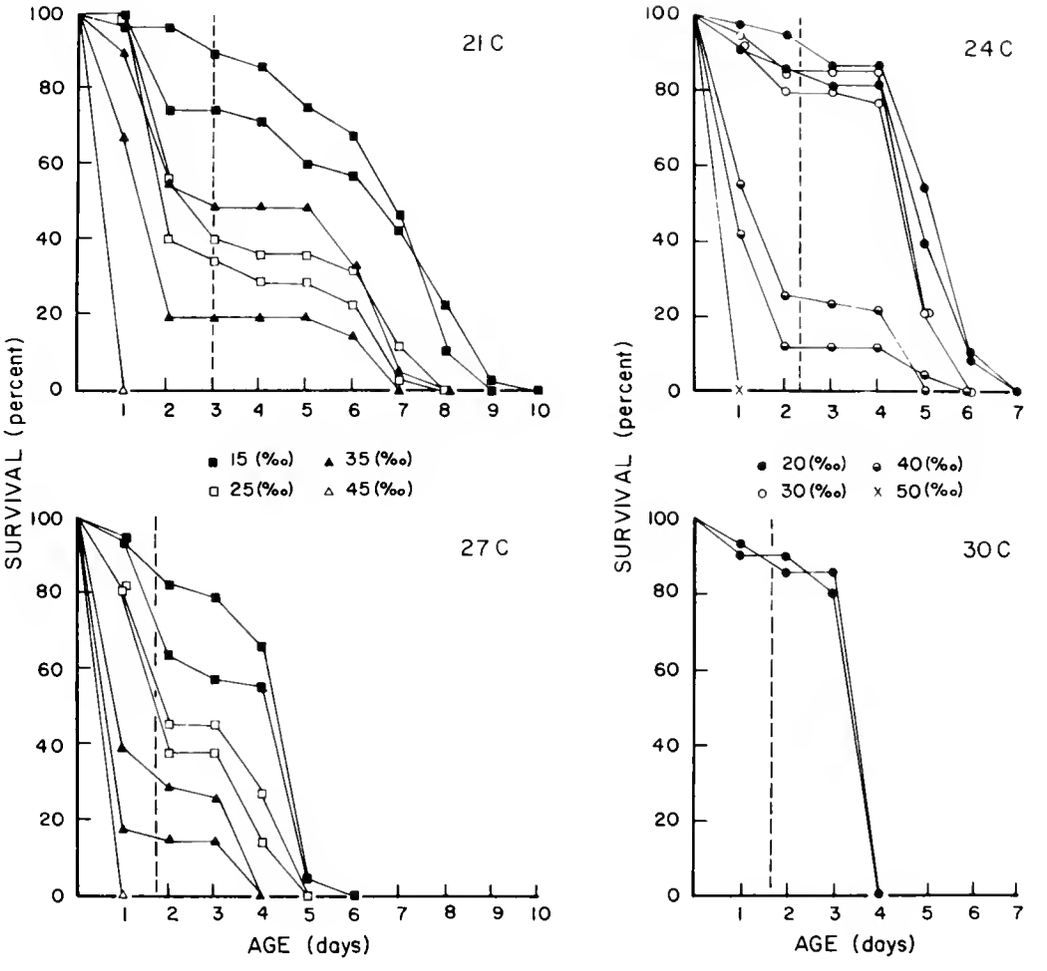


FIGURE 11.—Survival curves for unfed larvae at various temperatures and salinities in Series A. There were two replicate groups of larvae at each treatment, and the vertical dashed lines indicate the time of complete yolk absorption at each temperature.

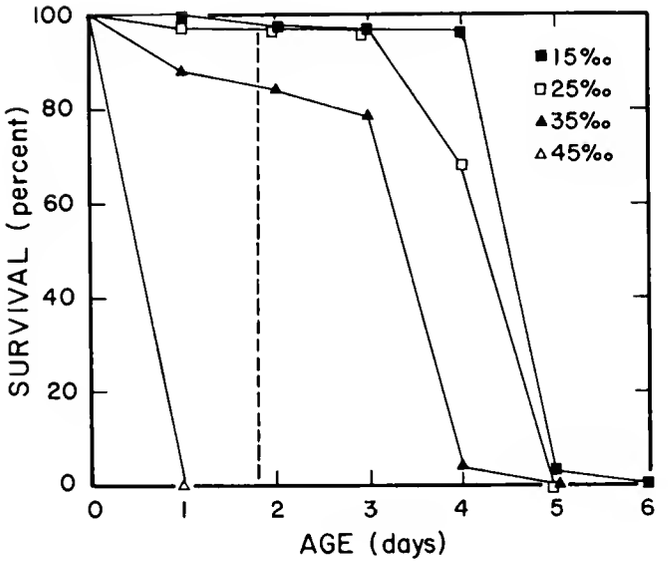


FIGURE 12.—Survival curves for unfed larvae in various salinities at 27°C, Series B. Vertical dashed line indicates the time of complete yolk absorption.

response to temperature and salinity by fitting a second order polynomial to the data and presenting response surfaces calculated from this equation (e.g., Costlow et al. 1960; Alderdice and Forrester 1967; Haefner 1969). This procedure was applied by computer to the results for fertilization, total hatch, and viable hatch, and the resulting equations are given in Table 8. Analysis of variance (ANOVA) showed that, although regression accounted for most of the variance in these data, deviations from regression were highly significant for all equations. This probably reflects the difficulty of fitting a second order polynomial to data of this sort, especially when abrupt thresholds are present, as between 10 and 15‰ and 18° and 21°C. A higher order polynomial, or a nonlinear model (Lindsey et al. 1970), would no doubt yield a better fit. Nonetheless, the second

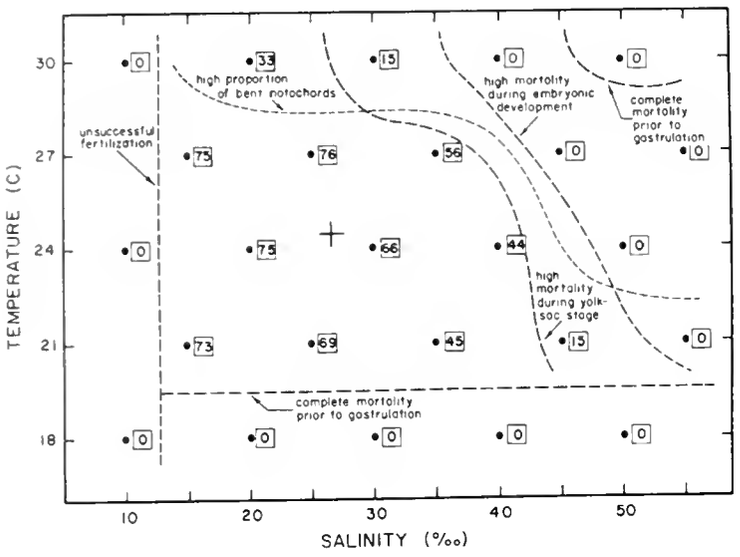


FIGURE 13.—Summary of the effects of temperature and salinity on early development of bairdiella. Closed circles identify treatment combinations utilized in the experiments, and the numbers in squares beside them give the mean values for viable hatch in Series B. The cross marks the estimated position of maximum viable hatch.

significance of interaction by existing statistical techniques.

Acclimation of Spawning Fish to Low Salinity

On 20 October 1971 it was discovered that only 4 of the 26 fish acclimated to 15‰ seawater were females, whereas 15 of the 26 fish at 33‰ were females. The random assignment of fish to the two tanks had somehow resulted in a great disparity in their sex ratios. Two of the four female fish from 15‰ biopsied on 20 October 1971 had well-developed ovaries, showing that gonadal maturation can take place in a salinity of 15‰. The two well-developed females, as well as one of the poorly developed ones, were spawned with hormone injections; the oocyte size-frequency distributions from biopsies of the three fish shortly before injection are shown in Figure 14.

TABLE 8.—Multiple regression equations for percentage fertilization, total hatch, and viable hatch, as functions of temperature and salinity. Y = arcsin (percentage) $^{1/2}$, X = temperature (C), X_2 = salinity (‰).

		Fertilization
Series A:	Y =	$-3.89030 + 0.25964X_1 + 0.10770X_2 - 0.00476X_1^2 - 0.00125X_2^2 - 0.00128X_1X_2$
Series B:	Y =	$-2.76156 + 0.14033X_1 + 0.12125X_2 - 0.00240X_1^2 - 0.00149X_2^2 - 0.00055X_1X_2$
		Total hatch
Series A:	Y =	$-8.55800 + 0.72293X_1 + 0.04177X_2 - 0.01482X_1^2 - 0.00073X_2^2 - 0.00014X_1X_2$
Series B:	Y =	$-13.40397 + 1.06566X_1 + 0.10817X_2 - 0.02115X_1^2 - 0.00157X_2^2 - 0.00070X_1X_2$
		Viable hatch
Series A:	Y =	$-3.91134 + 0.31755X_1 + 0.02932X_2 - 0.00645X_1^2 - 0.00046X_2^2 - 0.00017X_1X_2$
Series B:	Y =	$-9.99277 + 0.81039X_1 + 0.07829X_2 - 0.01620X_1^2 - 0.00117X_2^2 - 0.00066X_1X_2$

order equations are useful in that they allow computation of optimal conditions (Box 1956). The resulting values (Table 9) show a thermal optimum at about 24°C for total and viable hatch in both series, and optima of 23° and 25°C for fertilization in Series A and Series B, respectively. The calculated salinity optimum for fertilization was considerably higher in Series B than in Series A (36 vs. 31‰), but in both series the optimal salinities for hatching were below those for fertilization, ranging from 26 to 29‰. The optimal responses estimated at these points from the equations (Table 9) are below the maximal values actually recorded (cf. Tables 2 and 7), another indication of the lack of fit of the second order polynomial. The calculated positions of the optima, however, are the best available estimates of the true optima. These experiments were designed primarily to cover wide ranges of the two factors under consideration, and the arrangement of treatments unfortunately does not allow testing of the

TABLE 9.—Optimum temperatures and salinities for fertilization, total hatch, and viable hatch, estimated from the regression equations (Table 8). Also listed are the optimum percentage fertilization, total hatch, and viable hatch, calculated from the regression equations at the estimated temperature and salinity optima.

Item	Temperature (°C)	Salinity (‰)	Percentage
Fertilization:			
Series A	23.1	31.3	50.3
Series B	25.1	36.1	85.8
Total hatch:			
Series A	24.3	26.3	47.6
Series B	24.7	28.9	94.3
Viable hatch:			
Series A	24.3	27.4	11.2
Series B	24.5	26.6	67.3

The freezing point depression of blood serum from fish acclimated to 15‰, determined by the melting point method of Gross (1954), was 0.64 ± 0.066°C (mean ± SD, n = 12 fish), and that of fish from 33‰ was 0.63 ± 0.076°C (n = 12 fish). The two groups did not differ significantly, nor was

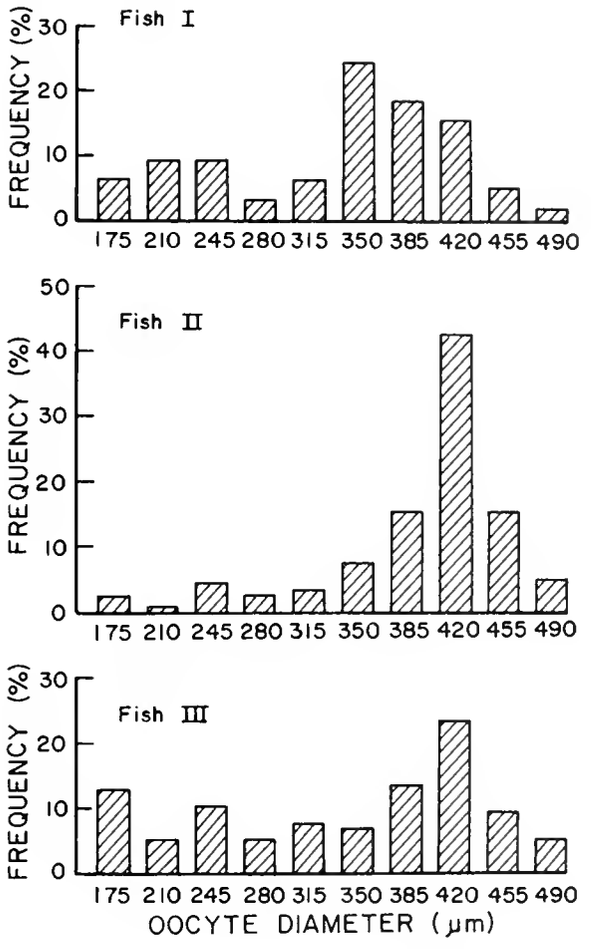


FIGURE 14.—Oocyte size-frequency distributions, based on ovarian biopsies, from fish acclimated to 15‰.

TABLE 10.—Fertilization success for eggs obtained from fish acclimated to 15‰.

Salinity (‰)	Percentage fertilization		
	Fish I	Fish II	Fish III
10	0	0	0
15	19.7	73.8	42.2
20	24.2	89.8	53.4
30	2.5	31.1	88.5
40	0.9	18.7	79.2
45	0	21.2	85.3
50	0	20.4	63.3

TABLE 11.—Percentage total and viable hatch of fertilized eggs at various salinities for eggs from fish acclimated to 15‰. For each fish, there were two replicate groups of eggs at each salinity.

Salinity (‰)	Fish I		Fish II		Fish III	
	a	b	a	b	a	b
			Total hatch			
15	23.4	22.0	87.1	79.8	97.0	92.6
20	30.5	44.2	86.7	86.3	97.0	95.7
30	10.9	2.0	46.9	66.0	97.9	94.9
40	—	—	80.0	80.9	84.8	68.8
45	—	—	71.2	71.4	65.7	76.3
50	—	—	35.9	31.0	22.8	45.8
			Viable hatch			
15	17.0	20.0	66.3	50.5	79.2	72.6
20	27.1	26.9	62.7	70.3	82.7	76.5
30	8.7	0	37.5	49.2	84.3	79.9
40	—	—	43.0	56.1	55.3	44.7
45	—	—	18.1	12.6	19.4	22.9
50	—	—	0	0	0	0

there a significant difference between sexes within each group (Mann-Whitney *U* test; Siegel 1956).

The fish with poorly developed ovaries (Fish I) became listless and swam in a disoriented manner after the hormone injection; 5 days after spawning, it still spent most of its time resting on its side on the bottom of the tank. At this point the fish was sacrificed and dissected, revealing some large, hydrated eggs with coalesced yolk, 665-735 μm in diameter, along with many unhydrated eggs still in their follicles, measuring 350 μm in diameter. Eggs obtained from the hormone-induced spawning of this fish showed low fertility, significant numbers being fertilized only at 15 and 20‰, with a maximum of 24.2% fertilized at 20‰ (Table 10). The hatching success of fertilized eggs was also poor, with a maximum total hatch of 44.2% at 20‰ (Table 11). A few embryos and larvae produced by this fish displayed various degrees of cyclopia, a deformity rarely seen in other batches of eggs.

As expected, the two ripe fish produced much better eggs, with maximum fertilization percentages of almost 90% (Table 10). Eggs from Fish II had a lower optimum salinity than those from Fish III and were more sensitive to high salinities (Table 10). No fertilization took place at 10‰, as was the case with eggs from fish living at 33‰.

Hatching at 15, 20, and 30‰ was better in eggs from Fish III than in those from Fish II, despite the better fertilization success of the latter at 15 and 20‰ (Table 11). Hatching at 40, 45, and 50‰ was comparable in the two batches of eggs. Eggs from Fish II hatched more successfully at 15 and 20‰ than at 30‰, whereas those from Fish III hatched equally well at 15, 20, and 30‰. The incidence of postmature unhatched eggs was similar to that in eggs from Series A and Series B, with most appearing at 15 and 20‰, few at 30‰, and very few or none above 30‰.

The hatching success at various salinities (20, 30, 40, and 50‰) of the best batch of eggs from fish living at 15‰ (i.e., from Fish III) was compared with that of the best batch of eggs from fish at 33‰ (Series B) at the same temperature (24°C) and salinities, by ANOVA (an arcsin-square root transformation was applied to the percentages).

Neither total nor viable hatching success differed significantly between the two groups. Therefore, acclimation of spawning fish to a low salinity did not affect the salinity tolerance of the eggs in any detectable way. Effects of acclimation salinity on egg size and buoyancy will be discussed elsewhere (May in preparation).

DISCUSSION

Fertilization and early development in *Bairdiella icistia* are stenothermal and stenohaline processes. The approximate limits for successful development, from fertilization to yolk exhaustion, are 20° to 28°C and 15 to 40‰, although a certain interaction of the two factors is apparent, development being more successful at the higher salinities when the temperature is relatively low, and at the higher temperatures when the salinity is relatively low. The limits within which successful reproduction can take place are defined by the most sensitive stages and events in development. The lower limit of salinity for bairdiella reproduction is defined by fertilization, since eggs cannot be fertilized at 10‰ or below, even though eggs fertilized at a higher salinity will develop at 10‰. However, the lowest salinity at which eggs remain buoyant may in some cases determine the lower salinity threshold for successful reproduction (May 1972). The upper salinity limit, and both the upper and the lower limits of temperature, are defined by the abilities of the embryos to develop. Fertilization is successful at 18°C but development is not; likewise, fertilization does take place at 30°C, and at salinities of 45‰ and above, but the hatching of viable larvae is greatly curtailed.

Fertilization in bairdiella is more limited by salinity than temperature over the ranges studied. The complete block to fertilization which occurs at 10‰ may be related to an inability of spermatozoa to function properly at this salinity. Although the egg itself seems to be unharmed by water of 10‰, at this salinity spermatozoa never attain the high intensity of activity that they do at higher salinities. At 15‰, where spermatozoan activity is more intense than at 10‰ but less intense than at higher salinities, fertilization occurs but is poorer than at higher salinities. Fairly high salinities seem to aid fertilization: the calculated optimum salinities for fertilization were higher than the optima for hatching in both Series A and Series B. It is possible that low calcium levels at low salinities inhibit the activity of spermatozoa (Yanagimachi and Kanoh 1953). In general, the greater the intensity of spermatozoan activity, the shorter is the overall duration of activity (Figure 3). Thus a shortlived but extremely high level of spermatozoan activity may be necessary for fertilization in bairdiella, perhaps because penetration of the micropyle requires a considerable expenditure of energy on the part of the spermatozoa. This implies that the actual process of fertilization takes place during the first few seconds after hydration of the sperm, when spermatozoan activity is maximal. Haydock (1971) reports that bairdiella spermatozoa are no longer able to fertilize eggs 30 s after sperm hydration. In such a situation, experimental technique could have a marked influence on the success of artificial fertilization, since a delay of a few seconds between hydration of the sperm and contact of the sperm with eggs could significantly reduce the percentage of eggs which become fertilized. A technical problem of this sort may explain the puzzling differences in fertilization success between eggs from Fishes II and III, acclimated to 15‰ (Table 10).

Several previous investigations of salinity effects on spermatozoan activity in other fishes provide interesting contrasts with the present results. Ellis and Jones (1939) found that spermatozoa of Atlantic salmon, *Salmo salar*, a fish which spawns in fresh water, were active for over 180 min in seawater diluted to 15 and 20% and that the duration of activity dropped off sharply above and below these salinities. Working with the longjaw mudsucker, *Gillichthys mirabilis*, Weisel (1948) observed that spermatozoa showed only feeble activity in seawater diluted to 17-24%, but activity was intense in 25% seawater and above; the duration of spermatozoan activity was maximal (over 50 h!) in 25% seawater and decreased at higher salinities, as it did in the case of bairdiella. Yamamoto (1951) found that spermatozoa of the flounder, *Limanda schrenki*, were active in normal seawater and in seawater diluted to 50%, but showed no activity (and no fertilizing capability) in 25% seawater. Hines and Yashouv (1971), on the contrary, found that mullet, *Mugil capito*, spermatozoa exhibited a gradual increase in duration of activity with increasing salinity up to the salinity of normal seawater, rather than a threshold. Dushkina (1973) reported that spermatozoa of Pacific herring, *Clupea harengus pallasi*, were most active at higher salinities (17-23‰), but remained active longest at the

lowest salinities (0.3-0.5‰), as was true for bairdiella; however, in herring the duration of spermatozoan activity was much longer (4-8 days at 6-7°C) and some fertilization occurred even in fresh water. Spermatozoan activity and its response to salinity appear to be extremely variable among fish species, which is hardly surprising in view of the diversity of habitats and modes of reproduction of fishes.

The large proportion of postmature unhatched eggs at low salinities (Table 6) reflects a high incidence of malformations under these conditions, the embryos being physically unable to break from the chorion. Edema seen among larvae in low salinities suggests that deformities and the inability to hatch may be related to osmotic problems. Battle (1929) noted a similar difficulty in hatching among embryos of fourbeard rockling, *Enchelyopus cimbrius*, in low salinities and attributed it to abnormally developed musculature, which prevented movements required to free the embryo from the egg case. An inability to complete hatching at low salinities has been reported for other species as well (Ford 1929; McMynn and Hoar 1953; Alderdice and Forrester 1967; Dushkina 1973). The generalization that gastrulation and hatching are the two developmental stages most sensitive to physical disturbance (e.g., Holliday 1969) seems valid in the case of bairdiella.

The finding that unfed bairdiella survive longest in low salinities and low temperatures is not unique. Nakai (1962) and Hempel and Blaxter (1963) likewise found that starving larvae of *Sardinops melanosticta* and *Clupea harengus* survived longer at lower salinities, and more rapid mortality among unfed larvae at higher temperatures has been observed on a number of occasions (e.g., Qasim 1959; Bishai 1960; Hempel and Blaxter 1963; Alderdice and Velsen 1971; Hamai et al. 1971). High temperatures increase metabolic rate, accelerate yolk absorption (May 1972), and no doubt hasten death from starvation. The effect of high salinities on larval physiology is less certain: a salinity effect on embryonic or larval oxygen consumption has not been demonstrated except after abrupt transfer (Holliday 1969), and salinity has only a small effect on the rate of yolk absorption in bairdiella (May 1972). High salinities may increase larval mortality by causing osmotic or ionic changes in the interior milieu, although the larvae of some species have proved capable of osmoregulating over rather wide ranges of salinities (Holliday 1969). Lower levels of activity have been observed among larvae of some species in low salinities (Hempel and Blaxter 1963; Holliday 1965), and may reduce their metabolic demand and thus extend their survival time (Holliday 1965).

The salinity tolerance of bairdiella eggs is not significantly affected by acclimation of the parent fish to low salinity (15‰). This might suggest that the enhanced survival at low salinities which Solemdal (1967) observed in eggs from the Finnish population of flounder, *Pleuronectes flesus*, has a genetic basis. If acclimation of spawning fish to low salinities does not cause an increase in embryonic tolerance to low salinities, one might expect that high-salinity acclimation would be similarly ineffectual in aiding embryonic survival at high salinities. This supposition should be verified experimentally; but, if valid, it implies that salinity responses determined on eggs from fish living in ordinary seawater should be accurate predictors of reactions to different salinities in nature, except where genetic adaptation has occurred. This could be a significant advantage in cases where it is important to estimate the effects of rising salinities in specified habitats, such as the Salton Sea or the Gulf of California, where high salinities may in the future pose a threat to existing stocks of fish.

Because of the unusual chemical nature of the Salton Sea, it is impossible to estimate the salinity tolerance of bairdiella eggs in Salton Sea water from the present data concerning their responses in ordinary seawater. There is evidence that the ionic composition of Salton Sea water has a deleterious effect on the survival of eggs and larvae (Lasker et al. 1972; May 1972), so that the upper salinity limits defined in the present study are probably higher than those which hold for bairdiella in the Salton Sea.

The spawning season of bairdiella occurs during a period of rapidly rising temperatures. In the Salton Sea this species spawns mainly in April and May, with a peak of spawning probably in mid-May (Whitney 1961; Haydock 1971). Maximum surface temperatures in the Salton Sea are plotted in Figure 15, where the spawning time of bairdiella is also shown. It is clear that some bairdiella may spawn in water of 30°C or higher, although most spawning is probably finished before temperatures reach this level. Whitney (1961) reports finding bairdiella eggs in 1955 as late as 1 August, which means they could have been exposed to the undoubtedly lethal temperature of

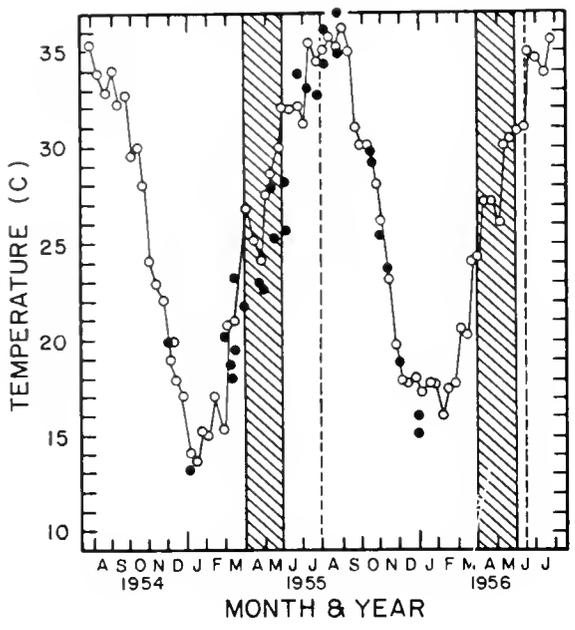


FIGURE 15.—Maximum surface temperatures in the Salton Sea. Open circles: measurements made at Sandy Beach, Salton Sea, from August 1954 to July 1956 (after Carpelan 1961). Closed circles: measurements made at various stations on the Salton Sea during 1967 (after Young 1970). The shaded areas indicate the major spawning period of *Bairdiella icistia*, and the vertical dotted lines indicate the latest records of bairdiella eggs in the plankton in 1955 and 1956, according to Whitney (1961).

35°C. Such late spawning by bairdiella seems unlikely, however, and Whitney may have collected eggs of the orangemouth corvina, *Cynoscion xanthulus*, which spawns during the summer and probably produces similar eggs, rather than bairdiella. In any event, it seems possible that late spawning bairdiella in the Salton Sea could release their eggs in water with a temperature high enough to reduce embryonic and larval survival severely. In view of the temperature-salinity interaction which occurs in the case of both embryonic and larval tolerance, bairdiella which spawn at relatively low temperatures early in the season will probably have a selective advantage as the salinity of the Salton Sea rises.

In the absence of detailed information on the distribution of bairdiella and the physical conditions obtaining in its native habitat, the Gulf of California, it is difficult to apply the present findings to the ecology of this species in that area. However, the utilization of Colorado River water for irrigation has caused an increase in the river's salinity (Wolman 1971); if this, and the accompanying reduced flow of fresh water into the upper Gulf of California, results in a significant rise in salinity in areas where bairdiella spawn, the combined action of salinity stress and heat in this arid region could adversely affect early survival in the local bairdiella population. The warm brine effluent from a proposed desalination plant in this area (Thomson et al. 1969) could aggravate the situation considerably if dispersal of the effluent is not adequate.

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FITTING THE GENERALIZED STOCK PRODUCTION MODEL BY LEAST-SQUARES AND EQUILIBRIUM APPROXIMATION[1]

WILLIAM W. FOX, JR.[2]

ABSTRACT

A least-squares method for fitting the generalized stock production to fishery catch and fishing effort data which utilizes the equilibrium approximation approach is described. A weighting procedure for providing improved estimates of equilibrium fishing effort and an estimator of the catchability coefficient are developed. A computer program PRODFIT for performing the calculations is presented. The utility and performance of PRODFIT is illustrated with data from a simulated pandalid shrimp population.

The production model approach to fish stock assessment is simply an adaptation of the Lotka-Volterra population equations into the situation of a population exploited by man. The earliest such adaptation was by Graham (1935) in assessing the potential production from North Sea fish stocks. The major development of this approach in fisheries management, though, is due to Schaefer (1954, 1957) who initiated it as a management tool for the yellowfin tuna fishery of the eastern tropical Pacific Ocean. While there has been an attempt at a detailed extention of the production model approach to multispecies fisheries (Lord 1971), the usual application has been on a single species stock.

Mathematical formulation of the production model begins with the general differential equation

$$dP/dt = P_t g\,(P_t) - P_t h(f_t) \qquad (1)$$

where P_t is the population size at time t, $P_t g(P_t)$ is the population production function encompassing the effects of reproduction and natural mortality (and growth in weight if biomass is the population unit), and $h\,(f_t)$ is the fishing mortality coefficient exerted by f_t units of fishing effort. Fishing effort is assumed to be standardized from nominal fishing effort such that $qf_t = F_t$, where F_t is the instantaneous coefficient of fishing mortality and q is a constant (the catchability coefficient), giving $qf_tP_t = dC/dt$, the rate of catch. At equilibrium, that is $dP/dt = 0$, the catch rate equals the production rate such that an equilibrium yield, Y, is obtained

$$Y = qfP = Pg(P). \qquad (2)$$

The most general assumptions about the form of $P_t g(P_t)$ are that it should 1) approach zero as P_t approaches some environmental capacity, P_{max}, and 2) increase to some maximum at a population size smaller than the environmentally limited size. Practically, the function should be simple, since in any case the approach is a gross simplification of population dynamics. The most flexible, simple function advanced for $P_t g\,(P_t)$ is a simple case of Bernoulli's equation (Chapman 1967; Pella and Tomlinson 1969)

$$P_t g(P_t) = HP_t^m - KP_t \qquad (3)$$

where H, K, and m are constant parameters.[3] Equation (3) includes the logistic function when $m = 2$ (Schaefer 1954, 1957) and the Gompertz function $[K'P_t - H'P_t \ln P_t]$ as $m \rightarrow 1$ (Fox 1970). Equation (3), hereafter referred to as the generalized stock production model after Pella and Tomlinson (1969), approaches zero at $P_{max} = (K/H)^{1/(m-1)}$ and has a maximum $P_{opt} = [m^{1/(1-m)}] \cdot P_{max}$.

Three equilibrium relationships can be derived by the substitution of Equation (3) in Equation (2) to obtain

1) Yield and population size

$$Y = HP^m - KP, \qquad (4)$$

2) Population size and fishing effort

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[3]When formulated as in Equation (3), H and K are positive for $m < 1$, but are negative for $m > 1$.

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$$P = \left(\frac{K}{H} + \frac{q}{H} f\right)^{\frac{1}{m-1}} \quad (5)$$

3) Yield and fishing effort

$$Y = f\left(\frac{Kq^{m-1}}{H} + \frac{q^m}{H} f\right)^{\frac{1}{m-1}} \quad (6)$$

The critical points, useful as management implications and previously derived by Pella and Tomlinson (1969), are:

$$f_{opt} = K\left(\frac{1}{m} - 1\right)/q \quad (7)$$

$$P_{opt} = [K/(mH)]^{\frac{1}{m-1}} \quad (8)$$

and

$$Y_{max} = H[K/(mH)]^{\frac{m}{m-1}} - [K^m/(mH)]^{\frac{1}{m-1}}, \quad (9)$$

where f_{opt} is the amount of fishing effort required to produce Y_{max}, the maximum sustainable average yield (MSAY),[4] and P_{opt} is the equilibrium population size obtained at f_{opt}. Figure 1 demonstrates the flexibility of the generalized stock production model with three values for m (0.5, 2.0, 4.0); each curve has the same value for P_{max} and Y_{max}.

In utilizing the production model for analysis of the status of a particular population, the usual basic assumptions are that 1) the model is being applied to a closed single unit population, 2) the concept of equilibrium conditions[5] applies to the population under analysis, and 3) the age-groups being fished have remained, and will continue to remain, the same. If one is able to obtain data which represent equilibrium conditions at three or more population levels, then no additional assumptions are needed to fit the production model. In most fishery data sets, however, no real period of equilibrium conditions will exist. Using data from the transitional states of a population requires the additional assumptions that both 1) time lags in processes associated with population change and 2) deviations from the stable age structure at any population level have negligible effects on the production rate, $P_t g\ (P)_t$ (Schaefer and Beverton 1963).

Schaefer (1954, 1957) pioneered the use of transitional state data for fitting a production model (the logistic form) to catch and fishing effort data. Schaefer's (1957) method for estimating the parameters consisted of approximating differential equation (1) with two finite difference equations and then iteratively solving them. Pella and Tomlinson (1969) greatly improved upon Schaefer's method by demonstrating that a catch history of a fishery could be predicted from the fishing effort history, initial estimates of the production model parameters, and the integrated form of Equation (1). Then final parameter estimates could be obtained by a pattern search routine which finds those parameters which minimize the residual sum of squared differences between

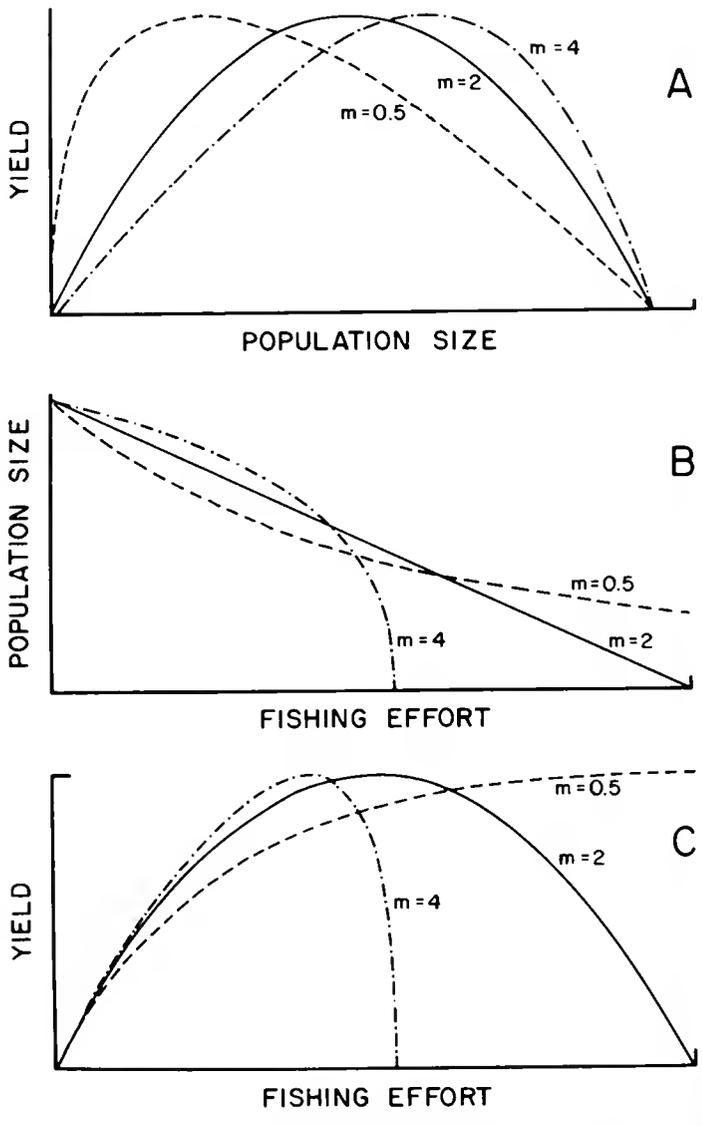

FIGURE 1.—Equilibrium relationships of the generalized stock production model for three values of m. (A) Equilibrium yield and population size; (B) population size and fishing effort; (C) equilibrium yield and fishing effort.

[4] Y_{max} is usually referred to as the maximum sustainable yield (MSY). The term MSY, however, does not convey that in reality the yield will fluctuate due to changes in the population even if the fishing effort and catchability coefficient remain constant. Hence, the "equilibrium yield" curve represents a curve of yield that is sustainable at some average level.

[5] The definition of equilibrium adopted here, essentially that of Beverton and Holt (1957), is: given a constant rate of fishing, including zero, a population will achieve a state where, on the average, it will not change in size or characteristics.

the observed and predicted catches. While these two estimation methods are very different in their degree of sophistication, they are fundamentally the same in that both methods utilize the prediction of population transitional state changes by the production model. For convenience, this approach will be subsequently referred to as the transition prediction approach.

Gulland (1961) established a second approach to fitting production models with transitional state data. Gulland's approach estimates the level of fishing effort which, if equilibrium obtained, would produce, on the average, the observed level of catch per unit effort in each year of the fishery. Then the set of paired catches per unit effort and estimated equilibrium fishing effort units are fitted to one of the equilibrium relationships given by, or derived from, Equation (4), (5), or (6). This approach will be referred to subsequently as the equilibrium approximation approach.

Clearly, the transition prediction and equilibrium approximation approaches are basically different. The transition prediction approach is obviously intimately based upon the transition state population assumptions. On the other hand, the degree to which the equilibrium approximation approach is dependent on these assumptions is unclear. This paper presents a least-squares method and a computer program PRODFIT, which uses the equilibrium approximation approach to estimate the parameters (and indices of their variability) of the generalized stock production model. A weighting procedure for providing improved estimates of equilibrium fishing effort and an estimator of the catchability coefficient are developed. The utility and performance of computer program PRODFIT is illustrated by fitting deterministic and stochastic data from a simulated pandalid shrimp population. Some cursory comparisons between the equilibrium approximation and transition prediction approaches are made by repeating the pandalid shrimp simulated data fits with GENPROD, the computer program written by Pella and Tomlinson (1969).

FITTING METHOD

The equilibrium approximation approach was first outlined in Gulland (1961), but is more fully explained in Gulland (1969:120). Gulland's method involves relating the annual catch per unit effort in year i, U_i, to the fishing effort averaged over some number of years, T. Gulland (1961) first defined T as the mean life expectancy of an individual in the fishable population, or Z^{-1}, where Z is the instantaneous total mortality coefficient and the value of Z^{-1} is rounded off to the nearest integer. Subsequently, Gulland (1969) defined T as the average fishable duration of a year class (again to the nearest whole year)—he provided the following example: if recruitment is at 4 yr and if most of the catch in year i consists of 4 to 9 yr-old fish, then the average fishable duration is about 3 yr so U_i would be related to an average of f_i, f_{i-1} and f_{i-2}. The general formulation for the averaged fishing effort in year i is

$$\bar{f}_i = \frac{1}{T} \sum_{j=i-T+1}^{i} f_j \tag{7}$$

A discussion of the rationale for, and performance of, Gulland's averaging method is given by Gulland (1969:120).

Weighted Average Fishing Effort Method

In this paper a different tack is taken which results in approximating equilibrium fishing effort with a weighted average. The catch per unit effort of the incoming year class j in year i, U_{ij}, is related to the amount of effort in year i; that of the previous year class, $U_{i,j-1}$, is related to the fishing effort in years i and $i-1$; that of the year class which entered 2 yr previously, $U_{i,j-2}$, is related to the fishing effort in years i, $i-1$, and $i-2$; and so forth. The catch per unit effort of the total fishable population, assuming equal catchability, is

$$U_i = U_{i,j} + U_{i,j-1} + U_{i,j-2} + \cdots + U_{i,j-k+1}$$

for k year classes. For the simplest case where the incoming year class is recruited at the beginning of each year's fishing season, therefore,

$$U_i \sim \{k \cdot f_i + (k-1) \cdot f_{i-1} + \cdots + f_{i-k+1}\}. \tag{8}$$

Equation (8) suggests a weighted average of fishing effort over the total number of years that a year class contributes significantly to the fishery, or

$$\bar{f}_i = \{k \cdot f_i + (k-1) \cdot f_{i-1} + \cdots + f_{i-k+1}\} / \{k + (k-1) + \cdots + 1\}. \tag{9}$$

An arithmetic average rather than a geometric average is suggested because most applications are on catch in weight, i.e. while year classes decline exponentially in terms of numbers they concomitantly increase in terms of mean weight per individual.

The weighting procedure can be more precise if it is known when during the year of record that recruitment occurs. For example, if recruitment occurs at midseason during the year of record for a fishable population of three year classes, $\bar{f}_i$ changes from $\left\{3f_i + 2f_{i-1} + f_{i-2}\right\}/6$ to $\left\{2.5f_i + 1.5f_{i-1} + 0.5f_{i-2}\right\}/4.5$. Further precision is gained if k is varied from year to year with the level of fishing effort, since at high fishing rates fewer year classes will contribute significantly to the catch than at low fishing rates. Further adjustments can be made for unequal catchability among the year classes.

The unweighted method of averaging the fishing effort, Equation (7), and the new weighted method, Equation (9), will be compared in a subsequent section of this paper.

Estimation Procedure

Gulland (pers. commun.)[6] prefers an eye-fitted curve for estimating the equilibrium relationship between U_i and f_i because of the oversimplification of the method and the errors associated with usual catch and effort data. However, these reasons should not defer the seeking of a more precise method of fitting a curve nor the taking advantage of error estimation schemes, if the simplifications and assumptions are kept in mind. On the contrary, it will be demonstrated that, at least for some controlled conditions, the equilibrium approximation approach provides reasonably good results.

Equation (5) may be written in terms of catch per unit effort and averaged fishing effort as

$$U_i = [(Kq^{m-1}/H) + (q^m/H)\bar{f}_i]^{1/(m-1)} \quad (10)$$

or simply

$$U_i = (\alpha + \beta \bar{f}_i)^{1/(m-1)}. \quad (11)$$

Equation (11) is a nonlinear function with three parameters which does not require simultaneous estimation of the catchability coefficient, q. The critical points in terms of the parameters of Equation (11) are

$$f_{opt} = (\alpha - \alpha m)/(m\beta) \quad (12)$$

$$U_{opt} = (\alpha/m)^{1/(m-1)} \quad (13)$$

and

$$Y_{max} = \frac{(\alpha - \alpha m)(\alpha/m)^{1/(m-1)}}{m\beta}. \quad (14)$$

Given the data set $\left\{U_i, \bar{f}_i\right\}$, where $i = 1 \ldots n$ observations, the least-squares criterion for estimating the parameters α, β, and m is to minimize the function

$$S = \sum_{i=1}^{n} W_i(U_i - \hat{U}_i)^2 \quad (15)$$

where the W_i are statistical weights, and $\hat{U}_i$ are the predicted equilibrium catches per unit effort from Equation (11). The statistical weights,

$$W_i = (\hat{U}_i)^{-2}, \quad (16)$$

are derived from the assumption of the multiplicative error structure as suggested by Fox (1971). Weighting as in Equation (16) will usually give the greatest weight to observations at the highest level of averaged fishing effort; in many cases these also will be the most recent observations. Giving greater weight to observations at high effort levels will tend to give the greatest weight to observations with the greatest temporal and spatial coverage of the population. In addition, giving the greatest weight to the most recent data is especially advantageous when approaching the Y_{max} level during a period increasing fishing effort because the observations nearest the Y_{max} level receive the greatest weight.

Up to now no mention has been made on the estimation of the catchability coefficient, q. This is because experience with GENPROD and stochastic simulation studies have indicated that poor results are frequently obtained from the simultaneous estimation of q (Pella and Tomlinson 1969; Fox 1971). Once that α, β, and m have been estimated, q may be treated as a conditional probabilistic variable and estimated as a mean value. Two tacks were selected, the difference method and the integral method.

[6]John A. Gulland, Food and Agricultural Organization, Rome, Italy.

The difference method involves writing Equation (1) as a finite difference equation for the production model in terms of catch per unit effort and the estimates for α, β, and m as

$$\frac{1}{q}\frac{\Delta U_i}{\Delta t} = \frac{1}{\hat{\beta}} U_i^{\hat{m}} - \frac{\hat{\alpha}}{\hat{\beta}} U_i - f_i U_i \qquad (17)$$

for each year i; Δt is taken as one unit, Equation (17) is divided through by U_i, summed over the $n - 2$ yr that ΔU_i can be estimated, and then solved for $\hat{q}_S$,

$$\hat{q}_S = \left[\sum_{i=2}^{n-1} \frac{\Delta \hat{U}_i}{U_i} \right] / \left[\frac{1}{\hat{\beta}} \sum_{i=2}^{n-1} U_i^{\hat{m}-1} - (n-2)\frac{\hat{\alpha}}{\hat{\beta}} - \sum_{i=2}^{n-1} f_i \right] \qquad (18)$$

where

$$\Delta \hat{U}_i = (U_{i+1} - U_{i-1})/2. \qquad (19)$$

This method has provided reasonable estimates with the logistic ($m = 2$) and Gompertz ($m \rightarrow 1$) forms of the production model for several fisheries (Fox 1970).

Pella and Tomlinson (1969) observed that Equation (19) can be a poor estimator of the change in stock size during year i under certain circumstances. The integral method avoids this problem by writing Equation (17) as a differential equation

$$\frac{dU}{U\left(-\frac{\hat{\alpha}}{\hat{\beta}} - f^* + \frac{1}{\hat{\beta}} U^{\hat{m}-1}\right)} = q\, dt, \qquad (20)$$

where f^*, the effective effort having been exerted between years i and $i+1$, is estimated by

$$\hat{f}^* = (f_i + f_{i+1})/2. \qquad (21)$$

The integral of Equation (20) after rearranging some terms is

$$\hat{q}_I = \ln\left[\left| (zU_t^{1-\hat{m}} + \frac{1}{\hat{\beta}}) / (zU_{t+1}^{1-\hat{m}} + \frac{1}{\hat{\beta}}) \right| \right] / (z\hat{m} - z) \qquad (22)$$

where

$$z = -\hat{\alpha}/\hat{\beta} - \hat{f}^*.$$

The fact that Equation (22), as an estimator of q, gives negative values when the stock changes in one direction, depending on whether m is greater or less than 1, is remedied by taking the absolute value of q. Also, since q is constrained against being less than zero, the geometric mean will probably be a better estimator than the arithmetic mean (this will be demonstrated to be so in at least one case), such that

$$\hat{q}_I = e^{\sum_{i=1}^{n-1} \ln|\hat{q}_i| / (n-1)} \qquad (23)$$

becomes the integral estimator.

Variability Measures

Some measure of the variability of the parameter estimates can be made using the "delta" method (Deming 1943). If S is the weighted residual sum of squares for the final parameter estimates, a variability index matrix, V, is computed by

$$V = (X'WX)^{-1} S/(n-3) \qquad (24)$$

where W is an n by n diagonal matrix of the statistical weights, X is an n by 3-parameter matrix of first partial derivatives of Equation (11) with respect to each parameter (given in the Appendix). The diagonal elements of V are variability indices of the parameter estimates and the off-diagonal elements of V are covariability indices. Since Equation (11) is nonlinear, the independent variable is not without error, the errors in the dependent variable are correlated, and the statistical weights are random variables, it is virtually impossible to make probability statements about the accuracy of the parameter estimates (Draper and Smith 1966). However, V gives some index of the variability inherent in the data which is useful largely for comparative purposes between different fisheries and data sets. For convenience, an error index may be formulated as

$$E_{\hat{x}} = [100\sqrt{V(\hat{x})}]/\hat{x} \qquad (25)$$

where $\hat{x}$ is the estimated parameter and $V(\hat{x})$ is its corresponding variability index. Variability and error indices of Y_{max}, f_{opt}, and U_{opt} also may be computed by the "delta" method (see Appendix) and the elements of V (Equation 24).

Program PRODFIT

A computer program PRODFIT, in FORTRAN IV language, was written to perform the calculations described above. A brief description of the program's options and mode of operation is given below.

DATA INPUT OPTION. *Option 1*.—A catch

and fishing effort history, $\{C_i, f_i\}$, of $i = 1 \ldots n$ years length and a vector of significant year class numbers $\{k_i\}$ are read in. There may be embedded zeros, if they are true zeros and do not simply reflect a lack of information. The only real problem with unreal zeros, however, occurs in the estimation of q. The catch per unit effort vector is computed internally and the averaged fishing effort vector is computed by Equation (9) with SUBROUTINE AVEFF.

Option 2.—If one wishes to compute the averaged fishing effort vector by another method or if data are obtained which represent equilibrium conditions, then this option is selected and the vectors of catch per unit effort and averaged (or equilibrium) fishing effort $\{U_i, \bar{f}_i\}$ are read in directly. No estimate of q can be made, however.

STARTING VALUES OPTION. *Option 1.*—Initial estimates of the parameters are computed in SUBROUTINE INEST and the user provides the starting estimate for m, either 0, 1, or 2. *Option 2.*—Occasionally the data are so variable that INEST does not provide compatible starting values for the parameters. In this case, or in any case, the user may opt to enter directly all the initial parameter estimates.

MODEL OPTION. The user may allow PRODFIT to estimate m to any desired precision. Frequently, however, the data are so variable that no significant reduction in the residual sum of squares is obtained by varying m. The user then has the option to fix m at 2, the logistic model (Schaefer 1957); at 1, the Gompertz model (Fox 1970); or at 0, the asymptotic yield model.

WEIGHTING OPTION. The user may select the statistical weights as Equation (16) or may choose to not weight the observations, i.e., $W_i = 1$ for all i.

CATCHABILITY COEFFICIENT. The catchability coefficient, q, is estimated by Equation (22), but both the geometric and arithmetic averages are computed.

Program PRODFIT uses an adaptation of the same pattern search optimization routine, MIN, as contained in GENPROD (Pella and Tomlinson 1969) to locate the least-squares parameter estimates. A more sophisticated Taylor series approach (Draper and Smith 1966) was attempted initially, but severe distortion of the sum-of-squares space prevented reasonable convergence. In order to facilitate termination of the searching procedure, the sum-of-squares space is searched with m and a transformation of the parameters α and β to

$$U_{\max} = \alpha^{1/(m-1)} \tag{26}$$

$$Y_{\max} = \frac{(\alpha - \alpha m)(\alpha/m)^{1/(m-1)}}{m\beta} \tag{27}$$

where $U_{\max}$ is the unexploited population size in terms of catch per unit effort. Neither $U_{\max}$ nor $Y_{\max}$ change greatly with moderate changes in m.

The output of PRODFIT provides a listing of the input data, the transformed data, initial parameter estimates, the iterative solution steps, the final estimates of α, β, and m and their variability indices, the management implications of the final model $U_{\max}$, U_{opt}, f_{opt}, and $Y_{\max}$ and their variability indices, the observed and predicted values and error terms, and estimates of the catchability coefficient, q.

A listing of program PRODFIT and a user's guide are available on request from the author.

COMPARATIVE EXAMPLES OF THE EQUILIBRIUM APPROXIMATION METHODS

Two methods of averaging fishing effort which attempt to approximate equilibrium conditions have been presented, the unweighted method (Equation 7) and the new weighted method (Equation 9). In order to compare these two methods, catch histories for a simulated pandalid shrimp fishery (Fox 1972) were generated using a generalized exploited population simulation model GXPOPS (Fox 1973). It should be noted, however, that the comparisons are, for the most part, simply illustrative. It is virtually impossible to demonstrate conclusively which is the better method because there is an infinite choice of life histories, parameter values, fishing effort histories, and stochastic variation representations.

Equilibrium values for the unexploited population biomass in terms of catch per unit effort ($U_{\max}$), the maximum equilibrium yield ($Y_{\max}$), and optimum fishing effort (f_{opt}), were determined empirically by running the simulation model

(Table 1). The catchability coefficient, q, was assumed to be 1.0. Figure 2 presents the equilibrium values of catch per unit effort and yield at fishing effort values ranging from 0.0 to 1.3 for the simulated shrimp population. Above $f = 1.3$ the population level did not stabilize in 25 yr of simulation and at $f = 2.0$ the population was definitely extinguished. The equilibrium data for $f = 0.0$ to 1.3 were fit to the generalized stock production model with PRODFIT to illustrate the obtainable degree of correspondence. The generalized stock production model very closely approximates the equilibrium values for the simulated pandalid shrimp population being slightly low in the range of $f = 0.7$ to 1.1 and slightly high beyond $f = 1.1$ (Figure 2). The estimated parameters are also very close (Table 1).

TABLE 1.—Empirical management implications for the simulated pandalid shrimp population and those estimated for the generalized stock production model with PRODFIT.

Method	Y_{max}	U_{max}	f_{opt}	q	m
Empirical	5.60	17.96	1.02	1.0	—
PRODFIT	5.56	17.91	1.11	—	0.604

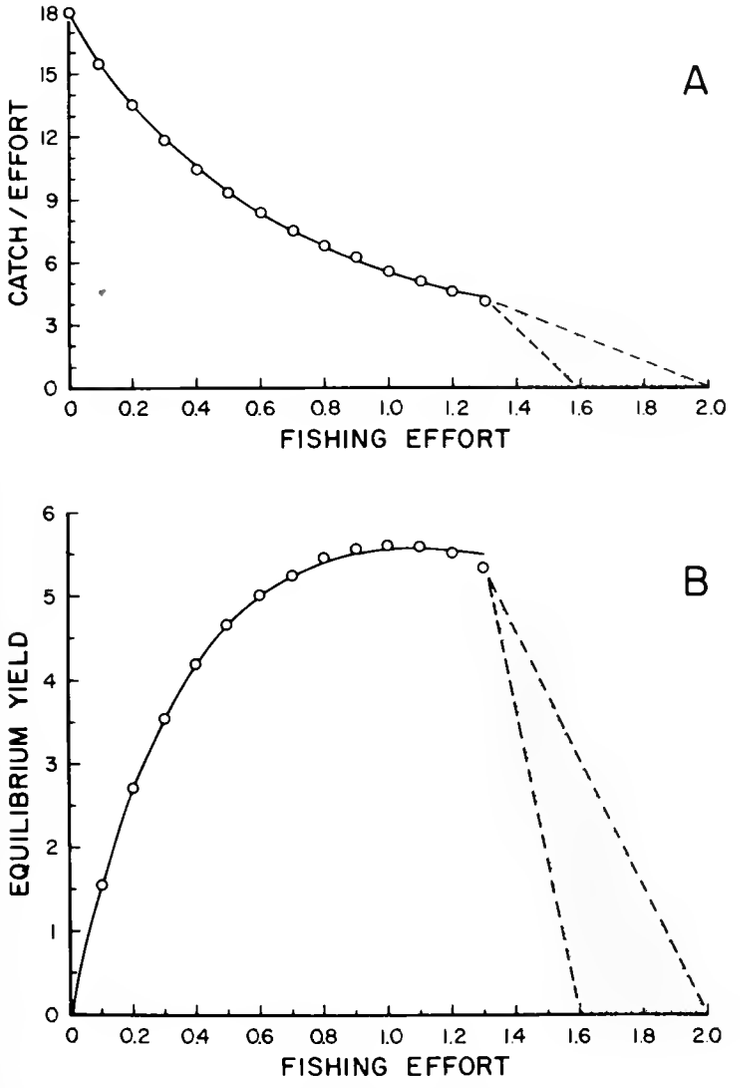

FIGURE 2.—Fit of the generalized stock production model (line) to simulated equilibrium values (circles) of (A) catch per unit effort and (B) yield by computer program PRODFIT. Shaded areas represent nonequilibrium.

The problem which confronts a fishery scientist is to estimate the parameters of Table 1, hence the equilibrium relationship of Figure 2, from catch and fishing effort data representing transitional rather than equilibrium states. To illustrate the efficacy of the equilibrium approximation approach and to provide a comparison between the two fishing effort averaging methods, a 12-yr fishing effort history was selected which approximates the rapid expansion of fishing for *Pandalus borealis* in Ugak Bay, Alaska. Exploiting the simulated shrimp population with the fishing effort history produced the catch and catch per unit effort history in Figure 3. Two comparisons were made, the first using the deterministic data shown in Figure 3 and the second introducing some random error.

Deterministic Comparison

The appropriate averaging time, k, for the weighted average method is four since the fishable part of the simulated shrimp population consists of four significant year classes. The appropriate averaging time, T, for the unweighted average method is 2 since the average duration of the fishable phase is 2 yr. The results of fitting the

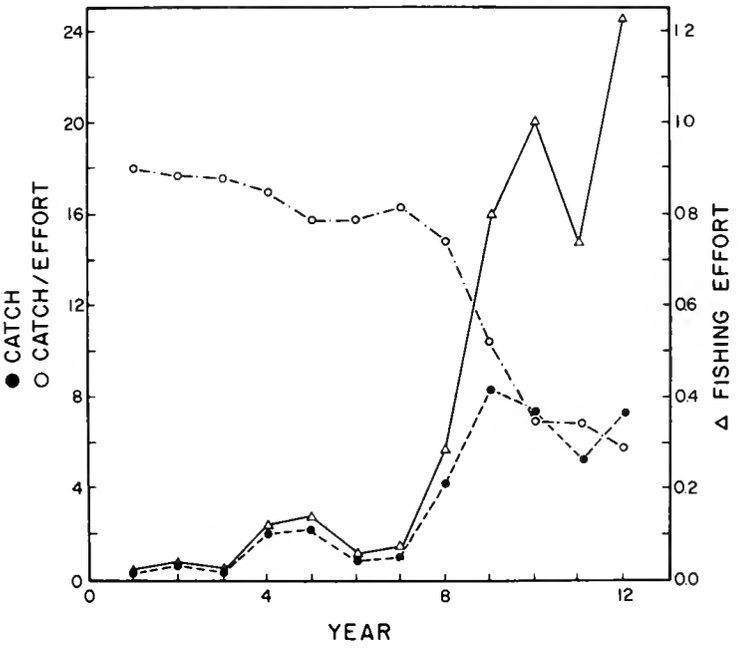

FIGURE 3.—Catch (dots) and catch per unit effort (circles) calculated with a fishing effort history (triangles) from the simulated pandalid shrimp population.

12-yr catch and fishing effort history by both methods for a range of averaging times are given in Table 2. Examination of the appropriate row for each method in Table 2 clearly reveals that for this example the superior estimates were produced by the weighted average method. In fact, the maximum error among the weighted average estimates of m, Y_{max}, and U_{max} (the parameters used in searching for the least-squares solution) at $k = 4$ is only 1%.

The effect of different averaging times on the estimates of the parameters m, Y_{max}, and U_{max} is the same for both effort averaging methods. By increasing the averaging time, the estimates of m and Y_{max} decrease and the estimate of U_{max} increases. The residual sum of squares is minimum at the appropriate averaging time for the weighted method (i.e. at $k = 4$). For the unweighted method, however, the minimum residual sum of squares is at 1 yr greater than the appropriate criterion.

Another way of comparing the weighted and unweighted averaging methods is to examine how well they estimated the equilibrium fishing effort. The equilibrium fishing effort was computed for each year's observed catch per unit effort (Figure 3), using the production model fitted to the equilibrium data (Table 1) for interpolation. The estimated equilibrium fishing effort by the weighted average method was closest in 10 of the 12 yr and had a mean absolute error of less than one-third of the unweighted method (Table 3).

Estimates of the catchability coefficient, q, by the integral method, Equation (22), —geometric and arithmetic means—and the difference method, Equation (18), for the weighted ($k = 4$) and unweighted ($T = 2$) fishing effort averaging techniques are given in Table 4. The best estimator within either effort averaging method was the integral method's geometric mean, with the weighted average fishing effort method being closest to the assumed value, 1.0.

TABLE 2.—Empirical and estimated parameters for the simulated pandalid shrimp catch history using the equilibrium approximation approach and two methods of averaging fishing effort.

Method	Averaging time (k or T)	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	[1]$\hat{q}$	Mean squared error
Empirical	—	[2]0.60	5.60	17.96	1.00	—
Weighted average fishing effort[3]	1	1.16	7.26	17.63	0.42	1.3830
	2	1.35	6.48	17.61	0.62	0.3293
	3	0.86	6.02	17.82	0.88	0.0686
	[4]4	0.60	5.67	17.97	0.87	0.0500
	5	0.53	5.21	18.01	0.75	0.0913
	6	0.51	4.76	18.02	0.62	0.1236
Unweighted average fishing effort[5]	1	1.16	7.26	17.63	0.42	1.3830
	[4]2	1.09	6.17	17.69	0.70	0.1323
	3	0.35	6.10	18.07	1.12	0.0529
	4	0.28	5.36	18.14	0.69	0.2797

[1]Integral method, geometric mean.
[2]Estimated, Table 1.
[3]Equation (9); Program PRODFIT, unweighted estimates option.
[4]Appropriate averaging time.
[5]Equation (7); Program PRODFIT, unweighted estimates option.

TABLE 3.—Comparison of two estimates of equilibrium fishing effort for the simulated pandalid shrimp population catch history.

Year	Equilibrium effort[3]	Weighted average estimate[1] Effort	Weighted average estimate[1] Error	Unweighted average estimate[2] Effort	Unweighted average estimate[2] Error
1	0.0000	0.0000	−0.0000	0.0000	−0.0000
2	0.0072	0.0116	−0.0044	0.0145	−0.0073
3	0.0109	0.0099	0.0010	0.0160	−0.0051
4	0.0412	0.0515	−0.0103	0.0575	−0.0163
5	0.0897	0.0891	0.0006	0.1210	−0.0313
6	0.0896	0.0801	0.0095	0.0880	0.0016
7	0.0692	0.0726	−0.0034	0.0500	0.0192
8	0.1327	0.1516	−0.0189	0.1685	−0.0358
9	0.4031	0.4195	−0.0164	0.5405	−0.1374
10	0.7461	0.7094	0.0367	0.9090	−0.1629
11	0.7800	0.7887	−0.0087	0.8785	−0.0985
12	0.9356	1.0025	−0.0669	0.9905	−0.0549
Mean absolute error			0.0147		0.0475

[1]Equation (9); $k = 4$.
[2]Equation (7); $T = 2$.
[3]Calculated from Table 1 parameters.

Stochastic Comparison

In the deterministic comparison, the catch and fishing effort data were known precisely, the catch per unit effort was always exactly proportional to the average population size, and the population did not fluctuate. However, the stochastic nature of population processes, temporal and spatial changes in the availability and vulnerability of the population to fishing, and the use of sample data to represent an entire fishery all introduce considerable variability in real catch and effort data. Under the assumption that the component sources of variability are independent and random variables with constant expected values and variances, an approximation of the overall variability

TABLE 4.—Estimates of the catchability coefficient, q, by three methods for the weighted and unweighted fishing effort averaging techniques. Actual value of q is 1.0.

Effort averaging method	Integral method[1] Geometric mean	Integral method[1] Arithmetic mean	Difference method[2]
Weighted $\bar{f}$[3]	0.8684	1.1949	1.3283
Unweighted $\bar{f}$[4]	0.6978	1.3558	2.6606

[1]Equation (22).
[2]Equation (18).
[3]Equation (9); $k = 4$.
[4]Equation (7); $T = 2$.

TABLE 5.—Empirical and estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation approach and two methods of averaging fishing effort.

Method	Replicate	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	[1]$\hat{q}$	Mean squared error
Empirical	—	[2]0.60	5.60	17.96	1.00	[3]0.0100
Weighted	1	1.03	5.80	17.49	0.53	0.0136
average	2	0.00	8.65	18.99	1.56	0.0107
fishing	3	0.60	5.73	17.97	0.87	0.0083
effort[4]	4	1.04	5.07	18.68	0.95	0.0047
	5	0.24	6.68	18.40	1.13	0.0145
	Mean	0.58	6.39	18.30	1.01	0.0104
	[5]$SE_{\bar{x}}$	0.21	0.62	0.26	0.17	0.0018
Unweighted	1	2.19	6.70	17.10	0.65	0.0110
average	2	0.44	6.64	18.62	1.74	0.0130
fishing	3	1.41	6.27	17.54	0.90	0.0100
effort[6]	4	2.17	6.45	18.06	0.89	0.0095
	5	1.34	6.26	17.79	0.95	0.0117
	Mean	1.51	6.46	17.82	1.03	0.0110
	$SE_{\bar{x}}$	0.32	0.09	0.25	0.19	0.0006

[1]Integral method, geometric mean.
[2]Estimate, Table 1.
[3]Assumed value.
[4]Equation (9); $k = 4$; Program PRODFIT, weighted estimates option.
[5]Standard error of the mean.
[6]Equation (7); $T = 2$; Program PRODFIT, weighted estimates option.

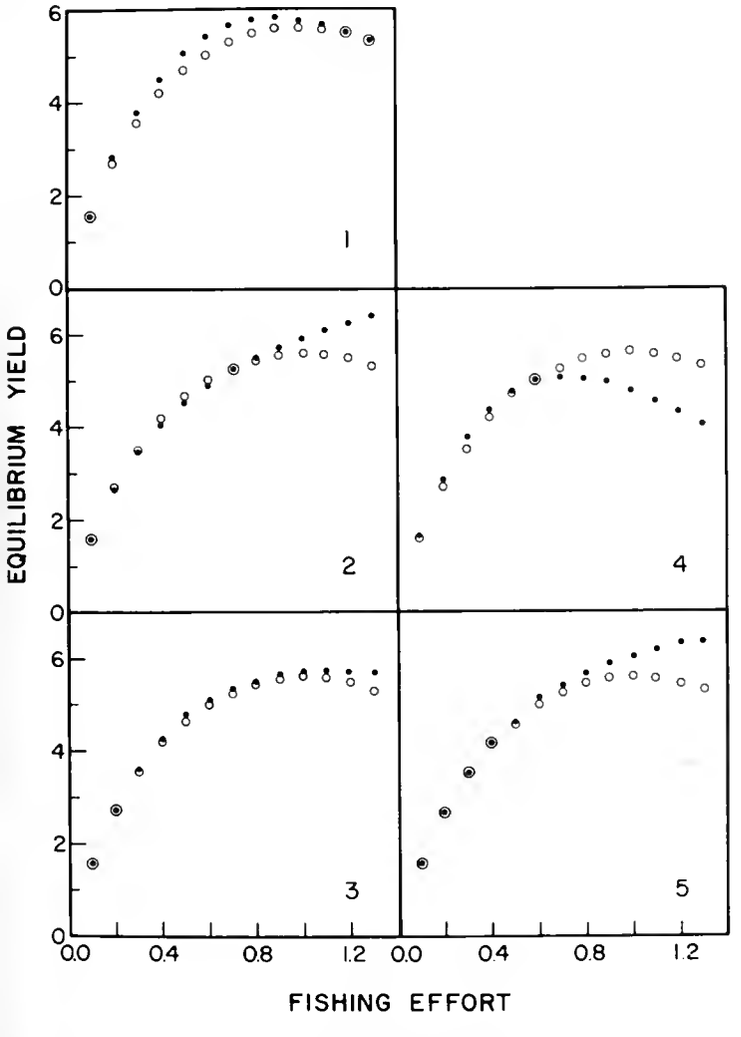

FIGURE 4.—Results (dots) of five stochastic simulated catch trials for the equilibrium approximation approach to fitting the generalized stock production model with the weighted averaging method. Circles are the true values.

structure is the multiplicative error model (Fox 1971)

$$C_i = C_i^* \cdot \epsilon_i \qquad (28)$$

where C_i is the observed catch in year i, C_i^* is the expected catch, and ϵ_i is a random variable with an expected value of 1 and standard deviation σ. In practice, however, the ϵ_i are usually correlated because some (or all) of the component sources of variability do not meet the assumptions.

An ideal (i.e., in the sense that the ϵ_i are independent and random) error structure was chosen to illustrate the estimation ability of the two equilibrium approximation methods, because the "true" error structure of any given population and fishery is unique and largely unknown. Five independent sets of 12 pseudorandom, normally distributed variables, δ, as with an expectation of zero and a standard deviation of 0.1 were produced with the Library Subroutine RAND (University of Washington Computer Center, Seattle). The sets of δ's were used to produce five stochastic catch data sets from the deterministic catch history (Figure 3) and Equation (28), with ϵ_i defined as $1 + \delta_i$.

The results of fitting the five replicate sets of catch and effort data by the weighted (Equation 9) and unweighted (Equation 7) averaging methods are given in Table 5. The effects of even moderate variability on the parameter estimates for both averaging methods are apparent. On the average, two (m and Y_{max}) of the three determining parameters (m, Y_{max}, and U_{max}) are closer to the empirical values for the weighted effort averaging method. The important observation, however, is that all the unweighted estimates of Y_{max} fall above the empirical value and that the average over the five replicates is significantly different from the empirical value with probability greater than 0.999.

Plots of the empirical equilibrium yields and those determined from the generalized stock production model parameters estimated by the weighted average method are compared in Figure 4. Equilibrium yield, for the most part, is estimated reasonably well in each replicate for the range of estimated "equilibrium" fishing effort, 0.0 to 1.0 (Table 3). The exception is replicate 4 where the empirical equilibrium yield is substantially underestimated above $f = 0.8$. Beyond the range of data, $f = 1.0$ to 1.3, the equilibrium yield is estimated reasonably well on the average, but not individually. None of the fitted models, of

course, reveal that there is no equilibrium yield in the range of f = 1.6 to 2.0 for the simulated shrimp population (Figure 2).

Table 6 provides a comparison of the catchability coefficient estimates by three techniques for each fishing effort averaging method. Clearly the best estimates were produced by the geometric mean for the integral method, with the mean estimate by the weighted average fishing effort procedure being slightly better than that of the unweighted average procedure.

COMPARATIVE EXAMPLES OF THE EQUILIBRIUM APPROXIMATION AND TRANSITION PREDICTION APPROACHES

Computer program GENPROD (Pella and Tomlinson 1969) was employed to fit the deterministic and stochastic catch and effort histories of the simulated shrimp to compare the results of the transition prediction and equilibrium approximation approaches. The reader is cautioned, as in the previous section, that these results are largely illustrative and should not be misconstrued as being valid for all cases in which a production model may be employed.

Deterministic Comparison

The comparison of equilibrium parameters in Table 7 reveals that the equilibrium approximation approach provided estimates that were closer to all the empirical values except m, where the two approaches estimated the same value as the empirical equilibrium fit. GENPROD estimated parameters which predicted the simulated catch history (Figure 3) extremely well—the largest error was only 0.05, the sum of squared errors was 0.00659, and the R statistic, a measure of improvement in the fit over simply using the mean catch as a predictor (Pella and Tomlinson 1969), was 0.99994. Utilizing the empirical equilibrium parameters in the generalized production model, however, resulted in a poorer, but still good, prediction of the transition state catches—the maximum error was 0.50, the sum of squared errors was 0.48515, and the R statistic was 0.99544. Apparently due to failure of the assumptions regarding population lag and age structure shifts or problems with precision in the numerical integration, the accuracy of some equilibrium parameter estimates by the transition prediction approach were sacrificed in order to reduce the sum of squared errors by nearly 99%.

TABLE 6.—Estimates of the catchability coefficient, q, from the five replicated stochastic catch histories by three methods for the weighted and unweighted fishing effort averaging procedures. Actual value of q is 1.0.

Effort averaging method	Estimation method	Mean $\hat{q}$	Range of $\hat{q}$
Weighted $\bar{f}$[1]	Integral method[2]		
	Geometric mean	1.008	0.53-1.56
	Arithmetic mean	1.660	1.27-2.41
	Difference method[3]	1.503	1.35-1.77
Unweighted $\bar{f}$[4]	Integral method		
	Geometric mean	1.028	0.65-1.74
	Arithmetic mean	1.546	1.12-2.11
	Difference method	4.459	2.22-10.47

[1]Equation (9); k = 4.
[2]Equation (22).
[3]Equation (18).
[4]Equation (7); T = 2.

Stochastic Comparison

The results of fitting the five replicate stochastic catch histories by the equilibrium approximation and transition prediction approaches are given in Table 8. Of the four common parameters (m, Y_{max}, U_{max}, and q), the equilibrium approximation approach estimates were closer to the empirical values of m, Y_{max}, and q, both on the average and for most of the replicates. The transition prediction approach estimates were closer, on the average, to the empirical value for U_{max}. The transition prediction approach provided one extremely poor estimate of q (replicate 3) and all replicate estimates are above the empirical value—the latter phenomenon could be related to the accuracy of the numerical integration scheme in GENPROD (Fox 1971). The additional parameter required by GENPROD, the ratio of the initial to unexploited population size (P_0/P_{max}), was estimated very well.

There is considerable variability in the estimates of the most frequently desired parameter, Y_{max}, by either approach (Table 8) in spite of assuming an ideal error structure (independent,

TABLE 7.—Empirical and estimated parameters for the simulated pandalid shrimp catch history using the equilibrium approximation and transition prediction approaches.

Approach	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	$\hat{q}$	$\widehat{P_0/P_{max}}$
Empirical	[1]0.60	5.60	17.96	1.00	1.00
Equilibrium approximation[2]	0.60	5.67	17.97	0.87	—
Transition prediction[3]	0.60	5.92	17.69	1.32	1.16

[1]Estimated, Table 1.
[2]Program PRODFIT, k = 4, unweighted estimates option.
[3]Program GENPROD, KK = 3, DEL = 3, unweighted estimates.

TABLE 8.—Empirical and estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation and transition prediction approaches.

Method	Replicate	$\hat{m}$	$\hat{Y}_{max}$	$\hat{U}_{max}$	$\hat{q}$	$\widehat{P_0/P_{max}}$	Mean squared error
Empirical	—	[1]0.60	5.60	17.96	1.00	1.000	[2]0.0100
Equilibrium approximation approach[3]	1	1.03	5.80	17.49	0.53	—	0.0136
	2	0.00	8.65	18.99	1.56	—	0.0107
	3	0.60	5.73	17.97	0.87	—	0.0083
	4	1.04	5.07	18.68	0.95	—	0.0047
	5	0.24	6.68	18.40	1.13	—	0.0145
	Mean	0.58	6.39	18.30	1.01	—	0.0104
	[4]$SE_{\bar{x}}$	0.21	0.62	0.26	0.17	—	0.0018
Transition prediction approach[5]	1	1.7	5.81	17.72	1.34	0.738	0.0105
	2	0.0	9.09	18.15	1.18	1.095	0.0131
	3	2.1	6.69	17.29	3.97	1.211	0.0086
	4	1.7	5.26	17.83	1.40	1.313	0.0053
	5	0.0	9.34	19.21	1.52	0.797	0.0126
	Mean	1.10	7.24	18.04	1.88	1.031	0.0100
	$SE_{\bar{x}}$	0.45	0.84	0.32	0.52	0.113	0.0014

[1]Estimated, Table 1.
[2]Assumed value.
[3]Program PRODFIT; $k = 4$, weighted estimates option.
[4]Standard error of the mean.
[5]Program GENPROD; KK = 3, DEL = 3, weighted estimates. The program was modified slightly from the version of Pella and Tomlinson (1969) by replacing f_{opt} with Y_{max} as one of the determining parameters to allow fitting the case where $m = 0$ (i.e. $f_{opt} = \infty$ at $m = 0$). Identical solutions were obtained for the remaining three cases with either version.

random and with constant expectation and variance), the observed catch being within 20% of the expected catch with probability 0.95, and the fishing effort being known without error. The maximum error for the equilibrium approximation approach was +54% (replicate 2) and for the transition prediction approach was +67% (replicate 5). The problem with these maximum errors (as well as an additional replicate of the transition prediction approach) was estimating m as 0.0, where Y_{max} occurs at infinite fishing effort. It is not unreasonable, however, to obtain $\hat{m} = 0.0$ since the data series is so short and the best value for m is about 0.60. Considering these results and the true relationship between yield and effort (Figure 2) it would be prudent to adopt an alternative m estimation strategy for short data series.

Alternative strategies which could be adopted for short data series are 1) to consistently assume one of the special cases of the generalized stock production model, either the logistic form ($m = 2$) or the Gompertz form ($m \rightarrow 1$), or 2) fit both special cases and select the one with the least sum of squared errors. Table 9 presents the parameters estimated by the two approaches through fixing the value for m at 1 (actually 1.001) and 2. For comparative purposes, the results of these alternative strategies are summarized in Table 10. Fixing m at 1 or 2 resulted in average estimates of Y_{max} nearer the empirical value with less variability than obtained by allowing m to be freely estimated for both the equilibrium approximation and transition prediction approaches. The empirical value of m is 0.6; hence assuming $m \rightarrow 1$ produced estimates nearer the empirical value of Y_{max} than assuming $m = 2$. For any given data set, however, one could not determine a priori which value of m to assume. The strategy of fitting both $m \rightarrow 1$ and $m = 2$ and then selecting that which provided the least-squares parameter estimates worked very well in comparison with freely estimating m under three criteria: 1) more accurate average estimate, 2) smaller average percentage error, and 3) smaller maximum overestimate. Comparing the equilibrium approximation and transition prediction approaches with the same three criteria reveals that the equilibrium approximation approach was superior [1) 0.5% vs. 5.2%, 2) 3.6% vs. 8.5%, and 3) 3.6% vs. 18.4%)].

DISCUSSION

The simple, illustrative calculations on the simulated pandalid shrimp population, of course, did not determine which of the approaches was better for general use in fitting the generalized stock production model. However, some additional guidance can be gained through examining some of their relative weaknesses with regard to the number of data points and the number of parameters they require.

The moving average of fishing effort in the equilibrium approximation approach results in the exclusion of points at the beginning of the data

TABLE 9.—Estimated parameters for the five replicated stochastic catch histories using the equilibrium approximation and transition prediction approaches for fixed estimates of m.

Method	m	Replicate	$\hat{Y}_{max}$	$\hat{U}_{max}$	$\hat{q}$	$\widehat{P_0/P_{max}}$	Mean squared error
Equilibrium approximation approach[1]	1	1	5.80	17.51	0.54	—	0.0136
		2	5.63	17.99	1.36	—	0.0155
		3	5.56	17.66	0.99	—	0.0087
		4	5.05	18.72	0.92	—	0.0048
		5	5.78	17.73	0.95	—	0.0166
		Mean	5.57	17.92	0.96	—	0.0118
	2	1	6.27	16.73	0.29	—	0.0182
		2	6.27	17.17	1.14	—	0.0267
		3	6.06	16.92	0.88	—	0.0139
		4	5.86	17.65	0.77	—	0.0115
		5	6.35	16.94	1.19	—	0.0260
		Mean	6.16	17.08	0.85	—	0.0193
Transition prediction approach[2]	1	1	5.44	18.18	1.10	0.778	0.0107
		2	6.00	18.16	1.79	1.014	0.0170
		3	6.39	17.81	2.97	1.058	0.0096
		4	4.66	18.08	1.07	1.162	0.0058
		5	6.10	18.40	1.87	0.715	0.0142
		Mean	5.72	18.13	1.76	0.945	0.0115
	2	1	5.95	17.61	1.38	0.720	0.0107
		2	6.47	17.83	2.40	0.962	0.0201
		3	6.63	17.37	3.62	1.210	0.0084
		4	5.30	17.73	1.35	1.361	0.0051
		5	6.51	17.89	2.29	0.604	0.0165
		Mean	6.17	17.69	2.21	0.971	0.0122

[1]Program PRODFIT; $k = 4$, weighted estimates option.
[2]Program GENPROD; KK = 3, DEL = 5, weighted estimates.

TABLE 10.—Summary of Y_{max} estimates by alternative strategies with the equilibrium approximation and transition prediction approaches for five replicated stochastic catch histories. Empirical value of Y_{max} is 5.60.

Method/strategy	$\hat{Y}_{max}$ Mean	Standard error of mean	Average percentage error	Range
Equilibrium approximation approach[1]				
1. Estimate m	6.39	0.62	17.8	5.07-8.65
2. Assume $m \rightarrow 1$	5.57	0.14	3.6	5.05-5.80
3. Assume $m = 2$	6.16	0.09	10.0	5.86-6.35
4. Least-squares, $m = 1$ or 2	5.57	0.14	3.6	5.05-5.80
Transition prediction approach[2]				
1. Estimate m	7.24	0.84	31.7	5.26-9.34
2. Assume $m \rightarrow 1$	5.72	0.31	10.0	4.66-6.39
3. Assume $m = 2$	6.17	0.25	12.4	5.30-6.63
4. Least-squares, $m = 1$ or 2	5.89	0.24	8.5	5.30-6.63

[1]Program PRODFIT.
[2]Program GENPROD.

set unless either there was no fishing prior to the first record of the set or some information is available on the approximate level of catch and effort. One should check carefully to ensure that critical points (those being the only points at high, low, or intermediate levels of fishing) are not excluded or that the fitted model does not deviate greatly from where they might reasonably be expected to lie. If fishing effort was reasonably constant or negligible prior to the first record, dummy data of length $k - 1$ can be employed to allow use of the first few data points. Also, since the average fishable duration, T, is less than the number of significant fishable year classes, k, the unweighted averaging method will result in fewer data being excluded In any case, the sensitivity of the parameter estimates to alternative averaging times should be explored.

No data points are excluded with the transition prediction approach, a positive factor which should be considered even if one is satisfied with the parameter estimates obtained with the equilibrium approximation approach. On the other hand, the transition prediction approach utilizes five parameters while the equilibrium approximation approach utilizes only three, so that with few significant year classes in the fishable population there is little difference between the required number of data points. For example, the transition prediction approach statistically

requires six points, while the equilibrium approximation approach with four significant year classes will require, in general, seven points. With a large number of significant year classes in the fishable population or a relatively high age at first capture, however, the major concern for either approach is the likelihood of failure of the transition state population assumptions.

The results summarized in Table 7 illustrate a general shortcoming in simultaneously estimating a large number of parameters, i.e. large deviations from model can be statistically reduced in a least-squares estimation procedure at the expense of the accuracy of certain "desired" parameters. The transition prediction approach, fitting a "free-form" type of curve with five parameters, is relatively more susceptible than the equilibrium approximation approach which fits a monotonically decreasing curve with only three parameters. On the other hand, estimates from the equilibrium approximation approach can be very sensitive to the placement of one data point in certain cases (e.g., a data point at an intermediate level of fishing with clusters of points at both low and high levels of fishing).

Utilizing the production model approach for assessing the effects of exploitation presents significant problems in addition to choice of the parameter estimation procedure or the length of the data series. These additional problems are 1) maintaining a constant catchability coefficient throughout the data series, 2) assessing the effects of changes in the constitution of the fishery, and 3) assessing the effects of time lags in population production processes.

The basic components of the overall effective catchability coefficient are 1) the relative efficiency of various types and classes of fishing gear and 2) the manner in which the gear is employed relative to the availability and vulnerability of the population, and its subunits, to capture. Heterogeneity in the efficiency of various gear classes, or vessels, within a fishing season can be alleviated by adjusting for their estimated relative fishing powers—currently the best method for estimating fishing power is by analysis of variance with the computer program FPOW (Berude and Abramson 1972). The major problem remaining, however, is adjusting for among-year changes in efficiency of the standard gear. Rothschild (1970) discussed and provided examples of problems associated with changes in the catchability coefficient related to areal deployment of the fishing gear. The expansion of fishing across a gradient of population density will increase or decrease the effective catchability coefficient depending on the direction of the density gradient and fishing expansion. Year-to-year shifts in the population location and density relative to the fishing effort deployment also could likewise create trends in the catchability coefficient. Age-specific differences in the catchability would cause shifting of the overall effective catchability coefficient with changes in fishing effort. For example, if the catchability of fish declined with age, then the overall effective catchability of the fishable population would increase with increasing fishing effort since the relative proportion of younger age groups would most likely increase.

Alterations in the constitution of the fishery probably are the most difficult problems to overcome satisfactorily. Expansion of the fishery across several stocks, either independent or with some mixing, can result in rather large shifts in the productivity estimates (Joseph 1970; Inter-American Tropical Tuna Commission 1972). Changes in the relative levels of fishing effort exerted by different gear types which exploit different age groups of the population, either voluntarily or through a change in minimum size limit regulations, can similarly have significant impact on the shape of the production model curve (Lenarz et al. 1974). The latter problem identifies a major shortcoming of the production model approach; i.e., the impact on total yield by altering the selectivity of fishing gear can not be assessed a priori without considerable additional information.

The effects of time lags in population production processes (e.g., reproduction, growth, and mortality, both density-independent and density-dependent) can result in either overestimation or underestimation of the population productivity, or in population cycling which may never result in reaching an equilibrium state (Wangersky and Cunningham 1957; Walter 1973).

In summary, both the equilibrium approximation and the transition prediction fitting methods are useful, one or the other more so under conditions outlined above. Application of the production model to catch and fishing effort data is relatively simple, the primary virtue of the approach. The interpretation of the results and the formulation of advice for managing the resource, however, can be extraordinarily complicated by a variety of

factors. Therefore, the proper perspective of production model analysis is that it is little more than a regression model, yet very useful for making "first estimate" projections of the relationship between the level of exploitation and expected equilibrium yield.

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APPENDIX

Miscellaneous Equations for PRODFIT

Elements of the X-matrix

Let $\hat{U}_i = (\alpha + \beta \bar{f}_i)^{1/(m-1)}$

Then

$$\frac{\partial \hat{U}_i}{\partial \alpha} = 1/(m-1)\,(\alpha + \beta \bar{f}_i)^{(2-m)/(m-1)}$$

$$\frac{\partial \hat{U}_i}{\partial \beta} = \bar{f}_i \times \frac{\partial \hat{U}_i}{\partial \hat{\alpha}}$$

$$\frac{\partial \hat{U}_i}{\partial m} = -(\alpha + \beta \bar{f}_i)^{1/(m-1)} \times \ln(\alpha + \beta \bar{f}_i)[1/(m-1)]^2$$

Derivatives for the Delta Method Variance Estimates

Y_{max}

$$\frac{\partial Y_{max}}{\partial \alpha} = Y_{max}[m/(m-1)]/\alpha$$

$$\frac{\partial Y_{max}}{\partial \beta} = -Y_{max}/\beta$$

$$\frac{\partial Y_{max}}{\partial m} = Y_{max} \times \ln(m/\alpha)/(m-1)^2$$

f_{opt}

$$\frac{\partial f_{opt}}{\partial \alpha} = (1/m - 1)/\beta$$

$$\frac{\partial f_{opt}}{\partial \beta} = -\alpha/\beta^2\,(1/m - 1)$$

$$\frac{\partial f_{opt}}{\partial m} = -\alpha/(\beta m^2)$$

U_{opt}

$$\frac{\partial U_{opt}}{\partial \alpha} = U_{opt}/[\alpha(m-1)]$$

$$\frac{\partial U_{opt}}{\partial m} = -U_{opt}\,[m \ln(\alpha/m) + m - 1]/[m(m-1)^2]$$

NET PHYTOPLANKTON AND THE GREATER THAN 20-MICRON PHYTOPLANKTON SIZE FRACTION IN UPWELLING WATERS OFF BAJA CALIFORNIA

THEODORE J. SMAYDA[1]

ABSTRACT

Between 26 March and 6 April 1973 various phytoplankton studies were carried out during the MESCAL II survey in an area measuring circa 105 km × 30 km, and centered approximately at Punta San Hipolito, Baja California. Upwelling was then in its early stages. The composition of 22 collections of net phytoplankton (No. 20 net), and the composition and abundance of the non-setose (i.e., excluding *Chaetoceros*, *Bacteriastrum*) size fraction >20 μm collected at various depths at 13 stations are reported here. The mean carbon content in the upper 50 m contained in the >20 μm non-setose size fraction was 533.5 mg C/m^2 for all stations, and ranged from 306 to 1,022 mg C/m^2 at individual stations. Based on a C/Chl *a* ratio of 40:1, the mean concentration in the euphotic zone represents circa 12% of the total phytoplankton carbon present. *Lauderia annulata* (28%) and several *Coscinodiscus* species (33%) accounted for most of the carbon found in the >20-μm size fraction, even though the latter comprised only about 10% of the mean population expressed as cell number. The mass occurrence of *Coscinodiscus* reported previously for Magdalena Bay during summer upwelling was not observed. The *Coscinodiscus* population and the non-setose component of the >20- μm size fraction contributed only 1.2% and 4%, respectively, of the daily caloric ingestion estimated for the crab, *Pleuroncodes planipes*, previously reported to graze heavily on *Coscinodiscus*. Sinking rates (61 to 144 m/h) of *Pleuroncodes* fecal material exceeded by onefold to fourfold those rates estimated for the various sizes of *Coscinodiscus* and zooplankton fecal pellets sampled during the survey. The abundant crab population is, thus, important in causing an exceptionally rapid deposition of unassimilated phytoplankton frustules and organic material onto the sea floor. Floristic changes accompanying upwelling were detectable. The occurrence of the unique diatoms *Coscinodiscus* (*Brenneckella*) *eccentricus* and *Planktoniella muriformis* in these waters is apparently reported for the first time. The present data together with earlier observations suggest that the net diatom community is similar in the coastal waters extending from San Diego, Calif., to the Gulf of Panama. The data do not support the idea that the abundance of *Pleuroncodes* in this upwelling system is causally linked to that of *Coscinodiscus*.

There is little information on the composition and abundance of the phytoplankton community in the upwelling waters off Baja California. The available data are mostly qualitative (Allen 1924, 1934, 1938; Balech 1960; Cupp 1930, 1934), aside from recent, cursory observations on phytoplankton cells >25 μm which are grazed by the red crab, *Pleuroncodes planipes* (Longhurst et al. 1967).

Unique mass blooms of *Coscinodiscus* have been observed by Longhurst et al. in the upwelled waters of Magdalena Bay. This phenomenon and the great abundance of *Pleuroncodes*, which grazes on *Coscinodiscus* cells, may be distinctive characteristics of this upwelling system. Smith et al.[2] have concluded that this crab is an important herbivore in the California Current upwelling system, where its role is comparable to that of the anchovy, *Engraulis ringens*, in the Peru Current. Longhurst (1968) has evaluated the potential fishery for this galatheid crab, which occurs in both the benthic and pelagic zones; some crabs exhibit diurnal migrations (Longhurst et al. 1967).

Pleuroncodes is generally distributed throughout this region (Blackburn 1969), while information on the regional distribution and abundance of *Coscinodiscus* is lacking. It is therefore unknown whether *Coscinodiscus* indeed generally characterizes the phytoplankton community in these upwelled waters. Clarification of this is relevant

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[2]Smith, K. L., Jr., G. R. Harbison, G. T. Rowe, and C. H. Clifford. Respiration and chemical composition of *Pleuroncodes planipes* (Decapoda: Galatheidae): Energetic significance in an upwelling system. Manuscr., 22 p. Woods Hole Oceanogr. Inst., Woods Hole, Mass.

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to the question of whether *Pleuroncodes'* occurrence is causally linked to that of *Coscinodiscus*.

Coscinodiscus and other heavily silicified diatoms sink to the sea floor, as documented for the Gulf of California (Round 1967, 1968). This deposition contributes skeletal remains (i.e., to the thanatocoenosis) and organic matter to the sediments. The abundance and sinking characteristics of this diatom population are also of interest, since *Pleuroncodes* also occurs in the benthos. During this benthic residence, when population densities up to 250 individuals/m^2 have been found (Smith et al. footnote 2), it may feed on detrital material (Longhurst et al. 1967).

Various studies on phytoplankton were carried out during the MESCAL II expedition of the RV *Thomas G. Thompson* in 1973 to study upwelling off Baja California, as a continuation of 1972 activities in this area (Walsh et al 1974). These included the routine, shipboard examination of both net phytoplankton and the >20-μm size fraction filtered from quantitative samples. The discovery that natural populations of a *Ditylum brightwelli* and, possibly, *Biddulphia mobiliensis* exhibited diel cell division has been reported (Smayda in press a).

Examination of the >20-μm size fraction was partly motivated by the need to know its composition and abundance, particularly that for *Coscinodiscus*. This was to evaluate the aforementioned relationship possibly occurring between *Pleuroncodes* and *Coscinodiscus*, and to establish the latter's importance during the initial stages of upwelling. This latter objective was prompted by the remarkable bloom found in Magdalena Bay during a later stage of the upwelling cycle. Finally, such data are needed to evaluate the sinking and turnover rates of the more heavily silicified and dissolution-resistant components of this size fraction which sink faster and represent an energy source for benthic secondary production.

METHODS

Between 26 March and 6 April 1973, 22 collections of net phytoplankton were made at 15 stations (multiple sampling on different days at some). A No. 20 (mesh opening of 69 μm) net 30 cm in diameter sampled the upper 50 to 100 m (depending on depth) for 30 min by repeated vertical oscillations, during which the net was lowered at a rate of ca. 30 m/min and retrieved at a rate of 10 m/min. The samples were examined microscopically soon after collection, after placing onto a slide an aliquot of the unpreserved, sedimented material from an unagitated sample.

Of the 15 stations sampled, 13 were located in a sampling block measuring about 105 km long and 30 km wide centered approximately at Punta San Hipolito off the coast of Baja California (Figure 1). The coordinates of the northern- and southernmost stations are lat. 27°6.7'N, long. 114°21.2'W and lat. 26°28.5'N, long. 113°45.5'W, respectively. The stations extended offshore from within sight of land to within, or near, the California Current; the inner- and outermost stations were at lat. 26°55.2'N, long. 114°02.2'W and lat. 26°51.2'N, long. 114°10.7'W, respectively. Stations 1 and 2 (not shown in Figure 1) were located about 460 km north of this main sampling area at lat. 30°57.8'N, long. 116°32'W and lat. 28°8.2'N, long. 115°39.2'W, respectively.

Quantitative samples were also collected at 13 stations from the surface to 50 m at 10-m intervals, and at 75 m with 5-liter Niskin Bottles. Seven stations (18 to 24) were sampled at 6-h intervals while following a drogue. From samples collected in the upper 30 m, 2 liters were usually filtered through a 20-μm mesh net, and 3 liters from greater depths. The apparatus used is illustrated in Durbin et al. (in press). The material

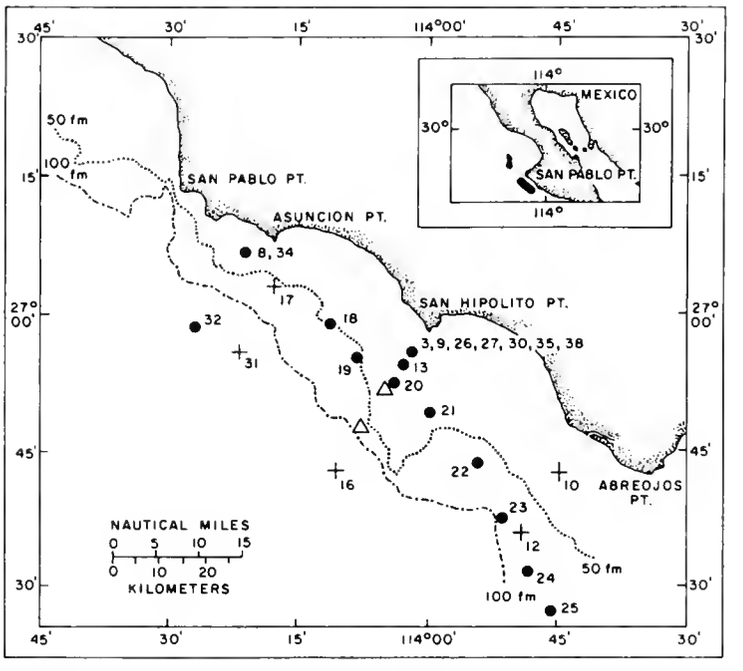

FIGURE 1.—Location of stations where collections of net phytoplankton (+) and net and water bottle samples (•) were made from 26 March to 6 April 1973 (except that net and water bottle collections were made only at Stations 26 and 38 at the frequently sampled station located off Punta San Hipolito). △ represents stations, along with Station 27, used to illustrate the occurrence of upwelling in Table 1; the outermost station is Station 29.

retained by the net was concentrated to 30 ml, preserved with hexamine + Formalin[3] and 1 ml of the concentrate then enumerated on board ship using a Sedgwick Rafter Counting Chamber. The concentrate was obtained by stopping filtration to leave about 1 cm of water above the filter.

As stated in the Introduction, cells in the size class >20 μm are frequently heavily silicified and sink to the sea bed. *Chaetoceros* and *Bacteriastrum* are usually not represented in the latter (Round 1968), presumably because of rapid dissolution of their silicon frustules. The various objectives of the present and other, ongoing studies during MESCAL II emphasized the *Coscinodiscus* and other non-setose genera, and also required real-time data for proper execution of the program. Shipboard enumeration of phytoplankton was therefore necessary. Quantitative shipboard enumeration of specimens belonging to genera characterized by setae is difficult; their setose nature makes them prone to movement within the counting chamber in response to the ship's vibrations and movement. For these various reasons, during the numerical census representatives of the genera *Chaetoceros* and *Bacteriastrum* and a species similar in general appearance to (but probably not) *Nitzschia frigida* were not enumerated.

Numerical abundance was transformed into carbon equivalents. From 10 to 40 cells of each species (depending on abundance) were measured to obtain the mean dimensions required to calculate cell volume using appropriate mensuration formulae. The carbon content was then calculated from Strathmann's (1967) equation

$$\log C = 0.758 (\log V) - 0.352$$

where V is the cell volume in μm^3. From this cellular estimate (pg per cell), the population carbon was computed. The constant 0.352 differs slightly from Strathmann's given value, and is based on additional diatom analyses (Eppley, pers. commun.).

The mean population per liter ($\bar{C}$) in the upper 50 m was calculated from:

$$\bar{C} = \frac{1}{2Z_5} [(C_0 + C_1)(Z_1 - Z_0) + (C_1 + C_2)(Z_3 - Z_2) + \ldots + (C_4 + C_5)(Z_5 + Z_4)]$$

where C_0, C_1, etc. are the observed cell (carbon) concentrations per liter at the surface (Z_0) and 10 m (Z_1), etc., down to 50 m (Z_5). Concentrations per square meter of sea surface down to 50 m were obtained from ($\bar{C}$) (5×10^4). Samples were collected at 75 m at only 9 of the 13 quantitative stations because of depth. This, together with the sparse populations usually found there, accounts for the emphasis on the upper 50 m.

RESULTS

Upwelling occurred during the field program. Table 1 presents some representative physical and chemical parameters along a transect of three stations sampled on 3 and 4 April near Punta San Hipolito (Figure 1). The inflow and upwelling of cold, nutrient-rich water at the nearshore station (27) is evident. Upwelling was usually more pronounced near and shorewards of the 50-fathom isobath. Details of this upwelling, which was in its early stages, and associated biotic responses will be presented elsewhere (Walsh, Kelley, Whitledge, Huntsman, and Pillsbury in prep.).

Net Phytoplankton

The species identified in the net material are listed in Appendix Table 1. Throughout the ship's track of ca. 700 km the No. 20 net phytoplankton was characterized by the genus *Chaetoceros*

TABLE 1.—Hydrographic conditions along a transect off Punta San Hipolito showing the occurrence of upwelling during 3 and 4 April 1973 (Stations shown in Figure 1).

Depth (m)	°C	‰	σ_t	μg at/liter PO_4	NO_3	SiO_2
Station 29 (lat. 26°48'N, long. 114°07.5'W) 0220						
0	16.04	34.122	25.08	0.47	0.98	1.23
10	16.04	34.119	25.08	0.54	0.98	1.10
20	15.67	34.127	25.17	0.55	0.98	0.98
30	15.65	34.112	25.16	0.63	1.31	1.53
40	13.68	33.957	25.47	1.05	3.94	7.52
50	11.87	33.736	25.65	1.40	9.18	13.34
75	11.51	33.821	25.79	1.65	14.43	18.83
Station 28 (lat. 26°51.5'N, long. 114°04.8'W) 0100						
0	15.69	34.044	25.10	0.51	0.66	1.75
10	15.25	34.002	25.17	0.63	0.66	2.48
20	14.35	33.912	25.29	0.82	1.31	4.91
30	13.64	33.930	25.45	1.06	3.94	8.52
40	11.94	33.690	25.60	1.22	8.20	11.29
50	11.84	33.922	25.80	1.67	14.43	16.95
Station 27 (lat. 26°55.2'N, long. 114°02.2'W) 1720						
0	13.53	34.080	25.59	1.15	7.03	11.87
10	13.26	34.086	25.65	1.32	7.91	12.39
20	13.04	34.092	25.70	1.57	10.94	15.36
30	12.26	34.063	25.83	1.83	14.28	18.85
40	11.81	34.141	25.98	2.12	20.08	22.68
50	11.36	34.243	26.14	2.34	23.72	27.05

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(*affinis, curvisetus, debilis, didymus, socialis*) in species and abundance. The genus *Coscinodiscus* was a conspicuous co-dominant, but varied in relative abundance from station to station. The remarkable colonial diatom *Planktoniella muriformis* (Loeblich et al. 1968; Round 1972) was also prominent throughout this region. Nonetheless, some apparent regional differences are noteworthy.

At Station 1 located near Punta Kolnett a very rich, diverse net plankton community occurred on 26 March dominated by *Chaetoceros* and *Nitzschia* spp. and *Thalassiothrix frauenfeldii*. *Asterionella japonica*, *Eucampia cornuta*, and *Lithodesmium undulatum* were other abundant diatoms. This community stands out from others in the importance of *Asterionella* (many small pennate diatoms were attached to the colonies), which was not found in subsequent net tows. Also unlike subsequent stations, *Phaeocystis* cf. *pouchetii* was common while *Coscinodiscus* spp. were not. Allen (1945) has reported extensive blooms of *Phaeocystis* off southern California. This colonial haptophycean is well known for its apparent adverse effects on certain fisheries in the North Sea during mass blooms.

The lack of nutrient data at Stations 1 and 2 prevents assessment of possible upwelling. However, when sampled on 27 March the upper 50 m of the latter station was considerably warmer (15.29°C at 0 m, 14.94°C at 50 m) than at Station 1 (14.53°C at 0 m, 11.42°C at 40 m). The net phytoplankton community was considerably poorer and dominated by *Ceratium* spp.; peridinians were frequent, and the diatoms *Biddulphia mobiliensis*, *Coscinodiscus* spp., and *Planktoniella sol* were common. This community suggests that upwelling was weak, if occurring.

The principal features of the net collections (n = 20) made in the intensive survey area (Figure 1) are: 1) the community at the deepwater stations (16, 31, 32) located seaward of the 50-fathom isobath was less abundant and differed somewhat relative to the shallower stations; 2) the composition at the latter stations was generally similar; and 3) a slight change in apparent species dominance occurred by the end of the 12-day sampling period.

At the outer, deepwater Station 16 (30 March) *Chaetoceros affinis* and *curvisetus* dominated; *Ceratium* and *Peridinium* spp. were also common. At Stations 31 and 32 (4 April), *Bacteriastrum* dominated together with the above *Chaetoceros* species and *decipiens* and *socialis*. *Coscinodiscus* spp. were subordinate; *Asterolampra marylandica* and cf. *Pyrocystis lunula* were frequent. The lower relative abundance and the difference in dominant species at these outer stations are also reflected in the quantitative samples (Table 2). The lowest mean concentration occurred at Station 32 (quantitative samples were not collected at Stations 16 and 31). The physical-chemical data indicate that upwelling was not occurring at Station 16 and was insignificant, if taking place, at Stations 31 and 32.

At the nearshore Station 34 (4 April), where the hydrographic conditions were similar to Station 27 (Table 1), the *Bacteriastrum* component important at Stations 31 and 32 was absent and *Thalassiosira rotula* dominated along with the *Chaetoceros* spp. This increased importance of *Thalassiosira rotula* relative to samples collected a week earlier is also noted in the series collected near Punta San Hipolito (Stations 3 to 38) (Figure 1). The nearshore communities were otherwise dominated by different proportions of *Chaetoceros* and *Coscinodiscus* spp. The *Coscinodiscus* component was especially prominent at Stations 10, 17, and 19, for example. (The net tows frequently contained pennate diatoms which might have been scoured from bottom sediments during upwelling.)

The apparent differences in net community composition, abundance, and species succession during the 10-day sampling period in the intensive survey area probably reflect variations in intensity of upwelling, which was just beginning based on aerial reconnaissance of sea-surface temperatures prior to the ship's arrival in the survey area. Between 28 March (Station 3) and 30 March (Station 13) cold water ascended 10 m at the fixed station near Punta San Hipolito (Figure 1; Pillsbury, pers. commun.).

Quantitative Samples

Numerical Abundance

The results of the quantitative census of the non-setose species in the >20-μm size fraction are presented in Table 2. The mean population level in the upper 50 m ranged from about 2,110 to 9,800 cells/liter. *Lauderia annulata* dominated numerically (from 35 to 60% of total abundance) throughout the area, except at the last station (38) sampled (3%) where *Thalassiosira rotula* dominated

TABLE 2.—The mean, non-setose population (cells/liter and μg C/liter) in the >20-μm size class in the upper 50 m. Lower value in cell abundance (i.e. *n/n*) represents number of dead cells.

Station	Time	Σ cells/carbon	*Actinoptychus undulatus*	*Biddulphia mobiliensis*	*Ceratium* spp.	*Coscinodiscus (Brenneckella) eccentricus*	Σ *Coscinodiscus* spp.	*Ditylum brightwelli*	*Eucampia cornuta*	*Guinardia flaccida*	*Lauderia annulata*	*Lithodesmium undulatum*	*Planktoniella muriformis*	*Planktoniella sol*	*Rhizosolenia* spp.	*Schroederella delicatula*	*Thalassiosira rotula*	OTHERS	% dead cells of *Coscinodiscus* spp.
13	1145	4,067	29/5	115/1	119	33	630/54	198/7	24	3	2,015/2	330	32	308/25	5/1	173	48	5	8.5
		11.05	0.07	0.72	0.25	0.08	4.83	1.49	0.01	0.01	2.68	0.48		0.20		0.17	0.06		
18	1800	3,995	47/6	254/15	29	35	631/49	284/6	57	16	1,396	589	87	335	3	177	48	7	7.8
		13.85	0.11	1.58	0.06	0.09	6.61	2.14	0.02	0.07	1.86	0.85		0.22		0.18	0.06		
19	0000	4,576	94	171	12	30	520/63	267	14	43	2,942	508	31	220	6	448/17	24	5	11.5
		16.13	0.23	1.06	0.02	0.08	7.26	2.01	0.004	0.18	3.92	0.74		0.15		0.45	0.03		
20	0600	3,321	22/3	59/2	12	7/1	309/27	125	2	22	2,008	306	20	197/3	5	116/34	114	3	8.7
		7.38	0.05	0.37	0.02	0.02	2.38	0.94	0	0.09	2.67	0.44		0.13		0.12	0.15		
21	1200	2,456	29/2	68/2	5	29	332/35	137	—	37	1,171/2	181/18	28	194/5	36/2	168	37	4	10.5
		8.31	0.09	0.42	0.01	0.07	4.37	1.03	—	0.15	1.56	0.26		0.13		0.17	0.05		
22	1800	9,806	45	232	10	55	479/29	552/15	123	91	5,665	719	37	746	11	841/19	190	10	6.1
		20.44	0.11	1.44	0.02	0.14	3.96	4.16	0.04	0.38	7.55	1.04		0.50		0.85	0.25		
23	0000	4,476	26/1	76/2	10	40	318/50	148/2	77	94	2,512	425	36	288/12	130/2	236/50	56	4	15.7
		8.96	0.06	0.47	0.02	0.10	2.27	1.16	0.02	0.39	3.35	0.62		0.19		0.24	0.07		
24	0600	3,595	21/1	80/2	17	97	191/17	64	—	101	1,957/10	314	7	538/13	52	113	38/5	5	8.9
		7.11	0.05	0.50	0.04	0.24	1.79	0.48	—	0.42	2.61	0.46		0.36		0.11	0.05		
25	1200	4,915	48	76	36	44	257/42	179	190	42	2,616	461	30	569	28	276	46	17	16.3
		9.13	0.12	0.47	0.07	0.11	1.90	1.35	0.06	0.18	3.48	0.67		0.38		0.28	0.06		
26	1800	3,248	26/2	88	1	12	508/50	78/2	10	8	1,526	148	6	46	—	170	618	3	9.8
		7.75	0.06	0.55	0	0.03	3.23	0.59	0.003	0.03	2.03	0.21		0.03		0.17	0.82		
32	1800	2,110	8	59	43	101/1	230/43	53/1	—	109	819	120	6	552	29	7	10	7	18.7
		6.12	0.02	0.37	0.09	0.25	2.88	0.40	—	0.46	1.09	0.17		0.37		0.01	0.01		
34	2140	8,653	10/2	54/1	12	11	406/16	272	46	43	3,835	486	12	151/2	7	1,318	1,990	—	3.9
		15.00	0.02	0.34	0.02	0.03	2.47	2.05	0.01	0.18	5.11	0.70		0.10		1.33	2.64		
38	0720	4,926	53/2	6	49	4	623/65	40	18/60	26	136/7	602/19	8	82	5	618	2,639/2	17	10.4
		9.03	0.13	0.04	0.10	0.01	3.10	0.30	0.005	0.11	0.18	0.87		0.05		0.62	3.51		
																			$\bar{x}$ = 10.5

(54%). The latter was also important at Station 34 (23%); the maximum, mean abundance of *Schroederella delicatula* (1,318 cells/liter) was also found here. *Coscinodiscus* spp. were usually next to *Lauderia* in numerical importance, and composed a maximum of 10 to 15% of the mean population. Table 3 lists the species of *Coscinodiscus* found. (*Coscinodiscus* "large species" may represent several species difficult to identify properly in the counting chamber.) *Planktoniella sol* contributed from about 2 to 25% of the mean population, and *Lithodesmium undulatum* usually around 7 to 12%.

The absolute abundance of the unique colonial aggregate, *Planktoniella muriformis*, which can have up to at least 530 cells/colony (Loeblich et al. 1968), is unknown; individual cells in the colonies were not counted. The mean number of colonies per liter in the upper 50 m ranged from 6 to 92, with the low levels (6 to 10) persistent at stations made after Station 25 (Table 2). The mean vertical distribution of this species shows a similar abundance (22 to 30 colonies/liter) in the upper 40 m (Table 4; Figure 2), contrary to expectations, and will be reconsidered later.

Species of *Rhizosolenia* >20 μm were not abundant, and included: *bergoni*, *calcar avis*, *imbricata* var. *shrubsolei*, *stolterfothii*. Diatoms which are included in OTHERS in Table 2, and their maximum abundance (cells per liter) are:

Asteromphalus heptactis (12)
Corethron pelagicum (19)
Dactyliosolen sp. (72)
Hemidiscus cuneiformis (84)
Leptocylindrus danicus (228)
Paralia sulcata (79)
Skeletonema costatum (152)
Stephanopyxis cf. *turris* (192)
Thalassionema nitzschioides (126)
Thalassiothrix cf. *mediterranea* var. *pacifica* (16)

TABLE 3.—The mean population as cells/liter (a) and μg C/liter (b) of the different *Coscinodiscus* species >20 μm in the upper 50 m.

Station		*(Brenneckella) eccentricus*	cf. *asteromphalus*	? *concinnus*	*eccentricus*	cf. *granii*	"large species"	Σ
13	a	33	118	3	465	3	41	663
	b	0.082	0.568	0.015	1.361	0.061	2.822	4.91
18	a	35	209	95	262	2	63	666
	b	.087	1.005	.467	.767	.041	4.337	6.70
19	a	30	202	103	135	4	77	551
	b	.075	.972	.506	.395	.082	5.300	7.33
20	a	7	152	36	104	0	17	316
	b	.017	.731	.177	.304	0	1.170	2.40
21	a	29	182	18	94	5	44	372
	b	.072	.876	.088	.275	.102	3.029	4.44
22	a	55	204	57	184	5	30	535
	b	.137	.981	.280	.539	.102	2.065	4.10
23	a	40	144	28	116	10	13	351
	b	.100	.692	.138	.340	.205	.895	2.37
24	a	97	64	51	64	4	14	294
	b	.241	.308	.251	.187	.082	.964	2.03
25	a	44	167	13	64	1	12	301
	b	.109	.803	.064	.187	.020	.826	2.01
26	a	12	176	18	283	11	18	518
	b	.030	.847	.088	.828	.225	1.239	3.26
32	a	101	125	17	42	34	20	339
	b	.251	.601	.084	.123	.696	1.377	3.13
34	a	11	95	24	271	0	16	417
	b	.027	.457	.118	.793	0	1.101	2.50
38	a	4	60	19	528	0	17	628
	b	.009	.289	.093	1.545	0	1.170	3.11

These species are listed only to indicate their presence; their actual abundance is probably greater, since most of these would routinely pass through a 20-μm mesh net depending on orientation of the cells during filtration.

Ceratium furca usually dominated the dinoflagellates >20-μm; populations of *Ceratium fusus* were persistent. Reproductive stages similar to those depicted by von Stosch (1964) for some ceratians were frequent. *Pyrocystis* was present, including an organism quite reminiscent of *Pyrocystis lunula* (vide Figure 559 in Schiller 1937) in shape and stages found. Maximum abundance was 60 cells/liter in the upper 10 m at Station 38 (13.96° to 14.31°C, otherwise similar to Station 27 (Table 1)). Various stages of the cf. *Pyrocystis lunula* cycle were also found during growth experiments carried out with mixed, natural populations. The dinoflagellate population was usually sparse, however, with no indication of red tide in the >20-μm size fraction either visually or microscopically. However, several weeks later, following temporary subsidence of upwelling, a red-tide outbreak occurred in these waters (Walsh, pers. commun.) similar to pre-upwelling blooms encountered during MESCAL I in March 1972 (Walsh et al. 1974).

A coccolithophorid similar to *Syracosphaera apsteini* (15 cells/liter) was found occasionally.

Noctiluca scintillans was frequently encountered in the samples, especially at Station 38, with evidence of active predation of the phytoplankton by *Noctiluca*.

Carbon Abundance

The mean carbon content in the upper 50 m for the dominant non-setose diatom component >20 μm, exclusive of *Planktoniella muriformis, Rhizosolenia* spp., and OTHERS is given in Table 2. The reason for excluding *Planktoniella muriformis* is because of the great difficulty to enumerate the cells within the colonies, whose size varied considerably. Insufficient specimens of the rarer *Rhizosolenia* and "other" species prevented reliable cell sizing to calculate cell volume.

The mean carbon content in the upper 50 m ranged from 6.12 to 20.44 μg C/liter at the various stations; the overall mean was 10.67 μg C/liter (Tables 2 to 4). Comparison of the percent of the total population represented by a species on a numerical and carbon basis shows an inherent inadequacy of the numerical census as a population monitor. For example, the *Coscinodiscus* spp. as carbon contributed from 16.7 to 53.4% of that in the >20-μm size fraction (exclusive of the non-setose species which were not monitored), while numerically they composed only from 4.8 to 16.7%. The corresponding means for all stations were about 36% and 11%, respectively. The six most abundant species as carbon ($\bar{x}$ = 10.67 μg C/liter) compared to their numerical ($\bar{x}$ = 4,732 cells/liter) importance in the upper 50 m are:

	μg C/liter	%	cells/liter	%
Lauderia annulata	2.97	27.8	2,227	47
Coscinodiscus "large species"	1.84	17.2	27	0.6
Ditylum brightwelli	1.38	12.9	184	3.9
Coscinodiscus cf. *asteromphalus*	0.71	6.7	148	3.1
Biddulphia mobiliensis	0.64	6.0	103	2.2
Thalassiosira rotula	0.61	5.7	454	9.6

For *Coscinodiscus* (*Brenneckella*) spp., the means are 3.53 μg C/liter (33.1%) and 458 cells/liter (9.7%). The *Coscinodiscus* (*Brenneckella*) spp. and the four other species given above compose 9.13

TABLE 4.—Mean vertical distribution as cells/liter and as equivalent carbon (μg C/liter) of the >20- μm non-setose size fraction at all stations between 30 March and 6 April 1973 in MESCAL II survey area (n = 12 (0 m), n = 13 (10-50 m), n = 9 (75 m))

Species	Depth (m)							$\bar{x}$ upper 50 m
	0	10	20	30	40	50	75	
Actinoptychus undulatus	36	41	48	36	18	13	8	34
	0.08	0.10	0.12	0.09	0.04	0.03	0.02	0.081
Biddulphia mobiliensis	177	185	121	66	47	19	5	103
	1.10	1.15	0.75	0.41	0.29	0.12	0.03	0.64
Ceratium spp.	66	68	28	5	0	2	0	27
	0.14	0.14	0.06	0.01	0	0.005	0	0.057
Coscinodiscus (Brenneckella) eccentricus	73	67	43	22	17	9	2	38
	0.16	0.17	0.11	0.05	0.04	0.02	0.005	0.092
Coscinodiscus cf. *asteromphalus*	286	228	150	96	112	18	33	148
	1.38	1.10	0.72	0.46	0.54	0.09	0.16	0.709
Coscinodiscus ? *concinnus*	49	64	46	13	30	17	16	37
	0.24	0.31	0.23	0.06	0.15	0.08	0.08	0.182
Coscinodiscus eccentricus	296	346	254	151	85	62	15	203
	0.87	1.01	0.74	0.44	0.25	0.18	0.04	0.593
Coscinodiscus cf. *granii*	11	8	3	10	2	2	0	6
	0.23	0.16	0.06	0.20	0.04	0.04	0	0.119
Coscinodiscus ("large species")	26	28	60	16	15	3	5	27
	1.79	1.93	4.13	1.10	1.03	0.21	0.34	1.838
Σ *Coscinodiscus (Brenneckella)*	741	741	556	308	261	111	71	458
	4.67	4.68	5.99	2.31	2.05	0.62	0.63	3.53
Ditylum brightwelli	304	346	247	98	73	3	4	184
	2.29	2.61	1.86	0.74	0.55	0.02	0.03	1.38
Eucampia cornuta	85	24	28	85	33	6	0	43
	0.03	0.01	0.01	0.03	0.01	0	0	0.015
Guinardia flaccida	69	109	66	24	17	2	0	50
	0.29	0.46	0.28	0.10	0.07	0.008	0	0.211
Lauderia annulata	3,393	3,761	3,597	1,479	580	46	30	2,227
	4.52	5.01	4.79	1.97	0.77	0.06	0.04	2.97
Lithodesmium undulatum	584	667	589	259	211	42	8	408
	0.85	0.97	0.85	0.38	0.31	0.06	0.01	0.59
Planktoniella muriformis (colonies)	24	24	27	32	30	12	11	26
Planktoniella sol	506	664	406	195	113	26	11	329
	0.34	0.44	0.27	0.13	0.08	0.02	0.007	0.22
Rhizosolenia spp.	24	29	64	11	6	1	1	25
Schroederella delicatula	601	456	705	220	116	47	0	364
	0.61	0.46	0.71	0.22	0.12	0.05	0	0.37
Thalassiosira rotula	442	420	969	585	57	34	0	454
	0.59	0.56	1.29	0.78	0.08	0.05	0	0.61
Σ cells/liter	7,028	7,100	7,424	3,403	1,532	352	138	4,732
Σ μg C/liter	15.51	16.59	16.98	7.17	4.37	1.04	0.77	10.67

μg C/liter, or 86% of the mean, and 3,426 cells/liter (72%).

Vertical Distribution

The mean vertical distribution of the species numerically and as carbon is given in Table 4. Selected examples of the types of vertical distribution characterizing certain species are given in Figure 2.

The standing stock declined sharply between 20 and 30 m; a uniform abundance characterized the upper 20 m. Both numerically and as biomass, the mean population at 30 m was about 45% of that at 20 m (Table 4). Expressed as carbon, and relative to the populations at 20 m, the mean populations at greater depths were only 25% (40 m), 6% (50 m) and 4.5% (75 m). About 62% of the mean carbon content of 533.5 mg C/m^2 in the upper 50 m occurred in the upper 20 m, where a mean of 16.42 μg C/liter is calculated. This pattern in vertical distribution is consistent with the mean compensation depth of about 23 m determined from Secchi disc measurements at 17 stations during this cruise leg.

The mean vertical carbon distribution of certain species (Figure 2) illustrates that peak abundance usually occurred in the upper 20 m. The phototaxic ceratians are most concentrated in the upper 10 m, with a rapid decrease (as percent of mean maximum abundance) with depth. The possibility that the "working distance" vertically within the water column varies between species is suggested by the representative distributions illustrated in Figure 2. The depth at which 50% of the mean maximum abundance occurred ranged from about 20 to 35 m between species, and from 25 to 55 m for the 25% level. Differences in light requirements, particularly that of growth at low intensities, might account for the observed distributions, if a physiological explanation can be applied. However, such distributions can also reflect differences in sinking rates, differential grazing, etc. Thus, while the underlying reasons are obscure, it is evident that the biomass distribution within and

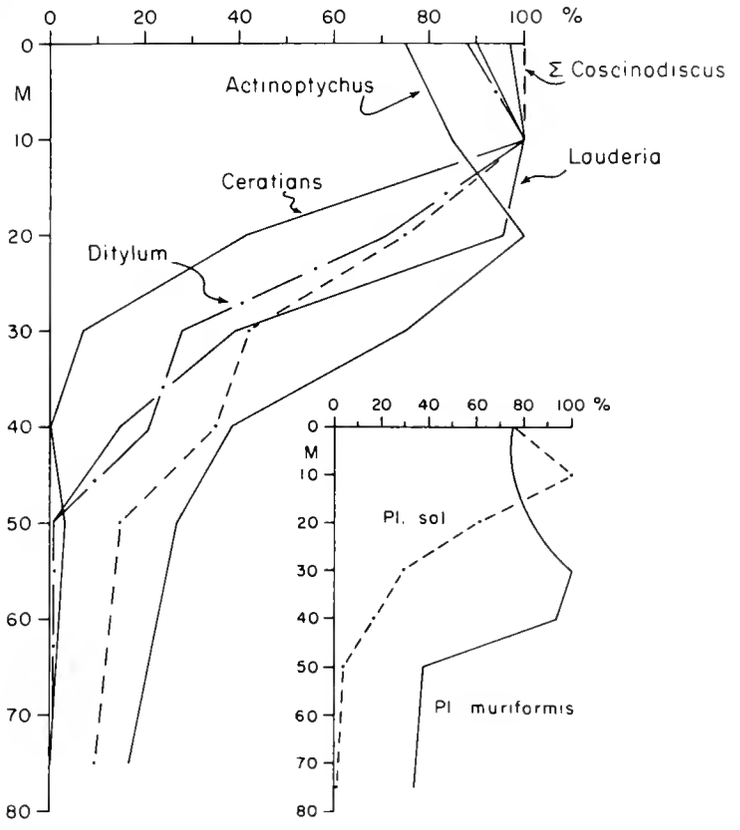

FIGURE 2.—The mean vertical distribution at all stations of *Actinoptychus undulatus*, *Ditylum brightwelli*, *Lauderia annulata*, *Planktoniella muriformis*, and *P. sol*, and for the combined *Ceratium* and *Coscinodiscus* species. Abundance is given as percent of the maximum mean abundance for each species presented in Table 4.

below the euphotic zone differs between species of phytoplankton.

BIOGEOGRAPHICAL COMMENTS

Planktoniella muriformis

Loeblich et al. (1968) described *Coenobiodiscus muriformis* as a new genus and species from north San Diego Bay, Calif., where blooms occur, and where it was reported to be in every sample collected since its first sighting in July 1966. Cultures were also established at 23° to 25°C. This unique, colonial diatom comprised up to 530 cells embedded in a one-cell thick gelatinous matrix which linked the cells in the girdle region. The circular to subcircular colonies have concave-convex shape and can be at least 500 μm in diameter. Round (1972) recently described a similar organism from the harbor at Tema in Ghana, Africa. (Environmental data were not given.) It differed from the San Diego population in the presence of considerably fewer cells per colony and slight microstructural variations. Nonetheless, Round concluded that these taxa were similar, and transferred this species to the genus *Planktoniella*.

This unique organism was conspicuous in the present survey, both in the vertical net tows and quantitative samples along the approximately 700-km track at temperatures ranging from about 11.5° to 16°C. In experiments to be described elsewhere in greater detail (Smayda in press b), the growth rate for colony increase was 2.9 and 2.0 "doublings" per day at ca. 15° to 18°C. These compare with daily colony doubling rates of 1.3 to 1.6 for cultured populations at 23° to 25°C calculated from data presented in Loeblich et al. (1968). The principal value of these data is the indication that active growth occurred under the upwelling conditions. Loeblich et al. and Round disagree as to whether all cells in the colony divide to produce a new colony, or whether growth without new colony formation can also occur.

The maximum recorded abundance of *Planktoniella muriformis* was 205 colonies/liter at the surface at Station 18. It was very common in the net tows. Thus, given its relative abundance at this time, its noteworthy appearance, and the long-term program of frequent net collections (especially during this time of year) in the coastal waters of southern and Baja California (including this survey area), carried out by Allen and Cupp, their failure to comment in any fashion on its presence is puzzling. Nor is it cited in any way in their periodic species lists for these waters (Cupp 1934; Allen 1938), or for the Gulf of California (Cupp and Allen 1938; Gilbert and Allen 1943), where floristic similarities are evident. Neither does Round (1967) mention it in his recent report on the net phytoplankton in the Gulf of California. Further, only this species and *Thalassiosira rotula*, of those found during this survey, were not found in the Gulf of Panama (Smayda 1966). Thus, the present observations suggest that *Planktoniella muriformis* is presently distributed in the Pacific Ocean from San Diego south to Punta Abreojos. But it is uncertain whether its presence and/or distribution in these coastal waters are relatively recent phenomena. Its apparent general rarity in nature and intriguing global distribution (off Baja California and Ghana) are also puzzling, although possibly an artifact of sampling. (The recent discovery of another remarkable colonial diatom, *Thalassiosira partheneia*, in the upwelling waters off Cape Blanc, Africa may also illustrate this latter problem (Schrader

1972).) It is also possible that differences in habitus account for this enigma. Loeblich et al. (1968) report that solitary cells present in cultures were unable to form colonies, and under certain conditions colonies reproduced themselves as "clusters of cells" or "a solitary pattern of growth" occurred. If the occurrence of variations in habitus correctly explains these biogeographical issues, then the factors triggering colony formation become of interest. Upwelling does not appear to be detrimental in this regard, at least during its initial stages in the survey area.

From its size, thickness, and concave-convex shape, it might a priori be presumed that *Planktoniella muriformis* is particularly well adapted for flotation and has a near-surface niche. However, the equal distribution in colony abundance in the upper 40 m is noteworthy, and contrasts to *Planktoniella sol*'s concentration in the upper 20 m (Figure 2; Table 4).

Coscinodiscus (Brenneckella) eccentricus

In the Gulf of Panama a unique centric diatom was found identified as *Brenneckella* sp. (Smayda 1966). It was characterized by an "outer, gelatinous" ring surrounding the girdle region in or on which coccolithophorids and other particulate matter were embedded. This organism was also commonplace in the present material (Tables 1, 4), and grew actively in one experiment when 2.9 divisions/day were measured (Smayda in press b). Gaarder and Hasle (1961) have reviewed its taxonomic history, the limited information on its distribution, and the potential relationships between the attached organisms and the host diatom. Based on electron microscopy, they concluded that the two species of *Brenneckella* described earlier are conspecific with *Coscinodiscus eccentricus*, a synonomy which is followed here. Nonetheless, it is listed separately as *Coscinodiscus (Brenneckella) eccentricus* in Tables 2 and 4 where mean values for the *Coscinodiscus* spp. are given.

Gaarder and Hasle suggest that the attachment of cocolithophorid cells to this diatom is a mere agglutination without any symbiotic significance. While this may be so, the relationship still remains intriguing. One may ask why other *Coscinodiscus* species, or centric diatoms, including *Planktoniella sol* characterized by an outer membrane, seemingly are invariably devoid of such epibionts.

DISCUSSION

Allen (1924, 1934, 1938) and Cupp (1930, 1934; Cupp and Allen 1938) carried out a long-term survey (approximately 1921 to 1937) of the net phytoplankton in the coastal, surface waters of southern and Baja California. These data are valuable principally in their suggestion that the net diatom community in these waters from San Diego to the Gulf of Panama is similar, inclusive of the Gulf of California (Cupp and Allen 1938; Gilbert and Allen 1943). Subsequent quantitative observations in the Gulf of Panama (Smayda 1963, 1966), net collections in the Gulf of California (Round 1967), and the present survey generally support this.

Diatoms dominated the net community (Table 4) in response to upwelling, then in its early stages. A red-tide outbreak occurred during mid-April in the survey area following a temporary subsidence of upwelling (Walsh pers. commun.). During the MESCAL I survey of 1972 in this same region the dinoflagellate *Gonyaulax polyedra* was dominant in March (Walsh et al. 1974). Its abundance then also probably reflects the occurrence of limited, if any, upwelling. Thus, annual variations in time of inception of upwelling in these waters, as well as variations within a given upwelling cycle, are reflected in the relative importance of dinoflagellates vis-à-vis that of diatoms. An abundance of diatoms will be an indication of nutrient enrichment, as is generally observed in upwelled waters.

The species composition of the diatom community is of considerable interest, given the observations of Longhurst et al. (1967). They reported that *Coscinodiscus* species, especially *C. eccentricus*, were important dominants of the upwelling communities in June and August 1964 near Magdalena Bay, lying south of the present survey area. Blooms of this genus are of exceptional interest. *Coscinodiscus*, a priori, is not generally expected to occur in great abundance pelagically in unmodified coastal and oceanic water masses. This is generally confirmed by worldwide observations, as reported in the extensive literature on phytoplankton surveys. The periodic, enormous spring blooms of *Coscinodiscus concinnus* in the North Sea are noteworthy and puzzling (Grøntved 1952).

This interest in local species composition is sustained, given the remarkable occurrence and abundance of the red crab, *Pleuroncodes planipes*,

(Longhurst 1968) in these waters. Although it is omnivorous, while herbivorous it grazes on phytoplankton cells >25 μm (Longhurst et al. 1967), i.e., the size class of *Coscinodiscus*. Indeed, these authors report active grazing on this genus under experimental conditions, and confirmed during the present study (unpubl.). Therefore, is an abundant *Coscinodiscus* community significant causally to *Pleuroncodes*, whose occurrence is a major biotic characteristic of the Baja California upwelling system? Some calculations will be made to evaluate this relationship, and to examine the other questions posed in the Introduction.

The maximum observed abundance of all *Coscinodiscus* (*Brenneckella*) spp. was 2,243 cells/liter; the mean abundance for all stations in the upper 50 m was 458 cells/liter (Table 4). This meager abundance contrasts with a mean of 4.3×10^6 cells/liter reported for *Coscinodiscus eccentricus* by Longhurst et al. (1967). In their study, this concentration represented only 8% of the total community, which was dominated by several *Nitzschia* species. *Coscinodiscus* cells of <20 μm diameter were also not present in bloom concentrations in the present material. Therefore, unlike in Magdalena Bay, this genus was not important numerically, at least during the initial stages of upwelling in the survey area.

It remains obscure whether a regional patchiness characterizes the abundance of *Coscinodiscus* during upwelling along the coast of Baja California, as for *Coscinodiscus asteromphalus* in the Gulf of California (Round 1967). Allen and Cupp referred repeatedly to such patchiness in other species in these waters. It is also possible that the *Coscinodiscus* bloom reported by Longhurst et al. represents a later state in a species succession. Finally, it might have represented an episodic bloom in response to local, unique factors, rather than reflect a general regional or successional phenomenon. Nonetheless, the reported summer abundance of *Coscinodiscus eccentricus* during upwelling in 1964 remains intriguing. The dynamics of *Coscinodiscus* populations in these waters warrant further study.

The dominant (non-setose) species numerically in the >20-μm fraction was *Lauderia annulata*, although blooms of *Schroederella delicatula* and *Thalassiosira rotula* characterized individual stations (Table 2). The total *Coscinodiscus* (*Brenneckella*) spp. represented only about 10% of the mean population numerically, but this represented 33% of the mean carbon; corresponding values for *Lauderia annulata* are 47% and 28%, respectively. Thus, although *Coscinodiscus* was not as abundant as in the Longhurst et al. survey it dominated the >20-μm biomass fraction during MESCAL II.

The percent of the total phytoplankton community represented by the >20-μm fraction can be established indirectly from chlorophyll determinations made at 10 of the stations for which quantitative >20-μm phytoplankton counts were also made. The mean concentration (based on 5 depths) in the upper 20 m was 3.46 μg Chl *a*/liter. This depth is near the compensation depth; chlorophyll determinations were not made at depths greater than this 1% level. The significant decrease in mean phytoplankton abundance between 20 and 30 m was pointed out previously (Table 4). The mean carbon content of the non-setose fraction >20 μm in the upper 20 m is 16.4 μg/liter.

Longhurst et al. (1967) give a mean carbon/chlorophyll *a* ratio of 258:1 for their material. This is exceptionally high, and contrasts with a mean (n = 17) of 110:1 characterizing the community dominated by *Gonyaulax polyedra* during the 1972 MESCAL I survey (Walsh et al. 1974). A mean ratio of 40:1 characterized diatom-dominated communities found throughout the euphotic zone in the Peru Current (Lorenzen 1968). Applying this conversion factor yields a mean carbon content of 138 μg C/liter in the upper 20 m in the present survey. If a similar carbon/chlorophyll ratio characterizes the >20-μm fraction (it may differ with cell size), then this size group (exclusive of setose species) contributes at least 12% of the viable phytoplankton carbon in the euphotic zone. *Lauderia annulata* and the *Coscinodiscus* (*Brenneckella*) species each contribute 3.5%. The non-setose component of this size grouping would appear to represent only a modest portion of the phytoplankton biomass in the euphotic zone. However, significant diel variations in this component occur, which indicate a high turnover rate. The fluxes and kinetics of this response are considered elsewhere (Smayda in press b).

Longhurst et al. (1967) estimated that the grazing rate of *Pleuroncodes* on phytoplankton was 540 liters/day per animal. Its mean abundance during MESCAL II was 1 animal/m^3 (Whitledge, pers. commun.), threefold greater than that during Longhurst and coworkers' study. The total phytoplankton population in the upper 20 m was

276 mg/m³, assuming a dry weight : carbon ratio of 2. Smith et al. (footnote 2) report a mean caloric content of 1,699 cal for *Pleuroncodes* during MESCAL II, and cite a caloric value of 3,814 cal/g dry wt for diatoms. From these data, a daily caloric ingestion of phytoplankton of 568 cal/m³ within the euphotic zone is calculated, which represents 33% of the total caloric content of the crab. *Coscinodiscus* would contribute only 1.2% of this daily caloric ingestion and the non-setose component of the >20-μm size fraction 4%, based on their contributions of 3.5 and 12%, respectively, to the phytoplankton standing stock in the upper 20 m. Even at the maximum growth rates of 3 divisions/day for *Coscinodiscus* observed during the survey (Smayda in press b) this genus would provide a negligible fraction of the daily caloric intake estimated for *Pleuroncodes*. This suggests that the *Coscinodiscus* population could not then support the *Pleuroncodes* population; other food sources were necessary.

Smith et al. (footnote 2) demonstrated that the respiration rate (as oxycaloric equivalents) of *Pleuroncodes* is only 3% of the ingestion rates calculated using the grazing rate proposed by Longhurst et al. (1967). Other calculations made by them support their notion that the grazing rate of 540 liters/day is too high, and partly accounts for the discrepancy between rates. Other factors which might contribute to the apparent feeding inefficiency of *Pleuroncodes* would be high energy losses as fecal material. Longhurst et al. observed the copious production of fecal material packed with *Coscinodiscus*. While the magnitude of this waste production during MESCAL II can not yet be evaluated, the relative rates of deposition of frustules and organic matter to the sediments when contained in fecal pellets and as free cells can be put into perspective.

The sinking rates (n = 24) of fecal pellets produced by freshly collected crabs, and determined on board ship (unpubl.), ranged from 61 to 144 m/h. These rates exceed by 1 to 4 orders of magnitude those calculated (Smayda 1970) for the different sizes of *Coscinodiscus* encountered, and that (5.2 m/hr) estimated (Smayda 1969) for the mean zooplankton fecal pellet size (320,000 μm³) collected routinely in the >20-μm fraction. Thus, while *Coscinodiscus* apparently contributed only a negligible fraction of the daily caloric ingestion of *Pleuroncodes*, the latter's ingestion and voidance in fecal material of this genus and other heavily silicified diatoms >20 μm represent a means of exceptionally rapid deposition onto the sea floor.

The mean carbon content of 138 μg/liter during the initial stages of upwelling compares with a mean standing stock of 566 μg C/liter at 20 stations reported for this region during the *Gonyaulax polyedra* bloom in March 1972 (from Table 1 in Walsh et al. 1974). The mean carbon content ranged from 23 to 100 μg/liter at three stations sampled over a 5-mo period off La Jolla, Calif. (Eppley et al. 1970). The mean concentration during upwelling south of the survey region during June 1964 ranged from 48 μg C/liter (from C/Chl *a* of 40:1) to 308 μg C/liter using data given by Longhurst et al. (1967). However, the data are too limited as yet for any meaningful comparison of regional or seasonal variations in apparent productivity in these coastal waters. They also indicated that the net plankton was usually more abundant in April (upwelling) between Punta Abreojos and Punta Eugenia, i.e., in the present survey area (Figure 1). However, quantitative data are needed to confirm this.

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APPENDIX TABLE 1.—List of phytoplankton taxa identified to species found in net tows and in >20-μm size fraction.

BACILLARIOPHYCEAE
- *Actinocyclus octonarius* Ehrenberg
- *Actinoptychus undulatus* (Bailey) Ralfs
- *Asterionella japonica* Castracane
- *Asterolampra marylandica* Ehrenberg
- *Asteromphalus heptactis* (Brébisson) Ralfs
- *Bacteriastrum hyalinum* Lauder
- *Biddulphia mobiliensis* Bailey
- *Biddulphia* cf. *sinensis* Greville
- *Cerataulina pelagica* (Cleve) Hendey
- *Chaetoceros affinis* Lauder
- *Ch.* cf. *costatus* Pavillard
- *Ch. curvisetus* Cleve
- *Ch. debilis* Cleve
- *Ch. decipiens* Cleve
- *Ch. didymus* Ehrenberg
- *Ch. peruvianus* Brightwell
- *Ch. socialis* Lauder
- *Ch. subsecundus* (Grunow) Hustedt
- *Corethron pelagicum* Brun
- *Coscinodiscus* cf. *asteromphalus* Ehrenberg
- *C. centralis* var. *pacifica* Gran et Angst
- *C. concinnus* W. Smith
- *C. curvatulus* Grunow
- *C. eccentricus* Ehrenberg
- *C. granii* Gough
- *C. perforatus* var. *pavillardi* (Forti) Hustedt
- *C. radiatus* Ehrenberg
- *Coscinodiscus (Brenneckella) eccentricus (Lohmann)* Gaarder et Hasle
- *Ditylum brightwelli* (West) Grunow
- cf. *Ethmodiscus rex* (Rattray) Hendey
- *Eucampia cornuta* (Cleve) Grunow
- *Guinardia flaccida* (Castracane) Peragallo
- *Hemidiscus cuneiformis* Wallich
- *Lauderia annulata* Cleve
- *Leptocylindrus danicus* Cleve

BACILLARIOPHYCEAE—Cont.
- *Lithodesmium undulatum* Ehrenberg
- *Paralia sulcata* (Ehrenberg) Cleve
- *Planktoniella muriformis* (Loeblich III, Wight et Darley) Round
- *Planktoniella sol* (Wallich) Schütt
- *Rhizosolenia alata* Brightwell
- *R. bergoni* H. Peragallo
- *R. calcar avis* M Schultze
- *R. delicatula* Cleve
- *R. imbricata* var. *shrubsolei* (Cleve) Schröder
- *R. robustum* Norman
- *R. stolterfothii* H. Péragallo
- *Roperia tessellata* (Roper) Grunow
- *Shroederella delicatula* (Peragallo) Pavillard
- *Skeletonema costatum* (Greville) Cleve
- *Stephanopyxis turris* (Greville) Ralfs
- *Thalassionema nitzschioides* (Grunow) Hustedt
- *Thalassiosira rotula* Meunier
- *Thalassiothrix frauenfeldii* Grunow
- *T. longissima* Cleve et Grunow
- *T. mediterranea* var. *pacifica* Cupp

DINOPHYCEAE
- *Ceratium furca* (Ehrenberg) Claparede et Lachmann
- *Ceratium fusus* (Ehrenberg) Dujardin
- *Dinophysis miles* Cleve
- *Gonyaulax* cf. *polyedra* Stein
- *Noctiluca scintillans* (Macartney) Kofoid et Swezy
- *Pyrocystis* cf. *lunula* Schütt
- *Pyrophacus horologicum* Stein

CHRYSOPHYCEAE
- *Distephanus speculum* (Ehrenberg) Haeckel

HAPTOPHYCEAE
- *Phaeocystis poucheti* (Hariot) Lagerheim

PRASINOPHYCEAE
- cf. *Halosphaera viridis* Schmitz

OPTIMUM ECONOMIC YIELD OF AN INTERNATIONALLY UTILIZED COMMON PROPERTY RESOURCE[1]

LEE G. ANDERSON[2]

ABSTRACT

The exploitation of a common property resource, specifically a fishery, by nationals of two countries is discussed using a simple general equilibrium analysis. The interdependence of their production possibility curves is used to describe the open-access equilibrium yield, local maximum economic yields, and a true international maximum economic yield. Finally a complete description of the conditions necessary for this international maximum economic yield and why they are different from those in a national fishery is presented.

The purpose of this paper is to analyse, using a simple general equilibrium model, the problem of the allocation of resources where common property or open access exists for some of them. The common property or open-access resource will be a fish stock. The economics of fisheries has been quite extensively developed. See for example Gordon (1954), Scott (1955), Crutchfield and Zellner (1962), Turvey (1964), Crutchfield (1965), Christy and Scott (1965), Smith (1969), Copes (1970), Scott and Southey (1970), Gould (1972), Southey (1972), and Anderson (1973). The present paper follows Scott and Southey and uses a production possibility (PP) curve model which takes into direct account all the resources of the economy and not just the fishery. This change in focus is especially useful for analysing economic aspects of international use of common property resources, a problem that has long been recognized but which has received very little treatment to date. The following quote from Christy and Scott (1965:223) summarizes the problem fairly well:

> "Two countries contemplating the same fishery may rightly make different choices about the intensity and combination of fishing activities .... These different valuations are ultimately the result of the obstacles to the movement of factors from one economy to another. More directly, they result from differences in population, national income, and tastes. It is a commonplace of the theory of comparative costs that the same industry may use a different technique in each country, depending on the structure of wages and prices in each place. But it has never, to our knowledge, been pointed out that the ocean is the main locale where these structures clash .... Of course, it is possible to exaggerate these discrepancies. Forces outside the fisheries tend to bring the national wage and price structure into line, through the movement of goods and the sale of services. And within the fishery itself the increasing international trade in this equipment, all tend to press toward a uniform set of labor-capital-fish price-ratios."

The model presented will allow a more formal analysis of these and other problems.

The first section of the paper describes a one country model of the economics of fisheries from a general equilibrium point of view. Results identical to the earlier works are derived as a starting point for discussion. The second section expands the model to consider two nations both having access to the same fish stock and describes the conditions necessary for an international open-access equilibrium yield, for local maximum economic yields (MEY), and for a true international MEY. The third section describes the conditions for an international MEY in more detail and shows the ways in which the countries can go about achieving them. Throughout the analysis is static.

I

Consider a country with a specified amount of resources, a given technology, and exclusive use (either through default or international law) of a fish stock. Using its resources, it can either produce manufactured goods (M) or fishing effort (E) which can be applied to the fish stock to catch fish. Let the implicit function for the PP curve between M and E be:

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$$G\ (E, M) = 0. \qquad (1)$$

Assume that it is quasi-concave so that there will be a concave transformation curve between E and M. Let the sustained yield curve of the fish stock (i.e. the production function) be expressed as:[3]

$$F(E) = aE - bE^2. \qquad (2)$$

Using this equation assumes that the fish stock will always be in a biologic equilibrium. F will increase until E is equal to $\frac{a}{2b}$ and will thereafter decrease. F will be zero when $E = 0$ and when $E = \frac{a}{b}$. As long as the maximum amount of E possible is greater than $\frac{a}{2b}$ but less than $\frac{a}{b}$, then the PP curve for M and F will be similar to the solid one in Figure 1. (Ignore for the moment the dotted one.) The slope of the curve is:

$$\frac{dF}{dM} = \frac{dF}{dE}\ \frac{dE}{dM} = -(a - 2bE)\ \frac{G_2}{G_1} \qquad (3)$$

where G_1 is the derivative of G with respect to its first argument, etc. Fish output will be at a maximum when E equals $\frac{a}{2b}$, not when all of the resources are used in the production of E. As long as the marginal productivity of E in fishing is negative, the PP curve will have a positive slope. Switching resources out of effort and into manufacturing will actually increase both F and M. Where E's marginal productivity in F is positive, the PP curve will have its normal negative slope. Because both $\frac{G_2}{G_1}$ and $(a - 2bE)$ increase as M increases (i.e. as E decreases), the curve will be concave to the origin. Also assume that there is a linearly homogeneous social utility function of the form

$$U = U\ (F, M). \qquad (4)$$

As pointed out in the literature cited above (see especially Turvey 1964 and Scott and Southey 1970), as long as no one regulates entry into the fishing industry, profit maximizing individuals will continue to produce or buy E as long as the value of the average catch per unit of E is greater than the price of effort. The effects of this are as follows. If E and M are produced in pure competition, then $-\frac{P_M}{P_E} = \frac{dE}{dM}$. Equilibrium will occur in the open-access fishery when $P_F \frac{F}{E}$ equals P_E; that is when the average return to effort equals its cost. [Smith (1969) has shown that under certain circumstances, the fishery will not reach an equilibrium. For the moment let us ignore this possibility although its effects will be discussed briefly below.] It can be shown therefore that with an open-access fishery and pure competition in the production of E and M, producers will arrange their production such that for any given price ratio the following condition will hold:

$$-\frac{P_M}{P_F} = \frac{F/E}{dM/dE}. \qquad (5)$$

Maximum consumer welfare occurs where the slope of the social indifference curve is equal to the price ratio. That is where

$$-\frac{U_2}{U_1} = -\frac{P_M}{P_F}.$$

Therefore a general equilibrium in the production and the consumption sectors of the economy will occur when

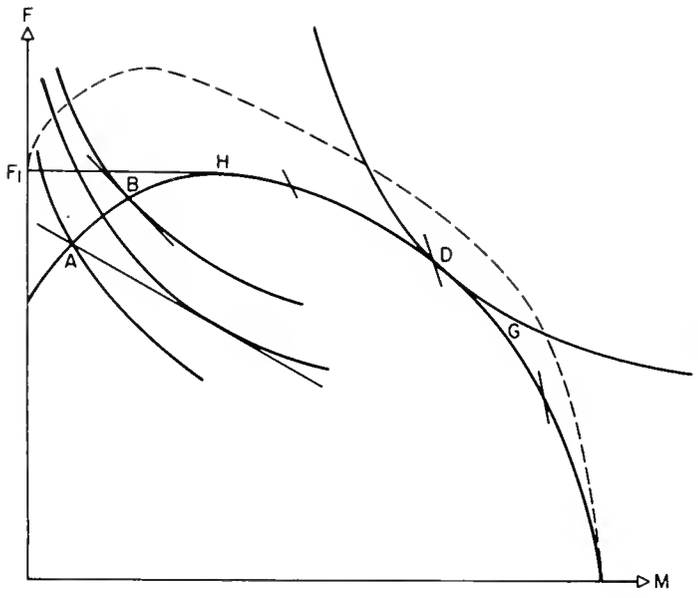

FIGURE 1.—The solid concave curve is the production possibility curve and the set of convex curves are the community indifference curves. Open-access equilibrium will occur at B, maximum sustainable yield at H, and maximum economic yield at D. In the two country model, a decrease in fishing effort in the other country will shift the production possibility curve to the dotted one.

[3]The sustained yield curve is the relationship between the amount of effort expended and the amount of fish that will be captured period after period. The particular expression here follows Schaefer (1957). Although other expressions have been discussed recently (see the papers by Southey and Gould cited above), Expression (1) is descriptive enough to capture the essentials of the argument.

$$-\frac{U_2}{U_1} = -\frac{P_M}{P_F} = \frac{F/E}{dM/dE} . \qquad (6)$$

Conditions for the maximization of social welfare, however, are:

$$-\frac{U_2}{U_1} = -\frac{P_M}{P_F} = \left[\frac{dF/dE}{dM/dE} \equiv \frac{dF}{dM}\right] . \qquad (7)$$

An expression for $\frac{dF}{dM}$ is given in (3) and $(F/E)/(dM/dE)$ can be expressed as:

$$(F/E)/(dM/dE) = -(a - bE)\frac{G_2}{G_1} . \qquad (8)$$

The ratio $\frac{F/E}{dM/dE}$ will increase in absolute size as M increases, and because of the assumption that the maximum E is less than a/b, it will always be negative, even when the slope of the PP curve is positive. It can be seen that when they are both negative, this ratio will be larger in absolute size than the slope of the PP curve at that point; i.e. it will have a steeper slope. The small lines on the PP curve in Figure 1 represent the ratio $\frac{F/E}{dM/dE}$ at that point.

In terms of Figure 1, open-access equilibrium will occur at point B where the slope of the indifference curve as it intersects the PP curve is equal to the ratio of $\frac{F/E}{dM/dE}$ at that point.[4] The social optimum is at point D where the indifference curve is just tangent to the PP curve. The common property or open-access equilibrium will always be to the left of the optimal point; therefore with open access, too many resources will be allocated to F under the market system. It is even possible that the market equilibrium will occur in the positive sloped segment of the PP curve.

By way of comparing the present analysis with the standard one, point H on Figure 1 is the point of maximum sustained yield for a fishery and point D is the MEY. The latter point has less fish but more manufactured goods than the former (and may even have less fish than the point where the unregulated fishery will operate). At MEY, however, no fish is produced unless its value is greater than its opportunity cost. Although MEY in the traditional literature refers to a specified amount of fish production, it assumes that the resources not in fishing are used efficiently in the production of other goods. Describing the model in terms of a PP curve makes this explicit.

Through proper regulation, the country can move to MEY. This could involve a ceiling on the amount of fishing effort allowed or the granting of property rights to the fishery to certain individuals. The former has been tried but usually by means of decreasing efficiency rather than by shifting resources to other types of production, and the latter can lead to monopoly or oligopoly unless the property rights are distributed widely or there are other fish stocks that can provide the necessary competition.

If the government only allows α units of effort, where α is less than the open-access amount of effort, and then distributes the rights to this number of units among a large enough group such that there is still pure competition in the market for both effort and fish, these people will be earning a rent per period, R, of $P_F F(\alpha) - P_E \alpha$ where $F(\alpha)$ is the amount of fish caught by α units of effort. Unless reductions in effort have perverse effects on price, average catch, or cost of effort, this rent will be positive. See Anderson (1973:513).

The optimal amount of effort is where the total amount of rent is a maximum (Christy and Scott 1965:8). By using the standard mathematical procedure it can be shown that the first order condition for R to be a maximum is:

$$P_F \frac{dF}{dE} = P_E .$$

Under the above assumptions, the open-access problem of the fishery has been solved in a way that keeps pure competition in the production of M and E. Therefore $-P_M/P_E$ is equal to dE/dM and so maximization of the rent of the fishery will guarantee that

$$-\frac{P_M}{P_F} = \frac{dF/dE}{dM/dE} = \frac{dF}{dM} \qquad (9)$$

This will mean that the conditions for the maximization of social welfare, expressed in (7) above, will hold. Therefore a policy that maximizes the rent from the fishery also maximizes social welfare.

In summary, a country with exclusive rights to an open-access fishery will operate inefficiently as

[4] As Scott and Southey (1970) point out, if there are increasing returns to scale and if the social utility function is not linearly homogeneous, it is possible that there may be multiple equilibria. I have ignored that complication for purposes of this paper.

long as there is no regulation of fishing effort. This will be because as long as the average returns to fishing are greater than the price of effort, private decision makers will continue to demand E. Also since E and F are directly related, there is always a direct relationship between P_E and P_F .

II

Now to turn to the case of more than one country exploiting the same fish stock, analysis of this is made very difficult by a variety of intriguing problems. For instance, technology may be so different in the two countries that it is very hard to find a common measure of fishing effort, tastes may be such that one country prefers small fish while the other prefers large ones and yet the sustained yield curve is dependent on the size of catch, each country may be using other criteria for harvesting the fish; for example, one may look at it as a place to put unemployed labor, or as a source of earning foreign exchange. For purposes of discussion these intricacies will not be considered.

Assume that two countries, country X and country Y, both with specified production capacities ($G^X(E_X, M_X) = 0$ and $G^Y(E_Y, M_Y) = 0$) and linearly homogeneous community welfare functions ($U^X = U^X(F_X, M_X)$ and $U^Y = U^Y(F_Y, M_Y)$,are the exclusive users of a fish stock with the sustainable yield curve (2) above. Since a unit of effort in country X, (E_X), is identical to one in Y, (E_Y), the sustained yield curve can be expressed as:

$$F(E_Y, E_X) = a(E_X + E_Y) - b(E_X + E_Y)^2.$$

As before the total catch from the fishery will reach a maximum when E_X plus E_Y is equal to $\frac{a}{2b}$ and will fall to zero if total effort gets as large as $\frac{a}{b}$.

The catch of one country will be in proportion to its effort in relation to total effort, therefore:

$$F_X(E_X, E_X) = \frac{E_X}{E_X + E_Y}\left[a(E_X + E_Y) - b(E_X + E_Y)^2\right].$$

This can be simplified to:

$$F_X = aE_X - bE_X^2 - bE_XE_Y . \qquad (10)$$

F_X will reach a maximum when E_X equals $\frac{a - bE_Y}{2b}$ and will fall to zero if it gets as large as $\frac{a - bE_Y}{b}$. The equation for F_Y is analogous.

The amount of fish that country X can catch using a specified amount of E_X depends upon how much E_Y country Y is producing and using. Similarly the catch of country Y depends upon the amount of E_X used by country X. Therefore, the shape and position of each country's PP curve for F and M is dependent upon the amount of E the other country uses. Let the two PP curves in Figure 1 be two possible ones for country X. The solid one is for the larger level of E_Y. Note that the lower curve gets further away from the higher one as M_X decreases. This is because $\frac{\partial F_X}{\partial E_Y}$, the vertical displacement of the curve due to a change in effort in country Y, is equal to $-bE_X$. Therefore, the higher the level of E_X, that is the lower the level of M_X, the greater will be the vertical displacement. The maximum amount of F_X will be at a higher amount of M_X (a lower amount of E_X) because F_X is a maximum when E_X is equal to $\frac{a - bE_Y}{2b}$.

Using this two country model let us consider the implications of three types of exploitation: 1) open access in both countries, 2) local MEY in both countries, and 3) a true international MEY.

From the above description, it can be seen that the shape and position of the PP curve for M and F in each country is dependent upon the level of effort used in the other. Therefore the open-access free market equilibrium in each country will depend upon the level of effort used in the other. The mathematical condition for an international open-access equilibrium is the following set of simultaneous equations:

$$\text{Country } X \quad \frac{U_2^X}{U_1^X} = \frac{F_X/E_X}{dM_X/dE_X} \qquad (11a)$$

$$\text{Country } Y \quad \frac{U_2^Y}{U_1^Y} = \frac{F_Y/E_Y}{dM_Y/dE_Y} . \qquad (11b)$$

This simply states that the open-access condition for each country (see Equation (6)) must hold in both simultaneously. In terms of Figure 1, each country must be operating at a point such as B.

Note however, that in country X, average catch (F_X/E_X) is a function of both E_X and E_Y. Therefore an equilibrium in country X can be reached only for a given level of E_Y, (i.e. for a given PP curve). Similarly an equilibrium in country Y is possible only for a given level of E_X. Therefore an international equilibrium is possible only at that combination(s) of E_X and E_Y where Equations (11a) and (11b) both hold simultaneously.

If free international trade between these countries is possible, the price ratios in both countries will be equalized, and so at the equilibrium, the marginal rates of substitution $\left(\frac{U_2}{U_1}\right)$ will also be equal. Therefore the following condition will hold:

$$\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} = \frac{F_X/E_X}{dM_X/dE_X} = \frac{F_Y/E_Y}{dM_Y/dE_Y}. \quad (12)$$

Graphically the international trade case can be interpreted as follows. For a given level of E produced in the other country, each country will produce at that point on the PP curve where the trade price ratio is equal to $\frac{F/E}{dM/dE}$. It will then trade along the price ratio line until welfare is maximized. Consider a country that would operate under autarky at point B in Figure 1. Under our assumptions the location of the PP curve is related to the amount of E being produced in the other country. If trade opens up with a lower $\frac{P_M}{P_F}$, the production point will move to A, but the consumption point will be at C because of imports of M and exports of F. From this it can be concluded that for each level of E produced in the other country, a decrease in $\frac{P_M}{P_F}$, i.e. a relative increase in P_F, will increase the amount of E produced locally.

As a sidelight notice that the decrease in $\frac{P_M}{P_F}$ actually decreased the welfare of the fish exporting country described in Figure 1. Trade allowed for a further misallocation of resources due to an expanding market for fish to such an extent that welfare fell. Of course, if the price line through A intersected the indifference curve through B, then welfare would have been increased in spite of the harmful effects. To be precise it should be noted that in the general equilibrium analysis, the amount of E produced by the other country will fall in most cases which will shift the PP curve out and may cause welfare to increase enough to overcome the initial loss. On the other hand, increases in $\frac{P_M}{P_F}$ brought about by trade will improve the allocation of resources and always increase welfare initially; however, the increase in E in the other country will have the opposite effect on welfare. So whether the country exports or imports fish, changes in the terms of trade may decrease welfare depending upon the direction and magnitudes of the changes caused by these two factors.

Equation (7) above states the condition for the maximization of social welfare (i.e. MEY) in the one country case. With free international trade, if both countries attempt to maximize welfare given the level of effort used in the other country, the condition for an international equilibrium is:

$$\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} = \frac{\partial F_X/\partial E_X}{dM_X/dE_X} = \frac{\partial F_Y/\partial E_Y}{dM_Y/dE_Y}. \quad (13)$$

The last two terms can be simplified to $\frac{\partial F_X}{\partial M_X}$ and $\frac{\partial F_Y}{\partial M_Y}$ respectively. These will be recognized as the slopes of the PP curves of the two countries. What this condition states is that for a local MEY, the marginal rate of substitution between M and F in each country must equal each other and they must also equal the internal marginal rate of transformation between M and F given the level of effort in the other country. In terms of Figure 1, each country will be operating at a point such as D, where the slope of the social indifference curve is equal to the slope of the existing PP curve. Notice that in equation (13), $\frac{\partial F_X}{\partial E_X}$ and $\frac{\partial F_Y}{\partial E_Y}$ are both partially determined by the level of effort in the other country, so that here again the equilibrium combination of E_X and E_Y must be simultaneously determined.

One main purpose of this paper is to describe the necessary condition for an international MEY. It is important to note at this time that they are different from Equation (13), the conditions of local MEY's given the level of effort in the other country. Since the level of effort in each country affects the PP curve, and hence potential welfare, in both countries, the maximizing conditions

must take this into account. With free international trade, these conditions are:[5]

$$-\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} = \frac{\frac{\partial F_X}{\partial E_X} + \frac{\partial F_Y}{\partial E_X}}{\frac{dM_X}{dE_X}} = \frac{\frac{\partial F_Y}{\partial E_Y} + \frac{\partial F_X}{\partial E_Y}}{\frac{dM_Y}{dE_Y}} \cdot \quad (14)$$

[5]This condition can be derived in the following manner. With international trade, the community welfare functions become

$U^X = U^X\ [F_X(E_X, E_Y) + F_T, M_X + M_T]$ and

$U^Y = U^Y\ [F_Y(E_Y, E_X) - F_T, M_Y - M_T]$

where F_T and M_T are the amounts of F and M respectively that are traded. If we wish to maximize the welfare of country X subject to a specified amount in country Y and to the productive capacities, we get the following Lagrangian function.

$$L = U^X + \lambda_1(U^Y - \bar{U}^Y) + \lambda_2 G^X(E_X, M_X) + \lambda_3 G^Y(E_Y, M_Y).$$

The first order conditions for a maximum (using the normal notation for derivatives) are:

(a) $\frac{\partial L}{\partial E_X} = U_1^X \frac{\partial F_X}{\partial E_X} + \lambda_1 U_1^Y \frac{\partial F_Y}{\partial E_X} + \lambda_2 G_1^X = 0$

(b) $\frac{\partial L}{\partial M_X} = U_2^X + \lambda_2 G_2^X = 0$

(c) $\frac{\partial L}{\partial E_Y} = U_1^X \frac{\partial F_X}{\partial E_Y} + \lambda_1 U_1^Y \frac{\partial F_Y}{\partial E_Y} + \lambda_3 G_1^Y = 0$

(d) $\frac{\partial L}{\partial M_Y} = \lambda_1 U_2^Y + \lambda_3 G_2^Y = 0$

(e) $\frac{\partial L}{\partial M_T} = U_1^X + \lambda_1 U_1^Y = 0$

(f) $\frac{\partial L}{\partial F_T} = U_2^X + \lambda_1 U_2^Y = 0.$

Note that Conditions (a) and (c) show that a change in the level of effort in one country has a direct effect on the level of welfare on the other. For this reason the Pareto conditions for an international optimum are different than in the standard case. Solving (e) for λ_1 substituting that expression in (a) and then dividing (b) by (a) yields

$$-\frac{U_2^X}{U_1^X} = \frac{\frac{\partial F_X}{\partial E_X} + \frac{\partial F_Y}{\partial E_X}}{-\frac{G_1^X}{G_2^X}}.$$

Similarly substituting the value of λ_1 into (c) and (d) and then dividing (d) by (c) yields

$$-\frac{U_2^X}{U_1^X} = \frac{\frac{\partial F_Y}{\partial E_Y} + \frac{\partial F_X}{\partial E_Y}}{-\frac{G_1^Y}{G_2^Y}}.$$

Since from (e) and (f) it can be shown that $-\frac{U_2^X}{U_1^X} = -\frac{U_2^Y}{U_1^Y}$, and by definition $-\frac{G_1^X}{G_2^X} = \frac{dM_X}{dE_X}$ and $-\frac{G_1^Y}{G_2^Y} = \frac{dM_Y}{dE_Y}$, it can be shown that Condition (12) holds.

Alternatively this condition can be written as:

$$-\frac{U_2^X}{U_1^X} = -\frac{U_2^Y}{U_1^Y} = \frac{\overset{(-)}{\partial F_X}}{\partial M_X} + \frac{\overset{(+)}{\partial F_Y}}{\partial M_X} = \frac{\overset{(-)}{\partial F_Y}}{\partial M_Y} + \frac{\overset{(+)}{\partial F_X}}{\partial M_Y} \cdot \quad (14')$$

Expression (14) is useful for comparisons with the open-access free market international equilibrium conditions in (12) and with the local MEY condition in (13), while Expression (14') is useful for tying the analysis to the PP curve.

In words these conditions state that the marginal rate of substitution for M and F and a special type of marginal rate of transformation (MRT) in both countries must equal each other. The marginal rate of transformation is special in that it considers the effect on fish production in both countries, of a change in manufacturing in only one. To be more precise a "socially optimal" international policy should guarantee that neither country expand their fishing effort unless the value of the extra yield, regardless of who catches it, is equal to the value of the extra M that must be foregone. That is country X should compare the opportunity value of producing effort with its effect on local catch $(\frac{\partial F_X}{\partial M_X})$ and with its effect on country Y's catch $(\frac{\partial F_Y}{\partial M_X})$. The same restriction must be placed on country Y's fishing industry also.

It is important to stress at this point that these international MEY conditions were derived by maximizing the level of welfare in one country while specifying a certain level in the other. That is, an initial distribution of the fishery is essential before the maximizing conditions for an international MEY can be utilized. This same condition will hold at many combinations of E_X and E_Y depending upon how the wealth of fishery is distributed. This is one of the major differences between a national MEY and an international MEY. The importance of the beginning distribution will be discussed in greater detail in Section III.

It can be shown from the equations for F_X and F_Y that $\frac{\partial F_X}{\partial E_X} + \frac{\partial F_Y}{\partial E_X}$ equals $\frac{\partial F_Y}{\partial E_Y} + \frac{\partial F_X}{\partial E_Y}$ and that F_X/E_X equals F_Y/E_Y. Therefore in both the open-access equilibrium (Condition 12) and at any true international optimum point (Condition 14), dM_X/dE_X must equal dM_Y/dE_Y. That is, the real cost of producing fishing effort will be the same in both countries. The difference is that only in the

latter is the proper amount of it produced. The equalizing mechanism in both cases is the trade in fish which is indirect trade in effort.

Figure 2 depicts the international MEY situation in terms of the PP curve of both countries. Expression (14′) says that the absolute value of the slope of the indifference curves in both countries $(-\frac{U_2}{U_1})$ must be less than the absolute value of the slope of their existing PP curves at the point of operation $(\frac{\partial F}{\partial M})$. That is at the equilibrium point, the slope of the indifference curve must be less steep than the slope of the PP curve. Therefore the slope of the price ratio line must also be less steep than the slope of the PP curve. What this means is that both countries must produce less fish than they would under normal free market conditions given the relative cost of producing F and M. The reason for this is that they must take into account the effect of their output levels on the production of fish in the other country. In the diagram the regulated price ratio common to both countries is represented by the two straight lines. Country X, producing at point A and consuming at point B, is importing M_T units of M and exporting F_T units of F. Country Y, producing at point A′ and consuming at point B′, is doing the reverse. Since at the equilibrium, producers in both countries are basing the production decision on the same price ratio, and since $\frac{dM_X}{dE_X} = \frac{dM_Y}{dE_Y}$, there will be no balance of payments problem; i.e. the value of F traded will equal the value of M traded.

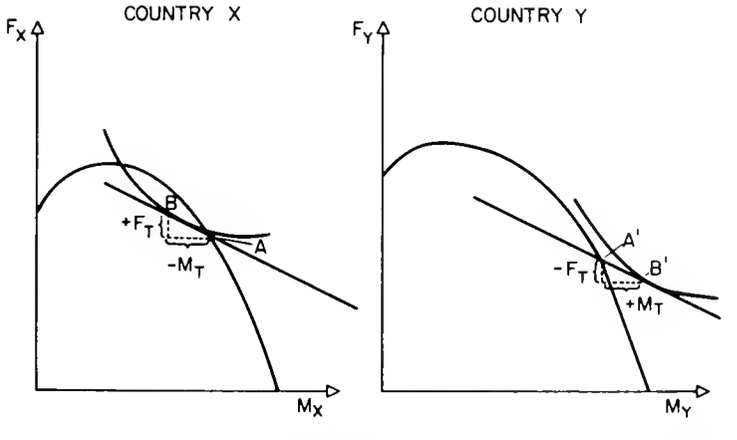

FIGURE 2.—In the two country case, the international maximum economic yield can be represented by the countries producing at A and A′ and consuming at B and B′, the difference being made up by international trade. The exact relationship between the slope of the indifference curves and the production possibility curves is expressed in Equations (14) and (14′).

Two technical points regarding this diagram should be pointed out. First, since there are international interdependencies involved, operation at the international MEY requires government regulation. Some form of taxes or other means of control will be necessary in each country to keep producers operating where the price ratio to consumers, as represented by the slope of the indifference curve, is different than the ratio of marginal costs of production, as represented by the slope of the PP curve. Second, it may seem strange that country X, the importer of fish, is consuming at a point inside its existing PP curve. (If the indifference curve for country Y through point B′ intersects the PP curve, that country will also be operating at a point where its welfare is not as large as it might be given its existing PP curve.) Would it not be to its advantage to stop trading and expand its own fishing by moving up its PP curve? In answering this question it must be remembered that the only reason country X's PP curve is as high as it is, is that country Y has reduced its level of effort. Only if country Y were foolish enough to keep its level of effort the same regardless of country X's behavior would the latter benefit from an increase in effort. It would gain welfare while country Y would lose. This discussion points out, however, that proper management of international fisheries will be difficult to enforce because one or both of the countries involved will be motivated to increase effort from the optimal point.

So far three distinguishable points on each PP curve can be identified: the open-access equilibrium point (where the slope of the indifference curve, or the international price line, as it intersects the PP curve equals $\frac{F/E}{dM/dE}$, i.e. point B in Figure 1); the local MEY optima given the level of effort in the other country (where the slope of the indifference curve or the international price line is equal to $\frac{\partial F}{\partial M}$, i.e. point D in Figure 1); and the point where the country contributes to an international MEY given the level of E produced abroad, i.e. at point A or A′ in Figure 2. With regard to the latter, only if both countries are operating in this fashion, is it a true international MEY, where the value of the net increase in fish production by the marginal unit of effort, regardless of its origin,

is just equal to the value of the resultant decrease in the production of M.

As a sidelight it is interesting to note that if one country unilaterally adopts a local optimum regulation policy given the level of effort in the other country, at the new equilibrium it will be using less effort and in most cases the other country will react to this by increasing their level of effort. Therefore, while the decrease in effort will increase its level of welfare (it will move from point B to point D in Figure 1), the increase in effort by the other country will shift the PP curve toward the origin, and this will reduce the gains. It is even possible that the shift of the PP curve could be large enough that at the new equilibrium the country actually loses welfare.

This has interesting implications for cases where international cooperation in fisheries management does not exist. National regulation policies must be derived taking into account the reaction of other countries to specific actions. Each country will have to know how the other will react to a change in its level of effort. Taking this into account, it should only reduce its own effort (i.e. transfer resources from producing effort into the production of M) as long as the resultant increase in welfare is greater than the decline due to any possible increase in foreign fishing.[6] If these reactions are not known, the determination of the proper regulation program will require some sort of game theory approach.

In conclusion it should be pointed out that simply because it is possible to list the conditions that are necessary for a certain type of equilibrium to exist does not mean that it will in fact exist. As Smith (1969) has pointed out, a fishery will reach a bionomic equilibrium only if certain relationships exist between the growth rate of the fish stock and the rate at which effort enters and leaves the fishery (either because of market forces or regulatory decree). As pointed out earlier, however, the present analysis is static and will ignore these complications.

III

It will prove useful to view the problem from a different angle. There are two countries each with its own productive capacity and preference function, and between them they share an open-access fishery. Given this information, it is possible to construct a welfare possibility curve for the two countries (Figure 3). Any point on the curve is the maximum amount of welfare that can be obtained for one country at the level of welfare specified for the other country given the productive capacities of both countries and the sustained yield curve of the fishery. At any point on the curve, Condition (14) holds. Therefore, at each point there is an international MEY from the fishery since in all cases the value of the last fish caught will be worth its opportunity cost. As is well known, there is no way of choosing one point on the curve from another.

To digress a moment, if there were no open-access resources or other market imperfections, the two countries through market-directed production and trade will end up at a point on that possibility curve. If they each operated independently, they could obtain a certain amount of welfare, say the amounts represented by point A. Under free market conditions, each would be motivated to change its output combination and then trade such that both would be better off at a point such as B. Point B is not inherently superior to any other point on the curve. It is merely the point where given the productive capacities and the preferences of the two countries, they will operate under the conditions of a free international market. At that point no country can be made better off without making the other one worse off. If for some reason there was a redistribution of productive capacity, the final equilibrium would still be on the curve but at a different point than B.

Now to turn back to the case of the open-access fishery, if neither country exploits the fishery and they do not engage in trade, then operating independently, each would be able to obtain a certain amount of welfare. Again let this point be represented by A in Figure 3. If free trade is introduced and if both countries begin to exploit the fishery taking into account the effect of their effort

[6] In formal mathematical terms the country must maximize welfare subject to its production constraint knowing that the equilibrium level of effort in the other country is a function of its own effort. The proper Lagrangian for country X and its first order conditions are:

$$L_1 = U^X[F_X(E_X, E_Y(E_X)), M_X] + \lambda_1 G^X(E_X, M_X)$$

$$\frac{\partial L_1}{\partial E_X} = U_1^X\left[\frac{\partial F_X}{\partial E_X} + \frac{\partial F_X}{\partial E_Y}\frac{dE_Y}{dE_X}\right] + \lambda_1 G_1^X = 0$$

$$\frac{\partial L_1}{\partial M_X} = U_2^X + \lambda_1 G_2^X = 0.$$

The first order condition with respect to E_X takes into account the total effect on the amount of fish caught by a change in effort. There is the direct change in catch and the indirect effect caused by a change in the level of effort in country Y.

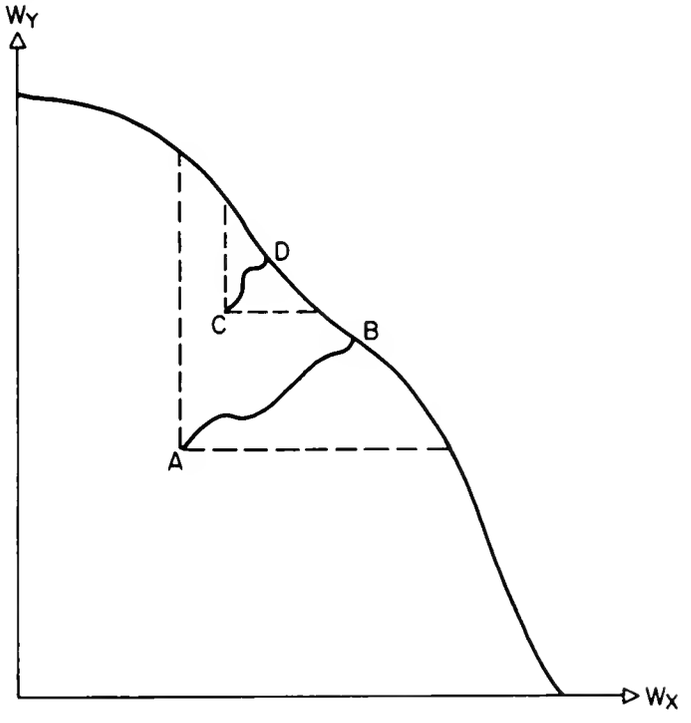

FIGURE 3.—Each point on the curve represents a distribution of the fishery where one country cannot be made better off without hurting the other. B represents the point where it is distributed on the basis of ability to harvest fish. C represents the distribution that is obtained by open-access exploitation. While both countries can benefit from changes from this point, note that in this case a move to the "ability" distribution at B represents a decrease in the welfare of country *Y*.

on the catch in the other country, a point such as B on the possibility curve will be reached. The wealth from the fishery will have been distributed between the two countries on their ability to produce the effort to harvest it. In fact, if the cost of effort was always less in one country, then at the MEY point, that country would be doing all the fishing and gaining all the wealth from the fish stock. The other country would gain from trade in goods but not from the fishery itself. There is nothing inherently superior about point B, however. There does not appear to be a moral argument that one country deserves the wealth from an international common property resource simply because it has a comparative advantage in the ability to capture it.

Under open-access conditions, the two countries will operate somewhere inside the welfare possibility curve, say at point C. This point is analogous to the solution of Equations (11a) and (11b). It is possible for both countries to increase their welfare by moving to a point such as D. Just how these gains can be obtained is discussed in detail below. But for now notice that in the case depicted here, if the countries are forced to move to point B (i.e. the point where the wealth from the fishery is distributed on the basis of ability to produce effort), country *Y* will suffer a decrease in welfare. This will not always be the case but will depend upon the position of C relative to that of B.

The point to be made from all this is that distribution is a critical part of determining the makeup on an international MEY. It is important to separate who obtains the wealth from the fishery from who harvests the fish. When the two are linked together, economic efficiency can be obtained only if the fishery is distributed according to ability to harvest. Under these conditions, therefore, one of the countries may suffer a decrease in welfare in the process of obtaining an international MEY. However if distribution and harvesting can be separated, an international MEY can be obtained using any criterion for distribution. Further, one can be obtained whereby both countries will improve their welfare from that at the open-access equilibrium.

The remainder of this paper will discuss a process for reaching an international MEY making explicit the distributional problem and its relationship with Condition (14). Let us consider how two countries that are operating at a point such as C in Figure 3 can move to an international MEY at a point such as D. Such a move would entail up to four mutually inderdependent types of trades between the two countries, including trade in mutual changes in fishing effort (essentially trades that alter, to the mutual advantage of both countries, the property rights to the fishery from those established by the rule of capture in the open-access fishery), trade in fishing effort or rights to fish when one country has the right to fish but the other can produce effort with less cost, and trade in the produced goods *F* and *M*. The first of these trades establishes a distribution of the fishery, and the rest insure that Condition (14) will hold for that distribution. These trades are interdependent since any trade can alter demand conditions if the gains are large relative to wealth. Each of these trades will be discussed separately so as to clarify the concepts involved. It should be remembered however, that the theoretical maximum advantage from international cooperation can not be achieved unless the trades are considered simultaneously.

First let us consider the potential for mutual gain from trade in mutual changes in fishing effort. Assume that two countries have reached an international open-access equilibrium with coun-

try X producing E_{X1} units of effort and country Y producing E_{Y1} units. (To be completely general this combination of effort can also be thought of as the one that both countries agree to use as an initial bargaining point.) Assume that under these conditions country X is operating at point A in Figure 4a. At that point, which is on social indifference curve I_1, there is a specified amount of E_Y (which determines the shape and position of X's PP curve) and E_X (which determines the position on the curve) being produced. There are other combinations of E_X and E_Y that will cause X to operate on I_1 however. For example, if E_Y remains the same and E_X is reduced (i.e. resources are shifted from the production of effort to manufacturing) such that there is a movement to point B, the level of social welfare will not change.[7] Smaller reductions of E_X that are matched by increases in E_Y will leave welfare unchanged if the increase in E_Y shifts the PP curve down such that the country is still operating on I_1. Similarly, increases in E_X, or reductions by more than is necessary to shift the country to point B, will result in constant welfare if there is a simultaneous reduction in E_Y large enough to shift the PP curve up by the appropriate amount.

This information can be more meaningfully displayed in terms of the property right indifference curves (PRI curves) in Figure 4b. The axis represent allowable levels of E_X and E_Y. These allowable levels are essentially property rights to the annual harvest that the specified amount of E will catch. They are labeled PR_X and PR_Y, but when there is no trade in effort, then E_X equals PR_X and E_Y equals PR_Y. Point A′ represents the international open-access equilibrium point. That is, E_{Y1} is the level of effort in country Y that will cause country X to be operating on the PP curve in Figure 4a, and E_{X1} is the amount of effort in country X that will cause it to operate at point A on that curve. Every other point in the diagram represents a different combination of effort in each country and, in effect, represents a distribution of the fishery. Point A′ is the distribution of the property rights by the rule of capture. Movements to the left represent reductions in the amount of allowable effort for country X, and downward

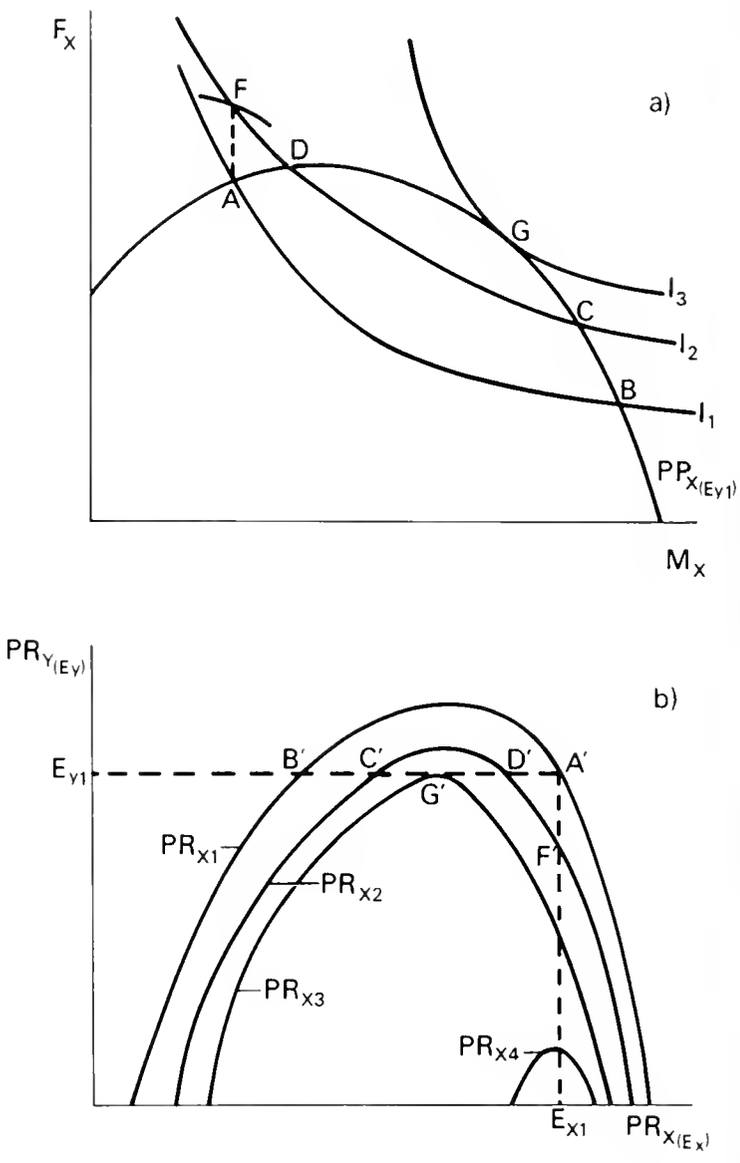

FIGURE 4.—The property right indifference (PRI) curves for each country follow directly from the relationship between their production possibility curves and indifference curves.

movements represent a reduction for country Y. PRI_{X1} is that collection of bundles of PR_X and PR_Y where country X is operating on social indifference curve I_1. Increases in PR_X (movements to the right) will only result in a constant welfare if it is matched by reductions in PR_Y. Small reductions in PR_X with PR_Y remaining unchanged, will normally increase welfare, and so for welfare to remain constant, PR_Y must increase. As reductions in PR_X get larger, however, welfare will remain constant only if there are reductions in both PR_X and PR_Y. Similarly, PRI_{X2} and PRI_{X3} are combinations of PR_X and PR_Y where the level of welfare is the same as along I_2 and I_3, respectively.[8] It

[7]Throughout it is assumed that there is free mobility of resources between fishing and manufacturing. As has been correctly pointed out in the past, this is not always the case. Rather there is a time lag of perhaps as much as a generation involved. This fact should be considered when making practical applications of the model.

[8]The curves will be concave from below. For reductions in allowable levels of effort, the greater the reduction, the greater is the increase in F_X that is necessary to keep welfare constant, and at the same time, the effect of decreases in the allowable

follows then that any distribution of property rights to the fishery represented by a point inside the area delineated by PRI_{X1} will lead to an improvement in welfare in country X over that which is obtained at the international open-access equilibrium. Note that because of the shape of the curve, welfare in country X can actually be increased in some cases where its allowable level of effort decreases while that for the other country goes up. This is possible because at the open-access equilibrium, country X can gain from switching some resources from producing effort to producing the other good and, up to a point, these gains are possible even if country Y increases effort. (Points A, B, C, D, F, and G are analogous to A′, B′, C′, D′, F′, and G′.) The reader should be aware by now of the similarity between these curves and trade indifference curves in international trade theory. Before using these curves in the analysis of the problem at hand, however, a few more points are in order. The short line through I_2 at F is meant to represent the slope of the PP curve if E_X remains constant and E_Y decreases so that country X is operating at F. A decrease in PR_Y will cause the slope of X's PP curve to decrease at every level of M_X.[9] As pictured here it has decreased from a positive to a negative. If it decreases such that it is steeper than the social indifference curve at that point, then the PRI curve will look like PRI_{X4}. That is, the PRI curve will not have a negatively sloped segment to the left of the open-access equilibrium amount of effort for country X. This means that reductions in the allowable level of effort in country X, with the amount in country Y held constant, will always result in a reduction in welfare for country X. Along the same line if country X pursues a local maximizing policy (i.e. it operates at point G in Figure 4a), the international equilibrium will be at point G′ in Figure 4b. This means that under no circumstances will country X be better off if it unilaterally decreases its allowable effort and it will always be worse off if country Y increases its level of effort. This is not the case if the international equilibrium is at point A′.

Figure 5a is similar to Figure 4b except that PRI curves for country Y have been added. PRI_{Y1} has the same meaning for country Y as does PRI_{X1} for country X and is constructed in an identical fashion.

Any distribution of property rights represented by a point inside the area delineated by PRI_{Y1} would result in an increase in the welfare of country Y. It follows then that any combination that is in the area common to both PRI_{X1} and PRI_{Y1} (see hatched area of Figure 5a) will increase the welfare of both countries over that achieved by the open-access "law of capture" distribution of the rights to the fishery. Note again that it is possible for both countries to be better off in some cases where the trade involves a reduction in property rights in one country and yet an increase in the other.

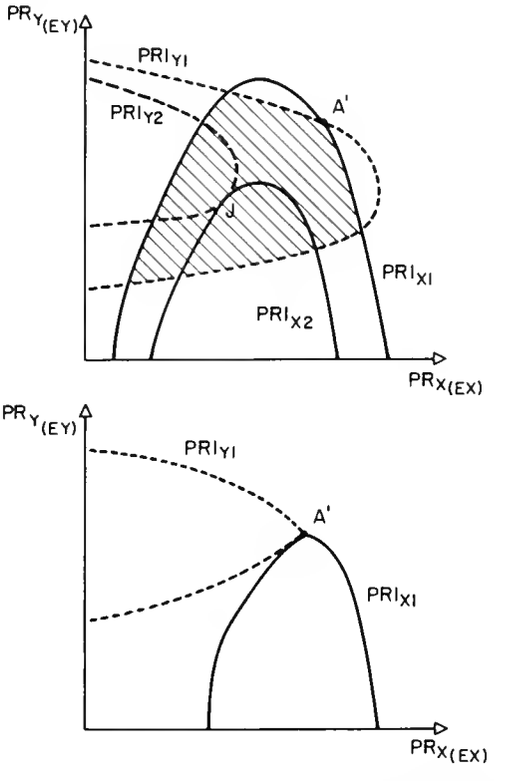

FIGURE 5.—The area common to the initial property right indifference (PRI) curves of both countries represents those distributions of the fishery where both countries will be better off than at the open-access equilibrium. In some special cases, there is no such area (see b).

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level of effort in country Y on F_X decreases as E_X increases (i.e. $\frac{\partial F_X}{\partial E_Y} = -bE_X$). Therefore greater reductions in PR_Y will be necessary to compensate for equal reductions in PR_X as the amount of E_X is reduced from the international equilibrium level. For increases in PR_X, the greater the increase the smaller is the marginal increase in fish caught and yet the greater must be the increase in catch in order to keep welfare constant. Therefore greater reductions in PR_Y will be necessary to compensate for equal increases in PR_X as the amount of E_X is increased from the international equilibrium level.

[9] $$\frac{\partial F_X}{\partial M_X} = -(a - 2bE_X - bE_Y)\frac{G_2^X}{G_1^X}$$

and so

$$\frac{\partial\left(\frac{dF_X}{dM_X}\right)}{\partial E_Y} = b\,\frac{G_2^X}{G_1^X}.$$

Therefore, as E_Y decreases, the slope will decrease.

It is also possible that in some cases there may be no changes in both E_X and E_Y that will benefit both countries. If both countries adopt a local optimum regulation policy, the PRI's will be of the general shape of those depicted in Figure 5b. In this case, there have to be mutual reductions in order for either country to gain, but as pictured here, there are no mutual reductions that will benefit both countries.

If the governments have the power to control the level of effort in their countries, then it is possible for both of them to increase their welfare by each agreeing to a change in the property right distribution such that the new combination lies within the area described. And further gains are possible if the PRI's for the countries are not tangent at the new point. In other words, given that the equations for the PRI's are of the form $W_{PR} = W_{PR}(PR_X, PR_Y)$, further gains are possible unless

$$\frac{\frac{\partial W_{PR}^X}{\partial PR_X}}{\frac{\partial W_{PR}^X}{\partial PR_Y}} = \frac{\frac{\partial W_{PR}^Y}{\partial PR_X}}{\frac{\partial W_{PR}^Y}{\partial PR_Y}}, \qquad (15)$$

that is, unless the slopes of the PRI curves are equal. Formally this says that the ratio of the change in welfare in country X due to a change in property rights in country X and to a change in rights in country Y must be equal to the ratio of the change in welfare in country Y due to a change in rights in country X and in country Y. This can be rewritten in terms of the earlier notation as:

$$\frac{U_1^x \frac{\partial F_x}{\partial E_x} + U_2^x \frac{dM_x}{dE_x}}{U_1^x \frac{\partial F_x}{\partial E_y}} = \frac{U_1^y \frac{\partial F_y}{\partial E_x}}{U_1^y \frac{\partial F_y}{\partial E_y} + U_2^y \frac{dM_y}{dE_y}}. \qquad (15')$$

The change in welfare in either country due to a change in its allowable effort is equal to the change in welfare due to a change in F times the change in F due to a change in allowable effort plus the change in welfare due to a change in M times the amount of M that must be given up to produce the extra allowable effort. The change in welfare in the other country is simply the change in welfare due to a change in F times the change in F due to a change in allowable effort in the first country.

Where the final trading position will be and hence what the exact gain to each country is cannot be accurately determined in advance. It depends however upon the international free market equilibrium distribution of the property rights to the fishery which determine the position of the PRI's, the trading ability of the two countries, the extent of the knowledge concerning each other's PRI's, and the number and particular composition of any small trades that lead up the final equilibrium. It would be possible to construct offer curves from the PRI's similar to the ones used in international trade theory, but since trade in mutual changes in property rights will necessitate intergovernmental negotiations and since they will, more than likely, take place on a lump-sum basis, the equilibrium determined by their intersection would be of doubtful significance.

To summarize this discussion let us consider point J in Figure 5a, which is one possible final trading position. Notice that it is not possible to redistribute the property rights from that point without forcing one of the countries to suffer a loss in welfare; that is, there are no further changes in the distribution of the property rights that will be mutually beneficial. This is one of the conditions that must hold for an MEY of an international fishery. It determines the amount of fish that should be caught and the distribution of the rights to catch it. An important point to remember however is that this condition will not guarantee that the fish are caught at the lowest possible cost, and yet this is a very important aspect of MEY.

Let us now consider the potential for mutual gains from trade in actual property rights or in fishing effort. Such trade is not possible unless the rights to fish have been formalized either at the open-access equilibrium or at some other mutually agreed upon point. Again it should be remembered that this is only one type of trade, and the degree to which each country is willing to engage in it depends to some extent upon the makeup of the other trades.

Just because a country has the right to fish does not mean that it should necessarily produce the effort to catch the fish. For instance, if the opportunity cost of producing effort is cheaper in X, then both countries can gain if X expands the production of effort and then sells the increase to Y, who must make a corresponding reduction in its production of effort. If the price of effort for these international sales is between that in each country, both will be able to gain. Country X will gain because it is getting more for the effort that it cost to produce. Country Y will gain because it can buy

effort cheaper than it can produce it at home. These mutually beneficial trades can continue until the opportunity cost of producing effort is the same in both countries, i.e. until:

$$\frac{dM_X}{dE_X} = \frac{dM_Y}{dE_Y} . \qquad (16)$$

The same thing could be accomplished by X purchasing rights to apply effort from Y until the MRT's for E and M are equal. Assume for simplicity that $P_F^Y = P_F^X$. Initially the price for a right to use one unit of effort would have to be somewhat above the rent the right-holder in Y would earn by doing the fishing himself. ($R_Y = P_F^Y \frac{F(\alpha)}{\alpha} - P_E^Y$, where α in this case is the total of the allowable efforts from both countries.) People in X will be able to pay more than that since P_E^X is less than P_E^Y. In trade equilibrium the prices of fish and effort are the same in both countries, and therefore the rents in both countries will be identical and no further gains from trade are possible.

While the above will not change the amount of fish produced, it will make sure that effort is being produced at a minimum cost. The savings can be used to produce more of the manufactured good which can be distributed such that both countries are better off.

Now that two of the possible types of trade have been discussed, it will prove worthwhile to show exactly how they can be interrelated.

Trade in E or in fishing rights may have an effect on the bargaining for the distribution of property rights. To see this, assume that after such bargainings country X is at point D in Figure 4a and at that point $\frac{dM_X}{dE_X}$ is less than $\frac{dM_Y}{dE_Y}$. If it produces q more units of E but sells them to Y who reduces its production of E by the same amount, the PP curve will not change. Initially X will operate somewhere horizontally to the left of point D because it had to give up units of M_X to get the extra units of E. Y will be willing to pay sufficient units of M to X such that it will ultimately operate somewhere horizontally to the right of D and will therefore show an increase in welfare. Therefore at point D′ in Figure 4b, which represents the rights to fish and not the actual amount of E produced in each country, the welfare of X will increase. By similar analysis it can be shown that if trade is possible, Y will always be at a higher level of welfare at D′ also. This means that the PRI's of both X and Y will change shape and position. Therefore more than likely there will be the possibility of further mutually beneficial trades in the distribution of fishing rights.

The final type of trade to consider is trade in the final products M and F. If the relative prices are different in the two countries, mutually beneficial trades can be arranged. These trades can continue to be mutually beneficial until the marginal rate of substitution in both countries is the same, i.e. until:

$$\frac{U_2^X}{U_1^X} = \frac{U_2^Y}{U_1^Y} . \qquad (17)$$

These trades will be affected by trades in E and also in changes in the allocation of the property rights.

On a practical note it must be admitted that few countries will be willing to let their international trade policy in all goods be dictated by their fishery management program. Therefore it is unrealistic to assume that they will drop all restrictions on international trade on this account.

This means that even after the rights to fish have been distributed, there are four things that can be traded: fish, manufactured goods, effort, and rights to fish. Because the prices of the last two are directly related to those of the first two, the relative demands for M and F will determine the equilibrium set of prices. It is impossible to predict, however, just what the actual trade bundle will be. For instance, nothing in the model allows us to predict whether X will export effort or import fishing rights if it has a comparative advantage in producing effort. The outcome of that, however, will affect its exports or imports of F.

Although the exact makeup of the international MEY position cannot be described, Conditions (15), (16), and (17) must hold simultaneously for it to be in effect. (Condition (15) sets a distribution from which no further mutual gains are possible, and Conditions (16) and (17) guarantee that Condition (14) above will hold for that distribution.) That is all potential mutual gains (where a mutual gain could consist of one country being made better off and the other remaining the same) by (1) altering the distribution of the rights to use effort, (2) trading in actual rights or in effort itself, or (3) trading in final goods, have been achieved. This point (say at point D in Figure 3) is a Pareto point that can be reached by mutually advanta-

geous trades between the two countries given their initial positions which include their productive capacity and the rights to the fishery that they have obtained by the right of capture. At this point there will be an MEY to the fishery. The proper amount of fish will be harvested and at the lowest cost possible. But since there is nothing sacred about these initial positions, point D is not inherently superior to any other point on the curve. If the world order somehow alters their initial positions, for instance, by saying that since Y is a poor country it should be able to expand its effort and X should do the opposite, the same types of trades will still be possible, and they will lead to a point on the curve that is more advantageous to country X than was point D. This point would also be an MEY given the distribution of productive capacity and of the wealth of the fishery. The distribution of the rights to the fishery is very important in determining the MEY of the fishery. Let us consider some of the practical implications of this discussion. First, before an international fishery can be optimally managed, the wealth from it must be distributed. The exact makeup of the distribution is not important, but it is possible, in most cases, to find a distribution whereby both countries are better off than at the initial bargaining point. The rights to the fishery should be transferable if the country owning them is to receive the maximum possible benefit. This way, it can sell the rights or hire effort from other countries to utilize them if it does not have a comparative advantage in producing effort. Therefore, unless the upcoming Law of the Sea Conference can agree to some sort of distribution of the wealth of the fishery and make allowances for possible trades in the makeup of the distribution bundle and also in fishing rights and effort, there is little hope for economically rational management of international fisheries.

The results of this two country, one fishery model can be expanded in a fairly straightforward fashion to a situation where there are many countries that simultaneously exploit several different fisheries. An international open-access equilibrium will occur when, in each country, the average returns from fishing the various stocks are equal to the average cost of providing effort. The distribution of the wealth from the fisheries will depend on the ability of each of the countries to produce the effort that is most efficient for a particular fishery. The more efficient producers will capture a larger share of the fisheries. If perfect international trade in fish products is not possible, then the distribution of the fishery by the "rule of capture" will also depend upon the tastes of the countries. A country that has the potential to harvest a certain type of fish very efficiently but has little desire for the product and cannot use it in international trade will not exploit that stock very extensively.

The usefulness of unilateral regulation in this situation will probably be less than in the two country case. Any reduction in effort will more than likely be met by an increase from one of the other countries. Therefore, while the country will show an increase in the amount of other products it can produce, it is entirely possible that the value of its total production will fall due to the decrease in catch.

Proper international regulation must take into account the effect that effort from one country will have on the yields to other countries exploiting the same stocks. With this consideration in mind, each country can benefit from some program of reallocation of the rights to the fish stocks from that which exists under open access. To achieve the maximum potential benefits, this program should include the possibility of trade in effort, fishing rights, and final products. The existence of many countries will of course make it much more difficult to specify the set of redistributions that would be beneficial to all concerned and even more difficult to get the countries to agree to one combination within that set. A major problem with international regulation is that allocational requirements are just as important as economic efficiency requirements. But given a mutually agreed upon allocation (i.e. a certain allowable level of effort in each country for all fisheries), the efficiency requirements can be met. The problem is to get agreement on a distribution plan with many different countries involved.

SUMMARY AND CONCLUSIONS

In the first section of the paper the general equilibrium model was used to derive the familiar result that in an open-access fishery too many resources will be allocated to the production of fishing effort. Using this model it is possible to explicitly take into account the lost production of other goods. In the second section the general equilibrium model was expanded to include two countries exploiting the same open-access fishery. The amount of effort used in one country will af-

fect the production possibilities in the other by changing the catch per unit of effort. Therefore, there is a direct technical relationship between the two countries. An international open-access equilibrium will exist when the average return to effort is equal to the marginal cost of providing it. (Whether or not such an equilibrium will ever be reached is another question.) The international optimum is where the marginal increase in the value of the fish caught (regardless of the country in which it is landed) is equal to the marginal cost of producing the last unit of effort in both countries. Using this model, two interesting points can be made. First, under open access, what are normally considered to be improvements in the terms of trade, for either the exporter or the importer of fish, can in some circumstances lead to a decrease in welfare. Also attempts at unilateral management can lead to decreases in welfare depending on the way in which the other country's fishing industry reacts. Proper regulation policies should directly take these things into account.

The topic of the third section was the necessary conditions for an MEY of an international fishery. The discussion with its implicit assumptions of governments that are willing and able to negotiate in an open and far ranging manner at zero cost, free trade in all goods, regulation methods that are not at the expense of efficiency, a physically independent fish stock that is only available to two countries, showed if negotiation is possible that an international MEY can be reached. This point will be the MEY of the fishery. (Even if the assumption about the possibility of free trade in final goods is dropped, the analysis of trade concerning the distribution of property rights to the fishery and trade in rights or effort is still valid. Therefore, even if there are different price and cost structures in the two countries, there is a basis for selecting a second best total amount and composition of fishing effort.)

It is also pointed out that there are many points that satisfy the conditions of an international MEY and that the distribution of the rights to the fishery (especially where the wealth from the fishery is large relative to the productive capacities of the countries) and, to a lesser extent, the differences in negotiating ability have an effect on which one will apply at any point in time. (There will not be one point that can be called MEY as in the case of a national fishery.) This is important because fishery negotiations typically work in the reverse. They try to find some optimum total amount of effort that should be applied and then they divide it in some equitable fashion, but it is impossible to choose an optimum amount unless the distribution has already been determined.

With regard to the argument that the underdeveloped countries should be granted preferential treatment in the distribution of the ocean's living resources, the model points out that if this is accepted, it does not mean that they should necessarily do the fishing. Rather, if they do not have a comparative advantage in the production of fishing effort, they would be better off by either selling their rights to the fish or by hiring fishing effort from other countries.

In conclusion this paper has formalized the analysis of the problems of international fisheries management that earlier writers only briefly discussed. To their list of problems of different prices, taste, and cost structures, it adds the effect that the distribution of the wealth of the fishery itself can have on the final outcome. It presents the three conditions for an MEY of an internationally utilized fishery. More generally the conditions guarantee the proper production bundle of all goods and its optimal distribution given the productive capacity of the countries and of the fishery and the distribution of wealth.

Although the discussion has been in terms of a fishery, the analysis could be expanded to other common property resources, such as air and watersheds, deep-sea mineral sources, etc. by taking proper consideration of the various physical characteristics of the resource involved.

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IMPACT OF THERMAL EFFLUENT FROM A STEAM-ELECTRIC STATION ON A MARSHLAND NURSERY AREA DURING THE HOT SEASON

WILLIAM E. S. CARR[1] AND JAMES T. GIESEL[2]

ABSTRACT

Seine samples of fishes were collected during the hot season from three similar marshland creeks situated at various distances from a steam-electric station near Jacksonville, Fla. Thermal effluent from the electric station is discharged directly into one creek and enters a second creek on the initial stage of each rising tide. The third creek remained at ambient temperature. Fishes collected in the samples were analyzed for species composition and for density and biomass per unit area. A total of 48 species belonging to 23 families were identified. Thirty-seven species were collected at least once in the ambient temperature creek whereas 30 species were collected in the creek receiving the maximum amount of thermal effluent.

Twenty species appearing in the samples are categorized as utilizable species because they are used by man either as food or for various fishery products. Specimens of all utilizable species were juveniles. In the thermally affected creeks, both the numbers and the biomass per unit area of juveniles of utilizable species were 3- to 10-fold smaller than those obtained in collections from the ambient temperature creek. When data for the entire hot season are considered, the creek receiving the largest input of thermal effluent supported a population of fishes having approximately 19% of its numbers and 32% of its biomass composed of juveniles of utilizable species. In contrast, the ambient temperature creek supported a population having approximately 73% of its numbers and 83% of its biomass composed of such species. Whereas juveniles of two species of mullet (*Mugil curema* and *M. cephalus*) accounted for the majority of the utilizable fishes using the thermally affected creeks as a nursery area, large numbers of juveniles of at least five additional utilizable species occupied the ambient temperature creek. These species were as follows (in order of decreasing abundance): tidewater silverside, *Menidia beryllina*; spot, *Leiostomus xanthurus*; Atlantic menhaden, *Brevoortia tyrannus*; silver perch, *Bairdiella chrysura*; and Atlantic thread herring, *Opisthonema oglinum*.

There is no longer any doubt that estuarine areas play a vital role in the life cycles of the majority of species of finfish and shellfish that are harvested annually in coastal fisheries. The role of estuaries as nursery areas for both sport and commercial species is now well documented (Skud and Wilson 1960; Smith et al. 1966; Sykes and Finucane 1966; Carr and Adams 1973; others). The majority of sport and commercial species must inhabit estuarine areas during at least part of their life cycles. Most frequently it is the early juvenile stages that exhibit the most pronounced estuarine dependence.

Thermal additions from power plants are considered to pose a potentially serious threat to valuable estuarine habitats. Krenkel and Parker (1969) have estimated that the amount of water required for condenser cooling by power plants in this country will increase from 50 trillion gallons per year in 1968 to 100 trillion gallons per year by 1980. This latter amount represents approximately one-fifth of the total land runoff in the contiguous United States. The immense volumes of water required for cooling by power plants are most readily obtained by building these plants adjacent to estuaries or in other coastal locations. The fact that estuarine areas "are among the most productive natural ecosystems in the world" (Schelske and Odum 1962) raises the question as to whether meeting the increasing needs for electricity by our growing population is best satisfied by using estuarine areas as the receiving waters for ever increasing discharges of thermal effluents.

Although a large literature exists concerning various biological facets of "thermal pollution" (reviews are provided by Naylor 1965; Wurtz and Renn 1965; Krenkel and Parker 1969; Jensen et al. 1969; Coutant 1970, 1971; Sylvester 1972; others) we are aware of no published studies that

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attempted to measure in situ the impact of thermal additions upon the capacity of an estuarine habitat to continue functioning as a viable nursery area, particularly for species of sport and commercial significance. Nugent (1970) provided one of the most complete studies on the effects of a thermal effluent on the estuarine macrofauna in the vicinity of a power station south of Miami, Fla. Nugent concluded that there were both beneficial and harmful effects attributable to the thermal additions but that the overall impact was "detrimental to many of the economically valuable animals of the waterway." Nugent found that during the hot summer months the heated effluent decreased the number of fishes present in the discharge area and also contributed to the death of certain organisms. However, the methods used in this study for the collection of fishes (gill nets, traps, and hoop nets) are unsuitable for the collection of many juvenile specimens and are somewhat inappropriate for estimates of density and standing crop. Grimes (1971) and Grimes and Mountain (1971) studied the effects of a thermal effluent upon marine fishes in the vicinity of a power station near Crystal River, Fla. Their major conclusions were that the natural seasonal abundance and the diversity of fishes were slightly altered by fishes being attracted into the heated area during late fall and early winter and by being repulsed during the summer. However the collecting methods and the station locations used in this study make the data difficult to assess in terms of the impact of the thermal effluent on the nursery area capacity of the affected area.

The current study was designed to evaluate in quantitative terms the impact that the discharge of a thermal effluent by a steam electric station had upon the capacity of an estuarine habitat to continue functioning as a nursery area during the hot season. This study was conducted in a marshland area to the northeast of Jacksonville, Fla. The data were obtained by analyzing the contents of seine samples taken from shallow-water stations located in three marshland creeks situated in the vicinity of the power station.

METHODS

Description of Study Area

San Carlos Creek, a small marshland creek draining into the St. Johns River, receives the discharge of thermal effluent from the Northside Generating Station (NGS) operated for the city of Jacksonville by the Jacksonville Electric Authority (see Figure 1). The NGS is situated in a relatively undeveloped marshland area to the northeast of Jacksonville approximately 10 miles west of the juncture of the St. Johns River with the Atlantic Ocean. Currently the NGS has two, of an anticipated three, oil-fired steam-electric units on line. Units 1 and 2 of the NGS (550-MW generating capacity) discharge approximately 280,000 gallons/min of thermal effluent directly into San Carlos Creek via outfalls situated 150 ft apart. The completion of Unit 3 (550 MW) in 1976 will result in the discharge of an additional 280,000 gallons/min of thermal effluent into this same creek. Cooling water for the NGS enters via a flume from the St. Johns River and the heated effluent is discharged into San Carlos Creek at a point approximately 0.75 mile upstream from the river.

San Carlos Creek and two other physically similar creeks located adjacent to the site described above were used for the collection of fishes described in the current study. San Carlos Creek not only receives directly the thermal effluent from

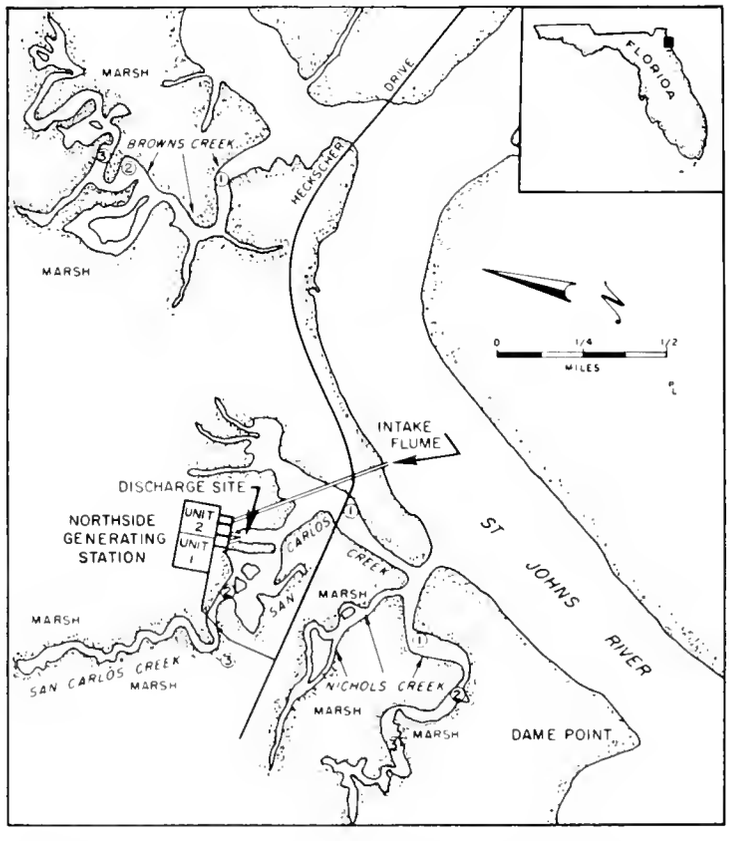

FIGURE 1.—Study area showing location of Northside Generating Station and marshland creeks adjacent to St. Johns River north of Jacksonville, Fla (see inset). Locations of sampling stations in San Carlos Creek, Nichols Creek, and Browns Creek are indicated by numbers. Juncture of river and ocean is situated about 10 miles to the east.

the NGS but on each rising tide this effluent is backed up by tidal action and much of it is retained within the confines of this creek. At this time the thermal effects extend to the uppermost reaches of the creek. A second creek, Nichols Creek (see Figure 1), receives an injection of thermal effluent during the initial stage of each rising tide. Nichols Creek converges with San Carlos Creek just prior to the juncture of both with the river. A major branch of a third creek, Browns Creek, is situated approximately 1 mile east of San Carlos Creek and is completely beyond the zone of thermal influence produced by the power plant. Browns Creek served as a "control" creek that remained at ambient temperature.

The three creeks are physically quite similar in terms of their size, depth, and contiguous marshland and upland areas. The substrate in each consists primarily of soft black mud rich in organic material. Scattered bars of a firmer sand-mud composition are present. Each creek is lined on either side with marsh grasses, primarily *Spartina alterniflora* and *Juncus roemarianus*. No submerged sea grass or other attached macrophytes are present in the creek beds themselves. The major variables affecting differentially the habitats of the three creeks are the thermal effluent, the chemical agents used in the cleaning of condenser tubes, and the clearing and alteration of the landscape necessary for the construction of the power plant.

Sampling Stations

Three sampling stations were established in each of the three creeks (see Figure 1). One of the stations in each creek was situated near the creek mouth whereas the other two were situated at appropriate distances upstream. The station sites in each creek were selected such that two stations were situated at the sites of juncture of small adjoining creeklets and the third at the edge of a bar. During the hot season of 1973, samples were taken from all nine stations during June and July and from seven of the stations in September.

Collecting Methods

Fishes were collected at all stations with a bag seine (50 × 6 ft) constructed of 3/8-inch stretch mesh netting. The dimensions of the area seined in each sample were measured with a steel tape at the time the sample was taken. Areas sampled at the stations varied somewhat according to the particular configuration of each seine haul; these areas ranged from 102 to 403 m^2 per station. During each sampling period, all seine hauls were made during the day on consecutive days within 1.5 h of low tide. Specimens were preserved immediately in 20% Formalin[3]-seawater and later washed with tap water and stored in 75% isopropyl alcohol. Determinations of biomass are based on weights of preserved specimens. Invertebrates obtained in the samples were also retained for future analysis.

A Beckman electrodeless induction salinometer was used to obtain measurements of temperature and salinity.

Quantitative core samples and plankton samples were also taken but their analyses are incomplete and they are not reported here.

Presentation of Data

To minimize the number of tables and figures necessary for the presentation of data, analyses of the samples taken from the three stations in each creek have been pooled for each monthly collection. Although this method prohibits comparisons of variations between individual stations within a particular creek, this procedure provides a more direct means of analyzing and comparing the overall population structure within each creek.

RESULTS

Table 1 presents temperature and salinity measurements taken from San Carlos Creek, Nichols Creek, and Browns Creek during the study period. The temperature data from Browns Creek, which is beyond the range of thermal influence produced by the power station, can be used as a measure of the daytime ambient temperature regime for a creek in this area. During the June sampling period, the average recorded temperature of water discharged by Units 1 and 2 of the NGS into San Carlos Creek was from 5.6° to 7.7°C above the average temperatures recorded at the three stations in Browns Creek. During July, San Carlos Creek received water from the power station that averaged 8.0° to 8.9°C higher than the averages recorded in Browns Creek. During September, this differential increased to 9.1° to 10.8°C. The highest temperature that we recorded

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Daytime measurements of temperature and salinity recorded during the hot season of 1973 from three creeks in the vicinity of the Northside Generating Station, Jacksonville, Fla.

Item	San Carlos Creek			Nichols Creek			Brown Creek			Outfalls in San Carlos Creek	
	Stn. 1	Stn. 2	Stn. 3	Stn. 1	Stn. 2	Stn. 3	Stn. 1	Stn. 2	Stn. 3	Unit 1	Unit 2
23-27 June:											
Temperature, °C:											
Maximum	35.9	35.0	36.4	31.1	32.6	34.6	30.5	30.5	[1]27.9	36.5	37.8
Minimum	30.3	31.0	30.0	27.8	28.2	27.6	26.7	26.9		31.8	33.9
Average	33.1	33.1	33.5	29.4	29.9	30.2	28.5	28.5		34.1	36.2
Salinity, ‰:											
Maximum	30.6	30.1	29.0	27.0	26.6	25.6	27.5	26.2	[1]21.7	31.0	31.0
Minimum	20.7	24.7	18.2	18.9	18.3	18.7	18.3	17.7		23.3	24.2
Average	25.9	27.3	25.6	21.9	21.9	21.7	22.6	22.3		26.5	26.8
25-26 July:											
Temperature, °C:											
Maximum	38.0	38.2	39.2	37.5	37.3	35.8	31.2	30.6	31.6	39.7	39.4
Minimum	30.4	33.9	32.8	30.1	30.4	31.6	29.2	29.7	29.8	36.9	38.5
Average	35.3	35.7	35.5	32.3	32.4	32.9	30.2	30.2	30.5	38.5	39.1
Salinity, ‰:											
Maximum	31.2	29.8	31.0	31.5	31.3	29.3	27.5	27.3	27.2	30.8	30.8
Minimum	23.3	26.2	26.6	23.5	23.6	24.1	25.5	21.8	21.7	25.7	25.2
Average	28.1	28.9	28.8	27.4	27.6	26.0	26.5	25.2	25.1	29.2	29.2
19-20 September:											
Temperature, °C:											
Maximum	37.3	37.7	37.9	36.2	—[2]	35.0	29.7	29.6	27.5	37.6	38.4
Minimum	30.6	32.3	32.1	28.5		27.9	27.3	26.5	27.0	37.4	37.8
Average	34.3	36.2	36.3	31.5		31.4	28.4	27.9	27.3	37.5	38.1
Salinity, ‰:											
Maximum	26.4	24.3	24.3	24.8	—[2]	24.7	27.2	26.2	26.4	23.2	24.0
Minimum	19.5	22.1	22.7	18.1		21.6	21.9	20.8	19.6	20.6	21.0
Average	22.0	23.2	23.5	22.4		23.4	24.6	22.7	23.0	22.0	22.5

[1]Only one recording.
[2]Not recorded.

was 39.7°C taken at the outfall of Unit 2. The data shown in Table 1 suggest that the thermal regime present in Nichols Creek was somewhat intermediate between that of the other two creeks. However this is not entirely the case. During the initial phase of each rising tide, tidal action causes the injection of heated effluent from the power plant up the entire length of Nichols Creek. On 19 September, we recorded this injection as it reached and later passed Station 1 in this creek (see Figure 2). The highest temperature recorded at Station 1 during this day was 36.2°C. The passage time of this injection of hot water was approximately 2 h with temperatures greater than 34°C lasting approximately 1 h. Only a slight drop in temperature was apparent when the hot water reached Station 3 situated approximately 0.6 mile away (see Figure 2). Hence, whereas the minimum and average temperatures in Nichols Creek are more similar to those of Browns Creek than to those in San Carlos Creek, the maximum temperatures in Nichols Creek are more similar to those in San Carlos Creek. Consequently, at the onset of each rising tide (twice daily), organisms living in Nichols Creek are subjected to a period of 1- or 2-h duration during which the water temperature is markedly above ambient and almost as high as that in San Carlos Creek.

Table 2 provides a list of the species of fishes collected from the three creeks during the hot season of 1973. A total of 48 species belonging to 23 families were collected. Aside from the Cyprinodontidae and certain of the Gerreidae and

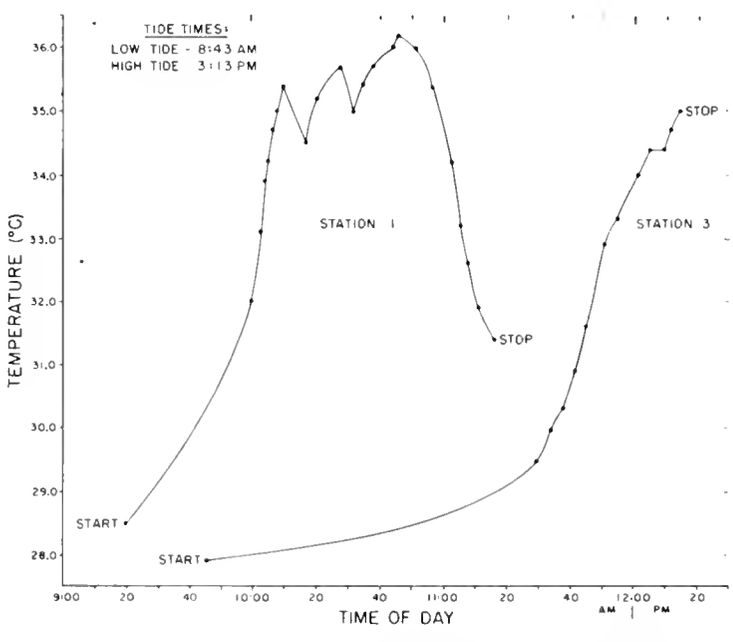

FIGURE 2.—Recordings of water temperature taken in Nichols Creek on the initial stage of rising tide, 19 September 1973. Appearance of thermal effluent from the power plant is indicated by the sudden increases in temperature at Stations 1 and 3.

TABLE 2.—List of fishes collected during the hot season of 1973 from three creeks in the vicinity of the Northside Generating Station, Jacksonville, Fla.

Family	Scientific name	Common name[1]	Class[2]	Species utilized[3]
Elopidae	*Elops saurus*	Ladyfish	J	X
Clupeidae	*Brevoortia tyrannus*[4]	Atlantic menhaden	J	X
	Opisthonema oglinum	Atlantic thread herring	J	X
Engraulidae	*Anchoa hepsetus*	Striped anchovy	J	
	Anchoa mitchilli	Bay anchovy	J	
Synodontidae	*Synodus foetens*	Inshore lizardfish	J	
Ariidae	*Arius felis*	Sea catfish	J	
Batrachoididae	*Opsanus tau*	Oyster toadfish	J	
Belonidae	*Strongylura marina*	Atlantic needlefish	J	
Cyprinodontidae	*Cyprinodon variegatus*	Sheepshead minnow	J-A	
	Fundulus grandis	Gulf killifish	J-A	
	Fundulus heteroclitus	Mummichog	J-A	
	Fundulus majalis[5]	Striped killifish	J-A	
Poeciliidae	*Gambusia affinis*	Mosquitofish	J-A	
	Poecilia latipinna	Sailfin molly	J-A	
Atherinidae	*Menidia beryllina*	Tidewater silverside	J	X
Syngnathidae	*Syngnathus floridae*	Dusky pipefish	J	
Carangidae	*Caranx hippos*	Crevalle jack	J	X
	Chloroscombrus chrysurus	Atlantic bumper	J	
	Selene vomer	Lookdown	J	
	Trachinotus falcatus	Permit	J	X
Lutjanidae	*Lutjanus griseus*	Gray snapper	J	X
Gerreidae	*Diapterus olisthostomus*	Irish pompano	J	
	Eucinostomous argenteus	Spotfin mojarra	J-A	
	Eucinostomous gula	Silver jenny	J	
	Gerres cinereus	Yellowfin mojarra	J	X
Sparidae	*Archosargus probatocephalus*	Sheepshead	J	X
	Lagodon rhomboides	Pinfish	J	X
Sciaenidae	*Bairdiella chrysura*	Silver perch	J	X
	Cynoscion nebulosus	Spotted seatrout	J	X
	Leiostomus xanthurus	Spot	J	X
	Micropogon undulatus	Atlantic croaker	J	X
	Pogonias cromis	Black drum	J	X
	Sciaenops ocellata	Red drum	J	X
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish	J	X
Mugilidae	*Mugil cephalus*	Striped mullet	J	X
	Mugil curema	White mullet	J	X
Gobiidae	*Gobionellus boleosoma*	Darter goby	J	
	Gobionellus hastatus	Sharptail goby	J-A	
	Gobionellus smaragdus	Emerald goby	J	
	Gobiosoma bosci	Naked goby	J	
	Microgobius gulosus	Clown goby	J-A	
Triglidae	*Prionotus tribulus*	Bighead searobin	J	
Bothidae	*Citharichthys spilopterus*	Bay whiff	J	
	Etropus crossotus	Fringed flounder	J	
	Paralichthys lethostigma	Southern flounder	J	X
Cynoglossidae	*Symphurus plagiusa*	Blackcheek tonguefish	J	
Tetraodontidae	*Sphoeroides nephelus*	Southern puffer	J	

[1]Common names recommended by Bailey (1970) are used.
[2]J = juvenile; A = adult.
[3]Species utilized refers to either sport species or to species cited by Lyles (1969:463-487) as being used by man for tood or related fishery products.
[4]Some of these specimens may have been *B. smithii* and/or hybrids of *Brevoortia smithii* as described by Dahlberg (1970). Since they were all juvenile specimens the major characters given by Dahlberg for distinguishing between the three possibilities were extremely difficult to apply with certainty.
[5]According to Carter R. Gilbert (pers. commun.) of the Florida State Museum, some of these specimens may have been *F. similis*. The taxonomic status of the two species on the northeast coast of Florida is somewhat uncertain.

Gobiidae, all of the specimens were juveniles that were using the creeks as a nursery area. Twenty of the species are utilized directly by man, i.e., are species used for food and/or related fishery products including sport species and bait fishes. Subsequent references to "utilizable species" refer to those used by man as defined above.

Tables 3-5 provide monthly summaries of the numbers of individuals and the estimated densities of all fish species collected from the three creeks. Of the 48 species obtained in one or more collections, 30 were collected at least once in San Carlos Creek, 23 were collected in Nichols Creek, and 37 appeared in Browns Creek. Four species, *Cyprinodon variegatus* and three species of gobies (*Gobionellus smaragdus*, *Gobiosomo bosci*, and *Microgobius gulosus*), were collected only in San Carlos Creek thereby suggesting that they preferred the high temperature regime afforded there. However, the three species of gobies appeared only in the June samples. Eleven other species of temperature tolerant fishes were present in San Carlos Creek at densities that were either as great, or greater, than the densities present in the ambient temperature creek. These species were as follows (in order of decreasing

TABLE 3.—Collections of fishes from three stations on San Carlos Creek during the hot season of 1973. Area seined in June was 706 m², in July was 563 m², and in September was 563². Total area seined was 1,832 m².

Family	Species	June collection		July collection		September collection		Total collections	
		No.	No./100 m²	No.	No./100 m²	No.	No./100 m²	No.	No./100 m²
Elopidae	*Elops saurus*	3	0.4	—	—	1	0.2	4	0.2
Clupeidae	*Brevoortia tyrannus*	—	—	4	0.7	—	—	4	0.2
	Opisthonema oglinum	—	—	6	1.1	—	—	6	0.3
Engraulidae	*Anchoa hepsetus*	1	0.1	—	—	—	—	1	0.05
Belonidae	*Strongylura marina*	1	0.1	—	—	—	—	1	0.05
Cyprinodontidae	*Cyprinodon variegatus*	10	1.4	4	0.7	12	2.1	26	1.4
	Fundulus grandis	62	8.8	161	28.6	179	31.6	402	21.9
	Fundulus heteroclitus	192	27.2	669	118.8	405	72.1	1266	69.2
	Fundulus majalis	15	2.1	44	7.8	50	8.9	109	5.9
Poeciliidae	*Gambusia affinis*	—	—	5	0.9	2	0.4	7	0.4
	Poecilia latipinna	40	5.7	44	7.8	31	5.5	115	6.3
Atherinidae	*Menidia beryllina*	2	0.3	—	—	5	0.7	7	0.4
Lutjanidae	*Lutjanus griseus*	—	—	—	—	4	0.7	4	0.2
Gerreidae	*Diapterus olisthostomus*	—	—	—	—	1	0.2	1	0.05
	Eucinostomous argenteus	137	19.4	36	6.4	693	123.1	866	47.3
	Eucinostomous gula	—	—	—	—	3	0.5	3	0.2
	Gerres cinereus	1	0.1	2	0.4	3	0.5	6	0.3
Sparidae	*Lagodon rhomboides*	1	0.1	—	—	—	—	1	0.05
Sciaenidae	*Cynoscion nebulosus*	1	0.1	—	—	2	0.4	3	0.2
	Leiostomus xanthurus	44	6.2	—	—	—	—	44	2.4
	Pogonias cromis	4	0.6	—	—	—	—	4	0.2
	Sciaenops ocellata	1	0.1	—	—	—	—	1	0.05
Mugilidae	*Mugil cephalus*	40	5.7	13	2.3	1	0.2	54	2.9
	Mugil curema	211	29.9	292	51.9	42	7.5	545	29.7
Gobiidae	*Gobionellus boleosoma*	5	0.7	—	—	—	—	5	0.3
	Gobionellus hastatus	12	1.7	2	0.4	—	—	14	0.8
	Gobionellus smaragdus	2	0.3	—	—	—	—	2	0.1
	Gobiosoma bosci	1	0.1	—	—	—	—	1	0.05
	Microgobius gulosus	3	0.4	—	—	—	—	3	0.2
Bothidae	*Citharichthys spilopterus*	3	0.4	—	—	—	—	3	0.2
	Total	792	111.9	1,282	227.8	1,434	254.6	3,508	191.5
	Total utilizable species	308	43.5	317	56.4	58	10.2	683	37.1

abundance): *Fundulus heteroclitus*, *Eucinostomous argenteus*, *Mugil curema*, *F. grandis*, *Poecilia latipinna*, *F. majalis*, *Gobionellus hastatus*, *Gambusia affinis*, *Gerres cinereus*, *Elops saurus*, and *Lutjanus griseus*.

Eleven species, *Synodus foetens*, *Opsanus tau*, *Syngnathus floridae*, *Chloroscombrus chrysurus*, *Selene vomer*, *Micropogon undulatus*, *Chaetodipterus faber*, *Prionotus tribulus*, *Etropus crossotus*, *Paralichthys lethostigma*, and

TABLE 4.—Collections of fishes from three stations on Nichols Creek during the hot season of 1973. Area seined in June was 819 m², in July was 815 m², and in September 714 m². Total area seined was 2,348 m².

Family	Species	June collection		July collection		September collection[1]		Total collections	
		No.	No./100 m²	No.	No./100 m²	No.	No./100 m²	No.	No./100 m²
Clupeidae	*Brevoortia tyrannus*	1	0.1	—	—	—	—	1	0.04
Engraulidae	*Anchoa mitchilli*	36	4.4	—	—	—	—	36	1.5
Ariidae	*Arius felis*	—	—	1	0.1	—	—	1	0.04
Cyprinodontidae	*Fundulus grandis*	77	9.4	55	6.7	—	—	132	5.6
	Fundulus heteroclitus	346	42.2	766	94.0	10	1.4	1122	47.8
	Fundulus majalis	4	0.5	4	0.5	—	—	8	0.3
Poeciliidae	*Poecilia latipinna*	—	—	12	1.5	—	—	12	0.5
Atherinidae	*Menidia beryllina*	13	1.6	11	1.3	102	14.3	126	5.4
Carangidae	*Caranx hippos*	—	—	—	—	2	0.3	2	0.1
	Trachinotus falcatus	—	—	1	0.1	—	—	1	0.04
Gerreidae	*Diapterus olisthostomus*	1	0.1	—	—	—	—	1	0.04
	Eucinostomous argenteus	168	20.5	246	30.2	103	14.4	517	22.0
	Eucinostomous gula	—	—	49	6.0	12	1.7	61	2.6
Sparidae	*Archosargus probatocephalus*	—	—	1	0.1	—	—	1	0.04
	Lagodon rhomboides	—	—	1	0.1	—	—	1	0.04
Sciaenidae	*Bairdiella chrysura*	—	—	—	—	1	0.1	1	0.04
	Leiostomus xanthurus	105	12.8	47	5.8	6	0.8	158	6.7
	Pogonias cromis	—	—	1	0.1	—	—	1	0.04
Mugilidae	*Mugil cephalus*	121	14.8	7	0.9	1	0.1	129	5.5
	Mugil curema	653	79.7	183	22.5	35	4.9	871	37.1
Gobiidae	*Gobionellus boleosoma*	1	0.1	—	—	—	—	1	0.04
	Gobionellus hastatus	1	0.1	—	—	—	—	1	0.04
Bothidae	*Citharichthys spilopterus*	8	1.0	—	—	1	0.1	9	0.4
Cynoglossidae	*Symphurus plagiusa*	2	0.2	—	—	—	—	2	0.1
	Total	1,537	187.5	1,385	169.9	273	38.1	3,195	136.0
	Total utilizable species	893	109.0	252	30.9	147	20.5	1,292	55.0

[1]Station 2 not sampled in September due to mechanical problems.

TABLE 5.—Collections of fishes from three stations on Browns Creek during the hot season of 1973. Area seined in June was 685 m², in July was 676 m², and in September was 285 m². Total area seined was 1,646 m².

Family	Species	June collection		July collection		September collection[1]		Total collections	
		No.	No./100 m²	No.	No./100 m²	No.	No./100 m²	No.	No./100 m²
Elopidae	*Elops saurus*	—	—	1	0.1	—	—	1	0.06
Clupeidae	*Brevoortia tyrannus*	551	80.4	420	62.1	—	—	971	59.0
	Opisthonema oglinum	—	—	103	15.2	—	—	103	6.3
Engraulidae	*Anchoa hepsetus*	21	3.1	—	—	1	0.4	22	1.3
	Anchoa mitchilli	265	38.7	377	55.8	16	5.6	658	40.0
Synodontidae	*Synodus foetens*	3	0.4	—	—	1	0.4	4	0.2
Batrachoididae	*Opsanus tau*	1	0.1	—	—	1	0.4	2	0.1
Belonidae	*Strongylura marina*	1	0.1	—	—	—	—	1	0.06
Cyprinodontidae	*Fundulus grandis*	2	0.3	3	0.4	1	0.4	6	0.4
	Fundulus heteroclitus	717	105.0	342	50.6	9	3.5	1,068	64.9
	Fundulus majalis	1	0.1	—	—	—	—	1	0.06
Poeciliidae	*Gambusia affinis*	2	0.3	4	0.6	6	2.1	12	0.7
Atherinidae	*Menidia beryllina*	222	32.4	2,288	338.5	80	28.1	2,590	157.4
Syngnathidae	*Syngnathus floridae*	1	0.1	—	—	1	0.4	2	0.1
Carangidae	*Caranx hippos*	1	0.1	1	0.1	1	0.4	3	0.2
	Chloroscombrus chrysurus	—	—	—	—	2	0.7	2	0.1
	Selene vomer	2	0.3	1	0.1	—	—	3	0.2
Lutjanidae	*Lutjanus griseus*	—	—	1	0.1	4	1.4	5	0.3
Gerreidae	*Eucinostomous argenteus*	14	2.0	79	11.7	44	15.4	137	8.3
	Eucinostomous gula	2	0.3	44	6.5	2	0.7	48	2.9
	Gerres cinereus	—	—	1	0.1	—	—	1	0.06
Sparidae	*Lagodon rhomboides*	10	1.5	1	0.1	—	—	11	0.7
Sciaenidae	*Bairdiella chrysura*	77	11.2	38	5.6	4	1.4	119	7.2
	Cynoscion nebulosus	—	—	—	—	1	0.4	1	0.06
	Leiostomus xanthurus	912	133.0	134	19.8	25	8.8	1,071	65.1
	Micropogon undulatus	9	1.3	2	0.3	—	—	11	0.7
	Sciaenops ocellata	4	0.6	—	—	—	—	4	0.2
Ephippidae	*Chaetodipterus faber*	—	—	2	0.3	—	—	2	0.1
Mugilidae	*Mugil cephalus*	61	8.9	31	4.6	1	0.4	93	5.7
	Mugil curema	238	34.7	206	30.5	21	7.4	465	28.3
Gobiidae	*Gobionellus boleosoma*	1	0.1	1	0.1	—	—	2	0.1
Triglidae	*Prionotus tribulus*	—	—	1	0.1	—	—	1	0.06
Bothidae	*Citharichthys spilopterus*	5	0.7	4	0.6	—	—	9	0.6
	Etropus crossotus	—	—	—	—	1	0.4	1	0.06
	Paralichthys lethostigma	1	0.1	—	—	—	—	1	0.06
Cynoglossidae	*Symphurus plagiusa*	1	0.1	13	1.9	—	—	14	0.9
Tetraodontidae	*Sphoeroides nephelus*	2	0.3	—	—	2	0.7	4	0.2
	Total	3,127	456.2	4,098	605.8	224	79.4	7,449	452.7
	Total utilizable species	2,086	304.2	3,229	477.0	137	48.3	5,452	331.4

[1]Station 1 not sampled in September due to mechanical problems.

Sphoeroides nephelus, were collected only in Browns Creek and not in either of the thermally affected creeks. However, none of the species listed above made a major contribution to the total density of fishes in this ambient temperature creek. Among the other species entirely absent from San Carlos collections, only two species, *Anchoa mitchilli* and *Bairdiella chrysura*, made a significant contribution to the fish density in Browns Creek. When considered alone, the differences cited above might be construed to suggest that the nursery capacity of thermally affected San Carlos Creek is not markedly different from that of Browns Creek which functions at ambient temperature. However, a critical comparison of the densities, the biomasses, and the population structure of the fishes in the three creeks reveal some important differences that are described below.

Figure 3 illustrates the relative densities of both total fishes and utilizable fishes as they appeared in the monthly samples. The figure shows that the following three major differences existed between the populations present in the thermally affected creeks (San Carlos and Nichols) and the population present in the ambient temperature creek (Browns):

1. In June and July the density of total fishes was highest in the ambient temperature creek.
2. Throughout the entire study period the density of utilizable species was markedly higher in the ambient temperature creek.
3. In the ambient temperature creek, the majority of the population consisted of juveniles of utilizable species, whereas in the thermally affected creeks the majority consisted of species not utilized by man.

In June and July the estimated density of total

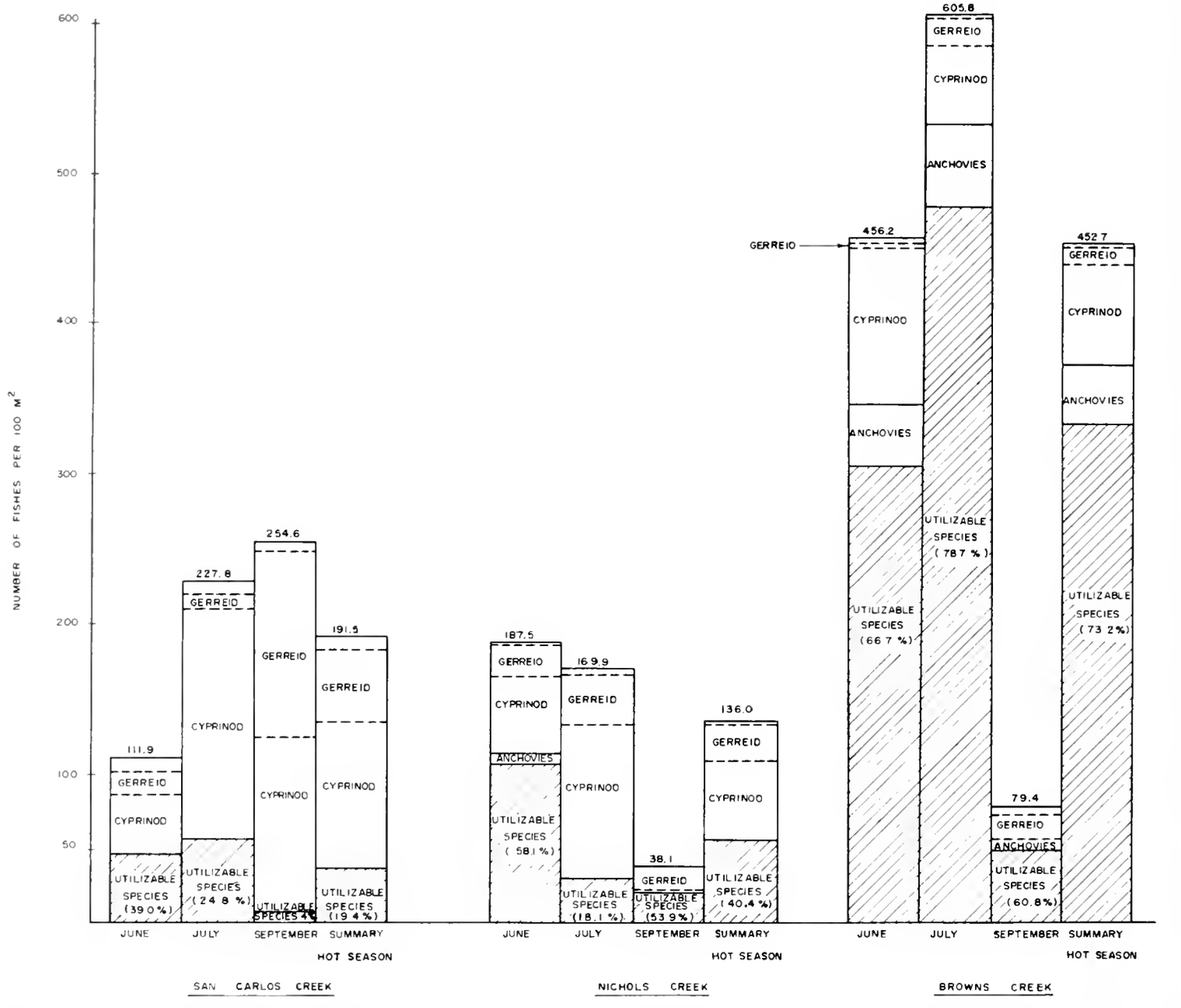

FIGURE 3.—Densities of fishes in the three creeks as estimated from seine collections. Species used by man as food or fishery products are combined and termed Utilizable Species. Percent of each collection that was represented by utilizable species is indicated. Cyprinod = all species of Cyprinodontidae. Gerreid = all species of Gerreidae except for *Gerres cinereus*. The histogram for each creek depicting "Summary Hot Season" was compiled on the basis of the total area sampled during the entire study period.

fishes in Browns Creek was three to four times higher than the estimated density in San Carlos Creek. However, in September the estimated density in San Carlos Creek was about three times higher than that in Browns Creek. The basis for this apparent September reversal between the two creeks was due primarily to the expected early fall emigration of juveniles of migratory species, many of which are utilizable species. The estimated density of total fishes in Browns Creek was two to four times higher than the density in Nichols Creek throughout the entire study period.

Of greater significance than the differences in total density of fishes described above, are the marked differences that existed between creeks in the estimated densities of utilizable species (see Figure 3). In June and July, the estimated density of utilizable species in Browns Creek was seven to eight times greater than in San Carlos Creek. In September following the emigration of juveniles of many migratory species, the estimated density of utilizable species in Browns Creek was still nearly five times greater than that recorded in San Carlos Creek. When data for the entire hot season are pooled, Browns Creek displayed an overall density of utilizable species approximately nine times greater than that in San Carlos Creek. In Nichols Creek the estimated densities of utilizable species were generally somewhat higher than those in San Carlos Creek yet markedly lower than those

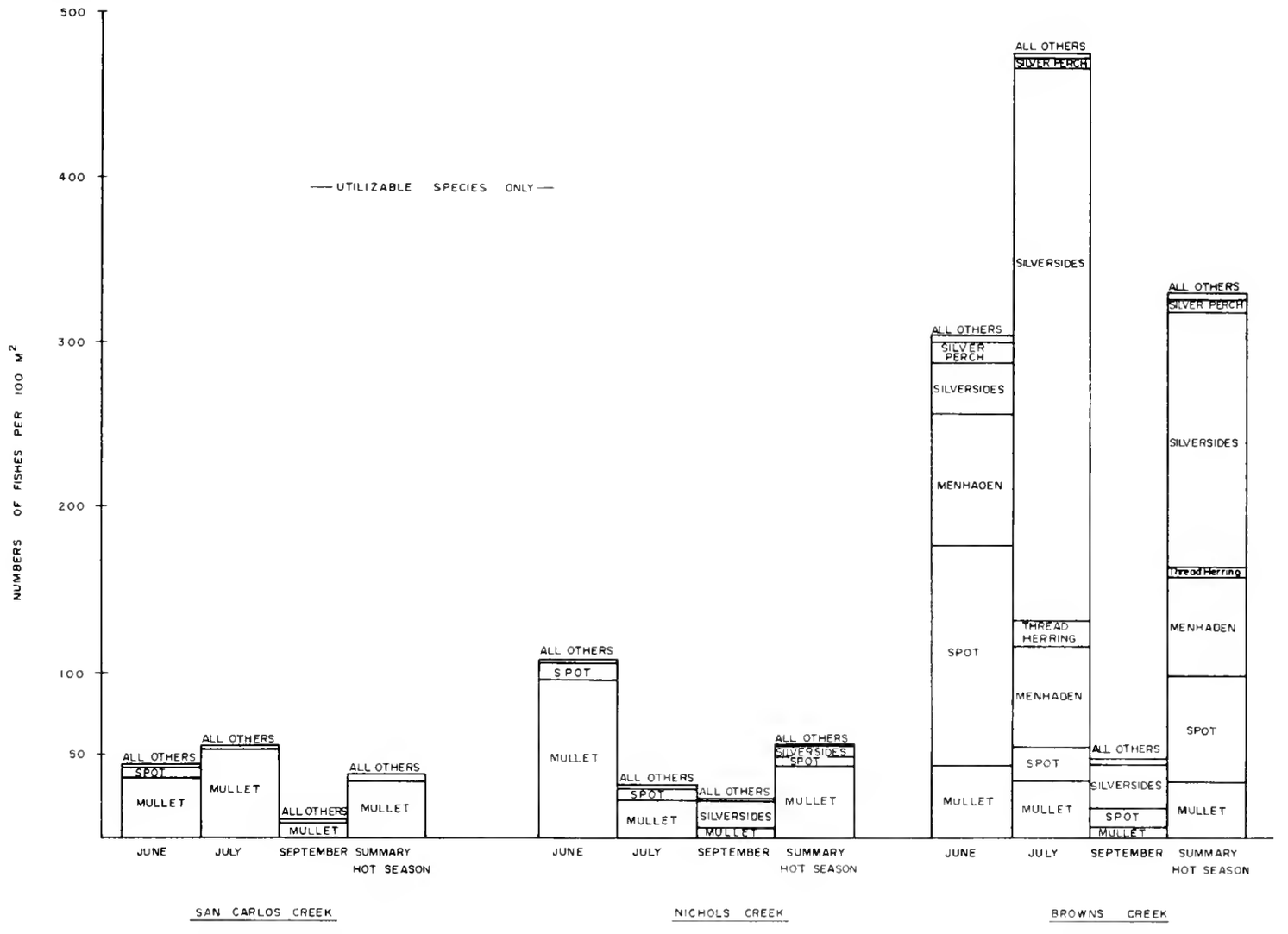

FIGURE 4.—Densities of utilizable species in the three creeks as estimated from seine collections. Histograms depicting "Summary Hot Season" compiled as described in Figure 3.

in Browns Creek. The injection of hot water that was forced through Nichols Creek twice each day (see Figure 2) obviously decreased the value of this second creek as a nursery area for utilizable species.

Figure 3 also illustrates the change in overall population structure that has occurred in response to the thermal effluent. Whereas in Browns Creek 61 to 79% (average 73.2%) of the total fishes in the monthly collections were utilizable species, in San Carlos Creek only 4 to 39% (average 19.4%) of the total specimens could be so categorized. Hence in contrast to the situation in the ambient temperature creek, the majority of the fishes occupying San Carlos Creek during the hot season are species not utilized by man. Dominant among this latter group of temperature tolerant fishes were two species of cyprinodonts (*Fundulus grandis* and *F. heteroclitus*) and the gerreid *Eucinostomous argenteus*. Whereas these three species alone accounted for 72% of the total fishes collected in San Carlos Creek, these same species accounted for only 16% of the total fishes collected in Browns Creek. In Nichols Creek the portion of the population consisting of utilizable species was generally greater than that in San Carlos Creek yet considerably less than that in Browns Creek.

Figure 4 illustrates the relative abundance of the various utilizable species collected in the three creeks. In San Carlos Creek, two species of mullet (*Mugil curema* and *M. cephalus*) alone accounted for 76 to 96% of the total utilizable species collected. In Browns Creek, mullet accounted for only 8 to 16% of the utilizable species. Five other species made major contributions to the array of utilizable species present in Browns Creek. These other species were (in order of decreasing abundance): tidewater silverside *Menidia beryllina*, spot *Leiostomus xanthurus*, Atlantic menhaden *Brevoortia tyrannus*, silver perch *Bairdiella chrysura*, and Atlantic thread herring *Opisthonema oglinum*. Silver perch *Bairdiella chrysura* were entirely absent from the San Carlos collections.

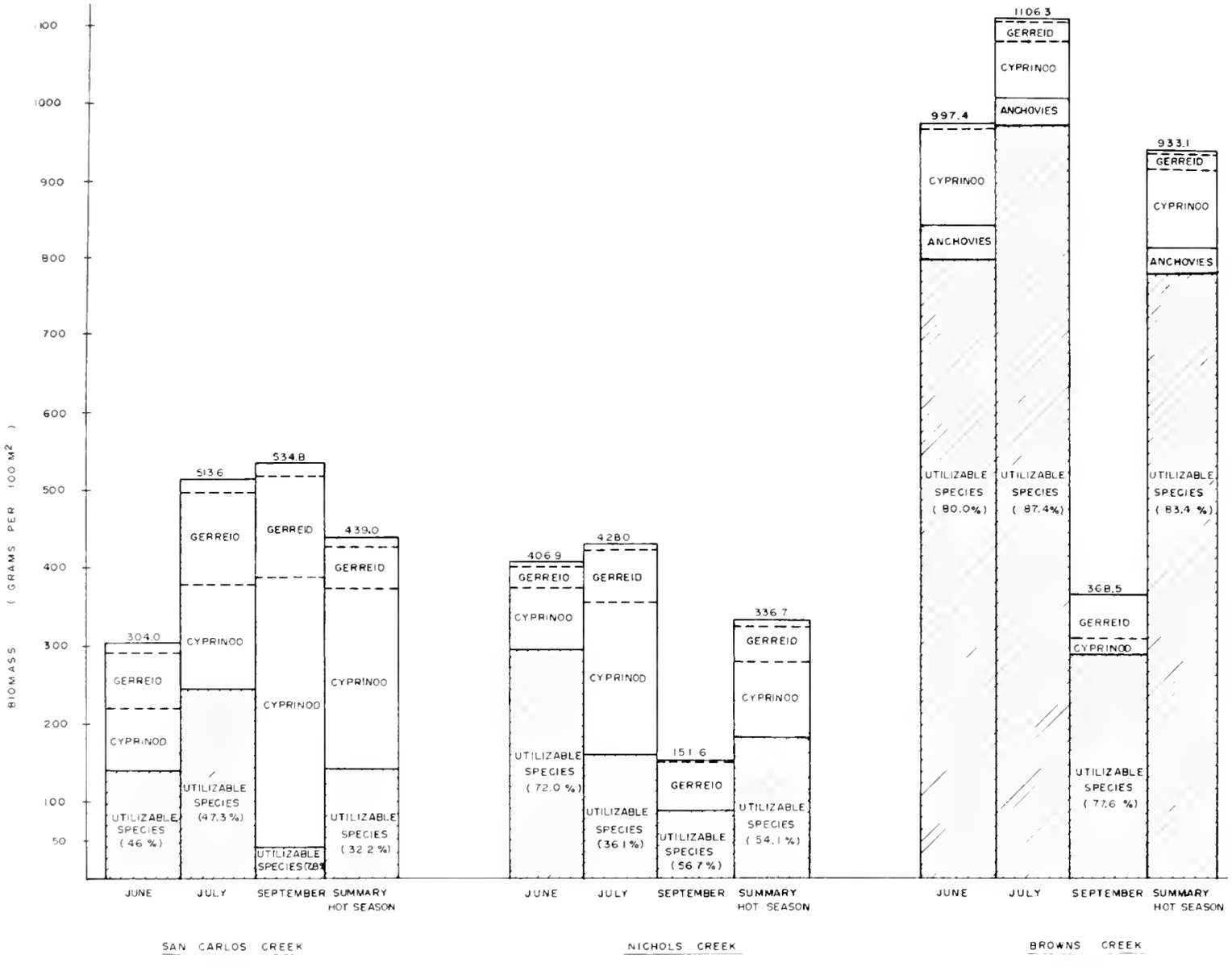

FIGURE 5.—Biomass per 100 m² of fishes in the three creeks as estimated from seine collections. Presentation as in Figure 3.

Figure 5 illustrates the biomass distributions that were computed from the weights of fishes obtained in the samples. The figure shows that the differences in overall standing crops (grams per 100 m²) between the creeks conform quite closely to the differences in density described earlier. In June and July the estimated standing crop of total fishes in Browns Creek was approximately 2 to 3 times greater than that in San Carlos Creek and 2.5 times greater than that in Nichols Creek. In September, following the aforementioned emigration of juveniles of many transient species, the estimated standing crop in San Carlos Creek was 1.5 times greater than that in Browns Creek. However, even in September, Browns Creek continued to support a standing crop approximately 2.5 times greater than that in Nichols Creek.

Of greater significance than the overall differences in biomass described above, are the marked differences in utilizable species that existed between creeks. Throughout the entire collecting period, the biomass of utilizable species (grams per 100 m²) was from four to seven times greater in Browns Creek than in San Carlos Creek and from three to six times greater in Browns Creek than in Nichols Creek. Whereas in Browns Creek the bulk of the biomass was distributed among utilizable species, in San Carlos Creek the bulk of the biomass was distributed among species not utilized by man. In San Carlos Creek, three species of nonutilized fishes (*F. grandis*, *F. heteroclitus*, and *E. argenteus*) accounted collectively for 45 to 85% (average 62%) of the total biomass. In Browns Creek these same species accounted for only 8 to 16% (average 11.9%) of the total biomass.

Figure 6 illustrates the biomass distributions among the various utilizable species. In San Carlos Creek, the two species of mullet alone accounted for 73 to 97% (average 86.7%) of the

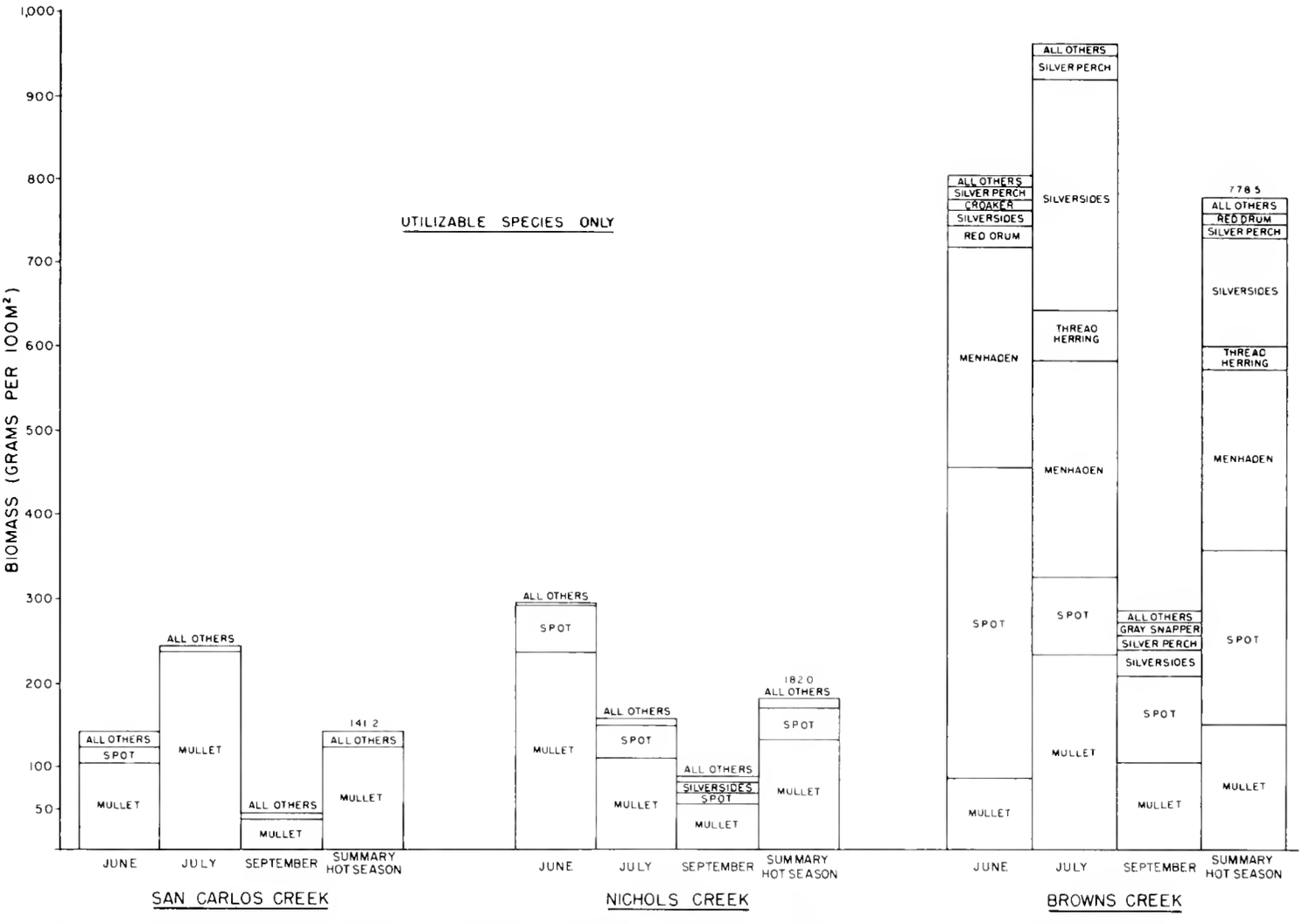

FIGURE 6.—Biomass per 100 m² of utilizable species in the three creeks as estimated from seine collections. Histograms depicting "Summary Hot Season" compiled as described in Figure 3.

biomass of utilizable species. In Browns Creek, the mullet accounted for only 11 to 37% (average 19.2%) of this biomass. The same five species that were cited earlier made the most significant additional contributions to the biomass of utilizable species in Browns Creek.

DISCUSSION AND SUMMARY

Elevated water temperature resulting from the discharge of condenser cooling water by the two units of the Northside Generating Station in Jacksonville, Fla. has a detrimental effect on the capacity of two marshland creeks to serve as a nursery area for juvenile fishes during the hot season. Evidence for this detrimental effect is based upon the marked differences in both the density of fishes and the species composition which exist between an ambient temperature creek and two creeks receiving thermal effluent. To the best of our knowledge this is the first field study in which quantitative measurements have been reported on the effects of a thermal effluent on the capacity of an estuarine receiving water to continue serving as a nursery area for juvenile specimens, especially those of species having direct value to man. Although only the results of the 1973 study have been reported here, a preliminary, less-extensive study conducted at the same site in July and September of 1971 revealed the same basic types of differences that are described herein.

From the standpoint of coastal fisheries operations, the major detrimental effect of the thermal effluent is to decrease the suitability of the habitat for juveniles of species used by man as food and related fishery products. In the thermally affected creeks, both the numbers and the biomass of juveniles of utilizable species were 3- to 10-fold smaller than those encountered in the ambient temperature creek. Regarding these species, our data clearly show that whereas the creek receiving the largest input of thermal effluent affords a nursery habitat dominated almost entirely by

mullet (primarily *Mugil curema*), the creek functioning at ambient temperature affords a nursery habitat for a much greater array of utilizable species. In both of the thermally affected creeks there was a marked diminution in the numbers and the biomass of the following seven species of utilizable fishes (listed in order of decreasing abundance in ambient temperature creek): tidewater silverside *Menidia beryllina*, spot *Leiostomus xanthurus*, Atlantic menhaden *Brevoortia tyrannus*, silver perch *Bairdiella chrysura*, Atlantic thread herring *Opisthonema oglinum*, Atlantic croaker *Micropogon undulatus*, and pinfish *Lagodon rhomboides*.

The shallow-water habitats afforded by marshland creeks are especially important to estuarine fishes during the hot season. As shown by McErlean et al. (1973), both the number of species and the number of individuals that rely on the shallow shore zone of the estuary are maximal in summer and spring. This is due in part to the time of spawning in many species, frequently in late winter or in the spring, and to the subsequent immigration into estuarine areas of juveniles of the many transient species. The September decline in both the number and the biomass of fishes that occurred in the ambient temperature creek (Browns Creek) is similar to the fall decline described by McErlean et al. for shallow-water stations in the Patuxent River.

In the review by Wurtz and Renn (1965) on water temperature and aquatic life, the following statements were made: "Although there are historic records of fish surviving natural temperatures of 100°F, this is unusual. Waters with temperatures that regularly exceed 95°F would not be expected to support a large, or diverse, fish population." It is noteworthy that throughout the period of this study, June through September, daily temperatures in San Carlos Creek routinely exceeded 95°F (35°C). In July and September, the average daytime temperatures recorded at all stations in this creek were, with but one exception, greater than 95°F (see Table 1). A maximum temperature of 102.6°F (39.2°C) was recorded at one station in July. Although the overall population of fishes found in San Carlos Creek was neither large nor very diverse, 15 species exhibited no marked diminution in numbers, and a few species were actually more abundant here than in the ambient temperature creek. Among the species of temperature tolerant fishes recorded in the current study, the gray snapper was reported by Nugent (1970) as being a species whose numbers were not diminished by the thermal effluent of a power plant situated to the south of Miami. Although the gray snapper was the most abundant species collected in the gill net samples reported by Nugent, it was a very minor member of the fish population sampled in our study. Nugent also reported that the tarpon, *Megalops atlantica*, was equally abundant at both heated and control stations. In the current study large tarpon were seen during midsummer within a few hundred yards of the outfall of the power plant in San Carlos Creek although no specimens were collected. Nugent reported a decrease in the numbers of white mullet (primarily adults taken by gill nets) at stations in the area of elevated temperature during the hot season. In the current study the estimated density of juvenile white mullet was quite similar in all of the creeks. Trembley (1961) reported that mummichogs from the Delaware River, acclimated to 32.2°C, had an LD_{50} (mean lethal dose) of 39.4°C. If this LD_{50} approximates that in our own study area then the presence of large numbers of this species in San Carlos Creek indicates that it is literally thriving in an environment in which the temperatures encountered daily during July are very close to the upper limits for survival.

The current study was directed primarily at an analysis of the effects of a thermal effluent and related conditions upon the population of juvenile fishes utilizing a nursery habitat during the hot season. It might be contended that the effects described herein for juvenile fishes do not necessarily apply to the population of adult fishes using the same heated creeks. However, de Silva (1969) surveyed literature relating to differential tolerances exhibited by both juveniles and adults of several species. He concluded that many juveniles appear to tolerate eurythermal conditions, while adults tend to be broadly stenothermal. If the above generalization is correct, then one would predict that the effect of the thermal effluent on the population of adult fishes would be even more extreme during the hot season than the effects we recorded regarding the juvenile fishes.

We recognize that some of the population changes ascribed to elevated water temperatures in the current study may be due in part to other factors operating in concert with temperature. As was pointed out by Mihursky and Kennedy (1967), temperature tolerance limits of aquatic organisms are affected by a number of other variables such as

dissolved oxygen and carbon dioxide, salinity, and a variety of toxic substances. The St. Johns River in the vicinity of Jacksonville receives a multitude of pollutants in addition to thermal effluent. It is impossible to quantify the relative role played by other pollutants in altering the fish populations in the thermally affected creeks. However, since our control creek (Browns Creek) probably received the same array of extraneous pollutants from the river as did the heated creeks, it is possible to use the fish population found in Browns Creek as an indicator of how the system is faring without the addition of the thermal effluent and the various chemicals associated with power plant operation.

It is not the intent of this report to criticize the Northside Generating Station or the Jacksonville Electric Authority for the effects that the operation of their power plant is having upon the nursery area capacity of the adjacent marshland. It is realized that this plant is operating within the guidelines dictated by appropriate State and Federal agencies. Further, it is recognized that the acreage of marshland affected by this plant represents only a minute portion of the total marshland habitat available in this area. However, it is the intent of this report to show that massive discharges of thermal effluent do have a very obvious detrimental effect on the capacity of an estuarine receiving water to continue functioning as a nursery area for a variety of important species. This particular detrimental effect has received inadequate attention in the past. Since nursery areas represent one of our most valuable estuarine resources, it is imperative that this resource and its impairment should be given proper consideration during the site selection stages that precede the construction of future power plants.

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ADDITIONAL STUDIES OF THE FISHES, MACROINVERTEBRATES, AND HYDROLOGICAL CONDITIONS OF UPLAND CANALS IN TAMPA BAY, FLORIDA

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ABSTRACT

Hydrological and biological data from a concluding study of upland canals in Tampa Bay, Fla., are presented and compared with those collected the previous year. Critically low levels of dissolved oxygen occurred more frequently and over a longer period of time in the second year. Most affected were the inland portions of the canal system where the number of species declined markedly over the previous year. Impoverishment of fauna on or near the bottom is expected to recur during summer months because of oxygen depletion resulting from a combination of continuing accumulation of decomposing organic sediment, warm water, and little circulation in the dead-end canals.

In order to create waterfront property while not violating legislation that curtails dredging and filling of wetlands below the mean high-water line, land developers in Florida and elsewhere are digging access canals that lead from open water to upland acreage (Barada and Partington 1972). Florida's shoreline has already been extensively altered by such practice (McNulty et al. 1972), and further alteration can be expected because of ever-increasing demand for waterfront property. If the coastal zone is to be managed wisely, information on the suitability of these man-made waterways as habitat for aquatic organisms is urgently needed.

In June 1970 a small, upland canal system in Old Tampa Bay, Fla., was completed (Figure 1). This offered a unique opportunity to study the development of and changes in ecological conditions in upland canals. The fishes, macroinvertebrates, and hydrological conditions occurring in the canals during the first year following completion of the system were described by Lindall et al. (1973). In that study, however, the unusual occurrence of red tide (caused by *Gymnodinium breve*) and drought produced conditions that were atypical for the area. Conditions during our second year were more typical. Further studies by us are unlikely owing to closure of the laboratory at St. Petersburg Beach and relocation of personnel. Thus, we present the results from our follow-up study in this paper. We discuss the hydrological conditions and biota found in the canals during the second year and make comparisons with those found in the first year.

STUDY AREA AND METHODS

The study area, known as Tanglewood Estates, is located on the southwest shore of Old Tampa Bay in northeast St. Petersburg, Fla. (Figure 1). Development of the canal system, sampling procedures, sampling gear, and station descriptions were reported previously (Lindall et al. 1973). Briefly, sampling consisted of trawling at each station in the canals with concomitant measurements of temperature, salinity, and oxygen. Sampling was conducted monthly from October 1971 through September 1972.

TEMPERATURE

Water temperatures at the control and canal stations are shown in Figure 2. At the control station (Station 1) surface and bottom temperatures ranged from 20.0° to 29.3°C and were nearly identical in any one sampling period. The greatest difference was in December when the bottom was 1.1°C higher than the surface. Canal stations showed greater temperature ranges than the control station. They ranged from 20.0° to 30.6°C at the surface and 17.8° to 29.7°C at the bottom. With few exceptions, water temperature at the bottom

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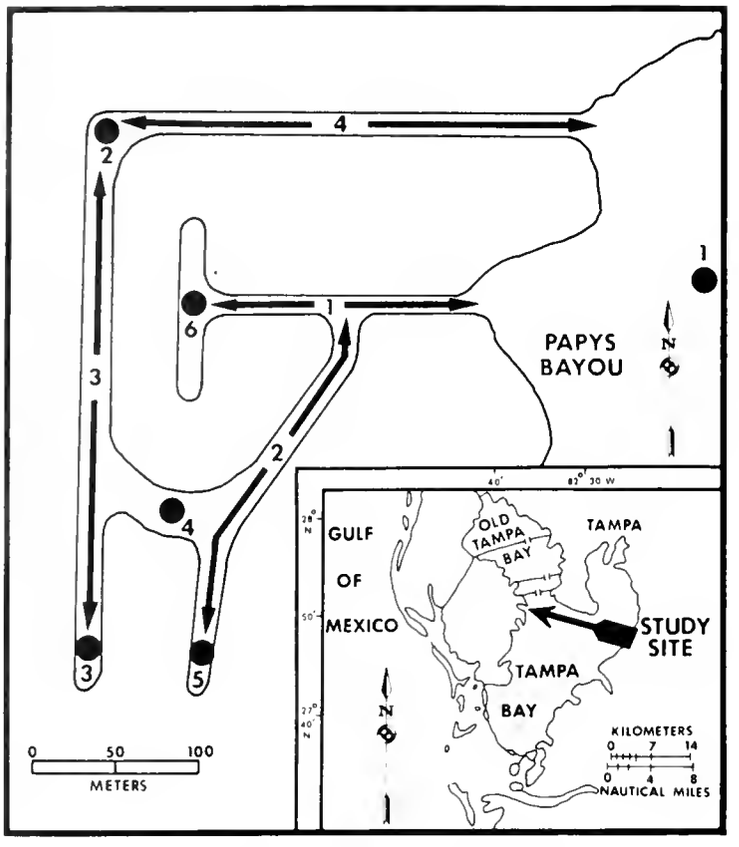

FIGURE 1.—Tampa Bay, Fla., showing location of study area and sampling stations (hydrologic station • ; trawl station ⟷).

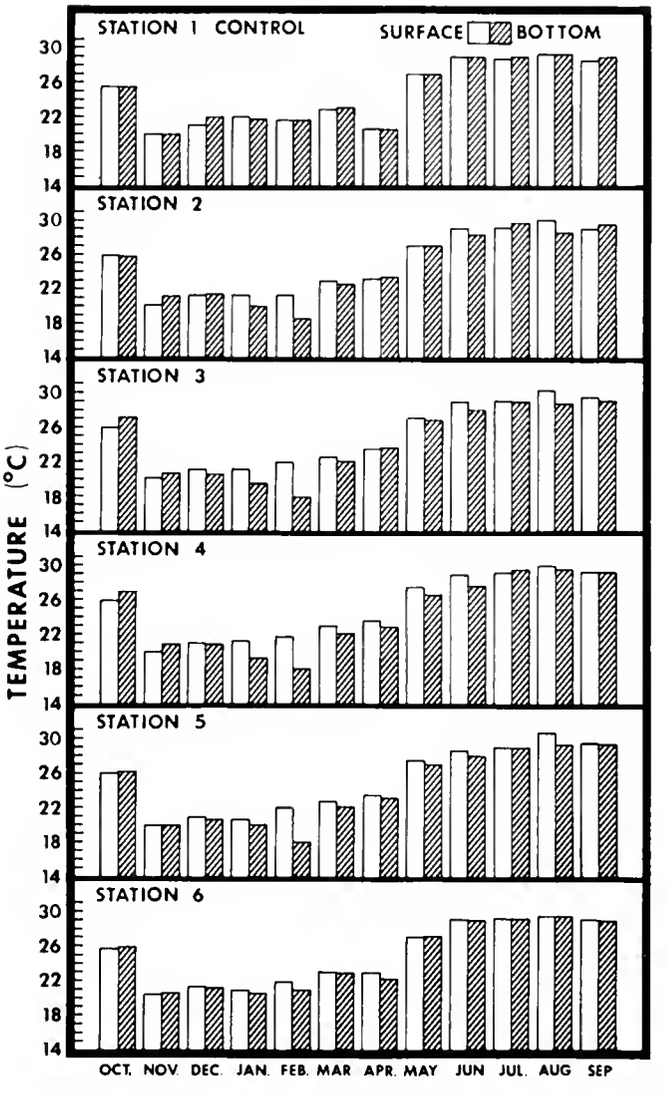

FIGURE 2.—Monthly water temperature at the surface and bottom of all hydrologic stations, October 1971-November 1972.

of the canals was lower than at the surface in any one sampling period. A definite thermocline was noted in January and February with the most inland stations exhibiting the greatest differences between surface and bottom temperatures. The greatest difference was at Station 5 in February when the bottom was 4.0°C lower than the surface.

In the previous year's study, the greatest difference was at Station 4 (February 1971) when the bottom was 1.8°C lower than at the surface (Lindall et al. 1973).

SALINITY

Surface and bottom salinities at the control station ranged from 19.1 to 28.0‰ during the study and were nearly identical in any one sampling period (Figure 3). The greatest difference was in May when the bottom was 0.7‰ lower than the surface. Surface salinities at canal stations were similar to those at the control station, ranging from 19.1 to 28.5‰. With few exceptions, however, salinity at the bottom of the canals was higher than at the surface in any one sampling period. The greatest difference was at Station 3 in October when the bottom was 4.5‰ higher than the surface.

Stratification of salinity was also noted in the previous year's study (Lindall et al. 1973). Differences between surface and bottom were not as pronounced during most of that study because drought conditions prevailed throughout most of the year. Heavy rains in August 1971 ended the drought. Thus, greater differences between surface and bottom salinities (as much as 15‰) were recorded in the previous study than in the present study.

OXYGEN

Dissolved oxygen levels at each station are shown in Figure 4. Only at the control station were surface and bottom values similar, differing no more than 0.3 ml/liter in any one sampling period. At this station the lowest observed concentration was 2.2 ml/liter (July 1972). Surface oxygen values in the canals ranged from 2.4 to 6.2 ml/liter and were similar to those at the control station throughout the year. Oxygen at the bottom

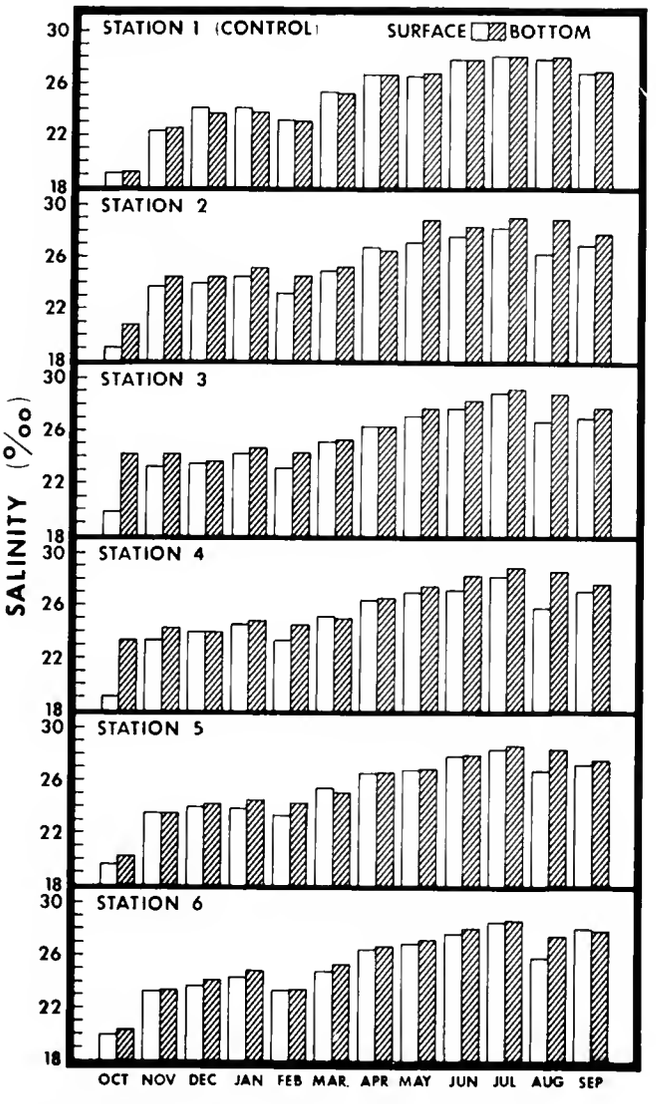

FIGURE 3.—Monthly salinity at the surface and bottom of all hydrologic stations, October 1971-November 1972.

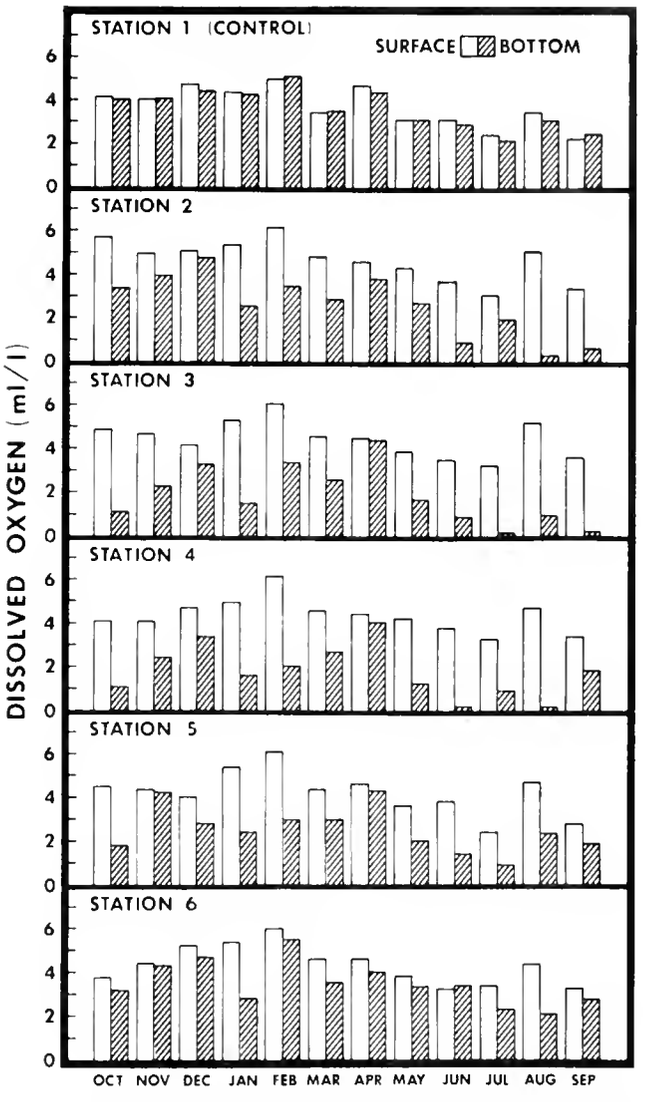

FIGURE 4.—Monthly dissolved oxygen at the surface and bottom of all hydrologic stations, October 1971-November 1972.

of the canals was always less than at the surface with the single exception of Station 6 in June. Moreover, about 50% of the bottom samples taken throughout the year at stations farthest from the bayou (Stations 3-5) contained less than 2.0 ml/liter of oxygen; several were anoxic or nearly so. At Station 6, closest to the bayou, oxygen levels were never observed to be less than 2.1 ml/liter. Trent et al. (1972) also reported oxygen depletion at inland portions of housing development canals in Galveston Bay, Tex., during the summer.

Results of the previous year's study showed severe oxygen depletion in the canals during the summer months following a red tide (caused by *Gymnodinium breve*) outbreak (Lindall et al. 1973). In that study decaying fish killed by the red tide placed additional oxygen demand on the system and precluded the determination of the extent to which dissolved oxygen would have been depressed in the absence of red tide. In the present study, no red tide occurred, but oxygen was again depleted at the bottom of the most inland stations in the canals during the summer. In fact, low dissolved oxygen occurred more frequently and over a longer period of time (October 1971 and May through September 1972) than in the previous year.

FISHES AND MACROINVERTEBRATES

Thirty-eight species and 9,502 individuals of vertebrates and invertebrates were collected in the canals during the year (Table 1). Of the 38 species, 34 were finfish, 1 was the diamondback terrapin, *Malaclemys terrapin*, and 3 were commercially important invertebrates (blue crab, *Callinectes sapidus*; pink shrimp, *Penaeus duorarum*; and brief squid, *Lolliguncula brevis*). Fourteen of the 34 species of finfish did not occur in the previous year's catch. These 14 species, however, made up less than 1% of the total catch.

TABLE 1—Monthly occurrence and number of individuals of vertebrates and invertebrates collected with otter trawl at all stations from October 1971 through September 1972.

Species	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Total No.	Total %
Vertebrates:														
Anchoa mitchilli	429	1,360	3,368	1,516	296	360	0	1,005	42	6	22	449	8,853	93.2
Anchoa hepsetus	0	0	0	0	0	0	0	208	1	0	1	0	210	2.3
Bairdiella chrysura	0	0	19	0	0	0	4	29	41	1	1	0	95	1.1
Chaetodipterus faber	0	0	9	0	0	0	1	1	16	5	1	1	34	0.5
Syngnathus scovelli[1]	0	0	0	0	4	1	0	7	5	0	0	0	17	0.2
Lagodon rhomboides	0	0	0	0	0	2	6	3	3	0	0	0	14	0.1
Gobiosoma bosci	0	1	1	0	2	4	0	2	3	0	0	0	13	0.1
Pogonias cromis	0	0	1	1	0	2	8	0	0	0	1	0	13	0.1
Lucania parva[1]	0	0	1	1	2	2	0	4	0	0	0	0	10	0.1
Diapterus plumieri[1]	0	0	4	0	2	0	0	0	0	0	2	1	9	0.1
Eucinostomus argenteus	0	0	7	1	0	0	0	1	0	0	0	0	9	0.1
Menticirrhus americanus	0	1	0	0	0	0	0	5	0	2	1	0	9	0.1
Cynoscion arenarius	0	0	0	0	0	0	0	3	0	1	2	2	8	0.1
Orthopristis chrysoptera	0	0	0	0	0	0	4	1	0	0	0	0	5	0.1
Eucinostomus gula	0	0	0	0	0	0	0	0	4	0	0	0	4	0.1
Trinectes maculatus[1]	0	0	4	0	0	0	0	0	0	0	0	0	4	0.1
Cynoscion nebulosus	0	0	0	0	0	0	0	3	0	0	0	0	3	0.0
Microgobius gulosus	0	0	0	0	0	0	0	0	0	1	1	1	3	0.0
Opisthonema oglinum	0	0	0	0	0	0	1	2	0	0	0	0	3	0.0
Sciaenops ocellata	0	0	1	1	1	0	0	0	0	0	0	0	3	0.0
Sphoeroides nephelus	0	2	0	0	1	0	0	0	0	0	0	0	3	0.0
Chilomycterus schoepfi[1]	0	0	0	0	0	0	0	1	1	0	0	0	2	0.0
Epinephelus itajara[1]	0	0	0	1	0	0	0	0	0	1	0	0	2	0.0
Gobiosoma robustum[1]	0	0	0	0	0	1	0	1	0	0	0	0	2	0.0
Hippocampus erectus[1]	0	0	0	0	1	0	0	0	0	0	1	0	2	0.0
Leiostomus xanthurus	0	0	0	0	0	2	0	0	0	0	0	0	2	0.0
Malaclemys terrapin	0	0	0	0	0	0	0	0	1	0	0	1	2	0.0
Monacanthus hispidus[1]	0	0	0	0	0	1	0	1	0	0	0	0	2	0.0
Syngnathus louisianae[1]	0	0	0	0	0	0	0	1	0	1	0	0	2	0.0
Archosargus probatocephalus	0	0	0	0	0	0	0	0	1	0	0	0	1	0.0
Arius felis	0	0	0	0	0	0	0	0	0	0	1	0	1	0.0
Elops saurus[1]	0	0	0	0	1	0	0	0	0	0	0	0	1	0.0
Harengula pensacolae[1]	0	0	0	0	0	0	0	1	0	0	0	0	1	0.0
Hippocampus zosterae[1]	0	0	0	0	0	0	0	0	0	1	0	0	1	0.0
Lactophrys quadricornis[1]	0	0	0	0	0	0	0	0	0	1	0	0	1	0.0
Invertebrates:														
Lolliguncula brevis	0	0	1	0	1	11	7	17	21	13	0	15	86	0.9
Callinectes sapidus	0	4	11	8	5	4	10	2	3	0	1	1	49	0.5
Penaeus duorarum	0	1	5	6	1	0	0	1	1	3	3	2	23	0.2
Total species	1	6	13	8	12	11	8	22	14	12	13	9	38	
Total individuals	429	1,369	3,432	1,535	317	390	41	1,299	143	36	38	473	9,502	100.0

[1]Did not occur in catches from August 1970 through August 1971 (Lindall et al. 1973).

The four species of finfish caught in greatest abundance represented 97% of the total number of specimens (Table 1). They were the bay anchovy, *Anchoa mitchilli*; striped anchovy, *A. hepsetus*; silver perch, *Bairdiella chrysura*; and Atlantic spadefish, *Chaetodipterus faber*. The bay anchovy alone accounted for more than 93% of the total number caught.

In the previous year's study (Lindall et al. 1973) the four dominant species of fish, representing 92% of the catch, were bay anchovy (7,557 individuals—72%); spotfin mojarra, *Eucinostomus argenteus* (921 individuals—8.8%); spot, *Leiostomus xanthurus* (821 individuals—7.8%); silver jenny, *Eucinostomus gula* (372 individuals—3.5%). The latter three species combined consisted of only 15 individuals in the present study and made up only 0.2% of the catch (Table 1). Each of these three species is a bottom feeder (Darnell 1958; Springer and Woodburn 1960; Carr and Adams 1973), and the prolonged period of low dissolved oxygen at the bottom of the canals probably accounted for the 99% reduction in their numbers.

The brief squid was the most abundant invertebrate (54% of all invertebrates collected) and made up about 1% of all animals collected during the year. Based on the previous year's catch, the number of squid in the canal system declined by about 78%, while the total numbers of pink shrimp and blue crab remained about the same.

Of the 38 species collected during the year, most occurred at Station 4 (28 species), followed by Station 1 (21 species), Station 3 (18 species), and Station 2 (14 species). Compared with the previous year, the number of species collected at Stations 1 and 4 were about the same, but those at Stations 2 and 3 declined markedly (30% and 50% respec-

tively). We were not surprised to find fewer species at Stations 2 and 3, because these stations are farthest from the bayou and were most affected by the critically low oxygen levels. As evidence, catches at the four trawl stations during the summer period of low dissolved oxygen (July-August) are compared in Figure 5. The vast majority of species and individuals occurred nearest the bayou (Stations 1 and 4) during this period of stress.

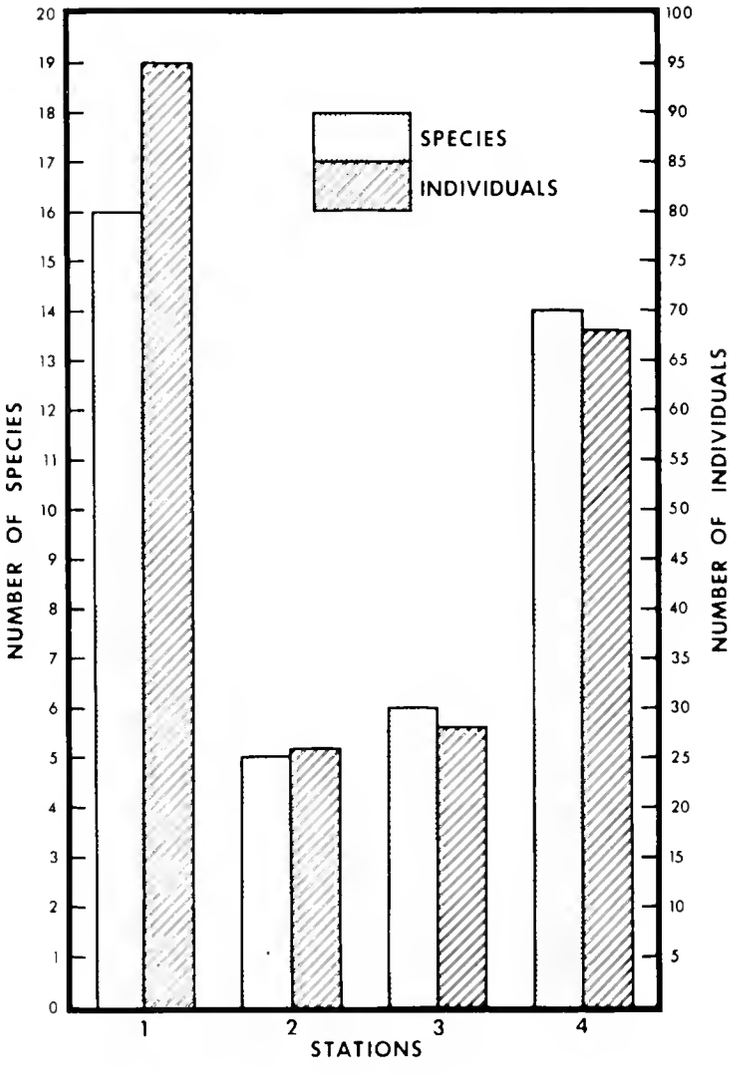

FIGURE 5.—Number of species and individuals caught at each trawl station during the summer period of low dissolved oxygen (June through August 1972).

CONCLUSIONS

The upland canal system known as Tanglewood Estates is poorly designed with respect to providing year-round, quality habitat for estuarine species of fish and shellfish. Apparently caused by prolonged periods of low dissolved oxygen at the bottom of the canals, the numbers of squid (*Lolliguncula brevis*) and three species of finfish (*Eucinostomus argenteus*, *E. gula*, and *Leiostomus xanthurus*) were drastically reduced in the second year of the system's existence. We believe that the ability of the canal system to provide adequate oxygen for respiration of bottom-dwelling fishes is becoming progressively worse. The main causative factors are: 1) lack of water exchange with the adjacent bayou, 2) water depths greater than the depth of the photic zone, thus preventing photosynthesis by benthic flora, and 3) continuing accumulation of decomposing soft sediments (Hall and Lindall[4]).

The major advantages of upland canal development, as opposed to bayfill development, are that bay bottom is not adversely altered and water circulation patterns are not altered significantly. In fact, estuarine area is increased. However, as long as land developers continue to design upland canals with dead ends and excessive depths, oxygen depletion and the resulting impoverishment of fauna on or near the bottom can be expected to be a recurring problem in summer months.

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A REEVALUATION OF THE COMBINED EFFECTS OF TEMPERATURE AND SALINITY ON SURVIVAL AND GROWTH OF BIVALVE LARVAE USING RESPONSE SURFACE TECHNIQUES

R. GREGORY LOUGH[1]

ABSTRACT

The combined effects of temperature and salinity on larval survival and growth of *Crassostrea virginica, Mercenaria mercenaria*, and *Mulinia lateralis* as reported in the literature were critically examined using response surface techniques. The late veliger larvae generally have a greater tolerance to both temperature and salinity than the developing embryos. Each species shows its own characteristic change in temperature-salinity tolerance as it develops and approaches the range normally tolerated by the adults as it matures. Maximum growth of the veliger larvae required higher temperatures and somewhat higher salinities than maximum survival. Differences in temperature-salinity ranges estimated for maximum survival and growth were significantly different for all three species. In each case growth showed a significant temperature-salinity interaction. Response surface plots are given for early larval survival and late veliger survival and growth. Inferences of tolerance studies are made to the fields of pollution and aquaculture.

Recent studies of the combined effects of temperature and salinity on early development of bivalve larvae have been done by Davis and Calabrese (1964) for *Crassostrea virginica* and *Mercenaria mercenaria*, Brenko and Calabrese (1969) for *Mytilus edulis*, Calabrese (1969) for *Mulinia lateralis*, Lough and Gonor (1971, 1973a, b) for *Adula californiensis*, and Goodwin (1973) for *Panope generosa*. However, only Lough and Gonor (1973a, b) have critically examined the effects of temperature and salinity on bivalve larval life by multiple regression analyses and the fitting of response surfaces to survival, growth, and respiration of early and late stage larvae. The use and evaluation of this response surface technique in marine ecology has been reviewed in detail by Alderdice (1972). This technique not only facilitates the prediction of an organism's response to a wide range of untested conditions but also visually represents any change in its response at various stages of development. The experimental data from the above mentioned species have been critically analyzed by response surface techniques to reevaluate the combined effects of temperature and salinity on larval survival and growth. The results for *Crassostrea virginica, Mercenaria mercenaria*, and *Mulinia lateralis* are given in this paper.

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METHODS

The mathematical model used in the analyses was of the form:

$$Y = b_0 + b_1 (T) + b_2 (S) + b_3 (T^2) + b_4 (S^2) + b_5 (T \times S)$$

where Y = percentage survival or growth
b_0 = a constant
T = linear effect of temperature
S = linear effect of salinity
T^2 = quadratic effect of temperature
S^2 = quadratic effect of salinity
$T \times S$ = interaction effect between temperature and salinity

The coefficients in the model (b's) were estimated by a stepwise multiple regression computer program contained in the Oregon State University Statistical Program Library. F-levels were set equal to zero to enter and remove variables. This allowed all variables to come into the equation by a forward selection process, their order of insertion determined by using the partial correlation coefficient as a measure of their importance. The contribution a variable makes in reducing the variance of the equation can also be considered by looking at the various values given as the program proceeds. One of the more useful is the square of the multiple correlation

coefficient, R^2, defined as the sum of squares due to regression divided by the total sum of squares corrected for the mean. It is often stated as a percentage, $100R^2$. The larger R^2 is, the better the fitted equation explains the variation in the data. Values of R^2 can be compared at each stage of the regression program. A t-test also is made indicating the equality of the individual regression coefficients to zero and their level of significance.

The calculated regression coefficients from a particular equation were fitted by computer to a full quadratic equation in temperature and salinity in order to print a contour diagram of the response surface. The computer program was instructed to print 20% contour intervals, wide enough to exclude the approximate ±10% experimental error reported by the authors. Temperature and salinity scales on all plots were set to range from 0 to 40 in order to facilitate response comparison and to allow the overall form of the surface to be visualized. Contours extrapolated beyond the experimental data are given as dotted lines.

Analysis of covariance methods, as used in Lough and Gonor (1973a, b), were used to test the significance of the difference between the estimated polynomials for early and late larval survival and between late survival and growth.

RESULTS

Crassostrea virginica

Davis and Calabrese (1964) first reared the larvae for 2 days at six levels of temperature and nine levels of salinity to study the effect of these factors on early development, or the period from fertilization to approximately the veliger stage. To learn what effect these same combinations of temperature and salinity had on late larval development, larvae were initially reared from eggs for 2 days at normal seawater conditions (24.0°C, 27.5‰) and then transferred at the veliger stage to the experimental conditions.

Tables of the multiple regression analyses are given in the Appendix and will not be referred to in this section. Survival to 2 days of development was affected most by the linear and quadratic effects of salinity and the linear effect of temperature. Maximum survival of the 2-day-old larvae (80% survival contour) was estimated to occur at temperature and salinity conditions between 19° and 30.5°C and 19 and 30‰ (Figure 1), which is in good agreement with the experimental results.

The analysis of survival of 10-day-old larvae, after 8 days of rearing at experimental conditions, indicated that the linear and quadratic effects of temperature and the quadratic effect of salinity significantly affected survival. Maximum survival after 8 days (60% survival contour) was estimated to occur above 21°C and between 8 and 30.5‰ (Figure 2). The 10-day-old larvae showed a tolerance to much higher temperature and a wider salinity range than the 2-day-old larvae. Analysis of covariance showed a significant difference (1% level) between the 2- and 8-day survival polynomials further substantiating that the range of temperatures and salinities tolerated by the late veliger larvae were significantly different than that of the early embryos.

Growth of the larvae during 8 days was affected most by the interacting effect of temperature and salinity and the quadratic effect of salinity. Maximum growth (100% response contour) was estimated to occur at temperatures and salinities above 19°C and 33‰ (Figure 3).

There was a significant difference (1% level) between the polynomials estimated for 8-day

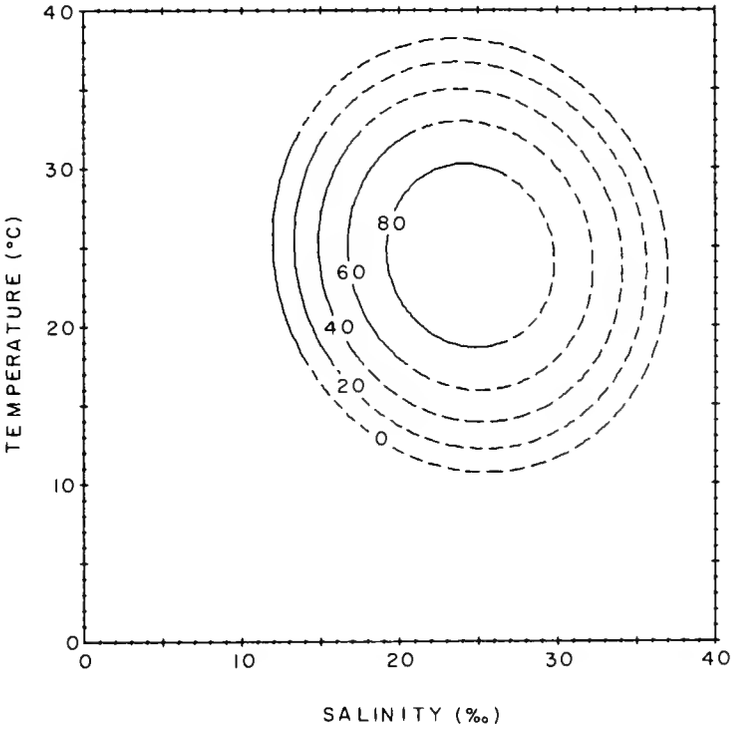

FIGURE 1.—Response surface estimation of percent survival of *Crassostrea virginica* larvae after 2 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

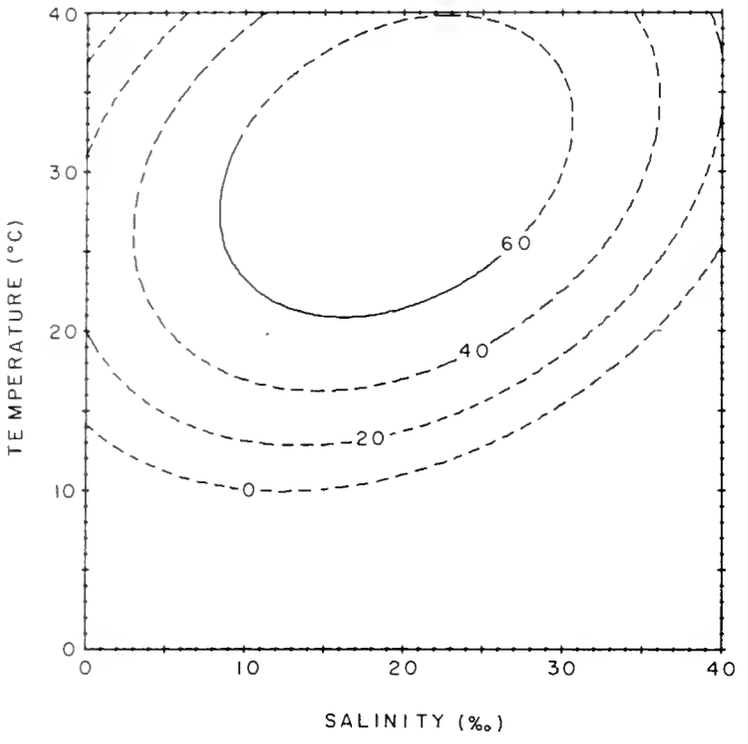

FIGURE 2.—Response surface estimation of percent survival of *Crassostrea virginica* veliger larvae after 8 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

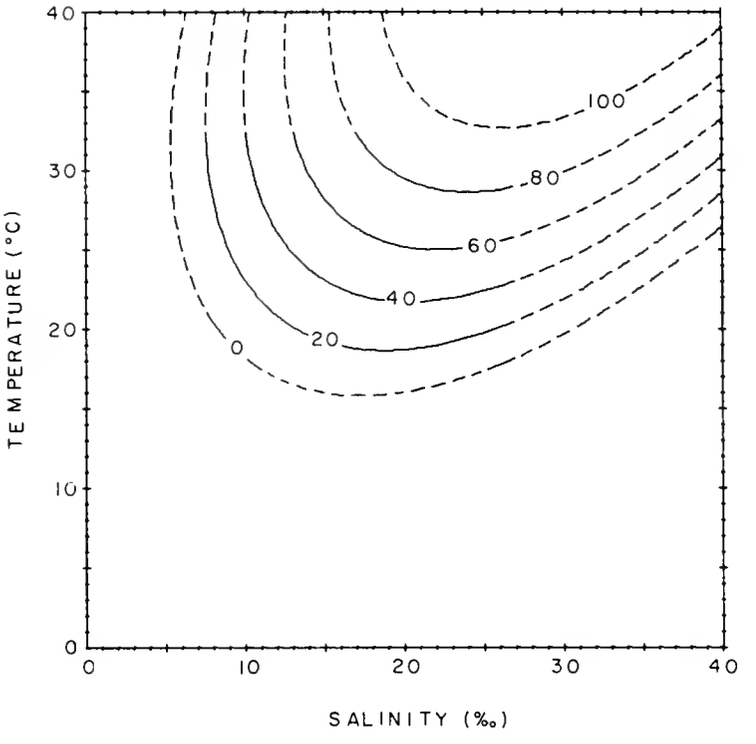

FIGURE 3.—Response surface estimation of percent growth of *Crassostrea virginica* veliger larvae after 8 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

survival and growth indicating a significantly higher salinity range is required for optimum growth than is required for optimum survival.

An analysis of combined 8-day-survival and growth data indicated that the linear effect of temperature, the interacting effect of temperature and salinity, and the quadratic effect of salinity were the more important factors explaining the data. Optimum (80% contour) temperature and salinity conditions for maximizing both larval survival and growth was estimated at above 30°C and between 18 and 35‰.

Mercenaria mercenaria

The same experimental design with the exception of nine levels of temperature and six levels of salinity was used by Davis and Calabrese (1964) to study the larval tolerance of this species.

Survival to 2 days of development, or from fertilization to veliger stage larvae, was affected most by the quadratic effects of salinity and temperature, and the interacting effect of temperature and salinity. The response surface for 2-day-old larvae clearly shows the skewed contours resulting from the interaction effect (Figure 4). Maximum survival to 2 days of development (100% survival contour) was estimated to occur at temperatures and salinities above 7.2°C and 28‰. Their experimental data show maximum survival between 17.5° and 30°C at a salinity of 27‰.

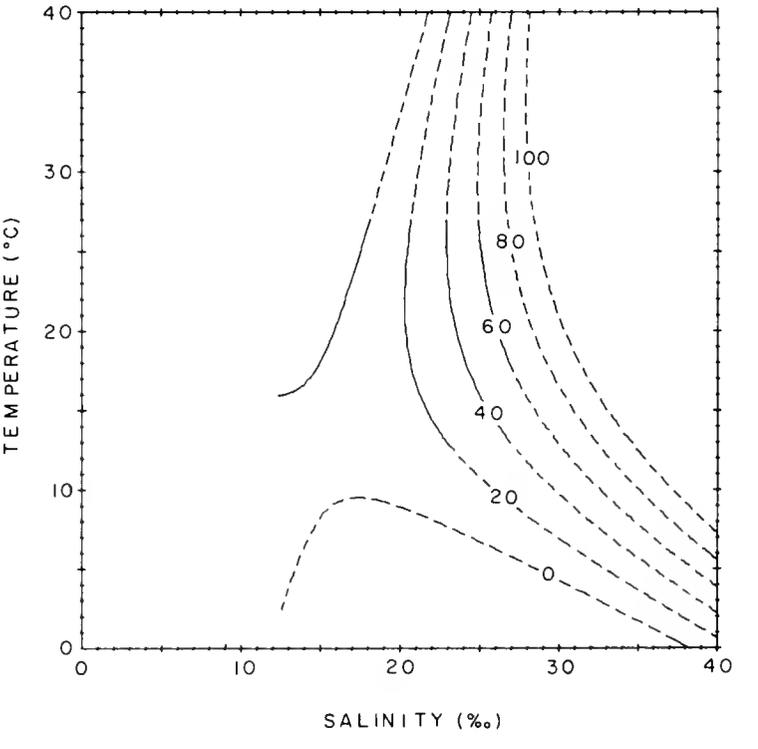

FIGURE 4.—Response surface estimation of percent survival of *Mercenaria mercenaria* larvae after 2 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

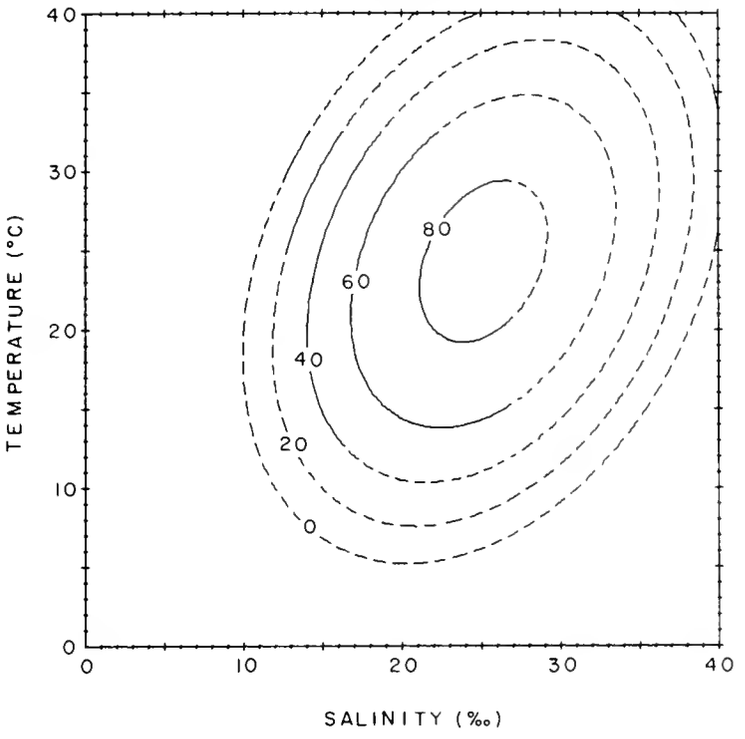

FIGURE 5.—Response surface estimation of percent survival of *Mercenaria mercenaria* veliger larvae after 10 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

Late larval survival after 10 days of rearing at the experimental conditions indicated that the linear and quadratic effects of salinity and the interacting effect of temperature and salinity were the more important factors affecting survival. Maximum survival of these 12-day-old larvae (80% survival contour) was estimated to occur between temperatures and salinities of 19° and 29.5°C and 21 and 29‰ (Figure 5). Although the late larvae had a much narrower temperature tolerance than the developing embryos, the late larvae showed a significantly greater tolerance to low salinity. This difference in tolerance of these two life stages was further substantiated by the fact that there was a significant difference (1% level) between the 2- and 10-day survival polynomials.

Growth of the larvae during the 10-day experimental period was most affected by the interacting effect of temperature and salinity and by the linear and quadratic effects of temperature, and the linear effect of salinity. Maximum growth (80% contour) was estimated to occur at temperatures and salinities between 22.5° and 36.5°C and 21.5 and 30‰ (Figure 6). There was a significant difference (1% level) between the polynomials estimated for 10-day survival and growth indicating that the higher temperatures and salinities required for optimum growth are significantly different than those conditions estimated for optimum survival. Larval survival and growth estimated by these techniques above the experimental temperature and salinity of 32.5°C and 27.0‰ are questionable. Higher temperature and salinity levels need to be added to the experimental design to more carefully define the response surface.

The combined 10-day survival and growth analysis indicated that they were affected by all of the variables of temperature and salinity, but by salinity more than by temperature. Optimum temperature and salinity conditions (80% contour) for maximizing both larval survival and growth to 12 days was estimated at 21.5° to 33°C and 22 to 31‰.

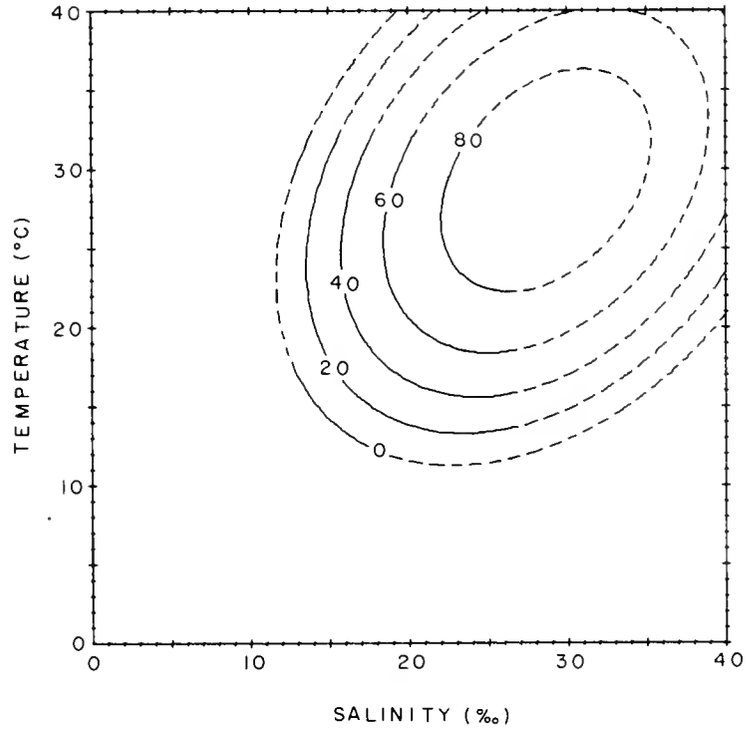

FIGURE 6.—Response surface estimation of percent growth of *Mercenaria mercenaria* veliger larvae after 10 days of development at experimental temperature and salinity combinations given in Davis and Calabrese (1964).

Mulinia lateralis

Six levels each of temperature and salinity were used to investigate the tolerances of early and late development of this species by Calabrese (1969) in the same manner as used for the other species.

Survival of the early embryos for 2 days under the experimental conditions was affected by all the variables except the interacting effect of

temperature and salinity. Maximum survival of the 2-day-old larvae (80% contour) was estimated to occur at temperatures between 18.5° and 24.5°C and salinities between 22 and 28.5‰ (Figure 7).

The analysis of survival after 6 to 8 days of rearing beyond the veliger stage indicated that the linear and quadratic effects of temperature and the interacting effect of temperature and salinity were the more important variables affecting survival. Response surface estimation predicted 80% survival at temperatures between 8.5° and 26.5°C and salinities above 12‰ (Figure 8). A significant difference (1% level) was calculated by the analysis of covariance for the 2- and 6- to 8-day survival polynomials. The veliger larvae showed a much greater tolerance to low temperatures and a wider range of salinities than the early embryos.

Growth of the veliger larvae was most affected by the interacting effect of temperature and salinity, the quadratic effect of salinity, and the linear effect of temperature. Maximum growth (60% contour) was estimated to occur at temperatures between 18° and 38°C and salinities above 16.5‰ (Figure 9). The axis of the growth contours are observed to lie diagonal to the factor axes showing the effect of the temperature-salinity interaction. There was a significant (1% level) difference between the polynomials estimated for the 6- to 8-day survival and growth indicating that the higher temperatures required

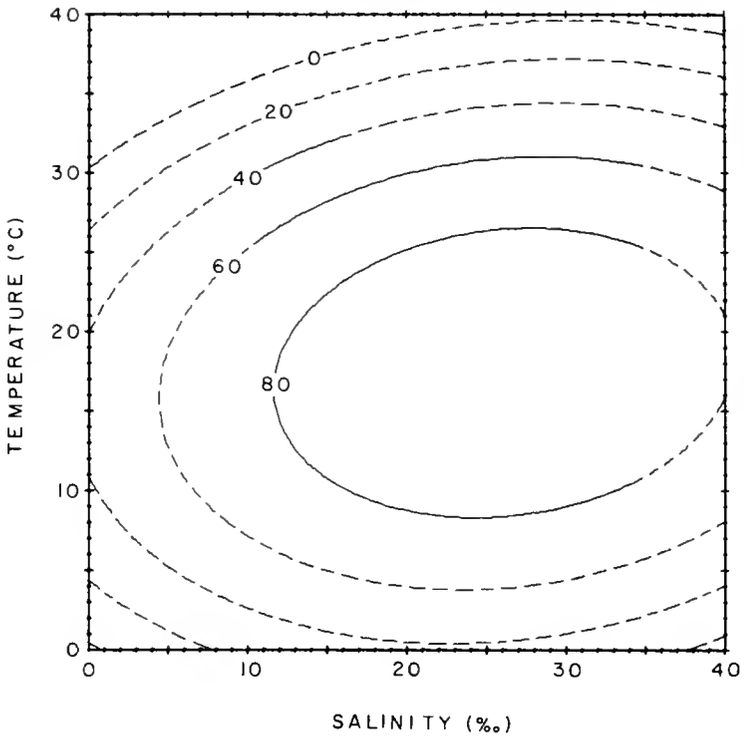

FIGURE 8.—Response surface estimation of percent survival of *Mulinia lateralis* veliger larvae after 6 to 8 days of development at experimental temperature and salinity combinations given in Calabrese (1969).

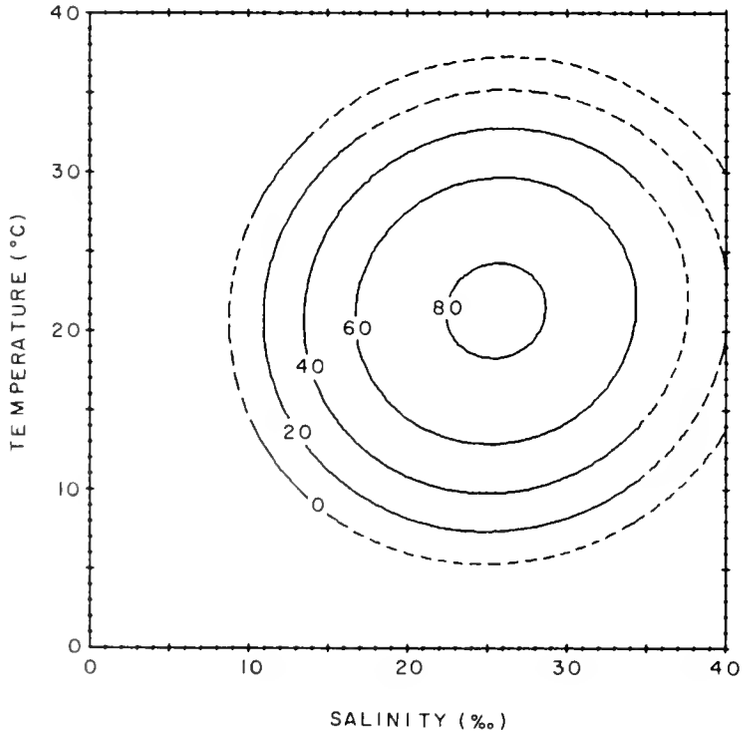

FIGURE 7.—Response surface estimation of percent survival of *Mulinia lateralis* larvae after 2 days of development at experimental temperature and salinity combinations given in Calabrese (1969).

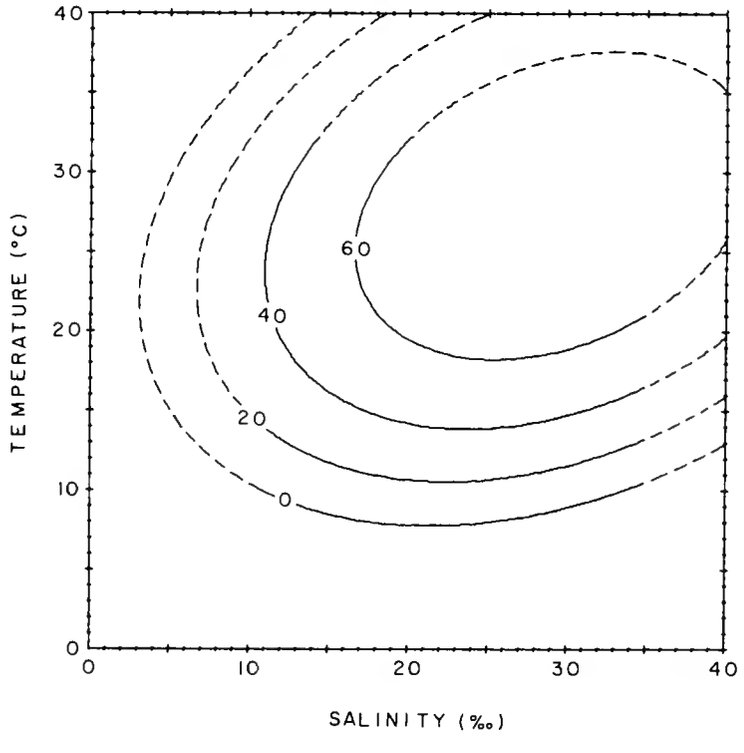

FIGURE 9.—Response surface estimation of percent growth of *Mulinia lateralis* veliger larvae after 6 to 8 days of development at experimental temperature and salinity combinations given in Calabrese (1969).

for optimum growth were significantly different than those required for optimum survival.

Analysis of the combined 6- to 8-day survival and growth indicated that the interacting effect of temperature and salinity and the linear effect of temperature were the more important variables explaining the data, although only 30.4% of the variance was explained by the combined polynomial. Optimum temperature and salinity conditions (80% contour) for maximizing both larval survival and growth to 8 to 10 days of age were predicted between 20° and 26°C and 23 and 32‰.

DISCUSSION

Despite the fact that the adults of the three species studied are euryhaline to varying degrees, their early embryos and larvae have a comparatively narrow salinity range. Early larvae of *Mercenaria mercenaria* appear to be much more tolerant to high temperatures than the other two species, but require essentially oceanic salinities.

The older larvae, having been reared from fertilization to the veliger stage at optimum conditions, now appear to have a generally greater tolerance to both temperature and salinity. The late larvae of *C. virginica* appear to tolerate a higher temperature range than the early larvae while *Mulinia lateralis* late larvae seem to tolerate best temperatures at the lower end of its range. Late larvae of *Mercenaria mercenaria* are able to tolerate low salinities somewhat better than the early larvae, but their temperature range is quite restricted. The observed progressive change in their temperature-salinity tolerance with time approaches the range normally tolerated by the adults. This same progressive change was observed for the larvae of *Adula californiensis* by Lough and Gonor (1973a, b).

The range of temperature-salinity conditions estimated for maximum growth was significantly different from that estimated for maximum survival of the same late stage larvae. Maximum predicted growth occurred at higher temperatures and at somewhat higher salinities than those for maximum survival for all three species studied. All three species showed a significant temperature-salinity interaction effect for growth. Growth, classically, is positively correlated with temperature up to some limit; however, the role of salinity appears to complicate the temperature effect.

The combining of late larval survival and growth to maximize both responses seems intuitively pleasing as one would expect a compromise situation in nature. An organism probably can operate most effectively when it is in a set of environmental conditions which maximize all its biological responses. It has been shown by Lough and Gonor (1973a, b) that temperatures for maximum growth response may be an abnormal stress environment which ultimately results in high mortality. Similarly, low temperatures may be suitable for larval survival but not necessarily highly productive for recruitment and growth to the adult population. Although the optimum temperatures and salinities usually can be estimated from the raw data, the statistical techniques used in this study allow one to define and interpret an organism's response to a matrix of environmental factors and to determine whether the response(s) between stages of development or sampling intervals is significantly different.

INFERENCES

Tolerance studies of various stages or at various times in the life history of an organism are especially important to pollution studies. Different stages of crab larvae have been shown to have different temperature-salinity tolerances of ecological significance (Costlow et al. 1960, 1962, 1966). This study demonstrates that different periods in the life of bivalve larvae also differ in their tolerance to temperature and salinity. The determination of water quality standards based on only one stage in the life of an organism is not realistic. All stages of development are important, particularly when the synergistic effect of a pollutant is studied. Davis and Hidu (1969) found it was necessary to evaluate the effects of pesticides on all stages of clam and oyster larvae as their tolerances are markedly different.

The field of aquaculture also may benefit from these tolerance studies. Based on this study a long-term experimental program should be undertaken to maximize both survival and growth recognizing that different stages of an organism may have different optimum conditions. Possibly,

larvae should be reared at one set of conditions from fertilization to veliger stage and then transferred to another set of conditions for the late stages. Juvenile clams may have yet another set of optimum conditions different than those of the late larval stage. The larvae and the adults are two distinct morphological and physiological organisms and occupy distinctly different ecological environments.

Recent work by Costlow and Bookhout (1971) on the cyclic effect of temperatures on the larval development of an estuarine mud crab, *Rhithropanopeus harrisii*, emphasizes the need for more research on the fluctuating environmental variables that normally occur in nature. The possible stimulating or inhibiting effect of fluctuating temperatures on bivalve larval survival and growth in relation to both pollution and aquaculture should be investigated in the future.

ACKNOWLEDGMENT

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APPENDIX

APPENDIX TABLE 1.—Multiple regression analyses of *Crassostrea virginica* larvae.

Step number	Variable	R^2	F-level	df	Level of significance	Coefficient	T-value	Level of significance
				2-day survival				
1	S	0.661	77.857	(1,40)	1%	32.8617	8.007	1%
2	S^2	.793	24.818	(2,39)	1%	−0.6234	6.706	1%
3	T^2	.795	.356	(3,38)	N.S.	−0.5195	5.715	1%
4	T	.889	31.397	(4,37)	1%	27.7755	5.821	1%
5	$T \times S$	.894	1.875	(5,36)	N.S.	−0.0971	1.369	N.S.
	Constant					−643.9149		
				8-day survival				
1	T	0.426	38.600	(1,52)	1%	10.221	2.992	1%
2	T^2	.493	6.781	(2,51)	1%	−0.2006	3.008	1%
3	$T \times S$	.501	.778	(3,50)	N.S.	0.0996	2.492	5%
4	S^2	.625	1.612	(4,49)	N.S.	−0.1455	3.687	1%
5	S	.643	2.430	(5,48)	N.S.	2.6621	1.559	N.S.
	Constant					−104.389		
				8-day growth				
1	$T \times S$	0.642	93.200	(1,52)	1%	0.2450	6.645	1%
2	S^2	.907	144.539	(2,51)	1%	−0.2329	6.401	1%
3	S	.918	7.139	(3,50)	1%	4.1512	2.636	5%
4	T	.919	.317	(4,49)	N.S.	7.5246	2.389	5%
5	T^2	.927	5.365	(5,48)	1%	−0.1425	2.316	5%
	Constant					−152.2672		
				8-day survival and growth				
1	T	0.431	80.437	(1,106)	1%	8.8727	2 182	5%
2	$T \times S$	.528	21.559	(2,105)	1%	0.1723	3.620	1%
3	S^2	.602	19.110	(3,104)	1%	−0.1892	4.028	1%
4	T^2	.619	4.587	(4,103)	1%	−0.1715	2.160	5%
5	S	.629	2.807	(5,102)	5%	3.4066	1.676	N.S.
	Constant					−128.3283		

APPENDIX TABLE 2.—Multiple regression analyses of *Mercenaria mercenaria* larvae.

Step number	Variable	R^2	F-level	df	Level of significance	Coefficient	t-value	Level of significance
				2-day survival				
1	S^2	0.561	43.513	(1,34)	1%	0.2439	0.611	N.S.
2	$T \times S$	.581	1.555	(2,33)	N.S.	0.3947	2.345	5%
3	T^2	.640	5.223	(3,32)	1%	−0.1219	2.039	N.S.
4	T	.648	.678	(4,31)	N.S.	−2.7229	0.819	N.S.
5	S	.653	.449	(5,30)	N.S.	−12.2188	0.670	N.S.
	Constant					110.3864		
				10-day survival				
1	S	0.488	49.560	(1,52)	1%	15.6884	4.021	1%
2	S^2	.594	13.307	(2,51)	1%	−0.4142	4.570	1%
3	T^2	.609	1.894	(3,50)	N.S.	−0.2630	4.916	1%
4	$T \times S$	.732	22.546	(4,49)	1%	0.2111	3.295	1%
5	T	.769	7.591	(5,48)	1%	7.4766	2.755	1%
	Constant					−201.8315		
				10-day growth				
1	$T \times S$	0.631	88.900	(1,52)	1%	0.2438	4.532	1%
2	T^2	.739	21.109	(2,51)	1%	−0.3305	7.262	1%
3	T	.829	26.270	(3,50)	1%	12.3631	5.363	1%
4	S^2	.841	3.706	(4,49)	5%	−0.3702	4.835	1%
5	S	.885	18.518	(5,48)	1%	14.0885	4.303	1%
	Constant					−288.6339		
				10-day survival and growth				
1	S	0.463	91.215	(1,106)	1%	14.5902	4.532	1%
2	S^2	.535	16.411	(2,105)	1%	−0.3876	5.164	1%
3	$T \times S$	.590	13.881	(3,104)	1%	0.2316	4.378	1%
4	T^2	.685	31.236	(4,103)	1%	−0.2987	6.719	1%
5	T	.736	19.522	(5,102)	1%	9.9556	4.418	1%
	Constant					−243.0117		

APPENDIX TABLE 3.—Multiple regression analyses of *Mulinia lateralis* larvae.

Step number	Variable	R^2	F-level	df	Level of significance	Coefficient	t-value	Level of significance
				2-day survival				
1	S	0.156	6.269	(1,34)	5%	14.4237	4.949	1%
2	S^2	.390	12.705	(2,33)	1%	−0.2942	4.916	1%
3	$T \times S$	.421	1.708	(3,32)	N.S.	0.0284	0.554	N.S.
4	T^2	.478	3.359	(4,31)	5%	−0.3256	5.440	1%
5	T	.709	23.769	(5,30)	1%	13.1265	4.875	1%
	Constant					−240.8807		
				6- to 8-day survival				
1	T^2	0.353	18.540	(1,34)	1%	−0.1976	7.190	1%
2	T	.627	24.193	(2,33)	1%	6.0749	4.914	1%
3	$T \times S$	.716	10.002	(3,32)	1%	0.0307	1.305	N.S.
4	S^2	.724	.898	(4,31)	N.S.	−0.0781	2.843	1%
5	S	.760	7.013	(5,30)	1%	3.5437	2.648	5%
	Constant					−2.8961		
				6- to 8-day growth				
1	$T \times S$	0.498	33.698	(1,34)	1%	0.0993	2.646	5%
2	S^2	.605	8.979	(2,33)	1%	−0.1258	2.867	1%
3	T^2	.641	3.220	(3,32)	5%	−0.2120	4.833	1%
4	T	.765	16.222	(4,31)	1%	8.9352	4.528	1%
5	S	.796	4.584	(5,30)	1%	4.5735	2.141	5%
	Constant					−113.4013		
				6- to 8-day survival and growth				
1	$T \times S$	0.102	7.963	(1,70)	1%	0.0650	1.438	N.S.
2	T^2	.120	1.408	(2,69)	N.S.	−0.2048	3.876	1%
3	T	.262	13.046	(3,68)	1%	7.5051	2.377	1%
4	S^2	.278	1.491	(4,67)	N.S.	−0.1020	1.930	N.S.
5	S	.304	2.489	(5,66)	5%	4.0586	1.578	N.S.
	Constant					−58.1487		

SWIM-BLADDER STATE AND STRUCTURE IN RELATION TO BEHAVIOR AND MODE OF LIFE IN STROMATEOID FISHES

MICHAEL H. HORN[1]

ABSTRACT

Fourteen of the 15 genera of stromateoid fishes possess a relatively small (0.6-3.4% of body volume), euphysoclistous swim bladder which forms early in life (3-5 mm standard length) and regresses in all genera except possibly *Nomeus* before maturity (150-200 mm standard length) is reached. The organ is thus an almost exclusive characteristic of the juveniles which occupy surface layers (upper 100-150 m) in coastal and oceanic waters.

The gas gland of the swim bladder consists of cuboidal to irregularly shaped cells 6-46 μm in greatest dimension. The retia mirabilia range in length from 0.4 to 2.0 mm and in diameter of individual capillaries from 4 to 10 μm. The area of the gas gland and the length of the retia relative to the size of the swim-bladder lumen are great compared to the same in other epipelagic fishes and are similar to those of deeper living, mesopelagic fishes. The relatively large gas-secreting complex is considered to be an adaptation for rapid and efficient gas secretion in maintaining hydrostatic equilibrium as the juvenile fishes swim in the surface layers, frequently in association with floating objects, where pressure changes are greatest with depth.

Swim-bladder loss accompanies changes in behavior and mode of life and is part of the transition from the juvenile to the adult stage of life. Hovering and high maneuverability as principal components of locomotor behavior in juveniles give way to continuous swimming in adults which are generally independent of floating objects and occupy a greater depth range. The relative length of the paired fins changes with age and varies among the species. *Peprilus triacanthus* and *P. simillimus*, negatively buoyant, active swimmers, have long pectoral fins as adults whereas *Schedophilus medusophagus*, a neutrally or nearly neutrally buoyant, slow-moving fish, has short pectoral fins. Both *P. simillimus* and *S. medusophagus* have high levels of lipid which may serve to replace the swim bladder in a buoyancy function when the fishes are adults.

The swim bladder (or gas bladder), a gas-filled organ unique to bony fishes, has its greatest functional significance as a hydrostatic device, i.e., one that provides neutral or nearly neutral buoyancy to the fish. It is one of the most plastic of vertebrate organs (Marshall 1960) and occurs in a great diversity of fishes from a variety of habitats. The swim bladder is not necessary for life as it is absent in many fishes, but according to Fänge (1966) about one-half of the 20,000 existing species have it as adults and even more as larvae or juveniles. The organ, owing to its diversity of form and widespread occurrence, should reflect in its presence or absence and structure the behavior and mode of life of the fishes possessing it. In stromateoid fishes, the swim bladder regresses in 13, possibly 14, of the 15 genera, and the regression seems to be associated with other morphological changes and changes in mode of life (Horn 1970a).

The swim bladder of stromateoid fishes has received little mention in the literature partly due to its absence or reduced state in adults. Goode and Bean (1895) and Jordan and Evermann (1896) stated that the organ was "usually absent" in the Stromateidae, and the former as well as Grey (1955) reported its absence in the Tetragonuridae. Fowler (1936) in his treatment of several stromateoid genera indicated that the swim bladder was "present or absent." Goode and Bean (1895) stated that it was present in *Nomeus* as did Haedrich (1967) for *Ariomma*. Based upon an examination of approximately one-half of the species in the group, I have found the organ to be present at some stage (larval and/or juvenile) in the life of all stromateoid genera except *Pampus*. Even in *Pampus* it may be present at an early stage since larvae or small juveniles (< 20 mm SL, standard length) were not studied.

The perciform suborder Stromateoidei consists of 6 families, 15 genera, and about 60 species (Haedrich and Horn 1972) and is characterized by toothed saccular outgrowths in the gullet and by

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small teeth approximately unilateral in the jaws (Haedrich 1967). The larvae and juveniles occur mainly in the surface layers of the ocean and are frequently associated with animate or inanimate floating objects. The adults, ranging in maximum size from about 30 to 120 cm, form a diverse group of temperate and tropical species which variously occupy a wide range of depths in coastal and oceanic waters (including mesopelagic and bathypelagic levels). The Centrolophidae (six genera) are either coastal or oceanic, the Stromateidae (three genera) are coastal, the Amarsipidae (one genus), Nomeidae (three genera), and Tetragonuridae (one genus) are oceanic, and the Ariommidae (one genus) are benthopelagic on the continental shelf and slope.

The purposes of the present paper are to 1) describe the morphology and histology of the stromateoid swim bladder, 2) compare the dimensions and capabilities of the stromateoid swim bladder with that of other fishes of similar and different habitats, and 3) discuss the relationship of swim-bladder state and structure to the behavior and mode of life of stromateoids based upon the results of the present and other studies.

MATERIALS AND METHODS

The majority of specimens examined (Table 1) for swim-bladder structure and other morphological detail were preserved although fresh or frozen material of several species was studied. Observations on the behavior of certain species were made and are briefly described in appropriate sections of the paper.

Specimens in addition to those personally collected were obtained from the following institutions: British Museum (Natural History), London; Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; Institute of Oceanographic Sciences, Wormley, England; Natural History Museum of Los Angeles County, Los Angeles, Calif.; Scripps Institution of Oceanography, La Jolla, Calif.; Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla; Woods Hole Oceanographic Institution, Woods Hole, Mass.; and Zoological Museum, Copenhagen, Denmark.

Swim-bladder dimensions were measured with an ocular micrometer in either a dissecting or compound microscope or, in large specimens, with dial calipers. Swim-bladder and body volumes were determined by displacement and/or, for the former, calculated on the assumption that the bladder was a prolate spheroid ($v = 4/3\pi ab^2$, where a and b are the major and minor semiaxes (see Capen 1967)). Volume measurements were made from swim bladders that were in most cases well expanded. Ten percent was allowed for shrinkage of preserved material.

Transverse or longitudinal serial sections of the swim bladder of 13 genera and species were cut at 8-μm thickness and stained with haemalum and eosin.

Buoyancy determinations were made by weighing each fish in air and in water of known temperature and salinity. Results are expressed as the percentage of the air weight that each fish weighed in seawater.

TABLE 1.—Stromateoid specimens examined for swim bladder and other morphological characteristics.

Family and species	Number of specimens	Size range (mm SL)
Centrolophidae:		
Hyperoglyphe antarctica	4	23.4- 34.9
Hyperoglyphe perciformis	2	35.8, 47.7
Schedophilus huttoni	1	22.9
Schedophilus maculatus	2	70.2, 77.5
Schedophilus medusophagus	7	10.4-285.0
Centrolophus maoricus	3	15.1-127.8
Centrolophus niger	2	124.0, 231.0
Icichthys lockingtoni	20	3.5-268.0
Seriolella punctata	2	132.0, 162.6
Seriolella violacea	3	12.8- 84.0
Psenopsis cyanea	2	94.2, 104.2
Stromateidae:		
Stromateus brasiliensis	7	75.7-167.3
Stromateus fiatola	9	12.5- 93.5
Stromateus stellatus	5	17.5- 99.4
Peprilus burti	3	57.4- 95.1
Peprilus paru	10	28.6-123.0
Peprilus simillimus	17	2.0-135.0
Peprilus triacanthus	10	12.0-120.4
Pampus argenteus	7	24.6- 49.0
Pampus chinensis	6	25.4- 67.3
Amarsipidae:		
Amarsipus carlsbergi	3	22.0- 67.5
Nomeidae:		
Cubiceps caeruleus	1	18.5
Cubiceps carinatus	1	8.5
Cubiceps gracilis	10	16.5-330.0
Nomeus gronovii	13	11.6-142.7
Psenes arafurensis	2	17.0, 18.0
Psenes cyanophrys	17	9.1-120.0
Psenes maculatus	1	33.6
Psenes pellucidus	2	26.9, 34.8
Unidentified (probably *Psenes*)	5	3.4- 12.3
Tetragonuridae:		
Tetragonurus cuvieri	13	4.0-242.0
Ariommidae:		
Ariomma bondi	7	20.9-124.3
Ariomma indica	1	59.7
Ariomma melanum	2	each 134.1
Ariomma regulus	3	123.3-150.0
Ariomma sp. (either *A. bondi* or *A. melanum*)	1	16.5
Total number of specimens	204	

RESULTS

Swim-Bladder Structure

The stromateoid swim bladder is of the physoclistous, two-chambered type usually found in perciform fishes (Horn 1970a) (Figure 1). The delicate, thin-walled sac lies in the upper part of the body cavity above the gut and below the kidney and is closely invested by the dorsal peritoneum. A muscular diaphragm (not always visible) divides the bladder into anterior and posterior chambers (Figures 1, 2), the latter of which serves a gas-resorbing function (a euphysoclistous condition). The gas gland, associated with the anterior chamber, typically forms a U-shape and may be single or divided into two or more lobes (Figure 1). Cells composing the gland are cuboidal to irregular in shape and usually in two or more layers (Figures 2-5). Some cells appear to be either syncytial or of the giant type found widely distributed in marine euphysoclists (Fänge 1953) and in some deep-sea fishes (Marshall 1960). The retia mirabilia are unipolar,

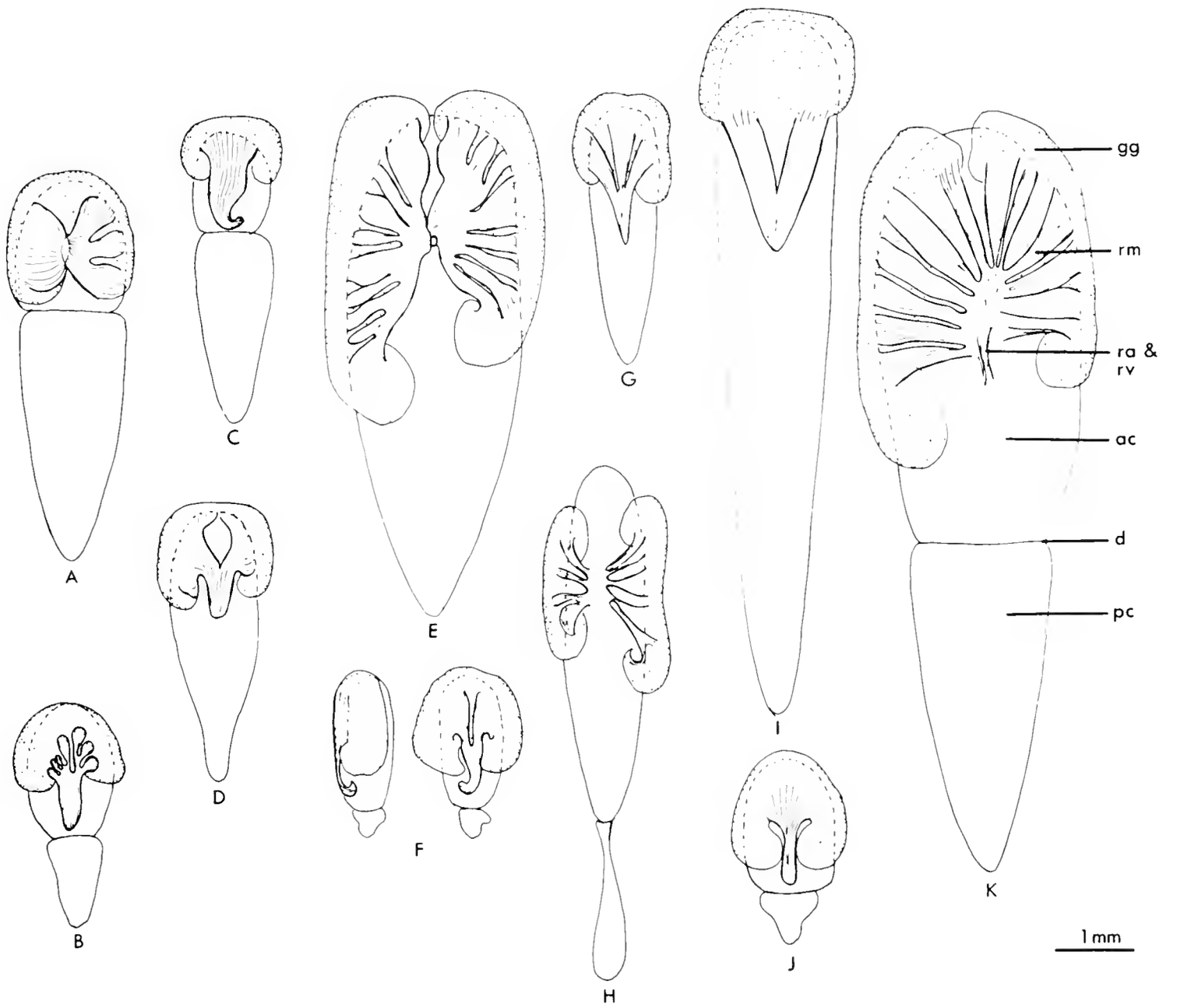

FIGURE 1.—Ventral view of the swim bladder of 11 species of stromateoids (all drawn to same scale). **gg**, gas gland (slightly flattened and expanded); **rm**, rete mirabile; **ra** and **rv**, retial artery and retial vein; **ac**, anterior chamber; **d**, diaphragm; **pc**, posterior chamber. **A**, *Ariomma bondi*, 24.2 mm SL; **B**, *Centrolophus maoricus*, 15.1 mm SL; **C**, *Tetragonurus cuvieri*, 28.8 mm SL; **D**, *Seriolella violacea*, 12.8 mm SL; **E**,*Cubiceps gracilis*, 30.5 mm SL; **F**, *Schedophilus medusophagus*, 17.4 mm SL (lateral and ventral view); **G**, *Psenes cyanophrys*, 11.5 mm SL; **H**, *Nomeus gronovii*, 26.4 mm SL; **I**, *Stromateus fiatola*, 34.1 mm SL; **J**, *Icichthys lockingtoni*, 16.3 mm SL; **K**, *Hyperoglyphe antarctica*, 34.9 mm SL.

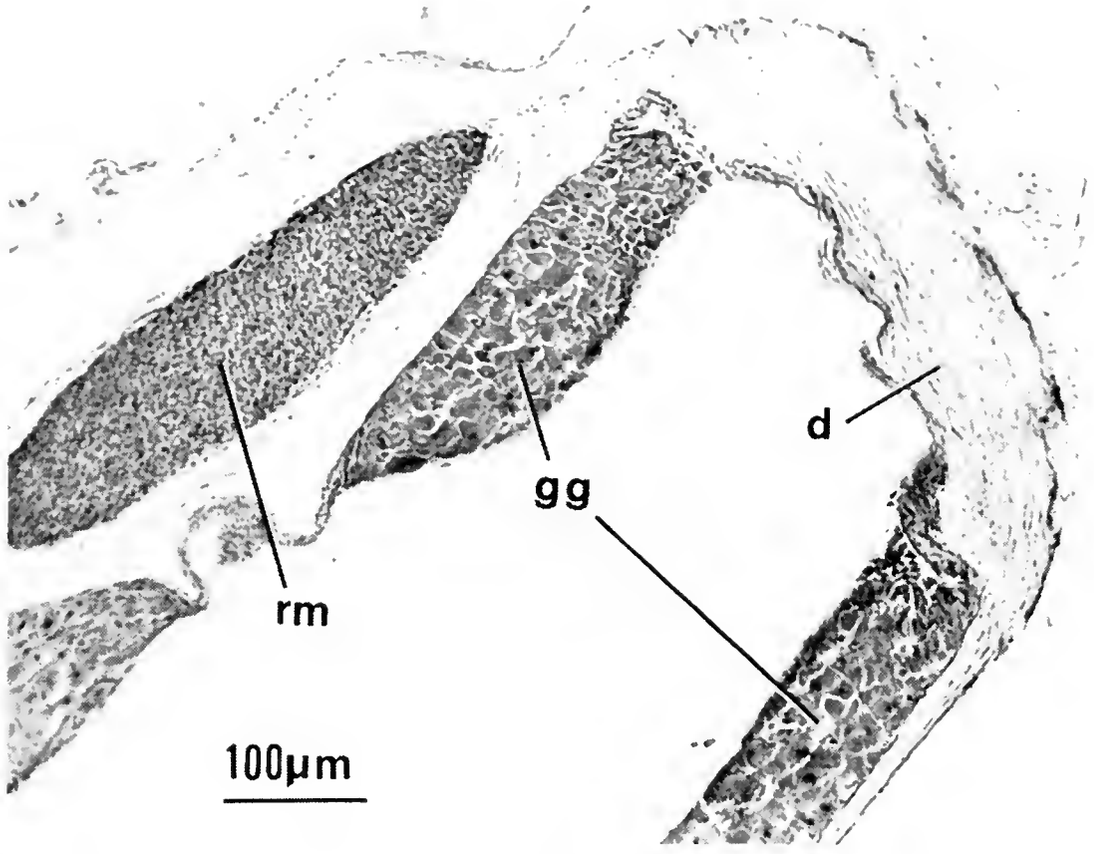

FIGURE 2.—Sagittal section of the anterior chamber of the swim bladder of *Ariomma bondi*. d, diaphragm; gg, gas gland; rm, rete mirabile. (From same specimen as Figure 1A.)

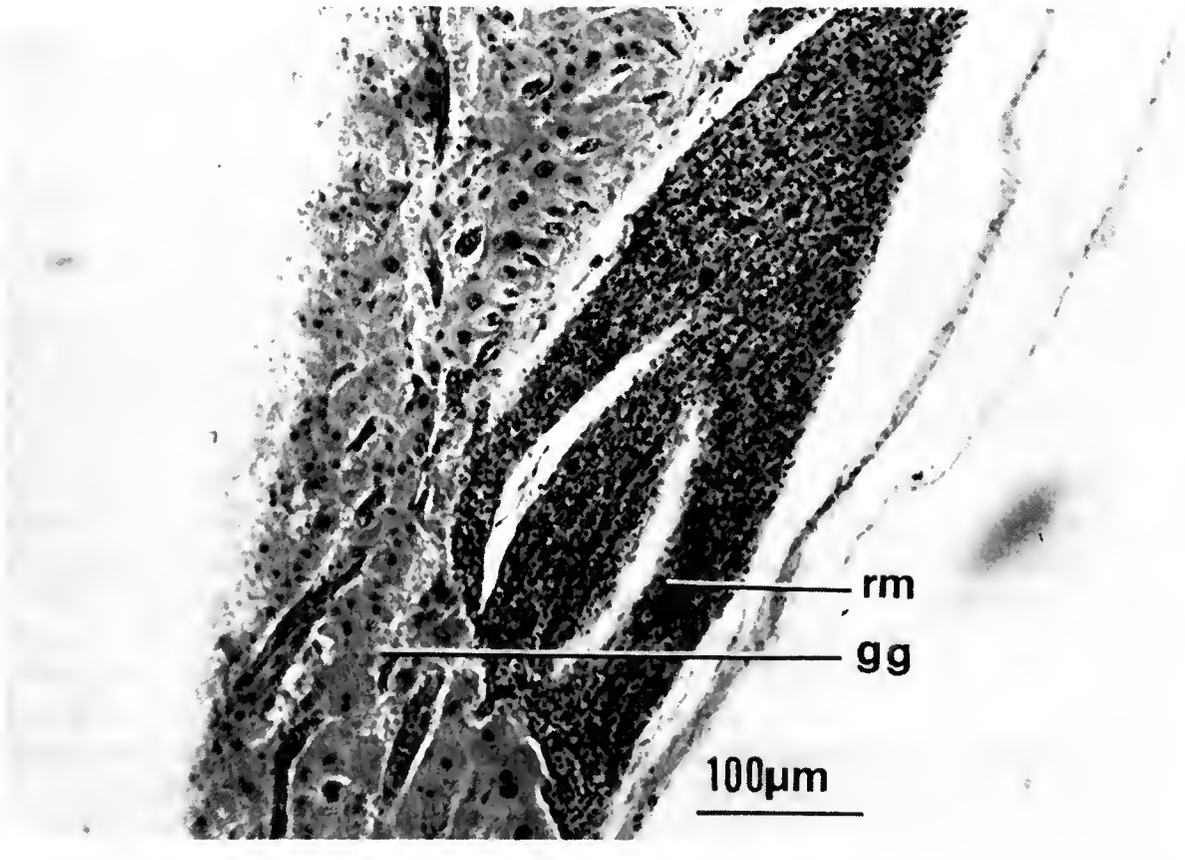

FIGURE 3.—Sagittal section of the gas secreting complex of the swim bladder of *Cubiceps gracilis*. gg, gas gland; rm, rete mirabile. (From same specimen as Figure 1B.)

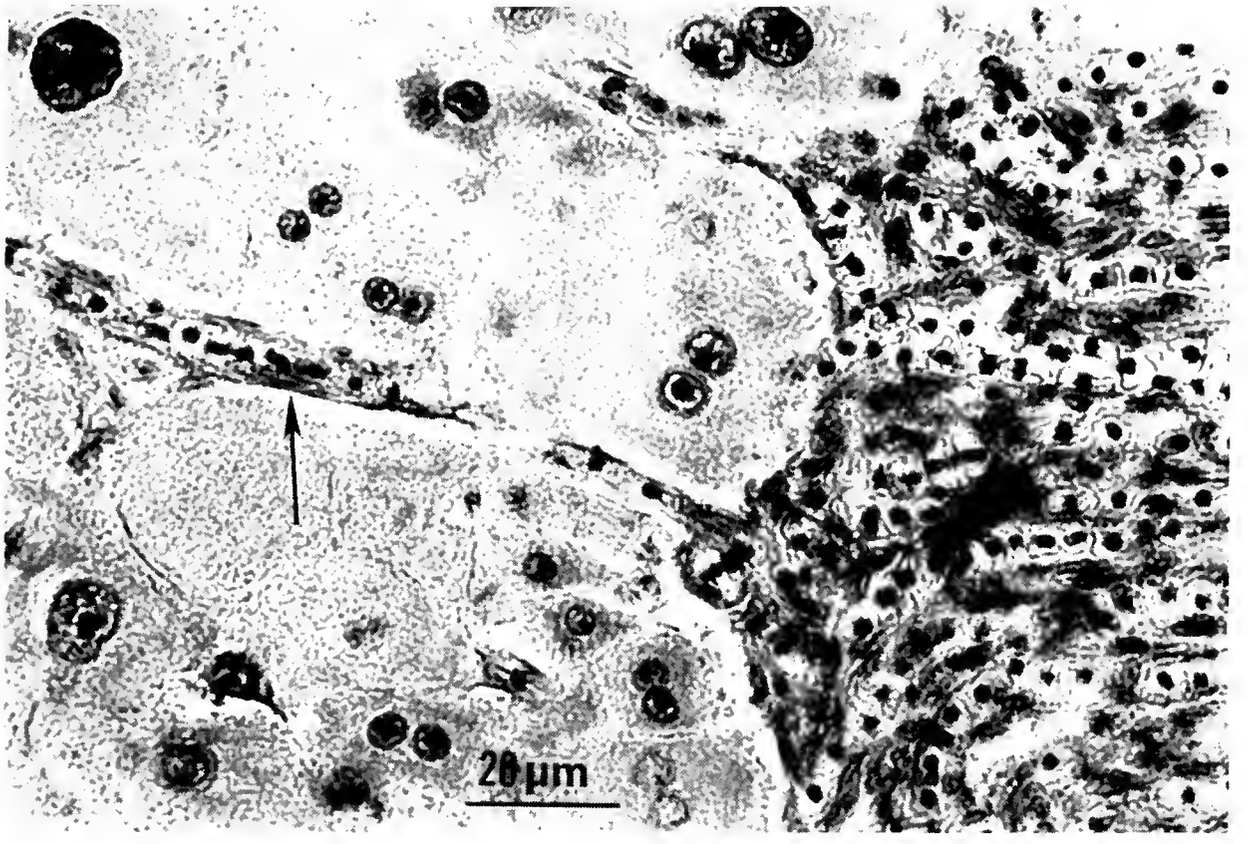

FIGURE 4.—Gas gland cells and retial capillaries of the swimbladder of *Cubiceps gracilis*. Arrow points to retial capillary between gas gland cells. (From same specimen as Figures 1E and 3.)

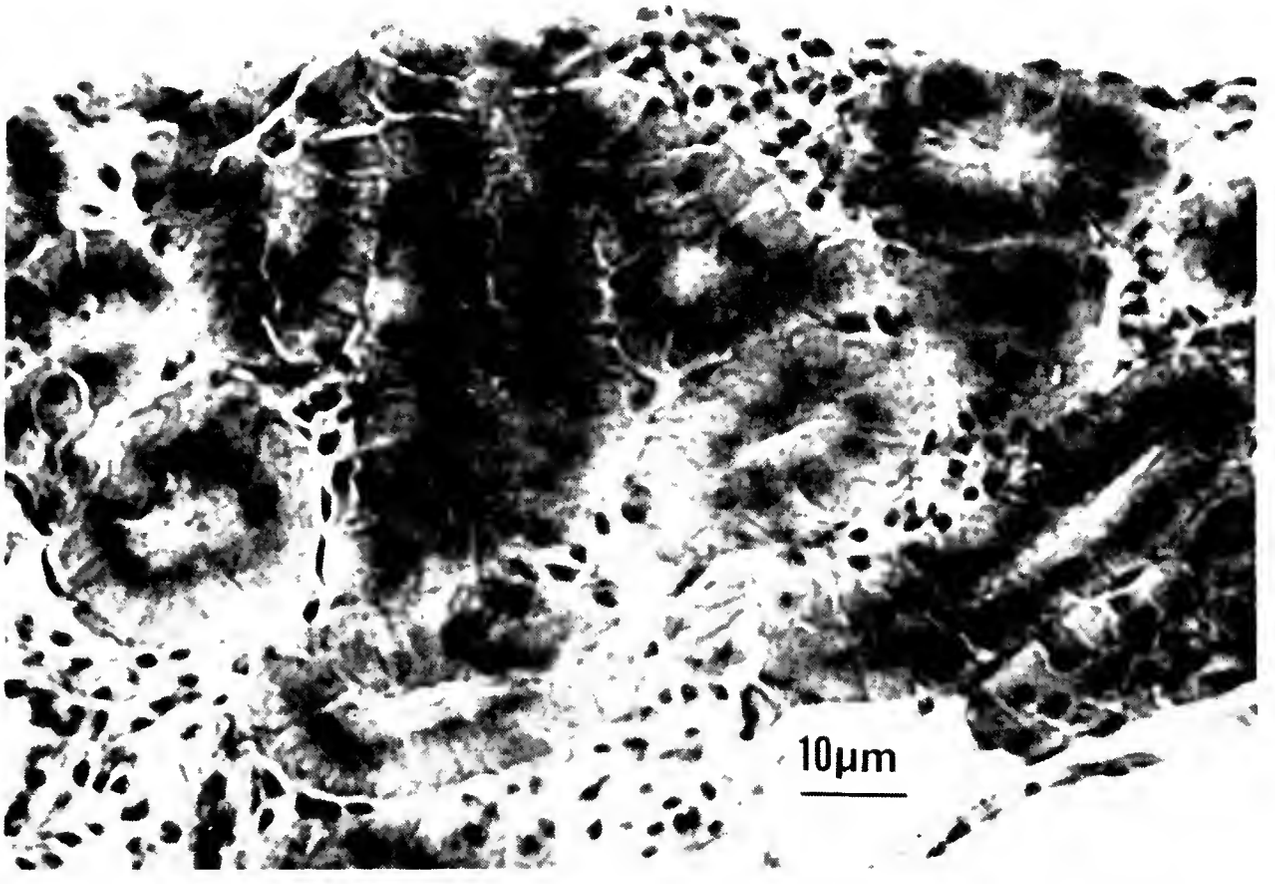

FIGURE 5.—Gas gland of *Peprilus triacanthus*, 16.5 mm SL, showing arrangement of cells. (Transverse section.)

i.e., the artery and vein subdivide to form parallel capillaries which enter the gas gland (Figures 3, 4, 6). Retial orientation varies from a position parallel to the long axis of the swim bladder to one that is perpendicular (Figure 1). Size characteristics of swim-bladder components are given in Table 2. Distinctive features of the swim bladder of the six stromateoid families are described below.

Centrolophidae

Swim-bladder volume in the fishes examined varied from less than 1% of body volume in *Schedophilus* to greater than 3% in *Hyperoglyphe*. Size (greatest dimension) of the gas gland cells ranged from 10-17 μm in *Hyperoglyphe* and *Seriolella* to 20-40 μm in *Schedophilus*. Retial length ranged from 1.1 mm in *Seriolella* to 2.0 mm

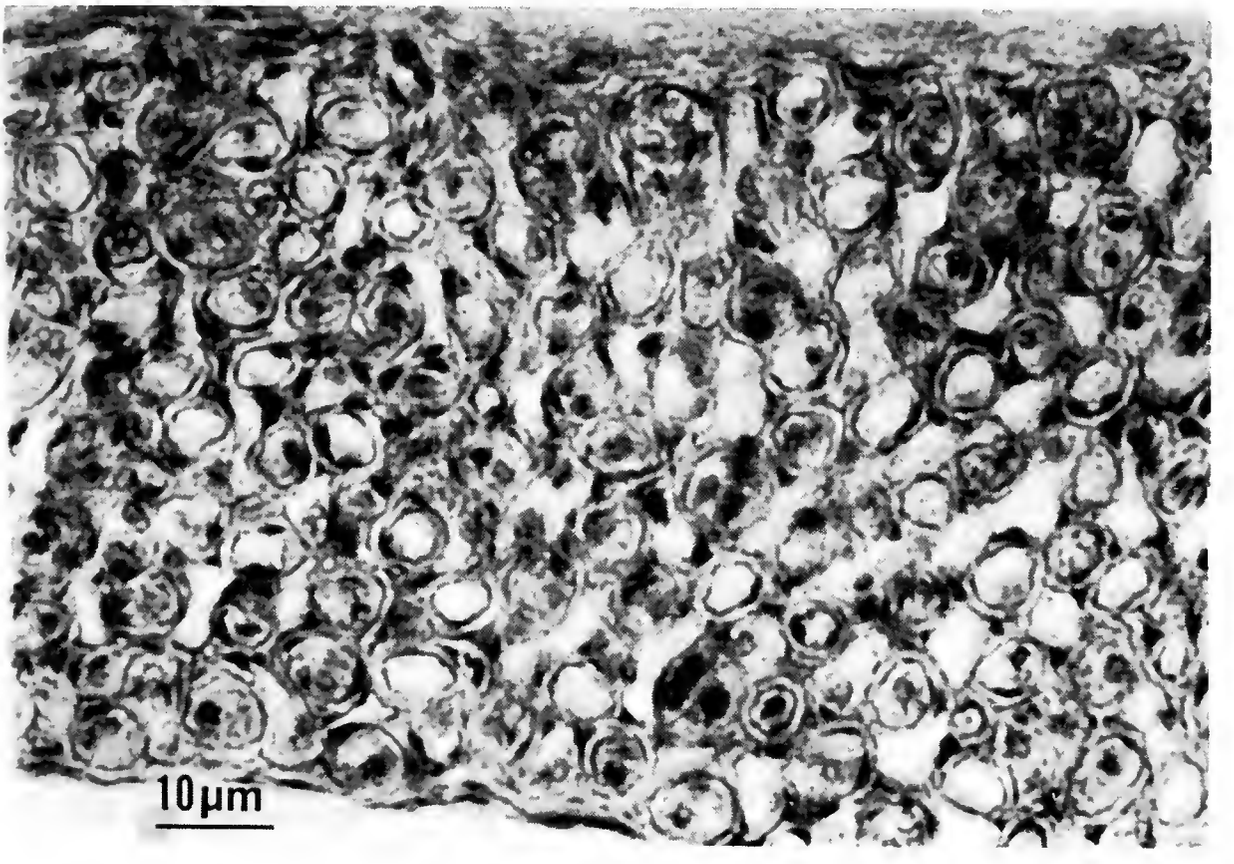

FIGURE 6.—Transverse section through the rete mirabile of the swim bladder of *Tetragonurus cuvieri*. (From same specimen as Figure 1C.)

TABLE 2.—Size characteristics of the swim-bladder lumen, gas gland, and rete mirabile in 12 species of stromateoids.

		Lumen			Gas gland		Rete mirabile			
Species	Size (mm SL)	L × W (mm)	Vol (mm^3)	Vol (%)	Area (mm^2)	Cell size (μm)	Capillary diam (μm)	Length (mm)	Total number of capillaries	Total capillary length (m)
Hyperoglyphe antarctica	34.9	9.8 × 2.7	37.0	3.4	5.4	10-17	7-10	1.3-2.0	2,000	2.6 -4.0
Schedophilus medusophagus	17.4	2.1 × 0.8	—	—	1.8	20-40	8-10	1.3	800	1.04
Icichthys lockingtoni	16.3	2.4 × 1.2	2.0	3.0	2.1	15-20	6-8	1.4	1,000	1.4
Seriolella violacea	12.8	3.5 × 1.1	—	—	1.0	10-17	4-8	1.1-1.2	1,200	1.3 -1.4
Stromateus fiatola	34.1	9.1 × 2.0	—	—	2.9	10-20	6-8	1.8-2.0	1,500	2.7 -3.0
Peprilus triacanthus	16.5	2.5 × 1.0	3.0	2.3	0.8	6-10	5-6	0.8	600	0.48
Amarsipus carlsbergi	22.0	2.0 × 0.8	0.7	—	1.0	8-20	4-8	0.7-0.9	1,100	0.77-0.99
Cubiceps gracilis	30.5	6.6 × 2.3	21.0	3.3	8.7	25-40	8-10	1.1-1.9	3,000	3.5 -5.7
Nomeus gronovii	26.4	6.7 × 1.0	3.5	0.7	1.6	—	—	0.4-0.6	—	—
	27.4	6.8 × 1.3	—	—	2.5	10-30	5-6	0.5-0.6	2,000	1.0 -1.2
Psenes cyanophrys	14.1	3.7 × 1.2	2.5	2.1	0.7	—	—	1.0	—	—
	18.6	5.1 × 1.6	—	—	6.0	25-40	5-6	0.8-0.9	1,500	1.2 -1.35
Tetragonurus cuvieri	28.8	3.8 × 1.0	2.0	0.6	0.6	8-20	4-10	1.3	1,000	1.3
Ariomma bondi	23.3	6.5 × 1.3	7.0	2.9	3.6	—	—	0.9	—	—
	24.2	5.0 × 1.4	5.0	1.7	3.7	20-46	8	0.6-0.9	2,500	1.5 -2.25

in *Hyperoglyphe*. Retial orientation was generally parallel to the long axis of the bladder, and the retial bundle either remained single anteriorly as in *Icichthys* (Figure 1J) or variously branched into smaller bundles perpendicular to the long axis as in *Hyperoglyphe* (Figure 1K). The rete bundle of *Schedophilus* had a sharp turn near the posterior end producing a sigmoid outline (Figure 1F). Swim-bladder shape which depends to a large degree upon secretory and absorptive states varied from elongate with a large posterior chamber to short and bulbous with either a small posterior chamber or no posterior chamber visible.

Stromateidae

The organ was similar in structure and shape to that of the Centrolophidae. The gas gland cells of *Peprilus triacanthus* were small (6-10 μm) and were arranged in loops and rings (Figure 5). In one *P. triacanthus* (16.5 mm SL) the retial blood vessels formed a single bundle posteriorly which expanded anteriorly over the gas gland whereas in two somewhat larger juveniles (22.2 and 33.9 mm SL) the retia were more nearly perpendicular to the long axis of the bladder and consisted of 7 or 8 distinct branches.

Amarsipidae

The swim bladder was similar to that of the Centrolophidae. The rete originated posteriorly as a single bundle and divided anteriorly into 7 or 8 distinct branches before entering the gas gland.

Nomeidae

Swim-bladder volume ranged from 0.7% in *Nomeus* to 3.3% of body volume in *Cubiceps* and gas gland size from 10-30 μm in *Nomeus* to 25-40 μm in *Cubiceps* and *Psenes*. Retial length varied from 0.4 mm in *Nomeus* to 1.9 mm in *Cubiceps*. The retia were divided into several branches and in position were more nearly perpendicular than parallel to the long axis of the bladder (Figure 1E, H). Small juvenile *Psenes cyanophrys* (9.1 and 14.1 mm SL) had retia almost parallel to the long axis of the bladder (Figure 1G) whereas larger juveniles (e.g., 60.8 mm SL) tended to have retia which were more nearly perpendicular to the long axis and more highly branched. The pattern, seen also in *Peprilus triacanthus*, may be part of the regression process that the swim bladder undergoes.

Tetragonuridae

The sac was small (0.6% of body volume) and elongate. The retial bundle was parallel to the long axis of the bladder and, as in *Schedophilus medusophagus*, had an S-shaped turn near the posterior end (Figure 1C). The gas gland was relatively small and located at the anterior end of the lumen.

Ariommidae

The swim bladder was relatively large (up to 2.9% of body volume) and elongate. The gas gland cells were in the upper range of size (20-46 μm) among the stromateoids examined, and the retia were broad, fanlike and perpendicular to the long axis of the bladder (Figure 1A).

Size at Swim-Bladder Inflation

The swim bladder becomes functional early in the life of stromateoids. Whether the larval fishes gulp air at the surface or whether gas is secreted to initially fill the bladder was not determined. Examination of larvae of four genera indicated that the organ in one species was almost completely developed at 3.0 mm SL and in three others at slightly larger sizes. Specimens of *Peprilus simillimus* as small as 3.0 mm SL had what appeared to be a fully developed swim bladder whereas in smaller individuals, e.g., 2.7 mm SL, the sac was inflated but the gas gland and retia were incomplete. The bladder was absent in a fish of 2.4 mm SL. A series of larvae, 3.4-5.0 mm SL, of an unidentified species of *Psenes* had an inflated swim bladder, and larvae of *Tetragonurus cuvieri* as small as 4.0 mm SL had a gas-filled sac which was visible through the semitransparent body wall. Individuals of *Icichthys lockingtoni*, 5.0 and 7.5 mm SL, had an inflated sac and an apparently fully developed gas gland and retial complement.

Swim-Bladder Regression

The swim bladder regresses, becomes nonfunctional, and finally disappears before the adult stage is reached in all stromateoid genera except *Pampus* in which the organ is apparently absent and possibly *Nomeus* in which the largest individual examined (142.7 mm SL) had a functional swim bladder. The regression is a

TABLE 3.—Surface area of the gas gland (mm^2) and length of the rete mirabile (mm) relative to swim-bladder volume (mm^3 or ml) or dimension (length × width, in mm) in the European eel, certain shallow-sea and deep-sea fishes, and in 12 species of stromateoids. Total capillary length (m) = retial length × number of retial capillaries. Retial lengths of stromateoids are means of individuals for each species.

Species	Size (mm SL)	Gas gland area × 1,000/swim-bladder volume (mm^3)	Retial length × 1,000/swim-bladder dimension	Total capillary length/swim-bladder volume (ml)
European eel[1]				
Anguilla anguilla	—	—	—	30
Shallow-sea (epipelagic):[1]				
Cypsilurus cyanopterus	290.0	8	0.5	—
Danichthys rondeletii	214.0	8	1.3	—
Exocoetus volitans	159.0	6	5	—
Petalichthys capensis	—	—	1.5	—
Hyporhamphus sp.	112.0	40	8	—
Scomberesox saurus	—	—	2	—
Gadus minutus	—	—	13	—
Capros aper	—	—	18	—
Deep-sea:[1]				
Gonostoma denudatum	81.0	—	76	—
Pollichthys mauli	43.0	—	125	—
Bonapartia pedaliota	67.0	—	71	—
Vinciguerria attenuata	43.5	140	34	—
Vinciguerria nimbaria	—	—	—	150
Argyropelecus aculeatus	23.0	140	38	50
Polyipnus laternatus	36.0	—	143	100
Astronesthes niger	41.0	250	111	—
Astronesthes similis	104.0	170	—	—
Myctophum punctatum	71.0	200	40	20
Benthosema suborbitale	24.0	500	—	—
Lampanyctus guntheri	53.0	330	142	—
Diaphus rafinesquei	—	—	21	—
Melamphaes megalops	56.0	60	250	30
Stephanoberyx monae	83.5	—	63	—
Chiasmodon niger	104.0	250	71	—
Stromateoids:				
Hyperoglyphe antarctica	34.9	140	63	89
Schedophilus medusophagus	17.4	—	1,000	—
Icichthys lockingtoni	16.3	1,000	500	700
Seriolella violacea	12.8	—	333	—
Stromateus fiatola	34.1	—	100	—
Peprilus triacanthus	16.5	250	333	167
Amarsipus carlsbergi	22.0	—	500	—
Cubiceps gracilis	30.5	500	100	214
Nomeus gronovii	26.4	500	77	—
Psenes cyanophrys	11.5	1,000	333	—
Tetragonurus cuvieri	28.8	330	333	650
Ariomma bondi	23.3	500	111	380

[1]Data from Marshall (1960).

gradual process which makes difficult the determination of the exact time of loss of function. Several stages are recognizable in the process although they vary in appearance, and both the stages and the overall regression vary in duration among and within species. Estimated ranges of fish size during which regression occurs in nine stromateoid species are given in Table 4.

Early in the regression the gas gland contracts and thickens and the sac begins to decrease in size. Later the gas gland and retia mirabilia become atrophied as the cells and capillaries lose integrity (Figure 7). A yellowish-white material, possibly lipid, frequently invests the gas gland. Finally, the swim-bladder wall is resorbed, and the gas secreting and absorbing complexes become indistinct. A large stromateoid (> 100-200 mm SL, see Table 4) may have either a small irregularly shaped mass of yellowish-white material lying in the dorsal mesentery (Figure 7) as the only remnant of the swim bladder or no visible trace at all of the organ.

DISCUSSION

Relative Dimensions and Capabilities of the Swim Bladder

Volume

Mean percentage volumes were relatively small, 0.6-3.4% (Table 2), and generally below the 3.1-5.7 range for the swim bladder calculated by Alexander (1966) to be necessary for neutral buoyancy in seawater. A number of mid-water fishes also have swim bladders of low volume

TABLE 4.—Size ranges during which swim-bladder regression occurs in nine species of stromateoids and during which the same species have been observed in association with animate (mainly coelenterate) or inanimate floating objects. Former ranges derived from data of present study and latter from sources listed.

Species	Size during regression (mm SL)	Size during association (mm SL, FL, or TL)[1]	Associated species or object	Source[2]
Centrolophus niger	50-75	30-40 TL	*Rhizostoma pulmo*	Mansueti 1963
		103-477 SL	*Mola mola*	Mackay 1972
Icichthys lockingtoni	40-65	55 TL	*Pelagia noctiluca*	Mansueti 1963
		16.3 SL	*Pelagia noctiluca*	Specimen label (MCZ)
		180.5 TL	*Pelagia noctiluca*	Mansueti 1963
Stromateus fiatola (including *S. fasciatus*)	50-75	10-40 TL	*Rhizostoma pulmo*	Mansueti 1963
		10-40 TL	*Cotylorhiza tuberculata*	Mansueti 1963
		127 TL	Unidentified medusa	Mansueti 1963
		12.5-28.2 SL	*Cassiopeia carbonica*	Specimen label (ZMC)
Peprilus triacanthus	75-100	10-20 TL	*Chrysaora quinquerirrha*	Mansueti 1963
		51-64 TL	*Cyanea capillata*	Mansueti 1963
		50-73 TL	Unidentified medusa	Mansueti 1963
Peprilus paru (including *P. alepidotus*)	60-100	18-69 TL	*Chrysaora quinquecirrha*	Mansueti 1963
		13 TL	*Chrysaora quinquecirrha*	Mansueti 1963
		147 TL	Unidentified medusa	Mansueti 1963
		28.6 SL	Unidentified medusa	Specimen label (BMNH 1956.11.12.12)
Cubiceps gracilis	40-75	42 SL	Unidentified medusa	Specimen label (BMNH 76.6.21-2)
Nomeus gronovii	Swim bladder present at ≥150 SL	20 FL	Drifting raft	Gooding and Magnuson 1967
		51-76 TL	*Physalia pelagica*	Mansueti 1963
		127-152 TL	*Stomolophus meleagris*	Mansueti 1963
		142.7 SL	*Physalia pelagica*	NIO specimen, HMS *Discovery II* Stn. 6688-3
Psenes cyanophrys (including *P. pacificus*)	110-130	15-124 FL	Drifting raft	Gooding and Magnuson 1967
		10-133 SL	Flotsam	Hunter and Mitchell 1967
Tetragonurus cuvieri	40-60	34 SL	Unidentified medusa	Specimen label (BMNH 76.6.21.23)

[1]SL = standard length, FL = fork length, TL = total length.
[2]MCZ = Museum of Comparative Zoology, Harvard University.
ZMC = Zoological Museum, Copenhagen.
BMNH = British Museum (Natural History), London.

(Capen 1967; Kleckner and Gibbs 1972) and even a relatively small gas-filled sac provides some degree of buoyancy which may be significant depending upon what other lift or buoyancy devices are utilized. Larval and juvenile stromateoids, the stages which have the organ, have a different mode of life (see below) and are in some species at least probably less dense than adults. Only a 1% reduction in specific gravity of a fish lowers the required percentage volume for neutral buoyancy from 3.1%, the lower value in Alexander's (1966) calculated range (which was based upon specific gravities of adults), to 2.2% (Horn 1970a). Thus, even a small swim bladder would be an important contribution to buoyancy. Data on specific gravities of young stromateoids which might help to explain the range of percentage volumes found within the group are not yet available.

Gas Gland

The area of the gas gland relative to swim-bladder volume is similar to that in a number of deep-sea fishes and much greater than that of a series of epipelagic or shallow-sea ones (Table 3). Marshall (1960) stated that the large gas gland of deep-sea fishes, especially vertical migrators, may be an adaptation for rapid gas secretion as the fish descends. Even though juvenile stromateoids occur only in the epipelagial, the adaptive significance of a large gas gland would be the same for them as for deep vertical migrators since stromateoids range over depths in the upper 100-150 m where pressure changes are greatest (e.g., the pressure at 10 m is 2× that at the surface). Maintaining association with animate floating objects as many stromateoids do requires that fishes range, even if slowly, over depths in the surface layers and in so doing secrete gas during descents if the hydrostatic advantage of the swim bladder is to be effected. Thus, the main selective value of the large gas gland may be for making fine adjustments to buoyancy. At least some of the epipelagic fishes listed in Table 3 have a narrow vertical range near the surface and would not require as large a gas gland.

The size and structure of the gas gland cells vary widely among stromateoids, a common situation in both shallow-water (Woodland 1911; Fänge 1953) and deep-sea fishes (Marshall 1960). Cells measured in stromateoids ranged from 6 to 46 μm (Table 2), although some other cells in a few species appeared to be multinucleate and syncytial or similar to the giant cells (50-150 μm) described by Fänge (1953) and Marshall (1960). The gland consisted of relatively large cells in a

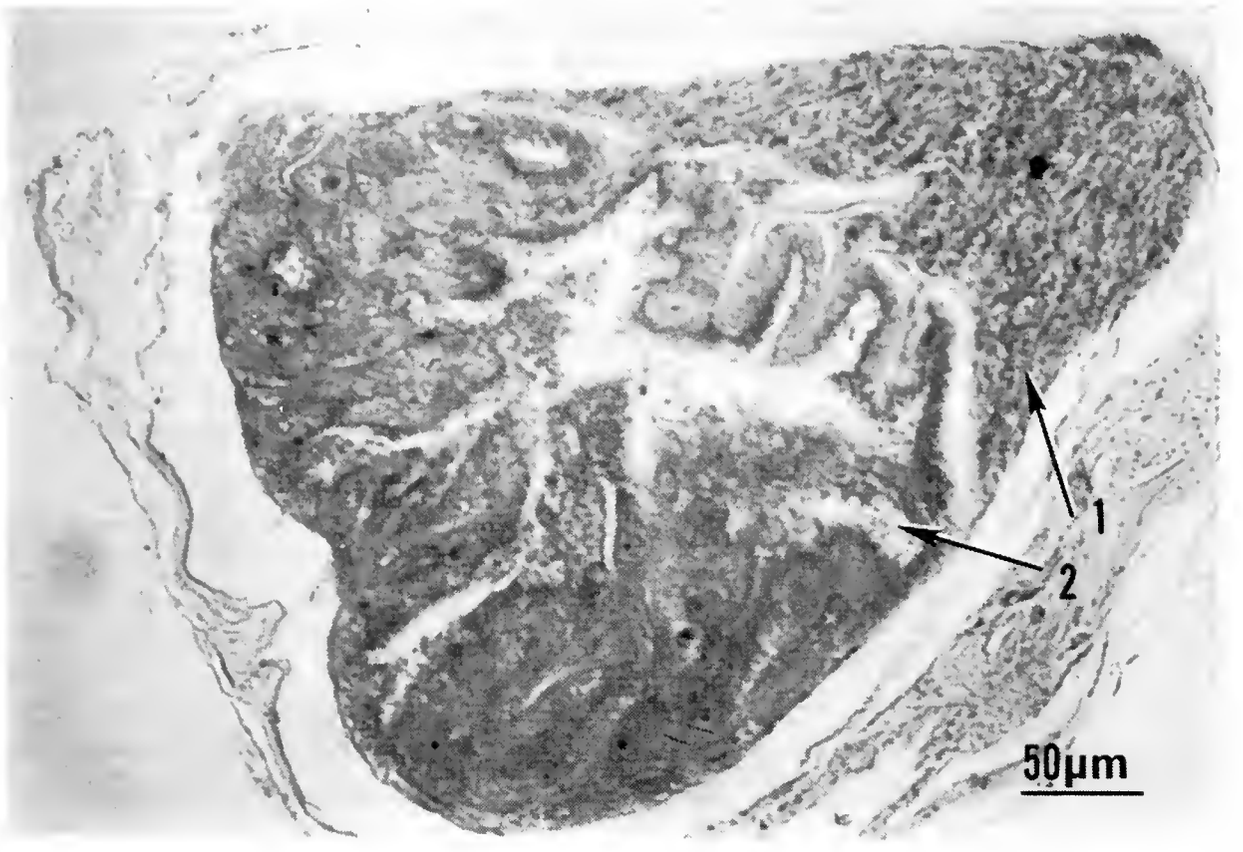

FIGURE 7.—Transverse section through the regressed swim bladder of *Ariomma indica*, 59.7 mm SL. Arrow (1) points to regressed rete mirabile, arrow (2) to regressed gas gland.

complex, multilayered arrangement as in *Ariomma bondi* (Figure 2), or, less frequently, of small cells arranged in circles or loops as in *Peprilus triacanthus* (Figure 5). The functional significance of cells of either different sizes or arrangements is poorly understood.

Rete Mirabile

Retial length in stromateoids ranged from 0.4 to 2.0 mm (Table 2), similar to the 0.75 to 2.0-mm range listed by Marshall (1972) for upper mesopelagic (200-600 m) fishes. The ratio of retial length to swim-bladder dimension (length × width) (Table 3) as an approximation of relative development is high in stromateoids and similar to that of Marshall's (1960) deep-sea group which includes some vertical migrators. The stromateoid ratio is much higher than that of other epipelagic fishes and demonstrates that the retia, as with the gas gland, which together form the gas-secreting complex, are relatively well developed in stromateoids. In addition, the total length of the retial capillaries (retial length × number of retial capillaries) in relation to swim-bladder volume is similar to or exceeds that for the eel, *Anguilla anguilla*, and certain deep-sea fishes (Table 3).

Marshall (1972) pointed out that the only flexible adaptation to increase the surface available for countercurrent gas exchange is an increase in length of the retial capillaries. An increase in length will not only lead to increased gas exchange but also slow the rate of bloodflow and so further enhance the efficiency of exchange (Marshall 1960). Marshall (1972) showed that the deeper the living space of a fish the greater the absolute length of the retia. On the basis of the pattern of retial length and depth of living described by Marshall, the predicted depth zone for larval and juvenile stromateoids would be the upper mesopelagial.

Besides length, the diameter of the retial capillaries of stromateoids shows a somewhat greater similarity to that of deep-sea fishes than to other epipelagic fishes. Stromateoids have capillary bores of 4-10 µm (Table 2) whereas epipelagic fishes listed by Marshall (1960) had diameters of greater than 10 µm. Deep-sea fishes with large erythrocytes have retial capillaries 7-18 µm in diameter and those with small, nonnucleated erythrocytes such as *Maurolicus* and *Vinciguerria* have retial capillaries 2-10 µm in diameter (Marshall 1972). The smaller the diameter the greater the efficiency of gaseous exchange (Marshall

1960), although decreased bore is an adaptation limited in most fish species by the size of the erythrocytes.

Swim-Bladder Regression in Relation to Behavior and Mode of Life

Data from the present study and other sources on depth distribution, association with floating objects, and locomotion and buoyancy make it possible to formulate a general outline of the changes in behavior and mode of life that accompany the regression of the swim bladder and which are part of the transition from the juvenile to the adult state.

Depth Distribution

Adult stromateoids generally occupy a wide range of depths either over the continental shelf or in the open ocean, whereas larvae and juveniles of all or nearly all species occur in the surface layers (mainly the upper 100 m) (Haedrich 1967, 1969; Horn 1970a). Larval nomeids (*Psenes* and *Cubiceps*) are important constituents of the epipelagic fauna; this is known especially for the eastern tropical Pacific (Ahlstrom 1971, 1972). The Centrolophidae and Tetragonuridae were listed by Ahlstrom (1969) as two of the principal families of deep-sea fishes which had larvae in the surface layers of the California Current region. The stromateid, *Peprilus simillimus*, occurs mainly in the upper 50 m of coastal waters off California and Baja California (Ahlstrom 1959), and ariommid larvae and juveniles apparently live in the surface layers although the adults are benthopelagic (Horn 1972). Thus, swim-bladder loss occurs as the fishes increase their range of vertical distribution.

Association with Floating Objects

Beginning at a small size (≤ 10 mm SL) and usually ending before maturity is reached (≤200 mm SL), stromateoids commonly associate with a wide variety of animate and inanimate floating objects (Mansueti 1963; Haedrich 1967; Horn 1970a) and during the period that the swim bladder is functional (Table 4). The associations are not obligatory but rather, as Mansueti (1963) described them, temporary ecological phenomena in which the objects (e.g., jellyfishes or flotsam) are essentially passive hosts and the fishes active opportunists. Scyphozoan medusae of several genera form a major group of associates particularly of stromateids and to some extent of centrolophids, nomeids, and tetragonurids (Mansueti 1963). The nomeid, *Nomeus gronovii*, and the Portuguese man-of-war, *Physalia*, form the apparently most intimate and enduring of "fish-jellyfish" associations. Certain stromateoids have also been found inside pelagic ascidians (Grey 1955), beneath the ocean sunfish, *Mola* (Mackay 1972) and beneath floating plants such as *Sargassum* (Haedrich 1967). Several species occur beneath flotsam, and the nomeid, *Psenes cyanophrys*, is one of the more abundant fishes under drifting objects (Hunter and Mitchell 1967, 1968; Gooding and Magnuson 1967). Drift associations are not well understood but probably provide one or more ecological advantages such as food, protection, or visual stimuli.

Juvenile stromateoids in their coloration and maneuverability are well adapted for life beneath floating objects, especially coelenterates. Young fish typically have a banded, mottled, or blotched pattern whereas adults are generally uniform in color or are dark above and pale below. The duration of the juvenile color pattern is similar to the period when the fishes are associated with floating objects, and the patterns according to Haedrich (1967) serve as protective coloration beneath the shifting shadows of objects, especially jellyfishes. *Nomeus* which retains its association with floating objects longer than most or all other stromateoids also retains its mottled color pattern in the largest specimens known.

Maneuverability and avoidance by the fish appear to be of primary importance in all or most stromateoid-coelenterate associations (Mansueti 1963; Horn 1970a). *Peprilus triacanthus* placed in tanks with a medusa, *Chrysaora quinquecirrha*, gradually increased the amount of time spent near the jellyfish and after 72 h remained within a 4-cm distance of the bell at least 75% of the time (Horn unpubl. data). Hovering and rapid turning were significant parts of the locomotor behavior of the fish in avoiding the tentacles of the medusa. Contact of the skin of the fish by the tentacles resulted in nematocyst firing as evidenced by the clinging of the tentacles to the fish's body causing the fish to rapidly swim away. In a two-way feeding relationship, *P. triacanthus* frequently nibbled at the manubrium and tentacles of the medusa, while weakened or otherwise slow-moving fish were captured and ingested by the medusa.

Although Lane (1960) reported that *Nomeus* can survive doses of *Physalia* toxin as much as 10 times the amount that would kill other fishes of the same size and type, *Nomeus* is stung if forced into contact with the tentacles (Lane 1960) and can be killed if touched by the tentacles according to Zahl (1952). Maul (1964) found that *Schedophilus* (= *Mupus*) *ovalis* also suffered large weals on the body from nematocysts when in contact with *Physalia* and that safety for the fish must be due in part to its ability to avoid contact with the tentacles. Mansueti (1963) concluded that in all fish-jellyfish associations the former skillfully maneuver between tentacles and generally avoid being stung but that contacts are inevitable.

Locomotion and buoyancy

The differences in locomotor behavior found between juvenile and adult stromateoids that have been observed illustrate the importance of maneuverability for juveniles and correspond to swim-bladder loss and increased independence of floating objects as maturity is reached. The paired fins are important locomotor devices among stromateoids. The pectoral fins are moved in a rotary manner for maintaining position in juveniles of *Peprilus triacanthus* and *Schedophilus medusophagus* when hovering beneath floating objects (pers. obs.) and sculled for effecting continuous swimming at less than maximum speeds in these species (Horn 1970b, unpubl. obs.) and in other stromateoids such as *Cubiceps gracilis* (Figure 8). I have observed adults of both *P. triacanthus* and *P. simillimus* in public aquaria and calculated that the pectorals are used at least 80-90% of the time as a main propulsive force at cruising speeds. The pelvic fins which may be absent (all stromateid species except one) or small (as in certain centrolophids) are well developed in juveniles of certain species. Pelvics are large in *Nomeus* and apparently important for increasing maneuverability and enhancing protective coloration for a fish living among the tentacles of *Physalia*.

The relative length of the paired fins changes with age and varies among the species (Haedrich 1967; Horn 1970b). Extremes are represented by *P. triacanthus* and *S. medusophagus* (Figures 9, 10). In *P. triacanthus* (which lacks pelvic fins) the relative length of the pectoral fin increases rapidly until the fish reaches about 75-80 mm SL beyond which the fin length ceases to increase (Figure 9). This fish size is in the range of that when the swim bladder regresses and the fish deserts its coelenterate host (Table 4). Individuals of *P. triacanthus* greater than 75-80 mm SL are negatively buoyant (see below) and swim continuously using mainly the long pectorals which also generate dynamic lift. In *S. medusophagus* the relative length of the paired fins decreases with age (Figure 10), a pattern opposite that of *P. triacanthus*. The swim bladder regresses in a size range of about 40-60 mm SL corresponding closely to the size interval during which the marked change in paired fin length occurs and apparently during which the fish deserts its coelenterate host

FIGURE 8.—*Cubiceps gracilis*, 68 mm SL, swimming in plastic container and using pectoral fins as principal locomotor force. Swim bladder of this fish partially regressed (see Table 4). Specimen captured at the surface in the North Atlantic.

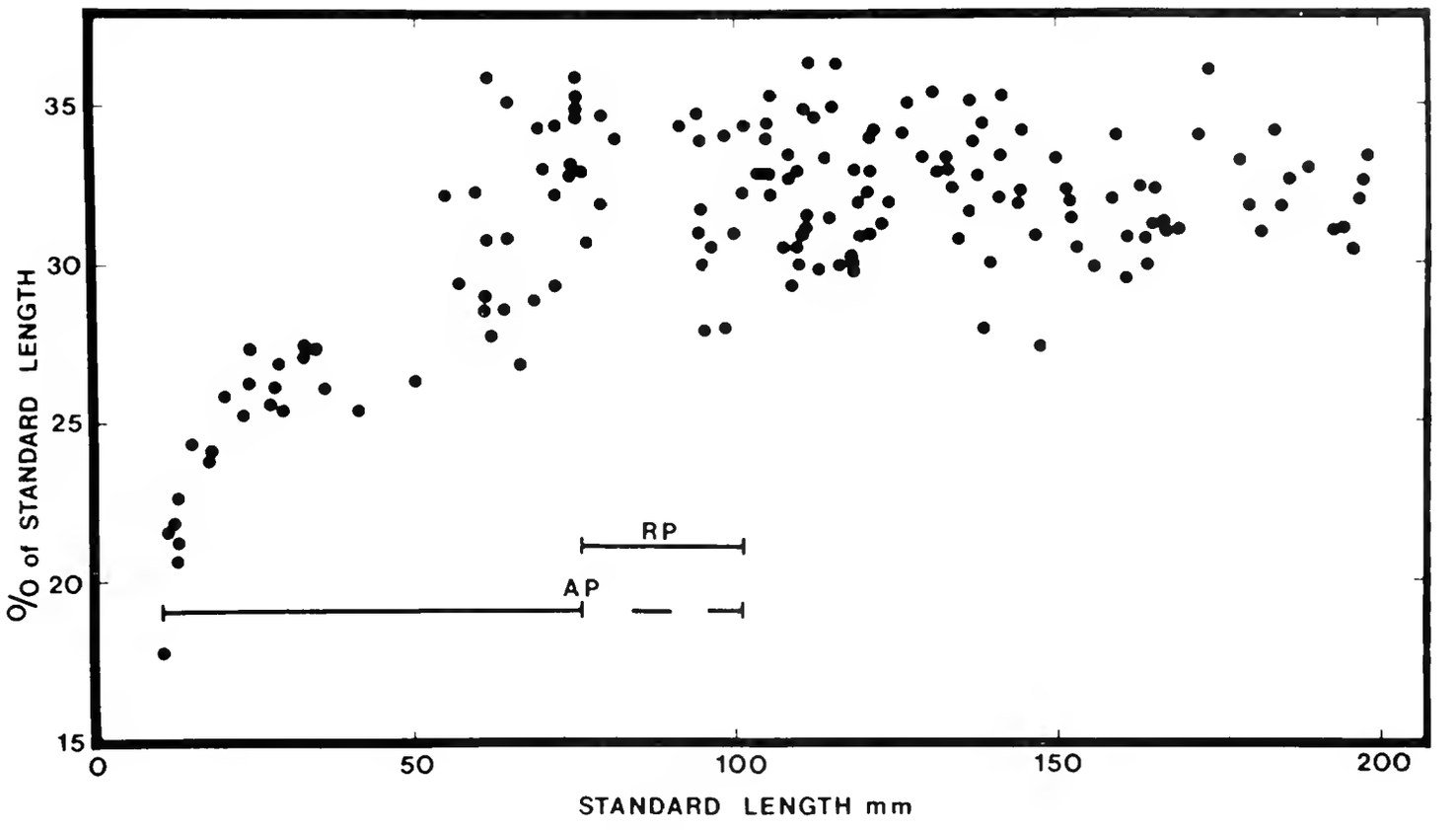

FIGURE 9.—Scatter diagram of pectoral fin length as a percentage of standard length in *Peprilus triacanthus*. RP, regression period, or size interval during which swim bladder regresses; AP, association period, or size interval during which fish associates with floating objects (dashed part of line indicates less frequent association) (see Table 4).

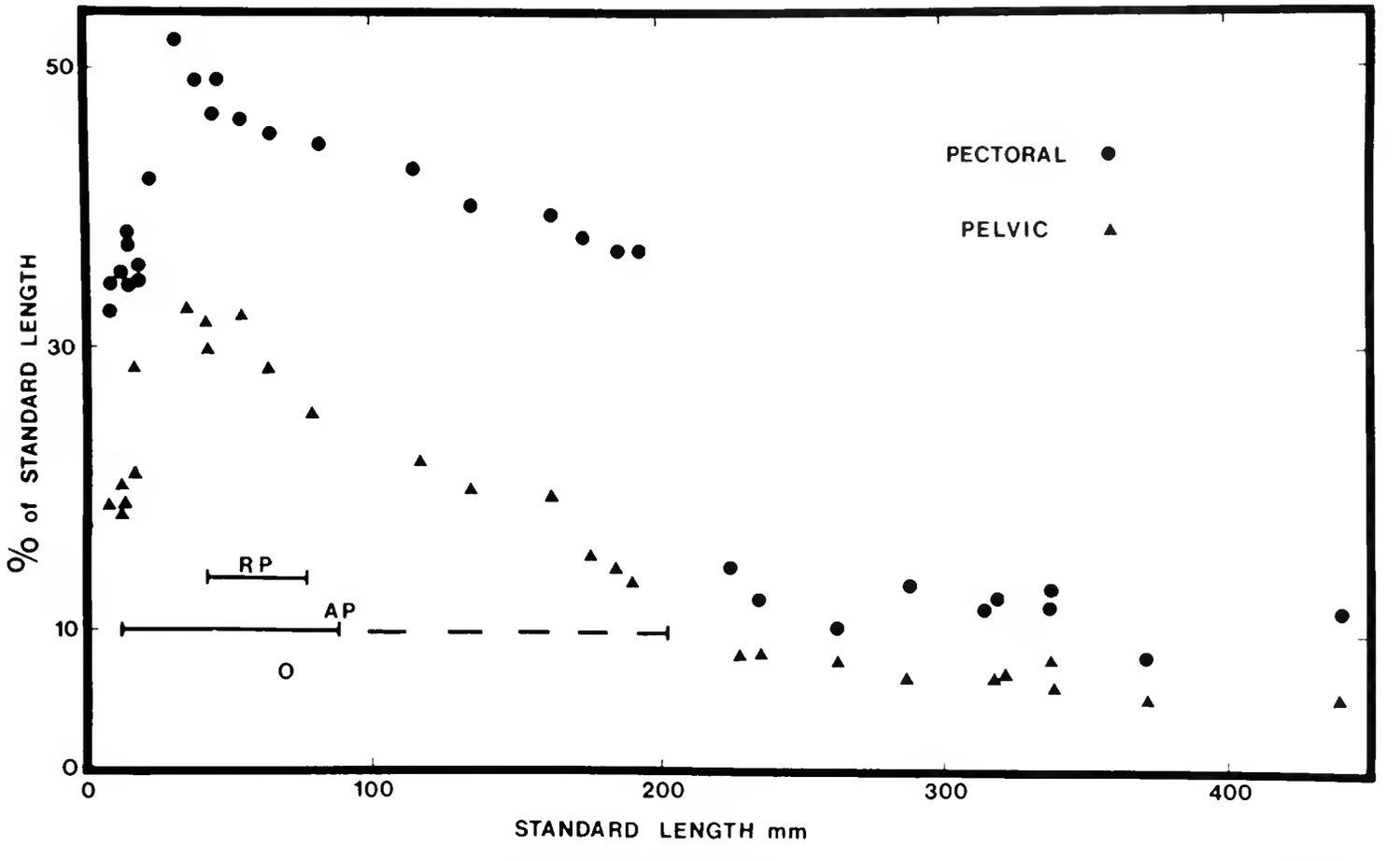

FIGURE 10.—Scatter diagram of pectoral fin and pelvic fin lengths as a percentage of standard length in *Schedophilus medusophagus*. RP and AP as in Figure 9.

(Mansueti 1963). Unlike *P. triacanthus*, *S. medusophagus* becomes neutrally buoyant or nearly so (see below) and has a poorly ossified skeleton and soft musculature (Bone and Brook 1973). Adult *S. medusophagus* swim slowly and continuously in near anguilliform manner and with only a minor part of the propulsive force provided by the small pectorals (pers. obs.). Because of the fish's low density, little or no lift is required from locomotor activity.

Changes in the level of buoyancy and in the nature of the buoyancy mechanism may coincide with swim-bladder loss and other changes occurring as stromateoids mature although the data are as yet insufficient to permit conclusions to be reached. *Peprilus triacanthus* and a closely related species, *P. simillimus*, are negatively buoyant as adults (weight in water 1.4-2.3% of weight in air) (unpubl. data). Juvenile *S. medusophagus* (85-200 mm SL) are slightly negatively buoyant (Bone and Brook 1973) whereas a larger (285 mm SL) specimen was found to be neutrally buoyant in surface seawater (unpubl. data). Large amounts of lipid have been found in adults of both *P. simillimus* and *S. medusophagus* especially in the skull and spine (Lee et al. in press). Bone and Brook (1973) found relatively low amounts of lipid in juvenile *S. medusophagus*, an indication that lipid content may increase with size in this species. Lipids may serve to partially replace the swim bladder in a buoyancy function as the organ regresses in *P. simillimus* and *S. medusophagus*, two morphologically and ecologically dissimilar stromateoids. *Peprilus simillimus*, an active, continuous swimmer with long pectoral fins, has a relatively well ossified skeleton, firm musculature, and is negatively buoyant, whereas *S. medusophagus*, a slow moving, continuous swimmer with short pectoral fins, has poorly ossified bones and soft, loosely packed muscles, and approaches or attains neutral buoyancy.

Increased lipid content as a buoyancy replacement for the swim bladder would be advantageous for *P. simillimus*, *S. medusophagus*, and probably other stromateoids that range over the upper several hundred meters of the water column since the low coefficient of compressibility of lipid compared to gas reduces the stress of pressure changes with depth. Nevenzel et al. (1969) pointed out the advantage of lipid for a vertically migrating midwater fish, and Butler and Pearcy (1972) discovered that in two such species, the myctophids *Stenobrachius leucopsarus* and *Diaphus theta*, swim bladder-to-body volumes were inversely related to body size and lipid content indicating that lipids assume the primary buoyancy function as the swim bladder regresses with age. An additional advantage of stored lipid, especially triglycerides, may be as an energy source (Lee et al. in press). Bone (1973) has suggested that vertically migrating myctophids can be grouped into functional types based on swim-bladder state, lipid content, density, and size of the pectoral fins. Stromateoids are not classed as a principal group of vertical migrators partly because of their relative rarity, but many species do have a broad vertical range. With more data, it may be possible to divide stromateoids into functional groups according to characteristics similar to those listed by Bone (1973) for myctophids.

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DISTRIBUTION AND RELATIVE ABUNDANCE OF SEVEN SPECIES OF SKATES (PISCES: RAJIDAE) WHICH OCCUR BETWEEN NOVA SCOTIA AND CAPE HATTERAS[1]

JOHN D. MCEACHRAN[2] AND J. A. MUSICK[3]

ABSTRACT

Data collected during eight groundfish surveys of the area from Nova Scotia to Cape Hatteras, North Carolina, and during five seasonal surveys of Chesapeake Bight were used to define the distribution and relative abundance of *Raja eglanteria, R. garmani, R. laevis, R. erinacea, R. ocellata, R. senta,* and *R. radiata.* Ancillary distributional data for the area from the Straits of Florida to Cape Hatteras and the areas off northern Nova Scotia and the Gulf of St. Lawrence were used qualitatively to extend the distributional study.

Raja eglanteria is a Carolinian species abundant north of Cape Hatteras only during the warmer months. *Raja garmani*, a skate of the outer continental shelf and upper slope, consists of two populations which have different temperature preferences. *Raja laevis* is the most widespread species studied and does not appear to be as abundant as the other skates in any region of the study. *Raja erinacea*, a Virginian to boreal species, occurs from southern Nova Scotia to Cape Hatteras in shallow water but is present at depths down to 384 m. *Raja ocellata* is a Virginian to boreal species distributed similarly to *R. erinacea* except that the former is widespread in the Gulf of St. Lawrence and off northern Nova Scotia. *Raja senta*, a boreal species, frequently occurs on the northern offshore banks of Nova Scotia and at temperatures as low as −1.3°C. *Raja radiata* is a boreal to arctic species.

Raja erinacea and *R. ocellata* are sympatric over the greater part of their ranges as are *R. senta* and *R. radiata*. The two pairs of species have complementary distributions. *Raja ocellata* has slightly lower temperature preferences than *R. erinacea*, and *R. radiata* is more widespread and has wider temperature tolerances than *R. senta*.

The genus *Raja* is represented by *R. eglanteria, R. garmani, R. laevis, R. erinacea, R. ocellata, R. senta* and *R. radiata* along the continental shelf of North America between Nova Scotia and Cape Hatteras, NC. Notes on the occurrence and distribution of these species have been summarized by Bigelow and Schroeder (1953, 1954), Leim and Scott (1966), and McEachran (1973); however, most of this information is based on scattered regional studies. The present study presents data gathered during comprehensive groundfish surveys of the area from Nova Scotia to Cape Hatteras and defines the distribution and relative abundance of each species, as well as cooccurrence among species.

MATERIALS AND METHODS

Data used in this study were divided into two categories: 1) quantitative data used to determine relative abundance of the skates, and 2) qualitative data used only to determine the temperature, depth, and geographical ranges of the skates.

Data supplied by National Marine Fisheries Service (NMFS) Biological Laboratory at Woods Hole, Mass. (now Northeast Fisheries Center) and by the Virginia Institute of Marine Science (VIMS) at Gloucester Point, Va. were used to determine relative abundance. The former data consisted of eight groundfish surveys of the continental shelf (27-366 m) from LaHave Bank, off southeastern Nova Scotia, and the Gulf of Maine to Cape Hatteras. A total of 2,247 stations were made during the winters of 1968-70, the summer of 1969, and the autumns of 1967-70 (Table 1) by the RV *Albatross IV*, except that part of 70-06 was conducted by the RV *Delaware II*. The survey area was divided into 58 strata according to depth and geographical area, and three or more stations were randomly selected within each stratum per cruise (Figure 1) (Grosslein 1969). A No. 36 Yankee trawl equipped with a cod end liner of 0.25-inch bar mesh and

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TABLE 1.—Groundfish surveys conducted by the Biological Laboratory of the National Marine Fisheries Service at Woods Hole, Mass (now Northeast Fisheries Center).

Cruise	Dates	Season	No. of stations
67-21	17 Oct.- 9 Dec. 1967	Autumn	271
68-03	4 Mar.- 16 May 1968	Winter	262
68-17	10 Oct.- 26 Nov. 1968	Autumn	275
69-02	5 Mar.- 10 Apr. 1969	Winter	266
69-08	14 July- 18 Aug. 1969	Summer	267
69-11	8 Oct.- 23 Nov. 1969	Autumn	276
70-03	12 Mar.- 29 Apr. 1970	Winter	289
70-01	15 Oct.- 20 Nov. 1970	Autumn	341
Total			2,247

18 inch rollers on the ground rope was towed at 3.5 knots for 0.5 h at each station. Distance of tow averaged 1.75 miles.

Prior to data analysis, the 58 sampling strata were grouped into five ecological subareas according to hydrography and substratum. Schopf and Colton (1966) stated that the southern Nova Scotian shelf, Gulf of Maine, and Georges Bank have different bottom temperatures and faunal assemblages. Although Georges Bank and Nantucket shoals (northern section of the mid-Atlantic Bight) have similar bottom temperatures and faunal assemblages (Schopf and Colton 1966), the area extending from Georges Bank to Cape Hatteras was subdivided because of its great size. The southern section of the mid-Atlantic Bight consisted of strata 61 to 76; the northern mid-Atlantic Bight was composed of strata 1 to 12 and 25; Georges Bank was made up of strata 13 to 23; the Gulf of Maine included strata 24, 26 to 30, and 36 to 40; and the Nova Scotian shelf consisted of strata 31 to 35, 41, and 42. All four depth zones (27-55, 56-110, 111-183, 184-366 m) were sampled in the first three subareas; the three deeper zones were surveyed in the Gulf of Maine; and only two zones, 56-110 and 111-183 m, were sampled on the Nova Scotian shelf.

Preliminary examination of the skate data indicated contagion as Taylor (1953) and Roessler (1965) had demonstrated for trawl catch data in general. A logarithmic transformation tends to normalize contagious distributions (Pereyra et al. 1967), so skate counts were transformed to log $(X + 1)$. Transformed values were used to determine the geometric mean numbers (indices of abundance) of skates per stratum per cruise. The indices of abundance were weighted by dividing them by the area of the strata to correct

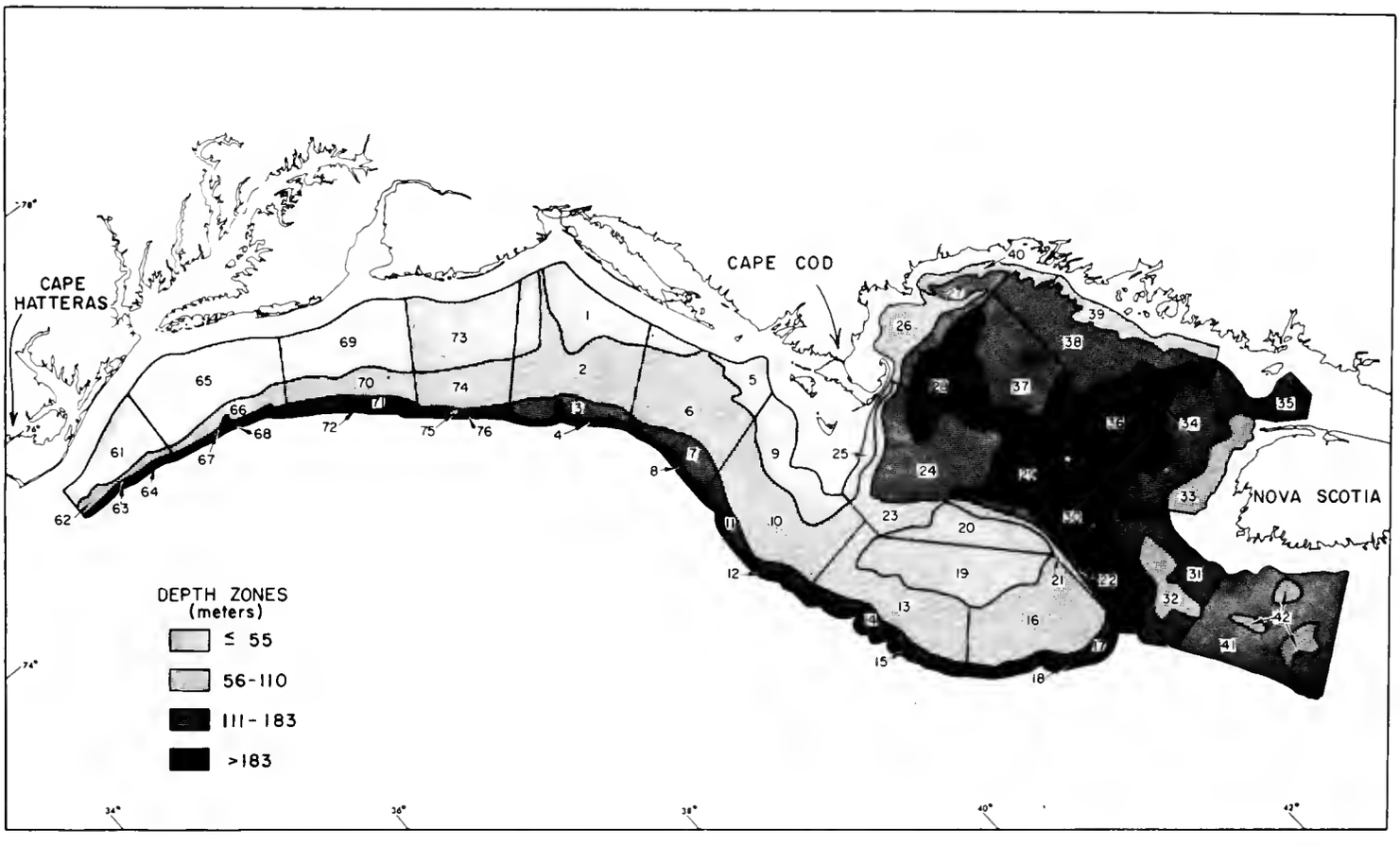

FIGURE 1.—Strata sampled by the RV *Albatross IV* and *Delaware II*, 1967-70. Strata numbers 43-60 were not included in the surveys.

for areal differences between strata. Area of the strata are listed in Table 2.

Indices of abundance for all stations, within temperature intervals of 1°C for each of the five ecological subareas, were calculated for each species. Indices were not weighted. Length frequencies were calculated for strata sets corresponding to each of the four depth intervals (27-55, 56-110, 111-183, 184-366 m) within each of the subareas. This analysis gave the percentages that each 3-cm length increment contributed to the total catch of a species within each of the strata sets of the subareas.

Hurlbert's (1969) index of association was used to determine the level of cooccurrence based on presence and absence of two species at the same stations. Species pairs with a significant positive index were compared by the product moment correlation (simple correlation coefficient) to determine if the two species were positively or negatively related by numbers. The correlation indices were computed from transformed abundance values [log $(X + 1)$] at stations where the two species cooccurred. According to Hurlbert (1969), a negative correlation, showing an inverse relationship in numbers of individuals between the species, may indicate that the two species compete for the same resources.

The VIMS data included five seasonal groundfish surveys of the Chesapeake Bight (lat. 38° 43′N to 35°13′N) in 9 to 274 m during the four seasons of 1967 and winter of 1968. This area was divided into grids of lat. 15′ by long. 12.5′. A 1-h tow was made in each grid per survey with an Atlantic western trawl without rollers (Musick and McEachran 1972).

The Chesapeake Bight was divided into two areas, one north and one south of the Virginia Capes (lat. 37°N) for data analysis. Index of abundance (geometric mean) was computed for each of the species (*R. eglanteria, R. garmani, R. erinacea,* and *R. ocellata*) captured during the VIMS survey, by depth zone (0-18, 19-37, 38-73, 74-110, 111-165, 166-274 m) and by temperature intervals of 1°C, north and south of lat. 37°N separately. This index was not weighted by area of the depth zone.

The qualitative data were obtained from the NMFS Exploratory Fishing and Gear Research Base at Pascagoula, Miss. (now Southeast Fisheries Center, Pascagoula Laboratory) for the area from the Straits of Florida to Cape Hatteras,

TABLE 2.—Area of sampling strata.

Stratum number	Area (mi²)	Stratum number	Area (mi²)	Stratum number	Area (mi²)
1	2,516	21	424	40	578
2	2,078	22	454	41	3,752
3	566	23	1,016	42	589
4	188	24	2,569	61	1,318
5	1,475	25	390	62	243
6	2,554	26	1,014	63	86
7	514	27	720	64	60
8	230	28	2,249	65	2,832
9	1,522	29	3,245	66	555
10	2,722	30	619	67	86
11	622	31	2,185	68	52
12	176	32	712	69	2,433
13	2,374	33	816	70	1,024
14	656	34	1,766	71	281
15	230	35	1,097	72	105
16	2,980	36	4,069	73	2,145
17	360	37	2,108	74	1,273
18	172	38	2,560	75	139
19	2,454	39	730	76	60
20	1,221				

and from the Fisheries Research Board of Canada Biological Station at St. Andrews, New Brunswick for the area off northeastern Nova Scotia, including Banquereau, Sable Island Bank, Western Bank, and the Gulf of St. Lawrence. Distributional data from south of Cape Hatteras were collected from 1961 to 1968, and data from northeastern Nova Scotia and the Gulf of St. Lawrence were collected from 1960 to 1970. Several vessels and different types of trawling gear were used.

Small specimens of *R. erinacea* and *R. ocellata* are difficult to distinguish (McEachran and Musick 1973), and field personnel often misidentified them. Records of species not verified by the authors were evaluated with discretion. Records were not used when the correct species could not be determined.

RESULTS AND DISCUSSION

Seasonal bottom isotherms were plotted from the RV *Albatross IV* surveys of 1969 because this was the only year that included a summer cruise, and the winter and autumn temperature profiles appeared typical. Temperatures were lowest during the winter survey, and isotherms in the mid-Atlantic Bight tended to parallel the coast line (Figure 2), as stated by Bigelow (1933). During the summer cruise a mass of cold water, surrounded by warmer water, extended southward almost to the Virginia Capes, a condition previously described by Bigelow (1933). Temperatures were warmest during the autumn survey.

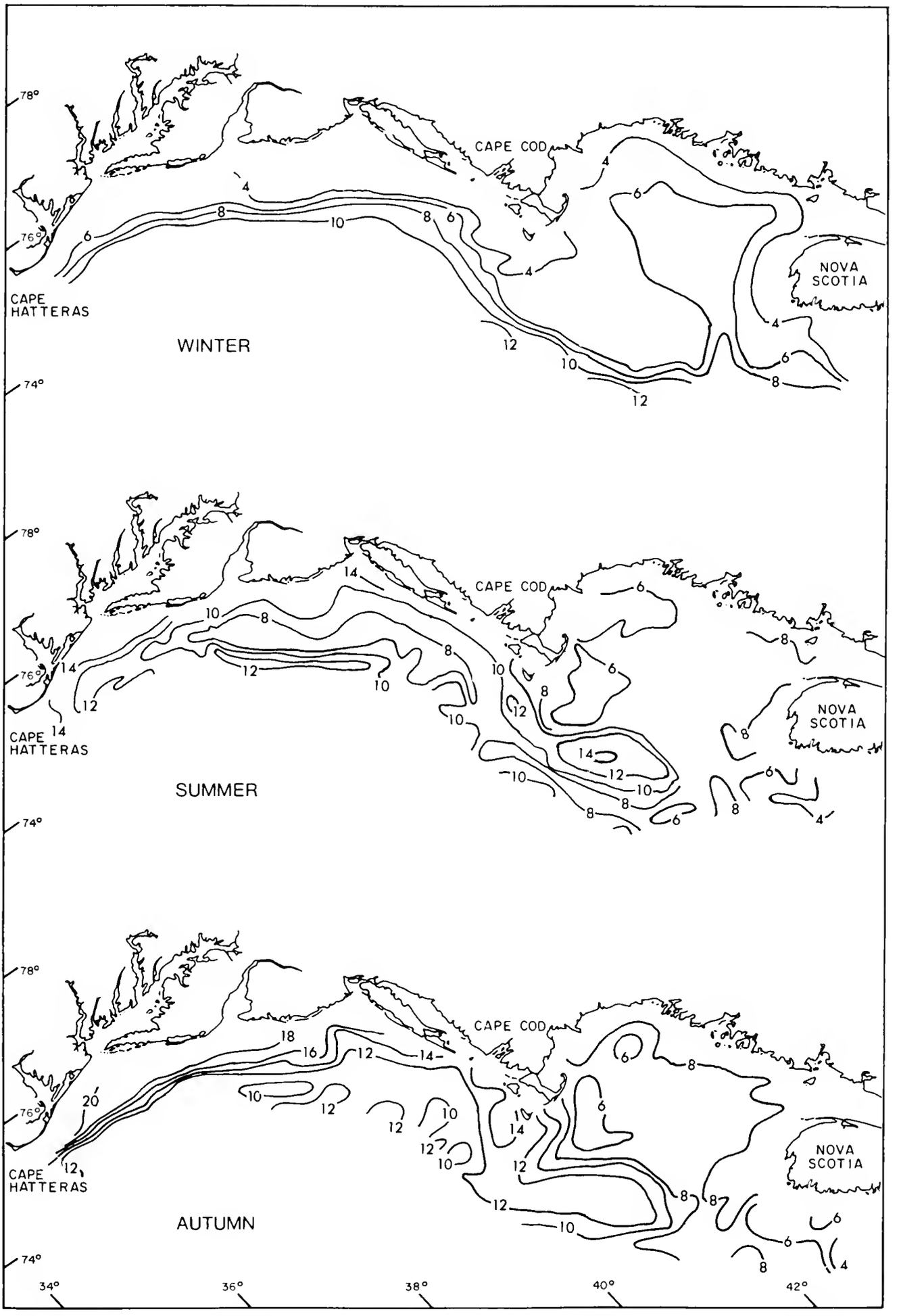

FIGURE 2.—Bottom isotherms plotted from measurements taken during winter, summer, and autumn 1969 surveys of the RV *Albatross IV*. Temperatures are in degrees Celsius.

The summer survey was conducted during July and August, and the autumn survey during October and November (Table 1). Waters of intermediate depths of both the mid-Atlantic Bight and Georges Bank reach their maximum temperatures in October (Bigelow 1927, 1933; Schopf and Colton 1966).

Length frequencies by strata sets revealed that small to large specimens of each species were found together and all length sizes were pooled for the distributional analyses of each species. Small specimens of *R. erinacea* and *R. ocellata* were seldom captured. The young of these two species may lie outside the sampling region or may be less vulnerable to the gear used. Richards et al. (1963) also noted the absence of young *R. erinacea* on the fishing grounds of Block Island and Long Island sounds where the larger individuals were abundant.

Charts showing the distribution by strata, and histograms showing the distribution by temperature were illustrated for the *Albatross IV* cruises of 1969. Only the four most abundant species (*R. erinacea, R. ocellata, R. senta,* and *R. radiata*) were included. Distribution by temperature and depth zones was illustrated for two species (*R. eglanteria* and *R. garmani*) captured during the VIMS survey of the Chesapeake Bight.

Raja eglanteria

Raja eglanteria was captured from the southern section of the mid-Atlantic Bight to about midway along the eastern coast of Florida. A few individuals were taken in the southern section of the mid-Atlantic Bight on all *Albatross IV* cruises, except for summer 1969 and winter 1970. During the VIMS survey of the Chesapeake Bight *R. eglanteria* was more abundant in shoal water during the spring and summer than during the autumn and winter (Figure 3) and was more abundant in the Chesapeake Bight during the summer and autumn than in the winter and spring. It was captured between 5° and 26°C in the Chesapeake Bight and was most abundant between 9° and 20°C (Figure 4). South of Cape Hatteras it was taken from 9° to 27°C. Over its entire range, it was most abundant at depths less than 111 m. *Raja eglanteria* was captured only at 9 of the 676 stations which were in water deeper than 110 m. It was taken at 5 of the 43 deeper stations during the VIMS survey but at only 4 of the 633 deeper stations south of Cape Hatteras, thus it has a greater tendency to inhabit deeper water in the northern part of its range.

Raja eglanteria, a Carolinian species in the sense of Johnson (1934) and Hedgpeth (1957), occurs north of Cape Hatteras all year but is abundant there only during the warmer months. Bigelow and Schroeder (1953) stated that it is most abundant from the sublitoral zone to about 55 m. However, Edwards et al. (1962) captured it in 280 and 329 m off Cape May, N.J. during the winter. In autumn, *R. eglanteria* leaves the embayments and shallow areas of the mid-Atlantic Bight (Bigelow and Schroeder 1953; Schwartz 1961; Massman 1962; Fitz and Daiber 1963; Schaefer 1967) and moves offshore and southward. *Raja eglanteria* was not captured in the mid-Atlantic Bight during the summer *Albatross IV* cruise probably because the species is concentrated then at depths less than 27 m. Apparently many individuals that summer in the southern part of the Chesapeake Bight move around Cape Hatteras during the autumn or early winter. The individuals south of Cape Hatteras inhabit slightly warmer water as suggested by Bigelow and Schroeder (1953) and do not appear to move into deeper water during the winter. Dahlberg and Odum (1970) reported that this species is resident year-round in Georgia estuaries.

Raja garmani

Raja garmani was captured in deep water from Nantucket Shoals to the Straits of Florida. Between Nantucket Shoals and Cape Hatteras it was most abundant in the southern section of Chesapeake Bight. Over the Chesapeake Bight it was found between 33 and 196 m and generally deeper than 73 m (Figure 5), and appeared to move shoreward in the summer. In the Chesapeake Bight *R. garmani* was captured at temperatures of 6° to 17°C and was most abundant bewteen 9° and 13°C (Figure 6). Between Cape Hatteras and Georgia it was found in 66 to 123 m at 17°C; off Georgia and northern Florida it was captured in 77 to 155 m at 11° to 19°C. From northern Florida to the Straits of Florida it occurred in 99 to 366 m at 17°C, and all but one of the captures were in 183 to 366 m.

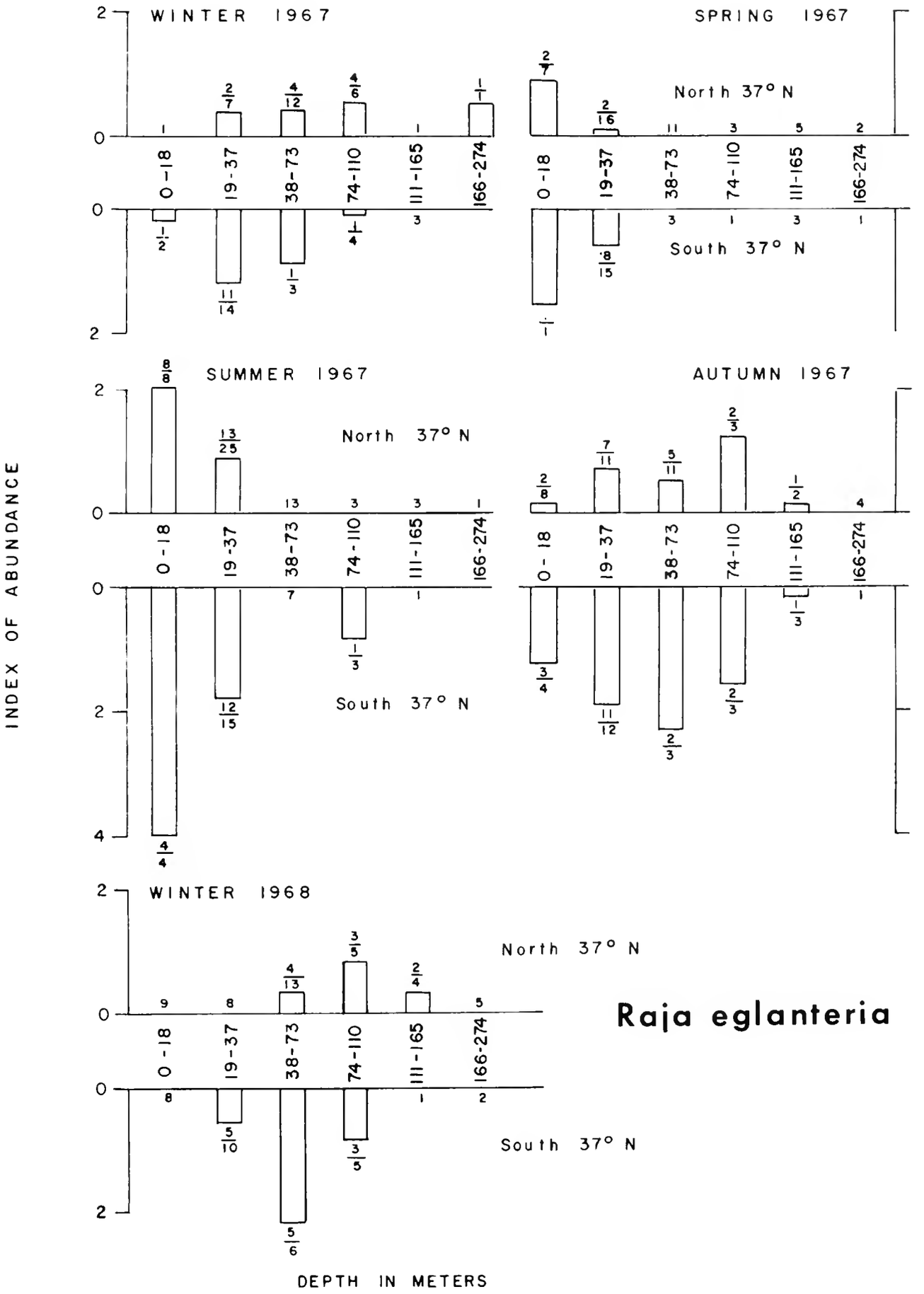

FIGURE 3.—Index of abundance (geometric mean) of *Raja eglanteria* captured in Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of lat. 37°N were analyzed separately. The fraction over each bar is the ratio of the number of stations at which the species was captured to the total number of stations in each stratum. Whole numbers represent the number of stations in the strata in which no specimens were captured.

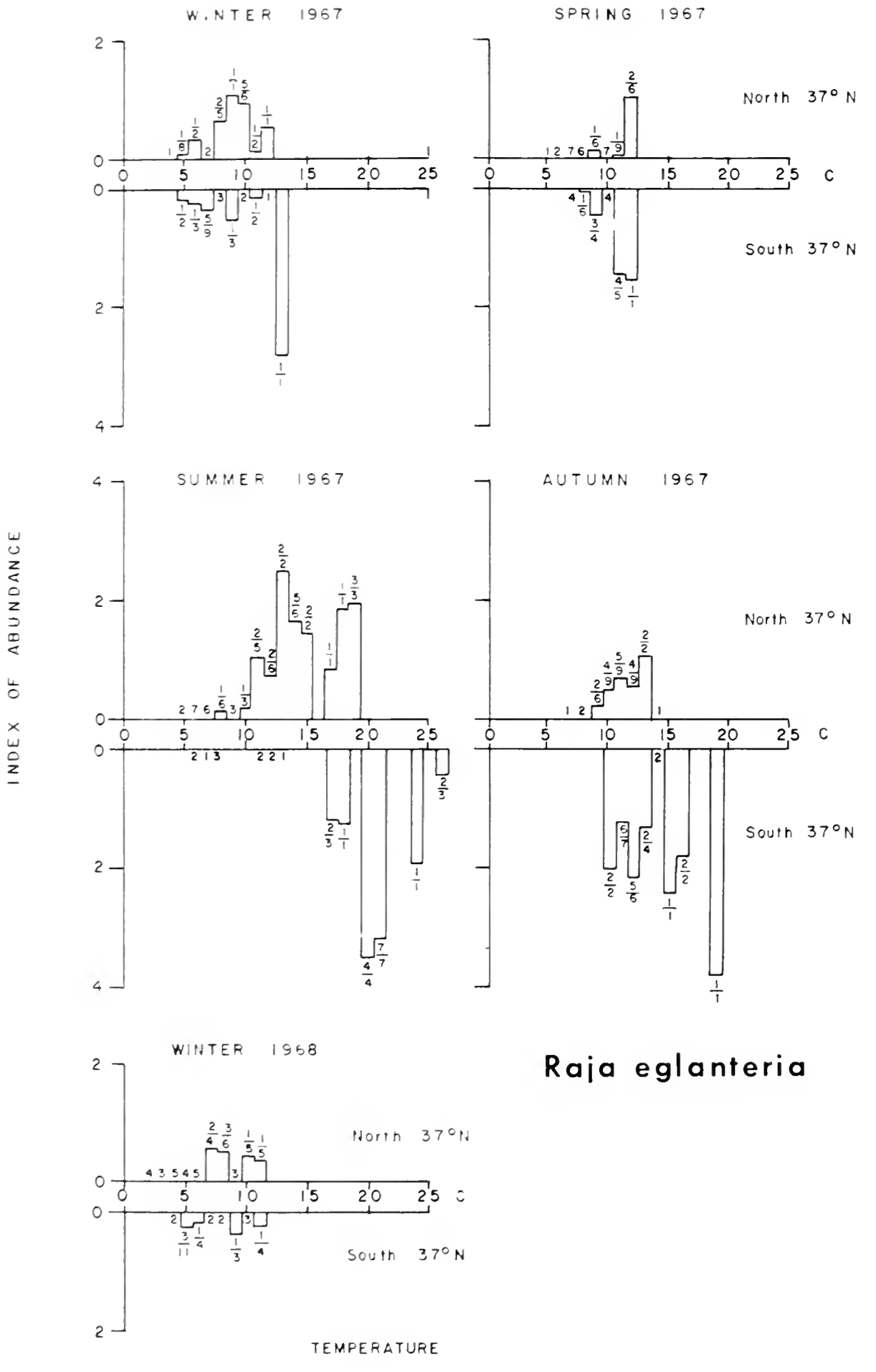

FIGURE 4.—Index of abundance (geometric mean) of *Raja eglanteria* captured in the Chesapeake Bight during each cruise within temperature intervals of 1°C. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for explanation of fractions and whole numbers.

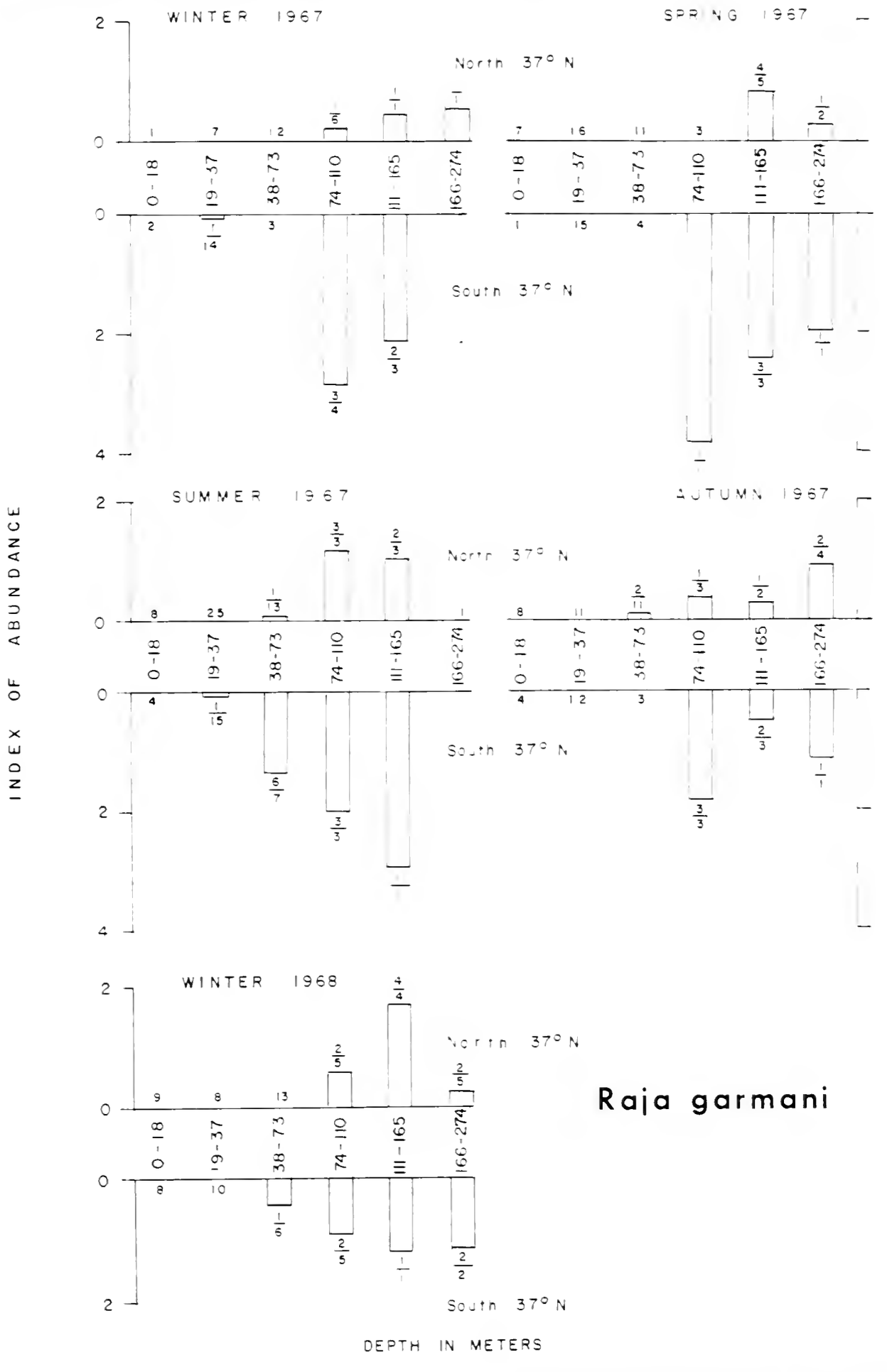

FIGURE 5.—Index of abundance (geometric mean) of *Raja garmani* captured in the Chesapeake Bight during each cruise within each depth stratum. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for an explanation of fractions and whole numbers.

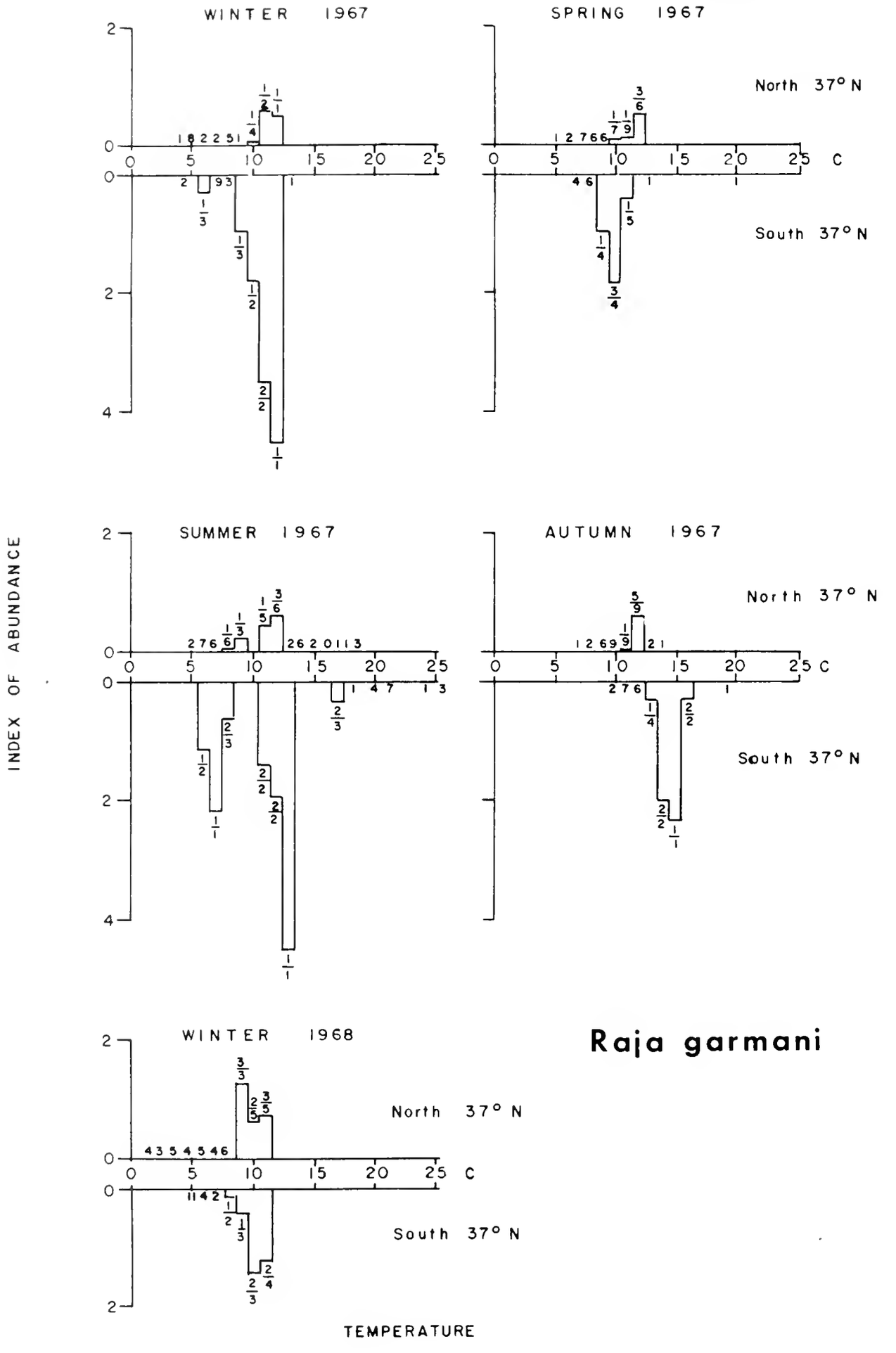

FIGURE 6.—Index of abundance (geometric mean) of *Raja garmani* captured in the Chesapeake Bight during each cruise within temperature intervals of 1°C. Data collected north and south of lat. 37°N were analyzed separately. See Figure 3 for explanation of fractions and whole numbers.

Raja garmani probably does not occur regularly on the eastern slope of Georges Bank, contrary to Schroeder (1955), because no specimens were captured there during the *Albatross IV* cruises. The depth and temperature ranges of 51 to 494 m and 5.3° to 15°C given by Bigelow and Schroeder (1953) are close to those for the area north of Cape Hatteras in the present study. It has more limited depth range and is found in warmer water in the southern part of its range than in the northern part as stated by Bigelow and Schroeder (1953). Staiger (1970) stated that it is found between the 119- and 366-m isobaths on Pourtales Terrace, and north of Pourtales Terrace it occurs in 183 m up the coast of Florida. This species appears to have separate populations, one north and the other south of Cape Hatteras. North of Cape Hatteras mature specimens are 335 mm TL (McEachran 1970) to 439 mm TL and south of Cape Hatteras they are mature between 250 and 314 mm TL. The differences in temperature ranges north and south of Cape Hatteras may be due to differences in physiological requirements of the two populations.

Raja laevis

Raja laevis was captured from the Gulf of St. Lawrence, along the northeastern coast and offshore banks of Nova Scotia, to the northeastern coast of Florida. During the *Albatross IV* cruises it was taken from the Nova Scotian shelf to the southern section of the mid-Atlantic Bight and was most frequently taken in the northern section of the mid-Atlantic Bight, the eastern part of Georges Bank, eastern Gulf of Maine, and the Nova Scotian shelf. No specimens were obtained from the western Gulf of Maine. Seasonal changes in abundance were not evident. In the Gulf of St. Lawrence, *R. laevis* was found in 315 m at 4.7°C. Off northeastern Nova Scotia it was caught at depths of 24 to 375 m at 1.2° to 10.7°C. Depths and temperatures at capture for the area from southern Nova Scotia to Cape Hatteras ranged from 38 to 351 m and 3° to 20°C. *Raja laevis* was caught in 302 to 368 m off northeastern Florida.

Raja laevis is the most widespread of the species studied, but too few were taken during this study to elaborate on its distribution. Bigelow and Schroeder (1953) stated that this species occurs from the tidemark to about 750 m at 1.2° to 20°C. The southern limit of its range remains in doubt because of the apparent confusion of this species with *R. floridana* which has been captured from Cape Lookout, N.C. to Dry Tortugas, Fla. (Bigelow and Schroeder 1968). *Raja floridana* is very similar to *R. laevis* (Bigelow and Schroeder 1962) and the specimens used to describe *R. floridana* came from some of the same stations at which Bullis and Thompson (1965) listed *R. laevis*. The senior author has examined the specimens identified as *R. laevis* at the United States National Museum and University of Miami School of Marine and Atmospheric Sciences, and all of those from south of Cape Hatteras have proven to be *R. floridana*. Also *R. laevis* does not occur in the species lists of Struhsaker (1969) or Staiger (1970). Thus it is likely that many or all of the records of *R. laevis* from south of Cape Hatteras refer to *R. floridana*.

Raja erinacea

Raja erinacea was recorded from the Gulf of St. Lawrence; off Cape Breton, Nova Scotia; Western Bank; and two specimens were positively identified from Sable Island Bank. It was the most abundant species captured on Georges Bank and in the northern section of the mid-Atlantic Bight. It was rarely taken in the western Gulf of Maine (Figure 7). *Raja erinacea* was most abundant in Chesapeake Bight during the winter and those that remained there during the summer moved into deeper water.

Throughout its range, *R. erinacea* was generally caught at depths less than 111 m, but was occasionally taken at depths greater than 183 m, especially in the northern section of the mid-Atlantic Bight and on Georges Bank where it occurred as deep as 329 m. Edwards et al. (1962) captured *R. erinacea* as deep as 384 m off New Jersey, thus the species is not as restricted to shallow water as stated by Bigelow and Schroeder (1954) who reported that 159 m was the maximum depth of the species. Temperatures at depth of capture ranged from 2° to 19°C with most captures occurring between 2° and 15°C. The recorded temperature range of the species is 1.2°C (Tyler 1971) to 21°C (Bigelow and Schroeder 1953).

Raja erinacea is a Virginian to boreal species whose center of abundance is in the northern section of the mid-Atlantic Bight and on Georges Bank. Only in these areas was it found yearround over almost the entire range of temperatures recorded for the areas (Figures 8-10). In

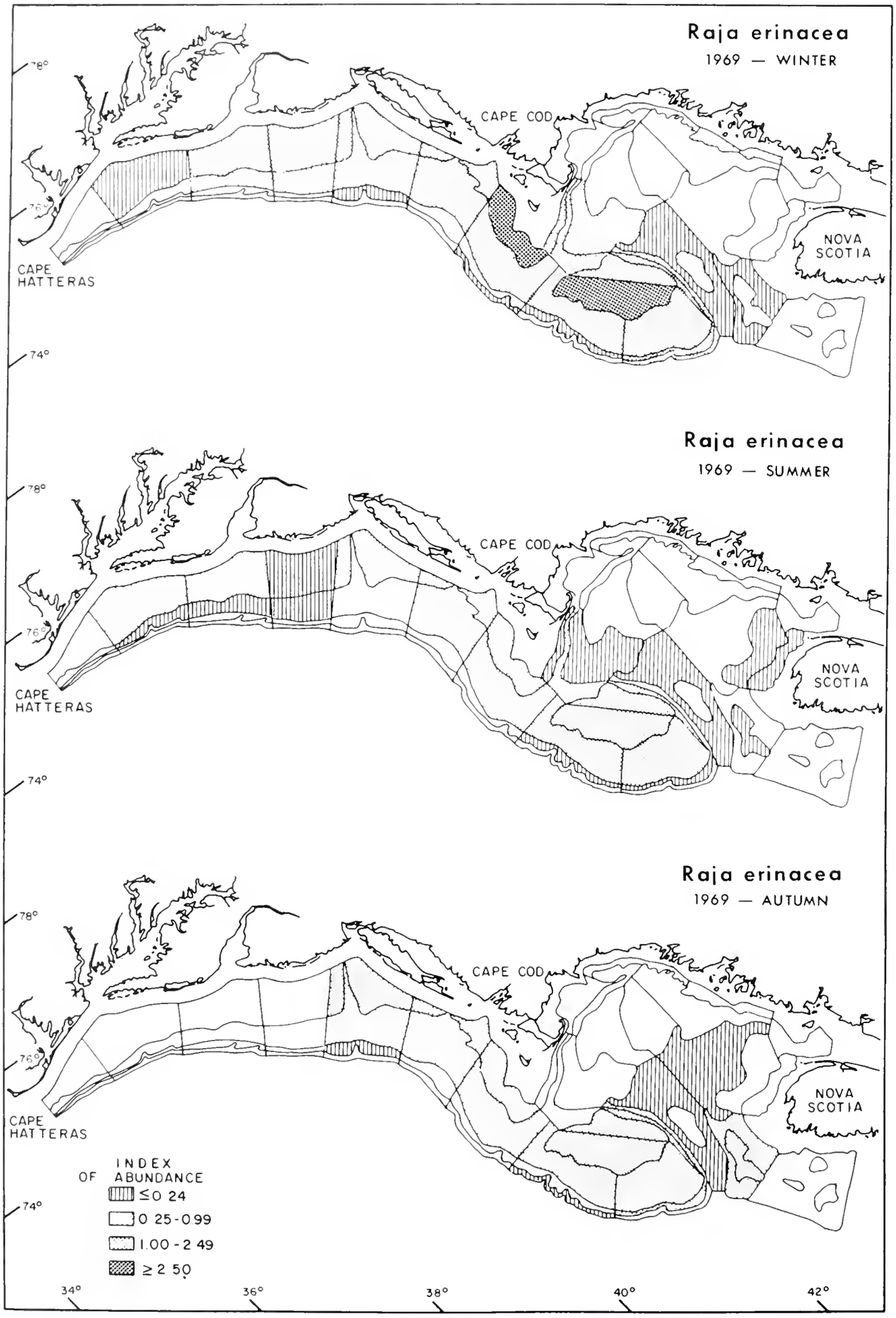

FIGURE 7.—Index of abundance (geometric mean) of *Raja erinacea* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

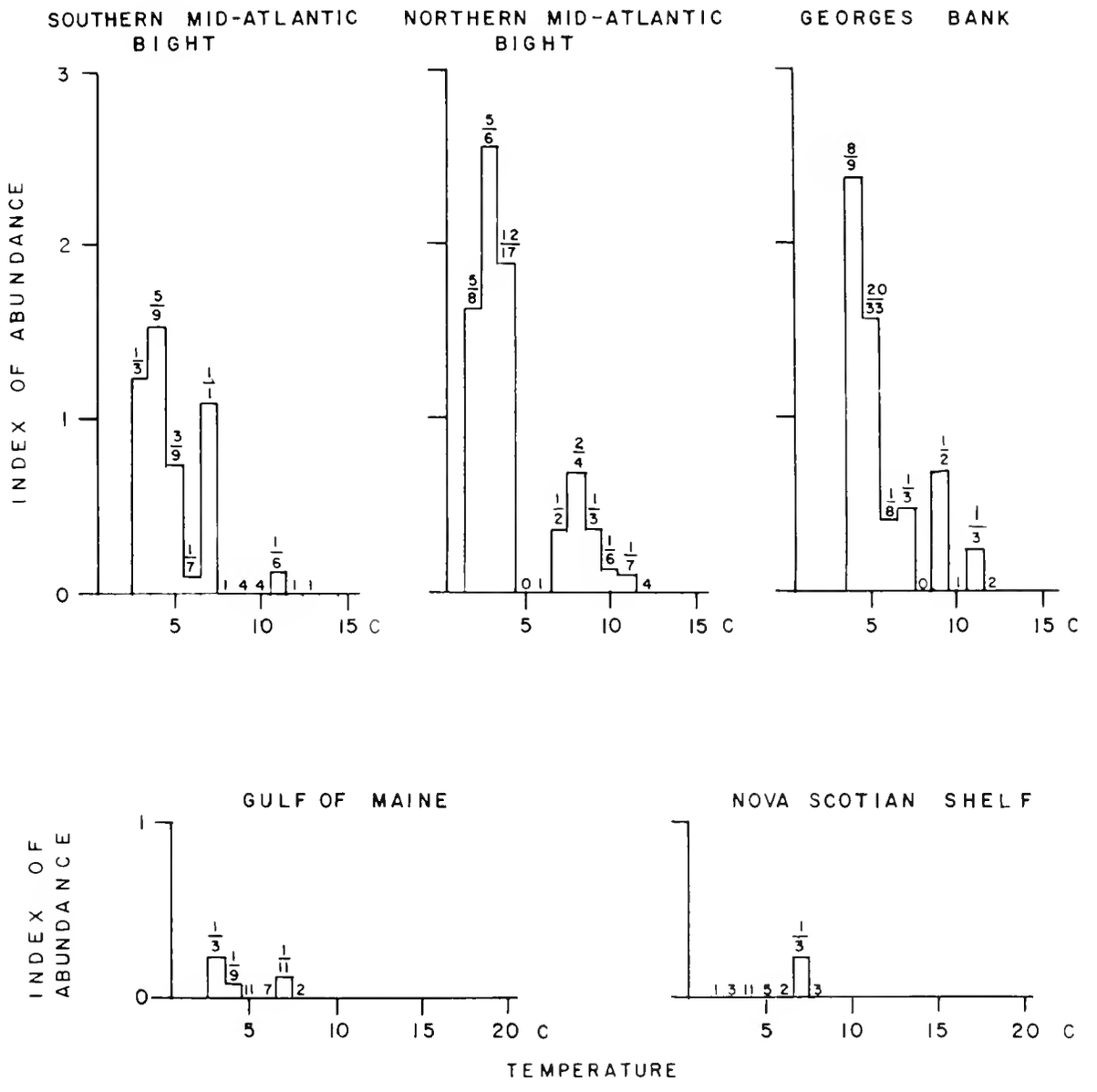

FIGURE 8.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

the southern section of the mid-Atlantic Bight it was usually caught in the lower part of the area's temperature range, and on the Nova Scotian shelf in the upper part of the temperature range.

Along the inshore fringe of its range the species moves onshore and offshore with seasonal temperature changes as stated by Bigelow and Schroeder (1953); Merriman et al. (1953); Fitz and Daiber (1963); Richards (1963); Schaefer (1967); and Tyler (1971, 1972). *Raja erinacea* also moves north and south with seasonal temperature changes along the southern fringe of its range. Contrary to Bigelow and Schroeder (1953) and Leim and Scott (1966), *R. erinacea* probably does not regularly occur off Nova Scotia north of LaHave Bank, and it may be entirely absent in the Gulf of St. Lawrence (McEachran 1973).

Raja ocellata

Raja ocellata was frequently taken in the Gulf of St. Lawrence, off northeastern Nova Scotia, and the offshore banks of Banquereau, Sable Island, and Western Bank. It was second to *R. erinacea* in abundance on Georges Bank and in the northern section of the mid-Atlantic Bight (Figure 11). *Raja ocellata* was much more abundant in the southern section of the mid-Atlantic Bight during the winter than during the remainder of the year. This species was most frequently captured in water shallower than 111 m, but was occasionally caught deeper than the maximum depth of 110 m recorded by Bigelow and Schroeder (1953). In the Gulf of Maine it was taken at 205 m, and in the Gulf of St.

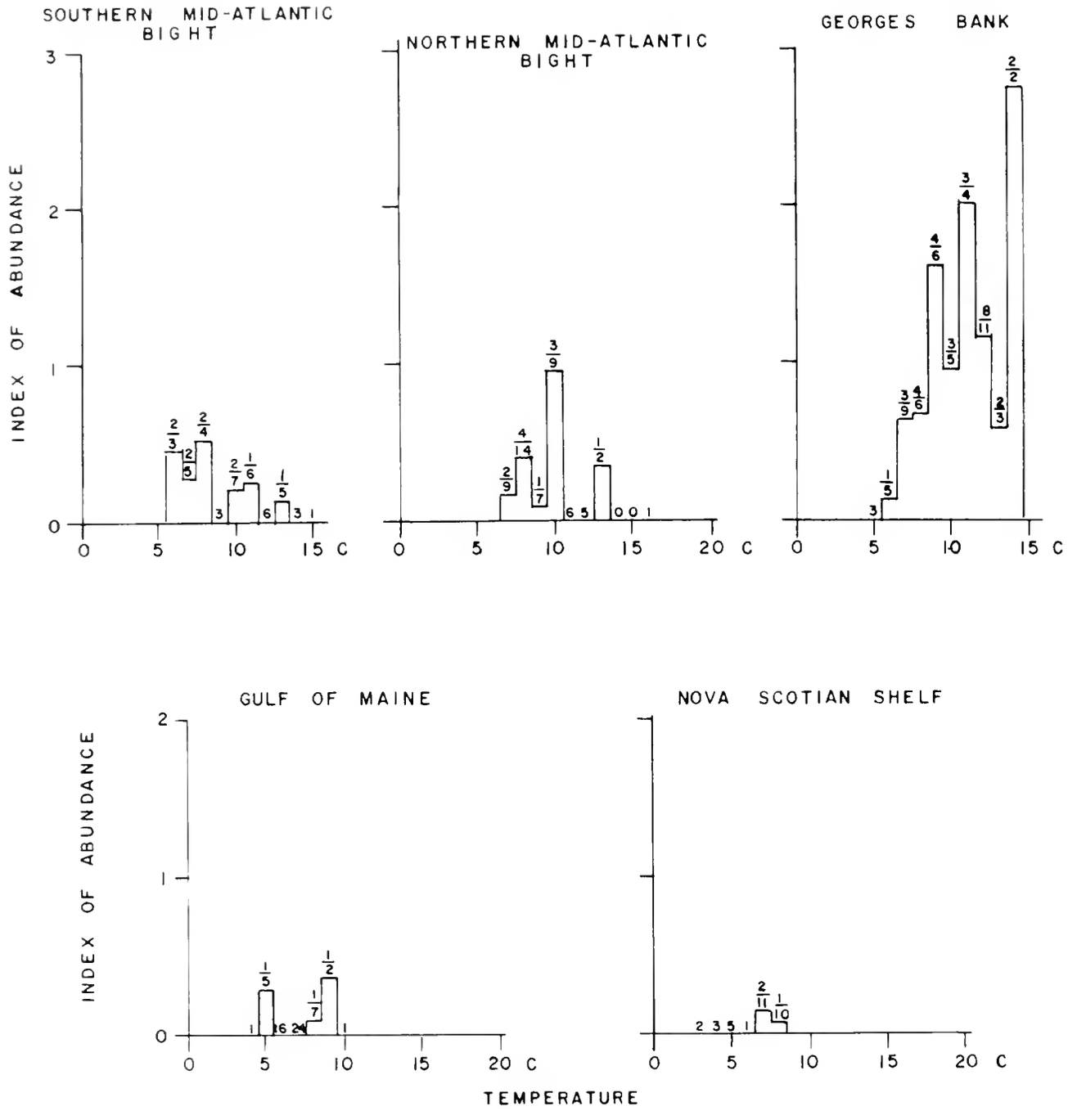

FIGURE 9.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Lawrence as deep as 371 m. Temperatures at depth of capture ranged from −1.2° to 4.8°C in the Gulf of St. Lawrence, 1.1° to 12.7°C off northeastern Nova Scotia, and 2° to 15°C from southern Nova Scotia to Cape Hatteras. Only in the Gulf of St. Lawrence was *R. ocellata* taken at temperatures below its previously recorded temperature range of 1.2°C (Tyler 1971) to 19°C (Bigelow and Schroeder 1953).

Raja ocellata is a Virginian to boreal species whose center of abundance is on Georges Bank and in the northern section of the mid-Atlantic Bight. In both subareas it was found year-round over almost the entire temperature range for the areas (Figures 12-14). It was captured only at the lower part of the temperature range recorded for the southern section of the mid-Atlantic Bight and at higher temperatures recorded for the Nova Scotian shelf.

This species was widespread in the Gulf of St. Lawrence, off northeastern Nova Scotia, and the offshore banks, and it was not as abundant as *R. erinacea* in the southern mid-Atlantic Bight. All reports of *R. erinacea* from the Gulf of St. Lawrence and most records of it from northern Nova Scotia probably refer to *R. ocellata*.

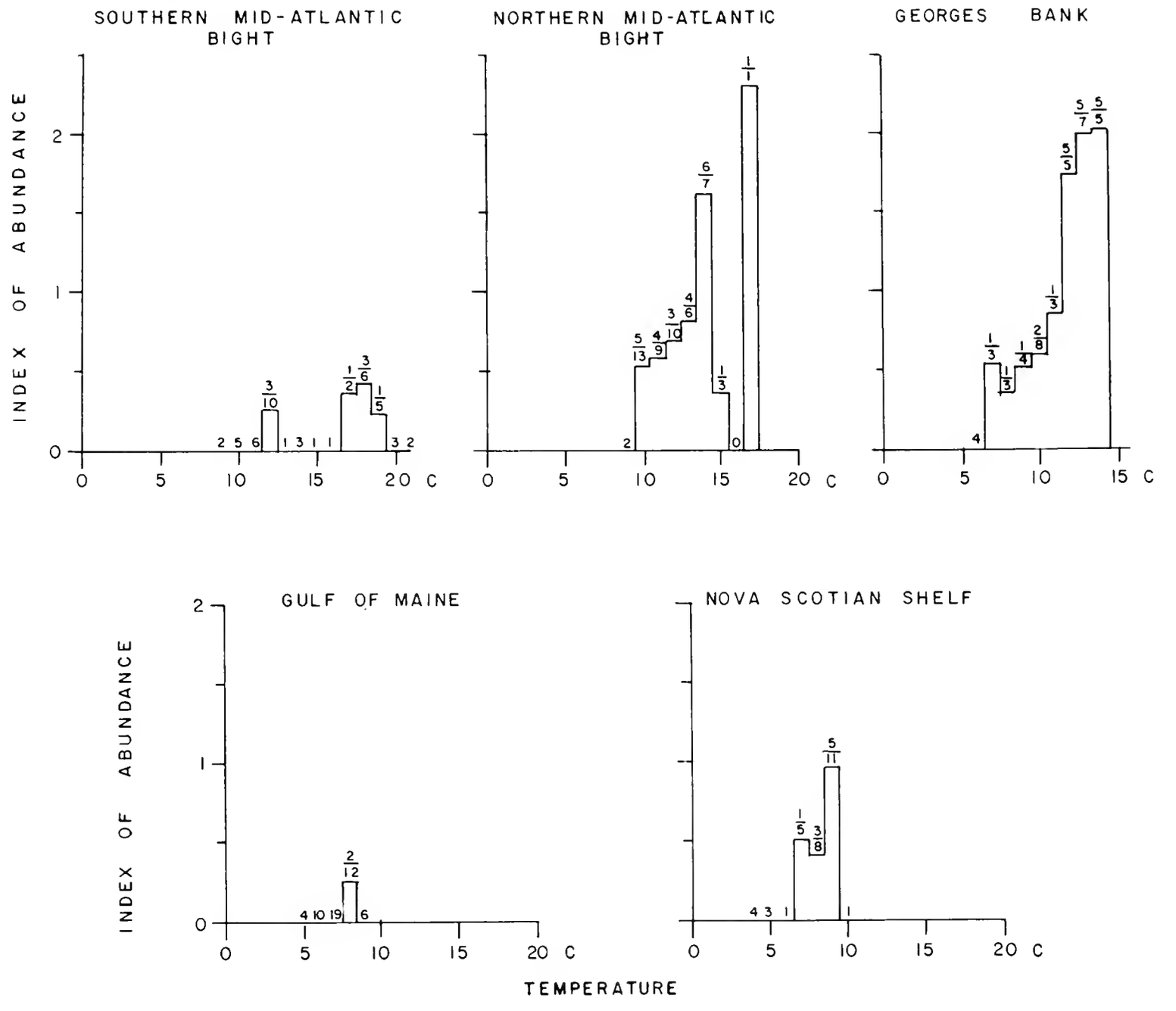

FIGURE 10.—Index of abundance (geometric mean) of *Raja erinacea* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Raja senta

Raja senta was taken in the Gulf of St. Lawrence, along the northeastern coast of Nova Scotia and, contrary to the reports of Bigelow and Schroeder (1953) and Leim and Scott (1966), it was fairly abundant on the offshore banks of Banquereau, Sable Island, and Western. It was found throughout the Gulf of Maine, off southern Nova Scotia, and on Georges Bank (Figure 15). No seasonal trends in abundance were noted. Depth of capture ranged from 31 to 413 m but it was most abundant below 110 m. Bigelow and Schroeder (1953) stated that *R. senta* occurred between 46 and 874 m and was most abundant between 91 and 457 m. This species was found at temperatures from 0.5° to 4.8°C in the Gulf of St. Lawrence, −1.3° to 11.8°C off northeastern Nova Scotia, and 2° to 10°C from southern Nova Scotia to Georges Bank. In the northern part of its range, it was occasionally caught at temperatures less than 2°C, which Bigelow and Schroeder (1953) stated was the minimum temperature for the species.

Raja senta is a boreal species whose center of abundance occurs in the Gulf of Maine, where it is found over the greater part of the range of temperatures (Figures 16-18). It is found only at the lower part of the temperature range on Georges Bank.

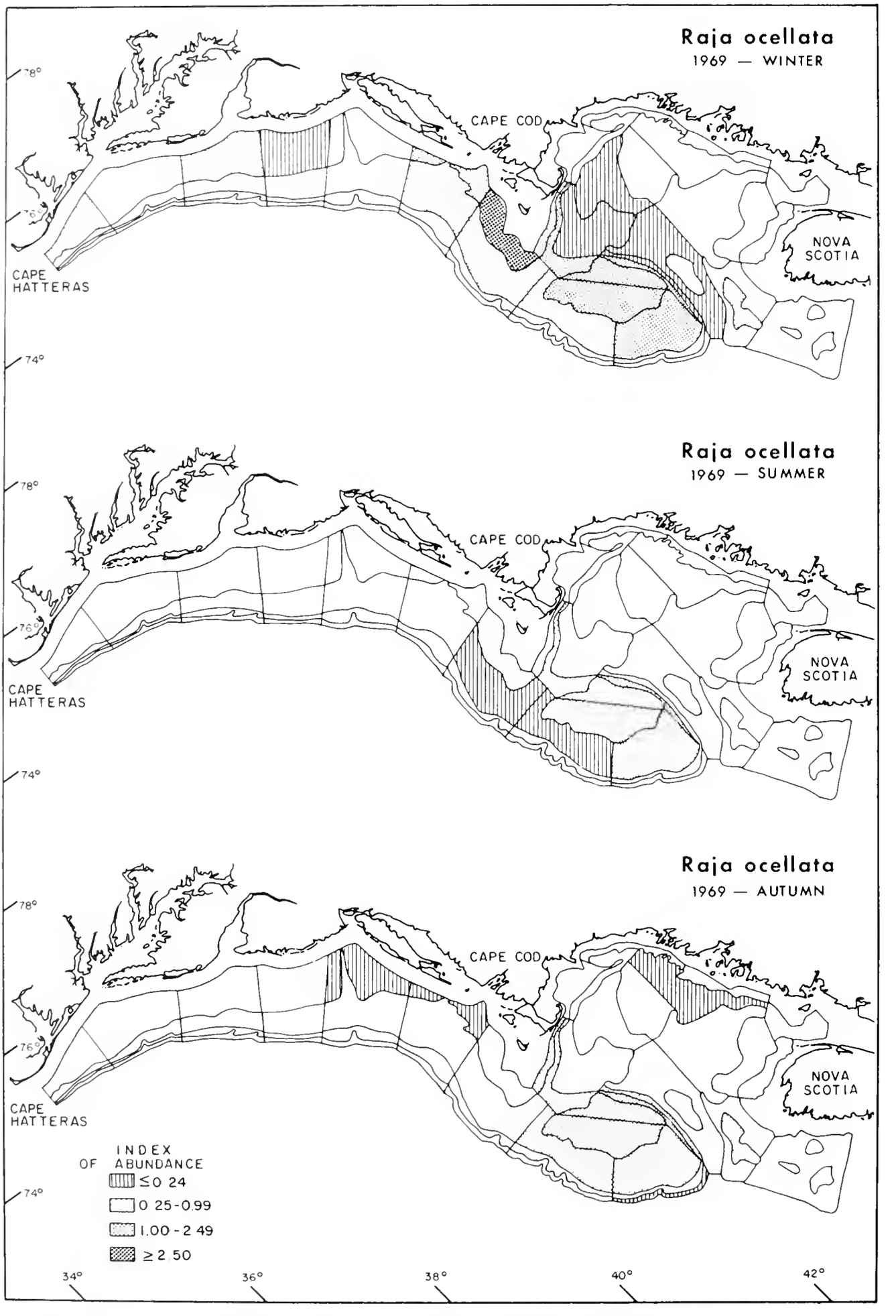

FIGURE 11.—Index of abundance (geometric mean) of *Raja ocellata* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

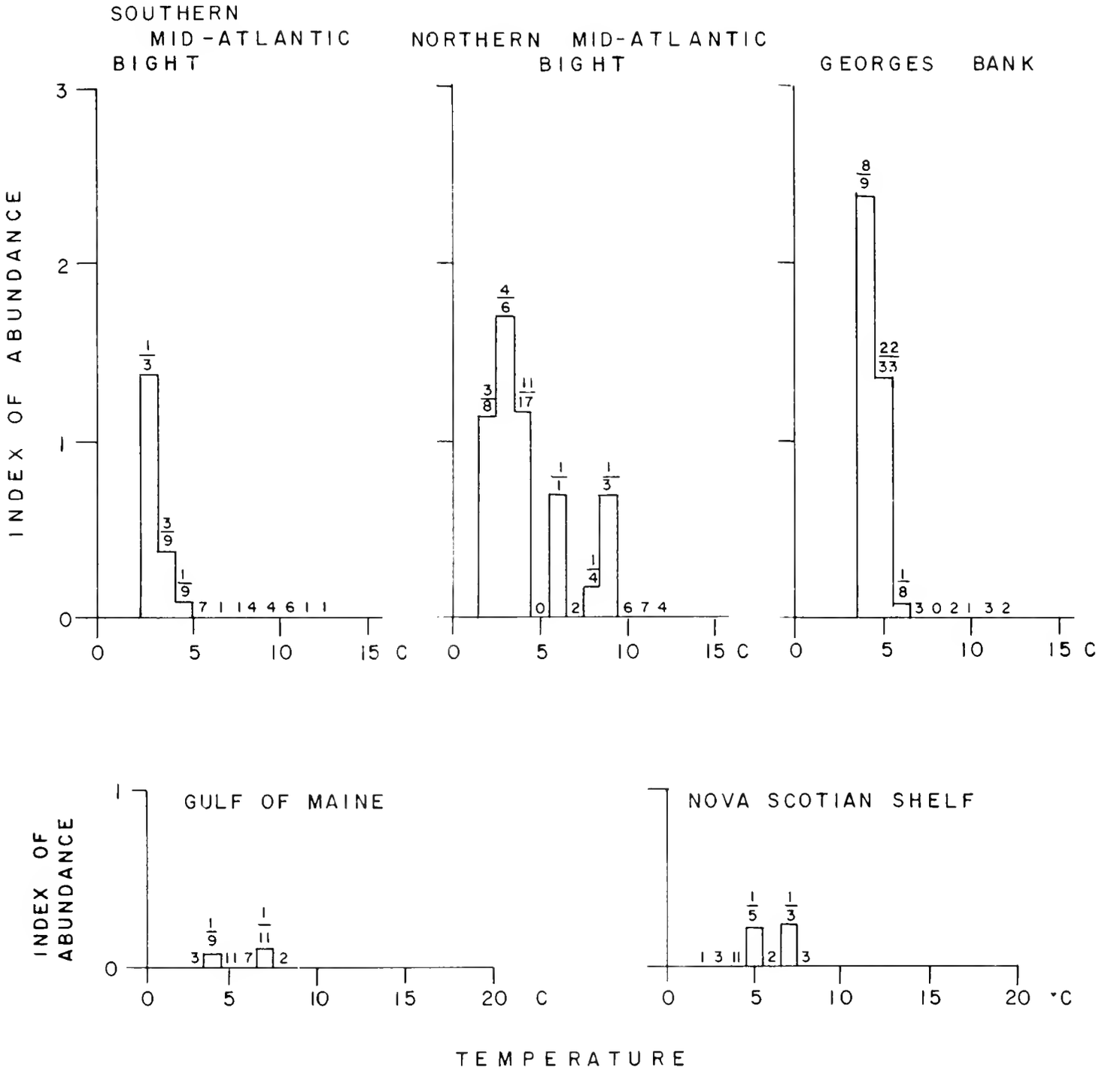

FIGURE 12.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Raja radiata

Raja radiata was the most abundant skate encountered in the Gulf of St. Lawrence, off northeastern and southeastern Nova Scotia, and in the Gulf of Maine. It was widespread along the eastern and northwestern slopes of Georges Bank (Figure 19). *Raja radiata* occurred between 27 and 439 m but was most abundant between 111 and 366 m. Bigelow and Schroeder (1953) listed a depth range of 18 to 896 m for this species in the western Atlantic. Temperatures at which it was captured ranged from −1.3° to 14°C. The previously recorded temperature range was −1.4°C (Backus, 1957) to 10°C (Bigelow and Schroeder 1953).

Raja radiata is a boreal to arctic species whose center of abundance in the western Atlantic extends northward from the Gulf of Maine probably as far as the Gulf of St. Lawrence. It

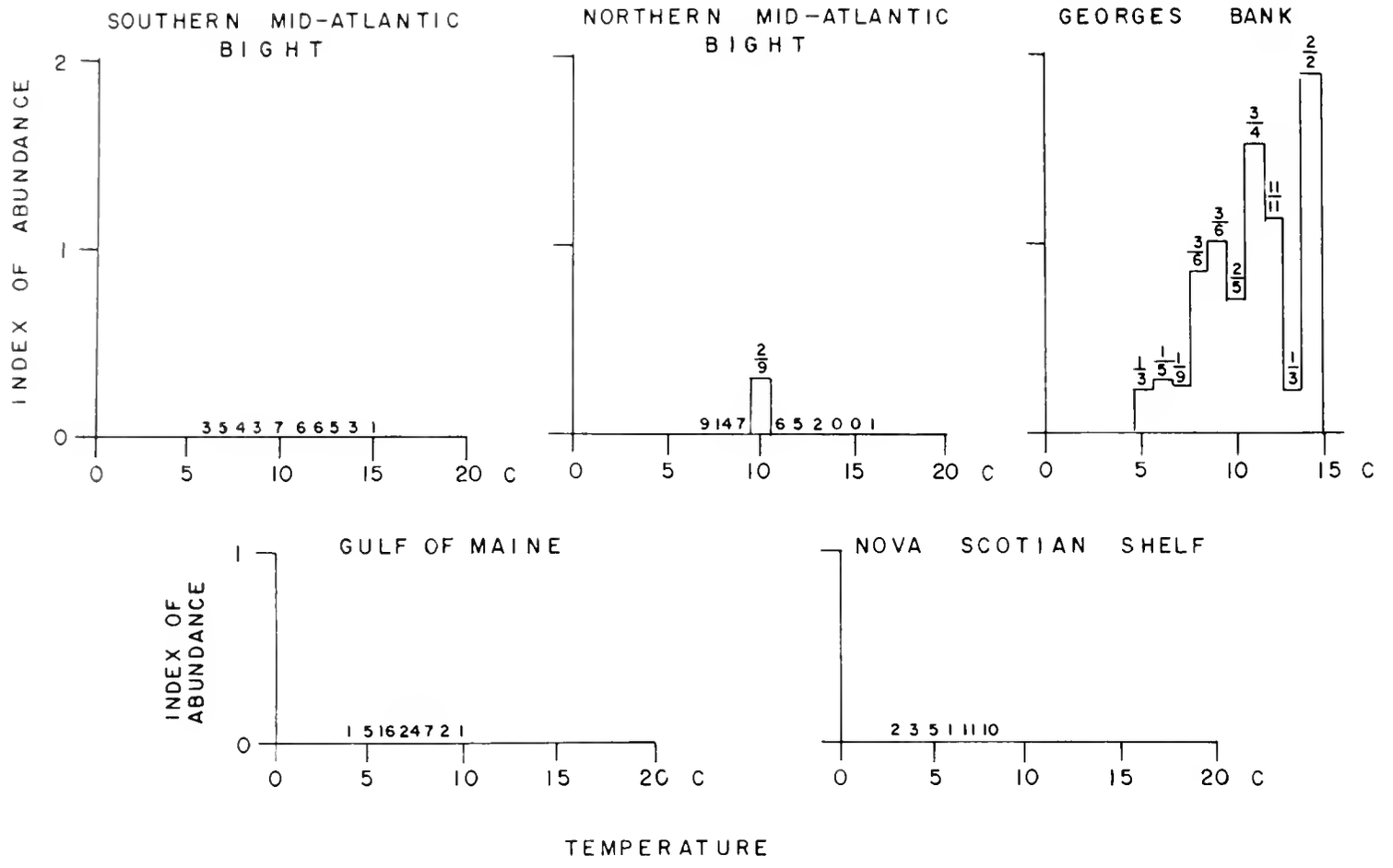

FIGURE 13.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

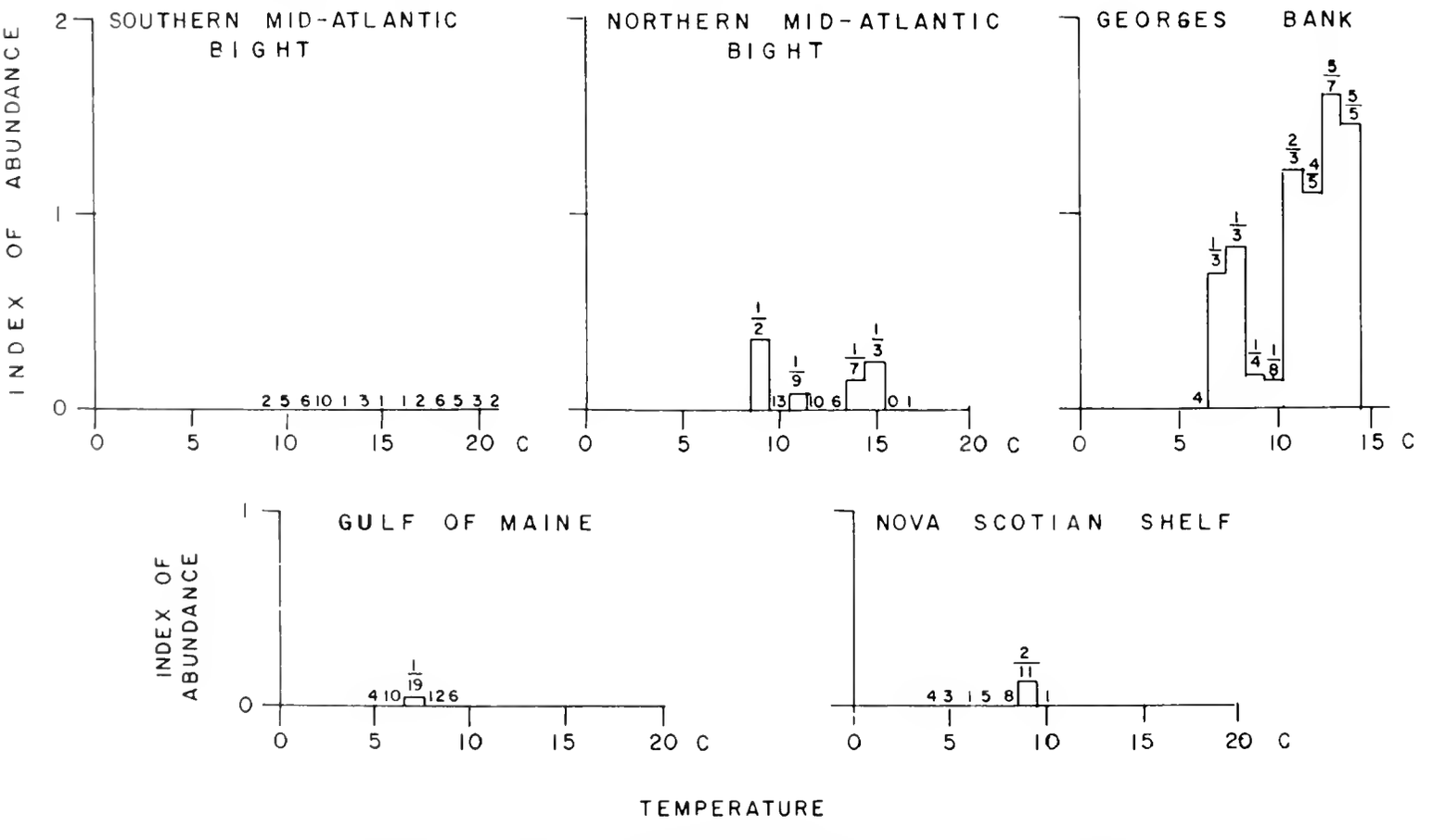

FIGURE 14.—Index of abundance (geometric mean) of *Raja ocellata* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

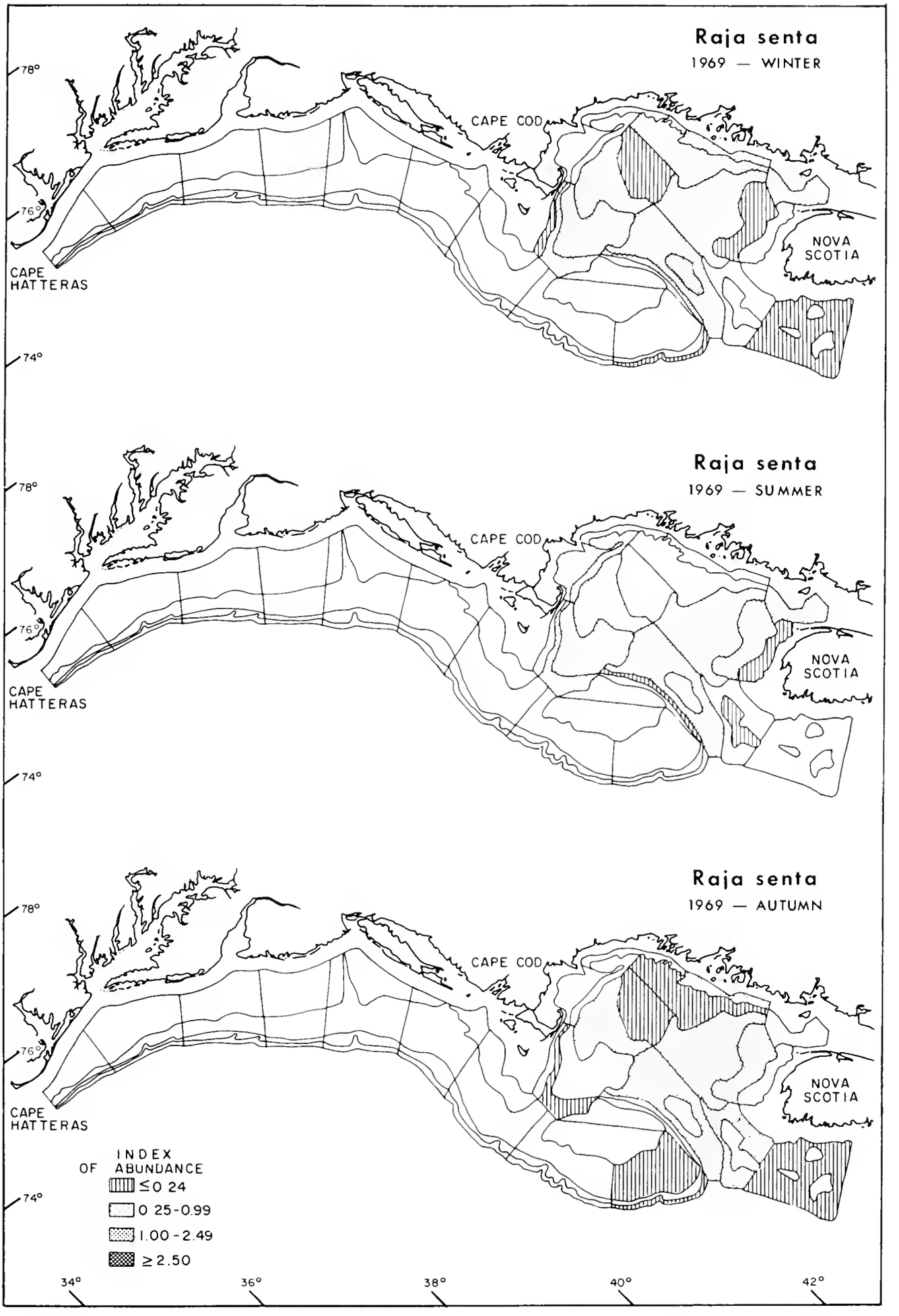

FIGURE 15.—Index of abundance (geometric mean) of *Raja senta* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

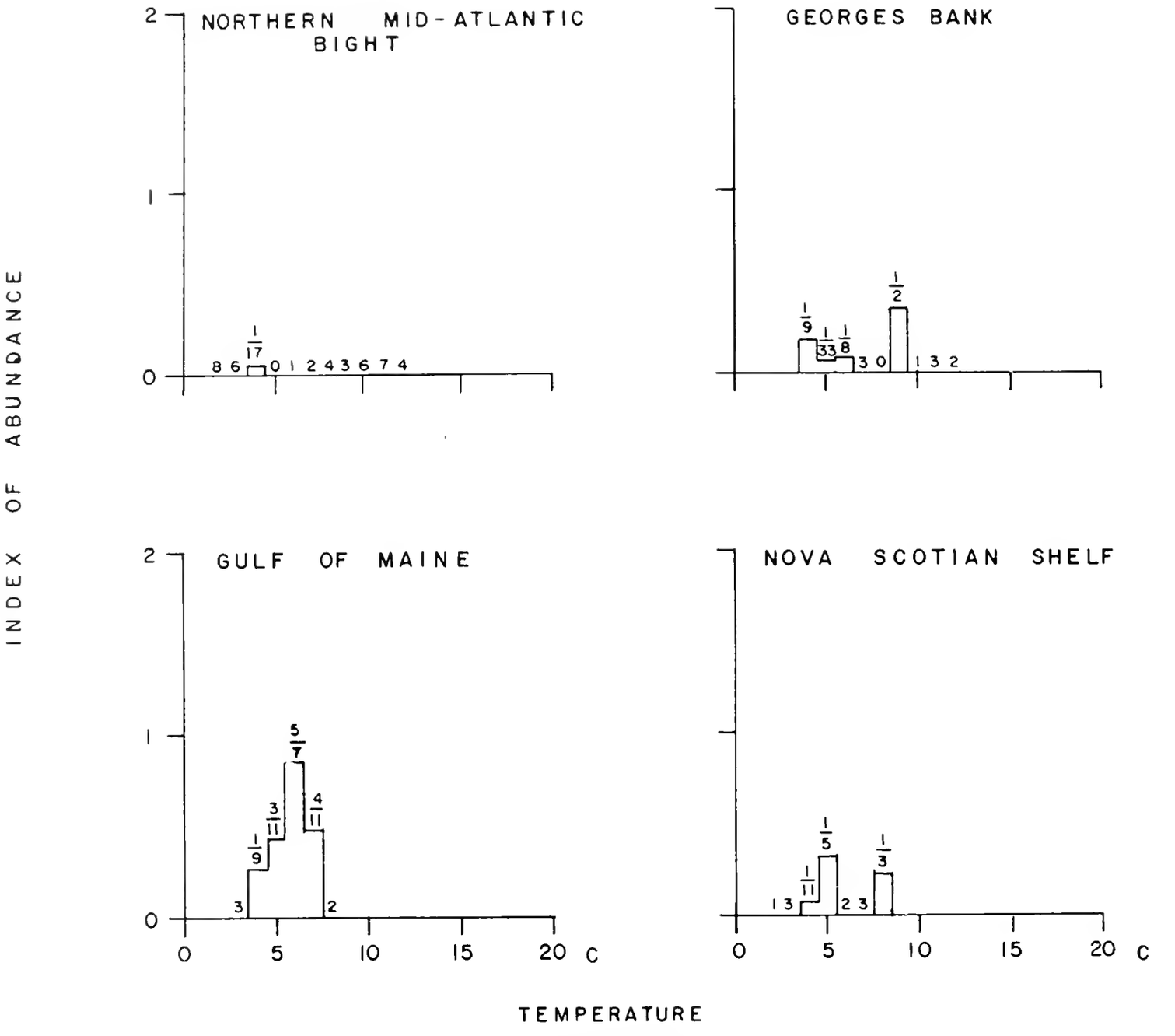

FIGURE 16.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

was found over almost the entire temperature range in the Gulf of Maine and off southeastern Nova Scotia. (Figures 20-22).

INTERSPECIFIC RELATIONSHIPS

Five of the species cooccurred significantly with one or more of the other species (Table 3). *Raja laevis* was associated with both *R. erinacea* and *R. ocellata* for half or more of the *Albatross IV* cruises. *Raja erinacea* and *R. ocellata* cooccurred significantly during all of the survey cruises and were positively associated by abundance. The product moment coefficients for the *Albatross IV* winter, summer, and autumn cruises of 1969 were: $r = 0.656$, 0.471, and 0.640. Percent of the variation in y associated with x was: 43%, 22%, and 41% respectively. The slopes of all three regressions were significant at the 1% probability level. No reason was apparent for the low correlation obtained during the summer cruise. *Raja senta* and *R. radiata* had the highest coefficient of association, and these two species were often negatively associated with *R. erinacea* and *R. ocellata*. *Raja senta* and *R. radiata* were not correlated by numbers; the coefficients for the *Albatross IV* winter, summer, and autumn cruises of 1969 were: 0.310, 0.081, and 0.283. Only a

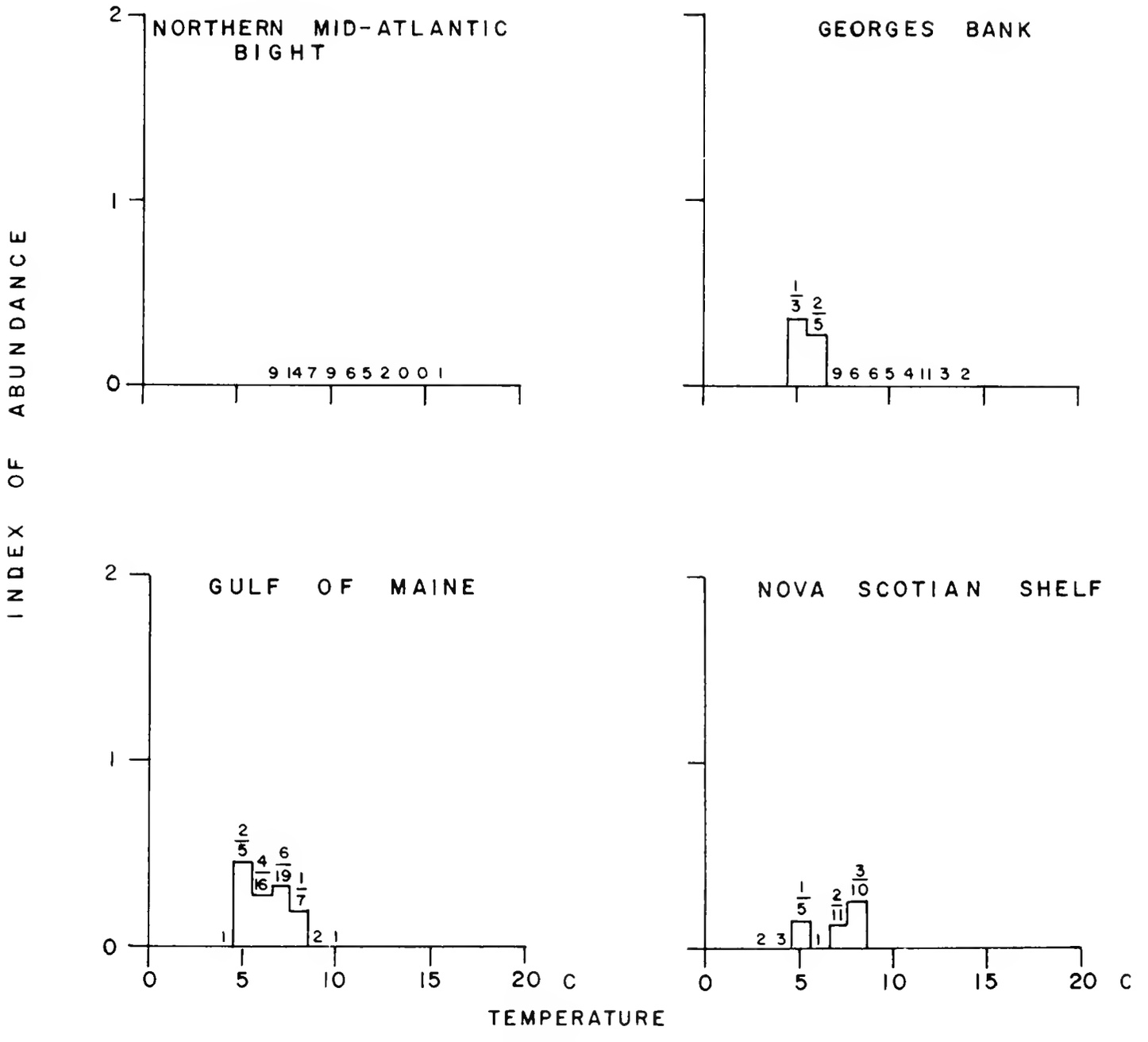

FIGURE 17.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

small part of the variance could be assigned to the correlation, and the slopes were not significant at the 5% probability level.

Raja erinacea and *R. ocellata* are predominantly found at depths less than 111 m in areas which, according to Uchupi (1963) are covered with sand or gravel. They have similar responses to seasonal temperature changes. In the southern periphery of their ranges they move southward during the colder months of the year and offshore and northward during the warmer months of the year. Within their centers of abundance, neither species undergoes a seasonal migration, each being able to tolerate the seasonal temperature extreme. *Raja ocellata* appears to have a slightly lower temperature preference as suggested by the difference in latitudinal distribution of the species. The apparent rareness of the species pair in the Gulf of Maine may be due to insufficient sampling. The shallowest depth zone (27-55 m) was not sampled during the *Albatross IV* cruises. Although the species have similar habitat requirements their positive correlation by numbers suggests that they are not competing for the same resources. Also a study of the food habits of the two species indicates that *R. erinacea* feeds largely on epifaunal organisms, and *R. ocellata* predominately selects infaunal organisms (McEachran 1973).

Raja laevis is found in the same areas as the

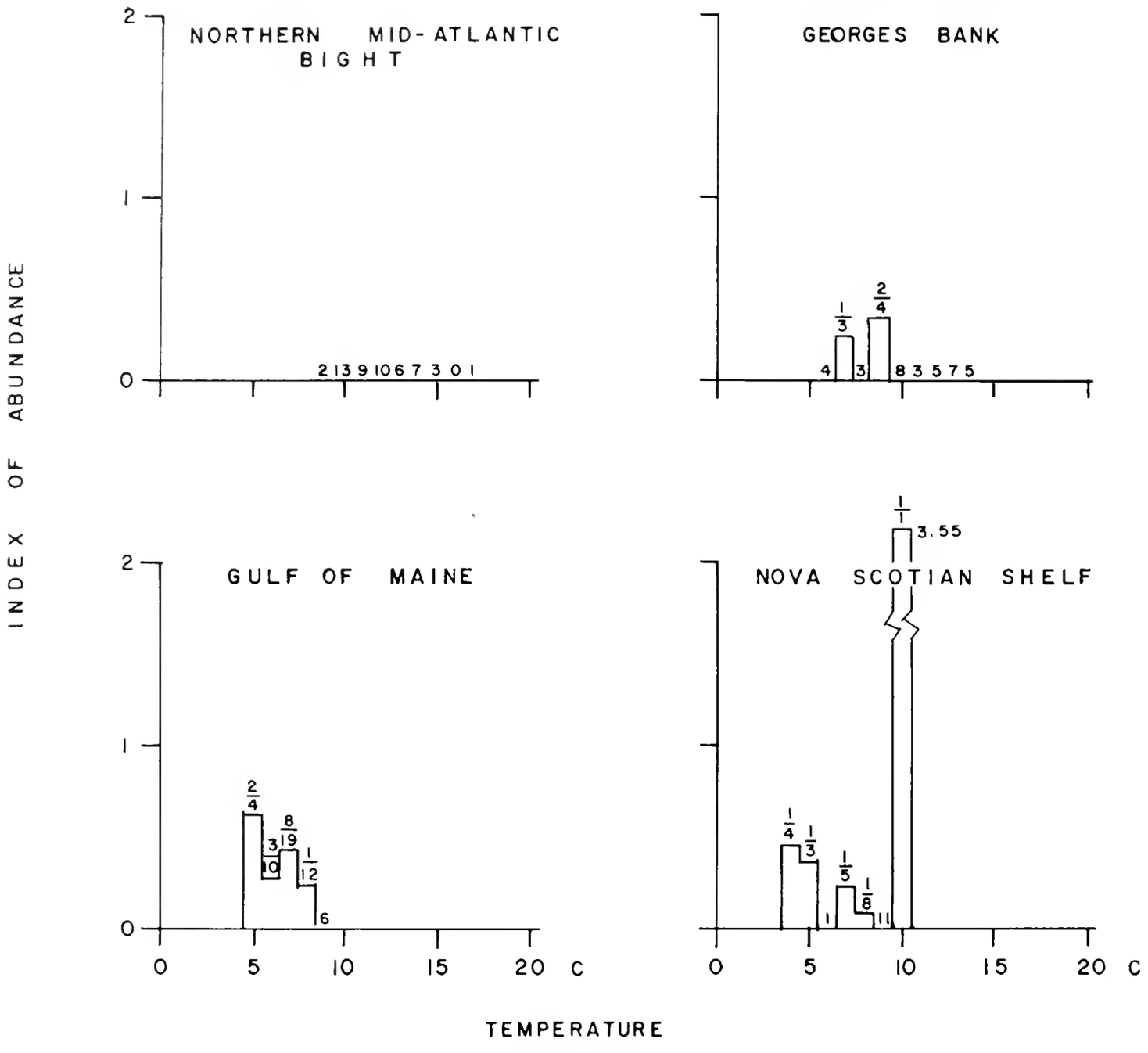

FIGURE 18.—Index of abundance (geometric mean) of *Raja senta* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

above species pair but has wider substratum and depth tolerance. Its low abundance may in part be explained by its considerably larger maximum size (Bigelow and Schroeder 1953) which makes it less available to the sampling gear.

The distribution of the *R. senta-R. radiata* species pair complements that of the *R. erinacea-R. ocellata* species pair. The former is found predominately in areas which, according to Uchupi (1963), were covered with sandy silt to silt and clay. They are taken over a narrower and lower temperature range than *R. erinacea-R. ocellata* and generally occur below 110 m. In the southern periphery of their ranges they are limited to a narrow band on the continental slope where the waters are thermally stable (Bigelow, 1933). Neither species appears to make seasonal movements. *Raja radiata* appears to have a wider temperature range and a lower temperature preference, and it is the more abundant of the two. The low abundance of *R. senta* may explain the lack of a positive or negative correlation by numbers between the species.

SUMMARY

Below the geographical, temperature and depth distribution of each species, based on literature

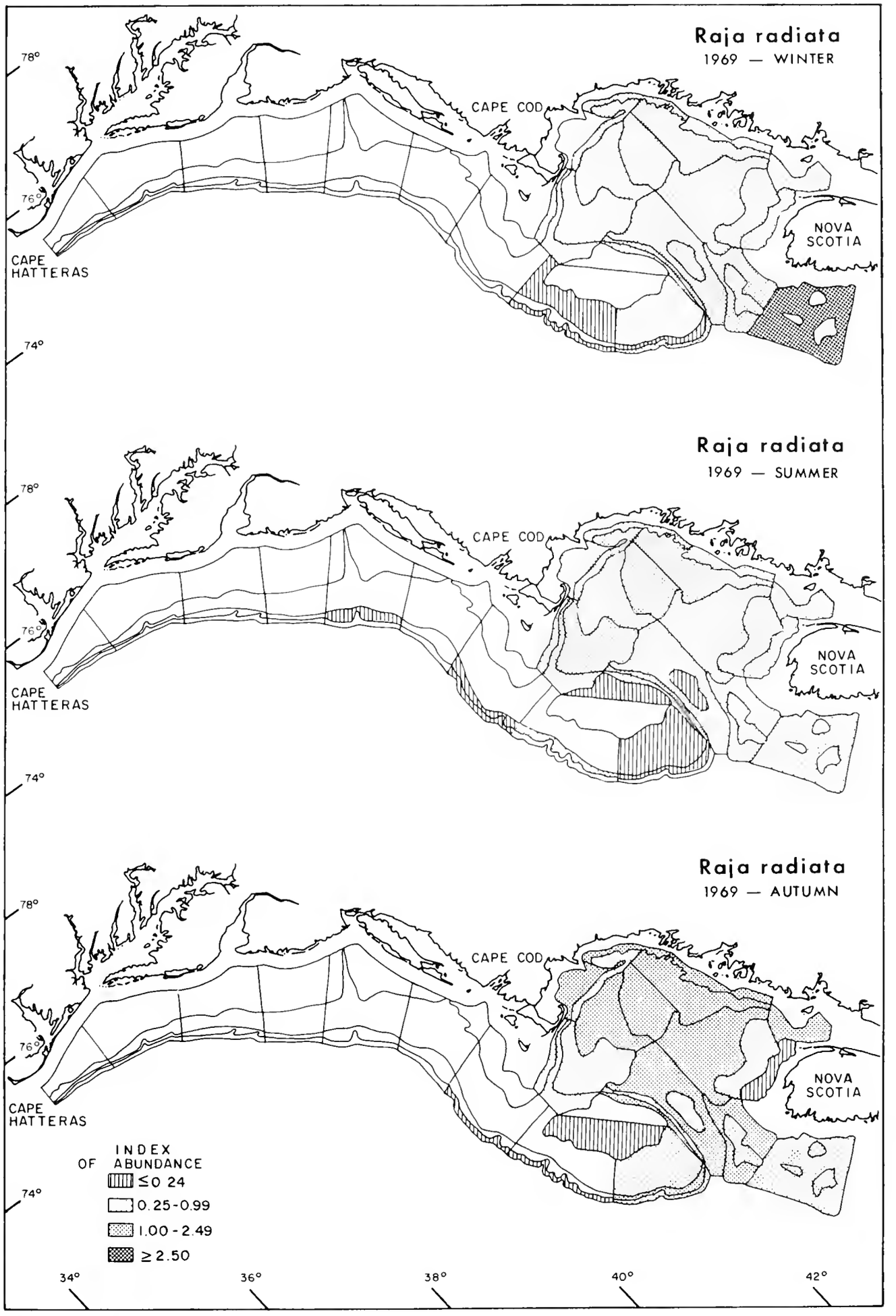

FIGURE 19.—Index of abundance (geometric mean) of *Raja radiata* captured by sampling strata during the winter, summer, and autumn 1969 cruise of the RV *Albatross IV*.

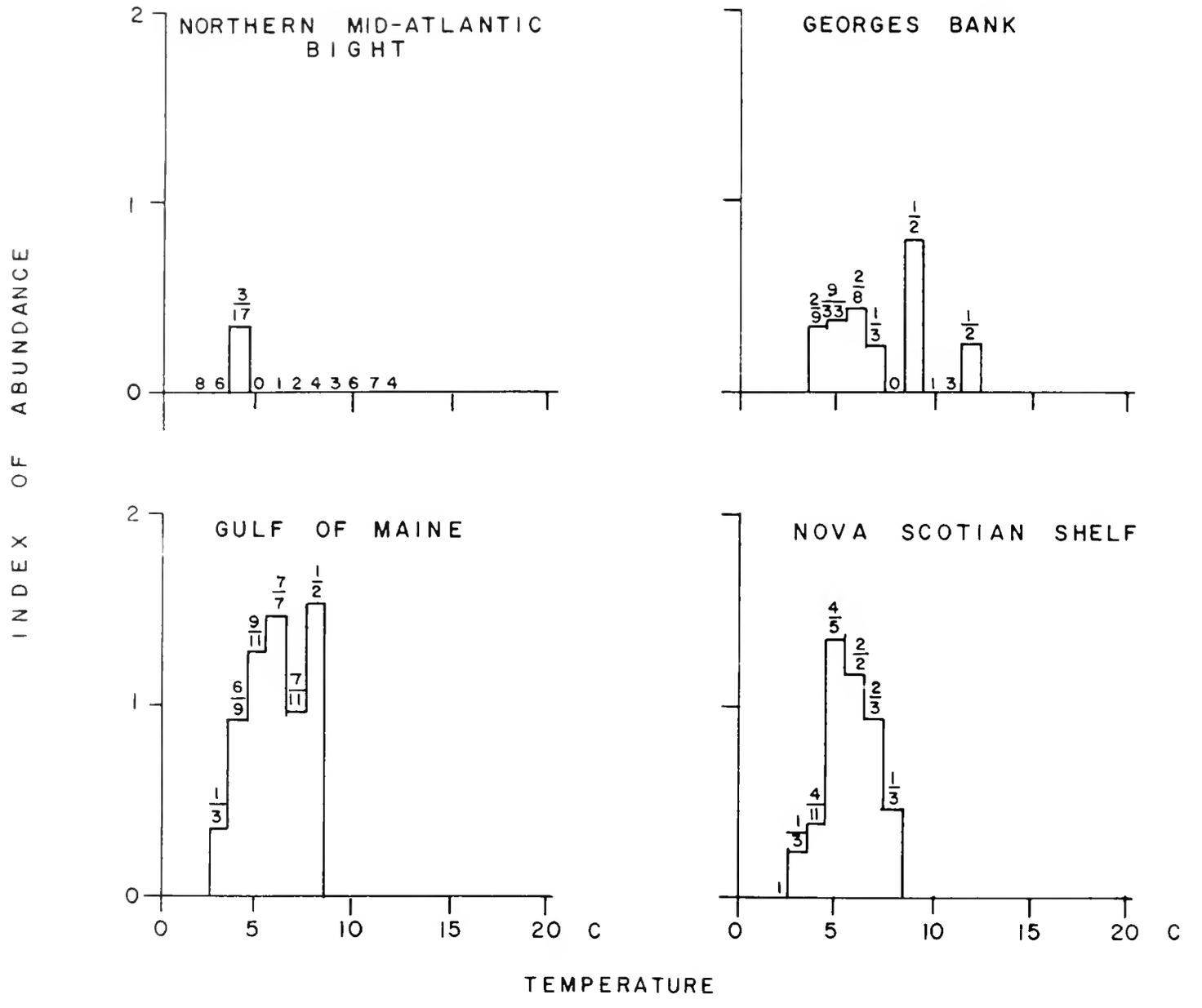

FIGURE 20.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during winter 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

reports (Bigelow and Schroeder 1953; Leim and Scott 1966; and McEachran 1973) and findings in the present study, are summarized.

Raja eglanteria is found from Long Island to northern Mexico but is rare off southern Florida. It occurs from the shore zone to 329 m at 5° to 27°C, but is most abundant between the shore zone and 111 m at 9° to 20°C.

Raja garmani occurs from the offing of Nantucket Shoals to the Dry Tortugas, Fla. North of Cape Hatteras, N.C., it is found in 37 to 366 m at 6° to 17°C, and south of there it occurs from 66 to 366 m at 11° to 19°C.

Raja laevis extends from the southern Newfoundland banks and the Gulf of St. Lawrence south to North Carolina. It is found from shore to 750 m at 1.2° to 20°C.

Raja erinacea regularly occurs from southern Nova Scotia to Cape Hatteras. It is found between shore and 384 m at 2° to 21°C but is most abundant in water shallower than 111 m at 2° to 15°C.

Raja ocellata is found from the Newfoundland banks and southern Gulf of St. Lawrence to Cape Hatteras. It occurs from shore to 371 m at −1.2° to 19°C but is most abundant in water shallower than 111 m at 2° to 15°C.

Raja senta occurs from the southern Newfoundland banks and the Gulf of St. Lawrence to South Carolina. It occurs from 31 to 974 m at −1.3° to 14°C but is most abundant below 110 m at 2° to 10°C.

Raja radiata extends from Labrador, west Greenland, Hudson Bay, Grand Banks, and Gulf of St. Lawrence to South Carolina. It occurs from

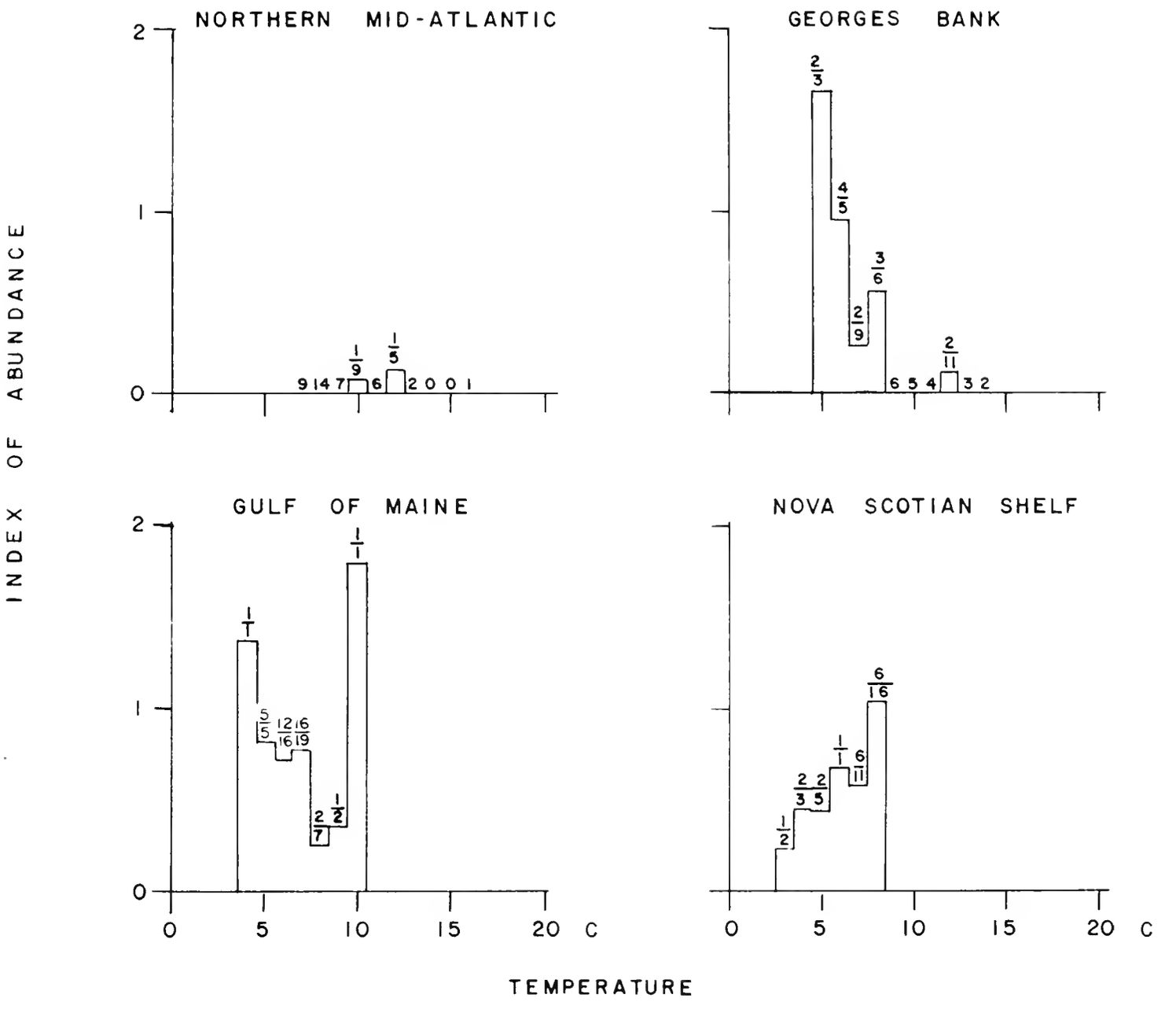

FIGURE 21.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during summer 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

18 to 996 m at −1.4° to 14°C but is most abundant below 110 m at 2° to 10°C.

Raja erinacea and *R. ocellata* are sympatric species with very similar habitat requirements. *Raja ocellata* has slightly lower temperature preferences than *R. erinacea* and occurs farther to the north than the latter. *Raja senta* and *R. radiata* are sympatric species; *R. radiata* has wider temperature range and is more widespread than *R. senta*.

ACKNOWLEDGMENTS

We are very grateful to the Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA; the Fisheries Research Board of Canada Biological Station at St. Andrews, New Brunswick; and the Southeast Fisheries Center Pascagoula Laboratory, NMFS, NOAA for furnishing data for this study. The two former institutions also permitted the senior author to take part in their groundfish surveys.

The Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA gave access to their computer programs and computer facilities to summarize data. The VIMS survey of Chesapeake Bight was supported in part by the NMFS under P.L. 88-309, Project 3-5-D, Jackson Davis, Principle Investigator.

Special thanks is given to Marvin Grosslein of the Northeast Fisheries Center Woods Hole

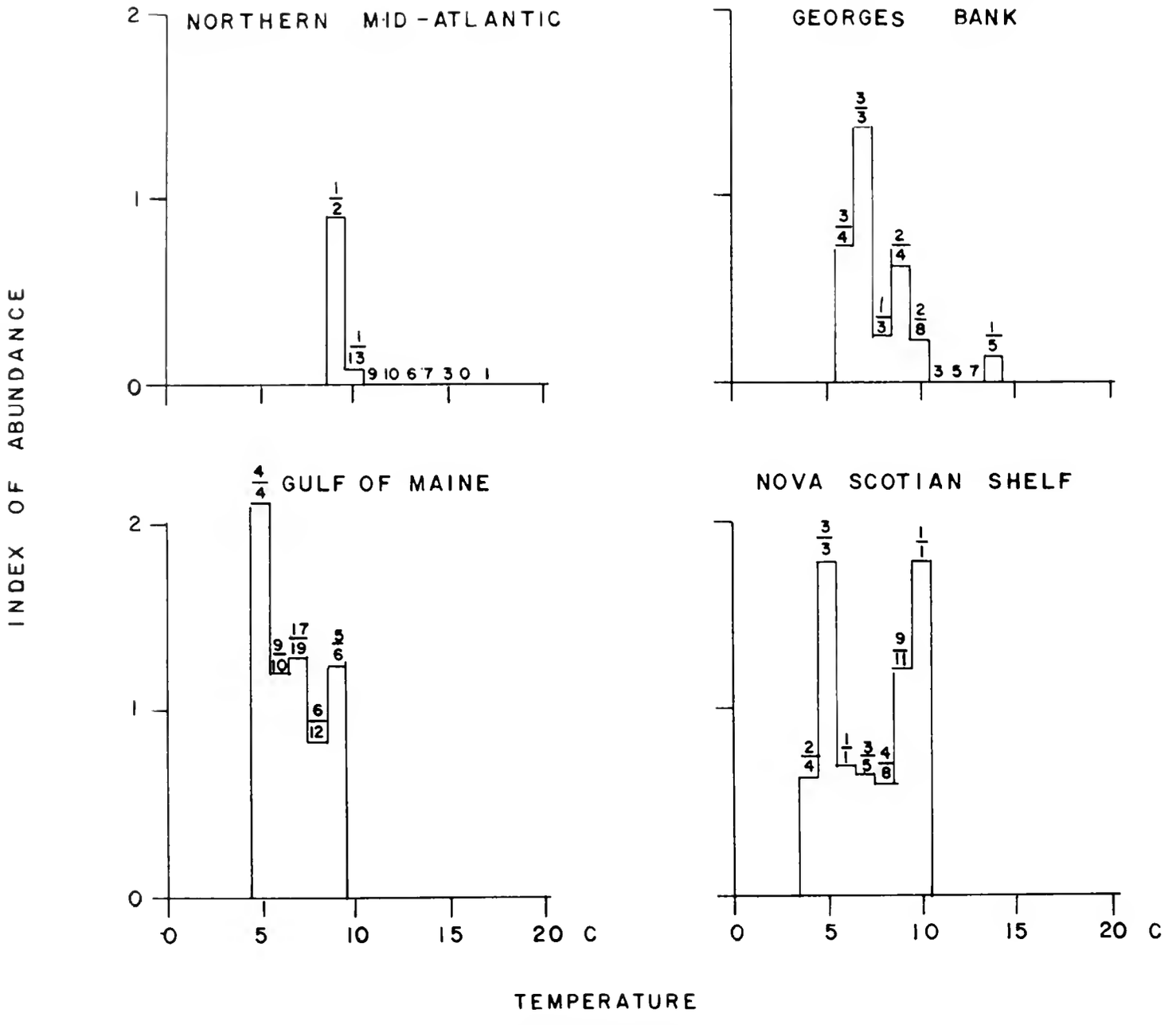

FIGURE 22.—Index of abundance (geometric mean) of *Raja radiata* captured in each subarea during autumn 1969 within temperature intervals of 1°C. See Figure 3 for explanation of fractions and whole numbers.

Laboratory, NMFS, NOAA for his cooperation during all phases of this study. John B. Colton, Jr., also of the Northeast Fisheries Center Woods Hole Laboratory, NMFS, NOAA supervised the construction of the isotherm charts. The following VIMS staff members and students contributed greatly to this study: Mark E. Chittenden and George C. Grant reviewed the manuscript; Russel L. Bradley and Kay Stubblefield did the drafting; Ken Thornberry did the photographic work; and Charles Wenner, Linda Mercer, Ken Able, Doug Markle, and Jim Weaver assisted with data collection.

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TABLE 3.—Coefficients of interspecific association for *Raja ocellata*, *R. erinacea*, *R. senta*, *R. radiata*, and *R. laevis*.

Cruise and species	*R. ocellata*	*R. erinacea*	*R. senta*	*R. radiata*
Cruise 67-21:				
R. erinacea	0.61**	—	—	—
R. senta	−0.02	−0.71	—	—
R. radiata	−0.28	−0.53**	0.60**	—
R. laevis	−0.02	0.00	0.00	0.00
Cruise 68-03:				
R. erinacea	0.67**	—	—	—
R. senta	0.00	0.00	—	—
R. radiata	−0.04	−0.32	0.84**	—
R. laevis	0.25*	0.53**	0.00	0.27
Cruise 68-17:				
R. erinacea	0.52**	—	—	—
R. senta	0.00	0.00	—	—
R. radiata	−0.85**	−0.54**	0.78**	—
R. laevis	0.14	0.45	0.00	0.00
Cruise 69-02:				
R. erinacea	0.63**	—	—	—
R. senta	−0.35	−0.34	—	—
R. radiata	−0.31	−0.23	0.95**	—
R. laevis	0.54**	0.36	−0.01	−0.03
Cruise 69-08:				
R. erinacea	0.71	—	—	—
R. senta	0.00	−0.62**	—	—
R. radiata	−0.56*	−0.42*	0.75**	—
R. laevis	0.72**	0.84**	−0.09	−0.02
Cruise 69-11:				
R. erinacea	0.57**	—	—	—
R. senta	−0.70	−0.85*	—	—
R. radiata	−0.21	−0.54**	1.00**	—
R. laevis	0.48	0.79**	0.00	0.34
Cruise 70-03:				
R. erinacea	0.53	—	—	—
R. senta	−0.01	−0.42	—	—
R. radiata	−0.12	−0.38	1.00**	—
R. laevis	0.13	0.47*	−0.09	0.01
Cruise 70-06:				
R. erinacea	0.41**	—	—	—
R. senta	−0.82**	−0.84**	—	—
R. radiata	−0.61**	−0.44**	0.80**	—
R. laevis	0.01	0.01	0.00	0.51

*Significant at the 0.05 probability level.
**Significant at the 0.01 probability level.

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THE GENERAL FEEDING ECOLOGY OF POSTLARVAL FISHES IN THE NEWPORT RIVER ESTUARY[1]

MARTIN A. KJELSON, DAVID S. PETERS, GORDON W. THAYER, AND GEORGE N. JOHNSON[2]

ABSTRACT

Food preferences, feeding intensity and chronology, evacuation rates, and daily rations were determined for postlarval stages of Atlantic menhaden, *Brevoortia tyrannus* (25-32 mm); pinfish, *Lagodon rhomboides* (16-20 mm); and spot, *Leiostomus xanthurus* (17-24 mm). Four copepod taxa, *Centropages, Temora, Acartia,* and Harpacticoida, made up 76-99% of the total gut contents. Postlarval feeding intensity was greatest during early daylight hours. Postlarval menhaden lost an estimated 60% of their orginal gut contents due to the stress of handling and capture. Similar stress caused no food loss in either postlarval pinfish or spot. Gastrointestinal evacuation of copepods and *Artemia* nauplii were described by linear regression. Evacuation rates varied directly with the amount of food in the gut. Rate constants were used in conjunction with information on the chronology of gut contents to determine daily rations. Daily ration estimates as a percent of the fish's wet body weight were: menhaden, 4.9%; pinfish, 3.5%; spot, 4.3% and 9.0%. The ration estimates for spot in terms of calories per fish per day were similar to the metabolic needs estimated from oxygen consumption measurements but were lower than the estimates from oxygen consumption for menhaden and pinfish.

Larval and postlarval fish are significant consumers in aquatic ecosystems, yet our knowledge of their feeding habits and daily food consumption is incomplete. This paper deals with the general feeding ecology of the postlarval stages of three common estuarine fishes. Four major aspects are discussed. These include 1) food preferences, 2) feeding intensity and chronology, 3) evacuation rate, and 4) daily ration.

Postlarval Atlantic menhaden, *Brevoortia tyrannus*; pinfish, *Lagodon rhomboides*; and spot, *Leiostomus xanthurus*, were collected during March of 1972 and 1973 from the Newport River estuary, Carteret County, N.C. The fish (hereafter referred to as larvae) were taken near Pivers Island, approximately 2.5 km inside the Beaufort Inlet. Pinfish and spot were collected using a seine and dip nets, while menhaden were captured in a channel net (Lewis et al. 1970) and with dip nets. One additional group of samples was collected in bongo nets. Most fish were frozen immediately following capture, thus stopping their digestive processes. The only exceptions to preservations by freezing were the bongo net samples which were placed in 5% Formalin.[3]

Food preferences were determined by examining the contents of entire digestive tracts. The gut contents from 120 fish of each species collected throughout the day were combined and individual food items identified, counted, and measured. Copepodite and adult copepods composed 99-100% (by both number and volume) of the identifiable food items in the digestive tracts. The average-sized copepod fed upon by each larval species was determined by measuring 100 copepods chosen from the combined digestive tract contents of all larvae collected in a 24-h period.

Diel periodicity of digestive tract contents indicated the intensity and chronology of feeding by the larvae. Twenty fish of each species were collected at 4-h intervals for 24 consecutive hours.

Larval evacuation rates for copepods and for *Artemia salina* were determined from laboratory experiments performed at 15°-17°C and 25-30‰; conditions which typify larval collection sites during March. Copepod evacuation was determined by collecting larvae from the estuary, placing them in food-free seawater tanks, and observing the decrease in their gut contents through time. At the time of initial capture

[1]This research was supported through a cooperative agreement between the National Marine Fisheries Service and the U.S. Atomic Energy Commission.

[2]Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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and every 3 or 4 h thereafter, at least 10 fish were killed and the copepods present were counted. Evacuation of newly hatched *Artemia* nauplii was measured by allowing unfed larvae to feed to satiation on high prey densities (0.3 to 3.0 nauplii/cm^3), placing them in a food-free environment, and then periodically removing larvae for determination of remaining gut contents. Sampling of both copepod- and *Artemia*-fed fish continued periodically from the time of feeding until more than one-half of the fish had empty tracts.

Linear regression equations of log-transformed data were used to describe the evacuation process (Peters et al. 1974). The equations were of the form:

$$\log_{10} C = A + Bt$$

where C = 1 + the mean number of copepods or *Artemia* present in the gut
t = time
$A + B$ = regression terms

Instantaneous evacuation rates were calculated from the equation $\frac{dC}{dt} = 2.303\ BC$ (Peters and Kjelson in press).

Daily rations were calculated using information on diel periodicity of gut content and instantaneous evacuation rates. Previous calculations of fish rations (Bajkov 1935; Seaburg and Moyle 1964) have assumed a constant evacuation rate, but more recent data (Tyler 1970; Elliot 1972) indicate that digestive rate changes with the quantity of food in the digestive tract.

Our method of calculating daily ration (Peters and Kjelson in press) accounts for changes in evacuation rate which accompany diel changes of feeding intensity. To calculate the rations, we first determined an average instantaneous evacuation rate (in copepods per hour) for each of the 4-h sampling periods in the diel cycle. This average rate was the geometric mean of the instantaneous evacuation rates at the beginning and end of the period. Since each period lasted 4 h, the estimate of food evacuated during the period was four times the average instantaneous hourly evacuation rate. The total food evacuated per day was achieved by summing the six 4-h evacuation estimates, and is an estimate of the daily ration, because average ingestion rate must equal the rate at which material leaves the gut whether by assimilation or expulsion.

Daily rations were calculated initially as copepods per fish per day and then transformed to percent of the larval body weight and calories per fish per day. Dry weights of ingested copepods were estimated from the length-weight relationship:

$$W = 6.274L - 0.153$$

where W = dry weight in micrograms
L = copepod length, based on Heinle's (1966) data for all stages of *Acartia tonsa*

Copepod dry weights were converted to wet weights using a factor of 9.1 based upon our measurements of the wet/dry ratio for zooplankton, and were compared to wet weights of the fish to compute the daily ration as a percent of live body weight. Daily caloric intake was computed using our estimation of 0.555 cal/mg wet weight of an average size copepod during March, based on microbomb calorimeter measurements of mixed estuarine zooplankton (Thayer et al. 1974).

FOOD PREFERENCES

The larvae we collected were feeding primarily upon copepods, a common food source for both freshwater and marine fish larvae (Werner 1969; May 1970). Copepods composed 99% (by volume and number) of the gut contents of larval spot, pinfish, and menhaden (Table 1). Four copepod taxa (*Centropages, Temora, Acartia,* and Harpacticoida) were dominant. Diatoms, amphipods, barnacle larvae, crab zoea, and ostracods, although present in some larvae, were rare.

TABLE 1.—Relative (percent) composition by number of the major taxa in the total gut contents of three species of larval fish.

Taxa	Larval species		
	Pinfish	Spot	Menhaden
Harpacticoida	32	32	22
Centropages	28	28	40
Temora	3	21	6
Acartia	13	8	30
Other copepods	23	10	1
Other organisms	1	1	1
Total	100	100	100

Prey size is an important factor in determining the individuals selected by planktivorous fish (Ivlev 1961; Brooks and Dodson 1965; Kjelson 1971). The larval fish we studied appeared to restrict the majority of their feeding to items of a size ranging between 300 and 1,200 μm. Our observations of the mean length of ingested copepods showed that the larger menhaden larvae (26-31 mm, $\bar{x}$ = 29 mm TL) ingested 750-μm copepods with an estimated copepod wet weight of 0.04 mg, while the smaller spot (17-22 mm, $\bar{x}$ = 19 mm TL) and pinfish larvae (16-20 mm, $\bar{x}$ = 18 mm TL) fed upon 600-μm copepods with an estimated wet weight of 0.03 mg. Small zooplankters such as copepod nauplii, barnacle larvae, or small adult copepods such as *Oithona* (all present in the plankton tows) were rarely found in gut contents. Copepods larger than 1.2 mm were in the plankton, but were rarely consumed. Perhaps copepods were the only food items of the appropriate size present in sufficient abundance. Had we collected smaller larvae, it is possible food preferences may have been for smaller food items such as copepod nauplii and copepodites and adults of small-sized species as well as phytoplankton. May (1970) stressed the fact that larval fish require progressively larger prey as they grow. However, since larvae smaller than the size we collected are rarely found in the Newport River estuary, we feel our data indicates that smaller planktonic forms are relatively unimportant to the larval fish studied in this estuary.

Thayer et al. (1974) found that as a yearly average, copepods represented 81% of the zooplankton numbers and 85% of the zooplankton biomass retained by a No. 10 mesh plankton net. Since larval fishes enter the Newport River estuary during winter and spring, the consumption of copepods by these three larval species may, in part, explain the decrease in copepod abundance observed by Thayer et al. (1974) during this period. They noted that the four copepod taxa utilized by these larvae decreased from a mean of 81% of the copepod biomass during March 1970 and 1971 to a mean of 48% of the biomass during the summer.

FEEDING CHRONOLOGY AND INTENSITY

All three larval fishes had the highest food content in their digestive tracts during daylight hours (Figures 1-3). Periodicity of gastrointestinal contents indicates that each population begins feeding near dawn and reaches a maximum gut fullness near midday. The rapid single increase in the gut content of the three species indicates they have one major burst of feeding activity per day (Figures 1-3). Other studies (Blaxter 1965; Schumann 1965; Braum 1967; June and Carlson 1971) have shown that larval fish generally do not have food within their digestive tracts when captured at night, suggesting that larval fish do not feed at low light intensities.

Considerable variation was observed in the amounts of food present in larval guts (Figures 1-3). The variation is probably due to differences in prey abundance or capture and handling techniques, although other factors such as fish size and copepod size may also be important. During our 24 h sampling the variation in numbers of copepods in individual fish was high at some times and low at others. The ratio of the standard error of the estimate to the mean varied from 4 to 48% for spot with a mean of 21%; for menhaden the ratio varied from 0 to 100% with a mean of 40%; and for pinfish it varied from 0 to 100% with a mean of 43%. Spot larvae

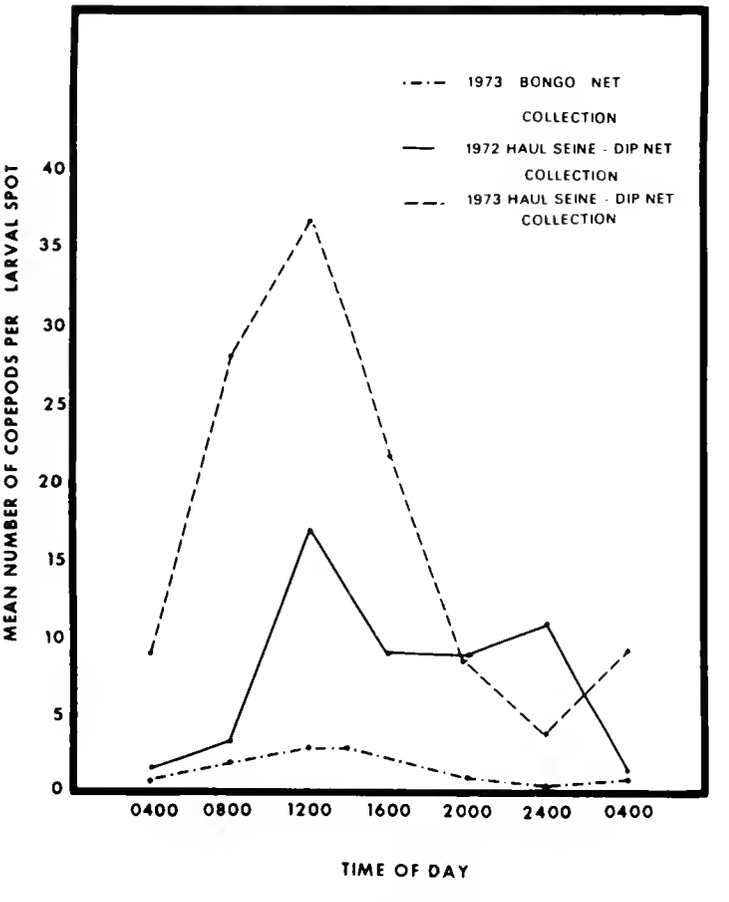

FIGURE 1.—Variation in diel cycle of gastrointestinal contents in postlarval spot.

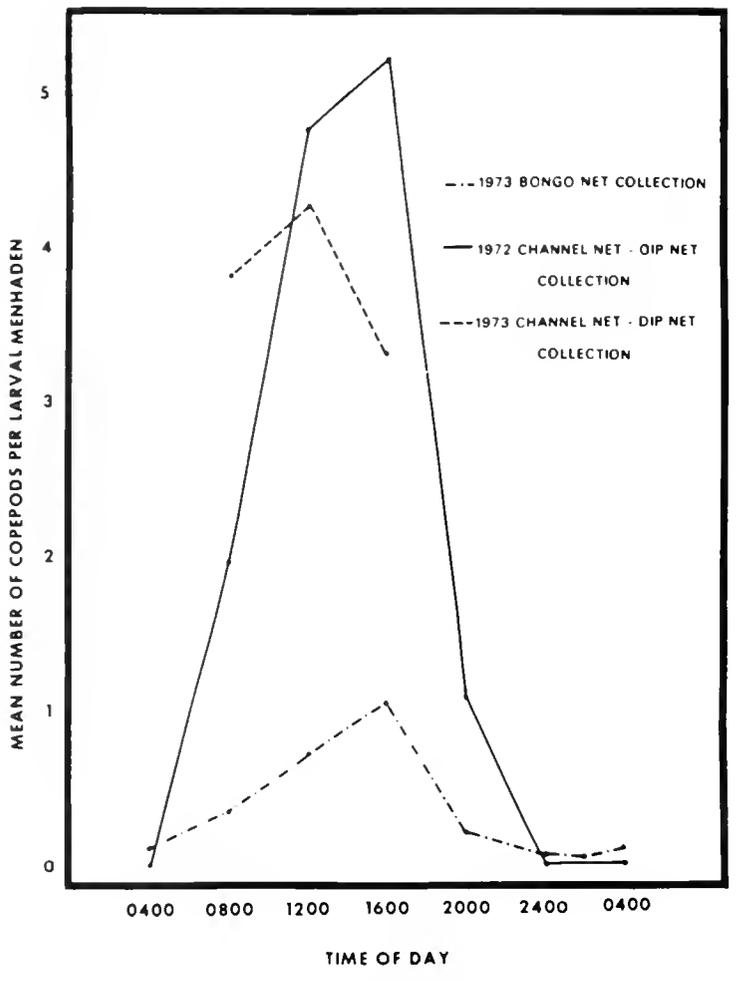

FIGURE 2.—Variation in diel cycle of gastrointestinal contents in postlarval Atlantic menhaden.

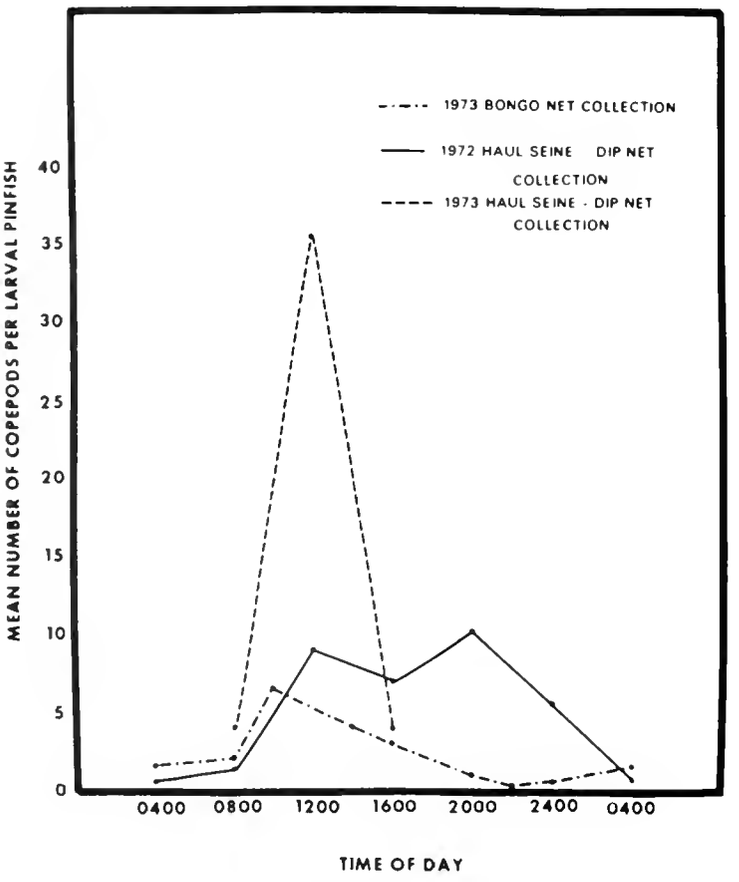

FIGURE 3.—Variation in diel cycle of gastrointestinal contents in postlarval pinfish.

(18-24 mm, $\bar{x}$ = 21.5 mm) collected by dip net at one location and between 0830 and 1030 h over a 4-day period had little variation in their mean gut contents. Spot larvae collected 2 April averaged 25.3 copepods/fish (SE = 2.3), on 3 April, 21.3 (SE = 2.0), and on 5 April, 26.3 (SE = 3.7). The similarity of food quantity in the larval digestive tracts suggests that prey abundance may have remained relatively constant over the 4-day period thus allowing the fish to consume similar amounts of food.

ESTIMATES OF LARVAL GUT CAPACITIES

Laboratory feeding experiments were conducted at 15°-16°C to estimate the maximum gut capacity of the larvae. The fish were fed high densities of *Artemia* nauplii until their digestive tracts were completely packed from esophagus to anus. Menhaden (28-32 mm, $\bar{x}$ = 30 mm TL) fed for 20 min on a concentration of *Artemia* nauplii, 3 nauplii/cm^3, had an average of 145 nauplii/fish in their digestive tracts (SE = 9.6). Spot larvae (19-23 mm, $\bar{x}$ = 21 mm TL) fed for 15 min on 0.3 nauplius/cm^3 had an average of 89 (SE = 7.0) nauplii/fish; and pinfish (16-20 mm, $\bar{x}$ = 18 mm TL) fed for 1 h on 0.3 nauplius/cm^3, had an average of 75 (SE = 15.1) nauplii/fish. By comparing individual *Artemia* and copepods of the four major taxa side by side under a microscope, we estimated that the volume of two 450-μm *Artemia* nauplii were equivalent to that of one 650-μm copepod. Using 0.5 as a conversion factor, we calculated maximum gut capacities in terms of copepods. Menhaden larvae of 30 mm have a gut capacity of 72 copepods, 21-mm spot a gut capacity of 44 copepods, and 18-mm pinfish a gut capacity of 37 copepods. These estimates of gut capacity were comparable to the maximum numbers of copepods observed in the digestive tracts of larval fish collected in the estuary for spot (36.5 copepods/fish) (Figure 1) and pinfish (35.3 copepods/fish) (Figure 3), but not for menhaden (5.2 copepods/fish) (Figure 2). This large difference between gut capacity and observed gut contents suggests that menhaden larvae either feed very little under natural conditions, and never approach the estimated maximum gut capacity or capture and/or handling causes them to regurgitate or defecate causing inaccuracy in our estimate of natural gut content. To test

the latter possibility, we performed a variety of experiments to determine if handling and capture technique influences the quantities of food observed in the larval gut.

EFFECTS OF SAMPLING TECHNIQUE ON GUT CONTENT

Larvae of all three species were first collected by a 3-m channel net with an attached live box. Captured fish were counted, identified, divided into two groups, and transferred (underwater) into separate containers. One group of fish was anesthetized with 0.12 g/liter MS-222 (tricaine methanesulfonate) and then dissected, while the other group was transferred carefully into the posterior end of a 20-cm bongo net (keeping them underwater throughout transfer). The net was towed for 5 min, and after retrieval the larvae were removed, identified, and counted to assure that none were lost and that no new larvae were captured. The fish were then dissected to determine the number of copepods present in their guts. Menhaden lost 68% of their gut contents when exposed to the stress of bongo tows, whereas gut contents of larval spot and pinfish before and after the bongo tow did not differ statistically (Table 2). The amounts of food present in all three species of larvae collected at the Beaufort Inlet in the 24-h bongo samples were lower than the food quantities observed in larvae collected by the other techniques inside the estuary (Figures 1-3). Thus, factors other than the stress of capture may be responsible for the low gut contents in larvae collected in the bongo nets: 1) copepod abundance may have been lower at the Beaufort Inlet sampling site than further inside the estuary, 2) the use of Formalin (restricted to bongo samples) to kill and preserve the larvae may have caused defecation of the copepods prior to analysis (June and Carlson (1971) showed that larval menhaden when placed in Formalin had violent spasms accompanied by defecation), and 3) larvae collected in midchannel by bongo nets may not be feeding as actively since they are exposed to a greater tidal current (perhaps the protected inshore waters of the estuary may allow the larvae to feed more efficiently and result in fish with greater numbers of prey in their digestive tracts).

No significant differences were observed in the food contents of spot larvae collected by routine seining and those collected by seining with a more gentle sampling technique (Table 3). In routine seining, the larvae were picked out of the seine as it lay on the shore and placed in a bucket of ice water. The gentle sampling technique consisted of surrounding a body of water with the seine and then concentrating the larvae, taking care that fish were not forced against the net. Once concentrated, the larvae were dipped out of the water in a bucket and anesthetized with MS-222. The results of our sampling experiments indicate that routine field sampling techniques used to collect spot and pinfish larvae probably caused little loss of food from the digestive tracts.

TABLE 2.—The effect of bongo net tow stress upon the amount of food observed in larval menhaden, pinfish, and spot.

Capture technique	Menhaden[1]	Pinfish[2]	Spot[3]
	Mean number copepods/fish ± one SE		
Channel net	7.4 ± 2	1.3 ± 0.6	6.4 ± 4.4
Channel net + bongo net tow	2.4 ± 0.7	0.8 ± 0.3	7.0 ± 2

[1] n = 22 larvae.
[2] n = 18 larvae.
[3] n = 5 larvae.

EFFECTS OF HANDLING TECHNIQUE ON GUT CONTENT

In the laboratory, handling stress did not reduce the food quantities present in larval spot and pinfish, but did reduce the amount of food remaining in larval menhaden (Table 4). Two groups

TABLE 3.—Comparison of food quantities, mean number of copepods per fish ± one SE, present in larval spot (22-33 mm, $\bar{x}$ = 27 mm) collected by haul seine using rough and gentle handling techniques. Ten fish were collected per sample.

Date	Gentle	Rough
April 2	84.5 ± 7.4	78.6 ± 5.3
April 3	69.7 ± 5.9	66.9 ± 5.5

TABLE 4.—The effects of handling on the retention of *Artemia* nauplii in digestive tracts of larval Atlantic menhaden, pinfish, and spot. Rough handling is approximately equivalent to field capture by dip net and haul seine.

Species (Range mm)	Experiment 1		Experiment 2	
	Gentle	Rough	Gentle	Rough
	Mean number ± one SE			
Menhaden[1] (28-32)	71 ± 15	29 ± 10	145 ± 10	76 ± 11
Pinfish[2] (16-20)	37 ± 4	34 ± 5	35 ± 9	43 ± 6
Spot[2] (19-23)	51 ± 5	47 ± 5	89 ± 7	92 ± 10

[1] n = 18 larvae per sample.
[2] n = 36 larvae per sample.

of unfed larvae of each species were offered identical concentrations of *Artemia* nauplii. One group was handled roughly to represent the physical stress associated with field capture, while the other group was handled gently. The roughly handled fish were chased around the tank with a dip net for 10 to 30 s, captured with the net, allowed to suffocate in air, and then dissected. After feeding, the other fish were anesthetized by carefully adding an aqueous solution of MS-222 to the tank and then were dissected immediately to determine the numbers of nauplii in their digestive tracts. The roughly handled menhaden had only 40 to 52% of the *Artemia* numbers present in the guts of the gently handled menhaden (Table 4). The loss of food in menhaden larvae probably was due to the stress-related defecation or regurgitation and thus, may explain the consistently low quantities of food observed in larval menhaden captured in the estuary. Roughly handled pinfish and spot larvae showed no significant decrease in gut contents (Table 4). The curved digestive tract of larval spot and pinfish may prevent rapid passage of food, while the straight tubelike gut of menhaden may permit easy loss of food. This gut shape difference may account for the differences we observed.

A separate experiment was conducted to determine if the technique used to kill menhaden larvae in the handling experiments (exposure to air and suffocation versus anesthesia with MS-222) influenced the amount of food remaining in the gut. No difference was found. Fish killed by suffocation had a mean of 19 *Artemia* nauplii/fish (SE = 4.7), while fish anesthetized with MS-222 had a mean of 20 *Artemia* nauplii/fish (SE = 4.2).

EVACUATION RATES

Estimated regression coefficients for the equations describing the evacuation of copepods and *Artemia* nauplii are provided in Tables 5 and 6. Certain factors may alter the reliability of our estimates of evacuation rate under natural estuarine conditions. Bias may result from the temperature difference between estuarine waters from which fish were captured (14°-15°C) and the aquaria temperature during evacuation experiments (16°-17°C). The effect of a 2° temperature change on evacuation rate of larvae is unknown, although a similar change significantly increases the evacuation rates in some juvenile marine fish (Peters and Kjelson in press). Although our regression model could probably be improved, the r^2 values (Tables 5, 6) indicate the model is reasonable. Initial analysis included data collected until all the fish were empty. This resulted in nonlinearity near the end of evacuation due to bias near the end of evacuation period where more weight was given to the slower evacuating fish. Thus, by including in the regression analysis data from only those samples in which at least half of the larvae contained some food, this bias was decreased and the linear regression model appeared to represent larvae evacuation adequately.

TABLE 5.—Linear regressions describing evacuation of copepods in Atlantic menhaden, pinfish, and spot larvae. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of copepods per larva})$ and t = hours since feeding. n = the number of data points.

Species	Mean TL (Range mm)	A	B	n	r^2	Temperature (°C)
Menhaden	29 (27-31)	1.14	−0.17	3	0.98	16
Pinfish	17 (15-20)	0.94	−0.10	3	0.86	16
Pinfish	16 (13-19)	0.68	−0.08	4	0.98	17
Spot	20 (17-23)	0.91	−0.10	5	0.98	17

INFLUENCE OF HANDLING AND CAPTURE ON EVACUATION

Evacuation experiments using *Artemia* nauplii were performed to determine if handling and capture influenced the rate of evacuation. Each

TABLE 6.—Linear regressions describing evacuation of *Artemia* nauplii in Atlantic menhaden, pinfish, and spot larvae under varied handling conditions. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of } \textit{Artemia} \text{ per larva})$ and t = hours since feeding. n = the number of data points.

Species	Mean TL (Range mm)	A	B	n	r^2	Handling condition	Temperature (°C)
Menhaden	29 (27-32)	2.36	−0.28	5	0.96	Gentle	15
Menhaden	29 (27-32)	2.04	−0.34	3	0.86	Rough	15
Pinfish	16 (14-18)	1.64	−0.26	4	0.97	Gentle	16
Pinfish	16 (14-17)	1.73	−0.28	3	0.92	Rough	16
Spot	20 (18-23)	2.12	−0.19	5	0.94	Gentle	16
Spot	20 (18-23)	2.11	−0.18	5	0.95	Rough	16

of the three larval fish species were fed concentrated amounts of *Artemia* (> 0.3 nauplius/cm^3) and allowed to feed until their digestive tracts were full. Each species then was transferred to food-free containers and separated into two groups, one handled roughly and another handled gently. Fish were sampled immediately and every 2 h thereafter. The rough treatment was similar to that used to study the influence of handling on gut content. The gently handled fish were sampled by dipping them carefully out of the tank with a beaker and anesthetizing them prior to dissection. The similarities of the regression coefficients (Table 6) for fish of the same species under the two treatments indicate that evacuation rates were not affected by rough treatment. The higher B value for roughly handled menhaden was not significantly different. Thus, our use of laboratory evacuation data to represent the normal evacuation in nature appears reasonable.

The regression coefficients for *Artemia* nauplii evacuation were larger (B values ranging from -0.18 to -0.34) than those for copepod evacuation (B values ranging from -0.08 to -0.17) for all three species (Tables 5, 6). This was expected since the *Artemia* nauplii were estimated to be only one-half the volume of copepods ingested by the larvae.

Food quality may also affect evacuation rate. Rosenthal and Hempel (1970) working with herring larvae found that *Artemia* nauplii were not digested as completely as copepods. We also observed that copepods become transparent in the posterior gut, whereas *Artemia* nauplii remained opaque.

The variation in the numbers of prey per larva between individual menhaden and pinfish larvae increased with each successive sampling period (0, 2, 4, 6, and 8 h after feeding stopped), but fluctuated in spot. The increasing variation in menhaden and pinfish may be explained by differences in individual evacuation rates. Food densities and gut capacities were relatively constant for the individual larva and thus, the initial numbers of prey per larva were similar. Varied individual evacuation rates would influence the amounts present in the tracts of the fish sampled at later times and therefore increase the variation. Individual fish may have significantly different evacuation rate constants as has been shown for juvenile pinfish (Peters and Hoss 1974).

DAILY RATIONS

The estimated daily rations for the three larval fish species varied between 3.5 and 9.0% of the mean wet weight of the fish or from 38 to 99 copepods/fish·day. The daily ration estimate for menhaden larvae (Table 7) was corrected by a factor of 2.5 to account for the fact that menhaden larvae lose approximately 60-68% of their gut contents during capture and subsequent handlings (Tables 2, 4). Since pinfish and spot larvae did not lose food from their gut when put under the stress, no correction factor was used.

Two estimates of daily ration, based upon both the 1972 and 1973 haul seine-dip net collections (Figure 1), are provided for spot larvae (Table 7). The two spot rations (4.3% and 9.0% of the body weight) differ considerably, probably due to differences in food availability.

Measurements of larval metabolic expenditures based on O_2 consumption (D. E. Hoss and W. F. Hettler, Jr., Atlantic Estuarine Fisheries Center,

TABLE 7.—Daily rations calculated from feeding studies and O_2 consumption measurements at 15°-17°C for larval Atlantic menhaden, pinfish, and spot in the Newport River estuary, N.C.

Species (range mm)	Mean larvae wet weight (mg)	Number copepods/ fish·day	Percent of body weight	Calories/ fish·day	Calories/fish·day estimated from O_2 consumption[1, 2]
1972:					
Menhaden (27-32)	43	53	4.9	1.18	3.0
Pinfish (16-20)	32	38	3.5	0.63	1.2
Spot (17-23)	33	47	4.3	0.78	1.2
1973:					
Spot (17-23)	33	99	9.0	1.65	1.2

[1]From Hettler and Hoss, unpubl. data.
[2]3.38 cal/mg O_2.

National Marine Fisheries Service, NOAA, pers. commun.) are higher than three of our four larval ration estimates (Table 7). Our menhaden ration of 1.18 calories/fish·day was 40% of the 3.0 calculated from Hoss and Hettler's measurements of respiration rate, indicating that for this species our estimate is probably low. Our pinfish ration was also lower, being 52% of that calculated from the O_2 consumption method. Our menhaden estimate is highly dependent on a very tentative factor used to adjust for handling effects. More accurate measurement of this conversion factor would probably provide better correlation with metabolic costs. Our 1972 spot ration was 66% of maintenance needs and may be indicative (as with pinfish and menhaden) of natural food shortages or environmental conditions not optimal for feeding on the dates of collection in 1972. The 1973 spot ration was nearly twice that estimated from O_2 consumption measurements and provides sufficient energy for general metabolism and growth.

We must consider our larval ration estimates as tentative in light of the high variability in the ration estimates for spot. This variation is due to differences in natural gut content, possibly as a result of differences in food availability on the sampling dates. Extensive sampling under the varied environmental conditions and zooplankton abundances and repeated evacuation rate measurements will provide us with more accurate estimates of their daily ration.

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THE LARVAL DEVELOPMENT OF PACIFIC *EUPHAUSIA GIBBOIDES* (EUPHAUSIACEA)

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ABSTRACT

The larval development of *Euphausia gibboides* is described and illustrated, including nauplius stages I and II, metanauplius stage, calyptopis stages I-III, and furcilia stages I-VI; dominant and variant forms, with respect to reduction in number of terminal telson spines, were found in furcilia IV-VI. Identification of developmental stages was substantiated by the study of a series of juveniles of *E. gibboides*, the largest of which had characters of both the furcilia phase and the adult. Larvae were studied in plankton samples from several areas within the range of the species in the Pacific Ocean; variation in size of calyptopes in different areas is described.

Euphausia gibboides Ortmann is a relatively large euphausiid of the temperate and tropical Pacific. It is closely related to *E. sanzoi* Torelli and *E. fallax* Hansen and with them forms a "*Euphausia gibboides* group" (Brinton 1962). In the North Pacific, *E. gibboides* is found in the transition zone between lat. 30° and 45°N and extending southward to about lat. 20°N in the east where it is considered a major species of the California Current system; in the South Pacific it occurs in the eastern equatorial zone. *Euphausia sanzoi* has been found in the Red Sea and western Indian Ocean, and *E. fallax* in the western tropical Pacific. The distributions of these species are discussed by Brinton (1962, 1967a, b, 1973), Brinton and Gopalakrishnan (1973), Roger (1967), and Mauchline and Fisher (1969). The distribution of the larvae of *E. gibboides* in the California Current is shown by Brinton (1967a, b, 1973).

Hansen (1911) divided the species of the genus *Euphausia* Dana into four groups with respect to armature of carapace and abdomen; of these, groups A and D were considered to be "well separated" but groups B and C "somewhat badly defined." Group C, the largest of the four, contains 12 of the 32 species now recognized in the genus: *E. mucronata*, *E. paragibba*, *E. pseudogibba*, *E. hemigibba*, *E. gibba*, *E. lamilligera*, *E. distinguenda*, *E. sibogae*, *E. gibboides*, *E. fallax*, *E. sanzoi*, and *E. vallentini* (*E. alvae* and *E. consuelae*, both considered difficult to evaluate are not included) (Boden et al. 1955). An early furcilia of *E. hemigibba* (Lebour 1949) and a late furcilia of *E. distinguenda* (Hansen 1912) have been identified, but a series of developmental stages has been described for only one of the group C species, *E. vallentini* (John 1936). In his investigation of the adults and larvae of the southern species of *Euphausia*, John has shown the affinity of *E. vallentini* and certain species of group B with which it may now be associated (Mauchline and Fisher 1969). Studies of the larvae of additional species should aid not only in identification of planktonic forms but also in definition of specific relationships within the genus.

The present paper provides descriptions of the developmental stages of *Euphausia gibboides*; it is part of a larger study whose purpose is to identify and describe larvae of the three species of the "*Euphausia gibboides* Group" and to compare the larval morphology of these closely related forms.

METHODS AND MATERIALS

Larvae of *E. gibboides* were obtained from preserved plankton samples in the Marine Invertebrate Collections of the Scripps Institution of Oceanography. They were sorted from net hauls, taken with the standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) 1-m net (Ahlstrom 1954), which were known to contain larvae and juveniles of the species. The positions of these tows are given in Table 1; station data for the samples are given by Snyder

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TABLE 1.—The area, station number, and position of samples from which larvae of *E. gibboides* were obtained.

Area	Cruise	Station	Position (Lat., Long.)
North Pacific:			
Eastern	CalCOFI 6304	60.140	34°65.0'N, 129°19.5'W
	CalCOFI 6304	70.90	34°53.0'N, 125°13.0'W
	CalCOFI 6304	70.100	34°33.0'N, 125°13.0'W
	CalCOFI 6304	110.70	28°36.0'N, 118°18.0'W
	CalCOFI 6304	117.90	26°47.5'N, 118°50.0'W
	CalCOFI 6304	120.120	25°12.5'N, 120°22.5'W
	CalCOFI 6304	133.80	24°14.5'N, 116°17.5'W
	CalCOFI 6307	117.80	27°07.5'N, 118°06.0'W
Western	Transpac	56A + B	41°49.0'N, 166°38.6'E
	Transpac	76A	39°56.4'N, 143°38.5'E
Equatorial Pacific:			
Eastern	Shellback	187	1°39.5'N, 92°05.0'W
	Shellback	188	1°06.5'N, 93°14.5'W

and Fleminger (1965) and in University of California Data Reports (Scripps Institution of Oceanography 1964a, b).

The larvae were grouped by developmental phase, measured, and dissected for detailed study of appendages. The identification of eggs, nauplii, and metanauplius is based on their relative abundance in samples in which calyptopes and furcilia of *E. gibboides* were clearly the dominant euphausiid larvae. Identification of calyptopis and furcilia stages, based on morphology, distribution, and relative abundance with juveniles and adults of *E. gibboides*, was substantiated by the study of a series of juvenile forms the largest of which had characters of both the furcilia phase and the adult.

The identification of calyptopis I was confirmed by rearing after the manuscript had been accepted for publication. A gravid female of *E. gibboides*, caught in a mid-water trawl collection at lat. 27°35.5'N, long. 115°52.0'W, deposited her eggs soon after capture and larvae which hatched from the eggs were cultured through the first four developmental stages. I am indebted to Edward Brinton and Annie Townsend who undertook the rearing study of *E. gibboides* aboard RV *Alexander Agassiz* during Leg I of Scripps Institution of Oceanography Expedition Krill, May-June 1974.

Reviews of the literature dealing with the larval development of the Euphausiacea and discussions of their larval phases are given by Mauchline and Fisher (1969) and Gopalakrishnan (1973). The nomenclature used in the description of *E. gibboides* is modified from Sars (1885) as follows.

Nauplius phase (two stages): Body oval, unsegmented, without compound eyes; 3 pairs of limbs present, antennulae uniramous, antennae and mandibles biramous and natatory.

Metanauplius phase (one stage): Body unsegmented, with carapace; only 2 pairs of limbs present (antennulae and antennae); mandibles, maxillules, maxillae, and maxillipeds (first thoracic legs) present as bud-like prominences.

Calyptopis phase (three stages): Body divided into two principal sections; abdomen becomes segmented; thoracic segments develop but are much compressed; compound eyes imperfectly developed, immobile and covered by hood-like expansion of carapace; mandibles, maxillae, and maxillipeds distinct and functional; thoracic legs posterior to first leg and pleopods not present; uropods develop.

Furcilia phase (variable number of stages): Compound eyes more fully developed, mobile, and projecting beyond sides of carapace; antennae at first retaining original natatory structure, later transformed to adult form with scale and developing flagellum; legs and pleopods develop; method of locomotion thus changes as setose pleopods replace modified antennae for swimming; photophores develop; terminal telson spines become reduced in number, last furcilia stage with 1 terminal telson spine and 3 posterolateral spines.

Juvenile phase: Begins when telson has 2 posterolateral and 1 terminal telson spines, the adult number.

Individuals were straightened on a glass slide in a drop of preservative for measurement with an ocular micrometer. Measurements of developmental phases were as follows.

Egg: Diameter of capsule and width of perivitelline space measured only in specimens with undeveloped embryos.

Nauplius: Length between midpoints of anterior and posterior margins; width at widest point.

Metanauplius: Length between midpoints of anterior margin of rostral hood and posterior margin of abdomen; width of rostral hood at widest point; width of body at widest point posterior to rostral hood; measurements exclude spinose fringe on rostral hood and telson spines.

Calyptopis: Total length between midpoints of anterior margin of carapace and posterior margin of telson; carapace length from center of anterior margin to distal point on posterior margin excluding dorsal spine; carapace width at widest point on anterolateral margins; measurements exclude spinose fringe of carapace and telson spines.

Furcilia: Total length between midpoints of anterior margin of carapace and posterior margin of telson, the carapace measurement excludes spines until median spine appears and then is made from tip of spine, the telson measurement excludes spines until development of 1 terminal spine in last stage and then is taken from tip of spine; carapace length from posterior margin of orbit to distal point on posterior margin excluding spine in furcilia I; rostrum width at widest point proximal to eyestalks, excluding spines; eye height on cornea between upper and lower lobes measured in lateral view.

Juvenile: Total length as in last furcilia stage.

The range, mean ($\bar{x}$), and standard deviation (SD) of each measurement with number of specimens measured (n) is given in Tables 5-8.

Larvae were placed in glycerine for dissection. The description of setation and form of appendages is based on dissection of at least 10 specimens of each developmental stage. The common form of each appendage is figured; when the setation varies within a stage, the number of appendages with each setation observed is given in parentheses behind the number of setae. Only changes in setation or structure from the preceding stage are noted. Drawings were prepared with a Wild M-20 microscope[2] equipped with drawing attachment.

RESULTS

Developmental Stages

The following larval forms of *E. gibboides* were found: nauplius phase, stages I, II; metanauplius phase, one stage; calyptopis phase, stages I-III; furcilia phase, stages I-VI. There was no variation in the number of stages in nauplius, metanauplius, and calyptopis phases or in the first half of the furcilia phase in which stages are defined by the pattern of pleopod development. In the later furcilia stages, usually characterized by the sequential reduction in number of terminal telson spines, dominant and variant forms were found. The features used to differentiate furcilia in the initial sorting were: number and position of setose and non-setose pleopods, form of antenna, number of terminal telson spines, total length, and relative abundance. The furcilia identified are listed in Table 2.

When representatives of each stage were dissected and studied in more detail, two forms of the furcilia with 3 terminal telson spines were found; one was the dominant furcilia V and the other an advanced form which was comparable in size and development to the furcilia with 1 terminal telson spine. There also were two forms of furcilia with 2 terminal telson spines; the smallest was equivalent to furcilia V and the largest to furcilia VI. The relatively large furcilia with 2 and 3 telson spines considered to be variants of furcilia VI lacked the 2nd (middle) pair of posterolateral spines on the telson of the next instar developing beneath the cuticle and presumably would be classified as juvenile after the

TABLE 2.—The furcilia identified during initial survey.

Stage		Form of antenna	Pairs of pleopods		No. terminal telson spines
			Non-setose	Setose	
I		natatory	1	0	7
II		natatory	3	1	7
III		natatory	1	4	7
IV	dominant	natatory	0	5	5
	variant	natatory	0	5	7
	variant	natatory	0	5	6
	variant	natatory	0	5	4
V	dominant	juvenile	0	5	3
	variant	juvenile	0	5	5
	variant	juvenile	0	5	4
	variant	juvenile	0	5	2
VI		juvenile	0	5	1

TABLE 3.—Some of the characters used to group variant forms of furcilia stages IV-VI.

Character	Stage IV	Stage V	Stage VI
No. terminal telson spines: Dominant	5	3	1
Variant	7, 6, 4	5, 4, 2	3, 2
Antenna: Form	natatory	juvenile	juvenile
Right mandible: Dentate process near incisor teeth	+	+	–
Maxillule: Pseudexopod bud	–	–	+
Pleopod 5: Endopod setae	1	2	4

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

next molt. A few of the details which helped to clarify the relationship between furcilia with variant forms are noted in Table 3.

The total number of dominant and variant forms of furcilia IV-VI in samples examined and the percentage of each form within these stages is given in Table 4. The potential variation in reduction of the number of terminal telson spines was estimated by counting the number of spines developing on the telson of the next instar when possible. The range observed in each form is shown in Table 4.

John (1936) in describing larvae of species of *Euphausia* from the Southern Ocean noted that the "furcilia stages recognized by the number of terminal spines on the telson are not such natural groups as those recognized by the character and number of the pleopods"; this appears to be true as well for *E. gibboides*. As observed in other species (Mauchline and Fisher 1969), there is a general correlation between size of furcilia and the number of terminal telson spines (Tables 7, 8). As the larvae become larger, on the average, the number of spines usually decreases, and stages may be characterized by size, number of spines, and relative abundance. Furcilia identified by a wider range of developmental details, however, seem to be grouped more naturally.

Description of Stages

Nauplius I (Figure 1A)

Body egg-shaped, with 3 pairs of appendages. Antennule (Figure 6A) uniramous, unsegmented, with 1 seta and 2 small spines terminally, and 1 small subterminal spine.

Antenna (Figure 7A) biramous, unsegmented; exopod with 4 setae and tiny tooth distally; endopod with 2 setae and small spine terminally and 1 subterminal seta.

Mandible (Figure 7G) biramous, unsegmented; endopod and exopod each with 3 setae.

TABLE 4.—The number of dominant and variant forms of furcilia IV, V, and VI observed, the percentage of each form within stage, and the variation in number of terminal telson spines on developing telson of next instar among individuals of each form.

Stage	No. terminal telson spines	No. larvae	% of stage	No. terminal telson spines in next instar
IV dominant	5	242	88.6	5, 4, 3, or 2
variant	7	9	3.3	5
variant	6	17	6.2	5, 4, or 3
variant	4	5	1.8	3 or 2
V dominant	3	122	78.7	3 or 1
variant	5	11	7.1	3
variant	4	14	9.0	3, 2, or 1
variant	2	8	5.2	1
VI dominant	1	78	66.1	1
variant	3	21	17.8	1
variant	2	19	16.1	1

Nauplius II (Figure 1B)

Body longer, with 2 pairs posterior spines, outer pair very small.

Antennule (Figure 6B) with 2 setae and 1 spine terminally, and a small subterminal spine.

Antenna (Figure 7B) with 5 setae and sometimes a rudimentary 6th seta on exopod. Endopod with 3 setae and a small spine terminally, and 1 subterminal seta.

Mandible as in nauplius I.

Metanauplius (Figure 1C, D)

Carapace produced into wide rostral hood fringed with marginal spines; anterior margin with 3 or 4 relatively long pairs interspersed; posterolateral lobes curved ventrally around body; dorsal crest prominent, without spines. Abdomen short, posterior margin with median indentation and 5 pairs of spines; 3rd pair relatively long bearing setules, other pairs small and fused with telson, one or both of inner pair sometimes rudimentary. There are only 2 pairs of functional appendages.

Antennule (Figure 6C) with 2 setae, 1 aesthetasc (sensory seta), and 1 spine terminally and a small subterminal spine.

Antennal exopod and endopod (Figure 7C) articulated with basal segment which may show incipient segmentation. Exopod with 6 setae on 5 small distal segments; terminal segment, too small to be visible in figure, bears 2 setae. Endopod with 4 setae and 2 small spines distally and 1 subterminal seta on inner margin; rudiment of proximal 2nd marginal seta sometimes present.

Mandibles, maxillules, maxillae, and maxillipeds present as rudimentary buds.

Calyptopis I (Figure 2A-C)

Carapace with distinctive broad rostral hood fringed with small marginal spines; lateral

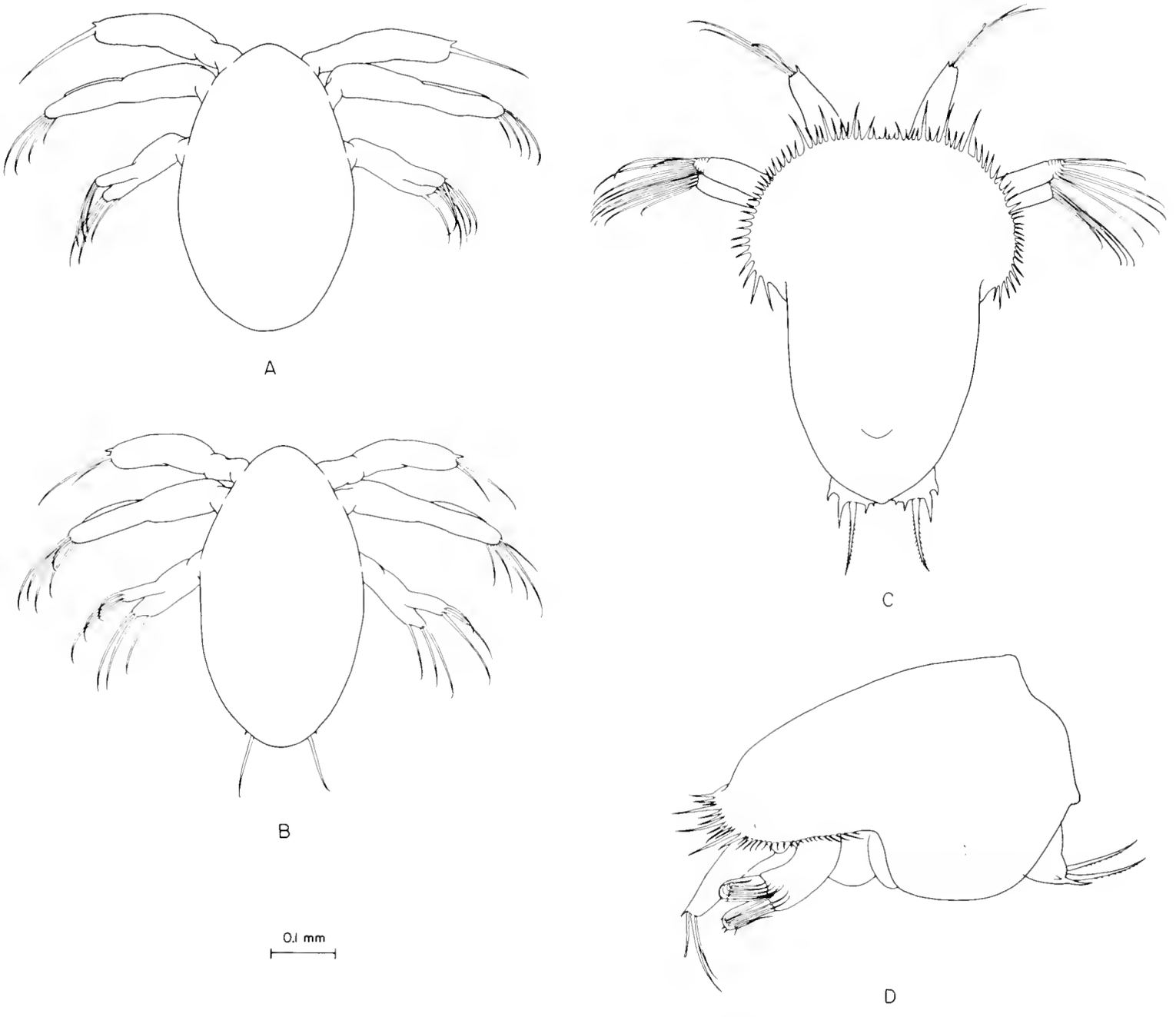

FIGURE 1.—Nauplius I: **A**, dorsal view. Nauplius II: **B**, dorsal view. Metanauplius: **C**, dorsal view; **D**, lateral view.

margins constricted behind eyes; posterior margin produced into strong dorsal spine; dorsal crest prominent. Compound eyes widen as they develop during stage, striated body of photophore visible. Thoracic segments may be visible; abdomen unsegmented.

Antennule (Figure 6D) 2-segmented, basal segment with 2 dorsal setae, 1 medial seta, and medial spine on distal margin; small terminal segment with 2 aesthetascs, 3 setae, 1 strong medial spine and tiny spine.

Antenna (Figure 7D) with 2-segmented protopod. Exopod with 7 setae on 5 distal segments; terminal segment with 3 setae, subterminal segments with 1 seta each. Endopod with 4 terminal setae and 2 setae on inner margin, the proximal marginal seta may be rudimentary; in addition to setules, distal marginal seta and 2 terminal setae bear small spinules and 3rd terminal seta armed with proximal row of comblike setules. This setation remains unchanged until furcilia V.

Mandibles (Figure 7H) asymmetrical; both with narrow plate near *pars molaris* and tuft of setae at base of plate; right mandible with dentate process near incisor teeth; when mandibles close dentate process bends inward toward mouth, the lower plates overlap. Conical anterolateral process and small prominent lateral knob present; lateral knob disappears in furcilia I, and anterolateral process decreases in size gradually up to late furcilia stages.

Maxillule (Figure 8A) with 6(1) or 7(20) setae

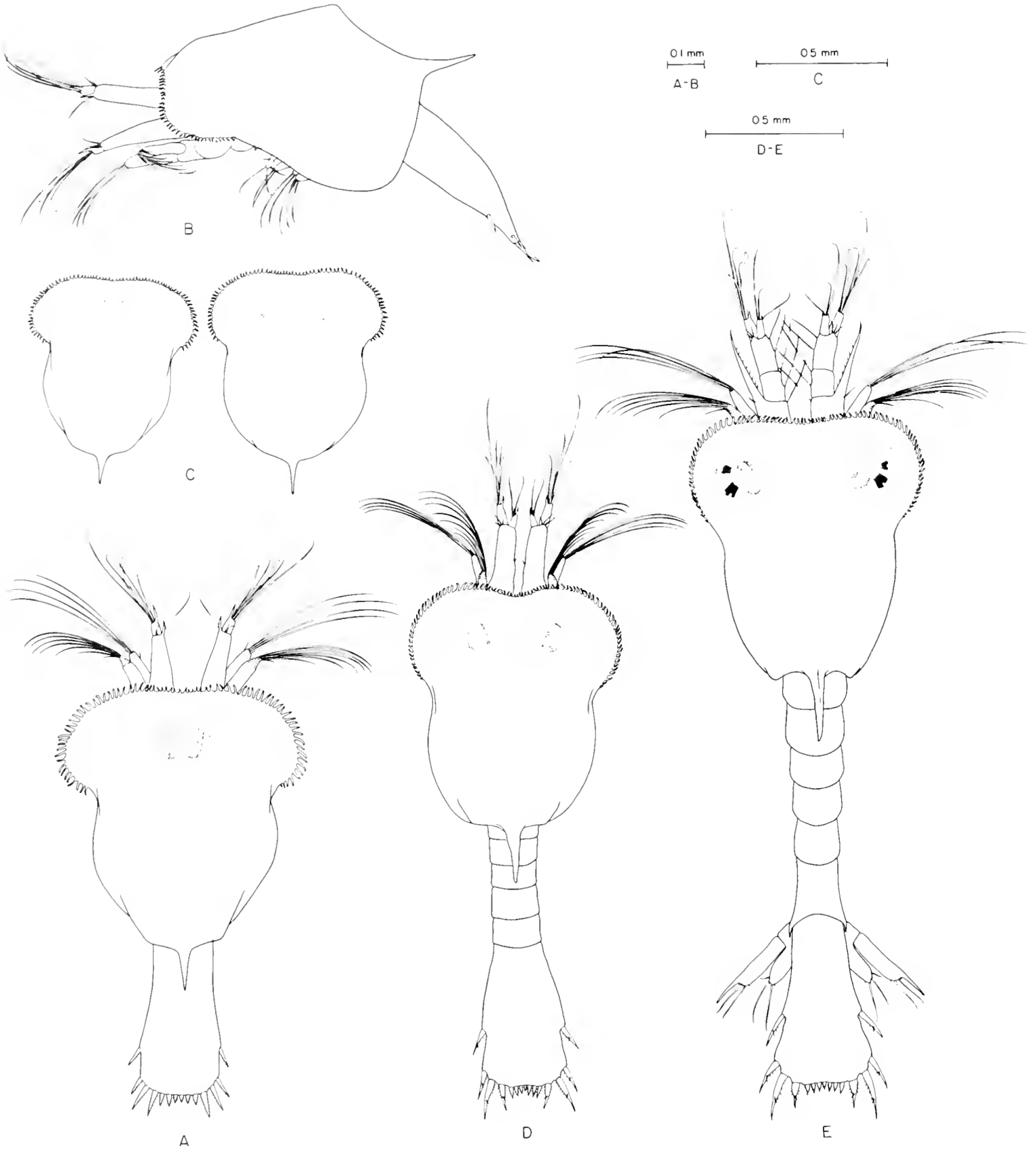

FIGURE 2.—Calyptopis I: **A**, dorsal view; **B**, lateral view; **C**, development of eyes within stage. Calyptopis II: **D**, dorsal view. Calyptopis III: **E**, dorsal view.

on coxal endite, 1 of 2 large setae distinctively armed distally with strong triangular spines rather than setules; basal endite with 3 spines armed with spinules. Endopod 2-segmented, terminal segment with 3 and proximal segment with 2 setae. Exopod a small lobe with 4 plumose setae. Setation of endopod does not change until furcilia V and that of exopod does not change throughout larval development.

Maxilla (Figure 8H) with 5 setose lobes on inner

margin (proximal 2 considered coxal and distal 3 basal although segmentation is unclear); setation of medial lobes 1-5 progressing distally is 8-4-4-4-3; 2 setae on lobe 1 and 1 seta on lobes 2-4 situated submarginally on posterior face. Endopod 1-segmented with 3 setae; exopod represented by 1 plumose seta on lateral margin. There is no change in setation in calyptopis phase.

Maxilliped (Figure 9A) usually with 5 setae on coxa, 4 marginal and 1 (sometimes absent) on posterior face, 4(3) or 5(17) setae were observed. Basis with 6 setae. Endopod 2-segmented; terminal segment with 4 and proximal segment with 3 setae; 1 distal seta on basis and 1 on proximal segment of endopod situated submarginally on posterior face; 1 marginal seta on basis and 1 on first segment of endopod relatively short and stout with tiny marginal spinules. Exopod with 4 terminal setae and 1 proximal seta near indistinct articulation with basis. Fine marginal hairs present as figured.

Telson with 1 pair of lateral spines, 3 pairs of posterolateral spines and 6 terminal spines, posterolateral spine 3 (inner) slightly longer than central posterolateral spine 2; terminal spines and posterolateral spine 3 armed with spinules on lateral margins, lateral spines and posterolateral spines 1 and 2 with spinules on inner margins only.

Calyptopis II (Figure 2D)

Broad rostral hood of carapace with more pronounced inward curve between eyes; dorsal crest less prominent. Abdomen with 5 segments.

Antennule (Figure 6E) biramous. Peduncle unsegmented but may be constricted with segmentation of calyptopis III visible beneath cuticle; distal margin with 3 dorsal setae and inner margin with 1 seta. Outer ramus with 2 aesthetascs, 1-3 setae and 2-4 spines terminally; inner ramus short, with 2 setae and 1-4 spines.

Maxillule (Figure 8B) with 6(3) or 7(15) setae on coxal endite; basal endite with 5 spines.

Maxilliped with 4(1) or 5(19) setae on coxa.

Telson, with addition of small median spine, armed with 7 terminal spines; posterolateral spine 2 now longest; lateral and posterolateral spines with relatively large dorsal spinule slightly more than halfway to tip.

Calyptopis III (Figure 2E)

Carapace with rudiment of small denticle on posterolateral margin present in furcilia I (Figure 4A). Abdomen with 6 segments; 6th segment, now separate from telson, with pair of biramous uropods.

Antennule (Figure 6F) with 3-segmented peduncle, basal segment produced distally into strong lateral spine extending to or slightly beyond tip of inner ramus, inner margin of spine setose. Peduncle segments 1-3 with 1-2-2 plumose setae on inner margins; segment 3 with dorsal lobe bearing 3 setae on distal margin; basal segment with 1 large lateral seta at base of spine. Inner flagellum about two-thirds length of outer flagellum and may have 3rd terminal seta; otherwise setation of rami unchanged.

Mandible armature (Figure 7I) unchanged.

Maxillule with 7 setae on coxal endite and 5 spines on basal endite; no variation observed.

Maxilla usually unchanged, with setation of 8-4-4-4-3 on lobes 1-5; lobe 3 varied with 3(1) or 4(20) setae and lobe 5 with 2(1) or 3(20) setae.

Maxilliped (Figure 9B) usually with 6 setae on coxa, 5(3) or 6(16) setae were observed.

Uropod (Figure 11Q) biramous; protopod with ventral spine above endopod; exopod with strong posterolateral spine, 2 small spines and 2 setae distally; endopod incompletely articulated with protopod, bearing 1 spine and 2 setae distally and 1 small subterminal dorsally projecting seta.

Telson armature unchanged.

Furcilia I (Figures 3A, 4A)

Eyes large, stalked and moveable, with 3-lobed appearance due to arrangement of ommatidia and concentrations of pigment as well as constrictions in cornea; lower lobe largest and most distinctly defined; convex middle lobe especially contributes to characteristic shape of eye. Carapace emarginate behind eyes; rostrum broad, blunt, fringed with small spines; posterior margin produced into dorsal spine; posterolateral margins with denticle; dorsal crest near midlength. First segment of abdomen with pair of non-setose pleopods; developing photophore between pleopods sometimes with faint pigment. Small anal spine present.

Antennule (Figure 6G) with lateral spine of peduncle segment 1 extending to distal margin

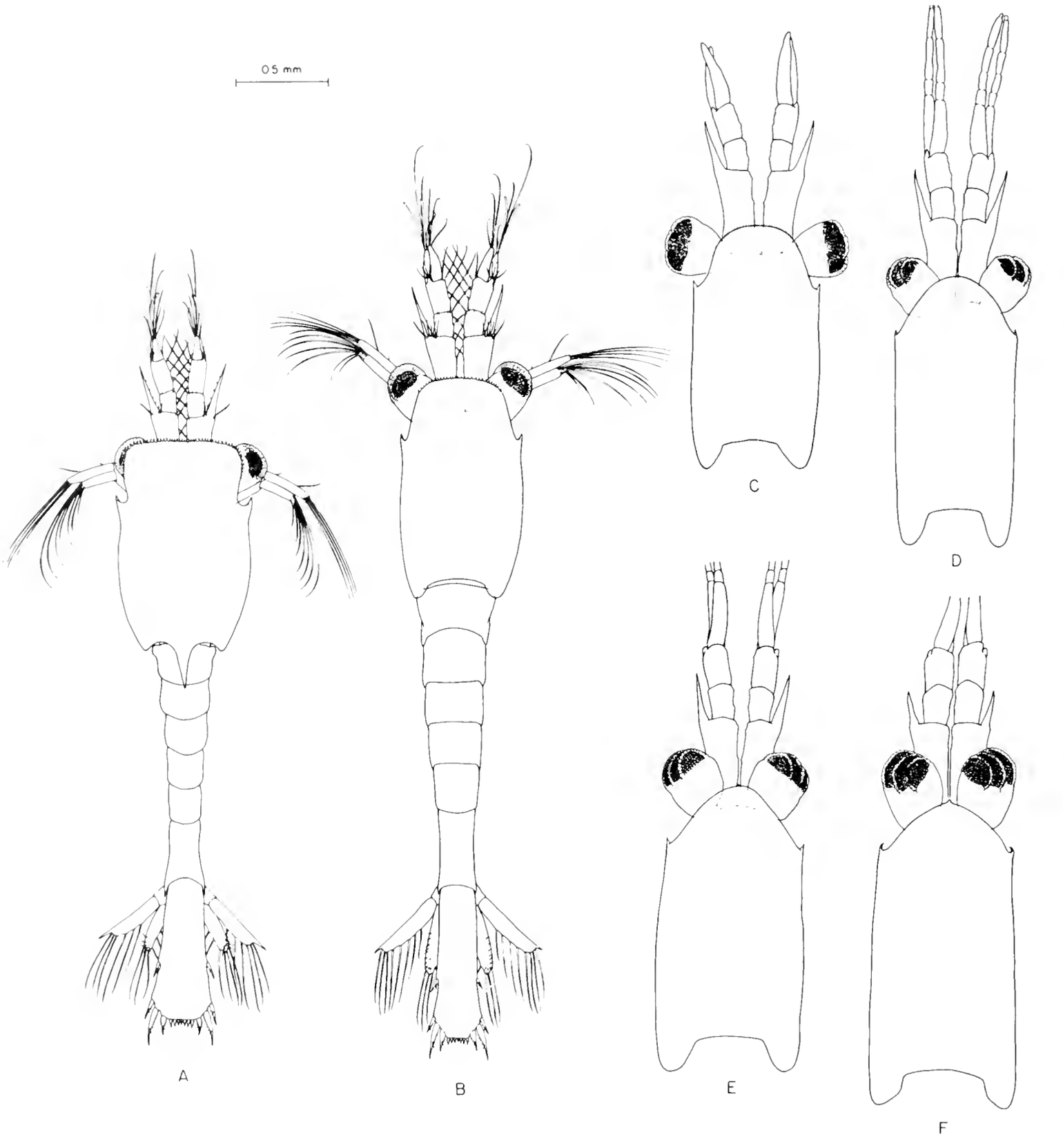

FIGURE 3.—Dorsal view: **A**, furcilia I; **B**, furcilia II; **C**, furcilia III; **D**, furcilia IV; **E**, furcilia V; **F**, furcilia VI.

of segment 3; spine with 5 pairs of setae spaced along inner margin and small setae between; peduncle segments 1 and 2 each with 2 plumose setae on inner margin and small dorsal setae; segment 3 with 3 setae on inner margin, a 4th slightly ventral seta on distal margin, and 4 setae on dorsal lobe. Flagella usually of equal length; outer ramus with 1 aesthetasc at about midlength of inner margin; terminal setation of flagella apparently unchanged but too frequently broken to determine. In subsequent furciliar stages numbers of setae on dorsal surface increase but

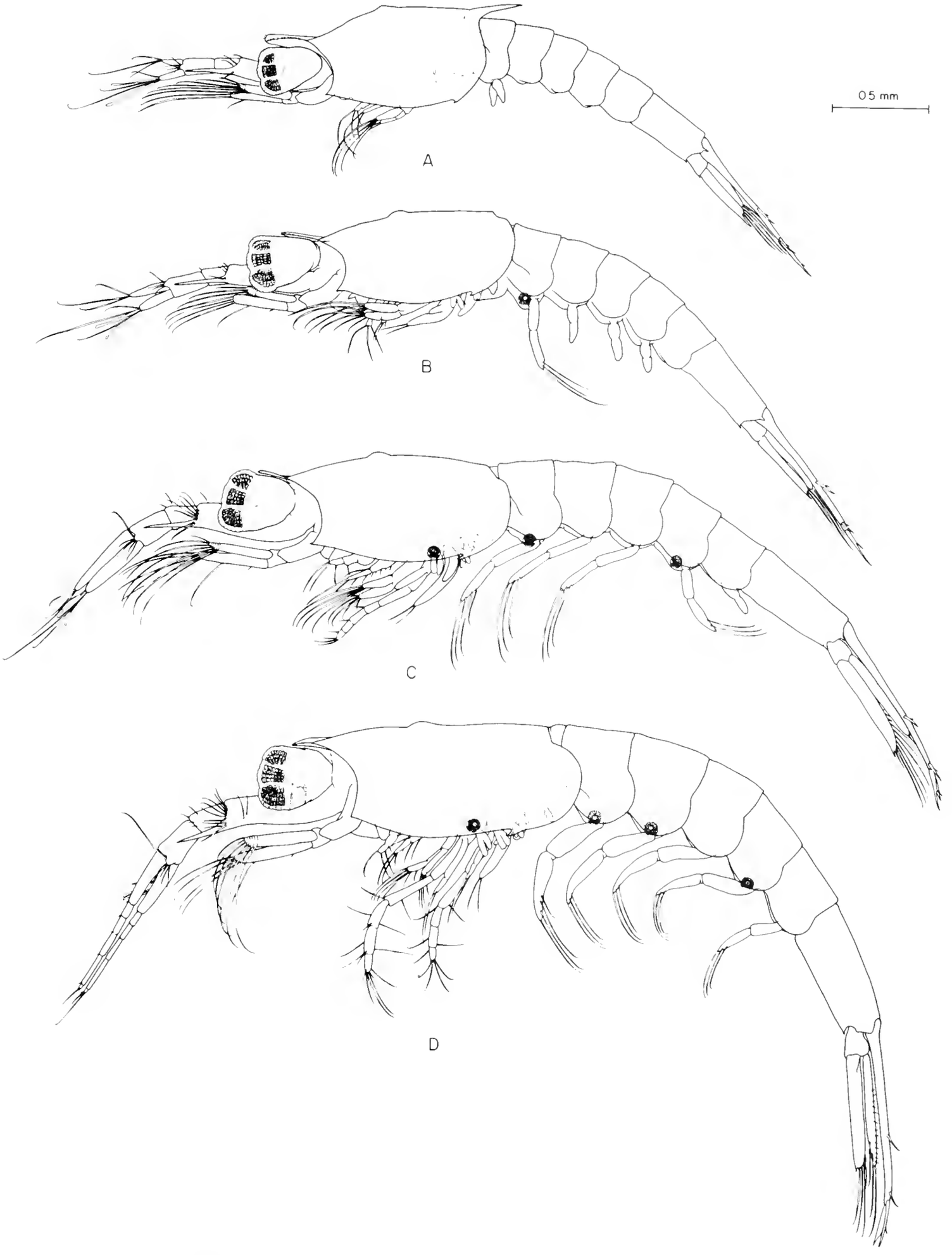

FIGURE 4.—Lateral view: **A**, furcilia I; **B**, furcilia II; **C**, furcilia III; **D**, furcilia IV.

number of plumose setae on medial margin remain the same; the lateral spine on segment 1 gradually decreases in length.

Maxillule with 6(2) or 7(20) setae on coxal endite; basal endite (Figure 8C) with 6(1) or 7(21) spines.

Maxilla (Figure 8I) usually with setation of 8-4-5-4-3 on inner lobes 1-5; lobe 3 now bears 5 setae; lobe 1 variable, with 7(1) or 8(20) setae.

Maxilliped with 5 setae on terminal segment of endopod (Figure 9C); coxa with 5(3) or 6(18) setae.

Leg 2 (Figure 10A) present, rudimentary; bud of leg 3 sometimes visible.

Pleopod (Figure 11L) non-setose and unsegmented, or with incipient segmentation and bud of endopod.

Uropod (Figure 11R) with 6 plumose setae on exopod; endopod articulated with protopod, bearing 6 marginal plumose setae and 3-5 small dorsal setae.

Telson (Figure 12A) with posterolateral spine 2 relatively longer.

Furcilia II (Figures 3B, 4B)

Rostrum of carapace a little narrower, with smaller marginal spines; posterior margin without dorsal spine; lobes of eye more defined (Figure 6K). Abdomen with 1 pair setose and 3 pairs non-setose pleopods on segments 1-4 respectively; photophore on segment 1 pigmented and functional, developing photophore on segment 4 sometimes with faint pigment.

Antennule (Figure 6H) with 5 setae on dorsal lobe of peduncle segment 3 one of which projects dorsally; this setation, with dorsally oriented seta becoming longer and stronger, is found in subsequent furcilia stages. Flagella now approximately as long as 3rd segment of peduncle.

Maxillule (Figure 8D) with 7(1) or 8(23) setae on coxal endite; basal endite with 7 marginal spines and often, in 16 of 24 appendages, with small seta on proximal margin.

Maxilla usually with setation of 8-4-5-5-3; lobe 3 variable with 5(23) or 6(1) setae and lobe 4 (Figure 8J) with 4(3) or 5(21) setae.

Maxilliped usually with 6 setae on terminal segment of endopod (Figure 9D), 5(3) or 6(21) setae were observed; coxa with 5(1) or 6(23) setae.

Leg 2 (Figure 10B) with endopod bearing 2 terminal setae and unsegmented or with 2 or 3 weakly defined segments; exopod rudimentary, without setae; gill bilobed; developing photophore on coxa sometimes with faint pigment. Leg 3 (Figure 10H) rudimentary, or with bud of exopod and gill. Bud of leg 4 may be present.

Setose pleopod 1 (Figure 11M) with 6 plumose setae on exopod, small endopod with single seta and median hook; non-setose pleopods 2-4 as in furcilia I.

Uropod (Figure 11S) with 8(21) or 9(1) setae on exopod, endopod with 7 marginal and 11 or 12 dorsal setae. This is the last stage in which numbers of setae can be counted; in preserved specimens the marginal setae are too frequently broken to attempt enumeration.

Telson (Figure 12B) narrower, posterolateral spine 3 wider basally.

Furcilia III (Figures 3C, 4C)

Carapace with rostrum narrowing, anterior marginal spines may be very small remnants. Abdomen with 4 pairs setose and 1 pair non-setose pleopods on segments 1-4 respectively; photophores on segments 1 and 4 pigmented and functional; developing photophore on segment 2 sometimes with faint pigment.

Antennular flagella (Figure 6I) almost twice as long as peduncle segment 3 and may be 2-segmented; outer flagellum with 2 aesthetascs on inner margin one of which bifurcates distally.

Mandible with anterolateral process about one-half as long as that figured for calyptopis III.

Maxillule with 8 setae on coxal endite; basal endite (Figure 8E) with 7(1), 8(4), or 9(17) spines on medial margin and 1 small seta on proximal margin.

Maxilla usually with setation of 8-4-6-5-3; lobe 3 (Figure 8K) now with 5(2) or 6(20) setae; lobe 5 variable with 2(1) or 3(20) setae.

Maxilliped with 5(3) or 6(16) setae on coxa and 6 on terminal segment of endopod.

Leg 2 (Figure 10C) with endopod 5-segmented, articulation with basis indistinct, setation variable, terminal segment with more than 2 setae; exopod with 0(7), 1(5), or 2(5) setae; gill bilobed; photophore pigmented and functional. Leg 3 (Figure 10I) with endopod unsegmented or with a few (less than 5) weakly defined segments, setation variable, distal segment usually with 2 terminal setae, 2(21) or 3(1) setae were observed; exopod rudimentary, without setae; gill bilobed.

Leg 4 (Figure 10N) rudimentary, with bud of exopod and small bilobed or simple bud of gill; endopod usually without terminal setae, 0(22) or 1(2) seta were observed. Leg 5 present as bud. Leg 7 rudimentary with gill bud and developing photophore.

Setation of pleopods on abdominal segments 1-4 as follows: pleopod 1 (Figure 11N) — endopod 2, exopod 6(8), 7(11), or 8(1); pleopods 2-4 — endopod 1, exopod 6. Non-setose pleopod of segment 5 as in furcilia I. Endopod of pleopod 1 with *appendix interna*, a small medial lobe with tiny hooks.

Telson (Figure 12C) narrower; posterolateral spine 3 quite broad, inner margin smooth except for 1 or 2 tiny distal spinules near larger dorsal spinule. Five terminal spines of furcilia IV may often be seen beneath integument.

Furcilia IV (Figures 3D, 4D)

Rostrum of carapace usually with smooth margin, there may be tiny remnants of marginal spines but no median spine. Abdomen with 5 pairs of setose pleopods; photophores on segments 1, 2, and 4 pigmented and functional; developing photophore on segment 3 sometimes with faint pigment.

Antennular flagella (Figure 6J) with about 6 or 7 segments, segmentation usually indistinct; outer flagellum with 3 aesthetascs, 1 proximal to pair on medial margin, 1 aesthetasc no longer bifurcate.

Maxillule with 8(12) or 9(10) setae on coxal endite (Figure 8F); basal endite with 8(1) or 9(21) marginal spines and 1 seta on proximal margin.

Maxilla usually unchanged, with setation of 8-4-6-5-3; lobe 4 variable with 5(20) or 6(2) setae.

Maxilliped (Figure 9E) with 5(4) or 6(18) setae on coxa; basis with 6(9) or 7(10) setae. Endopod becoming 3-segmented as small terminal segment forms with setation of 3-2-4 for segments 1-3.

Leg 2 (Figure 10D) with endopod larger, more setose, and becoming geniculate with terminal 3 segments reflexed as in adult; exopod with 4(3) or 5(6) setae (seldom intact); gill bilobed. Leg 3 (Figure 10J) with endopod 5-segmented, sometimes slightly reflexed, articulation with basis indistinct, setation variable, terminal segment with more than 2 setae; exopod with 2(1), 3(1), or 4(12) setae; gill bilobed. Leg 4 (Figure 10O) endopod with few (less than 5) weakly delineated segments, terminal segment with 2 setae, other setation variable; exopod usually without setae, 1 of 15 appendages examined with 1 seta; gill bilobed. Leg 5 (Figure 11A) rudimentary with bud of exopod and bilobed or simple bud of gill. Bud of leg 6 present. Leg 7 (Figure 11I) with gill bilobed or with small bud of 3rd lobe, photophore may have pigment. Leg 8 (Figure 11F) represented by bilobed or trilobed gill.

Pleopod setation as follows: pleopod 1 (Figure 11O) — endopod 3(2) or 4(17), exopod 8; pleopod 2 — endopod 2, exopod 7(1) or 8(19); pleopod 3 — endopod 2, exopod 7(3) or 8(15); pleopod 4 — endopod 2, exopod 7(8) or 8(9); pleopod 5 — endopod 1, exopod 6.

Telson (Figure 12D) with 5 terminal spines, the 3 terminal spines of next instar often visible beneath cuticle.

VARIANT FORMS. — A small furcilia IV with 6 telson spines was less mature in that leg 4 had 1 terminal seta and exopods of pleopods 3 and 4 had only 6 setae. A furcilia IV with 4 telson spines showed bud of 3rd lobe of gill on leg 2.

Furcilia V (Figures 3E, 5A)

Rostrum usually with smooth margin, there may be a very small median spine. Photophores on abdominal segments 1-4 now pigmented.

Antennule with lateral spine of peduncle segment 1 extending to about midpoint of segment 3, none of the specimens available had flagella intact.

Antenna (Figure 7E) transformed, no longer natatory; basal segment with distolateral spine; endopod with 8 segments, 3 peduncular and 5 flagellar, division of terminal segment not always distinct; exopod (scale) with 13 or 14 plumose marginal setae.

Mandible (Figure 7J) with anterolateral process now considerably reduced in size.

Maxillule with 8(1) or 9(22) setae on coxal endite; basal endite with 9(21) or 10(2) marginal spines and 1(21) or 2(2) small setae on proximal margin. Endopod with segmentation weak or indistinct; in 6 of 21 appendages examined 1-segmented with 1 seta on lateral margin as figured for furcilia VI (Figure 8G).

Maxilla usually with setation of 8-4/5-6-6-3; lobe 2 (Figure 8L) variable with 4(15) or 5(9) setae and lobe 4 with 4(1), 5(4), or 6(19) setae.

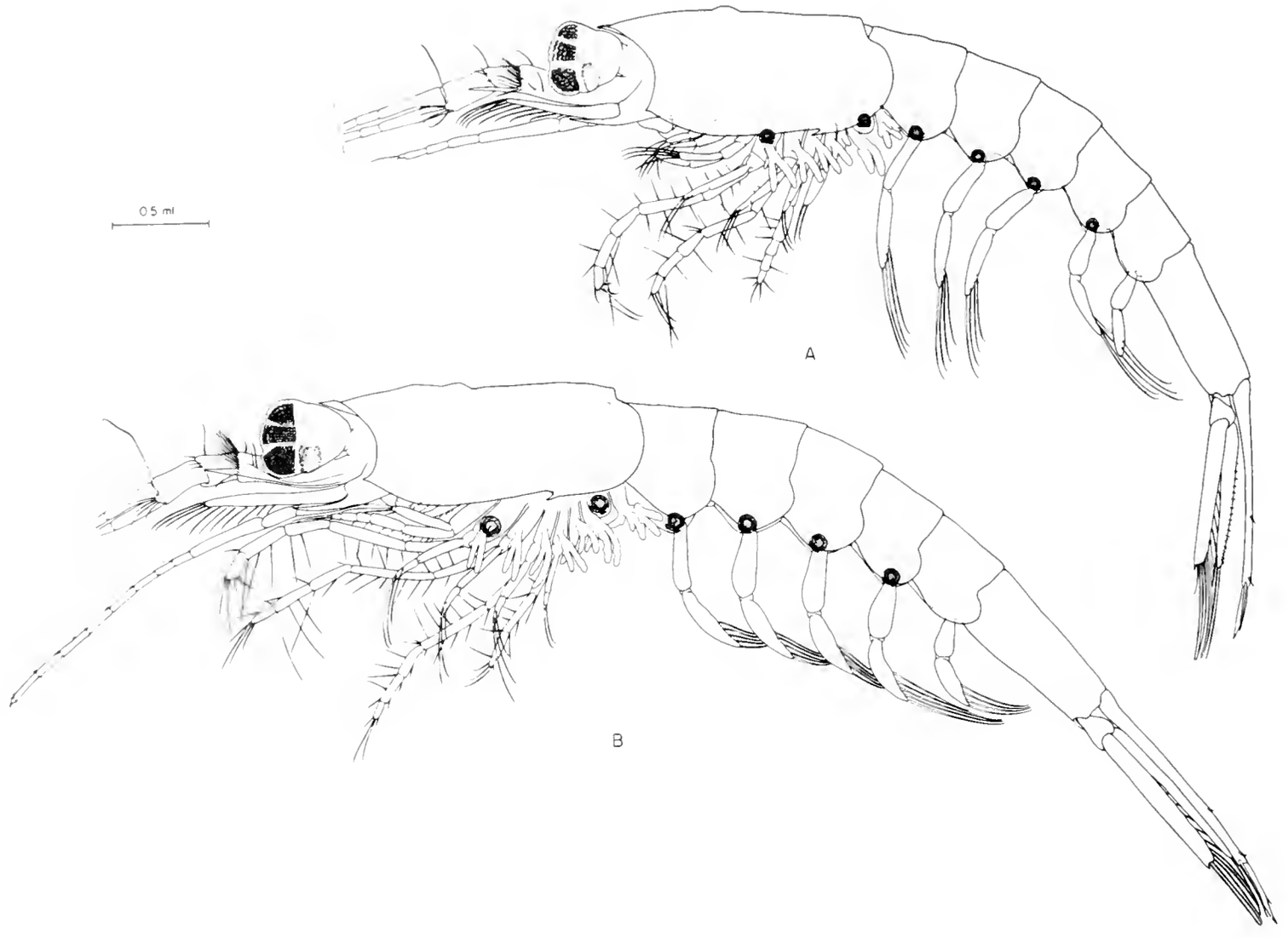

FIGURE 5.—Lateral view: **A**, furcilia V; **B**, furcilia VI.

Maxilliped (Figure 9F) with increasingly variable setation; coxa with 5(2), 6(12), 7(9), or 8(1) setae; basis with 6(2), 7(9), or 8(12) setae. Endopod lengthened, usually with 3 segments; 4 of 20 appendages examined with 4 or 5 segments indicated, distal segments weakly delineated; setations of 3-2-4, 3-1-1-4, and 3-2-0-1-4, progressing distally, were observed.

Leg 2 (Figure 10E) with dactyl of endopod becoming modified; exopod with 6 setae; gill usually with bud of 3rd lobe. Leg 3 (Figure 10K) with endopod reflexed, longer and more setose; exopod with 5(8) or 6(8) setae; gill with bud or sizeable rudiment of 3rd lobe. Leg 4 (Figure 10P) with endopod 5-segmented, articulation with basis never clear, setation variable, terminal segment with more than 2 setae; exopod with 4(16) or 5(1) setae; gill bilobed. Leg 5 (Figure 11B) with endopod unsegmented or weakly segmented with less than 5 segments, with 1(9) or 2(13) terminal setae and sometimes a few marginal setae; exopod with 0(22) or 1(1) seta; gill bilobed. Leg 6 (Figure 11D) rudimentary with gill bud, may be slightly bifid. Leg 7 (Figure 11J) with pigmented photophore; gill sometimes with bud of 3rd or 4th lobes. Leg 8 (Figure 11G) ramified, with varying numbers of lobes.

Setation of pleopods as follows: pleopod 1 — endopod 4, exopod 8(11), 9(5), or 10(2); pleopod 2 — endopod 4, exopod 8(7), 9(11), or 10(1); pleopod 3 — endopod 4, exopod 8(15) or 9(5); pleopod 4 — endopod 3(1) or 4(19), exopod 8; pleopod 5 — endopod 2, exopod 6(1), 7(17), or 8(5).

Telson (Figure 12E) narrow, with 3 terminal spines, 3rd pair of posterolateral spines lengthening relatively; single terminal spine of final furcilia may often be seen beneath cuticle.

VARIANT FORM. — A small furcilia V with 5 telson spines had antennal flagellum of about 5 segments, endopod of leg 5 without terminal setae, and endopod of pleopods 3-5 with 2, 2, and

1 setae respectively, one of the endopods of pleopod 5 had rudiment of 2nd seta.

Furcilia VI (Figures 3F, 5B)

Rostrum usually with small median spine.

Antennule with lateral spine of peduncle segment 1 about as long as segment 2; outer flagellum may have additional proximal aesthetasc; one apparently intact inner flagellum with 10 segments.

Antennal scale (Figure 7F) with approximately 15 or 16 setae; one intact flagellum with 3 peduncular and 11 flagellar segments.

Right mandible (Figure 7K) now without dentate process near incisor teeth; toothed plates relatively smaller; rudimentary palp may begin to increase in size.

Maxillule (Figure 8G) with 9(15) or 10(9) setae on coxal endite; basal endite with 9(4) or 10(20) marginal spines and 1(8) or 2(16) small setae on proximal margin. Endopod of 1 segment with 1 proximal lateral seta; terminal and medial setation unchanged. Coxa now with rudiment of pseudexopod.

Maxilla (Figure 8M) usually with setation of 8-6-6-6-3; lobe 2 variable with 4(2), 5(4), or 6(18) setae. Exopod represented by 1 (22) or 2(2) setae; endopod rounder.

Maxilliped (Figure 9G) modifying to adult form; coxa with 5-9 setae, long seta on posterior face no longer present; basis with 8(22) or 9(2) setae. Endopod of 5 segments with variable setation; articulation with basis not clear. Exopod still with 4 terminal setae.

Leg 2 (Figure 10F, G) with endopod more setose, dactyl with a few more "cleaning" comb setae; exopod with 6 setae; gill trilobed. Leg 3 (Figure 10L, M) with long terminal setae on dactyl of endopod; exopod with 6 setae; gill with bud of 3rd lobe or trilobed. Leg 4 (Figure 10Q) with endopod reflexed; exopod with 5(1) or 6(14) setae; gill with bud or larger rudiment of 3rd lobe. Leg 5 (Figure 11C) with endopod 5-segmented and setation variable, terminal segment with more than 2 setae; exopod with 1(2), 2(4), 3(2), or 4(10) setae; gill trilobed. Leg 6 (Figure 11E) with endopod unsegmented and nonsetose; exopod without setae; gill trilobed; exopod and gill may be rudimentary. Legs 7 (Figure 11K) and 8 (Figure 11H) with increasing number of gill lobes.

Pleopods with setation as follows: pleopod 1 (Figure 11P) — endopod 4(5), 5(10), or 6(7), exopod 9(7) or 10(12); pleopod 2 — endopod 4(14), 5(7), or 6(2), exopod 9(2), 10(13), or 11(3); pleopod 3 — endopod 4(17), 5(1), or 6(3), exopod 9(2), 10(13), or 11(1); pleopod 4 — endopod 4(21) or 6(2), exopod 9(10) or 10(7); pleopod 5 — endopod 3(1) or 4(20), exopod 8.

Telson (Figure 12F) quite slender with 1 terminal spine and 3 pairs posterolateral spines; posterolateral spine 2 was missing on one side in 5 of 12 larvae dissected. Developing telson of next instar is without spine 2 on either side.

VARIANT FORMS. — In furcilia VI with 2 and 3 telson spines, basis of maxilliped sometimes with 7 setae and exopod of leg 2 with 6, 7, or 8 setae. Once in furcilia with 3 telson spines, lobe 3 of maxilla with 7 setae and right mandible with tiny remnant of dentate process.

Measurements

The eggs assumed to be those of *E. gibboides* have a relatively wide perivitelline space. The measurements, in millimeters, of 100 eggs from one sample (6304-110.70) are: diameter of capsule, range = 0.61-0.75, $\bar{x}$ = 0.69, SD = 0.03; perivitelline space, range = 0.13-0.19, $\bar{x}$ = 0.16, SD = 0.01.

The measurements of developmental stages are given in Tables 5-8. The growth factor (mean length in stage divided by mean length in preceding stage) for dominant forms is as follows:

Stage	*Growth factor*	*Stage*	*Growth factor*
		Furcilia I	1.23
Nauplius II	1.04	Furcilia II	1.17
Metanauplius	1.08	Furcilia III	1.14
Calyptopis I	2.03	Furcilia IV	1.10
Calyptopis II	1.55	Furcilia V	1.10
Calyptopis III	1.39	Furcilia VI	1.12

There was variation in size of comparable developmental stages between the different areas from which samples were studied. The lengths of calyptopis stages are compared in Table 9. The larvae sampled in April 1963 (Cruise 6304) in the eastern North Pacific became larger, on the average, during the calyptopis phase in the

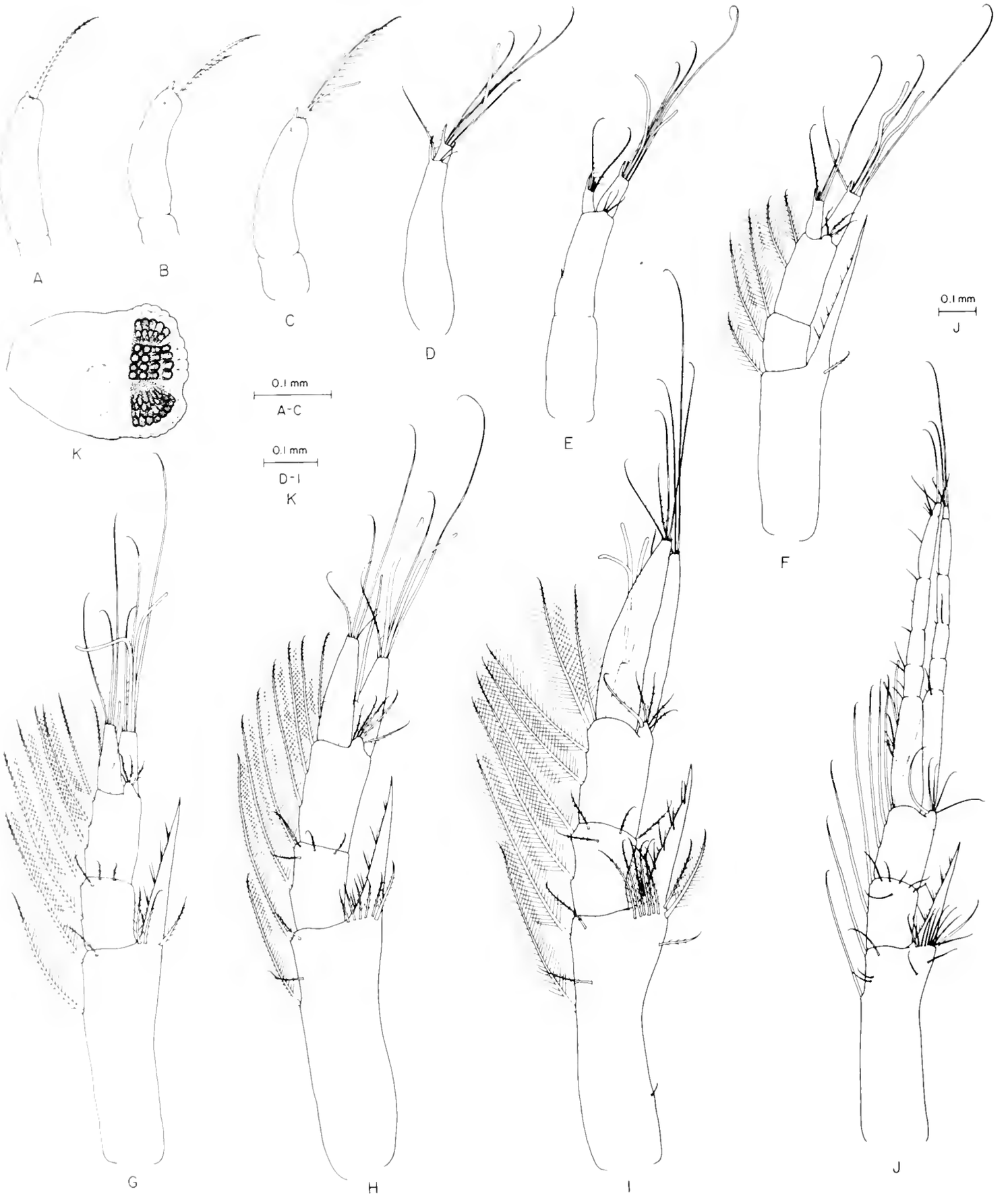

FIGURE 6.—Antennule: **A**, nauplius I; **B**, nauplius II; **C**, metanauplius; **D**, calyptopis I; **E**, calyptopis II; **F**, calyptopis III; **G**, furcilia I; **H**, furcilia II; **I**, furcilia III; **J**, furcilia IV. Eye: **K**, furcilia II.

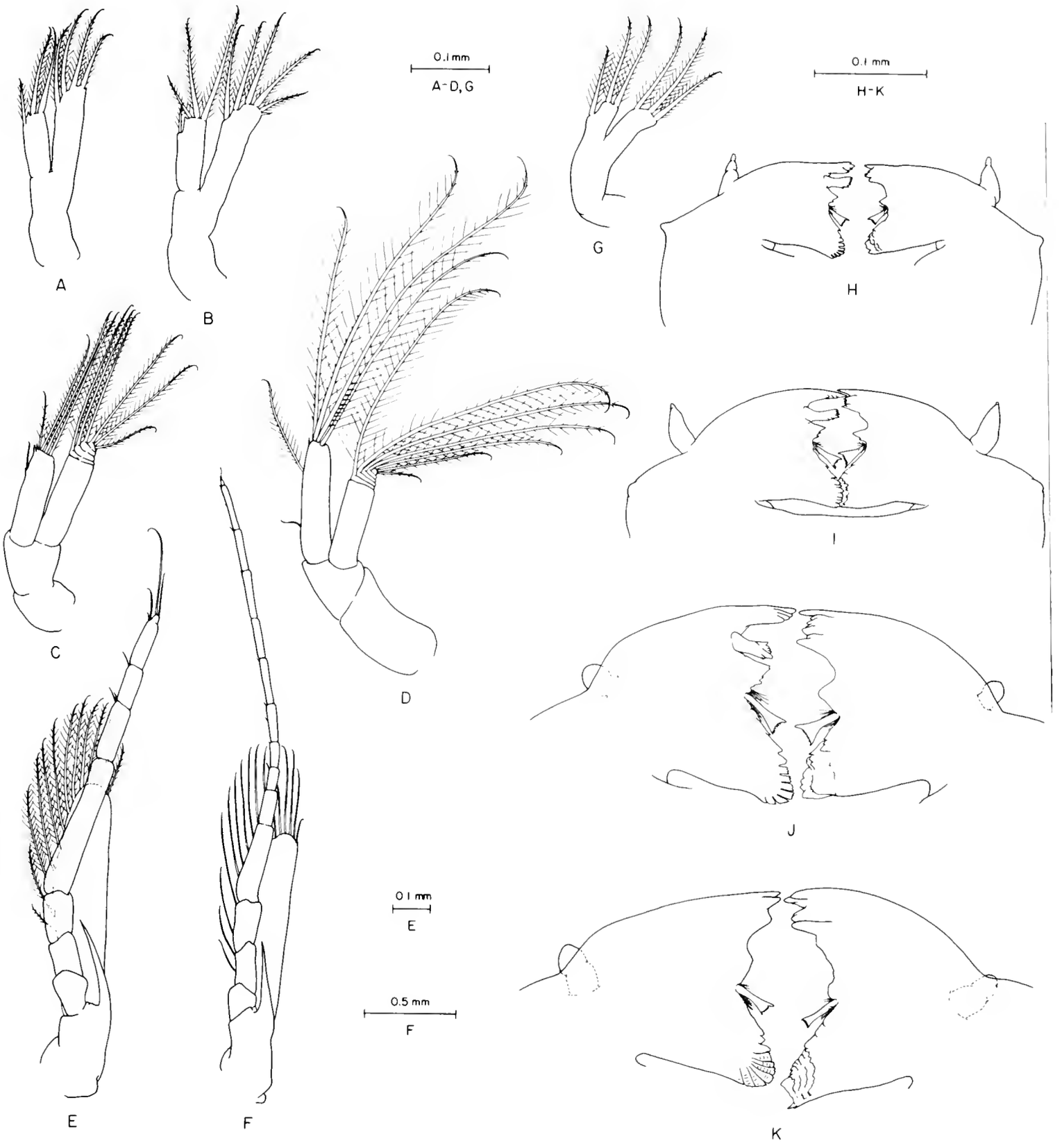

FIGURE 7.—Antenna: **A**, nauplius I; **B**, nauplius II; **C**, metanauplius; **D**, calyptopis I; **E**, furcilia V; **F**, furcilia VI. Mandibles: **G**, nauplius I; **H**, calyptopis I; **I**, calyptopis III; **J**, furcilia V; **K**, furcilia VI.

FIGURE 8.—Maxillule: **A**, calyptopis I; **B**, calyptopis II; **C**, furcilia I, basal endite; **D**, furcilia II; **E**, furcilia III, basal endite; **F**, furcilia IV, coxal endite; **G**, furcilia VI. Maxilla: **H**, calyptopis I; **I**, furcilia I; **J**, furcilia II, lobe 4; **K**, furcilia III, lobe 3; **L**, furcilia V, lobe 2; **M**, furcilia VI.

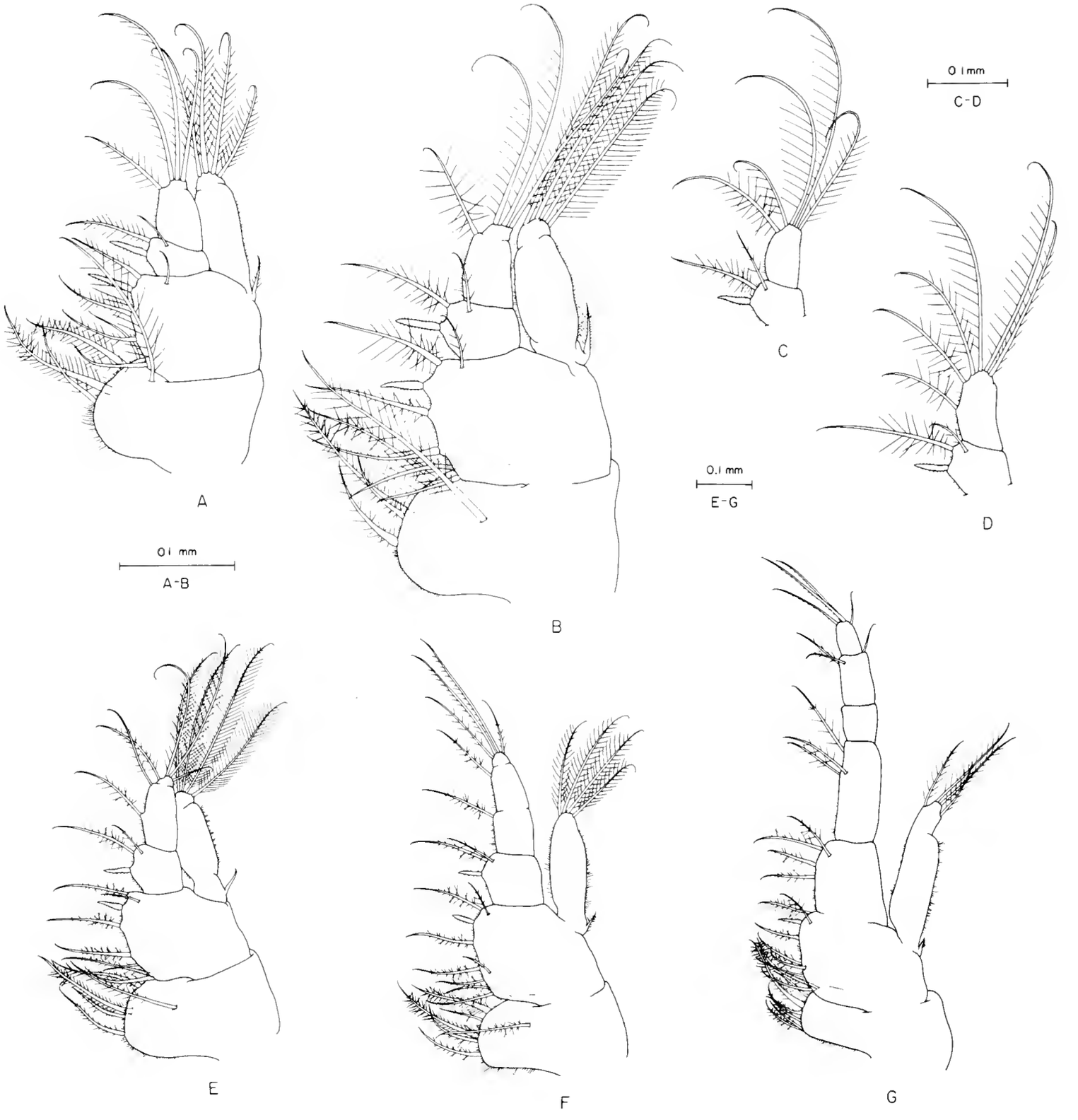

FIGURE 9.—Maxilliped (leg 1): **A**, calyptopis I; **B**, calyptopis III; **C**, furcilia I, endopod; **D**, furcilia II, endopod; **E**, furcilia IV; **F**, furcilia V; **G**, furcilia VI.

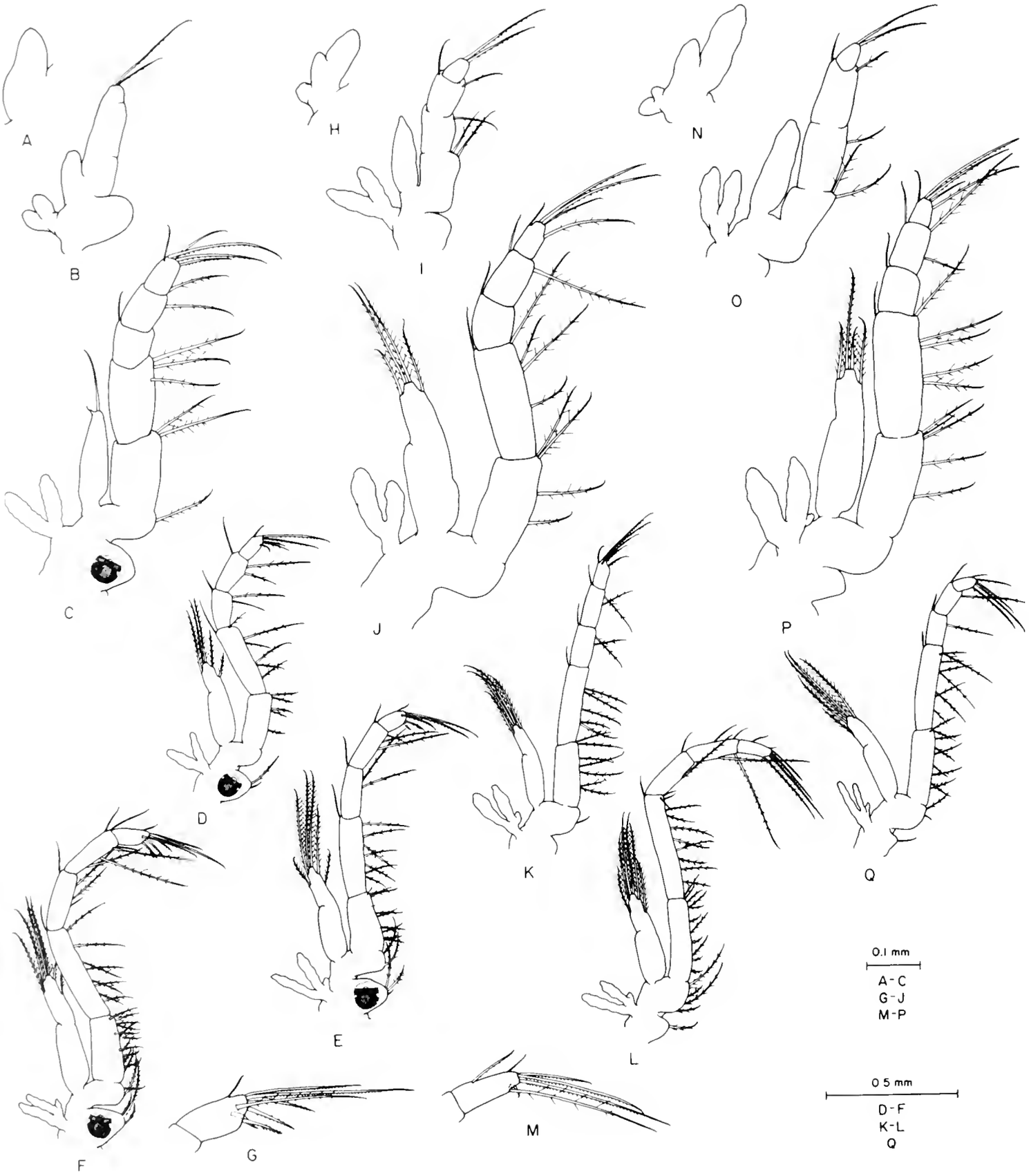

FIGURE 10.—Thoracic legs. Leg 2: **A**, furcilia I; **B**, furcilia II; **C**, furcilia III; **D**, furcilia IV; **E**, furcilia V; **F**, furcilia VI; **G**, dactyl, furcilia VI. Leg 3: **H**, furcilia II; **I**, furcilia III; **J**, furcilia IV; **K**, furcilia V; **L**, furcilia VI; **M**, dactyl, furcilia VI. Leg 4: **N**, furcilia III; **O**, furcilia IV; **P**, furcilia V; **Q**, furcilia VI.

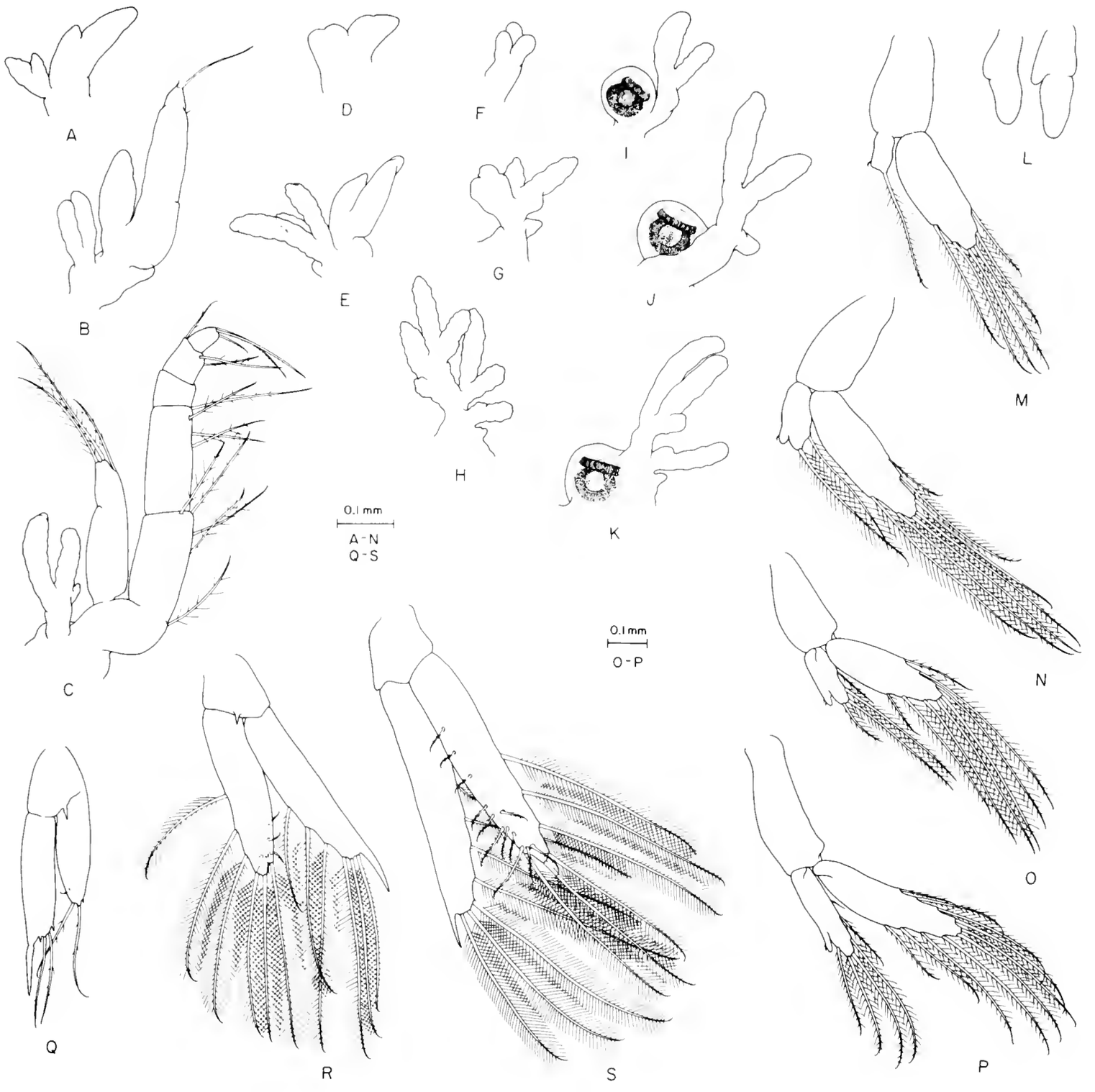

FIGURE 11.—Thoracic leg 5: **A**, furcilia IV; **B**, furcilia V; **C**, furcilia VI. Leg 6: **D**, furcilia V; **E**, furcilia VI. Leg 7: **I**, furcilia IV; **J**, furcilia V; **K**, furcilia VI. Leg 8: **F**, furcilia IV; **G**, furcilia V; **H**, furcilia VI. Pleopod 1: **L**, furcilia I; **M**, furcilia II; **N**, furcilia III; **O**, furcilia IV; **P**, furcilia VI. Uropods: **Q**, calyptopis III; **R**, furcilia I; **S**, furcilia II.

more northern areas. In the sample from August 1963 (6306-117.80), the sizes of developmental stages were similar to those found in the same general area in the spring. There is insufficient information at this time to consider the effects of environmental conditions on the rate of larval growth and development in *E. gibboides*, but similar variation has been observed in other species of euphausiids (Einarsson 1945; Mauchline 1965).

The range and mean of carapace width in calyptopis stages expressed as percent of carapace length is given in Table 10 as the proportional anterolateral expansion of carapace appears to be a useful character for identification of *E. gibboides*. Comparison by area shows

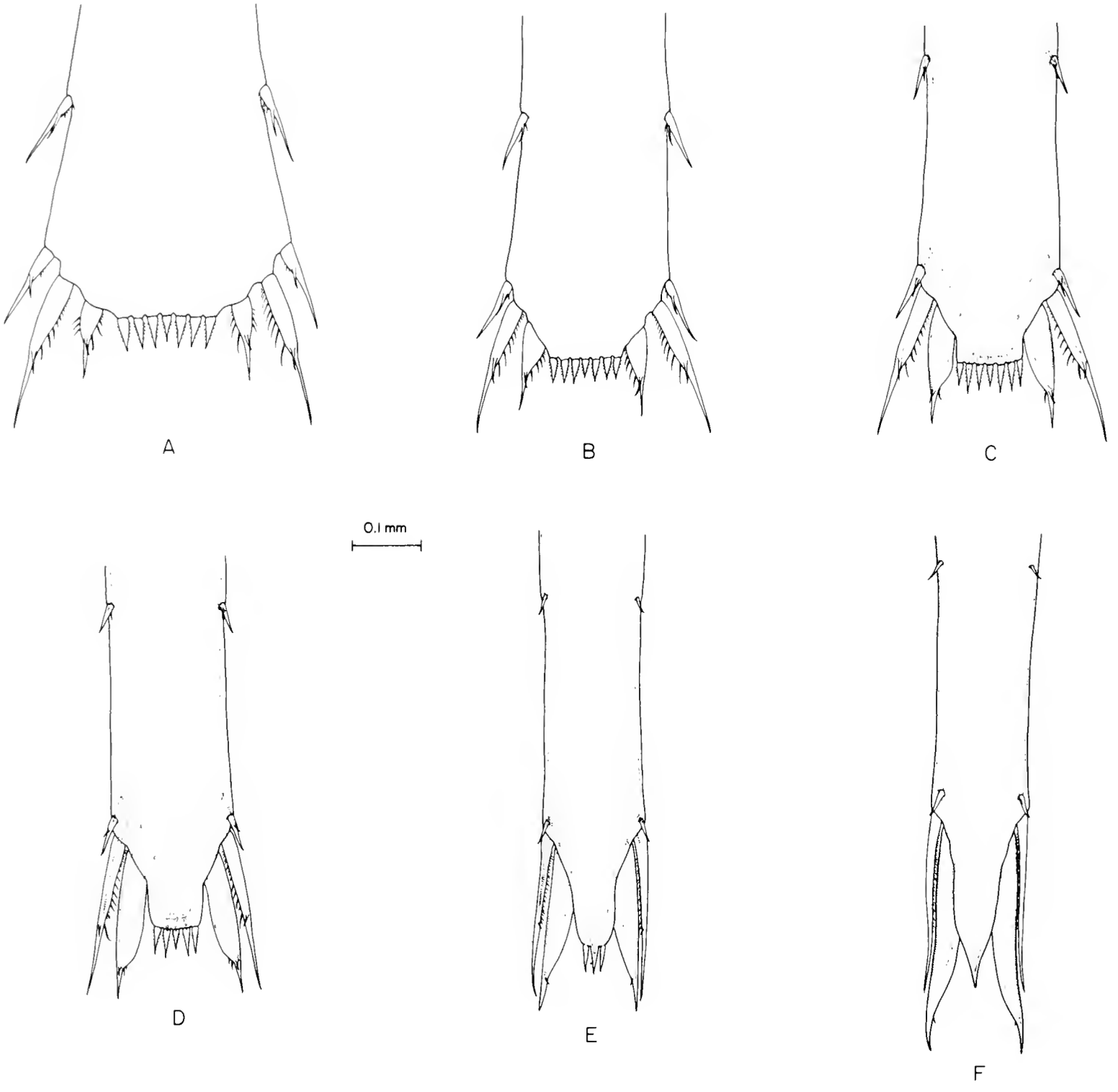

FIGURE 12.—Telson: **A**, furcilia I; **B**, furcilia II; **C**, furcilia III; **D**, furcilia IV; **E**, furcilia V; **F**, furcilia VI.

that the average ratio tends to increase in northern and western Pacific samples.

Juveniles

There was a good series of related juvenile euphausiids in the net haul from station 6304-117.90. Sixty-four were measured and examined in some detail. The smaller juveniles had the distinctive 3-lobed eye described for furcilia stages of *E. gibboides* while some of the larger individuals had the characteristic eye as well as a small dorsal spine on the posterior margin of the 3rd segment of the abdomen and a small dorsal lappet with triangular pointed tip on the margin of the 1st segment of the antennule. The abdominal spine and shape of rudimentary lappet together with the relatively large eye identify the juveniles as *E. gibboides* (Boden et al. 1955). The shape of the eye provides continuity with the

larvae described and confirms their identification.

The juveniles examined ranged from 5.3 to 8.2 mm in total length and a dorsal spine appeared on the 3rd segment of the abdomen at a length of 6.8 mm. A 3-lobed eye was found in a 7.2-mm individual. At 7.0 mm, the constriction between the upper and middle lobes of the eye may disappear; the lower large lobe remains well defined and, although the pigment still appears darker in the lateral position of the middle lobe, the eye becomes increasingly 2-lobed in appearance. The antennule may have a small lappet in 6.3-mm individuals, but the pointed triangular tip was not seen in animals less than 7.0 mm in length, and then it was not always directed outward as in the adult. The lobe and keel of the 2nd and 3rd antennular segments respectively were not developed. A rostral spine may be missing or very small in the early

TABLE 5.—Measurements of nauplius and metanauplius stages.

Stage	Total length (mm)	Width of body (mm)	Width of rostral hood (mm)
Nauplius I:			
Range	0.48-0.53	0.29-0.32	—
$\bar{x}$	0.51	0.30	
SD	0.02	0.01	
n	12	12	
Nauplius II:			
Range	0.51-0.56	0.28-0.32	—
$\bar{x}$	0.53	0.30	
SD	0.01	0.01	
n	12	12	
Metanauplius:			
Range	0.53-0.61	0.28-0.36	0.38-0.45
$\bar{x}$	0.57	0.32	0.42
SD	0.02	0.02	0.02
n	38	38	38

TABLE 6.—Measurements of calyptopis stages.

Stage	Total length (mm)	Carapace width (mm)	Carapace length (mm)
Calyptopis I:			
Range	1.09-1.27	0.59-0.71	0.69-0.79
$\bar{x}$	1.16	0.64	0.72
SD	0.03	0.03	0.02
n	124	124	124
Calyptopis II:			
Range	1.66-1.98	0.65-0.87	0.79-0.93
$\bar{x}$	1.80	0.76	0.86
SD	0.07	0.05	0.03
n	158	158	157
Calyptopis III:			
Range	2.34-2.71	0.75-0.99	0.89-1.09
$\bar{x}$	2.51	0.86	1.00
SD	0.09	0.06	0.05
n	149	149	148

TABLE 7.—Measurements of furcilia stages I-III.

Stage	Total length (mm)	Carapace length (mm)	Rostrum width (mm)	Eye height (mm)
Furcilia I:				
Range	2.85-3.37	0.75-0.85	0.51-0.65	0.24-0.28
$\bar{x}$	3.09	0.80	0.58	0.25
SD	0.10	0.02	0.03	0.01
n	123	104	107	109
Furcilia II:				
Range	3.19-3.94	0.79-0.97	—	0.26-0.32
$\bar{x}$	3.61	0.88		0.29
SD	0.14	0.04		0.01
n	104	98		103
Furcilia III:				
Range	3.80-4.57	0.91-1.09	—	0.30-0.34
$\bar{x}$	4.10	1.02		0.32
SD	0.13	0.04		0.01
n	143	82		83

TABLE 8.—Measurements of furcilia stages IV-VI.

Stage	Total length (mm)	Carapace length (mm)	Eye height (mm)
Furcilia IV:			
dominant — 5 ts (telson spines)			
Range	4.20-4.93	1.01-1.19	0.32-0.38
$\bar{x}$	4.53	1.10	0.34
SD	0.15	0.04	0.02
n	58	56	59
variant — 7 ts			
Range	4.34-4.85	1.05-1.17	0.32-0.36
$\bar{x}$	4.63	1.11	0.34
SD	0.16	0.05	0.01
n	7	5	7
variant — 6 ts			
Range	4.16-4.79	1.03-1.17	0.30-0.36
x	4.47	1.08	0.34
SD	0.20	0.05	0.02
n	11	10	10
variant — 4 ts			
Range	4.36-4.61	1.07-1.15	0.34-0.36
$\bar{x}$	4.51	1.10	0.34
SD	0.12	0.03	0.01
n	5	4	5
Furcilia V:			
dominant — 3 ts			
Range	4.61-5.41	1.11-1.31	0.36-0.40
$\bar{x}$	4.98	1.20	0.37
SD	0.21	0.06	0.02
n	46	43	46
variant — 5 ts			
Range	4.57-5.25	1.09-1.27	0.36-0.40
$\bar{x}$	4.87	1.17	0.37
SD	0.24	0.05	0.01
n	10	9	9
variant — 4 ts			
Range	4.65-5.33	1.11-1.31	0.34-0.38
$\bar{x}$	4.96	1.19	0.37
SD	0.20	0.06	0.01
n	13	11	13
variant — 2 ts			
Range	5.01-5.29	1.17-1.29	0.36-0.40
$\bar{x}$	5.19	1.25	0.38
SD	0.09	0.04	0.02
n	7	6	8
Furcilia VI:			
dominant — 1 ts			
Range	5.13-5.90	1.17-1.45	0.38-0.44
$\bar{x}$	5.58	1.33	0.40
SD	0.21	0.06	0.02
n	36	35	35
variant — 3 ts			
Range	5.13-5.78	1.19-1.43	0.38-0.40
$\bar{x}$	5.40	1.28	0.40
SD	0.17	0.05	0.01
n	15	14	15
variant — 2 ts			
Range	5.17-5.78	1.23-1.41	0.38-0.42
$\bar{x}$	5.46	1.30	0.40
SD	0.21	0.05	0.01
n	11	10	7

TABLE 9.—Variation in total length of calyptopis stages between the different areas from which samples were studied.

Sample	Calyptopis I				Calyptopis II				Calyptopis III			
	Range	$\bar{x}$	SD	*n*	Range	$\bar{x}$	SD	*n*	Range	$\bar{x}$	SD	*n*
Equatorial Pacific:												
Eastern												
Shellback 187 + 188	1.11-1.17	1.14	0.02	9	1.70-1.94	1.82	0.07	13	2.36-2.63	2.49	0.07	21
North Pacific:												
Eastern												
6304-133.80	1.11-1.21	1.16	0.03	19	1.66-1.82	1.76	0.04	20	2.36-2.55	2.43	0.05	20
6304-120.120	1.09-1.19	1.15	0.02	20	1.66-1.80	1.72	0.04	20	2.34-2.50	2.40	0.05	9
6304-117.90	1.11-1.21	1.15	0.03	20	1.68-1.88	1.77	0.05	20	2.36-2.55	2.45	0.05	20
6304-110.70	1.09-1.19	1.16	0.03	20	1.72-1.86	1.80	0.04	20	2.34-2.67	2.51	0.09	20
6304-70.90 + 100	1.09-1.21	1.15	0.04	21	1.72-1.92	1.82	0.05	20	2.46-2.69	2.56	0.08	11
6304-60.140	1.13-1.27	1.19	0.04	11	1.82-1.98	1.88	0.05	19	2.55-2.71	2.62	0.05	15
6307-117.80	1.09-1.17	1.13	0.02	10	1.72-1.86	1.80	0.05	10	2.40-2.59	2.50	0.06	10
Western												
Transpac 56A + B	—	—	—	—	1.80-1.86	1.84	0.02	6	2.46-2.71	2.58	0.08	11
Transpac 76A	1.11-1.23	1.18	0.06	4	1.68-1.90	1.81	0.06	20	2.44-2.65	2.55	0.06	20

juveniles; it is well developed in larger individuals but never more than one-half the length of the eyestalk in specimens examined.

DISCUSSION

The larvae of many species of the genus *Euphausia* have not been studied but, although preliminary, it may be useful to note ways in which *E. gibboides* larvae differ from related identified forms. The described larvae of *Euphausia* which have features such as armature of carapace or telson similar to those of *E. gibboides* during some phase of development belong to the following species:

Group A *E. brevis* — (Gurney 1942)
E. krohnii — (Sars 1885; Lebour 1926; Frost 1934)
E. diomediae — (Ponomareva 1969)
E. eximia — (author unpubl.)
Group B *E. pacifica* — (Boden 1950; Banse and Komaki 1966[3]; author unpubl.)
Group D *E. longirostris* — (Tattersall 1924; John 1936)
E. spinifera — (Tattersall 1924; John 1936; Sheard 1953)
Euphausia sp. (Ruud 1932; Lebour 1949; Boden 1955)

A metanauplius with marginal fringe of spines on the rostral hood of the carapace is found in *E. brevis, E. krohnii, E. eximia, E. diomediae, E. pacifica,* and Ruud's *E.* sp. as well as in *E. gibboides.* The metanauplius figured by Ruud differs from the others, however, in that the

[3]Banse, K., and Y. Komaki. 1966. Studies of Euphausiidae (Crustacea) off the Washington and Oregon coasts. Annual Report to NSF (Natl. Sci. Found.), Grant No. GB-3360, 6 p. Unpubl.

TABLE 10.—Carapace width expressed as percent of carapace length in calyptopis stages of *E. gibboides* (the number measured is given in Table 9).

Sample	Calyptopis I		Calyptopis II		Calyptopis III	
	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$
Equatorial Pacific:						
Eastern						
Shellback 187 + 188	86.1-91.4	89.3	85.7-92.9	90.1	83.7-91.8	87.7
North Pacific:						
Eastern						
6304-133.80	83.3-91.4	87.4	83.3-90.0	86.0	80.0-85.7	83.1
6304-120.120	83.3-91.2	87.1	82.1-90.0	85.5	80.4-88.6	83.5
6304-117.90	85.3-94.4	88.1	82.5-90.7	86.4	79.6-87.5	83.4
6304-110.70	82.8-91.4	86.8	82.9-90.5	86.5	80.0-87.8	83.8
6304-70.90 + 100	86.1-94.4	90.1	86.0-97.7	91.6	80.0-94.0	86.0
6304-60.140	86.5-91.9	90.1	88.9-95.3	91.0	86.8-92.4	88.8
6307-117.80	87.9-91.4	88.9	87.8-90.5	89.3	90.0-86.3	83.3
Western						
Transpac 56A + B	—	—	90.5-97.6	94.4	88.2-95.8	90.4
Transpac 76A	83.8-91.7	87.8	85.7-93.0	89.6	84.6-90.6	88.0

entire margin of carapace, not only the rostral hood, is spinose. *Euphausia brevis*, *E. krohnii*, and *E. eximia*, unlike *E. gibboides*, have two small dorsal spines on the carapace; *E. diomediae*, the only other species of Group A identified has instead a "sharp eminence" which, as figured (Ponomareva 1969, Figure 1c), is considerably higher and sharper than the dorsal prominence of *E. gibboides*. The metanauplius of *E. pacifica* has a dorsal crest more like that of *E. gibboides* but may prove, with further study, to be consistently smaller; 25 specimens measured from one location by the author ranged from 0.44 to 0.48 mm in total length with an average of 0.46 mm. A metanauplius with fringed rostral hood and two small dorsal spines is figured by Boden (1955) as one of the larval stages of *E. lucens*. It appears, however, that the larvae are those of another species of the genus (Bary 1956), and the form of the metanauplius suggests that it might belong to a species of Group A *Euphausia*.

Calyptopis stages with spinose anterior margin of carapace are found in all of the species listed above except *E. pacifica*. The calyptopes of Group A species may be easily distinguished from those of *E. gibboides* by relative width of carapace; they do not have the anterolateral expansion over the eyes. The carapace of the two species of Group D is wide but, unlike *E. gibboides*, with a very high peaked dorsal crest. Also, the entire margin of the carapace of *E. longirostris* is spinose, the first calyptopis is not described but presumably it does not differ from calyptopes II and III in this respect. The third calyptopis of Lebour's *E.* sp. (1949, Figure 4, 3-4) resembles *E. gibboides* in width of carapace, but the lateral margins of the carapace are spinose. The carapace of the calyptopis I described by Boden (1955, Figure 12) is expanded anterolaterally, but it appears to be proportionally longer than the carapace of *E. gibboides*. The relative lengths of the posterolateral spines of the telson also differ; the 3rd posterolateral spine is relatively short; as figured it is no longer than the terminal spines. The second and third calyptopes of this species have relatively narrow carapaces.

The most useful character for the identification of furcilia stages of *E. gibboides* is the relatively large 3-lobed eye; width of rostral plate and form of pleopods and telson may be helpful as well in differentiating furcilia with spinose anterior margin of carapace. Furcilia of *E. gibboides* may be separated from those of Group A *Euphausia* as follows:

Furcilia with 1 pair of non-setose pleopods — the rostral plate appears to be of greater width in *E. gibboides*;

Furcilia with both setose and non-setose pleopods — in Group A *Euphausia* there is usually only one form and it has 1 setose plus 4 non-setose pairs of pleopods on abdominal segments 1-5 respectively (Sheard (1953) reports numerous variants in the furciliar development of a species identified as *E. recurva*), *E. gibboides* has two forms, 1 setose plus 3 non-setose and 4 setose plus 1 non-setose pair of pleopods;

Furcilia with 5 pairs of setose pleopods — the inner margin of the 3rd (inner) posterolateral spine of the telson is smooth except for tiny distal spinules in larvae of *E. gibboides* and spinose in larvae of Group A.

A single character is sufficient to separate furcilia of *E. gibboides* from those of *E. longirostris* and *E. spinifera*; both Group D species have a dorsal spine on segment 3 of the abdomen beginning in furcilia I. The furcilia with 1 pair of non-setose pleopods figured as *E.* sp. by Lebour (1949, Figure 4, 5-6) differs from *E. gibboides* in relative length of posterolateral spines 2 and 3 of the telson; as drawn they are almost equal in length. The telson of the second furcilia which, like *E. gibboides*, has 1 setose and 3 non-setose pairs of pleopods is not figured, and details of the two forms are not described. The first furcilia figured by Boden (1955, Figure 15) also differs from *E. gibboides* in length of posterolateral spines of the telson; the 2nd pair are almost the same length as the 3rd pair and only a little longer than the 1st pair. The second furcilia of the species has 1 setose and 4 non-setose pairs of pleopods as found in species of Group A *Euphausia*.

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NEW RECORDS OF ELLOBIOPSIDAE (PROTISTA (*INCERTAE SEDIS*)) FROM THE NORTH PACIFIC WITH A DESCRIPTION OF *THALASSOMYCES ALBATROSSI* N.SP., A PARASITE OF THE MYSID *STILOMYSIS MAJOR*

BRUCE L. WING[1]

ABSTRACT

Ten species of ellobiopsids are currently known to occur in the North Pacific Ocean—three on mysids and seven on other crustaceans. *Thalassomyces boschmai* parasitizes mysids of genera *Acanthomysis, Neomysis,* and *Meterythrops* from the coastal waters of Alaska, British Columbia, and Washington. *Thalassomyces albatrossi* n.sp. is described as a parasite of *Stilomysis major* from Korea. *Thalassomyces fasciatus* parasitizes the pelagic mysids *Gnathophausia ingens* and *G. gracilis* from Baja California and southern California. *Thalassomyces marsupii* parasitizes the hyperiid amphipods *Parathemisto pacifica* and *P. libellula* and the lysianassid amphipod *Cyphocaris challengeri* in the northeastern Pacific. *Thalassomyces fagei* parasitizes euphausiids of the genera *Euphausia* and *Thysanoessa* in the northeastern Pacific from the southern Chukchi Sea to southern California, and occurs off the coast of Japan in the western Pacific. *Thalassomyces capillosus* parasitizes the decapod shrimp *Pasiphaea pacifica* in the northeastern Pacific from Alaska to Oregon, while *Thalassomyces californiensis* parasitizes *Pasiphaea emarginata* from central California. An eighth species of *Thalassomyces* parasitizing pasiphaeid shrimp from Baja California remains undescribed. *Ellobiopsis chattoni* parasitizes the calanoid copepods *Metridia longa* and *Pseudocalanus minutus* in the coastal waters of southeastern Alaska. *Ellobiocystis caridarum* is found frequently on the mouth parts of *Pasiphaea pacifica* from southeastern Alaska. An epibiont closely resembling *Ellobiocystis caridarum* has been found on the benthic gammarid amphipod *Rhachotropis helleri* from Auke Bay, Alaska. Where sufficient data are available, notes on variability, seasonal occurrence, and effects on the hosts are presented for each species of ellobiopsid.

The family Ellobiopsidae (Protista (*incertae sedis*)) is a heterogeneous group of parasites and epibionts found on various crustaceans (mostly planktonic) and on the benthic polychaete worm *Nephthys ciliata* Müller. The Ellobiopsidae have been classified at various times as protistans, colorless algae, fungi, or protozoans. The recent work of Galt and Whisler (1970) suggests including the parasitic ellobiopsids among the dinoflagellates.

The parasitic ellobiopsids are multinucleate protistans with reproductive structures outside the host and absorptive portions inside. The reproductive structures often resemble a large mold; consequently, much of the descriptive terminology of ellobiopsids is mycological. The reproductive parts of an ellobiopsid (Figure 1) consist of a short primary stalk passing from the organ of fixation through the cuticle of the host and one or more trophomeres which branch from the primary stalk. The trophomeres in turn bear one or more gonomeres at their distal end.

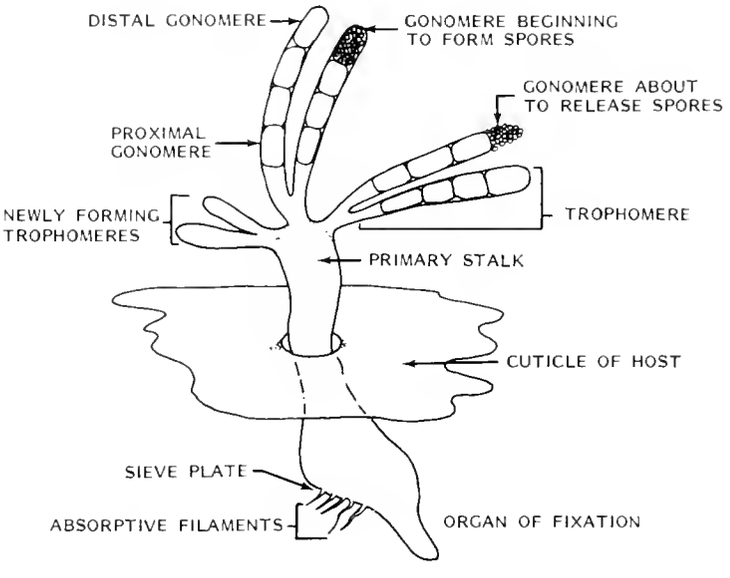

FIGURE 1.—Schematic of an ellobiopsid (*Thalassomyces* sp.)

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The mature distal gonomeres further subdivide to produce motile biflagellate spores (Galt and Whisler 1970).

The internal portion of a parasitic ellobiopsid, the organ of fixation, may be compact (like a bulb or taproot—Figure 1) or may be branching (rhizomorphous). The compact forms bear ridged sieve plates from which extend fine protoplasmic filaments. These filaments are believed to absorb nutrients from the host. The internal portions are difficult to observe without staining and sectioning techniques and have not been used much for taxonomic purposes.

The nonparasitic epibionts of the genus *Ellobiocystis* Coutiere do not have an internal organ of fixation but attach directly to the host's cuticle. These epibionts superficially resemble single trophomeres of the parasitic ellobiopsids but usually have a single gonomere. They are small and attached singly or in clusters to the mouth parts of various shrimps, mysids, and amphipods. Only the morphology of the *Ellobiocystis* spp. has been described. The inclusion of *Ellobiocystis* spp. in the Ellobiopsidae is very questionable.

Other than their morphology, little is known about the ellobiopsids of the genus *Thalassomyces* or their effects on hosts. The development of reproductive spores has been described (Galt and Whisler 1970); however, the mode of infection, time required to mature, and true incidence of infection remain subjects of speculation. Some of the parasitic ellobiopsids sterilize the hosts and probably exert some control on the molting cycle of crustacean hosts. Undoubtedly, the parasites draw heavily on the metabolic resources of the hosts, which conceivably would increase mortality and decrease reproduction in the host populations.

Ellobiopsids were first recognized as a component of the northeastern Pacific fauna when McCauley (1962) recorded *Thalassomyces capillosus* (Fage) as a parasite of the shrimp *Pasiphaea pacifica* Rathbun. Since then eight additional ellobiopsids have been recognized in zooplankton collections from the eastern North Pacific. Only two species of ellobiopsids have been reported from the western North Pacific. In the following discussions for each species, I summarize observations, some new and some from the literature, on the occurrence and hosts of the North Pacific ellobiopsids. I list synonymies only for references to material from the North Pacific. For convenience only, I have treated those ellobiopsids found on mysids first and those found on amphipods, euphausiids, shrimp, and copepods second.

ARTIFICIAL KEY TO ELLOBIOPSIDS FOUND ON MYSIDS

The published keys to the ellobiopsids (Kane 1964; Collard 1966) do not give complete coverage to the ellobiopsids found on mysids. Kane's key is restricted to genera of ellobiopsids, and Collard's key covers only 9 of the 11 known species of *Thalassomyces*. Identification of the known species of *Ellobiocystis*, and *Ellobiopsis* and most *Thalassomyces* is possible by reference to the summaries by Boschma (1949, 1957, 1959). The following key supplements Collard's but treats only the ellobiopsids found on mysids. Two of the species, *T. nouveli* (Hoenigman 1954) and *T. niezabitowskii* (Hoenigman 1960), are known only from the Mediterranean Sea; and *Ellobiocystis caridarum* (Coutiere) while not known from North Pacific mysids is found on Antarctic mysids (Boschma 1949, 1959) and has been found on the North Pacific decapod shrimp *Pasiphaea pacifica*.

1. No root system of attachment to host; attached to oral appendages. Mature parasite consists of single trophomere with one or more gonomeres . . . . . *Ellobiocystis caridarum* (Coutiere)
   Root system of attachment to host; not attached to oral appendages. Mature parasite with many trophomeres branching from stalk(s) . . *Thalassomyces* (2)
2. Parasite attached to ventral surface of first abdominal segment. Long pendulous umbellate trophomeres; usually only one gonomere per trophomere (length of mature gonomere 1.5 to over 2 times the diameter) . . . *T. fasciatus* (Fage)
   Site of attachment usually dorsal thoracic, but variable. Trophomeres not pendulous; usually more than one gonomere per trophomere (2-4) . . . . . (3)
3. Mature gonomeres flattened spheres. Mean length-diameter ratio less than 1 . . . . . *T. nouveli* (Hoenigman)
   Mature gonomeres globular to oval. Mean length-diameter ratio greater than 1 . . . . (4)

4. Primary stalks widely spaced when more than one per host. Mature gonomere length-diameter ratio 0.7-1.9 (mean about 1.2) .....(5)
   Primary stalks closely spaced when more than one per host. Mature gonomere length-diameter ratio 1.5-2.4 (mean about 2) .....*T. albatrossi* n.sp.
5. Mature terminal gonomere shape ellipsoid, with the distal end the same size as the proximal end, to spherical .....
   .....*T. boschmai* (Nouvel)
   Mature terminal gonomere shape ovoid, with the distal end smaller than the proximal end, to spherical .....
   .....*T. niezabitowskii* (Hoenigman)

ELLOBIOPSIDS OF NORTH PACIFIC MYSIDS

Thalassomyces boschmai (Nouvel 1954)

Thalassomyces sp.—Wing (1965), Hoffman and Yancey (1966), Thorne (1968).
Thalassomyces boschmai—Galt and Whisler (1970), Vader (1973b).

Ellobiopsids of the genus *Thalassomyces* have been observed on Mysidae from Alaska (Wing 1965; Hoffman and Yancey 1966); from Puget Sound (Thorne 1968); and from southern British Columbia (J. Galt, Friday Harbor Laboratory, University of Washington, Friday Harbor, WA 98250, pers. commun.). New collections of Alaska mysids (Table 1) plus supplementary material from Puget Sound enabled me to identify these ellobiopsids as *T. boschmai.*

Characteristics of *T. boschmai*

The identification of *Thalassomyces* spp. parasitizing mysids is based on external portions so variable that for definitive identifications, several characters must be examined. The external characters used to identify a species are the total size or height of the parasite, length of trophomeres, number of trophomeres per primary stalk, number of gonomeres per trophomere, and size and shape of gonomeres. The number of primary stalks and the site of attachment are also useful characteristics. Differences between specimens from different localities may be associated with local races and may to some extent be phenotypically associated with the host species.

TABLE 1.—Records of *Thalassomyces boschmai* found on mysids in Alaska, 1963-67.

Area, collection number, and species of host	Number of mysids with *T. boschmai*	Number of *T. boschmai*
Little Port Walter[1]		
AB66-243		
Acanthomysis pseudomacropsis	4	4
Neomysis kadiakensis	70+	80+
AB66-244		
Acanthomysis pseudomacropsis	2	2
Neomysis kadiakensis	9+	23+
Auke Bay[2]		
AB65-108		
Acanthomysis pseudomacropsis	8	8
Neomysis kadiakensis	8	10+
Katlian Bay[3]		
AB67-45		
Acanthomysis pseudomacropsis	1	1
AB67-46		
Meterythrops robusta	2	2
Kachemak Bay[4]		
Acanthomysis pseudomacropsis	3	6

[1]Taken in light-baited trap; lat. 56°23'N, long. 134°39'W; 7-8 September 1966.
[2]Taken in light-baited trap; lat. 58°21'N, long. 134°40'W; 24 June 1964.
[3]Taken in Isaacs-Kidd mid-water trawl; lat. 57°10'N, long. 135°21'W; 21 April 1967.
[4]Collection of Hoffman and Yancey (1966); lat. 59°27'N, long. 151°33'W; October, December 1963 and February 1964. No collection number because material was lost.

The height of the North Pacific *T. boschmai* ranges from 0.75 to 1.70 mm; most of the specimens are between 1.30 and 1.50 mm. The maximum height is larger than the 1.25 mm given by Hoenigman (1954) for *T. boschmai* found on *Leptomysis gracilis* G. O. Sars, but in the Pacific, host mysids are much longer than the Mediterranean *Leptomysis* (13 mm). *Neomysis kadiakensis* Ortman are often over 20 mm long. Boschma (1959) noted a positive relationship between the size of the host and the size of the parasite *T. fagei* (Boschma) on euphausiids.

Mature trophomeres constitute most of the external mass of an ellobiopsid parasite. Within a parasite, the lengths of the trophomeres appear uniform, but they vary greatly between parasites. Lengths of trophomeres from 18 parasites found on *Acanthomysis pseudomacropsis* (Tattersall) and *N. kadiakensis* were from 0.72 to 1.32 mm. Because gonomeres are lost during sporulation, old trophomeres are generally 0.3 to 0.7 mm shorter than those that still have three or four gonomeres.

The number of trophomeres per primary stalk depends on the state of development and the condition of preservation. Dichotomous branching close to the point where the trophomeres

join the primary stalk makes it difficult to determine the number of trophomeres in a dense tuft, or the number that may be developing, or those that may have been lost. Counts of trophomeres on 21 *T. boschmai* from southeastern Alaska ranged from 13 to 46 (mean 28.6). Hoffman and Yancey (1966) examined six parasites which had 7 to 20 trophomeres each. Nouvel and Hoenigman (1955) found a maximum of 32 (mode 16) trophomeres for 21 Mediterranean *T. boschmai* from Cabo do Palos, Spain.

The number of gonomeres on a mature trophomere of *T. boschmai* is usually three, rarely four. Trophomeres having no gonomeres or up to two are immature, damaged, or are degenerating after sporulation. Degenerating trophomeres may be recognized by the small rudiments of protoplasm left after sporulation (Nouvel and Hoenigman 1955).

The size and shape of the gonomeres, especially the distal gonomere (Figure 1), are used as taxonomic characters, but most descriptions give little information on the variability of gonomere characters. I measured gonomere lengths and diameters and computed length-diameter ratios for 10 *T. boschmai* from each of two sites in southeastern Alaska and one in Puget Sound for comparison with data from central Alaska (Hoffman and Yancey 1966) and the western Mediterranean (Nouvel and Hoenigman 1955) (Table 2). The ranges of lengths and diameters were greater in specimens from southeastern Alaska and Puget Sound than in those from central Alaska or the Mediterranean, although the mean sizes were similar. A weighted *t*-test (Ostle 1963) confirmed (95% level) that ellobiopsids from different host species of mysids but within the same collection belong to the same statistical population; that is, all the ellobiopsids within each collection may be considered as one species. Tests for significant differences between means indicated that *T. boschmai* from the three collections were from different populations, but the broad overlap of gonomere size ranges, especially the length-diameter ratios (Figure 2), makes specific distinction unwarranted.

Occasionally an ellobiopsid will form more than one primary stalk by internal budding. This produces two or more stalks which separately penetrate the host's cuticle. The stalks are usually less than 1 mm apart. Budding described for *T. boschmai* and *T. nouveli* in the Mediterranean (Hoenigman 1954) is rare in the North Pacific *T. boschmai*. I examined 130 ellobiopsids from the North Pacific and found only one instance of apparent budding—a *T. boschmai* on an *A. pseudomacropsis* from Katlian Bay, Alaska.

On mysids, *T. boschmai* usually occur either on the dorsal surface of the host's carapace or on the last thoracic segment, although some are found on the dorsal, lateral, or ventral surface of the abdomen. In contrast, the most frequent sites of attachment on *L. gracilis* are the frontal plaque and rostral areas (Hoenigman 1954; Nouvel 1954; Nouvel and Hoenigman 1955).

Less than 10% of the parasitized mysids I examined had more than one *T. boschmai*. In one case a mysid had four ellobiopsids, and another mysid bore scars from four ellobiopsids. Hoenigman (1954) observed one *L. gracilis* with seven *T. boschmai*. When two or more ellobiopsids occur on a mysid, they usually are widely separated; one ellobiopsid may be on the thorax and the other(s) may be on various parts of the abdomen or rostrum. Two of the three hosts described by Hoffman and Yancey (1966) had both ellobiopsids on the carapace; in the third, the second ellobiopsid was on the abdomen.

Observations of Living *T. boschmai*

Collard (1966), Vader and Kane (1968), and Galt and Whisler (1970) have described living *Thalassomyces* spp. I briefly observed three living *T. boschmai* on *A. pseudomacropsis* from the first Auke Bay collection (AB65-108). In the live *T. boschmai*, the external portions were transparent and colorless except for a slight yellow tint at the base of the primary stalk. Perhaps the tinting is caused by the same melanic pigment deposited by the host at the margin of the pore through the host's cuticle. Deposition of pigments at the site of injury or parasitism is a frequent occurrence among crustaceans. The parasites stand out from the host's carapace, which gives the appearance of a flexible cluster of grapes that twist and turn slightly as the host swims. The live ellobiopsids I observed had about 40 trophomeres each with one to four gonomeres per trophomere. Many distal gonomeres were pebbled as described by Collard (1966) and Galt and Whisler (1970). I observed that some gonomeres had the amorphous drop of protoplasm described by Collard, but I did not find the

TABLE 2.—Ranges, means, and 0.95 confidence intervals (CI) of means for lengths, diameters, and length-diameter ratios of terminal gonomeres of *Thalassomyces boschmai* parasitizing mysids in collections from the western Mediterranean, Washington, southeastern Alaska, and central Alaska.

Host mysid and number of gonomeres measured		Length (mm)			Diameter (mm)			Ratio length to diameter		
		Range	Mean	0.95CI	Range	Mean	0.95CI	Range	Mean	0.95CI
					Western Mediterranean (Cabo do Palos, Spain)					
Leptomysis gracilis[1]										
	8	0.240-0.300	0.258		0.205-0.240	0.228		1.00-1.46	1.14	
	7	0.155-0.185	0.172		0.150-0.170	0.158		1.00-1.17	1.09	
Total	—	0.155-0.300	—	—	0.135-0.250	—	—	—	—	—
					Washington (Puget Sound)					
Neomysis kadiakensis										
	1	—	0.208		—	0.250		—	0.83	
	5	0.24-0.27	0.251		0.19-0.24	0.223		0.96-1.44	1.14	
	7	0.21-0.26	0.232		0.16-0.22	0.180		1.04-1.44	1.31	
	4	0.30-0.36	0.319		0.26-0.28	0.269		1.12-1.35	1.19	
	5	0.32-0.36	0.339		0.27-0.30	0.282		1.09-1.33	1.21	
	4	0.24-0.28	0.251		0.18-0.24	0.200		1.20-1.33	1.26	
	3	0.23-0.26	0.239		0.22-0.24	0.231		0.96-1.10	1.03	
	4	0.30-0.33	0.305		0.24-0.29	0.260		0.98-1.22	1.14	
	3	0.25-0.28	0.262		0.18-0.20	0.193		1.32-1.40	1.36	
	1	—	0.305		—	0.190		—	1.61	
Total	37	0.21-0.36	0.273	±0.014	0.18-0.30	0.228	±0.014	0.96-1.61	1.22	±0.06
					Southeastern Alaska (Little Port Walter)					
Acanthomysis pseudomacropsis										
	10	0.19-0.22	0.198		0.17-0.22	0.198		0.94-1.00	1.00	
Neomysis kadiakensis										
	10	0.24-0.29	0.263		0.20-0.26	0.223		1.00-1.41	1.18	
	10	0.22-0.25	0.235		0.19-0.24	0.224		0.90-1.25	1.05	
	10	0.22-0.29	0.259		0.22-0.26	0.236		0.90-1.25	1.10	
	10	0.29-0.34	0.314		0.26-0.31	0.295		1.00-1.17	1.06	
	10	0.24-0.38	0.298		0.24-0.34	0.287		0.71-1.17	1.04	
	10	0.22-0.26	0.242		0.19-0.23	0.210		1.00-1.25	1.15	
	10	0.31-0.41	0.350		0.24-0.29	0.275		1.08-1.42	1.28	
	10	0.26-0.36	0.278		0.24-0.31	0.241		1.00-1.44	1.15	
	10	0.19-0.24	0.214		0.19-0.24	0.206		0.90-1.12	1.03	
	10	0.19-0.26	0.226		0.19-0.24	0.204		1.00-1.25	1.11	
	10	0.22-0.29	0.247		0.17-0.22	0.197		1.00-1.67	1.26	
Total	120	0.19-0.41	0.260	±0.012	0.17-0.34	0.233	±0.009	0.71-1.67	1.10	±0.04
					Southeastern Alaska (Auke Bay)					
Acanthomysis pseudomacropsis										
	11	0.15-0.31	0.205		0.13-0.23	0.168		0.79-1.71	1.23	
	11	0.17-0.28	0.228		0.14-0.18	0.156		1.21-1.87	1.46	
	13	0.24-0.32	0.291		0.18-0.28	0.230		1.08-1.39	1.27	
	10	0.13-0.17	0.157		0.14-0.16	0.150		0.86-1.14	1.04	
	10	0.24-0.38	0.319		0.22-0.31	0.261		0.84-1.73	1.24	
	10	0.27-0.29	0.282		0.18-0.24	0.212		1.21-1.56	1.34	
	5	0.27-0.30	0.280		0.17-0.29	0.202		0.96-1.70	1.44	
Neomysis kadiakensis										
	10	0.20-0.25	0.231		0.15-0.23	0.173		1.08-1.39	1.25	
Total	80	0.13-0.38	0.230	±0.019	0.13-0.31	0.181	±0.014	0.79-1.87	1.28	±0.05
					Central Alaska (Kasitsna Bay)					
Acanthomysis pseudomacropsis[2]										
	—	—	—	—	0.14-0.21	0.17	—	—	—	—

[1]Data from Nouvel and Hoenigman (1955). The authors gave the total length and diameter ranges shown but did not give the total number of gonomeres used to figure these ranges.
[2]Data from Hoffman and Yancey (1966).

gonomeres of *T. boschmai* to be adherent as Collard found for *T. californiensis* Collard.

Effect of Host

Adult and juvenile mysids are parasitized by *T. boschmai*. I made no histological studies of sterilization, but in the 130 parasitized mysids examined, no brooding females occurred and reduced oostegites were common. Sterilization may not always result, for Nouvel and Hoenigman (1955) found a brooding female *L. gracilis* parasitized by *T. boschmai*. Because the length of time for development of the parasite or the eggs of the mysids is not known, the specimen observed by Nouvel and Hoenigman may have deposited her eggs before being parasitized. The parasite must also affect the host's molting and growth because

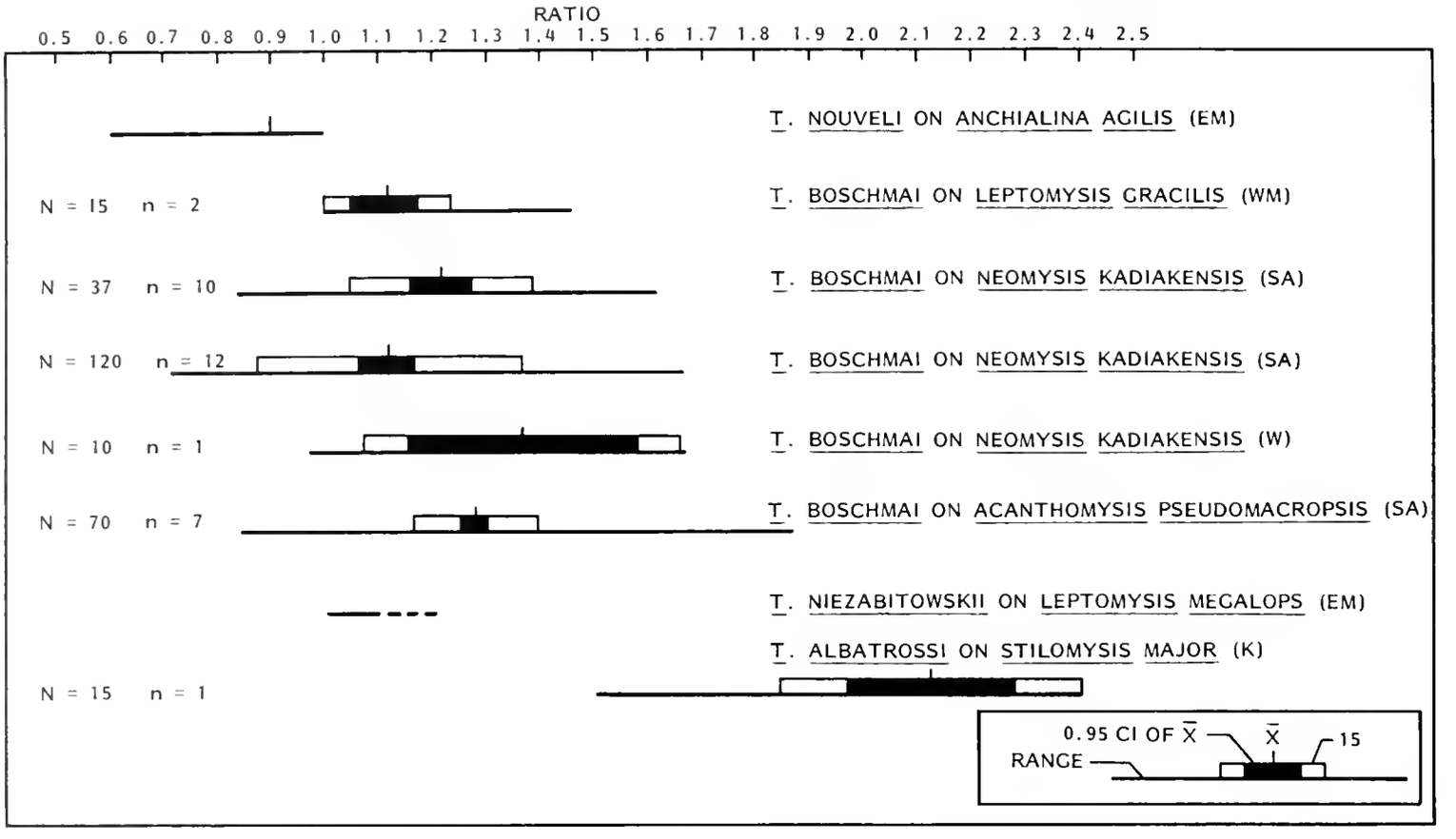

FIGURE 2.—Length-diameter ratios of *Thalassomyces* found on Mysidae from the eastern Mediterranean (EM), western Mediterranean (WM), Washington (W), southeastern Alaska (SA), and Korea (K). The horizontal line represents the sample range, the vertical line the sample mean; the black rectangle represents the 0.95 confidence limits of the mean, and the distance from the mean line to the edge of the white rectangle represents 1 standard deviation; N = number of gonomeres measured and n = number of parasites (the numbers are unknown for *T. nouveli* and *T. niezabitowskii*).

the external portions of the parasite could hardly be retained during a molt. The control over molting could be by starvation as postulated by Wickstead (1963) or by disturbance of the host's neuroendocrine system as postulated by Hoffman and Yancey (1966). The close association of other *Thalassomyces* with the nervous system (Boschma 1959; Kane 1964; Collard 1966) or the gonadal areas (Einarsson 1945; Boschma 1959) suggests some hormonal control over growth, molting, and maturation of the host.

The behavior of the parasitized mysids is not noticeably affected. The swimming speed and maneuverability of parasitized and nonparasitized mysids appear to be the same; flexing and twisting of the ellobiopsids as they are dragged through the water apparently do not affect the host.

Hosts of *T. boschmai*

This species has been recorded as a parasite of *L. gracilis* and *Gastrosaccus lobatus* (Nouvel) in the Mediterranean Sea (Nouvel 1954; Hoenigman 1954, 1960, 1963; Nouvel and Hoenigman 1955). Five mysids are known as hosts of *T. boschmai* in the eastern North Pacific. In Puget Sound, *Acanthomysis macropsis* (Tattersall), *A. nephrophthalma* Banner, and *N. kadiakensis* are hosts (Thorne 1968). In Alaska, *A. pseudomacropsis* (Wing 1965, Hoffman and Yancey 1966), *N. kadiakensis* (Wing 1965), and *Meterythrops robusta* S. I. Smith have been observed parasitized by *T. boschmai*. *Meterythrops robusta* is a new host record.

Seasonal Occurrence

Thorne (1968) reported a seasonal pattern of incidence of infection by mysids (the percentage of *N. kadiakensis* with ellobiopsids) by *T. boschmai* at Port Orchard, Puget Sound, Wash. The incidence of infection at Port Orchard was low in the winter and spring (1 to 8% of adults, 1 to 21.5% of immatures) and rose in the late summer to a maximum in October (17% of adults, 35% of immatures). A seasonal pattern of infestation is not clear in the Alaska material. Although the

number of infected hosts and the proportion of hosts with more than one parasite were greatest in the late summer, this may be an artifact of sampling methods. Long-term sampling with plankton nets at Auke Bay and Little Port Walter has not captured parasitized mysids and generally has not taken large numbers of mysids. The light-baited trap is exceptionally effective in capturing mysids but has been used only in summer. Although no quantitative data are available for the Auke Bay sample (AB65-108—Table 1), it contained several thousand mysids. The two Little Port Walter collections contained about 9,000 and 7,000 mysids respectively (Table 3).

Thalassomyces albatrossi n.sp.

?*Amallocystis fasciatus*—Tattersall (1951), Boschma (1959).
Thalassomyces fasciatus—Collard (1966).
Thalassomyces n.sp.—Vader (1973b).

Type location:[2] *Albatross* stn. 4867, lat. 36° 31'N, long. 129°46'E; depth 150 fathoms; 1 August 1906. USNM 82439.

Holotype: One slide with several gonomeres and trophomeres separated and mounted whole. Remainder left on the host. Host: *Stilomysis major* Tattersall, female, 26 mm long; carapace length, 7.9 mm.

Paratype: Immature, bearing two tufts or stalks of trophomeres, intact on host. Host: *S. major*, female, from USNM 81268.

Location: *Albatross* stn. 4862, lat. 36°20'N, long. 129°50'E; depth 184 fathoms; 31 July 1906.

Disposition of types: Holotype and paratype deposited in Division of Crustacea, Smithsonian Institution, U.S. National Museum, Washington, D.C., as Type USNM 24366 and USNM 24367.

[2]The locale on the original collection labels is Cape Clonard, Japan. Political changes since 1906 have resulted in name changes, the area now being referable to near Yonghae, South Korea.

Specific Diagnosis

The external portion of the parasite is visible as one to four tufts of trophomeres located middorsally on the host's thorax. In the mature parasite, each tuft contains up to 50 trophomeres, which arise by close dichotomous branching from the primary stalk. Trophomeres are 0.80 to 1.70 mm long. Each trophomere bears one to four gonomeres, usually three. Mature distal gonomeres are oval to elongate in shape—0.4 to 0.7 mm long and 0.25 to 0.35 mm in diameter. The length of the distal gonomere is 1.5 to 2.4 times the diameter. The penultimate and proximal gonomeres are usually shorter than the distal gonomere but have about the same diameter.

[Diagnosis Propria: Pars parasiti externa apparet unus ad quattuor racemi trophomerorum medio dorso in animalis thorace positi. In maturo parasito, unusquisque racemorum fert ad quinquaginta trophomera, quae in duas partes proximas ex stirpe principali dividuntur. Trophomera sunt 0.80 ad 1.70 mm longa. Unumquidque trophomerorum fert unum ad quattuor gonomera, plerumque tria. Matura gonomera distalia sunt conformatione ovata ad praelonga—0.4 ad 0.7 mm longa et 0.25 ad 0.35 mm per medium. Longitudo gonomeri distalis est 1.5 ad 2.4 eius gonomeri dimetientes. Gonomera paenultima et proximalia sunt plerumque breviora quam gonomera distali, sed sunt per medium fere eadem.]

This species differs most clearly from other closely related *Thalassomyces* (*T. boschmai*, *T. niezabitowskii*, and *T. nouveli*) found on mysids by having much longer terminal gonomeres (which exceed 0.4 mm), a more elongate shape of the gonomeres, and three or four tufts of

TABLE 3.—Species and number of mysids and incidence of *Thalassomyces boschmai* in two light-baited trap samples at Little Port Walter, 7-8 September 1966.

Species	AB66-243 (2-h set)		AB66-244 (7-h set)	
	Number of mysids caught	Number of mysids parasitized by *T. boschmai*	Number of mysids caught	Number of mysids parasitized by *T. boschmai*
Acanthomysis pseudomacropsis	1,680	4	4,960	2
Acanthomysis sp.	1,600	0	290	0
Neomysis kadiakensis	5,630	70+	1,160	9+
Mysis litoralis	<20	0	740	0
Total	8,930	74+	7,150	11+

trophomeres rather than one or two per parasite. It differs from *T. fasciatus* by being attached to the dorsum of the host's thorax rather than the ventral abdomen, by bearing multiple gonomeres on each trophomere rather than one or rarely two, and by having much shorter lengths of the trophomeres (not including the gonomeres —about half that of *T. fasciatus*).

Description of Holotype

Externally, the holotype consists of three tufts of trophomeres attached to the dorsal carapace (Figure 3). The prior existence of a fourth tuft is indicated by a scar on the host's carapace. Dense packing of the trophomeres and the apparent loss of some by breakage during preservation and handling made it impossible to determine the exact number of trophomeres in each tuft. Examination at 40× magnification indicated the following approximate numbers: 45 in the left anterior tuft, 20 in the left posterior tuft, and 35 in the right posterior tuft. The trophomeres branch dichotomously close to the primary stalk, which gives an appearance of many trophomeres arising directly from the primary stalk. The trophomeres are of various lengths—0.8 to 1.7 mm. Each trophomere (Figure 4a, b) is composed of a short basal portion and one to three gonomeres, usually three. A few trophomeres appear to have lost a fourth gonomere.

The gonomeres (Figure 4) vary in shape from oval to elongate; a few distal gonomeres are small and cone shaped. The penultimate and proximal gonomeres vary considerably in length but are of similar diameter to the normal distal gonomeres (0.25 to 0.32 mm). The dimensions of 15 distal gonomeres (measured in situ) are summarized in Table 4.

The host specimen, which was preserved in ethyl alcohol, was partially dehydrated, brittle, and broken at the third and fourth thoracic

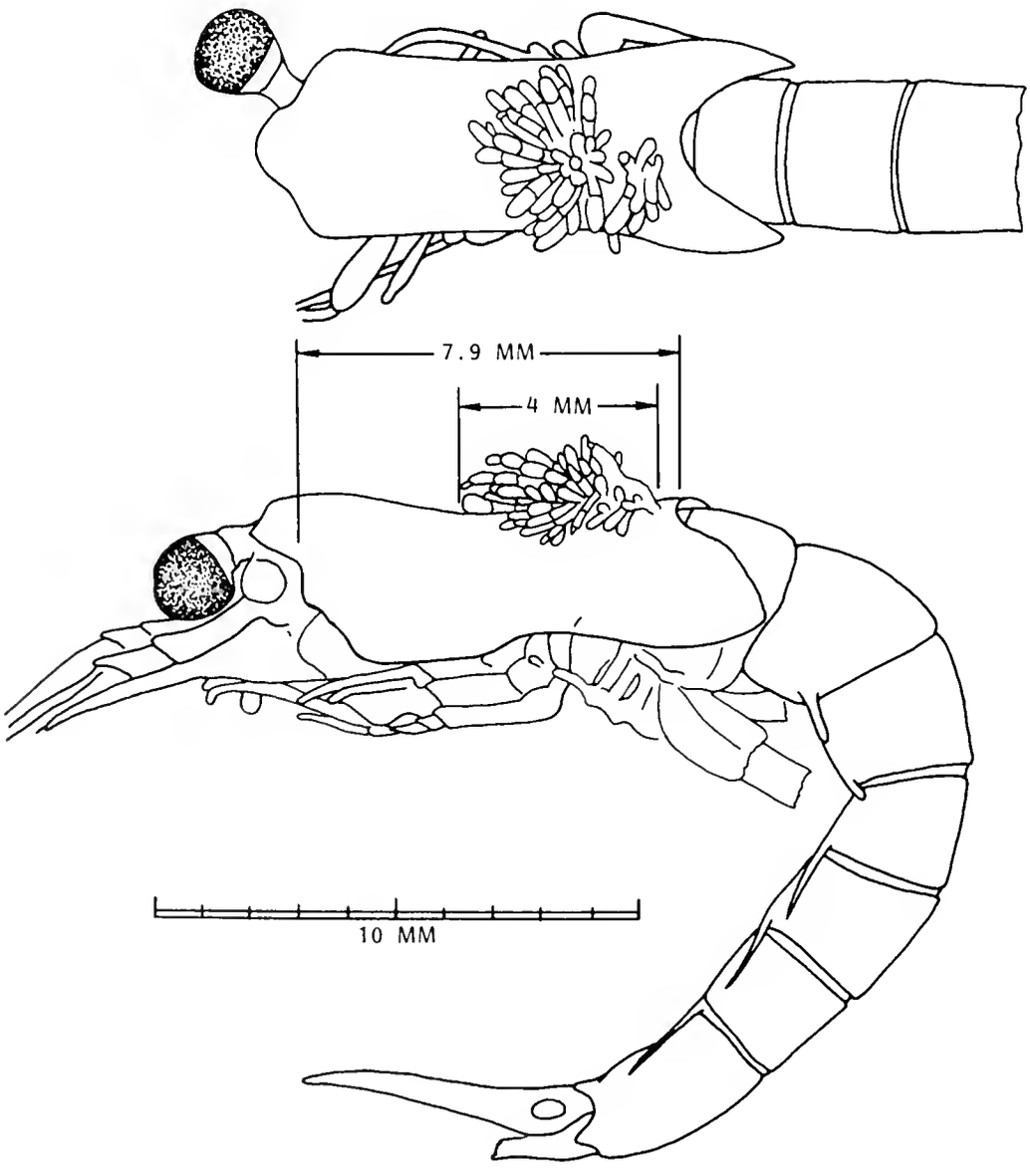

FIGURE 3.—Holotype of *Thalassomyces albatrossi* n.sp. on *Stilomysis major*. A. Lateral view. B. Dorsal view.

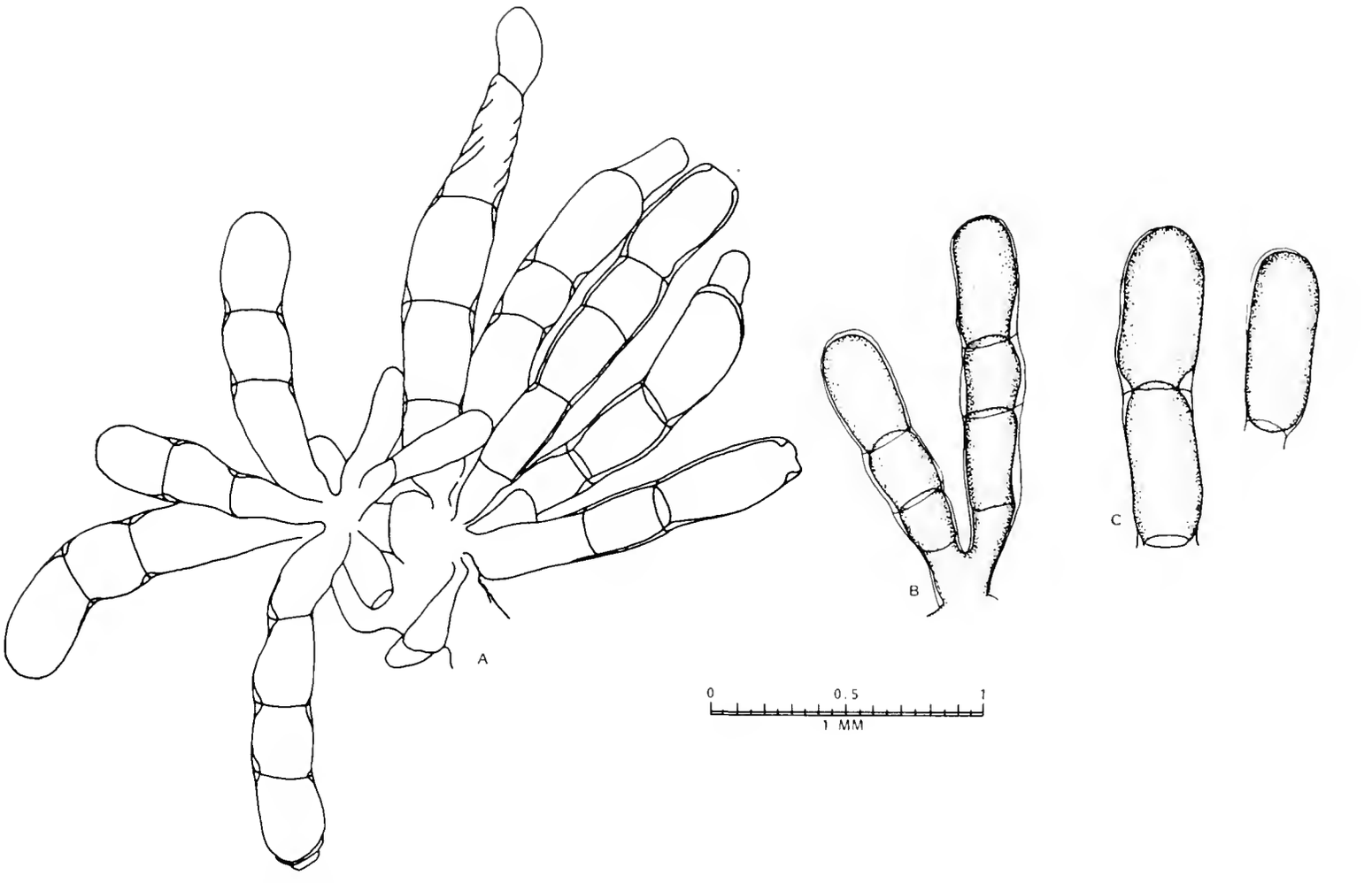

FIGURE 4.—Holotype of *Thalassomyces albatrossi* n.sp. A. Cluster of trophomeres. B. Pair of trophomeres, each bearing three gonomeres. C. Separate gonomeres.

TABLE 4.—Dimensions of 15 distal gonomeres from holotype of *Thalassomyces albatrossi* n.sp.

Dimension	Range (mm)	Mean (mm)	SD	0.95 CI of mean
Length	0.41-0.68	0.57	0.07	0.04
Diameter	0.25-0.32	0.27	0.03	0.01
Length-diameter ratio	1.5-2.4	2.1	0.3	0.15

segments—the site of attachment to the ellobiopsid. Histological studies were not done because of this damage. Each of the three primary stalks passes through the carapace of the host. Just inside the carapace there is a connection between the left pair of stalks. A similar connection between the right stalk and the left anterior stalk is indicated by a torn piece of an ellobiopsid projecting from the right stalk toward the left anterior stalk. Below the connection between the left pair of stalks is a small (about 1.5 mm long) elongate conical organ of absorption (fixation), which appears to have passed through or between the ovaries of the host. The organ is similar to that figured for *T. nouveli* by Hoenigman (1954).

Description of Paratype

The paratype is an immature ellobiopsid consisting of two primary stalks which pass through the carapace of the host. None of the trophomeres bear more than two gonomeres; several of them have no gonomeres and appear to have been damaged in handling or by drying after preservation. Because of the withered state of the specimen, no accurate measurements of either the trophomeres or the gonomeres can be made. The gonomeres on one of the stalks are, however, thinner than those on the other. No sporulating gonomeres are present.

Specimens Examined

In the discussion that followed his description of *S. major*, Tattersall (1951) states that two specimens were parasitized by an ellobiopsid resembling *T. fasciatus* (Fage). Subsequent authors accepted this tentative identification by Tattersall, but my examination of the ellobiopsids from his material revealed only *T.*

albatrossi. I have examined 15 *S. major* from three of Tattersall's collections. Two of the collections (USNM 82439—2 *S. major*, and USNM 81268—10 *S. major*) contained the holotype and paratype respectively of *T. albatrossi*. In the third collection (USNM 82440—three *S. major; Albatross* stn. 4861; lat. 36°19'N, long. 129°47'E; 163 fathoms; 31 July 1906) I found a female *S. major* bearing four scars from an ellobiopsid.

Effect on the Host

The mysid specimens bearing the type and paratype ellobiopsids were females of mature size but with reduced oostegites. This apparent sterilization agrees with observations of Fage (1941), Einarsson (1945), and Nouvel (1941), who noted that ellobiopsids sterilize their hosts. A scarred mature female *S. major* in USNM 82440 was brooding young but appeared to have been parasitized earlier by an ellobiopsid. The scars consisted of holes in the carapace, probably caused by the primary stalks of the parasite. Each of the four holes had a heavy deposit of pigment at the margin that was surrounded by a clear area. Thus, it appears that the sterilization by ellobiopsids may be temporary, as suggested by Wickstead (1963), or it may be influenced by the age of the host at the time of infection.

Distribution

The new species has been reported only from the eastern coast of Korea, the type locality of the parasite and its host.

Derivation of Name

The specific name *albatrossi* is selected to honor the U.S. steamer *Albatross*, the vessel from which the parasitized mysids were collected. The many biological collections made from the *Albatross* during 39 yr of service to the U.S. Fisheries Commission and later to the U.S. Bureau of Fisheries have been of immeasurable value in the investigation of life in the oceans.

Thalassomyces fasciatus (Fage 1936)

Amallocystis fasciatus—Pequegnat (1965).
Thalassomyces fasciatus—Vader (1973b).

Thalassomyces fasciatus is a large species known to parasitize only lophogastrid mysids of the genus *Gnathophausia*. Pequegnat (1965) found it on *G. ingens* (Dohrn) and *G. gracilis* Willemoes-Suhm off central Baja California. It has also been collected in the Santa Cruz Basin off California (S.B. Collard, Marine Environmental Sciences Consortium, Dauphin Island, AL 36528, pers. commun.). Boschma (1959) recorded this ellobiopsid on *G. gigas* Willemoes-Suhm from Spain; on *G. ingens* from Morocco, the Lesser Antilles, and the Maldive Islands; and on *G. zoea* Willemoes-Suhm from Portugal, Guiana, the Fiji Islands, and New Zealand.

Thalassomyces fasciatus attaches to the ventral surface of the first abdominal somite of the host. The gonomeres are oval and about twice as long as wide (0.4 by 0.2 mm), and normally, there is only one gonomere per trophomere (Boschma 1959). The trophomeres are long (1.5 mm total length) and joined in groups of five or six to the primary stalk (Fage 1941). In these aspects *T. fasciatus* differs from the *T. albatrossi* n.sp. found on *S. major* by Tattersall (1951), which were erroneously believed to be *T. fasciatus* by Boschma (1959) and Collard (1966). The size of the gonomeres and total length of trophomeres (including the gonomeres) in the two species are similar, although my specimens of *T. albatrossi* have a greater number of gonomeres per trophomere than *T. fasciatus* and therefore do not appear to be as long and pendulate.

ADDITIONAL RECORDS OF NORTH PACIFIC ELLOBIOPSIDS

Besides the three species of *Thalassomyces* found on mysids, seven other ellobiopsids have been found on crustaceans in the North Pacific. The following sections summarize current knowledge about the hosts and distribution of these seven ellobiopsids.

Thalassomyces marsupii Kane 1964

Thalassomyces marsupii—Galt and Whisler (1970), Vader (1973b).

Thalassomyces marsupii is found inside the marsupium of host amphipods. The mature parasites resemble compact egg masses. Usually the whitish spherical gonomeres are smaller than the

eggs of the host species. An infected amphipod carries one, rarely two, parasites. The mature parasites may completely fill the marsupium of small amphipods and occasionally protrude beyond the marsupium of an immature host. In large or heavily pigmented amphipods, *T. marsupii* is easily overlooked unless specifically searched for. On male amphipods, *T. marsupii* are more easily noticed although they are often obscured by the thoracic legs and coxal plates of the host.

Thalassomyces marsupii parasitizes both pelagic and benthic amphipods and appears to have a worldwide distribution. The recorded pelagic hosts are hyperiids of the genus *Parathemisto: P. gaudichaudii* (Guerin) in the North Atlantic, Benguela Current, and Southern Ocean (Kane 1964); *P. abyssorum* Boeck in the North Atlantic (Vader and Kane 1968) and Arctic (Tencati and Geiger 1968); *P. gracilipes* Norman in the North Sea (R. A. McHardy, Department of Oceanography, The University, Southampton, England, pers. commun.); and *P. pacifica* Stebbing in Puget Sound (Galt and Whisler 1970). A similar parasite has been observed on *Cystisoma* sp., a hyperiid, in the North Pacific (T. H. Bowman, Division of Crustacea, Smithsonian Institution, U.S. National Museum, Washington, DC 20560, pers. commun.). The recorded epibenthic gammarid hosts of *T. marsupii* are: *Eusirus leptocarpus* G. O. Sars, *E. longipes* Boeck, *Rhachotropis aculeata* (Lepechin), *R. macropus* G. O. Sars, and *R. helleri* Boeck, all family Eusiridae, from several North Atlantic locales (Vader and Kane 1968).

I have observed *T. marsupii* on three species of amphipods in southeastern Alaska: the hyperiids *Parathemisto pacifica* and *P. libellula* (Lichtenstein) and the pelagic gammarid *Cyphocaris challengeri* Stebbing (family Lysianissidae). *Parathemisto libellula* and *C. challengeri* are new host records as well as geographic range extensions for *T. marsupii*. The parasitized amphipods were collected with a 1.8-m Isaacs-Kidd mid-water trawl by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) in Lynn Canal and Chatham Strait. The sampling program continued from March 1964 to February 1967; each year eight stations (Figure 5) were sampled quarterly at depths of 15 and 100 m. Beginning with the August 1965 samples, I kept records of the occurrence of *T. marsupii* on

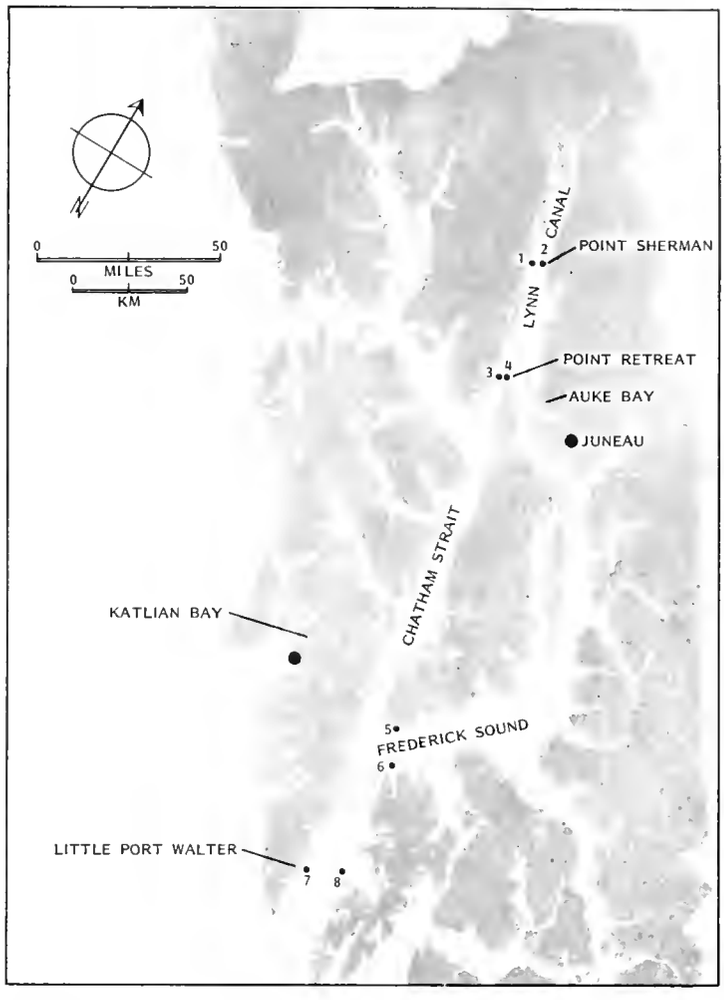

FIGURE 5.—Locations in southeastern Alaska where ellobiopsids were collected.

Alaska amphipods. The parasitized amphipods were found mostly in the 15-m samples. *Cyphocaris challengeri* was the most frequent host, and the highest incidence of parasitism occurred in the August samples (Table 5).

The internal portions of the parasite were not examined, but the external morphology, size, and site of attachment correspond closely to Kane's original description. Most of the specimens I examined were forming gonomeres. A few gonomeres had begun cleavage to form spores. The sporulating gonomeres were not as deeply sculptured nor as dark as those described by Kane (1964).

Thalassomyces fagei (Boschma 1948)

Thalassomyces fagei—Hoffman and Yancey (1966), Komaki (1970), Vader (1973b).

The euphausiid *Thysanoessa raschii* (M. Sars) is the most common host of *Thalassomyces fagei* in Alaska waters. I have examined parasitized

TABLE 5.—Occurrence of *Thalassomyces marsupii* on three species of amphipods taken in quarterly sampling with a 1.8-m Isaacs-Kidd mid-water trawl (August 1965 to February 1967) in southeastern Alaska.

Cruise date and station number	*Cyphocaris challengeri*		*Parathemisto libellula*		*Parathemisto pacifica*	
	Number collected	Number parasitized	Number collected	Number parasitized	Number collected	Number parasitized
August 1965						
1	107	3	80	0	4	0
2	176	5	89	0	3	0
3	10	1	4,144	0	9	0
4	228	3	494	0	40	0
5	62	3	3	0	4	0
6	43	2	0	—	4	0
7	20	3	6	0	3	0
8	44	3	13	0	2	0
November 1965						
8	19	1	1	0	2	0
February 1966						
8	124	1	0	—	0	—
September 1966						
1	2	0	465	1	0	—
2	0	—	1,350	10	0	—
3	0	—	60	3	15	0
4	<50	1	130	5	18	1
5	272	0	43	0	12	1
6	1,346	12	382	0	159	0
February 1967						
6	21	1	6	0	0	—

specimens collected in sampling by the National Marine Fisheries Service (NMFS) in southeastern Alaska, south-central Alaska, the eastern Bering Sea, and the southeastern Chukchi Sea. Hoffman and Yancey (1966), who reported that *T. fagei* parasitized *Thysanoessa raschii* in Kachemak Bay, south-central Alaska, followed the development of external portions of the ellobiopsids from April through June. Examination of euphausiids collected during 4 yr (1962-66) of plankton sampling by NMFS in southeastern Alaska indicates that the ellobiopsids are most evident during May. Maturing ellobiopsids are seen on *T. raschii* as early as April and occasionally as late as December. A similar pattern of occurrence was described by Mauchline (1966) for *Thalassomyces fagei* on euphausiids in the North Atlantic.

Euphausia pacifica Hansen is abundant in lower Chatham Strait, southeastern Alaska, but is rarely parasitized by *T. fagei*. *Euphausia pacifica* bears this ellobiopsid off southern California (S. B. Collard, Marine Environmental Sciences Consortium, Dauphin Island, AL 36528, pers. commun.). An unidentified *Thalassomyces* was found on *E. pacifica* and *Thysanoessa longipes* Brandt in British Columbia (T. H. Butler, Biological Laboratory, Fisheries Research Board of Canada, Nanaimo, B.C., pers. commun.). In view of the wide distribution (Jones 1964) and known occurrence on at least 19 species of euphausiids (Vader 1973b), the British Columbia *Thalassomyces* is probably *fagei*. Komaki (1970) records *T. fagei* parasitizing *E. similis* G. O. Sars from Suruga Bay, Japan and *Thysanoessa inermis* (Krøyer) from the Bering Sea.

Thalassomyces capillosus (Fage 1938)

Amallocystis capillosus—McCauley (1962).
Thalassomyces capillosus—Collard (1966), Hoffman and Yancey (1966), Vader (1973a, b).

Thalassomyces capillosus is a parasite of the pelagic shrimp *Pasiphaea pacifica* from Coos Bay, Oreg., (McCauley 1962) to Prince William Sound, Alaska (Hoffman and Yancey 1966). I found nearly 700 *T. capillosus* in varying stages of development the year-round on *Pasiphaea* collected with a 1.8-m Isaacs-Kidd trawl in Chatham Strait and Lynn Canal. They were most abundant during the late spring and early summer, when it was not unusual to find 5 to 10% of the *Pasiphaea* in a sample parasitized; in one sample (May 1965 at the southern end of Chatham Strait) 47 of 115 *Pasiphaea* were parasitized by *T. capillosus*. *Thalassomyces capillosus* is also common in British Columbia (T. H. Butler, Biological Laboratory, Fisheries Research Board of Canada, Nanaimo, B.C., pers. commun.). Although *T. capillosus* are common in the northeastern Pacific, Vader (1973a) records only about

100 specimens in literature published on Atlantic *Pasiphaea* spp.

This parasite apparently has both physiological and morphological effects on the host shrimp. As noted by Bergan (1953), male and female shrimp were both parasitized; none of the parasitized females were carrying eggs, which indicates that the parasite must have sterilized the host. Although Bergan (1953) found no evidence that the root system of the parasite penetrates the host's gonads, it is possible that the parasite controls the sexual development and molting processes of the host either by influencing hormone production (Hoffman and Yancey 1966) or by a starvation effect (Wickstead 1963). In addition to the effect on growth and reproduction, *T. capillosus* causes a characteristic upward deflection of the host's rostrum (Boschma 1959; McCauley 1962; Hoffman and Yancey 1966). It is not known whether the deformation of the rostrum occurs before or after the primary stalks break through the cuticle of the host. The ellobiopsid is frequently lost or degenerates, but the upturned rostrum remains as evidence of parasitism. It was primarily on the basis of the upturned rostrum that *Pasiphaea principalis* Sund was erroneously distinguished from *P. tarda* Krøyer (Boschma 1959).

Thalassomyces californiensis Collard 1966

Thalassomyces californiensis n.sp.—Collard (1966).

Thalassomyces californiensis—Vader (1973a, b).

Thalassomyces californiensis is a parasite of the shrimp *Pasiphaea emarginata* Rathbun off the coast of central California (Collard 1966). *Thalassomyces californiensis* superficially resembles *T. capillosus*, but the primary stalks penetrate the eye stalks of the host rather than the base of the rostrum. Five to 20 primary stalks may be associated with each organ of fixation (Collard 1966) rather than the one to four primary stalks found in *T. capillosus*. Collard did not find any major morphological or histological changes caused by this parasite.

Thalassomyces species (not identified)

Thalassomyces sp.—Collard (1966).

A third species of *Thalassomyces* infects *Pasiphaea chacei* Yaldwyn in southern Baja California but is unidentified. This parasite is found on the anterior part of the abdomen (R. Lavenberg, Los Angeles County Museum of Natural History, Los Angeles, CA 90007, pers. commun.).

Ellobiopsis chattoni Caullery 1910

Ellobiopsis chattoni—Hoffman and Yancey (1966).

Hoffman and Yancey (1966) reported *E. chattoni* as a parasite of the calanoid copepod *Metridia longa* (Lubbock) in Auke Bay, southeastern Alaska. During monthly sampling of the Auke Bay vicinity by the NMFS from August 1962 to January 1964, copepods parasitized by *E. chattoni* were found from late July through December; 5 to 25% of the *M. longa* were parasitized and peak infestation was in late October and early November. Hoffman and Yancey (1966) found only *M. longa* infected by *E. chattoni* despite the availability of other potential calanoid hosts—*Calanus finmarchicus* (Gunnerus), *Pseudocalanus minutus* (Krøyer), and *Acartia clausii* Giesbrecht. Wickstead (1963) noted a similar 100% host specificity of *E. chattoni* on *Undinula vulgaris* var. *major* Sewell in the Zanzibar Channel.

There may be a large seasonal and yearly variation in the rate of infection by ellobiopsids and perhaps even in the species of copepod infected. I sampled zooplankton monthly in Auke Bay and near Point Retreat (Figure 5) from September 1969 through October 1970. During this time, *E. chattoni* did not infect *M. longa* but did infect *P. minutus*; the level of infection was very low, however: one to six *P. minutus* were taken each month from the thousands of potential hosts examined, but no distinct seasonal trend of infection was evident.

Ellobiocystis caridarum (Coutiere 1911)

Sampling with the 1.8-m Isaacs-Kidd mid-water trawl in southeastern Alaska yielded many *Pasiphaea pacifica* (a pelagic shrimp) with the epibiont *E. caridarum* on their mouth parts. Boschma (1959) discussed the difficulties in identifying the various species of *Ellobiocystis*

described by Coutiere. Boschma also examined the question of including the genus *Ellobiocystis* within the family Ellobiopsidae and of including various epibionts described by With (1915), Monod (1926), and Sewell (1951) within the genus. I follow Boschma (1959) in considering the *Ellobiocystis* found on *P. pacifica* to belong to the collective species *E. caridarum* s.l. This constitutes the first record of *E. caridarum* s.l. outside of the Atlantic and Antarctic oceans.

Ellobiocystis caridarum attach as single trophomeres directly to the mouth parts of the host. There is no branching of the trophomeres, and no organs of adsorption penetrate the cuticle of the host. The trophomeres may occur singly or in small groups attached to the labia, mandibles, maxillae, or maxillipeds. Single trophomeres on the oral appendages are usually attached near the base of a seta, sometimes directly to a seta. When on the mandibles, the trophomeres are located between the teeth. Groups of trophomeres, each trophomere separately attached to the host's cuticle, may contain 12 or more individuals when on the labia but usually contain less than 8 when attached to the maxilla or maxillipeds. I have seen nearly 50 *E. caridarum* on a single *Pasiphaea*.

The size and form of *E. caridarum* s.l. found on *P. pacifica* in southeastern Alaska are as variable as the size and form figured by Boschma (1959) for the *E. caridarum* found on *P. semispinosa* Holthuis. The maximum observed length of trophomeres of Alaska specimens was 1.17 mm and of gonomeres was 0.54 mm; the maximum diameter of trophomeres was 0.56 mm and of gonomeres was 0.42 mm. The shapes of the gonomeres varied from ovals, slightly longer than wide, to rods eight times longer than wide. Each maturing trophomere carried one gonomere; less than 1% of the trophomeres had two or three gonomeres.

The incidence of *E. caridarum* s.l. on *P. pacifica* is not known, primarily because the epibiont is not readily noticeable in either the living or preserved state. When searched for, *E. caridarum* have been found on *P. pacifica* of a wide size range (30 to 80 mm total length) and during all months of the year. The proportion of the *P. pacifica* having *E. caridarum* varies but is usually less than 10%. In one exceptional sample (AB65-15, southern Chatham Strait, May 1965), 84% (263 of 314) were infested.

Ellobiocystis species?

Monod (1926) figured an epibiont found on the mouth parts of the Antarctic amphipod *Podocerus septemcarinatus* Shellenberg (= *Platophium hystricoides* Monod). This epibiont has been provisionally classified as *Ellobiocystis caridarum* by Boschma (1959). Vader and Kane (1968) reported a similar epibiont on the mouth parts of *Rhachotropis macropus* from western Norway. The taxonomic status of these epibionts still is uncertain (W. Vader, Zoologisk Avdeling, Tromsø Museum, Tromsø, Norway, pers. commun.).

I found small epibionts like those figured by Monod (1926) on the amphipod *R. helleri* from Auke Bay, Alaska. The small bean-shaped organisms (Figure 6) are attached to the labia, mandibles, and maxillipeds of the host by a short stalk. Lengths range from 0.10 to 0.13 mm. The separation of body and stalk is more distinct than in the *E. caridarum* figured by Boschma (1959) or than in material from *Pasiphaea pacifica* that I have seen. None of the epibionts on *R. helleri* are divided into gonomeres or spores. Although these epibionts superficially resemble early stages of developing *E. caridarum*, their proper identification remains in doubt.

SUMMARY

1. *Thalassomyces boschmai* is found on the mysids of the genera *Acanthomysis, Neomysis*, and *Meterythrops* in the northeastern Pacific.

2. *Thalassomyces albatrossi* n.sp. is described as a parasite of *Stilomysis major* from the western Pacific off Korea.

3. *Thalassomyces fasciatus* is found on *Gnathophausia ingens* and *G. gracilis* from Baja California and southern California.

4. *Thalassomyces marsupii* is found on the amphipods *Parathemisto pacifica, P. libellula*, and *Cyphocaris challengeri* from the inside coastal waters of southeastern Alaska and *P. pacifica* from Puget Sound.

5. *Thalassomyces fagei* has been found on the euphausiid *Thysanoessa raschii* from southeastern Alaska, the Bering Sea, and the Chukchi Sea and on *Euphausia pacifica* from California and southeastern Alaska.

6. *Thalassomyces capillosus* is common on the shrimp *Pasiphaea pacifica* in the coastal waters

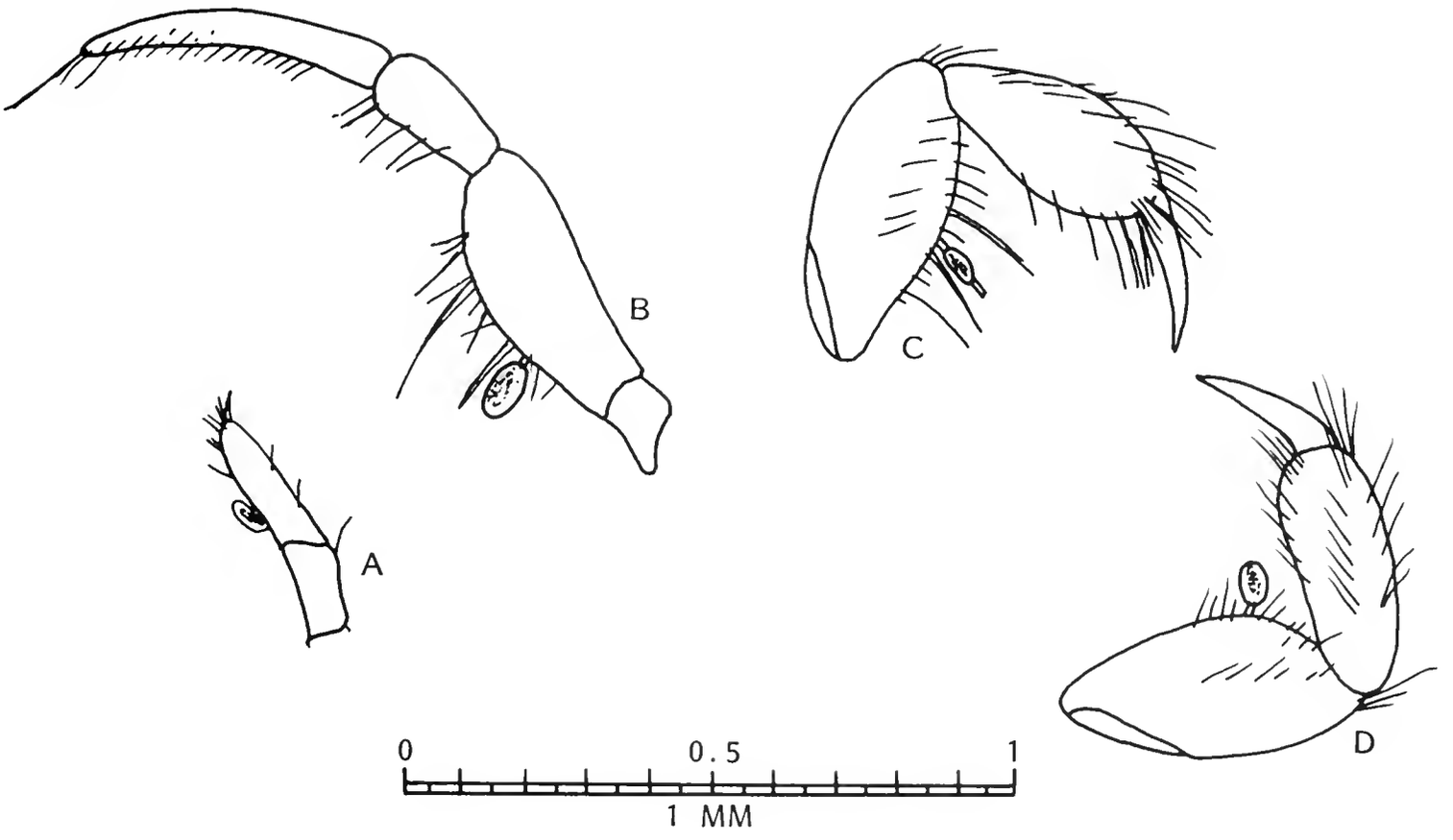

FIGURE 6.—*Ellobiocystis* sp.? on mouth parts of the amphipod *Rhachotropis helleri*. A. Palp of first maxilla. B. Mandibular palp. C. and D. Maxilliped palps.

of the northeastern Pacific during all seasons of the year.

7. *Thalassomyces californiensis* is found on *P. emarginata* from southern California.

8. *Ellobiopsis chattoni* is found on the copepod *Metridia longa* from Auke Bay, Alaska, from July through December; peak abundance is in late October and early November. *Pseudocalanus minutus* is also a host of *E. chattoni*.

9. *Ellobiocystis caridarum* is found in a wide variety of growth forms on *Pasiphaea pacifica* from southeastern Alaska during all seasons of the year. Incidence of infestation by *E. caridarum* may be as high as 84% of the *Pasiphaea*. This is the first report of *E. caridarum* from the North Pacific.

10. A small epibiont resembling *E. caridarum* has been found on the mouth parts of the amphipod *Rhachotropis helleri* from Auke Bay, Alaska.

11. Known North Pacific ellobiopsids, their hosts, and the geographical range of the ellobiopsids are summarized in Table 6.

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TABLE 6.—North Pacific ellobiopsids, known North Pacific range, and known North Pacific hosts.

Ellobiopsid	Known North Pacific range of ellobiopsid	Known North Pacific hosts
Thalassomyces albatrossi n.sp	Eastern Korea	*Stilomysis major*
Thalassomyces boschmai	Puget Sound, Wash., to Kachemak Bay, Alaska	*Acanthomysis macropsis* *Acanthomysis pseudomacropsis* *Acanthomysis nephrophthalma* *Neomysis kadiakensis* *Meterythrops robusta*
Thalassomyces fasciatus	Southern Baja California to Santa Cruz Basin, Calif.	*Gnathophausia gracilis* *Gnathophausia ingens*
Thalassomyces capillosus	Southern Oregon to Prince William Sound, Alaska	*Pasiphaea pacifica*
Thalassomyces californiensis	Central California	*Pasiphaea emarginata*
Thalassomyces sp.	Baja California	*Pasiphaea chacei*
Thalassomyces fagei	Southern California to southeastern Chukchi Sea; Suruga Bay, Japan	*Euphausia pacifica* *Euphausia similis* *Thysanoessa inermis* *Thysanoessa longipes* *Thysanoessa raschii*
Thalassomyces marsupii	Puget Sound, Wash., to southeastern Alaska	*Parathemisto pacifica* *Parathemisto libellula* *Cyphocaris challengeri*
Ellobiopsis chattoni	Southeastern Alaska	*Metridia longa* *Pseudocalanus minutus*
Ellobiocystis caridarum	Southeastern Alaska	*Pasiphaea pacifica*
Ellobiocystis sp.	Southeastern Alaska	*Rhachotropis helleri*

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A DESCRIPTION OF ATLANTIC MACKEREL, *SCOMBER SCOMBRUS*, EGGS AND EARLY LARVAE

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ABSTRACT

The development of laboratory-reared Atlantic mackerel, *Scomber scombrus*, eggs and early larvae is described in order to augment published descriptions of this species. The eggs are spherical, have a diameter of 1.01 to 1.28 mm, and have a single, yellowish oil globule, 0.22 to 0.38 mm in diameter. Melanophores, first visible after blastopore closure, assume a distinct pattern on the embryo. Melanophores are present on the oil globule but are absent from the yolk surface except immediately prior to hatching. Hatching occurs at 90 to 102 h after fertilization at an average incubation temperature of 13.8°C. Bodily pigmentation of the larvae undergoes considerable change during yolk absorption; eye pigmentation is apparent at 66 h after hatching. The yolk is fully absorbed by 137 h after hatching, and teeth are present in 192-h-old larvae.

To complement ichthyoplankton survey work underway at the Sandy Hook Laboratory, eggs of a few fish species have been artificially spawned and reared in the laboratory. These series of known identities were obtained for comparison with eggs and larvae from plankton samples. The purpose of this paper is to present descriptive information on the eggs and early larvae of Atlantic mackerel, *Scomber scombrus* Linnaeus 1758, and, in so doing, to augment previous descriptions of the young stages of this species, particularly of the eggs.

Previous publications containing helpful information on identification of North American Atlantic mackerel eggs and larvae are by Sette (1943), who included descriptive notes on eggs and larvae and compared them with young stages of other species present in the same waters, and by Bigelow and Schroeder (1953), who presented a brief egg and larval description and illustrated four larval stages. Other, less helpful, descriptive notes on North American Atlantic mackerel eggs and larvae are by Moore (1899), Dannevig (1919), Bigelow and Welsh (1925), Sparks (1929), Merriman and Sclar (1952), Wheatland (1956), and Marak and Colton (1961). Worley (1933) described the rate of embryonic development of Atlantic mackerel at various temperatures. Other papers describing eggs and larvae of Atlantic mackerel, probably of a separate European race (Garstang 1897-99), include Cunningham (1891-92a, b), Ehrenbaum (1905-09), Bigelow and Welsh (1925), Sella and Ciacchi (1925), and Padoa (1956). However, adequate descriptions of Atlantic mackerel eggs are lacking in the literature because descriptive information by most of the above authors is limited to reports of egg and oil globule diameters. Illustrations, where presented, are of little use in differentiating this from other species. The reported egg dimensions vary greatly and overlap those of other species present at the same time and in some of the same areas as Atlantic mackerel. Regarding this problem, Sette (1943) described a technique of plotting oil globule diameter against egg diameter for all eggs in hauls containing troublesome mixtures. In these scatter diagrams the Atlantic mackerel eggs remained discrete from other species' eggs.

The congeneric chub mackerel, *Pneumatophorus diego* (= *Scomber japonicus*) eggs and larvae from the eastern Pacific Ocean were described by Fry (1936), Orton (1953), and Kramer (1960) and from the western Pacific Ocean by Uchida et al. (1958), Dekhnik (1959), and Watanabe (1970). The papers by Orton, Kramer, and Watanabe contain very detailed and useful descriptions. Eggs and yolk-sac larvae of *S. scombrus* and *S. japonicus*, judged by my specimens and the above-mentioned descriptions, are similar, but differ in that: *S. japonicus* late-stage eggs and early yolk-sac lar-

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vae have more melanophores on the yolk surface than *S. scombrus*; and *S. scombrus* larvae, during and at the end of yolk absorption have several dorsal trunk melanophores, whereas few *S. japonicus* at this stage have any such pigmentation. In those *S. japonicus* which have dorsal melanophores on the trunk, it is apparently limited to a single patch near the 23rd myomere (Fry 1936; Uchida et al. 1958; Kramer 1960). Separation of the two species of *Scomber* early-stage eggs, before blastopore closure, may be impossible on the basis of morphological characters. Other factors, such as spawning time and area, and the proximity of older, identifiable stages, may be necessary for subjective identifications.

PROCEDURES

Running ripe Atlantic mackerel were caught by hook and line off Fire Island, Long Island, N.Y., during the morning of 2 June 1967. Several hundred eggs were stripped from one female and fertilized in a liter jar containing a small amount of seawater. The water was renewed about 20 min after introduction of the eggs and sperm, and the jar placed in a water bath to minimize temperature changes. The water temperature generally increased during egg incubation and larval life and ranged from 12.1° to 14.4°C for eggs and from 14.1° to 15.2°C for larvae (Table 1). Larvae were not fed and none survived longer than 8 days past hatching. Samples of the developing eggs and larvae were removed at intervals and preserved in dilute Formalin.[2]

While the following descriptions of eggs were based mainly on cultured eggs, planktonic eggs were utilized in obtaining dimensions (Table 2) and in confirming pigmentation, which tended to be faded and obscure in the cultured specimens. Owing to the internally damaged condition of early-stage eggs from plankton samples only middle- and late-stage eggs from that source were used for the above purposes. In the early-stage eggs the yolk and oil globule membranes ruptured and allowed the yolk and fractured oil globule to mix with perivitelline fluid. Planktonic eggs were taken by Gulf V high-speed samplers, with 0.4-m mouth and 0.52-mm mesh openings.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Dimensions of Atlantic mackerel larvae, cultured series.

Hours from hatching	Number of larvae	Culture temp. (°C)	Standard length (mm)		Total length (mm)	
			Mean	Range	Mean	Range
0	3	14.1	3.25	3.03-3.36	3.39	3.16-3.50
6	10	14.1	3.47	3.30-3.58	3.62	3.47-3.75
18	7	14.1	3.59	3.44-3.70	3.76	3.61-3.84
42	8	14.4	3.77	3.67-3.84	3.99	3.89-4.05
66	3	14.6	3.85	3.78-3.94	4.08	4.00-4.16
137	7	15.2	3.92	3.84-4.03	4.14	4.05-4.19
166	3	15.1	4.02	3.81-4.25	4.24	4.03-4.47
192	2	14.8	3.97	3.75-4.19	4.21	3.97-4.45

The samples were taken in step-oblique tows at depths between 0 and 33 m, at a speed of 5.0 knots.

DESCRIPTION OF THE EGG

Dimensions

Formalin-preserved Atlantic mackerel eggs are spherical and have clear and unsculptured shells (Figure 1). The mean diameter of eggs from plankton samples is 1.13 mm (range 1.01 to 1.28 mm) and of those that were cultured is 1.20 mm (range 1.13 to 1.25 mm, Table 2). The cultured eggs were stripped from a single female, while those from plankton samples undoubtedly were spawned by many. This may account for the smaller range in egg diameter from the cultured series and the difference in mean diameters from the two sources. Differential shrinkage of egg diameter, due to varying time in preservation, between cultured and planktonic eggs is assumed negligible, as all eggs were measured more than a year after preservation.

The egg contains a single oil globule which is generally spherical and yellow or pale amber. Its diameter ranges from 0.22 to 0.38 mm, with a mean for all samples of 0.29 mm (Table 2). In many of our preserved samples, from both the cultured and planktonic eggs, the oil globules were fractured or distorted. The dimensions presented here lie within the range of those given by previous authors who have studied Atlantic mackerel. Published observations on eggs of this species from western North Atlantic waters report a range in egg diameter of 0.88 to 1.38 mm, with mean or modal values of 1.15 to 1.30 mm, and an oil globule diameter of 0.24 to 0.32 mm (Moore 1899; Dannevig 1919; Bigelow and Welsh 1925; Sparks 1929; Sette 1943; Merriman and Sclar 1952; Wheatland 1956; Marak and Colton 1961).

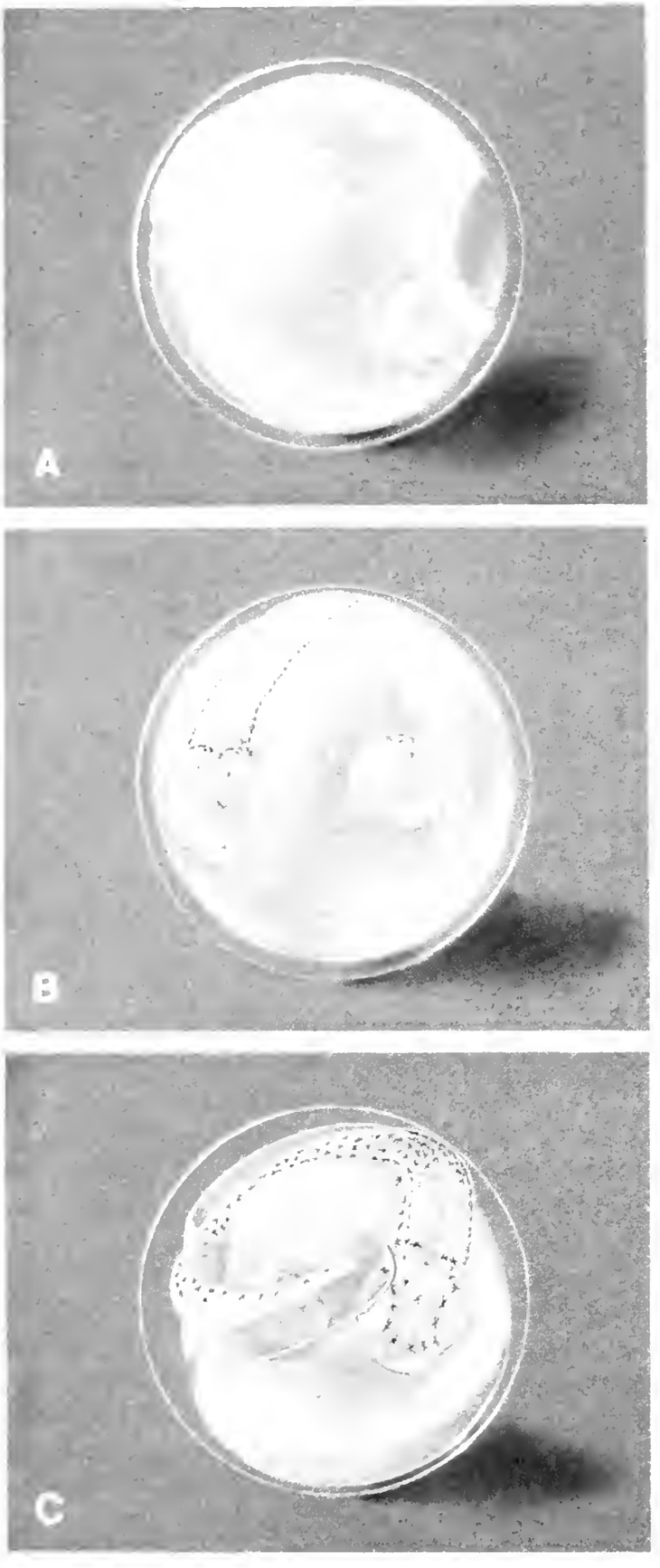

FIGURE 1.—Atlantic mackerel eggs: A, early stages; B, middle stage; C, late stage.

Perivitelline Space

In live eggs, the perivitelline space occupies about one-twentieth of the eggshell diameter, or about 0.05 mm. The eggs illustrated (Figure 1) are idealized only to the extent that the width of perivitelline space conforms to the observations on live eggs.

Pigmentation

Two large yellow chromatophores were observed in the live eggs at 60 and 85 h after fertilization. These chromatophores were situated on either side of the embryo immediately behind the head. No further notes on chromatophores of this color were kept. By the time I observed the eggs and larvae, several months after preservation, only melanophores were observed. All further comments on pigmentation refer to melanophores.

Development

Following the criteria of Ahlstrom and Ball (1954), this paper describes the development of the Atlantic mackerel egg in three stages: early (fertilization to closure of the blastopore), middle (blastopore closure to the twisting of the tail), and late (tail twisting to hatching). The early stage terminated shortly after 36 h, as the blastopore was 0.3 mm across at that time; the middle stage was completed by 72 h, when the tail was observed twisted; and the late stage lasted till hatching, by 102 h after fertilization. Incubation temperature ranges of the three stages were: early, 12.1° to 14.4°C; middle, 13.8° to 14.2°C; and late, 14.1° to 14.2°C.

Early-Stage Eggs (Figure 1A)

Early-stage Atlantic mackerel eggs are characterized by the dimensions given above and by the presence of a single yellow oil globule. The oil globule is off-center at the vegetal pole, opposite the blastodisc at first and, with development of the embryo, slightly posterior to the tail at the time of blastopore closure. There are no visible myomeres, pigmentation, or formed eyes.

Middle-Stage Eggs (Figure 1B)

Soon after the blastopore closes, pigmentation becomes visible on the embryo as numerous, scattered fine points on the dorsal surface of the thoracic region and a few back along the trunk.

TABLE 2.—Dimensions of Atlantic mackerel eggs from the cultured series and plankton samples taken during May and June 1966.

Item	Egg diameter (mm)			Oil globule diameter (mm)		
	No.[1]	Mean	Range	No.[1]	Mean	Range
Cultured series:						
Early stage	537	1.19	1.13-1.25	371	0.29	0.24-0.36
Middle stage	43	1.20	1.17-1.24	36	0.32	0.27-0.36
Late stage	42	1.20	1.16-1.22	42	0.32	0.28-0.33
Total cultured	622	1.20	1.13-1.25	449	0.30	0.24-0.36
Plankton samples, middle- and late-stage eggs:						
19 May 1966						
38°01.5'N, 74°59.0'W	54	1.18	1.06-1.28	53	0.32	0.27-0.38
17 June 1966						
41°17.0'N, 70°48.0'W	163	1.14	1.01-1.27	156	0.28	0.22-0.35
41°12.0'N, 70°47.0'W	114	1.12	1.02-1.26	113	0.31	0.24-0.38
41°07'N, 70°46.0'W	62	1.08	1.02-1.21	62	0.28	0.22-0.32
Total plankton	393	1.13	1.01-1.28	384	0.29	0.22-0.38

[1]Discrepancies between numbers of specimens in these columns are due to fractured or distorted oil globules, which were not measured.

As development progresses, these pigment cells become more intense and increase in number on the trunk where they tend to line up in two dorsolateral rows. The lateral melanophores in the thoracic region become dendritic and dense, while the middorsal melanophores fade. This distinct thoracic pattern persists until hatching. Melanophores appear on the anterior surface of the oil globule at the same time as those on the embryo.

The width of the head increases to almost twice that of the tail. The embryo increases in length, growing past the oil globule and encircling three-fourths of the egg by the end of this stage. The tail twists and flexes near the oil globule until it lies flat against the yolk surface. A finfold begins to develop on the posterior one-third of the embryo. Optic vesicles become prominent and up to six myomeres are discernible.

Late-Stage Eggs (Figure 1C)

At the start of the late stage, there are two dorsolateral rows of melanophores extending back from just behind the brain, well past the oil globule; there are few melanophores below these rows on the flanks. There is always pigment on the anterior half of the oil globule, and usually some on the snout and in a row behind the eyes across the head. During this stage, trunk melanophores migrate; they become scattered on the flanks and in some specimens a few melanophores posterior to the oil globule nearly reach the ventral edge of the body by the time of hatching. Pigment is lacking on the extreme caudal portion of the body. Melanophores on the oil globule darken and increase in number and coverage, so that just before hatching they are scattered over most of the oil globule. As many as 24 myomeres are visible prior to hatching. The dorsal line of melanophores behind the eyes persists on most embryos. The eyes are unpigmented through hatching.

The embryo increases in length until it encircles the yolk, with the tail overlapping the head just before hatching. The oil globule lies midway along the body, at the posterior end of the yolk sac, at hatching. The finfold deepens and extends forward to occupy the posterior two-thirds of the embryo. Before hatching the alimentary tract is visible posterior to the oil globule and terminates at the edge of the ventral finfold.

DESCRIPTION OF LARVAE

Rate of Development

Hatching occurred between 90 and 102 h after fertilization at an average incubation temperature of 13.8°C (range 12.1° to 14.4°C). This was a slightly faster rate of development than that reported by Worley (1933). At this temperature (13.8°C), interpolation of Worley's data would indicate a time to hatching of about 120 h. The yolk-sac stage ended by 137 h, for the yolk in all specimens was absorbed by that time.

Pigmentation at Hatching (Figure 2A)

Melanophores are distributed as follows: some tend to be in dorsolateral rows, extending on each side from the snout over the eyes to about nine-tenths of the body length, while others are

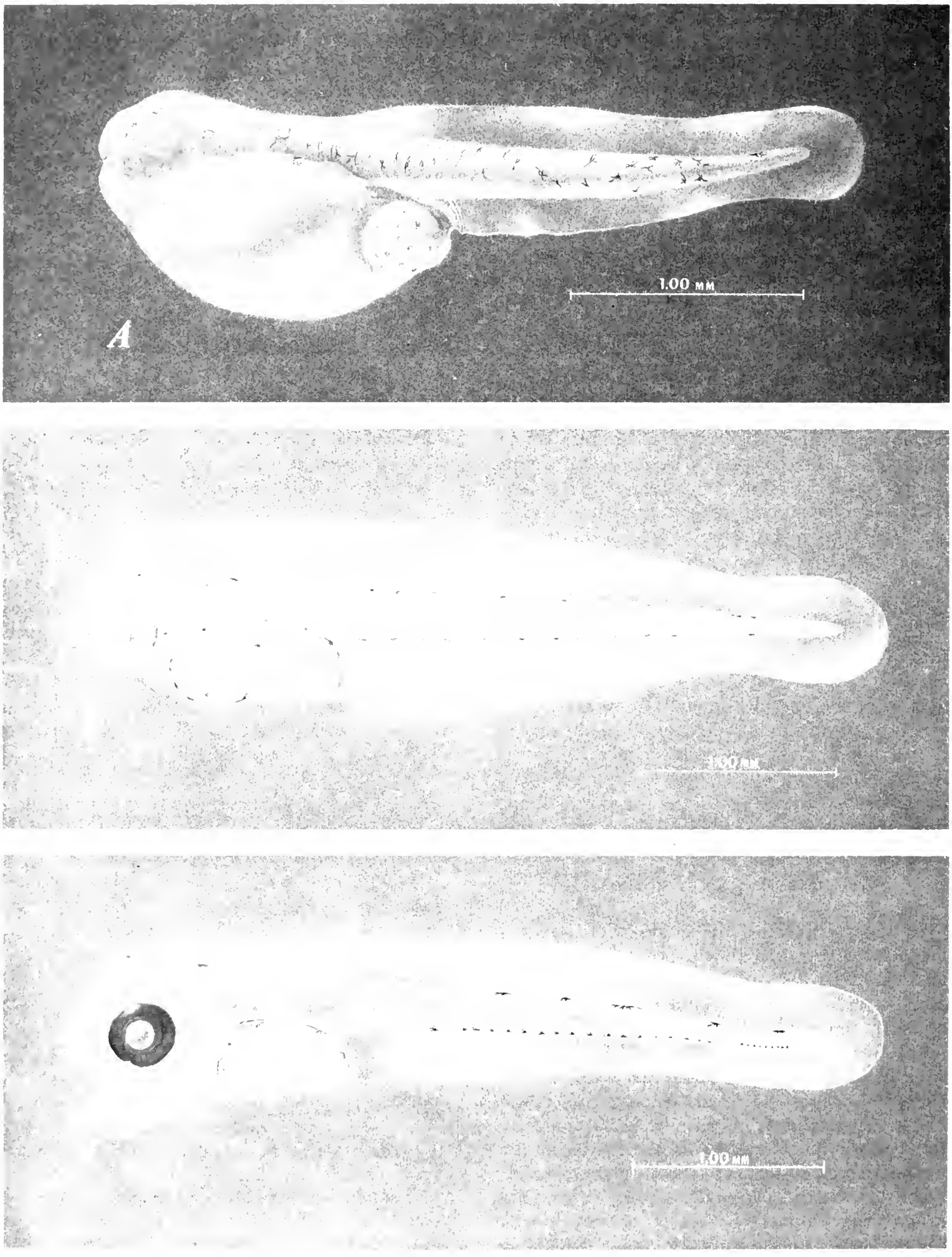

FIGURE 2.—Atlantic mackerel larvae: A, shortly after hatching; B, 66 h after hatching; C, 192 h after hatching.

scattered on the flanks; they are found on the nape; one on each side of the yolk-sac close to the otocysts; and scattered on the oil globule.

Subsequent yolk-sac stages undergo marked pigmentation changes, including the migration and formation, or initial appearance of melanophores. Orton (1953) reported similar melanophore migration in *Pneumatophorus japonicus diego* (= *S. japonicus*) eggs and yolk-sac larvae.

Head Pigmentation

Pigment on the head becomes reduced to a few melanophores dorsal to the eyes and on the nape (Figure 2B, C). At 66 h, pigment forms in the eyes. Some specimens, between 137 and 192 h, have a melanophore on the ventral midline between the developing dentaries where the basihyal forms.

Abdominal Pigmentation

Melanophores present on the oil globule at hatching and at 6 h start migrating to the ventral surface of the yolk sac by 18 h, and are mostly on that surface by 42 h. Subsequently, these melanophores tend to coalesce on two areas: on the forward end of the gut cavity between the cleithra (Figure 2B, C) and, in some specimens, on the ventral surface of the hindgut. This pigmented area on the hindgut varies in occurrence, intensity, and location.

At 18 h, some of the melanophores which were on the sides of newly hatched larvae, above the middle of the yolk sac, are migrating ventrally and inward above the yolk mass. By 66 h, this pigment is situated over the dorsum of the midgut and hindgut. Older specimens, up to 192 h, all have intense or large dendritic melanophores directly above the gut cavity (Figure 2C).

Caudal Pigmentation

The two dorsolateral rows of melanophores, already somewhat scattered on the flanks at hatching (Figure 2A), migrate toward the bases of the dorsal and anal finfolds; this condition is complete by 66 h (Figure 2B). Those melanophores at the dorsal finfold base decrease to about 6 by 192 h and are located on the posterior half of the larva; those in the ventral row increase to about 20 to 25 and extend from near the vent back to the caudal extremity, exclusive of finfold.

Myomeres

At 102 h, only 23 or 24 myomeres were observed in the unhatched eggs. Others most certainly present were obscured by the opacity of the yolk. In the newly hatched larvae, however, the full complement of 31 myomeres was evident.

Finfold

In newly hatched larvae, a continuous finfold extends posteriorly on the dorsal surface from slightly behind the auditory vesicle, around the caudal extreme, then forward on the ventral surface to the yolk sac. The finfold broadens, lengthens, and reaches the top of the head by 66 h where it persists to 192 h. With development, the ventral finfold extends forward to the anus, and as the yolk sac decreases in length the preanal finfold occupies the area between the anus and yolk sac. Actinotrichia are barely visible in the caudal portion of the finfold on newly hatched larvae and become more evident on older stages (Figure 2).

Alimentary Canal

The hindgut, observable in the ventral finfold of larvae at hatching as a narrow tract, is much thickened at 18 h. Mouth rudiments are present on 66-h larvae, and by 137 h, when the yolk material is completely absorbed, the mouth is open. A pair of recurved teeth occur on each jaw at 192 h (Figure 2C).

Otocysts

The otocysts are visible at hatching. Developing otoliths are barely visible at 42 h and are plainly evident by 66 h (Figure 2).

Pectoral Buds

The newly hatched larvae have pectoral buds. By 66 h, these buds have fleshy bases, fan-shape membranes, and appear functional (Figure 2A, B).

SUMMARY

For identification purposes, it is useful to summarize some of the more prominent features of Atlantic mackerel eggs and early larvae. The

egg has an average diameter of 1.08 to 1.20 mm, and contains a single, yellowish oil globule averaging 0.28 to 0.32 mm in diameter. A distinctive pigment pattern forms on the embryo after the blastopore closes. The eyes remain unpigmented through hatching.

Pigmentation on the larvae undergoes considerable change during the yolk-sac stage. Newly hatched larvae have scattered melanophores on the dorsal and lateral surfaces of the head and trunk and on the oil globule. By the time the yolk is used up, pigment coalesces onto the dorsal and ventral surfaces of the trunk, above the brain and gut, and forms in the eyes. Teeth are present in 192-h-old larvae, at a size of 4.0 mm standard length.

ACKNOWLEDGMENT

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THE CONCENTRATION OF MERCURY, COPPER, NICKEL, SILVER, CADMIUM, AND LEAD IN THE NORTHERN ADRIATIC ANCHOVY, *ENGRAULIS ENCRASICHOLUS*, AND SARDINE, *SARDINA PILCHARDUS*

MALVERN GILMARTIN[1] AND NOELIA REVELANTE[2]

ABSTRACT

Levels of mercury, copper, nickel, silver, cadmium, and lead were determined in various tissues of the northern Adriatic anchovy, *Engraulis encrasicholus*, and sardine, *Sardina pilchardus*. throughout a 7-month fishing season. The highest concentrations of nickel, silver, cadmium, and lead occurred in the skin and gills, with little interspecific differences and no unusually high values. The highest concentrations of mercury and copper occurred in internal tissues, with the anchovy showing markedly higher concentrations than the sardine. Total mercury concentrations in anchovy muscle ranged from 70 to 215 nanograms per gram wet weight, concentrations 2-4× greater than in the same or similar anchovy species off northwestern Africa, southeastern United States, and California.

The Adriatic Sea extends 800 km into the heartland of the European continent, and is bordered by Italy, Yugoslavia, and Albania. The extended coastal shelf of the northern portion is an important fishery region, exploited heavily by both Italy and Yugoslavia.

Unfortunately, with restricted exchange to the open Mediterranean, the Adriatic displays many of the characteristics of a narrow trapped sea. Furthermore, the shallow northern region receives industrial wastes disproportionate to its area from large industrial centers located along the eastern coast at Rijeka and Pula, Yugoslavia, and more extensive industrial concentrations on the Gulf of Trieste and the western coast near Venice, Italy. More significantly, the Reno, Po, Adige, and Isonzo rivers discharge their industrial pollutant loads into the northern Adriatic. The Po alone is the second largest and perhaps most heavily polluted river entering the entire Mediterranean, and has a drainage area more than three-quarters the total area of the Adriatic itself. In 1972, 76 plants were discharging their waste water directly or indirectly into the Venice lagoon, and 10,000 of the 64,000 hectares of the lagoon were considered seriously polluted. Consequently, it is estimated that about 70% of the total organic load of industrial waste entering the Adriatic Sea from the west is concentrated in the northern part of the sea (General Fisheries Council for the Mediterranean 1972).

In contrast, although the deeply indented eastern coast has more than twice the shoreline of the western coast, population density and industrialization are markedly lower, and no major rivers flow into the Adriatic from the east. However, the level of industrialization and population density is increasing on both coasts of the Adriatic, and already the level of some heavy metals (e.g. mercury) in water and edible marine organisms in the open Adriatic may be at, or even slightly above, the acceptable safety level (General Fisheries Council for the Mediterranean 1972).

Recent research has drawn attention to the increasing hazards of heavy metal pollution in the marine environment (Ruivo 1972). Continental shelf fisheries, such as those of the shallow northern Adriatic, are especially threatened by these materials since large amounts can be introduced into restricted areas by coastal waste water runoff and the fallout of aerosols.

Therefore, a preliminary survey of the levels of mercury and copper, and the potentially toxic metals nickel, silver, cadmium, and lead in the sardine *Sardina pilchardus* Walbaum and the

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anchovy *Engraulis encrasicholus* Linnaeus was conducted during 1972 and 1973 to establish currently occurring levels of these elements and to produce a baseline for future reference.

The Fishery

The total fish catch landed in the eastern Adriatic remained relatively stable from 1964 through 1971, at 25,000-30,000 metric tons (Food and Agriculture Organization of the United Nations 1972), with an additional 2,000-3,000 metric tons taken annually for noncommercial use. Three small pelagic species of clupeids consistently compose at least 70% of this catch (Table 1), about 85% of which is canned, the balance being sold fresh. No significant fish meal industry currently utilizes these species.

There is strong evidence that the sardine is already fished to capacity, but that the anchovy may be significantly underexploited (Major 1970). The two species selected for the initial survey were the sardine, the most abundant and commercially most important species in the Adriatic, and the anchovy, the species suspected of having the greatest potential for increased production.

The Stock

The population structure and migration patterns of the Adriatic sardine and anchovy are not well understood. Gamulin (1956) opined that the sardine population migrates offshore annually from the very shallow waters of the northern Adriatic to somewhat deeper waters (60-120 m), but not into the central Adriatic, a behavior pattern typical of the species (Larrañeta 1960). Zavodnik (1968) presented similar evidence, noting that the species is completely absent from the shallow coastal zone by December. Krajnović and Dekaris (1968) found serological evidence that various subpopulations pass the Istrian coast during these migrations.

Evidence for anchovy migrations, e.g. based on seasonal variations in catch statistics at various ports, appears somewhat clearer. Piccinetti (1970) suggests that the population "winters" off Ancona and farther south off the western coast of the Adriatic, and during the spring migrates eastward and then northward along the Dalmatian coast, reaching the Istrian islands and peninsula during early summer. Continuing into the Gulf of Trieste and westward to Venice during autumn, the population returns to its "wintering" grounds by December.

While it is difficult to define exact migratory routes, or to delimit subpopulations, the evidence suggests that a composite stock of sardine and anchovy exists in the northern Adriatic, and that the Rovinj fishery "samples" much of this stock as it migrates past the Yugoslav Istrian peninsula.

MATERIALS AND METHODS

Sampling

During 1972 the major fishing season off Istria extended from June to December, rather than the more common May to October season. Samples were collected throughout the 1972 season and during the first few months of the 1973 season from the catch landed at the Mirna Cannery in Rovinj, Yugoslavia. These fish were usually caught within the preceding 12-18 h, within 15-30 km of Rovinj, using night light and purse seine.

Each sample usually consisted of at least six "representative" sardines and six "representative" anchovies selected from the catch, although often 50, and occasionally up to 60, fish were collected. Samples were immediately taken to

TABLE 1.—Yugoslavia's marine fisheries catch, 1964-71.

Species[1]	Nominal catch in thousands of metric tons							
	1964	1965	1966	1967	1968	1969	1970	1971
Sardina pilchardus (sardine)	5.4	9.4	9.1	11.2	13.5	13.5	10.9	14.7
Clupea sprattus (sprat)	5.0	5.7	3.4	2.5	3.2	2.0	5.5	3.8
Engraulis enchrasicholus (anchovy)	4.9	2.2	4.8	7.3	4.8	4.0	3.0	3.1
Scomber scombrus (Atlantic mackerel)	2.6	0.8	2.3	1.2	1.1	0.5	0.3	0.1
Boops boops (greater amberjack)	1.3	0.7	1.4	1.4	1.4	1.3	1.1	1.0
Maena maena, M. smaris (mullet)	1.3	1.1	1.0	1.0	0.9	0.8	0.7	0.3
Misc. marine fishes (18 spp.), Crustacea, and Mollusca	4.8	6.1	5.3	5.4	5.0	4.8	4.1	7.8
Total marine catch	25.3	26.0	27.3	30.0	29.9	26.9	25.6	30.8

[1]All scientific and common names from Bini (1965).

the Center for Marine Research in Rovinj, weighed and their standard length determined. Each fish was then dissected into component parts, e.g. skin (including scales), gills, muscle. These components were then pooled according to type, weighed, dried to a constant weight at 110°C, ground to homogeneous meal in a porcelain mortar, and stored in a glass desiccator until analyzed.

Analytical Methods

Standard chemical procedures (Christian and Feldman 1970; Fletcher 1970; Uthe et al. 1970; Stainton 1971) as modified by Knauer and Martin (1972) were used. For all elements except mercury, two 1-g aliquots of sample plus 10 ml 70% redistilled HNO_3 were added to 30-ml beakers, which were covered with watch glasses and refluxed at 90°C for 2 h, followed by evaporation to dryness. After charring, the samples were redissolved in 5 ml 70% HNO_3, followed by the dropwise addition of 30% H_2O_2 until the samples remained clear. At this point the samples were evaporated to 5 ml, cooled, and diluted to 25 ml with distilled water.

All samples were analyzed on a Perkin-Elmer 303 atomic absorption spectrophotometer.[3] Various combinations of fuels and oxidants, as recommended in the Perkin-Elmer manual, were used for each element. Small differences between signal and base line in some of the Cd, Ni, and Ag analyses may have introduced error.

Procedures for mercury differed slightly. Approximately 0.2-0.4 g dry weight of sardine and anchovy tissues were weighed into 20-ml Neutraglas disposable ampoules, followed by the addition of 3 ml of a 2:1 solution of concentrated H_2SO_4 and HNO_3. Samples were heated on a hotplate overnight at 80°C, cooled in ice, followed by the addition of 8 ml 6% $KMnO_4$ until the solution just turned pink. Subsequently 2 ml of sample digest were drawn into a 10-ml disposable syringe, followed by the addition of 2 ml reductant, and partitioning. The mercury was partitioned between liquid and air on a vortex mixer by drawing the syringe back to 10 ml (leaving a 6-ml air space). The vapor was then injected into a specially constructed 3-ml (total volume) glass absorption cell which had been mounted on the burner assembly of a Perkin-Elmer 303 atomic absorption spectrophotometer. A Westinghouse hollow cathode mercury lamp was used as an energy source. Three sets of blanks and three sets of standards consisting of .10, 20, and 30 ng mercury ($HgCl_2$) in triplicate were interspersed within a given sample run.

Calibration

During the analyses, aliquots of National Bureau of Standards Orchard Leaves No. 1571 were routinely analyzed for each element (Table 2). Similar standardizations conducted by Knauer (1972) during his study of metals in the northern anchovy, *Engraulis mordax*, and an interlaboratory calibration using both the destructive analytical techniques with atomic absorption spectrophotometry and non-destructive activation analysis (Knauer 1972; Goldberg 1972), indicate that our standardizations compare well with other laboratory analyses for these elements (Table 2).

[3]Reference to trade names does not imply endorsement by the National Fisheries Service, NOAA.

TABLE 2.—Comparative standardizations of elemental concentrations in National Bureau of Standards Orchard Leaves No. 1571 in micrograms per gram (Hg in nanograms per gram).

Laboratory	Hg $\bar{x}$	Hg c.v.	Cu $\bar{x}$	Cu c.v.	Ni $\bar{x}$	Ni c.v.	Ag $\bar{x}$	Ag c.v.	Cd $\bar{x}$	Cd c.v.	Pb $\bar{x}$	Pb c.v.
National Bureau of Standards	155	± 15	12.0	± 0.3	1.3	± 0.2			0.11	± 0.02	45.0	± 3.0
Hopkins Marine Station[1]												
Knauer	160	± 17	12.0	± 1.0	0.6	± 0.3	<0.05		0.21	± 0.1	41.0	± 3.8
Gilmartin and Revelante	166	± 22	10.0	± 1.0	2.3	± 0.4	0.15	± 0.04	0.30	± 0.1	41.0	± 4.3
Skidaway[1]	150	± 30	9.9	± 0.5					0.32	± 0.06	40.9	± 3.3
Battelle-Northwest[2]	180	± 20	11.2	± 1.3			<0.02		0.23	± 0.06		
Puerto Rico Nuclear Center[2]	170	± 50	11.8								[1]50.0	

[1]Flameless atomic absorption spectroscopy.
[2]Neutron activation analysis.

RESULTS

The six metals studied are considered from the viewpoint of differences in concentrations between the two species, variable concentrations in different tissues, and seasonal variations. Results are expressed in $\mu g\ g^{-1}$ wet weight for all elements except mercury, which is expressed in $ng\ g^{-1}$ wet weight. These can be converted to dry weight using the factors presented in Table 3.

Mercury

The seasonal distribution of mercury in various tissues in both the sardine and anchovy ranged from 5 to 610 $ng\ g^{-1}$ wet weight (Table 4). During

TABLE 3.—Sample size, length data, and wet:dry ratio for sardine and anchovy tissues analyzed for metal concentrations.

Date	n	Length (cm) Mean	Range	Wet:dry weight ratios Skin	Gills	Muscle	Digest.	Liver	Kidney	Gonad	Brain
Sardine:											
9 June 72	6			2.18	3.81	3.79	3.90	2.80			
10 July 72	6	12.90	12.7-13.2	1.38	4.57	3.71	3.22	3.56			
17 Aug. 72	6	16.14	15.5-16.5	2.36	4.62	4.04	4.48	3.47			
29 Sept. 72	5	15.28	14.6-16.0	1.53	4.30	3.54	2.43	3.76			
31 Oct. 72	6	17.85	7.0-18.8	1.56	4.36	3.55	2.33	4.64			
5 Dec. 72	6	15.08	14.4-16.0	1.82	4.14	3.86	4.00	1.67			
28 Mar. 73	6	17.69	16.7-18.3	1.88	5.31	3.94	4.45	4.04			
4 May 73	16	15.29	14.7-16.0	1.87	4.34	3.90	4.49	3.58	3.20	3.78	
8 May 73	51	15.39	14.1-17.4	1.81	4.44	4.10	4.58	3.47	2.87	3.99	3.94
24 May 73	49	14.93	14.1-15.8	2.05	4.09	3.88	4.40	3.41	3.78	4.69	4.23
6 June 73	45	15.54	14.6-16.6	2.23	4.17	3.70	3.54	3.55	3.51	3.69	4.04
Mean				1.88	4.38	3.82	3.80	3.45	3.34	4.04	4.07
Anchovy:											
9 June 72	6			1.73	3.92	3.47	2.65	2.56			
10 July 72	6	12.67	12.4-13.0	1.68	4.96	3.74	2.22				
17 Aug. 72	6	14.50	13.6-15.8	1.34	4.12	3.12	1.96	2.81			
3 Oct. 72	6	13.98	13.3-14.8	1.30	4.75	3.23	2.06	3.32			
31 Oct. 72	6	14.52	14.2-14.8	1.50	4.86	2.97	2.58	3.99			
6 Dec. 72	6	14.43	14.2-14.6	1.36	5.64	3.49	3.33	3.70		4.72	
29 Mar. 73	6	14.40	14.1-14.6	1.87	6.92	4.53	3.41	3.84			
24 May 73	60	13.37	12.2-14.8	1.81	3.70	3.89	4.16	3.35	3.19	4.09	3.81
6 June 73	52	14.75	13.2-16.6	2.52	4.10	4.03	5.21	3.46	4.32	3.56	4.06
Mean				1.68	4.77	3.61	3.06	3.38	3.76	4.12	3.94

TABLE 4.—Concentrations of total mercury ($ng\ g^{-1}$ wet weight) in tissues of sardine *Sardina pilchardus* and anchovy *Engraulis encrasicholus* from the Adriatic Sea.

Date	Skin[1]	Gills	Muscle	Digest.[1]	Liver	Kidney	Gonads	Brain	Tot. fish
Sardine:									
9 June 72	70		105	ND					80
10 July 72	35		40	ND					30
17 Aug. 72	10		135	90					110
29 Sept. 72	25		95	60					75
31 Oct. 72	35		115	110					105
5 Dec. 72	5		85	80					65
28 Mar. 73	105	25	115	100	155				100
4 May 73	30	35	80	80	160	260	20	15	60
8 May 73	60	35	90	115	215	455	40	35	85
24 May 73	45	30	95	60	210	220	30	35	80
6 June 73	70	45	120	115	210	330	75	35	165
Mean	45	35	100	75	190	315	40	30	85
Anchovy:									
9 June 72	75		120	ND					105
10 July 72	40		75	125					75
17 Aug. 72	55		215	ND					190
3 Oct. 72	ND		165	ND					140
31 Oct. 72	200		155	ND					160
6 Dec. 72	190		215	185					165
29 Mar. 73	70	25	85	140	215	295			65
24 May 73	80	45	70	110	255	370	35	25	75
6 June 73	145	60	175	215	415	610	80	35	170
Mean	95	45	140	85	295	425	60	30	125

[1]ND = not detected.

the early part of the study period, insufficient material was available to determine levels in certain tissues, but very significant species differences were noted between fish collected at the same point in time. In most instances mercury was present in greater amounts in specific anchovy tissues and the mean whole fish concentration was about 50% higher in anchovies.

The highest concentrations of mercury were noted in the liver and kidneys. On an annual mean basis the skin and gills of the sardine contained relatively low levels of mercury relative to other body tissues. In contrast, anchovy skin contained higher levels, especially during winter months when concentrations of 190-200 ng g^{-1} wet weight were observed. The greatest seasonal variation occurred in the digestive tract, where mercury ranged from not detected to 215 ng g^{-1}.

Copper

Copper levels ranged from 0.6 to 8.5 $\mu g\ g^{-1}$ wet weight (Table 5). As with mercury, anchovy tissues often contained higher concentrations of copper than corresponding sardine tissues, although the differences between the two species were not nearly so pronounced. The highest concentrations were observed in the liver of both species, with the skin of the anchovy consistently having significantly higher concentrations of copper than that of the sardine. On occasion the digestive tract of the anchovy contained up to 5.4× the concentrations in comparable sardine samples.

TABLE 5.—Concentrations of copper ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle	Digest.	Liver	Total fish
Sardine:						
9 June 72	1.8	1.0	0.9	1.4	3.7	1.09
10 July 72	1.5	0.9	1.2	1.5	—	1.05
17 Aug. 72	1.2	0.6	0.9	1.0	2.5	0.96
29 Sept. 72	1.2	0.7	1.1	0.8	3.4	0.94
31 Oct. 72	0.9	0.7	0.9	1.4	2.1	0.97
5 Dec. 72	1.9	1.1	1.0	1.7	3.5	0.98
Mean	1.4	0.8	1.0	1.3	3.0	1.0
Anchovy:						
9 June 72	1.8	0.8	0.7	1.7	4.0	1.05
10 July 72	2.0	0.9	0.6	1.9	2.8	0.96
17 Aug. 72	3.1	0.8	0.8	2.9	3.9	1.09
3 Oct. 72	[1]17.5	0.8	0.8	4.3	3.2	1.52
31 Oct. 72	2.8	0.8	0.8	3.3	1.0	1.14
6 Dec. 72	2.5	0.6	0.6	1.5	8.5	0.98
Mean	2.4	0.8	0.7	2.6	3.9	1.1

[1]Suspect value — excluded from mean.

Nickel and Silver

In contrast with mercury and copper, the concentrations of nickel and silver rarely showed significant differences between the two species. Nickel was consistently detected in muscle tissue whereas silver was not, and nickel was occasionally observed in anchovy livers but not sardine (Tables 6, 7). Although data indicate higher concentrations in the gills and skin, these may be artifacts introduced by scatter caused by bone matrix in the gills and clays in the skin. The concentrations reported are therefore considered maximal estimates.

TABLE 6.—Concentrations of nickel[1] (μg^{-1} wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle[2]	Digest.	Liver[2]	Total fish
Sardine:						
9 June 72	1.3	0.9	ND	0.3	ND	0.54
10 July 72	2.7	0.8	0.5	0.3	ND	0.53
17 Aug. 72	2.2	0.5	ND	0.1	ND	0.56
29 Sept. 72	2.9	0.5	0.3	1.0	ND	0.56
31 Oct. 72	1.5	0.7	0.3	ND	ND	0.59
5 Dec. 72	4.5	1.0	ND	0.6	ND	0.59
Mean	2.5	0.7	0.2	0.4	ND	0.6
Anchovy:						
9 June 72	1.7	0.9	0.3	0.4	ND	0.56
10 July 72	1.7	0.6	0.4	1.7	0.3	0.74
17 Aug. 72	1.1	0.2	0.3	0.6	0.2	0.58
3 Oct. 72	1.4	0.8	0.3	0.3	ND	0.46
31 Oct. 72	3.4	0.7	0.2	0.6	1.1	0.64
6 Dec. 72	5.8	0.9	0.2	0.9	ND	0.85
Mean	2.5	0.7	0.3	0.8	0.3	0.6

[1] = maximal estimates due to matrix problem.
[2]ND = not detected.

TABLE 7.—Concentrations of silver[1] ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin[2]	Gills	Muscle[2]	Digest.[2]	Liver[2]	Total fish
Sardine:						
9 June 72	0.3	0.1	ND	ND	ND	<0.09
10 July 72	0.3	0.1	ND	ND	ND	<0.08
17 Aug. 72	0.4	0.2	ND	ND	ND	<0.10
29 Sept. 72	0.6	0.1	ND	ND	ND	<0.10
31 Oct. 72	0.2	0.2	ND	ND	ND	<0.09
5 Dec. 72	0.7	0.2	ND	<0.1	ND	0.10
Mean	0.4	0.2	ND	ND	ND	0.1
Anchovy:						
9 June 72	0.4	0.1	ND	ND	ND	<0.08
10 July 72	0.5	0.1	ND	ND	ND	<0.08
17 Aug. 72	0.4	0.2	ND	ND	ND	0.08
3 Oct. 72	0.2	0.2	ND	ND	ND	0.09
31 Oct. 72	ND	0.2	ND	ND	ND	<0.07
6 Dec. 72	0.5	0.1	ND	<0.1	ND	<0.10
Mean	0.3	0.2	ND	ND	ND	0.1

[1] = maximal estimates due to matrix problem.
[2]ND = not detected.

Cadmium

Concentrations of cadmium in various anchovy and sardine tissues ranged from less than 0.1 to 1.4 $\mu g\ g^{-1}$ wet weight (Table 8). No significant difference was observed between the two species, except for the anchovy liver which had consistently higher levels than all other tissues. Higher concentrations occurred in the skin of both species.

Lead

Lead concentrations in sardine tissues paralleled those in the anchovy (Table 9). High concentrations occurred in the gills and skin of both species, and a tendency for higher levels in anchovy liver late in the year was observed. The lowest values tended to occur in muscle tissue, with seasonal means ranging from not detected to 1.2 $\mu g\ g^{-1}$ wet weight.

TABLE 8.—Concentrations of cadmium ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle[1]	Digest.[1]	Liver[1]	Total fish
Sardine:						
9 June 72	0.2	0.2	<0.1	0.1	0.2	0.11
10 July 72	0.3	0.2	<0.1	0.3	ND	0.11
17 Aug. 72	0.4	0.1	ND	ND	0.4	0.10
29 Sept. 72	0.5	0.1	ND	ND	0.2	0.09
31 Oct. 72	0.3	0.1	ND	0.1	0.1	0.10
5 Dec. 72	0.5	0.2	ND	0.3	0.1	0.11
Mean	0.4	0.2	<0.1	0.1	0.2	0.1
Anchovy:						
9 June 72	0.4	0.2	<0.1	0.2	0.9	0.16
10 July 72	0.3	0.3	0.1	0.4	0.5	0.13
17 Aug. 72	0.5	0.3	<0.1	0.2	0.7	0.13
3 Oct. 72	0.2	0.1	ND	0.2	0.5	0.09
31 Oct. 72	0.4	0.2	<0.1	0.2	ND	0.12
6 Dec. 72	0.6	0.1	<0.1	0.2	1.4	0.20
Mean	0.4	0.2	<0.1	0.2	0.7	0.1

[1]ND = not detected.

TABLE 9.—Concentrations of lead ($\mu g\ g^{-1}$ wet weight) in tissues of sardine and anchovy from the Adriatic Sea.

Date	Skin	Gills	Muscle[1]	Digest.[1]	Liver[1]	Total fish
Sardine:						
9 June 72	4.5	3.0	0.4	ND	ND	1.23
10 July 72	4.9	4.5	0.1	ND	ND	0.94
17 Aug. 72	4.3	2.6	ND	ND	ND	0.82
29 Sept. 72	5.3	1.9	ND	2.2	ND	0.84
31 Oct. 72	3.3	2.4	ND	0.7	ND	1.38
5 Dec. 72	6.8	3.1	ND	0.3	ND	1.40
Mean	4.9	2.9	0.1	0.5	ND	1.1
Anchovy:						
9 June 72	2.7	4.3	ND	ND	ND	0.99
10 July 72	5.2	3.7	ND	0.4	ND	0.99
17 Aug. 72	5.7	3.9	ND	0.3	1.1	0.51
3 Oct. 72	1.6	2.6	ND	1.3	1.5	0.73
31 Oct. 72	7.0	3.1	1.2	0.7	3.4	1.16
6 Dec. 72	6.5	3.9	0.3	0.4	[2]11.0	1.37
Mean	4.8	3.6	0.3	0.5	1.2	1.0

[1]ND = not detected.
[2]Suspect value — excluded from mean.

DISCUSSION

The six heavy metals considered during this study fall into two groups with regard to distribution in tissues and differences in concentrations between the two species: nickel, silver, cadmium, and lead, with no major interspecific differences and the highest concentrations occurring in the skin and gills, and mercury and copper, with marked interspecific differences and the highest concentrations occurring in internal tissues.

The highest concentrations of nickel, silver, cadmium, and lead were observed in the skin and gills, perhaps associated with adsorption. A significant interspecific difference was observed with nickel and lead, with these elements being nondetectable in the sardine liver but frequently being detected in anchovy liver, suggesting a difference in feeding habits and/or migration routes of the two species.

A tendency for increasing lead concentrations in the skin during winter was evident, related perhaps to wind-induced roiling of sediments into the water column during this period. The northern Adriatic is known to have relatively high concentrations of metal pollutants in the bottom sediments (Selli et al. 1972; Štirn pers. commun. 1973). A comparison of the concentrations of these metals in various tissues of the Adriatic and northern anchovies (Table 10) indicated that both nickel and cadmium occurred at approximately the same level. The relatively high nickel concentrations reported for the skin of the Adriatic anchovy could be an artifact introduced by analytical techniques (Table 2).

Copper and mercury showed a very different distribution pattern, with concentrations highest in the digestive tract and liver of the two clupeids, and seasonal means 2 to 3× greater than in the skin and gills, suggesting that ingestion may be the primary entry route into the organism. Concentrations in anchovy muscle tissue were markedly higher than in the sardine, contrasting with Establier's (1972) report that there were no differences in mercury concentration between these species off northwest Africa.

TABLE 10.—Mean elemental concentrations in *Engraulis mordax* collected from Monterey Bay, Calif. (Pacific) from Knauer (1972) and in *E. encrasicholus* from Rovinj, Yugoslavia (Adriatic) (mercury: ng g^{-1} wet weight: other elements: $\mu g\ g^{-1}$ wet weight).

Element	Location	Skin	Gills	Muscle	Digest.	Liver	Gonads
Mercury	Pacific	10	30	40		90	15
	Adriatic	95	45	140		295	55
Copper	Pacific	1.6	3	1.6	5	3	2
	Adriatic	2.4	0.8	0.7	2.6	3.9	
Nickel	Pacific	0.4	0.7	ND	1.1	ND	ND
	Adriatic	2.5	0.7	0.3	0.8	0.3	
Silver	Pacific	0.2	0.4	0.01	0.07	ND	0.4
	Adriatic	0.3	0.2	ND	ND	ND	
Cadmium	Pacific	0.2	0.3	0.03	2.8	1	0.3
	Adriatic	0.4	0.2	<0.1	0.2	0.7	
Lead	Pacific	3	4.8	0.2	1.2	ND	0.2
	Adriatic	4.8	3.6	0.3	0.5	1.2	

ND = not detected.

The calculated concentrations of mercury in the whole sardine range from 100 to 645 ng g^{-1} dry weight, with a seasonal mean of 320. These values compare favorably with the 580 ng g^{-1} dry weight reported by Ui (1971) for sardine collected in coastal waters 2 to 3 km north of Porto Corsini, on the Italian side of the northern Adriatic. Levels of mercury found in the northern Adriatic anchovy were relatively high when compared with levels in the same or similar species in other parts of the world. Mean concentrations of 140 ng g^{-1} wet weight were found in muscle tissue, and values in excess of 200 ng g^{-1} were observed (Table 4). The same species from the Gulf of Cádiz and off northwestern Africa contained 60 and 50 ng g^{-1} wet weight respectively (Establier 1972); and the northern anchovy, *Engraulis mordax*, occupying the same ecological niche (see Baxter 1967), contained concentrations in muscle tissue averaging 40 ng g^{-1} wet weight (Knauer and Martin 1972). These last data are directly comparable, since the analyses were conducted in the same laboratory using the same techniques and equipment.

Short-lived, low trophic level fish such as the anchovy have a tendency to concentrate low levels of mercury relative to longer-lived higher order carnivores, e.g. tunas and billfishes (Rivers et al. 1972), yet the higher concentrations of mercury in internal tissues indicate an accumulation in the Adriatic anchovy as well. However, it should be noted that the source of such mercury is not necessarily lower trophic level organisms. On entering the sea, mercury is immediately bound to proteinaceous materials, and if not adsorbed or absorbed by organisms, is often present in detritus/matrixlike suspended matter (see Keckes and Miettinen 1972, for review). Since massive amounts of suspended matter are found in feeding areas, filter feeders cannot avoid ingesting it (Leong and O'Connell 1969).

While mercury input to the sea results from a combination of natural processes, such as weathering and atmospheric fallout, and from various anthropogenic processes, a number of recent studies have focused on the pollution resulting from increasing urbanization and industrialization along the northern Adriatic coast, in particular within the Po River watershed (Štirn 1965, 1970; Majori, Morelli, Diana, and Rausa 1967; Majori, Rausa, Morelli, and Diana 1967; Majori et al. 1968; Majori 1968; Panella 1968a, b, 1970; Cescon and Grancini 1971; General Fisheries Council for the Mediterranean 1972). Three factories in northern Italy use the same acetaldehyde process as the Japanese Minimata plant (Ui and Kitamura 1971), and two of these are located on the coast at Ravenna and Venice, offshore of which are the spring spawning grounds of the anchovy (Štirn 1969). In addition, the wintering grounds of the anchovy lie to the south, in an area influenced by the Po River (Štirn 1969; Piccinetti 1970).

The rate of mercury elimination by fish is slow, e.g. 267-700 days (Keckes and Miettinen 1972). This time scale easily spans annual migrations encompassing the northern Adriatic and emphasizes the necessity for international consideration of the potential pollution of the region. Although the levels of mercury observed in this study are well within the tolerances established by most countries (e.g. 200 ng g^{-1} muscle wet weight in Switzerland, 500 ng g^{-1} in the United States, and 1,000 ng g^{-1} in Italy and Japan), it is likely that with increasing anthropogenic input to the northern Adriatic, concentrations will increase, perhaps to prohibitory levels. Thus it is essential that monitoring continue, especially of the clupeid *Engraulis encrasicholus*, which not only concentrates mercury to a greater degree than the sardine, but which may represent one of the few significantly underutilized fish resources of the northern Adriatic Sea.

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THE CORRELATION BETWEEN NUMBERS OF VERTEBRAE AND LATERAL-LINE SCALES IN WESTERN ATLANTIC LIZARDFISHES (SYNODONTIDAE)[1]

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ABSTRACT

The 10 species of Synodontidae in the western Atlantic have a positive correlation between numbers of vertebrae and pored lateral-line scales. A ratio of close to 1:1 exists for all species, with individuals having from four more to two fewer scales than vertebrae, and the majority having at least one more scale than vertebrae. Geographic variation is suggested by vertebral counts of four species, and possible taxonomic heterogeneity is indicated by the counts of a fifth species. Scale counts are bilaterally symmetrical in most individuals and differ by one scale in most of the rest. Vertebral and scale counts are given for type specimens at the U.S. National Museum of Natural History.

The principal purpose of this paper is to describe the complements and correlations of vertebrae and pored lateral-line scales in samples of the western Atlantic species of Synodontidae, as a contribution to the knowledge of their morphology and to facilitate specific identification of various life history stages.

The species of the lizardfish family Synodontidae have been distinguished in part by differences in number of pored lateral-line scales for juvenile and adult stages (e.g. Norman 1935; Anderson et al. 1966a, b) and in number of myomeres for larval and prejuvenile stages (Gibbs 1959). Accurate scale counts may be impossible in damaged or small specimens, and myomeres are difficult to count in all but young stages. Numbers of myomeres in individual fish are equal or about equal to numbers of vertebrae, but species complements of vertebrae in synodontids have not been analyzed or utilized.

For the 10 species of lizardfishes in the western Atlantic, we have determined that:

1) complements of vertebrae and intraspecifically variable with a relatively normal distribution around the mean (as occurs with complements of scales and myomeres);
2) numbers of vertebrae have a positive correlation to numbers of pored lateral-line scales;
3) in individuals, the number of vertebrae is in a ratio of close to 1:1 to the number of pored lateral-line scales, with scales ranging from two less to four more than vertebrae in our samples, and the majority of specimens of all species having more scales than vertebrae.

MATERIALS AND METHODS

Specimens used in this study are in the collections of the Florida State Museum (formerly in the Tropical Atlantic Biological Laboratory, Miami, Fla. and the Biological Laboratory at Brunswick, Ga.), the Academy of Natural Sciences of Philadelphia, and the U.S. National Museum of Natural History (USNM). Some of the specimens used in these analyses were specifically selected from material previously reported by us (Anderson et al. 1966a) to encompass high and low values in scale counts of the various species or to obtain geographic coverage.

Identifications, measurements, and counts were made as described by Anderson et al. (1966a) with the following additions:

Vertebrae—counted from the anteriormost centrum articulating with the occipitals to and

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including the triangular-shaped last or ultimate centrum articulating with the hypural bones. All counts were made from X rays. Vertebral counts for individual specimens are used twice in correlations with paired (bilateral) scale counts. Specimens with obvious abnormalities in vertebral structure were not included in the tabulations.

Pored lateral-line scales—counted from the first pored scale in the lateral line to and including the last pored scale in the lateral line, lateral to the median base of the caudal-fin rays. Specimens with one or more scales missing from the lateral line were included in the tabulations, if the position of the scale pockets or the remaining scales were adequate to allow an accurate reconstruction. Bilateral counts were made for each specimen, and the counts for both sides of each fish were included in all tables and in the correlations with vertebrae. The term scale or scales refers specifically to pored scales in the lateral line.

RESULTS

Vertebrae

Vertebrae in our samples of the 10 western Atlantic species range from 44 to 62. We know of one higher count for a synodontid—the holotype of *Synodus ulae* from Hawaii has 64 vertebrae. Statistics based on vertebral samples for the western Atlantic species are listed in Table 1 and graphically depicted in Figure 1. Samples of at least six of the species are probably too small (and possibly too heterogeneous) to adequately define the ranges of vertebral complements for these species. This is obvious from comparison of skewedness of the range and/or standard deviations and the relatively large values of the standard errors. For the two species for which we have the largest and most reliable samples, *Sy. foetens* and *Sy. intermedius*, the relation of variance to meristic complement is similar to that we have noted in some other fish families—the species with the larger number or larger range of elements has the greater variance. The extremely high variance and extensive range of vertebrae in *Saurida caribbaea* suggest a taxonomic or ontogenetic problem as yet unidentified.

Intraspecific geographic variation in these lizardfishes has not been investigated, but our limited samples of four of the species suggest that it may exist. *Synodus intermedius* appears to have fewer vertebrae in tropical continental waters and more in insular areas than in temperate and subtropical continental waters.

Area	n	$\bar{x}$
U.S.—Mexico	37	48.2
Honduras—Surinam	21	47.6
Brazil	25	48.6

These samples are relatively homogeneous, and the means of the three samples are significantly different ($P < 0.01$, anova). *Synodus foetens* may have a parabolic cline in mean vertebral number, with lower average numbers in tropical areas and higher average numbers to the more temperate north and south.

Area	n	$\bar{x}$
U.S.—Mexico	98	59.6
Honduras—Surinam	9	58.1
Brazil	10	59.6

TABLE 1.—Statistics from numbers of vertebrae, numbers of pored lateral-line scales, and correlation coefficients of the two variates from samples of the 10 species of western Atlantic Synodontidae.

Species	Vertebrae						Scales				Correlation (*r*)
	No.	Range	Mean	SD	SE	Var.	No.	Range	Mean	Var.	
Synodus foetens	118	56-62	59.4	1.4082	0.1296	1.98	236	57-63	61.1	2.11	0.86
Synodus saurus	14	56-58	57.6	0.6667	0.1693	0.40	28	58-60	58.9	0.57	0.20
Synodus synodus	11	55-57	55.7	0.9045	0.2727	0.82	20	55-58	56.1	0.68	0.44
Synodus intermedius	85	47-50	48.2	0.7661	0.0831	0.59	170	47-51	49.1	0.94	0.76
Synodus poeyi	19	44-48	45.6	1.2996	0.2965	1.69	38	43-48	45.8	3.00	0.83
Trachinocephalus myops	11	54-57	55.4	0.9244	0.2787	0.85	22	54-58	56.4	0.92	0.37
Saurida brasiliensis	10	46-48	46.7	0.8233	0.2603	0.68	20	47-49	48.2	0.56	0.52
Saurida normani	11	49-52	50.9	1.1362	0.3423	1.30	22	52-56	54.0	1.38	0.84
Saurida suspicio	11	49-52	51.3	0.9045	0.2727	0.82	22	52-54	52.8	0.47	0.50
Saurida caribbaea	27	48-58	54.2	2.6651	0.5129	7.10	38	51-60	56.2	8.69	0.96

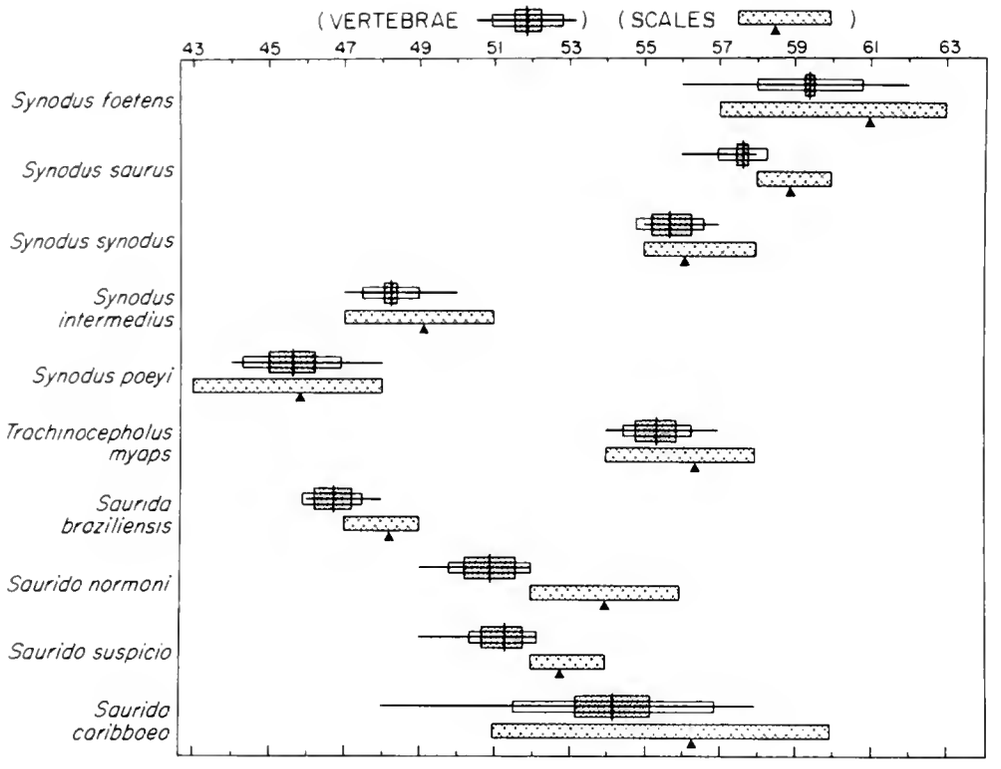

FIGURE 1.—Numbers and statistics of vertebrae and scales of the 10 species of western Atlantic Synodontidae. Vertebrae: range—horizontal line; mean—vertical line; standard deviation, one on each side of the mean—open rectangle; standard error—two on each side of the mean—shaded rectangle. Scales: range—cross-hatched bar; mean—small triangle.

Synodus saurus from the eastern Atlantic (5 specimens) had a range in vertebrae of 55-59, greater than the western Atlantic (14 specimens) vertebrae range of 56-58. *Trachinocephalus myops* had varying but similar vertebral ranges in small samples encompassing its extensive geographic range.

Area	n	$\bar{x}$	*Range*
U.S.—Brazil	11	55.4	54-57
Nigeria	1	55.0	55
Philippines	7	53.1	52-54
Hawaii	5	54.8	54-55

Abnormalities in vertebral structure (specimens not included in the tables or figure) occurred in 11 of 317 western Atlantic specimens examined. In six, pairs of vertebrae were shortened with irregular and expanded ossifications at their adjoining ends. In five, a single centrum in the caudal region was elongated and had two neural spines (in two), two hemal spines (in two), or double neural and hemal spines (in one).

Scales

Pored lateral-line scales in our samples of the 10 western Atlantic species range from 43 to 63 (Table 1). We have not confirmed any higher or lower values for these or other species of the family. Ranges in scale complements that we have confirmed for specimens from the western Atlantic, with clarification where these ranges differ from those given by Anderson et al. (1966a), are:

Synodus foetens 57-64; the range of 56-65 given by Anderson et al. was in error, as determined by our reexamination of the material originally reported. *Synodus saurus* 56-60; the range of 55-62 given by Anderson et al. included a low count for an eastern Atlantic specimen and a published but unsubstantiated high count. *Synodus synodus* 54-59. *Synodus intermedius* 47-51; the range of 45-52 given by Anderson et al. was in error, as determined by our reexamination of the material originally reported. *Synodus poeyi* 43-48. *Trachinocephalus myops* 53-59; the

range of 51-61 reported by Anderson et al. was based on previously published records from other geographic areas. *Saurida brasiliensis* 43-49; the range of 40-50 reported in Anderson et al. was based on a low count previously published and currently unconfirmable and on a high count that we have since confirmed in a specimen from the eastern Atlantic. *Saurida normani* 51-56. *Saurida suspicio* 52-54; a high count of 56 previously published has not been confirmed by us. *Saurida caribbaea* 51-60; examination of additional specimens has enlarged the range of 54-60 given by Anderson et al.

Many of the specimens used in the confirmations above are not included in Table 1, because corresponding vertebral counts were not made.

Bilateral symmetry in scale numbers characterized one-half to three-quarters of the specimens of each species. In the total sample, 62% were bilaterally symmetrical. Asymmetry appears to be random, 20% having more scales on the left side and 18% having more scales on the right side. Asymmetry was of only one scale difference in all species, except in our largest species sample. In *Sy. foetens*, which also has the greatest number of scales, of 118 specimens 3 had two more scales on one side than the other, 52 had one more scale on one side than the other, and 63 were bilaterally symmetrical.

Correlations

Frequency distributions of numbers of vertebrae and associated numbers of pored lateral-line scales are shown for the two species for which we examined the largest number of specimens, *Sy. foetens* (Table 2) and *Sy. intermedius* (Table 3). The trend of positive correlation is apparent from visual inspection of both tables. The coefficients of correlation (Table 1) document the positive nature of the correlation, *Sy. foetens* (r = 0.86) and *Sy. intermedius* (r = 0.76) (Table 1).

The same kinds of data for the other eight species are given below, with number of vertebrae separated by a hyphen from the number of scales and followed in parentheses by the frequency for that combination:

Synodus saurus, vertebrae 56-58 scales (2), 57-58(1), 57-59(4), 57-60(1), 58-58(7), 58-59(8), 58-60(5). *Synodus synodus*, 55-55(3), 55-56(7), 56-55(1), 56-56(1), 56-57(2), 57-55(1), 57-56(2), 57-57(2), 57-58(1). *Synodus poeyi*, 44-43(4), 44-44(2), 44-45(3), 44-46(1), 45-43(1), 45-44(2), 45-45(1), 45-46(2), 46-44(1), 46-45(2), 46-46(2), 46-47(9), 47-48(4), 48-48(4). *Trachinocephalus myops*, 54-56(3), 54-57(1), 55-54(1), 55-55(2), 55-56(3), 55-57(2), 56-56(1), 56-57(5), 56-58(2), 57-56(1), 57-57(1). *Saurida brasiliensis*, 46-47(4), 46-48(6), 47-49(6), 48-48(3), 48-49(1). *Saurida normani*, 49-52(3), 49-53(1), 50-53(2), 51-53(1), 51-54(3), 51-55(4), 52-54(2), 52-55(5), 52-56(1). *Saurida suspicio*, 49-52(1), 49-53(1), 51-52(7), 51-53(3), 52-53(7), 52-54(3). *Saurida caribbaea*, 48-51(2), 49-51(3), 50-52(2), 52-53(3), 52-54(1), 54-55(1), 54-56(1), 54-58(2), 55-57(2), 55-58(3), 55-59(5), 56-57(3), 56-58(4), 56-59(1), 57-59(2), 58-60(2).

TABLE 2.—Frequency distributions of numbers of vertebrae and pored lateral-line scales in 118 *Synodus foetens*.

Scales	Vertebrae						
	56	57	58	59	60	61	62
63	—	—	—	—	10	25	2
62	—	—	—	4	57	15	2
61	—	—	4	15	21	4	—
60	—	1	19	14	2	—	—
59	4	15	5	2	2	—	—
58	4	7	—	1	—	—	—
57	—	1	—	—	—	—	—

TABLE 3.—Frequency distributions of numbers of vertebrae and pored lateral-line scales in 85 *Synodus intermedius*.

Scales	Vertebrae			
	47	48	49	50
51	—	1	9	2
50	—	5	37	2
49	2	44	16	—
48	26	21	—	—
47	2	3	—	—

The correlation coefficients of the samples for all species are positive, ranging from 0.96 for *Sa. caribbaea* to 0.20 for *Sy. saurus* (Table 1). The species with the larger number of specimens (19 to 118) generally had the higher correlation coefficients (r 0.76 to 0.96). Of the species with a lesser number of specimens (11 to 14), one had a high positive value (0.84), and the others were low (0.20 to 0.52). We suspect that the relatively low value of positive correlation for five of the species is due to the small and somewhat heterogeneous samples used for these species.

Statistics describing the samples of vertebrae and scales for each species (from Table 1) are illustrated in Figure 1. The nature of positive

correlation of vertebrae and scales for the 10 species is apparent in this figure.

The ratio of scales to vertebrae is nearly 1:1 for the 10 species, but in each species the total number of scales averages slightly more than the total number of vertebrae (50% or more of the scale counts in any species are greater than the vertebral counts). In species of *Saurida* the number of scales averages from one to three more than the number of vertebrae and ranges from an equal number of each to four more scales than vertebrae. In species of *Synodus* and in *Trachinocephalus* the number of scales averages one or two more than the number of vertebrae and ranges from two fewer to three more scales than vertebrae. Of 118 *Sy. foetens* 10% had three more scales than vertebrae, 57% had two more scales, 27% had one more, 5% had an equal number, and 1% had one less scale than vertebrae.

The positional relationship of scales to vertebrae in lateral aspect was investigated. In a *Sy. foetens* with 62 pored lateral-line scales on each side and 60 vertebrae, pins were inserted at the posterior margins of certain numbered lateral-line scales on the left side, and the specimen was X-rayed. The first scale was lateral to the junction of the 4th and 5th centra, the 30th scale was lateral to the junction of the 32nd and 33rd centra, the 60th scale was lateral to the last centrum, and the last scale was lateral to the posterior ends of the hypural bones and overlapping anterior ends of the median caudal-fin rays. Similarly, in a *Sy. intermedius* with 49 scales on each side and 48 vertebrae the first scale was lateral to the 4th centrum, the 47th scale was lateral to the 48th centrum, and the last scale was lateral to the posterior ends of the hypural bones.

DATA ON TYPE SPECIMENS AT USNM

Counts of vertebrae and pored lateral-line scales on type specimens of 12 nominal species of Synodontidae in the U.S. National Museum of Natural History are recorded here for use in future studies. The four data items following the collection number for each type specimen are, in sequence, number of vertebrae, number of left-side scales, number of right-side scales, and standard length in millimeters:

Synodus binotatus Schultz, holotype USNM 140801, 53-54-ca. 54-86.5. *Synodus cinereus* Hildebrand, holotype USNM 53079, 57-58-59-112. *Synodus englemani* Schultz, holotype USNM 140815, 59-60-60-104. *Synodus evermanni* Jordan and Bollman, one of 11 syntypes USNM 41144, 47-48-48-142. *Synodus jenkinsi* Jordan and Bollman, holotype USNM 41171, 60-ca. 60-61-282. *Synodus lacertinus* Gilbert, holotype USNM 44300, 61-63-62-129. *Synodus marchenae* Hildebrand, holotype USNM 120171, 60-62-62-50.5. *Synodus sechurae* Hildebrand, holotype USNM 127829, 57-58-58-130. *Synodus simulans* Garman, paratype USNM 153607, 60-ca. 62-ca. 61-ca. 45. *Synodus ulae* Schultz, holotype USNM 52671, 64-ca. 63-ca. 63-177. *Saurida eso* Jordan and Herre, holotype USNM 57847, 59-62-61-290. *Saurida normani* Longley, holotype USNM 107330, 52-52-53-320.

In these type specimens the ratio of nearly 1:1 for number of vertebrae and scales suggests a positive correlation of these two variates in the species that they represent.

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ACUTE TOXICITY OF AMMONIA TO SEVERAL DEVELOPMENTAL STAGES OF RAINBOW TROUT, *SALMO GAIRDNERI*

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ABSTRACT

Median tolerance limits derived from 24-h bioassays demonstrated that fertilized eggs and alevins of rainbow trout, *Salmo gairdneri*, were not vulnerable to 3.58 ppm un-ionized ammonia at 10°C (pH 8.3). At the end of yolk absorption, rainbow trout fry increased in susceptibility dramatically; their median tolerance limit values were about 0.072 ppm, the same as for adult trout. Fertilization of eggs was not prevented in un-ionized ammonia solutions up to 1.79 ppm, the highest exposure tested.

Much information is available on the toxicity of ammonia to juvenile and adult trout, but the paucity of information on the toxicity of ammonia to fertilized eggs and larvae of teleosts is surprising since these life stages are often assumed to be relatively sensitive. Several studies have examined ammonia toxicity to adult trout (Lloyd 1961; Ball 1967; Wilson et al. 1969), including the effects of increased ammonia toxicity to trout at lower oxygen levels (Downing and Merkens 1955) and decreased toxicity at higher carbon dioxide levels (Lloyd and Herbert 1960). Temperature, oxygen, pH, carbon dioxide, and bicarbonate alkalinity influence the toxicity of ammonia and are discussed in a report by the European Inland Fisheries Advisory Commission (1970). Exposure of juvenile or adult salmonids to ammonia has been associated with decreased growth (Brockway 1950; Burrows 1964; Larmoyeux and Piper 1973), gill damage (Burrows 1964; Reichenbach-Klinke 1967), and other sublethal physiological effects (Reichenbach-Klinke 1967; Fromm and Gillette 1968; Lloyd and Orr 1969), and similar effects may occur with salmonid eggs and alevins. Exposure to ammonia has also been associated with increased incidence of disease in juvenile and adult salmonids (Burrows 1964; Larmoyeux and Piper 1973) and in salmonid alevins (Wolf 1957).

The only study of toxicity of ammonia to eggs and larvae (Penaz 1965) involved three stages of eggs and two stages of yolk fry of *Salmo trutta*. Penaz observed an increase in sensitivity of the eggs with age to brief (120 min) exposures to ammonia at pH 8 and temperatures of 5.68° to 3.56°C. A similar pattern was observed with longer exposures (10 h) of newly hatched and 12-day-old alevins to ammonia at pH 8 and temperatures of 11° and 16.9°C. The early eggs were resistant to the highest dose he tested—50 mg/liter of un-ionized ammonia. These data suggest changes in sensitivity with development, but the changes in lengths of exposure and temperature make it difficult to compare differences between eggs and alevins.

We used a series of bioassays to determine the stage of development at which eggs and larvae of rainbow trout, *Salmo gairdneri*, were most susceptible to acute ammonia toxicity. Such information is needed to establish realistic limits for survival of eggs and larvae in both natural and hatchery environments. Knowledge of concentrations of ammonia that may limit survival is particularly important in hatchery operations where it is advantageous to maintain the greatest density of fish and eggs per unit water flow.

MATERIALS AND METHODS

Freshly fertilized rainbow trout eggs were obtained from Bowden National Fish Hatchery, W.V., (courtesy of the U.S. Bureau of Sport Fisheries and Wildlife) and transported to the laboratory within 6 h.

About 2,000 of the eggs were poured under water into 4-inch-square trays with nylon screen bottoms at about 25 to 35 eggs per tray. For incubation the trays were put into a 10°C water

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bath that recycled through both charcoal and a gravel bacterial filter at a rate of 3 gallons/min. Ammonia levels were measured periodically and never attained 0.1 ppm. All ammonia analyses were made by separating ammonia by diffusion (Conway and Cooke 1939) and followed by nesslerization of the separated ammonia. For the ammonia bioassays, the small trays were transferred directly to the experimental medium. By conducting the bioassays in the same trays in which the eggs or larvae were incubated, we did not have to pipette them to other containers—a process that might have injured them.

Two series of duplicated ammonia toxicity bioassays were conducted according to standard procedures outlined by Doudoroff et al. (1951) and results were expressed as 24-h median tolerance limits (24-h TLm)[3]. The bioassays were conducted every 4 to 7 days from fertilization to the completion of yolk sac absorption. Toxicity of ammonia to adult rainbow trout (length 7-9 inches) was also measured with static bioassays (12 fish per concentration tested, 1 fish per 10-liter aquarium) at the same water temperature and pH used with the eggs and larvae.

All bioassays were conducted in aged tap water (total hardness 5.94 ppm as calcium carbonate at pH 7.8) adjusted to pH 8.3 with tris buffer (final concentration 0.05 M). Ammonia, in the form of ammonia sulfate, was added to arrive at the various test concentrations. The resulting conditions made the ammonia toxicity assays more severe than would normally be encountered because the toxicity of ammonia increases as pH increases due to the conversion of ionized NH_4^+ into the un-ionized NH_3 form. At 10°C and pH 8.3, 3.58% of the ammonia in water is un-ionized, considerably more than the 0.19% un-ionized ammonia at pH 7 (Trussell 1972).

Since the un-ionized form of ammonia has been identified as the toxic form, we report our results in units of un-ionized ammonia rather than total ammonia.

Several water quality parameters were measured at the beginning and end of the bioassays, since changes could affect the results. Ammonia levels never dropped below 93% of the initial bioassay concentrations during the course of the 24-h experiments. Very low levels of un-ionized ammonia (0.011 ppm) were detected in the control exposures after 24 h. The tris buffer prevented any changes in pH from occurring during the 24-h tests. Dissolved oxygen remained above 91% saturation in the shallow egg-alevein bioassay containers and above 88% saturation in the adult bioassays (measured with YSI oxygen probe).[4] Carbon dioxide was not measured in any of the bioassays.

We tested the influence of ammonia on egg fertilization and viability during the water-hardening stage by exposing some eggs to ammonia at Bowden Hatchery on the day our experimental eggs were collected. Approximately 200 to 300 eggs from one female were stripped into each of several pans containing tris buffered water (pH 8.3, temperature 8°-10°C), some with added ammonia at concentrations up to 1.79 mg/liter of un-ionized ammonia. Milt from at least two young males was stripped into each pan of water and eggs 15 to 30 s later. Buss and Corl (1966) determined that fertilization must be completed within the first 1 or 2 min because the sperm are viable in water for only a few seconds. By replacing the ammonia solutions with fresh water in one-half of the pans after 2 or 3 min of ammonia exposure and in the remaining pans after 1 h, we hoped to separate the effects of ammonia on fertilization per se from the effects on the viability of the fertilized eggs during the water-hardening stage of the first hour. The effects were measured by determining the percentage of eggs that hatched.

RESULTS AND DISCUSSION

Neither fertilized eggs, embryos, nor alevins (embryo after hatching) were susceptible to a 24-h exposure of un-ionized ammonia (3.58 mg/liter) until about the 50th day of development (Figure 1). At that time, susceptibility increased dramatically and continued to increase until most of the yolk was absorbed (when alevins became fry). The median tolerance limits (24-h TLm) for 85-day-old fry were 0.068 mg/liter, slightly less than the 0.097 mg/liter value we observed for adult trout; in the bioassays for both the fry and the adults, temperature was 10°C and pH was 8.3.

Buss and Corl (1966) found that the viability of eggs of brook trout, *Salvelinus fontinalis*, and

[3]24-h TLm = the concentration resulting in 50% survival after 24-h exposures.

[4]YSI = Yellow Springs Instrument Company, Inc., Yellow Springs, Ohio. Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

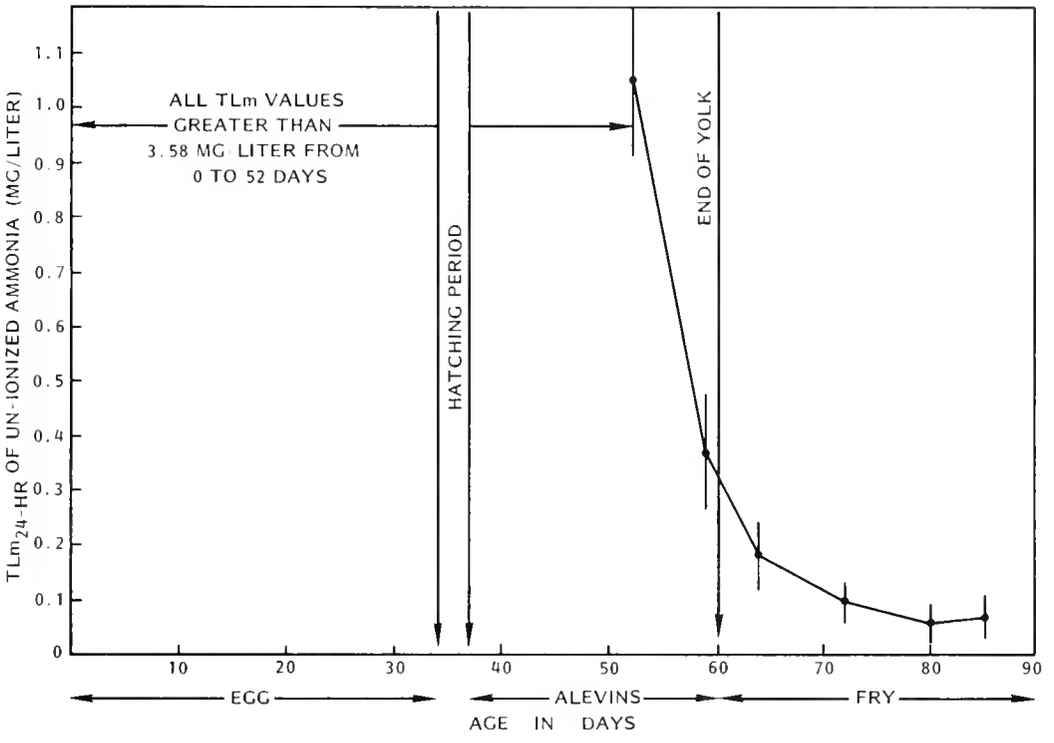

FIGURE 1.—Twenty-four-hour median tolerance limits (TLm) of un-ionized ammonia to eggs and alevins of rainbow trout (10°C, pH 8.3). Points indicate mean of two bioassays; bars indicate the range. Adult trout 24-h TLm was 0.097 mg/liter (10°C, pH 8.3).

brown trout, *Salmo trutta*, drops significantly after 15 s in water—in our experiments this was about the minimum time lapse between stripping eggs into the water and introduction of sperm. Because we did not control the time lapse before sperm introduction precisely enough, we cannot evaluate any subtle effects of ammonia on prevention of fertilization. It was obvious, however, that high ammonia concentrations did not cause complete loss of eggs or sperm (Table 1) because more than half of the eggs were fertilized at all ammonia exposures. No obvious differences in the percentages of eggs that hatched were noticed between ammonia exposures of 2 or 3 min and 1 h, even at the highest concentrations of un-ionized ammonia (1.79 mg/liter) we tested. The fertilization and water-hardening stages are similar to later stages (before 50 days of development) in their relative insensitivity to ammonia when compared with older fry with absorbed yolks (after about 60 days of development).

Our observations of great resistance of eggs and alevins of rainbow trout to ammonia toxicity are consistent with results of ammonia toxicity studies of Penaz (1965) and with other studies of other toxicants. Trout eggs and sac fry were only slightly susceptible to endrin at concentrations that seriously affected adults (Wenger 1973). Burdick et al. (1964) observed that a high proportion of lake trout, *Salvelinus namaycush*, fry from normal appearing eggs containing 2.95 ppm DDT or more died. The sensitive fry died at the completion of yolk absorption when feeding would normally begin. Eggs of "common trout" were less susceptible to anionic detergent toxicity (sodium alkylsulphate) than alevins, whose sensitivity continued to increase for 6 wk (Wurtz-Arlet 1959). Eggs of two salmonids were about one-tenth as sensitive to a commercial formulation of rotenone and derivatives as fry at the same temperature (Garrison 1968). A study of zinc toxicity by Skidmore (1965) showed that eggs of zebrafish, *Brachydanio rerio*, were relatively less susceptible than newly hatched fish.

It appears then that eggs and developing embryos are resistant to several toxicants, including ammonia. One obvious explanation for the resis-

TABLE 1. — Effect of ammonia on fertilization.

Concentration of un-ionized ammonia	Percentage[1] hatch at exposure of	
	2-3 min	1 h
0 mg/liter	66.8	68.4
0.0358 mg/liter	74.3	70.1
1.79 mg/liter	58.2	68.8

[1]Percentage hatch of each group of 250 eggs.

tance may be the protection afforded the embryo by the surrounding egg membranes which separate the internal from the external environment. However, in a second study of zinc toxicity to zebrafish embryos, Skidmore (1966) found no evidence of protection of the embryo by the egg membranes. He found that embryos with ruptured outer membranes actually survived longer in a zinc sulphate solution than embryos of the same age with an intact membrane. If the outer egg membrane impermeability were a major factor in preventing ammonia toxicity, all alevins would be instantly vulnerable at hatching. No sudden susceptibility to toxicants in newly hatched fish was observed in this study or in several others.

We can see no satisfactory explanation for the observed high resistance to ammonia and other toxicants during early developmental stages of teleosts. The higher resistance of sac fry than eggs to toxicants indicates that the egg membranes are not always protective barriers and that the explanation is more complex.

In our study, the susceptibility to ammonia developed during the transition from alevin to fry, toward the end of yolk absorption. This transition, although gradual, is probably more of a physiological change than the changes that occur at hatching. The newly hatched alevins are more "embryo" than "juvenile." They normally reside in the incubation gravels, have few voluntary responses to changes in their environment, and continue to develop by catabolizing their yolk. As the alevin develops and becomes prepared for emergence, susceptibility to some toxicants increases. The alevins are now more juvenile than embryo, even to the point of preemergent feeding as concluded by Dill (1967) for sockeye salmon alevins.

Our results indicate that rainbow trout embryos and alevins are safer from ammonia toxicity than are older salmonids (Burrows 1964; Larmoyeux and Piper 1973). A dramatic increase in the excretion of ammonia (Rice and Stokes in press) and sensitivity to ammonia appears to begin about the time the fry complete absorption of their yolk. Chronic exposure to ammonia would probably exert its greatest effects beginning at this stage also.

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NOTES

ADDITIONAL EVIDENCE SUBSTANTIATING EXISTENCE OF NORTHERN SUBPOPULATION OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

The northern anchovy, *Engraulis mordax* (Girard), ranges from Queen Charlotte Islands, British Columbia, to Cape San Lucas, lower Baja California. A study of variations in meristic characters (McHugh 1951) and genetic studies using serum transferrins (Vrooman and Smith 1971) generally support the hypothesis that three distinct subpopulations exist within this species' total geographic range. The dividing lines between subpopulations apparently occur at Point Conception, Calif. (delineating the northern and central elements), and at Cedros Island, central Baja California (delineating the central and southern elements).

Extensive spawning activity by the central and southern subpopulations is evidenced from the results of comprehensive egg and larvae surveys conducted since 1951 by the California Cooperative Oceanic Fisheries Investigations (Baxter 1967). Although these surveys suggest that the time-space distributions of spawning effort by these two subpopulations tend to overlap, evidently each achieves enough reproductive isolation to generate genetic differences between serum transferrins. Apparently, then, the central and southern subpopulations are capable of independently producing their own recruitment.

Until recently, the evidence for independent spawning by the northern subpopulation was not extensive. Ahlstrom (1968) noted that, in 1949 and 1950, anchovy larvae were found in moderate abundance off the Oregon coast. LeBrasseur (1970) indicated that a small number of larvae were taken in a 1958 survey of Queen Charlotte Sound, British Columbia. Waldron[1] stated that no eggs or larvae were taken in incidental samples off the Washington-Oregon coast in 1966 but that a few anchovy larvae were obtained during a comprehensive survey in the spring of 1967.

Such meager results might lead one to believe that the few larvae observed in northern waters were merely the result of incidental spawning activity. A conclusion might then be made that the northern subpopulation does not independently produce its own recruitment but relies instead upon an influx of anchovies from the two southern subpopulations.

In 1969, however, Richardson (1973) encountered such extensive numbers of anchovy larvae during a May-October survey of larval fishes off the Oregon coast (lat. 42°00′-46°30′N, coastline—long.129°30′W) that the above conclusions seemed to be refuted. Her results indicated the presence of a spawning stock of anchovies associated with the warm, near-surface waters of the Columbia River plume. Moreover, the peak of spawning seemed to be correlated with that period in summer when warm plume water (>14°C) was a dominant oceanographic feature.

Evidence from Length-Frequency Distributions

An analysis of age- and length-frequency distributions played a major role in determining stock structure for the Pacific sardine, *Sardinops sagax*. A similar analysis of length-frequency distributions was undertaken for the northern anchovy. The following review outlines the rationale and criteria applied in the sardine analysis and adapted for this study.

Early sardine investigators at first hypothesized that three subpopulations composed this species' total west coast population[2]. However, in addition to evidence of only sporadic spawning activity (Ahlstrom 1954), age- and length-frequency distributions obtained from the so-called northern subpopulation failed to reveal the presence of the most recently produced age-groups, i.e., the 0's, 1's, and 2's (Harry 1948). These ages, however, were often observed in samples from the central and southern subpopulations. The consistent absence of 0's from northern samples presumably confirmed a lack

[1]Waldron, K. D., Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash., pers. commun. 1971.

[2]A northern subpopulation supposedly ranged from British Columbia southward to central California, while central and southern subpopulations resided respectively off southern California and lower Baja California.

of independent spawning activity by that subpopulation of sardines (Harry 1949). The consistent presence of 0's, of course, would have indicated that independent spawning had occurred.

Figure 1 presents the length-frequency distributions analyzed in this study. These anchovy lengths were obtained from four exploratory fishing surveys conducted from Cape Flattery, Wash., to Yaquina Bay, Oreg., during 1966-67. These surveys occasionally encountered schools of anchovies containing small fish which became gilled in the meshes of the survey gear (Figure 2). It was speculated that these small anchovies were the result of recent spawning activity in the Washington-Oregon area.

To analyze these length distributions, one must first know the range of lengths associated with individuals belonging to age-group 0. Clark and Phillips (1952) indicated that 0-age anchovies begin entering the southern California live-bait fishery at lengths ranging from 5 to 9 cm. Miller (1955) stated that 0-age fish begin entering the southern California commercial fishery at 8.5-9.0 cm. Tillman (1972) concluded that anchovies are at least 6 mo old when they enter the commercially exploitable population at 9 cm. Figure 3 presents the ranges, medians, and median quartiles of the lengths of anchovy larvae obtained by Richardson (1973). These indicate that, in the northern subpopulation, 0-age anchovies approach 6 cm after 5 mo of growth. Thus, a length range of 0-9 cm should define those anchovies which resulted from spawning, at least, during the past 6 mo. This range was used to define the 0-age component in all length-frequency distributions.

Applying this criterion, the bar graphs of Figure 1 indicate that 0-age anchovies indeed were present in the northern subpopulation during the years surveyed. Lengths less than 4 cm were not found, but the 4-9 cm range composed, respectively, 11.6, 19.8, 87.0, and 39.0% of these four length-frequency distributions. The results shown for November-December 1966 and February 1967 are particularly striking, having major modes located respectively at 6 and 5.5 cm. These latter two distributions result from the facts that anchovies tend to school by size and that the later 1966 and early 1967 surveys primarily encountered schools of small fish. Therefore, following the rationale discussed at the beginning of this section, the presence of such juveniles would tend to confirm the

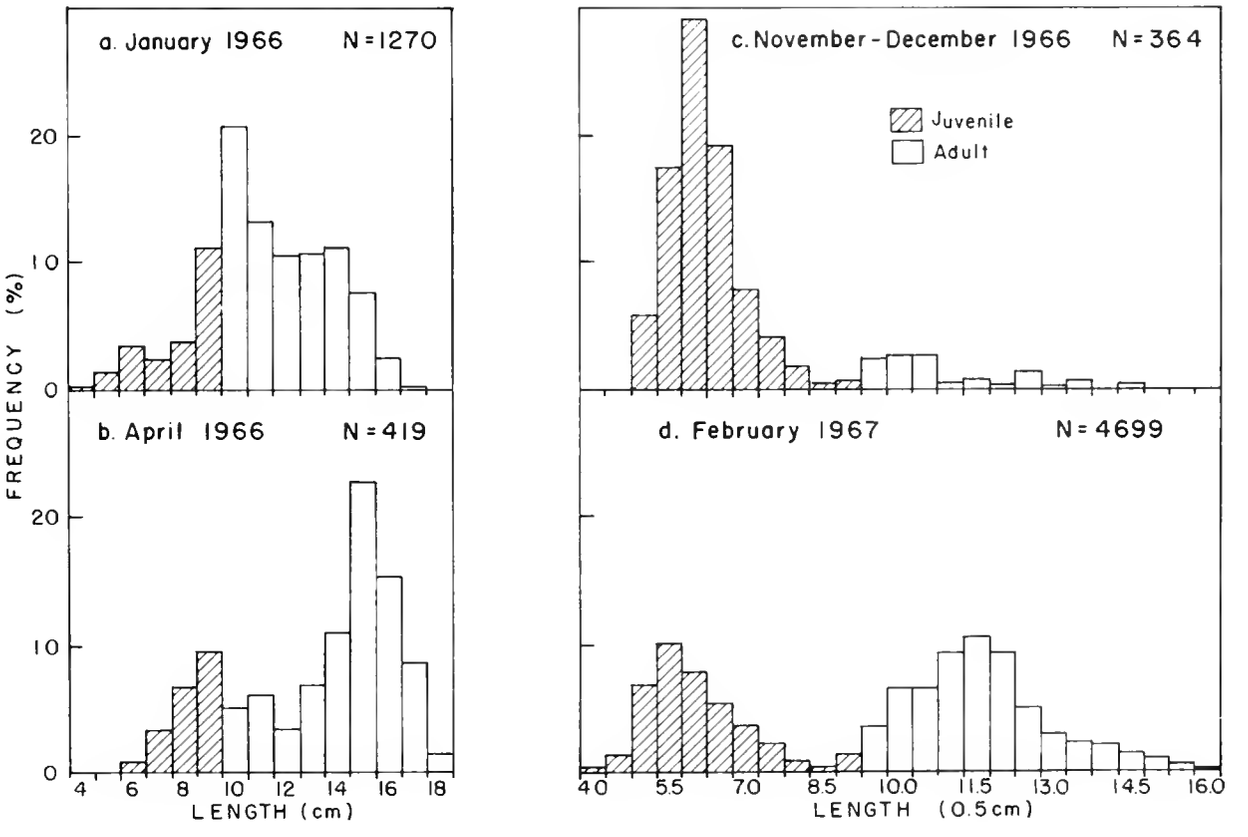
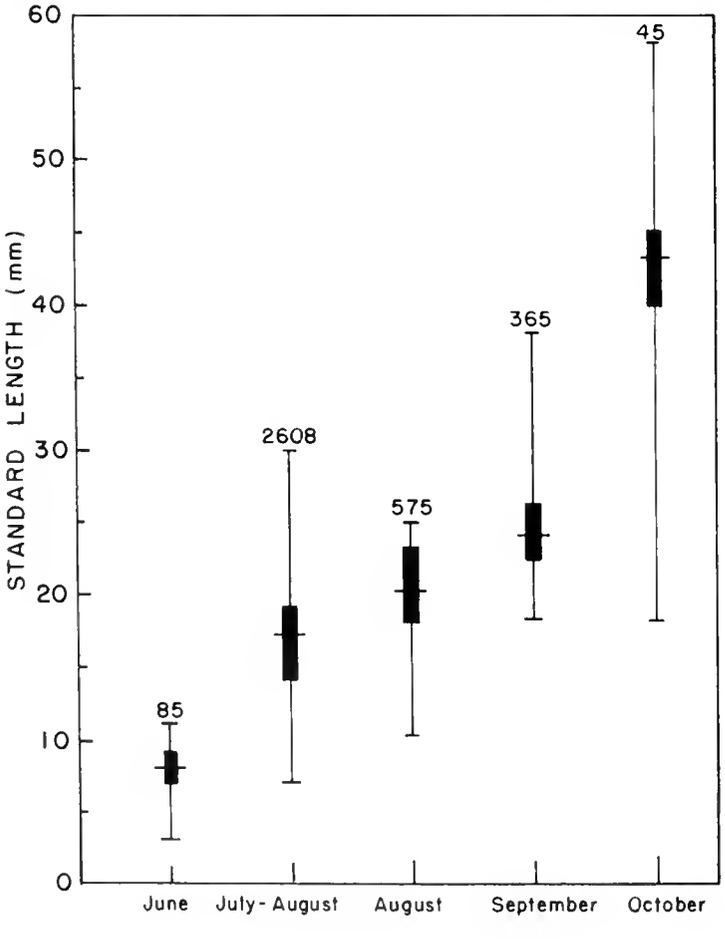


FIGURE 1.—Composite length-frequency distributions of juvenile and adult northern anchovy sampled off Washington-Oregon during 1966-67.

FIGURE 2.—Juvenile northern anchovy gilled in the meshes (½-¾ inch) of a mid-water trawl off the Washington-Oregon coast.



occurrence of independent spawning activity by the northern subpopulation of anchovies.

Discussion

Figure 1 gives the results of surveys which took place during the winter or spring. Since the northern subpopulation apparently spawns during the summer, then these figures indicate that spawning occurred during the summer which preceded each survey period. In other words, Figure 1a and b indicate that spawning occurred during the summer of 1965, resulting in recruitment of 0-age fish during January-April 1966. Moreover, Figure 1c and d indicate that spawning occurred in the summer of 1966, resulting in recruitment during November 1966-February 1967. Thus, according to Richardson's data and this analysis, independent spawning by the northern subpopulation seems to have occurred

FIGURE 3.—Ranges, medians, and median quartiles of lengths of northern anchovy larvae obtained during May-October 1969 off Oregon (Richardson 1973).

quite regularly rather than incidentally (occurring at least in 1965, 1966, and 1969).

Consequently, it is concluded that the presence of anchovies in northern waters does not represent a mere expansion of this species' geographic range—an expansion that well might have accompanied its recent fivefold increase in total population size. The previously mentioned genetic and meristic evidence, the results of recent larvae surveys, and the above length-frequency analysis would all seem to refute such a conclusion. Moreover, since this subpopulation was the mainstay of a substantive fishery for live bait during the 1940's (Pruter 1966), it seems to have been a persistent feature of the Washington-Oregon coast even before the dramatic expansion of the anchovy biomass which followed the demise of the sardine. Thus the weight of evidence seems to indicate that the northern subpopulation of anchovies is one of three independent population elements, all of which are capable of spawning and producing their own recruitment.

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COMMENT. INTRODUCTION OF *CODIUM* IN NEW ENGLAND WATERS

Genus *Codium* is one of the most common forms of seaweed found in almost every latitude but, until recently, has been absent from the east coast of North America. *Codium* attaches to rocks, pilings, old molluscan shells, and also shells of living oysters, scallops, and mussels. This algae has a number of common names, such as spaghetti grass, staghorn, deadman's fingers, and Japanese weed. It grows rapidly and often becomes so dense that it sometimes creates undesirable conditions on cultivated and natural shellfish beds, as well as in some other environments. At times it becomes buoyant enough to float and to carry along with it mollusks, to the shells of which it is attached. Mass mortalities of *Codium* are usually followed by quick decomposition, creating adverse conditions that result in the death of mollusks and other bottom forms.

No *Codium* was known to exist in New England waters until approximately the end of the 1950's, when the first specimens of *Codium fragile* were reported from several aquatic areas adjacent to Long Island. Since then it has become established in the waters of New England, spreading as far north as the State of Maine. According to a recent article (Quinn 1971) "It is now a dominant seaweed in the waters of Eastern Long Island and

can be found from Barnegat Bay, N.J., to Boothbay Harbor, Me."

Because of its wide distribution in the new environment, *Codium* now causes serious impact on local ecology and also creates serious problems on shellfish beds. There is some question, naturally, as to when the first introduction of this algae occurred and how this somewhat undesirable "immigrant" was brought into our eastern waters. Quinn (1971) quotes Mueller, who, apparently without any evidence, speculates that "It was imported on the backs of oysters from Europe and Japan." Since I am responsible for the introduction of the European oyster, *Ostrea edulis*, into the waters of New England (Loosanoff 1951, 1955), I wish to comment on this matter.

The European oysters were brought to Long Island Sound in October 1949, when I was the Director of the United States Bureau of Commercial Fisheries Biological Laboratory at Milford, Conn. The shipment was comprised of approximately 2 bushels of the mollusks, ranging in age from 1 to 3 yr. They were shipped in a vegetable compartment of a large refrigerator on a Holland-American Line passenger ship and spent about 13 days in transit.

The introduction of *O. edulis* was made in accordance with the decision reached after my consultations with members of the shellfish industry, as well as with leading marine biologists of that period, including Paul S. Galtsoff of the United States Bureau of Commercial Fisheries and Thurlow Nelson of Rutgers University. Federal authorities approved the importation and the Director of the State of Maine Sea and Shore Fisheries, who was extremely interested in planting European oysters into those waters, gave me a small sum of money to pay for that shipment. The latter fact, obviously, discredits Mueller's statement, quoted by Quinn, that "The oysters were removed from Milford and Woods Hole without permission and introduced into local waters."

In introducing European oysters it was our desire to establish a second commercial species of bivalves in the waters of Maine. At that time only one mollusk, the soft-shell clam, *Mya arenaria*, was commercially utilized in that region. However, because of extremely heavy mortality among the *Mya* in the mid-1940's, this species became almost extinct for a period of several years. As a result, many shore communities which depended upon soft-shell clam fisheries were deprived of the chief means of their livelihood. Therefore, it seemed logical to me that a second shellfishery should be developed in those waters, namely that of *O. edulis*. If successful such a development would enhance the economy of the region. *Ostrea edulis* was chosen for the cold waters of Maine because, in addition to its high quality as human food, it is able to propagate at a considerably lower temperature than the American oyster, *Crassostrea virginica*.

In bringing the oysters from Europe, I dealt with my friend, Peter Korringa, who is now Director of the Netherlands Institute for Fishery Investigations. At that time he was already considered one of the world's leading shellfish experts. Being fully aware of the possibility of introducing undesirable exotic species which might accompany the European oyster, our group of American biologists, as well as Korringa, decided to take precautionary measures considered sufficient to prevent such an occurrence. The problem was discussed at great length in correspondence between Korringa and myself, and I still have in my files several of Korringa's letters attesting to this exchange. For example, in his letter of March 1949, Korringa wrote "I can kill any germs in the shell by disinfecting the consignment before shipment." In May of the same year he wrote again "I will disinfect very carefully every oyster we ship you with the chemicals we find satisfactory to that end." In his recent letter to me, dated 27 November 1973, Korringa wrote as follows: "I suggested to treat the oysters by bathing them in a mercury solution, using the organic fungicide we used on large scale against infection with shell disease. This kills hundred procent all organisms on the outside of the shell which cannot withdraw in a hermetically closed shell. You see from my correspondence that I have treated the oysters with this disinfectant before shipping them. Therefore I feel sure that *Codium fragile* cannot have been introduced in the American Atlantic waters with our oysters."

When the oysters arrived at Milford, they were again carefully examined, washed with fresh water, and dipped in a weak solution of copper salt. At that time, however, we were not concerned as much with the introduction of *Codium*

as we were afraid of bringing along a highly destructive fungus causing so-called "oyster shell-disease." Because of Korringa's assurance, however, we were quite certain we would eliminate this and any similar dangers.

The small shipment of European oysters was later divided into two parts, one taken to the U.S. Bureau of Commercial Fisheries Laboratory at Boothbay Harbor, Maine, where some of the oysters were suspended off the dock, the other part kept in Milford Harbor, remaining there under the observation of my associates and me for several years. Not in a single instance did I, other members of Milford Laboratory, or John B. Glude, Director of the U.S. Bureau of Commercial Fisheries Laboratory at Boothbay Harbor, or his colleagues, notice or report to me the presence of *Codium* on the oyster shells. Therefore, considering the chemical treatment that was given the oysters before they were placed in open American waters and because of the results of our long-term observations of these oysters at both Milford and Boothbay Harbor, it is improbable that *Codium* was brought into the waters of New England "on the backs of the European oysters."

There are several much more plausible explanations as to the way *Codium* was introduced to our Atlantic coast. In my opinion, it was brought into our waters during World War II. At that time, to avoid being torpedoed by German submarines along the open Long Island coast, many freighters coming from Europe to the port of New York traveled through the well-protected inside passage—Long Island Sound. At times, these vessels were so numerous that many of them had to be anchored in Long Island Sound for several weeks before they could be unloaded at New York piers. I was then engaged in the study of plankton of Long Island Sound—in relation to propagation of oysters—running, sometimes, 14-h sampling series from a small boat. Several of our collecting stations were then located on the Bridgeport and New Haven oyster beds where seed oysters were dredged each fall and planted on cultivated beds of Long Island, Rhode Island, Massachusetts, and even Maine (Loosanoff 1966).

To avoid the wind and heavy wave action we would usually position our boat on the lee side of anchored freighters. Often we were so close to those vessels that we could converse with members of their crews. Many of these ships were of European registry and, because of the war, most of them were not able to undergo proper bottom cleaning for several years. As a result of this neglect, the ship bottoms were covered with heavy layers of marine fouling organisms. Sometimes such layers, as had been reported by Woods Hole investigators, were as much as 2, or even 3, feet thick (Woods Hole Oceanographic Institution 1952). The fouling mass was composed of many forms, including mussels, tunicates, and, no doubt, a variety of other organisms. The *Codium* was also present and sometimes clearly visible. While the freighters were riding at anchor, frequently large chunks of the fouling mass broke off and fell to the bottom of the Sound. We witnessed this phenomenon on numerous occasions.

Thus, it appears logical that *C. fragile* gained entrance into the waters of eastern United States from the bottoms of European freighters during World War II. This possibility, however, seems to be ignored; the blame is placed instead, directly or indirectly, on a small, properly handled shipment of European oysters which was brought from Holland to Milford in 1949 (Quinn 1971).

It may be mentioned, in conclusion, that, as originally planned, the European oysters planted in Boothbay Harbor not only survived in the new environment but reproduced under a new set of ecological conditions and became firmly established within a large area (Welch 1966). Therefore, these excellent "immigrants" may soon become the second commercial shellfish crop of Maine. Secondly, *Codium*, although a nuisance and a highly undesirable invader in some respects, and for introduction of which we claim no "credit," may be a welcome addition to localized biosystems by providing extensive, rich-in-food, protective nursery areas to the advanced larval stage and juveniles of many fishes and of such important species of commercial invertebrates as the American lobster, *Homarus americanus*, and the blue crab, *Callinectes sapidus*.

I wish to thank John B. Glude for reading this manuscript and offering constructive suggestions.

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1952. Marine fouling and its prevention. U.S. Nav. Inst., Annapolis, 388 p.

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ERRATA

Fishery Bulletin, Vol. 72, No. 4

KENNEDY, V. S., W. H. ROOSENBURG, M. CASTAGNA, AND J. A. MIHURSKY, "*Mercenaria mercenaria* (Mollusca: Bivalvia): Temperature-time relationships for survival of embryos and larvae," p. 1160-1166.

1) Page 1161, right column, line 13, correct line to read:
(25 mm) in an 8 × 11 matrix (see Figure 1,
2) Page 1163, the figure legends for Figures 2 and 3 were switched in printing. The legend for Figure 2 should be under the second drawing in the left column and that for Figure 3 should be under the drawing in the right column.

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Notes

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Vol. 73, No. 2 April 1975

(Continued on back cover)

Seattle, Washington

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NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

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Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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Seattle, Washington

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Notes

HEAT EXCHANGE IN THE YELLOWFIN TUNA, *THUNNUS ALBACARES*, AND SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND THE ADAPTIVE SIGNIFICANCE OF ELEVATED BODY TEMPERATURES IN SCOMBRID FISHES

JEFFREY B. GRAHAM[1]

ABSTRACT

Thunnus albacares and *Katsuwonus pelamis* are warm-bodied fish and use retia mirabilia as countercurrent heat exchangers. Both species have four sets of lateral exchangers, two epaxial and two hypaxial, each consisting of a large cutaneous artery and vein and rete. *Katsuwonus pelamis* has a central exchanger, located within the haemal arch, which consists of the dorsal aorta, the posterior cardinal vein, and a large vertical rete. The central heat exchanger in *T. albacares*, while also in the haemal arch, is simpler, consisting of two small "wing-shaped" retia on either side of the dorsal aorta and cardinal vein.

The adaptive significance of the specialization for heat conservation is discussed. Body temperatures, thermal profiles, and the natural histories of different warm-bodied species are compared, and warm fishes are contrasted with scombrids that do not conserve heat. The skipjack tunas, *Euthynnus* and *Katsuwonus*, have well-developed central heat exchangers and are much warmer than *T. albacares*. Higher body temperatures in skipjacks seems related to their requirement for a higher basal swimming speed and their faster burst speed.

Comparisons on the basis of existing knowledge about the two phyletic groups of *Thunnus* reveal few differences in swimming ability or factors related to locomotion. The bluefin group, consisting of *T. thynnus*, *T. maccoyii*, and *T. alalunga*, however does contrast with the yellowfin group (*T. albacares*, *T. atlanticus*, and *T. tonggol*) by maintaining generally higher body temperature differentials, having incomplete vertebral circulation through the absence of a posterior cardinal vein, and occurring at higher latitudes.

Scombrids (mackerels, bonitos, and tunas) are pelagic, oceanic fishes that are highly adapted for continuous swimming. Some of the more advanced scombrids (principally frigate mackerels, *Auxis;* skipjack tunas, *Euthynnus* and *Katsuwonus;* and tunas, *Thunnus*) have evolved the capacity to conserve heat generated by the continuous metabolic activity of their swimming muscle and thus maintain body temperatures that are warmer than ambient seawater (Carey et al. 1971; Carey 1973). There has been convergent evolution for this specialization in mackerel sharks (Isuridae) a highly active, continually swimming group (Carey and Teal 1969a).

Warm-bodied fish retain heat by using retia mirabilia (= wonderful network) as countercurrent vascular heat exchangers. The principal advantage of a high and fairly constant body temperature is facilitation of continuous swimming by increasing the frequency of muscular contractions, thus increasing available swimming power (Carey et al. 1971). Also, warm-bodied fish probably achieve a marked independence from environmental temperature permitting them to make rapid vertical and latitudinal migrations without the necessity of thermal acclimation.

In their extensive review of warm-bodied fish, Carey et al. (1971) described two types of heat exchanger, lateral and central. Lateral heat exchangers (Figure 1) are present in many warm-bodied species but are best developed in the genus *Thunnus* where they consist of four sets of longitudinal subcutaneous arteries and veins (two epaxial and two hypaxial), each with adjoining layers of retial vessels that penetrate the red muscle near the midplane (Gibbs and Collette 1967; Carey et al. 1971). Large, highly developed central heat exchangers (Figure 1) are found in *Euthynnus*, *Katsuwonus*, and *Auxis*. These are located below the vertebral column, in the haemal arch, and consist of a large vertical rete formed from branches of the dorsal aorta and the posterior

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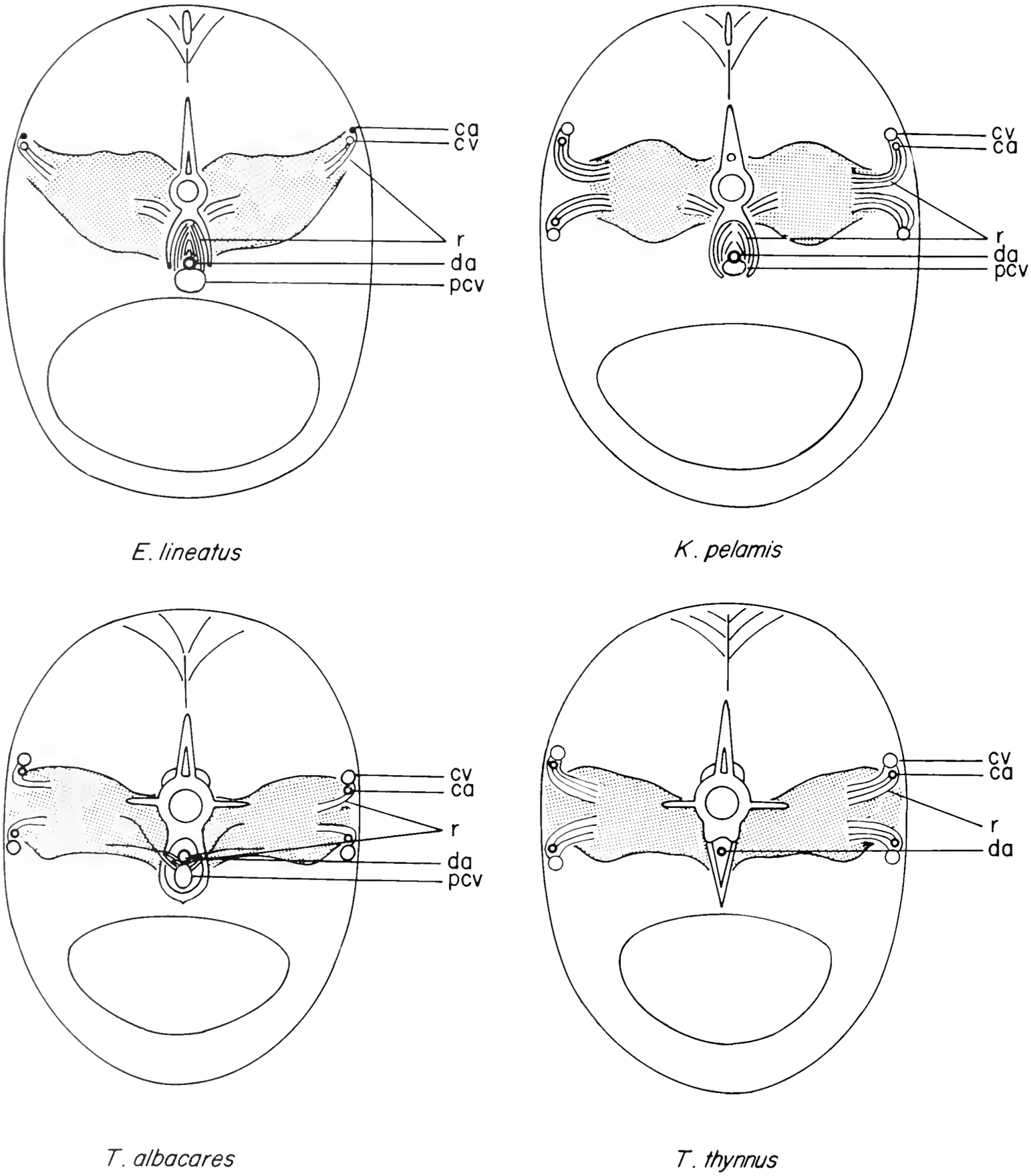

FIGURE 1.—Transverse sections of four warm-bodied species showing the position of central and lateral retia mirabilia (r) that function as vascular heat exchangers. The major blood vessels supplying retia are: dorsal aorta (da), posterior cardinal vein (pcv), cutaneous arteries (ca), and veins (cv). Veins are shown with larger diameters and thinner walls. Red muscle distribution (shaded areas) is also depicted. Noted that the position of cutaneous arteries and veins in *Euthynnus lineatus* is reversed compared to that in other species and that only an epaxial pair is present. Also, *Thunnus thynnus* does not have a posterior cardinal vein. Frigate mackerels (*Auxis*) are not shown but are very similar to *Euthynnus*. Data contained in this figure are from various sources cited in the text.

cardinal vein (Kishinouye 1923; Godsil 1954; Carey et al. 1971; Carey 1973; Graham 1973).

Kishinouye (1923: 377; see discussion of *Neothunnus*, a synonym of *T. albacares*) described a special subspinal vascular plexus or "kurochiai" in the yellowfin tuna, *T. albacares* (Bonnaterre), and recent studies have indicated that this structure is a central heat exchanger (Carey et al. 1971; Carey 1973). The kurochiai has not been fully described, nor has the relationship between it and *T. albacares'* well-developed lateral heat exchangers been considered. Body temperatures of fresh-caught and swimming yellowfin tuna are known to be less than those of skipjack tunas and some other tuna when measured under similar conditions (Barrett and Hester 1964; Carey and Teal 1969b; Stevens and Fry 1971; Carey 1973), but where heat is distributed in the body (thermal profiles) has not been determined for either *T. albacares* or the skipjack tuna *K. pelamis* (Linnaeus).

The purpose of this study is to investigate the relationship between body temperature and the types of heat exchanger in *T. albacares*. The patterns observed for this species and *K. pelamis* are compared with those of other warm-bodied fish. Body temperatures and thermal profiles of fresh-caught *T. albacares* and *K. pelamis* are reported, and their central heat exchangers are described. The general structure and circulation pattern of these species' heat exchangers are compared with those of the bluefin tuna *T. thynnus*, and other skipjack tunas, *Euthynnus*, and are discussed in terms of their relation to differences in body temperature, morphology, swimming capability, and the natural history of these species. Studies of this type may enable us to understand why there are different kinds of heat exchangers and how these evolved.

MATERIALS AND METHODS

Eleven *T. albacares* (360 to 700 mm fork length; weight, 1 to 5 kg) and four *K. pelamis* (500 to 600 mm, 3 to 4 kg) were caught by surface trolling in the Gulf of Panama and brought on board within 30 to 90 s of being hooked. Red and white muscle temperatures of these specimens were immediately taken with a fast-reading hypodermic thermistor probe (Yellow Springs Instrument No. 513)[2] that had been calibrated against a mercury thermometer. Measurements were made deep (near the vertebrae), midway from the vertebrae to the skin, and subcutaneously at several positions along the fishes' lateral midplane, from the operculum to the tail, in order to determine the relative contribution of the lateral and central heat exchangers to heat distribution. All temperatures were rounded to the nearest 0.5°C. Body temperatures of shaded fish remained fairly constant during the first 10 min after capture, and all measurements were made within this time.

A criticism that has been directed against the measurement and interpretation of temperature data from fresh-caught fish is that burst swimming to catch a troll lure, or frenzied swimming, together with struggling once hooked may increase body temperatures above typical values. This probably has some validity, but the effects of struggling and handling seem generally overrated. With telemetry, Carey (1973) has shown that free-swimming *T. thynnus* have body temperatures very similar to captured fish. Also, Barrett and Hester (1964) found that immediately captured yellowfin tuna and those that had been tethered for a few minutes had similar temperatures.

Large frozen *T. albacares* (800 to 1,400 mm, 8 to 42 kg) were obtained from a commercial fishing vessel, and a range of sizes was dissected to determine red muscle distribution, the position, size, and structure of the heat exchangers, and the dimensions of retial vessels. Specimens of *K. pelamis* were also dissected, and measurements were made.

RESULTS

Body Temperatures

Average deep, intermediate, and subcutaneous red muscle temperatures of eight *T. albacares* (caught in surface water of 28.5°C) were 30.5°, 30.5°, and 29.5°C. Three specimens caught in 30°C water had average deep body temperatures of 32.5°C. Elevated temperatures in *T. albacares* occur along the body from the pectoral fins to as far as the third or fourth finlet. The warm region also extends laterally through a large portion of the red muscle. Highest body temperatures were always found in the red and white muscle along and near the lateral midplane of the body. *Katsuwonus pelamis* is warmer than *T. albacares*, and its warm

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

region extends laterally to just below the skin. The average deep, intermediate, and subcutaneous red muscle temperatures of four *K. pelamis* (caught in 28.5°C surface water) were 35°, 35°, and 33°C. Deep white muscle temperatures in these fish averaged 34°C; brain temperatures were 33°C. The temperatures reported here for *T. albacares* and *K. pelamis* are in good agreement with those found for these species by other investigators (Barrett and Hester 1964; Stevens and Fry 1971).

Heat-Exchanger Structure and Red-Muscle Distribution

Thunnus albacares

The distribution and structure of the lateral heat exchangers found for *T. albacares* in this study agree fully with those described by Gibbs and Collette (1967) and are summarized here with new notes on variations related to size. Epaxial and hypaxial arteries and veins subdivide from their respective trunks at about vertebrae no. 10 and extend along the body to about two-thirds of the way from the second dorsal fin to the tail (vertebrae no. 29 or 30) where they are rejoined by a commissure. One row of retial vessels originates from the lateral edge of each artery and vein, and this is consistent with the observations of Kishinouye (1923, as *Neothunnus*). *Thunnus albacares*' lateral retia are long and strongly curved towards the center of the body. Retial curvature was not observed in specimens smaller than 3 kg. Cutaneous vessel diameters increase dramatically with increased size, ranging from 0.5 to 1.0 mm (artery and vein) in a 1.1-kg specimen to 6.0 to 8.0 mm in a 42-kg fish. Retial vessels ranged from 0.05 to 0.1 mm in diameter.

The central heat exchanger in *T. albacares* extends from the first to the second dorsal fins (vertebrae no. 8 or 9 to 20) and is situated immediately below the vertebrae in the haemal arch. This structure is composed of the dorsal aorta, the posterior cardinal vein, and their small vessels that form two "wing-shaped" retia (Figure 2). Diameters of the dorsal aorta and posterior cardinal vein only increase slightly with increasing size, ranging from 1.5 to 3.0 mm in a 2.7-kg fish to 3.5 to 4.0 mm in a 42-kg specimen. This contrasts markedly with the large weight-related change in the diameters of the lateral blood vessels. The central retia originate as thick bundles in the haemal arch, then extend supralaterally and pass through vertebral foramina into the red muscle. In the muscle these vessels flatten into broad continuous sheets of alternating veins and arteries (0.1 to 0.2 mm in diameter) that are only one layer thick (Figure 2). This layer penetrates far into the muscle, from 18 mm in a 2.7-kg fish to 40 mm in a 42-kg fish.

Red muscle in *T. albacares* appears in thin bands along each side of the fish at the level of the vertebrae (Figure 2). Only red fibers from the hypaxial muscles actually reach the vertebrae, but epaxial and hypaxial muscle both extend well toward the fishes' side. Longitudinally, red muscle extends from behind the transverse septum (vertebrae no. 6 or 7) to as far as the fifth finlet (vertebrae no. 28 or 29) and is fairly uniform in thickness and shape (cf. Kishinouye 1923, Plate XVII, as *Neothunnus*). As was found for *E. lineatus* (Graham 1973) and, as would be expected, there is good agreement in the lineal distribution of red muscle and the lateral and central heat exchangers of *T. albacares*.

Katsuwonus pelamis

Except for its higher position in the body, the central exchanger of *K. pelamis* (Figure 3) is very similar to that of *Euthynnus* and *Auxis*, consisting of the closely associated dorsal aorta and posterior cardinal vein and a thick vertical rete, all in the haemal arch (Kishinouye 1923; Godsil 1954; Graham 1973). Just posterior to the pectoral fins in a 580-mm (about 4 kg) specimen, the following vessel diameters were measured: dorsal aorta, 2.0 mm; posterior cardinal vein, 4.0 mm; retial vessels, 0.05 to 0.1 mm. At its center (Figure 3), vessels in the central rete of this fish were 8.0 mm long.

Lateral heat exchangers are better developed in *K. pelamis* than in either *Euthynnus* or *Auxis* (Figure 1). Both epaxial and hypaxial sets of cutaneous vessels, with retia, are present, but they are further apart than in *T. albacares* (Figure 1), reflecting the laterally thicker wedge of red muscle in *K. pelamis* (see below). The cutaneous vessels are smaller than in *Thunnus*. The most developed retial vessels occur anteriorally but are variable in their position, length, and the direction they penetrate red muscle (cf. Godsil and Byers 1944, Figure 15).

Red muscle in *K. pelamis* is thicker than in *T. albacares* but does not appear to extend as far into the tail. In a transverse section (Figure 3), both

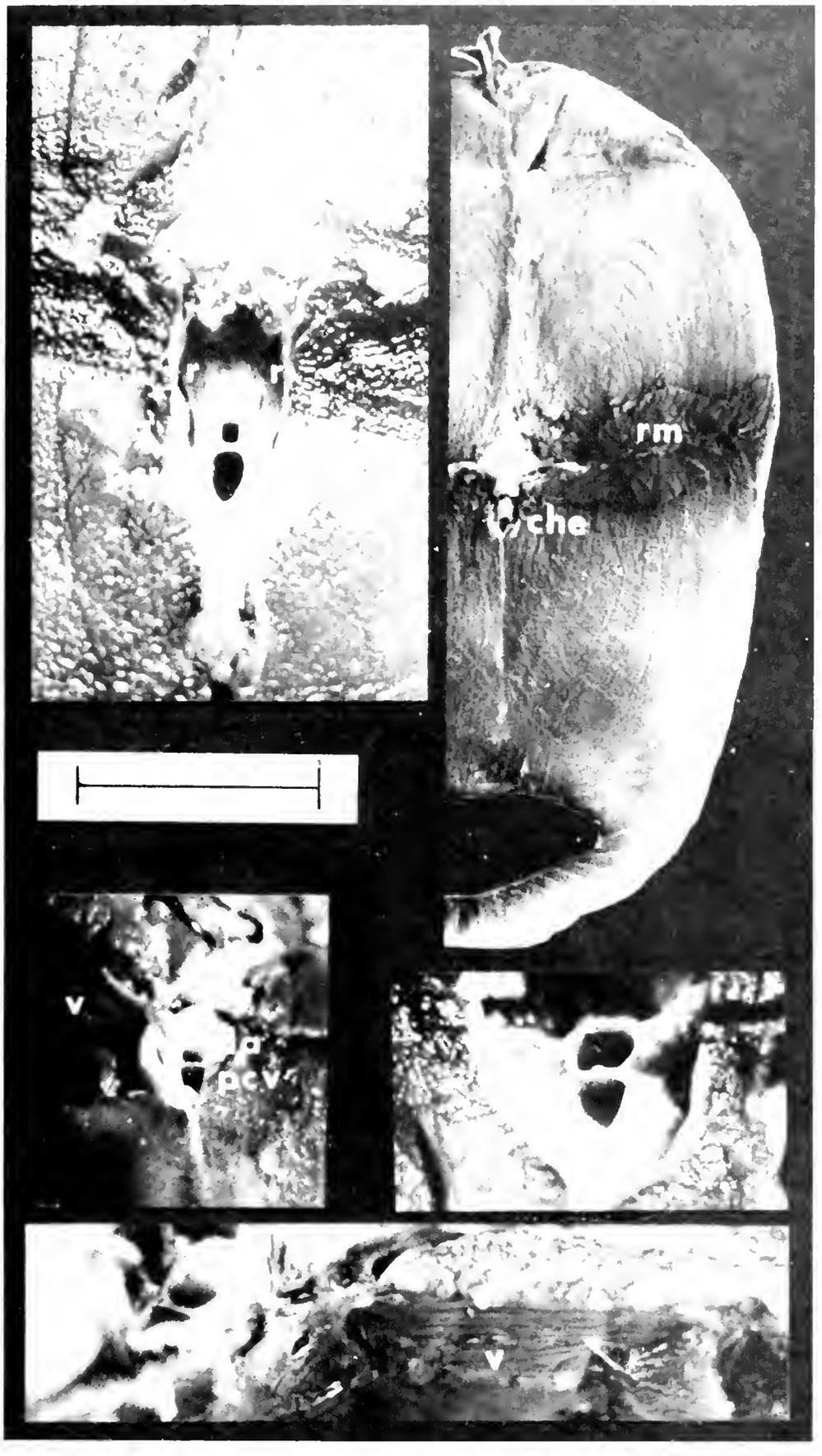

FIGURE 2.–Central heat exchanger of *Thunnus albacares*. (Top right, scale = 6.5 cm): Transverse sections showing the position of red muscle (rm) and the central heat exchanger (che). (Top left, scale = 1.5 cm): Transverse section of the che showing the dorsal aorta (da), posterior cardinal vein (pcv), and retia (r). (Middle right, scale = 2 cm): A close view of the che showing the da, pcv, and two wing-shaped retia that proceed supralaterally from the vessels. (Middle left, scale = 1.2 cm): A ventrolateral view of the da, pcv, and the sheet of vessels (v) outside the haemal arch that penetrate red muscle. (Bottom, scale = 2.0 cm): Ventrolateral view showing the che on the left and the thin sheet of vessels in red muscle.

hypaxial and epaxial red muscle reach the vertebrae. Longitudinally, shape as well as thickness of red muscle varies at different points (cf. Kishinouye 1923, Plate XVII). Generally, red muscle in *K. pelamis* appears to have more ligaments than *T. albacares*. In both species the myomeres are continuous through red and white muscle (Figures 2, 3), but red and white muscle are easily distinguished and separate with slight teasing.

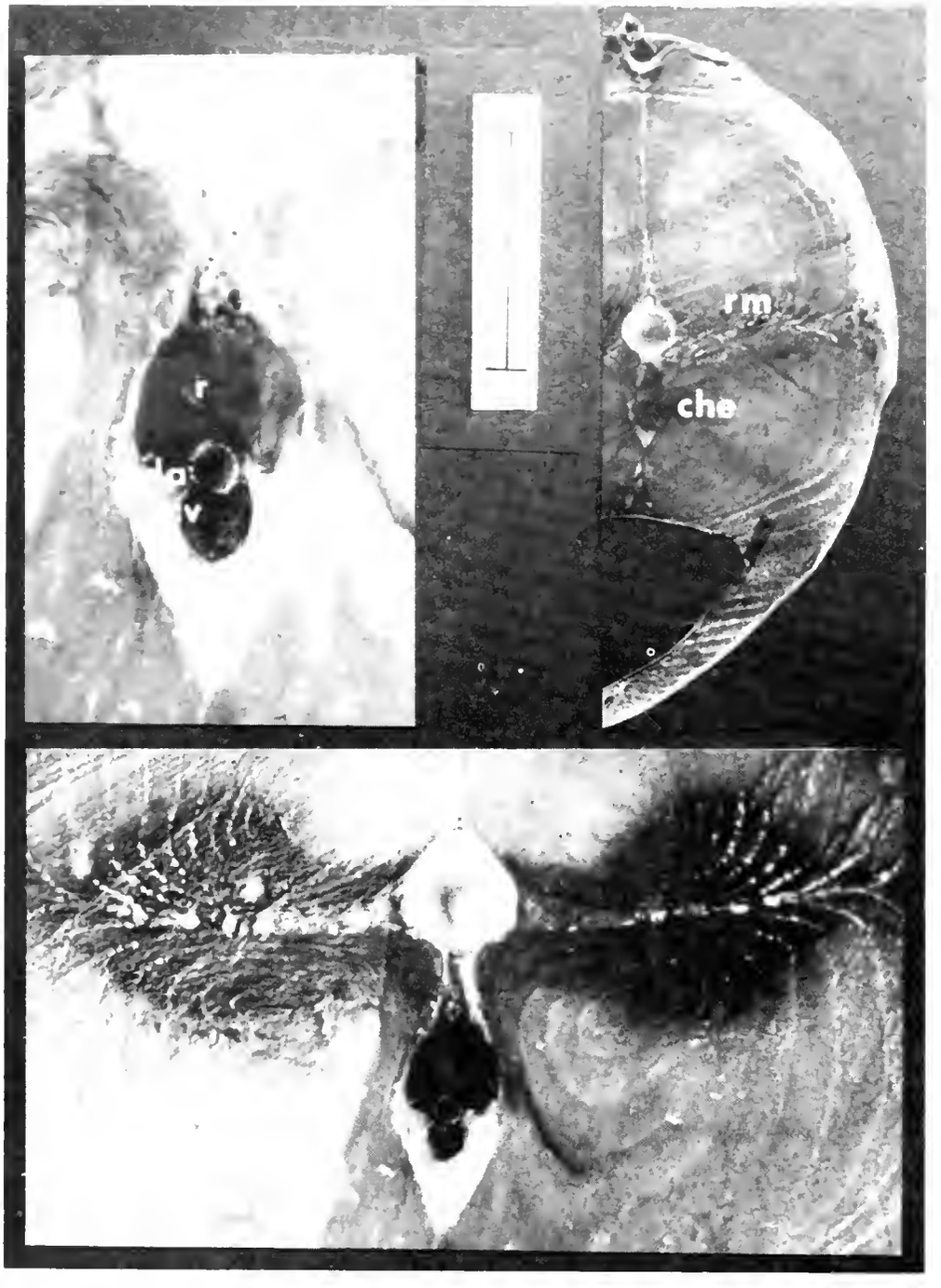

FIGURE 3.—Central heat exchanger of *Katsuwonus pelamis*. (Top right, scale = 5.6 cm): Transverse section showing the position of the central heat exchanger (che) and red muscle (rm). (Top left, scale = 1.1 cm): Close view of the rete (r), the dorsal aorta (da), and the posterior cardinal vein (pcv) in the haemal arch. (Bottom, scale = 1.9 cm): Red muscle and the central heat exchanger.

COMPARISON OF *KATSUWONUS, EUTHYNNUS, AUXIS,* AND *T. ALBACARES*

Differences in Heat Exchangers

Central heat-exchanger differences can be summarized as follows: *Katsuwonus, Euthynnus,* and *Auxis* have only a single vertical rete whereas *T. albacares* has two much smaller retia. *Thunnus albacares'* central exchanger is immediately below the vertebral centrum (Figures 1 and 2) while in *K. pelamis* it is lower, about midway between the vertebrae and the coelomic cavity, and in *Euthynnus* and *Auxis* it is quite low, occurring just above the coelom (Kishinouye 1923; Godsil 1954; Graham 1973). In *E. lineatus* and *E. alletteratus,* and *K. pelamis* that I have examined, and in *Auxis* (Godsil 1954), the dorsal aorta is actually embedded in the dorsal side of the posterior cardinal vein and is surrounded by a vast network of retial vessels which in effect bathes the aorta in venous blood. This structure has been interpreted as allowing the rete to occupy a full arc over the vessels, thus maximizing its heat-exchanging area (Graham 1973).

Both *K. pelamis* and *T. albacares* have two pairs of lateral exchangers. *Katsuwonus* has two

somewhat variable rows of retial vessels in each lateral exchanger while *T. albacares* only has one. *Euthynnus* and *Auxis* (Figure 1) have only a small pair of epaxial heat exchangers.

Thermal Profiles of Fish with Central Exchangers

Lateral midplane thermal profiles of *T. albacares* and *K. pelamis*, taken in the red muscle just posterior to the pectoral fins, illustrate general differences in thermal profiles and body temperatures between these species, *E. lineatus*, and *T. thynnus* (Figure 4). *Katsuwonus* and *Euthynnus* have much warmer core temperatures than *T. albacares*, but warmest temperatures in *Euthynnus* are restricted to a fairly narrow zone around the vertebral column. *Euthynnus'* profile therefore seems related to its poorly developed lateral exchangers (also red muscle is very thick in the center and thinner laterally, Figure 1) and, based on structural similarities, this type of thermal profile would be predicted for *Auxis*. *Katsuwonus* on the other hand, with its lateral exchangers has heat widely distributed across its body.

Thunnus albacares, with a small central exchanger and well-developed lateral exchangers has a widely distributed warm region although it is much cooler than *K. pelamis* and *E. lineatus* (Figure 4). The dimensions of *T. albacares'* cutaneous vessels increase at a much faster rate with increased body weight than do the dorsal aorta and posterior cardinal vein, and in larger fish a greater proportion of blood flow would occur through lateral vessels which might change the thermal profile.

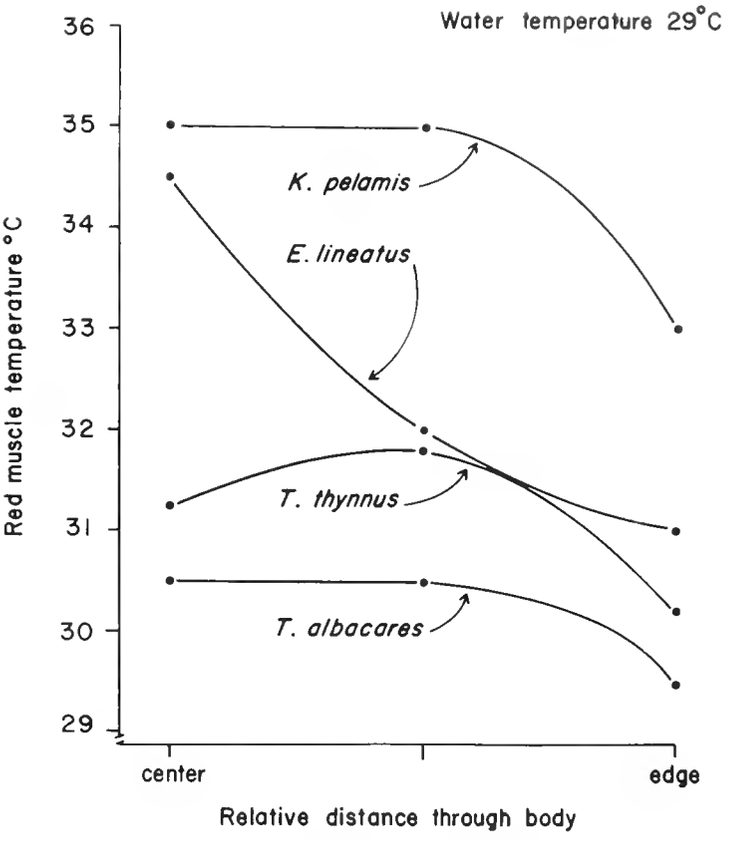

FIGURE 4.—Lateral midplane thermal profiles from the center (near the vertebrae) to the edge (subcutaneous) of red muscle in four species of warm-bodied fish. (Data for *Thunnus thynnus* were provided by F. G. Carey, that for *Euthynnus lineatus* are from Graham 1973).

COMPARISONS WITHIN THE GENUS *THUNNUS*

Heat Exchangers and Thermal Profiles in *T. albacares* and *T. thynnus*

Comparative studies of the vascular anatomy of *Thunnus* show different levels of structural complexity in the heat-exchanging systems (Kishinouye 1923; Godsil and Byers 1944; Gibbs and Collette 1967) which relate to thermal profiles and body temperatures. In *T. thynnus*, lateral heat exchangers are used solely (Carey and Teal 1966). Two rows of retial vessels emanate from each cutaneous artery and vein (only one row occurs in *T. albacares*), and these extend axially for a long distance (Carey et al. 1971). Reliance upon cutaneous circulation is so extensive in *T. thynnus* that the dorsal aorta is reduced in diameter and the posterior cardinal vein is absent. In warm water *T. thynnus* is about the same temperature as *T. albacares*, but its thermal profile (Figure 4) reflects the exclusive presence of lateral heat exchangers in that warmest temperatures are found in the middle of the muscle, while the center of the fish is cooler (Carey et al. 1971). (Again, thermal profiles probably change with body size.)

Anatomical Features and Phyletic Groupings Related to the Presence or Absence of Complete Vertebral Circulation

In their comprehensive study of the genus *Thunnus*, Gibbs and Collette (1967) recognized seven species which, on the basis of 18 characters, were separated into two phyletic groups: the bluefin tuna group, *T. thynnus*, *T. alalunga*, and *T.*

maccoyii; and the yellowfin tuna group, *T. albacares, T. atlanticus,* and *T. tonggol.* (The seventh species, *T. obesus,* has traits in common with both groups and will be discussed later.) Several of the characters used (Gibbs and Collette 1967, Table 4) to distinguish these groups are related to the presence or absence of complete vertebral circulation (both a dorsal aorta and posterior cardinal vein present). The yellowfin tuna group has a posterior cardinal vein, the bluefin tuna group does not. Another striking difference is the presence of large striations and vascular cones on the livers of fish in the bluefin tuna group. The importance of this is discussed below.

There are several structural modifications in the vertebrae of the yellowfin tuna group which permit the passage of more or larger blood vessels through the haemal arch. Prezygapophyses arise far more ventrad on the haemal arch, postzygapophyses are longer, and the inferior foramina are larger (Gibbs and Collette 1967, Figures 10-13). In describing these vertebrae, Gibbs and Collette (1967:80) remarked that the development of the vertebral openings and processes in the yellowfin tuna group is almost as complex as that in *Auxis, Euthynnus,* and *Katsuwonus.* The presence of complete vertebral circulation and appropriate modifications in the vertebral column suggested to me that other species in the yellowfin tuna group, in addition to *T. albacares,* may have central heat exchangers. I have examined a preserved section of vertebral column from *T. atlanticus* (collected in the Gulf of Mexico and sent to me by F. G. Carey) and *T. tonggol* (obtained by G. Sharp) both of which have a central exchanger like that of *T. albacares.*

ADAPTIVE SIGNIFICANCE OF DIFFERENT HEAT EXCHANGERS, BODY TEMPERATURES, AND THERMAL PROFILES

Heat exchangers in *T. albacares* differ from those of *K. pelamis* and *E. lineatus,* and among these three species, there are marked differences in body temperatures and thermal profiles (Figure 4). *Thunnus albacares* and *T. thynnus* also have different heat exchangers, different body temperatures, as well as different thermal profiles depending on body size. Are there morphological features related to locomotion, or ecological factors, such as geographical distribution patterns or feeding behavior, that would explain thermal and anatomical differences between *K. pelamis* or *E. lineatus* and *T. albacares* or between species of *Thunnus*?

Comparisons Within the Genus *Thunnus*

The morphologies and locomotion of *T. thynnus* and *T. albacares* have not been compared. There are some data; however it is diffuse and mostly anecdotal, and it does not suggest functional differences in these two species or in the bluefin and yellowfin tuna groups of *Thunnus.*

If species in the yellowfin and bluefin tuna groups are compared on the basis of existing body-temperature data (cf. Carey et al. 1971, Table 1), it is apparent that species in the yellowfin tuna group have lower relative temperatures than those in the bluefin tuna group. Ambient water temperatures are not the same for these different species, and only a general comparison is possible. Still, these differences agree with the known differences in *T. albacares* and *T. thynnus* (Carey and Teal 1969b; Carey 1973) and are suggestive of a general trend of body-temperature differences that might in turn reflect a significant functional difference between the two taxonomic groups.

A feature in the natural history of species in the yellowfin and bluefin tuna groups that clearly separates them, and relates to their anatomical and temperature differences as well, is the water temperature that they normally inhabit. *Thunnus maccoyii* and *T. alalunga* of the bluefin tuna group occur only in cool water while *T. thynnus,* because of its thermoregulatory ability, is wide ranging and may occur in waters from 6° to 30°C but seems most common in the range 16° to 22°C (Gibbs and Collette 1967; Carey and Teal 1969b). Of the yellowfin tuna group, *T. albacares* usually occurs from 20° to 28°C (Schaeffer et al. 1963), and both *T. tonggol* and *T. atlanticus* are strictly tropical species (Gibbs and Collette 1967).

Several facts suggest that incomplete vertebral circulation in the bluefin group is a specialization for living in cooler water and that central heat exchangers are a primitive character related to the occurrence of the yellowfin tuna group in tropical waters. First, central heat exchangers, being restricted to within the haemal arch, are, of necessity small and therefore have limited heat-exchanging capacity. Thus, in cool water, and, given that red muscle is large and located at varying distances away from the vertebrae, a small central heat

exchanger may prove insufficient to maintain a warm temperature. Carey and Teal (1966, 1969b) pointed out the obvious insulative value of having a large lateral heat exchanger between the warm muscle and cool water. Also, in cool water it may not be efficient for heat conservation to pump a large volume of cool blood (from the gills) into the center of the body via the dorsal aorta, and this might explain why the dorsal aorta in *T. thynnus* is small. Indeed, the lower core temperature found in *T. thynnus* may result from the small volume of unheated blood that does flow through the dorsal aorta. Another vascular specialization that appears directly related to the cool-water distribution of the bluefin tuna group is the presence of vascular bundles on their livers which enables these fish to warm their viscera, thus facilitating digestion in cooler water.

A consideration of the bigeye tuna, *T. obesus*, substantiates the idea that central heat exchangers and ultimately complete vertebral circulation are lost as tuna species evolve into cooler habitats. Although *T. obesus* and *T. albacares* have practically the same latitudinal distributions (Gibbs and Collette 1967), the former occurs in deeper and therefore cooler water (Kishinouye 1923:390 as *Parathunnus mebachi*, a synonym for *T. obesus*). This aspect of the distribution of *T. obesus* thus makes it intermediate, in terms of its thermal habitat, to that of the bluefin and yellowfin tuna groups. *Thunnus obesus* is also morphologically intermediate to the bluefin and yellowfin tuna groups of *Thunnus*. It has complete vertebral circulation and vascular bundles on its liver (Gibbs and Collette 1967) yet, F. G. Carey (pers. commun.) who has extensively studied this species reports that it does not have a central heat exchanger. With respect to body temperatures, thermal profiles, and the structure of its lateral heat exchangers, *T. obesus* closely resembles *T. thynnus* (Carey and Teal 1966). Thus for the bigeye tuna, which in terms of adapting to cool water appears to be at an intermediate position between the yellowfin and bluefin tuna groups, a central heat exchanger is not present although complete vertebral circulation persists. With respect to the latter, however, and perhaps underscoring the de-emphasis of vertebral circulation, it is relevant to point out that although *T. obesus* does have a posterior cardinal vein, Godsil and Byers (1944:114) describe it as "relatively small" and note that it fuses anteriorly with the right cutaneous vein.

Elevated Body Temperatures and Locomotion in Skipjack Tunas and *T. albacares*

Studies of scombrid locomotion (Fierstine and Walters 1968; Magnuson 1970, 1973) suggest that elevated body temperature in skipjacks, while related to their requirement for a faster typical (basal) speed, primarily contributes to their higher burst swimming speed.

Magnuson (1970, 1973) pointed out that scombrids are negatively buoyant and that the skipjack tunas, which lack a gas bladder, are even more negatively buoyant than is *T. albacares*. To compensate for this, and to maintain hydrostatic equilibrium, skipjack tunas must swim more rapidly. Magnuson has argued that the need for a faster basal speed correlates well with a significantly higher amount of red muscle found in skipjack tunas (about 8% of body weight in *Katsuwonus* and *Euthynnus*, compared with 7.4% in *T. albacares* of the same size) and with their slightly greater amounts of blood hemoglobin (Magnuson 1973, Table 7).

The amount of red muscle of course bears an important relationship to body temperature. In warm-bodied fish, retia supply blood to red muscle which is highly aerobic. Red muscle is the principal organ used for basal swimming (Rayner and Keenan 1967), and therefore it is the principal site of thermogenesis. (White muscle mainly functions in burst swimming.) Thus skipjack tunas, to maintain a high basal speed, have a large mass of red muscle, and it could be logically concluded that to augment power output, the capacity to conserve heat and keep swimming muscles warm has evolved in skipjack tunas. The difficulty with this idea however is that other scombrids such as the Pacific bonito, *Sarda chiliensis*, have minimum speed requirements as high as those of the skipjack tunas (Magnuson 1973), but are not warm-bodied, nor do they have high hemoglobin levels or large amounts of red muscle. This obviously indicates that elevated body temperatures and high amounts of hemoglobin and red muscle in the skipjack tunas, while contributing to the sustenance of a high basal speed, must have other functions as well.

Further comparison of *Sarda* with *Euthynnus* provides valuable insight to the significance of elevated body temperature to burst swimming. *Sarda velox* and *E. lineatus* (Figure 5) attain about the same size and are morphologically

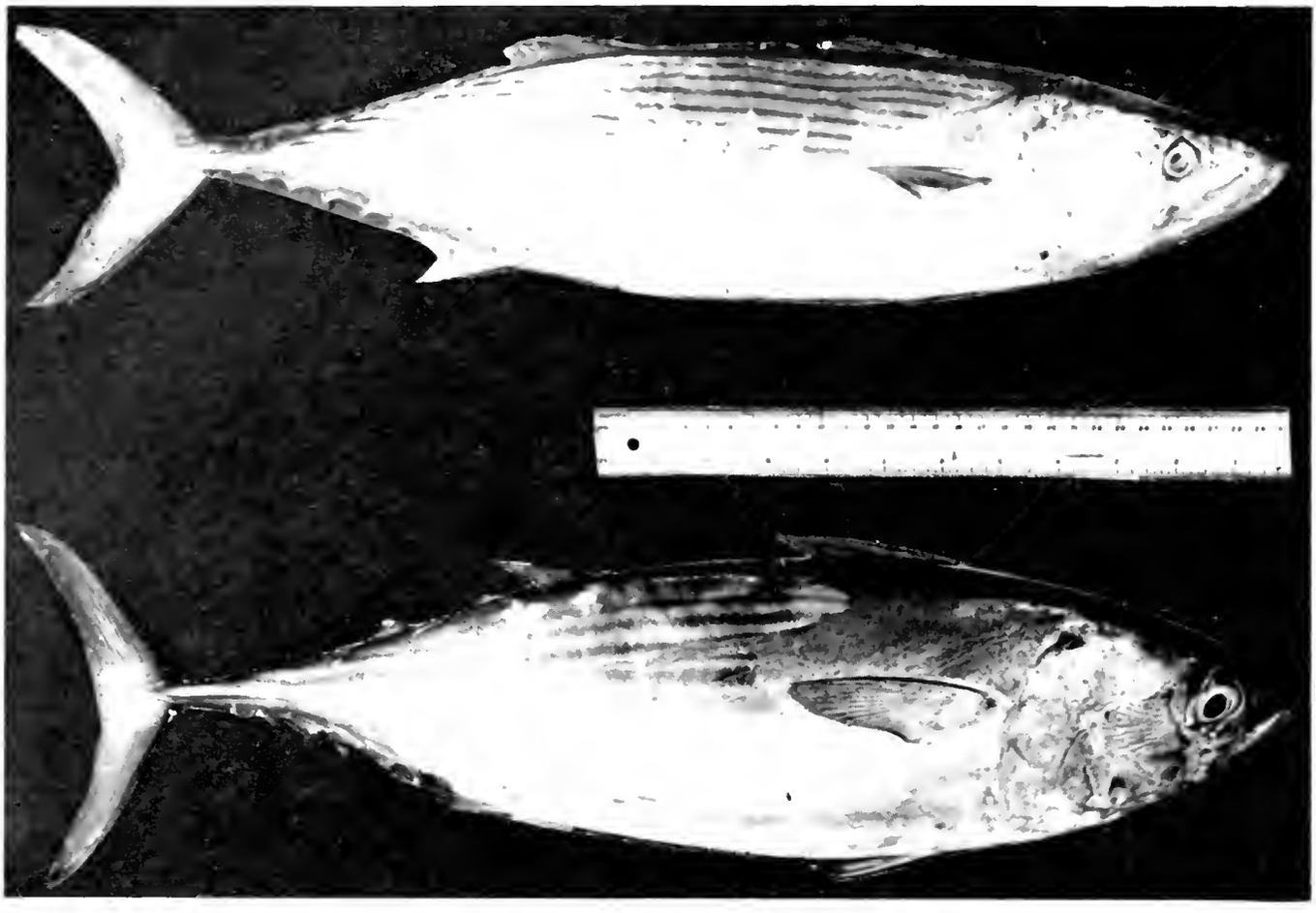

FIGURE 5.–The bonita, *Sarda velox*, (top) and the skipjack tuna, *Euthynnus lineatus* (bottom). Note differences in body shape and pectoral and caudal fin size and shape.

similar. These species also have similar distributions and, in the Gulf of Panama, they occur in the same areas and eat similar prey (crustaceans, squid, and small fishes; pers. obs.) although *Sarda* has a bigger mouth and large teeth. The different mouths and other differences suggest that the swimming capability of these species are also different. *Sarda* has a smaller pectoral fin (Magnuson 1973; Figure 5, this paper) and a lower caudal fin aspect ratio (Fierstine and Walters 1968, Table 7). Its red muscle is not as well developed as that in *Euthynnus* (Fierstine and Walters 1968:17), and *Sarda* has much less blood hemoglobin (Klawe et al. 1963). Finally, a very striking difference exists in the maximum burst speeds of *E. affinis* and *S. chiliensis* (Magnuson 1973, Table 6). In fact, the three warm-bodied species listed by Magnuson (Table 6), all have burst speeds nearly double those of *S. chiliensis*, suggesting that elevated body temperatures, coupled with morphological adaptations, greatly increase the maximum swimming speed. The principal contribution of high body temperature to burst swimming is probably the maintenance of a thermal profile that warms large portions of white muscle.

For *Katsuwonus*, *Euthynnus*, and *T. albacares*, which are all tropical species, there are differences in several structures related to locomotion such as caudal fin aspect ratio and the amount, distribution, and shape of red muscle (Fierstine and Walters 1968). It is reasonable to assume that these differences, combined with elevated body temperature, must confer different capabilities for acceleration, maneuverability, and sustained swimming on different species. One difficulty with the data presently available however is that *T. albacares* grows to be much larger than skipjack tunas, and allometric growth is known or thought to occur in several locomotion-related structures (see discussions by Gibbs and Collette 1967; Magnuson 1973). Without quantitative data on growth patterns of these features, their contribution to locomotion cannot be fully evaluated.

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EXPERIMENTAL STUDIES OF ALGAL CANOPY INTERACTIONS IN A SEA OTTER-DOMINATED KELP COMMUNITY AT AMCHITKA ISLAND, ALASKA

PAUL K. DAYTON[1]

ABSTRACT

Studies on the results of competitive interactions between three kelp canopy guilds were conducted in a community in which herbivorous invertebrates have been largely removed from shallow water (approximately 20 m) by sea otters. Small sea urchins observed in the haptera of kelps all disappeared following the canopy removal, suggesting that the canopy itself offers a modest refuge from their predators. Experiments prove that the largest alga, *Alaria fistulosa*, behaves as a fugitive species with respect to *Laminaria* and *Agarum* species in spite of the structural dominance of a floating canopy. Vegetative regeneration may give *Laminaria longipes* an advantage over other *Laminaria* species, *Alaria*, and presumably *Agarum cribrosum* following disturbances in very shallow water (<5 m). *Laminaria* species suppress *Agarum* growth (and recruitment) in moderate depths (5-20 m) where either *Laminaria* or *Agarum* suppresses growth of red algal turf beneath them, and where both *Laminaria* and *Agarum* must be removed to allow recruitment and growth of *Alaria fistulosa*. Although kelps were observed to depths of 30 m, their lower distribution appears primarily limited by sea urchin grazing.

Few natural communities are so influenced by one population as is the nearshore marine community dominated by the sea otter, *Enhydra lutris* Linn. The nearshore community at Amchitka Island, Alaska, is especially interesting in this regard because for almost 40 yr it has had a sizable sea otter population. This population has been at or near its carrying capacity for at least 20 yr (Kenyon 1969; Estes and Smith 1973), and is thus one of the few localities where the sea otter can be found in a natural balance with the rest of its community. The sea otter exerts its powerful influence in shallow water, where its predation on diverse kinds of invertebrates is remarkably efficient. In addition to drastically reducing populations of motile herbivores (McLean 1962; Ebert 1968; Lowry and Pearse 1973; Estes and Palmisano 1974), the sea otters eat many sessile animals and may release the algae from potential space competition with many potentially competitively important species such as the bivalves *Mytilus edulis*, *Modiolus modiolus*, and *Pododesmus macroschisma*, and the barnacles *Balanus* spp. The algal community at Amchitka Island, then, offers unusual opportunities to evaluate algal-algal interactions in the natural absence of herbivores and animal space competitors. Such interactions might suggest important competitive components of the algal "niches."

The sublittoral association of perennial algae at Amchitka has four separate canopies (Figure 1). *Alaria fistulosa* P. et R. is a conspicuous kelp with long floating fronds that form a canopy on the surface (Kibbe 1915). The thickest *Alaria* canopy is usually found in relatively shallow (< 5 m) water. The second canopy level is composed of the following stipitate *Laminaria* species: *L. groenlandica* Rosenvinge, *L. dentigera* Kjellman, *L. yezoensis* Miyabe, and *L. longipes* Bory. This canopy can be found from the intertidal to depths of approximately 20 m. The third canopy is usually composed of *Agarum cribrosum* Bory with short stripes and large broad fronds lying prostrate on the substratum. This canopy of prostrate kelp occurs between 10 and 20 m. Finally there is a turf composed of numerous species of red algae and occasional clumps of green algae, especially *Codium ritteri* Setch. et Gardn. and *Cladophora* spp. The fact that the canopies tend to occupy nonoverlapping patches in shallow (< 10 m) water suggests that there are competitive interactions between the species comprising the canopies. This paper discusses tests of a series of hypotheses

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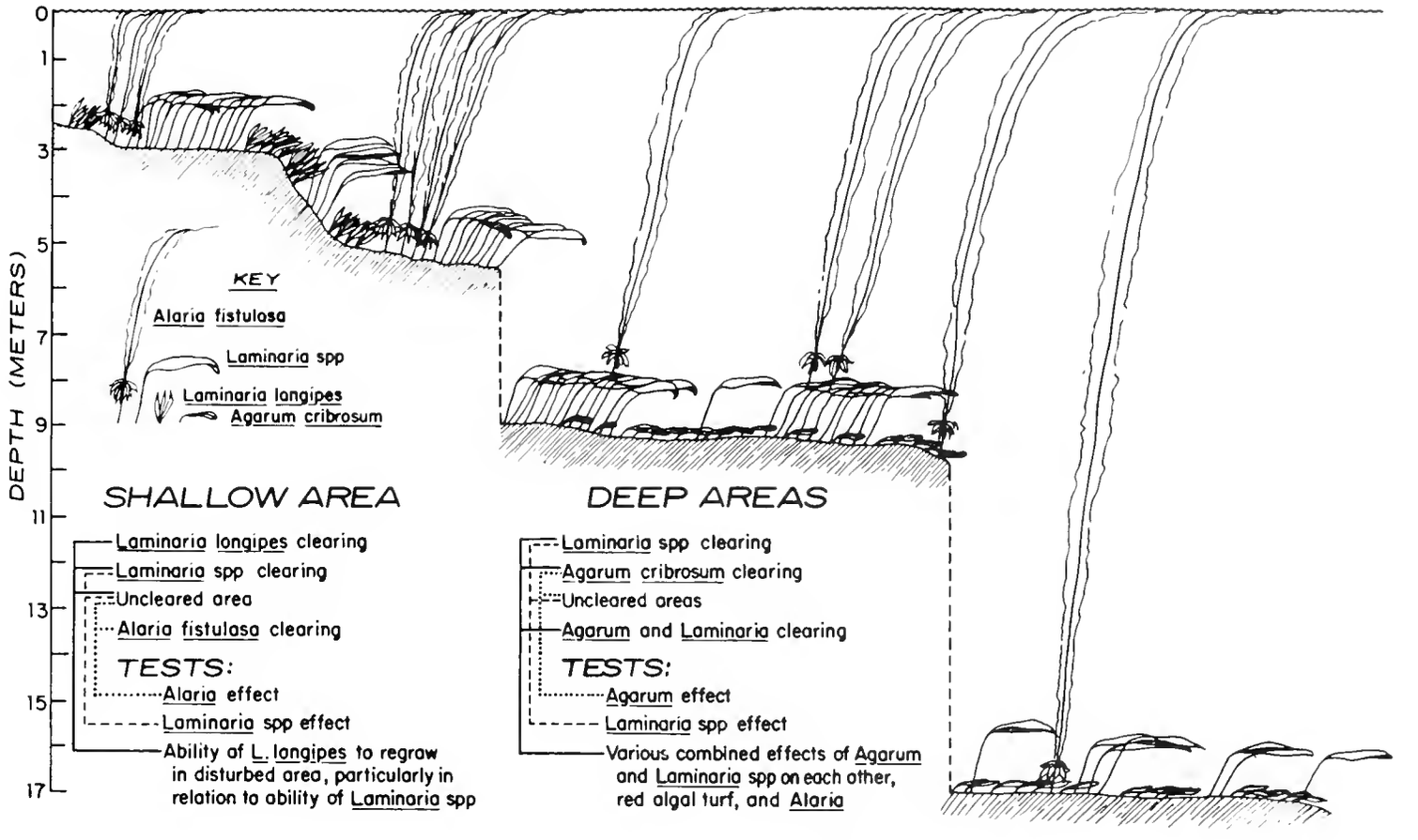

FIGURE 1.—Drawing of the kelp canopies at three different depths. *Laminaria* spp. refers to the large and very similar stipitate *L. groenlandica*, *L. dentigera*, and *L. yezoensis* which seem to occupy broadly overlapping depth profiles but form identical canopies because the stipe lengths and frond sizes are very similar. Diagrams of the experimental design testing hypotheses about the competitive effects between canopies is included for the two manipulated areas.

about the competitive effects these canopies have on each other, the role of physical disturbance in canopy composition, and a gradient of herbivore pressures in deeper waters, where the sea otter foraging becomes less efficient.

METHODS

This research was done in July 1971 and April 1972 in a small bay between the remains of the old Constantine jetty and Kirilof Point on the Bering Sea. A total of 34 dives were made during the study. There were two study sites, a nearshore shallow (< 5 m) area beside an old quarry and a deeper (>7 m) reef about 150 m offshore. Immediately offshore in the shallow area there is a very heavy summer canopy of *Alaria* mixed with a dense growth of annual brown algae such as *Cymathere triplicata* (P. et R.) J. Ag., *Desmarestia intermedia* P. et R., and numerous species of red algae representing such genera as *Ptilota*, *Hypophyllum*, etc. Offshore from this dense algal band, but still in the shallow area, are distinct patches of *Alaria* with thick canopies floating on the surface and patches of a very solid secondary *Laminaria* canopy. There are two *Laminaria* growth forms in the more shallow (< 5 m) area: *L. groenlandica*, *L. dentigera*, and *L. yezoensis* are solitary plants with one heavy 50-150 cm stipe per plant; *L. longipes* has thin multiple 20-40 cm stipes from a single rhizomelike holdfast (Markham 1968, 1972). The third prostrate canopy is represented in shallow water by scattered individuals of the heavy brown alga *Thalassiophyllum clathrus* (Gmelin) P. et R. The deeper offshore reef has a scattered and relatively thin (0-20%) canopy of *Alaria* and in the more shallow (7-12 m) levels a very thick canopy cover of *Laminaria* spp. With increasing depth the *Alaria* density decreases and the *Laminaria* is gradually replaced by *Agarum cribrosum* which forms the third prostrate canopy.

The experimental sites were chosen on the basis of distinct patches of the respective canopies to be manipulated and on the ease of shore access and relocation. Pruning shears were used to clear areas by cutting the stipes just above the holdfasts. In every case an immediately adjacent area was monitored as a control.

Methods of estimating percent canopy cover varied. The *Alaria* canopies represent visual estimates. The 100% covers were very thick and in these cases the floating stipes seemed to form an almost impenetrable wall in the water column. A few photographs taken of the *Alaria* canopy in areas where it had less than 100% cover suggest that the visual estimates in these locations were conservative. The other percent cover estimates were made with the aid of 0.25 or 0.16 m^2 quadrats which, in larger areas, were placed haphazardly, and in restricted experimental areas were placed systematically in such a way that the entire experimental area was sampled. The actual measurements were usually taken planimetrically from photographs as defined earlier (Dayton 1971). There were a number of cases in which visual estimates were used because of camera malfunction, running out of film, etc. I have compared such visual estimates with planimeter measurements and found that they are usually within 5% and always within 10% of each other (Dayton 1971, 1975). The data are presented as means because the actual sample numbers varied (but except where stated, were never fewer than 10); the variance is given as standard error.

RESULTS

Shallow Area

This area is covered with an extremely thick growth of algae and is generally characterized by a conspicuous absence of herbivores (Estes and Palmisano 1974). I was surprised to find sea urchins[2] among the *Laminaria* (especially *L. longipes*) haptera and holdfasts upon removing the canopies for the experiments discussed below. The sea urchins may exist in these sheltered refuges because the canopy is both very dense and relatively close (25-35 cm) to the substratum, thus seriously reducing the foraging efficiencies of their visual predators. This sea urchin-refuge hypothesis was supported by the observation that the sea urchins remained untouched in both clearings from 3 and 6 July through 8 July, but all were gone on 9 July. I suspect that they were taken by a sea otter that found the cleared patches, as one was observed foraging in the vicinity on the morning of 9 July. However, predation by the common eider, *Somateria mollissima* (Williamson and Emison 1969), and emigration are other possible explanations. At any rate, the small size (< 15 mm) and scarcity of these sea urchins do not seriously affect the contention that the herbivores have largely been eliminated from this area. The elimination of the grazing pressures makes the competition-based hypotheses discussed below more meaningful.

Hypothesis I

The *Alaria fistulosa* canopy excludes *Laminaria* spp. This hypothesis was tested (a) by cutting *Alaria* from several rocks and observing whether *Laminaria* recruited in the absence of *Alaria* and (b) by cutting *Laminaria* and observing potential *Alaria* recruitment. *Alaria* and probably *Laminaria* spp. were fertile at the time of the cutting. Significantly more *Laminaria* recruitment into *Alaria* clearings than into uncleared controls would support the hypothesis, whereas significantly more *Alaria* recruitment into *Laminaria* clearings than into the control would negate the hypothesis and suggest the truth of the converse hypothesis, that *Alaria* behaves as an opportunistic or fugitive species (Dayton 1973, 1975) in the presence of competition with the competitively dominant *Laminaria* spp. The results of such clearings at a depth of 5 m (done 3 and 4 July 1971) are presented in Table 1. The

[2]Opinions are divided whether the Amchitka sea urchin is *Strongylocentrotus drobachiensis* or *S. polyacanthus*.

TABLE 1.—Effects of canopies of *Alaria fistulosa* and *Laminaria* spp. on each other and on the cover of red algae in the nearshore experimental area (25 m^2) at 3-5 m depth. The data are presented as percent cover with the variance presented as the 95% confidence interval about the mean. Data presented without variance were visual estimates. Control no. 1 suffered heavy algal loss from winter storms. The mean density of *A. fistulosa* in the April 1972 *Laminaria* removal experiment was 14.7 (± 1.1, SE) in ten 100 cm^2 quadrats.

	Alaria removal		*Laminaria* removal		Control no. 1		Control no. 2	
Canopy species	July 71	April 72	July 71	April 72	July 71	April 72	July 71	April 72
Alaria fistulosa	[1]75	20.3 ± 20.0	5	100	45	100	10	5
Laminaria spp.	35.7 ± 15.0	39.2 ± 12.1	[1]87.2 ± 7.9	0	[2]100 ± 0	25.3 ± 20.0	100 ± 0	100 ± 0
Red algal turf	40.4 ± 10.7	45.6 ± 13.6	15.3 ± 8.6	45.5 ± 4.6	10.2 ± 5.8	40.2 ± 12.0	5.4 ± 5.3	15.8 ± 7.9

[1]Signifies that the canopy was experimentally removed.
[2]Canopy ripped out during winter storms.

Alaria forming a 75% canopy were removed from a 25 m² area and no significant change was observed in the *Laminaria* or red algal turf canopies by April 1972. But the removal of an 87% cover of *Laminaria* produced dramatic (5-100%) increases in the *Alaria* cover and a significant ($P<0.001$) increase in the red algal turf covers (t-test run on data normalized with an arcsine transformation). The 100% *Laminaria* cover in Control no. 1 suffered heavy damage when two large boulders, rolled about by winter storms, reduced *Laminaria* densities and resulted in significant increases in recruitment of *Alaria* and red algal turf covers ($P<0.01$). In addition to the extremely heavy *Alaria* recruitment in the *Laminaria* removal areas, there were also patches of *Rhodymenia palmata* (L.) Greville, *Ptilota* spp., *Desmarestia* spp., *Cymathere triplicata*, *Chaetomorpha melagonium* (Weber et Mohr) Jutz., and *Coilodesme* spp. No significant changes were observed in Control no. 2. To a certain extent these observations could be explained by a very slow growth rate of *Laminaria* spp. But certainly the hypothesis that *Alaria* dominates in competition over *Laminaria* was negated, and these data strongly support the conclusion that despite the expected competitive advantage gained by forming a surface canopy, *Alaria fistulosa* is not a competitive dominant, but a fugitive species colonizing areas released from competition with the dominant *Laminaria* canopy.

Hypothesis II

The rhizoidal growth pattern of *Laminaria longipes* allows an efficient recovery following a disturbance (Markham 1968). The hypothesis suggests that the removal of an *L. longipes* canopy results in the area being succeeded by its own extensive vegetative regrowth, in contrast to the invasion of many individuals of fugitive species seen following the removal of a mixed species canopy of *Laminaria groenlandica*, *L. yezoensis*, and *L. dentigera*. This hypothesis was tested by cutting the stipes near the holdfasts of a 100% cover of *L. longipes* from a 10 m² patch at a depth of 3 m on 7 July 1971. Fifteen ¼ m² quadrats observed after the 100% canopy was removed showed the following mean substratum covers: 57% (± 4.9, SE) *L. longipes* holdfasts, 7% (± 1.8, SE) sponges and compound tunicates, and 22% (± 5.2, SE) coralline algae, mainly *Clathromorphum* spp. They also showed mean ¼ m² densities of the sea urchin, *Strongylocentrotus* sp., of 17.5 (± 3.8, SE) and the asteroid, *Leptasterias aleutica*, of 1.0 (± 0.3, SE). Spores of the three other *Laminaria* species and of *Alaria* were potentially available from many plants on rocks on three sides of the clearing.

By April 1972, the clearing had been completely recolonized by *L. longipes*, despite the proximity of large plants of the other species. The recovery was so complete that the clearing could only be recognized after a long search located a few "landmarks" (sponges, compound tunicates, and a *Laminaria yezoensis* holdfast with the stipe cut by pruning shears) photographed the previous year. This strongly supports the hypothesis that the rhizoidal growth pattern of *L. longipes* is an effective adaptation for the recovery of its canopy following a disturbance and is in marked contrast to the heavy *Alaria* recruitment following the removal of a nearby *Laminaria* spp. canopy. I was unable to test the obvious hypothesis that this capacity for vegetative growth gives *L. longipes* an advantage over the other *Laminaria* spp. in a disturbed area, but loses a competitive advantage in less disturbed areas because the other *Laminaria* species have a higher, more effective canopy.

Offshore Area

An exploratory dive was made on the deeper offshore reef to investigate the relationship between sea urchin densities and the various algal canopies. Samples were taken from haphazardly placed ¼ m² quadrats. Five samples taken in the 12-15 m range showed means of 44% (± 23.3, SE) cover of *Laminaria* spp. and 62% (± 15.7, SE) cover of *Agarum cribrosum*, and a mean density of 11.2 (± 3.8, SE) sea urchins per ¼ m². In the 15-21 m depth range five samples provided means of 36% (± 13.0, SE) canopy cover of *Laminaria* and 80% (± 4.9, SE) canopy cover of *Agarum* with a mean sea urchin density of 6.4 (± 3.2, SE) per ¼ m². Few identifiable foliose algae were seen below 21 m, but there was a high mean sea urchin density of 30.4 (± 3.7, SE) per ¼ m². In these deeper areas there was almost a complete substratum cover of the encrusting coralline algae *Clathromorphum* spp. and the green alga, *Codium ritteri*. Only four *Alaria* plants were encountered in these 17 samples; all were growing from the top portion of one Laminaria stipe at 11 m.

On 11 and 12 July 1971, a study site was chosen and the data in Figure 2 labelled July 1971 were collected. The differences between these data and those given in the preceding paragraph give an idea of the variation in this area. The inverse relationship between the percent cover of *Laminaria* and *Agarum*, in which the *Laminaria* decreases and the *Agarum* increases with depth and sea urchin density, suggests that in shallow water *Laminaria* competition suppresses the growth of *Agarum*, but that *Agarum*, which has been demonstrated to be highly distasteful to *Strongylocentrotus drobachiensis* (Vadas 1968), is more successful in the presence of a moderate density of grazers. Finally, *Agarum* itself may also have an important competitive effect against *Alaria* and the foliose red algal turf. Grazing pressure and limiting light conditions probably cause the severe reduction of foliose algae in deeper water. These data demonstrating high densities of sea urchins at depths below 20 m agree with the observations of Barr (1971), Estes and Smith (1973), and Estes and Palmisano (1974). This suggests that sea otters at Amchitka do not forage effectively below 18-20 m.

That the experimental area could not be continuously monitored meant that it was not possible to manipulate the sea urchin density, but competitive effects of the algae at this depth were readily testable by selective removal of algal species.

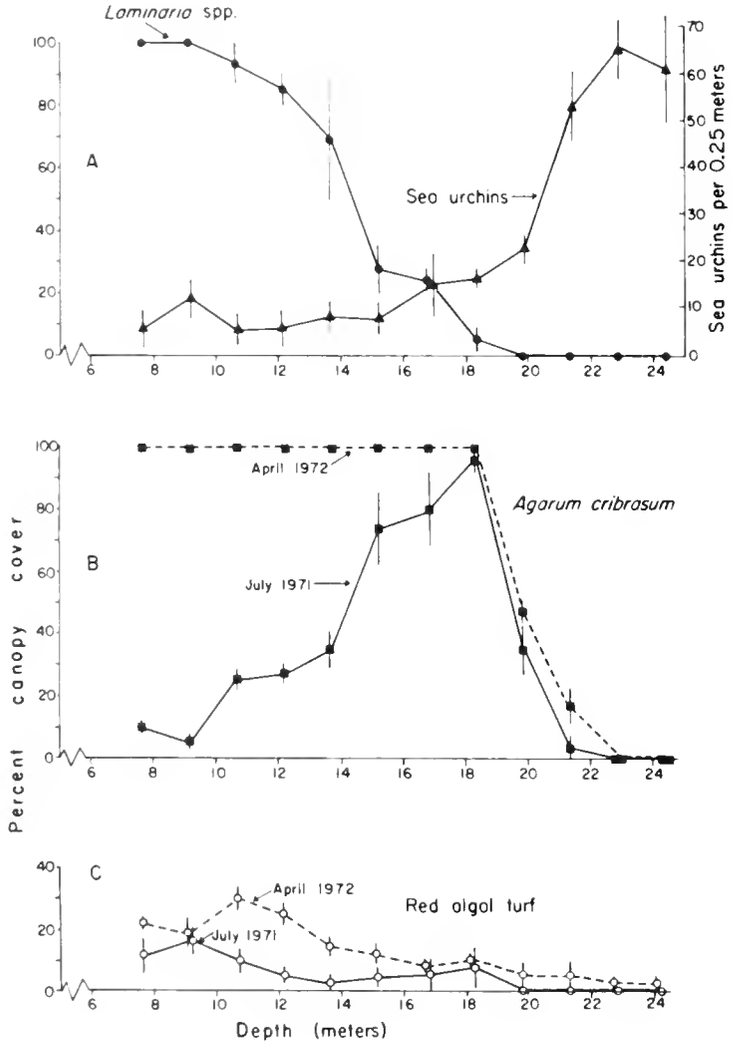

FIGURE 2.—Mean sea urchin densities and percent covers of *Laminaria*, *Agarum*, and red algal turf canopies at increasing depths before (July 1971) and after (April 1972) the *Laminaria* canopy was removed. Figure 2A contrasts the decreasing *Laminaria* cover with increasing sea urchin density in July 1971. Note that the *Agarum* canopy cover at that time shown in Figure 2B is nearly complete only at those depths at which there is reduced *Laminaria* coverage and relatively low sea urchin density. After removal of *Laminaria*, the *Agarum* canopy increased dramatically at the shallower depths. The increase of red algal cover after *Laminaria* removal is shown in Figure 2C. Variance is presented as the 95% confidence interval around the mean.

Hypothesis III

The presence of *Laminaria* spp. has no effect on other algae. This hypothesis was tested by removing a 2-m wide strip of *Laminaria* from the area where the data in Figure 2A were collected. The hypothesis was negated as both *Agarum* and the foliose red algae canopies significantly increased their covers (Figure 2B, C). The spectacular increase in the cover of the *Agarum* canopy certainly resulted partially from growth of the fronds; however, samples taken in April 1971 and repeated in July 1972 at approximately the same spots along the experimental *Laminaria* removal strip, showed that the mean *Agarum* density increased significantly from 4.1 ($\pm$ 0.6, SE; ten ¼ m^2 samples) plants to 15.6 plants per ¼ m^2 (was calculated from ten 1/16 m^2 samples with a mean of 3.9; $\pm$ 0.4 SE). The increase in canopy cover of the red algal turf was less spectacular, but a one-tailed Wilcoxon matched-pairs signed-ranks test of mean percent canopy cover at all depths considered shows a significant ($P<0.005$) general increase after the *Laminaria* were removed, this despite the fact that April may be early in the season for red algal growth. Thus the *Laminaria* canopy in the presence of an *Agarum* canopy has an important effect on other algal species.

Hypothesis IV

The *Agarum cribrosum* canopy alone has no effect on the other algae. This hypothesis was tested by clearing 45-85% covers of *Agarum* from 4 m^2

plots at 9.1- and 16.8-m depths in July 1971. In both cases a 100% canopy of *Laminaria* persisted throughout the experiment. A slight recovery of the *Agarum* population was observed the following April (Table 2), but no significant differences were observed in the numbers or percent cover of the other species. Thus there is, at present, no reason to negate the hypothesis.

Hypothesis V

The *Agarum cribrosum* canopy in the absence of the *Laminaria* canopy has an important effect on the other species of algae. This hypothesis was tested by removing both *Agarum* and *Laminaria* canopies from 4 m^2 plots at 9.1- and 16.8-m depths. These clearings were then compared to those in the adjacent *Laminaria*-only removal experiments at the same depths (Figure 2C). A strict interpretation of this comparison suggests that either a *Laminaria* or *Agarum* canopy or both is sufficient to prevent an increase of red algal turf cover because there is, at those two particular depths, no significant increase of red algal turf in either the *Laminaria*-only or *Agarum*-only removal experiments (Figure 2C, Table 2). This interpretation is equivocal, however, as Hypothesis III demonstrated a slight but significant *Laminaria* effect on the red algal turf. There is no equivocation regarding the effect of the combined *Laminaria* and *Agarum* canopies on the red algal turf which increased from 7 to 49% at 9.1 m and 1 to 38% at 16.8 m (Table 2). These are much more dramatic increases than were observed in the *Laminaria*-only removal areas and convincingly argue for a strong *Agarum* effect in the absence of *Laminaria*. Some of the red algae in this experiment were *Ptilota asplenoides* (Esper) C. Ag., *Laingia aleutica* Wynne, *Hypophyllum ruprechtianum* Zinova, *Constantinea rosa-marina* (Gmelin) P. et R., *Pantoneura juergensii* (J. Ag.) Kylin, *Cirrulicarpus gmelini* (Grunow) Tokida et Masaki, *Turnerella* sp., *Callophyllis flabellulata* Harvey, and *Nienburgia prolifera* Wynne.

The most impressive effect of the *Agarum* canopy in the absence of *Laminaria* was its inhibition of *Alaria* recruitment. In each of the two quadrats from which both *Laminaria* and *Agarum* were removed, the *Alaria* cover, consisting of a heavy recruitment of juvenile plants, increased from 0 to 100% canopy cover (Table 2). The *Alaria* response was particularly impressive because the dense *Alaria* recruitment completely filled, but was perfectly contained within, the *Agarum*-and-*Laminaria* removal patches. The mean density increased from 0 to 22.8 *Alaria* plants per 1/16 m^2 ($\pm$ 3.5, SE). In contrast to this result in the *Agarum*-and-*Laminaria* removal area, there was no *Alaria* recruitment in the rather extensive area from which *Laminaria* alone was removed (Figure 2). This result also contrasts sharply with those of the shallow *Laminaria* removal experiments (Table 1), in which no *Agarum* canopy level existed. An adjacent control was monitored for each experimental clearing; no changes were observed in any of the controls.

The above comparisons demonstrate that both the secondary *Laminaria* canopy and the tertiary *Agarum* canopy individually can significantly reduce the recruitment of *Alaria*, the species which forms the primary surface canopy. Further evidence of the intense competition in the deeper area where both understory canopies exist is provided by the observation that, of 100 *Alaria* plants surveyed, 79 were utilizing secondary substrata with their holdfasts attached high on *Laminaria* stipes (Figure 1).

TABLE 2.—Effects of *Agarum cribrosum* and combined *Agarum-Laminaria* spp. canopies on each other, red algal turf, and *Alaria fistulosa* at 9.1-m and 16.8-m depths in the offshore study site. Each experimental clearing area was 4 m^2. The data are presented as percent cover with the variance presented as the 95% confidence interval about the mean; data presented without variance are visual estimates.

	Depth: 9.1 m				Depth: 16.8 m			
	Agarum (only) removal		*Agarum* and *Laminaria* removal		*Agarum* (only) removal		*Agarum* and *Laminaria* removal	
Canopy species	July 71	April 72	July 71	April 72	July 71	April 72	July 71	April 72
Laminaria	100 ± 0	100 ± 0	[1]100 ± 0	0	100 ± 0	100 ± 0	[1]100 ± 0	0
Agarum	[1]65.3 ± 23.4	11.5 ± 10.2	[1]45.5 ± 16.1	25.8 ± 11.9	[1]85.2 ± 33.4	17.5 ± 7.1	[1]77.4 ± 12.7	11.5 ± 4.0
Red algal turf	11.5 ± 12.9	8.4 ± 10.7	7.0 ± 4.9	49.2 ± 14.0	2.1 ± 5.6	0	1.2 ± 4.0	37.5 ± 10.2
Alaria	0	0	0	100 ± 0	0	0	0	100 ± 0

[1]Signifies that the canopy was experimentally removed.

DISCUSSION

The pattern emerging from these and other (McLean 1962; Lowry and Pearse 1973; Estes and Palmisano 1974) studies of sea otter-dominated communities is that by consuming the populations of invertebrate herbivores, the sea otter has an extremely important role in maintaining the structure of shallow algal communities. In this study, high densities of sea urchins are found below 18-20 m, suggesting that this depth is the lower limit of effective sea otter foraging in this area. It is interesting to note that this depth is much more shallow than the 30-fathom profile speculated by Kenyon (1969). In addition, this seems to be a much more shallow limit to efficient foraging than is exhibited by the California population of sea otters, as I have seen evidence of their foraging to at least 30 m in the Carmel Bay region.

Strong competitive interactions between species of benthic algae appear well expressed in the shallow nearshore waters of the Aleutian Islands which have sea otters. The shallower (3-5 m) waters, subject to severe storm disturbance, are functionally dominated by *Laminaria* species. When the larger *Laminaria* spp. (*L. groenlandica*, *L. dentigera*, and *L. yezoensis*) are removed, either experimentally or by natural storm disturbance, their space is quickly utilized by *Alaria fistulosa*. In contrast, the rhizomelike holdfast with multiple meristems of *L. longipes* appears to be an effective adaptation to disturbance, as it allowed quick regrowth of stipes and fronds after their experimental removal. In deeper water (12-20 m), where there are many sea urchins, *Agarum cribrosum* is one of the dominant algal species. *Agarum*, however, loses in competition for light to solid canopies of *Laminaria* spp., which have erect stipes supporting their fronds above the nearly prostrate *Agarum*. When freed from *Laminaria* competition, *Agarum* significantly increases its cover and abundance. When both *Laminaria* and *Agarum* are removed, there is a bloom of red algal turf and of *Alaria fistulosa*. These tests of competition-based hypotheses are probably valid despite the various depth-related changes in the physical environment because each was compared to immediately adjacent controls.

It is interesting to note that despite having potentially long-lived individuals and the competitively superior adaptation of a floating canopy, *Alaria fistulosa* behaves as a fugitive species with its densest distribution in the highly disturbed immediate offshore area, occurring farther offshore only in areas where two understory canopy levels are removed or by growing on *Laminaria* stipes. This is surprising because quite the opposite situation seems to exist in the southern California kelp community, where *Macrocystis pyrifera* forms a heavy surface canopy which may inhibit the growth of the understory species (North and Shaeffer 1964; Dayton unpubl. data). Although *Alaria* was observed in depths of over 25 m, its lower distribution appears to be restricted primarily by sea urchin grazing.

Other research (Estes and Palmisano 1974; Palmisano in prep.) contrasts the nearshore and intertidal communities of Amchitka with nearby otter-free islands and convincingly demonstrates the powerful role the sea otters have in structuring the nearshore community. This paper has experimentally demonstrated competitive trends between different canopy guilds in an algal community which contains an unusually high number (four) of *Laminaria* species which have semirigid stipes. It is tempting to speculate an evolutionary hypothesis in which the sea otters reduce the herbivore pressure and thus allow a competitive differentiation of niches of these large stipitate kelps. Such hypothetical evolutionary thought has the common and serious flaw of ignoring the roles of extinct species, many of which may have left large and important "vacant niches" (such as those left by the mammal extinctions of the late Pleistocene discussed in Martin and Wright 1967). This problem is particularly acute in the Bering Sea, as Steller in 1751 (reference in Gard et al. 1972) reported the giant sea cow, *Hydrodamalis gigas* (Zimmermann 1780), eating algae in the nearshore and tidal beaches of the Komandorskiye Islands. The large populations reported by Steller and various Russian and German sailors of this huge (ca. 10 tons, Scheffer 1973) kelp-eating (Stejmeger 1936) sirenian surely had important consequences to the kelp populations that weaken any present day speculation of the evolutionary consequences of kelp competition. It may be reasonable, however, to pose the hypothesis that by consuming invertebrate herbivores, particularly sea urchins, the sea otter was indirectly responsible for the high productivity of large algae necessary to maintain the sea cow populations. Such an hypothesis is supported by the overlap of the otter

and sea cow populations in the Pleistocene (Jones 1967; Kenyon 1969; and Gard et al. 1972). This relationship is nicely diagrammed in Scheffer's (1973) touching story of the last day of the sea cow.

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PRODUCTION OF TWO PLANKTONIC CARNIVORES (CHAETOGNATH AND CTENOPHORE) IN SOUTH FLORIDA INSHORE WATERS[1]

M. R. REEVE AND L. D. BAKER[2]

ABSTRACT

Seasonal changes in biomass and production of two planktonic carnivores, *Sagitta hispida* Conant and *Mnemiopsis mccradyi* Mayer, were followed in a subtropical inshore marine environment. Production was estimated as the product of mean daily biomass (calculated from the sampled biomass and computed mortality rates) and daily growth rate. The latter was determined from laboratory culture experiments at three temperatures. Seasonal fluctuations of ctenophore biomass and production were much greater than those of chaetognaths. Mean daily production in milligram carbon per square meter was 2.00 and 4.80 for *Sagitta* in Card Sound and Biscayne Bay respectively, and 1.01 for *Mnemiopsis* in Biscayne Bay. The ctenophore was absent from Card Sound, possibly because the zooplankton standing crop was an order of magnitude lower than in Biscayne Bay (excluding ctenophores). Average production/biomass ratios were 0.31 for *Sagitta* and 0.12 for *Mnemiopsis*.

Most production data for zooplankton are restricted to the herbivorous copepods in temperate and cold waters (see review of Mullin 1969; Mullin and Brooks 1970; Riley 1972). Estimates for carnivores are very few and include *Sagitta elegans* (McLaren 1969; Zo 1969; Sameoto 1971) and *Pleurobrachia bachei* (Hirota 1974).

As pointed out by Mullin (1969) there is no simple technique for the measurement of production of natural populations of zooplankton comparable to the relatively routine ^{14}C uptake method for the determination of primary production by phytoplankton. Unlike the phytoplankton, which share a common characteristic of a single trophic level, zooplankton extend over at least two trophic levels, and an individual species may vary its trophic status on the basis of food availability or life history stage. In addition, zooplankton range in size from 20 μm or less to 20 cm or more and have widely differing growth and reproduction rates. Attempts to measure total zooplankton production have been made, especially where a single species dominates the population over a period (e.g., Cushing and Vucetic 1963) or where a single group (such as copepods) dominates and is treated as a unit (e.g., Riley 1972), and most recently by relating respiration to temperature and body weight and applying these data to the plankton biomass of the Kuroshio (Ikeda and Motoda in press).

The data reported below are based on the individual species approach, using experimentally determined growth rates to compute production from environmental biomass estimates for two planktonic carnivores, widely separated phylogenetically but dependent upon the same source of food.

STUDY SITE AND SAMPLING METHODS

The study area consisted of Biscayne Bay and Card Sound which form part of an extensive system of shallow, warm, semiestuarine, and semienclosed interconnected water bodies typical of the coastal region of a large part of Florida. Zooplankton sampling programs were conducted at 4 stations on 28 dates throughout 1971 in Card Sound and at 11 stations on 26 dates from October 1970 to February 1972 in central Biscayne Bay. Detailed reports of these programs were given by Reeve and Cosper (1973) and Baker (1973), respectively.

In both locations, surface tows were made with a metered, ½-m mouth diameter net of 200-μm mesh. In addition, a similar net of 64-μm mesh was used in Card Sound. In Biscayne Bay, a 1-m, 705-μm mesh net with a 14-liter flexible, vinyl cod end was employed to collect ctenophores. It was not used routinely in Card Sound because ctenophores

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were not encountered. Zooplankton were thus collected from both locations using two nets (which were towed simultaneously), one of which (the 200-μm mesh) was common to both locations.

An extensive series of samples was collected in Card Sound to check on the adequacy of the 64- and 200-μm mesh ½-m mouth diameter nets in sampling the entire size range of the population of *Sagitta hispida*. In comparisons between a 64- and 35-μm mesh, the size-frequency distribution of the population was not significantly different. Absolute numbers often differed, but this was attributable to the rapid clogging of 35-μm mesh, which rendered flowmeter readings unreliable, and was why this mesh was not used routinely. The 64-μm mesh net, which filtered less than 50% of the volume of water of the 200-μm mesh in the same time, collected fewer of the larger size chaetognaths than the 200-μm mesh, indicating that a greater proportion of the larger animals were avoiding the smaller meshed net. Comparative tests between the 200-μm ½-m diameter net and a 200-μm 1-m net (which filtered 3 times more water) did not indicate that the larger net caught either a larger absolute number, or a higher percentage, of the larger size classes per volume filtered. These data are available by writing to the first author. It appeared, therefore, that the two standard ½-m nets utilized in the sampling program quantitatively collected the entire size range of this species in the surface water.

Vertical distribution of *S. hispida* Conant in the 3-m water column was investigated on six dates during the year using both towed nets and a pump as described by Reeve and Cosper (1973). There was considerable variability in vertical distribution between sampling dates, due in part to variability in incident radiation and water turbidity, but it was estimated that the numbers per cubic meter from surface hauls should be multiplied by a factor of 1.54 to obtain a mean water column density per cubic meter in the 3-m deep water column. This factor was very close to the 1.45 calculated for the plankton as a whole, by Reeve and Cosper (1973). As noted previously (Reeve and Walter 1972), *S. hispida* has the ability to attach itself to substrates in the laboratory and lays its eggs on surfaces in clumps. It does not attach significantly until near maturity and even then, most of the population is usually to be found swimming in the water column in aquaria. We believe that the biomass estimates of our plankton samples were not biassed downwards due to this behavioral pattern, as eggs are usually laid at night while the plankton samples were taken during the day, and the vertical sample series gave no indication of a higher proportion of older animals nearer the bottom. On the other hand, comparisons of the size-frequency distribution of a population sampled with a towed net and with an Okelmann sledge lightly skimmed across the bottom, which is an effective means of sampling the benthic *Spadella*, usually yielded a few mature individuals in the larger size classes which were absent from the net. The sledge, however, only provided a qualitative sample and it was not possible to adjust the biomass of Table 1 to take these few animals into account. Our biomass estimates are, therefore, slightly underestimated on this account. No estimates of egg numbers were made, since *Sagitta hispida* does not deposit them in the water column, but attaches them to objects on the bottom.

Ctenophores presented different sampling problems. Lobate ctenophores, such as the genus *Mnemiopsis*, tend to break up easily in nets and are rapidly disintegrated in the usual fixatives. Baker (1973) reported that transference of individual, newly hatched larvae by pipette from one beaker to another would result in the disappearance without a trace of over 90% of these 200-μm diameter animals. It was futile, therefore, to attempt to assess the numbers of eggs or the smallest larvae from net tows, and probably some of size class A (0.8-4.4 mm) were also fragmented beyond recognition. Even so, the pattern of distribution of biomass between the size classes (Table 1) suggests that the fraction contributed by the smallest unsampled or inadequately sampled members of the population is small. It may be presumed that animals in the larger size classes were not avoiding nets, since *Mnemiopsis* is a weak swimmer with no rapid escape behavior, and hence were sampled adequately. No feasible method was devised of making tows near the bottom of this shallow water column with a 1-m mouth diameter net, and pumps were impractical for sampling ctenophores. The only indication we have that *Mnemiopsis* does not exhibit any marked vertical layering are observations by scuba.

Analysis of Samples

The chaetognaths of the preserved samples (all of which belonged to the species *S. hispida*) were

TABLE 1.–Summary of biomass and production data for *Sagitta* and *Mnemiopsis* by size class averaged over the entire survey period.

	Sagitta Size class (live length)								*Mnemiopsis* Size class (live volume)				
	A <2.5	B 2.5–3.7	C 3.8–4.9	D 5.0–6.2	E 6.3–7.4	F 7.5–8.7	G 8.8–9.9	H 10.0–11.3	A 0.0021	B 0.052	C 0.92	D 15.0	E 28.0
Numbers per cubic meter	87.4	66.0	33.3	13.7	3.32	0.40	0.031	0.008	2.90	1.50	0.225	0.157	0.075
Mean duration (days)	12	4.7	2.8	2.7	1.7	2.0	5.5	9	8.7	2.0	17	10	16
Ash-free dry weight per organism (μg)	2.18	10.1	29.5	71.2	132	218	349	531	19.7	507	12,100	140,000	278,000
Ash-free dry weight per size class (μg/m³)	191	667	982	975	438	87.2	10.8	4.2	57.0	761	2,730	22,000	20,900
Daily net production (μg ash-free dry wt/m³)	72.5	244	289	290	63.1	13.1	0.78	0.17	60.9	452	936	1,800	1,860
P/B	.38	.37	.29	.30	0.14	0.15	0.07	0.04	1.1	0.59	0.34	0.08	0.09
Growth 21	0.25	0.25	0.25	0.25	0.25	0.25	0.083	0.044	0.50	0.50	0.21	0.069	0.069
Coefficient 26	0.35	0.35	0.35	0.35	0.35	0.35	0.074	0.007	0.78	0.78	0.23	0.071	0.071
31	0.41	0.41	0.41	0.41	0.41	0.11	0.041		0.65	0.65	0.23	0.069	0.069
Mortality 21		<0.01	0.04	0.15	0.40	0.85	1.5	0.3	<0.01	1.8	<0.01	0.08	
Coefficient 26		<0.01	<0.01	0.55	0.30	3.5	2.0		<0.01	1.1	0.03	0.07	
31		<0.01	0.30	0.90	2.0	4.0			<0.01	0.76	0.05	0.09	

counted and measured in the laboratory. The Card Sound samples from the four stations were pooled for each net on each sampling date in proportion to the filtered volumes they represented (Reeve and Cosper 1973). Aliquots of each pooled sample were taken such that they contained between 50 and 100 organisms. The total body length of each animal was measured (see Reeve 1970). The entire sample was examined for mature animals. The lengths were tabulated in 1-mm preserved length size classes (see next section for conversion to live length). Since two values were obtained for each size class from the Card Sound samples (i.e., one for each mesh size) the larger number was taken as the correct one, on the assumption that the smaller value was due either to avoidance by larger animals of the 64-μm mesh, or escape of the smaller animals through the 200-μm mesh.

The pooled 200-μm Biscayne Bay samples were treated similarly. The numbers of *S. hispida* in Biscayne Bay were estimated by adjusting the numbers in each size class in the 200-μm net to total number on the basis of ratios computed for the 64- and 200-μm counts from Card Sound.

Analysis of ctenophore samples from the 1-m net presented special difficulties, because there was no known satisfactory method of preservation of lobate ctenophores. Following Miller (1970) analysis was performed on deck immediately after recovery of the net (see Baker 1973). The contents of the cod end were emptied into a stack of wire sieves of arbitrarily chosen decreasing mesh sizes (25-, 12.5-, 6.25-, 3.0-, and 0.7-mm mesh openings) immersed in seawater. The ctenophores from each sieve, except the smallest, were transferred to a graduated cylinder and the total volume of organisms retained by each sieve measured. The average volume per individual retained in each sieve was determined either by counting the total number of animals in each sieve or, in the case of the larger animals, by direct volume displacement of randomly selected individual ctenophores. It was impractical to follow this routine with the smallest animals (0.7-mm sieve) since their total volume was too small to be measured accurately. Instead, they were resuspended in seawater, transferred to plastic bags, and returned to the laboratory where they were counted. No attempt was made to assess the number and hence production of ctenophores smaller than 0.7 mm in diameter.

Conversion of Raw Data to Other Units

The shrinkage in length of *S. hispida* with Formalin[3] preservation was estimated by measuring over 100 live animals from a freshly caught 200-μm mesh sample, and repeating this 10 and 420 days following preservation of that collection in a 5% formaldehyde solution buffered with methenamine, which was the standard preservative for all plankton samples. The degree of shrinkage was judged by the extent of the downward shift in the peak of the length/frequency histogram. Half the total shrinkage (12.5% of the original length) occurred within the first 10 days. Assuming a linear rate of shrinkage after day 10, and preservation time of the samples before analysis varying from 1 to 9 mo, the degree of shrinkage was computed to be 20% with a range of ± 3.5%. This mean estimate was used to adjust size classes from preserved to live length.

Live length was converted to dry weight using the relationship obtained from a linear regression analysis of more than 40 separate weight determinations of animals over their entire size range. Animals to be weighed were rinsed in isotonic ammonium formate and dried at 60°C. The ash-free (i.e., organic) dry weight was previously determined to be 90.7% of the dry weight (Reeve et al. 1970). The mean carbon and nitrogen content of *S. hispida* was determined by a Perkin-Elmer elemental analyzer to be 44.9% with a standard error of ± 1.0% and 11.9% ± 0.2% of the ash-free dry weight from 23 separate estimations over its entire size range. The raw biomass units for ctenophores were obtained in terms of live volume. Over 100 separate determinations of animals over their entire size range were made for wet (drained), dry (at 60°C), and ash (at 500°C) weights. Live volume was approximately numerically equal to wet weight (1.000 ml = 0.958 ± 0.002 g standard error). Dry weight was 4.43% ± 0.40% of wet weight and ash-free dry weight was 21.90% ± 0.15% of dry weight.

Eighteen separate determinations of carbon and nitrogen content of *Mnemiopsis mccradyi* Mayer were made which yielded unusually low values 8.72% ± 0.06% and 2.32% ± 0.07% of the ash-free dry weight of carbon and nitrogen respectively. A value of 44.9% carbon was reported for *Sagitta* (above), and Curl (1962) quoted values for various planktonic crustaceans between 44 and 52%. Even his value for *Mnemiopsis* sp. was considerably higher at 20.6%. Hirota (1974) assumed a 50% carbon content of organic weight for *Pleurobrachia bachei* in his calculations, because analysis by wet combustion with acid dichromate was unsuccessful due to problems with chloride ion interference (J. Hirota, pers. commun.).

We considered the possibility that our analyses were also yielding incorrect results and tested three possible sources of error: a) interference in the analysis by the unusually large amount of inorganic salts present in the ctenophore tissue, b) errors of dry weight determination, and c) errors of ash weight determination. Mixtures of bovine serum albumin (5-15%) and sodium chloride did not reduce the theoretical yield of carbon when combusted in the elemental analyzer. Since, however, the dried ctenophore material was a more intimately bound complex of organic and inorganic substances, which might be more resistant to complete combustion, potassium persulfate was added to promote complete oxidization (see Strickland and Parsons 1968). No increase in carbon yield was achieved by this method. The reliability of dry and ash weight determinations affects the reliability of the carbon value since the numbers so obtained are used in its computation. The possibility of any significant loss of organic matter during drying at 60°C was checked by performing carbon analyses on freeze-dried material. The previously derived mean value remained unchanged. Finally, ash weights were determined at a temperature 100°C lower than previously. Slightly higher ash weights resulted, which in turn slightly increased the computed carbon level to 10.3% of the ash-free dry weight. Since any significant source of error in this determination has so far eluded us, we report production values below for ctenophores and chaetognaths in terms of ash-free dry weight for direct comparison and in terms of the analyzed carbon. Mullin (pers. commun.), on the basis of unpublished observations, suggested that the weight lost on ashing may be largely "bound" water, and that in *Pleurobrachia bachei*, at least, only about 12% of the ash-free dry weight is organic matter. This suggests that comparisons based on carbon content are more valid than those based on "organic" or ash free-dry weight.

Growth Rates

Growth rates of populations of the ctenophore

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and chaetognath were determined in the laboratory using larvae hatched from wild adults according to methods detailed by Reeve and Walter (1972) for *S. hispida* and Baker and Reeve (1974) for *M. mccradyi*. Three separate populations of the chaetognath and two of the ctenophore were grown at each of three temperatures (21°, 26°, 31°C), which corresponded to the mean monthly minimum, annual mean, and mean monthly maximum temperatures (to the nearest 1°C) off the laboratory dock in Biscayne Bay over 11 yr (unpubl. records). Food was provided in the form of naturally occurring zooplankton of suitable size (see previously cited information on culture technique), consisting mostly of the copepods *Acartia tonsa* and *Paracalanus parvus*, maintained at a level such that no more than 50% were grazed down over 24 h.

Growth rates were measured as length increase to avoid sacrificing any members of the populations and the data converted to ash-free dry weight as previously described. Total length of *Mnemiopsis* was measured from the aboral to the oral pole (or tip of the oral lobes in adults) as described in detail by Baker (1973).

Production Calculation

The method of calculating production was that employed by Mullin and Brooks (1970) and Hirota (1974), where for each size class an exponential coefficient of daily growth (G) and mortality (M) is obtained from laboratory growth rate and field size-frequency data.

The growth coefficients were computed from the slope of the line relating the logarithm of increase in ash-free dry weight and age (Figure 1) following Crisp (1971). Data from each rearing experiment were combined for each species at the specified temperature. For *S. hispida*, the semilogarithmic relationship is linear over most of its size range until growth levels off at maturity (Reeve and Walter 1972). The termination of the linear (i.e., constant exponential growth) phase was arbitrarily set at 20, 25, and 30 days at 31°, 26°, and 21°C respectively, and the slope of the line calculated by linear regression analysis. At each temperature, slopes at two points beyond the linear phase were required, and these were derived by extrapolation on the basis of the remaining data points and other (unpubl.) data on lengths of

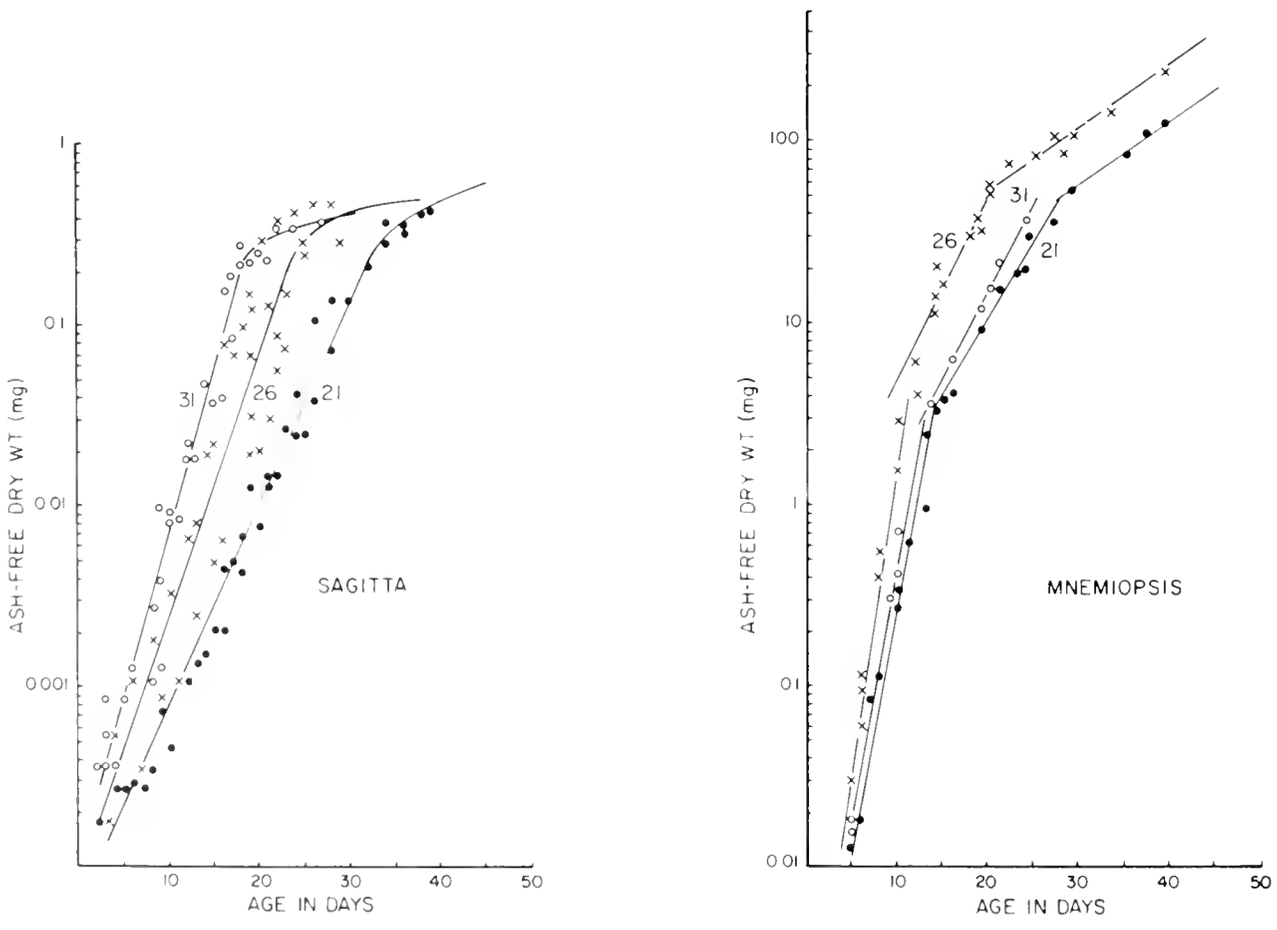

FIGURE 1.—Growth rate of *Sagitta* and *Mnemiopsis* at three different temperatures.

animals older than those surviving in these experiments. The potential errors in such a procedure are minimal, because the coefficients are tending towards zero and the biomass involved in the two largest size classes is only a small percentage of the total.

The *Mnemiopsis* growth curves were treated differently because their slopes decreased progressively with age. In order to facilitate computation of the required slopes, the curves were divided into segments, the junctions of which were assigned by visual inspection to be at 3- and 50-mg ash-free dry weight. The slopes of the individual segments A, B, and C were individually calculated from the population mean points within them by linear regression analysis. Unlike *S. hispida*, where growth rate is proportional to temperature between 21° and 31°C, *M. mccradyi* grows faster at 26°C than at either end of the range. Survival was poor at 31°C, populations dying out by the 25th day. Since no points exist from which to compute a slope for segment C at 31°C, it was taken to be the same as that for the 21°C experiments, since segments A and B at the two temperatures are almost identical.

Sampling dates were divided into three groups on the basis of the proximity of the ambient water temperature to 21°, 26°, and 31°C so that growth coefficients derived for these temperatures could be applied to the standing stock data. Similarly, mean mortality coefficients were derived for the three temperature ranges by averaging the numbers of animals in each size class over the sampling dates in each temperature range. These mean numbers were used to obtain mean ratios of Y/X (as did Mullin and Brooks 1970) where X and Y are the numbers of the earlier and later of two successive size classes. This ratio, and the duration of development in each of the two successive size classes, enables calculation of the exponential coefficient of daily mortality between the two size classes using computer-generated tables. We recognize that this procedure is an approximation which probably oversimplifies actual conditions by making unproven assumptions regarding constancy of mortality rate with time and between adjacent size classes, yielding a single value for m rather than a measure of its possible range (see Fager 1973).

The duration of development in each size class at each temperature range was estimated from the arbitrarily defined limits of each size class and the laboratory growth rate data.

Net production of a size class on a given sampling date, taking into account animals which die before the end of the day, is the product of the mean biomass and the daily exponential coefficient of growth for that temperature range. The day is assumed to start at the time of sampling, and the mean biomass ($\overline{WN}$) of that size class over the subsequent 24 h is obtained by application of the relationship given by Mullin and Brooks (1970) which utilizes the initial biomass, growth, and mortality coefficients. The initial biomass (WN in ash-free dry weight) is the product of sampled numbers (N) and mean ash-free dry weight (W) of an individual organism of that size class. Summing the production values for each size class provides an estimate of the total net production of the population on that day. No attempt was made to estimate egg production in either species.

Net production was determined for chaetognaths of the Card Sound population only; values quoted below for the Biscayne Bay population are estimated by applying the mean population production/biomass ratio for Card Sound to estimated total biomass in Biscayne Bay. An estimate of annual production is obtained by taking each sampling date as the midpoint of each sampling period, summing the product of daily production and number of days in that sampling period, and summing the total production for each sampling period and adjusting for 365 days. In the ctenophore population, which was sampled for 17 mo, and passed through two biomass peaks which Baker (1973) considered to be an annual winter event (Table 2), two values were computed (see Table 3), one for 365 days from the beginning and one for 365 days up to the end of the sampling program.

Results and Discussion

Seasonal Changes

Summaries of the population dynamics and production data are contained in Tables 1 and 2, computed as detailed above from tabulations by sampling date and size class. Figure 1 contains the laboratory growth rate data. The standing stock and production data are summarized in Tables 1 and 2, and are derived from the Card Sound population of *Sagitta* and the Biscayne Bay population of *Mnemiopsis*, since these populations had been the most effectively sampled. For each size class (Table 1) averaged over the entire

TABLE 2.—Summary of biomass and production data by sampling data averaged over all size classes.

Sagitta				*Mnemiopsis*			
Date	Biomass mg ash-free dry wt/m³	Production mg ash-free dry wt/m³/day	P/B	Date	Biomass mg ash-free dry wt/m³	Production mg ash-free dry wt/m³/day	P/B
1/06/71	3.82	0.95	.25	10/12/70	18.02	2.64	.15
1/23/71	2.86	0.62	.22	10/23/70	135.59	12.12	.09
2/06/71	2.94	0.74	.25	11/20/70	314.31	27.80	.09
2/16/71	7.09	1.44	.20	12/15/70	81.97	6.92	.09
3/05/71	3.68	0.94	.26	1/15/71	18.31	2.09	.11
3/19/71	1.56	0.40	.26	2/15/71	23.56	2.35	.10
4/02/71	4.89	1.28	.26	3/12/71	5.46	0.67	.12
4/16/71	4.10	0.96	.23	4/08/71	20.34	1.63	.08
4/30/71	11.98	3.11	.26	5/07/71	17.77	1.49	.08
5/14/71	5.53	1.77	.32	6/03/71	0.22	0.04	.18
5/28/71	2.50	0.69	.28	7/01/71	0.87	0.12	.14
6/11/71	4.46	1.54	.35	7/26/71	0.17	0.01	.06
6/25/71	1.24	0.46	.37	8/25/71	—	—	—
7/09/71	1.58	0.60	.38	9/17/71	0.06	<0.01	.06
7/23/71	0.10	0.04	40	9/30/71	0.58	0.09	.16
8/06/71	0.56	0.23	.41	10/14/71	1.29	0.14	.11
8/20/71	0.25	0.10	.40	10/28/71	3.27	0.64	.20
9/03/71	0.48	0.19	.40	11/12/71	8.86	1.30	.15
9/09/71	0.62	0.24	.39	11/24/71	6.80	1.07	.16
9/14/71	6.03	2.26	.37	12/02/71	56.55	6.14	.11
9/21/71	2.00	0.66	.33	12/20/71	20.89	2.16	.10
9/28/71	3.47	1.24	.36	1/06/72	200.35	15.66	.08
10/14/71	4.85	1.67	.34	1/21/72	103.59	7.38	.07
10/26/71	6.06	2.23	.37	2/03/72	7.69	0.75	.10
11/09/71	0.99	0.37	.37				
11/23/71	3.93	0.97	.25				
12/07/71	5.21	1.27	.23				
12/15/71	1.16	0.30	.26				

sampling period, the mean numbers, live length (or volume for *Mnemiopsis*), ash-free dry weight per organism, and ash-free dry weight per size class are tabulated. The mean net daily production of each size class (per cubic meter) averaged over the entire period using the information on daily rates of growth and mortality and the average duration of each size class (over the three temperatures) is also provided.

Seasonal changes in production reflected those of biomass generally as indicated in the production/biomass ratios (Table 2), which varied between 0.20 and 0.41 (mean, 0.31) for *Sagitta* and 0.059 and 0.20 (mean, 0.12) for *Mnemiopsis*. The ratios were highest in *Sagitta* in the summer when growth rates were maximum, but biomass and production was at its lowest. In *Mnemiopsis*, which also exhibited minimum summer biomass and production levels, the ratio tended to be low relatively, as was growth rate. This summer low point of biomass and production is a confirmation of the experience of some nine seasons of observation by the first author and is characteristic of the 200-μm net plankton of Card Sound and Biscayne Bay as a whole (for a discussion of which, see reviews of Reeve and Cosper 1973 and Reeve in press).

Throughout the rest of the year the chaetognath biomass of Card Sound and Biscayne Bay fluctuated much less widely than that of the ctenophores in Biscayne Bay. The biomass of *Sagitta* ranged (excluding July-September) between 1- and 12-mg ash-free dry wt/m³ in Card Sound and an estimated 2- and 20-mg ash-free dry weight in Biscayne Bay, whereas for ctenophores the range was 0.2 to 314 mg/m³. The mean annual biomass of *Sagitta* in Card Sound and Biscayne Bay was 3.36- and 8.04-mg ash-free dry wt/m³ and for *Mnemiopsis* in Biscayne Bay was 25.2- to 42.5-mg ash-free dry wt/m³ (reckoning 12 mo from the date of the first sample or 12 mo prior to the date of the last sample).

The range of net daily production rate in terms of ash-free dry weight for *Sagitta* at the surface from Card Sound and *Mnemiopsis* from Biscayne Bay was 0.04 to 3.1 and < 0.01 to 27.8/m³, respectively. Table 3 contains production estimates on an annual basis computed for surface and average water column (for *Sagitta* only) as ash-free dry weight and carbon per cubic meter. For *Mnemiopsis*, carbon production is computed both on the basis of the carbon content of *Sagitta* and the experimentally determined carbon content for *Mnemiopsis*. Daily production estimates per cubic meter and per square meter are also computed in terms of experimentally determined carbon content. As noted above, the two values in each case for *Mnemiopsis* incorporate successive annual production peaks.

TABLE 3.—Mean annual and daily production of the *Sagitta* populations of Card Sound and Biscayne Bay and *Mnemiopsis* population of Biscayne Bay.

	Annual production					
	mg ash-free dry wt/m³		mgC/m³		Daily production	
	Surface	Average water column	Carbon 44.9%	Carbon by analysis	mgC/m³	mgC/m²
Sagitta						
Card Sound	357	542	244	244	0.67	2.00
Biscayne Bay	855	1,200	584	584	1.60	4.80
Mnemiopsis						
Biscayne Bay	695/1,409		312/633	60.6/123	0.17/0.34	0.50/1.01

Details of methods for the calculation of production for populations with continuous breeding occur in Winberg (1971) and Crisp (1971). They are essentially similar to the method used here and by Mullin and Brooks (1970) and Hirota (1974) except that no adjustment is made to the sampled biomass (WN) to compute the mean biomass ($\overline{W}\overline{N}$) during the 24 h immediately following the taking of the sample. This additional step, which we also performed, requires considerable extra effort (depending on the number of size classes and sampling dates involved) as well as access to computer services. In these warm waters, however, where growth and mortality rates may be less variable than in regions of more pronounced seasonality, the increase in W tends to cancel out the decrease in N, the difference between WN and $\overline{W}\overline{N}$ for *Sagitta* and *Mnemiopsis* being less than 10% (93 and 108%, respectively).

Mortality coefficients tended to increase progressively with age in *Sagitta* and with increasing temperature. These environmental observations correspond to the conditions of laboratory cultures with respect to temperature, but in cultures young animals tend to die off more rapidly than juveniles and immature animals (Reeve and Walter 1972). A variety of interacting factors, including differences in predation pressure and food adequacy, may be responsible. In the ctenophore population the pattern of mortality is uniformally low except in size class B which corresponds to the time of change from tentaculate larva to lobate adult. The unmeasurable mortality of size group A can be partly attributed to sampling inefficiency, though this was shown not to be the case for *Sagitta* (see above).

Problems of Measuring Growth Rate

In animals such as copepods, with life history stages marked by recognizable and abrupt changes (i.e., molts), division of the cycle into parts may be accomplished on the basis of some biologically meaningful criteria. Both chaetognaths and ctenophores exhibit more gradual transformation from newly hatched larva to mature adult, and size class separation is based on arbitrary limitations such as preserved length or sieve size. The only real validity of the particular size classes used here is that they represent a progression from the youngest to the oldest animals. Factors such as variability of size of animals of the same age at different temperatures and imprecision of raw measurements (larger ctenophores may pass through a mesh slightly smaller than their diameter by their own weight deforming their shape) tend to blur the sharpness of the line separating one size class from the next. The arbitrary choice of size classes resulted in large variations in the durations of development of each size class. In *Sagitta* the mean duration (i.e., averaged over the three experimental temperatures) of the initial size class was 12 days, shortening to 2 days as length increased rapidly, and increasing to 9 in the last size class as a final length was approached in the adult. In *Mnemiopsis* size class durations proved to be even more erratic (see Table 1).

On the basis of the definitions used by Reeve (1970) for *S. hispida*, the larval, juvenile, immature, and mature stages correspond approximately to size classes A and B, C and D, E and F, and G and H, respectively. For *M. mccradyi* the tentaculate larva extends to size class C and the first eggs are also produced by size class C animals (29 mm and larger).

The most satisfactory way to determine growth and mortality in a population is to follow the increase in size and decrease in numbers of a cohort of the population over successive sampling dates by inspection of size-frequency histograms (Winberg 1971; Crisp 1971). In warmer waters, although biomass may fluctuate widely, breeding

tends to extend over most or all of the year and distinct cohorts can rarely be identified.

Growth rate, therefore, was measured in the laboratory, and in as large a volume as practical (30-70 liters). No attempt was made to simulate natural food levels. There were various reasons for this. Mean annual zooplankton concentrations of the 200-μm mesh, which is the food source of older *Sagitta* and *Mnemiopsis* (Reeve and Walter 1972; Baker 1973), were of the order of magnitude of 1 organism/liter, an impractically low concentration to work with in these volumes. It is certain that any environmental concentration estimated from a net tow is an average of several small-scale patches of higher and lower density. We have some information from direct observation by scuba (unpubl. data) that patch densities at least an order of magnitude greater occur, as well as information (also unpubl. data) that both *Sagitta* and *Mnemiopsis* can ingest food several times faster following a period of starvation than they do under conditions of a constant supply of food. *Sagitta* is capable, under certain conditions, of ingesting within 1 to 2 min all the food it consumes in 24 h under conditions of continuous abundant food supply.

Despite the fact that feeding habits and environmental food concentrations are poorly understood at present, it is clear that for carnivorous zooplankton, at least, maintaining a continuous supply of food at mean environmental concentrations in small-scale experimental conditions, would be as artificial as maintaining a continuous abundant supply, even though there must obviously be a relationship between total food supply and production in the environment. The latter method does provide a standard (i.e., maximum) growth rate. When better data become available on the interrelationships of feeding, food supply, and growth rate, the production estimates computed on that basis can be revised downward. At present, there is little information available to even guess to what extent these growth rates and hence production estimates are overestimations. Hirota (1974) reported surprisingly little difference in growth rates of *Pleurobrachia* in experiments at food concentrations ranging between 1 and 350 μgC/liter, but pointed out that in the 70-m^3 tank in which the low food concentration occurred, food organisms were not uniformly distributed because some species were concentrated at the surface during the day. In Card Sound and Biscayne Bay the mean annual concentration of food from the 200-μm net (the size range fed to adult *Sagitta* and postlarval *Mnemiopsis* in our experiments) was 0.8 and 8.1 μgC/liter. Taking into account all organisms down to a 20-μm retaining mesh those figures would be increased by a factor of 5 (Reeve and Cosper 1973).

Production Comparisons

Sameoto (1971) obtained a value for the net production of *S. elegans* in Nova Scotia waters (ranging in temperature approximately from 0.5° to 14°C) of 200 mgC/m^2 per yr in a 50-m water column, and McLaren (1969) reported a similar range of values for this species from Ogac Lake on Baffin Island (49-196 and 318). Those authors estimated production/biomass ratios between 1.0 and 2.1 on an annual basis. These figures compare with annual net production of *S. hispida* in Card Sound and estimated in Biscayne Bay of 730 and 1,750 mgC/m^2 per yr and production/biomass ratio of 109 on an annual basis. With a mean annual biomass two orders of magnitude lower, therefore, *S. hispida* in Card Sound exceeds the net production of *S. elegans* in St. Margaret's Bay, Nova Scotia by virtue of its rapid growth rate and short generation time. The disparity would be even greater on a cubic meter basis because Card Sound is comparatively shallow.

Hirota (1974) quoted a value for net annual production of the ctenophore *Pleurobrachia bachei* in waters off California (ranging in temperature approximately from 12.5° to 20°C) of 5,415 mg ash-free dry weight/m^2 per yr, and a daily production/biomass ratio of 0.02. These figures compare with an annual net production of *M. mccradyi* in Biscayne Bay of 2,086 to 4,227 mg ash-free dry weight/m^2 per yr and a production/biomass ratio of 0.12. As in the previous comparison, annual production of different species in different regions is surprisingly similar on a water column (square meter) basis. The growth rate of *M. mccradyi*, however, is some 5 times faster, and its production is supported by a water column depth of 3 m rather than in excess of 40 m in the case of *Pleurobrachia bachei*.

The 10-fold difference in the mean annual standing stock of 200-μm mesh zooplankton between Card Sound and Biscayne Bay (and in phytoplankton pigment) is probably a reflection of the poor water exchange and limited land drainage into Card Sound as compared with Biscayne Bay (Reeve and Cosper 1973). These

differences in plankton biomass are accompanied by differences in biomass for both *Sagitta* and *Mnemiopsis*. In surface net tows from the 200-μm mesh, the biomass of the chaetognath in Biscayne Bay is 2.4 times that in Card Sound. The ctenophore is totally absent from Card Sound (except for rare isolated individuals). Baker (1973), relating stations with low plankton standing stock to low ctenophore levels in Biscayne Bay, suggested that the Card Sound plankton could not support a ctenophore population.

Since the waters of Card Sound are contiguous with those of Biscayne Bay to the north, and neritic waters to the east, where ctenophores are often abundant, the phenomenon of their exclusion from Card Sound can hardly be a physical one. A possibility is that chaetognaths are more efficient in collecting food at lower densities than are ctenophores.

It is of interest that the seasonal variations of biomass and production of the ctenophore populations both in Biscayne Bay and off California are extreme, to the extent that in both cases the months of peak production account for about two-thirds of the annual total. In the case of *S. hispida* this value is about one-fifth. There is probably some correlation between this extreme population instability of *M. mccradyi* and the suggestion above that its absence from Card Sound is related to its inefficiency in collecting food at low concentrations compared to *S. hispida*. The dry weight of other zooplankton from the 200-μm mesh net in Card Sound (Reeve and Cosper 1973) never exceeds the minimum value in central Biscayne Bay (Baker 1973).

It is possible to get a rough estimate of the relationship between production of *S. hispida* and *M. mccradyi* and the rest of the zooplankton by utilizing the standing stock data for that period in the two reports referred to immediately above. The mean annual dry weight of zooplankton (excluding ctenophores and corrected for detritus) was 2.02 and 5.28 mg/m^3 in the 200- and 64-μm mesh net respectively in Card Sound and 19.8 mg/m^3 in the 200-μm mesh net in central Biscayne Bay. Assuming the ratio between 64- and 200-mesh plankton in Card Sound is applicable to Biscayne Bay, and the ash-free dry weight is the same percentage of dry weight as determined for *S. hispida*, the mean annual ash-free dry weight in Card Sound and central Biscayne Bay was 6.62 and 64.9 mg/m^3 respectively. Since it appears that even the youngest larvae of *Mnemiopsis* and *Sagitta* do not utilize food organisms much smaller than those retained by the 64-μm mesh, and since neither carnivore appears to be able to utilize other sources of potential food such as detritus or phytoplankton (Reeve and Walter 1972; Baker and Reeve 1974), the plankton biomass quoted above is the only source of nutrition for these carnivores. If a production/biomass ratio the same as that determined for *S. hispida* is applied to these biomass figures, the net production available to these carnivores is 2.05- and 20.1-mg ash-free dry weight/m^3 per day. Since these figures are for surface waters, they may be related to the equivalent values for *Sagitta* and *Mnemiopsis* derived earlier. The daily net production of *S. hispida* in Card Sound and Biscayne Bay is then 47.7 and 11.7% of the production of potential food in those areas. For *M. mccradyi* in Biscayne Bay it was 9.5 or 19.2% depending on which production peak was included (see above). The total percentage for the two species is then 47.7 for Card Sound and 21.2 or 30.9 for central Biscayne Bay. If the ratio of production to food ingested is taken to be 50% on the basis that immature animals are responsible for most of the production, and would have higher growth efficiencies than the 30-40% range for adults quoted by Reeve (1972), then the chaetognaths in Card Sound appear to utilize all the rest of the zooplankton above 64 μm. For Biscayne Bay, the chaetognaths and ctenophores together utilize between 40 and 60% of the available food. As explained earlier, these are overestimated because the growth rates were maximum growth rates, but they do support the contention that there is little potential food reserve in Card Sound for other carnivores, and that *Sagitta* is more efficient in competing for the available supply. This is in agreement with the fact that in Card Sound, its population was as high as 42% of that in central Biscayne Bay, while for larger decapod larvae, fish larvae, and ctenophores (the other major first-order plankton carnivores) the values were approximately 25, 25 (see Reeve in press), and 0%.

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EFFECTS OF ACCLIMATION ON THE TEMPERATURE AND SALINITY TOLERANCE OF THE YOLK-SAC LARVAE OF *BAIRDIELLA ICISTIA* (PISCES: SCIAENIDAE)[1]

ROBERT C. MAY[2]

ABSTRACT

Eggs of the hairdiella, *Bairdiella icistia*, were fertilized and incubated in various combinations of temperature and salinity, and the salinity and upper thermal tolerances of the yolk-sac larvae were determined. The upper thermal tolerance was enhanced by acclimation to high temperatures and low salinities. Acclimation to low salinities enhanced the lower salinity tolerance of larvae at 24 h after exposure to test conditions, but an acclimation effect on the upper salinity tolerance was not apparent until 48 h after exposure. Yolk-sac bairdiella larvae are more tolerant than the embryonic stages and less tolerant than adults to extremes of temperature and salinity.

Techniques for inducing gonadal maturation and spawning under laboratory conditions are well developed for the bairdiella, *Bairdiella icistia* (Jordan and Gilbert), a sciaenid fish native to the Gulf of California and now present in the Salton Sea (Haydock 1971; May 1975). Hence bairdiella eggs and larvae are extremely favorable material for studying various facets of early development in a marine fish, and detailed information on the effects of temperature and salinity on fertilization, embryonic development, and hatching in this species has already been presented (May 1975). The present paper is concerned with the effects of acclimation on the tolerance of yolk-sac bairdiella larvae to temperature and salinity.

Acclimation has been defined as "the process of bringing the animal to a steady state by setting one or more of the conditions to which it is exposed for an appropriate time before a given test (Fry 1971:14)." In the case of yolk-sac larvae of tropical fish species which develop very rapidly, the term acclimation has a somewhat special meaning, since it necessarily refers to the conditions obtaining during embryonic development. Virtually no studies of acclimation in this context have heretofore been published. Although salinity has been shown to affect the upper thermal tolerance of adult fish (e.g., Garside and Jordan 1968), no comparable work has been reported for fish larvae. This paper investigates the upper thermal tolerance of newly hatched bairdiella larvae and the modifying influence of acclimation, i.e., the influence of temperature and salinity during embryonic development. Since there is little likelihood that bairdiella larvae would encounter lower lethal temperatures in nature (May 1975), their lower thermal tolerance is not considered here. In addition to upper thermal tolerance, the upper and lower salinity tolerance of larval bairdiella and the effect of the acclimation salinity are also considered in this paper. This information, together with results on embryonic tolerances described earlier (May 1975) and available information concerning adult tolerances, should lead to a conclusion as to which stage in the life history of bairdiella is the most sensitive to temperature and salinity.

METHODS

General

Bairdiella eggs were obtained from fish which had been held in normal seawater (33‰) and induced to mature and spawn in the laboratory, as described previously (May 1975). Eggs were artifically fertilized at specified temperatures (within ±0.2°C) and salinities (±0.5‰) and maintained under the same conditions until hatching in specially designed incubators (May

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1975). These conditions (which remained constant from fertilization to hatching, plus the period of time between hatching and transfer to the test conditions) constituted the conditions of acclimation. Larvae were not fed during the experiments. Test salinities were prepared by dilution with deionized water from a stock solution of 60%, which had been made by adding artificial sea salts to seawater (May 1975).

Upper Thermal Tolerance

Larvae were acclimated to temperatures of 21°, 24°, 27°, and 30°C, and to salinities of from 15 to 45‰ (Table 1), covering the ranges of these two factors within which successful embryonic development can take place (May 1975). Since developmental rates were more rapid at the higher temperatures (May 1975), the period of acclimation (fertilization to transfer to test vials) was shorter at the higher acclimation temperatures. The median tolerance limit (TLm)[3] of yolk-sac larvae to high temperatures was determined by the method of Doudoroff (1942). Larvae were transferred directly from the acclimation conditions to a series of 25-ml capped vials maintained in the dark at a series of high temperatures in a thermal gradient block (Thomas et al. 1963) within 5 to 10 h after hatching, at which time they were 1.8 to 2.0 mm in length. The highest test temperature was 36°C, and between five and eight test temperatures, 1.5°C apart, were used depending on the acclimation temperature; the salinities in the test vials were the same as the acclimation salinities. Approximately 10 larvae were placed in each vial, and the test temperatures did not vary by more than ±0.1°C. Antibiotics were added to the water in the vials (May 1975), and the survival of larvae under optimal conditions in these vials was comparable to that in larger containers. The number of larvae surviving at each test temperature was recorded at 0.5, 1, 3, 6, 12, 24, 48, and 72 h after transfer, and for each time the TLm—the temperature at which just 50% of the larvae survived the given time interval—was estimated by graphical interpolation as described by Doudoroff (1942). At each observation, larvae which showed no movement were removed from the vials by pipette and examined under a dissection microscope. If the heart was not beating and the larva was opaque, the larva was considered dead and was discarded; live larvae were returned to the vials. In one instance (see Results) moribund larvae were found and counted as dead.

[3]The term "median tolerance limit" and the symbol TLm are recommended in "Standard Methods" (American Public Health Association 1971).

TABLE 1.—Acclimation conditions for larvae used in determination of heat tolerances.

Acclimation salinity (‰)	Acclimation temperature (°C)			
	21	24	27	30
15	×		×	
20		×		×
25	×		×	
30		×		×
35	×		×	
40		×		
45	×			

Salinity Tolerance

Larvae were acclimated to salinities of 15, 20, 25, 30, 35, and 40‰, and their upper and lower salinity TLm's were determined by transferring larvae directly to a series of 25-ml vials containing test salinities ranging from 0 (deionized water) to 58‰. Between five and seven larvae were transferred to each vial within 8 h after hatching. Because of limited material, only the upper TLm was determined for larvae from an incubation salinity of 40‰, and only four larvae from this salinity were available for each vial. The temperature during fertilization, incubation, and testing was maintained at 24 ± 0.2°C by thermostatically controlled water baths, and vials were kept under continuous room light of low intensity (May 1975). The number of larvae surviving at each salinity was recorded 24, 48, and 72 h after transfer, and the upper and lower TLm's were estimated graphically for each time interval as in the case of thermal tolerance. Larvae were considered dead on the basis of the same criteria used in the study of thermal tolerance.

RESULTS

Upper Thermal Tolerance

The upper TLm dropped with increasing time intervals (Figures 1-4), and there was a leveling off of the time-temperature curves in the lower salinities as time increased. Most of the time-temperature curves have been separated by eye-fit lines into two major segments, the horizontal segment defining the "incipient lethal temperature"

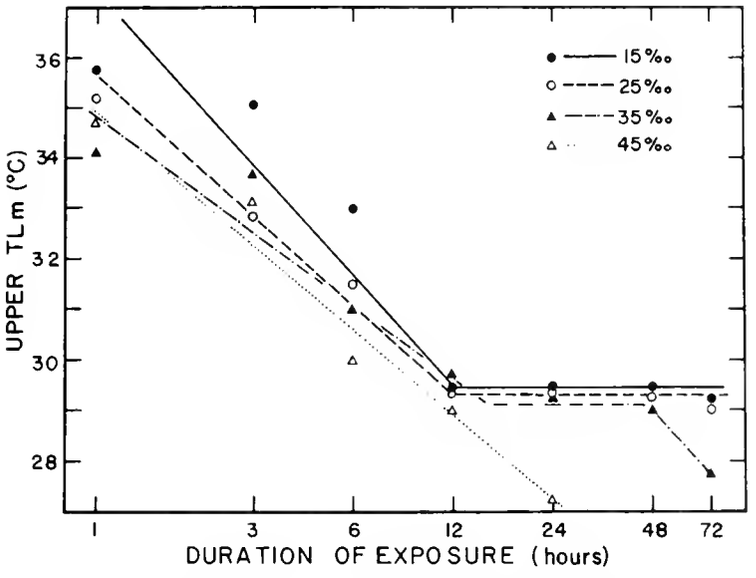

FIGURE 1.—Heat tolerance of larval bairdiella acclimated to 21°C in various salinities. The upper median tolerance limits (TLm) are plotted for various durations of exposure. The time scale is logarithmic, and lines were fitted by eye.

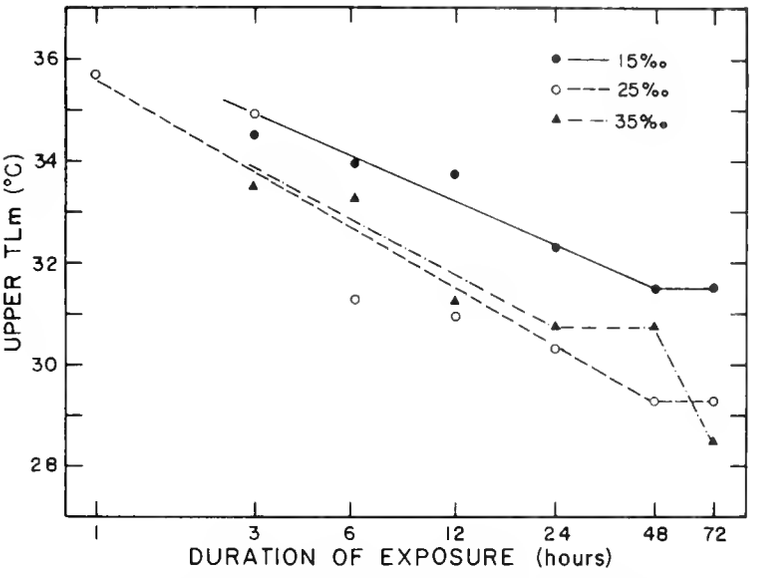

FIGURE 3.—Heat tolerance of larval bairdiella acclimated to 27°C in various salinties.

(Brett 1956), but in several curves there is a suggestion of an early plateau during the first few hours of exposure to the test conditions (Figures 1, 3, 4). At any given time the TLm was usually higher in the lower salinities. Since the highest test temperature used in the experiments was only 36°C, at acclimation temperatures above 21°C the 50% mortality point was usually not reached until 3 or more hours after exposure to the test conditions. Survival was very poor among larvae from eggs maintained at 30°C (a temperature highly stressful to eggs—May 1975) in 30‰, and at 24 h, survival in this group was below 50% at all test temperatures. For purposes of comparison, the 24-h upper TLm has been plotted against salinity for various acclimation temperatures (Figure 5); in this graph the increase in TLm at lower salinities is clear, as is the general increase in TLm effected by higher acclimation temperatures. In a salinity of 15‰, all larvae alive at 12 and 24 h in the 21°C acclimation group were moribund in test temperatures of 30°C and higher, i.e., they were contorted and totally immobile and unresponsive to touch, although their hearts were beating and they were not opaque. These larvae have been considered dead for the purpose of data presentation; if considered alive, they would raise the calculated 12-h upper TLm from 29.5° to 32.1°C (Figures 1, 5). At the salinity of normal seawater, the 24-h upper TLm of larval bairdiella lies

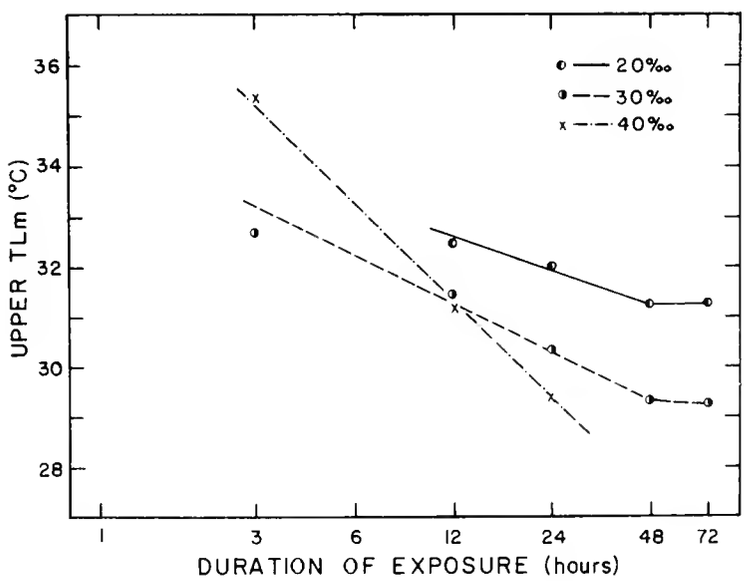

FIGURE 2.—Heat tolerance of larval bairdiella acclimated to 24°C in various salinities.

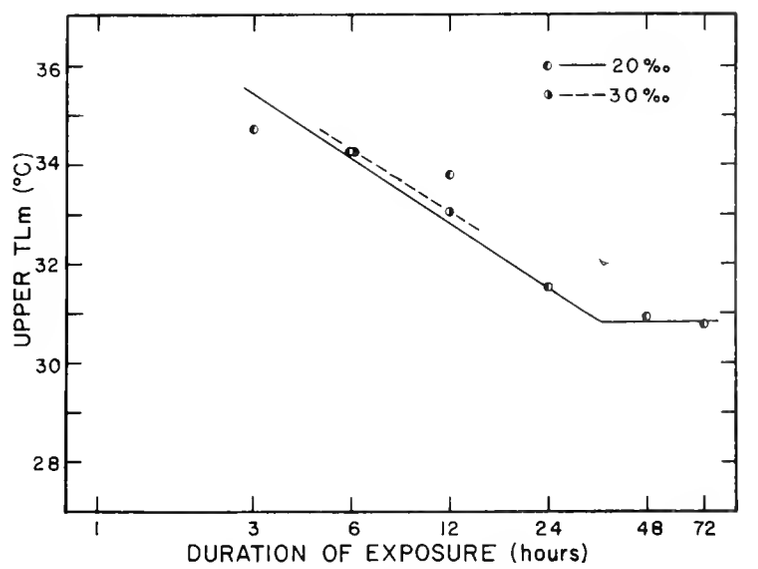

FIGURE 4.—Heat tolerance of larval bairdiella acclimated to 30°C in two salinities.

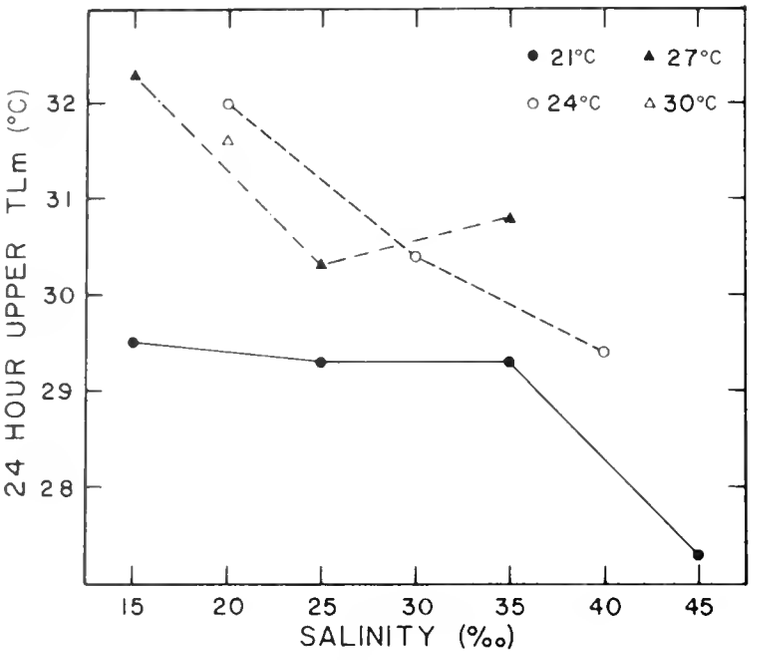

FIGURE 5.—Twenty-four hour upper median thermal tolerance limits (TLm) at various salinities for larvae acclimated to 21°, 24°, 27°, and 30°C.

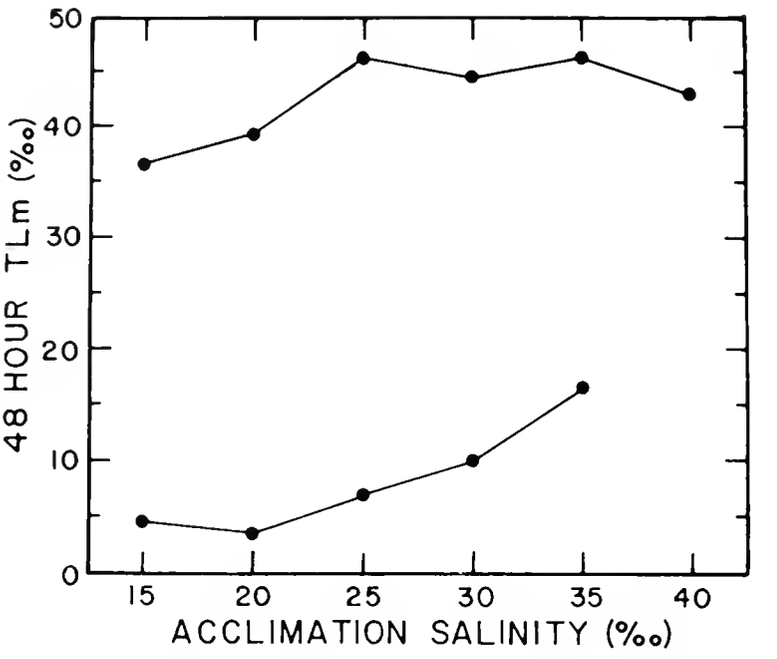

FIGURE 7.—Upper and lower median tolerance limits (TLm) of salinity for a 48-h exposure.

between 29° and 31°C, depending on the acclimation temperature. Larvae could resist higher temperatures for shorter periods of time.

Salinity Tolerance

The 24 h upper TLm for salinity was not greatly affected by the acclimation salinity and ranged from 43 to 48.5°/oo, but the 24-h lower TLm was appreciably higher among larvae incubated at higher salinities (Figure 6). The lower TLm's (24 h) for larvae acclimated to 15 and 20°/oo were 4.2 and 3.5°/oo, respectively, whereas those for larvae acclimated to 30 and 35°/oo were 10 and 16.5°/oo, respectively. The major difference between the 24-h TLm's and those for 48 and 72 h is the progressive lowering of the upper TLm for larvae acclimated to low salinities (Figures 7, 8). The upper TLm for larvae from 15°/oo shifted from 46.2°/oo at 24 h, to 36.6°/oo at 48 h, and to 30.0°/oo at 72 h; between 24 and 72 h, the upper TLm remained the same (43°/oo) for larvae acclimated to 40°/oo, and decreased only from 48 to 46.2°/oo for

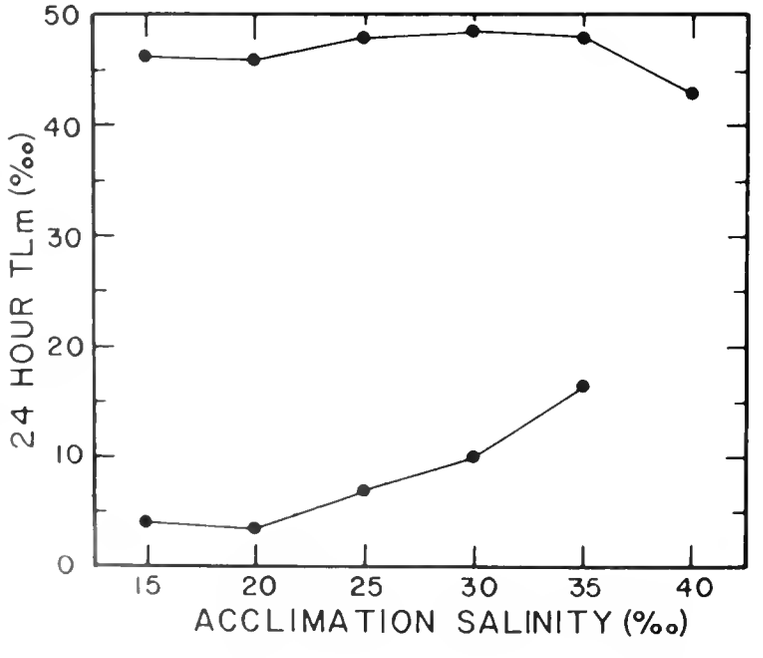

FIGURE 6.—Upper and lower median tolerance limits (TLm) of salinity for a 24-h exposure. Larvae were acclimated to various salinities at 24°C.

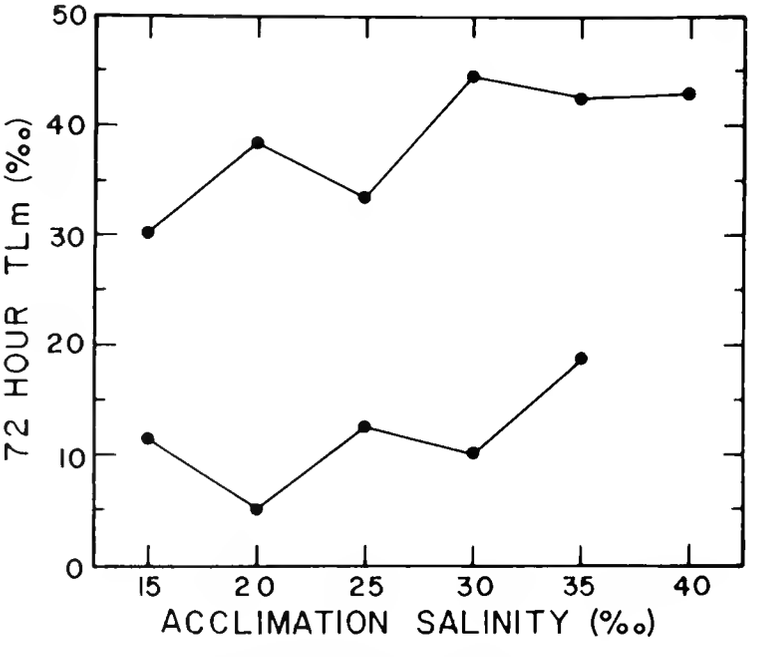

FIGURE 8.—Upper and lower median tolerance limits (TLm) of salinity for a 72-h exposure.

those acclimated to 35‰. There was little change in the lower TLm's between 24 and 48 h, but a slight rise occurred between 48 and 72 h in all but the 30‰ acclimation group.

DISCUSSION

Fry et al. (1946) define the "zone of tolerance" as the range of any environmental factor within which an animal can live indefinitely, and the "zone of resistance" as the range within which the animal can live for only a finite period of time, depending on the level of the factor. The zone of tolerance is bounded by the upper and lower "incipient lethal levels." In work on the upper thermal tolerance of fishes, the incipient lethal level is defined by an abrupt flattening of the time-temperature curve at a temperature below which less than 50% of the exposed individuals succumb (Brett 1956). Some of the curves generated in the present study (Figures 1-4) suggest that the incipient lethal level has been reached, but curves from the higher salinities lack a horizontal segment. This points up a difficulty in working with early larvae: at 24°C the larval yolk supply is 95% consumed by about 40 h after hatching (May 1974), and this occurs even sooner at higher temperatures. The 48- and 72-h TLm's therefore apply to starving larvae. Unlike adult fish, larvae which hatch from pelagic eggs are extremely sensitive to food deprivation (e.g., Lasker et al. 1970) and begin dying of starvation soon after yolk absorption if food is not provided for them, and unfed bairdiella larvae die sooner at high temperatures and salinities (May 1975). Therefore, prolonging these tests would not have helped in defining the upper incipient lethal temperature for larvae in the higher salinities—the TLm would simply continue to fall. Even at the lower salinities, the TLm would decline after a sufficient period of time; the curves for a salinity of 35‰ (Figures 1, 3) show how a flat segment is reached, only to be followed by another drop in TLm. A further difficulty in estimating tolerance limits for warmwater larvae is that these larvae develop morphologically at an extremely rapid rate and are very different organisms 1 or 2 days after hatching than they are at hatching. Newly hatched bairdiella are poorly developed and rather inactive (May 1975), whereas by 45 h after hatching (at 24°C) they have acquired functional eyes and an open mouth and are quite active. In this situation, consideration of the TLm at a more or less arbitrary time after exposure to the test conditions, such as 24 h, is at least a useful approach for comparative purposes.

Larval bairdiella are more sensitive to high temperatures when the salinity is also high, as are bairdiella gametes and developing embryos (May 1975). This adds further weight to the suggestion (May 1975) that in nature, eggs spawned late in the season at high temperatures will have a reduced chance of contributing recruits to the population when natural salinities rise as they are doing in the Salton Sea. The survival of bairdiella larvae in the Salton Sea would be significantly reduced at temperatures above 31°C, and temperature data from the Salton Sea (May 1975) indicate that some larvae could be exposed to thermal stress of this level or greater. The highest TLm is reached in 15‰, the lowest salinity in which larvae were tested and the nearest to being isosmotic with larval body fluids. Older fishes of various species are also most tolerant of high temperatures in isosmotic or nearly isosmotic salinities (Arai et al. 1963; Strawn and Dunn 1967; Garside and Jordan 1968; Simmons 1971). The added burden of osmotic work seems to reduce the ability of both larval and adult fish to tolerate extremely high temperatures.

It is clear that acclimation can alter the tolerance of early bairdiella larvae to both temperature and salinity, even though the rapid developmental rate of bairdiella eggs restricts the period of acclimation to between 20 and 40 h (the time between fertilization and transfer to test conditions, which is a function of incubation temperature). Incubation of bairdiella eggs at higher temperatures produces larvae with a higher upper thermal TLm. However, increasing the acclimation temperature from 27° to 30°C does not increase the upper TLm, even though the TLm's are generally above 30°C. Hence the lethal levels determined for an acclimation temperature of 27°C may represent "ultimate" incipient lethal temperatures (Fry et al. 1946), but here again one must consider the unique problems of working with early larvae. If the effect of thermal acclimation on the tolerance of yolk-sac larvae is to be studied, acclimation must take place during embryonic development, but the embryos are more sensitive to temperature than are the larvae to which they give rise (cf. May 1975). A temperature of 30°C is extremely stressful for developing eggs, and the larvae produced at this temperature survive poorly, a trait magnified at higher salinities.

The response of these larvae to elevated temperatures is therefore not a true reflection of thermal "acclimation," as the term is generally used, but is more a reflection of thermal stress during sensitive periods of morphogenesis. In an analogous way, salinity stress on embryos during acclimation at 40‰ probably accounts for the observation that the larvae have a reduced upper TLm for salinity when compared with larvae acclimated to 30 and 35‰.

Thermal acclimation has also been shown to affect the thermal tolerance of larval herring (Blaxter 1960), menhaden (Lewis 1965), and salmonids (Bishai 1960; Iwai 1962), although only Blaxter's study utilized larvae which hatched from eggs maintained at the acclimation temperature. The mechanisms involved in thermal acclimation during early development have never been investigated, but the present results for bairdiella suggest that they must be activated quite rapidly, within a day or two at most. A similarly rapid rate of acclimation to warm temperatures has been found in older fish (Brett 1970; Allen and Strawn 1971), so that a similar mechanism may be operating in both cases. Factors involved in setting thermal tolerance limits in fishes are little understood (Fry 1967), but thermal inactivation of enzymes has been suggested as a possible mechanism (Hochachka and Somero 1971).

Holliday and Blaxter (1960) found that the salinity prior to hatching had a limited effect on the salinity tolerance of larval herring. This effect was more pronounced in the present experiments with larval bairdiella, but there was a delay in the appearance of the acclimation response to high salinities. The upper TLm (salinity) was similar for all acclimation salinities 24 h after initial exposure to the test conditions, but at 48 h the larvae acclimated to high salinities had a higher TLm than those from low salinities (a very slight indication of the same phenomenon can be discerned in the results of Holliday and Blaxter 1960). This observation is difficult to explain, especially in view of the rudimentary state of our knowledge of larval osmoregulatory mechanisms; perhaps it is related to the opening of the mouth between 35 and 45 h after hatching (May 1974), which could expose the internal larval tissues more directly to the ambient salinity. Incubation at low salinities enables larvae to tolerate much lower salinities than larvae incubated in more saline water. Again, it is difficult to speculate on how this effect might be mediated.

Early larvae of *Bairdiella icistia* are more tolerant than the embryonic stages and less tolerant than adults to extremes of temperature and salinity. Very few bairdiella eggs develop normally at 30°C (May 1975), and 15 to 40‰ is the approximate salinity range for normal fertilization and embryonic development. In contrast to the eggs, 50% of the newly hatched larvae are capable of withstanding temperatures between 30° and 33°C for 24 h or longer, except at the lowest acclimation temperature and highest salinity; and with proper acclimation, larvae can tolerate salinities ranging from about 4 to 48‰ for 24 h, or 5 to 45‰ for 72 h. Juvenile and adult bairdiella must tolerate temperatures ranging from 10° to 34° or 35°C in the Salton Sea (Carpelan 1961). These fish have been found in freshwater (R. G. Hulquist, California Department of Fish and Game, pers. commun.) and can tolerate Salton Sea water with a salinity of 52.5‰ for 96 h after direct transfer from ordinary Salton Sea water (approximately 38‰), and 58‰ for over a week after gradual acclimation (Hanson 1970). The early larvae of some other species have also been shown to be more tolerant of temperature and salinity than their eggs. McCauley (1963) reports that prolarvae of the sea lamprey, *Petromyzon marinus*, are considerably more tolerant of high temperatures than are the eggs, and data presented by Holliday (1965) show that newly hatched herring, *Clupea harengus*; plaice, *Pleuronectes platessa*; and Atlantic cod, *Gadus morhua*, larvae are more tolerant of both high and low salinities than are their respective eggs. However, in the case of the herring and plaice, further larval development and metamorphosis are accompanied by a decrease in salinity tolerance (Holliday 1965), a pattern quite different from that found in bairdiella.

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THE INTERACTION OF ECONOMIC, BIOLOGICAL, AND LEGAL FORCES IN THE MIDDLE ATLANTIC OYSTER INDUSTRY

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ABSTRACT

Economic, environmental, and legal forces are contributing factors in the decline of the Middle Atlantic oyster industry. This paper determines the interactions and importance of these forces by quantifying and integrating some of the relevant variables into a supply and demand model of the oyster industry. The statistical results yield significant and expected parameter values with useful information on price and income demand elasticities. Also implications of common property legal frameworks on resource utilization are revealed. The main conclusions are that efforts to rehabilitate the industry by cleaning up pollution, replacing cultch, and encouraging legal private property rights may have large social values.

The historically important Middle Atlantic oyster industry is currently recognized as having many of the symptoms of a declining industry. Economic, biological, and legal forces are contributing causal factors in the fishery's decline. This paper attempts to integrate some of these variables into an estimable supply and demand model explaining oyster price and output movements over time for the region. Economic and biological variables are directly included in the model while the legal dimension is focused on indirectly by comparing empirical results for data generated from different common property structures.

The multidimensional approach reveals information on price and income elasticities, substitutability relationships, and the effect a common property regulatory framework has on resource overutilization and depletion. The regional orientation taken in this paper, rather than a national or international focus, provides a departure from much of the traditional fishery analysis and enables the effects of alternative property right structures between states to be observed.[2]

The impact property rights structure has on economic efficiency and biological growth has been discussed widely in the theoretical literature of fishery modelling.[3] Less however has been written on empirical analyses of the effects property rights have on economic and biological efficiency.[4] Consensus among the discussants is that common property leads to overexploitation of fish stocks and perhaps extinction of a species. Common property right systems result in less efficient resource allocation than private right systems since the former do not ensure that the total costs of an individual harvester's exploitation of the resource are borne fully by him. Private property internalizes the costs of the harvester's actions thereby forcing the producer to bear not only all of the costs of his actions but also to capture all of the benefits.

MIDDLE ATLANTIC OYSTER FISHERY

The American Eastern oyster represents the resource base of both the Gulf and Atlantic coasts oyster industries. Following a brief mobile larval stage, the oyster connects permanently to a firm subaqueous material such as rock or shell deposits.

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[2]Recent empirical work confined primarily to economic factors and directed towards species and regions different from our analysis includes Bell (1968), Doll (1972), and Waugh and Norton (1969).

[3]Much has been written in fishery economics on the effects of biological stock depletion due to common property legal structures. Some of the earlier treatments that are still widely referred to can be found in Gordon (1954) and Scott (1955). For more recent theoretical analyses see Fullenbaum et al. (1972), and Smith (1969). In the context of this literature, common property means that any member of a community has the right to harvest the fish stock.

[4]Notable exceptions in the fishery literature where the effects of legal ownership frameworks have been quantified include Bell (1972) and O'Rourke (1971). For example Bell estimates the redundant effort employed in the American lobster fishery which is subject to common property. He concludes that approximately 50% of current fishing effort is required to achieve economic efficiency.

Also the authors, in an unpublished paper (Efficiency and Property Rights in the U.S. Oyster Industry, 1974), estimate that in 1969 oystermens' income would have increased by almost 50% if all coastal states had relied on leasing of oyster beds.

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Its habitat is the intermediate salinity waters of the seacoast's intertidal zone and of inland rivers and bays. Water current, temperature, and biological productivity, in addition to salinity, are determinants of the resource productivity of a given parcel of subaqueous land.

The property right structure characterizing oyster grounds varies widely among states. Courts have granted rights to subaqueous land to the people of each state for their own common use. State legislatures exercise these rights. The federal government has been granted the right to a 3-mile coastal zone and Congress in turn has ceded back to the states land and resource use rights within this zone.[5] States have responded in similar ways to the exercise of their rights to the oyster resource. In general, natural oyster beds have been set aside as a common fishery for state residents,[6] whereas other submerged land parcels are available for private leasing. However, great variation among the states exists in the proportion of area and quality of land set aside for public or common use versus private use depending on how broadly administrators define the term "natural oyster bed."[7] An examination of the proportion of oyster catch by weight on private grounds to total catch by state reveals ratios ranging from a maximum of 1 to 0 for certain states in recent years. Within the Middle Atlantic region the two states with property rights in Delaware Bay (i.e., Delaware and New Jersey) can be characterized as essentially private property states, whereas Maryland and Virginia, which share the Chesapeake Bay, have significantly lower private to total catch ratios.[8]

Private property rights in oystering tend to promote efficiency in several ways. First, exclusive user rights provide incentives for firms to pursue a policy of investing in cultch and maintaining it at a desired level as influenced by market conditions. Second, congestion and overexploitation of the oyster resource is unlikely to occur since there is no pressing need to harvest quickly so as to not lose the resource's benefits. Finally, a communal property structure tends to lower efficiency by requiring the use of obsolete technology in order to prevent depletion of the resource stock. Inefficient technology often takes the form of obsolete capital regulated into use by legislative codes. In general, states relying on common property right structures tend to impose greater restrictions on the use of capital than private property states.[9]

Between 1947 and 1968 the annual U.S. domestic oyster harvest declined from 63.1 to 55.6 million pounds. Imports increased from an insignificant 111 thousand pounds to 15.5 million pounds during the same years. Accounting for inventory changes, total consumption of oyster meat consequently expanded by 8.2 million pounds. Concurrently, both ex-vessel and wholesale prices rose. Between 1950 and 1968 ex-vessel prices rose 38% and wholesale prices rose 89%.[10]

Significant regional differences in oyster catch trends characterize the post-World War II period. In general, the Gulf region has increased its landings while landings in the Middle Atlantic region (defined to include the states of New York, New Jersey, Delaware, Maryland, and Virginia) have declined by 45%. Delaware and New Jersey harvests especially have fallen dramatically, no doubt in large part due to disease which affected stocks beginning in 1958. It is during this period of both relative and absolute decline that we shall estimate the underlying factors explaining changes in quantities and prices for the Middle Atlantic oyster industry.

MODEL

Economic variables such as prices and quantities are generally explained by economists through the use of supply and demand models. Prices and quantities are determined through the equilibration of supply and demand forces which incorporate the effects of various predetermined

[5]See Power (1970) for a detailed description of court decisions involving rights to submerged land.

[6]Legislative codes usually prohibit nonresidents from entering the industry. See Power (1970:216-223) for a discussion of the constitutionality of these restrictions.

[7]Maryland, for example, classifies a natural bed as one such that the natural growth of oysters "... is of such abundance that during the preceding five years the public has resorted to them for livelihood," Power (1970:220). Courts reportedly view one individual declaration of one day's work in a 5 yr period as sufficient evidence of the existence of a natural bed. Most states employ a less restrictive definition for a natural bed.

[8]It is useful to note that private property rights may be institutionally arranged in a multitude of ways. The usual manner of leasing subaqueous lands to a relatively few individuals is by no means the only way of introducing private property, and in fact is often objected to as prejudicial to individual freedom. A more acceptable arrangement pointed out by a reviewer may be for states to assume control of beds and issue permits to harvest a given quantity of oysters.

[9]For example, in the predominantely common property right state of Maryland power dredging is prohibited in the harvest of oysters. Consequently any dredging takes place through the use of sail-powered craft called skipjacks, the newest of which is around 50 yr old.

[10]All data presented in this section are from *Fishery Statistics of the United States*, Bureau of Commercial Fisheries. National retail price data are not readily available.

(independent) variables on the endogenous (dependent) variables price and quantity. A general application of this methodology to any commodity would specify that quantity supplied (Q_s) is dependent on input cost factors, prices of goods related in supply, and price of the product. Quantity demand (Q_d) is usually hypothesized to depend on current price, income, and prices of related goods in demand.

When specifying such a model for oyster markets several modifications to the supply specification of the above general framework are employed. Although from supply theory input factors include technological, environmental, and biological variables, data limitations restrict the inclusion to a single biological factor, the MSX disease.[11] It is hypothesized that the protozoan oyster parasite commonly referred to as the MSX disease has a negative impact on the oyster industry during the period of analysis. Also since no strong relationships between the production of oysters and other goods is readily apparent, we omit prices of related goods from the oyster supply relationship.

The last modification of the supply relationship for oysters and probably the most unique feature of the model is the hypothesis that quantity supplied is a function of price lagged 1 yr rather than current price. As in the case of agricultural commodities, quantity supplied of oysters can be considered a function of past price and natural phenomena and hence fixed in the short run. In the fishery case a fixed supply is usually based on the presence of lags in generating fishing effort (e.g. securing capital and making occupational choices). Lagged price can be expected to positively influence current fishing effort.[12] In fishery estimation with annual data however, the assumption of such long lags in adjusting fishing effort may be inappropriate and the inclusion of lagged price as a determinant of effort will likely be a weak determinant of supply.

An additional rationale is therefore necessary for including price lagged 1 yr as a determinant of supply. We hypothesize that lagged price has a negative impact on current supply due to a depletion effect. In fishery production not only current effort, but current biological stock determines current production. If current biological stock is negatively related to past effort, then variables explaining past effort may bear a strong relation to current supply. Price lagged 1 yr (or alternatively distributed lags of past prices if data were plentiful) may be closely related to past effort. Accordingly we hypothesize that price lagged 1 yr is a proxy for past levels of effort and thus negatively related to current biological stock. Also if the negative relationship that lagged price has on current biological stock is strong enough to offset the positive relationship lagged price has on current fishing effort, the net impact of lagged price on current supply might be negative.

Furthermore we expect the negative depletion effect of lagged price to be stronger in fisheries subject to common property. Thus lagged price is likely to have a slight positive effect on supply in fisheries subject to private property due to the positive effort effect. For fisheries subject to common property the negative depletion effect is expected to offset the positive effort effect yielding a negative relationship between lagged price and quantity supplied.

The structural equations and equilibrium condition of the fixed supply model applied to oyster markets are written below with expected parameter signs appearing above each explanatory variable.

$$\text{Supply } Q_s = S(\overset{-}{\text{MSX}}, \overset{+}{P}_{t-1})$$

$$\text{Demand } Q_d = D_1(\overset{-}{P}, \overset{+}{I}, \overset{+}{P_r})$$

$$\text{Equilibrium conditions } Q_s = Q_d = Q$$

where MSX, P_{t-1}, P, I, and P_r are the MSX disease, price lagged 1 yr, current price, income, and the price of a related good, respectively. In the supply equation a negative relationship with MSX is hypothesized a priori, and lagged price may be positive or negative depending on the intensity of depletion. In demand, current price is expected to have a negative effect according to the law of

[11]Little technological change has occurred during the period of analysis due in part to state regulation mandating old technologies as a conservation device. Environmental factors such as pollution and siltation have doubtless had a negative impact on oyster supplies, but unfortunately little systematic and consistent information is available through time.

[12]We note that although lagged price may positively affect current effort the total effect on current harvest (i.e. supply) depends on what effect lagged price has on the current biological stock of the resource. For reasons explained below the net affect of lagged price on current supply might actually be negative if stocks have been reduced to the point of depletion. For an example of the short-run supply assumption (i.e., supply is independent of current price) in the fishery area, see Bell (1968). It should be noted that Bell's empirical work is quite successful using monthly data.

demand, the income effect is positive if oysters are a normal good, and the related good (poultry) is most likely a substitute for oysters.

Since the fixed supply assumption removes the simultaneity from the model, both the supply and demand functions can be interpreted as reduced forms, and estimated directly by ordinary least squares regression techniques without regard to problems of identification. The demand function is solved for its only endogenous variable, price, and estimated in this form. The reduced form equations estimated later in the paper are written below.

$$\text{Supply } Q = S(\overset{-}{\text{MSX}}, \overset{+}{\underset{-}{P_{t-1}}})$$

$$\text{Demand } P = D_2(\overset{+}{I}, \overset{+}{P_r}, \overset{-}{Q})$$

where Q is predetermined.

In addition to conclusions concerning parameter signs and elasticity values, implications of property right structures are revealed in the model. It is hypothesized that in states relying more heavily on common property rather than private leasing of subaqueous beds, the depletion effect should be greater. The lagged price variable in supply should thus have a negative coefficient value for common property right areas.

DATA

Regression analyses are performed on the above model for the Middle Atlantic and Delaware Bay regions. The Middle Atlantic region is defined to include the five contiguous coastal states of Virginia, Maryland, Delaware, New Jersey, and New York. This region includes the productive subaqueous resources of Chesapeake Bay, Delaware Bay, and part of Long Island Sound. The Delaware Bay area includes the states of Delaware and New Jersey only. We anticipate depletion to be a more important factor in the regional analyses which are dominated by the high production levels of Maryland and Virginia. These Chesapeake Bay states (especially Maryland) rely to a greater extent on common property than do the Delaware Bay states. The latter states allow much more extensive private leasing, and hence supply a greater proportion of their oysters from private leaseholds which may be expected a priori to be less subject to overfishing with the ensuing depletion.

Time series annual data on quantities landed (in pounds) and implicit prices are obtained from *Fishery Statistics of the United States* (1940-1970) compiled by the Bureau of Commercial Fisheries of the U.S. Department of Commerce and the U.S. Department of the Interior. Data on the price of a related commodity in demand (i.e., the price of poultry) and personal income are obtained from the Bureau of Labor Statistics (U.S. Department of Labor) and the *Survey of Current Business* (U.S. Department of Commerce), respectively. The biological variable representing the MSX disease included in the oyster supply function of the model was obtained from site sampling of oysters in the Delaware River.[13] The regions of consumption and production are not identical in that the consumption area includes a somewhat larger area. Precise definitions of the variables used are given below.

- Q Quantity per capita of oyster landings (measured as pounds per person) for Delaware Bay includes Delaware and New Jersey, and regional quantities include the five states of Delaware, New Jersey, Maryland, Virginia, and New York. Population refers to the seven-state region including New York, Pennsylvania, New Jersey, Delaware, Maryland, District of Columbia, and Virginia.
- P Price of oysters measured in dollars per pound (meat weight).
- P_{t-1} Price of oysters lagged 1 yr.
- MSX Biological variable referring to a protozoan oyster parasite commonly called the MSX disease.
- I Personal income per capita (deflated by the Consumer Price Index for all items) for the seven-state region including New York, Pennsylvania, New Jersey, Delaware, Maryland, District of Columbia, and Virginia.
- P_{ch} National average price per pound for chickens (live weight).

EMPIRICAL RESULTS

We now turn to a brief discussion of the detailed findings, and conclude with some general remarks and policy implications. Tables 1 and 2 present the

[13]The average annual prevalence of the MSX disease in a test sample of oysters in the Delaware River was obtained from H. Haskin of Rutgers University. These percentages were zero before 1957 and exceeded 50% in some later years.

TABLE 1.—Middle Atlantic supply and demand regressions.

Equation	Endogenous variable	Constant	Predetermined variables: MSX	I[3]	P_{ch}	P_{t-1}	Q[3]	Statistics[1] R^2 DW	Elasticities[2] Price	Income
Supply	Q[3]	1.733	−0.581			−1.202		0.85		
			(−3.14)*			−(6.29)*		0.48		
Supply	ln Q[4]	−0.136	−1.001			−0.319		0.68		
			(−3.60)*			−(3.05)*		0.39		
Demand	P	0.802		0.00002	0.010		−0.507	0.54	1.0	
				(0.20)	(4.12)*		(−3.14)*	0.76	0.1	
Demand	ln P[4]	−14.110		1.582	0.425		−0.421	0.53	2.4	
				(3.28)*	(2.59)*		(−1.50)	0.64	3.8	

[1] R^2 and DW refer to the unadjusted coefficient of determination and the Durbin-Watson statistic for autocorrelation, respectively.

[2] The formulae used in calculating price and income elasticities are $\frac{-dQ}{dp} \cdot \frac{P}{Q}$ and $\frac{dQ}{dI} \cdot \frac{I}{Q}$, respectively. In the regressions not utilizing logarithms mean values of variables are used to fix the point elasticities.

[3] Quantity and Income are measured in per capita form.

[4] All variables are measured in natural logarithms except MSX.

* Refers to statistical significance at the 0.05 level.

TABLE 2.—Delaware Bay supply and demand regressions.

Equation	Endogenous variable	Constant	Predetermined variables: MSX	I[3]	P_{ch}	P_{t-1}	Q[3]	Statistics[1] R^2 DW	Elasticities[2] Price	Income
Supply	Q[3]	0.223	−0.409			0.003		0.70		
			(−8.05)*			(0.22)		0.77		
Supply	ln Q[4]	−1.718	−4.317			−0.155		0.66		
			(−5.99)*			(−0.77)		0.98		
Demand	P	0.165		0.0003	0.008		−1.169	0.55	3.4	
				(3.18)*	(2.43)*		(−2.42)*	1.06	4.1	
Demand	ln P[4]	−18.290		2.090	0.407		−0.170	0.66	5.9	
				(5.04)*	(2.51)*		(−2.51)*	1.24	12.3	

[1] R^2 and DW refer to the unadjusted coefficient of determination and the Durbin-Watson statistic for autocorrelation, respectively.

[2] The formulae used in calculating price and income elasticities are $\frac{-dQ}{dp} \cdot \frac{P}{Q}$ and $\frac{dQ}{dI} \cdot \frac{I}{Q}$, respectively. In the regressions not utilizing logarithms mean values of variables are used to fix the point elasticities.

[3] Quantity and Income are measured in per capita form.

[4] All variables are measured in natural logarithms except MSX.

* Refers to statistical significance at the 0.05 level.

empirical results of the supply and demand model applied to oyster data for the years 1940 to 1970 in the Middle Atlantic and Delaware Bay regions. Numerical estimates of the coefficients along with t values in parentheses are obtained through the use of either linear or log linear regression analysis and ordinary least squares as the method of estimation.

In general, parameters have expected signs and are significant for at least the 0.05 level. The coefficient of determination is reasonably high in most regressions indicating that the included predetermined variables explain a large fraction of the variation in the endogenous variables. Since the linear and logarithmic equation forms do not differ greatly there is no evidence of nonlinearities.

In the supply equations the MSX variable displays a strong negative impact on quantity, and is more significant (i.e., larger t values) in the Delaware Bay regressions. Biological evidence indicates that the disease had a greater impact on Delaware Bay production than on Chesapeake Bay production although Virginia was hard hit during much of the period of analysis.

Lagged price has a negative and highly significant impact on supply for the Middle Atlantic region indicating that the depletion effect dominates the effort effect where common property prevails. In contrast the Delaware Bay results indicate that lagged price is not a significant determinant of supply in a private property right structure.

In the price (implicit demand) equations oysters display a significant positive income response in most regressions.[14] Oysters thus appear to be a normal good whose demand is likely to grow as consumer income rises over time. Since the price of chickens is a positive determinant of demand in all regressions, the relationship between the two commodities is one of substitution. The negative coefficient for quantity supports the law of

[14] Preliminary cross sectional analyses conducted by National Marine Fisheries Service Economic Research Laboratory indicate much weaker income effects (and possibly negative) for oysters.

demand indicating demand for oysters to be price-responsive.

In order to determine meaningfully how responsive quantity demanded is to price and income changes, it is useful to investigate the elasticities implied by the statistical results. Tables 1 and 2 indicate high elasticities in both the Middle Atlantic and Delaware Bay regions implying that oysters are price elastic and normal with respect to consumer income responses. If supplies were to increase in the future, one would expect increasing revenues for the oyster industry.[15] Similarly we might expect consumer demand for oysters to increase by larger percentages than real personal income in the future. Efforts to rehabilitate the oyster industry by cleaning up water pollution, discouraging overfishing, and replacing oyster cultch may thus have large social values.

Although the statistical results do lend support to the model, they are certainly not without difficulties. The time series problem of positive serial correlation is present throughout, thus detracting from the reliability of the results. The Durbin-Watson statistics in general indicate either positive autocorrelation or indeterminancy for the Middle Atlantic and Delaware Bay regions respectively using a two-tailed test at the 0.05 level of significance.[16] An additional problem impairing both estimation and prediction is structural change with data over a long time period. Parameters therefore may not remain constant with time series data. Also variables omitted from the model may have caused shifts in the functions over time. All of these problems make prediction hazardous and definitive conclusions should await further testing based on new data sets.

CONCLUSIONS

In general the statistical results support the model of supply and demand forces in the Middle Atlantic oyster industry. Estimates are generated on income and price elasticities of demand and lend optimism to the current rehabilitation efforts directed toward the oyster industry. The MSX disease has clearly had a debilitating effect, however, and must be solved as a condition of successful industry recovery.

The common property characteristics of the industry have also harmed the industry's progress. There exists evidence of overfishing in common property states, and hence less than optimal exploitation of the natural resource stocks. The results indicate that depletion is a much more serious problem for the Chesapeake Bay states than for the Delaware Bay states where private leasing of subaqueous lands is more prevalent. However, the reverse is true concerning the MSX disease characteristics of the regions.

[15]It has been reported by the Delaware State Department of Natural Resources and Environmental Control that oyster spat count recently have been the highest in several years indicating augmented supplies to be highly probable in the future.

[16]When first differences are used to remove serial correlation, R^2 and t values fall to unacceptably low levels although serial correlation is removed.

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THE REPRODUCTIVE BIOLOGY OF THE PROTOGYNOUS HERMAPHRODITE *PIMELOMETOPON PULCHRUM* (PISCES: LABRIDAE)

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ABSTRACT

Pimelometopon pulchrum, California sheephead, a labrid fish of the eastern Pacific Ocean, was collected the year round at Catalina Island, Calif., and comparative material was taken at Guadalupe Island, Mexico. Individuals at Guadalupe were dwarfed relative to those at Catalina. *Pimelometopon pulchrum* is a protogynous hermaphrodite, the ovarian elements undergoing massive degeneration as spermatogenic crypts proliferate in the gonads of transitional individuals. Sexual changes occur between breeding seasons. Individuals from both populations mature as females at age four; most of those at Catalina function as females for 4 yr and then change sex, at a length of around 310 mm. Sexual transformation occurs earlier on the average at Guadalupe; most individuals are male by age seven. In both populations, more rapidly growing fishes apparently change sex sooner than other individuals of the same age, and fishes that grow slowly may not change sex at all. Spawning appears to occur in July, August, and September in the Catalina population. Individuals probably spawn several times in a breeding season. The weight of active, prespawning ovaries increases at a rate approximately proportional to the third power of the length of the fish. Ovary weight increases in a linear fashion with age in the Catalina population. The rate of increase with age would be less in the Guadalupe population due to dwarfing.

The three coloration phases of *P. pulchrum* are described, two of which are found in adult individuals. The uniform coloration is made up mostly of mature female and immature fishes. About 5% of the mature uniform individuals were males at Catalina, and about 12% at Guadalupe. The bicolored phase is made up exclusively of males and late transitional individuals. Data from field transects revealed that there were about five uniform individuals to every bicolored male. Based on an estimated yearly survival rate of about 0.7, the mature sex ratio at Catalina was approximately two females for every male. The ratio at Guadalupe was closer to three females for every two males, due in part to the earlier sex changes seen there.

Sequential hermaphroditism, a phenomenon characterized by an individual changing from one sex to another at some point in its life history, is widespread in teleost fishes (Atz 1964; Reinboth 1970). In some species, individuals change from male to female (protandry) and in others the situation is the reverse (protogyny).

Most of the published information on the life histories of sequentially hermaphroditic species has dealt with the distribution of the sexes with size, sometimes correlated with a histological investigation of the gonads (Atz 1964; Reinboth 1970). However, in order to interpret the full implications of the sexual patterns seen in sequential hermaphrodites, data on the age distribution, age-specific fecundity, and the sexual transformation schedule of the population are needed (Warner in press).

There are a few protogynous fish species for which the information is nearly complete. For example, Moe (1969) provided excellent data on the life history pattern, gonadal transformation, and survival rate of the serranid *Epinephelus morio*. Natural sex reversal in the synbranchid *Monopterus albus* has been extensively studied both in the field and laboratory (Liem 1963, 1968; Chan 1971), but little is known about its age-specific fecundity and survival pattern. A similar situation exists for the labrid *Coris julis* (Reinboth 1957, 1962; Roede 1966), where again we lack information on the demography of the population. Among the Labridae, perhaps the most complete information exists on the seven Caribbean species of the genera *Thalassoma*, *Halichoeres*, and *Hemipteronotus* studied by Roede (1972). An unfortunate limitation was placed on Roede's work by the tropical location, which precluded age determination from growth rings on scales or otoliths.

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Pimelometopon pulchrum (Ayres), the California sheephead, is a labrid of the subfamily Bodianinae. It is confined to temperate waters, ranging from Monterey Bay, Calif., to Cabo San Lucas at the tip of Baja California, Mexico (Miller and Lea 1972). Individuals can reach a large size (over 800 mm standard length [SL]) and are commonly found off southern California along rocky shores at depths between 5 and 50 m. In this report, it is demonstrated that *P. pulchrum*, like many other labrids, is a protogynous hermaphrodite. In addition, data are presented on age and growth, on the distribution of the sexes in relation to color, size, and age, and on the observed patterns of fecundity and survival. The study embraces two widely separated populations, chosen to reflect how differences in the demography of the population might lead to the observed differences in the schedule of sexual transformation (discussed in Warner in press).

MATERIALS AND METHODS

Source of Materials and Times of Sampling

Pimelometopon pulchrum was taken by means of a hand spear while either skin diving or using scuba. The main collecting area was at Fisherman's Cove on the northeast shore of Santa Catalina Island, Calif., near the University of Southern California Marine Station (lat. 33°27′N, long. 118°29′W). A total of 341 individuals of *P. pulchrum* were processed from samples taken the year round at monthly intervals. Collections began in December 1969 and continued, with occasional gaps, until July 1971; monthly samples were between 20 and 30 individuals.

The other area sampled in this study was at Guadalupe Island, Mexico, located approximately 200 km west of Punta Baja, Baja California. Collections were made along the protected east side of the island, concentrating on an area 3 km from the southern tip known as Lobster Camp (lat. 29°01′N, long. 118°14′W). Year-round sampling at Guadalupe Island was not possible, and the 130 individuals taken there were from three expeditions, January 1970 (16 specimens), April 1970 (53 specimens), and May 1971 (61 specimens).

Supplemental collections were made at La Jolla, Calif., including a sample of large individuals from a spearfishing meet on 19 July 1970.

The standard length of each fish was measured, and its coloration noted. Several dorsal spines were removed and frozen, and the gonads were fixed in bouin's fluid.

Age Determination Methods

Age determination by counting annular marks on the otoliths or scales was precluded in *P. pulchrum*. The otoliths are extremely small and difficult to locate, and the central portions of nearly all the scales were either clear or irregularly banded, indicating regeneration.

The bones and spines of *P. pulchrum* did show regular markings, and younger fish could be successfully aged by counting the marks on either the bones (opercula or cranial ridges) or the dorsal spines. However, the proximal portions of the bones tended to thicken and obscure the earlier marks on older California sheephead and only dorsal spine annuli could be used for age determination.

Dorsal spines were prepared as follows: the flesh was removed by means of a household enzyme product (Ossian 1970) and the spines were air dried. The classical methods of decalcification and/or thin sectioning (e.g., Cuerrier 1951) were not used. Instead, a high-speed grinding tool with a thin abrasive disc was used to cut cleanly through the spine at a point just distal to the swollen portion of the base. The spinous portion was then thrust through an opaque light shield so that only the cut base protruded. A strong microscope light was directed to the lower portion of the shield so that the only light visible on the other side then came through the projecting base of the spine. The hyaline layers of the spine transmit much more light and the illuminated pattern, resembling tree rings, is easily seen in a dissecting microscope.

The second dorsal spine was used for primary counts; the ring patterns on the other spines were identical, and were used to verify counts for individuals. Counts on each spine were made by two people and were used in the analysis of growth only when they agreed. False rings, probably caused by abnormal growth conditions, were identifiable in young individuals by their proximity to other annuli and their tendency to be incomplete.

Rarely, older fish showed a marked degeneration of the central portion of the spine, which became hollow and oil-filled, making age determination from spines impossible.

A series of measurements of 100 spines was made with an ocular micrometer at a magnification of 30×. At this magnification, one ocular micrometer unit equals 0.033 mm. The radius was measured at midspine on a line perpendicular to and beginning at the indentation axis. Distances from the center of the spine to each annulus were recorded for back calculation of length, along the radius line. Finally, the distance from the spine margin to the outermost annulus was measured for determination of the time of annulus formation.

Methods of Reproductive Biology

In the laboratory, each gonad was blotted dry, weighed, and a segment of one lobe was dehydrated in alcohol and embedded in paraffin. Slides were prepared of cross-sections of the lobe, cut at thicknesses of 5, 10, and 25 μm; thicker sections have less tendency to collapse and were made to ensure that the overall configuration of the cross-section could be observed. Sections were stained with ehrlich's hematoxylin and eosin.

Each gonad was classified according to sex and state of development. Assignment of a developmental class depended on the predominate stage of gametogenesis seen in the gonad. The division of gametogenic stages is as follows:

Oogenesis was divided into five stages, following criteria detailed for a variety of species by Kraft and Peters (1963), Smith (1965), and Moe (1969).

Stage 1. Very small (15-30 μm in diameter) oocytes with a large nucleus, single nucleolus, and a relatively small amount of basophilic cytoplasm.

Stage 2. (30-50 μm) Previtellogenic oocytes with a strongly basophilic cytoplasm and multiple nucleoli around the nucleus margin.

Stage 3. (150-300 μm) Vitellogenesis begins with the deposition of yolk vesicles in the less darkly staining cytoplasm. A thin zona radiata can be seen in late stage 3.

Stage 4. (280-450 μm) Cytoplasm filled with yolk vesicles and globules; the zona radiata well developed and strongly acidophilic.

Stage 5. (450-1,050 μm) Mature or nearly mature oocytes, uniform in appearance due to the coalescence of the yolk globules. The nucleus is eccentric and the zona radiata is thin and nonstriated. These oocytes are often extremely irregular in outline and Roede (1972), who noted the same irregularity in mature eggs of other labrids, probably correctly attributed this to distortion during fixation and staining. This stage was seldom seen, but several specimens were seen with eggs in the ovarian lumen and stage 5 oocytes still within the follicle.

Spermatogenesis occurs in small crypts, in which all the cells are at the same stage. The development and appearance of the spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and mature sperm follows very closely the descriptions given by Hyder (1969) for *Tilapia* and by Moe (1969) for *Epinephelus morio*, and will not be repeated here.

The gonadal development classes, intended to parallel those of Moe (1969) and Smith (1965), were designated as follows:

Class 1. Immature female. Stages 1 and 2 oocytes present, atretic or brown bodies (Chan et al. 1967) absent. The ovarian lamellae are pressed closely together and the lumen is small.

Class 2. Resting mature female. Oocyte stages 1, 2, and 3 present, with stage 2 predominating. Atretic bodies are usually present.

Class 3. Active mature female. Oocyte stages 3 and 4 predominate in the lamellae. In late class 3, stage 5 oocytes are also present.

Class 4. Postspawning female. Ovary is disrupted, with many empty follicles in the lamellae. Some degenerating stages 4 and 5 oocytes are usually found in the lamellae and lumen, respectively.

Class 5. Transitional. Seminiferous crypts begin to proliferate in the lamellae, but some stage 2 oocytes can be seen. These oocytes degenerate and decrease in number as spermatogenic activity begins to dominate the gonad.

Class 6. Inactive male. Crypts containing primary and secondary spermatocytes predominate; few spermatids and mature sperm are seen.

Class 7. Active male. Spermatids and tailed sperm increase in abundance until, in the ripe phase, sperm are densely packed in the collecting ducts and many crypts have coalesced.

Class 8. Postspawning male. Ducts are still expanded, but few sperm can be seen in them. Many new crypts containing spermatogonia are present. This apparently is a short-lived stage that rapidly gives way to the resting (class 6) testis.

Fecundity determinations were made by count-

ing yolky oocytes. A thick cross-section of the ovary was cut from near the middle of the lobe, weighed, and then agitated to dislodge as many oocytes as possible from the ovarian lamellae. Oocytes remaining in the lamellae were teased out so that a complete count could be made. An estimate of the number of yolky oocytes per gram of ovary could then be made directly from the sample. The total number of eggs in the ovary was then approximated by multiplying by the total weight of the ovary.

Relative abundance of coloration types was estimated directly from field observations. To eliminate the effects of any differential depth distribution, visual transects were either run perpendicular to depth contours or were compiled from a series of equal length runs parallel to successive contours. Transects were approximately 50 m in length. The number of California sheephead in each color phase was recorded. It was assumed that both coloration types are equally visible, and this is probably valid. California sheephead are not secretive when adults; only juveniles tend to remain close to cover. Larger males appear warier than other individuals, but still remain in sight. The problem in observing California sheephead is not in avoidance, but inquisitiveness. Occasionally transects had to be aborted because of the tendency of *Pimelometopon* to follow the diver.

RESULTS

Age and Growth

Van Oosten (1929) set forth criteria for the acceptance of annuli on scales or bones as yearly marks. These criteria apply equally well to spines, and are as follows: (1) The spine must remain constant in identity and grow proportionally with the fish. (2) Only one mark must be formed each year. (3) The body lengths calculated by using prior annuli on the spine (back-calculated lengths) should agree with the actual lengths of younger age groups.

The criteria will be discussed in order.

(1) Dorsal spines were certainly constantly identifiable in all individuals of *P. pulchrum* examined. The relationship of spine radius to standard length (Figure 1) is satisfactorily expressed in a linear fashion ($r = 0.787$) and there is no apparent indication of allometric growth of the spine, at least for fishes of lengths greater than 130 mm. Much of the scatter in the data is due to variability in the location of the cut made across the tapering spine.

(2) The increment of distance from the last annulus to the outer edge of the spine should increase with the time since the formation of that mark. If one mark is formed each year at a particular time, the average marginal increment should drop to near zero at the time of annulus formation, then steadily increase for the rest of the year. This pattern is shown (Figure 2) for 77 California sheephead from Catalina taken throughout the year. Successive age groups did not differ in time of annulus formation, so the data are combined for all aged fish. The distinct hyaline bands appeared to be formed in June and July, at the beginning of the period of warming water in the Catalina area (Quast 1968). Formation of growth marks has been found to occur in other inshore California fishes at a similar time (Joseph 1962; Norris 1963; Clarke 1970). Ring formation also overlaps with the initiation of reproductive activity, although egg production and spawning continue well into September (see below).

(3) Lengths of *P. pulchrum* at previous ages were calculated by a modified direct-propor-

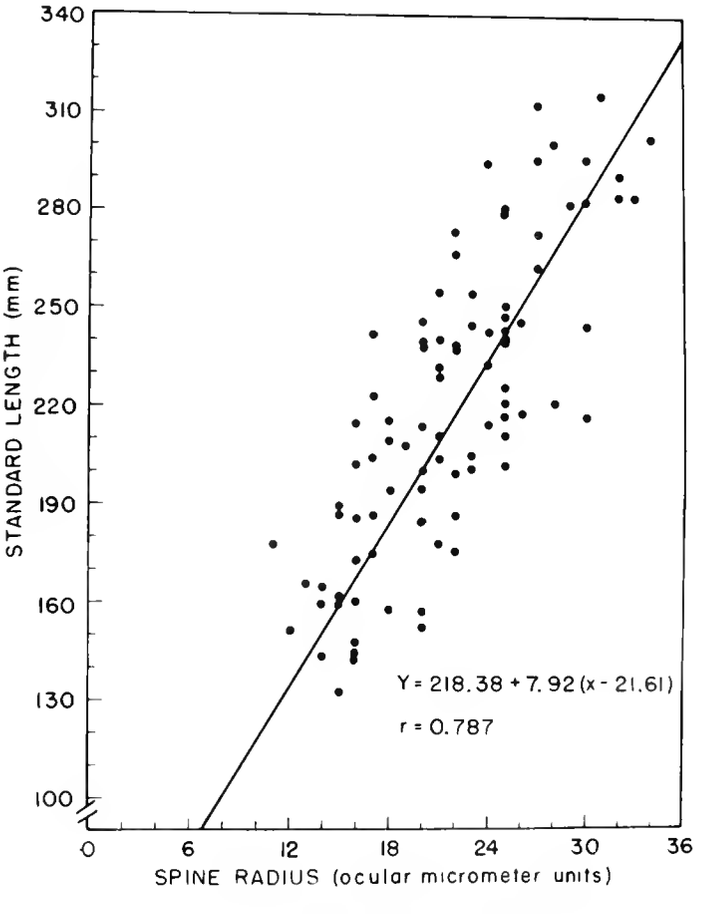

FIGURE 1.—The relationship of dorsal spine radius to standard length for 117 specimens of *Pimelometopon pulchrum* from Catalina Island. One ocular micrometer unit equals 0.033 mm at 30×.

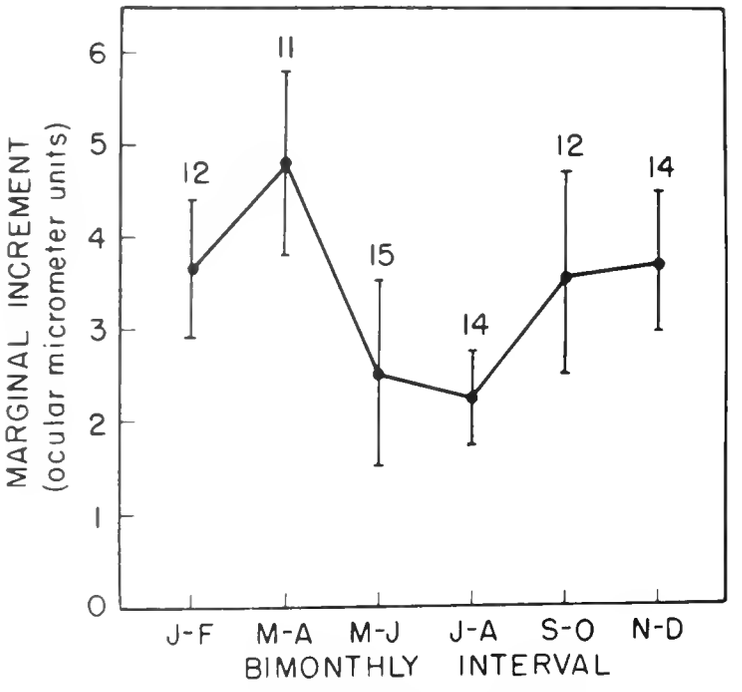

FIGURE 2.—Mean marginal increments for six bimonthly intervals from 78 specimens of *Pimelometopon pulchrum* from Catalina Island. Sample sizes are shown for each interval, and 95% confidence limits for the mean are drawn on either side of each point.

Table 1 shows the back-calculated lengths for 100 California sheephead from Catalina over eight age groups, derived from spine radius measurements. The means from back calculation are also given in Figure 3 for comparison with empirical data. The mean standard lengths for each age (Figure 3) demonstrate good agreement with the back-calculated data.

There appears to be a slight slowing of growth after the fourth year in the Catalina California sheephead population. This may reflect the onset of a diversion of a significant amount of energy into egg production, since most 4-yr-old fish examined were mature females (see below). A second period of more rapid growth is suggested after the seventh year, at an age where many of the Catalina California sheephead are beginning to transform from female to male. There is no evidence for a decrease in the rate of growth up to age 13, where the average standard length is 470 mm. *Pimelometopon pulchrum* is quite capable of growing larger than this, and some individuals have very long lifespans. Fitch and Lavenberg (1971) mention a 32-inch (815-mm) male aged at 53 yr, and an 8.3-kg female, no length given, that was 30 yr old. Although exact age determination becomes difficult for large and old individuals, it is occasionally possible. The largest California sheephead encountered in this study were a 592 mm SL male, 20 yr of age, and a 538 mm SL male which had lived 18 yr. Size-age distributions can vary for different locations. In a sample taken by the California Department of Fish and Game at a spearfishing meet at San Pedro, Calif., on 28 March 1971, the mean standard length for males was 661 mm (range 545-745 mm) and for females was 450 mm (range 294-656 mm).

The pattern at Guadalupe Island is different from that at Catalina (Figure 4). While the sample

TABLE 1.—Back-calculated lengths for age groups 1 through 8 of *Pimelometopon pulchrum* from Catalina Island.

Age group	N	Mean length of subsample (mm)	Mean length of total sample (mm)	Back-calculated lengths (mm) for ages 1	2	3	4	5	6	7	8
1	8	100	116	97							
2	16	158	155	100	127						
3	22	198	197	106	139	168					
4	17	231	238	124	152	178	200				
5	11	246	245	130	164	185	203	225			
6	11	286	272	129	159	191	212	230	251		
7	7	289	294	128	163	190	225	247	274	295	
8	8	359	368	145	183	220	254	279	299	320	343
Overall means of calculated lengths				117	150	184	214	242	272	308	343
Number of individuals				100	92	76	54	37	26	15	8

tionality method given by Rounsefell and Everhart (1953) as follows:

$$\frac{L' - C}{L - C} = \frac{S'}{S}$$

where L = length of the fish at the time the spine was obtained, L' = length at the time a particular annulus was formed, S = total length of the spine radius, and S' = length along the spine radius to the annulus in question. The term C is a factor used to correct for the length obtained before the spine was formed, and is estimated by the intercept of the length axis on a fish length versus spine radius plot (Figure 1). In the case of the Catalina California sheephead population, C was equal to 47.2 mm.

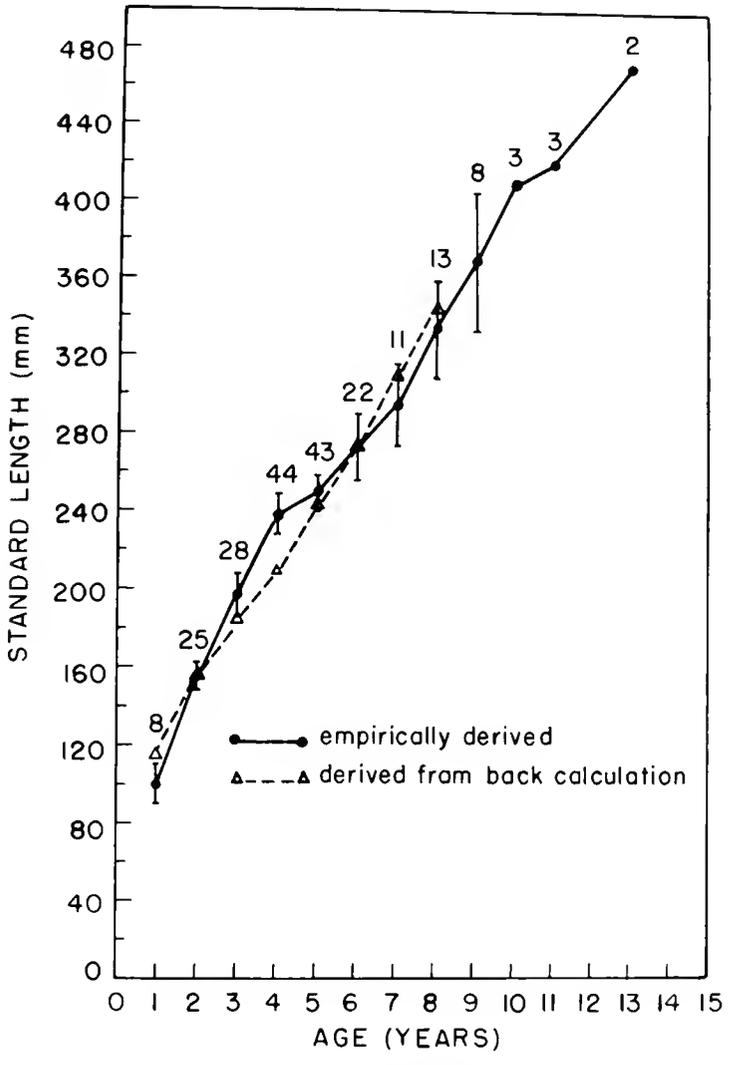

FIGURE 3.—Mean standard length versus age in the Catalina population of *Pimelometopon pulchrum*. Sample sizes are shown for each interval, and 95% confidence limits for the mean are drawn on either side of each point. Means for back-calculated lengths are shown for comparison.

is smaller and more variable than that from Catalina, a marked tendency towards dwarfing is clear. Judging from the mean lengths of each age class, the Guadalupe California sheephead complete their first year of growth at a standard length about 20 mm shorter than those at Catalina. For each of the next 3 yr they fall behind an additional 10 mm, after which relative growth slows even more. By the eighth year, the mean standard length of Guadalupe California sheephead is a full 100 mm less than that found at Catalina.

In spite of the dwarfing, the Guadalupe population shows some interesting parallels with Catalina. The slowing of the average rate of growth at the time of maturity (age four) is more striking here, and growth appears to pick up again after the sixth year, by which time at Guadalupe most individuals are males (see below). This suggests that an increase in the growth rate is associated with sex changes, a topic covered more fully in the discussion. In the Catalina population, both the increase in growth rate and the maximum number of sex changes occur about a year later than in the Guadalupe population.

Anatomical Features of the Gonad and Sexual Transformation

The gonad of *P. pulchrum* consists of two hollow sacs in the extreme dorsal part of the body cavity. Genital arteries and veins run through the dorsal part of each lobe, giving off segmental branches. The wall of each lobe consists of connective tissue and smooth muscle.

The internal structure is made up of germinal epithelium in a series of folds or ridges, the gonadal lamellae. These are numerous in the female, but few in the male. There is a small

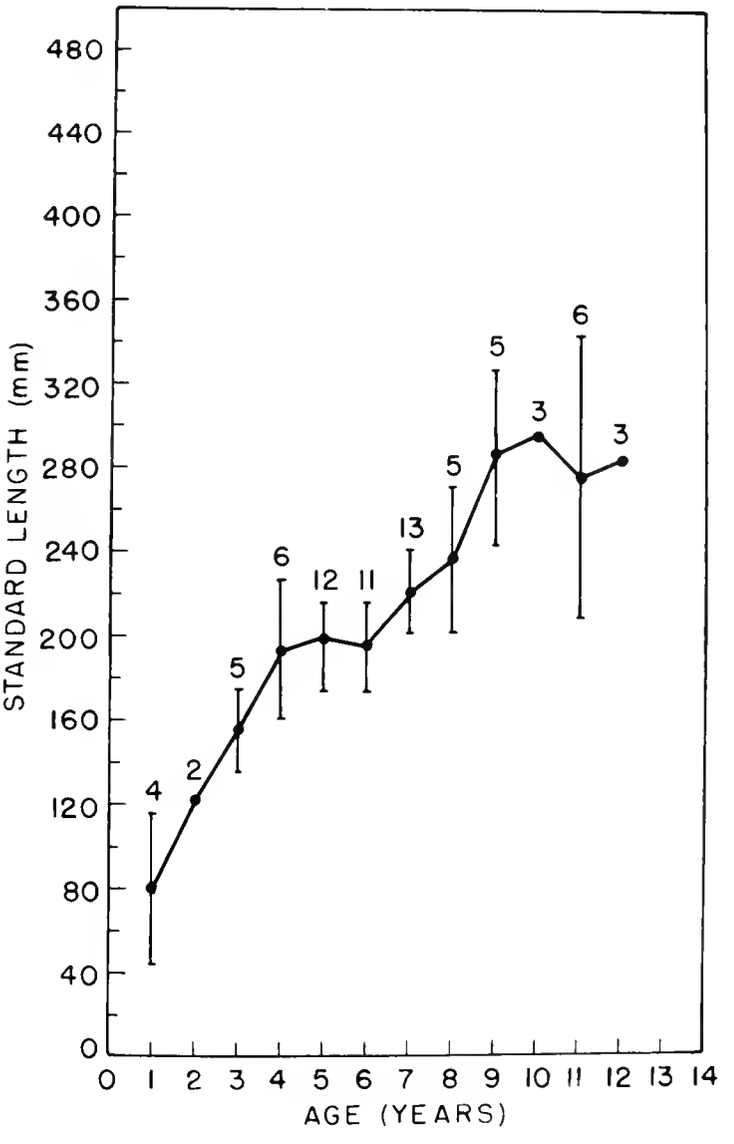

FIGURE 4.—Mean standard length versus age in the Guadalupe Island population of *Pimelometopon pulchrum*. Sample sizes are shown for each age, and 95% confidence limits are drawn on either side of each point.

alamellar portion in the most ventral section of the gonad, similar to that described by Smith (1965) for some serranids.

In the female, oogenesis takes place within the lamellae. When the egg ripens, it breaks into the central lumen, which leads to the common oviduct. Some oocytes are interrupted in their normal development and undergo a degeneration into various types of corpora atretica (Figure 5). These have been described briefly for serranids by Smith (1965) and in detail for *Monopterus albus* by Chan et al. (1967). Chan and his colleagues discuss the possible endocrine function of atretic structures, and state that all types of corpora atretica eventually end up as brown or yellowish bodies which are long lasting in the gonad. In *P. pulchrum*, brown bodies can usually be found near the gonad wall and in the central portion of the lamellae. Judging from the number of these terminal phase corpora atretica in resting (class 2) females compared with the usually greater number of earlier stage atretics (Chan et al. 1967) in postspawning females, the brown bodies are probably formed from more than one degenerating oocyte.

Brown bodies are also found in male gonads; some of these are almost certainly the result of oocyte degeneration in the previous female phase (Figure 6), while others may be the result of degeneration and coalescence of unshed sperm.

During sexual transformation, crypts of developing spermatocytes appear, first at the base of the ovarian lamellae, and then throughout the gonad (Figure 7). Unshed eggs and nonvitellogenic (stage 2) oocytes are gradually reabsorbed and the number of lamellae visible in cross-section are reduced. The basic structure of the gonad remains ovarian, with a central lumen into which the lamellae protrude. The lumen however no longer functions in gamete transport and sperm are collected in a series of sinuses on the periphery of the gonad, reaching the outside by means of ducts in the wall of the now unused oviduct. This is very similar to the anatomy described by Reinboth (1962, 1970) for other labrid secondary (sex-reversed) males. No testes of the primary type were seen.

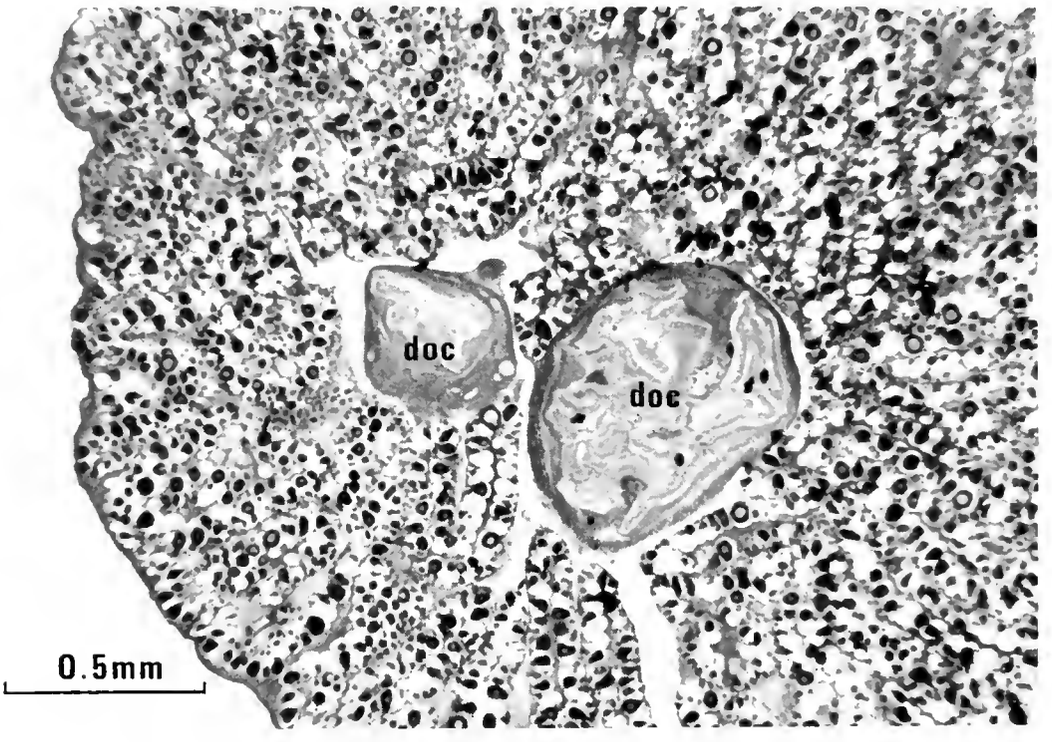

FIGURE 5.—Degenerating oocytes (doc) in the lumen of a resting ovary of *Pimelometopon pulchrum*. Specimen number PP411, 217 mm SL.

Transformation Schedule

To illuminate the life history patterns of the California sheephead populations, the gonad development classes were grouped in the following way:

Immature: Class 1 only.
Female: Classes 2, 3, and 4.
Transitional: Class 5 only.
Male: Classes 6, 7, and 8.

The distribution of sexual types by standard

length for *P. pulchrum* from Catalina Island (Table 2) and Guadalupe Island (Table 3), as well as the relative frequencies for each size grouping (Figure 8), are similar in both localities in that the small size classes are made up exclusively of immature females. Mature females are most abundant in the next size classes, and then become less numerous as males begin to predominate in the

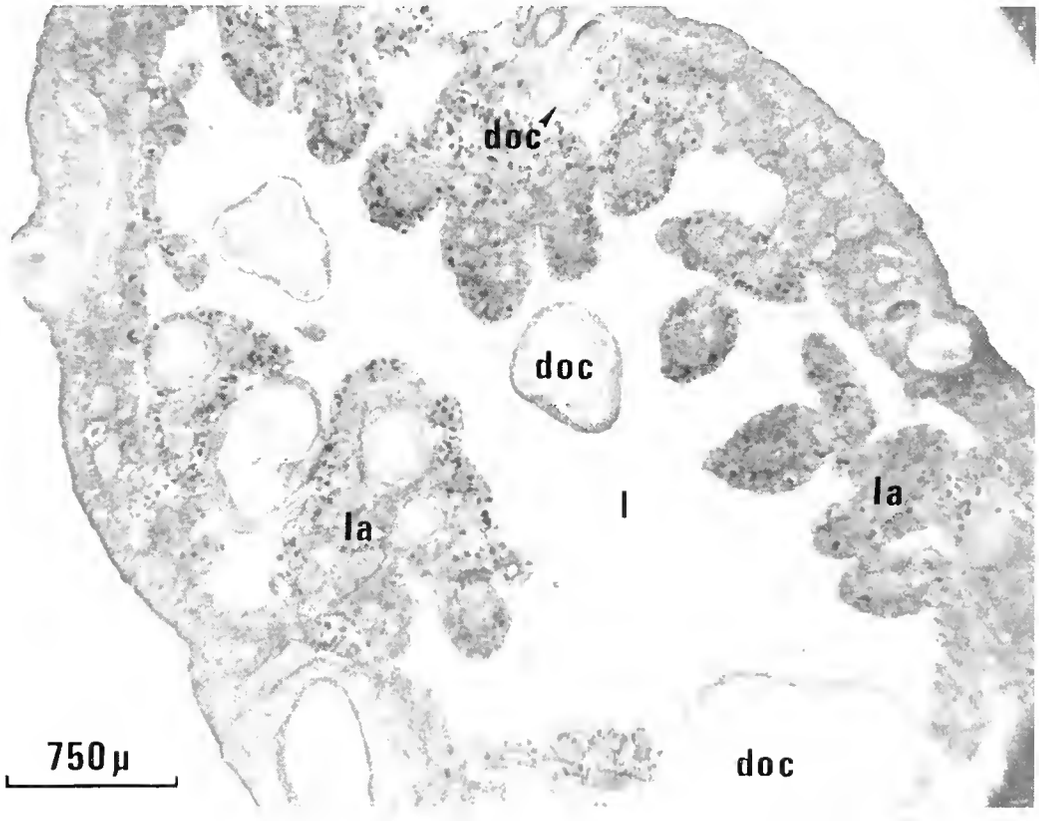

FIGURE 6.–Degenerating oocytes (doc) in the lumen (l) and lamellae (la) of the gonad of a transitional individual of *Pimelometopon pulchrum*. Specimen number PP405, 317 mm SL.

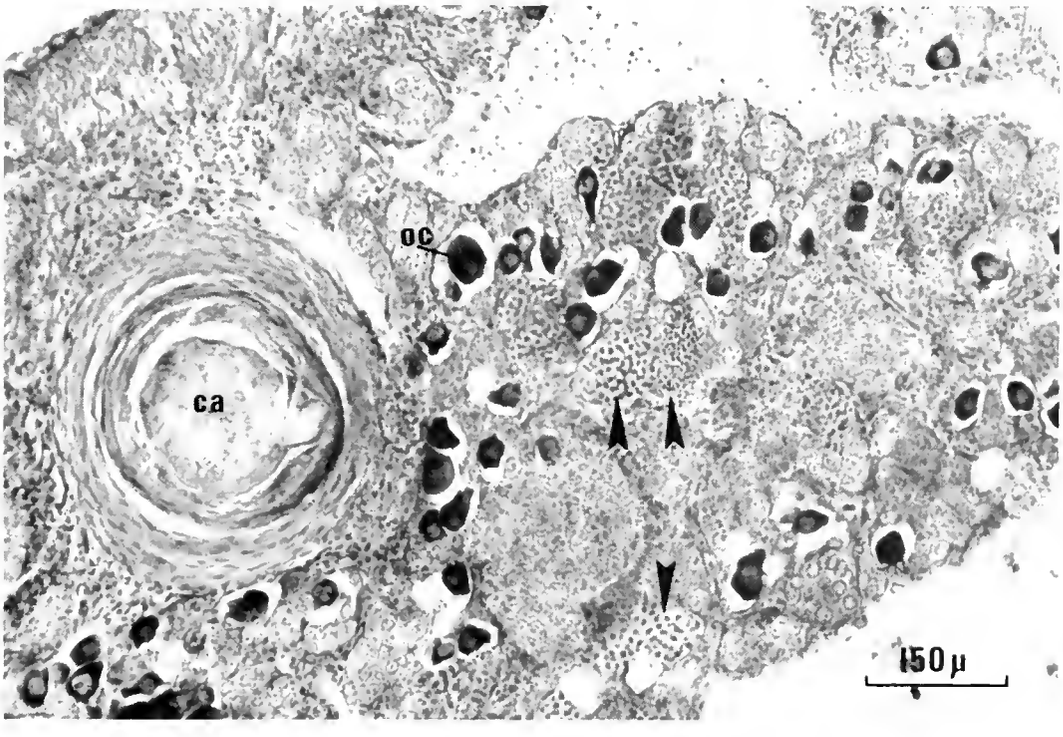

FIGURE 7.–Spermatogenic crypts (shown by arrows) developing in a gonadal lamella of a transforming *Pimelometopon pulchrum*. Stage 2 oocytes (oc) and a corpus atreticum (ca) can also be seen. Specimen number PP405, 317 mm SL.

TABLE 2.—Frequency of sexual types in each 20-mm size class for the Catalina Island population of *Pimelometopon pulchrum*.

Standard length (mm)	Number of fish	Immature	Mature female	Transitional	Mature Male
< 100	7	7	0	0	0
100-119	5	5	0	0	0
120-139	6	6	0	0	0
140-159	28	28	0	0	0
160-179	18	18	0	0	0
180-199	25	24	1	0	0
200-219	34	15	19	0	0
220-239	40	6	33	0	1
240-259	49	2	39	5	3
260-279	33	0	25	4	4
280-299	23	0	15	2	6
300-319	14	0	9	1	4
320-339	10	0	3	0	7
340-359	16	0	5	0	11
360-379	9	0	1	0	8
380-399	7	0	2	0	5
> 400	17	0	1	0	16
Totals	341	111	153	12	65

TABLE 3.—Frequency of sexual types in each 20-mm size class for the Guadalupe Island population of *Pimelometopon pulchrum*.

Standard length (mm)	Number of fish	Immature	Mature female	Transitional	Mature Male
< 100	5	5	0	0	0
100-119	5	5	0	0	0
120-139	3	3	0	0	0
140-159	8	1	7	0	0
160-179	12	0	9	0	3
180-199	15	0	10	0	5
200-219	16	0	5	1	10
220-239	11	0	2	1	8
240-259	16	0	4	2	10
260-279	10	0	2	2	6
280-299	6	0	1	0	5
300-319	7	0	1	0	6
320-339	7	0	1	0	6
340-359	2	0	0	0	2
360-379	3	0	0	0	3
380-399	1	0	0	0	1
> 400	3	0	0	0	3
Totals	130	14	42	6	68

largest sizes. Transitionals were found in intermediate sizes, in numbers which varied seasonally (see below).

At Catalina, most California sheephead mature at standard lengths between 190 and 230 mm. Sexual transformation occurs over a broader size range beginning at 250 mm, with a peak of activity apparently occurring at standard lengths between 310 and 330 mm.

The dwarfing phenomenon found in the Guadalupe population is again evident (Table 3, Figure 8). Maturity begins at a length near 140 mm, and the majority of individuals are male by a length of 210 mm. Peak transformation activity appears to occur in the population in fishes ranging from 190 to 230 mm in standard length.

The actual time courses for all these events become evident when the relative frequencies of

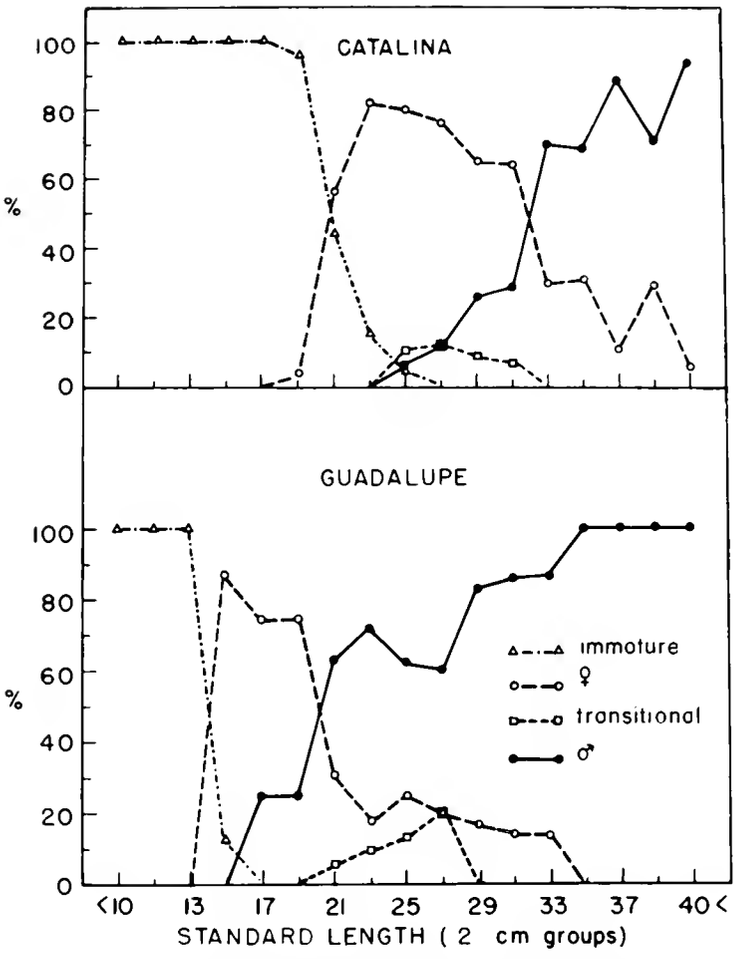

FIGURE 8.—Proportions of each sexual type in successive 2 cm standard length groupings for the Catalina Island (top) and Guadalupe Island (bottom) populations of *Pimelometopon pulchrum*.

TABLE 4.—Frequency of sexual types in each year class of *Pimelometopon pulchrum*.

	Age class	Number of fish	Immature	Mature female	Transitional	Mature male
Catalina population	1	7	7	0	0	0
	2	33	33	0	0	0
	3	34	34	0	0	0
	4	42	5	35	1	1
	5	40	0	33	2	5
	6	27	0	16	3	8
	7	15	0	9	1	5
	8	14	0	4	0	10
	9	8	0	2	0	6
	10+	8	0	1	0	7
Totals		228	79	100	7	42
Guadalupe population	1	4	4	0	0	0
	2	2	2	0	0	0
	3	5	5	0	0	0
	4	4	0	4	0	0
	5	10	0	5	1	4
	6	13	0	7	0	6
	7	14	0	2	3	9
	8	9	0	2	0	7
	9	6	0	0	1	5
	10+	13	0	3	0	10
Totals		80	11	23	5	41

the sexual types in each age class are graphed (Figure 9). The curves are based on the frequency distributions listed in Table 4.

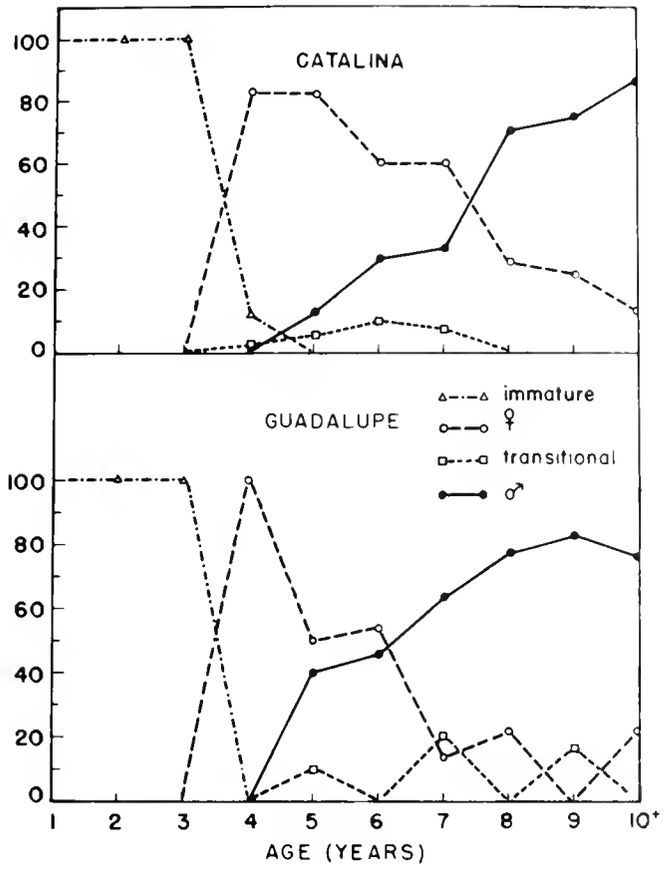

FIGURE 9.—Proportions of sexual types in each year class of *Pimelometopon pulchrum* from Catalina Island (top) and Guadalupe Island (bottom). The last age grouping consists of all fishes 10 or more years old.

In both populations, sexual maturity begins in the fourth year of life for virtually all members. By using age groupings, the skewness introduced by the dwarfing at Guadalupe is removed, and differences in the transformation activity time schedule in the two populations are revealed. At Guadalupe, males are present in essentially the same abundance as females in age classes 5 and 6, and strongly predominate at age 7 and thereafter. Therefore the majority of California sheephead at Guadalupe Island spend no more than 2 or 3 yr as functional females.

Transformation generally occurs later in the Catalina population. Most individuals are functional females for at least 4 yr, and males predominate only after age 8.

Distribution of Gonad Development Classes with Time

The active state of gonads may be determined directly through histological examination or inferred from the appearance and the size of gonad (gonad indices).

The seasonal distribution of mature gonad development classes for 166 California sheephead from Catalina is shown in Figure 10. As expected, immature fishes, which are not shown in the Figure, occur throughout the year. Resting stage females (class 2) were encountered from August through May, and predominated from October to April. Active females (class 3) were present May

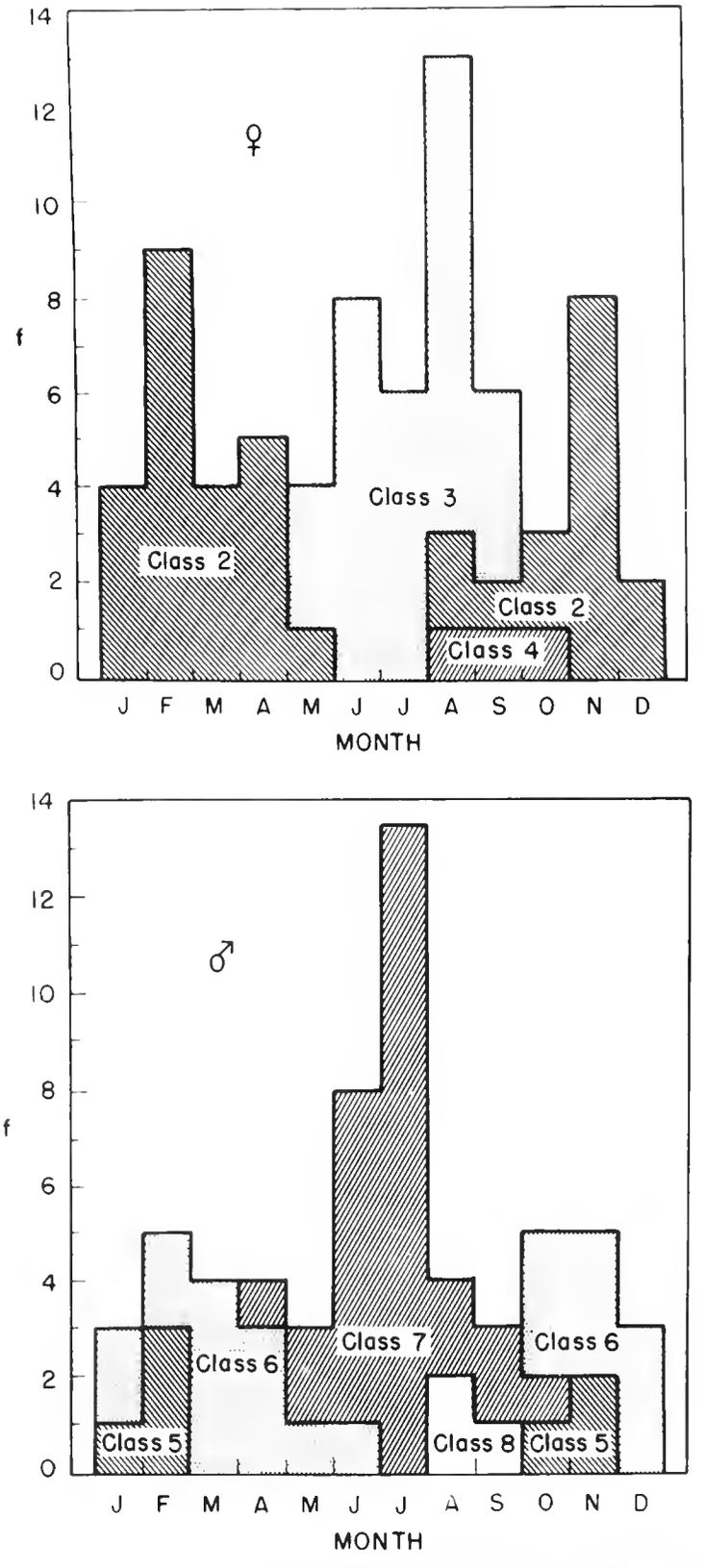

FIGURE 10.—Number of individuals of *Pimelometopon pulchrum* in each mature gonadal development class from monthly samples taken at Catalina Island.

through September. Late class 3 gonads were seen in July, August, and September, and most spawning activity probably takes place in these months. Females with postspawning ovaries (class 4) were captured in low numbers from August to early October. Class 4 appears short-lived, quickly receding into a resting class (class 2) or transitional (class 5) phase.

Transitional individuals were found only from October to March at Catalina. Those taken in October and November were all in the early stages of transformation, with many stage 2 oocytes and a few scattered spermatogenic crypts in evidence. Transitionals captured in February at Catalina or in May at Guadalupe were more advanced, with few stage 2 oocytes and spermatogenic crypts dominating the gonad.

Most males at Catalina were inactive (class 6) from October through April, closely paralleling the period seen for females. Active gonads predominated in samples from fish taken in May through September. Again the pattern suggests that spawning activity takes place from August through early October.

Further support for designating this period as the spawning season comes from the gonad indices (Figure 11) of Catalina females caught in different months. These reflect a similar pattern seen in the analysis of gonad development states. After a quiescent period from October through April, the ovaries begin to increase in size until a maximum is reached in June and July. Spawning reduces the average index steadily from then until September. The resting value is then seen again, remaining constant through the winter.

The index used was gonad weight scaled to compensate for different lengths of individuals. When only the mature females less than 310 mm in standard length are included in the analysis, the relationship between gonad weight and standard weight is sufficiently linear (Pearson correlation coefficient = 0.845 [$P < 0.001$] on 24 individuals caught in June) that the use of the following formula is justified:

$$\text{Gonad index} = \frac{(\text{gonad weight in grams})\,(100)}{(\text{standard length in mm})}$$

The size range used includes the great majority of reproductive females at Catalina.

An analysis of the spawning season of *P. pulchrum* at Guadalupe Island was not possible due to the lack of year-round sampling.

Multiple Spawning and Fecundity

Two or more distinct groups of ripening oocytes were usually apparent in the ovaries of *P. pulchrum* examined in June and July. The size distribution of yolky oocytes in an ovarian cross-section (Figure 12) from a female, 244 mm SL, captured at Catalina in mid-July, shows that there is one group of eggs ready to be spawned, and that two other distinct groups are undergoing vitellogenesis. This type of successive maturation of several groups of oocytes is termed asynchrony, and is characteristic of species that have comparatively long breeding seasons and multiple spawnings by individuals within each season (Yamamoto and Yamazaki 1961).

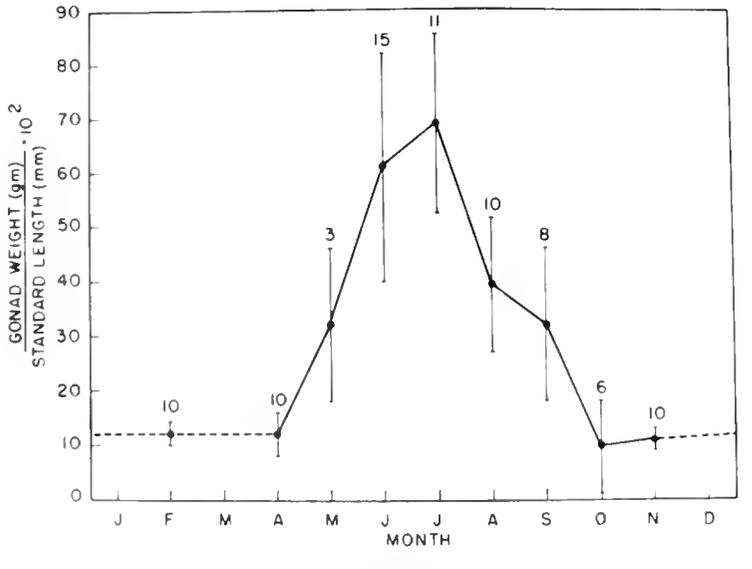

FIGURE 11.—Average gonad indices for monthly samples of mature female *Pimelometopon pulchrum*, all of standard lengths less than 300 mm. Sample sizes are shown above the bracketed lines, which are the 95% confidence limits of the mean.

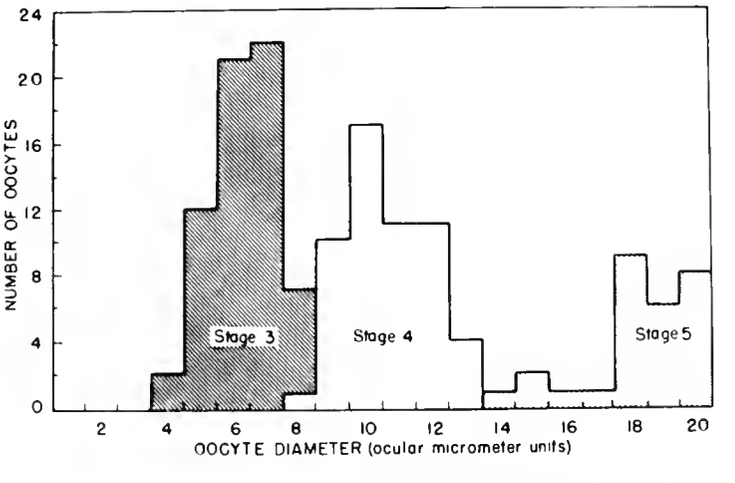

FIGURE 12.—Size distribution of yolky oocytes in an ovarian cross-section of a 244 mm SL female of *Pimelometopon pulchrum* captured 22 July at Catalina Island. The oocytes are also classified according to their degree of development.

Further evidence for multiple spawning is seen in the ovaries from some females captured in August and early September. There were a few mature eggs free in the lumen and numerous empty follicles in the lamellae, both indications of recent spawning. At the same time, another group of vitellogenic oocytes were observed developing in the lamellae and these would presumably have been spawned at a later time.

As Yamamoto and Yamazaki (1961) point out, the presence of multiple spawning complicates any determination of the number of eggs produced each year by an individual fish. Estimates can be made from an analysis over time of frequencies of egg diameters, such as that done by Clark (1934) for *Sardinops caerula*. Such analyses require a large sample over the mature size range and this was not available for *P. pulchrum*.

Counts of the yolky oocytes in subsamples of ovaries made for California sheephead females captured in July (Table 5) are probably overestimates of the number of eggs spawned during the season. This is because, as pointed out above, the relationship between the number of these oocytes and the number actually spawned depends on the survival rate of the oocytes to maturity and the proportion that are actually ejected from the body. The smaller numbers of stage 5 oocytes relative to stages 3 and 4 (Figure 12) indicates a loss during development. There are certainly some eggs left in the lumen of postspawning females. These degenerate and are presumably absorbed during the resting phase.

TABLE 5.–Estimates of the total number of vitellogenic oocytes and density of those oocytes in the ovaries of *Pimelometopon pulchrum* captured at Catalina Island in July 1970.

Standard length (mm)	Date of capture	Weight of ovary (g)	Estimated number of yolky oocytes, total	Estimated number of yolky oocytes per gram of ovary
209	7/24	6.87	36,068	5,250
235	7/22	16.69	74,270	4,450
238	7/22	16.53	76,870	4,650
254	7/19	28.00	171,500	6,125
280	7/22	17.23	88,300	5,125
311	7/19	50.02	296,600	5,930
314	7/19	19.80	113,850	5,750
330	7/19	34.07	167,600	4,920
359	7/19	41.63	258,100	6,200

Mean and 95% confidence limits of oocyte density, oocytes per gram = 5,377 ± 499.

For an analysis of the functional significance of sequential hermaphroditism, actual egg numbers are less important than data on the relative values for age- or size-specific fecundities (Williams 1966; Warner in press). As long as the number of eggs per unit weight of ovary does not vary appreciably with size or age, weights of active prespawning ovaries can be used to represent relative fecundities. The last column of Table 5 shows there is no apparent effect of fish length on egg density within the ovary.

Comparison of ovary weights and standard lengths for mature females captured at Catalina in June and July (Figure 13) shows that fecundity increases exponentially with the length. The exponential equation:

$$W = 1.31 \times 10^{-3} L^{2.95}$$

(W = gonad weight, L = standard length) indicates that the increase of gonad weight with

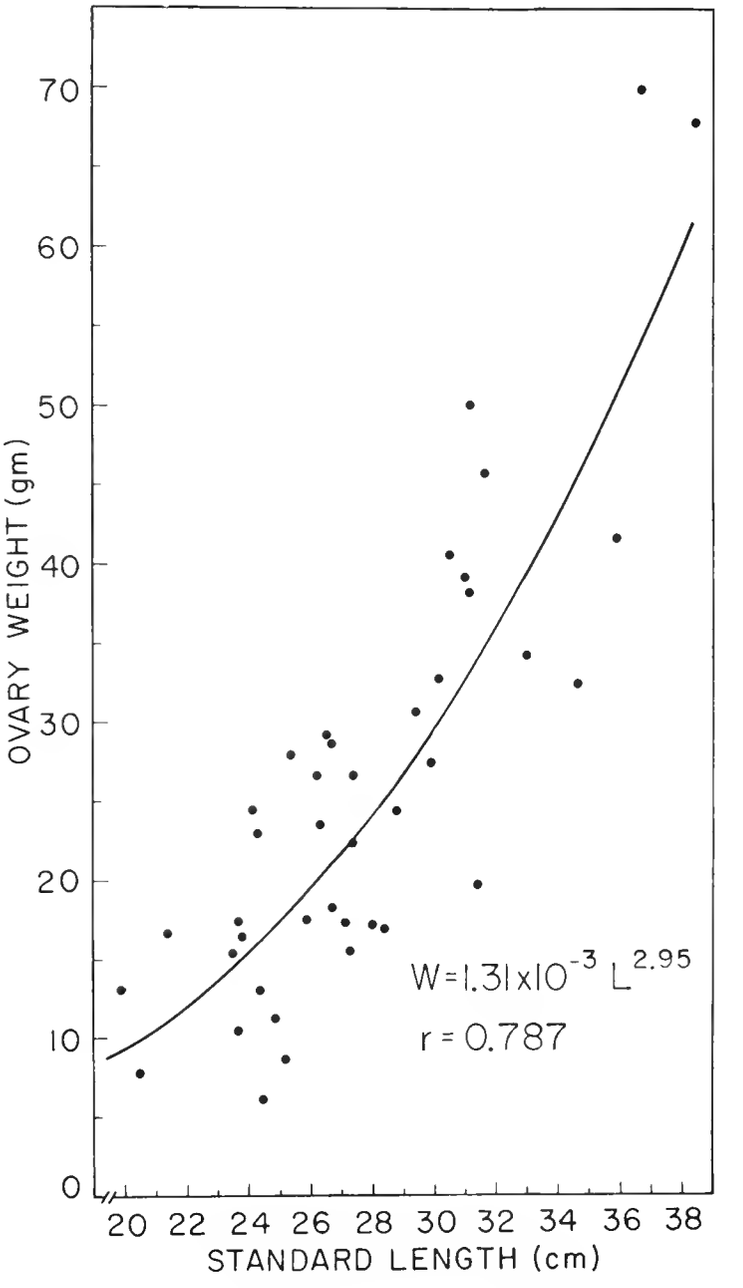

FIGURE 13.–Ovary weight versus standard length for females of *Pimelometopon pulchrum* captured in June and July at Catalina Island.

length conforms to a simple cube law relationship, which would be expected if gonad weight remains some constant proportion of the total weight. The exponent 2.95 was determined by a least-squares regression fit to a logarithmic transformation of the data. The confidence limits around the regression line become increasingly large with higher values of W and L, and the curve should not be used for extrapolations beyond the range of the data. Ovary weights in relation to age are shown in Figure 14. There are few data for the older age classes, but there is a definite positive correlation of the fecundity and the age of the individual.

Coloration, Sex, and Field Distribution of Coloration Types

The California sheephead is found in three main color phases (Crozier 1966), all of which are closely correlated with sexual state.

For the first year, *P. pulchrum* has juvenile coloration, a gold or salmon body color with black spots on the anal fin, the anterior and posterior portions of the dorsal fins, and on the caudal peduncle, and with a silver lateral stripe extending from the eye to the caudal fin. Crozier (1966) stated that the initial body color was gold, and this was gradually replaced by the reddish adult shade. The juvenile coloration was seldom seen in individuals over 100 mm SL, and has never been found in sexually mature individuals.

The most common color pattern of *P. pulchrum* is a uniform rose or salmon color, covering the entire body with the exception of the chin, which is usually white in mature individuals. The median and pelvic fins are darker than the body, ranging from dusky red to black. The pectoral fins usually match body color. Uniform coloration may be obscured by a melanistic condition which causes the entire body to appear brown. This occurs in varying degrees, making the fish appear almost black in extreme cases. Eleven percent of the uniformly colored fish captured at Catalina were designated melanistic, as were one-third of all uniform types at Guadalupe.

A uniform coloration is characteristic of immature fish as well as mature females. Histological analysis indicated, however, that the relationship was not perfect. At Catalina, 3.5% of the individuals designated uniform in color were discovered to have male gonads. When only sexually mature uniformly colored California sheephead were tallied, 5.1% were male. These males ranged

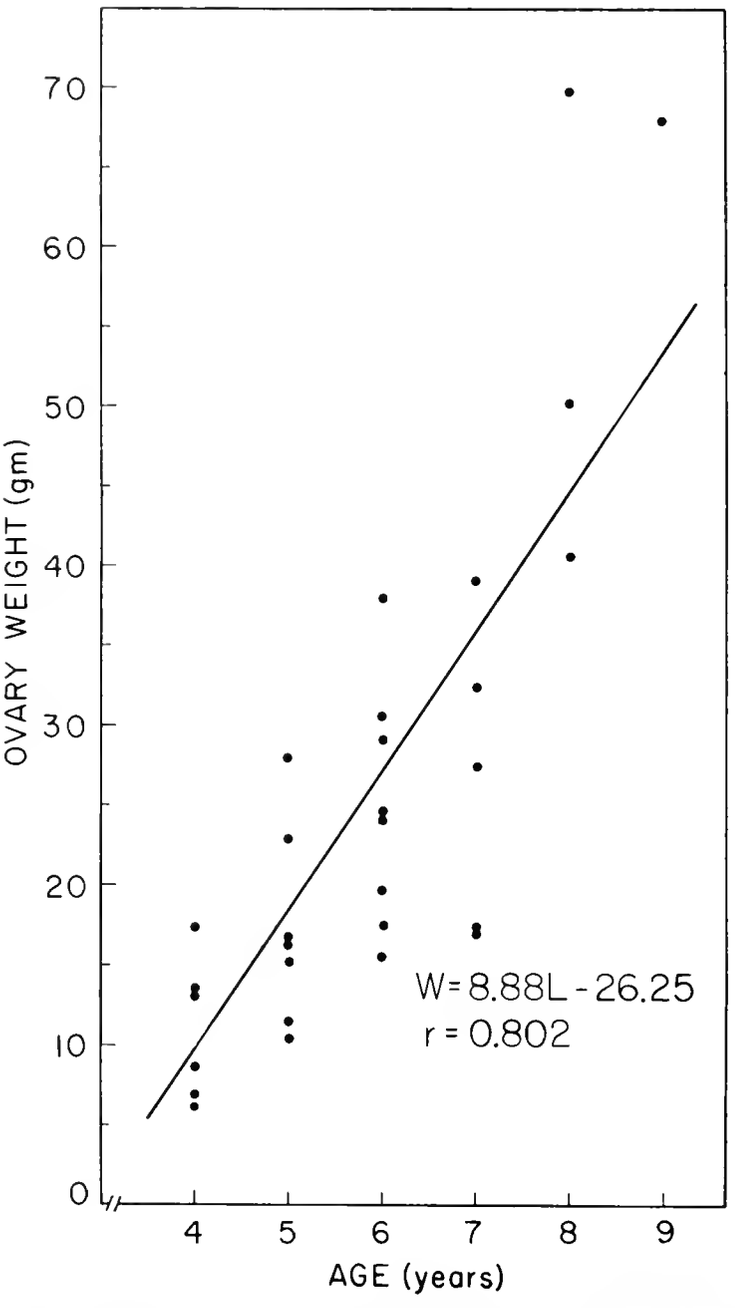

FIGURE 14.–Ovary weight versus age for females of *Pimelometopon pulchrum* captured in June and July at Catalina Island.

in length from 245 to 315 mm. and were captured in June, July, and December. Examination of a large series of gonad cross-sections from these individuals revealed a few stage 2 oocytes within the lamellae from two captured in July. This can be taken as evidence for a recent sex change. All the others had gonads of completely normal male appearance.

Field notes revealed that all of these individuals were melanistic, and 70% were recorded as having some male external characteristics, such as a small nuchal hump or slight differential darkenings of either the head or tail regions (see below). This suggests the possibility that some of these individuals may have been incorrectly typed due to the ground color being obscured by melanin.

Males in uniform coloration are more frequent in the Guadalupe population. A total of 6 out of 57 (10.5%) uniformly colored individuals were males. Elimination of immature fish from the count raises the figure to 12.3% males. Four of the six were melanistic, one of these with slight male characteristics. The other two individuals possessed normal uniform coloration with no darkening.

In the third color phase the head region, including the opercle, is dark brown or black. The chin remains white, and the midsection retains the reddish hue of the uniform type. The caudal portion, beginning approximately on a line connecting the initial soft rays of the dorsal fin with the anterior limit of the anal fin, is also dark brown or black. The median fins and pelvics remain generally dark in color, and the pectorals may acquire a dark band at their tips.

This coloration is found exclusively in males and some transitionals (see below). It is usually accompanied by two other male secondary sexual features common in the Bodianinae, the nuchal hump and filamentous extensions of the median fins. The hump appears to increase in relative size as the male gets larger, making the head appear increasingly angular in profile. No individual with this bicolored pattern was found to have functional ovaries. During the breeding season, the pattern serves as an excellent indicator of a functional male.

Individuals classified as transitional varied in coloration. Of 11 transforming California sheephead for which coloration records exist, 3 were scored uniform in color and 2 as bicolored. The remaining 6 were recorded as intermediate in coloration, usually involving a slight darkening of the head, caudal region, or both. The three uniform individuals were classed as early transitionals (large amounts of stage 2 oocytes still in the gonad); the two bicolored fishes were classed as late transitionals (only a few degenerating oocytes in the gonad cross-sections).

The distribution of uniform and bicolored types in field populations, determined by visual transects (Table 6) shows that bicolored males are present in remarkably similar proportions in both localities, occurring in a ratio of about 5.5 uniform individuals to every bicolored individual. Confidence limits for estimating the proportion of bicolored individuals were calculated from a binomial distribution, $n = 216$ and 407 for Catalina Island and Guadalupe Island, respectively (Dixon and Massey 1969).

TABLE 6.–Numbers of coloration types in two populations of *Pimelometopon pulchrum*, determined by a series of visual transects.

Locality	No. of transects	No. of uniform type	No. of bicolored type	Proportion p of bicolored types and 95% conf. limit
Catalina Island	70	183	33	0.153 ± 0.048
Guadalupe Island	93	343	64	0.157 ± 0.035

DISCUSSION

Anatomical Features of the Gonad and Sexual Transformation

The ovary of *P. pulchrum* is essentially identical with that of the labrid *Coris julis*, which was studied in detail by Reinboth (1962). Reinboth, however, did distinguish between the testes of those *C. julis* born as males (primary males) and those that become males through sex reversal (secondary males). In the former, the testis appears rather solid and flattened, and sperm are transported by means of a single vas deferens in each lobe. The secondary male has a testis like that described here for *P. pulchrum*. The two types differ in the structure of the vas deferens posterior to the gonadal lobes, which surrounds the old oviduct in secondary males, but is a simple tube in primary males (Reinboth 1970).

When primary and secondary males are present in a single species, Reinboth (1970) termed the species diandric. When only secondary males are present, the species is termed monandric. To Reinboth's (1970) list of monandric species (*Labrus turdus*, *L. merula*, *L. bergytta*, *Hemipteronotus novacula*, and possibly *L. bimaculatus*) we may add *P. pulchrum*. Other labrid species have been studied without regard for the primary-secondary male phenomenon (Atz 1964; Reinboth 1970), and cannot be categorized with certainty as monandric or diandric.

The transition from a functional ovary to a testis has been described in detail for labrid fishes in both naturally occurring situations (Reinboth 1962; Sordi 1962; Okada 1962; Roede 1972) and under the influence of hormone administration (Reinboth 1962, 1963; Roede 1972). These reports are essentially in agreement with the present observations on *P. pulchrum*. There is no evidence of synchronous hermaphroditism (Atz 1964:147) in the Labridae, but Robertson (1972) found spermatogenic crypts in the ovaries of 28 of 29 females of

Labroides dimidiatus, and 15 of these had crypts with sperm or spermatids. Thus, the possibility of encountering a synchronously hermaphroditic labrid species should not be ruled out.

Transformation Schedule

Pimelometopon pulchrum fits the general labrid pattern of size and sex distribution. No males were found smaller than 230 mm SL at Catalina Island, and none smaller than 150 mm at Guadalupe. The longer size classes (above 350 mm and 230 mm at Catalina and Guadalupe, respectively) contain mostly males.

Data for labrid sexuality are usually in the form of size frequency distributions of males and females within a species (Atz 1964; Remacle 1970; Roede 1972). Some of these studies have been confounded by the presence of two distinct color patterns, the investigators wrongly assuming strict sexual dichromatism (see below). An additional complication is the possibility of two different types of males being present in some species, usually with different life histories and behavior (Reinboth 1970). Both of these problems are eliminated by histological examinations of the gonad, which also reveals the presence of intersexual or transitional individuals.

The absence of males from the smaller size classes at least suggests protogyny. However, similar patterns can also result from samples of a species exhibiting differential growth rates for the sexes (e.g., see Strasburg 1970, for weight and sex distributions of blue marlin, *Makaira nigricans*), and this should be taken into consideration.

Fourteen of the fifteen labrid species either reviewed or dealt with originally by Roede (1972) had similar patterns of length-sex distribution. Females predominated in the smaller size classes, males in the larger. The proportion of males in the smaller sizes (usually associated with a particular color pattern; see below) varied from practically none in some species of *Halichoeres* and *Hemipteronotus* up to nearly 30% for *Stethojulis strigiventer* (Randall 1955). Males became increasingly common as length increased and the longest size classes consisted almost exclusively of males.

Species of the genus *Symphodus* (*Crenilabrus*) appeared to exhibit a different pattern, with nearly equal numbers of males and females in the small size classes (Sõljan 1930a, b). Remacle (1970) believed that sex reversal is a rare phenomenon in this genus.

Age determinations allow several more inferences about the sexual life history of a species. When few or no young males can be found, there is strong evidence for protogyny since the possibility of differential growth is eliminated. The rate of transformation in different age classes can be estimated, and this provides an idea of how long the average individual spends in different sexual phases. Finally, by comparing the distribution of sex versus length with sex versus the age of the individual, it may be possible to assign a more critical role to one or the other as a causative factor for sex reversal.

The age at first maturity (4 yr) does not differ for *P. pulchrum* at Catalina and Guadalupe Islands, but the distribution of sexual transformation with age differs markedly. Most individuals in both populations function at least 1 yr as females. At Guadalupe, many change sex after 1 yr, and most are males within 3 yr after maturing. Most sex reversals occur at Catalina between the seventh and eighth year, 4 yr after maturing as a female. Some individuals remain female for shorter or longer periods of time. The oldest female encountered in this study was 17 yr old.

The dwarfing phenomenon at Guadalupe, which should bring about a slower rate of increase of fecundity with age, would have enough effect to decrease the optimum age of transformation in that population when compared to the Catalina population. This will be discussed in detail elsewhere (Warner in press).

Lonnberg and Gustafson (1937) determined the ages of a series of specimens of *Labrus bimaculatus* (as *L. ossifagus*) which they correlated with sexual state. They found that sex reversal occurred in individuals from age seven onward, and was associated with a color change from red to blue-striped. Females were found in diminishing numbers up to age 18, mostly confined to the red phase. Males in the red phase ranged from around 3 to 7 yr old; blue-striped males got as old as 25.

Other protogynous teleosts which have been investigated regarding age of transformation show a variety of patterns in the distribution of sex reversal over their life-span. Liem (1963) demonstrated that sex transformation in the synbranchid rice eel *Monopterus albus* occurs mainly when individuals reach about 30 mo of age (about 35 cm in length). Few fishes in nature deviated from this pattern. Liem (1963) was able

to induce earlier transformations by starving the individuals. Moe (1969) has carefully worked out the age distribution of sex reversal in the serranid *Epinephelus morio*, and found a rather smooth period of transition from female to male over at least 5 yr (ages 5 to 10), at a rate of about 15% of the individuals in a year class reversing per year. In a less comprehensive survey, McErlean and Smith (1964) estimated that transformation occurred at age 10 or 11 in *Mycteroperca microlepis* (Serranidae), and speculated that the age of the fish had more effect on sex reversal than the length.

To determine the effect of individual size on sex transformation in *P. pulchrum*, mean lengths of males and females in each age class were compared (Figure 15). If length is closely related to sex reversal, one would expect males to be larger than females of the same age, and this was found in both the Catalina and Guadalupe populations. In every age grouping where sample size permitted statistical analysis, males tended to be larger than females. Five of the seven groups tested (one-sided t-test for difference in means) were significantly different at the 5% level or less, and the remaining two were significant at the 10% level.

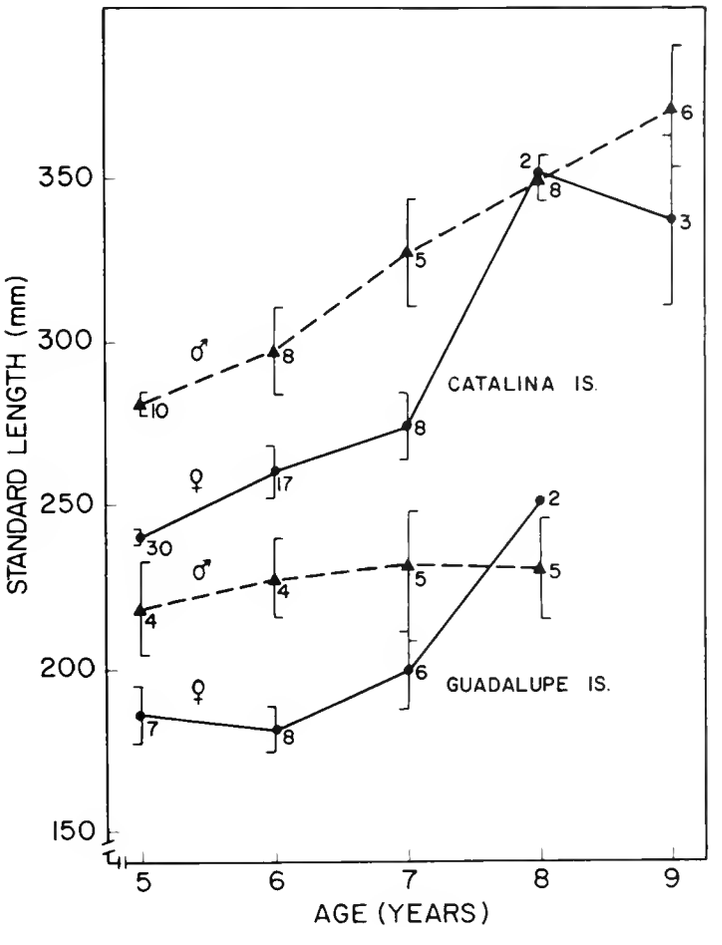

FIGURE 15.—Mean lengths for successive age classes of males and females of *Pimelometopon pulchrum*. Sample sizes are shown for each point, and standard error brackets are given when samples are large enough. For clarity, standard error brackets for males point to the right, and brackets for females point to the left.

An assessment of the effect of age on sex reversal was made in similar fashion, comparing the mean ages of males and females in successive size groupings (Figure 16). If sex reversal were closely related to the age of an individual, then males would tend to be older than females in a given length group. The relationship between age and sex is less strong (Figure 16). Sample sizes are not large, and the range of ages encountered in a sample is small relative to measured length values, so fewer significant results might be expected. Only one size group was found where males were significantly older than the females. However, the existence of several large negative t values in groups where the age of females is greater than that of males supports the idea that size is more important than age in effecting sex change.

The high average age of females in the larger size groupings of both populations (Figure 16) was not expected, and suggests that the individual growth rate may also be involved in sex reversal. The large separation between male and female mean ages begins with the 300-mm size grouping at Catalina, and the 200-mm group at Guadalupe. Inspection of Figure 8 reveals that at about these lengths, the proportions of males and females undergo an abrupt shift. A large percentage of the individuals in the populations apparently reverse sex at these sizes. Furthermore, the difference in ages between males and females of lengths above these "critical" sizes appears to be significant. The mean age of females larger than 300 mm at Catalina is 7.9, a full year older than males in the same size range ($t_{31} = 1.51$, $P<0.10$). Similarly, females larger than 200 mm at Guadalupe have a mean age of 9.5 yr, and males at that size range average 7.0 yr ($t_{32} = 2.80$, $P<0.001$). Thus the females that pass through the "critical" lengths without changing sex appear to be those individuals with relatively low rates of growth, suggesting both that slow growing individuals tend to be refractory to sex change, and that fishes with high rates of growth change sex more readily. The data of Figure 15 support this idea, as males are faster growing (larger) members of each age class. A check of the back-calculation information revealed that the growth rates of the large females were consistently low throughout their lifetime, and those of the small males had been high relative to other members of the age class.

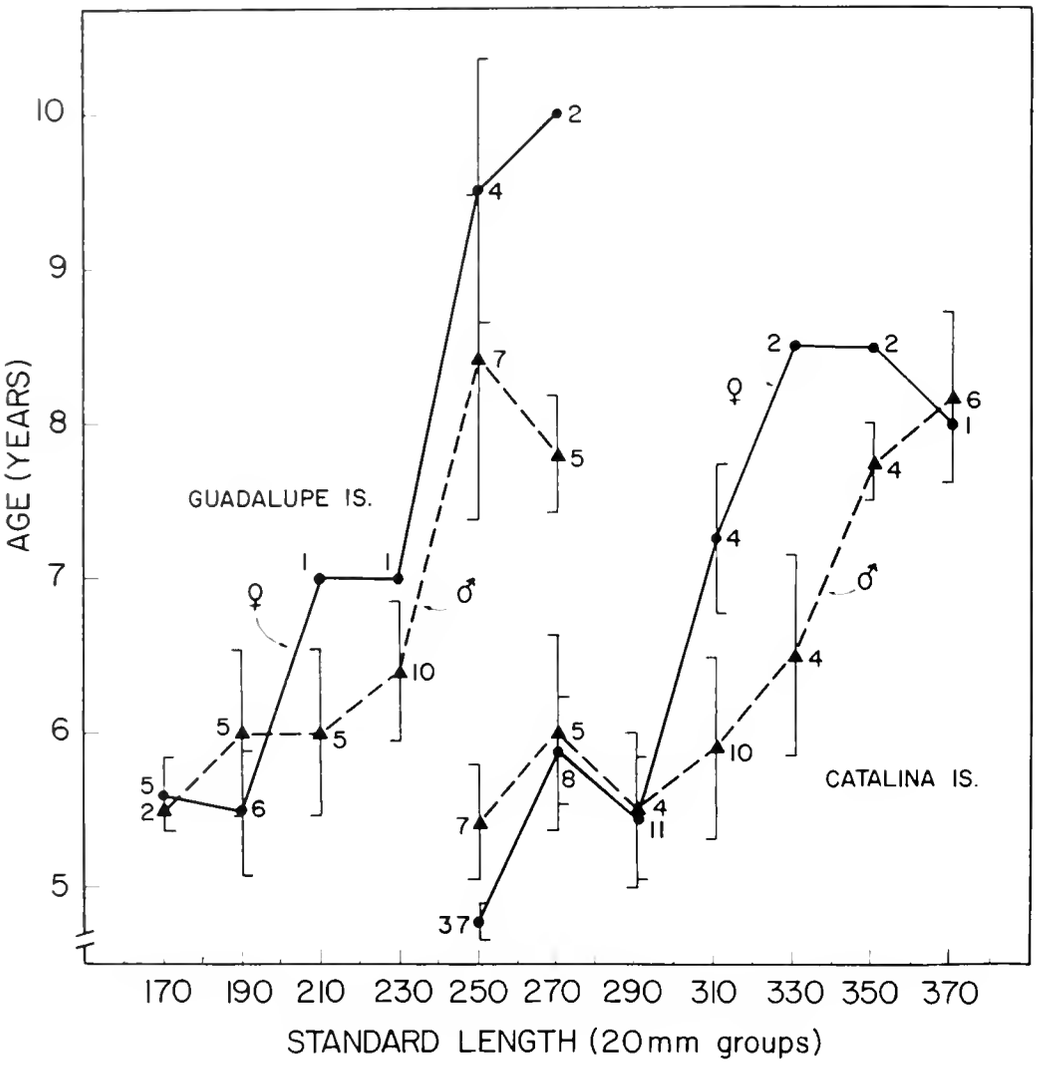

FIGURE 16.—Mean ages for successive 20 mm standard length groupings of male and female *Pimelometopon pulchrum*. Sample sizes and standard errors are shown as in Figure 15.

The best picture, then, that can be drawn from the present information is that rapidly growing individuals may transform sooner than other fishes of the same age. The bulk of the population, growing at the average rate, eventually reaches a "critical" size where most of them change sex. Fishes that grow slowly may not change sex at all.

The Breeding Season, Multiple Spawning, and Fecundity

Breder and Rosen (1966) have summarized the information available on the spawning seasons of labrids. In temperate species, most activity occurs over a period of approximately 3 mo, most commonly in April, May, and June. The Catalina population of *P. pulchrum* is exceptional in this case, since spawning occurs from August to October. The two other wrasses commonly found at Catalina Island also spawn later in the year than other labrids. *Oxyjulis californica* spawns from May until October (Bolin 1930), and *Halichoeres semicinctus* probably spawns in late June, July, and August (D. R. Diener, pers. commun.). The relatively late spawning seasons of these species may be caused by upwelling along the southern California coast which usually persists well into June or July, resulting in a delay of inshore water warming until that time (Quast 1968).

Multiple spawning has not often been considered in studies of labrid breeding seasons. Roede (1972) stated that labrids have "continuous, successive spawning cycles," and based this view upon the presence of many vitellogenic oocyte stages in mature ovaries of the seven species she investigated. She contended there is no resting stage of the ovary, but a series of year-round spawnings. At all times of the year she was able to find ovaries with several stages of developing oocytes as well as the stage 2 recruitment stock. This clearly is not the case in *P. pulchrum*, where the winter-resting ovary contains virtually no signs of vitellogenesis. Active ovaries of the California sheephead strongly resemble those pictured by Roede (1972, plates II and III) for *Halichoeres* and *Hemipteronotus*. The successive spawnings within a restricted season indicated for *P. pulchrum* may then be a curtailed version of a

year-round condition in its presumably tropical ancestor, representing an adaptation to the fluctuations of food availability characteristic of temperate regions.

The size-specific increases in fecundity seen in Catalina *P. pulchrum* are, of course, common in most long-lived fishes. Many of the Guadalupe females were not sexually active when the sample was taken and no fecundity data are available. However, it can be predicted that the average fecundity of Guadalupe Island individuals will increase much more slowly with age than that of individuals from Catalina, due to the low growth rate of the Guadalupe individuals discussed in an earlier section. If the active ovary weight increases with size in a fashion similar to that seen at Catalina (Figure 13), the average ovary weight for a 4-yr-old fish at Guadalupe would be approximately 8 g. Age class 4 California sheephead at Catalina had ovaries with an average weight of 13.13 g. The difference increases with age. Six- and eight-year-old individuals at Guadalupe should have ovaries weighing 9 and 15 g respectively. Weights for the same ages at Catalina were 23.1 g and 53.5 g.

In the Catalina population, there may be an abrupt increase in the fecundity of fishes remaining female after age seven; this is the age where most sexual transformations occur (compare Figures 9 and 14). If such an increase does exist, it may be an indication of compensation by those remaining females for the relative gain in age-specific reproductive potential experienced by individuals that do change sex. A more complete discussion of relative male and female age-specific fecundities can be found elsewhere (Warner in press).

The Relationship of Color and Sex

Pimelometopon pulchrum appears to follow the general labrid coloration pattern quite closely, with a preponderance of females and immatures in the initial uniform color phase, and the terminal bicolored phase containing only males. Thus the designation of the uniform phase as the "female" coloration and the bicolored phase as the "male" coloration (Jordan and Evermann 1898; Fitch and Lavenberg 1971; Miller and Lea 1972) is more or less correct, especially when immatures are included under the uniform designation (Barnhart 1936; Roedel 1948). Dichromatism, however, is not necessarily an indication of sexual dimorphism in the Labridae, and extensive sampling is usually needed before the relationship between sex and coloration can be accurately described.

Many labrid species exhibit a number of color phases, and these have often been attributed to sexual dimorphism or to differences between immatures and adults. Roede (1972) has reviewed a number of cases where such an interpretation was incorrect, being based on casual observation or small samples. Apparently there is no strict distribution of sex with color in the Labridae and the only generalization possible is that females tend to strongly predominate in the "first adult" (Roede 1972) colors, and the terminal-phase coloration is made up almost exclusively of males.

In most species investigated, males make up 10 to 35% of the first adult-colored individuals (Roede 1972). In *Gomphosus varius* (Strasburg and Hiatt 1957), *Halichoeres maculipinna*, *H. garnoti*, and *Hemipteronotus martinicensis* (Roede 1972), no males are found in the initial color phase. In contrast, Sõljan (1930a, b) found that 48% of the *Symphodus* (*Crenilabrus*) *ocellatus* examined in the first adult phase were males.

The terminal-phase coloration appears to be much more closely restricted as to sex. Of 14 labrid species exhibiting color phases mentioned by Roede (1972), the terminal phase consisted exclusively of males in all but two (*Halichoeres garnoti* and *H. bivittatus*). When other coloration classes are described, intermediate between the initial and terminal phases, the proportions of males and females in them are also intermediate. Roede (1972) notes that where color changes are more gradual, as in *H. garnoti* and *H. bivittatus*, the relationship between size and sex is the least exact.

Sex Ratio and an Estimate of Survival

Roede (1972) believed that her collections were true random samples of populations and was able to estimate the sex ratio in the seven labrid species she investigated. There were two to four times as many females as males in all but one species (*Hemipteronotus splendens*), which had an equal sex ratio.

The samples of *P. pulchrum* were not considered random and direct sex ratio estimates could not be made. Field transects at Catalina and Guadalupe islands yielded a ratio of about 5.5 uniformly colored individuals to every bicolored male. To estimate the sex ratios of mature individuals, the

proportion of immatures and males in the uniform group must be known, and this requires some knowledge of mortality rates.

A rough estimate of mortality can be made from the transect data and the known color composition of each age. The yearly survival rate is calculated using a modification of a simple fisheries estimate (Ricker 1958). The rate is assumed to be constant, and can be estimated as:

$$\hat{s} = \frac{N_{t+1}}{N_t}$$

where N is the number of individuals in a particular age class in a sample. Where a large number of age classes are available, one can weight the classes according to their abundance and separate two or more ages from the numerator and denominator, giving, for example:

$$\hat{s}^2 = \frac{N_3 + N_4 + \ldots + N_r}{N_1 + N_2 + \ldots + N_{r-2}}$$

For the Catalina population of *P. pulchrum*, the formula used was:

$$\hat{s}^6 = \frac{N_8 + N_9 + \ldots + N_{13}}{N_2 + N_3 + \ldots + N_7}$$

In this first approximation we assume that bicolored fishes are all 8 or more years old, and younger fish (ages 2 through 7) are uniform. The decision to use age 7 as the dividing point comes from Figure 9, where between ages 7 and 8 the proportion of females drops to a low level and the males become predominant.

From Catalina transect data, $\hat{s}$ is estimated by:

$$\hat{s}^6 = \frac{33}{183} \text{ and } \hat{s} = 0.735.$$

The transect ratio can then be adjusted to compensate for bicolored individuals younger than age 8 and uniform individuals older than age 7 by using proportions derived from Table 4, and each age's contribution to the numerator or denominator can be weighted according to the first estimate of survival derived above. The new estimate of survival from the adjusted transect ratio is not very different from the original, $\hat{s} = 0.71$.

A similar estimate for the Guadalupe Island population, assuming in this case that the uniform individuals are ages 2 through 7 (see Figure 9) and adjusting as before, is $\hat{s} = 0.69$.

Mature sex ratios can now be estimated. Using 0.7 as the yearly survival rate, about 36% of the uniform individuals seen at Catalina should be mature, and approximately 5% of those individuals would be male. The ratio of mature males to mature females from field transects would then be derived as:

$$\frac{33 + (183 \times 0.36 \times 0.05)}{183 \times 0.36 \times 0.95} = \frac{36}{63} = 0.57$$

or about two females for every mature male.

For Guadalupe, about a third (34%) of the uniform individuals should be mature, and 90% of these would be female. The sex ratio at Guadalupe would then best estimated as:

$$\frac{64 + (343 \times 0.34 \times 0.1)}{343 \times 0.34 \times 0.9} = \frac{76}{105} = 0.72$$

or approximately three females for every two males.

An artifact of protogynous hermaphroditism is the concentration of females in the younger ages. Thus, the observed sex ratio depends on when the animals change sex, and upon the mortality occurring from year to year. Mortality causes sex ratios to be biased towards females and these become even more biased the greater the average age of transformation is in the population. This effect can be seen by comparing the estimated sex ratio of the Guadalupe population (0.72), where most females change sex within 3 yr after maturity, with that of Catalina (0.57), where transformation is relatively delayed.

The deviations of sex ratio from unity seen here should not be taken as contradictions of the theories put forth on the adaptiveness of the 1:1 ratio (Fisher 1930; Bodmer and Edwards 1960; Kalmus and Smith 1960), as these were developed for nonhermaphroditic species, and sought to equalize the lifetime reproductive potentials for males and females. In sequential hermaphrodites, the same individual functions as both male and female at sometime in its life, and the question becomes one of changing sex at the proper time to maximize the individual's reproductive potential (Warner in press).

SUMMARY

Year-round sampling of a population of the California sheephead, *Pimelometopon pulchrum*, was carried out at Catalina Island, Calif., and comparative material was collected from a population at Guadalupe Island, Mexico.

Age determinations indicate individuals in the Guadalupe population are dwarfed relative to

those at Catalina. The growth rate is lower for Guadalupe fishes and in both populations there may be a slowing of growth at the onset of maturity, as well as an increase in the growth rate after sexual transformation.

Pimelometopon pulchrum is a protogynous hermaphrodite. During the sex change from female to male, the ovary degenerates and spermatogenic crypts dominate the gonad. The basic structure of the gonad remains ovarian however, with lamellae protruding into a central lumen. Sperm transport is through a series of ducts on the periphery of the gonad and oviduct.

Catalina California sheephead attain sexual maturity at age 4, at a standard length of about 200 mm. Most function as females for 4 yr and then change sex, at a length of about 310 mm. Some individuals may transform earlier or later, or not at all. The Guadalupe population also matures at age 4, at a length of about 140 mm. But transformation occurs at an earlier age, with most individuals becoming males by age 7. Peak transformation activity occurs in fishes between 190 and 230 mm SL at Guadalupe.

Gonad development states and gonad indices of Catalina California sheephead suggest that spawning occurs in July, August, and September and that sexual transformation occurs in the winter months between breeding seasons.

Spawning probably takes place a number of times in a single breeding season, which complicates the determination of the actual number of eggs produced by a female each year. Ovary weight, however, can give a good indication of relative age and size-specific fecundities, since egg density does not appear to vary with fish length. The ovary weight of *P. pulchrum* increases exponentially with length and linearly with the age of the individual in the Catalina population.

At Guadalupe, the average fecundity probably increases more slowly with age when compared to Catalina, due to the low average rate of growth.

Pimelometopon pulchrum has three color phases. Juvenile coloration occurs in individuals usually less than a year old and smaller than 100 mm in length, and never in sexually mature individuals.

The uniform coloration is found in immatures and mature females. Melanization may obscure the ground coloration, but it appears that about 5% of the mature uniform individuals were males at Catalina, and 12% at Guadalupe.

Bicolored fishes are exclusively males or late transitionals and usually have a nuchal hump and filamentous extensions of the median fins.

Field observations indicate that there are about 5.5 uniformly colored individuals to every bicolored male at both Catalina and Guadalupe.

Individual size appears to have a greater effect on the sex change than does age, and rapidly growing fishes may change sex sooner than slow growing individuals of the same age, which may not change sex at all.

With the assumption of constant, age-independent mortality, the annual survival rate at both Catalina and Guadalupe was estimated as about 0.7, as judged from the field transect data.

The mature sex ratio at Catalina was approximately two females for every male. At Guadalupe the ratio was closer to three females for every two males, due in part to the earlier sexual transformation seen there.

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AN INVERSE CORRELATION BETWEEN MERISTIC CHARACTERS AND FOOD SUPPLY IN MID-WATER FISHES: EVIDENCE AND POSSIBLE EXPLANATIONS

ROBERT KARL JOHNSON[1] AND MICHAEL A. BARNETT[2]

ABSTRACT

In five species of mid-water fishes, *Chauliodus sloani*, *Diplophos taenia*, *Pollichthys mauli*, *Vinciguerria lucetia*, and *V. nimbaria*, the central values of meristic counts (anal fin rays, vertebrae, longitudinal photophore rows) and three measures of biological productivity (phosphate-phosphorus concentration, net primary production, zooplankton standing stocks) are correlated negatively. For the species and areas studied the meristic variation observed cannot be related to temperature, salinity, dissolved oxygen, or any other physical or chemical factor known to affect meristic variation in fishes. It is hypothesized that this relationship between meristic counts and measures of food availability involves differences in egg size, fecundity, size at hatching, and size at comparable stages of larval development between populations in different areas, and that these differences in turn reflect adaptations to low food densities in areas of low productivity and higher predator densities in areas of higher productivity.

Meristic characters have been widely used in studies of fish populations and species. Unlike body proportions or coloration, meristic characters are fixed usually at or before metamorphosis and remain constant throughout the life of an individual. Variation in meristic characters stems from both genetic variation between populations and species, and from environmental variation, which, within genetically controlled limits, can directly affect the number of parts formed in developing embryos and larvae. Recent reviews of factors known to affect meristic characters in fishes include Barlow (1961), Blaxter (1969), Garside (1966), and Fowler (1970).

An inverse relationship between vertebral and/or other meristic counts and water temperature at the time of early development has been demonstrated in numerous studies (see above review articles). Experimental studies have shown that in many cases the effect of temperature upon meristic characters occurs within a restricted period of time, the so-called sensitive period, and that variations in temperature before and after this period have no effect (Hempel and Blaxter 1961). The sensitive period may vary with different structures with the result that the timing, magnitude, and in some cases the direction of response of different structures to temperature variation differs among different species (Fowler 1970).

Hubbs (1926), Barlow (1961), and others, have suggested that the relationship between meristic counts and temperature involves differential effects of temperature on rate of growth versus rate of differentiation, with the result that accelerated growth is associated with a shortening of the sensitive period, resulting in the laying down of fewer parts. The conclusion is that conditions retarding growth rates are associated with elevated meristic counts, conditions accelerating growth rates are associated with lowered meristic counts. This explanation has been extended to factors other than temperature known to affect meristic characters in fishes: dissolved oxygen concentration (Alderdice et al. 1958), salinity (Forrester and Alderdice 1966; Blackburn 1967), carbon dioxide concentration, light intensity, exposure to X-rays, etc. (see Fowler 1970).

In 1972, we reported a significant negative correlation between certain meristic counts in *Diplophos taenia* and three measures of food supply: net primary production, phosphate-phosphorus concentration, and zooplankton standing stocks (Johnson and Barnett 1972). To our knowledge, this was the first suggestion of a

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possible relationship between meristic counts and measures of food supply. We did not offer any explanation for this relationship in the earlier report. In the present paper we extend our information on *D. taenia* to the Atlantic Ocean, present corroborative evidence for the relationship between meristic counts and food supply based on four other species of mid-water fishes, and attempt to show that the relationship for the species and areas studied is with food supply and not temperature, salinity, or dissolved oxygen. We hypothesize that this relationship between meristic counts and food supply reflects differences in egg size, fecundity, size at hatching, and size at comparable stages of larval development between populations in different areas, and that these differences represent adaptations to low food densities in areas of low productivity and higher predator densities in areas of higher productivity.

METHODS

Collection and Analysis of Data

Methods of taking counts follow those of Grey (1964), Morrow (1964), and Johnson (1970). Photophore rows in a generalized stomiatoid fish are illustrated in Morrow (1964: Figure 73), but our nomenclature for segments of photophore rows follows that of Johnson (1970). All vertebral centra were counted including the compound element supporting the parhypural and hypurals (Weitzman 1967). Standard statistical texts have been used as reference material (especially Tate and Clelland 1957; Sokal and Rohlf 1969). Agreement between sets of ranks is assessed via the tau coefficient of correlation or Kendall's coefficient of concordance, W (see Tate and Clelland 1957).

Localities Studied

We have studied specimens from eight areas (Figure 1): 1) the eastern tropical Pacific (ETP) off Mexico; 2) the central North Pacific (CNP) off the Hawaiian Islands; 3) the central equatorial Pacific (CEP) at long. 145° to 150°W; 4) the western equatorial Pacific (WEP) around long. 170°E; 5) the Philippine Sea (PS); 6) the South China Sea (SCS); 7) the Gulf of Guinea (GG); and 8) the central North Atlantic (CNA) including the Sargasso Sea. All of these areas are tropical oceanic habitats and represent a wide range of physical and biological features.

Measures of Biological Productivity

The measures used to assess relative richness of food supply are phosphate-phosphorus concentration, net primary production, and zooplankton standing stocks. These three variables are highly intercorrelated (Cushing 1971). These measures were chosen because there are published attempts at contouring values of these variables on an oceanwide basis and because values for them are commonly reported in more regionally oriented studies.

Despite many problems in both sampling and interpretation associated with attempts to contour values of biological variables on an oceanwide basis and to integrate values based on a limited number of measurements over a full year, we were forced to accept such attempts as the principal basis for ranking our eight study areas with respect to the three measures of food supply. Where possible we relied on synoptic studies presenting contours on an oceanwide basis: net primary production (as mg-C/m^2 per day, Koblentz-Mishke et al. 1970; as g-C/m^2 per year, Ebeling 1962 based on Fleming and Laevastu 1956), zooplankton concentration (as parts/10^9 by volume in the upper 150 m of the Pacific Ocean, Reid 1962), and phosphate-phosphorus concentration (as μg-at/liter contoured at 100 m in the Pacific Ocean, Reid 1962). Where these studies did not cover several of our study areas, we used regional studies (SCS: Angot, Steemann Nielsen in Wyrtki 1961; Sorokin 1973; GG: Raymont 1963, Corcoran and Mahnken 1969, Kinzer 1969, Zeitschel 1969, Riley 1972; CNA: Menzel and Ryther 1961, Raymont 1963, Corcoran and Mahnken 1969, Zeitschel 1969, Riley 1972).

We compared the contours or values for each of the three measures of productivity over all eight study areas and then ranked the eight areas with respect to each other for each measure (Table 1). As expected (Cushing 1971), the ranks for the three measures over the eight areas are highly concordant ($W_{3,8} = 0.85$, $P < 0.01$, concordance coefficient corrected for ties, see Tate and Clelland 1957). This highly significant concordance increases our confidence in this approach to ranking the eight areas with respect to productivity and allows summation of the ranks of the three measures of food supply over each area, yielding a rank-sum. We then ranked this rank-sum and obtained the following rank-index order of productivity, from highest to lowest: 1) eastern

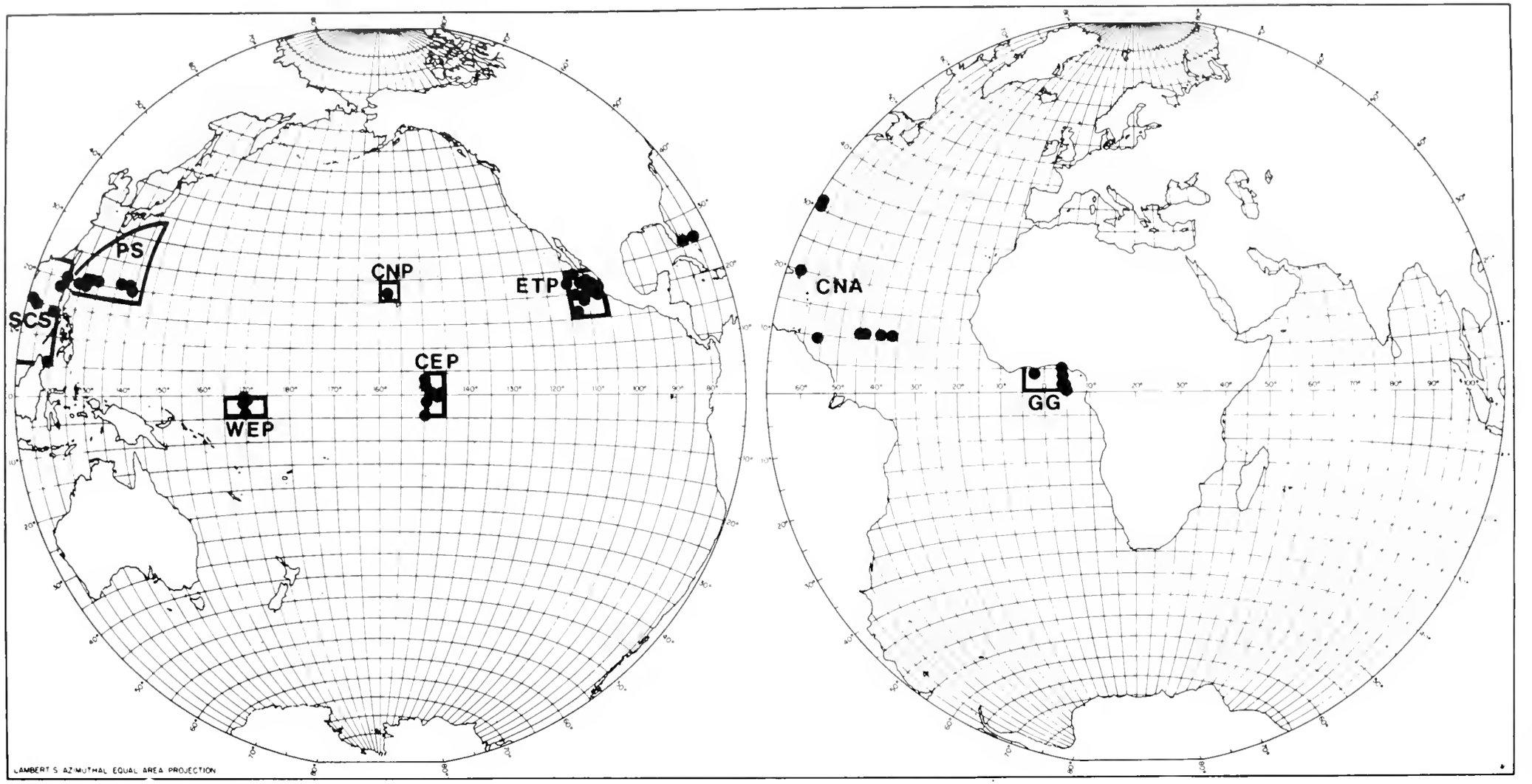

FIGURE 1.–Study areas: ETP = eastern tropical Pacific; CEP = central equatorial Pacific; CNP = central North Pacific; WEP = western equatorial Pacific; PS = Philippine Sea; SCS = South China Sea; GG = Gulf of Guinea; CNA = central North Atlantic. Localities for *Diplophos taenia* indicated by closed circles. Localities for other species were within boundaries of study areas as indicated except that all specimens of *Vinciguerria nimbaria* from the central North Atlantic were from the Ocean Acre area near lat. 32° to 33°N, long. 64°W.

TABLE 1.–Computation of rank-sum index of productivity. This table was produced by reproducing the contours or values presented by each of the authors cited in the text for each of the three measures of productivity–net primary production (NET), zooplankton concentration (ZOO), and phosphate phosphorus concentration (PO_4-P)–within the geographic limits of each of the eight areas and then ranking the eight areas with respect to one another for each measure.

Area	NET rank	ZOO rank	PO_4-P rank	Sum of ranks	Rank-sum
ETP	1	1	1	3	1
GG	2.5	3.5	2	8	2
SCS	2.5	[1]3.5	4.5	10.5	3
CEP	4	5	3	12	4
WEP	7	2	4.5	13.5	5
PS	5	6	7.5	18.5	6
CNA	6	7	6	19	7
CNP	8	8	7.5	23.5	8

$W_{3,8} = 0.85$, $P < 0.01$

[1]Data from Brinton (pers. commun.)

tropical Pacific, 2) Gulf of Guinea, 3) South China Sea, 4) central equatorial Pacific, 5) western equatorial Pacific, 6) Philippine Sea, 7) central North Atlantic, and 8) central North Pacific. In establishing the relationship between meristic counts and productivity we have compared central values of meristic counts with this rank-index value for productivity.

RESULTS

Diplophos taenia Günther

Diplophos taenia, a circumtropical mesopelagic gonostomatid, is the only species included in this study to occur in all eight study areas. Results for counts of anal fin rays, LLP photophores, and IPVALA photophores are illustrated in Figure 2. In nearly all cases counts are highest in areas of lowest productivity, lowest in areas of highest productivity, and intermediate in areas of intermediate productivity. Agreement between mean values for photophore row segments in terms of rank order by area, e.g. all four segments in the IC row, is highly significant ($W_{4,8} = 0.81$, $P < 0.01$, Table 2), as is the agreement between mean values for anal fin rays, LLP photophores, and IPVALA photophores ($W_{3,8} = 0.94$, $P < 0.01$, Table 3). This concordance allows computation of a rank-sum index for mean values of meristic counts (Table 3).

There exists no significant correlation between the observed meristic variation and temperature over the six Pacific areas ($tau_6 = 0.13$, $P > 0.20$, Table 4). Temperature data was taken from a chart of temperature at 100 m in the Pacific Ocean

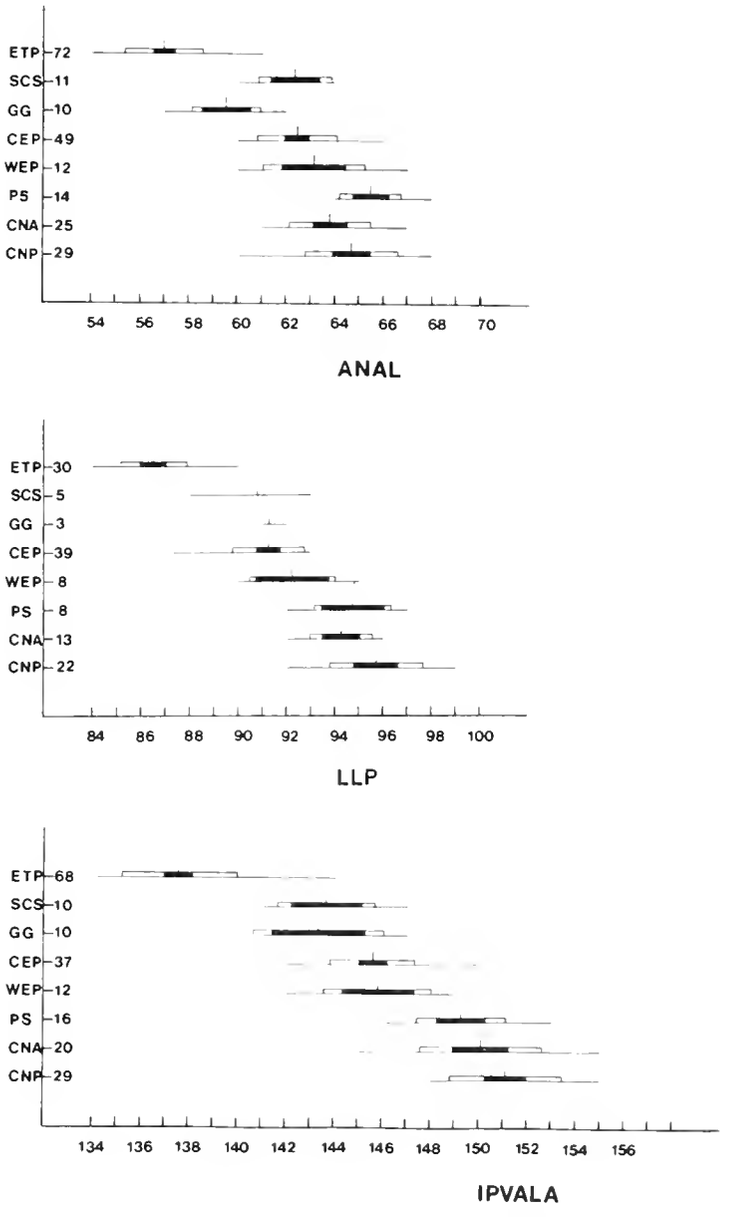

FIGURE 2.–*Diplophos taenia*. Comparison of mean (vertical line), 95% confidence limits for the mean (closed bar), one standard deviation on either side of the mean (open bar plus closed bar), and range (horizontal line) for anal fin rays (top), LLP photophores (middle), and IPVALA photophores (bottom) for specimens from eight study areas (Figure 1). Numbers on ordinate are number of specimens examined.

TABLE 2.–Agreement between segments of IC row of photophores in *Diplophos taenia*. Values are given as mean)rank. Number of specimens (n) is given for counts of IP and represent the minimum number of specimens counted for each character for each area.

Area	n	IP	PV	VAV	AC	Sum of ranks
ETP	74	15.7)8	24.9)8	15.1)8	42.0)8	32
GG	10	16.6)6	27.1)2.5	15.9)5	42.9)7	20.5
SCS	10	16.4)7	25.6)7	16.0)4	44.7)6	24
CEP	50	16.9)5	26.2)6	15.8)6	45.18)4	21
WEP	12	17.0)4	26.4)5	15.7)7	45.17)5	21
PS	18	17.1)3	26.9)4	16.3)2	46.67)3	12
CNA	25	17.4)1	27.5)1	16.2)3	46.72)2	7
CNP	29	17.3)2	27.1)2.5	16.6)1	47.5)1	6.5

$W_{4,8} = 0.812$, $P < 0.01$

TABLE 3.—*Diplophos taenia*, computation of rank-sum index of meristic counts and comparison with rank-sum index of productivity (from Table 1). Values are given as mean (number of specimens).

Area	Anal fin Mean	Anal fin Rank	LLP Mean	LLP Rank	IPVALA Mean	IPVALA Rank	Sum of ranks	Rank-sum	Productivity rank-sum
ETP	57.0 (72)	8	86.5 (30)	8	137.5 (68)	8	24	8	1
GG	59.5 (10)	7	91.3 (5)	5	143.3 (10)	7	19	6.5	2
SCS	62.3 (11)	6	90.8 (3)	7	143.6 (10)	6	19	6.5	3
CEP	62.4 (49)	5	91.2 (39)	6	145.54 (37)	5	16	5	4
WEP	63.2 (12)	4	92.2 (8)	4	145.75 (12)	4	12	4	5
PS	65.4 (14)	1	94.8 (8)	2	149.2 (16)	3	6	2	6
CNA	63.8 (25)	3	94.2 (13)	3	150.2 (20)	2	8	3	7
CNP	64.7 (29)	2	95.7 (22)	1	151.7 (29)	1	4	1	8

$W_{3,8} = 0.942$, $P < 0.01$ $\quad$ $\text{Tau}_8 = -0.893$, $P < 0.01$

TABLE 4.—*Diplophos taenia*. Comparison of rank-sum index of meristic counts (from Table 3) with temperature at 100 m ranked over the six Pacific areas. Temperature data taken from Brinton (1962).

Area	Rank Counts	Rank Temperature
CNP	1	5
PS	2	3.5
WEP	3	1
CEP	4	2
SCS	5	3.5
ETP	6	6

$\text{Tau}_6 = +0.13$, $P > 0.20$

given by Brinton (1962). The 100-m depth was chosen arbitrarily, but the conclusion holds if surface temperatures, whether summer or winter, are chosen. Meristic counts for *D. taenia* are lowest in specimens from the eastern tropical Pacific where temperature values are also the lowest. This is exactly opposite to the result expected if temperature were involved in determining the meristic variation observed over the six areas. In fact the data show no relationship between meristic counts and temperature for these areas. Values of salinity in the open ocean are far too conservative to be involved in determining the observed variation (Hubbs 1925; Sverdrup et al. 1942; Barlow 1961; Blackburn 1967). Although the eastern tropical Pacific is well known for a marked oxygen minimum layer (Brandhorst 1959), and oxygen concentration variation may affect the development of meristic characters (Alderdice et al. 1958; Garside 1959, 1966), in all eight areas oxygen is essentially saturated in the wind-mixed surface layer where the larvae and probably the eggs of *D. taenia* occur. The low counts (relative to other areas) of specimens of *D. taenia* from the eastern tropical Pacific run counter to what might be expected if dissolved oxygen concentrations were involved in determining the observed meristic variation.

The rank-sum indices of meristic counts and productivity are significantly and negatively correlated ($\text{tau}_8 = -0.893$, $P < 0.01$, Table 3).

Pollichthys mauli (Poll)

Pollichthys mauli ranges from the western North Atlantic to the Philippine Sea. We have examined specimens of this species from the Gulf of Guinea, and the Philippine and South China seas. Results for IPVALA photophore counts (Table 5) parallel the results for *Diplophos taenia;* the counts from Philippine Sea specimens are significantly higher than counts from specimens from the South China Sea and Gulf of Guinea.

TABLE 5.—*Pollichthys mauli*, IPVALA photophores.

Area	68	69	70	71	72	73	74	75	76	77	78	*n*	Mean ± 95% limits
GG	1	7	5	6	1	4	—	—	—	—	—	24	70.46 ± 0.635
SCS	—	—	1	7	2	1	—	—	—	—	—	11	71.27 ± 0.528
PS	—	—	—	—	—	1	1	3	2	1	2	10	75.70 ± 1.170

Vinciguerria lucetia Garman

Vinciguerria lucetia is endemic to the eastern Pacific (Ahlstrom and Counts 1958; Craddock and Mead 1970; Gorbunova 1972). The work of Ahlstrom and Counts (1958) has made the early life history of *V. lucetia* the best known of any of the species included in this report. We have not examined any specimens of *V. lucetia* in connection with this work, but the following results of the study of this species by Ahlstrom and Counts (1958) seem to be particularly relevant to this paper: 1) In *V. lucetia* the total number of myotomes is formed in late-stage eggs, prior to hatching. 2) Metamorphosis in *V. lucetia* is marked by a period of rapid change in body proportions without a marked change in standard length. The completion of metamorphosis is signaled by the complete development of all photophores, including the late-forming photophores of the posterior VAV and mid-AC segments. 3) Metamorphosis occurs at a smaller size south of lat. 25°N than north of lat. 27.5°N, with meta-

morphosis at an intermediate size in specimens from lat. 25° to 27.5°N. Mean values of vertebral and IPVALA counts are lowest in specimens taken from areas where metamorphosis occurs at a smaller size. A delay in vertebral ossification is found in specimens from areas where metamorphosis occurs at a larger size. 4) Ahlstrom and Counts (1958) report a north to south cline in mean values for IPVALA photophore counts and relate this to temperature. An east to west cline is also suggested by their data (Figure 3), with mean IPVALA counts lowest near the American continent and increasing with distance offshore. Values for productivity measures in the eastern tropical Pacific tend to fall off with increasing distance from land (Reid 1962; Koblentz-Mishke et al. 1970). If variation in photophore numbers in *V. lucetia* is related to variation in productivity, we would expect mean IPVALA counts at a given latitude to be lower near the continent and higher with increasing distance from land. Data from Ahlstrom and Counts (1958) confirm this expectation (Figure 3) for all but two latitudinal transects. Along these two transects, one just to the north of the equator, the second centered at about lat. 12°N, mean values obtained for IPVALA counts do not change or actually decrease to the westward, an apparent contradiction of our hypothesis. However, these two zonal transects fall along zonal areas of high or elevated productivity far to the westward of the American continent, and this is true for net primary production, zooplankton standing stocks, or, as illustrated (Figure 3), phosphate-phosphorus concentration. Williams (1972) relates these zonal belts of elevated productivity to the divergence systems at the equator and at the North Equatorial Countercurrent-North Equatorial Current boundary. Williams (1972) states that the zonal band at lat. 10° to 12°N is best shown by data for zooplankton stocks, but we note that this band is quite apparent for phosphate-phosphorus concentration (Reid 1962). Thus the apparently discrepant values of mean IPVALA counts from specimens of *V. lucetia* taken along these two zonal transects in fact tend to further corroborate the hypothesized inverse relationship between meristic counts and productivity.

Vinciguerria nimbaria (Jordan and Williams)

Vinciguerria nimbaria is nearly circumtropical in distribution but does not occur in the Medi-

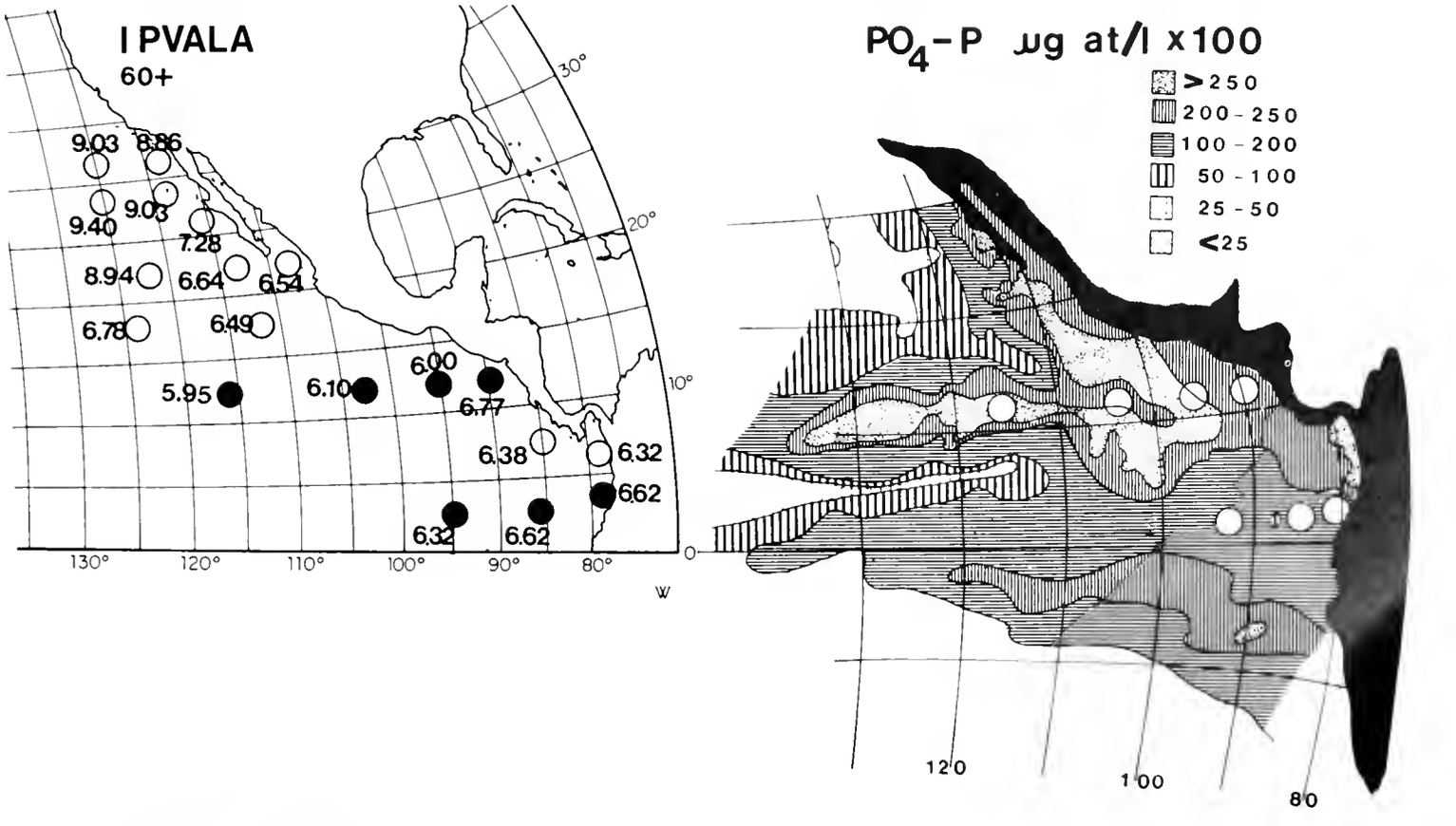

FIGURE 3.—*Vinciguerria lucetia*. Left: IPVALA photophores; values given are means based on five or more specimens taken at each locality (see text for additional explanation, data from Ahlstrom and Counts 1958). Right: phosphate phosphorus data simplified from Reid (1962).

terranean Sea nor in the eastern tropical Pacific (Ahlstrom and Counts 1958; Craddock and Mead 1970; Gorbunova 1972). The development of larvae of *V. nimbaria* is apparently quite similar to the development of larvae of *V. lucetia* (Ahlstrom and Counts 1958; Silas and George 1971). We have examined specimens of *V. nimbaria* from all of our study areas except the eastern tropical Pacific (where *V.nimbaria* is replaced by *V. lucetia*) and the western equatorial Pacific (no material available).

Counts of IPVALA photophores for specimens of *V. nimbaria* are given in Table 6. Mean values for specimens from the South China Sea, central equatorial Pacific, Philippine Sea, central North Atlantic, and central North Pacific agree in perfect rank-order with the rank-sum index of meristic counts for specimens of *Diplophos taenia* from these five areas (Table 3). The mean value of counts of IPVALA photophores of Gulf of Guinea specimens does not fit this trend, it is too high. All of our material of *V. nimbaria* from the Gulf of Guinea came from a single collection at the University of Miami (UMML 21902, lat. 0°54′ to 1°05′N, long. 4°53′ to 4°51′E, 23-24 May 1965). We have neither additional material of nor information on *V. nimbaria* from the Gulf of Guinea, and, for the present, we are unable to explain these anomalous results.

The values obtained for specimens of *V. nimbaria* from other study areas support our hypothesis of an inverse relationship between meristic counts and productivity. This is true for both IPVALA photophore (Table 6) and vertebral (Table 7) counts.

Counts for Arabian Sea (AS, Table 6) specimens of *V. nimbaria* are taken from Silas and George (1971). They studied specimens taken off the Malabar Coast of India and found larvae of *V. nimbaria* to be most abundant along the edge of the continental shelf from Mangalore to south of Cochin. Cushing (1971) discusses the strong upwelling system occurring along this coast during the period of the Northeast Monsoon, and notes

TABLE 7.—*Vinciguerria nimbaria*, vertebrae.

Area	39	40	41	42	*n*	Mean ± 95% limits
SCS	6	5	—	—	11	39.45 ± 0.351
CEP	1	23	7	—	31	40.19 ± 0.175
PS	—	3	12	8	23	41.22 ± 0.290
CNP	—	—	6	21	27	41.78 ± 0.168

that high values of productivity occur in this area over at least half of the year and are associated with the upwelling system. Silas and George (1971) found *V. nimbaria* larvae to be most abundant during the upwelling season. Values for productivity measures in this area given by Cushing (1971) approach values for the eastern tropical Pacific, are certainly larger than values for the Philippine Sea, central North Atlantic, and central North Pacific, and probably significantly larger than values for the central equatorial Pacific and South China Sea. We therefore expected values for meristic counts of specimens of *V. nimbaria* from off the Mangalore Coast to be the lowest of any of these six areas. They are (Table 6).

Chauliodus sloani Bloch and Schneider

Chauliodus sloani occurs in tropical and temperate waters from the North Atlantic to the eastern Pacific, although throughout large oceanic areas it is replaced by other species of *Chauliodus*. The remaining six species of *Chauliodus*, including the recently described *C. vasnetzovi* Novikova, are limited to smaller areas, each entirely within one ocean basin (Morrow 1961; Gibbs and Hurwitz 1967; Novikova 1972).

We have examined specimens of *C. sloani* only from our Philippine Sea and central North Pacific study areas, but data from other sources (Ege 1948; Blache 1964; Gibbs and Hurwitz 1967) have made it possible to compare our results for *C. sloani* with counts for this species from other areas, and with counts for the closely related species *C. pammelas* Alcock and *C. schmidti* Ege (Table 8). IC photophore counts of *C. sloani* from central gyral areas (CNP, CNA, PS) are higher than counts from specimens taken in the South

TABLE 6.—*Vinciguerria nimbaria*. IPVALA photophore counts. AS = study area of Silas and George (1971) along Malabar Coast of India in the Arabian Sea, data taken from their study. Counts presented as the average between right and left sizes of each specimen.

Area	64	64.5	65	65.5	66	66.5	67	67.5	68	68.5	69	69.5	70	70.5	71	71.5	72	72.5	73	*n*	Mean ± 95% limits
AS	2	1	1	1	2	—	1	—	1	—	—	—	—	—	—	—	—	—	—	9	65.56 ± 1.023
GG	—	—	—	—	—	—	—	—	—	—	2	2	5	2	7	1	1	—	—	20	70.43 ± 0.380
SCS	—	—	2	1	10	4	2	1	4	—	—	—	—	—	—	—	—	—	—	24	66.46 ± 0.378
CEP	—	—	—	—	2	2	1	2	14	6	4	1	—	—	—	—	—	—	—	32	67.98 ± 0.302
PS	—	—	—	—	1	2	1	4	24	26	20	37	83	36	16	4	2	1	—	257	69.60 ± 0.126
CNA	—	—	—	—	—	—	1	—	1	2	1	4	2	1	—	—	—	—	—	12	69.12 ± 0.623
CNP	—	—	—	—	—	—	—	—	—	—	—	3	18	15	5	1	1	—	—	43	70.34 ± 0.157

TABLE 8.—IC photophore variation in three species of *Chauliodus*. (NIO, northern Indian Ocean, TAA, TAB, areas of eastern tropical Atlantic discussed in text).

Species	Area	58	59	60	61	62	63	64	65	66	67	68	69	*n*	Mean ± 95% limits
C. pammelas[1]	NIO	1	4	12	4	–	–	–	–	–	–	–	–	21	59.90 ± 0.350
C. schmidti[3]	TAA	–	–	1	7	32	14	–	–	–	–	–	–	54	62.09 ± 0.186
C. schmidti[2]	TAB	–	–	–	3	16	14	7	5	–	–	–	–	45	62.89 ± 0.335
C. sloani[3]	SCS	–	–	–	–	1	16	69	91	25	2	–	–	204	64.32 ± 0.117
C. sloani	PS	–	–	–	–	–	–	–	3	2	4	4	–	13	66.69 ± 0.714
C. sloani[3]	CNA	–	–	–	–	–	–	–	–	3	6	3	1	13	67.15 ± 0.543
C. sloani	CNP	–	–	–	–	–	–	–	2	9	7	2	–	20	66.45 ± 0.386

[1]Gibbs and Hurwitz 1967.
[2]Blache 1964.
[3]Ege 1948.

China Sea. This agrees with results for other species discussed in this paper.

The only character diagnostically separating *C. schmidti* from *C. sloani* is the lower number of serial photophores in *C. schmidti* (Morrow 1961; Blache 1964). Similarly Gibbs and Hurwitz (1967) concluded that the only characters separating *C. pammelas* from *C. sloani* were lower meristic counts (IC, VAV, vertebrae) in *C. pammelas* and greater development of the gill filaments in *C. pammelas*, with filaments both longer and with a greater number of lamellae per side. Gibbs and Hurwitz (1967) noted that the greater gill filament development of *C. pammelas* is correlated with a well-marked oxygen minimum layer in the northern Indian Ocean habitat of this species. Gill filament length may vary intraspecifically in some wide-ranging mid-water fish species (Johnson 1974).

Both *C. schmidti*, inhabiting the eastern tropical Atlantic, and *C. pammelas*, inhabiting the northern Indian Ocean, are limited to areas of high biological productivity (Ryther and Menzel 1965; Gibbs and Hurwitz 1967; Cushing 1971). Both are distinguished from *C. sloani* by lower counts of serial photophores (and vertebrae in *C. pammelas*), and essentially only by these lower counts. In both cases the lower counts apparently agree with our hypothesized relationship between meristic counts and productivity. The counts for *C. schmidti* are from specimens taken in two areas: TAA, along the west African coast from lat. 03°56′ to 18°22′N, to the west and north of our Gulf of Guinea study area; and TAB, along the west African coast from lat. 01°20′ to 17°53′S, to the south of our Gulf of Guinea study area (Ege 1948; Blache 1964). The counts for *C. pammelas* are from specimens taken between lat. 08° and 14°N, long. 58° to 66°E, in the Arabian Sea (Gibbs and Hurwitz 1967).

In view of other results presented in this paper, particularly those for *Diplophos taenia*, we suggest that a reexamination of the status of both *C. pammelas* and *C. schmidti*, with additional study of meristic variation in *C. sloani* throughout the range of this species, are in order.

Results of the Antipodes Transect

An essentially experimental opportunity to test the hypothesized relationship between meristic counts and productivity was afforded by fishes taken by the Antipodes Expedition of the Scripps Institution of Oceanography in 1970. On this expedition 22 mid-water trawl collections were taken in the Philippine Sea and six mid-water trawl collections were taken in the South China Sea (Figure 4). Because of the 2,000 m or more sill depth separating these geographically contiguous areas, the upper water mass in both areas is the same and differences in physical parameters are minimal. Although the South China Sea is poorly known, there is little doubt that at least nearshore areas or areas over shelves of the South China Sea are substantially more productive than offshore areas in the Philippine Sea (Wyrtki, 1961; Sorokin 1973).

We predicted: 1) that values of meristic counts for species occurring in both the South China Sea and Philippine Sea would be lower in specimens from the South China Sea, and 2) that values of meristic counts for species occurring in the Philippine Sea would be lower in specimens taken near land and increase with increasing distance from shore.

In all four cases thus far examined (Figure 4) where differences exist in values of meristic counts from the two areas, the counts are significantly lower in specimens from the South China Sea. This supports our first prediction.

Vinciguerria nimbaria was the only species taken in sufficient abundance to allow a test of our

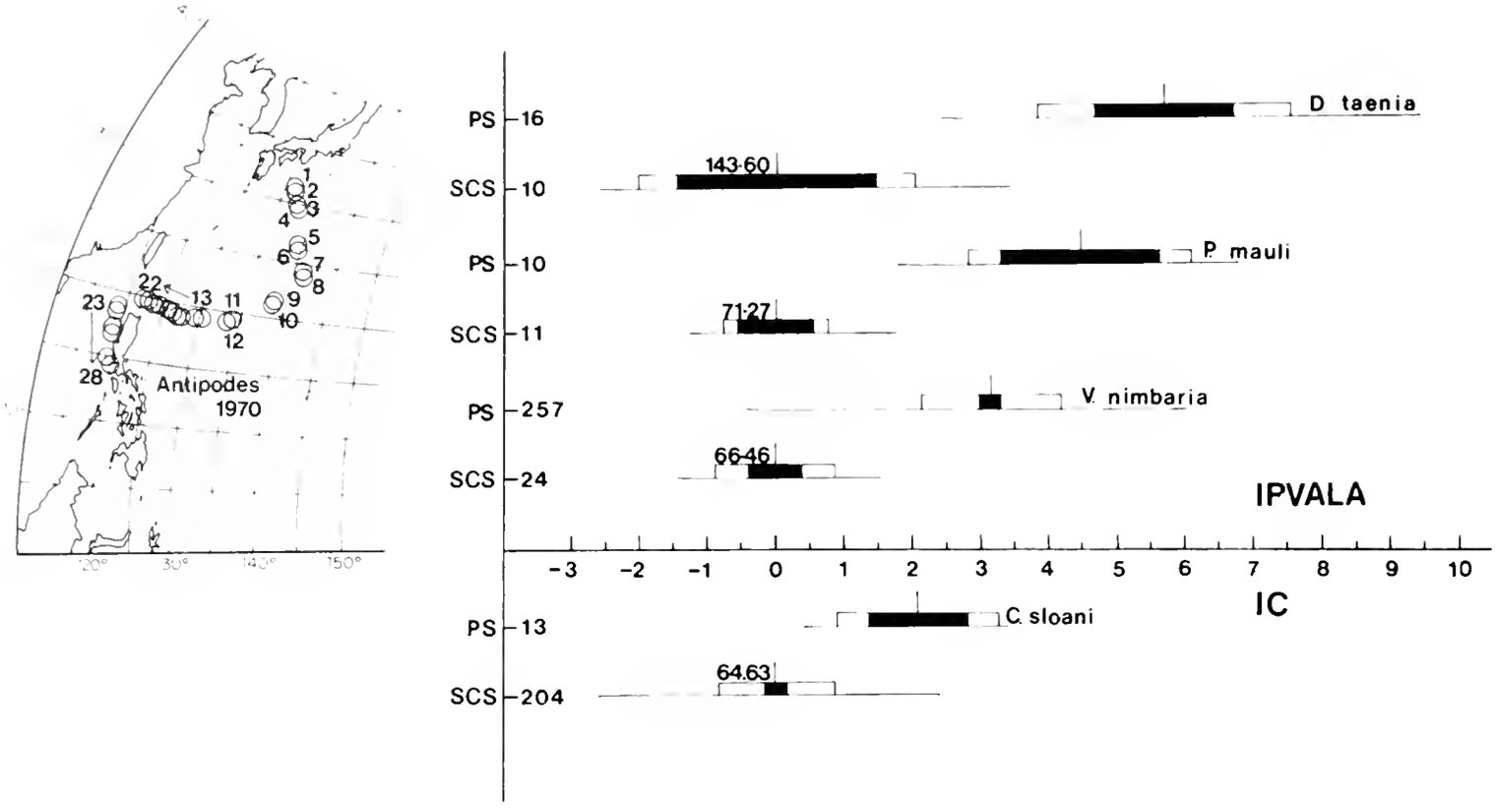

FIGURE 4.—Left: Antipodes Expedition station positions. Right: Comparison of IPVALA and IC photophore counts between specimens from South China Sea (SCS) and Philippine Sea (PS). Data presented as in Figure 2 except that mean values for South China Sea material of all four species have been set equal to zero and all other statistics are plotted as deviations from this zero point. Data for *Chauliodus sloani* from SCS are from Ege (1948); the rest is original data.

second prediction. In Table 9 mean IPVALA counts for Philippine Sea specimens of *V. nimbaria* are tested for relationship with distance of site of collection from land (Japan, Ryukyu Islands, Luzon, but not Bonin or Volcano islands). While the highest mean counts were found in specimens from the 4 stations most distant from land, the data show no relationship between mean counts and distance from land (tau_{11} = -0.273, $P > 0.20$). Mean IPVALA values for specimens from each of the 11 pairs of Philippine Sea stations are significantly higher than the mean IPVALA values for specimens from the South China Sea.

DISCUSSION

One fact and two assumptions are prerequisite to our discussion of the possible explanations for the relationship between meristic counts and measures of food supply. The fact: in *Diplophos taenia*, *Vinciguerria lucetia*, and *V. nimbaria*, the values of the meristic characters we have studied are fixed at or before metamorphosis (Ahlstrom, pers. commun., Ahlstrom and Counts 1958, Silas and George 1971). This is probably also true for *Pollichthys mauli* and *Chauliodus sloani*. This means that any explanation involves factors operating on eggs and/or larvae. The assumptions: 1) that the meristic variation observed is not the result of selection for certain absolute values of the meristic counts, and 2) that the same basic mechanism underlies the variation in counts for all five species in the area studied (in this discussion we ignore results for specimens of *V. nimbaria* from the Gulf of Guinea).

There are four possibilities: 1) that the observed variation is ecophenotypic, i.e. nongenetic modification of the phenotype resulting from the effects of differing food availability conditions upon early growth and development of meristic characters; 2) that the observed variation is a by-product and indicative of genetic differences between populations in these eight areas, and that these differences reflect differing selective pressures resulting from differing conditions for early growth; 3) that the observed variation is a combination of ecophenotypy and genetic differences; and 4) that the real explanation is none of these, that a causal relationship between meristic characters and productivity does not exist, and that we have overlooked the real meaning of our results. We are unable to deal with the third pos-

TABLE 9.—IPVALA photophore counts of *Vinciguerria nimbaria* from the Philippine and South China seas. Antipodes station positions given in Figure 4. Distance from shore (Philippine Sea stations only) given in rank order from nearest to land to most distant offshore. R_m = rank of mean, R_d = rank of distance offshore.

Antipodes stations	65	65.5	66	66.5	67	67.5	68	68.5	69	69.5	70	70.5	71	71.5	72	72.5	*n*	Mean ± 95% limits	R_m	R_d
1, 2	–	–	–	–	–	–	2	–	1	1	3	1	1	–	1	–	10	69.80 ± 0.895	4	4
3, 4	–	–	–	–	–	–	3	4	3	2	4	3	3	–	–	–	22	69.47 ± 0.456	8	5
5, 6	–	–	–	–	–	–	2	2	2	1	12	8	1	–	–	–	28	69.84 ± 0.308	3	8
7, 8	–	–	–	–	–	–	1	–	2	4	10	3	1	–	–	1	22	69.95 ± 0.374	2	11
9, 10	–	–	–	–	–	–	–	–	–	2	3	2	3	–	–	–	10	70.30 ± 0.420	1	10
11, 12	–	–	–	–	–	–	1	1	2	–	1	1	–	–	–	–	6	69.17 ± 0.930	10	9
13, 14	–	–	–	–	–	1	1	1	2	3	4	1	–	–	–	–	13	69.31 ± 0.531	9	7
15, 16	–	–	–	–	–	–	1	–	1	–	1	2	1	–	–	–	6	69.83 ± 1.124	5	6
17, 18	–	–	–	–	1	1	5	6	2	1	6	3	1	–	–	–	26	69.06 ± 0.440	11	3
19, 20	–	–	–	–	–	–	1	4	–	3	3	1	1	1	–	–	14	69.54 ± 0.604	7	2
21, 22	–	–	1	2	–	2	7	8	5	20	36	11	4	3	1	–	100	69.59 ± 0.209	6	1
Philippine Sea, mean = 69.60 ± 0.126																		Tau_{11} = –0.273 P>0.20		
23, 24	1	1	5	1	–	1	–	–	–	–	–	–	–	–	–	–	9	66.06 ± 0.524		
25, 26	1	–	1	1	–	–	3	–	–	–	–	–	–	–	–	–	6	66.92 ± 1.345		
27, 28	–	–	4	2	2	–	1	–	–	–	–	–	–	–	–	–	9	66.56 ± 0.524		
South China Sea, mean = 66.46 ± 0.378																				

sibility and ignore the fourth possibility in our subsequent discussion.

We believe that the observed meristic variation is the result of genetic differences between populations and not the result of an ecophenotypic effect of food availability conditions on development of meristic characters. We present evidence available to support this belief, but we note that this evidence is not conclusive.

A statement of the ecophenotypic explanation is easily made. The meristic variation observed could result if the effect of low food densities upon the development of meristic characters parallels the effect of low temperature, retarding growth rates more than differentiation rates, and lengthening the period of determination of meristic characters. Because the effect of low food availability upon egg maturation appears to be a reduction of egg number and not egg size (Anokhina 1960; Blaxter 1969), any ecophenotypic effect of low food density upon meristic characters would have to operate between the onset of feeding and metamorphosis. Riley (1966) and Blaxter (1969), among others, have found for the species they have studied that the time to reach metamorphosis may be significantly increased by decreasing the density of food. Therefore an indispensable condition of the ecophenotypic explanation is that for the species studied, the final values of meristic counts are determined after the onset of feeding. If so, the meristic variation observed might result from a concordant increase in the length of the period of determination of meristic characters with a delay in time to reach metamorphosis in larvae from areas of lower productivity.

Three facts resulting from the study of the development of the eggs and larvae of *Vinciguerria lucetia* by Ahlstrom and Counts (1958) appear to support the ecophenotypic explanation: 1) Ahlstrom and Counts did find a direct relationship between size at metamorphosis (no developmental time scale is available for any of the species studied) and numbers of longitudinal photophores and vertebrae; 2) vertebral ossification and photophore formation in *V. lucetia* occur in larvae 11 mm SL or more in size, well after yolk-sac absorption and presumably after the onset of feeding; and 3) the distances between samples of *V. lucetia* utilized in construction of Figure 3 are small, much less in most cases than the distances between the eight study areas for the other species discussed in this paper. Yet the results for *V. lucetia* along the east to west transect lines apparently agree with results for the other mid-water species. We find it difficult to believe that the results for *V. lucetia* are explainable in terms of genetically distinct populations distributed along these inshore to offshore transects.

Three lines of evidence appear to contradict the ecophenotypic explanation in favor of the explanation hypothesizing that the observed meristic variation is the result of genetic differences between populations. (1) in *Vinciguerria lucetia* the total number of myomeres are formed in late stage eggs (Ahlstrom and Counts 1958). Since the number of myomeres, vertebral counts, and longitudinal photophore row counts are usually highly intercorrelated, the ecophenotypic explanation appears to be invalid in

this case. (2) The data for *Vinciguerria nimbaria* may indicate the existance of separable populations in our different study areas. This is suggested by the results for the Antipodes transect (Table 9) in which is found no clear evidence for an onshore to offshore trend toward higher IPVALA counts, despite the fact that the productivity measures are higher inshore and decrease (rapidly) to seaward (Reid 1962; Koblentz-Mishke et al. 1970). Mean values of IPVALA photophore counts for specimens from each of the 11 pairs of Philippine Sea stations are significantly higher than the mean value for South China Sea specimens. This may suggest that genetically distinct, separable populations of *V. nimbaria* are found in each area. Gill raker counts for *V. nimbaria* (Table 10) apparently support this suggestion in that counts of gill rakers are discordant with counts of IPVALA photophores (Table 6) and vertebrae (Table 7). For the four Pacific areas the counts of vertebrae and IPVALA photophores for *V. nimbaria* agree in perfect rank-order with the IPVALA photophore counts for *D. taenia* (Table 10). That this is not true for gill raker counts may indicate the existence of separable populations of *V. nimbaria* in the South China Sea, central equatorial Pacific, and the North Pacific central gyral areas (Philippine Sea, central North Pacific). (3) The ecophenotypic explanation implies that in areas of low productivity elevated meristic counts result from retardation of growth and that this retardation is the result of the average survivor being underfed compared to larvae in areas of higher productivity. As year class strength in pelagic fish populations is probably largely determined in early stages of larval life and not by the total number of eggs produced or mortality during advanced prerecruit stages (Hempel 1965), it seems likely that selection would strongly favor any mechanisms that tended to protect the larvae of mid-water fishes occurring in areas of low productivity against starvation. The possible materials on which this selection might operate and the possible consequences on meristic characters form the basis for a second explanation of the observed meristic variation, that it is the by-product of genetic differences between separable populations in areas of low and high productivity.

Hempel (1965), Blaxter (1965), and others, concerned mainly with pelagic clupeoid fishes, have developed strong evidence that under normal circumstances the main restriction on the success of a year class occurs within a short period of larval life, the critical period of Hjort (1914, 1926) and others (e.g. Marr 1956; Schumann 1965). Selection has apparently resulted in adaptive mechanisms tending to balance the two main dangers to larval survival: the danger of starvation and the danger of predation (Blaxter and Hempel 1963; Hempel 1965).

Blaxter (1965), Hunter (1972), and others, have shown that at the onset of feeding, just before or at the time of yolk-sac absorption, surprisingly small differences in size can significantly affect the probability of larval survival. Hunter (1972) has shown for northern anchovy *Engraulis mordax* Girard, larvae that slight increments in size are associated with highly increased searching abilities, highly increased success of attempted feeding acts, and vastly diminished minimum prey density requirements for survival. Blaxter (1965) discusses the significance of the greater spectrum of particle sizes available to larger larvae in terms of increased diversity of available prey organisms. Similar findings have been reported for other fish larvae (e.g. Arthur 1956; Einsele 1965). Size at hatching, at least for Atlantic herring, *Clupea harengus* Linnaeus, is a direct function of egg size; larger larvae hatch from larger eggs. Fecundity is inversely proportional to average egg size (Baxter 1959; Blaxter and Hempel 1963; Blaxter 1969).

We believe that the meristic variation between populations occurring in areas differing in productivity values is the result of adaptations involving the adjustment of egg and larval size to the productivity regime. We believe that these adaptations reflect differences between areas of low and high productivity in the relative impor-

TABLE 10.—*Vinciguerria nimbaria*, comparison of gill raker counts with vertebral and longitudinal photophore row counts.

V. nimbaria, total gill rakers on first gill arch.

Area	17	18	19	20	21	22	23	24	25	26	*n*	Mean ± 95% limits
GG	—	—	—	—	—	—	3	6	10	1	20	24.45 ± 0.386
SCS	4	7	3	1	—	—	—	—	—	—	15	18.07 ± 0.489
CEP	—	—	—	4	13	13	1	—	—	—	31	21.35 ± 0.277
PS	—	2	26	54	31	2	—	—	—	—	115	20.04 ± 0.147
CNA	—	4	8	—	—	—	—	—	—	—	12	18.67 ± 0.313
CNP	—	—	3	6	3	—	—	—	—	—	12	20.00 ± 0.469

V. nimbaria and *Diplophos taenia*, comparison of counts, given as mean (rank.

	Vinciguerria nimbaria			*Diplophos taenia*
Area	Gill rakers	IPVALA	Vertebrae	IPVALA
SCS	18.1 (1	66.5 (1	39.4 (1	143.6 (1
CEP	21.4 (4	68.0 (2	40.2 (2	145.5 (2
PS	20.0 (2.5	69.6 (3	41.2 (3	149.2 (3
CNP	20.0 (2.5	70.3 (4	41.8 (4	151.7 (4

tance of two principal dangers to larval survival: starvation versus predation.

We hypothesize that selection on mid-water fish populations inhabiting areas of low productivity has favored mechanisms tending to offset the danger of larval starvation, and that these populations will exhibit: 1) larger average egg size, 2) lower fecundity, and 3) larger average larval size at hatching and at comparable stages of development than populations living in areas of higher productivity. Advantages that might accrue to larger larvae in areas of lower productivity include increased mobility, a wider possible search volume, increased diversity of potential prey organisms, and a longer period of survivorship solely on yolk reserves.

The danger of starvation is presumably lower in areas of higher productivity but the danger of predation, resulting from presumed higher densities of potential predators on fish larvae, may be greater. Here selection may have favored increased fecundity tending to offset the danger of increased predation on larvae. We believe that in areas of higher productivity populations of mid-water fishes will exhibit: 1) smaller average egg size, 2) increased fecundity, and 3) smaller average larval size at hatching and at comparable stages of development than populations living in areas of lower productivity.

In developing this hypothesis we have largely followed Hempel's (1965) explanation for variations in egg size and fecundity between populations of herring in the eastern North Atlantic and North Sea. We note that there exists no evidence for increased predation pressure on larval populations of mid-water fishes in areas of higher productivity. It is possible to retain the main features of our hypothesis without including predation pressure by relating variation in fecundity and egg size solely to food density requirements. By definition, selection will favor maximizing reproductive output, thereby favoring fewer larger larvae in areas of low productivity where the danger of larval starvation is greater, and favoring higher fecundity (with the concomitant of smaller eggs and larvae) in areas where the danger of starvation is lessened.

There exists limited available evidence to support these predictions. Ahlstrom and Counts (1958) showed that egg size and size at hatching in *Vinciguerria lucetia* are directly related, the smallest larvae (at a defined stage of development) are found in areas where average egg diameters are least. They also showed that mean values of vertebral and IPVALA photophore counts are lowest in those areas where egg and larval size is least and where metamorphosis occurs earliest (i.e. at smallest size). Although no small larvae were available for this study, we were able to compare development in prejuvenile specimens of *V. nimbaria* from the central North Pacific with specimens from the central equatorial Pacific. In *V. nimbaria* the last four VAL photophores are late-forming, are laid down serially from anterior to posterior, usually the left member of a pair of VAL photophores develops just before the right, and the number yet to develop can be determined uniquely from the one to one correspondence with the posterior photophores in the VAV segment. In Figure 5 standard lengths of all available prejuvenile specimens of *V. nimbaria* from the central North Pacific and central equatorial Pacific are plotted against the number of VAL photophores left to appear. If this character can be used as an index to comparable stages of development, then at comparable stages of development the larvae from the area of lower productivity are the larger, as predicted.

We believe that the correlation between meristics and productivity results from a correlation between meristics and egg size, and that egg size and, hence, size at hatching are genetically determined features reflecting adaptation to productivity conditions. A number of authors have stated or suggested that such a correlation exists (Ahlstrom and Counts 1958; Lindsey 1958, 1961; Garside

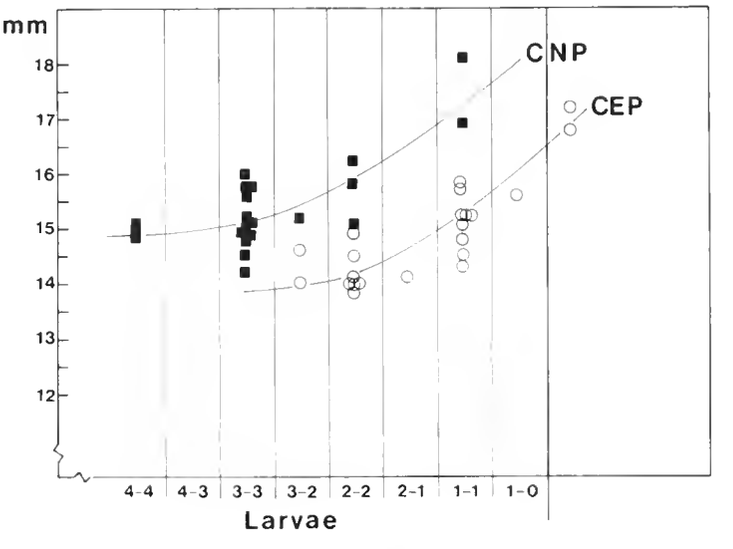

FIGURE 5.–Size of larvae of *Vinciguerria nimbaria* from the central North Pacific (CNP) and the central equatorial Pacific (CEP) at comparable stages of development. Ordinate: standard length in millimeters. Abscissa: number of VAL photophores yet to form (determined from VAV count) on each side of each specimen. Lines fitted by eye.

and Fry 1959). Lindsey and Ali (1971) have recently argued against this suggested relationship, despite the fact that their data showed a direct relationship between the number of anal fin rays and egg size in the medaka, *Oryzias latipes*. Blaxter and Hempel (1963) found no relationship between incubation time and egg size in herring, but did find a positive correlation between time to yolk sac absorption and egg size. If this correlation is true for the mid-water fishes considered in this report, if the correlation continues beyond the point of yolk sac absorption, and if the meristic characters in question are determined after hatching, it might result in a longer period of determination of these characters in larvae from larger eggs.

We lack essential developmental and ecological information to complete our hypothesis. We know little or nothing for most mid-water species about age and size at first spawning, number of spawnings per female, fecundity, seasonality of reproduction, course of larval development, or factors actually determining survivorship of larvae. The answer to the question of mechanism awaits the comparison of these population parameters between populations in areas of high and low productivity.

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MATERIAL EXAMINED

Diplophos taenia. The material examined of this species is listed in Johnson and Barnett 1972. Supplementary station list of materials examined for a study of meristic variation in *Diplophos taenia* Guenther. Ref. Ser. Scripps Inst. Oceanogr. 72-4, 1-8 (unpublished manuscript available from the Library, Scripps Institution of Oceanography, La Jolla, Calif).

Pollichthys mauli. GG: 24 (28.5-46.9), UMML 22881 (1), UMML 24132 (1), UMML 24237 (1), UMML 24266 (3), UMML 24658 (6), UMML 27884 (6), UMML 27929 (5), UMML 28159 (1). SCS: 11 (21.1-31.1); SIO 61-744 (1), SIO 69-20, (10); PS: 10 (33.8-49.9); SIO 70-308 (1), SIO 70-309 (1), SIO 70-334 (2), SIO 70-337 (2), SIO 70-340 (4).

Vinciguerria attenuata. SCS: 71 (13.0-37.8); SIO 70-341 (5), SIO 70-343 (5), SIO 70-344 (52), SIO 70-345 (5), SIO 70-346 (3), SIO 70-347 (1). PS: 71 (13.0-28.1); SIO 70-308 (12), SIO 70-309, (10), SIO 70-310 (6), SIO 70-311 (12), SIO 70-314 (11), SIO 70-318 (1), SIO 70-333 (15), SIO 70-334, (1), SIO 70-337 (2).

Vinciguerria nimbaria. GG: 20 (21.0-37.5); UMML 21902 (20). SCS: 35 (11.7-32.0); SIO 70-341 (4), SIO 70-343 (5), SIO 70-344 (10), SIO 70-345 (5), SIO 70-346 (5), SIO 70-347 (6). PS: 729 (11.6-39.9); SIO 70-306 (63), SIO 70-308 (6), SIO 70-309 (18), SIO 70-310 (23), SIO 70-311 (29), SIO 70-314 (45), SIO 70-318 (52), SIO 70-326 (7), SIO 70-327 (3), SIO 70-328 (12), SIO 70-329 (22), SIO 70-331 (2), SIO 70-332 (11), SIO 70-333 (173), SIO 70-334 (15), SIO 70-336 (6), SIO 70-337 (14), SIO 70-339 (2), SIO 70-340 (226). CEP: FMNH (Field Museum of Natural History) 77100 32 (16.9-36.0). CNA: USNM,

Ocean Acre Stations, all material from ca. lat. 32-32.5°N., long 64°W. 12(19.1-35.8); 12-17C (1), 12-18A (2), 12-18B (2), 12-28B (1), 12-34C (1), 12-35C (1), 12-62 (1), 12-80 (1), 12-81 (1), 12-86 (1). CNP: 49 (14.1-31.0); UH 69-11-5 (49).

Chauliodus sloani. PS: 14 (42.2-214.5); SIO 70-306 (3), SIO 70-311 (2), SIO 70-326 (1), SIO 70-334 (8). CNP: 20, SIO 71-301 (1), SIO 71-307 (1), SIO 71-309 (5), SIO 71-373 (1), SIO 72-11 (2), SIO 72-16 (1), SIO 72-22 (1), SIO 72-25 (2), SIO 73-142 (1), SIO 73-149 (1), SIO 73-155 (1), SIO 73-158 (2), SIO 73-159 (1).

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SPIN-LABELING TECHNIQUES FOR STUDYING MODE OF ACTION OF PETROLEUM HYDROCARBONS ON MARINE ORGANISMS

WILLIAM T. ROUBAL[1] AND TRACY K. COLLIER[2]

ABSTRACT

Spin-labeling studies of membrane-contaminant interaction are being conducted by biochemists at the Northwest Fisheries Center in Seattle, Washington. The aim of these studies is to gain a better understanding of the mode of action of hydrocarbon contaminants at the molecular level. Basic spin-labeling theory together with experimental results are presented and discussed. Spin-labeling holds great promise not only for environmental studies but also for drug research, toxicology, and pharmacology as well.

The interaction between contaminants and living systems commences when contaminants combine with so-called active sites in living tissue. Active sites are varied in nature, but often they are groups of molecules assembled in a special fashion such as those which comprise membranes and associated enzymes or other biopolymers.

Although the exact nature of contaminant-host interaction may not be known in each and every case, experimental data from biochemical/biophysical studies allow us to draw certain conclusions about interactions. With detailed investigations, collected data may even allow us to draw a fairly accurate picture concerning the molecular basis of physiological changes which contaminants are able to induce.

Admittedly, investigations such as these are difficult to perform. The molecular complexity of living systems defies ready characterization, and it is even more difficult to relate alterations in molecular organization to the subsequent physiological changes wrought by this contaminant-host interaction.

Recent years have seen an upsurge of interest in membranes and how membrane structure is modified when invaded by such things as drugs and insecticides. The reasons are several: membranes house cells, control the influx and efflux of nutrients and metabolites; membranes control and form the basis for the transmission of electrical signals (nerve impulses) when nerve receptor sites are stimulated. Any major alteration to normal membrane structure may be expected to play some role in animal physiology, especially if the contaminated membrane is associated with neural function or other viable life processes.

Membranes consist of a sandwich of phospholipids, sterols, and proteins; individual membranes are microscopically thin. The thinness and complexity of membranes make their study most difficult. One way of characterizing membranes is by measuring their electrical properties (conductance, resistance, capacitance, etc.). However, with respect to contaminant-host interaction, it is more desirable to be able to deduce structural features such as lipid fluidity, protein-lipid interaction, and arrangements of constituents in dynamic tissue preparations. This, then, precludes the use of electron microscopy or other methods which are incompatible with maintaining tissue in a viable unchanged condition.

THE THEME OF THIS REPORT—SPIN-LABELING

Several years ago, it was observed that certain free radical derivatives of fatty acids could be introduced into membrane preparations without unduly disturbing the natural arrangement of native membrane constituents (Jost et al. 1971). Furthermore, it was shown that these free radicals would associate with and align in membranes

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much the same way as do the nonradical natural fatty acids present in membranes (Libertini et al. 1969; Hubbell and McConnell 1969; Schreier-Muccillo et al. 1973). By using appropriate instrumentation, it was found that these radicals could be used as submicroscopic probes (or labels) for investigating membrane structure. This has become known as spin-labeling, and forms the underlying theme of this paper. This report describes our work on contaminant-host interaction in fingerling salmon. To show how these studies were performed, we need to arm ourselves with some basic background information. Let us review briefly some very important points concerning radicals, electrons, and nuclei.

THE FOUNDATION OF SPIN-LABELING

Free Radicals

Many free radicals are known or have been isolated. Most, as we know, are quite reactive chemically, and unless conditions conducive to their formation and stabilization (trapping) are maintained, radicals normally disappear once formed. Radical reactivity stems from the fact that radicals, by definition, are molecules which contain one or more unpaired electrons. Two radical partners normally pair together to yield end products with the normal complement of two electrons per chemical bond. This is the usual covalent bond and is characteristic of organic compounds.

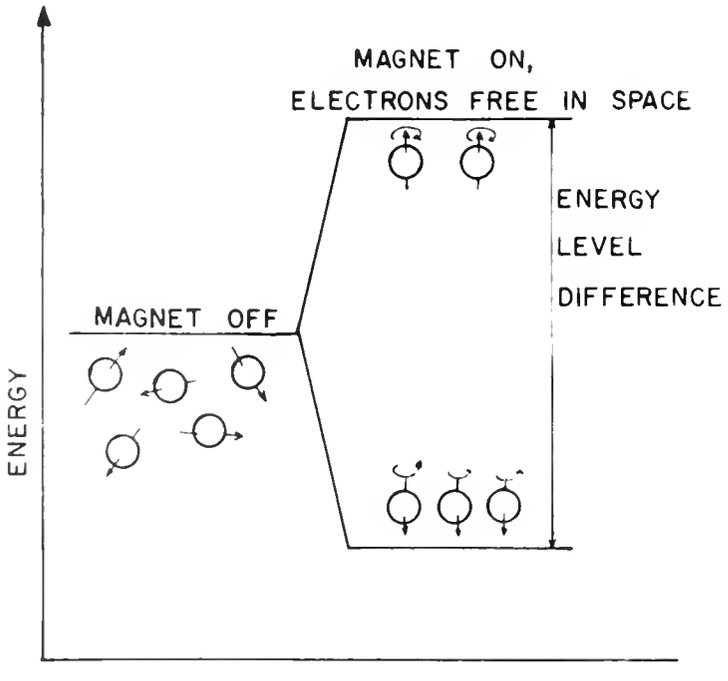

FIGURE 1.—Resonance condition for isolated electrons. In the absence of external field, energy levels are indistinguishable. When a magnetic field is applied, two levels (and only two levels, by quantum mechanical restrictions) are populated by electrons. By employing X-band microwaves (9 GHz) with the proper energy ($h\upsilon$ = gβH; see for instance, Roubal 1972), flipping between levels occur and the absorption of microwave energy is observed.

There is one class of free radicals, the nitroxides, which are stable under many of the usual laboratory conditions. Nitroxide stability derives from resonance and other contributing factors, but we need not discuss these here. Many nitroxides are relatively easy to synthesize, provided the necessary starting intermediates (some of which are rare) are at hand.

The important point to be made is the fact that nitroxides can be used to characterize biological systems. Nitroxides so used are called spin-labels; *spin* from the fact that it is the unpaired electron(s) (which is/are spinning) which forms the basis for the *label* or probe. Spin-labeling might just as conveniently be called spin-probing.

Spinning Electrons and Their Magnetic Properties

All electrons are in a state of motion; they all spin about on their axis. Spinning electrons are therefore moving charges of electricity. Thus electrons are magnetic. Spinning electrons therefore are influenced by an external magnetic field such as produced by a solenoid or electromagnet. When a sample of free radicals is placed between the poles of an electromagnet, the spin of the electron is described as clockwise or counterclockwise and is depicted in Figure 1.

Of immediate consequence is the fact that one spin condition is more stable than the other, and is so indicated by the reference to the energy of the system as shown. Although one population level is more stable than the other, the temperature of the system is always great enough to insure that the higher level contains just about as many electrons as the lower level. This is something akin to placing two bar magnets end to end. If they are aligned N-S N-S, we know from everyday experience that the interaction will be attractive and stable. If, on the other hand, we try to force them N-S S-N, we know again from experience that this is an unstable situation and requires an expenditure of energy (heat in the case of electrons, physical in the case of magnets) to maintain

them aligned in this fashion. Apart from this, however, the analogy extends no further, for in the realm of electrons and nuclear phenomena, quantum mechanical postulates hold and the common experience of our everyday world does not pertain.

The important point we want to make here is that we can induce an electron with one spin rotation to flip over and assume the alternate rotation. Energy is required to do this. To achieve flipping, the sample is irradiated (while between the poles of the electromagnet) by microwaves with a frequency of 9 gigahertz (GHz). Thus we see that what we are really talking about is just another type of spectroscopic method. The presence of free radicals is detected by measuring the loss of microwave energy. The actual instrument used for such studies is called the electron paramagnetic resonance (EPR) spectrometer (also called the electron spin resonance/ESR/spectrometer).

At this point we must consider other factors which contribute to the total magnetism of the system. Remember that the unpaired electron is not merely floating freely about in space. It belongs to a molecule. In fact it is coupled to a nucleus, and in the case of nitroxides, to a nitrogen nucleus, which is itself a magnetic entity. Thus in the presence of an external field, the nuclear magnetism can couple with the external field and alter the magnetism immediate to the electron. We must now consider this situation, called hyperfine splitting (hfs).

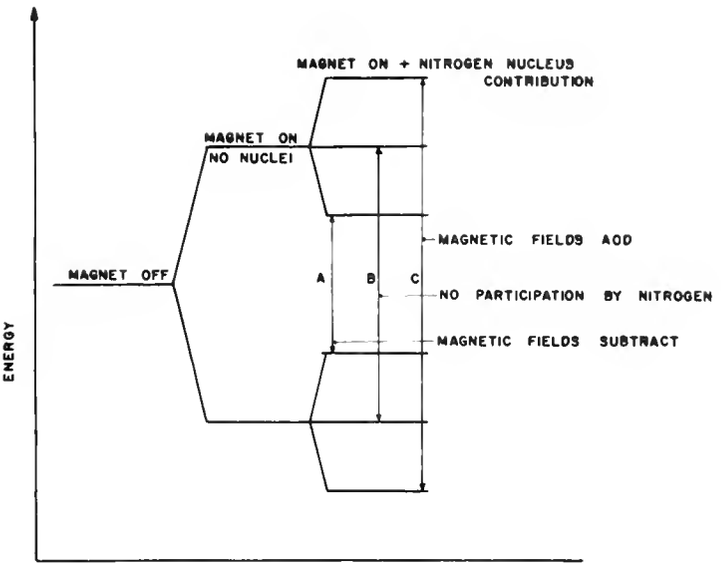

FIGURE 2.—Resonance condition for the case of one electron interacting with a nitrogen-N^{14} nucleus. Due to quantum mechanical restrictions, only those transitions shown are allowed.

Hyperfine Splitting (hfs)

Simply stated, it is found that the nitrogen magnetism can add to, subtract from, or be orthogonal (no interaction) to the external field. This is depicted in Figure 2.

Note that the situation of Figure 1 is now modified. The original resonance (flipping) condition is broken down into three resonances (hfs). The flipping from one level to the other is depicted by the double ended arrows A, B, and C. Certain restrictions are placed on flipping, and we find that only those shown are allowed. All levels are equally populated, and an actual EPR spectrum of a nitroxide in dilute solution is shown in Figure 3.

Spin-Label Spectra

While the spectrum of Figure 3 tells us most conclusively that we are dealing with a nitroxide, it serves no further purpose other than a possible quantitation of the amount of radical (number of spins) present. If all we ever measured were three sharp, hyperfine lines, we could not use nitroxides as spin-labels.

Fortunately, when a nitroxide is placed in an actual biological system, the hyperfine lines are modified both in shape, intensity (relative height), and in spacing. These spectral modifications are environment dependent, and it is this dependency which makes nitroxides valuable as probes for characterizing biological systems.

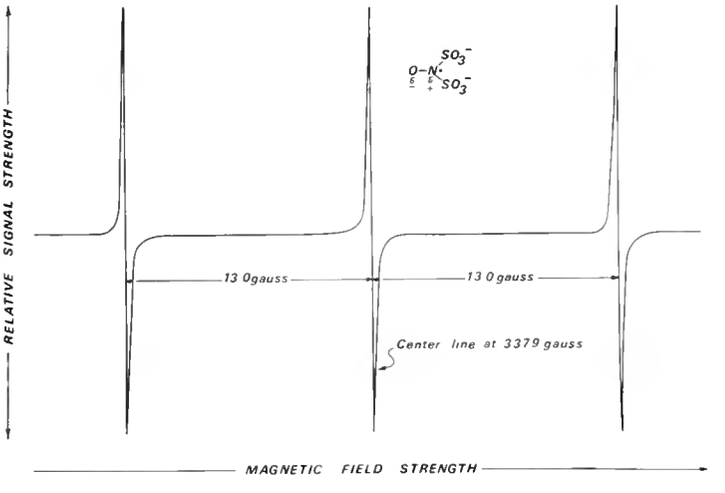

FIGURE 3.—EPR spectrum of the nitroxide compound potassium peroxylamine disulfonate (Freemy's salt) (10^{-3}M) in water at room temperature. Three hyperfine lines of equal intensity, and spaced 13 gauss apart, distinguish nitroxides in water.

It is sufficient to simply state that the unpaired electron is localized on nitrogen and this localization resides primarily in a p-orbital on nitrogen. p-Orbitals are dumbbell-shaped electron density regions in space, and the magnetic properties associated with an electron in such an orbital depends on the so-called tumbling frequency of the electron (how fast the p-orbital assumes a random distribution of orientations while part of the nitroxide in a biological system). An example of two limiting situations is shown in Figure 4. Spectrum 4A was recorded for a nitroxide in liquid glycerol, while 4B is for the frozen solution. Spectrum 4A tells us that moderate fast tumbling prevails, while 4B shows tumbling to be essentially quenched. The reader is referred to the literature (Roubal 1972) for a more thorough discussion on the dependency of spectral characteristics on tumbling frequency (label mobility).

Intermediate mobilities are characterized by a family of spectra. Examples are to be found in the recent spin-labeling study of a hapten combining site of trout antibody by Roubal et al. (1974). Using appropriate mathematical manipulations of recorded spectra, one can measure tumbling frequencies with accuracy. These frequencies together with other derived data provide quantitative characterization of labeling studies.

MEMBRANES AND MEMBRANE PROPERTIES

The importance of membranes in biological roles of living systems cannot be overemphasized. Membranes, as mentioned, are responsible for neural function. Membranes participate in ion-binding and in governing tissue permeability. Associated with membranes, especially mitochondrial membranes, are a variety of enzymes. Cytochrome oxidase and other electron transport enzymes are membraneous in nature. Membrane-bound enzymes require the proper conditions such as lipid fluidity, proper phase transition temperatures, and lipid-protein interactions for their function. The participation of membranes in neural control is well documented. Neural membranes contain molecular size pores which mediate sodium/potassium transport. The exact nature of these pores has not been delineated completely, but several lines of evidence suggest that pores consist of a cagelike arrangement of protein which spans the membrane from the inner to the outer surface. Membranes are considered to be the basis of life itself.

Membranes consist principally of proteins and lipids. Carbohydrates comprise 0-10% of the membrane mass. Lipids account for about 40% of the mass, and the balance is protein. Membranes are a matrix of lipids and proteins arranged in a bimolecular leaflet (Singer 1972; Green 1972), illustrated in Figure 5. The little circles represent phospholipid headgroups (choline, ethanolamine, serine, phosphatidic acid, etc.) while proteins are indicated by the larger "islands." Interspersed with the fatty acid tails (squiggly lines) are sterols and lesser tissue lipid components. Typical membranes are about 100 Å thick.

Membrane lipids are amphiphilic—provided

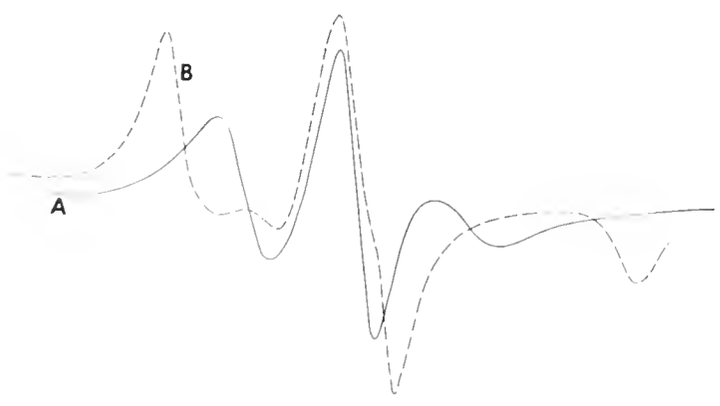

FIGURE 4.—Label II (see text) in glycerol.
A. In liquid glycerol at room temperature.
B. Frozen in glycerol at liquid nitrogen temperature.
Label mobility (effect of environment) is calculated by measurements of line widths, heights, intensity ratios, and spacing.

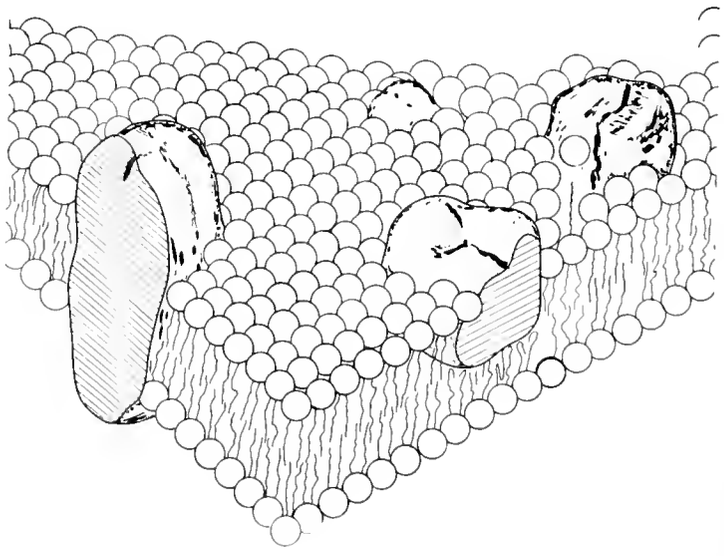

FIGURE 5.—Membrane bilayer leaflet. Small circles represent phospholipid headgroups. Squiggly lines are fatty acid tails. Large islands represent membrane protein. From Singer 1972. (Courtesy of S. J. Singer and New York Academy of Sciences.)

with polar headgroups and nonpolar tails of carbon-hydrogen chains. Thermodynamically, and for other reasons as well, the greatest stability for membrane structure results when membrane constituents are arranged as shown; polar surfaces are exposed to aqueous environments, and the fatty acid tails are tucked away out of contact with water.

QUESTIONS ABOUT CONTAMINANT-HOST INTERACTION

We would like to answer the following questions concerning membrane-contaminant interaction: a) are certain regions of membranes affected or is the whole membrane affected when invaded by contaminant? b) if the effect is localized, where is the localization? c) are there differences in membrane perturbations when treated on the one hand by paraffins, and aromatics on the other? d) can the differences, if they exist, be related to anything presently known about the toxicology of any of these contaminants?

EXPERIMENTAL METHODS AND RESULTS

The study was performed in two steps. First, an in vivo feeding study was undertaken. Here we used spin-labeled hydrocarbons (Roubal 1974) and fed them to fish. Second, an in vitro study was employed using excised tissue. In order to restrict our investigations of membranes (in vitro) to specified regions, the series of labels I, II, and III (Roubal 1974a) (Figure 6) were synthesized by the EPR group of this Center. The positively charged quarternary nitrogen of label I directs this portion of the label to the polar membrane surface, which in turn insures that the nitroxide nitrogen is situated at or very near to the membrane surface. The carboxyl groups of labels II and III direct the carboxyl end of these amphiphiles to the membrane surface, but now the nitroxide nitrogen lies some 12-15 Å below the membrane surface in II, and deep into the hydrophobic membrane interior in III. Thus we can "look" at the membrane's surface, subsurface, and interior.

In the feeding study, spin-labeled hydrocarbons were incorporated into fish food and fed to coho salmon, *Oncorhynchus kisutch*, fingerlings in a 2-day feeding study. Within an hour, or even less, after onset of intake of food by fish, the blood showed EPR activity. Using radiotracers, we have shown this activity to be associated with blood lipoproteins and albumins (Roubal 1974b), with lipoproteins making the greatest contribution to hydrocarbon transport in blood.

After an induction period of about a day, blood-associated labels (Roubal 1974b) slowly transfer to neural tissue and flesh. Weight for weight, the greatest concentrations are to be found in the spinal cord, lateral line nerve bundles, and brain. The nature of the EPR line shapes indicated that the invasion of hydrocarbon is site selective. All labeled paraffins appeared to intercalate with membrane in such a way that the nitroxide mobility is little impeded. In direct contrast to this, mobility of aromatics appeared to decrease. This in vivo study suggests that paraffins associate with molecularly fluid portions of membrane fatty acids, while aromatics associate with the more structured and rigid regions of membranes. In order to clarify these possible differences, an in vitro study was undertaken using labels I, II, and III (Roubal 1974a).

Neural tissue from untreated fish was carefully excised and placed in cold, 0.1 M phosphate buffer, pH 7.4 at 4°C, isotonic in NaCl. A sonicated dispersion of label, complexed to bovine serum albumin was added and allowed to transfer to neural membrane (overnight at 4°C). Membranes were then inserted directly into the EPR spectrometer, and the spectra were recorded immediately. After

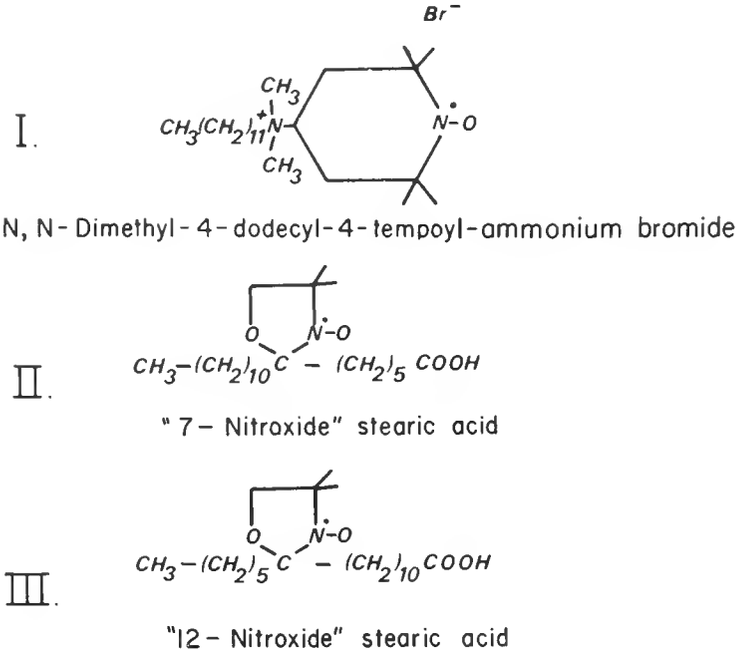

FIGURE 6.—Lipid-intercalating spin-labels.
Label I reports on surface conditions.
Label II reports on subsurface conditions.
Label III reports on interior conditions.

the spectrum for one sample was obtained, the tissue was returned to a large volume of fresh, cold buffer to which test hydrocarbon (in separate tests) was incorporated via sonication. Final hydrocarbon concentration in buffer was 15-25 ppm. Hydrocarbons included benzene, toluene, ethyl benzene, hexane, heptane, octadedecane, and cyclohexane. Actual uptake of paraffin hydrocarbon by tissue membrane, as measured by gas-liquid chromatography (GLC), was on the order of 1 ppm. Aromatics were present in higher amounts (5-10 ppm). Tissue was exposed to hydrocarbon in buffer for 1 h. At the end of this period, tissues were withdrawn, rinsed well, and the EPR spectra were re-recorded.

A comparison of the in vitro spectra for controls with those same samples after hydrocarbon treatment provided evidence that a differentiation in binding sites for paraffins and aromatic compounds does indeed exist (Figure 7).

DISCUSSION

We can explain rather easily the preference of paraffins seeking the interior of membranes—paraffins are nonpolar, very soluble in neutral hydrocarbons, such as those which comprise the hydrogen-carbon chains (or tails) of phospholipid fatty acids. Hence, thermodynamically, system stability is enhanced by mutual interaction of paraffin hydrocarbon with lipid tails.

Aromatics, on the other hand, are unique, for in addition to their ready solubility in many organic environments, aromatic compounds are fashioned from conjugated double bond systems with pi-electron unsaturation. These factors give aromatics the ability to form quasi-chemical complexes with other molecules which can act in electron acceptor-donor roles.

The surface of the membrane contains many different sites, both polar, nonpolar, and electron-interactive. It appears that some of these sites contain the necessary properties which make binding of aromatics possible. A charge-transfer mechanism (Kier 1971) may direct aromatics away from the membrane interior to the surface.

These site preferences for paraffins and aromatics may account in part for the differences we observe for retention of these substances in living tissue. For instance, in other studies (Roubal 1974b) we have shown via GLC, spin-labels, and radiotracers that paraffins are retained in living tissue for long periods of time; aromatics are not. What is more, paraffins are relatively nontoxic, while aromatics generally are quite toxic, even at low levels.

The molecular basis for physiological phenomena is associated in a very direct way with important membrane properties. Ion-binding, lipid protein (enzyme) interaction, lipid phase-transition temperatures, and lipid fluidity are all involved in one way or another. Membrane disor-

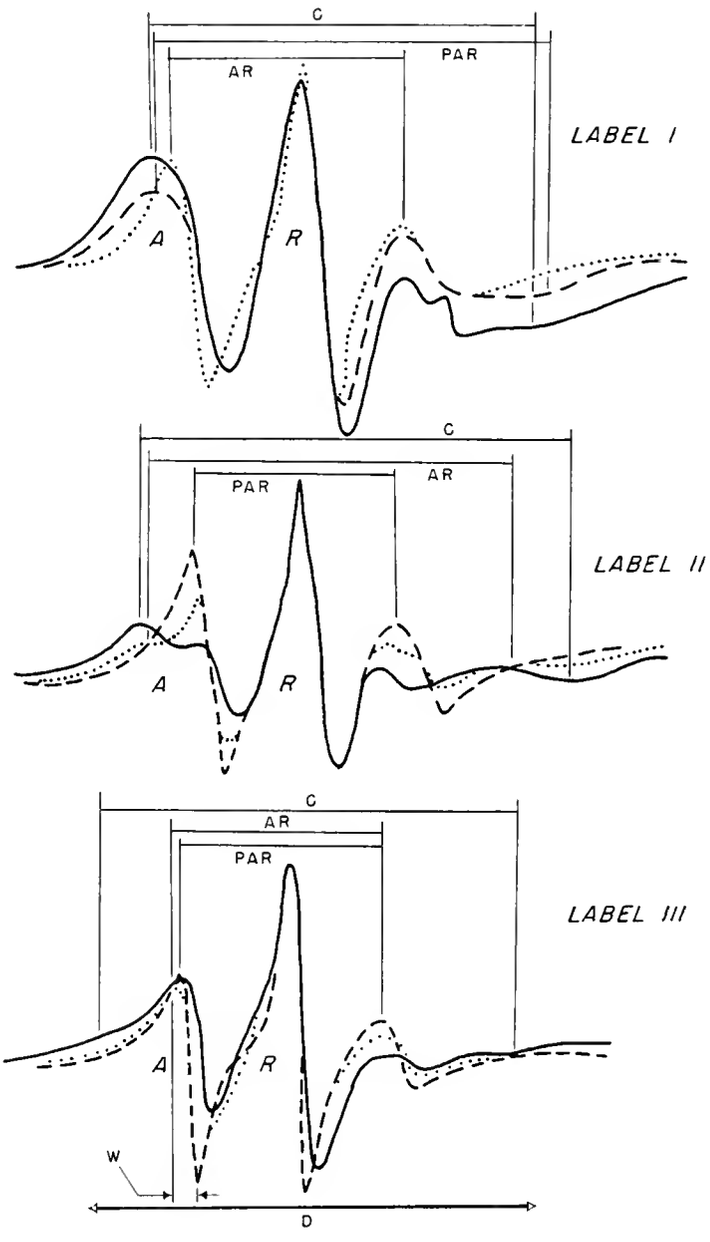

FIGURE 7.—Spin-label spectra of aromatic-treated and paraffin-treated coho salmon spinal cord (SC).
SC + Label I (+ treatment).
SC + Label II (+ treatment).
SC + Label III (+ treatment).
Changes in the A/R (line height) ratio, narrowing of peak widths (W), and shifts in distance D to lesser values provide data for characterizing influence of treatments (Roubal 1972; Roubal 1974a). C, spinal cord control.
AR, treatment by aromatics.
PAR, treatment by paraffins.

ganization is considered to involve alterations in these properties. Accordingly, on invasion of membrane primarily by aromatics, surface perturbations as indicated by spin-labeling spectra reflect changes in ion-binding properties of phospholipid headgroups, enzyme activity, and permeability changes.

From the standpoint of membranes, paraffins are tolerated up to a point, by shunting them into internal reaches of membrane, away from active metabolic processes. Our spin-labeling studies show lipid fluidity to be altered when tissue is exposed to paraffins. These changes are rather diffuse, however, and not associated with any one portion of the membrane interior. Such alterations however, could be operative in altering ion transport.

We contend, therefore, that aromatic-membrane interaction is of paramount concern. This is especially true when behavioral/physiological patterns are to be explained. Additional insight into these areas will necessitate further biophysical studies—both spin-labeling and broad-based electrophysiological studies.

FUTURE OUTLOOK ON SPIN-LABELING

Spin-labeling was first described only as recently as about 1968. Since then, a vast array of labels have been described. New instrumentation has evolved, and the technique has grown from a tool of limited application to one of major importance. For many biochemical and biophysical studies, the technique stands prominently above other methods. Applied to drug studies, pharmacology, immunology, cancer research, enzymology, and protein structure studies, spin-labeling promises to play an ever growing role. Environmentalists, biologists, zoologists, and food scientists now apply this tool to their studies. The future of spin-labeling is bright indeed.

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TELECONNECTIONS BETWEEN NORTHEASTERN PACIFIC OCEAN AND THE GULF OF MEXICO AND NORTHWESTERN ATLANTIC OCEAN

JAMES H. JOHNSON AND DOUGLAS R. MCLAIN[1]

ABSTRACT

Anomalous large-scale air-sea interactions that took place over the Gulf of Mexico and the Atlantic Ocean off the southeastern coast of the United States in the winter of 1957-58 caused a change of sea-surface temperatures from near average values to cold anomalies of nearly 3.0°C in some regions. Evidence suggests that the mechanism for the anomalous change in sea temperatures derived from frequent outbreaks of cold, North American continental air flowing over the Gulf and ocean waters with consequent anomalously high evaporation and sensible heat exchange. A contributing factor may have been divergence of surface waters with associated upwelling in regions of high cyclonic activity.

These severe outbreaks of cold continental air over the eastern seaboard may be related to air-sea interactions in the Pacific, thousands of miles distant. It is not clear what the full consequences of these events are to fisheries. The evidence which is available suggests that they are significant and warrant continued investigation.

In recent years large-scale air-sea interactions have captured the interest of a number of oceanographers and meteorologists. Motivated by the desire to develop and improve extended meteorological forecasts, Namias (1959, 1963, 1972, and in numerous other articles) has been one of the foremost investigators in studying these interactions. Most of his work has centered in the temperate latitudes of the northern hemisphere. Bjerknes (1966a, b, 1969) has studied large-scale interactions in the tropical Pacific Ocean, especially, processes associated with the El Niño phenomena. He has shown a relationship of fluctuations in the atmospheric Hadley circulation to large-scale anomalies of ocean temperatures. He suggests that an anomalously high heat supply in the equatorial Pacific, characterized by high equatorial ocean temperatures, intensifies the Hadley circulation providing more than normal flux of angular momentum to the mid-latitude belt of westerly winds, thus affecting the weather over the North American continent. He suggests that regular monitoring of sea temperatures in the eastern tropical Pacific is indispensable in long-range weather forecasting for North America.

Also motivated to develop improvements in long-range weather forecasting, Quinn (1972) has shown that large-scale interactions over the equatorial Pacific may affect the weather over the continental United States. He suggests that extensive dry-zone developments in the equatorial zone, which are associated with low sea-surface temperatures, may contribute to ridge development in the upper air circulation over the Northeast Pacific and, conversely, wet-zone developments (high equatorial sea temperatures) are associated with trough formation. Furthermore, he describes the effects downstream over the United States following development of these troughs and ridges and implies that now it may be possible, if these extreme developments are detected early enough, to make long-range weather predictions over North America.

Rowntree (1972), recently carrying out computer model studies, has confirmed that a sea temperature maximum in the tropical eastern Pacific leads to a persistent trough in the mid-latitude flow to the north.

Regions of the ocean particularly responsive to the overlying atmosphere lie to the east of large continental land masses. Jacobs (1951), Manabe (1957), Wyrtki (1966), and Hishida and Nishiyama (1969) have shown that in wintertime the temperate western Pacific Ocean loses large amounts of heat through evaporation and sensible heat exchange because of the overflow of cold, dry Siberian air masses. Parker (1968) pointed out a similar effect in the winter of 1966 in the northwestern Gulf of Mexico.

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This paper extends the findings of several of the authors mentioned above by describing the development of large-scale sea-surface temperature anomalies in the winter of 1957-58 in the Gulf of Mexico and off the U.S. eastern seaboard and suggests that these anomalies are associated with ridges and troughs in the upper air circulation. These, in turn, are associated with air-sea interactions in the Pacific. It further describes conditions in other winters where similar situations developed and suggests that changes in abundance and distribution of some fish populations both in the Pacific and Atlantic may be caused by events of this nature.

DATA SOURCES

Data used in heat budget calculations and in the description of sea-surface temperatures and anomalies were obtained from Tape Data Family 11 obtained by Fleet Numerical Weather Central and the Navy Oceanographic Office from the National Climatic Center, Asheville, N.C. This file contains merchant ship weather reports, some of which date back to 1854. Computer programs were developed to compute monthly averages by year of sea-surface temperature and heat exchange by 5° blocks.

Numerous studies have been made to determine the accuracy of sea-surface temperatures reported by merchant vessels in their weather reports. Saur (1963) found that in the Pacific the average injection temperature bias from that of a bucket temperature taken at the surface was about +1.2°F, and Franceschini (1955) noted similar results in the Gulf of Mexico. The latter suggested, however, that commercial vessel reports could be used for practical purposes such as meteorological and oceanographic research and for forecasting air mass modification over the Gulf. Because uncertainties remain concerning the relation between temperature at the sea surface and that at the injection intake depth of merchant vessels, no attempt was made in this study to apply a correction.

OBSERVATIONAL EVIDENCE OF ANOMALOUS AIR-SEA EVENTS

The Anomalous Winter of 1957-58

Charts of the height of the 700-mb (millibar) pressure surface (on the average about 10,000 feet above the surface of the earth in temperate latitudes) are particularly significant in air-sea interaction studies because the mass circulation of the atmosphere can be inferred from them including areas of cyclogenesis and movement of storms. Furthermore, mean 700-mb heights over the ocean are highly correlated with 700-mb temperatures, which in turn are measures of the vertical stability in the atmosphere over the ocean. For example, low temperatures at the 700-mb level, associated with negative 700-mb height anomalies, indicate instability in the atmosphere and loss of heat from the ocean through convective processes in the atmosphere.

O'Connor (1958) reported that the heights of the 700-mb surfaces during the winter of 1957-58 were very unusual. He reported the following three abnormalities in the 700-mb circulation in January 1958 (Figure 1) which persisted into February:

1. A trough in the east-central Pacific with 700-mb heights 550 feet below normal 700 miles south of Kodiak, Alaska,
2. A block in the Davis Straight where the 700-mb heights averaged 520 feet above normal and,
3. A trough in the southeastern United States (having 700-mb heights about 300 feet below normal) accompanied by strong northerly surface flow.

The trough along the eastern seaboard is particularly important. It suggests greater than normal penetration of cold continental air masses over the southeastern United States and adjacent waters. Indeed, the winter of 1957-58 will be remembered as one of the most severe of the century. Data taken at National Weather Service stations in the southeastern United States show slightly higher than normal air temperatures in November 1957 (Table 1). A small negative anomaly developed in December which increased substantially in January 1958 and reached a maximum in February. Monthly deviations of air temperature ranged up to 5.8°C below normal at stations along the northeast coast of the Gulf of Mexico.

Large negative sea-surface temperature anomalies also prevailed in February 1958 and were greatest in the northeastern Gulf in the same general area where shore station air temperature anomalies were highest (Figure 2). Stearns' (1964,

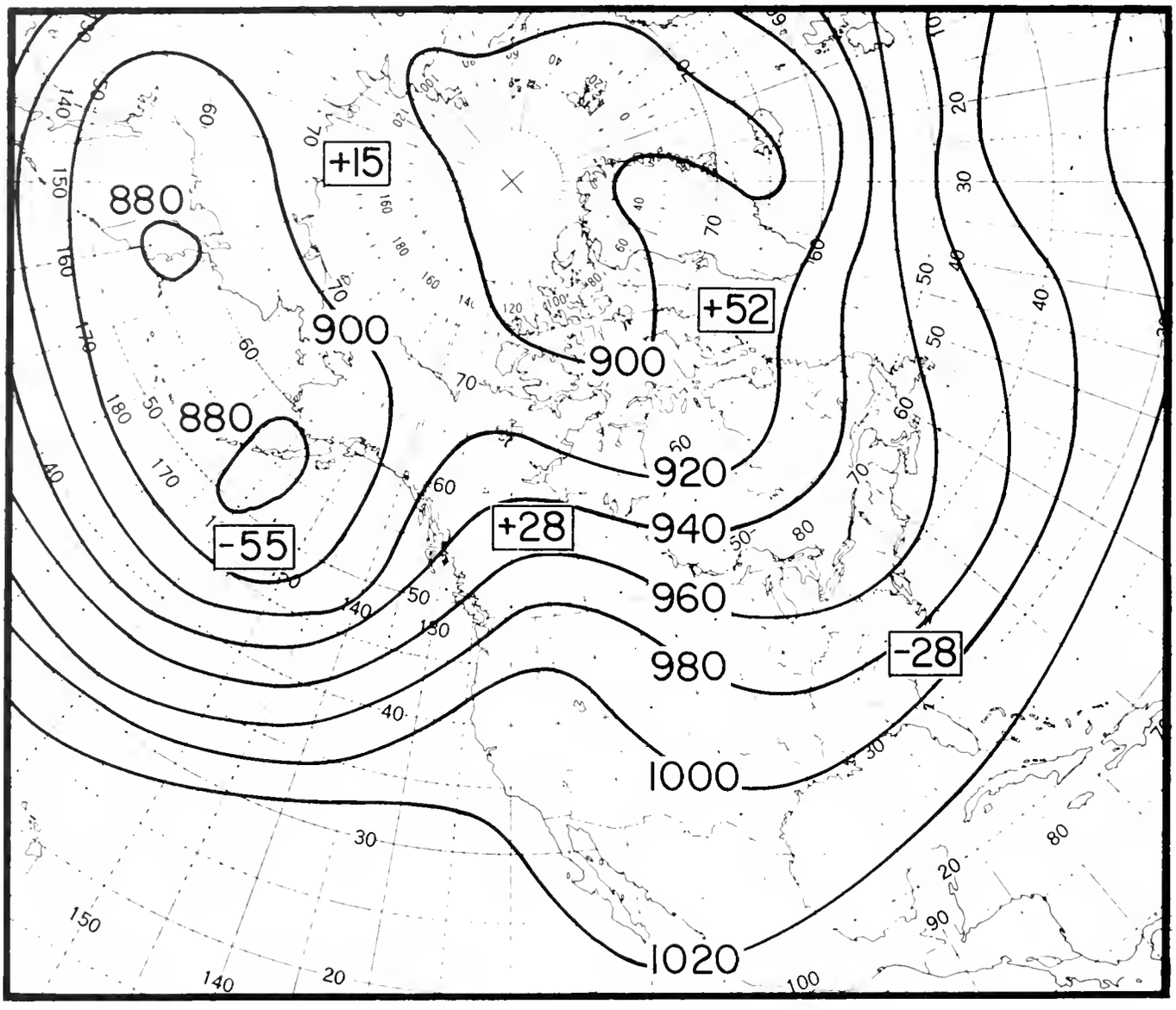

FIGURE 1.—700-mb heights and departures from normal, tens of feet, January 1958. Major departures are enclosed in boxes.

TABLE 1.—Monthly average air temperatures (°C) and departures from average (°C), November 1957-March 1958 at selected National Weather Service Stations.[1]

Station	November 1957		December 1957		January 1958		February 1958		March 1958	
	Temperature	Departure	Temperature	Departure	Temperature	Departure	Temperature	Departure	Temperature	Departure
New York, N.Y.	9.6	+1.6	4.8	+2.7	0.0	−0.4	−2.6	−2.8	4.5	−0.3
Wilmington, Del.	8.1	+0.6	3.3	+1.6	−0.7	−1.4	−2.6	−3.6	3.9	−1.9
Wilmington, N.C.	13.4	+0.2	9.6	+0.4	4.9	−3.8	4.9	−4.3	9.5	−3.1
Charleston, S.C.	15.4	+0.6	10.9	−0.3	7.0	−4.1	6.5	−5.0	11.8	−2.7
Savannah, Ga.	15.0	+0.8	10.3	−0.6	6.6	−4.3	6.8	−5.1	12.2	−2.6
Jacksonville, Fla.	18.5	+2.1	12.1	−1.5	9.1	−4.1	9.0	−5.2	15.1	−1.7
Miami Beach, Fla.	24.1	+0.8	19.9	−1.7	17.7	−3.4	16.6	−4.6	22.0	−0.3
Key West, Fla.	25.2	+1.6	20.3	−1.8	18.5	−3.0	17.5	−4.5	21.3	−1.8
Fort Myers, Fla.	22.0	+1.3	16.5	−2.1	13.9	−4.2	13.1	−5.6	18.8	−1.5
Pensacola, Fla.	16.2	+0.6	11.9	−0.9	8.3	−3.9	7.6	−5.7	14.3	−1.4
Mobile, Ala.	15.2	+0.4	11.2	−0.7	7.3	−4.2	6.9	−5.8	13.6	−1.6
New Orleans, La.	16.5	+0.5	12.9	−0.5	9.8	−3.5	9.1	−4.9	15.3	−1.7
Galveston, Tex.	17.2	−0.3	14.9	+1.3	10.7	−1.7	10.4	−3.6	14.3	−2.3
Corpus Christi, Tex.	17.3	−0.9	16.4	+1.5	12.8	−1.1	13.9	−1.8	15.7	−2.8

[1]Source: Local Climatological Data reports, U.S. Department of Commerce, National Weather Service.

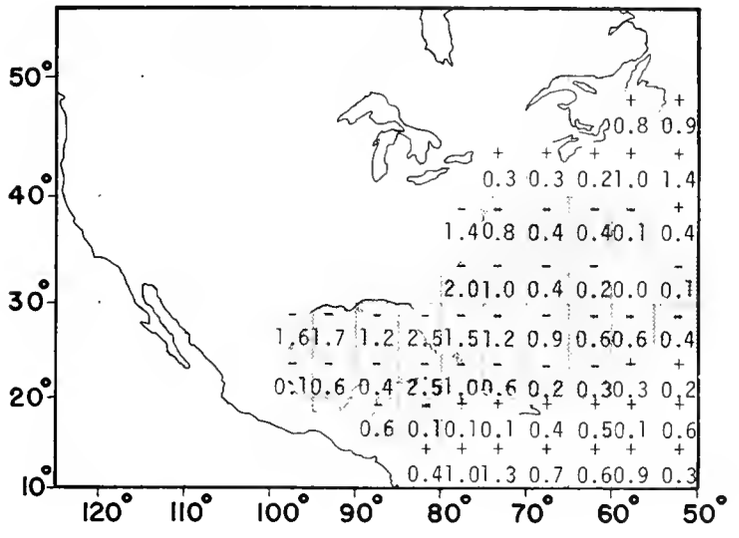

FIGURE 2.—Sea-surface temperature anomalies (°C) Gulf of Mexico and western Atlantic Ocean, February 1958. Shaded area colder than 20-yr (1948-67) mean.

1965) analysis of sea temperatures at coastal stations confirm the large winter sea temperature anomaly in coastal areas of southeastern United States. The extent of the anomaly was large, indeed, extending from below the Yucatan Straits northward throughout the Gulf to lat. 40°N off the eastern seaboard and to over a thousand miles offshore.

Important in this study is the anomalous change in sea temperatures in the winter of 1957-58 (Figure 3). The change from November to February shows that much higher than average cooling occurred over a broad expanse of the ocean during this winter. For example, the 1948-67 average change in sea-surface temperature in winter (November average - February average) is

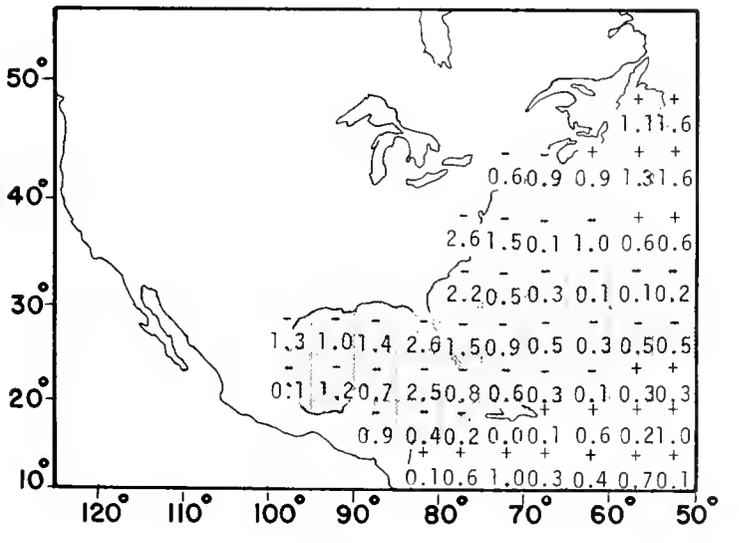

FIGURE 3.—Anomalous sea-surface temperature change (°C) November 1957 to February 1958. Shaded area indicates anomalous cooling.

about -2.7°C in the area lat. 25° to 30°N, long. 80° to 90°W. In the winter of 1957-58, however, the change in this area was -4.7°C—an anomalous change of -2.0°C.

Cause of Sea-Surface Temperature Change in the Winter of 1957-58

A variety of processes can cause changes in sea-surface temperatures. Some of these are horizontal and vertical advection and heat exchange at the air-sea interface.

In studies in the eastern Pacific Ocean, Clark (1972) has found that horizontal advective heat transfer processes in winter and spring have a greater effect in causing anomalous sea-surface temperature change than nonadvective processes. The latter have a greater effect in summer and fall. The area that he studied, however, was not subject to influence of a large continental land mass interacting with atmospheric circulation upstream from where heat exchange processes were calculated.

Horizontal advection into the Gulf of Mexico is mainly through the Yucatan Straits. Sea-surface temperature anomalies in these Straits ranged from -0.2°C to +0.4°C (Table 2) for a year preceding the maximum development in February 1958 of the severe cold anomalies in the Gulf of Mexico and along the eastern seaboard. This clearly suggests that horizontal advection was not the cause of the development of the cold anomalies.

Klein (1958) noted that the intensification of blocking in the 700-mb circulation in the northwest Atlantic in the winter of 1957-58 was associated with frequent outbreaks of cold air in the

TABLE 2.—Sea-surface temperatures and anomalies (°C) in 1° square (long. 85° to 86°W and lat. 21° to 22°N) in Yucatan Straits.

Date	Sea temperature °C	Anomaly °C
1957:		
January	26.2	−0.2
February	26.6	+0.3
March	26.4	−0.1
April	27.0	+0.1
May	28.0	+0.2
June	28.7	0.0
July	29.3	+0.1
August	29.7	0.0
September	29.5	−0.1
October	28.8	−0.2
November	28.0	0.0
December	27.5	+0.4
1958:		
January	26.2	−0.2
February	25.6	−0.7

eastern two-thirds of the United States. The contrast between this cold air and the air heated by the Gulf of Mexico and western Atlantic waters led to baroclinic deepening of coastal storms. In these regions of cyclonic activity, vertical advection may have caused some cooling through divergence of surface water and consequent local upwelling. Leipper (1967) has shown that hurricane Hilda, passing over the Gulf of Mexico in the early fall of 1964, indeed did cause significant cooling of surface waters through upwelling processes. However, the large area covered by anomalously low sea-surface temperatures in the winter of 1957-58, and other factors such as the frequent cold outbreaks over the entire eastern seaboard and the fact that the sea temperature anomalies appeared to occur over large areas contemporaneous with the overflow of cold air, suggests that the high rate of sea surface cooling was due to anomalously high loss of heat through evaporation and conduction of sensible heat.

To test this supposition formulae for calculation of the heat exchange at the air-sea interface have been employed. Laevastu (1965), Seckel (1962) and many others have provided these formulae. In this study the procedures for calculation of the energy exchange as presented by Johnson et al. (1965) are used. It is not the intent here to review the accuracy of the various techniques for estimating air-sea energy exchange. Because of the possible inaccuracies of input data and of the formulae, the exchange values should be viewed with caution and should be considered only as relative indices of the magnitude of energy flux at the air-sea interface. They appear, however, to be sufficiently accurate to permit detection of large-scale seasonal and nonseasonal variations.

The equation for the heat exchange at the air-sea interface is

$$Q_T = Q_I - Q_R - Q_B - Q_E - Q_H$$

where:

Q_T = Net heat gained or lost at the sea surface
Q_I = Incident solar radiation corrected for cloud cover
Q_R = Reflected radiation
Q_B = Back radiation
Q_E = Evaporation
Q_H = Conduction of sensible heat.

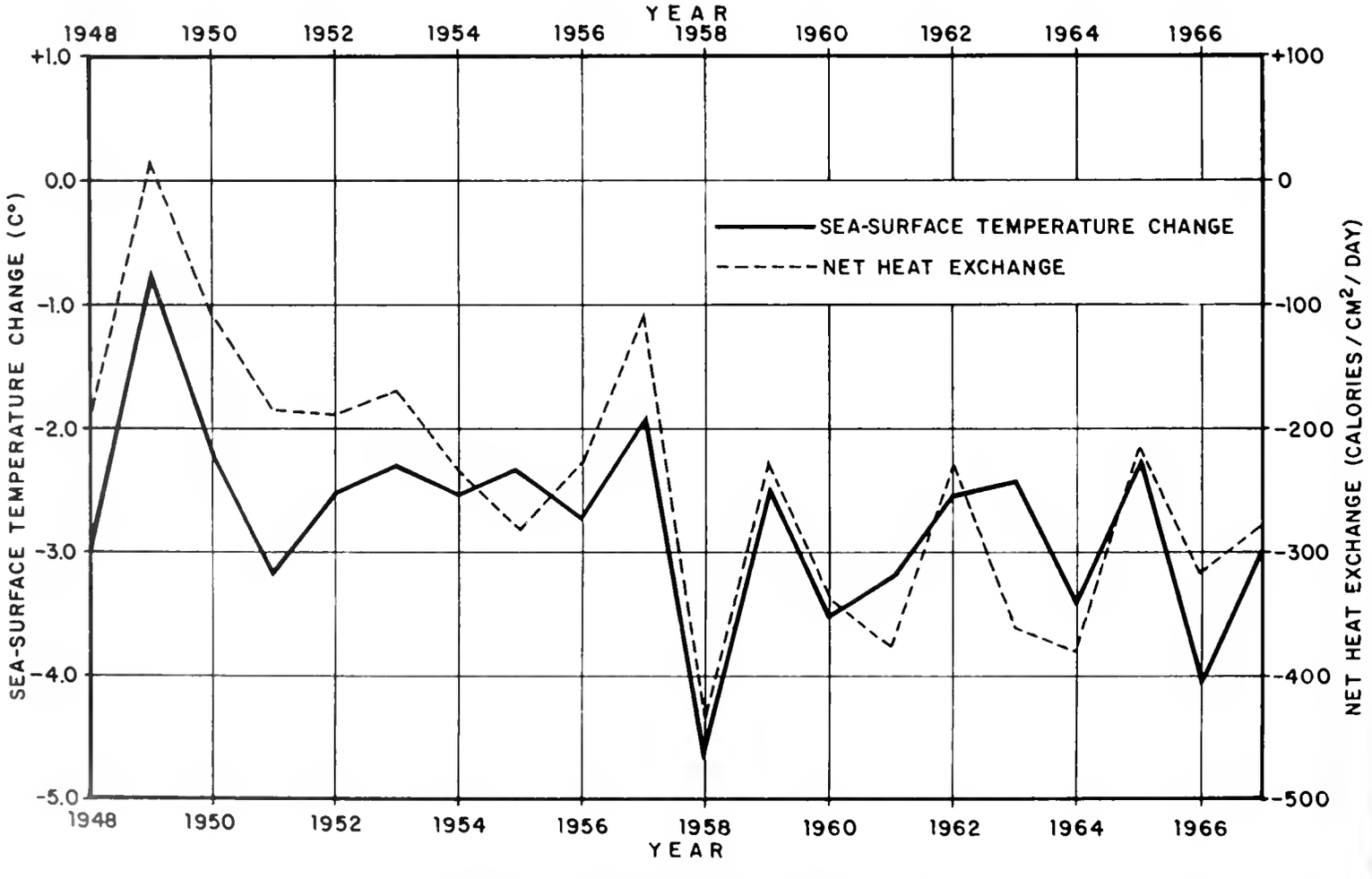

FIGURE 4.—Relation between net heat exchange at air-sea boundary and sea-surface temperature change winters of 1948-67 in the area bounded by long. 80° to 90°W and lat. 25° to 30°N.

The relation between Q_T and sea-surface temperature change in the winters of 1948-67 in the northern Gulf of Mexico is significant (Figure 4). Particularly noteworthy is the large net heat loss in the winter 1957-58 accompanied by the large sea-surface temperature change. The decrease in Q_I reaching the sea surface accounted for about 11% of the anomalous heat loss and increased Q_B about 12%. Q_E and Q_H, however, clearly stand out as significantly more important than the other heat budget elements in contributing to the large net loss of heat. Q_E contributed 57% of the anomalous heat loss and Q_H, 20%.

Data are not available that indicate the depth to which the sea temperature anomaly extended. One might speculate that it should extend throughout the mixed layer which on the average in the area of study is about 80 m in winter (Robinson 1973). For the three months December 1957-February 1958, the anomalous heat loss in the Gulf of Mexico in the area of lat. 25° to 30°N, long. 80° to 90°W was approximately 19,000 cal/cm^2. This should reflect an anomalous change in water temperature of about -2.4°C throughout the mixed layer which is very close to the anomalous -2.0°C change observed at the surface.

Though the immediate cause of the development of the cold anomaly appears to have been the flow of cold continental air over the Gulf and western Atlantic, the more general cause may have been due to large-scale interactions over the North Pacific Ocean. A large positive sea temperature anomaly appeared in the eastern Pacific in late 1957 and persisted throughout 1958 (Sette and Isaacs 1960) (Eber 1971). Namias (1959) explains that the contrast of anomalous warm ocean temperatures to the east of cold ocean temperatures, which was the situation in 1957 in the eastern Pacific, provided abnormal feedback in heat exchange processes to the atmosphere which provided the additional baroclinicity upon which cyclones could feed. This cyclogenesis helped maintain the deep Pacific trough south of Kodiak Island which was abnormally intense by the late fall of 1957. Downstream from this area of activity, a responsive ridge developed in the western United States (evident from Figure 1) and a deep trough along the Atlantic seaboard. This distribution is also consistent with the statistical findings of O'Connor (1969) who noted that when an anomalously deep trough forms in the 700-mb circulation in the east central Pacific, the chances for a trough off the eastern seaboard are high.

Air-Sea Interactions in Other Years

It is tempting to argue that events such as the 1957-58 occurrence described above occur so seldom that it is not worth the effort to study them and their effects on fisheries. Study of years when extreme conditions prevail, however, provides hints of the processes that are occurring in the natural system in other years. Definitive findings through study of more normal years are often difficult to obtain because processes involved may be obscured by the subtle interactions of a number of factors.

The interaction of the type described above may not be as infrequent as one might believe. A situation similar to the winter of 1957-58 seems to have occurred in the winter of 1939-40. O'Connor (1958) noted very cold air temperatures along the eastern seaboard in the winter of 1939-40 which were as intense as those in 1957-58. Although sea temperature records are sparse for winter months (December through February) of 1939-40, what data are available show an extremely cold and widespread anomaly in the Gulf of Mexico (Figure 5) and along the eastern seaboard where temperature anomalies of 5° and 6°C below normal were observed in February 1940.

Further analysis of these large-scale air-sea interactions suggest a possible relation between equatorial Pacific Ocean temperatures and those in the Gulf of Mexico. Bjerknes (1969) has shown that in the winters 1957-58, 1963-64, and 1965-66 high sea-surface temperatures prevailed in the eastern tropical Pacific Ocean. This is characteristic of El Niño years which are best known for the invasion of warm water off the Peruvian coast and effects on the anchoveta populations there. It is known also that in the winter of 1939-40 a severe El Niño was present in the eastern Pacific. In all of these winters cold sea-surface temperature anomalies prevailed in the Gulf of Mexico (Figure 5). There appears, then, to be a relation between sea temperature anomalies in the equatorial Pacific and anomalies in the Gulf of Mexico, that is, negative sea-surface temperature anomalies in the Gulf and western Atlantic in some situations may be related to positive sea temperature anomalies in the eastern equatorial Pacific through processes described by various authors mentioned previously and those described in this paper.

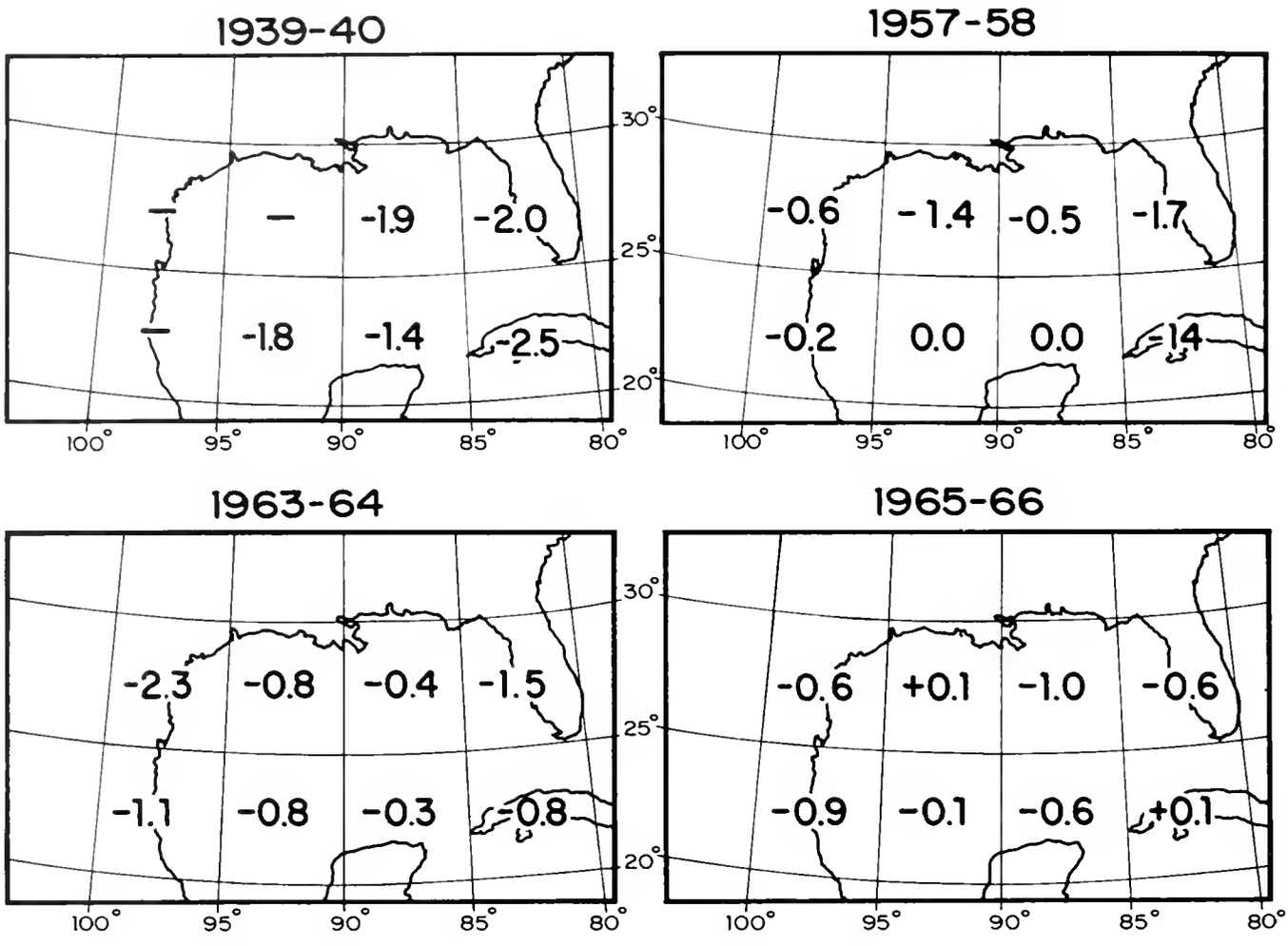

FIGURE 5.—Sea-surface temperature anomalies (°C) in the Gulf of Mexico for selected winters.

During the recent 1972-73 El Niño, however, a situation occurred where this relation did not exist. A trough did not develop off the eastern seaboard until late winter and was short-lived in nature. During most of the winter it was situated over the central United States. Consequently, the flow of cold, continental air over the Gulf of Mexico, especially in the eastern Gulf, was not as intense as in previous El Niño years, and thus not as much cooling of surface waters occurred in the Gulf of Mexico.

A situation opposite to the cold winters along the eastern seaboard described above occurred in the winter 1948-49. Very little cooling occurred in the waters of the Gulf, and the net heat exchange at the air-sea interface likewise was small (Figure 4). The sea-surface temperature anomaly patterns in the winter of 1948-49 compared to the winter 1957-58 are remarkably opposite in sign and magnitude (Figure 6). Whereas, cold sea temperature anomalies prevailed in the latter winter off the southeastern United States, widespread warm anomalies were present in the winter 1948-49. In this winter a distinct ridge developed over the eastern United States in the 700-mb heights, a trough over the western U.S., and another ridge in the northeast Pacific (Figure 7) which is consistent with the hypothesis given by Quinn (1972) and by the findings of Namias.

Namias (1972) suggested that the 1957-58 winter marked the beginning of a new climatic regime in the northern hemisphere. He shows, for example, that the winter mean air temperature at Atlanta, Ga. for the decade 1948-57 was about 5°F higher than the following decade. A trend is also noted in decadal differences of sea temperatures in the Gulf of Mexico. The 1948-57 decade average of February sea temperature was about 1.0°C higher than the 1958-67 February average. Somewhat lower sea temperatures generally prevailed along the entire eastern seaboard in the 1958-67 decade compared to the one preceding.

Sea temperatures and circulation off the U.S. west coast also showed a climatic change. Huang (1972) calculated that southward transport in the general area of the California Current from San Diego to long. 150°W in the period 1958-69 was less than in the previous decade. He showed further that the California Current annual sea temperatures were as much as 1.4°C above normal in the

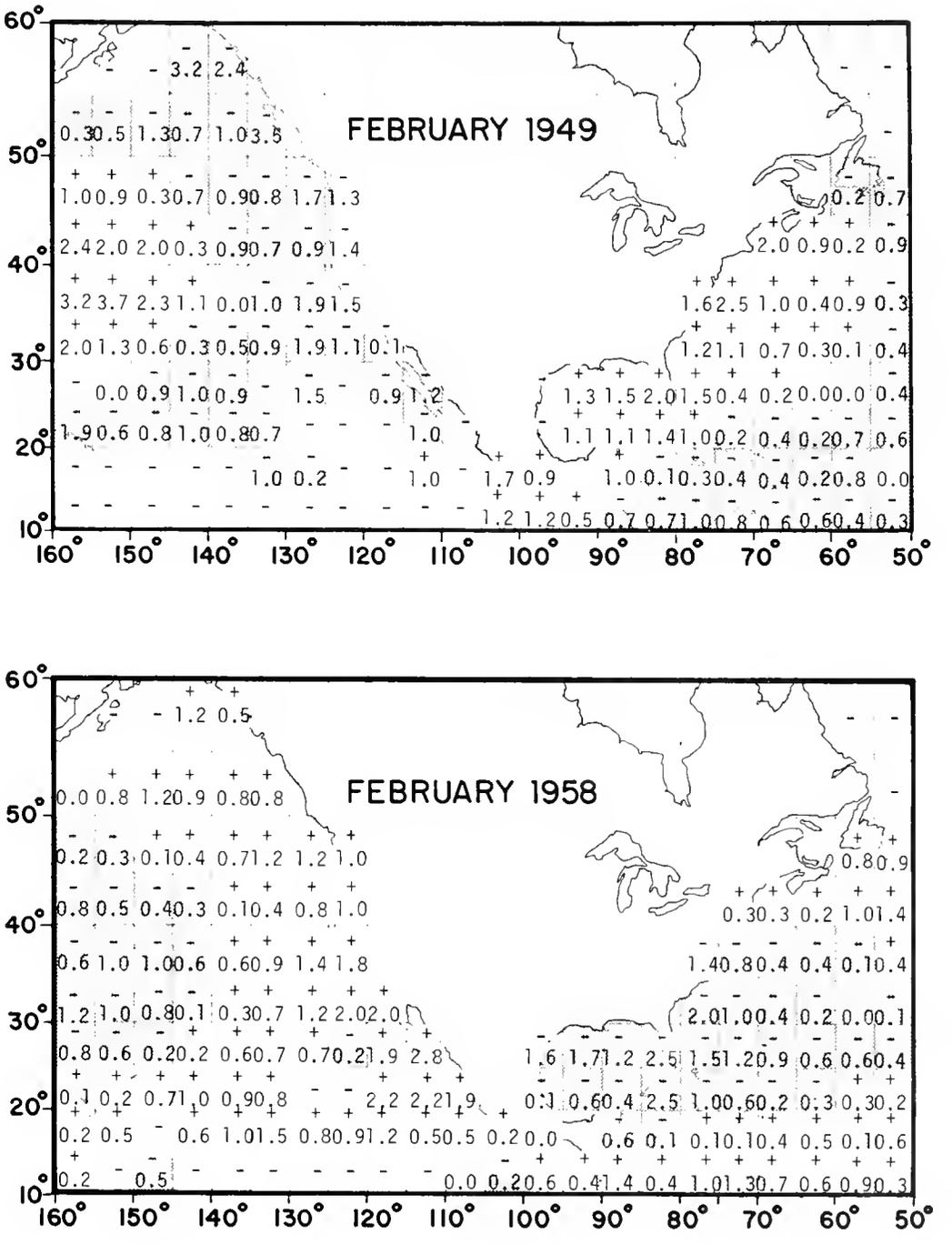

FIGURE 6.–Sea-surface temperature anomalies (°C) February 1949 and February 1958 in eastern Pacific and western Atlantic oceans. Shaded areas colder than 20-yr (1948-67) mean.

1958-69 period and the seasonal temperature departure in winter was greater than 2°C in some places. Apparently, this was caused by less advection of cold subarctic water southward.

DISCUSSION

The authors have attempted to show that development of sea-surface temperature anomalies in the Gulf of Mexico and along the U.S. eastern seaboard in wintertime may be related to the origin of the overlying air masses. In situations where trough development occurs in the upper air circulation over the eastern United States, cold continental air from North America is likely to flow over the Gulf and waters off the eastern seaboard causing excessive loss of heat through evaporation and conduction of sensible heat. Conversely, in situations where a ridge develops, warm air masses predominate, and loss of heat from the ocean is retarded. In fact, as Figure 4 indicates, the water in some winters may cool very little. Furthermore, an attempt has been made to show that the development of these

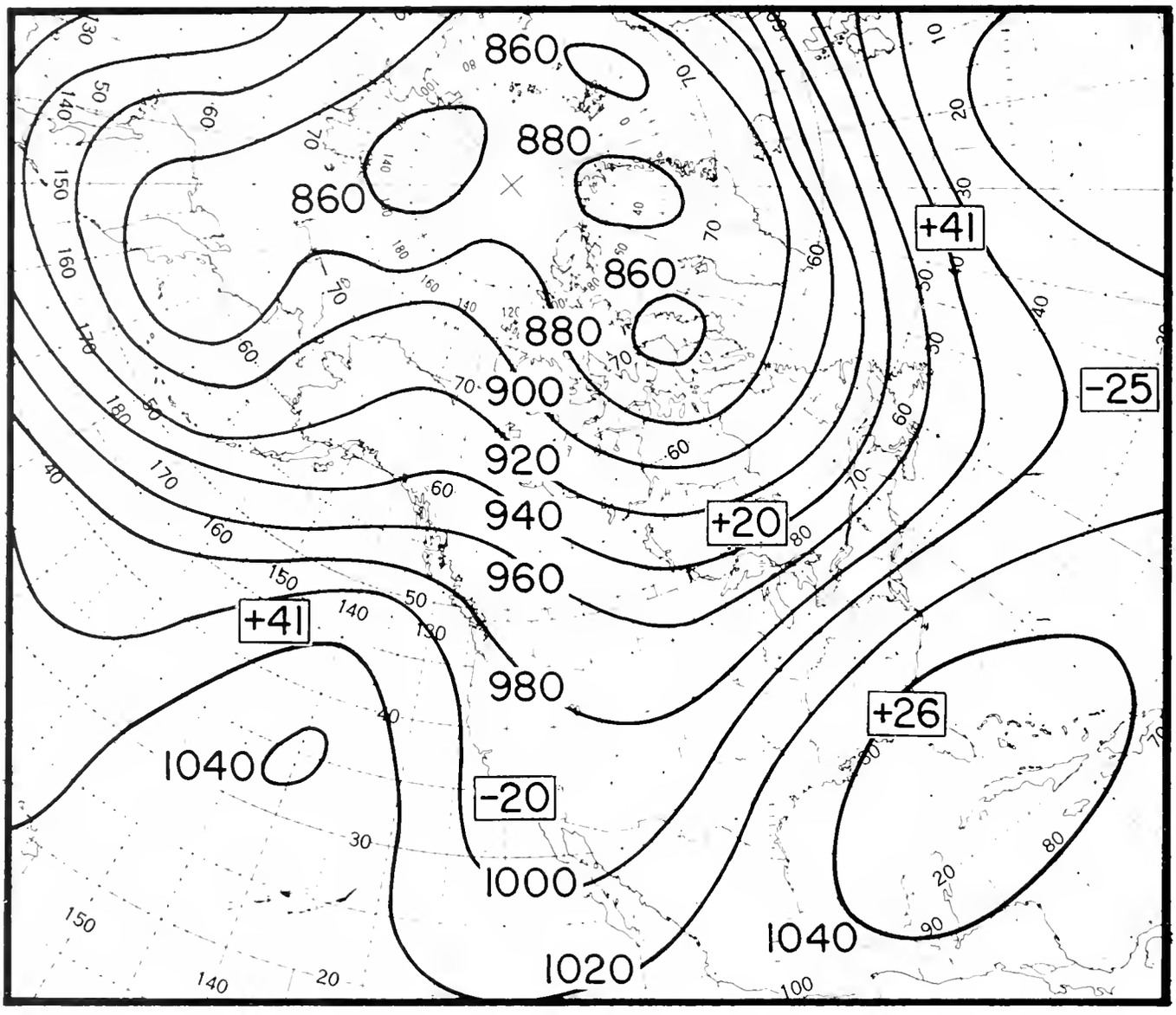

FIGURE 7.—700-mb heights and departures from normal, tens of feet, January 1949. Major departures are enclosed in boxes.

troughs and ridges in the upper air circulation may have been related to air-sea interaction processes in the Pacific Ocean.

It is interesting to speculate on the physical consequences following the development of a large-scale cold sea-surface temperature anomaly in the winter of 1957-58 in the Gulf of Mexico and western Atlantic. It is quite possible that further investigation will show differences of flow in the Gulf Stream. The fact that the anomaly developed in winter suggests that the water to the depth of the thermocline may be affected. A large cold mass of water of this type alters the density distribution over a large area and thus alters the surface circulation. The authors have noted an apparent drift of the anomaly away from the U.S. east coast northeastward until the early summer of 1958 when the surface anomalies were obscured, although it may be quite possible and even likely that the deeper waters were still colder than usual. The effects on Europe of this cold water mass after a period of eastward drift can only be speculated at this time. The fact that the anomaly could be traced for a time following its formation suggests an interesting possibility for further research.

The biological consequences of such large-scale air-sea interactions are even more complex. The effect of the warm sea temperature pool in the eastern Pacific in 1957 and 1958 on fish populations is well documented by Radovich (1961). Southern species were found much farther north than normal in the temperate northeastern Pacific apparently in response to the warm sea temperatures. In the western Atlantic and Gulf the effects of the cold anomaly were less evident although there is a suggestion from the work of Williams (1969) that the shrimp populations were affected.

Williams believes that catches of penaeid shrimp in the southeastern United States fluctuate in such a way as to suggest dependence on coastal temperatures. His studies show an apparent association of good catches with warm years and poor catches with cold years. The shrimp season following the cold winter of 1957-58 was particularly poor in several areas. His indices of cold and warm years are derived from coastal air temperatures which probably are a reasonable indicator of sea temperature variation in estuarine and coastal waters. Williams believes it might be possible to use winter coastal air temperatures as predictors for the succeeding year's catch when better definition and measure of fishing effort are available.

These hints of biological consequences of large-scale air-sea interactions point out possibilities for future research. Clearly, investigations of this nature will require a cooperative effort among meteorologists, oceanographers, and fishery biologists.

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GEOGRAPHIC AND HYDROGRAPHIC DISTRIBUTION OF ATLANTIC MENHADEN EGGS AND LARVAE ALONG THE MIDDLE ATLANTIC COAST FROM RV *DOLPHIN* CRUISES, 1965-66

ARTHUR W. KENDALL, JR.[1] AND JOHN W. REINTJES[2]

ABSTRACT

Atlantic menhaden, *Brevoortia tyrannus*, eggs and larvae were collected during eight ichthyoplankton cruises of the RV *Dolphin* from December 1965 to December 1966. On each cruise tows were made with a Gulf V plankton net at 92 stations along 14 transects from the coast to the edge of the continental shelf from Martha's Vineyard, Mass., to Cape Lookout, N.C. Larvae resulting from a protracted spawning season were taken throughout the year. Eggs were taken over the middle of the shelf in fall. Seasonal shifts in geographic pattern of larvae indicated spawning started in summer off New Jersey and New York, became widespread in the Middle Atlantic Bight in fall, and continued into winter off North Carolina. Larvae were equally distributed in shallow (0-15 m) and deep (18-33 m) tows during night and day. Larvae occurred over a water temperature range from 0° to 25°C and a salinity range of 29 to 36‰. Seasonal distribution of larvae suggests some of the annual variation in year classes may be due to cold-related mortality of larvae entering middle Atlantic estuaries in late fall.

Along the Atlantic coast spawning and early development of many fishes occur in the ocean. The distribution of early stages of most coastal species is inadequately known. Personnel of the Sandy Hook Marine Laboratory designed a program to determine the spawning times and localities of migratory coastal fishes through a series of cruises off the Atlantic coast from Martha's Vineyard, Mass., to Cape Lookout, N.C. From December 1965 to December 1966 eight survey cruises were conducted to collect fish eggs, larvae, and juveniles. These cruises, together with data on juvenile and adult distribution, provided information on the oceanic life history of most of the commercial and sport fishes of the region.

Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), an important commercial and forage fish, was among the species collected during this survey. The early life history of menhaden has puzzled scientists since early accounts by Baird (1873) and Goode (1879). The eggs and larvae were first described by Kuntz and Radcliffe (1917). After early development at sea, the larvae enter estuaries along the coast where they metamorphose into juveniles. June and Chamberlin (1959) concisely review the estuarine stage of menhaden.

The seasonal cycle of menhaden spawning has been inferred from ovary studies by Higham and Nicholson (1964). From Maine to eastern Long Island ovarian development starts in May and reaches a peak in October. The seasonal occurrence of sexually mature fish begins in New Jersey and Delaware in April, continues sporadically in summer, and reaches a peak in October. Around Cape Hatteras maturing fish were taken mainly in late fall; some are found as late as March.

Atlantic menhaden eggs and larvae have been collected offshore and in estuarine waters along the Atlantic coast (Table 1). These collections show a pattern similar to that found by Higham and Nicholson (1964). Spawning off New England occurs in late spring and early summer and again in early fall. Off the middle Atlantic coast eggs and larvae are found in late fall and in spring. Off North Carolina young occur in winter and spring.

Inlet and estuarine studies have collected larval menhaden as they emigrate from the ocean (Table 1). The time of entry varies considerably along the coast and from year to year in the same estuarine areas. In some years entry occurs in late fall, before lowest temperatures are reached. In other years entry occurs primarily as temperatures are warming in early spring. Larvae in the estuaries are apparently killed if winter temperatures fall below 3°C (Reintjes and Pacheco 1966). Emigration from the estuaries varies from late August in the north to January in the south, with some

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TABLE 1.—Collections of menhaden eggs and larvae, east coast of United States.

Reference	Sampling period: Years	Sampling period: Months	Sampling area	Occurrences
Open ocean				
Marak and Colton 1961	1953	Mar.-June	Georges Bank-Gulf of Maine	June—1 egg, off Martha's Vineyard
Marak, Colton, and Foster 1962	1955	Feb.-May	Georges Bank-Gulf of Maine	May—eggs, 130 km off Nantucket
Marak, Colton, Foster, and Miller 1962	1956	Feb.-June	Georges Bank-Gulf of Maine	June—larvae, off Woods Hole
Reintjes 1961	1953-54	all	Cape Hatteras-Florida	Dec.-Feb.—eggs Dec.-Mar.—larvae, off North Carolina
Massmann et al. 1962	1959-60	all	Off Chesapeake Bay	Nov.-Apr.—larvae
Reintjes 1969	1966	Dec.	Off North Carolina	Dec.—eggs, patch of several thousands
Bays and open sounds				
Bigelow and Schroeder 1953			Gulf of Maine	Oct. 1900—young fry, Casco Bay
Kuntz and Radcliffe 1917			Near Woods Hole, Mass.	Oct. 1915—eggs and larvae, Nantucket Sound Aug.—eggs, off Gay Head July—larvae, Woods Hole Harbor
Hildebrand and Schroeder 1928	1912-22		Chesapeake Bay	Jan.-May—large larvae
Pearson 1941	1929	May-Oct.	Lower Chesapeake Bay	May—larvae
	1930	Apr.-Dec.	Lower Chesapeake Bay	Apr.—larvae
	1931	Jan.-Mar.	Lower Chesapeake Bay	
Perlmutter 1939	1938	May-Oct.	Around Long Island	May-Oct.—eggs May-Sept.—larvae
Merriman and Sclar 1952	1943-46	all	Block Island Sound	Fall—larvae (see Wheatland 1956)
Wheatland 1956	1952-53	all	Long Island Sound	June-Oct.—eggs June and Sept.-Dec.—larvae
Richards 1959	1954-55	all	Long Island Sound	May-Oct.—eggs June-July and Sept.-Dec.—larvae
Deubler 1958	1955-57	Dec.-Apr.	Bogue Sound, N.C.	Winter and spring—larvae, common
Herman 1963	1957-58	all	Narragansett Bay	May-Aug. and Oct.—eggs June, July and Oct.-Feb. (most in Oct.)—larvae
Croker 1965	1960-61	all	Near Sandy Hook, N.J.	May-June—eggs Nov.-Dec.—larvae
Dovel 1971	1963-67	all	Chesapeake Bay	Spring and summer near Solomons, Md.—eggs Mar.-June and Nov.—larvae, upper Chesapeake Bay
Inlets				
Reintjes and Pacheco 1966	1955-61	Sept.-June	Indian River Inlet, Del.[1]	Oct.-May—larvae, month of peak occurrence varied with year from Dec.-Feb.
de Sylva et al. 1962	1956-58	all	Indian River Inlet, Del.[1]	Nov.-May—larvae
Tagatz and Dudley 1961	1957-60	all	Beaufort Inlet, N.C.	Jan. and Apr.-May—larvae
Lunz 1965	1964	Jan.-Mar.	Several South Carolina inlets	Feb.-Mar.—larvae
Lewis and Mann 1971	1966-68	Nov.-Apr.	Bogue and Beaufort inlets, N.C.	Nov.-Apr.—larvae
Smaller estuaries				
Warfel and Merriman 1944	1942-43	all	Morris Cove, Conn.	July-Nov.—larvae
Massmann et al. 1954	1950-52	Mar.-Oct.	Five Virginia tidal rivers	Apr.-May—larvae, brackish water
Pacheco and Grant 1965 Reintjes and Pacheco 1966	1955-61	Sept.-June	White Creek, Indian River, Del.	Nov.-June, most Feb.-June—larvae
Tagatz and Dudley 1961	1957-60	all	Neuse River, N.C.	Jan.-June and Sept.—larvae
Pearcy and Richards 1962	1959-60	all	Mystic River, Conn.	June-July—larvae
Dovel 1967	1965-66	all	Magothy River, Md.	Mar.—larvae
Wilkens and Lewis 1971	1967-69	all	White Oak River, N.C.	Jan.-Apr.—larvae

[1]Larvae emigrating from ocean.

juveniles overwintering in southern estuaries. Fish range from 50 to 160 mm when they leave the estuaries (June and Chamberlin 1959).

Recently Mansueti and Hardy (1967) amplified the descriptions of young menhaden and Reintjes (1969) reviewed the biology of the species.

This paper describes the occurrences of menhaden eggs and larvae in the *Dolphin* surveys and relates these findings to daylight, temperature, salinity, and depth, and to our understanding of menhaden early life history.

PROCEDURES

The eight ichthyoplankton cruises were made at approximately 6-wk intervals from December 1965 to December 1966 (Clark et al. 1969). On each cruise 92 stations were located along 14 transects from Martha's Vineyard to Cape Lookout (Figure 1). Stations were closely spaced inshore (9.3 km) along the transects and farther apart (27.8 km) offshore. The order that the transects were run and the time during the 24-h workday that stations were occupied varied among the cruises.

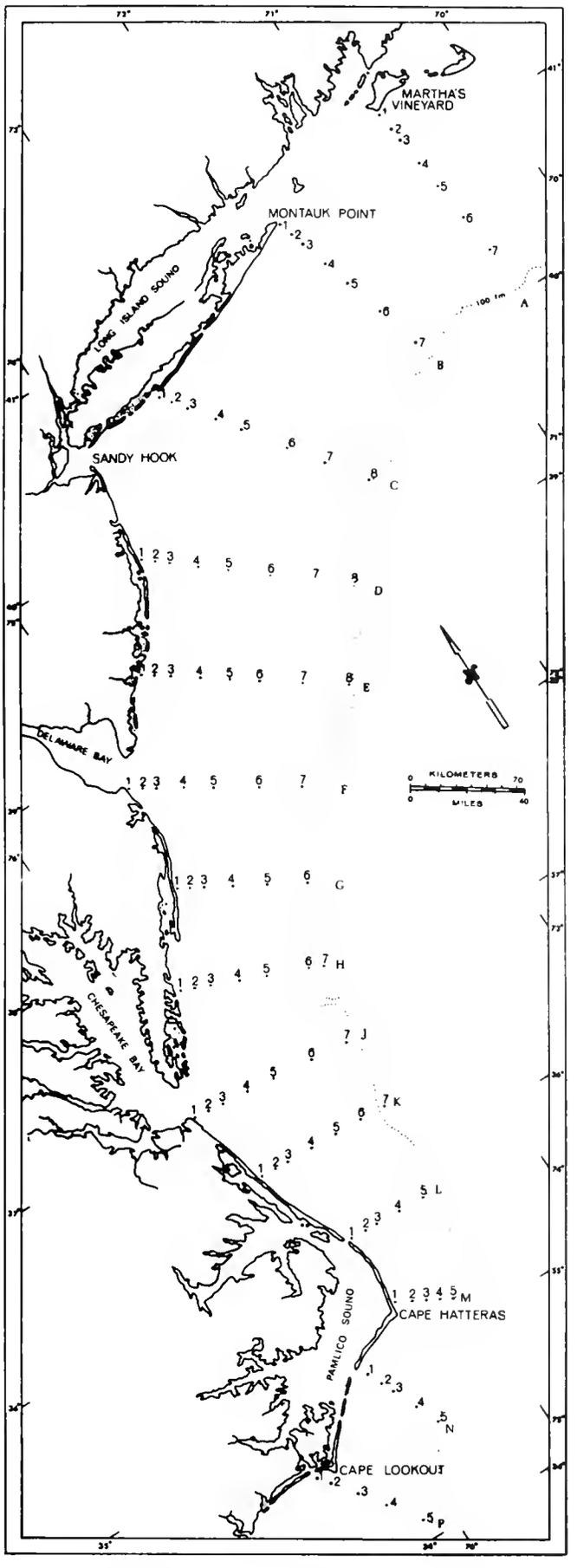


FIGURE 1.—RV *Dolphin* survey, 1965-66. Locations of transects and collecting stations.

Gulf V plankton samplers with 0.4-m openings and 0.52-mm wire mesh were towed for 30 min at 5 knots (2.6 m/s) in step-oblique tows at each station. Two nets were fished simultaneously at six 3-m depth intervals, from separate warps, one shallow (0-15 m) and one deep (18-33 m), where water depth permitted. In shallower water fewer depth intervals were sampled for longer time periods. Plankton samples were preserved in 4% buffered formaldehyde solution and brought to shore for sorting. Supplementary data collected at each station included water temperature and salinity with depth. A scaled-down Cobb midwater trawl was towed at about half of the stations to collect juvenile fishes.

Fish eggs and larvae were separated from the plankton in the laboratory. Clupeoid larvae were distinguished by their slender body, long gut, sparse pigment, and short dorsal and anal fin bases (Table 2), and separated from other larvae.

Several other fishes whose long slender larvae resemble clupeoids occur in the area but they differ in certain features. Lizardfish larvae have a large finfold, an adipose fin later in development, and a row of 6 to 12 paired dark patches ventrally along the body (Anderson et al. 1966). Other elongate salmoniform larvae generally have an adipose fin, photophores often, and oval or stalked eyes. Sand lance larvae have little pigment, but the dorsal and anal fins extend most of the length of the body (Norcross et al. 1961). Blennioid larvae have a short gut, with the anus forward of midlength of the body, and long dorsal and anal fin bases. Other larvae are excluded by myomere counts which fall outside the range for clupeoids (38-55) or by other distinctive characters not found on clupeoid larvae.

TABLE 2.—Distinguishing features of Atlantic coast clupeoid larvae.

Character	Distinguishing features
Body shape	Body slender and elongate, the greatest body depth less than 20% of total length. Anus in posterior third of body.
Fin positions	Dorsal — single, short, about two-thirds way back along body; no adipose fin. Anal — posterior to at least part of dorsal fin, not confluent with caudal fin. Pelvics — abdominal, at about midlength on the body.
Meristic counts	Myomeres (vertebrae) — 38-55. Dorsal fin rays — 9-22. Anal fin rays — 10-30. Principal caudal fin rays — 10 + 9.
Pigmentation	Little pigment except ventrally. Ventral pigment — small spots on throat, along the gut, and at base of caudal fin.
General	Eyes round, in orbits, not stalked. Gut straight with annular folding of the intestine.

Identification of menhaden eggs and larvae among the four other clupeid genera and two engraulid genera along the North American east coast was facilitated by published illustrations and descriptions (Kuntz and Radcliffe 1917; Mansueti and Hardy 1967; Houde and Fore 1973) and reported spawning areas and times (Reintjes 1961; Higham and Nicholson 1964). Menhaden larvae collected north of Cape Lookout are presumed to be *Brevoortia tyrannus*, since *B. smithi* occurs mainly farther south and spawns inshore (Reintjes 1962). The areas of larval occurrence of menhaden overlap Atlantic herring, *Clupea harengus harengus*, in the north, and round herring, *Etrumeus teres;* Spanish sardine, *Sardinella anchovia;* and Atlantic thread herring, *Opisthonema oglinum*, in the south.

Clupeoid larvae less than 8 mm are difficult to distinguish because the median fins and other characters are not formed. However, pigmentation, body shape, and gut length are helpful in small larvae. Among clupeoid larvae the stage of development at a particular size and area of capture are helpful. For each comparable stage of larval development, menhaden are larger than anchovies, Spanish sardine, and Atlantic thread herring, and smaller than Atlantic herring. Only round herring show the same development with size as menhaden but are easily distinguished by the relative length of the snout at all sizes.

Menhaden were counted and total length measurements of larvae less than 12 mm long were made to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope; those longer than 12 mm were measured with dividers and a steel rule or dial calipers to the nearest 0.5 mm. Samples containing more than 50 fish were usually randomly subsampled before measuring. To get a subsample of 25-50 larvae, the sample was floated in formaldehyde solution in a 150-mm petri dish scribed into quarters with two diameters; a random half or quarter of the dish was chosen for measuring. The process was repeated with the chosen fraction with samples of more than 200 specimens. When larvae showed slight damage, such as broken caudal rays, measurements were adjusted to approximate total length. Larvae identifiable, but too mutilated to be measured, were counted. For geographic distribution analysis, numbers of larvae at each station were adjusted to a standard tow as in Smith (1973) and Fahay (1974).

RESULTS

Geographic Distribution of Larvae

Menhaden larvae are more widely distributed than any other clupeoid in the northwest Atlantic. Larvae have been reported from Maine to Mexico in oceanic, estuarine, and fresh waters. South of Cape Hatteras Atlantic menhaden spawn in the cooler months (October to June), while along the Middle Atlantic states they spawn during the warmer months (June to November). Seasonal occurrences of larvae followed the annual north-south migration of adults. Small larvae were first collected in June near Delaware Bay. By October larvae were present from southern New England to Chesapeake Bay. In late fall they were found from New York to Cape Lookout. During the winter and spring larger larvae were present from Chesapeake Bay to Cape Lookout.

Small menhaden larvae were collected throughout the year except in late spring, indicating nearly continual spawning (Figure 2). Menhaden hatch at about 3 mm (Mansueti and Hardy 1967), but we caught few less than 5 mm. This was probably due in part to our inability to identify with certainty small larvae and in part to their fragile, slender form which caused them to be extruded from our nets. The largest larvae we collected were 30 mm, about the size at which they enter estuaries and transform into juveniles (Lewis et al. 1972).

It is not reasonable to attempt to determine a growth rate for menhaden larvae from our data. Small menhaden less than 8 mm were collected from June through February. Thus, spawning took place in our sampling area for 6 mo of the year. This protracted spawning season and probable geographic movements of larvae preclude the possibility of determining growth rate from this survey.

Data associated with collections of menhaden larvae are presented in the Appendix Table. Their occurrences are illustrated in Figures 4-11. From the irregular horizontal and vertical distributions and highly nonnormal catch frequency curve (Figure 3), it appears that the larvae are very unevenly and probably patchily distributed. The location and density of patches may be related to local currents and water conditions on a smaller scale than we sampled. This discussion follows the sequence of spawning, i.e. starting in late spring

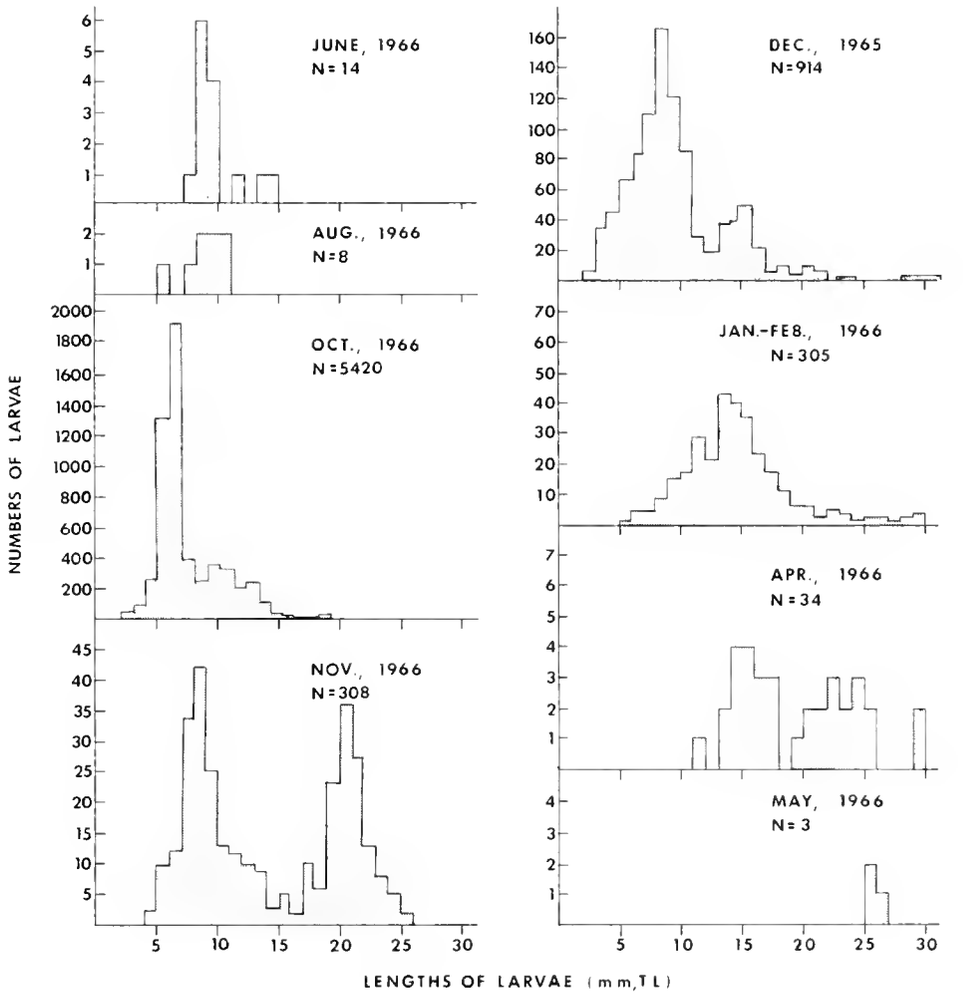


FIGURE 2.—Length-frequencies of menhaden larvae from the RV *Dolphin* survey, 1965-66.

1966. The cruises, however, began in December 1965. Thus, the cruises from December 1965 to May 1966 cover one spawning season and those from June 1966 to November-December 1966 cover the following season.

In late June a few larvae were collected nearshore off Delaware Bay (Figure 4). These larvae were small (7.8-14.4 mm), indicating they had been spawned recently. Spawning may have occurred in Delaware Bay since the larvae we

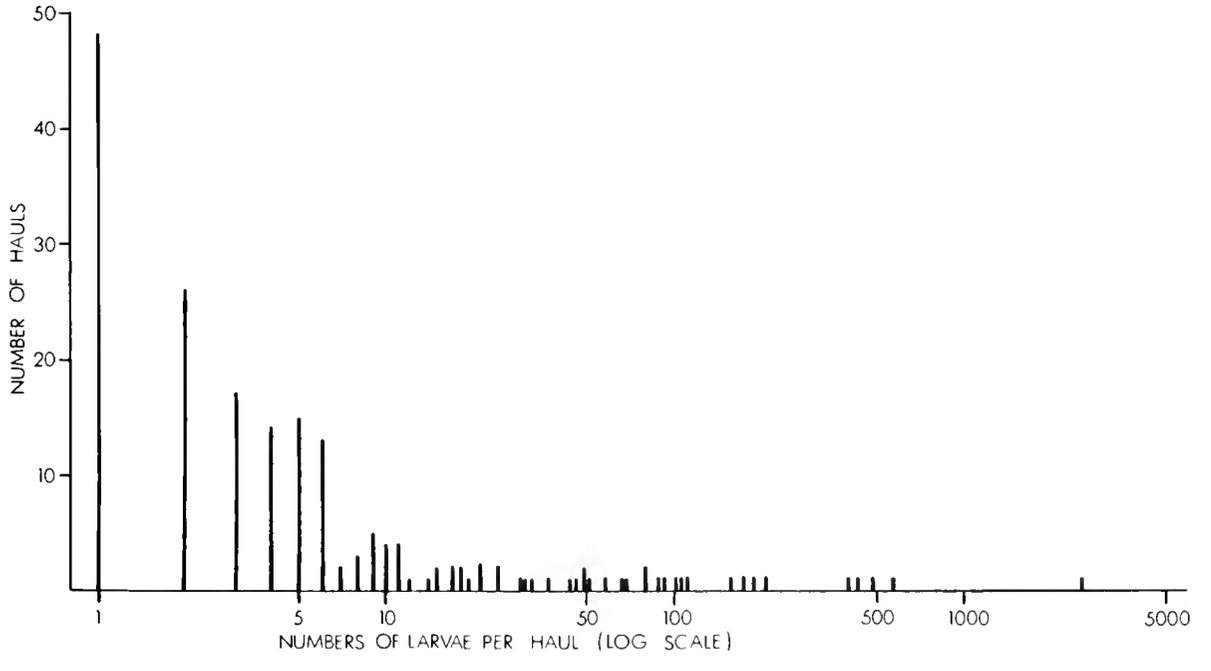


FIGURE 3.—Frequency distribution of menhaden larval catches per haul.

caught were concentrated close to its mouth. The distribution of the collections indicates spawning was not widespread. Stations north of these collections were sampled about 10 days earlier, possibly accounting for the limited distribution we observed. The absence of larvae to the north in these earlier collections would indicate spawning had recently started. Temperatures in June in the area of capture ranged from 15° to 19°C, and salinity varied from 30.3 to 32.1‰ (Figure 4). Hydrographic conditions within these ranges occurred widely along the coast during this cruise (Clark et al. 1969).

During our cruise in August there was evidence of limited spawning nearshore (Figure 5). A few small larvae, 5.6-10.5 mm, were taken off Long Island and New Jersey. Perhaps the earlier spawning in June was so limited that with dispersal during growth, insufficient larvae survived to be taken in our August sampling. Temperatures in the area of capture in August were warmer than in June, 18° to 22°C at the surface, and the seasonal thermocline was well developed about 15 m below the surface (Figure 5). Temperatures below the thermocline were less than 10°C. Larvae were collected only in the shallow net, indicating they were in the warm water above the thermocline. Salinity in the area of capture ranged from 30.1 to 31.0‰.

In October 5,420 larvae were collected that ranged from 3.5 to 18.5 mm (Figure 2). The length-frequency distribution was skewed to the left (mean 7.3 mm; mode 6.5 mm). Larvae were more widespread and in greater concentrations than during any other cruise (Figure 6). They occurred from Martha's Vineyard to Currituck Beach, N.C., and were abundant from Long Island to Maryland, near the middle of the shelf. They occurred nearshore from southern New England to New Jersey and near Chesapeake Bay. The fish

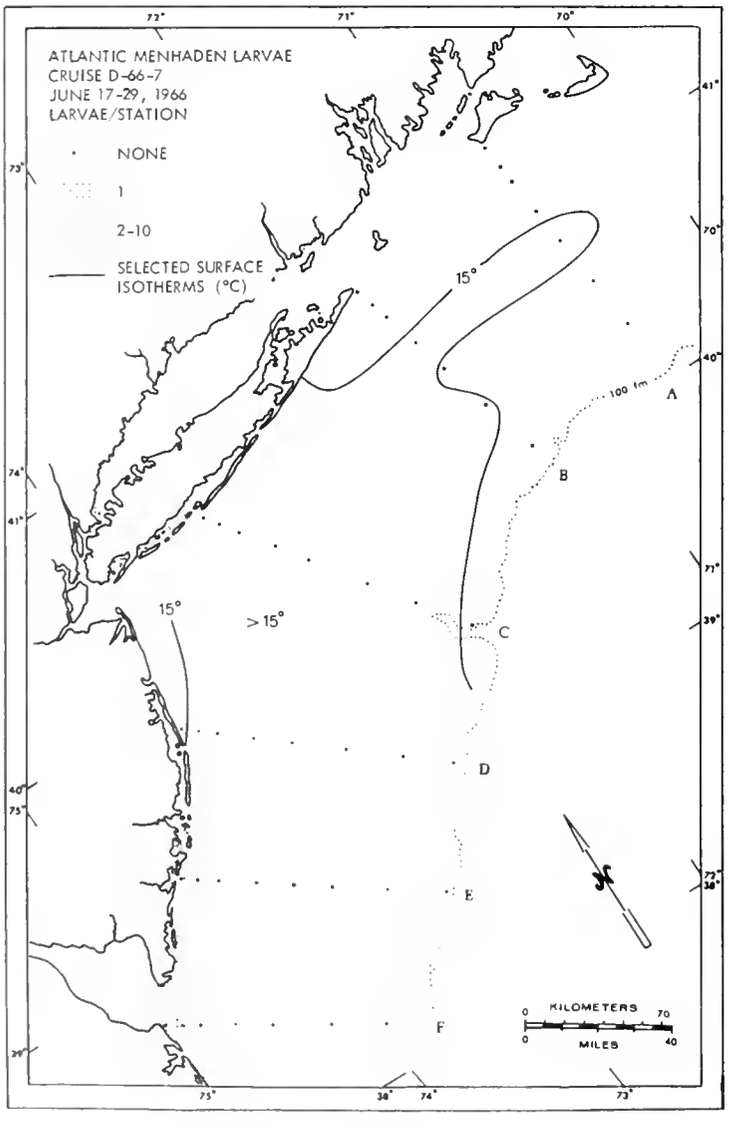


FIGURE 4.—Distribution and abundance of menhaden larvae in the June cruise.

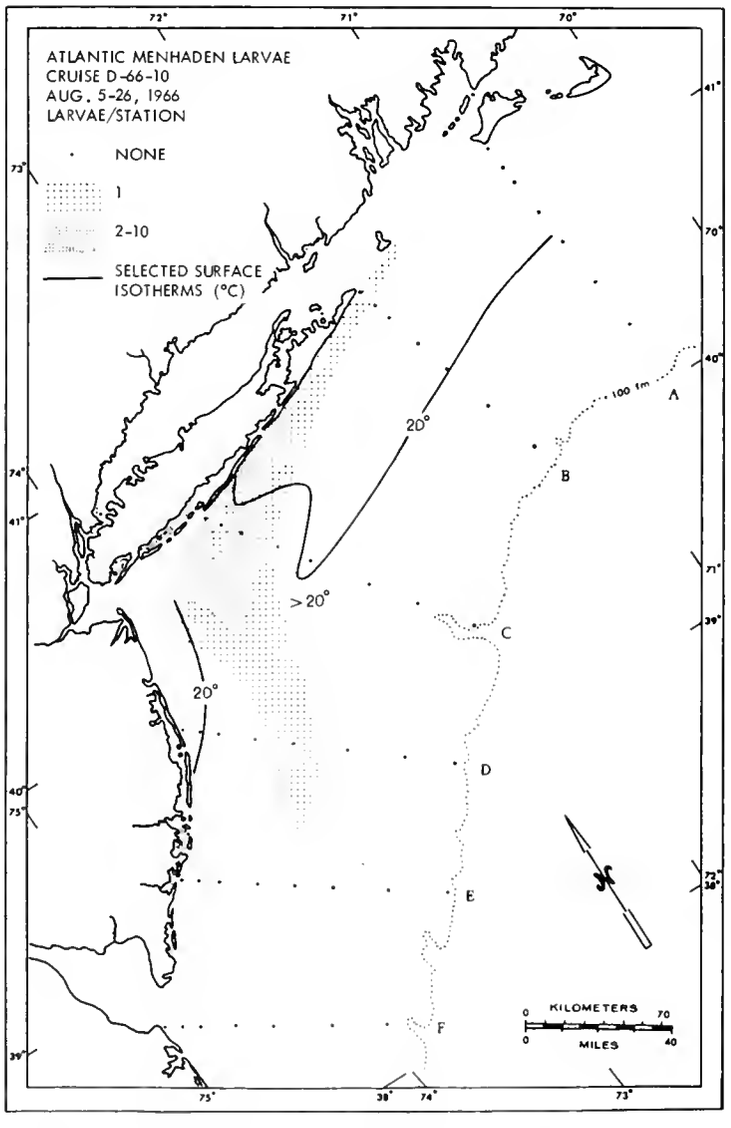
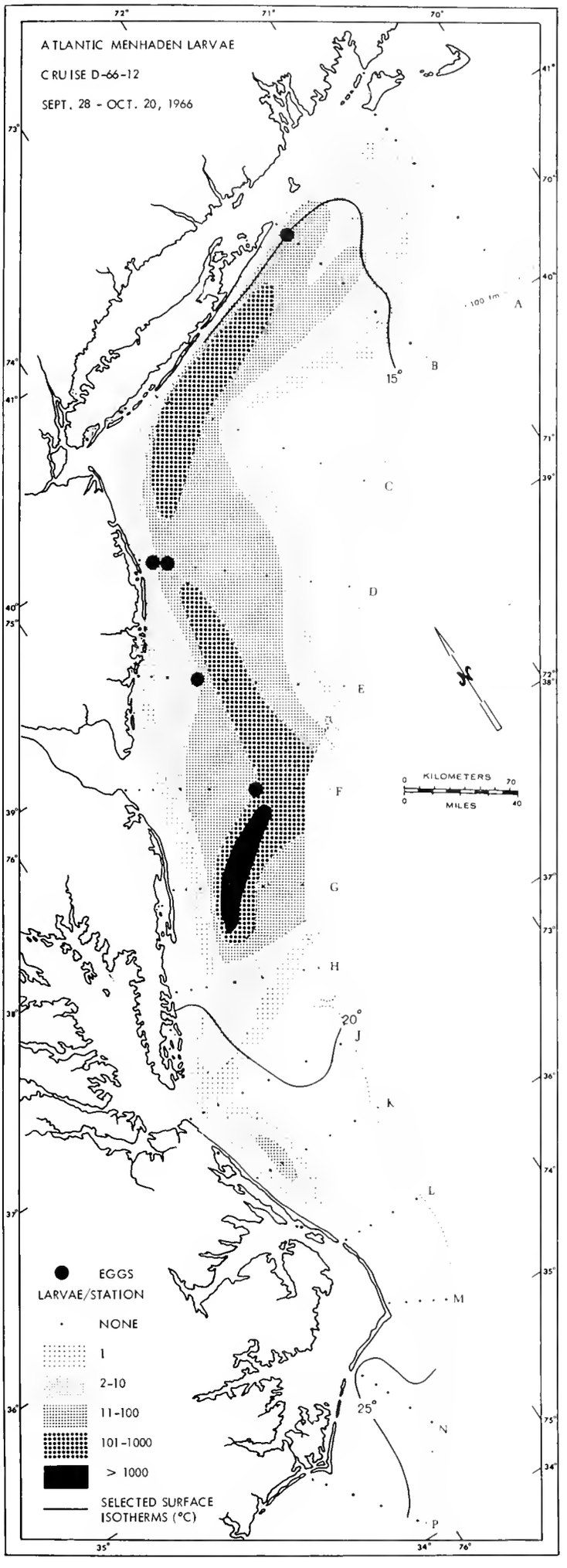


FIGURE 5.—Distribution and abundance of menhaden larvae in the August cruise.



were 8-12 mm in the northern part of the sampling range, from New York north. Fish in a broader size range, 4-12 mm, were present off New Jersey. Nearly all fish south of New Jersey were smaller, 4-8 mm.

In October the thermocline was breaking down but still present over much of the area, and surface temperatures were about 3°C cooler than in August (Figure 6). Salinity values were about the same as in August, mostly between 30.5 and 32.0‰, except near the mouth of Chesapeake Bay where they dropped to 28.0‰.

The cruise in late fall 1966 (Figure 7) shows a distribution pattern quite similar to the cruise in December 1965 (Figure 8). During both cruises, larvae occurred mostly nearshore from Long Island to North Carolina. They were most abundant near Cape Hatteras, where they were taken to the edge of the shelf.

In November 1966 there was a bimodal size distribution with one peak at 8 mm and the other at 20 mm (Figure 2). There were few larvae between 14 and 18 mm. In December 1965 the peak at 8 mm is similar to that in late fall 1966, but the second peak at 20 mm is not seen (Figure 2). Possibly this difference is due to year-to-year variation in spawning pattern in the area studied.

In the November and December cruises, small fish were found south of Delaware Bay and tended to occur at least 12 km offshore. Larger fish occurred mainly north of Chesapeake Bay and mostly within 15 km of shore. In transition areas between north and south and inshore and offshore areas, fish in a wide length range occurred at the same station and bimodal length-frequency curves were seen. This may indicate that spawning occurs in waves, and as the larvae grow they disperse from the area where they were spawned.

By late fall the thermocline was gone and surface isotherms roughly paralleled the coastline (Figures 7, 8). Larvae were taken over a wide range of temperature, from 7° to 25°C. Most collections were in water between 10° and 20°C. Salinity varied considerably between the two late fall cruises. In 1965, several patches of low saline water, less than 30‰, were found mostly near the shore (Clark et al. 1969). However, in 1966 salinity throughout the area was greater than31‰,except immediately outside Chesapeake Bay. The distribution of larvae is quite similar between these

FIGURE 6.—Distribution and abundance of menhaden larvae and distribution of menhaden eggs in the October cruise.

two cruises in spite of these differences in salinity.

In February menhaden larvae were taken from Virginia to Cape Lookout (Figure 9). They probably occurred farther south than we sampled since they were most abundant on our southernmost transect. Most larvae were taken between Cape Hatteras and Cape Lookout. Lengths presented a fairly symmetrical distribution with a peak at 13 mm (Figure 2). There is indication again that the larger fish were taken nearer to shore and farther north than the smaller fish. Few fish shorter than 8 mm were seen at this time, and the maximum length was 29 mm. Apparently, at about this size menhaden have either entered estuaries or can avoid our nets. In winter the temperature was 4°C at 11 of the 23 stations where menhaden were taken; it was less than 3°C at 4 stations (Figure 9). Water at these stations was practically isothermal with depth (Clark et al. 1969).

During April larvae occurred in approximately the same areas as in February (Figure 10). Fewer, larger larvae were taken between Chesapeake Bay and Ocracoke Inlet, N.C., than earlier. Larvae north of Cape Hatteras ranged from 21 to 29 mm. Off Ocracoke Inlet larvae were 11-19 mm. The larger larvae north of Cape Hatteras were taken nearshore; those farther south extended 37 km offshore. A bimodal length-frequency curve had peaks centered at 15 and 24 mm, although insufficient numbers of fish were collected to determine the statistical significance (Figure 2). By April, temperatures in the areas of capture were warmer than winter temperatures, above 8°C, and mostly between 10° and 12° (Figure 10). Salinity ranged from 30.3 to 35.6‰.

In May a few large (25-26 mm) larvae were taken off Virginia, inshore near Chesapeake Bay (Figure 11). These were apparently remnants of the early winter spawning, the rest of the larvae having already entered estuaries. Water in the areas of capture had warmed to 13° to 17°C (Figure 11). Salinity was generally lower, from 28.4 to 31.2‰, due to spring freshening nearshore (Clark et al. 1969).

Temperature-Salinity Relations

The catches of menhaden larvae during all cruises in the shallow net were compared

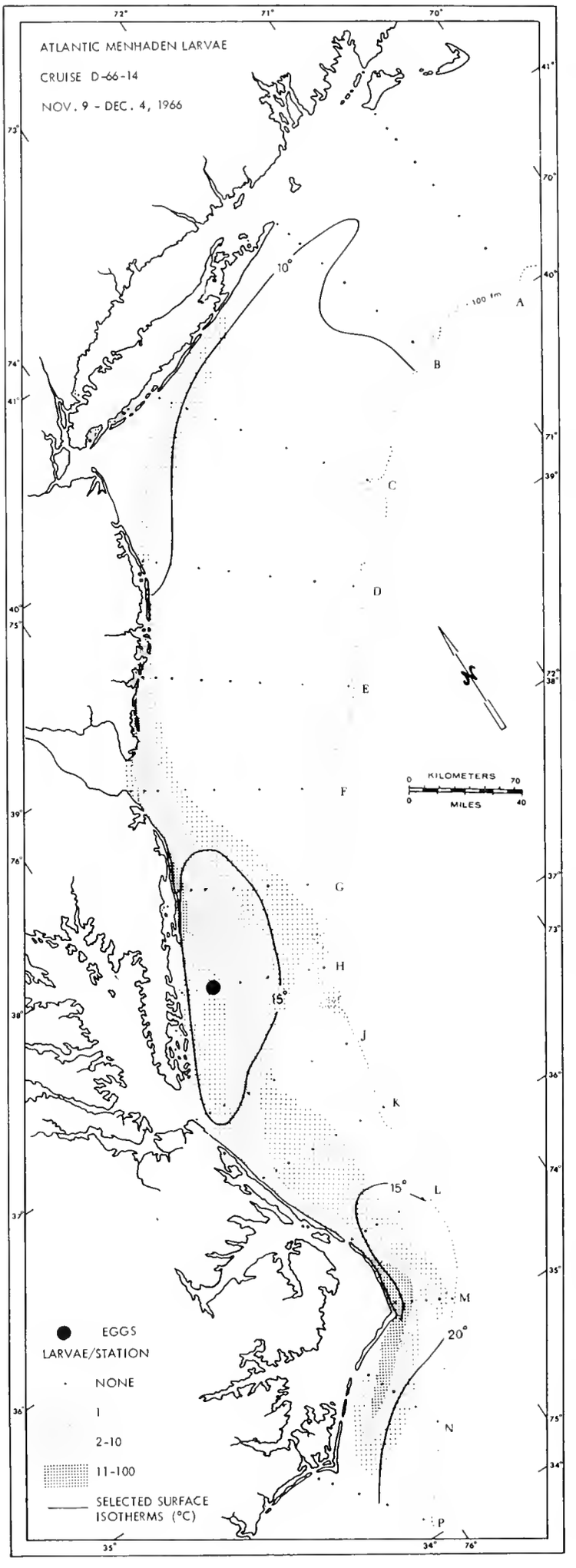
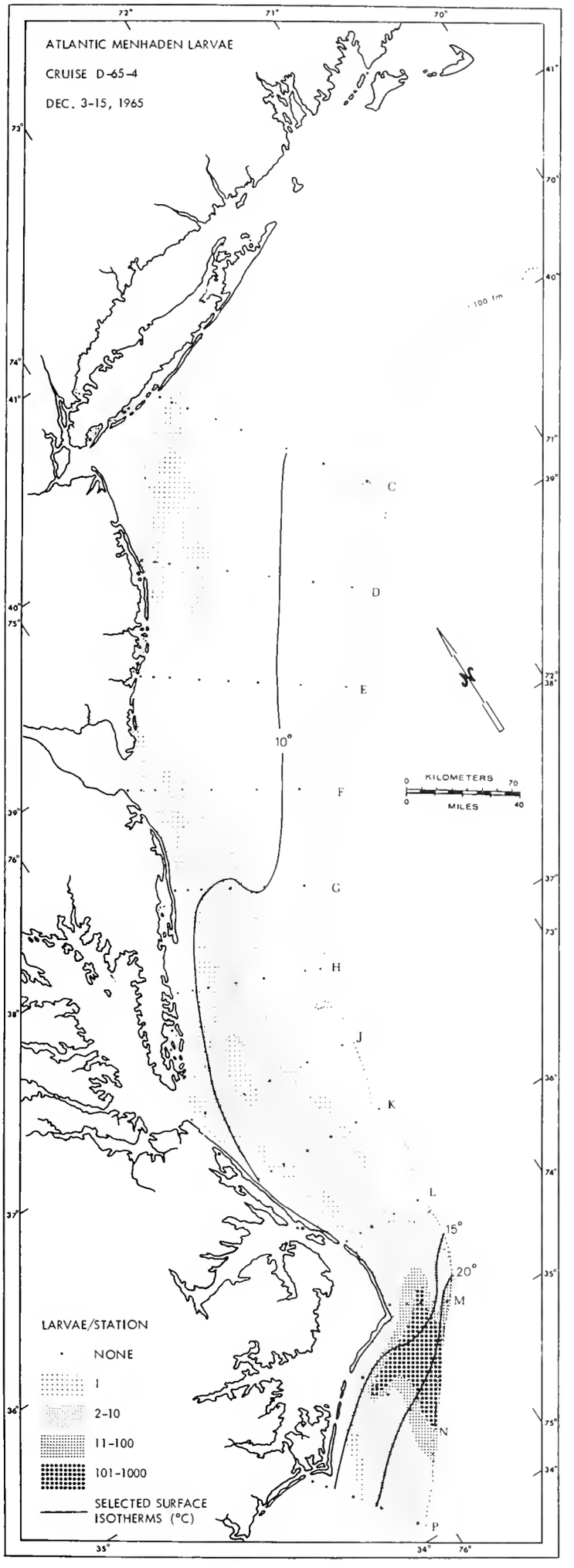


FIGURE 7.—Distribution and abundance of menhaden larvae and distribution of menhaden eggs in the November-December 1966 cruise.



graphically with observed surface temperatures and salinities. Surface observations were thought adequate since most larvae were collected when hydrographic conditions were nearly uniform with depth and menhaden larvae were scarce below the thermocline. Mean temperatures and salinities within the sampling depth range were also compared with catches and showed patterns similar to those discussed here.

Observed surface temperatures varied from -1° to 28°C (Figure 12). At each of nine whole-degree intervals between 6° and 19°C, more than 30 stations were occupied. More than 40 stations were occupied at 10° and 14°C. Menhaden occurred at stations when temperatures were between 0° and 25°C. The curve of positive stations (those where menhaden were taken) was similar in shape and range to that of total stations. The numbers of larvae taken at each temperature were plotted on a log scale. This plot was slightly skewed to the right, with modal catch at 18°C. Catches of over 100 larvae were made at temperatures from 9.3° to 20.5°C, with most between 15.8° and 18.5°C.

Surface salinity varied from 23 to 38‰, with a mode at 31‰ (Figure 13). Positive stations occurred over the entire range of salinities, with a mode at 30‰. The larval catch curve, on a log scale, is similar in shape to the total station curve, with a mode at 31‰. At stations with salinities between 30 and 36‰, a total of at least 200 larvae were taken within each part-per-thousand interval.

Diel-Vertical Comparisons of Larval Catches

Comparisons were made of the catches of larvae in shallow and deep tows made during night and day. These comparisons are on the basis of the volume of water sampled, which was assumed to be constant among the tows. The use of parametric statistics was precluded by the highly nonnormal catch frequency curve (Figure 3). Of the 172 tows with menhaden larvae, 48 contained only 1 larva, and 11 tows contained more than 100 larvae. Of the 11 tows with more than 100 larvae, 7 were taken in shallow tows during daylight. Altogether menhaden occurred in 85 daylight tows and 87 nighttime tows (Table 3). The distribution of catches was not significantly different with time of day (chi-square test; $P > 0.50$). Day and night

FIGURE 8.—Distribution and abundance of menhaden larvae in the December 1965 cruise.

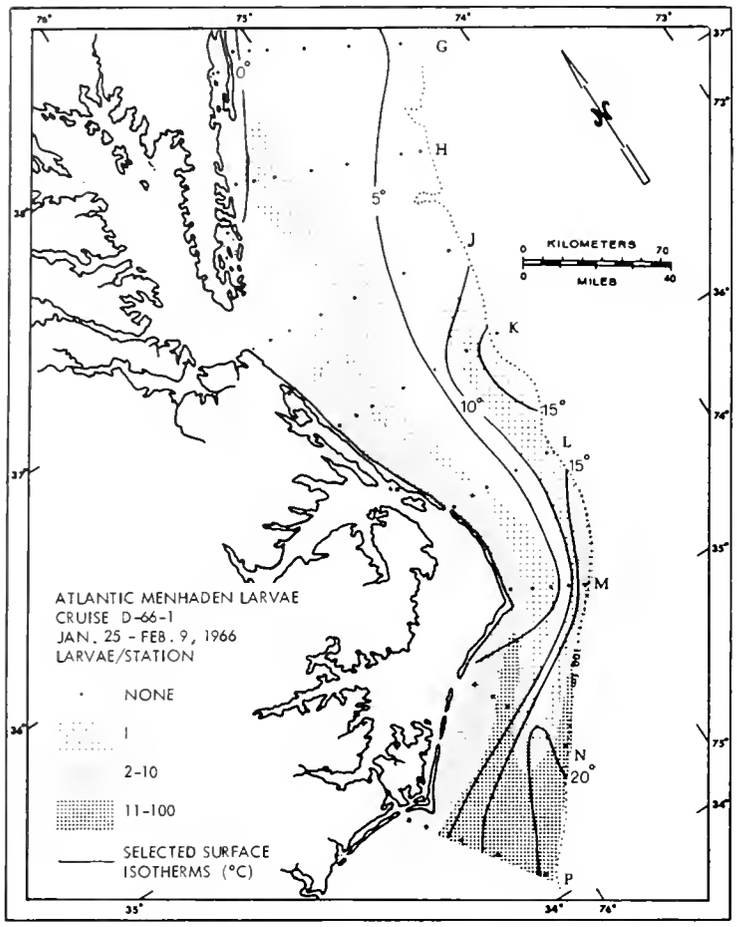


FIGURE 9.—Distribution and abundance of menhaden larvae in the February cruise.

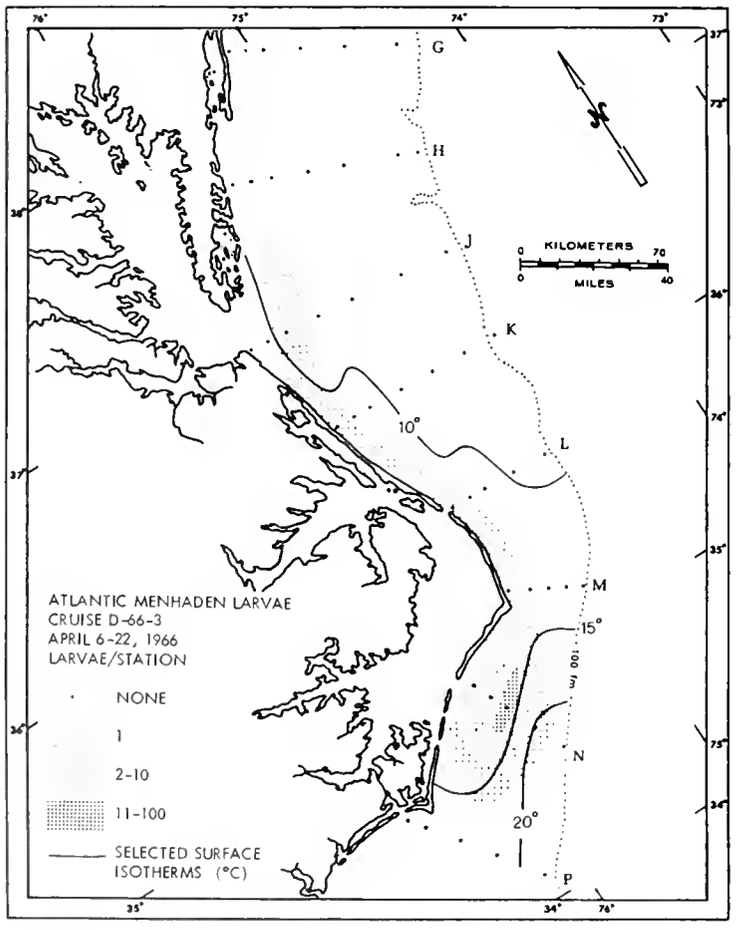


FIGURE 10.—Distribution and abundance of menhaden larvae in the April cruise.

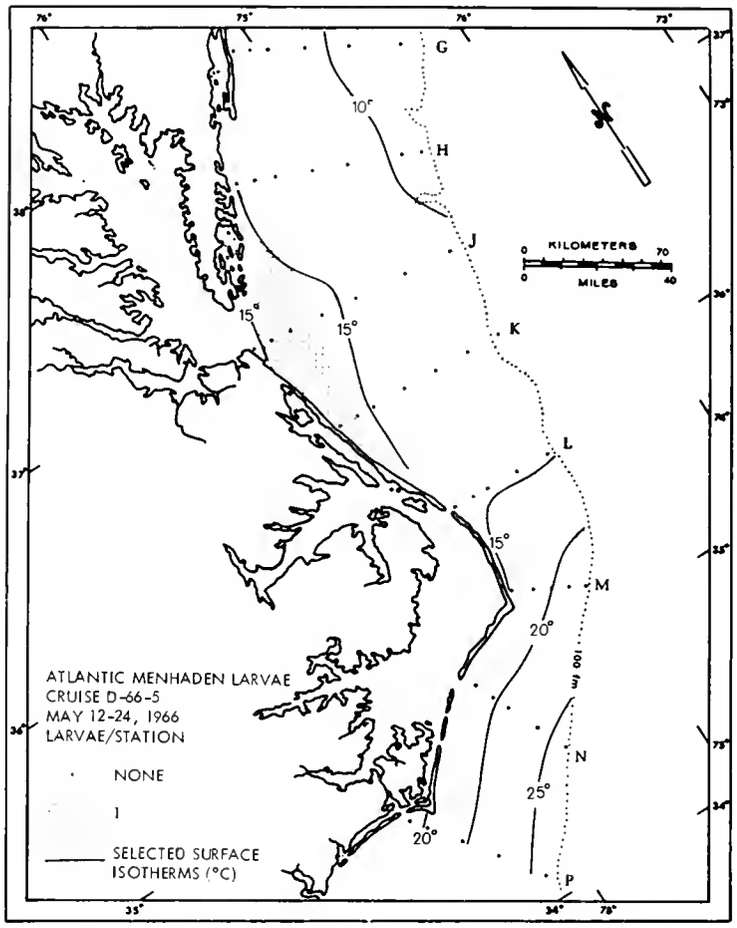


FIGURE 11.—Distribution and abundance of menhaden larvae in the May cruise.

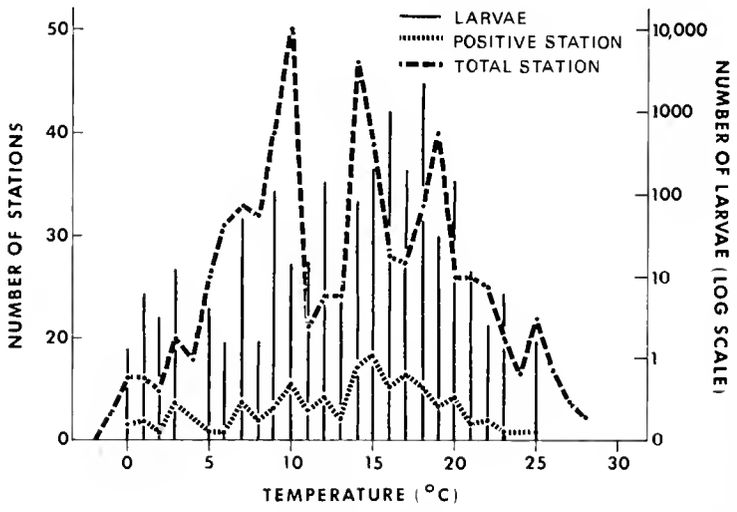


FIGURE 12.—Relation between surface temperature to menhaden larval catch and sampling effort.

tows were combined to compare the distribution of catches by the shallow and deep nets. By the shallow net, menhaden were taken in 138 tows and by the deep net in 34 tows (Table 3). The distribution of catches was not significantly different in the two nets ($P > 0.50$). Comparisons of size of larvae between day and night tows with the shallow and deep nets showed no significant differences.

Eggs

We found menhaden eggs at only six stations, five from the October cruise and one from the late fall cruise in 1966 (Figures 6, 7). All but one sample contained less than 100 developing eggs. The exceptional sample was from 85 km off Delaware Bay in October where about 2,000 eggs were taken. Precise counts were not possible due to the poor state of preservation of the samples when they were examined. Eggs were collected in areas where small larvae were taken. Apparently menhaden spawn as large schools producing dense patches of eggs (Reintjes 1969). During the short incubation time (48 h), these patches do not become dispersed. Thus the distribution of menhaden eggs at sea is probably more uneven than that of larvae. Chance was a dominant factor in catching menhaden eggs so distributed in our survey.

Mid-Water Trawl Catches

Sampling by mid-water trawl during the cruises collected a few larval and adult menhaden. Sampling effort was good in areas where the catches were made, so they probably reflect the actual geographic distribution of menhaden subject to capture by this type of sampling (Clark et al. 1969). A few large larvae, 21-37 mm, were taken in August off the Chesapeake Bay area. Age-0 fish, 89-177 mm FL (fork length) (Reintjes 1969), occurred close to shore from southern New England to Chesapeake Bay in late fall 1966. These probably represent young fish migrating south after spending the summer in estuaries (June and Chamberlin 1959). Other catches included two large fish, 305 and 361 mm FL, close to shore off southern New Jersey in May, and several age-0 fish off Oregon Inlet, N.C., in June.

DISCUSSION

Much speculation has surrounded the distribution of early stages of menhaden. Spawning times and places have been inferred from examination of gonads of adults (McHugh et al. 1959; Higham and Nicholson 1964) and nearshore and estuarine samples of larvae and juveniles (e.g. Richards 1959; Sutherland 1963; Pacheco and Grant 1965). Few studies have actually taken menhaden eggs and larvae to determine more directly the area of spawning (Reintjes 1961; Massmann et al. 1962). Controversy has concerned whether menhaden spawn in Chesapeake Bay (Hildebrand and Schroeder 1928) and whether there are two separate populations along the east coast, one spawning in spring and one in fall (Nicholson 1972). Annual variation in time of spawning and entry of larvae into estuaries may account for some of the confusion, since most studies have been short-termed and in a relatively small portion of the range of menhaden.

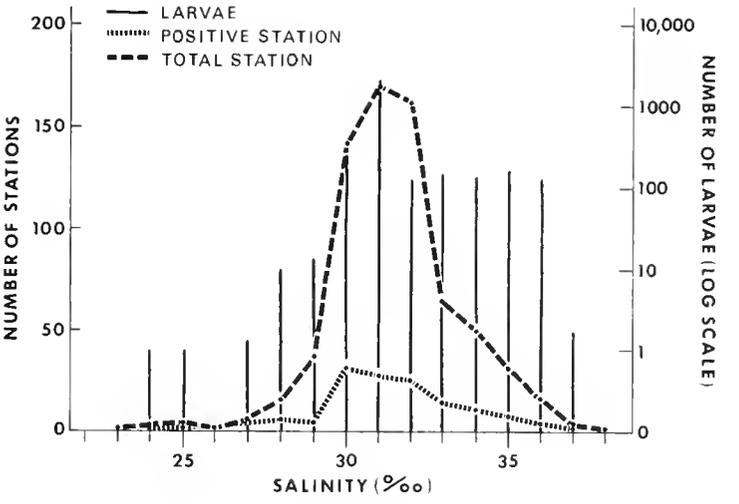


FIGURE 13.—Relation between surface salinity to menhaden larval catch and sampling effort.

Caution needs to be exercised in analyzing the present data since they were collected during a single year and do not encompass the entire range of spawning of menhaden (Reintjes 1969). During summer larvae were taken from our inshore stations to our farthest offshore station and at our most northerly station. The possibility of spawning within estuaries is indicated by the presence of

TABLE 3.—Diel and depth distribution of menhaden larval catches and mean lengths.

	Day			Night			Day and Night		
Larvae/tow	Shallow	Deep	Both	Shallow	Deep	Both	Shallow	Deep	All
	Number of tows								
1-2	29	9	38	34	2	36	63	11	74
3-4	7	3	10	7	4	11	14	7	21
5-20	18	3	21	18	6	24	36	9	45
>21	15	1	16	10	6	16	25	7	32
Total tows	69	16	85	69	18	87	138	34	172
Mean larvae/tow	68.2	6.4	56.0	19.1	48.2	25.6	43.0	27.2	39.8
Mean larval length (mm)	8.3	8.8	8.3	9.0	6.9	8.2	8.5	7.1	8.3

small larvae near their mouths. In winter they were found at our southernmost stations. Therefore, spawning could have taken place inshore and offshore of our stations and farther north and south of our sampling.

Our results on area of spawning confirm the conclusions of Higham and Nicholson (1964) and Nicholson (1972) that menhaden spawn during both their northward spring migration and their southward fall migration. We conclude that spawning apparently continues in winter in the south, based on our catches around Cape Lookout. Midsummer spawning may have occurred north of our sampling area, or may have been inhibited in 1966 by water cooler than usual.

Harrison et al. (1967) postulated that bottom drift of waters off Chesapeake Bay influence the success of year classes of menhaden. During years when bottom drift was weak and southwesterly, poor year classes occurred. However, our data and that of Massmann et al. (1962) do not indicate a preference for bottom waters by larger menhaden larvae. Larvae entering the estuaries are found throughout the water column (Lewis and Mann 1971), and later, in the estuaries, they are found primarily in surface waters (Massmann et al. 1954). Possibly the factors affecting bottom drift also affect the success of year classes, but in an indirect way.

Reintjes and Pacheco (1966) reported on inlet and nursery area collections in Indian River, Del., made over a 6-yr period (1955-61). Among the years studied, the peak in larval abundance at the inlet occurred in all months from December through March. Larvae were taken at the inlet from September through June in most years. It appeared that when temperatures at the inlet dropped to 3°C, larvae in the area were killed. In four seasons, when large catches of larvae were made at the inlet between December and February and temperature later dropped below 3°C, larvae were scarce or absent in upstream nursery areas. However, larvae taken in years when temperature remained above 3°C and those taken after the critical low temperature period were later represented in collections upstream.

Due to the extreme year-to-year variability in time of entry at the inlet at Indian River, it is difficult to relate our catches to these data. The few small larvae taken near Delaware Bay in June would probably have entered the estuary in July, a month when Reintjes and Pacheco (1966) reported none. We made large catches in this area in October. Larvae were also present offshore in November and December. In February, larvae were not taken north of Virginia and water temperature close to shore between Chesapeake and Delaware bays was less than 0°C. From these data, it would appear that 1965-66 was dissimilar to any year studied by Reintjes and Pacheco (1966) with regard to menhaden larvae near Delaware Bay. Presumably during 1965-66 larvae could have been taken in abundance in late fall but would have been killed by cold water in February. Subsequently no larvae would have entered in winter or spring, but some might have appeared in early summer.

Menhaden larvae were taken off Chesapeake Bay in waters 1° to 15°C by Massmann et al. (1962). Herman (1963) reported them in Narragansett Bay from 1° to 22°C. The larvae we collected at temperatures below 3°C did not appear decomposed as would be expected had they been dead when captured. Lewis (1965, 1966) has studied the effects of subjecting menhaden larvae to low temperatures and a range of salinities in the laboratory. He has shown that moderate salinities (10-20‰) enhance survival at low temperature as do lowered acclimation temperatures. At 7°C acclimation temperature, the lowest he used, and 2° to 4°C test temperatures, 50% mortality occurred in about 40 h at 24‰. Salinities in our areas of capture were 31 to 35‰—higher than those tested by Lewis (1966). If temperatures below 3°C in estuarine waters kill many menhaden (Reintjes and Pacheco 1966), it may be advantageous for larvae to remain in the ocean where temperature changes are more gradual. Menhaden entering estuaries are usually larvae less than 30 mm long, and in the estuary they rapidly transform by 38 mm (Lewis et al. 1972). Reintjes and Pacheco (1966) reported a few transforming specimens (greater than 34 mm) entering Indian River in May. That they are dependent on estuarine conditions for transformation is supported by the absence of transforming specimens and juveniles in our collections.

SUMMARY AND CONCLUSIONS

A total of 7,006 menhaden larvae were collected in 172, 0.5-h Gulf V plankton tows. The larvae were taken on eight cruises along the middle Atlantic coast throughout the year. Eggs were taken in a few tows in the fall. The catch distribution was nonnormal, with 48 tows catching only 1 fish and 1

tow catching 2,553 fish. No differences in larval catches or size were found in shallow and deep tows or during day or night. Small larvae, less than 8 mm, were taken from June through February, indicating a protracted spawning period. However, there was a seasonal shift in area of spawning. In late spring and summer limited spawning was occurring off New Jersey and New York. By early fall spawning was widespread from southern New England to Virginia. By late fall and early winter spawning was limited to areas between Delaware and North Carolina. Larger larvae were taken in the north in late fall and south of Delaware Bay in winter and spring.

Larvae occurred over a wide range of temperature, from 0° to 25°C. Several were taken in waters cooler than the 3°C limit found lethal in laboratory tests and inferred to be limiting in inlet sampling studies. Most larvae were collected at temperatures between 15° and 20°C. There was an inverse relationship between temperature and size of larvae.

Salinity seemed to have little influence on the distribution of larvae. They occurred at practically every salinity encountered and the frequency of salinities closely resembled the frequency of positive tows.

Our findings are similar to recent investigations of early life history of Atlantic menhaden based on inlet sampling of larvae, gonad studies, and scale annulus formation. It appears that spawning and early development at sea take place over a long period in a given coastal area, and the larvae resulting from this spawning may reach the inlets over a long seasonal time. In years with mild winters, successful immigration to estuarine areas may occur before the winter temperature minimum. However, under more severe conditions, when winter temperatures in the estuaries fall below 3°C, successful immigration may occur only as temperatures are increasing in spring because larvae entering estuaries during the fall may not survive the winter. This could account for some of the annual variation in year-class strength of Atlantic menhaden.

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APPENDIX TABLE—RV *Dolphin* 1965-66 ichthyoplankton survey. Data associated with Gulf V catches of Atlantic menhaden larvae.

CRUISE STAT. D65 4	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE	DATE 1965 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE	MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE	MEAN
C 2	0-15	1	1	19.7		312	2353	NIGHT	27	8.2 8.2	8.2	8.2	8.3	NONE	-	30.0 30.4	30.2
D 1	0- 6	6	6	18.7	15.4 23.8	512	1459	DAY	11	7.7 7.7	7.7	7.7	7.8	NONE	-	29.0 29.1	29.1
D 2	0- 9	1	1	20.2		512	1557	DAY	18	7.9 8.0	7.9	8.0	7.9	NONE	-	29.0 29.6	29.3
D 4	18-24	1	1	16.9		512	1905	NIGHT	33	8.5 8.5	8.5	8.5	8.5	NONE	-	29.4 29.7	29.5
E 1	0- 9	2	2	30.0	29.4 30.6	912	1707	NIGHT	17	7.2 7.3	7.3	7.3	7.0	NONE	-	28.4 28.6	28.5
E 2	0- 9	1	1	23.3		912	1803	NIGHT	17	7.3 7.4	7.3	7.3	7.4	NONE	-	24.3 24.6	24.5
E 4	0-15	1	1	21.0		1012	0119	NIGHT	20	9.1 9.2	9.2	9.2	9.1	NONE	-	30.1 30.2	30.1
G 3	0- 6	6	6	11.8	10.6 13.7	1012	2302	NIGHT	18	9.8 10.0	9.9	10.0	9.5	NONE	-	30.1 30.4	30.3
G 4	0-15	2	2	12.3	10.2 14.4	1012	2126	NIGHT	29	10.1 10.2	10.2	10.1	10.2	NONE	-	31.8 32.2	32.0
H 3	0- 6	2	2	12.1	10.2 14.0	1112	0812	DAY	23	10.8 10.9	10.9	10.8	10.9	NONE	-	28.3 28.4	28.3
H 4	0-15	2	2	11.9	10.9 12.8	1112	1237	DAY	25	10.7 10.7	10.7	10.7	10.7	NONE	-	28.1 30.0	29.2
J 2	0- 3	1	1	17.4		1212	1900	NIGHT	9	9.8 10.3	10.0	9.8	10.8	NONE	-	30.3 30.8	30.6
J 3	0- 6	5	5	16.5	13.7 18.9	1212	1030	DAY	16	10.0 10.9	10.5	10.0	10.9	NONE	-	30.5 32.1	31.4
J 4	0- 6	1	1	10.1		1212	0902	DAY	17	10.9 11.0	11.0	10.9	11.0	NONE	-	32.8 32.8	32.8
J 5	0-15	2	2	15.7	15.6 15.8	1212	0537	NIGHT	26	10.8 10.9	10.8	10.9	10.8	NONE	-	32.5 34.0	33.1
K 3	0-15	1	1	15.1		1312	0038	NIGHT	25	10.2 10.8	10.3	10.2	10.8	NONE	-	33.3 34.0	33.7
K 4	0-15	7	7	15.3	13.7 19.5	1312	0410	NIGHT	31	11.9 12.0	11.9	12.0	11.9	NONE	-	33.9 34.2	34.0
K 4	18-24	3	3	13.6	11.4 15.0	1312	0410	NIGHT	31	11.9 11.9	11.9	12.0	11.9	NONE	-	34.3 34.5	34.5
K 5	0-15	3	3	14.1	13.4 15.1	1312	0607	NIGHT	35	11.3 11.5	11.3	11.5	11.3	NONE	-	32.5 32.9	32.6
L 1	0- 6	1	1	15.2		1312	1939	NIGHT	18	11.3 11.5	11.4	11.3	11.7	NONE	-	33.8 34.6	34.2
L 3	0-15	1	1	18.3		1312	2152	NIGHT	35	12.1 12.4	12.3	12.4	12.2	NONE	-	34.1 34.2	34.2
L 3	18-24	7	7	12.5	9.1 15.9	1312	2152	NIGHT	35	12.2 12.2	12.2	12.4	12.2	NONE	-	33.9 34.1	34.0
M 1	0- 3	18	18	18.4	12.3 21.3	1412	1838	NIGHT	13	12.4 12.4	12.4	12.4	12.5	NONE	-	34.1 34.4	34.2
M 2	0- 9	79	36	14.2	10.1 18.4	1412	1730	NIGHT	18	12.6 12.7	12.6	12.7	12.6	NONE	-		
M 3	0-15	181	77	10.6	5.1 16.3	1412	1553	DAY	20	12.7 12.8	12.7	12.8	12.7	NONE	-	33.2 34.5	33.6
M 4	0-15	5	5	12.8	9.5 14.2	1412	1445	DAY	26	13.0 13.1	13.1	13.1	12.8	NONE	-	34.1 34.5	34.2
M 4	18-24	1	1	11.9		1412	1445	DAY	26	12.8 13.0	12.9	13.1	12.8	NONE	-	34.2 34.2	34.2
M 5	0-15	57	32	7.5	3.5 10.3	1412	1235	DAY	90	23.1 23.1	23.1	23.1	20.1	NONE	-		
M 5	18-33	4	4	9.7	7.8 11.5	1412	1235	DAY	90	22.5 23.1	22.8	23.1	20.1	NONE	-		
N 1	0- 6	5	5	15.3	12.5 19.0	1512	0005	NIGHT	19	14.3 14.4	14.3	14.4	14.3	NONE	-	34.6 34.8	34.7
N 2	0-15	206	81	6.2	2.9 15.2	1512	0058	NIGHT	24	18.4 18.8	18.5	18.4	19.4	NONE	-	35.1 35.8	35.5
N 3	0-15	10	10	8.2	4.9 11.2	1512	0341	NIGHT	25	17.5 17.5	17.5	17.5	17.8	NONE	-	35.3 36.5	35.8
N 4	0-15	34	32	7.5	4.1 12.7	1512	0520	NIGHT	45	19.1 20.6	20.1	20.6	17.6	NONE	-	36.3 36.8	36.6
N 4	18-33	21	21	9.1	5.0 11.7	1512	0520	NIGHT	45	17.6 18.9	18.2	20.6	17.6	NONE	-	36.1 36.2	36.1
N 5	0-15	172	49	8.2	3.9 11.2	1512	0900	DAY	128	20.5 20.5	20.5	20.5	17.0	NONE	-	36.3 36.3	36.3
N 5	18-33	49	45	8.6	5.3 12.7	1512	0900	DAY	128	19.9 20.4	20.2	20.5	17.0	NONE	-	36.3 36.3	36.3
P 4	0-15	9	8	9.2	7.7 12.0	1512	1630	DUSK	34	22.4 23.2	23.0	23.2	19.3	NONE	-	36.9 37.5	37.1
P 4	18-33	2	2	9.2	8.3 10.1	1512	1630	DUSK	34	19.3 22.3	21.5	23.2	19.3	NONE	-		
P 5	0-15	3	3	9.5	8.7 10.7	1512	1335	DAY	82	25.4 25.4	25.4	25.4	23.5	NONE	-	37.4 37.8	37.6

APPENDIX TABLE—Continued.

CRUISE STAT.	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE	DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE	MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE	MEAN
D66 1																	
H 2	0- 6	2	2	21.1	19.4 22.9	7 2	0200	NIGHT	16	0.5	0.7	0.6	0.5	0.7	NONE	-	31.6 32.0 31.8
H 3	0- 6	1	1	15.5		7 2	0059	NIGHT	22	1.5	1.6	1.6	1.5	1.6	NONE	-	32.2 32.4 32.3
J 5	0-15	1	1	23.5		7 2	1143	DAY	26	3.5	3.6	3.5	3.6	3.5	NONE	-	32.9 33.0 33.0
K 1	0- 6	3	3	16.8	9.5 29.4	8 2	0138	NIGHT	15	1.5	1.6	1.5	1.6	1.5	NONE	-	30.9 31.2 31.1
K 2	0-15	4	4	17.3	13.8 24.3	8 2	0038	NIGHT	25	1.5	1.9	1.6	1.8	2.1	NONE	-	31.2 32.1 31.6
K 3	0-15	1	1	17.0		7 2	2332	NIGHT	22	3.4	3.8	3.5	3.8	3.4	NONE	-	32.6 32.6 32.6
K 6	0-15	1	1	17.9		7 2	1938	NIGHT	50	14.4	14.8	14.7	14.4	13.2	NONE	-	34.9 35.1 35.0
L 1	0- 6	6	6	22.3	17.0 29.1	8 2	0711	DAY	19	2.0	2.4	2.2	2.4	2.0	NONE	-	31.9 31.9 31.9
L 2	0- 6	4	4	19.6	15.9 28.0	8 2	0824	DAY	23	3.3	3.4	3.4	3.3	3.4	NONE	-	32.4 32.4 32.4
L 5	18-33	1	1	17.0		8 2	1225	DAY	145	12.2	13.2	12.7	14.5	11.1	NONE	-	34.6 34.9 34.7
M 1	0- 6	3	3	23.6	17.4 27.4	8 2	1633	DAY	13	3.3	3.4	3.3	3.4	3.3	NONE	-	31.6 31.6 31.6
M 2	0- 6	2	2	18.3	17.7 20.0	8 2	1726	DUSK	20	3.7	3.8	3.8	3.7	3.9	NONE	-	31.7 31.7 31.7
M 3	0- 6	2	2	16.6	15.8 17.4	8 2	1822	NIGHT	20	3.9	3.9	3.9	3.9	4.0	NONE	-	32.3 32.3 32.3
M 5	0-15	2	2	17.2	14.5 19.9	8 2	2018	NIGHT	139	12.2	17.0	16.0	17.0	10.0	STRONG	9-16	34.0 35.1 34.7
N 1	0- 6	6	6	20.3	17.5 23.0	9 2	0034	NIGHT	19	5.5	5.8	5.6	5.5	6.4	NONE	-	31.3 31.5 31.4
N 2	0-15	5	5	13.9	11.5 18.0	9 2	0126	NIGHT	24	7.9	8.6	8.1	7.9	8.6	NONE	-	32.7 33.1 33.0
N 3	0-15	49	49	13.7	7.1 29.8	9 2	0218	NIGHT	30	7.7	9.0	8.3	7.7	10.6	NONE	-	32.6 32.9 32.8
N 5	0-15	15	15	11.9	5.7 17.5	9 2	0509	NIGHT	82	19.2	19.4	19.3	19.4	16.6	NONE	-	35.3 35.5 35.5
N 5	18-33	6	6	11.5	8.6 13.4	9 2	0509	NIGHT	82	18.5	18.8	18.6	19.4	16.6	NONE	-	35.3 35.4 35.4
P 1	0- 6	3	3	14.9	13.6 17.3	9 2	1337	DAY	16	6.5	6.5	6.5	6.5	7.1	NONE	-	33.5 33.5 33.5
P 2	0- 6	9	9	21.1	14.6 26.6	9 2	1244	DAY	17	7.2	7.6	7.4	7.6	6.5	NONE	-	33.2 33.3 33.3
P 3	0- 6	108	108	14.8	6.5 23.9	9 2	1154	DAY	17	9.1	9.6	9.3	9.6	9.1	NONE	-	33.8 33.9 33.8
P 4	0-15	45	44	12.6	7.1 17.9	9 2	1033	DAY	31	14.1	17.0	15.8	17.0	13.1	WEAK	7-10	34.9 35.4 35.2
P 5	0-15	21	21	10.1	7.0 16.0	9 2	0848	DAY	60	20.0	20.0	20.0	20.0	17.8	NONE	-	35.5 35.6 35.5
P 5	18-33	5	5	10.5	6.5 15.4	9 2	0848	DAY	60	19.6	19.9	19.8	20.0	17.8	NONE	-	35.4 35.5 35.5
D66 3	(M)			(MM TL)		1966 D M	(EST)		(M)							(M)	
J 3	0- 6	1	1	29.4		16 4	0825	DAY	19	8.9	8.9	8.9	8.9	8.5	NONE	-	31.8 31.8 31.8
K 1	0- 6	2	2	27.3	25.3 29.3	19 4	1528	DAY	17	10.3	10.4	10.4	10.3	10.4	NONE	-	31.0 31.4 31.2
L 1	0- 6	1	1	25.0		20 4	0635	DAY	17	9.6	10.7	10.1	10.7	9.2	NONE	-	30.3 30.7 30.4
M 1	0- 6	12	12	22.7	20.6 24.7	20 4	1001	DAY	16	11.3	11.6	11.5	11.6	11.0	NONE	-	30.1 30.6 30.3
N 1	0-15	3	3	15.2	14.1 17.0	20 4	1753	DAY	21	10.7	12.2	10.9	12.2	10.7	WEAK	0- 4	32.2 32.6 32.4
N 2	0- 6	1	1	14.0		20 4	1851	NIGHT	22	11.7	11.8	11.8	11.8	11.9	NONE	-	32.1 32.1 32.1
N 3	0-15	9	9	15.0	11.0 17.4	20 4	1948	NIGHT	29	9.9	12.5	11.3	12.2	9.9	STRONG	6-10	31.7 32.2 32.0
N 3	18-24	4	4	15.3	14.4 16.0	20 4	1948	NIGHT	29	9.9	10.0	10.0	12.2	9.9	STRONG	6-10	32.1 33.9 32.7
N 4	0-15	1	1	19.0		20 4	2125	NIGHT	49	20.9	21.0	21.0	21.0	18.5	NONE	-	35.5 35.6 35.6

APPENDIX TABLE—Continued.

CRUISE STAT.	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE		DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE		MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE		MEAN
D66 5	(M)			(MM TL)			1966 D M	(EST)		(M)							(M)			
J 2	0- 6	1	1	25.0			21 5	0505	DAY	14	13.7	15.2	14.3	15.2	13.5	WEAK	3- 4	28.4	31.2	30.0
J 3	0- 6	1	1	25.0			21 5	0547	DAY	19	13.9	16.9	15.3	16.9	13.0	STRONG	1- 5	25.9	30.7	28.6
K 1	0- 6	1	1	26.0			21 5	2119	NIGHT	18	12.8	16.3	14.4	16.3	11.8	STRONG	1- 6	29.7	30.4	30.1
D66 7	(M)			(MM TL)			1966 D M	(EST)		(M)							(M)			
E 1	0- 3	1	1	13.7			29 6	0705	DAY	14	15.8	17.1	16.4	17.1	14.7	NONE	-	32.0	32.1	32.0
F 1	0- 6	11	11	9.5	7.8	14.4	28 6	0833	DAY	17	18.5	18.5	18.5	18.5	18.5	NONE	-	30.8	30.9	30.8
F 2	0- 6	2	2	8.0	8.0	8.1	28 6	0917	DAY	24	18.5	18.7	18.6	18.7	14.9	NONE	-	30.3	30.6	30.5
D6610	(M)			(MM TL)			1966 D M	(EST)		(M)							(M)			
B 1	0-15	1	1	5.6			6 8	1249	DAY	20	17.5	18.5	17.7	18.5	17.5	NONE	-	30.1	30.3	30.2
C 1	0- 6	3	3	8.6	8.1	9.1	6 8	2343	NIGHT	19	19.8	20.6	20.5	20.6	12.3	STRONG	5-13	30.6	30.8	30.7
C 2	0-15	1	1	7.7			7 8	0037	NIGHT	28	13.3	20.2	18.2	20.2	9.6	WEAK	5-19	30.6	30.8	30.7
C 3	0-15	2	2	9.8	9.3	10.3	7 8	0139	NIGHT	32	14.5	20.3	18.8	20.3	7.9	STRONG	11-22	30.6	30.7	30.7
D 5	0-15	1	1	10.6			8 8	1515	DAY	37	20.1	22.2	21.5	22.2	8.6	STRONG	14-19	30.9	31.0	30.9
D6612	(M)			(MM TL)			1966 D M	(EST)		(M)							(M)			
A 2	0-15	1	1	8.0			1510	0209	NIGHT	30	14.0	14.3	14.2	14.3	12.9	NONE	-	31.2	31.3	31.2
A 2	18-24	4	4	4.4	4.1	4.7	1510	0209	NIGHT	30	13.2	13.9	13.6	14.3	12.9	NONE	-	31.3	31.5	31.4
A 4	0-15	1	1	9.3			1510	0615	DAY	49	14.2	14.3	14.2	14.3	10.1	STRONG	30-35	31.0	31.3	31.2
B 2	0-15	15	15	13.7	6.9	18.7	1410	1937	NIGHT	35	13.5	15.1	14.2	15.1	12.7	NONE	-	30.9	31.3	31.1
B 2	18-24	9	7	5.3	3.6	8.2	1410	1937	NIGHT	35	12.7	13.4	13.2	15.1	12.7	NONE	-	31.3	31.3	31.3
B 3	0-15	24	22	11.7	4.4	18.7	1410	2034	NIGHT	45	15.7	16.1	16.0	15.7	9.8	WEAK	25-39	31.3	31.5	31.4
B 3	18-33	31	27	5.9	4.0	11.1	1410	2034	NIGHT	45	12.9	15.9	14.8	15.7	9.8	WEAK	25-39	31.4	31.6	31.5
B 4	0-15	8	8	9.7	7.1	11.3	1410	1306	DAY	60	15.4	15.6	15.4	15.6	8.0	STRONG	29-42	30.7	31.0	30.9
B 4	18-33	2	2	9.8	9.7	10.0	1410	1306	DAY	60	13.8	15.5	15.3	15.6	8.0	STRONG	29-42	30.9	31.6	31.3
B 5	0-15	9	9	13.1	9.3	16.2	1410	1138	DAY	71	14.9	15.2	15.0	15.2	7.4	STRONG	26-42	30.7	31.0	30.8
B 5	18-33	4	3	9.8	6.9	9.7	1410	1138	DAY	71	12.9	14.9	14.5	15.2	7.4	STRONG	26-42	31.0	31.5	31.2
B 6	0-15	1	1	9.6			1410	0750	DAY	81	15.1	15.2	15.1	15.2	9.1	STRONG	33-46	31.5	31.7	31.6
C 2	0-15	155	65	11.6	5.0	18.2	1310	0912	DAY	25	15.7	15.9	15.8	15.9	11.9	STRONG	19-23	30.9	31.0	31.0
C 3	0-15	398	153	11.5	7.7	16.2	1310	1007	DAY	31	16.2	16.4	16.3	16.3	10.5	STRONG	24-30	31.0	31.2	31.1
C 3	18-24	4	4	10.9	9.3	12.2	1310	1007	DAY	31	16.1	16.2	16.2	16.3	10.5	STRONG	24-30	31.0	31.3	31.2
C 4	0-15	19	18	11.3	5.4	17.4	1310	1133	DAY	38	15.7	16.0	15.8	16.0	9.1	STRONG	25-32	30.9	31.0	30.9
C 4	18-33	1	0				1310	1133	DAY	38	9.7	15.6	13.6	16.0	9.1	STRONG	25-32	31.0	31.6	31.4

APPENDIX TABLE—Continued.

CRUISE STAT.	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE		DATE 1965 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE	MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE	MEAN
D6612(CON'D)																		
D 1	0- 6	2	2	7.6	5.1	10.2	610	0124	NIGHT	18	17.2	17.3	17.3	17.2	17.5	NONE	-	30.4 30.5 30.5
D 2	0- 6	5	5	6.9	4.4	8.7	610	0213	NIGHT	23	17.0	17.1	17.0	17.1	17.0	NONE	-	30.5 30.7 30.6
D 3	0-15	99	33	6.9	4.1	10.1	510	0308	NIGHT	24	16.8	17.0	16.9	17.0	16.8	NONE	-	30.8 30.9 30.8
D 4	0-15	24	17	9.1	4.7	12.8	1210	2336	NIGHT	27	16.3	16.4	16.4	16.4	15.4	NONE	-	30.8 31.2 31.0
D 4	18-24	105	41	6.3	4.7	12.8	1210	2336	NIGHT	27	15.4	16.2	15.9	16.4	15.4	NONE	-	31.0 31.3 31.2
D 5	0-15	11	10	7.8	5.0	10.0	1210	2204	NIGHT	36	16.5	16.6	16.6	16.6	11.0	WEAK	23-37	31.2 31.3 31.2
D 5	18-24	50	50	6.5	3.1	12.5	1210	2204	NIGHT	36	15.5	16.4	16.1	16.6	11.0	WEAK	23-37	31.2 31.4 31.3
D 6	0-15	17	17	12.0	9.3	13.7	1210	1801	NIGHT	54	16.4	16.4	16.4	16.4	7.4	STRONG	19-24	31.5 31.8 31.7
D 6	18-33	11	11	11.4	9.5	13.0	1210	1801	NIGHT	54	8.3	15.5	10.8	16.4	7.4	STRONG	19-24	31.1 31.7 31.3
E 1	0- 6	10	9	7.2	5.6	8.7	510	1501	DAY	16	17.7	17.9	17.8	17.7	17.9	NONE	-	30.3 30.6 30.4
E 3	0- 6	6	6	5.9	4.0	10.3	510	1323	DAY	22	17.4	17.4	17.4	17.4	16.9	NONE	-	30.8 30.9 30.8
E 4	0-15	3	2	11.5	10.0	13.0	1110	2034	NIGHT	29	16.4	17.2	17.0	17.2	13.0	STRONG	21-28	30.8 31.3 31.0
E 5	0-15	476	111	7.2	3.7	12.5	1110	2210	NIGHT	35	16.4	16.6	16.5	16.6	9.0	STRONG	22-31	31.2 31.4 31.3
E 5	18-24	563	99	6.6	2.9	13.7	1110	2210	NIGHT	35	15.3	16.4	16.0	16.6	9.0	STRONG	22-31	31.4 31.4 31.4
E 6	0-15	66	36	10.4	7.7	13.0	1210	0150	NIGHT	43	15.8	16.2	16.1	16.2	7.9	STRONG	19-24	31.2 31.5 31.4
E 6	18-33	9	9	9.6	4.9	12.2	1210	0150	NIGHT	43	7.9	15.4	10.4	16.2	7.9	STRONG	19-24	30.9 31.9 31.4
E 7	18-33	4	4	10.3	10.0	10.5	1210	0352	NIGHT	65	11.0	17.1	15.7	17.2	6.2	STRONG	26-39	31.7 32.3 32.1
F 4	0-15	4	4	6.2	4.7	6.9	510	0227	NIGHT	22	17.7	18.0	17.8	18.0	17.7	NONE	-	30.8 30.9 30.8
F 5	0-15	18	16	6.9	5.0	11.4	410	2151	NIGHT	35	17.4	17.9	17.7	17.9	14.2	WEAK	18-24	30.7 30.9 30.8
F 5	18-24	30	29	7.1	5.0	12.5	410	2151	NIGHT	35	14.9	17.0	16.1	17.9	14.2	WEAK	18-24	30.9 30.9 30.9
F 6	0-15	92	43	7.0	5.8	10.2	410	1953	NIGHT	54	16.4	17.3	17.0	17.3	6.8	STRONG	15-23	30.9 31.2 31.1
F 6	18-33	9	6	7.2	6.9	7.6	410	1953	NIGHT	54	7.5	14.4	9.9	17.3	6.8	STRONG	15-23	30.8 31.3 31.0
F 7	0-15	426	38	6.6	3.1	8.5	410	1552	DAY	91	17.8	18.2	18.1	18.2	10.2	WEAK	14-42	31.6 31.9 31.8
F 7	18-33	2	2	6.7	5.8	7.6	410	1552	DAY	91	10.6	16.8	14.3	18.2	10.2	WEAK	14-42	31.4 31.7 31.5
G 3	0-15	1	1	11.6			310	2231	NIGHT	22	18.2	18.3	18.3	18.2	18.3	NONE	-	31.0 31.0 31.0
G 4	0-15	2553	116	6.4	2.7	10.5	410	0627	DAY	31	18.1	18.2	18.2	18.2	15.8	NONE	-	31.0 31.1 31.0
G 5	0-15	79	37	7.1	2.7	10.3	410	0816	DAY	51	17.4	18.0	17.8	18.0	9.4	STRONG	19-26	30.9 31.0 30.9
G 5	18-33	2	2	7.3	7.2	7.4	410	0816	DAY	51	10.9	16.9	12.9	18.0	9.4	STRONG	19-26	31.0 31.2 31.1
G 6	0-15	29	24	7.0	3.9	9.7	410	1209	DAY	85	19.1	19.4	19.2	19.1	11.7	STRONG	26-40	31.5 31.9 31.7
G 6	18-33	6	5	7.4	6.3	10.3	410	1209	DAY	85	15.9	19.5	18.7	19.1	11.7	STRONG	26-40	31.8 32.3 32.1
H 4	0-15	10	10	10.3	8.0	11.3	310	1114	DAY	28	19.3	19.4	19.3	19.3	19.4	NONE	-	30.0 30.9 30.7
H 5	0-15	1	1	7.3			310	0950	DAY	39	19.6	19.7	19.7	19.7	14.0	NONE	-	30.8 30.9 30.9
H 5	18-33	5	5	7.4	6.9	8.0	310	0950	DAY	39	16.1	18.6	17.2	19.7	14.0	NONE	-	30.9 31.1 31.0
J 2	0- 3	2	2	5.9	5.5	6.4	110	1351	DAY	11	21.6	21.6	21.6	21.6	21.2	NONE	-	27.8 29.1 28.5
J 3	0- 6	2	2	3.9	3.5	4.4	110	1257	DAY	17	21.9	22.0	21.9	22.0	21.8	NONE	-	28.4 28.8 28.5
K 2	0-15	2	2	3.6	3.5	3.7	110	0825	DAY	22	21.4	22.0	21.9	22.0	18.9	WEAK	15-21	30.0 30.7 30.2
K 3	0-15	11	10	6.4	4.5	7.7	110	0924	DAY	25	19.9	21.9	21.5	21.9	16.3	WEAK	12-22	29.9 30.9 30.3

APPENDIX TABLE—Continued.

CRUISE STAT. D6614	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE		DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE		MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE		MEAN
C 2	0- 6	1	1	22.0			312	0645	DAWN	28	9.8	9.9	9.9	9.8	9.9	NONE	-	32.9	33.0	33.0
C 3	0-15	1	1	21.5			312	0537	NIGHT	34	10.1	10.3	10.1	10.3	10.1	NONE	-	33.0	33.1	33.1
D 1	0- 6	2	2	21.7	20.0	23.5	112	1854	NIGHT	14	9.4	9.4	9.4	9.4	9.3	NONE	-	32.1	32.3	32.2
E 1	0- 6	5	5	19.9	18.5	20.5	911	2248	NIGHT	11	12.5	12.6	12.6	12.5	12.8	NONE	-	31.1	31.3	31.2
F 1	0- 6	1	1	21.0			1111	0602	NIGHT	18	13.5	13.5	13.5	13.5	13.5	NONE	-	31.4	31.8	31.6
F 2	0- 6	3	3	20.7	19.5	21.5	1111	0515	NIGHT	20	13.6	14.3	14.0	13.6	13.9	NONE	-	31.8	31.9	31.8
F 3	0-15	2	2	15.2	15.0	15.5	1111	0432	NIGHT	26	14.5	14.7	14.6	14.7	14.2	NONE	-	32.5	32.8	32.6
G 1	0- 6	100	55	20.7	17.0	25.0	1111	1604	DAY	10	14.5	15.0	14.7	15.0	14.3	NONE	-	32.4	32.4	32.4
G 2	0- 6	5	5	16.5	14.5	18.0	1111	1657	NIGHT	17	14.4	15.0	14.6	15.0	14.0	NONE	-	32.6	32.6	32.6
G 3	0-15	5	5	18.6	15.0	24.0	1111	1753	NIGHT	16	15.2	15.7	15.5	15.6	15.5	NONE	-	32.6	32.9	32.8
G 4	0-15	1	1	5.0			1111	1919	NIGHT	29	15.0	15.5	15.4	15.4	13.0	NONE	-	32.9	33.1	33.1
G 5	0-15	1	1	9.3			1111	2234	NIGHT	49	14.3	14.8	14.6	14.8	10.5	STRONG	26-28	33.3	33.5	33.4
H 1	0- 6	1	1	15.0			1211	1312	DAY	10	14.7	14.9	14.8	14.9	14.7	NONE	-	32.0	32.2	32.1
H 3	0- 6	1	1	5.7			1211	1041	DAY	25	15.8	15.9	15.9	15.8	15.3	NONE	-	32.6	32.8	32.7
H 4	0-15	2	2	13.7	13.5	14.0	1211	0918	DAY	29	14.9	15.6	15.2	15.6	14.7	NONE	-	32.8	33.4	33.1
H 5	18-33	2	2	5.3	5.0	5.7	1211	0754	DAY	42	14.0	14.3	14.2	15.3	14.0	NONE	-	33.8	33.9	33.9
H 7	0-15	1	1	19.0			1211	0503	NIGHT	134	14.5	15.1	14.7	14.5	11.2	STRONG	43-52	33.8	34.6	34.0
J 2	0- 6	1	1	20.5			1311	0036	NIGHT	10	15.1	15.3	15.2	15.1	15.2	NONE	-	31.7	32.0	31.8
J 3	0- 6	1	1	10.6			1311	0202	NIGHT	16	15.0	15.2	15.1	15.2	15.3	NONE	-	32.3	32.4	32.4
J 4	0-15	6	6	9.3	7.4	12.5	1411	1348	DAY	22	14.9	15.0	14.9	14.9	15.0	NONE	-	33.2	33.3	33.2
K 1	0- 6	17	17	15.1	4.4	22.0	1811	0842	DAY	15	14.5	14.5	14.5	14.5	14.6	NONE	-	33.2	33.3	33.2
K 2	0-15	1	1	12.5			1811	0929	DAY	20	14.1	14.7	14.4	14.2	14.7	NONE	-	32.3	33.8	33.2
K 3	0-15	1	1	6.0			1811	1022	DAY	24	14.7	14.7	14.7	14.7	14.9	NONE	-	33.6	34.0	33.8
K 4	18-24	2	2	11.5	10.6	12.5	1811	0325	NIGHT	33	14.4	14.6	14.5	14.7	14.5	NONE	-	34.1	34.1	34.1
K 5	0-15	1	1	13.1			1811	0155	NIGHT	37	14.5	14.8	14.7	14.8	13.9	NONE	-	34.2	34.4	34.3
L 1	0- 6	3	3	10.9	10.2	11.9	1711	0838	DAY	21	14.2	14.4	14.3	14.2	15.1	NONE	-	31.0	31.6	31.2
L 2	0- 6	2	2	13.7	10.5	17.0	1711	0754	DAY	21	15.0	15.2	15.1	15.2	15.0	NONE	-	33.3	33.5	33.4
L 3	18-24	1	1	11.9			1711	0707	DAY	32	14.8	15.0	14.9	15.1	15.0	NONE	-	33.3	33.8	33.5
M 1	0- 6	43	43	9.7	6.6	14.0	1611	1530	DAY	26	14.8	14.9	14.8	14.9	14.7	NONE	-	33.4	33.5	33.5
M 2	0- 6	67	37	8.0	5.0	11.4	1611	1440	DAY	20	14.9	15.1	15.0	15.1	15.0	NONE	-	33.7	33.8	33.7
M 4	0- 6	10	10	9.9	6.5	11.4	1611	2339	NIGHT	41	17.5	17.6	17.5	17.6	17.9	NONE	-	35.0	35.1	35.1
N 1	0- 6	1	1	10.7			1611	1034	DAY	25	16.4	16.4	16.4	16.4	16.4	NONE	-	34.0	34.0	34.0
N 2	0-15	14	14	9.0	4.3	11.4	1611	0937	DAY	26	18.6	18.8	18.7	18.8	18.9	NONE	-	35.5	35.6	35.6
N 3	0-15	3	3	7.2	5.1	11.1	1611	0833	DAY	30	19.3	19.5	19.4	19.3	19.4	NONE	-	35.6	35.8	35.8

AGE AND GROWTH OF PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

THOMAS A. DARK[1]

ABSTRACT

The age and growth of Pacific hake, *Merluccius productus*, collected off California, Oregon, and Washington in 1964-69, were studied.

The age determination procedure was examined and considered to provide valid ages.

Several sources of variation in the age structure of the population were given cursory examination. Relative size of the year class and sampling area (average age tends to increase with latitude) contribute substantially to the variation of the population age composition while sex and sampling season have lesser effects.

Growth in length is rapid during the first 3 yr after which it slows and approaches an asymptote in the oldest ages, 10-13 yr. Females have a faster rate of growth than males and tend to survive 2 or 3 yr longer, to age 13. Growth in length can be adequately described by the von Bertalanffy growth equations: $l_t = 56.29\ (1\text{-}e^{-0.39\ (t\text{-}0.20)})$ for males and $l_t = 61.23\ (1\text{-}e^{-0.30\ (t\text{-}0.01)})$ for females. Year class variation in growth rate was detected by back-calculation, using the body length (Y) -otolith radius (X) relationship $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$. Growth in weight was determined by use of the length-weight equations: $\log W = -1.45990 + 2.55618 \log L$ for males and $\log W = -1.68944 + 2.69509 \log L$ for females. Males attain an average weight of about 1,211 g by age 11 and females reach an average weight of 1,374 g by age 13. Annual instantaneous growth rates in weight were computed and were found to decrease most during the fourth year for both sexes and very little growth occurred after the sixth year for males or after the ninth year for females.

The Pacific hake, *Merluccius productus*, is a common gadid fish that ranges from the Gulf of California to the Gulf of Alaska (Hart 1973) but is most abundant from Baja California to southern British Columbia (Alverson et al. 1964). There is apparently a single population offshore and another in Puget Sound, Wash. (Utter and Hodgins 1971). The Puget Sound population supports only a small fishery and is not considered in this report.

Feeding adult hake are usually found over the continental shelf and exhibit pronounced diel movement. During the day they are most commonly found in compact schools near the seabed, but as darkness approaches the schools rise and become more loosely structured. During their spawning period mature hake are more pelagic in behavior than during the rest of the year. They apparently spawn at intermediate depths in water 1,000 m deep or more and demonstrate little diel movement (Nelson 1967). Spawning occurs from January through April off northern Mexico and southern California (Ahlstrom and Counts 1955). Eggs and larvae are pelagic and are found mostly near the thermocline at depths of about 45 to 100 m. It is not clear at what age juvenile hake leave their pelagic phase and become more closely associated with the seabed. One-year-old hake are found in inshore waters off southern California, associated at times with schools of northern anchovy, *Engraulis mordax* (Dark et al. 1970). Hake, 1 to 3 yr old, are taken in shrimp trawls along the Oregon and California coasts (Morgan and Gates 1961). Pacific hake less than 4 yr old are rarely found north of Oregon. Most 4- to 13-yr-old hake mature and are found feeding off the coasts of Oregon, Washington, and southern British Columbia during the spring and summer. By early winter only a small portion of the summer population remains in these areas.

Temporal and areal distribution of the various life history stages suggest that adult Pacific hake undertake extensive annual migrations along the west coast of North America (Alverson and Larkins 1969). Most adult hake seem to move northward along the coasts of California, Oregon, and Washington in early spring on a feeding migration as far north as central Vancouver Island. In late fall the adults begin a return

[1] Northwest Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

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migration to the south which terminates in the spawning area off southern California and Mexico. The eggs and larvae drift onto the continental shelf and the young inhabit the waters of California and Oregon as 1-to-3 yr-olds. Some 3-yr-olds and most 4-yr-olds become sexually mature (Best 1963) and are recruited to the adult population.

Pacific hake were landed in small quantities in California ports as early as 1879. California landings from 1916 to 1951 varied from about 0.2 to 90 metric tons. An animal food fishery developed in 1952 creating an increased demand for low value species and hake landings increased to about 590 metric tons in 1956. From 1956 to 1968, landings averaged about 200 metric tons annually.

Prior to 1965 Washington and Oregon fishermen did not purposefully fish for hake and, in fact, considered them a nuisance species. In 1965 a small fishery was initiated under the guidance of the U.S. Bureau of Commercial Fisheries (BCF)[2] to examine the feasibility of efficiently harvesting Pacific hake off Washington and Oregon. Four vessels began fishing commercially in 1966 because favorable results were obtained from the feasibility study and a new fish reduction plant had begun operations at Aberdeen, Wash. During the same year a large Soviet trawl fleet appeared off the Washington-Oregon coast fishing for rockfish, *Sebastes* spp., and Pacific hake. Competition from the Soviet fleet was so severe that it seriously threatened the existence of the U.S. fishery. Negotiations between the United States and the Soviet Union in February 1967 resulted in an agreement which restricted the size of the Soviet fishing area off the southern Washington coast. The U.S. fleet was more successful in 1967 because of a reduction of Soviet competition and increased efficiency of U.S. vessels. This greater efficiency stemmed from the increased experience of fishermen, improved fishing gear, and greater scouting capability. The total U.S. catch in 1967 was 8,381 metric tons (catch-per-unit-effort [CPUE] = 4.5 metric tons/h), as compared to a total catch of 1,694 metric tons (CPUE = 3.0 metric tons/h) in 1966 (Nelson 1970). Soviet catches in 1966 and 1967 were about 136,050 and 170,590 metric tons, respectively. Since 1967 the Soviets have continued to fish for Pacific hake and annual catches have averaged about 140,000 metric tons. The U.S. fishery was discontinued in 1968 when the reduction industry, facing a depressed fish meal market, was unable to give vessel owners prices that were competitive with those offered by the shrimp and groundfish processors (Pereyra and Richards 1970).

An agreement pertaining to the joint exploitation of groundfish in the northeast Pacific Ocean was negotiated between the United States and the Soviet Union in 1967 and renegotiated in 1969 and 1971. Scientific meetings have been held annually to discuss problems of mutual concern such as assessing the size of the Pacific hake population, determining the effects of the fishery, and estimating rates of growth, mortality, and maximum sustainable yield. Recommendations resulting from the scientific meetings provide a basis for modification of the bilateral fishery agreement—which can be done every 2 yr.

Initial growth estimates were based on preliminary data but served to provide essential real time estimates of maximum sustainable yield. Subsequently, additional data have been collected allowing for refinement of early growth estimates. The objectives of the present study were to provide new estimates of the growth rate of Pacific hake and to examine some of the potential sources of variation. An analysis was made of the reliability of the age determination method used since age information is basic to growth studies. The variability in the age structure of the Pacific hake population was also examined since age composition is frequently used to evaluate relative year class strengths, mortality rates, and the effects of fishing.

SAMPLING

Collection Methods

Biological data were collected from two sources: "commercial" samples from the commercial fishery and "research" samples taken aboard research vessels.

Commercial samples were taken mainly in 1966-67 when a U.S. hake fishery was conducted off the Washington coast during May-September. A sampling station was established at the reduction plant in Aberdeen, Wash., where essentially all hake taken off Washington and Oregon were landed. An attempt was made to man the station every other week and to sample the catches as they were unloaded at the plant. Irregular landing schedules, especially in 1966, resulted in sporadic

[2]Presently, the National Marine Fisheries Service.

sampling. In some sampling weeks, landings were made during 3 or 4 days while in other weeks there were no landings. Landings were sampled as fish moved from the vessel to the plant over a conveyor system. Approximately 200 specimens were collected for each sample. Specimens were first dissected to determine the sex, then were measured (to the nearest centimeter) from the snout to the fork of the tail. An otolith was removed for age determination and, when time allowed, whole specimens were weighed to the nearest decagram.

To simplify the collection of otoliths, most otolith samples were stratified by 1-cm body length intervals. Otoliths were taken from five males and five females in each length interval until the sample was exhausted. Although average length-at-age information can be taken directly from such stratified samples, randomization was necessary to obtain unbiased estimates of age composition.

Research vessel samples were collected from 1964 through 1969 and were both stratified and random. Most research vessel samples were processed at sea for the same biological data as those taken from commercial samples. When weights were taken a small hand-held steelyard was used which provided more consistent readings than did spring scales.

The research vessel samples used herein are geographically and temporally restricted simply because it was beyond the capability of a single vessel to conduct more extensive sampling. The samples taken at the reduction plant in 1966-67 provided the best temporal coverage over a season, but their areal distribution was restricted mainly to fishing grounds off Grays and Willapa Harbors, Wash.

Sample Representativeness

Whereas the nature of available samples places constraints on some aspects of the following study, the large number and size of samples collected over several years and over a large part of the species' geographical range render them valuable in examining the reliability of earlier estimates of growth (Best 1963; Tillman 1968). Also, some of the more conspicuous variations in both growth rates and age composition can be examined.

Figure 1 gives a general representation of the distribution of sampling effort in 1964-69. The adult portion of the population (4- to 13-yr-olds) occurring off the coast of Washington during the summer was the most intensively sampled, especially in 1966-67 when commercial samples were taken. Research vessels sampled adults off Washington, Oregon, and California, mostly during the summers of 1965-67. Juveniles (1- to 3-yr-olds) were sampled only sporadically and much less intensively. In the winters of 1965 and 1968, research vessels searching off southern California and northern Mexico for spawning hake obtained some samples of 1- and 2-yr-old specimens. Very few 3-yr-old hake were captured, probably because there was relatively little sampling effort in areas where they were likely to be most abundant.

Commercial vessels fishing for Pacific hake off Washington used Cobb pelagic and BCF universal trawls (Johnson and High 1970). The stretched mesh size varied from 5.1 to 7.6 cm in the trawl bodies and cod ends. Research vessels used the

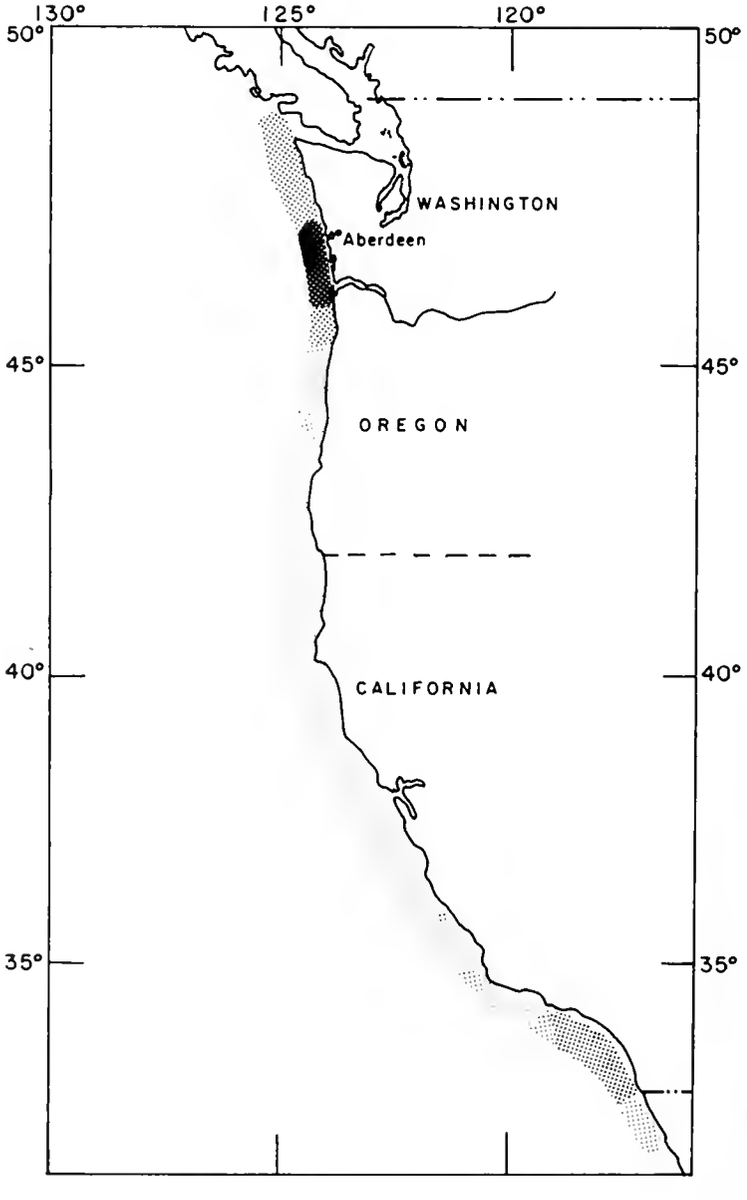


FIGURE 1.—Distribution of sampling effort for Pacific hake, 1964-69. (Darker stipling infers more intensive sampling.)

same trawls, but with 3.8-cm liners in the cod ends much of the time. Liners were used to determine the availability of the youngest age groups. Research and commercial samples were never taken in such a manner that length frequencies could be compared to isolate the effects, if any, of the 3.8-cm liner. But there was probably no significant selection for fish length without the liner since similar unlined trawls used in the Puget Sound hake fishery apparently retain all fish of 35 cm or greater.[3] Because very few hake off Washington were as small as 35 cm, sampling gear differences were not considered to be a significant source of sampling error. Therefore research and commercial samples taken in 1966-67 were combined at times to increase sample sizes and to improve temporal and areal sampling coverage.

DETERMINATION OF AGE COMPOSITION

Aging Technique

A prerequisite to any growth study is a method for reliably determining the age of individual fish. European investigators (Birtwistle and Lewis 1925; Hickling 1933; Bagenal 1954) found the otolith to be the most useful structure in determining the age of the European hake, *Merluccius merluccius*. Bigelow and Schroeder (1953) arrived at the same conclusion while studying the silver hake, *M. bilinearis*. Apparently Best (1963) was the first to age Pacific hake. He found that from the standpoint of availability otoliths were superior to scales as most scales were absent on trawl-caught specimens.

Our collection of otoliths was standardized in an effort to control sampling variation. Samplers attempted to always collect the otolith from the right side of the head to avoid any confounding effects due to possible otolith asymmetry. If the right otolith was damaged during the extraction process, the left otolith was accepted as an alternate (5-10% of all samples). Otoliths were thoroughly cleaned and preserved in a solution of 10-30% ethyl alcohol. Occasionally otoliths with a uniform chalky appearance were encountered and were cleared by dipping them in a weak solution of hydrochloric acid. This practice was followed with care to prevent the dissolution of annuli at the otolith edge.

Otoliths were placed in a petri dish with the bottom painted black, illuminated with a reflected light, and read under a dissecting microscope at a magnification of 6.6×. Each otolith was read by two readers and if the ages did not agree, as was the case in 25-40% of the otoliths processed, the otolith was examined by a third reader. The best estimate of age was taken as the age agreed upon by any two readers. When all three readers disagreed (about 5% of the readings), the middle reading was used. If one reader could not make a determination and agreement could not be reached by the other two, the otolith was considered unreadable. Generally there was a 3-5% rejection rate.

The majority of the hake otoliths were collected during the summer (May-September). Assuming that the past winter was represented by the last (most recent) translucent zone, the age was taken to be simply the total number of translucent zones on the otolith. The few winter (February-March) samples collected were composed mainly of fish completing their first or second year of life. The same aging criteria cited above were applied to winter samples, except those otoliths without a translucent zone were assigned to age "1" instead of "0." This was done on the premise that the translucent zone would have been deposited shortly after the sample was taken, since young of the year would not have been captured by the sampling gear.

Validity of Aging Technique

Because the use of otoliths in aging Pacific hake had not been completely evaluated, some attention was devoted to determining the reliability of the procedure. Graham (1929) gives three indirect methods of evaluating the use of scales and otoliths for age determination: 1) agreement with Petersen's (1895) method; 2) seasonal changes in scale or otolith margins; and 3) observation of a strong year class over a period of years.

The Petersen's (1895) method, which compares the relative abundance of age groups as determined by length distribution with age groups as determined by analysis of scales, otoliths, or other structures, is generally only applicable to the first three or four age groups. For Pacific hake, the length distributions of the age groups overlap extensively after age 3, restricting the use of the

[3]Larkins, H. A., H. H. Shippen, and K. D. Waldron. Features of a northern Puget Sound hake population. Unpubl. manuscr. Northwest Fish Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

method to the first three age groups. Because few 2- and 3-yr-old hake were present in the samples, Petersen's (1895) method could not be effectively applied.

According to Graham's (1929) second method, observations of the development of translucent and opaque zones on the perimeter of the otolith (based on data from a population that had been sampled periodically during a year) may provide an indication of the frequency with which the zones are formed. A single occurrence of a particular zone during a year would provide an annual mark which may be suitable for age determination. In European hake (Hickling 1933) opaque zones have been associated with good physical condition and growth whereas translucent zones have been associated with a lesser physical well-being and retardation or cessation of growth. Poor condition can result from a decrease in the food supply, the onset of maturation and spawning, or both.

For the present study a special effort was made to record the zone type on the edge of all hake otoliths collected during 1967. Samples were taken during March, April, May, June, and August. Otoliths from a sample collected in November 1969 were added to the above spring and summer samples for data on the winter appearance of the edge. It appears that there are long and overlapping periods when zones are deposited because most samples had some otoliths with opaque margins and others with translucent margins. One exception is the small, March 1967 sample that contains only 1-yr-olds. Even though opaque edges are plainly recognizable in the young age groups, all otoliths in this sample had translucent margins.

The persistent occurrence during the summer (the apparent growing season) of otoliths with a translucent edge may be at least partly because the newly deposited opaque material is not always detectable due to the thinness of the edge and the resulting transparency.

Figure 2 demonstrates that the frequency of opaque edges decreases rapidly with the age of the fish. This is almost certainly a bias resulting from the increased difficulty in distinguishing the zone type on the edge of the otolith as the fish becomes older. Opaque bands on the otoliths of young fish (1-4 yr) growing at a relatively fast rate are wide, dense, and readily distinguishable. As growth slows in older specimens, new opaque zones become narrower, and are not always apparent

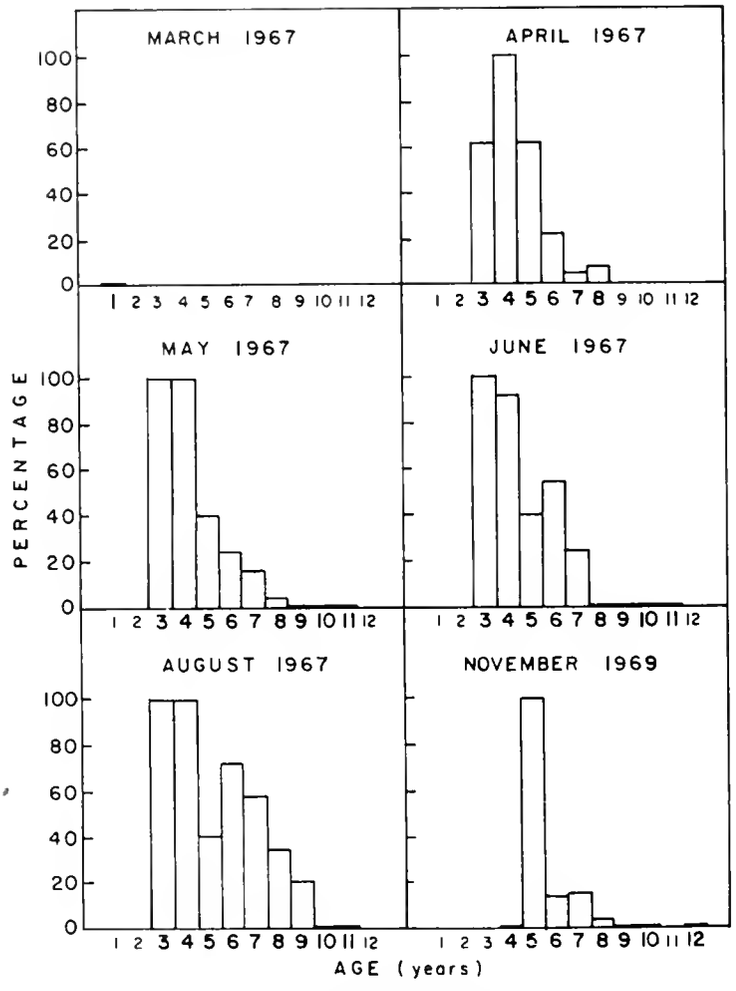


FIGURE 2.—Percentage of otoliths with opaque edges by age group (ages actually observed in bold print).

until late in the growing season or until bordered by a new translucent zone.

Because the zone type on the edge of the otolith is related to the age of the fish, a comparison of otoliths could be misleading if the sample age compositions vary to a large extent. Whereas the age compositions of the 1967 samples were similar, the age composition of the 1969 sample was noticeably different (Figure 3). To avoid the effects of advanced fish age on a reader's ability to accurately judge opaque zones at the otolith edge type, samples of 6-yr-olds taken in April-November and one sample of 1-yr-olds taken in March were compared in Figure 4. The graph suggests that Pacific hake start to deposit opaque material around April. The time of deposition may vary with age, but other age groups were not present in numbers adequate for comparison. The incidence of otoliths with opaque edges increased steadily through August when it peaked at about 72%. A dramatic decrease in otoliths with opaque edges occurred in the November sample. The foregoing analysis indicates that the physical well-being of Pacific hake improves in early spring

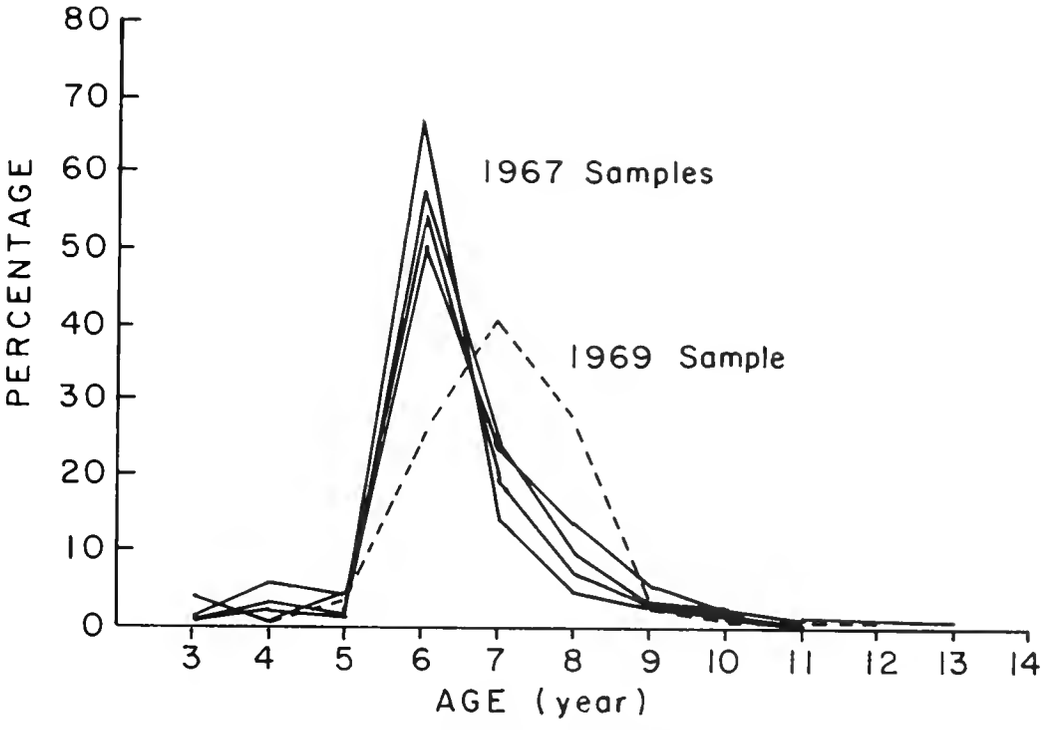


FIGURE 3.—Age composition of samples selected for analysis of zone type on the otolith edge.

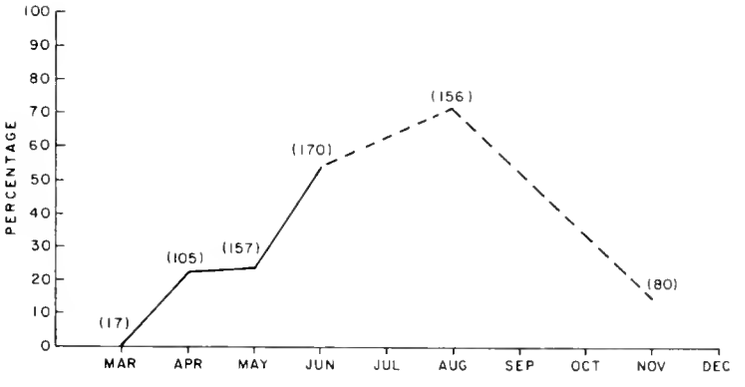


FIGURE 4.—Percentage of otoliths with opaque edges by month of collection, 1967-69. (Sample size occurs in parentheses.)

(indicated by the appearance of the opaque zone in the otolith edge). Growth occurs throughout the summer until sometime after August. The onset of maturation and the spawning migration in late fall probably place additional demands on the energies of the animal, resulting in slowed growth which is reflected in the appearance of the translucent zone at the otolith edge.

Although observations are not available during all months, the unimodal characteristic of the curve in Figure 4 strongly suggests that one opaque and one translucent zone are deposited each year and that the zones provide reliable annual marks. However, comprehensive monthly sampling is required to confirm unimodality.

The third method suggested by Graham (1929) is based on the rationale that if a predominant year class enters a population of fish and if the aging technique is reasonably reliable, then the year class should be observed progressing normally through the population age structure for several years.

Fortunately the 1961 year class of Pacific hake was extremely strong when it was partially recruited (designated as 4-yr-olds) to the adult hake population in 1965. In that year the 4-yr-olds comprised 15% of the adult population off Washington, while in other years from 1964 to 1969, 4-yr-olds contributed only 0-2%. In 1966 sampling indicated that over 50% of the adult population off Washington was composed of 5-yr-old hake. The dominance of the 1961 year class evidently continued through 1967, when over 70% of the population was 6-yr-olds; 1968 when about 64% was 7-yr-olds; and 1969 when about 24% was 8-yr-olds (Figure 5). In contrast, from 1964 to 1968, 8-yr-olds comprised only 2.4-13.7% of the population. This movement of the 1961 year class through the population age structure is accepted as additional evidence that the translucent zone represents a single annual mark.

Randomization of Age Samples

As noted previously some otolith samples used herein were collected aboard research vessels and are considered to be random, but the majority were commercial samples in which otoliths were

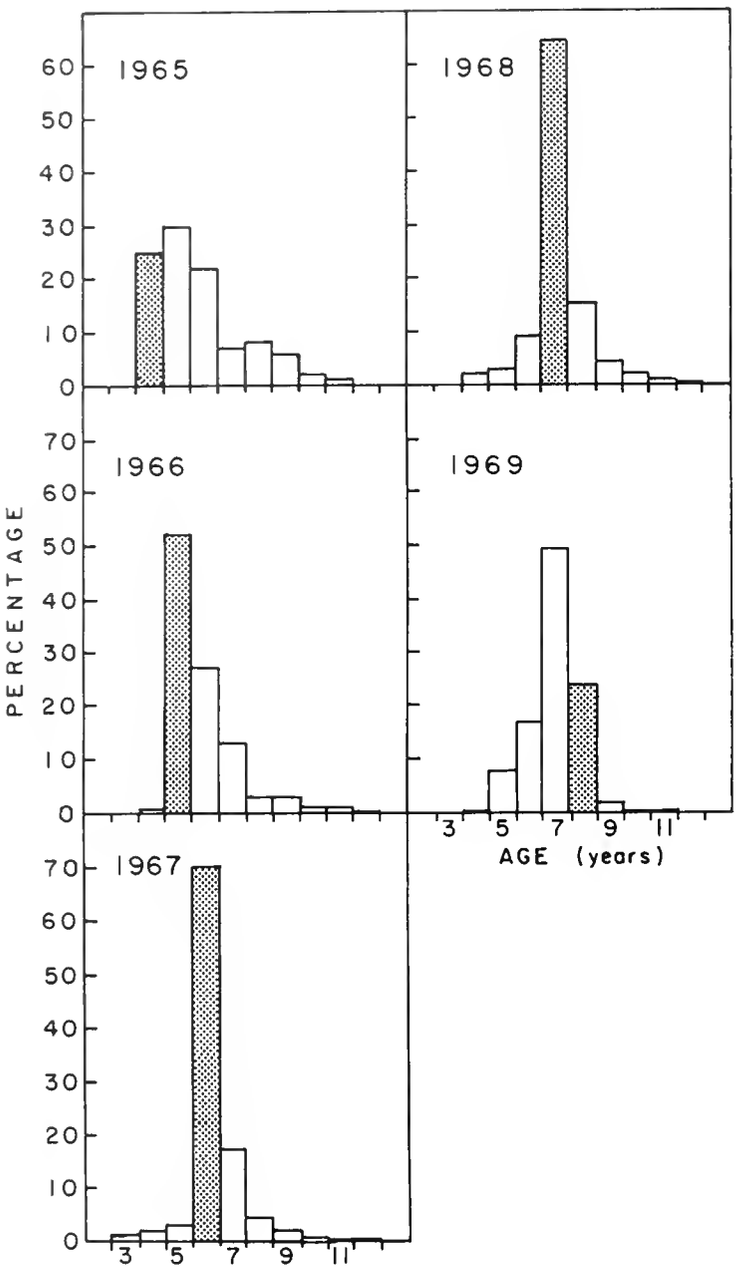


FIGURE 5.—Age composition of Pacific hake taken off Washington during May-August, 1965-69. (Shaded bar denotes the 1961 year class.)

collected in a stratified manner. Before the commercial samples could render representative age compositions, they had to be randomized. This was accomplished by constructing an age-length key for each sample. The percentage age frequency per length interval observed in stratified subsamples was applied to the length frequency distribution of the entire sample.

VARIABILITY IN AGE COMPOSITION

Several potential sources of variation in age composition were analyzed using research and commercial samples. Age composition is used for evaluation of the effects of fishing, estimation of recruitment, growth, and mortality. Therefore the major sources of sampling variation should be identified. The effects of annual, seasonal, latitudinal, and sexual variation are considered in this section.

Annual Variation

Annual variation in age composition was studied using samples collected off the Washington coast during May-September 1965-69. It has been assumed (Tillman 1968; Nelson and Larkins 1970) that Pacific hake are fully recruited to the fishery at age 5. If this assumption is valid and if recruitment and mortality rates are constant then one would expect, from a relatively unexploited population, a typical catch curve with the 5-yr-olds most numerous and the succeeding ages decreasing at a rate equal to the rate of natural mortality. This pattern was apparent in 1965 (Figure 5). The partially recruited 4-yr-olds were not as numerous as the 5-yr-olds which predominated. From age 5 there was a progressive decrease in the relative abundance of succeeding age groups until only a few 13-yr-olds remained. By examining the age compositions in subsequent years, it became obvious that the 4-yr-old age group in 1965 was considerably larger than usual. This was the first indication that the 1961 year class was unusually large. In 1966 the 1961 year class (5-yr-olds) was probably fully recruited and strongly dominated the age structure. The relative abundance of the incoming 1962 year class (4-yr-olds) was much smaller than the 1961 year class in the 1965 samples. The 1961 year class can be followed through the age composition in 1967-69. In 1969 the 1961 year class lost its dominance to the 1962 year class, but still produced extraordinarily large numbers of 8-yr-olds. Apparently the 1965-66 year classes were smaller than those observed previously since in the 1969 sample no 4-yr-olds were observed.

Obviously annual variation in age composition does occur in Pacific hake and is at least partly due to varying levels of recruitment of incoming year classes.

Seasonal Variation

In 1966-67 regular sampling of Pacific hake from off the southern coast (lat. 46°00′-46°59′N) of

Washington occurred throughout the fishing season. These samples were combined as "early" (collected in May-June), "middle" (July), and "late" (August-October) samples for the purpose of identifying any gross seasonal changes in age composition (Figure 6). The 1966 early sample contains somewhat fewer 5-yr-olds and more 6-yr-olds than either the middle or late samples which are very similar. For all practical purposes, the age compositions of the three 1967 samples are identical. There is little evidence in these comparisons to suggest that there is significant change in age composition during the time the Pacific hake are present in commercial quantities off southern Washington. The paucity of samples appropriate for further comparisons precludes assessment of seasonal age composition variation which may occur at other times and places.

Latitudinal Variation

Variation occurs in the age composition of Pacific hake samples taken from different portions of the latitudinal distribution (Nelson 1967; Tillman 1968). Table 1 is adapted from Tillman's table 14 to show the percentage age composition

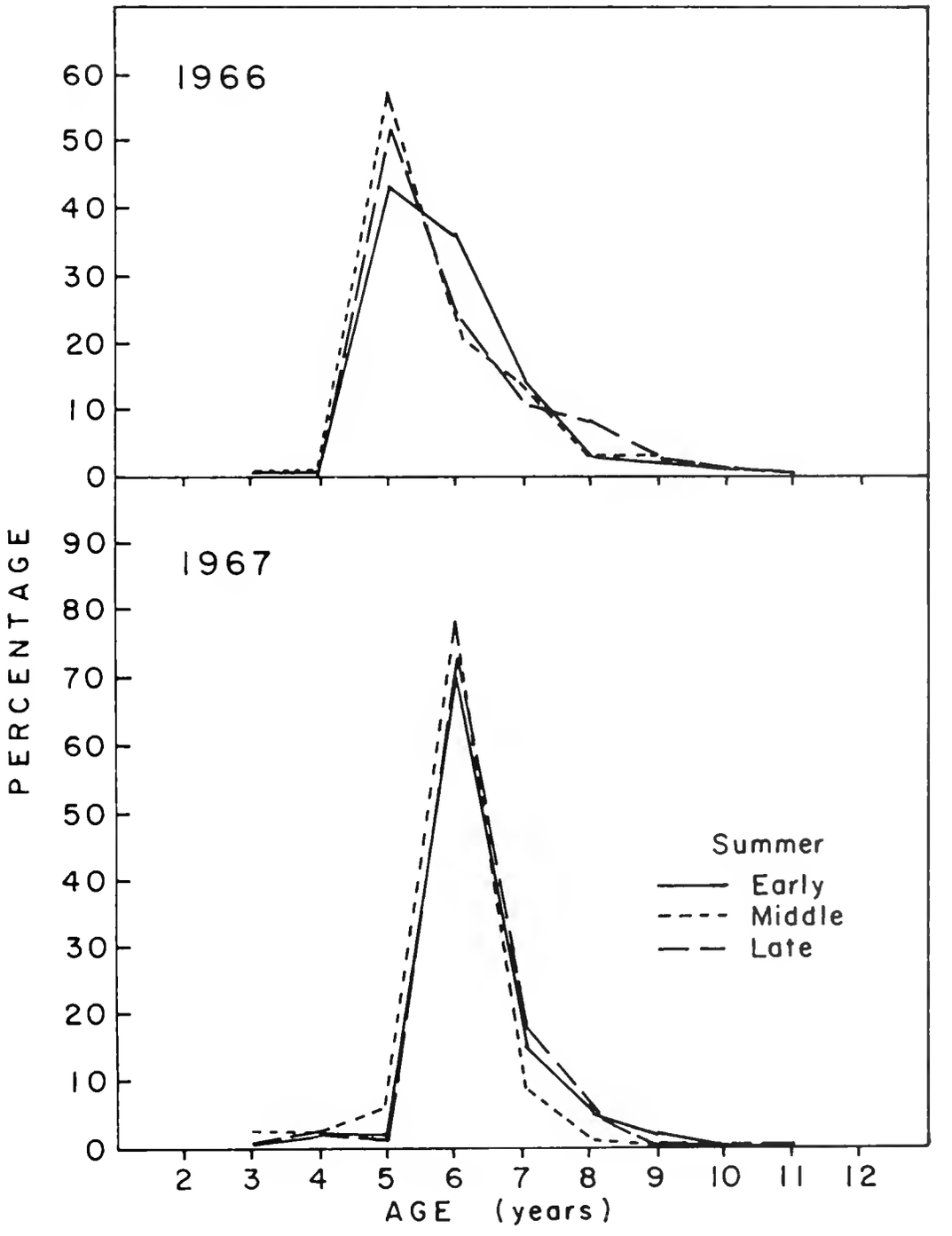


FIGURE 6.—Age composition of Pacific hake collected off southern Washington (lat. 46°00'-46°59'N) by early, middle, and late summer periods.

TABLE 1.—Age composition (percentage) of hake taken off Washington, Oregon, and California in 1965 by research vessels (adapted from Tillman 1968).

Age (years)	Washington			Oregon			California		
	Male	Female	Sexes combined	Male	Female	Sexes combined	Male	Female	Sexes combined
1	—	—	—	—	—	—	0.2	1.5	0.6
2	—	—	—	—	—	—	1.8	4.0	2.4
3	—	—	—	—	—	—	3.8	6.9	4.7
4	13.0	22.5	17.7	26.8	46.4	37.2	44.4	38.2	42.6
5	28.9	20.6	24.7	37.0	27.6	32.0	29.8	25.1	28.4
6	27.2	23.8	25.1	22.8	11.9	17.0	8.1	10.6	8.8
7	13.5	5.2	8.5	4.1	4.6	4.4	5.1	5.5	5.2
8	12.9	10.6	11.5	9.1	4.3	6.6	3.5	5.1	4.0
9	3.0	10.3	7.4	0.1	3.9	2.1	2.7	2.5	2.6
10	1.4	4.9	3.5	—	0.6	0.3	0.4	0.6	0.4
11	—	1.4	0.9	—	0.5	0.3	0.1	—	0.1
12	—	0.6	0.4	—	—	—	0.1	—	0.0
13	—	—	—	—	0.1	0.1	—	—	—
Sample size	1,474	2,196	3,670	810	914	1,724	1,586	670	2,256

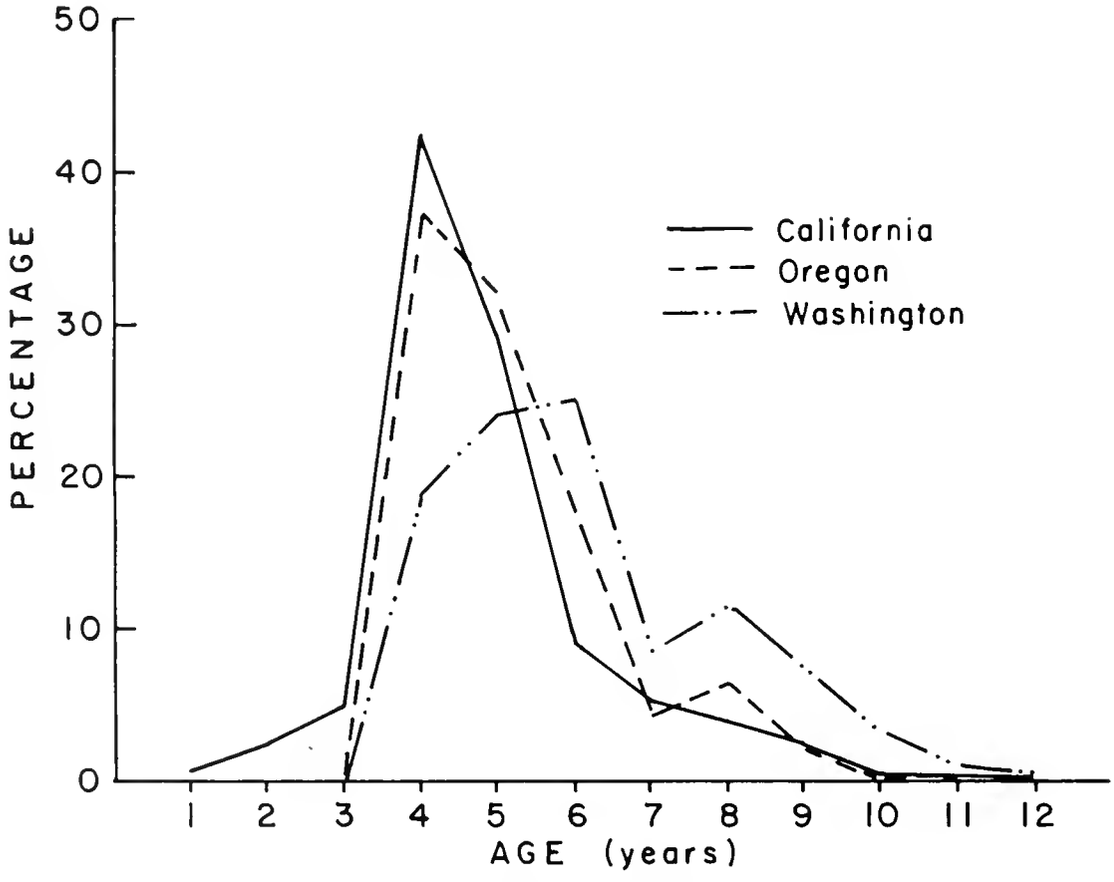


FIGURE 7.—Age composition of Pacific hake collected off California, Oregon, and Washington in 1965.

for research vessel samples taken off Washington, Oregon, and California in 1965. These samples were used because they provided the best geographic coverage and were taken with similar trawl gear, equipped with small-mesh cod end liners capable of capturing juvenile hake. The age composition of the California sample probably does not truly reflect the relative abundance of the age groups. The southern distribution and abundance of adult hake was a primary consideration at the time of sampling and, because the very young hake normally are not found associated with the adults, they probably were not taken in proportion to their abundance. Figure 7 shows, however, that samples taken off California included 1-, 2-, and 3-yr-olds, which did not occur in Washington and Oregon samples. Washington and Oregon samples composed of fish 4-yr-old and older were considered to be representative of the population in those areas. There is a smaller per-

centage of 4-yr-olds and a greater percentage of 5- and 6-yr-olds in the Oregon sample than in the California sample. Similarly, the Washington sample contains a much smaller percentage of 4-yr-olds and a greater percentage of nearly all the older age groups than does the Oregon sample. It cannot be clearly demonstrated whether there are in fact fewer 4-yr-olds in the hake population off Washington or whether additional older specimens are recruited, depressing the relative abundance of the 4-yr-olds. However, since 3-yr-old hake are not recruited to the Washington fishery and it is difficult to rationalize the sudden occurrence of additional large numbers of older, adult fish not found off Oregon and California, the most likely event is that the 4-yr-olds are only partially recruited off Washington and are not as numerous as they are off Oregon.

In May, July, and October 1965 and in August 1966, samples were available from off the Washington coast from lat. 46°00'N to 48°59'N. For each year the samples were grouped by half degree intervals of latitude and compared in Figure 8 to determine if changes in age composition among smaller spatial units than used in the foregoing discussion could be detected. The 1965 samples were collected during a period of several months but, as indicated in a previous section, seasonal (spring-fall) variation should not be a significant factor. Although there is considerable random variation in the relative abundance of an age group among areas, there appear to be some

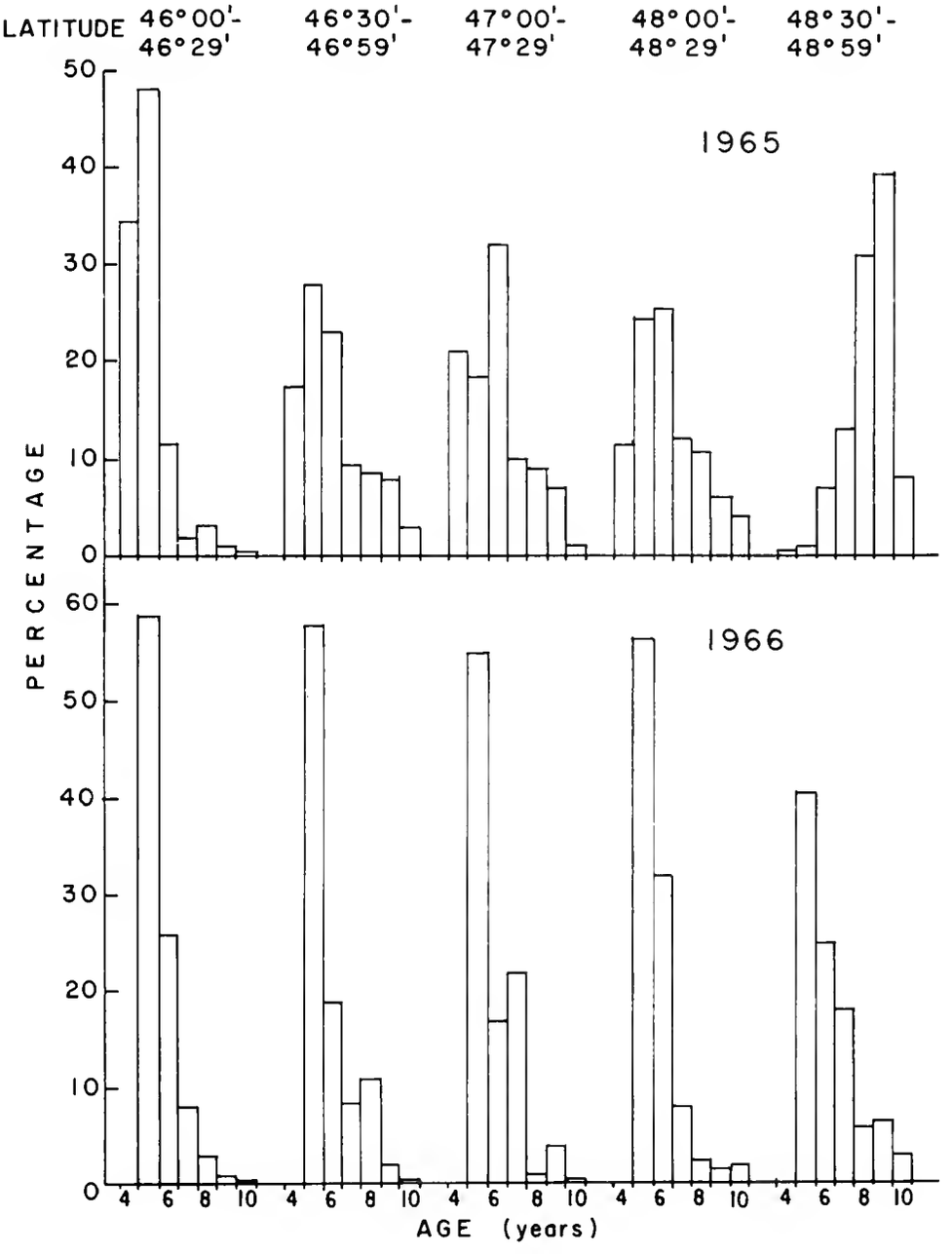


FIGURE 8.—Age composition of Pacific hake taken at various latitudes off Washington in 1965-66.

trends associated with latitude. Generally, the relative abundance of 4- and 5-yr-olds tended to decrease as sampling progressed from south to north while the relative abundance of 7- to 10-yr-olds tended to increase. This is consistent with observations over a larger sampling area.

In summary, 1-, 2-, and 3-yr-old Pacific hake are rarely encountered north of California and, as sampling progresses northward along the Washington coast, the younger age groups (4- and 5-yr-olds) contribute less to the population while the relative abundance of the older age groups (7- to 10-yr-olds) increases.

Such latitudinal stratification of age groups, apparently occurring to some extent even within 3 degrees of latitude, compounds the problem of representatively sampling the age composition of not only the entire hake population, but also the commercially available portion of the population. This spatial variation should be considered when comparing annual changes in age composition.

Sexual Variation

Pacific hake samples taken off Washington in 1965-69 were used to examine the variation in age composition between male and female components. The percentage of each sex by age group was calculated (Table 2) and plotted in Figure 9. The age compositions for males and females are similar in all years. The greatest difference occurred in 1965 when females contributed a larger proportion of the 4-yr-old group. In all years, a greater percentage of the females occurred in the older age groups (8 yr and older). These results correspond well with earlier observations (Best 1963; Tillman 1968) that females live longer and may be the sole survivors by age 11 and 12. Therefore sampling that is highly selective for sex would provide biased estimates of the relative abundance of older age groups.

GROWTH OF PACIFIC HAKE

Growth in Length

To determine the general shape of the growth curve for Pacific hake, average lengths-at-age by sex were computed using combined data from samples taken off Washington, Oregon, and California during 1965-69 (Table 3).

Growth of both sexes is quite rapid during the first 3 yr, then slows abruptly (Figure 10). Deceleration of the growth rate probably is not as pronounced as indicated. Latitudinal stratification of ages discussed previously is probably a result of stratification by size; therefore, mainly the larger members of the younger age groups would be recruited to the Washington-Oregon area where most samples were collected. Best (1963), for instance, computed the average lengths for small samples of hake (age groups 4-13 consisted of females only) taken off northern California and the 3- to 6-yr-olds were somewhat shorter than those in the Washington-Oregon samples (Figure 10). The most accurate growth curve for 2- to 6-yr-olds would probably fall somewhere between that based on Best's (1963) data and the curves generated from my data. Asymptotic growth has been shown for Cape hake, *M. capensis* (Botha 1969); silver hake (Fritz 1962); and Pacific hake in Puget Sound (see footnote 3). For the purpose of this study it is assumed that the growth curve for the length of coastal Pacific hake is also asymptotic.

Sexual differences in the size at age occur in most hake species (Hickling 1933; Hart 1948; Fritz 1962; Botha 1969), and the Pacific hake is no exception (Figure 10). Females are noticeably longer by age 4, but may be longer even at an earlier age. Larkins et al. (see footnote 3) reported that female Pacific hake of the Puget Sound population are slightly longer than males even as 1-yr-olds. This cannot be demonstrated for coastal hake because sex information was not available for 1-yr-olds and so few 2- to 3-yr-olds were collected that one cannot accept the estimated mean lengths by sex with confidence. Although sexual differences in growth exist, these differences are not large. The maximum difference in mean lengths is 3.12 cm occurring at 11 yr of age (Table 3).

Year class variation with respect to growth was examined by two means: 1) the comparison of age-length data collected in 1965-69, and 2) the back-calculation and comparison of growth rates for five year classes.

Mean body lengths by age for the 1956-62 year classes are found in Table 4 and compared in Figure 11. Only samples taken off the Washington coast were used so that successive year classes could be compared while minimizing any spatial effects. These growth curves generally fall into two sets. Individuals of the 1956-59 year classes were considerably larger at age than the members of the 1961-64 year classes. The growth curve for the 1960 year class falls between the two sets.

TABLE 2.—Age composition (percentage) of male and female hake taken each year off Washington, 1965-69.

Age (years)	1965		1966		1967		1968		1969	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
2	—	—	0.1	—	0.1	0.1	—	—	—	—
3	—	—	0.1	0.1	1.4	1.2	—	—	—	—
4	13.0	22.5	0.3	0.3	1.6	2.6	1.4	2.5	0.1	0.2
5	28.9	20.6	44.2	46.0	5.2	4.5	1.9	2.9	6.9	9.0
6	27.2	23.8	33.1	23.7	62.1	53.6	11.5	7.0	16.6	18.5
7	13.5	5.2	14.5	15.9	22.2	19.7	68.6	60.3	55.7	41.3
8	12.9	10.6	3.1	6.7	5.4	10.2	13.3	17.2	19.7	28.2
9	3.0	10.3	3.2	3.3	1.2	4.8	2.3	4.8	1.0	2.5
10	1.4	4.9	0.7	1.8	0.6	2.2	0.9	3.2	—	0.1
11	—	1.4	0.7	1.5	0.1	0.9	0.2	1.4	—	0.1
12	—	0.6	—	0.5	0.1	0.2	—	0.4	—	—
13	—	—	—	0.1	—	—	—	0.3	—	—
Sample size	1,474	2,196	1,355	1,724	1,195	1,432	1,047	1,546	1,009	811

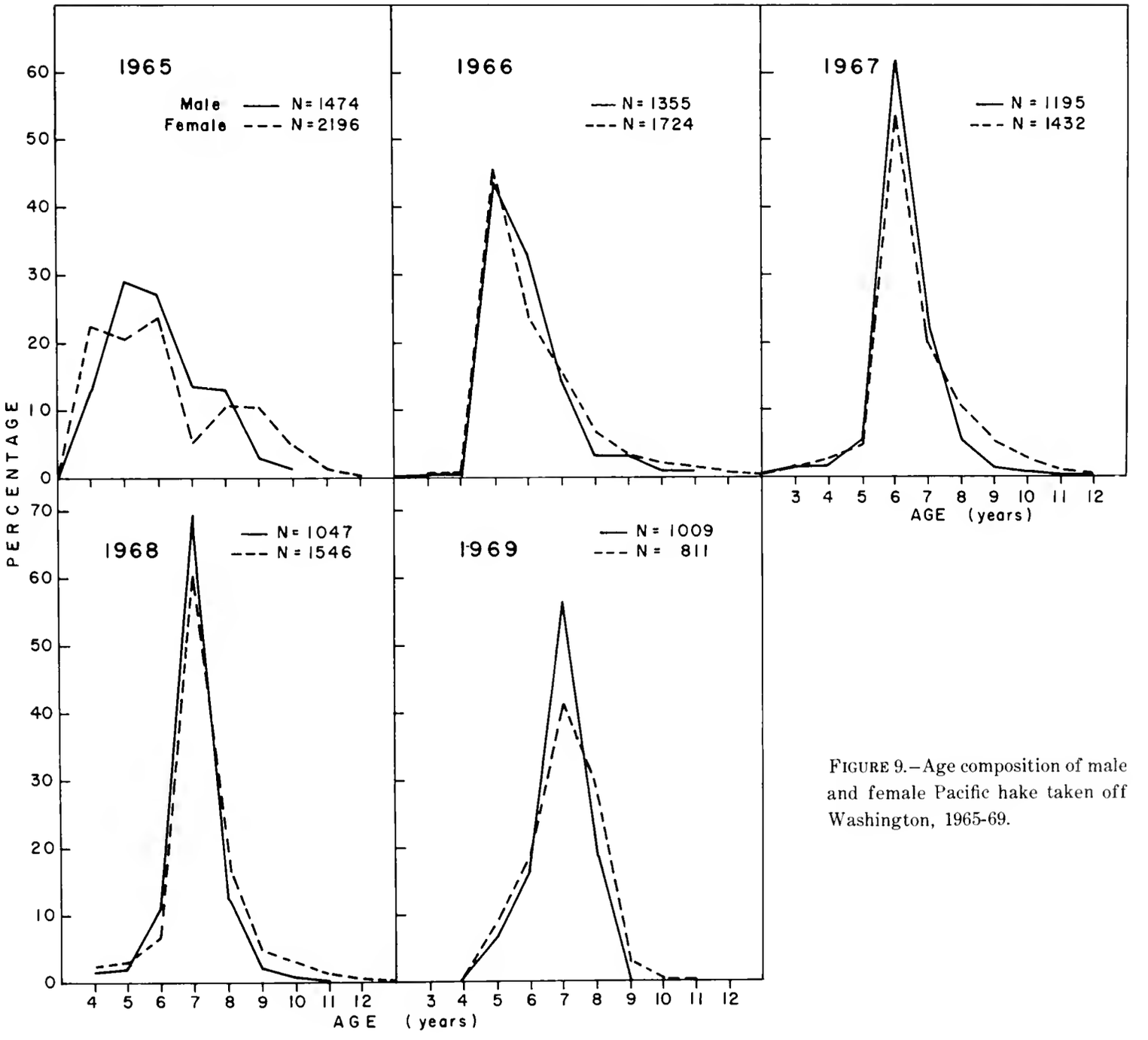


FIGURE 9.—Age composition of male and female Pacific hake taken off Washington, 1965-69.

TABLE 3.—Average body length at various ages for male and female hake taken off California, Oregon, and Washington during 1965-69.

Age (years)	Female		Male	
	Sample size	Mean length (cm)	Sample size	Mean length (cm)
1.0	385	[1]15.40	385	[1]15.40
2.0	36	28.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91	—	—
13.3	6	61.83	—	—
	[2]4,453		[2]4,201	

[1]Assigned value based on the mean of all 1-yr-old hake; sex determinations were not available for 1-yr-olds.
[2]Does not include the unsexed 1-yr-old group.

While there is little variation apparent within year class groups, length at age may vary by as much as 4 cm between year class groups.

These data suggest that some variation in growth can occur among year classes, but the irregular sampling of all ages, particularly the youngest, precludes construction of complete growth curves by year class using length-at-age data. Therefore a back-calculation technique was utilized to reconstruct the growth curves for several year classes as a means of further examining year-class variation.

Back calculation of body lengths was based on an otolith radius-body length relationship derived from hake samples collected in 1966-68. Approximately 10 otoliths (5 male and 5 female) per 1-cm body length interval were selected for

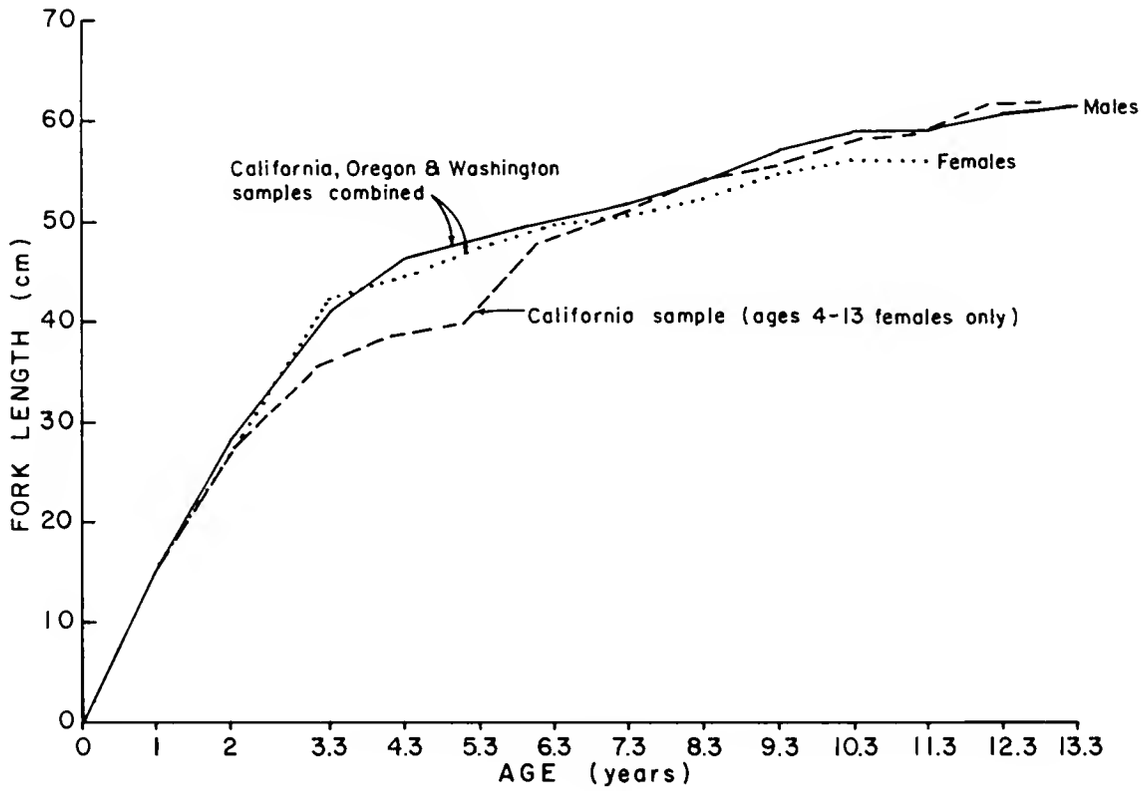


FIGURE 10.—Average fork lengths at various ages for Pacific hake collected off California, Oregon, and Washington combined, and from California alone (Best 1963).

TABLE 4.—Mean body length (cm) at various ages (in years) for 1956-62 year classes of hake.

1956		1957		1958		1959		1960		1961		1962	
Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length
—	—	—	—	—	—	—	—	—	—	—	—	3.0	35.6
—	—	—	—	—	—	—	—	—	—	4.3	44.9	4.5	47.8
—	—	—	—	—	—	5.7	52.5	5.3	48.9	5.5	48.2	5.3	48.7
—	—	—	—	6.7	53.9	6.3	52.6	6.5	51.6	6.3	49.2	6.3	49.7
—	—	7.7	54.2	7.3	53.9	7.5	54.8	7.3	53.2	7.3	50.6	7.5	50.6
8.7	54.9	8.3	55.2	8.5	56.1	8.3	55.9	8.3	54.1	8.5	51.8	—	—
9.3	57.4	9.5	56.8	9.3	56.5	9.3	56.6	9.5	54.2	—	—	—	—
10.5	57.8	10.3	59.7	10.3	58.2	10.5	57.0	—	—	—	—	—	—
11.3	58.7	11.3	58.0	11.5	60.0	—	—	—	—	—	—	—	—
12.3	60.0	—	—	—	—	—	—	—	—	—	—	—	—

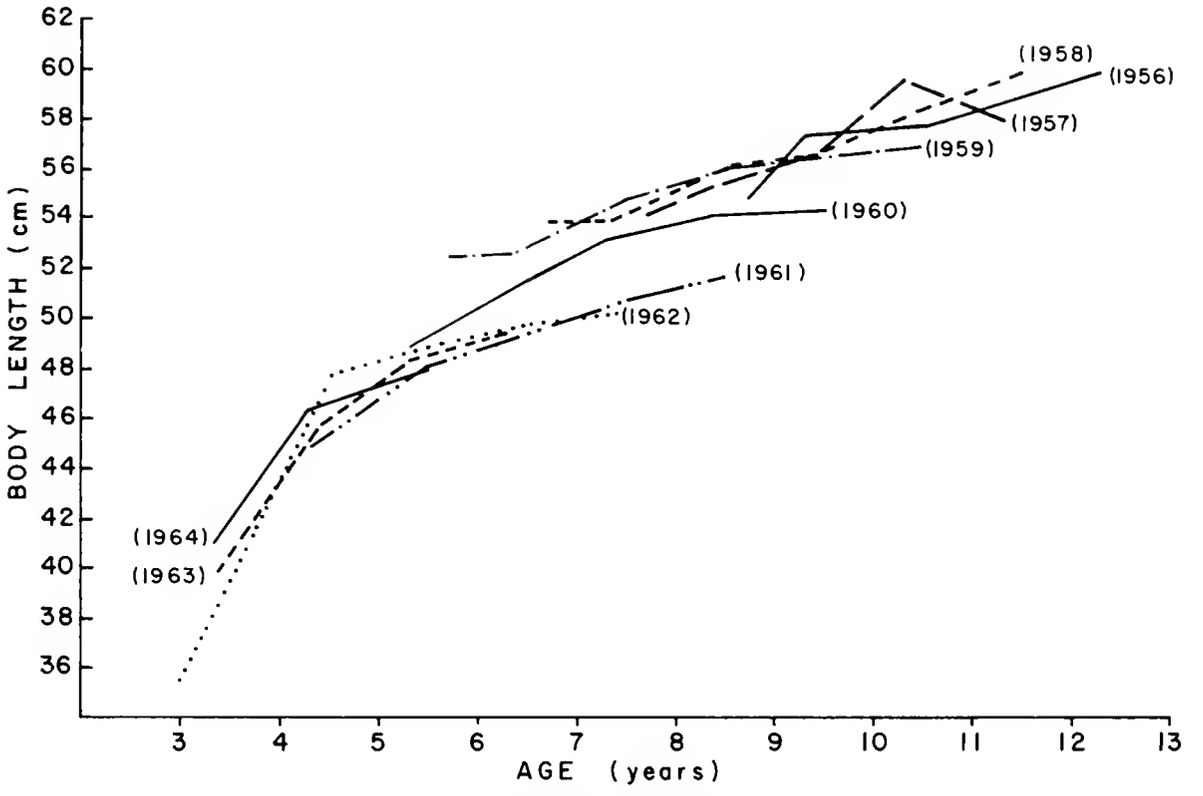


FIGURE 11.—Average fork lengths at various ages by year class (in parentheses) for Pacific hake taken off Washington, 1964-69.

analysis. A sample of 10 was not attained in those centimeter groups near the extremes of the length distribution nor in those length groups where 10 samples were taken but not all otoliths were readable. Fork lengths represented ranged from 11 to 68 cm. To facilitate the measuring all otoliths were photographed and enlargements made so that the prints were 16 times the size of the otoliths. Measurements were taken directly from each print. A midpoint was determined on the photograph of each otolith by measuring the distance from the anterior edge to the posterior edge of the first translucent zone and halving that measurement (Figure 12). Measurements were made from this midpoint to the anterior margin of each annulus and to the anterior edge of the otolith. When annuli were not clearly defined, measurements were not made.

The mean body length per centimeter of otolith radius was computed and plotted in Figure 13. A curve constructed from the individual observations (n = 370) is superimposed on the means. The curve was constructed from a third degree polynomial equation of the form $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$, where Y = estimated body length and X = otolith radius. This equation provided the best fit (smallest residual sum of squares and mean square) of the several functions examined (Table 5). The correlation

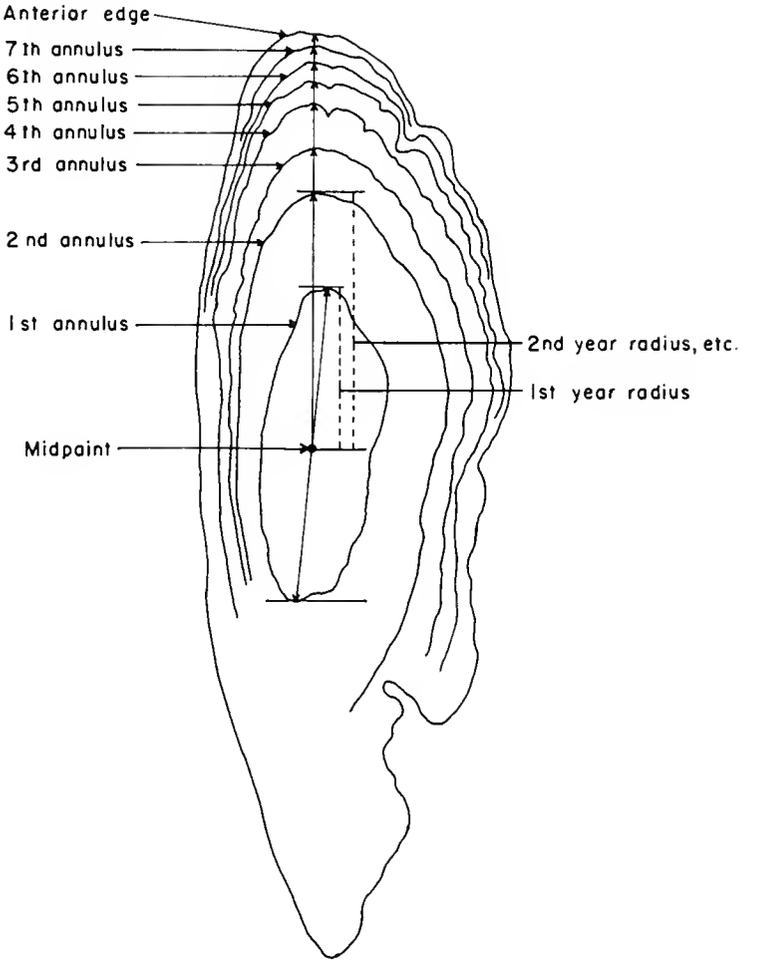


FIGURE 12.—Pacific hake otolith showing the calculated midpoint and measurement intervals from the midpoint to the anterior margins of successive annuli.

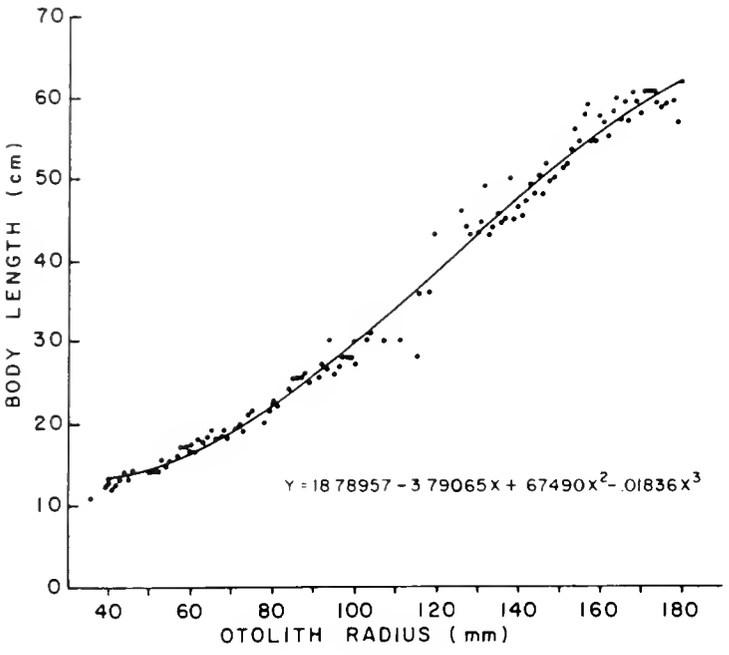


FIGURE 13.—A scattergram of mean body lengths per millimeter of otolith radius (as taken from a 16× photographic enlargement) and superimposed curve of the function used to back-calculate growth.

TABLE 5.—Functions examined for the best fit of otolith radius–body length data, corresponding residual sums of squares, and mean squares.

Function	Residual sum of squares	Mean square
$y = a + bx$	3,865	10.44
$y = a + bx + cx^2$	3,700	10.03
$y = a + bx + cx^2 + dx^3$	3,146	8.55
$y = ab^x$	7,611	20.57
$y = e^a x^b$	3,768	10.18

between estimated and observed values is 0.9860, so an improved fit was not attempted. The Y intercept is at 18.78957 cm indicating that the function does not adequately represent the otolith radius-body length relationship in fish less than 1 yr of age. Therefore the back calculation of body lengths beyond the range of the data fitted is obviously not meaningful.

The mean total otolith radii by age were used to back calculate lengths at age which are presented in Table 6 and compared in Figure 14 with observed lengths at age from combined 1965-69 samples. The atypical 1961 year class was excluded in this comparison. In spite of a certain amount of variation in the back-calculated curve (probably induced by the small sample size), the two curves correspond very well.

The lengths-at-age for five year classes (1957-61) were compared by back calculating the lengths of approximately equal numbers of males and females from each year class. Because there is some evidence in Table 7 that the radii of the first one or two annual marks increase as the total age increases, only otoliths from 7-yr-olds were used to avoid any possible age-related effects. Older specimens could not be used because they were not available in sufficient numbers and younger specimens had a growth history which was too brief. Fifteen otoliths of each sex for each of the 5 yr were selected. The desired sample size (30 per year class) was seldom obtained because many of the otoliths had deteriorated in storage so that opaque and hyaline zones could not be distinguished on the photographs.

Back-calculated lengths are presented in Table 8, and a comparison of back-calculated growth curves for the five year classes is made in Figure 15. It appears that year class variation was not great among the 1957-60 year classes, but that the members of the 1961 year class were on the average noticeably smaller at age than members of the other year classes. This latter observation

TABLE 6.—Mean otolith radii and back-calculated body lengths at various ages for Pacific hake.

Age (years)	Mean otolith radii (cm)	Calculated body lengths (cm)
1	6.08	16.57
2	9.06	26.19
3	12.53	41.13
4	13.50	45.44
5	13.60	45.88
6	14.43	49.45
7	14.80	51.00
8	16.44	57.30
9	15.79	54.92
10	17.29	60.11
11	17.74	61.44
12	18.30	62.92
13	17.90	61.88

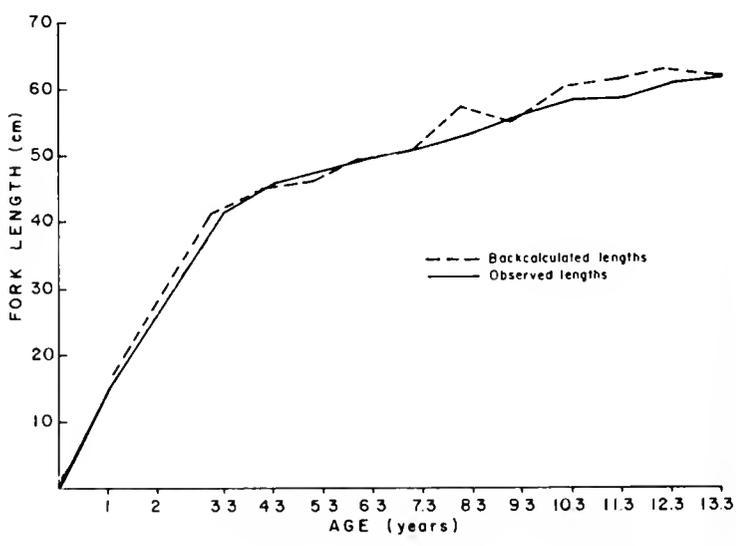


FIGURE 14.—A comparison of growth curves as constructed from observed and backcalculated fork lengths at various ages.

TABLE 7.—Mean radii (cm) of photographed otolith annuli by total age group.

Total age (years)	Annuli												
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th
1	5.96	—	—	—	—	—	—	—	—	—	—	—	—
2	5.85	8.87	—	—	—	—	—	—	—	—	—	—	—
3	7.10	10.13	12.53	—	—	—	—	—	—	—	—	—	—
4	6.34	9.73	11.66	13.13	—	—	—	—	—	—	—	—	—
5	6.57	10.03	11.50	12.87	13.57	—	—	—	—	—	—	—	—
6	6.38	9.73	11.51	12.79	13.79	14.32	—	—	—	—	—	—	—
7	6.16	9.59	11.60	12.97	13.89	14.37	14.71	—	—	—	—	—	—
8	6.18	9.86	12.02	13.63	14.90	15.61	16.15	16.50	—	—	—	—	—
9	6.33	9.80	11.56	12.89	14.05	14.53	14.94	15.39	15.66	—	—	—	—
10	6.44	9.92	11.65	13.39	14.57	15.66	16.21	16.73	17.14	17.50	—	—	—
11	6.60	9.84	11.38	13.08	14.42	15.52	16.00	16.54	16.94	17.36	17.66	—	—
12	6.75	10.85	12.75	14.50	15.50	16.10	16.60	17.60	17.90	18.10	18.40	18.60	—
13	7.15	10.45	12.20	13.40	14.35	14.95	15.35	15.75	16.20	16.55	16.90	17.25	17.65

TABLE 8.—Back-calculated body length (cm) at various ages for the 1957-61 year classes of Pacific hake.

Age (years)	Year class and (in parentheses) sample size				
	1957 (27)	1958 (15)	1959 (22)	1960 (27)	1961 (30)
1	19.02	18.64	16.45	16.85	16.95
2	31.16	31.01	30.36	29.92	28.50
3	38.71	39.05	38.65	37.11	37.06
4	44.61	40.66	46.09	46.12	43.58
5	49.31	50.14	50.92	50.38	47.60
6	52.28	50.98	53.74	52.65	49.88
7	54.10	54.61	55.51	54.20	51.48

corroborates the slow growth rate of the 1961 year class suggested by the length-age data presented previously. The 1961 year class was an extremely large year class numerically, exceeding by far the size of other year classes of record. Perhaps density-dependent growth was operative in this instance. The size of the 1961 year class may have been so large that the competition for food and space noticeably restricted the growth of individuals. It cannot be ascertained whether the members of smaller year classes might undergo density-dependent growth to a lesser extent or if the phenomenon is triggered only by unusually large year classes.

The von Bertalanffy growth equation is commonly used to describe asymptotic growth. It is used herein because it fits the data well and is readily incorporated in certain yield models. Von Bertalanffy's equation is $l_t = l\infty\ 1\text{-}e^{-k\ (t\text{-}t_0)}$), where l_t = body length at time t; $l\infty$ = estimated average maximum body length; k = rate of growth; t_0 = theoretical age when growth conforms to the von Bertalanffy equation. Since sexual differences in growth characteristics exist in Pacific hake, separate curves were fitted to male and female length data. Average length at age data from Table 3 were used to compute the growth curves. In this instance the growth of the 1961 year class was considered atypical and it was excluded from the analysis. A computer program[1] utilizing the method of Stevens (1951) was used to compute the constants for the von Bertalanffy equation. The resulting equations are: $l_t = 56.29\ (1\text{-}e^{-0.39\ (t\ -0.20)})$ for males and $l_t = 61.23\ (1\text{-}e^{-0.30\ (t\ -0.01)})$ for females. By comparison, Tillman's (1968) estimates of k were 0.41 for males and 0.19 for females. He reported that treatment of Best's (1963) data also yielded 0.19 for females. In the present study $l\infty$ for both sexes are reasonable estimates of average maximum body lengths. Males as long as 66 cm and females as long as 80 cm have been observed. Growth of Pacific hake is adequately represented by the von Bertalanffy equations as the curves fit the observed lengths-at-age very well (Figure 16). The curves are nearly superimposed until about age 5 when they begin to diverge and continue to do so with age. Although sex-specific growth rates are apparent, the growth rate of the entire Pacific hake population may be best represented by an equation based on data with the sexes combined. The growth equation with sexes combined is $l_t = 60.85\ (1\text{-}e^{-0.30\ (t\ -0.03)})$.

Growth in Weight

In 1964-69 length and weight data were collected on 2,417 male and 3,117 female Pacific hake taken from Washington to southern California. Lengths and weights were taken from fresh fish as they were unloaded from vessels at the processing plant and from research samples at sea. Fork lengths were taken to the nearest centimeter and weights to the nearest decagram. The majority of

[1]Program developed by George Hirschhorn, Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash.

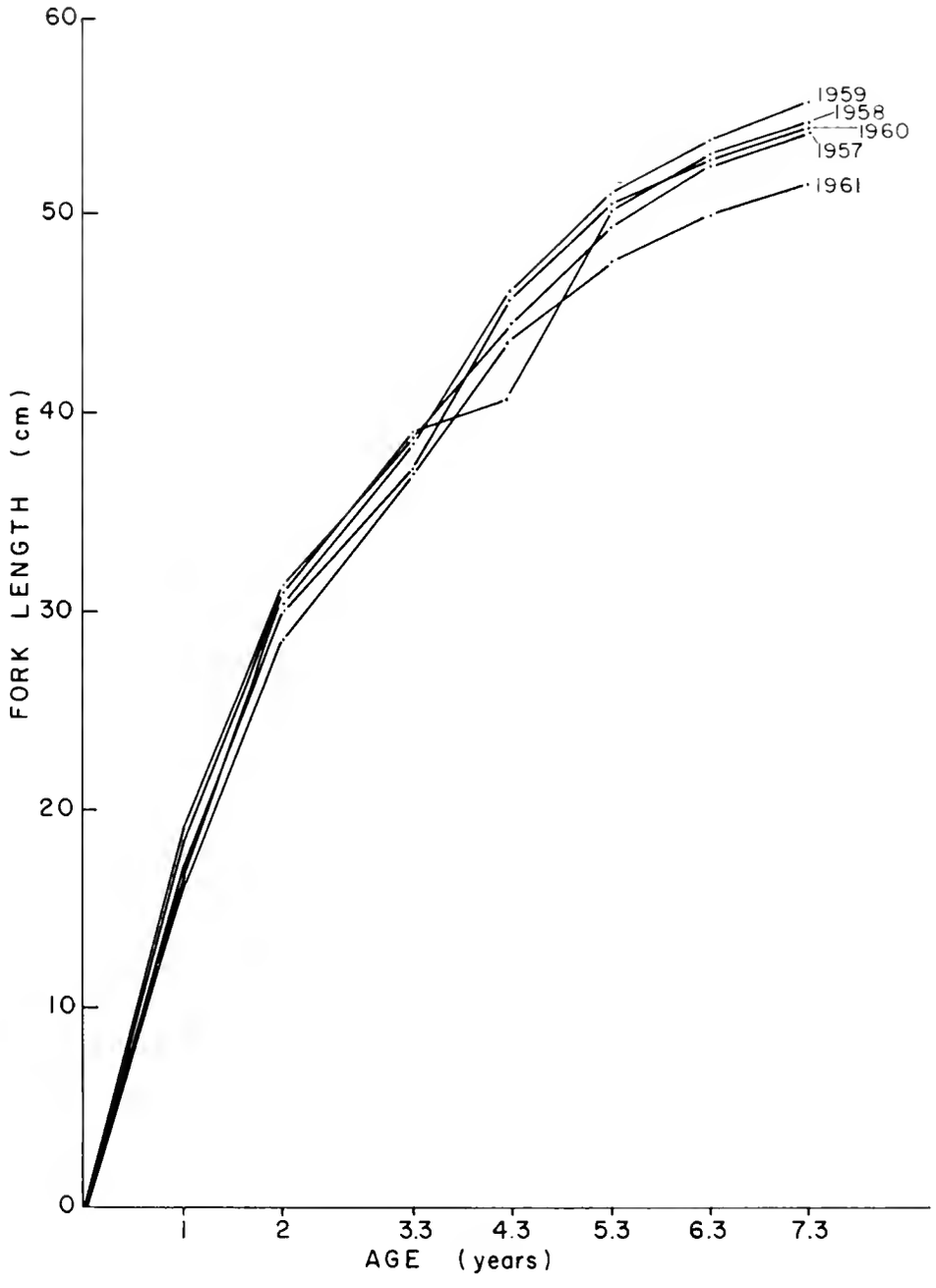
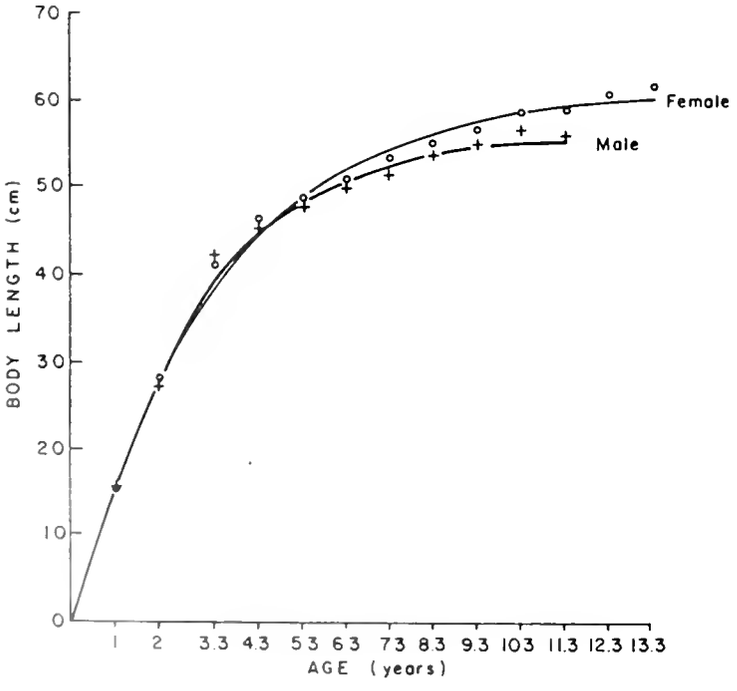


FIGURE 15.—Back-calculated growth curves for 1957-61 year classes. (Only otoliths from 7-yr-old specimens were used.)



observations were made from mature specimens in commercial samples, and therefore hake less than about 40 cm long were inadequately represented or not represented at all. The commercial data were fitted using the length-weight equation $W = aL^b$, where W = weight in grams, L = length in centimeters, and a and b are constants. In linear form this equation becomes $\log W = \log a + b (\log L)$. The length-weight relationships were calculated to be $\log W = -1.45990 + 2.55618 \log L$ for males and $\log W = -1.68944 + 2.69509 \log L$ for females (Figure 17).

Typically the exponent in the length-weight equation for most fusiform fishes approximates 3, implying isometric growth. On the basis of data

FIGURE 16.—Von Bertalanffy growth curves for male and female Pacific hake superimposed on mean body lengths at various ages. (o = females; + = males.)

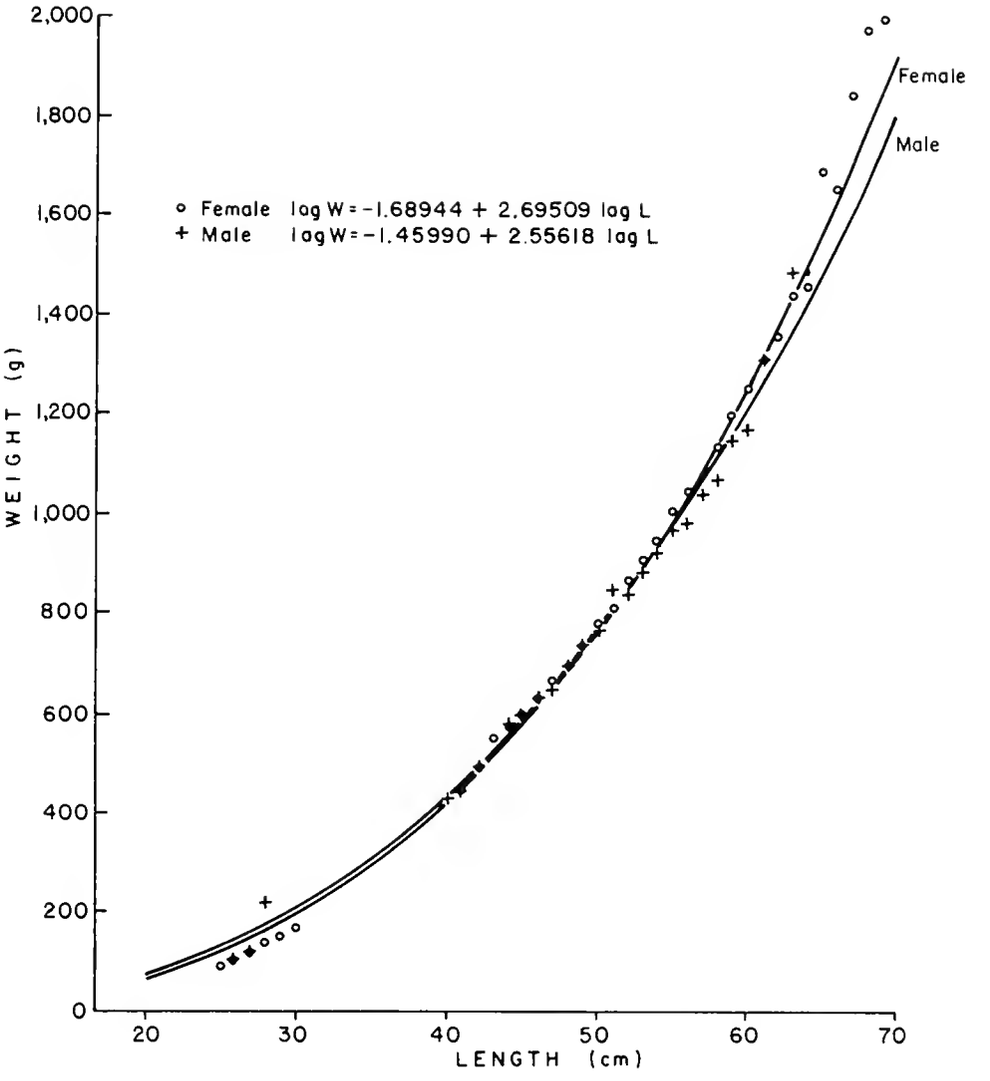


FIGURE 17.—Length-weight curves for male and female Pacific hake superimposed on mean body weights ($n \geq 5$).

from 58 female hake from California ports, Best (1963) estimated the exponent of the length-weight equation to be 3.0668. On the chance that the hake in commercial samples had lost weight between capture and delivery through the loss of body fluids, another pair of equations was fit to less extensive length-weight data taken aboard research vessels off Washington from freshly caught specimens. Student's t-test was used to test the null hypothesis that regression slopes calculated from research and commercial samples did not differ significantly from 3. All tests were significant at the 1% level (Table 9) and the hypothesis was rejected. A possible explanation is that because most specimens are in an immediate postspawning state as they arrive off Washington and Oregon, their weight relative to their length is less than it might be later in the year.

Growth in weight for males and females was calculated from the length-weight equations (Figure 18). These curves suggest that Pacific hake gain weight at an increasing rate until they are 3 yr old. After age 3 the rate of growth in weight decreases and remains roughly constant until death. By age 3, males have grown to approximately 50% of their total weight at 11 yr of age, whereas females by age 3 have attained about 40% of their total weight at 11 yr of age. The growth rates are sex specific and the curves begin to diverge noticeably between ages 3 and 4. At 11 yr of age females weigh on the average about 200 g

TABLE 9.—Results of t-tests to determine if slopes of length-weight regressions calculated from commercial and research samples differ significantly from 3. All comparisons were significant at the 1% level.

Sample type	Sum of deviations from mean (Σx^2)	Variance (Sxy^2)	Slope (b)	Sample size (n)	t
Commercial:					
Male	6.4064	0.0049	2.55618	2,417	16.02
Female	10.5651	0.0032	2.69509	3,117	17.62
Research:					
Male	2.6224	0.0154	2.63189	432	4.80
Female	4.2177	0.0075	2.65436	587	8.20

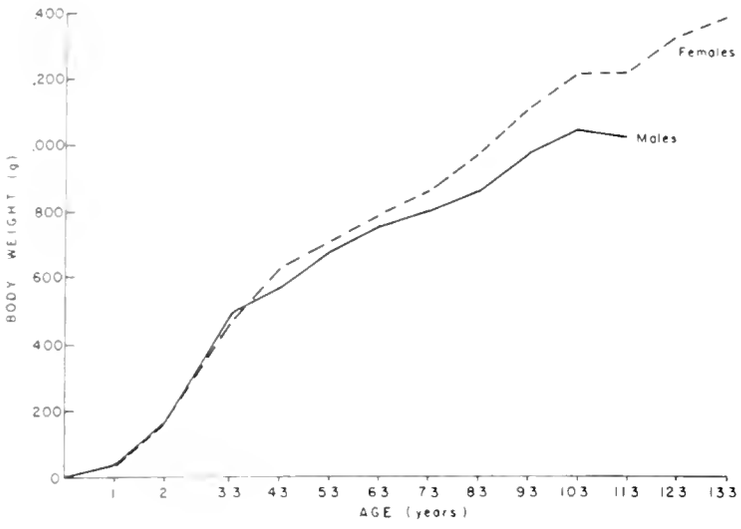


FIGURE 18.—Average body weight at various ages for Pacific hake collected off California, Oregon, and Washington, 1965-69.

more than males. For each sex, Table 10 gives average weight at age values, annual growth rates, and annual instantaneous growth rates, assuming exponential growth in weight.

SUMMARY AND CONCLUSIONS

Biological data from samples of Pacific hake taken in 1964-69 off the coasts of Washington, Oregon, and California were utilized to study the age and growth of the species.

TABLE 10.—Mean weight, annual increase in weight, and instantaneous growth rate at various ages for male and female hake taken off California, Oregon, and Washington, 1964-69.

	Male			Female		
Age (years)	Body weight (g)	Annual increase (%)	Instant. growth rate	Body weight (g)	Annual increase (%)	Instant. growth rate
1	37.6			32.4		
		318	1.43		400	1.61
2	157.0			162.9		
		216	1.15		183	1.04
3.3	496.0			459.5		
		15	0.14		36	0.31
4.3	570.0			626.5		
		18	0.17		13	0.12
5.3	674.6			703.5		
		12	0.11		12	0.11
6.3	751.0			786.2		
		6	0.06		8	0.08
7.3	798.2			853.6		
		7	0.07		13	0.12
8.3	856.8			966.8		
		13	0.12		14	0.13
9.3	964.1			1,102.5		
		8	0.08		9	0.09
10.3	1,040.6			1,207.2		
		0	0.00		0.3	0.00
11.3	1,014.8			1,211.1		
		—	—		8	0.08
12.3	—			1,319.6		
		—	—		4	0.04
13.3	—			1,374.0		
		—	—		—	—

The method of age determination from annuli on otoliths was examined, and all evidence suggests that the method provided reliable age data.

Several sources of variation in the age structure of the population were considered. The relative size of newly recruited year classes varied substantially, creating noticeably annual variation in the age composition. There was no detectable seasonal variation in the age composition of the hake population found off Washington from spring through fall. Latitudinal stratification of hake by age (known to occur over large geographical areas) was further examined, and some variation in age composition was found even among ½ degree intervals of latitude off the Washington coast. The relative abundance of the 4- and 5-yr-olds decreased as sampling progressed northward from the mouth of the Columbia River to the Strait of Juan de Fuca, while the relative abundance of 7- to 10-yr-olds increased. This stratification of ages by latitude supports the theory that there is a northward migration of hake in the early spring along the Pacific coast of North America with the older (larger) individuals tending to migrate farthest. There is little variation in age composition due to sex, except that the longer lived females tend to predominate from 8 to 10 yr of age and are usually the sole survivors at 11-13 yr of age.

Pacific hake grow rapidly in length during their first 3 yr after which growth slows and becomes asymptotic. At about 4 yr of age, females grow noticeably faster and by age 11 may average 3.12 cm longer than males. Individual males may reach 66 cm, while some females may reach 80 cm in length. Year class variation in growth rates was detected by analysis of age-length data and back calculation of growth from otoliths. The equation $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$ was used to describe the relationship of body length (Y) and otolith radius (X).

The extraordinarily large 1961 year class grew at a substantially slower rate than the 1957-60 year classes. This difference possibly is indicative of density-dependent growth. Growth in length can be expressed adequately by the von Bertalanffy growth equations:

$l_t = 56.29\ (1-e^{-0.39\,(t\,-0.20)})$ for males,
$l_t = 61.23\ (1-e^{-0.30\,(t\,-0.01)})$ for females, and
$l_t = 60.85\ (1-e^{-0.30\,(t\,-0.03)})$ for the sexes combined.

Growth in weight was determined by applying the length-weight equations:

$\log W = -1.45990 + 2.55618 \log L$ for males, and
$\log W = -1.68944 + 2.69509 \log L$ for females

to average length-at-age data. By age 3, males have grown to about 50% of their total weight at age 11, and females to about 40% of their total weight at age 11. At 11 yr of age females weigh on the average 200 g more than males. Males attain an average weight of about 1,015 g by age 11 and females reach an average weight of 1,374 g by 13 yr of age.

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EVALUATION OF THE RETURN OF ADULT CHINOOK SALMON TO THE ABERNATHY INCUBATION CHANNEL

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ABSTRACT

Adult returns of progeny of the 1964 year class of chinook salmon, *Oncorhynchus tshawytscha*, were determined for the Abernathy incubation channel, natural production, and hatchery sources. A total of 4,620,600 fry were released from the channel into Abernathy Creek (state of Washington) as unmarked fry. Natural production in the creek was estimated from spawning ground counts and fyke net sampling of migrants at 16,700 fry, or 0.36% of the total unmarked fish. A total of 557,649 hatchery fish were marked by feeding tetracycline, and 161,579 were both fin-clipped and fed tetracycline. All 2-, 3-, and 4-yr-old adult fish returning to the hatchery holding pond were examined for fin clips and fluorescent bands on the vertebrae. Returns from hatchery sources were 506 fish or 0.070%. Potential egg production was 865,000, or 76% of the original 1,142,604 eggs. Returns from the channel totaled 733 fish or 0.016%. Egg potential was 2,050,000, or 35% of the original 5,888,048 eggs. Returns attributed to Abernathy Creek totaled only three fish and egg potential was 0.2% of the original 2,880,000 eggs. Survival of this year class was considerably below the 9-yr average of 0.118%. Intuitively, costs favor incubation channel production over hatchery production. However, additional studies are needed to determine if contributions to the fisheries and survivals are comparable in years of better year class survival.

Spawning and incubation channels for salmon produce higher survivals of downstream migrants than do natural spawning grounds. Studies by Gangmark and Broad (1956), Lister and Walker (1966), Thomas and Shelton (1968), and others have shown that channels with flow and sediment control devices can produce many times as many migrant-sized fish as are produced by the parent stream. Little information is available on the percentage of fry produced in channels that return as adults. Such data are needed to determine the value of incubation channels for supporting and maintaining salmon runs.

In the present study, I compare the survival to the adult stage of chinook salmon, *Oncorhynchus tshawytscha*, from three sources: the Abernathy incubation channel (near Longview, Wash.); the Salmon-Cultural Laboratory hatchery adjacent to the channel; and natural spawning in Abernathy Creek.

MATERIALS AND METHODS

Problems were encountered in selecting the techniques to use to distinguish returning adults from the various sources. Fin-clipping presented two problems. First, fin-clipping of fry produced in the channel was undesirable mainly because of the small size of the fry (average weight, <0.5 g). The chance of injury or incomplete removal of fins would be high. Fin-clipping of hatchery fish has been shown to reduce adult returns by 43.3% (Weber and Wahle 1969). Second, the daily numbers of fry migrating varied widely (from a few thousand to over 120,000), depending upon water conditions. Fin-clipping at a practical rate would require that many fish be held beyond their normal migration date.

Marking channel and creek migrants with tetracycline would not be acceptable. Although marking fish in this manner using techniques developed by Weber and Ridgway (1962) had no detrimental effect on adult survival (Weber and Wahle 1969), the drug is normally administered in the food. The artificial feeding of channel fish might alter their characteristics and invalidate the survival evaluations. Attempts to mark small fish by immersion in solutions of tetracycline and 4% dimethyl sulfoxide have shown some favorable results (Richard C. Johnsen, pers. commun.), but the technique has not been sufficiently developed for reliable, large-scale marking.

For these reasons migrant fry from the incubation channel and Abernathy Creek were not

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marked. Rather, the numbers migrating downstream were determined and the returns were compared with returns from marked hatchery fish stocked in the creek. It is assumed that fish migrating from the channel and Abernathy Creek would have the same rates of survival. Table 1 summarizes the number, size, time of migration, and mark of each of the fish sources involved in the evaluation.

TABLE 1.–Summary of the number, size, time of migration, and mark of the various fish sources included in the evaluation.

Origin of migrants	Number	Size (g/fish)	Time of migration	Mark
Abernathy Creek	16,700	[1]0.5	[1]11/64-4/65	none
Incubation channel	4,620,600	0.5	12/64-4/65	none
Hatchery	61,000	8.2	5/65	2-OTC[2]
	445,500	4.8	5/65	2-OTC
	51,149	16.8	8/65	3-OTC
	161,579	16.8	8/65	3-OTC + fin clips

[1]Approximate size and time of migration based upon fyke net sampling.
[2]Oxytetracycline.

Migrants from the Incubation Channel

A total of 4,620,600 unmarked fry were released from the channel during the 1964-65 season. This number represents a 78.5% survival from the 5,888,100 eyed eggs planted. If the mortality of green eggs is also considered, the survival to migrant stage was 75.0%. A description of techniques for planting eggs and counting fry was given by Thomas and Shelton (1968).

Migrants from Abernathy Creek

Numbers of female chinook salmon which spawned in Abernathy Creek during the 1964 spawning season were estimated at 576 from spawning ground counts. On the basis of an average of 5,000 eggs per female, an estimated 2,880,000 eggs were deposited in the creek. Fry migrating downstream from this area were sampled with a fyke net, a method demonstrated to be reliable by Tait et al (1962). Recaptures from known numbers of marked fish released upstream indicated that the net sampled 13.3% of the migrating fish; the calculated survival of migrants from natural spawning was 16,700, or 0.58%. Flooding and superimposition of eggs during spawning are probably responsible for this low survival. These fish were unmarked and returning adults could not be distinguished from those which originated in the incubation channel.

Chinook salmon spawning area in Abernathy Creek extends for about 1 mile below the hatchery weir. Returns from natural spawners would not necessarily enter the hatchery holding pond.

Releases of Hatchery Fingerlings

All fish released from the Salmon-Cultural Laboratory hatchery were marked in some manner for later identification. Initially, all fish were marked in mid-April 1965 by feeding tetracycline after the technique developed by Weber and Ridgway (1962). All fish in a 100-fish sample examined in late April showed fluorescent bands on their vertebrae. Fish released into Abernathy Creek in May had two bands and those in August, three bands. These second and third marks were poor because the fish fed little, presumably because of the high level of drugs in the diet. Total hatchery fish released with only tetracycline marking totaled 557,649.

Two groups of fish used in a nutrition experiment received double fin clips, in addition to the tetracycline marks. These two groups served as controls in that the returning adults would be easily recognizable from the clipped fins, and a check of their vertebrae would indicate the persistence of the fluorescence. The fin-clipped groups, which numbered 161,579, were released in mid-August 1965.

Treatment of Adult Fish

All adult chinook salmon returning to the holding pond at the Salmon-Cultural Laboratory were examined during 1966-68. All fish returning as 2-yr-old jack salmon and as 3- and 4-yr-old adults were examined. Past records of age classification indicated that numbers of 5- and 6-yr-old adults in the Abernathy Creek spawning run are insignificant. Fish that returned to Abernathy Creek but not to the hatchery holding pond were not included in the evaluations. No attempt was made to sample the sport or commercial fisheries or to search the adjacent streams and hatcheries for strays. The evaluation is based only upon returns to the Salmon-Cultural Laboratory holding pond. No correction was made for strays from other hatcheries or streams that might enter the holding pond and be counted as survivors from the channel since their number would be insignificant (Worlund et al. 1969).

All adult fish were measured and the sex was

recorded. Scales were taken for age determination. Age determinations of fish returning to the hatchery in previous years had indicated the size range for 2-yr-old jack salmon, but 3- and 4-yr-old fish could not be separated by size. During the 1966 spawning season, a vertebra was removed from all fish smaller than the maximum length previously found for 2-yr-old fish, for determination of tetracycline marks. During the 1967 and 1968 spawning seasons, a vertebra was also removed from all fish in the size range of previous 3- and 4-yr-old fish.

Vertebrae were scanned under ultraviolet light by the technique described by Weber and Ridgway (1962). Vertebrae with tetracycline marks were classified as hatchery fish. The age of fish without vertebra marks was determined by examination of the scales. All unmarked fish of the correct age were considered to be recoveries from either the channel or creek. Tetracycline bands were visible in the vertebrae of all fin-clipped salmon.

Adult returns from two sources—the hatchery or Abernathy incubation channel and Abernathy Creek—were determined by measuring and aging fish and by identifying those with fin clips and tetracycline marks on vertabrae. Potential egg production was calculated on the basis of 5,000 eggs per female, the average number found in chinook salmon returning to the hatchery in previous years.

RESULTS

Adult Returns from Hatchery-Reared Fingerlings

Table 2 presents adult return data for both 1) the fin-clipped plus tetracycline-marked group and 2) the tetracycline-marked groups. Survival of fish that had been marked with both tetracycline and fin clip was low; of 161,579 fingerlings released, only 20 returned. Disease and parasite problems encountered during the summer rearing season probably contributed to the low survival. Fish released before the warm-water season appeared to have better survival. The total survival was 0.070%.

TABLE 2.—Number of male and female adult chinook salmon returns from 719,228[1] hatchery-reared fingerlings released from the Salmon-Cultural Laboratory hatchery, 1965.

Age at return (years)	Males	Females	Potential egg production (thousands)
2	209	0	0
3	90	96	480
4	34	77	385
Total	333	173	865

[1]Of this total, 557,649 fish were released with tetracycline bands and 161,579 with double fin clips and tetracycline bands.

Adult Returns from Abernathy Incubation Channel and Creek

The percentage returns of fish from the Abernathy incubation channel (0.016%) was considerably lower than that from the hatchery (Table 3). The higher ratio of female fish, however, resulted in a relatively higher number of eggs per returning fish.

The numbers of returning fish that originated in Abernathy Creek were insignificant. If the survival rate after migration is assumed to be identical for channel and creek migrants, only 0.36% of the 736 returning unmarked adults—or about 3 fish—were from the creek.

TABLE 3.—Number of male and female adult chinook salmon returns from 4,620,600 fry released at the Abernathy incubation channel, 1965.

Age at return (years)	Males	Females	Potential egg production (thousands)
2	16	0	0
3	202	220	1,100
4	107	188	940
Total	325	408	2,040

DISCUSSION

Survival was low from chinook salmon of the 1964 year class released from most Columbia River hatcheries, as they were in this experiment. Reasons for the poor survival are largely unknown. Although the evaluation of survival from several year classes would have been desirable, comparisons of survival from the different sources of young fish provide information on the relative survival of channel-reared and hatchery-reared fish, as well as an insight into the potential survival from an incubation channel. Ideally, sufficient adults should return to a salmon hatchery to provide 100% or more of the original egg supply. Assuming about 5,000 eggs per female and a 50:50 ratio of males to females, a chinook hatchery is self-sustaining when the return is about 0.045%.

TABLE 4.—Potential egg production of adult chinook salmon returns in relation to original egg numbers from which they were produced.

Source of downstream migrants	Return of adult salmon		Salmon eggs		
			Original number (thousands)	Potential production from adults	
	Number	Percent		Number (thousands)	Percent of original number
Salmon-Cultural Laboratory hatchery	506	0.070	1,143	865	76
Abernathy incubation channel	773	0.016	5,888	2,040	35
Abernathy Creek	3	0.016	2,880	7	0.2

Potential egg replacement of adult returns from the various sources is shown in Table 4. The adult return from the hatchery totaled 0.070%; however, more than 40% of the adult fish returned as 2-yr-old males. Only about 76% of the original eggs were replaced for this brood year. Although the percentage survival of hatchery fish was more than four times that of channel fish, the advantage in egg replacement was less than twofold. Even so, a channel could not operate long with a less than 35% replacement of eggs. If adults from natural spawning are assumed to enter the holding pond at an equal ratio with those from the channel, possible egg replacement from the creek source was only about 7,000.

The return of chinook salmon as 2-, 3-, and 4-yr-old, and sometimes as 5- and 6-yr-old fish, ensures overlapping of brood stocks. Consequently returns from year classes with poor survival are mixed with returns from other year classes, to help ensure that the hatcheries and streams may still have adequate egg supplies.

Production of salmon by incubation channels is usually evaluated only by the number of outmigrants produced and the total number of adults that return. The origins and ages of adults are seldom investigated.

Only relative comparisons can be made of survival from channel and hatchery releases due to variables such as time of release, size at release, and nutritional background. The channel had the sizable advantages of having very low costs for rearing the fry and no cost for food.

A 9-yr average of adult returns to the hatchery was 0.118%. Survival to adults from the 1963 year class of fish released by the hatchery was about 0.39%. There were no major differences in fish diet, times of stocking, or other known factors that might improve survival of this year class over that of the 1964 year class. If it is assumed that survivals of fish from the channel follow the same trends as do those from the hatchery, the more than fivefold greater hatchery returns for the 1963 year class would be reflected in channel production returns. This would provide more than sufficient egg production replacement. However, additional studies are needed to confirm this survival assumption.

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ECOLOGICAL STUDIES OF THE PUERULUS LARVAL STAGE OF THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS*[1]

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ABSTRACT

Ecological and related behavioral studies of the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*, involved the development and use of artificial and natural seaweed habitat traps, special paired neuston nets, and underwater night-lights for collecting and observing pueruli in nature. The results obtained indicate that pueruli first enter the coastal waters off San Diego, Calif., during May, and continue to appear regularly through September, but with no apparent relationship to lunar or temperature cycles.

Pueruli exhibit a strong attraction to floating habitat traps containing the surfgrass *Phyllospadix torreyi* and to bright lights at night. The results also suggest that the puerulus is a surface-swimming, pelagic form which may actively seek out specific nearshore areas for settlement, and thereby serve the important function of returning larval stages to areas suitable for demersal life of the young juveniles.

Previous studies of the California spiny lobster, *Panulirus interruptus* (Randall), and other spiny lobster species have concentrated primarily on either the adult or phyllosoma larval stages, leaving the biology of the intermediate, yet very important, puerulus and juvenile stages relatively unknown. This is particularly true for *P. interruptus*. Prior to the present study, essentially nothing was known about the ecological requirements or behavior of the puerulus or early juvenile stages, which together represent a period of 2-3 yr in the life history of this species. This is an unfortunate situation for an animal as heavily exploited by a commercial fishery as the California spiny lobster because, as Thorson (1950) has indicated, the abundance of any adult population is primarily dependent on the recruitment, survival, and growth of its larval and juvenile stages. Consequently, attempts to improve fishery yields through a better understanding of adult behavior and population ecology alone provide only a partial and temporary solution to the problem.

Increasing fishing pressure on the steadily declining stocks of *P. interruptus* and other spiny lobster species urges more than an academic interest in the ecological requirements of their puerulus and juvenile stages. On the basis of this information, for example, it may be possible to protect their natural habitats or to develop supplementary artificial habitats for them in nature. Techniques for culturing these stages under artificial conditions, as a means of supplementing natural stocks, must also be given serious consideration for the following reasons.

Evidence concerning *P. interruptus* (Johnson 1956, 1960, 1971) and other palinurid species (see, for example, Chittleborough and Thomas 1969) suggests that a majority of the phyllosoma and puerulus larvae may be lost from the population due to their long larval life (5-10 mo), during which they may be swept hundreds of kilometers offshore. Because of their small size, the surviving postpuerulus and early juvenile stages probably experience much higher predation mortality rates than do the adults (Winget 1968). In addition, evidence from limited studies of other spiny lobster species, including *P. argus*, *P. longipes cygnus*, and *Jasus edwardsii*, suggests that the nursery grounds of their postpuerulus and early juvenile stages are located in protected bays or estuaries (Sheard 1949; Lewis et al. 1952; Witham et al. 1964, 1968; Sweat 1968; C. B. Kensler, pers. commun.). If such estuarine nursery grounds are required by the early benthic stages of *P. interruptus*, reduction of this type of natural habitat as the result of commercial developments and water pollution may create a "weak link" in the life history of this species, at least within part of its geographical range.

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Aquaculture of *P. interruptus* or other palinurid lobsters, starting with the egg, has been attempted by several investigators as a means of bypassing what appears to be an inefficient recruitment process in nature. Yet all attempts to culture the phyllosoma larval stages from the egg through to the puerulus stage have been unsuccessful (for example, see Dexter 1972). This approach does not appear to be feasible at the present time, particularly on a mass culture basis, due to the long duration (5-10 mo in nature) and the poorly understood requirements of the delicate phyllosoma larval stages. In contrast, the succeeding puerulus and juvenile stages of spiny lobsters respond well to laboratory culture (Kensler 1967; Witham et al. 1968; Serfling and Ford in press a, b). Thus, if the puerulus stage of *P. Interruptus* proves to be abundant and relatively easy to collect in large numbers, particularly in certain offshore waters where these individuals might otherwise be swept away from coastal nursery grounds, it may be advantageous to supplement natural stocks by collecting pueruli and holding them in mass culture under controlled, optimal conditions through at least the early juvenile stages. These pueruli could either be reared directly to a marketable size under artificial conditions, or returned to the ocean, after passing the potentially critical early juvenile stages, for final growth and maturation. This approach to spiny lobster culture has also been proposed for *P. argus* by Ingle and Witham (1969).

The lack of ecological information on the puerulus stage of any spiny lobster species is due largely to the fact that investigators usually have been unable to collect more than a few individuals, despite extensive sampling in areas where they might be expected to occur. Consequently, the central question precluding further research has concerned the mode of life of the puerulus stage, i.e., whether it is primarily a benthic or pelagic form.

Evidence presented in the literature thus far supports about equally each side of the issue. Investigators who have failed to collect more than a few isolated pueruli, even after years of extensive sampling by conventional methods (Lewis et al. 1952; Johnson 1956, 1960, 1971; Harada 1957; Saisho 1966; Sims and Ingle 1966; Lazarus 1967), have concluded that the puerulus stage of their respective species is either primarily benthic, or concentrated in unknown pelagic areas. On the other hand, Gurney (1942), Sheard (1949), George and Cawthorn (1962), Chittleborough and Thomas (1969), and Chittleborough (1970) were able to collect small numbers of individuals in net hauls far out to sea, and thus suggested that the puerulus is a free-swimming stage.

Harada (1957) and Johnson (1960) reported collecting a few pueruli which were attracted to bright lights over shallow water at night, but both authors apparently believed they were lured from the bottom. Yet Lindberg (1955) reported that University of Hawaii personnel collected several pueruli of a *Panulirus* species which were attracted to surface night-lights in water several hundred meters deep, thereby eliminating the possibility that they were attracted from the bottom. Witham et al. (1968), Sweat (1968), Phillips (1972), and we have successfully attracted large numbers of pueruli to artificial habitat traps floating at the surface, thereby offering the first strong evidence that the puerulus is primarily a pelagic, surface-dwelling form.

Preliminary observations made originally by J. C. Van Olst (pers. commun.) in the spring of 1968, demonstrated that puerulus larvae of *P. interruptus* occurring in local coastal waters could be attracted to bright lights suspended underwater near the surface at night. This discovery prompted the following investigation into several aspects of puerulus behavior and ecology. The specific objectives of this study were: 1) to determine the mode of life of the puerulus stage of this species, e.g., whether it is primarily benthic or pelagic; and, having done so, 2) to develop and apply suitable field sampling techniques to study the general dynamics of puerulus recruitment with regard to seasonal, lunar, and daily periodicity, area of settlement, specific habitat preferences, and migratory behavior; and 3) to estimate the general abundance and possibility of collecting large numbers of this stage for use in aquaculture. Closely related studies were also conducted concurrently to investigate the habitat preferences and the natural growth rates of the early juvenile stages in nature, as well as the growth and survival of the juvenile stages at elevated temperatures in recirculating culture systems (Serfling 1972; Serfling and Ford in press a, b).

MATERIALS AND METHODS

The failure of standard sampling methods used by previous investigators to collect the puerulus

stage prompted the development of novel equipment and techniques. These included underwater night-lights of high intensity, floating artificial and natural seaweed habitat traps, and a special paired neuston net, which are described in the following sections.

Underwater Night-Lights

Most of the night-light observations and collections were made from an adjustable ladder platform near the end of the Scripps Institution pier, at the position shown in Figure 1, under a variety of environmental conditions. A standard motion picture projection lamp of either 500 or 1,000 W was waterproofed at the electrical connection with silicone sealant. The light was mounted on a pole and lowered 30-50 cm below the surface. This unit illuminated a spherical area 5-8 m in diameter, depending on water turbidity. When suspended in this way it provided much greater illumination than when suspended just above the surface. Pueruli attracted to the light were removed with a dip net and maintained alive for further studies.

Seaweed Habitat Traps

Pueruli placed in aquaria quickly settled and remained hidden in a variety of intertidal rock and plant substrates, but showed a preference for the surf grass *Phyllospadix torreyi*. They would continue to cling to any of these substrates, even when removed from the water. In an attempt to take advantage of this behavior, a variety of containers (Figure 2) for holding *Phyllospadix* and various species of red algae were floated under the lighted end of the Scripps Institution pier at the positions shown in Figure 1. The pier lights (three 200 W incandescent flood lamps mounted approximately 15 m above the water) apparently attracted pueruli to the pier, and the seaweed habitat traps provided convenient refuges in which they settled. The traps were retrieved and examined for pueruli every 4-6 days, providing a standard sampling system which could be operated continuously. The same types of habitat traps were also maintained on buoyed lines at several coastal locations in water 3-30 m deep, as discussed in a later section.

A variety of natural and artificial seaweed habitat trap designs, shown in Figure 2, were tested initially to develop a type most suitable for attracting pueruli. Included in the evaluation were several models of the "Witham" habitat design used by Witham et al. (1968) for collecting *P. argus* pueruli (Figure 2C). This trap was constructed of a synthetic fibrous material labeled "Conservation Web #200," manufactured by Minnesota Manufacturing and Mining Company.[3] The traps we developed and tested consisted of wood frames which contained either synthetic materials, e.g., burlap, foam rubber, nylon mop, and plastic screen and netting, or fresh natural seaweeds, held within either plastic cage sides (Figure 2A, B), or within net bags or wire screen (Figure 2D, E).

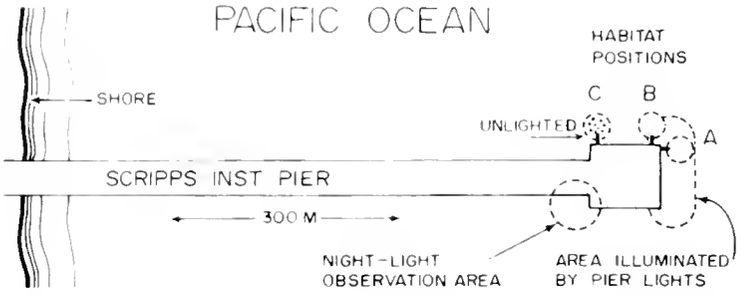

FIGURE 1.—Standard positions of puerulus habitat traps placed on the Scripps Institution pier, and the position from which night-light observations and collections of pueruli were made.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

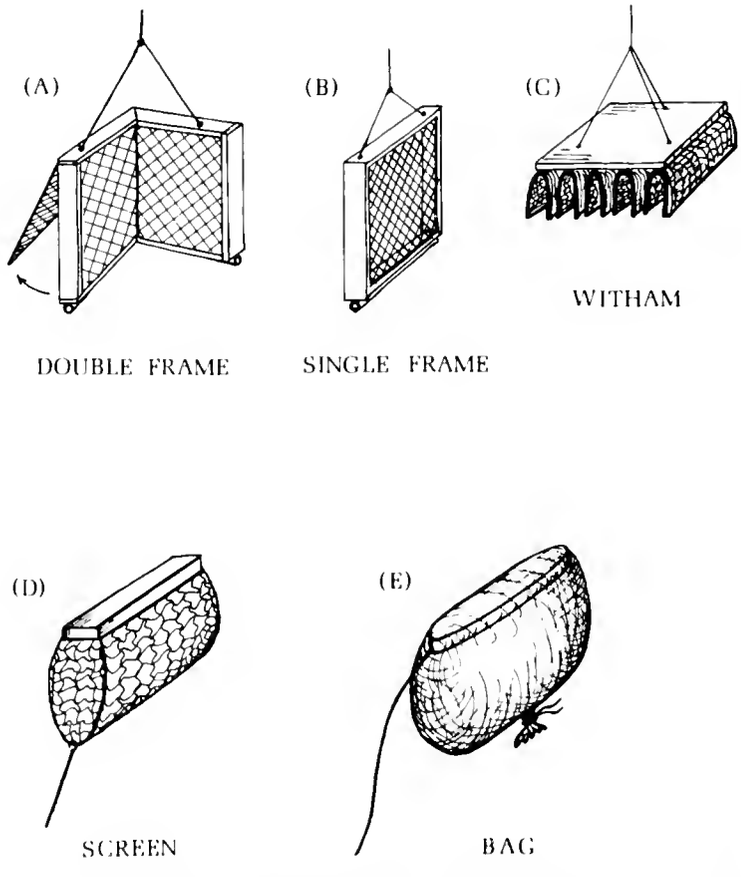

FIGURE 2.—Floating habitat trap designs employed in sampling puerulus larvae of *Panulirus interruptus*.

Suspension of the Habitat Traps

The strong surf and current conditions prevailing around the pier pilings required the development of a special system for suspending the habitat traps, as shown in Figure 3. This system allowed the trap to rise and fall during the tidal cycle, which has a vertical range of approximately 2.5 m, and in response to wave motion, thereby always remaining at the surface. The counterweight maintained a taut line and counteracted drag on the habitat trap caused by currents. No bottom anchor was necessary, thus eliminating problems of retrieval and fouling on kelp, and allowing the traps to be raised and lowered easily for examination. The traps also were held away from the pier pilings by the pole extension in order to prevent damage and entanglement.

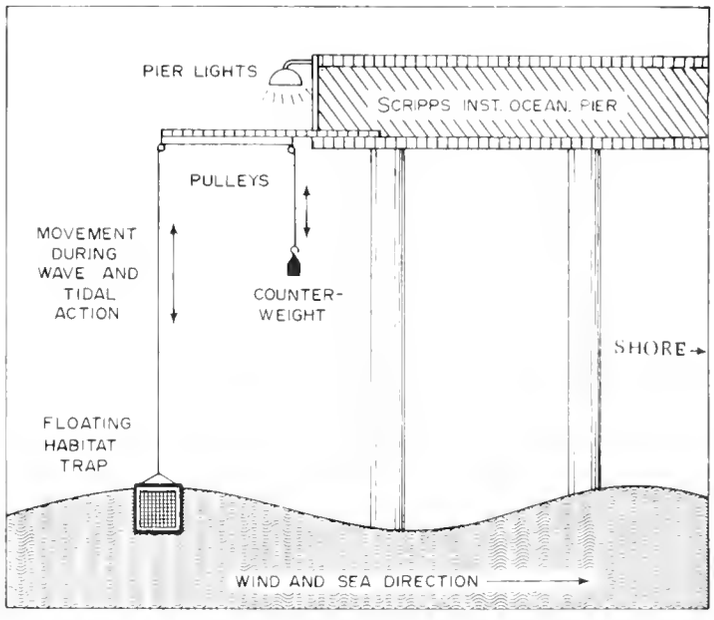

FIGURE 3.—The method employed in suspending habitat traps from the Scripps Institution pier.

Paired Neuston Nets

The results of night-lighting operations, discussed in a later section, suggested that the puerulus stage of *P. interruptus* swims within a few centimeters of the ocean surface. Thus, plankton or other nets towed below or near the surface probably would fail to catch this stage. Even surface tows made with a net breaking the surface might not be successful if it were trailed directly behind a vessel, because the "snow plow" action of the vessel might effectively push surface organisms away from the path of the net. Thus, paired neuston nets which could be mounted laterally on a small boat were developed to allow unobstructed surface water sampling, as shown in Figure 4. The presumed rarity of the puerulus stage required that these nets be of relatively large mesh size (5.0 mm) to allow reasonably fast towing speeds with a small boat (approximately 3 knots) and the filtration of large volumes of water. The short length and lateral position of the nets allowed their cod ends to be removed and emptied periodically without hauling the entire net from the water. The nets were towed with approximately 30% of the frontal area above water to ensure continual filtration of the top few centimeters of surface water, even during periods of low surface waves. The average frontal net area maintained submerged was approximately 0.7 square meter per net. Only rough estimates were made of the volumes and surface areas of water filtered during initial trials conducted during this study, as these were primarily concerned with evaluation of the sampler and with qualitative rather than quantitative results. The estimates of the water volume and surface area sampled were based on average boat speed and duration of the tow.

RESULTS

Night-Light Observations

Night-light observations were first conducted briefly in May 1968, and then resumed for a 2-mo period in September 1968. Night-light observations were also conducted again in the spring and summer of 1969, primarily to supplement information from the habitat traps also maintained during this period. The results of these observations, together with pertinent environmental data, are summarized in Table 1. During calm evenings in September 1968, pueruli were collected from the Scripps Institution pier at an average rate of approximately 4 per hour, with the highest rate reaching 12 pueruli collected within 90 min (8 per hour). No pueruli appeared during night-lighting conducted in October 1968, and further attempts were curtailed due to the onset of rough winter surf conditions which made the operation difficult. Night-lighting activities also were conducted at other San Diego localities during the period September-October 1968. These were: Quivira Basin in outer Mission Bay, Shelter Island in outer San Diego Bay, and the Imperial Beach pier. No pueruli were observed at any of these

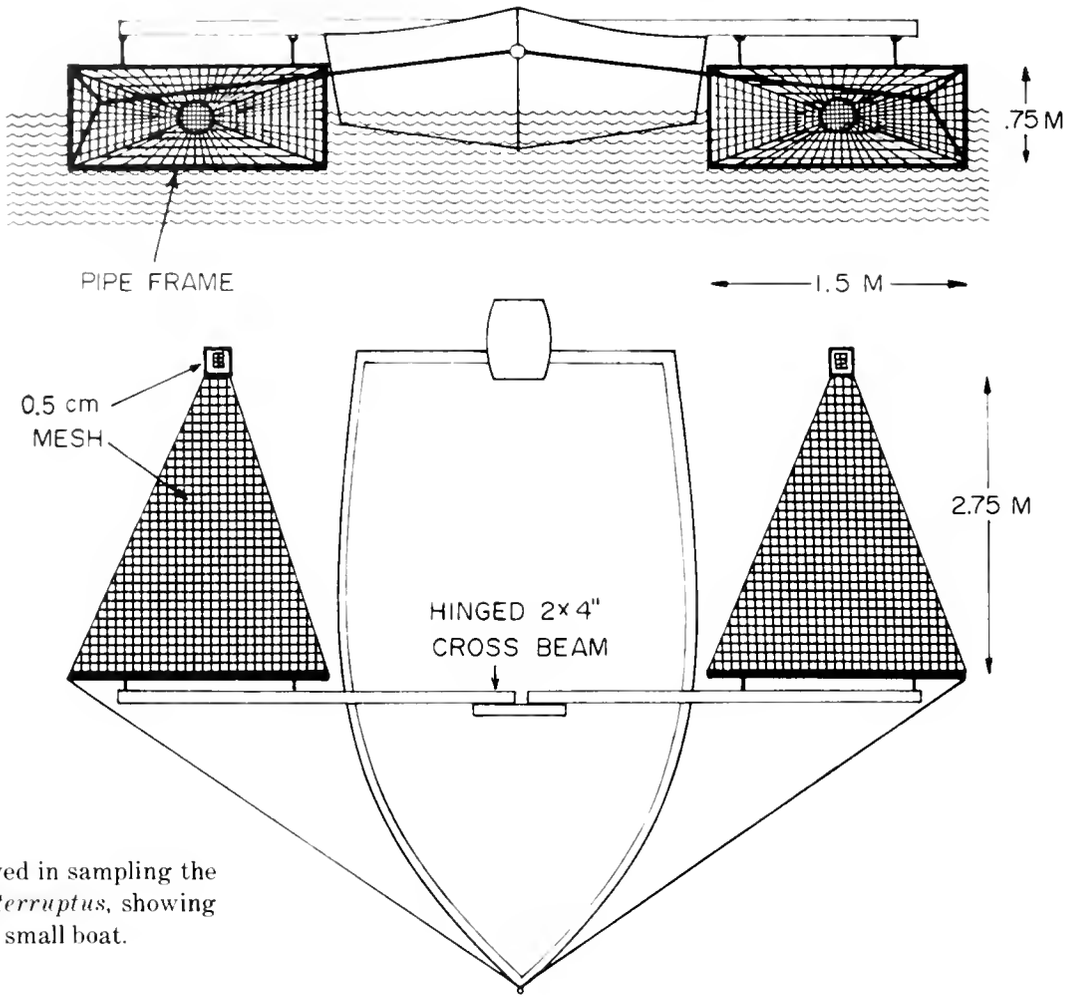

FIGURE 4.—Paired neuston nets employed in sampling the puerulus larval stage of *Panulirus interruptus*, showing the method used to deploy them from a small boat.

TABLE 1.—Results of night-light sampling for pueruli at the Scripps Institution pier and other San Diego localities.

Date	Number collected	Location	Time of sampling	Moon phase	Water temp. (°C)	Sampling period (min)	Suitability of conditions[1]
1968:							
May 15	0	Mission Bay	2000-2130	Full	16.0	45	Good
May 20	1	Scripps	2000-2130	Last Quarter	15.7	50	Fair
May 25	0	Mission Bay	1930-2030	New	16.4	60	Good
Aug. 28	9	Scripps	2130-2250	First Quarter	18.6	60	Good
Sept. 4	0	Imperial Beach	2030-2200	Full	20.7	80	Good
Sept. 7	4	Scripps	2200-2330	Full	20.0	40	Fair
Sept. 10	12	Scripps	2100-2230	Full—Last Quarter	20.5	90	Excellent
Sept. 16	3	Scripps	2000-2045	Last Quarter	20.7	40	Good
Sept. 26	4	Scripps	2000-2100	New—First Quarter	19.5	40	Fair
Oct. 2	0	Scripps	2230-2330	First Quarter—Full	18.3	50	Good
Oct. 10	0	Shelter Id.	2130-2250	Full—Last Quarter	18.5	80	Good
Oct. 20	0	Scripps	2200-2300	New	17.3	40	Good
Oct. 30	0	Scripps	2330-2430	First Quarter	16.8	30	Fair
1969:							
Apr. 5	0	Scripps	2030-2130	Full—Last Quarter	14.8	15	Poor
Apr. 20	0	Scripps	2130-2250	New—First Quarter	15.5	50	Good
May 7	0	Scripps	2030-2130	Last Quarter	15.9	20	Poor
May 15	0	Scripps	2130-2230	New	16.2	60	Good
May 23	6	Scripps	2145-2345	First Quarter	17.3	90	Good
June 4	3	Scripps	2200-2300	Last Quarter	18.1	30	Fair
July 10	14	Scripps	2100-2330	Last Quarter—New	20.5	90	Excellent
Aug. 7	6	Scripps	2130-2250	Last Quarter	21.5	70	Good
Sept. 12	4	Scripps	2210-2250	New	18.5	60	Fair
Sept. 22	0	Scripps	2030-2120	Full	18.0	20	Fair
Oct. 11	0	Scripps	2100-2230	New	18.0	50	Good
Oct. 20	0	Scripps	2000-2130	First Quarter	17.2	30	Fair

[1]The suitability of conditions for collecting pueruli was determined subjectively from general observations of current direction and velocity, wave height, and water clarity during the collecting period.

localities and work there was discontinued. Night-lighting observations during 1969 at the Scripps Institution pier provided a more complete picture of the apparent seasonal occurrence of pueruli, which first appeared in late May and were not observed after 4 September 1969.

These initial night-light studies allowed several interesting new observations on puerulus behavior. Previous investigators who reported that pueruli were occasionally attracted to night-lights (Harada 1957; Johnson 1960) presumed that the pueruli were lured off the bottom from rocky habitats where they had settled. However, this apparently was not the situation at the Scripps Institution pier for the following reasons.

The natural bottom substrate adjacent to the Scripps Institution pier for a radius of at least 500 m is entirely surf-washed sand. There is a small intertidal and subtidal rocky area approximately 500 m to the north, and an extensive rocky shoreline begins approximately 2 km to the south. While the pier pilings might afford a suitable habitat, we observed no pueruli or juveniles in several careful daytime and nighttime examination of the pilings, using scuba, during periods when there was active puerulus settlement in the habitat traps. In addition, direct observations of the free-swimming pueruli indicated that many individuals approached the light from a direction opposite that of the pilings. Perhaps most significant was the observation that the pueruli were seen swimming in only the top few centimeters of water; no individuals were ever seen approaching the light from a greater depth.

This opportunity to observe the free-swimming puerulus stage of *P. interruptus* thus demonstrated that, at least under these conditions, it is a surface-dwelling organism which occurs only in the top few centimeters of water. Consequently, the inconsistency or failure of standard plankton net tows to collect pueruli of this and other species probably is not due to the presumed benthic habits of this stage, but rather to improper sampling techniques. Only nets extending above the surface, and streamed parallel to the vessel's course with an unobstructed path, appear to be suitable. The likelihood of net avoidance accounting for previous failures seems minimal, as the pueruli of this species are relatively slow moving and easily captured in a hand held dip net, at least near a night-light.

Puerulus swimming speed in nature was measured by timing the passage of an individual between two lines suspended from a 2 m long, horizontally oriented pole, as it approached the underwater light. The mean swimming speed of six different pueruli under these conditions was 8 cm/s (range 6 to 9 cm/s). Individuals appeared to maintain this speed continuously, unless disturbed. In response to disturbance, they would spread their antennae and legs, sink slowly 5-20 cm, and then resume normal surface cruising with antennae held together and legs withdrawn. Illustrations of these swimming and sinking postures are shown in Figure 5.

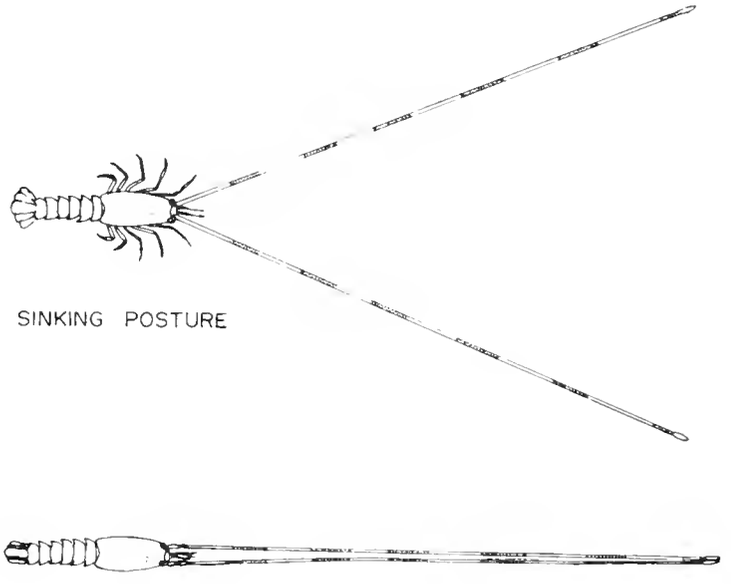

FIGURE 5.—Sinking and swimming postures of the puerulus larval stage of *Panulirus interruptus* as observed under a night-light.

Puerulus Pigmentation in Relation to Date of Settlement

Newly settled pueruli, or those collected during night-lighting, were always completely transparent. Pueruli held in open and closed system aquaria provided with *Phyllospadix* or other intertidal flora and fauna almost immediately began acquiring pigmentation, and this continued at a rapid rate. At temperatures of 18-20°C, pueruli would change from complete transparency to nearly complete pigmentation within 9-10 days, and would then moult into the first postpuerulus stage.

This occurred consistently among over 50 individuals we held in aquaria and observed systematically. Thus, the degree of pigmentation provided a reliable method of determining, within 1-2 days, the date of settlement. This technique

provided a more accurate means of evaluating possible correlations between puerulus recruitment and changing environmental factors than by merely recording the date on which the habitat trap was examined, as done by Witham et al. (1968) and Sweat (1968). In his later study, Parker (1972) provided a more detailed description of the pigmentation and transformation of the puerulus and postpuerulus stages of *P. interruptus*.

Laboratory observations indicated that once the puerulus settled in a suitable substrate, its transformation into a postpuerulus proceeded without delay. However, a few individuals which were held in containers without fresh *Phyllospadix*, algae, or rocks containing epifauna, remained as transparent pueruli for 2-3 wk until death, suggesting strongly that the presence of such suitable habitat features is necessary to induce transformation to the postpuerulus stage.

After settlement, pueruli became photonegative and were never again seen swimming. In order to test the related question of whether or not a settled puerulus might desert a habitat trap upon its removal from the water, and thus produce unreliable trap catch data, one seaweed frame habitat trap and one Witham trap containing known numbers of pueruli were returned to the water for 5-10 min on two different occasions, and then retrieved. No individuals left either the Witham or seaweed traps. This, and the laboratory observations described above, indicate that the number of individuals found in a habitat trap probably is a reliable estimate of the number that settled there.

Comparison of Habitat Trap Types

Habitat traps were mounted either singly or in groups of two or three from one main support bar in order that at least six different types could be tested simultaneously from the three available Scripps Institution pier positions (position A, B, or C, as shown in Figure 1). The exact pier position and combinations of traps were alternated from time to time, as indicated in Table 2, in order to compensate for possible variations in unknown factors influencing puerulus settlement, such as current direction, eddies near the pilings, and differences in daytime or nighttime light intensities. The results of comparative habitat trap design studies conducted during the summer of 1969 are summarized in Table 2. These results indicate that all habitat traps containing natural seaweed proved markedly superior to the Witham artificial habitat trap for this species (Figure 2C).

Only 5 pueruli were collected by two Witham habitat traps ($\bar{x}$ = 2.5 per trap), while 97 pueruli were collected by four seaweed habitats ($\bar{x}$ = 24.2

TABLE 2.—Results of a comparison of the catch effectiveness of habitat traps suspended off the Scripps Institution pier. The catches of pueruli per trap are also recorded in terms of the specific location of the trap at the pier (a, b, or c). Positions A and B were lighted, while position C was unlighted, as shown in Figure 1. For descriptions of the habitat trap designs, see Figure 2 and text.

Date traps examined 1969	Duration of sampling period (days)	Number of pueruli collected in habitat traps						
		Seaweed habitat traps				Witham habitat traps		Total collected
		Double frame	Single frame	Bag	Screen	#1	#2	
June 14	6	—[1]	2 a	—	—	0 a	—	2
20	6	—	—	—	—	—	—	—
27	7	—	—	—	—	0 a	—	0
July 2	4	0	7 a	—	—	1 a	—	8
5	3	3 b	1 a	—	—	0 a	—	4
9	4	3 b	1 a	—	—	0 a	—	4
13	4	2 b	1 a	—	—	0 a	—	3
17	4	3 b	0 a	—	—	0 a	—	3
23	6	3 b	1 a	—	—	1 b	—	5
28	5	1 b	1 a	—	—	0 b	—	2
Aug. 4	6	23 b	2 a	—	—	1 b	—	26
6	2	2 b	1 a	—	—	0 b	—	3
10	4	1 a	4 b	0 c	0 c	0 c	0 b	5
16	6	3 a	8 b	1 c	0 c	0 c	0 b	12
27	11	2 a	12 b	1 c	1 c	0 c	1 b	17
Sept. 4	8	1 a	1 b	0 c	0 c	0 c	1 b	3
12	8	0 c	0 c	2 b	1 b	0 c	0 b	3
19	7	0 c	1 c	1 b	0 b	0 c	0 b	2
27	8	0 c	0 c	0 b	0 b	0 c	0 b	0
Oct. 3	6	0 c	0 c	0 b	0 b	0 c	0 b	0
Total		47	43	5	2	3	2	102

[1]Habitat trap not in position at this time.

per trap), when all were in continuous use during the same 90-day time period from June through September 1969 (Table 2). Comparison of these catch figures by a chi-square test for equality indicates that the mean catch of the seaweed traps was significantly higher than that of the Witham traps ($P < 0.05$). The Witham habitat trap was not effective, either when new or moderately fouled with a variety of sessile organisms, yet the natural seaweed habitat traps appeared to catch well regardless of the condition of the plant material. Variations in the abundance of pueruli throughout the summer and differences in settlement in the different habitat positions, as discussed in subsequent sections, did not allow specific comparisons to be made between results of the habitat trap designs listed in Table 2. Yet general comparisons indicate that there were no major differences in catch between these trap designs that are not attributable to the environmental causes discussed in subsequent sections below. However, the nylon bag habitat trap (Figure 2E) proved to be the best in terms of cost, ease of use, and durability. It also appeared to catch as well as the other types, although tests were begun too late in the final puerulus settlement season during which we sampled to verify this. Thus, the bag trap design is recommended for future studies of this nature, and was used by Parker (1972) in a later study.

Habitat Trap Success in Relation to Position on the Pier

A comparison of the catch results of the "double" and "single" frame seaweed habitat traps, as shown in Table 2, indicates that more pueruli were consistently collected from the B than the A position on the Scripps Institution pier (Figure 1), when either type of trap was placed there. A combined total of 65 larvae was collected in the B position, versus only 24 in the A position by these two traps during the same 82-day period from 2 July to 19 September. A comparison of these catch figures by a chi-square test for equality indicates that the catch at position B was significantly greater than at position A ($P < 0.05$). No explanation for this difference is apparent at the present time, but it seems to indicate that there may be subtle environmental effects which influence puerulus settlement in habitat traps to a greater extent than do variations in trap design.

Significance of Nocturnal Illumination of Traps in the Attraction of Pueruli

The strongly positive phototactic response exhibited by the puerulus stage during night-lighting observations suggested that nocturnal illumination may play an important role in the successful operation of habitat traps. To evaluate this, additional traps were maintained in an unlighted area of the Scripps Institution pier (area C in Figure 1).

The results, summarized in Table 3, indicate that during the period from 10 August to 29 September 1969, when each trap design was maintained at both the lighted (positions A and B) and nonlighted (position C) pier locations, all traps caught more larvae in the lighted positions. A total of 38 larvae were collected over 132 "trap-days" (1 trap in place for a 24-h period = 1 trap-day) in the lighted position, versus only 4 per 132 trap-days in the nonlighted position. Comparison of these total catch values by means of a chi-square test for equality indicates that the value for the lighted positions was significantly greater than for the unlighted one ($P < 0.05$). This suggests that noc-

TABLE 3.—A comparison of the number of pueruli caught in lighted and nonlighted habitat traps. For detailed descriptions of trap types, and lighted and nonlighted pier positions, see text and Figures 1 and 2.

Type of habitat trap	Lighted (positions A and B)			Nonlighted (position C)		
	No. individuals collected per trap	Sampling period (days)[1]	Catch per 20 trap-days	No. individuals collected per trap	Sampling period (days)[1]	Catch per 20 trap-days
Double frame	7	29	4.8	0	15	0
Single frame	25	29	17.2	1	15	1.32
Bag	3	15	4.0	2	29	1.38
Screen	1	15	1.32	1	29	0.68
Witham "a"	—[2]	—	—	0	44	0
Witham "b"	2	44	0.48	—	—	—
Mean catch per 20 trap-days			5.4			0.68

[1]Number of trap days during the period of 10 August to 29 September only (see Table 1).
[2]Habitat trap not in place.

turnal illumination plays a major role in the successful use of these habitat traps for pueruli of *P. interruptus*. The fact that no pueruli were caught in the unlighted habitat traps maintained offshore, as discussed in the next section, provides additional strong support for this conclusion.

Habitat Traps Maintained Offshore

Unlighted habitat traps of the "bag" and "screen" designs were anchored in water 3- to 15-m deep in the San Diego area off Point Loma, La Jolla, and off the northeast shore of Catalina Island, Calif., at the positions shown in Figure 6a, b. This was done to monitor the recruitment of pueruli at other locations along the San Diego coastline, and on the leeward side of a large offshore island, as well as to determine the importance of lights in attracting pueruli by comparing these unlighted traps with those placed under the Scripps Institution pier lights. The traps placed offshore were checked and refilled with fresh *Phyllospadix* and red algae every 10-15 days during August and September 1969. Many were lost, apparently because of entanglement with kelp and boat propellers. However, the large number maintained successfully failed to collect any pueruli, despite the fact that puerulus settlement at the Scripps Institution pier was relatively high during this same period. The four traps maintained at Catalina Island were situated directly above a shallow rocky area, approximately 2-6 m in depth, where we had observed many small first year juvenile lobsters the previous winter. We presumed that the presence of these young juveniles indicated that this was an area of high puerulus recruitment. Thus, failure of the unlighted traps to collect pueruli at this location was particularly surprising.

The failure of these offshore habitat traps may have been due not only to the lack of nocturnal illumination, but also to the presence of large quantities of *Phyllospadix* and algal flotsam in the areas where they were maintained. The probability of a puerulus settling in a seaweed habitat trap under such conditions would be small, considering the large volume of seemingly equally suitable patches of floating surfgrass and algae present in these areas. In contrast, relatively few masses of plant flotsam of this kind were observed in the area around the Scripps Institution pier.

In an attempt to evaluate this, many clumps of floating *Phyllospadix* were collected and examined

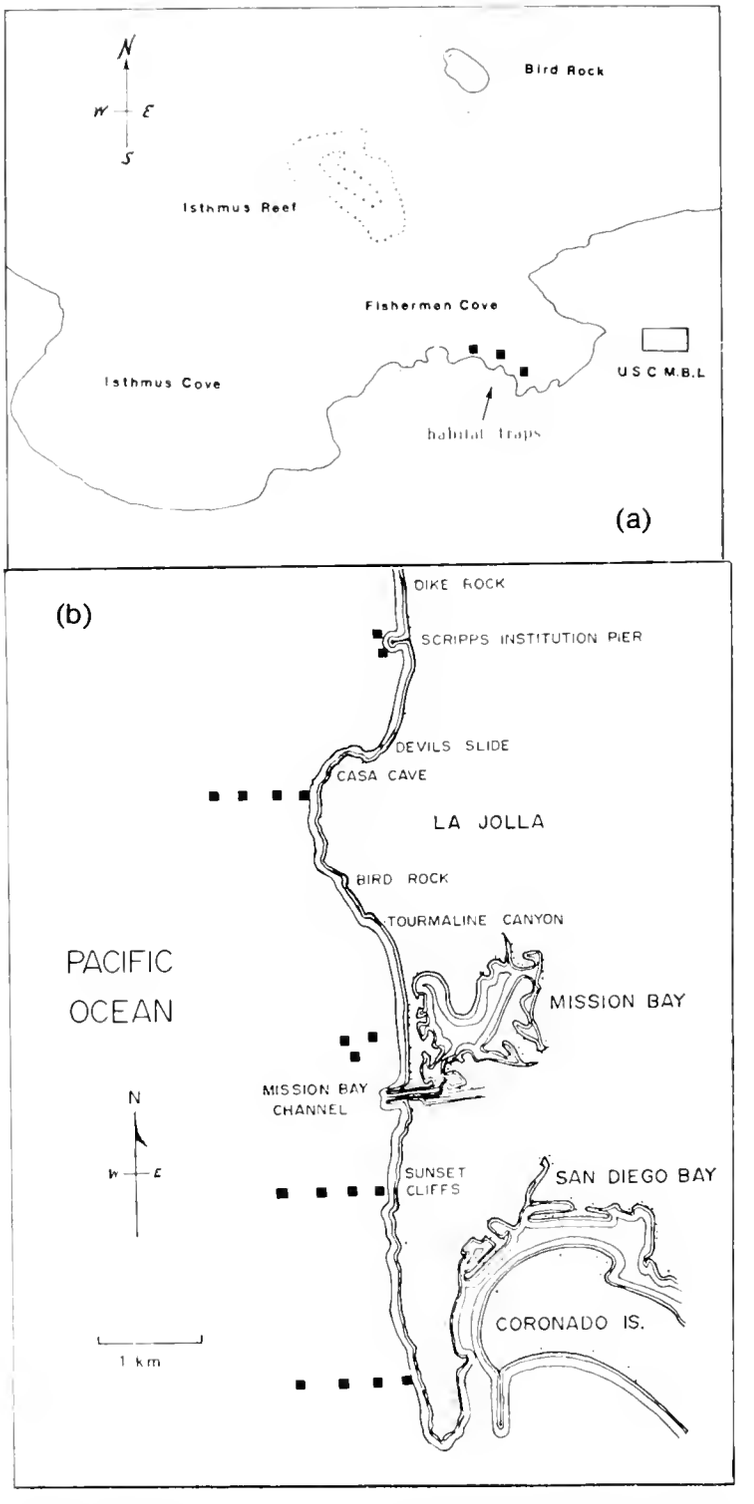

FIGURE 6.—Locations of sampling areas off northeastern Catalina Island (a) and San Diego (b) for puerulus and early juvenile *Panulirus interruptus*.

for pueruli while deploying and checking the offshore habitat traps. No pueruli were found in this manner, but only a relatively small percentage of this material was examined relative to that present, thus leaving the question open to further investigation.

Neuston Net Sampling

Semiquantitative sampling with the paired

neuston nets was initiated late in the study, during the period 3 September to 12 October 1969 (Table 4). The results of the habitat trap collections (Table 2) suggest that these towing operations were conducted during a period of very low puerulus abundance, yet two pueruli were collected during two separate towing efforts. Unfortunately, it was not possible to complete the development of these nets and begin sampling operations during the summer period of peak puerulus abundance.

Concurrent studies of the distribution and abundance of the phyllosoma larval stage of *P. interruptus* in the same inshore areas, using standard 1 m and larger conical nets in surface and oblique towing patterns, failed to catch any pueruli (W. E. Hazen and J. H. Rutherford, pers. commun.). In addition, considering that Johnson (1956, 1960) obtained only a few pueruli during 7 yr of extensive sampling with surface and oblique hauls of a 1-m conical net, our preliminary results suggest that use of this neuston net system probably is a more effective sampling technique and should be thoroughly evaluated in future studies. These results also strengthen the argument that the puerulus is pelagic, occurs at the surface, and is a temporary member of the neuston community.

TABLE 4.–Results of puerulus sampling with paired neuston nets.

Date 1969	Time	Surface area sampled (m^2)[1]	Water volume sampled (m^3)[1]	San Diego sampling localities	Number collected
3 Sept.	1400-1500	800	400	Mission Bay	0
10 Sept.	2000-2100	800	400	Mission Bay Channel	0
10 Sept.	2130-2230	800	400	Mission Bay Channel	1
20 Sept.	1800-1840	500	250	Off Pacific Beach	0
20 Sept.	1900-1930	300	150	Off Pacific Beach	1
7 Oct.	2000-2100	800	400	Off Pacific Beach	0
12 Oct.	1200-1330	1,000	500	Mission Bay Channel	0

[1]Estimated from average boat speed and duration of tow.

Relationship of Puerulus Settlement to Environmental Factors

Efforts to relate the influx of pueruli in major environmental factors, such as temperature, salinity, and lunar phase, were complicated by lack of information concerning other unmeasured or unknown variables which may have subtle effects on the settlement of pueruli in the habitat traps. These may include specific wave characteristics, current velocity and direction, and water turbidity. Therefore, the apparent low abundance of pueruli during some periods might be due to their failure to settle in the habitat traps, rather than their absence from coastal waters. Variations in surface salinity levels of water masses along the open coast when our sampling was conducted were very slight. Consequently, the influence of this factor probably was negligible and showed no obvious relationship to puerulus settlement, based on data available for the area of the Scripps Institution pier. Variations in wave heights and surf conditions occurring at the Scripps Institution pier during the summer also were relatively small. The range in height of swells recorded at the pier was 0.3-0.9 m (1-3 feet), and showed no obvious pattern in relation to puerulus settlement. However, the following general relationships between puerulus settlement and environmental conditions seem apparent.

Seasonal Periodicity

The results of night-lighting during 1969 (Table 1), and habitat trap sampling conducted in 1969 (Table 2) are presented together in Figure 7. These data indicate that the pueruli of *P. interruptus* began to appear in nearshore San Diego waters during late May, and occurred there continuously until mid-September, apparently reaching their greatest abundance during the first week of August. The habitat traps could not be maintained during rough winter surf conditions, and occasional night-light efforts during the winter were unsuccessful, so we were not able to establish conclusively that pueruli are absent from nearshore waters between October and May. However, evidence presented by Johnson (1960) on the seasonal periodicity of the later phyllosoma stages of *P. interruptus*, which are abundant only during the period from January to June, suggests that there would be no major influx of pueruli during the winter months, although a small number of individuals might be present throughout the year.

Relationship to Water Temperature

A comparison between surface water temperatures and puerulus trap catches obtained at the Scripps Institution pier indicates that the

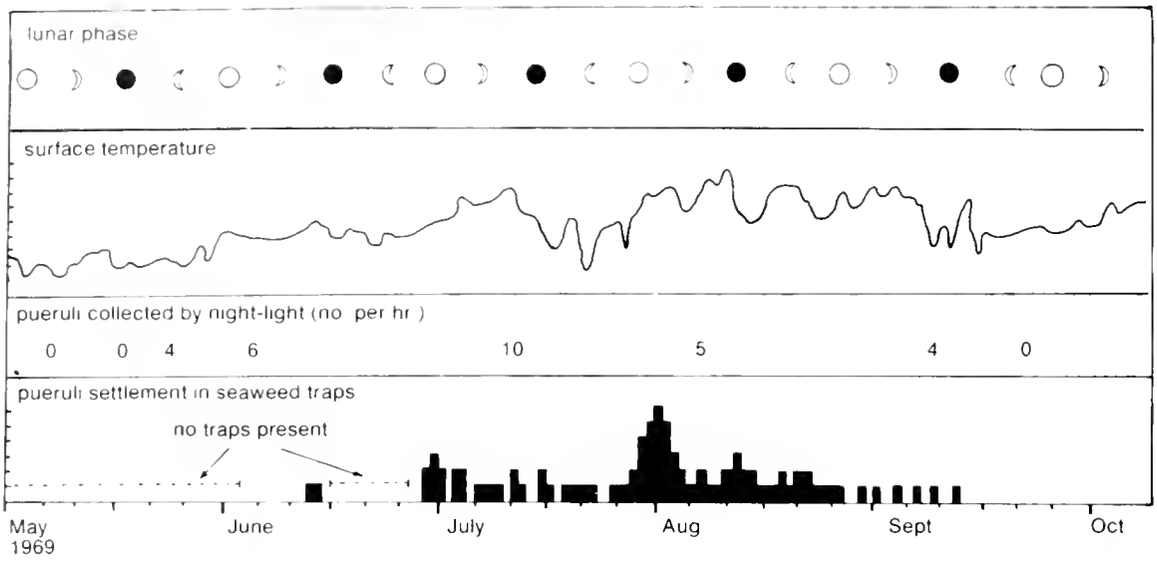

FIGURE 7.—Relationship of puerulus settlement to lunar, temperature, and seasonal cycles. The habitat trap catches are presented as catch per unit effort, and represent the total combined catch of two seaweed traps (primarily the single and double frame designs, Figure 2) maintained in the lighted pier positions (a and b). The date of original settlement for each puerulus was estimated within 1 to 2 days by its degree of pigmentation. Temperature data are from Scripps Institution pier records.

prevailing influx of pueruli corresponds with the seasonal period of highest temperatures, as shown in Figure 7. The peaks of puerulus settlement occurring during the first weeks of July and August also appear to correspond with periods of rising water temperatures. However, another possible interpretation of the settlement patterns shown in Figure 7 is that the low abundance of pueruli observed during the period of 10-25 July may have been caused by an influx of cold water originating from local submarine canyon upwelling, which occurs periodically. Such a cold upwelling water mass would not be expected to contain any pueruli if the surface-swimming habits attributed to this stage are correct, and could effectively prevent pueruli in warmer water masses from entering the pier area we sampled.

Lunar Perdicity

Studies by Witham et al. (1968) and Sweat (1968) of *P. argus* pueruli in Florida and by Phillips (1972) of *P. longipes cygnus* pueruli in Australia determined that puerulus settlement was highest during the new moon phase and did not occur at all during full moon periods. The abundance of *P. interruptus* pueruli, on the other hand, did not show any evident relationship to lunar phases. On two occasions during the first parts of July and August, there were apparent peaks in puerulus abundance during the full moon phase, as shown by the habitat trap results in Figure 7. Night-light and habitat trap collections and their relationship to lunar phases are summarized in Table 5. These data indicate that there were no lunar periods when pueruli of *P. interruptus* were not present and did not settle, and thus that they apparently do not respond to lunar cues, or at least not in the same manner as do species studied elsewhere.

Witham et al. (1968), Sweat (1968), and Phillips (1972) were unable to determine whether the absence of pueruli from their habitat traps during full moon periods was due to their absence from the area or their avoidance of the traps. The fact that pueruli of *P. interruptus* were present and settled in our habitat traps directly under the bright lights of the Scripps Institution pier in-

TABLE 5.—The relationship between lunar phases and puerulus abundance, as determined by habitat trap and night-light results. Total catches, given in detailed form in Tables 1 and 2, are presented below as catch per unit effort.

Lunar phase (eight equal divisions)		Habitat trap (mean catch/hour)[1]	Night-light (mean catch/hour)[2]
Full moon	(1)	5.0	3.0
	(2)	2.5	4.0
Last quarter	(3)	1.7	4.0
	(4)	1.7	10.0
New moon	(5)	2.0	1.0
	(6)	1.5	3.0
First quarter	(7)	1.8	6.5
	(8)	1.0	0.0

[1]Based on catches of the single and double frame traps only.
[2]Periods of poor conditions (i.e., unsuitable for observing pueruli) were excluded from calculation of the mean.

dicates that, at least for this species, illumination is not an inhibitory factor. In fact, it may serve as a stimulus for settlement.

In this regard it is important to note that persistent stratus overcast in the southern California coastal zone during the summer months results from upwelled water coursing southward from Point Conception. Thus, normal background illumination from the moon and stars generally is eliminated, although sky glow is present near major coastal cities. Consequently, at our sampling site the prevailing overcast and nocturnal illumination from the Scripps Institution pier lights could have masked any lunar effect, resulting in what we observed, puerulus settlement in traps during all moon phases.

Duration of the Puerulus Stage

Essentially nothing is known about the duration of the puerulus stage of any spiny lobster species. Sheard (1949) suggested that the puerulus of the western Australian spiny lobster, *P. longipes cygnus*, lasts for 2-3 wk, but offered no supporting evidence.

April was consistently the period of greatest abundance for the last phyllosoma stage (stage 11) of *P. interruptus*, based on evidence obtained by Johnson (1960) in extensive sampling during the period 1949-1957, as summarized in Figures 8 and 9. Most of the late stage phyllosoma larvae he collected were taken at stations 160-320 km (100-200 miles) offshore (Figure 9). Our data indicate that the greatest abundance of pueruli in coastal waters during 1969 was in early August, approximately 3½ mo after this peak in the abundance of stage 11 phyllosomes. Assuming that the duration of the eleventh phyllosoma stage extends for a period of 1 mo, and that shoreward migration is accomplished by the puerulus, rather than by the last phyllosoma larval stage (see subsequent discussion), then this suggests that the puerulus stage of *P. interruptus* may have an average duration of approximately 2½ mo. This timing is represented diagrammatically in Figure 8. Thus, a period of 2-3 mo appears to be a reasonable estimate for the average duration of the puerulus stage.

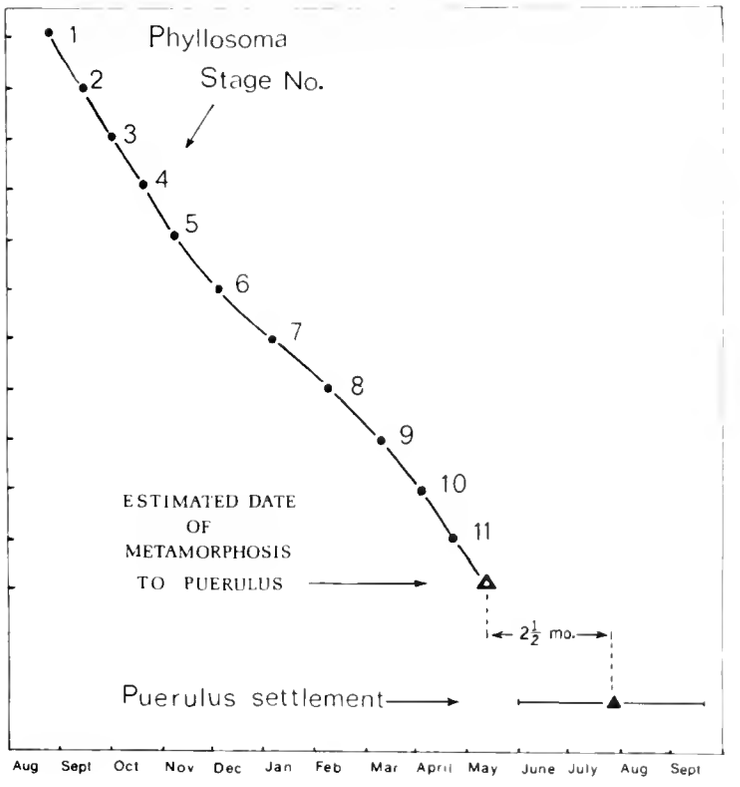

FIGURE 8.—Comparison of seasonal occurrence and dates of greatest abundance of the phyllosoma and puerulus larval stages. Data on the phyllosoma stages are from Johnson (1960).

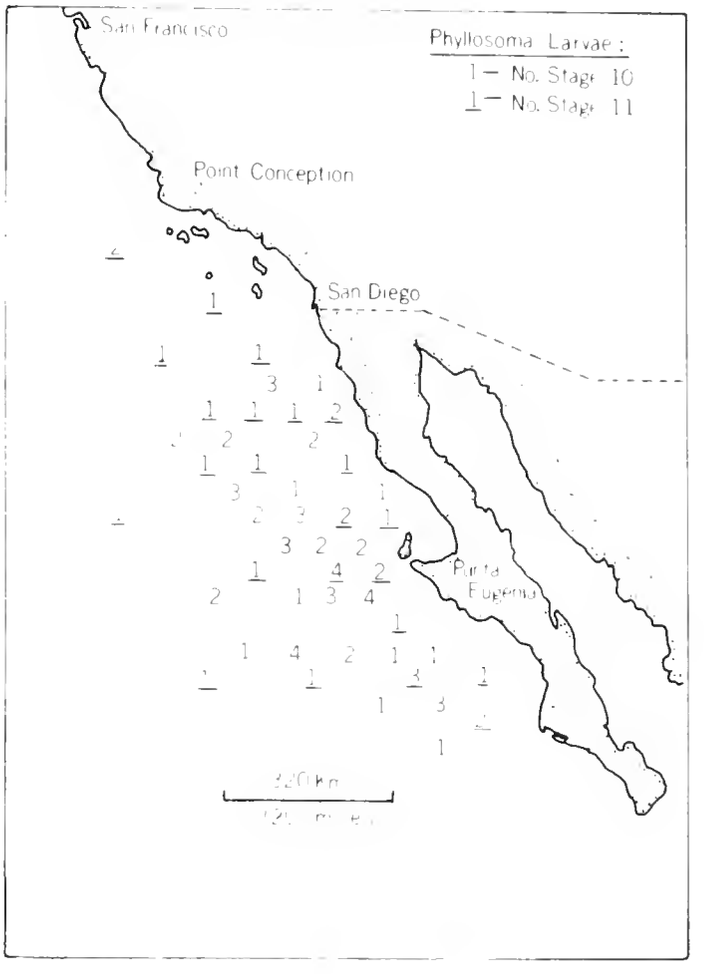

FIGURE 9.—Offshore distribution of the late stage phyllosoma larvae (stages 10 and 11) of *Panulirus interruptus* during the period from 1949 to 1955, as reported by Johnson (1960).

DISCUSSION

Mode of Life of the Puerulus Stage

Johnson (1960) and Lindberg (1955) speculated that the puerulus of *P. interruptus* is a benthic form, largely because it occurs so infrequently in standard net tows. However, the results of this study strongly suggest that it is a pelagic form, and in particular a member of the surface-dwelling neuston. Several lines of evidence support this conclusion. Our observations of many free-swimming pueruli which were attracted to night-lights revealed that the pueruli always swam in the top few centimeters of surface water, and no individuals were ever observed moving toward the light from deeper water. Pueruli were readily collected in habitat traps floating at the surface. However, the occurrence of pueruli at greater depths cannot be ruled out on the basis of habitat trap evidence alone because the traps were not maintained at greater depths. Although preliminary and very limited, our surface sampling with neuston nets yielded a much higher catch per unit effort than did standard near-surface and oblique tow sampling methods employed by previous investigators.

The puerulus stage of *P. interruptus* also has specialized physical characteristics which suggest that it is adapted to a pelagic existence. These include: 1) heavily setose pleopods and a streamlined body for efficient, forward swimming; 2) a transparent body completely devoid of pigmentation; and 3) extremely long, delicate antennae which appear unsuitable for a benthic existence because they quickly break off upon settlement. In addition, at the time the puerulus moults into the first postpuerulus stage, it loses the setose pleopods and acquires stronger antennae, an expanded cephalothorax, and walking ability typical of later demersal stages. In fact, pueruli we collected and held in aquaria were never observed walking upon the substrate, instead only clinging to algae or crevices in rocks and shells. A more detailed description of this transformation process from puerulus to postpuerulus was developed in a subsequent study by Parker (1972).

Both Witham et al. (1968) and Phillips (1972) reported that, in comparative tests between habitat traps maintained on the surface and traps anchored 1-4 m below the surface, all but a few pueruli of *P. argus* and *P. longipes cygnus* were collected in those at the surface. Phillips collected only 1 out of 38 pueruli in traps at 4-m depth, and Witham collected 12 from one trap anchored on the bottom in water 1 m deep, as compared to an average of 27 pueruli in surface traps located nearby.

Sweat (1968) utilized a multiple plankton net array for studying the depth preference of *P. argus* pueruli in the Florida Keys area. This system consisted of three conical plankton nets mounted from a bridge across a shallow channel connecting Florida Bay with the Atlantic Ocean. The nets were suspended at the surface, at mid-depth (1 m), and on the bottom (2.3 m), and were operated for 2-h periods within the new moon phase during evening flood tides. The largest proportion of the pueruli were collected by the mid-depth net (116 at the surface, 418 at 1 m, 61 at 2.3 m depth). However, this may have been due to the particular conditions in the channel, including its shallow depth, water turbulence, and the possibility that the pueruli were in the process of settlement at the time of sampling.

In general, these observations by Sweat (1968), Witham et al. (1968), and Phillips (1972) agree with ours on *P. interruptus*. The pueruli of these species seem to be restricted primarily to the ocean surface, at least just prior to settlement.

The Functional Significance of the Puerulus Stage

On the basis of morphology and our observations of its behavior, the puerulus stage of *P. interruptus* appears to be well adapted for directed, forward swimming, as shown in Figure 5, rather than for the passive, pelagic existence apparently exhibited by all phyllosoma larval stages of spiny lobsters. What, then, is the purpose of this directed swimming? A possible answer is suggested by considering the early life history of the scyllarid lobster, *Scyllarus americanus*, which also has a phyllosoma larval stage but no transitional puerulus stage, moulting instead directly into a nonswimming, benthic juvenile (Robertson 1968). Some other scyllarid species have a transitional form called a puerulus or, more properly, a nesto stage. The phyllosoma larval period of *S. americanus* is quite short (4-5 wk), thereby allowing the larvae a much greater chance of remaining near the shallow coastal areas suitable for later demersal life. In contrast, the phyllosomes of palinurid lobsters and other species of scyllarids may be carried several hundred kilometers out to

sea during their typical 5-10 mo larval existence. Obviously, the larvae must return not only to the coastal area, but also to very shallow nearshore zones if they are to transform and become established as demersal juveniles.

Previous investigators (Lindberg 1955; Johnson 1956, 1960, 1971; Saisho 1966; Sims and Ingle 1966; Lazarus 1967; Chittleborough and Thomas 1969; Chittleborough 1970) have postulated for several species that this recruitment in nearshore waters takes place during the phyllosoma stage, possibly through the action of countercurrents, upwelling, and eddies. Several studies, particularly those of Johnson (1960) and Chittleborough (1970), have shown clearly that large numbers of late stage phyllosoma larvae do remain well within the coastal areas in which the earlier larval stages occur. Evidence presented by Johnson (1960) also has shown that hydrography plays a major role in retaining a supply of late stage phyllosomes, and presumably pueruli, within reasonable distances from the coast. The presence, within one net haul, of several different phyllosome stages that must have been produced months apart, and the presence of late stage phyllosomes at the same locality, is good evidence that mixing processes and retaining eddies prevent wholesale flushing of these larvae from the coastal area. However, the late stage phyllosomes seem to be concentrated primarily in areas 50-250 km offshore, and the specific mechanism of onshore movement and recruitment has not been demonstrated.

If there were major active or passive movements of late stage phyllosomes toward shore, then one would expect to find relatively large numbers of them in shallow, inshore waters as well, or at least a trend in this direction. Most of the sampling reported by Johnson (1956, 1960) was conducted in waters 8 or more kilometers ($\geq$ 5 miles) offshore. However, studies of the distribution and abundance of phyllosoma larvae of *P. interruptus* in San Diego waters much closer inshore by W. E. Hazen and J. H. Rutherford (pers. commun.) during the summer months of 1969-1970, employing surface and oblique net tows, failed to collect any individuals older than stage 2. This suggests that the later stages occur either many kilometers offshore, as observed by Johnson (1956, 1960), or are concentrated in unknown areas.

For lack of evidence to the contrary, it has also been suggested that these phyllosoma larvae occurring far offshore are lost to the population and must perish. For similar reasons, Lindberg (1955) and Johnson (1960) have speculated that when these phyllosomes moult into the puerulus stage, the puerulus quickly settles to the bottom while still in deep water. Presumably, some of these are then able to migrate onshore to the shallow coastal nursery areas as benthic puerulus or postpuerulus forms.

However, in light of our behavioral observations on both pueruli and juveniles, another more likely explanation is that the puerulus stage may have evolved specifically for this purpose of recruitment. These observations suggest to us that the puerulus is a transitional, pelagic stage specifically adapted for directional swimming, and that it is capable of returning by active means to nearshore nursery areas suitable for settlement, thereby fulfilling the key role in recruitment. During this process, the surface-swimming and associated positive phototactic behavior of the puerulus stage probably aid it in locating the shallow nearshore areas which our related observations suggest are required as nursery grounds for the early juvenile stages.

Exactly how important a role the puerulus stage plays in the recruitment of the demersal population probably depends on three factors: 1) the degree of "assistance" contributed previously by the late phyllosoma stages which may move actively, e.g., by vertical migrations, into shoreward-directed currents or eddies; 2) how effective the puerulus is in travelling over long distances, with regard to both swimming speed and endurance; and 3) how well the puerulus can navigate, considering the fact that aimless wandering or swimming away from the coast would markedly reduce its probability of survival.

It seems reasonable to expect that the puerulus can swim nearly continuously, as other nektonic crustaceans, such as euphausiids, apparently do. If so, our estimate of an 8 cm/sec average swimming speed for the puerulus indicates it has the potential to travel approximately 7 km (4.3 miles) per day, or about 500 km (350 miles) during the period of 80 days estimated as the approximate average duration of this stage. Thus, the 160-320 km (100-200 mile) distance from shore at which Johnson (1960) found most late stage *P. interruptus* phyllosomes (Figure 9) could be within the basic swimming capabilities of the puerulus stage, even if part of the time was spent swimming against surface currents or in an inactive state.

The current patterns off the southern California and Baja California coasts are complex, and have

been studied extensively (see, for example, Johnson 1956, 1960; Wyllie 1966). During the summer months the California Current system has a generally southward trend, but displays retaining eddies and a net northward onshore drift in the northern range of *P. interruptus* larval distribution near the southern California coast and adjacent Channel Islands. There is a net southerly or offshore drift for water masses off most of Baja California. Even the apparent swimming capabilities of the puerulus stage probably would not allow it to move against these strong, offshore surface currents, particularly because an object in the surface waters would be vectored at a 45° angle, or westwardly, to the wind and current forces.

As a specific example of this problem, review of mean geostrophic flow at the surface off California and Baja California for the months of June-September during the typical period 1950-1964 (Wyllie 1966) reveals that there was a net surface transport southward from Point Conception to Cabo San Lucas offshore from approximately 80-320 km (50-200 miles). Northward flow near shore during these summer periods occurred only in the Southern California Bight (San Diego to Ventura), while net offshore transport apparently occurred from Bahia San Quintin south to Cabo San Lucas as a precursor to the California Current Extension.

Thus, it appears very likely that a majority of the late stage phyllosoma and puerulus larvae in the surface layers in this region, more than about 40-95 km (25-60 miles) offshore, depending on variations in the current system, were swept seaward by geostrophic flows which averaged greater than 46 cm/sec (0.9 knots) during this typical 15-yr interval. Such individuals undoubtedly are lost to the population. On the other hand, individuals present closer to shore, or in retaining eddies near the Southern California Channel Islands and the shallow Bahia Sebastián Vizcaino-Isla Cedros area (Johnson 1960), are within distances and ocean surface conditions which would allow their nearshore recruitment by directed swimming of the puerulus stage.

The Significance of *Phyllospadix* in the Settlement of the Puerulus Stage

The strong preference by the puerulus stage for the habitat traps containing *Phyllospadix torreyi*, as compared to generally similar synthetic material in the Witham traps, seems particularly significant in view of the fact that both Serfling (1972) and Parker (1972) discovered numerous early juvenile stages primarily in areas which had thick growths of this surfgrass. Comparative evaluations of habitat traps filled with *Phyllospadix* and other substrates, such as giant kelp (*Macrocystis pyrifera*) fronds and holdfasts, the eelgrass (*Zostera marina*), and *Mytilus* clumps, might prove useful as a means of improving collection success with the traps.

Preference tests involving various substrates typical of different nearshore habitats might also suggest other areas of natural puerulus settlement. In this regard, however, substrate preference tests of the puerulus and postpuerulus stages conducted in the laboratory by Parker (1972) suggest that these stages favor *Phyllospadix* over *Macrocystis*, *Zostera*, several species of red algae, sand, and rock.

Evaluation of the Natural Seaweed and Artificial Habitat Traps

In comparative tests conducted by Witham et al. (1968), their Witham habitat trap proved somewhat more successful than two other seemingly poor refuges, a tire and a shingle (102 versus 77 and 57 pueruli collected, respectively, over a 10-mo period). Phillips (1972), studying *P. longipes cygnus* in Australia, found that his artificial seaweed habitat trap design collected more pueruli than a modified Witham trap, but only by a factor of approximately two. In contrast, the results of our comparative evaluations (Table 2) indicate that the average number of pueruli caught by the two lighted natural seaweed habitat traps (single and double seaweed frame) was 47 per trap, while on lighted Witham artificial substrate trap caught only 5 pueruli over the same time period and at the same location. This suggests that the natural seaweed trap design was approximately nine times more effective than the Witham trap. Secondly, the lighted habitat traps, regardless of the design, caught more pueruli than did nonlighted ones at the Scripps Institution pier during the same time period (33 and 7 pueruli respectively), suggested that a lighted trap was approximately four to five times more effective than an unlighted one. Thus, the system developed in this study, utilizing a combination of both nocturnal illumination and natural seaweed, clearly is much more effective in collecting pueruli of *P. in-*

terruptus than the nonlighted artificial habitat system utilized by Witham et al. (1968).

This suggests that natural seaweed habitat traps filled with native flora characteristic of juvenile habitats, in combination with nocturnal illumination, could prove to be a more successful means of sampling the pueruli of other spiny lobster species as well. If so, use of this modified sampling technique might indicate that the abundances of *P. argus* pueruli in Florida and those of *P. longipes cygnus* in Australia actually are much greater than previously estimated by Witham et al. (1968), Sweat (1968), and Phillips (1972).

Implications for Aquaculture and Fishery Management

If the small numbers of pueruli captured during this study are representative of puerulus availability throughout the geographic range of *P. interruptus*, large-scale collecting of this stage for purposes of aquaculture and restocking is not feasible and probably could not be justified. However, other locations, particularly those closer to the center of adult and larval concentrations, such as the Bahia Sebastián Vizcaino-Isla Cedros area off Baja California (Figure 9), should be investigated as potential sites for such large-scale collecting operations, as well as for purposes of locating the primary areas of puerulus settlement.

It also seems reasonable that the habitat trap collecting system developed in this study, if standardized and employed on a wider geographic scale, could prove useful for monitoring fluctuations in year class recruitment of pueruli, and thereby provide a means of predicting fluctuations in the size of the demersal population in following years. For example, an extension of our study by Parker (1972) during the years 1970-71 indicates that puerulus settlement at the Scripps Institution pier was much less than we observed during the same months in 1969. If this reduced recruitment was representative of a wider geographic area, then the size of the adult population available to the commercial fishery within the succeeding 5-8 yr might be expected to show corresponding changes.

SUMMARY

Basic ecological and behavioral information was obtained about the recruitment process, habitat preferences, and general abundance of the puerulus larval stage of *Panulirus interruptus*.

Pueruli of *P. interruptus* exhibit a strong positive phototactic response, and could be lured to a bright underwater night-light from the surface water surrounding the Scripps Institution of Oceanography pier.

Direct observations of free swimming pueruli by this method demonstrated that this stage is typically pelagic rather than benthic, and swims at the surface in a continuous and directed manner. Estimates of swimming speed were obtained.

The surface swimming behavior of this stage indicates that it probably can be properly sampled quantitatively only by large nets towed horizontally at the surface. This may explain why few pueruli have been taken by other conventional sampling methods. Paired neuston nets were developed specifically for this purpose and pueruli seemed to be sampled effectively in this manner during preliminary evaluations.

Puerulus larvae also were collected effectively in floating habitat traps containing the surfgrass, *Phyllospadix torreyi*. A variety of natural seaweed habitat trap designs were tested, and all appeared to be about equally effective in collecting pueruli; however, a nylon bag habitat trap proved best in terms of cost and durability. All natural seaweed habitat traps were markedly superior in collecting pueruli compared to the Witham habitat trap design, formed of synthetic fibrous material.

Habitat traps maintained under the lighted end of Scripps Institution pier collected many more pueruli than those not subject to such artificial illumination. The failure of habitat traps placed offshore to collect any pueruli may have been due to the availability of abundant seaweed flotsam in the areas where they were maintained, as well as lack of artificial illumination. Both the presence of intertidal plants (particularly *Phyllospadix*) and nocturnal illumination appear to play significant roles in the settlement of puerulus larvae in habitat traps.

The results of night-lighting and habitat trap sampling indicate that off San Diego, Calif., the seasonal influx and settlement of puerulus larvae is continuous, beginning in May and ending in September.

Estimates based on a comparison of the peak periods of abundance for pueruli and the preceding final phyllosoma larval stage suggest that the puerulus stage of *P. interruptus* has a duration of approximately 2½ mo. This is followed by

settlement in shallow water and transformation to a benthic, postpuerulus form.

Based on observations of its surface swimming behavior and capabilities, preference for plant covered substrates, settlement behavior, and morphology, the puerulus appears to be a transitional, pelagic stage specifically adapted for directional swimming, whose function is to return from offshore by active means to nearshore areas suitable for settlement. Thus, it probably occupies the key role in recruitment.

The seemingly low abundance of pueruli in the southern California areas sampled suggests that it would not be practical or beneficial to attempt large collections there for purposes of aquaculture and restocking. However, other locations, including those closer to the center of the geographical range, should be investigated as potential large scale collecting sites.

Employed in a standardized manner, the habitat trap system developed in this study could prove useful in locating primary areas of puerulus settlement and in monitoring fluctuations in year class recruitment.

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A THEORETICAL TREATMENT OF UNSTRUCTURED FOOD WEBS

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ABSTRACT

In a recent paper, Isaacs has proposed a model for an unstructured food web in which the interconnections are so diverse that all heterotrophs in the system can be treated as if they were at the same average trophic position. This paper recasts the original model in terms of a 3 × 3 matrix using three empirical constants. In this form, the model can be easily generalized to one having nine constants and reflecting a more realistic view of the interactions among levels of a community.

Recent papers by Isaacs (1972, 1973) proposed an alternative to trophic level schemes for representing interactions among species. He termed this an unstructured food web and proposed a "matrix"[2] technique (Isaacs 1972) for evaluating the equilibrium distribution of energy (or matter) which would result from these interactions. In this paper we propose an alternative formulation of Isaacs' model which utilizes classical matrix and operator techniques.

SERIES APPROACH

Isaacs' model was originally proposed to account for Young's data (Young 1970) from the Gulf of California which indicated that cesium was not found concentrated in ratios one would expect from a simple food chain. Isaacs assumes that the principal interconnections in the marine food web are so diverse that all heterotrophs in the system (from microorganisms to vertebrates) can be treated as if they derived their food from a common source that is only coarsely differentiated. Therefore, the heterotrophs can all be treated as if they were at the same average trophic position. In this unstructured food web, Isaacs visualizes four levels of matter or energy: 1) source, 2) living tissue, 3) nonliving but retrievable matter, and 4) irretrievable matter. The source is assumed to be phytoplankton which is added to the system at a constant rate. The living matter consists of all heterotrophs, while the dead retrievable matter may consist of such sources of carbon as organic detritus or dissolved organic matter. The irretrievable component is that matter (or energy) which is forever lost to the system through such processes as respiratory combustion or mineralization. The "unstructured" nature of the food web comes from a set of coefficients which represent movement of material between these groups. The transitions are not in a trophic level line. Rather, groups two and three interact bilaterally and groups three and four can receive from other levels bypassing intermediates.

Isaacs calculates the final steady state values for the total living and dead material by summing two infinite series. To obtain these series, he introduces a "matrix" which is designed to aid in the formulation of each of the terms. The series take the form:

$$\begin{aligned} M'_t = {} & M_0 K_1 + M_0 K_1 (K_1 + K_3) \\ & + M_0 K_1 [K_1 (K_1 + K_3) + K_3 (K_1 + K_3)] \\ & + M_0 K_1[K_1 (K_1 + K_3)^2 + K_3 (K_1 + K_3)^2] \\ & + \ldots = \frac{M_0 K_1}{1 - (K_1 + K_3)} = \frac{M_0 K_1}{K_2} \end{aligned}$$

$$\begin{aligned} M''_t = {} & M_0 K_3 + M_0 K_3 (K_1 + K_3) \\ & + M_0 K_3 [K_1 (K_1 + K_3) + K_3 (K_1 + K_3)] \\ & + M_0 K_3 [K_1 (K_1 + K_3)^2 + K_3 (K_1 + K_3)^2] \\ & + \ldots = \frac{M_0 K_3}{1 - (K_1 + K_3)} = \frac{M_0 K_3}{K_2} \end{aligned}$$

where M_0 = increment of initial input periodically introduced into the

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[2]We have enclosed Isaacs' use of the word "matrix" in quotes because he has used the word in a common rather than in the standard mathematical sense. When the word appears without quotes in this text we are using it in the standard sense of a rectangular array of elements which operates on column vectors from the left to produce new column vectors.

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system at intervals equal to the time taken by one average step in the food web,

M'_t = total quantity of material in living tissue (level two),

M''_t = total in nonliving recoverable material (level three),

K_1 = a coefficient of conversion of matter (or energy) in food into living tissue,

K_2 = a coefficient of conversion of matter (or energy) in food into irretrievable form (e.g., by respiratory combustion or mineralization), and

K_3 = a coefficient of conversion of matter (or energy) in food into nonliving but retrievable form (e.g., organic detritus or dissolved organic matter).

Restrictions on coefficients are:

$$K_1 + K_2 + K_3 = 1,$$
$$0 < K_i < 1, \text{ where } i = 1, 2, \text{ or } 3.$$

MATRIX APPROACH

In our representation of the unstructured food web, source, living tissue, and nonliving but retrievable matter are taken to be components in a vector in a three-dimensional space. This vector can be written

$$\overline{w} = \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix}$$

where w_1 is the amount of matter (or energy) present in phytoplankton, w_2 is the amount present in heterotrophs, and w_3 is the amount present in retrievable dead material. The fourth level (loss) is the difference between the total input and the material present in the three other levels.

The matrix operator controlling movement of material from one level to another, using Isaacs' coefficients, takes the form:

$$A = \begin{pmatrix} 1 & 0 & 0 \\ K_1 & K_1 & K_1 \\ K_3 & K_3 & K_3 \end{pmatrix}$$

Each K represents the proportion of material transferred between the levels appropriate to its position in a time equivalent to one application of the matrix.

As Isaacs points out, three constants may not be sufficient. It is probably not reasonable to assume, for example, that all matter is converted to living tissue with the same coefficient of conversion or that both living and dead matter have the same conversion factor to irretrievable form. One advantage of our method is that it can be generalized to a more complex form. This cannot easily be done with Isaacs' original method because crossterms in the K's rule out viewing the steady state values as simple geometric series. The generalized form of the matrix for an unstructured food web with these additional coefficients is:

$$A = \begin{pmatrix} 1 & 0 & 0 \\ k_1 & k_4 & k_7 \\ k_2 & k_5 & k_8 \end{pmatrix}$$

where k_1 = conversion factor from source to living,

k_2 = conversion factor from source to dead retrievable,

k_3 = conversion factor from source to inrretrievable,

k_4 = conversion factor from living to living,

k_5 = conversion factor from living to dead retrievable,

k_6 = conversion factor from living to irretrievable,

k_7 = conversion factor from dead to living,

k_8 = conversion factor from dead to dead retrievable, and

k_9 = conversion factor from dead to irretrievable.

In this case,

$$k_1 + k_2 + k_3 = 1$$
$$k_4 + k_5 + k_6 = 1$$
$$k_7 + k_8 + k_9 = 1$$
$$0 < k_i < 1, \text{ where } i = 1 \text{ to } 9.$$

When this matrix acts upon the state vector $\overline{w}$ the result is somewhat more complex:

$$A\overline{w} = \begin{pmatrix} 1 & 0 & 0 \\ k_1 & k_4 & k_7 \\ k_2 & k_5 & k_8 \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix} = \begin{pmatrix} w_1 \\ k_1 w_1 + k_4 w_2 + k_7 w_3 \\ k_2 w_1 + k_5 w_2 + k_8 w_3 \end{pmatrix}.$$

Steady State Results

The eigenvectors and eigenvalves of a matrix

fully characterize its properties. For the matrix representing the Isaacs assumptions the following eigenvalues (λ's) and eigenvectors ($\bar{u}$'s) can be obtained:

$$\lambda_1 = 1 \qquad \lambda_2 = K_1 + K_3 \qquad \lambda_3 = 0$$

$$u_1 = \begin{pmatrix} 1 \\ \frac{K_1}{K_2} \\ \frac{K_3}{K_2} \end{pmatrix} \quad u_2 = \begin{pmatrix} 0 \\ \frac{K_1}{K_2} \\ \frac{K_3}{K_2} \end{pmatrix} \quad u_3 = \begin{pmatrix} 0 \\ 1 \\ -1 \end{pmatrix}.$$

Any initial state of the system (e.g., $\bar{w}$) can be written as a weighted sum of the eigenvectors

$$\bar{w} = c_1\bar{u}_1 + c_2\bar{u}_2 + c_3\bar{u}_3.$$

If we now apply A n times to this vector we obtain

$$A^n\bar{w} = c_1\lambda_1^n\bar{u}_1 + c_2\lambda_2^n\bar{u}_2 + c_3\lambda_3^n\bar{u}_3.$$

After a sufficient time (n very large), the second and third term will vanish, leaving an expression for the final state of the system:

$$\lim_{n\to\infty} A^n\bar{w} = c_1\bar{u}_1.$$

In Isaacs' terms $c_1 = M_0$ and the limiting values for the second and third compartments are M_t' and M_t'' respectively. Therefore

$$M_t' = M_0K_1/K_2$$
$$M_t'' = M_0K_3/K_2$$

which is exactly Isaacs' result.

For the nine constant model, there is also always a steady state distribution of matter in the system. By finding the eigenvector corresponding to an eigenvalue of one, we can obtain the following steady state values of M_t' (total quantity of material in living matter) and M_t'' (total in nonliving recoverable material) in terms of a constant input M_0:

$$M_t' = \frac{-k_1(k_8-1) + k_2k_7}{(k_4-1)(k_8-1) - k_5k_7} M_0$$

$$M_t'' = \frac{-k_2(k_4-1) + k_5k_1}{(k_4-1)(k_8-1) - k_5k_7} M_0.$$

Trophic Level Equations

In addition to values for total amounts of living and retrievable dead matter, Isaacs develops equations for general trophic levels. His equations can be generated by our approach if our original matrix is broken down into component parts and then applied to the steady state vector. For example, let us consider Isaacs' case (Isaacs 1973) of a subset of trophic levels which are complete and mutually exclusive. He considers strict herbivores, detrital feeders, and full predators to be such a subset.

Our original matrix A can be written in the following way

$$A = A_{S+R} + A_H + A_D + A_P$$

where

$$A_{S+R} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ K_3 & K_3 & K_3 \end{pmatrix}$$

$$A_H = \begin{pmatrix} 0 & 0 & 0 \\ K_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_D = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & K_1 \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_P = \begin{pmatrix} 0 & 0 & 0 \\ 0 & K_1 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

A_{S+R} = matrix responsible for the biomass in source and the retrievable dead matter,
A_H = matrix responsible for biomass in herbivores,
A_D = matrix responsible for biomass in detrital feeders, and
A_P = matrix responsible for biomass in predators.

To obtain the potential biomass for each of the trophic levels, we take the appropriate matrix times the steady state vector. Thus, the equation for the potential biomass of herbivores is obtained from

$$A_H\bar{u}_1 = \begin{pmatrix} 0 & 0 & 0 \\ K_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} M_0 \\ \frac{M_0K_1}{K_2} \\ \frac{M_0K_3}{K_2} \end{pmatrix} = \begin{pmatrix} 0 \\ M_0K_1 \\ 0 \end{pmatrix}.$$

Similarly, for detrital feeders

$$A_D \bar{u}_1 = \begin{pmatrix} 0 \\ \frac{M_0 K_1 K_3}{K_2} \\ 0 \end{pmatrix}$$

and for predators

$$A_P \bar{u}_1 = \begin{pmatrix} 0 \\ \frac{M_0 K_1^2}{K_2} \\ 0 \end{pmatrix}.$$

All of Isaacs' other equations for trophic level potential biomasses or fluxes can be obtained in a similar manner.

Equations for the potential biomass of trophic levels can also be calculated for the generalized model. This is done in a manner similar to that described in the previous section.

Strict herbivores (feeding on source):

$$M_m = M_0 k_1.$$

Omnivores (feeding on source, living and retrievable dead):

$$M_v = M_0 \left(\frac{-k_1 (k_8 - 1) + k_2 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$
$$= k_1 M_0 + k_4 M'_t + k_7 M''_t.$$

Particle feeders (feeding on source and retrievable dead):

$$M_\mu = M_0 \left(\frac{k_1 (k_4 - 1)(k_8 - 1) + k_2 k_7 (1 - k_4)}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$
$$= k_1 M_0 + k_7 M''_t.$$

Detrital feeders (feeding on retrievable dead):

$$M_d = M_0 \left(\frac{-k_2 k_7 k_4 + k_2 k_7 + k_1 k_5 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$
$$= k_7 M''_t.$$

Full predators (feeding on living):

$$M_P = M_0 \left(\frac{-k_4 k_1 (k_8 - 1) + k_4 k_2 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$
$$= k_4 M'_t.$$

Nonherbivorous omnivores (feeding on living and retrievable dead):

$$M_n = M_0 \left(\frac{-k_4 k_1 k_8 + k_1 k_4 + k_2 k_7 + k_1 k_5 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$
$$= k_4 M'_t + k_7 M''_t.$$

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DISTRIBUTION AND ECOLOGY OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, IN AN OFFSHORE AREA OF THE EASTERN TROPICAL PACIFIC OCEAN

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ABSTRACT

Distributions of skipjack tuna, *Katsuwonus pelamis*, were studied in the offshore eastern tropical Pacific between lat. 15°N and 5°S, long. 115° and 125°W, during two cruises in 1970 and 1971. Another cruise was made there with different methods in 1969. All cruises were between October and April. Various environmental properties were measured.

Catches of skipjack included fish smaller and larger than those generally taken near the American coast. This is consistent with previous hypotheses that mature adults and their larvae generally occur far offshore, whereas adolescents are generally coastal, in the eastern Pacific. The juveniles arriving near the coast and the older fish leaving it evidently cross the studied area on migrations from and to the spawning regions.

In 1970 and 1971 skipjack > 45 cm were most abundant in the equatorial upwelling and at the northern boundary of the North Equatorial Countercurrent, and scarce in the Countercurrent. Correlation coefficients between skipjack > 45 cm and skipjack forage in 1970 were positive and significant by the usual criteria, but the significance may in part be disputable because many other correlations involving skipjack were nonsignificant. The apparent significance was lost when juvenile skipjack (< 45 cm) were included with the larger ones. Juveniles may have different relations to environment. The 1971 data were scanty and yielded no significant correlations between skipjack and forage.

On the 1969 cruise forage was not studied. Skipjack were abundant in the Countercurrent, but at a prespawning stage, whereas postspawners predominated on the other cruises. Other studies suggest that skipjack larvae require relatively high temperatures, which occurred only in the Countercurrent on the 1969 cruise. Skipjack may be distributed according to the environmental requirements of their larvae when spawning and according to their own feeding requirements when not spawning.

Williams (1971) described plans for a series of cruises in two offshore areas of the eastern tropical Pacific Ocean. This report deals with results of two cruises made in 1970 and 1971 in one of the areas, bounded by lat. 15°N-5°S and long. 115°-125°W (Figure 1). The cruises were initiated by the National Marine Fisheries Service, Southwest Fisheries Center, and the Scripps Tuna Oceanography Research (STOR) Program, Institute of Marine Resources, University of California. They were designed to investigate on a seasonal basis the occurrence and relative abundance of skipjack tuna, *Katsuwonus pelamis*, in relation to environmental conditions. Coverage of

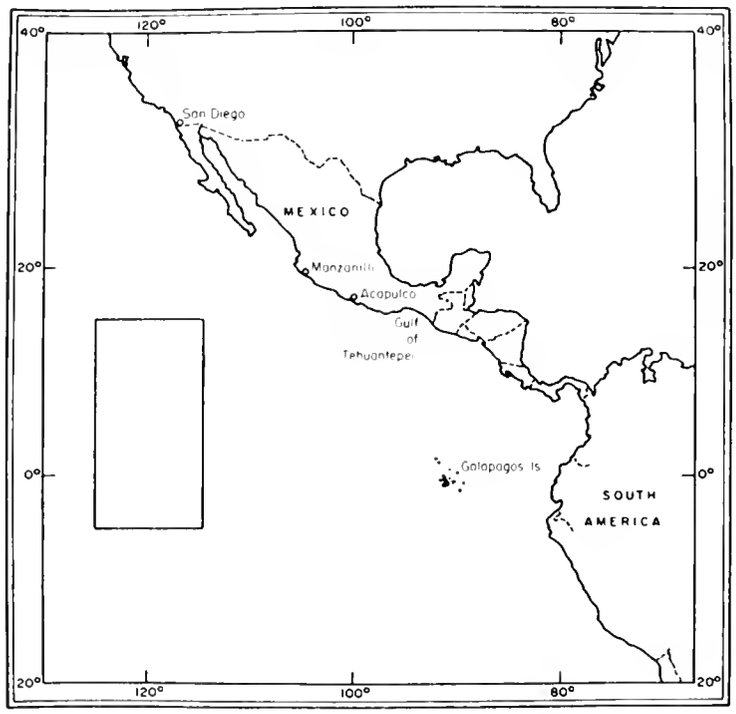

FIGURE 1.—Area of eastern tropical Pacific Ocean under investigation.

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offshore areas by the U.S. surface tuna fishery has been very limited, especially for skipjack. Coverage by the Japanese subsurface tuna fishery has been greater, but still poor for skipjack (Miyake 1968). The regulation of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific is expected to increase the need for information on skipjack in the offshore waters.

Work in coastal waters has shown that adult skipjack are most numerous when temperature is in the range 20° to 29°C (Williams 1970) and standing stock of skipjack forage is high (Blackburn 1965, 1969). Sea surface temperatures are in the suitable range for most of the year throughout the offshore eastern tropical Pacific (Wyrtki 1964; La Violette and Seim 1969; Love 1971b, 1972a, b, in prep.). Thus distribution of forage seemed likely to be a main factor in determining distribution of adult skipjack in offshore waters. The distribution of forage in that region was described from data of EASTROPAC Expedition (1967-68) by Blackburn and Laurs (1972), who expected that adult skipjack would prove to be distributed in the same way. One of the purposes of the present study was to test that expectation. The forage concentrations on EASTROPAC were characteristically high in certain zones of latitude and low in others, broadly corresponding to distributions of phytoplankton, zooplankton, and total micronekton (Love 1970, 1971a, in prep.; Blackburn et al. 1970; Owen and Zeitzschel 1970a).

Evidence, summarized by Williams (1972), indicates that most exploited skipjack in the eastern Pacific have a spawning origin in the central Pacific west of long. 130°W. It also suggests that the majority of the skipjack enter the present fishery, which is concentrated near tropical American coasts, during only 1 yr of their life history. They are then relatively small (average length about 50 to 55 cm, average weight 3 to 3.5 kg) and sexually immature. Thus it is probable that migration pathways exist for skipjack, both below and above these sizes, across the offshore eastern tropical Pacific.

Such pathways might occur at particular latitudes since forage concentrations and many other ocean conditions, including surface currents, are zonally oriented. On this basis Williams (1972) presented three qualitative models of the migration of young (recruit) skipjack from the central Pacific into the eastern Pacific fishing areas. The data from the present cruises may be useful for testing and modification of the models, and incorporation with other models of skipjack movement such as that of Seckel (1972).

PLAN OF THE INVESTIGATIONS

The inward skipjack migration models of Williams (1972) assumed that the routes were principally zonal across the offshore eastern Pacific. Mechanisms and timing of the migrations are probably dependent on oceanographic conditions and events in this region. The strategy for the present investigations was to have latitudinal sampling of fish and environmental parameters in meridional areas considered critical to the migrations. The area discussed in this paper includes the meridian of 119°W. It is important because the surface North Equatorial Countercurrent normally becomes intermittent or absent east of this meridian from January to May.

Each cruise had two parts (Williams 1971). Part I was a rapid meridional transect of the area along long. 119°W to monitor ocean conditions and compare them with previous data. These results showed the positions of zonal surface current boundaries and forage bands, and hence the latitudinal zones that were to be fished for skipjack.

In Part II detailed fisheries operations were carried out in the selected zones to a standardized plan based on a "unit area" of 2° latitude by 2° longitude, together with supporting environmental observations. Fishing was by multiple trolling during daylight. Figure 2 shows schematically the track and scheduled observations. The work time for each unit area, including entry and exit, was 96 h. Coverage in a zone of latitude could consist of any multiple of unit areas or fractions thereof (quadrants or 1° × 1° areas).

The first cruise in November-December 1970 utilized the vessels *Townsend Cromwell* (Cruise C 51) (R. Uchida, Chief Scientist) and *David Starr Jordan* (J 57) (F. Williams, Chief Scientist). The second cruise in March-April 1971, was made with only the *Jordan* (J 60) (M. Blackburn, Chief Scientist). The *Jordan* 60 cruise was severely curtailed due to illness of a crew member. On the first cruise the Part I transect was completed by the *Cromwell*; and data were sent by radio to the *Jordan*; subsequent Part II operations were carried out by both vessels.

This paper also discusses data from a cruise made by National Marine Fisheries Service, Hawaii, to the same area in October-November

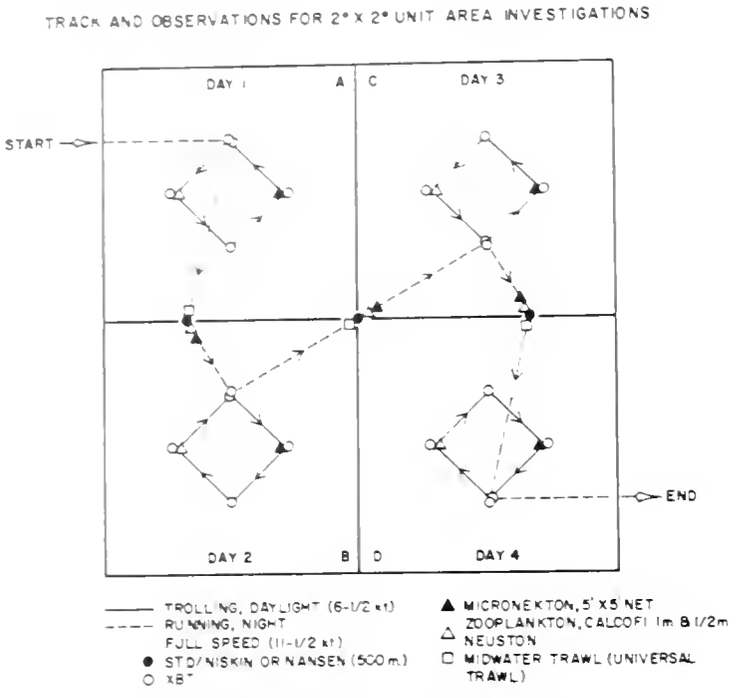


FIGURE 2.–Track and observations scheduled for each 2° × 2° unit area during Part II operations. [Dawn trawl haul was eliminated on cruise *Jordan* 60].

1969, in more detail than the previous cruise report by Hida (1970).

METHODS

This section deals with methods used on the 1970 and 1971 cruises. The Bissett-Berman[3] Salinity-Temperature-Depth probe (STD) and Sippican expendable bathythermograph (XBT) were used for measuring temperature and salinity. A Niskin 12-bottle rosette sampler coupled with the STD was used to collect water samples for salinity and oxygen. The STD system had digital (magnetic tape data logger) and analog chart outputs, as did the XBT system (punched paper tape and analog chart). STD/Niskin casts were normally made to 500 m and XBT drops to 450 m. Nansen bottle casts, for calibration of the STD system, were made at the start and finish of the Part I transect and at intervals during Part II fishing operations. On the Part I transect, STD/Niskin stations for temperature, salinity, and oxygen were made every 6 h, with one or more XBT drops between STD stations. In Part II operations, three STD stations were made at night in each 2° × 2° unit area, and five XBT drops between dawn and dusk on fishing tracks (Figure 2). Processing of the physical oceanographic data was as described by Taft and Miller (1970). Depth of the mixed layer was derived directly from analog charts of XBT and STD systems according to criteria of Owen (1970a).

Dissolved oxygen content of water samples from the Niskin sampler was determined, and data processed, as indicated by Owen (1970b). Discrete surface samples for chlorophyll *a* were taken at approximately noon and midnight and processed as described by Owen and Zeitzschel (1970b).

Zooplankton hauls were made and samples processed by the methods used on EASTROPAC Expedition (Laurs 1970). Oblique hauls from 200 m to surface were made with nets of 50 cm and 1 m mouth diameter in a paired frame. A wire angle of 45° was maintained during the haul at a speed about 1.5 to 2 knots. In Part II operations, one daylight haul was made during each of 4 days of fishing in a 2° × 2° unit area (see Figure 2), and three night hauls were made during the 4-day period. No hauls were made near dawn or dusk. Data were expressed in displacement volume in milliliters per 1,000 m^3.

Micronekton was sampled with a net 1.5 m square at the mouth, in oblique hauls from 200 m to surface at a ship speed of 5 knots (Blackburn 1968, 1970; Blackburn et al. 1970). During the Part I transect, micronekton hauls were made at approximately 12-h intervals following STD casts, one during daylight and one at night. In Part II operations, day and night hauls were made with the same frequency as for zooplankton (see Figure 2). Processing of the samples and estimation of volume of water strained was as discussed by the same authors, and total micronekton was expressed as displacement volume in milliliters per 1,000 m^3. A variable and generally large proportion of this micronekton consisted of organisms that skipjack are known or likely to eat (skipjack forage) in the eastern tropical Pacific. The micronekton catches were therefore sorted into forage and nonforage organisms (Blackburn and Laurs 1972). Forage organisms were all crustaceans, all cephalopods, all epipelagic fish and *Vinciguerria*. Nonforage organisms were all mesopelagic fish except *Vinciguerria* and all leptocephali.

The trolling gear used to catch skipjack and other fish was similar to that used in the albacore fishery off the U.S. west coast (Yoshida 1966). Feather jigs were fished with nylon traces and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

nylon parachute cord lines. The *Cromwell* could fish only 4 lines from the stern, compared with 11 fished by the *Jordan*, 8 from outriggers and 3 from the stern. On the *Jordan* the 4 lines on each outrigger were connected to a set of hydraulic power gurdies for rapid hauling.

Charts and sections were contoured by hand except those of dissolved oxygen content which were prepared by computer and Calcomp plotter. Gear and methods used for neuston and midwater trawl samples are not discussed because the results are not utilized in this report. The same applies to observations on birds, fish schools, and marine mammals.

RESULTS OF THE EXPERIMENTAL FISHING

Based on the position of the surface current boundaries and distributions of temperature and skipjack forage derived from Part I operations, the latitudinal zones investigated in Part II fishing operations were similar on the 1970 and 1971 cruises: 12°-14°N, 9°-11°N, 6°-8°N, 3°-5°N, 1°-3°N, and 2°-4°S. Figures 3 and 4 show the cruise tracks during Part II fishing operations in the above-mentioned zones. They also show approximate positions of surface current boundaries, which were obtained from data on thermocline topography.

The total fishing effort (number of line-hours) in or immediately adjacent to the study area was very much higher on the November-December 1970 cruise than in March-April 1971, because of the curtailment of the latter cruise (Table 1). The catch by species on each cruise is given in Table 2, which shows the number boarded and kept, tagged and released, and lost but identified, and the overall size range of each species. Skipjack was obviously the dominant species on each cruise.

TABLE 1.–Total fishing effort in the study area.

Period	Cruise no.		Line-hours fished	
			in unit areas	on passage
Nov.-Dec. 1970	*Jordan* 57	2,746	3,213	131
Nov.-Dec. 1970	*Cromwell* 51	467		
Mar.-Apr. 1971	*Jordan* 60		2,088	255

DISTRIBUTION AND RELATIVE ABUNDANCE OF SKIPJACK AND OTHER TUNA

This section deals with results from the 1970 and 1971 cruises. Relative abundance of skipjack was calculated in terms of catch per line-hour on track. Catch equals number boarded, tagged, and lost but identified. Fish taken when the vessel circled following an initial strike, or when chumming with live anchovy, are not included. Troll catches of skipjack made on track and separated, arbitrarily, by >10 min are considered to have come from separate schools or aggregations of fish, and an index of schools encountered per hour of trolling has been derived. There are highly significant positive correlations between catch/line-hour and schools/hour for each cruise ($r = +0.907$ for data of Table 3 and $+0.716$ for Table 4, both significant at the 1% level). Schools/hour is a more conservative indicator of relative abundance of skipjack than catch/line-hour because each

TABLE 2.–Summary of fish catch by species: Cruises *Jordan* 57-*Cromwell* 51, November-December 1970, and *Jordan* 60, March-April 1971.

Species	*Jordan* 57-*Cromwell* 51				*Jordan* 60			
	Boarded	Tagged	Lost but identified	Size range (cm)	Boarded	Tagged	Lost but identified	Size range (cm)
Skipjack *(Katsuwonus pelamis)*	114	67	~118	32.5- 71.0	61	8	49	41.8-70.0
Yellowfin tuna *(Thunnus albacares)*	30	4	5	26.2-111.5	2	–	–	33.5-44.7
Frigate mackerel *(Auxis thazard)*	2	–	–	30.2- 31.0	1	–	–	34.6
Unidentified tuna	–	–	12	–	–	–	–	–
Wahoo *(Acanthocybium solandri)*	4	–	1	52.0-110.0	–	–	–	–
Shortbill spearfish *(Tetrapturus angustirostris)*	–	–	1	–	–	–	–	–
Dolphin *(Coryphaena hippurus)*	8	–	–	20.5-114.5	6	–	~5	34.0-46.3
Pompano dolphin *(C. equiselis)*	4	–	2	26.5- ~50.0	–	–	–	–
Rainbow runner *(Elagatis bipinnulatus)*	–	–	–	–	1	–	–	81.5
Unidentified fish (lost)	–	–	10	–	–	–	10	–

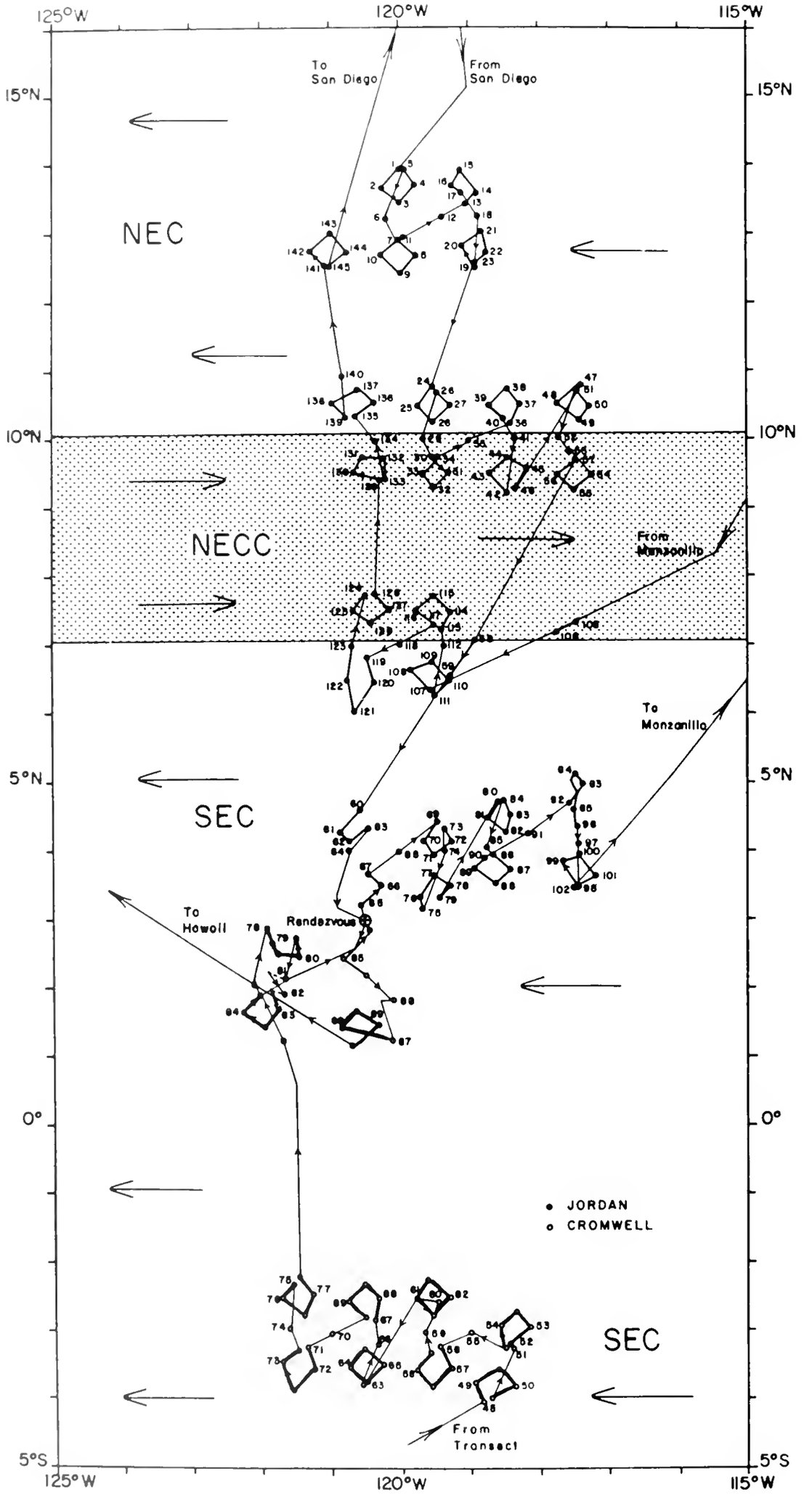


FIGURE 3.–Cruise tracks, Part II operations, *Jordan* 57-*Cromwell* 51, November-December 1970. Thickened lines indicate daylight fishing tracks. Approximate boundaries of surface currents are indicated.

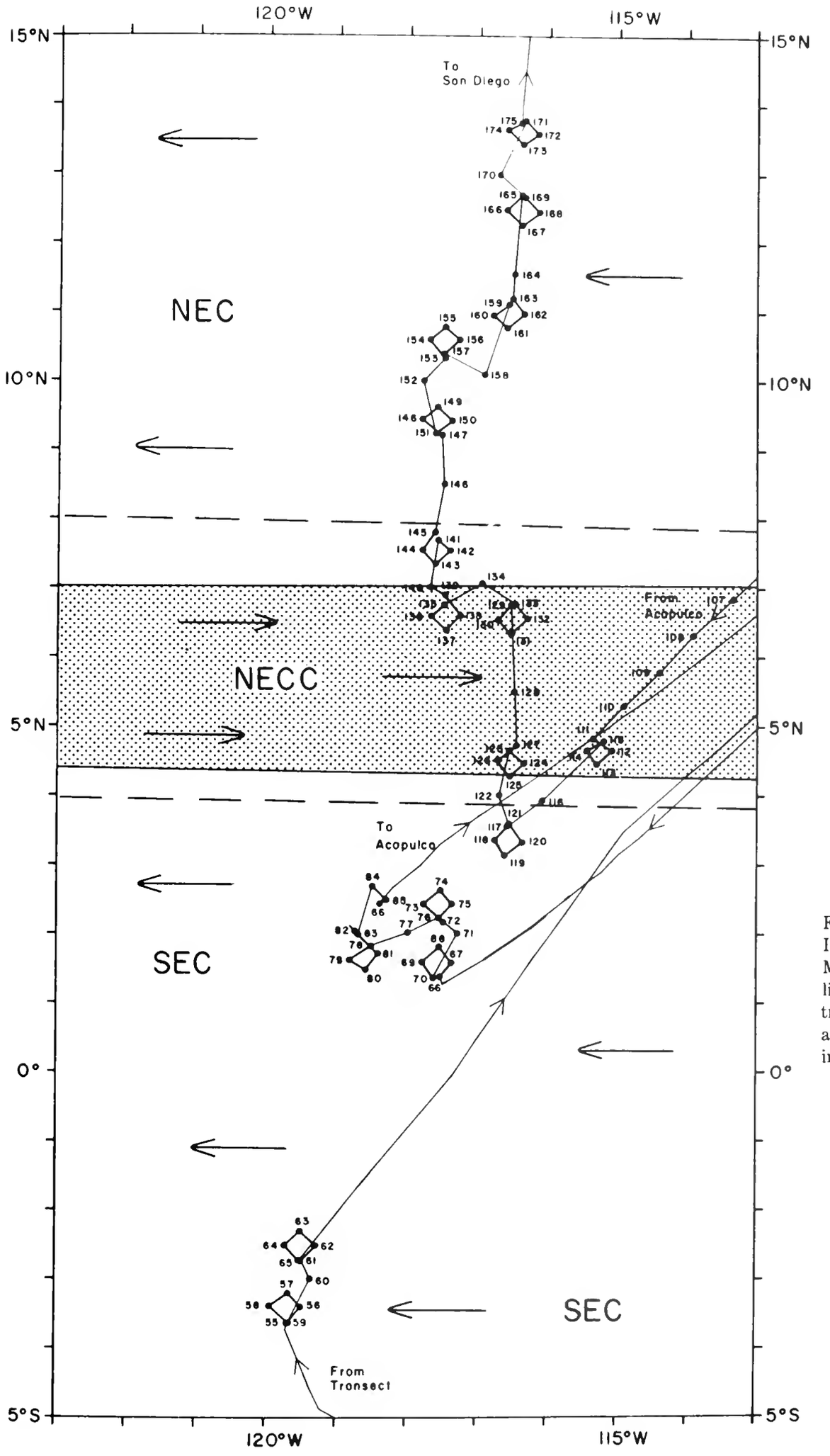


FIGURE 4.–Cruise tracks, Part II operations, *Jordan* 60, March-April 1971. Thickened lines indicate daylight fishing tracks. Approximate boundaries of surface currents are indicated.

TABLE 3.—Relative abundance of troll-caught skipjack and other tuna, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

Zone latitude	Current system	Catch/line-hour			Schools/hour skipjack
		Skipjack	Yellowfin	All tuna	
13°-14°N	NEC	0.072	0	0.072	0.10
12°-13°N	NEC	0.038	0.057	0.101	0.17
10°-11°N	NEC	0.064	0.022	0.099	0.17
9°-10°N	NECC	0.014	0	0.014	0.08
7°-8°N	NECC	0.075	0.004	0.079	0.10
6°-7°N	SEC	0.009	0	0.037	0.05
4°-5°N	SEC	0.100	0	0.100	0.10
3°-4°N	SEC	0.130	0.016	0.146	0.25
2°-3°N	SEC	0.015	0	0.015	0.06
1°-2°N	SEC	0.354	0	0.354	0.40
0°40′-1°N[1]	SEC	0.208	0	0.208	0.48
2°-3°S	SEC	0.096	0	0.096	0.13
3°-4°S	SEC	0.028	0	0.028	0.10

[1]Data on this line are from fishing on passage, <50 line-h.

TABLE 4.—Relative abundance of troll-caught skipjack and other tuna, Cruise *Jordan* 60, March-April 1971. Data in square brackets are from fishing on passage and are included in totals to the left.

Zone latitude	Current system	Catch/line-hour			Schools/hour skipjack
		Skipjack	Yellowfin	All tuna	
[16°-17°N	NEC	0.064	0	0.064	0.32]
13°-14°N	NEC	0.008	0.008	0.016	0.09
12°-13°N	NEC	0.054	0	0.054	0.08
10°-11°N	NEC	0.107	0	0.107	0.46
9°-10°N	NEC	0.134	0	0.134	0.17
7°-8°N	NEC	0	0	0	0
6°-7°N	NECC	0.031	0	0.031	0.09
4°-5°N	NECC/SEC	0.042	0.004	0.046	0.08
3°-4°N	SEC	0	0	0	0
2°-3°N	SEC	0.023 [0.019]	0	0.023 [0.019]	0.12 [0.10]
1°-2°N	SEC	0.067 [0.064]	0	0.067 [0.064]	0.17 [0.17]
2°-3°S	SEC	0.062	0	0.063	0.25
3°-4°S	SEC	0.039	0	0.029	0.16

aggregation is given equal weighting irrespective of the number of fish caught. The index does not reflect the size of the aggregations, which on both cruises were considered to be relatively small. No large surface schools of skipjack or other tuna were seen in the study area.

Tables 3 and 4 show the relative abundance of skipjack, yellowfin tuna and total tuna as catch/line-hour and skipjack as schools/hour for 1° latitudinal zones fished in Part II operations. Approximate boundaries of surface current systems are also indicated: NEC, NECC, and SEC mean North Equatorial Current, North Equatorial Countercurrent, and South Equatorial Current. In November-December 1970 the highest level of relative abundance of skipjack was between lat. 0°40′ and 2°N, with a secondary maximum at lat 3° to 5°N and other high levels north of the NECC and south of the Equator. Within the NECC at lat. 7° to 10°N, relative abundance in terms of catch rate was variable, but generally low in terms of schools encountered. With the added contribution of yellowfin and other tuna, there was a marked maximum north of the NECC. In March-April 1971, overall relative abundance was much lower, and the principal maximum was situated north of the NECC, between lat. 9° and 11°N. Secondary maxima occurred at lat. 1° to 3°N and south of the Equator. The relative abundance of skipjack in the NECC was again low.

In Figures 5, 6, 7, and 8, daily values of relative abundance (catch rates and schools) are plotted and contoured. The results are more difficult to interpret in this form, but there are some general agreements with the zonally averaged data.

Off-track Catches of Skipjack

Off-track troll catches of skipjack were made with the use of anchovy, *Engraulis mordax*, live bait on *Jordan* 57. On five occasions schools of skipjack were chummed with live bait, following initial jig strikes (4) or fish sighting (1). On two of these occasions the chumming and circling of the vessel produced a substantial additional catch. Use of live bait on cruises of this type is advantageous in order to increase sample size of fish.

Distribution of Skipjack by Time of Day

Percentages of the total numbers of skipjack schools encountered on track in each 1-h period have been calculated and are given in Table 5. Schools are defined as above. Some 60-min periods included station time (i.e., not fishing), and the numbers of schools per unit time have been adjusted. Variability in occurrence is considerable between cruises for 1-h periods. However, when presented by 2-h periods, the temporal occurrence of skipjack shows remarkable similarity on the two cruises. Surprisingly, fewest aggregations were encountered before 1000 h. Aggregations were encountered most frequently between 1200 and 1500 h, and again, as expected, in the predusk period, 1700 to 1759 h.

Biological Characteristics of Skipjack and Other Tuna

Size of Skipjack

Measurements of fish length (tip of snout to tip of median caudal fin rays) were made to the nearest millimeter on all fish. Table 6 shows the

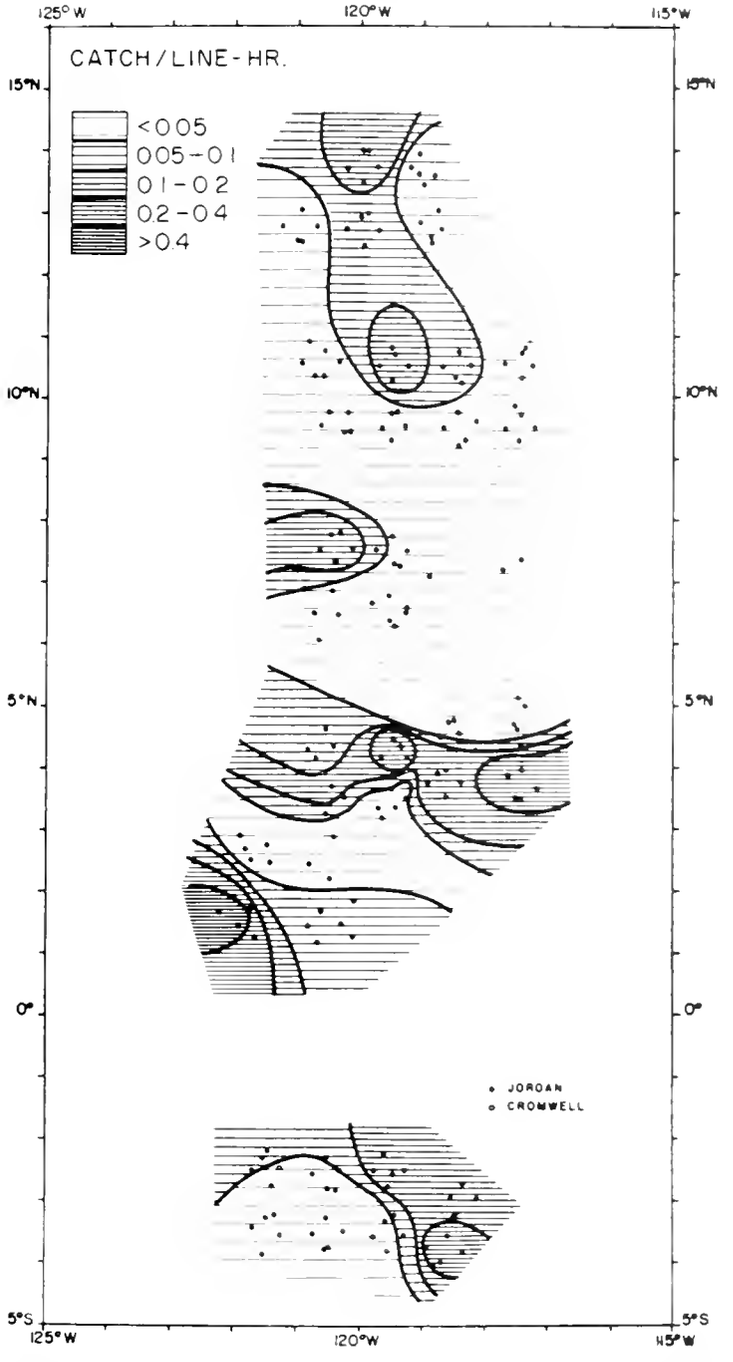


FIGURE 5.—Relative abundance of skipjack in catch/line-hour, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

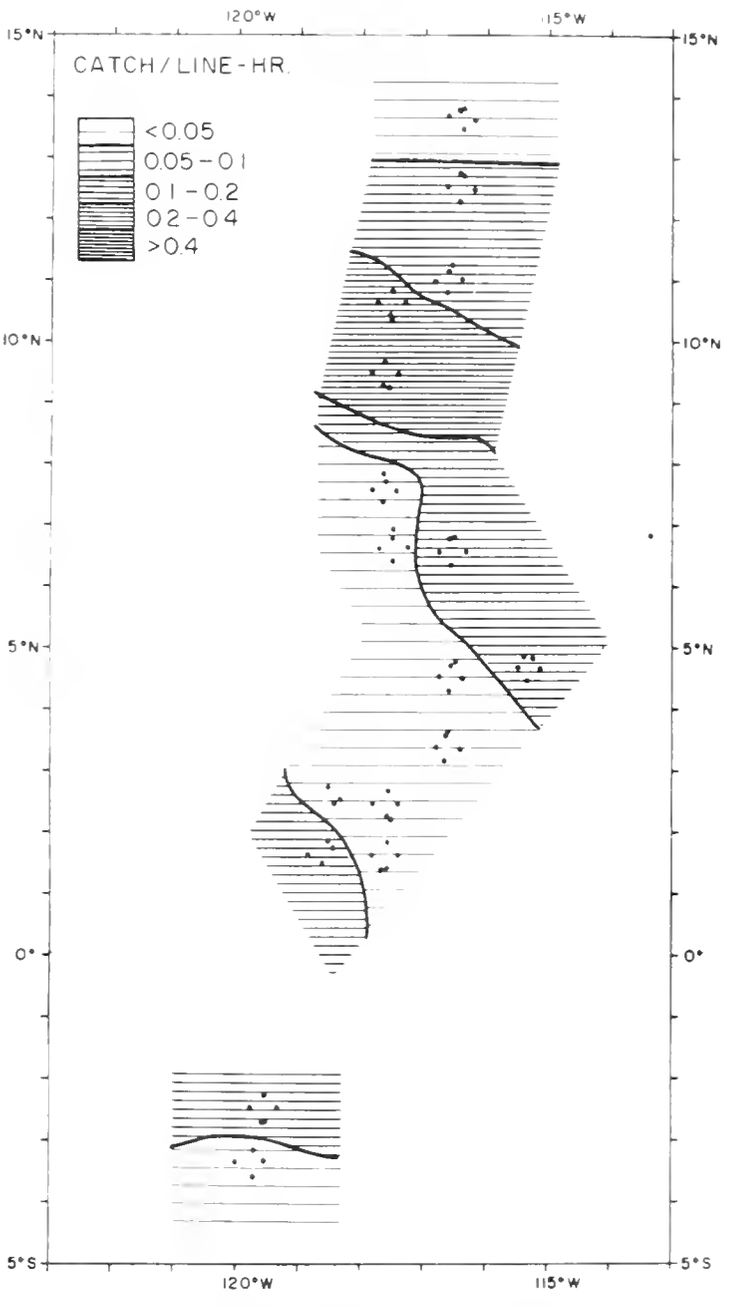


FIGURE 6.—Relative abundance of skipjack in catch/line-hour, cruise *Jordan* 60, March-April 1971.

percent of skipjack in three broad size categories for the two cruises. The most significant feature is that 13.3% of skipjack were <45 cm in November-December 1970, as against 2.9% on the next cruise.

The fish <45 cm were not distributed over a large part of the area, as fish >45 cm were, in November-December 1970. Of the small fish, 16 (85%) were from areas north of the NECC, lat. 10° to 14°N, and the remaining 3 (15%) from south of the NECC, lat. 0°30′ to 4°N; none were found in the NECC or south of the equator. Table 7 shows small skipjack (<45 cm) as percent of total in the latitudinal zones north of 10°N. It appears that the

TABLE 5.—Percent[1] of total number of skipjack schools encountered on track, by 1-h periods (all fishing days combined): Cruises *Jordan* 57-*Cromwell* 51, November-December 1970, and *Jordan* 60, March-April 1971.

Time period	*Jordan* 57-*Cromwell* 51		*Jordan* 60	
Start[2]-0659	3.7%	12.3%	12.2%	12.2%
0700-0759	8.6		0	
0800-0859	2.5	9.4	3.6	9.4
0900-0959	6.9		5.8	
1000-1059	8.8	16.0	10.6	16.2
1100-1159	7.2		5.6	
1200-1259	14.9	21.2	2.9	20.2
1300-1359	6.3		17.9	
1400-1459	7.5	14.8	15.8	21.6
1500-1559	7.3		5.8	
1600-1659	7.3	26.3	5.4	19.8
1700-1759	19.0		14.4	
Total fishing days	28		21	

[1]Adjusted data, see text p. 388.
[2]Mean start 0556 h and 0539 h on *Jordan* 57-*Cromwell* 51 and *Jordan* 60 respectively.

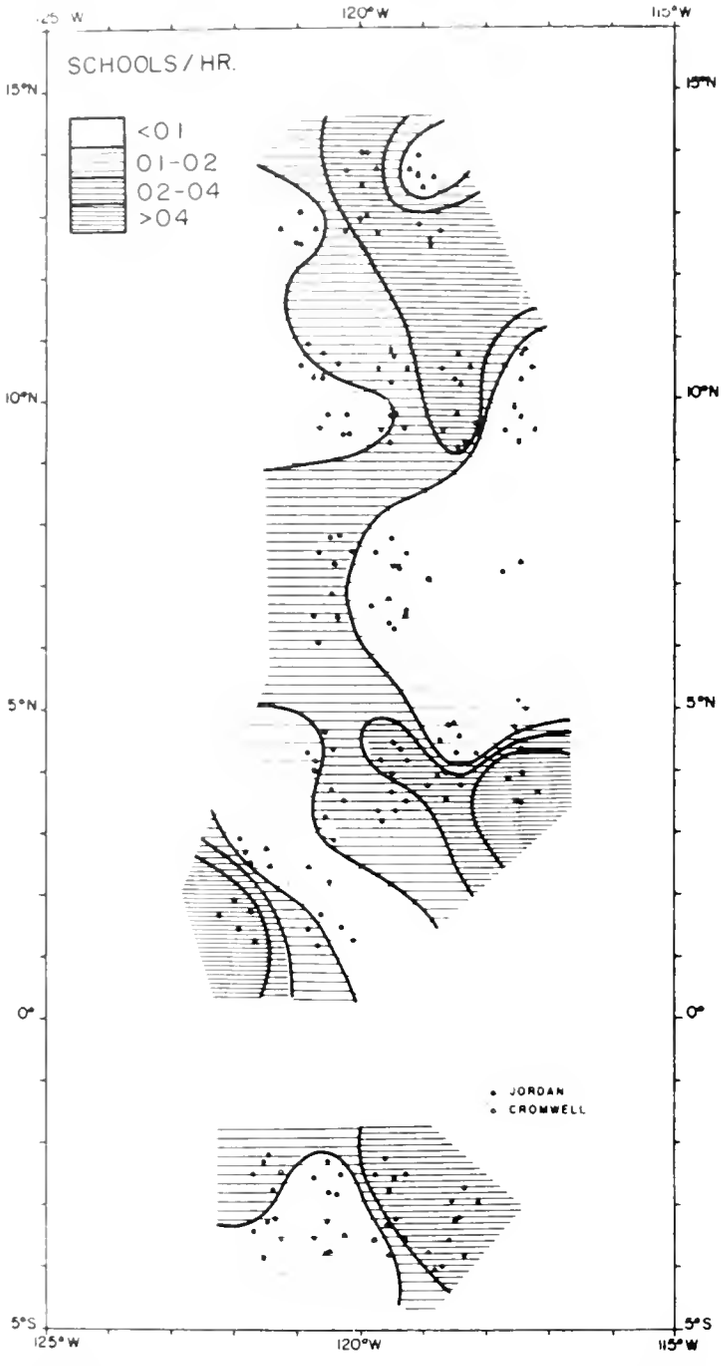


FIGURE 7.—Relative abundance of skipjack in schools/hour, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

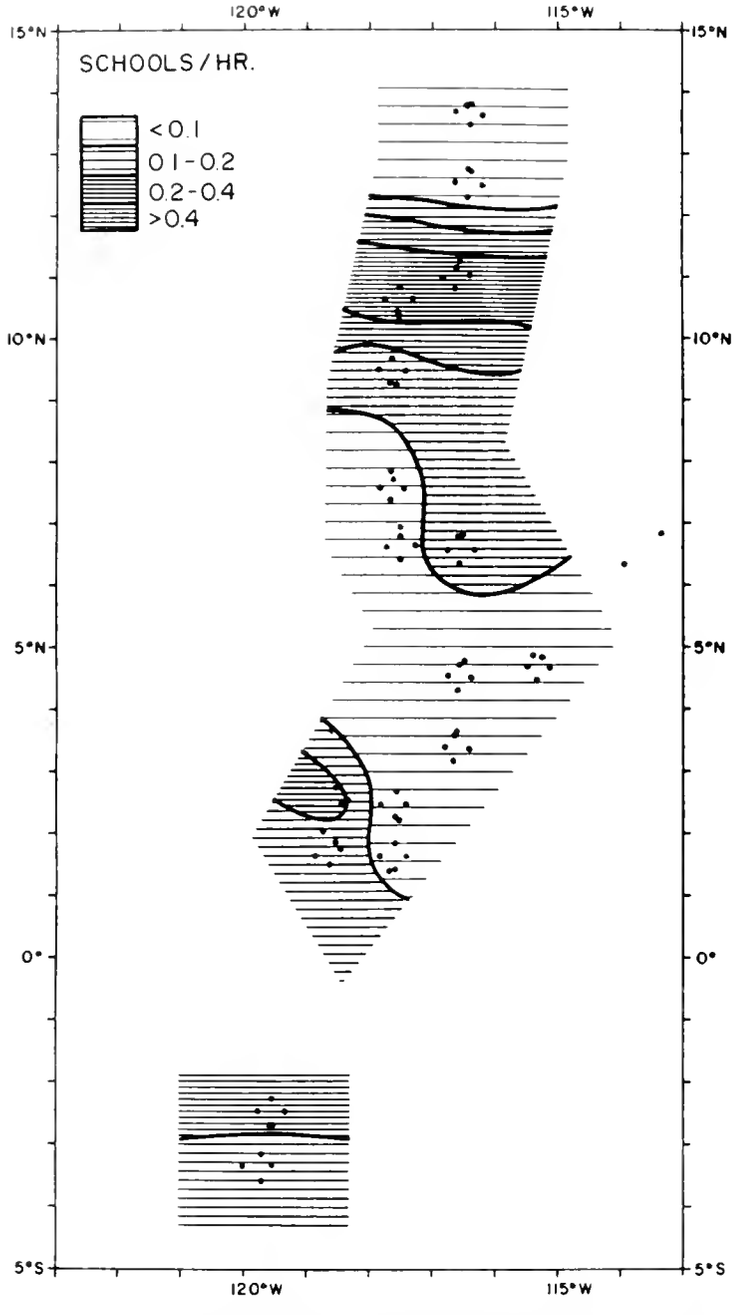


FIGURE 8.—Relative abundance of skipjack in schools/hour, cruise *Jordan* 60, March-April 1971.

fish <45 cm were largely segregated geographically from the medium and large ones. Figure 9 indicates a distinct separation in age as well. Small skipjack were very scarce in March-April 1971.

Figure 9 shows the percent length-frequency distributions of skipjack by 2-cm classes. In November-December 1970, the principal mode was at 58 cm, with a minor mode at 36 cm and perhaps another at 48 cm. The fish of modal size 36 cm could be about 14 to 15 mo old, if one accepts the growth rates for juveniles indicated by Yoshida (1971) and Joseph and Calkins (1969: from tagging data, averaged). This would suggest a spawning origin in the northern summer. Because no definite information is available on skipjack growth rates beyond this size, the age represented by the 58-cm mode is uncertain, but probably it is 2 to 3 yr. Whether the possible mode at 48 cm represents fish 1 yr or 6 mo between the other two modes is not known. If there were 6-mo difference, it would signify a spawning origin in the southern summer.

In March-April 1971, there is a single wide mode composed of fish >48 cm (peak 56 to 60 cm). The fish had about the same size distribution in all areas.

Skipjack in the eastern Pacific coastal fishery ranged from about 3 to 3.5 kg, with mean and modal lengths 50 to 55 cm, in the years 1955-71 (Miyake 1968; Inter-American Tropical Tuna

TABLE 6.–Skipjack in size categories as percent of total, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970 and *Jordan* 60, March-April 1971.

Size (cm)	Percent of total	
	Jordan 57-*Cromwell* 51	*Jordan* 60
<45	13.3	2.9
45-60	62.2	55.1
>60	24.5	42.0
Total skipjack	143	70

TABLE 7.–Small skipjack (<45 cm) as percent of total in latitudinal zones north of 10°N, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

Zone latitude	Size (cm)			No. of fish	Percent
	Category	Range	Mean		
12°-14°N	<45	32.5-39.8	35.5	13	76.5
	>45	48.8-56.5	54.2	4	23.5
10°-11°N	<45	33.4-34.7	34.2	3	13.6
	>45	45.0-65.0	58.0	19	86.4

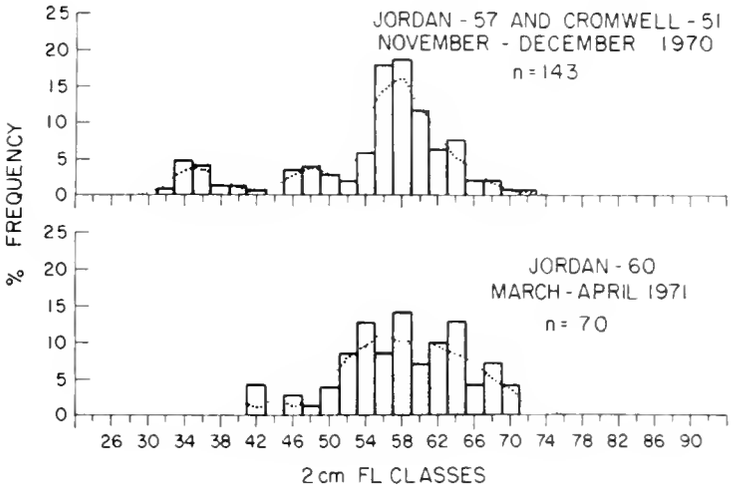


FIGURE 9.–Skipjack percent-length-frequency distribution in the study area. Smoothed curves are from 3-figure moving averages. Stated length indicates midpoint of class.

Commission 1966, 1972). The principal component of the Hawaiian catch usually consists of fish of modal sizes >60 cm (U.S. Bureau of Commercial Fisheries 1963; Rothschild 1965; Higgins 1966). The principal modes of skipjack caught in the study area, 56 to 60 cm on the two cruises, are intermediate between those in the eastern Pacific coastal fishery and the Hawaiian fishery. Purse seine samples of skipjack obtained in and near the study area in 1970 and 1971, which are mentioned later, had mean sizes from 58 to 61 cm.

Size of Other Tuna

Only 34 yellowfin tuna were boarded (39 caught) on the November-December 1970 cruise, and 2 in March-April 1971. None were taken south of lat. 3°N. Yellowfin ranged from 26 to 112 cm, with mean lengths for different aggregations ranging from 28.5 to 42.3 cm. The majority (68%) were <45 cm. These small yellowfin were mainly (83%) from the same latitudinal zone (10°-14°N) as the small skipjack. On three occasions schools of mixed small tunas–skipjack, yellowfin, and frigate mackerel (*Auxis*: 30 to 31 cm)–were sampled north of lat. 10°N. Small tuna of different species may occur together because of similar environmental and food requirements, and behavior.

Sex and Maturity of Skipjack

Sex ratios of skipjack for the two cruises were as follows:

November-December 1970:	Total 143, Sexed 72
	Males 24; females 33; indeterminate 15
Ratio:	Males to females, 1:1.4
March-April 1971:	Total 72, sexed 59
	Males 24; females 35
Ratio:	Males to females, 1:1.5

Gonad maturity was determined macroscopically in the field, and stages were classified as follows:

Immature, virgin	Roughly	1 - S
Immature, resting	equivalent	1
Maturing	to indicated	2
Spent	stages in	5 - A
Spent-recovering	Orange (1961)	5 - B

The number of gonads in each stage by size of fish are given in Tables 8 and 9.

In November-December the smallest spent or spent recovering female skipjack was 46.5 cm. In March-April the corresponding size for females was 49.8 cm, and for males 48.3 cm. These data support other evidence that first maturity in female skipjack in the Pacific is reached between 40 and 45 cm (Orange 1961; Waldron 1963; Kawasaki 1965).

A relatively large number of recently spawned fish, i.e., with spent and spent-recovering gonads, was taken on each cruise: 30% of the females and 7% of the males in November-December 1970, and

TABLE 8.—Number of skipjack gonads in each maturity stage by size of fish, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

Size class (cm)	Immature: Virgin M	Immature: Virgin F	Immature: Resting M	Immature: Resting F	Maturing M	Maturing F	Spent M	Spent F	Spent recovering M	Spent recovering F
<40	?	15 ?								
40-49.9		1	5	1						1
50-59.9			5	12	1			1	2	6
60-69.9			11	2		2				
≥70								2		

Totals: males (M) 24; females (F) 28; indeterminate (<40 cm) 15.

TABLE 9.—Number of skipjack gonads in each maturity stage by size of fish, Cruise *Jordan* 60, March-April 1971.

Size class (cm)	Immature: Virgin M	Immature: Virgin F	Immature: Resting M	Immature: Resting F	Maturing M	Maturing F	Spent M	Spent F	Spent recovering M	Spent recovering F
<40										
40-49.9				2					1	1
50-59.9			5	1	1				10	13
60-69.9					2	8			5	8
≥70						1				

Totals: males (M) 24; females (F) 34.

63% and 67%, respectively, in March-April 1971 (Tables 8, 9). Most others were at the immature resting stage. The spent-recovering fish appeared to be at a more advanced stage of recovery in March-April than in November-December 1970.

Data on other skipjack ovaries taken from or near the study area in 1970-71 are available from samples of purse seine-caught fish examined by the Inter-American Tropical Tuna Commission (C. L. Petersen, pers. commun.). Gonad indices were calculated by them according to Orange (1961), and data are given in Table 10.

The principal interest lies in the samples (mean lengths >57 cm) from long. 110°W westwards. It is assumed that gonad indices < 15.1 indicate immature (virgin or resting) or spent-recovering ovaries, 15.1 to 45 indicate maturing ovaries, and > 45 indicate mature or ripe ovaries. The occurrence of 35% of skipjack ovaries with indices > 45 in the middle of the study area in September 1970 may correspond to the 36% of ovaries in spent condition in fish >50 cm in the same area in November-December 1970 (Table 8). The sample from lat. 5°N, long. 110°W in April 1971 (Table 10) showed similar ovarian states to those in skipjack > 50 cm caught in March-April 1971 (Table 9): about 75% immature or spent-recovering, and 25% maturing, in each case.

Sex and Maturity of Yellowfin

In November-December 1970, 24 specimens of yellowfin under 50 cm were classified as immature, sex indeterminate; of 5 yellowfin from 50 to 60 cm, 3 were immature female, 1 was immature male, and 1 was indeterminate.

OBSERVATIONS ON THE ENVIRONMENT IN RELATION TO SKIPJACK

Temperature

The data from Part I operations on the 1970 and 1971 cruises were used to construct temperature

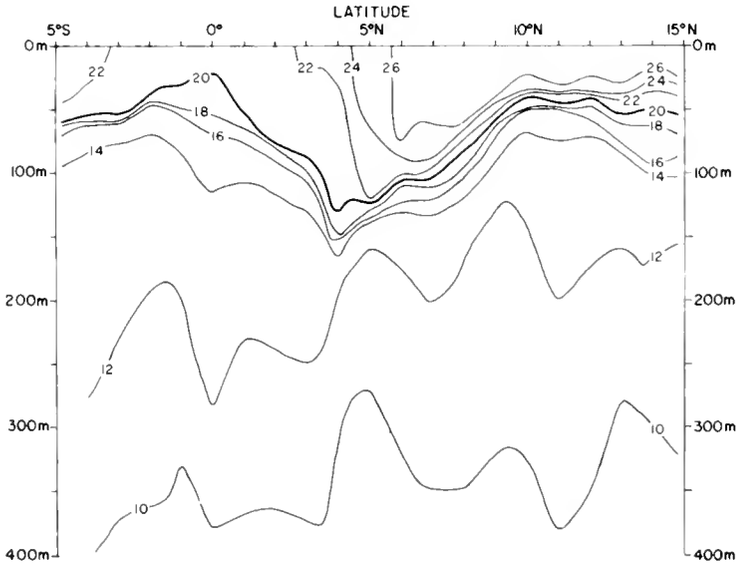


FIGURE 10.—Temperature (°C) section from lat. 15°N to 5°S along long. 119°W, cruise *Cromwell* 51, 1-7 November 1970.

TABLE 10.—Gonad indices of female skipjack caught by purse seine in northeastern tropical Pacific, 1970-71.

Date of capture	Approximate position: Lat. °N	Approximate position: Long. °W	Gonad indices: % <15.1	Gonad indices: %15.1-45	Gonad indices: % >45	Sample no.	Size (cm): Range	Size (cm): Mean
23 August 1970	5	135	48.9	46.8	4.3	50	53.5-63.8	59.9
8 September 1970	5	120	2.5	62.5	35.0	40	55.0-62.3	57.8
April 1971	5	110	76.0	24.0	0	50	54.3-67.6	60.5
30 April 1971	5	90	57.1	42.9	0	49	53.3-68.7	62.3
May 1971	5	90	32.0	60.0	8.0	59	57.8-70.0	64.5

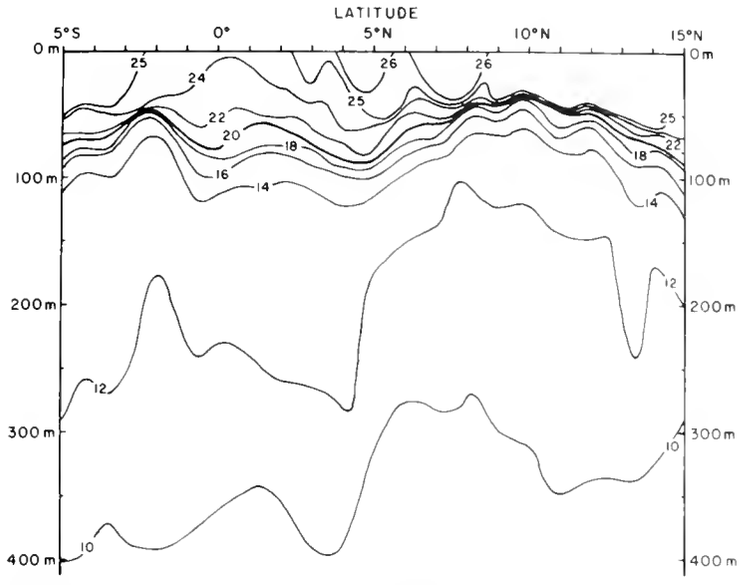
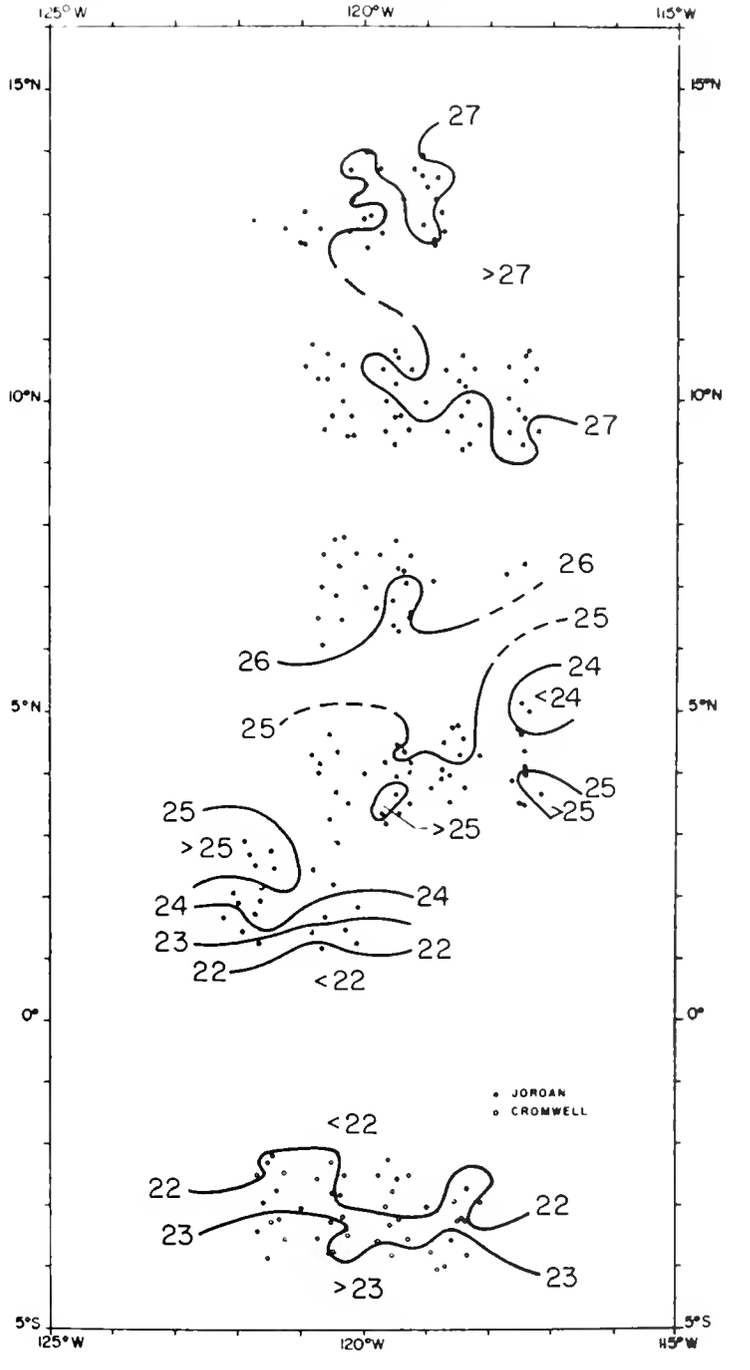


FIGURE 11.—Temperature (°C) section from lat. 15°N to 5°S along long. 119°W, cruise *Jordan* 60, 5-11 March 1971.



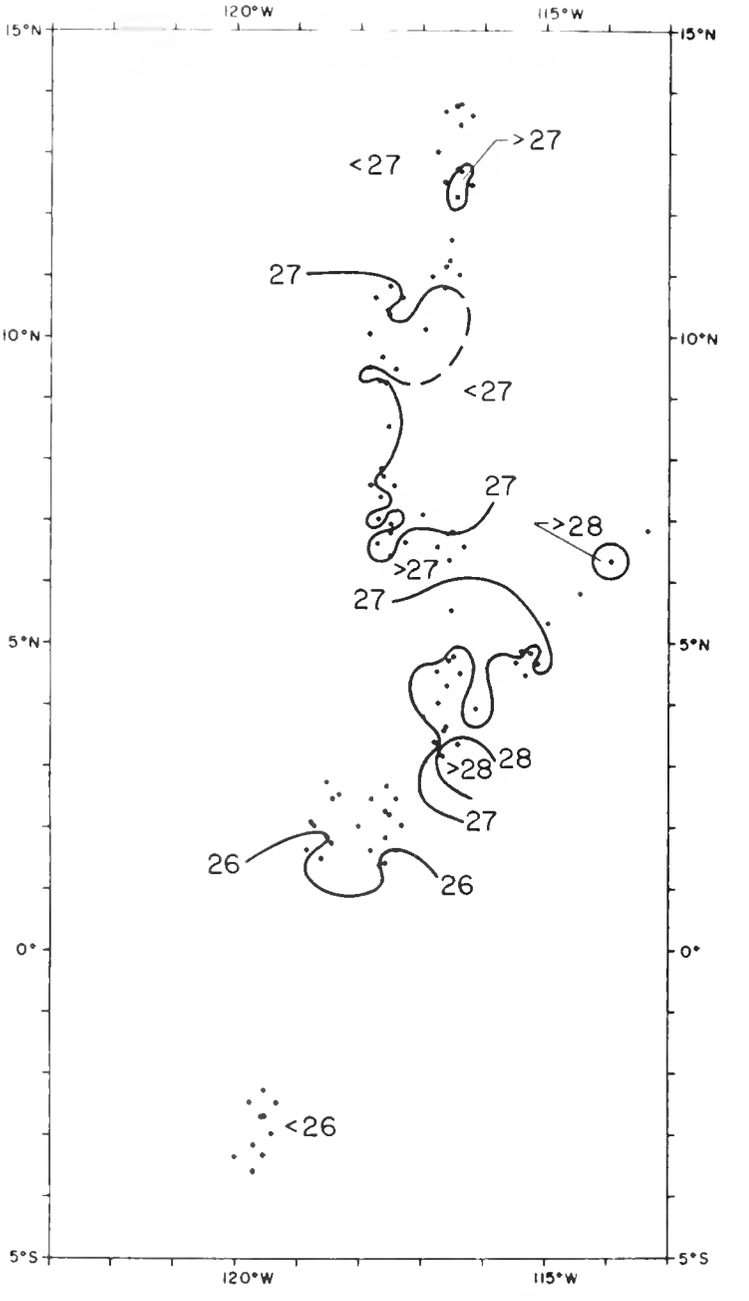


FIGURE 13.—Surface temperature (°C) during Part II operations, cruise *Jordan* 60, March-April 1971.

sections (Figures 10, 11). The temperature distributions were generally similar to those observed on the same meridian at the same time of year during EASTROPAC Expedition (M. Tsuchiya, pers. commun.). Surface temperatures suitable for skipjack, i.e., between 20° and 29°C, occurred at all latitudes on both cruises.

The distribution of surface isotherms (assumed synopticity) during Part II (fishing) operations on both cruises is shown in Figures 12 and 13. These figures have been compared, using overlays, with all charts of relative abundance of skipjack

FIGURE 12.—Surface temperature (°C) during Part II operations, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

(Figures 5, 6, 7, 8). The only apparent relationship between surface temperature and skipjack abundance appears to be the high abundance in the western part of the area of strong temperature gradient at lat. 1° to 3°N in November-December 1970.

Mixed Layer Depth

The depths (meters) of the bottom of the mixed layer are contoured at 20-m intervals in Figures 14 and 15 for Part II of the cruises. Figures 10 and 11 show the depths on Part I. Even though data are zonally discontinuous in parts of Figures 14 and 15, they are generally consistent with those of Cromwell (1958), Wyrtki (1964), and Love (1971b, 1972a, b, in prep.: EASTROPAC data).

In November-December 1970, the mixed layer depth was shallow (< 40 m) north of lat. 9°N, but south of there increased rapidly to > 100 m in the region of lat. 5°N. This ridge and trough are to be expected at the approximate northern and southern boundaries of the surface NECC. The gradient of change from this trough southwards to another ridge was particularly intense in the eastern edge of the area around lat. 4°N. In March-April 1971, the mixed layer was very shallow over most of the area surveyed south of lat. 10°N, becoming < 10 m in the region lat. 3° to 4°N. The even depth of the mixed layer from lat. 4° to 10°N

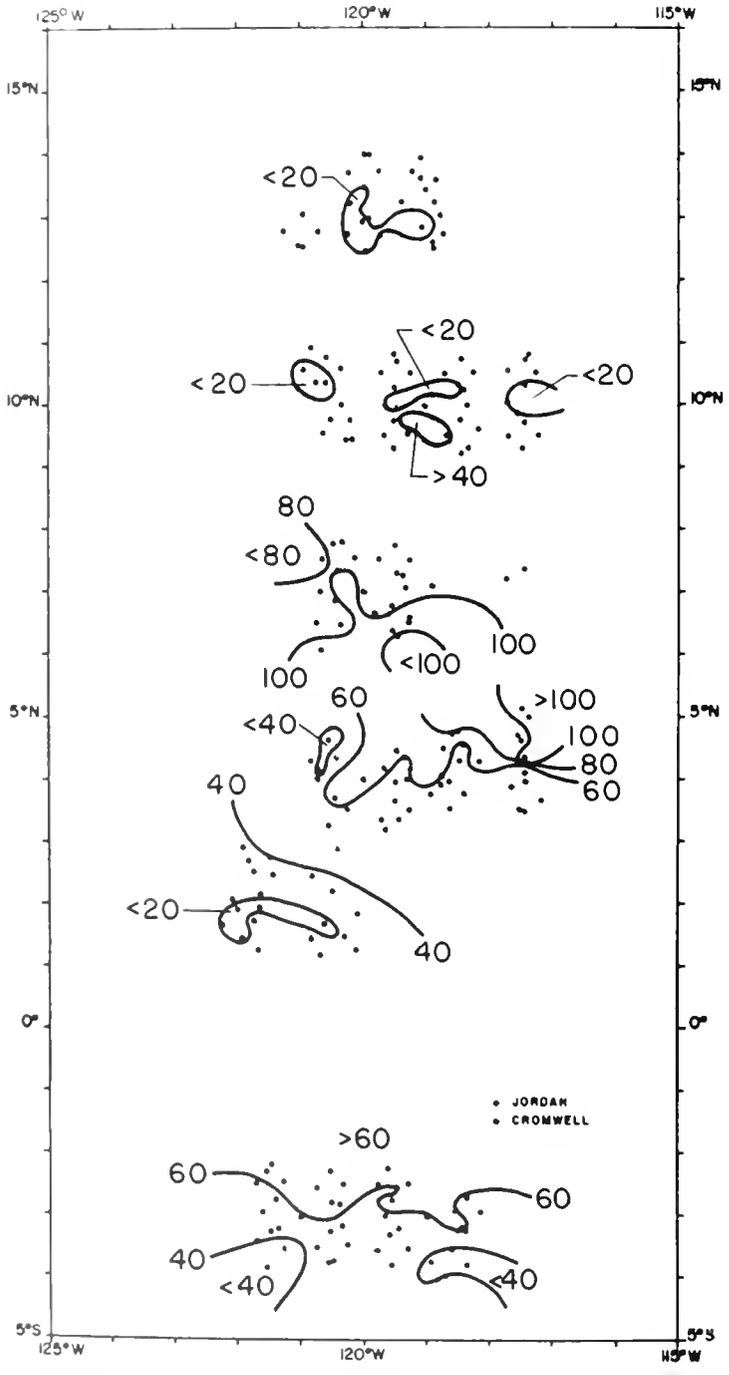


FIGURE 14.—Depth (m) of upper mixed layer, Part II operations, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

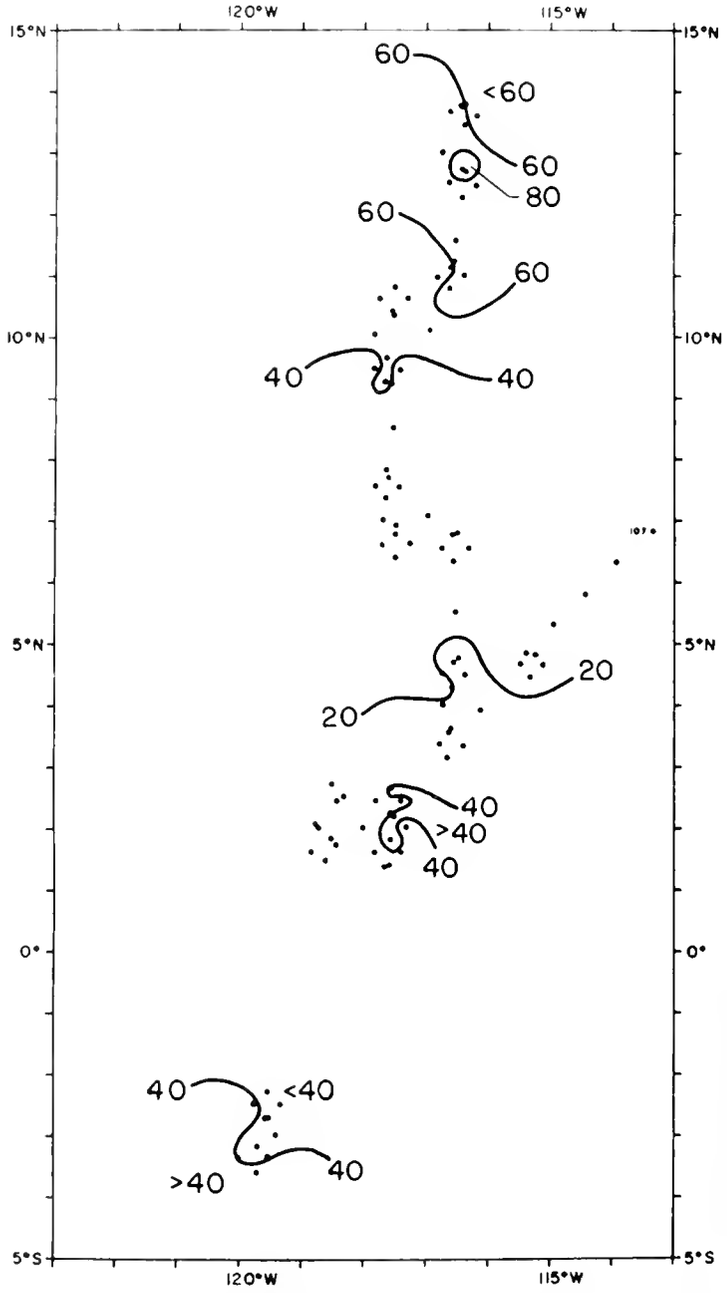


FIGURE 15.—Depth (m) of upper mixed layer, Part II operations, cruise *Jordan* 60, March-April 1971.

indicates the extreme weakness of the surface NECC at this time.

The charts of mixed layer depth have been compared by overlay with those of relative abundance of skipjack (Figures 5, 6, 7, 8). Areas of high relative abundance in November-December were generally close to ridges (< 40 m) in the mixed layer depth. There were exceptions, some of which are less obvious when utilizing schools/hour. There is no such trend in the March-April data.

Oxygen

Oxygen content (milliters/liter) was measured to 500 m, and sections showing oxygen distributions along the Part I transects of both cruises are presented in Figures 16 and 17. Sampling was also carried out in Part II fishing operations but for various reasons was more restricted than planned.

Figure 16 shows a strong oxycline (2 to 4 ml/liter) throughout the section of November 1971 parallel to the thermocline (Figure 10). In view of the probability of the lethal level of oxygen for skipjack being about 2.4 to 2.8 ml/liter (Anonymous 1973; R. Lasker pers. commun.), the depth of the 2.5-ml/liter isopleth may delimit the region of the water column suitable for skipjack. Its shallowest level in November-December 1970 (Figure 16) was about 50 m. In March-April 1971, (Figure 17) the oxycline was weaker and much reduced just north of the equator. The 2.5-ml/liter isopleth was on the average a little shallower than in November-December. The strong thermo-oxycline over most of the area on both cruises probably represented a bottom limit to vertical movement of skipjack, but even so at least the top 50 m of water were available to the fish.

The ridge in the oxycline at about lat. 10°N appears to be the western extension of the upper edge of the low oxygen-content water mass stretching out from the coast of Central America. (Tsuchiya 1968, Figure 7a, oxygen on the δ^{τ} = 400 cl/T surface, which there is at < 100 m).

Currents

The positions of the boundaries between the North Equatorial Current (NEC), the surface North Equatorial Countercurrent (NECC), and the South Equatorial Current (SEC) have been indicated schematically in Figures 3 and 4. They were based on the slope of the thermocline during Part I and II operations. In November-December 1970 the surface NECC was confined to a narrow band between lat. 7° and 10°N, with a geostrophic flow of < 1 knot (44 cm/s). On the second cruise in March-April 1971 the surface NECC was located between lat. 4° and 8°N during Part I operations, but a short time later in Part II it had narrowed to between lat. 4°30′ and 7°N. The geostrophic flow was lower than on the previous cruise, < 0.5 knot (< 25 cm/s), except at the southern boundary, where the subsurface NECC may have surfaced and geostrophic flow was about 1.25 knots (65 cm/s). Average current charts for the area (Wyrtki 1965) show the surface NECC absent east of long. 120°W at this time of year. EASTROPAC data (Love 1971b, 1972a; M. Tsuchiya, pers. commun.) show the surface current absent at this meridian and time in 1967, but present in 1968.

Data from XBT records of the return passage of the *Cromwell* from the study area to Hawaii in November 1970 have been used to construct a diagonal temperature section from lat. 3°N, long. 124°20′W to lat. 16°30′N, long. 146°06′W (Figure 18). From the slope of the thermocline, the approximate boundaries of the surface NECC along the transect are defined as lat. 6° to 8°N (southern boundary) and lat. 10° to 11°N (northern boundary).

Chlorophyll

In November-December 1970, the range of surface chlorophyll *a* values was 0.03 to 0.22 mg/m^3, with a maximum (> 0.20) between lat. 0°30′ and 2°00′S. A small area with chlorophyll values > 0.20 also existed at about lat. 2°30′N, long. 119°W. An area of low chlorophyll (< 0.05) was located at lat. 9° to 10°N, long. 117° to 119°W. During March-April 1971, surface chlorophyll ranged from 0.03 to at least 0.25 and probably to about 0.40 mg/m^3. Maxima (> 0.20) occurred from lat. 9° to 11°N and lat. 13° to 14°N, and a minimum (< 0.05) occurred from lat. 5° to 7°30′N, all east of long. 118°W.

Zooplankton

All four sets of zooplankton data (1-m and 0.5-m nets, day and night) from Part II operations show broadly similar distributions for the same cruise on contour charts, and it is unnecessary to show them for both nets. The 0.5-m net catches probably give a better representation of the standing stock of small herbivores than the 1-m net catches, and

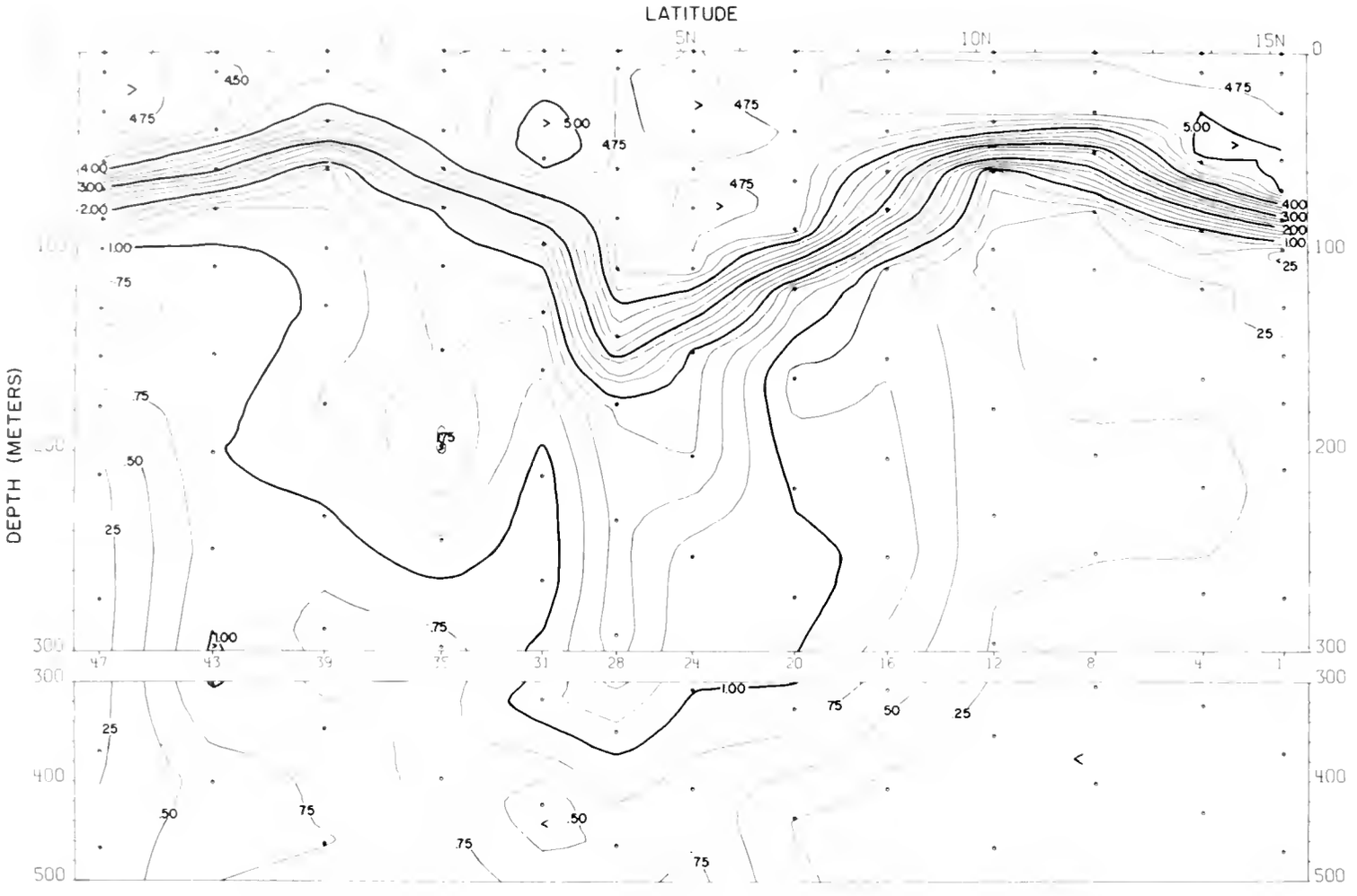


FIGURE 16.—Dissolved oxygen content (ml/liter), Part I transect, cruise *Cromwell* 51, 1-7 November 1970.

their distributions are charted here (Figures 19 to 22). Catches by the 1-m net are more likely to be related to skipjack tuna than those by the 0.5-m net, because more skipjack forage organisms occur in them. These relationships are investigated statistically in the next section.

The main features of the day and night zooplankton distributions in November-December 1970 are a maximum at about lat. 1° to 2°N, a minimum in the extreme north of the area, and a secondary minimum at about lat. 3° to 5°N. Maxima occurred in March-April 1971 at about lat. 3° to 6°N and 9° to 10°N; elsewhere at that period the catches were moderate with no conspicuous spatial minima except in the extreme north. Comparisons between Figures 19 to 22, and Figures 5 to 8, made by overlay, show no obvious relation between distributions of zooplankton and skipjack.

Skipjack Forage (and Zooplankton in Part)

One of the objectives of the cruises was to see if availability of offshore skipjack varied with the forage, as presumed by Blackburn (1965, 1969) and Blackburn and Laurs (1972); or with zooplankton, as suggested by Schaefer (1961); or with the arithmetic product of forage and zooplankton, as suggested by Riley (1963).

Charts of skipjack forage (in milliters/1,000 m^3), both day and night data, are shown in Figures 23 and 24 for both parts of the November-December 1970 cruise, and similarly in Figures 25 and 26 for the March-April 1971 cruise. Corresponding charts of total micronekton were very similar and are not given here. Data are available at Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif.

Measurements of day concentration of forage were more numerous than those of night concentration. Thus Figures 23 and 25 show more detail than Figures 24 and 26. Blackburn and Laurs (1972) showed that day and night distributions of forage were broadly similar in the area on a given cruise as far as locations of maxima and minima were concerned, although the night concentrations were about 10 times higher than day concentrations. Contours for day and night distributions were therefore drawn to agree with each other as

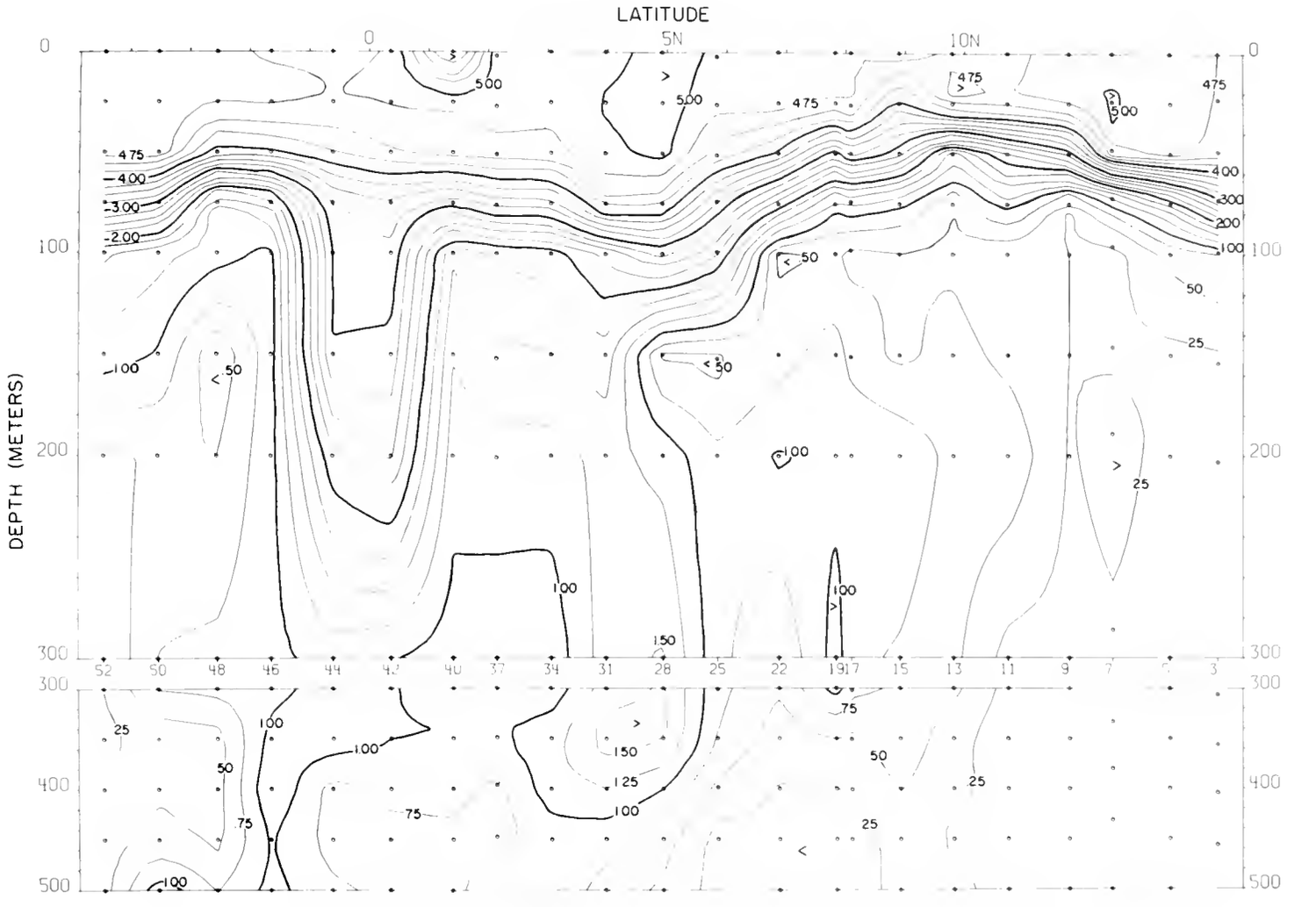


FIGURE 17.—Dissolved oxygen content (ml/liter), Part I transect, cruise *Jordan* 60, 5-11 March 1971.

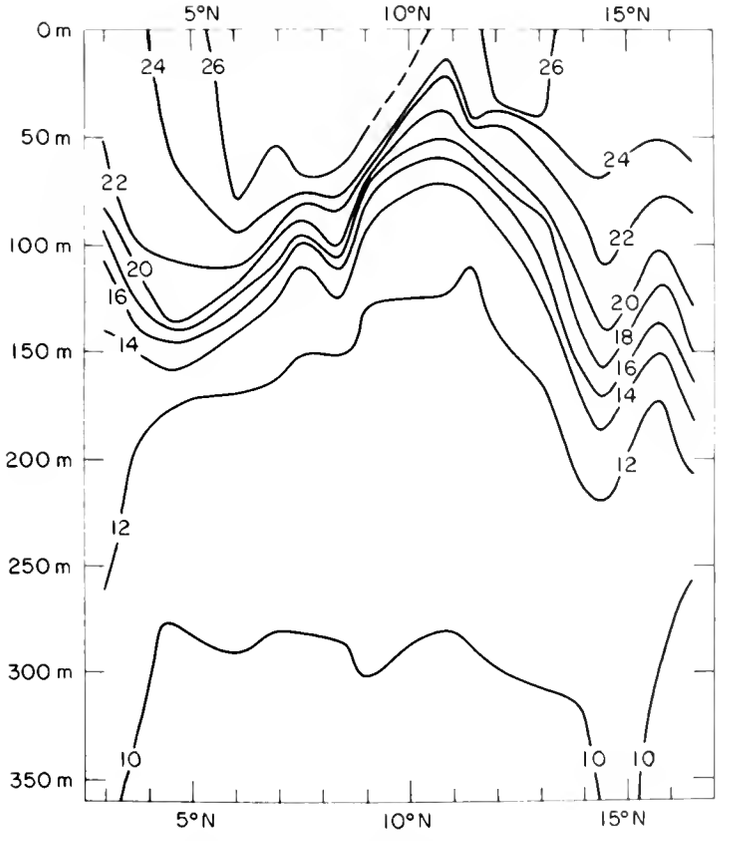


FIGURE 18.—Temperature (°C) section from lat. 3°N, long. 124°20'W, to lat. 16°30'N, long. 146°06'W, cruise *Cromwell* 51, November 21-26, 1970.

much as possible without violating the data. Fewer data were available for the March-April cruise than for the November-December one, for reasons given elsewhere.

According to Blackburn and Laurs (1972), the most conspicuous and consistent feature of day and night forage distributions in the study area is a zonally oriented maximum between lat. 0° and 5°N, which is probably associated with the equatorial upwelling as explained by King (1958). Figures 23 and 24 show this feature, and Figures 25 and 26 show one which is probably the same although it does not appear to be zonally oriented. Stations at the eastern end of the maximum in Figures 25 and 26 were occupied 13 days after the last stations at the western end were occupied, and the maximum could have moved north in the interval. Other maxima and minima in Figures 23 to 26 are smaller and less consistent in location between cruises.

The data from these micronekton net hauls, especially those for the March-April cruise which are very sparse, may not give a complete picture of the distribution of skipjack forage. On the March-

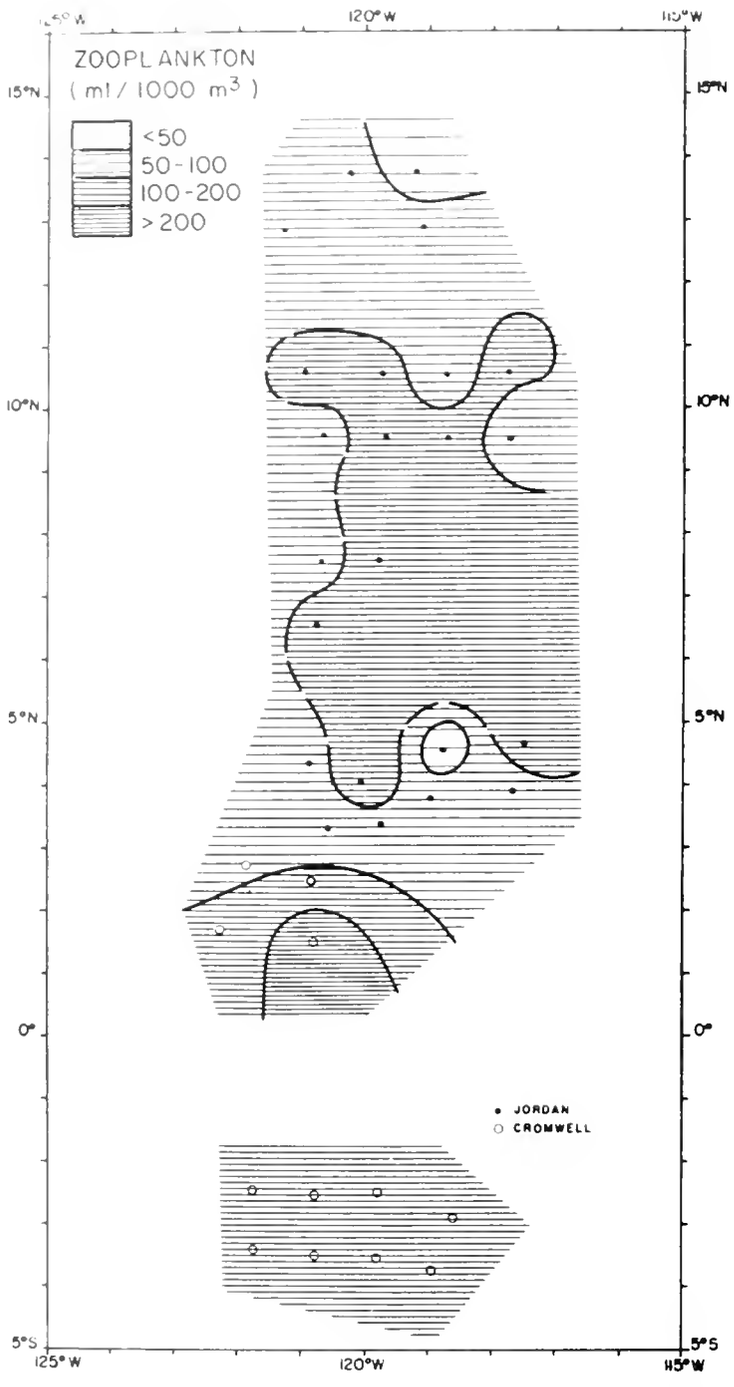


FIGURE 19.—Day standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

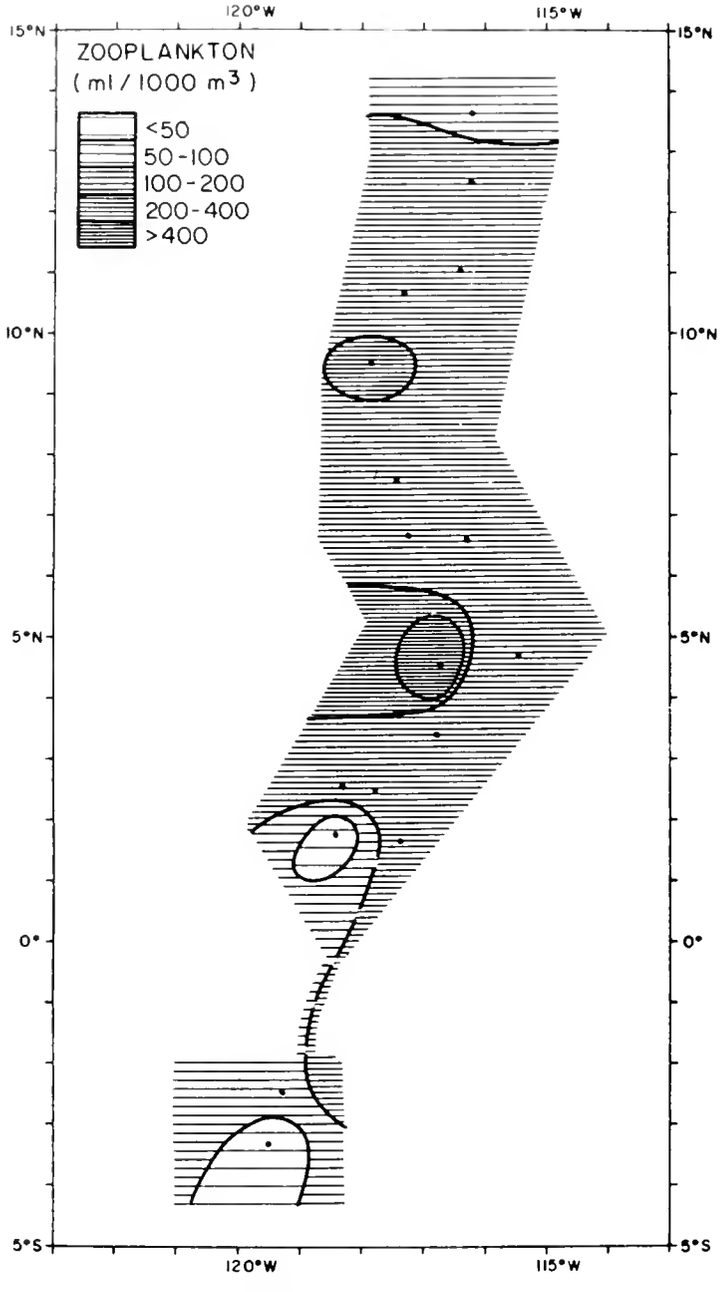


FIGURE 20.—Day standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruise *Jordan* 60, March-April 1971.

April cruise large catches of skipjack forage were obtained by midwater trawl as well as by micronekton net in the area of the maximum between lat. 0° and 5°N, and one was obtained also at about lat. 10°N where the micronekton net indicated a rather low concentration. This result from a single trawl haul thus indicates an area of rich forage of unknown extent at about lat. 10°N, which the sparse data from the micronekton net hauls do not show. The forage may have been patchy in this area.

The expected resemblance between the spatial distributions of forage and skipjack is not strongly evident when Figures 23 to 26 are compared with charts of skipjack availability on the same cruises (Figures 5 to 8). However, Table 3 shows that mean catch per line-hour and mean number of schools per hour for all fishing days in a zone of latitude was highest in November-December from lat. 1° to 5°N, where the principal forage maximum was located (Figures 23 and 24). Table 4 shows that the same indices were highest in March-April from lat. 9° to 11°N, where Figures 25 and 26 show no forage maximum, although one may have existed there as explained above. A secondary skipjack maximum occurred in March-April in the equatorial region, south of lat. 3°N, where a forage maximum was present.

Attempts were made to correlate forage con-

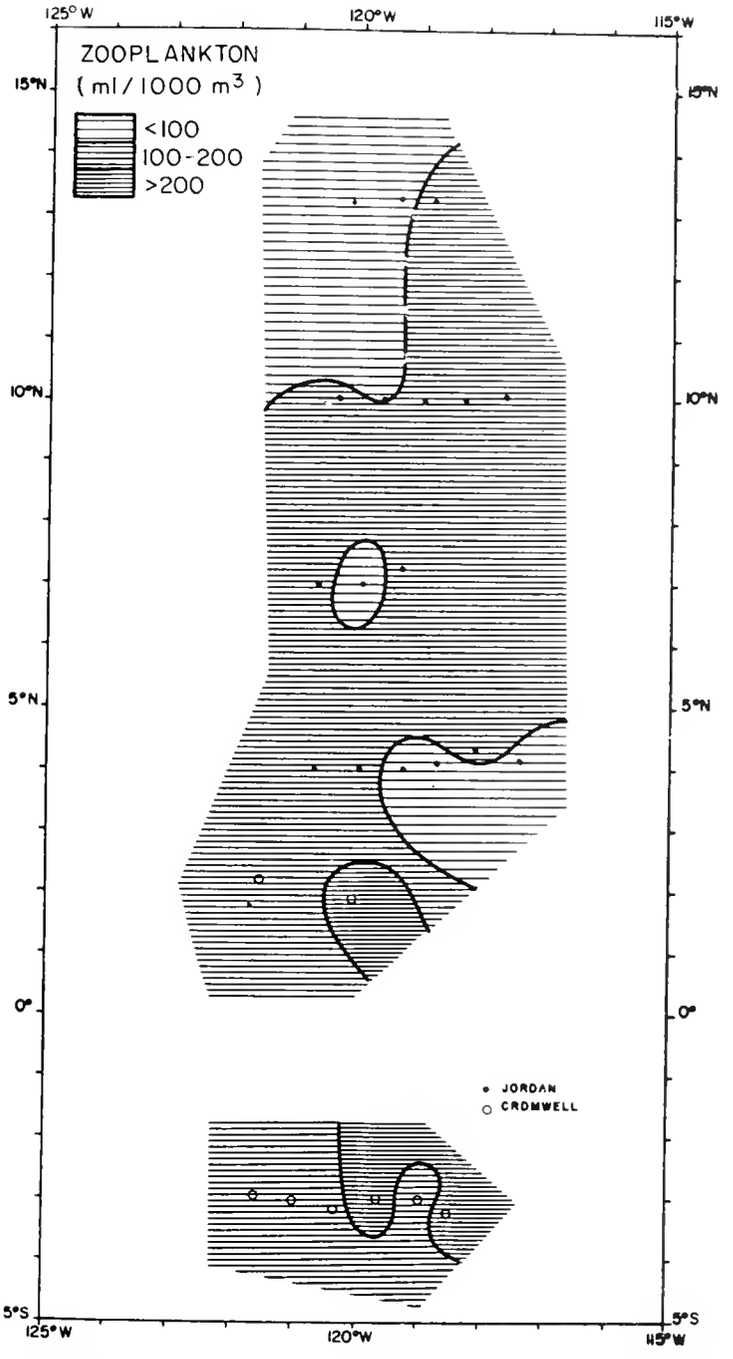


FIGURE 21.—Night standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

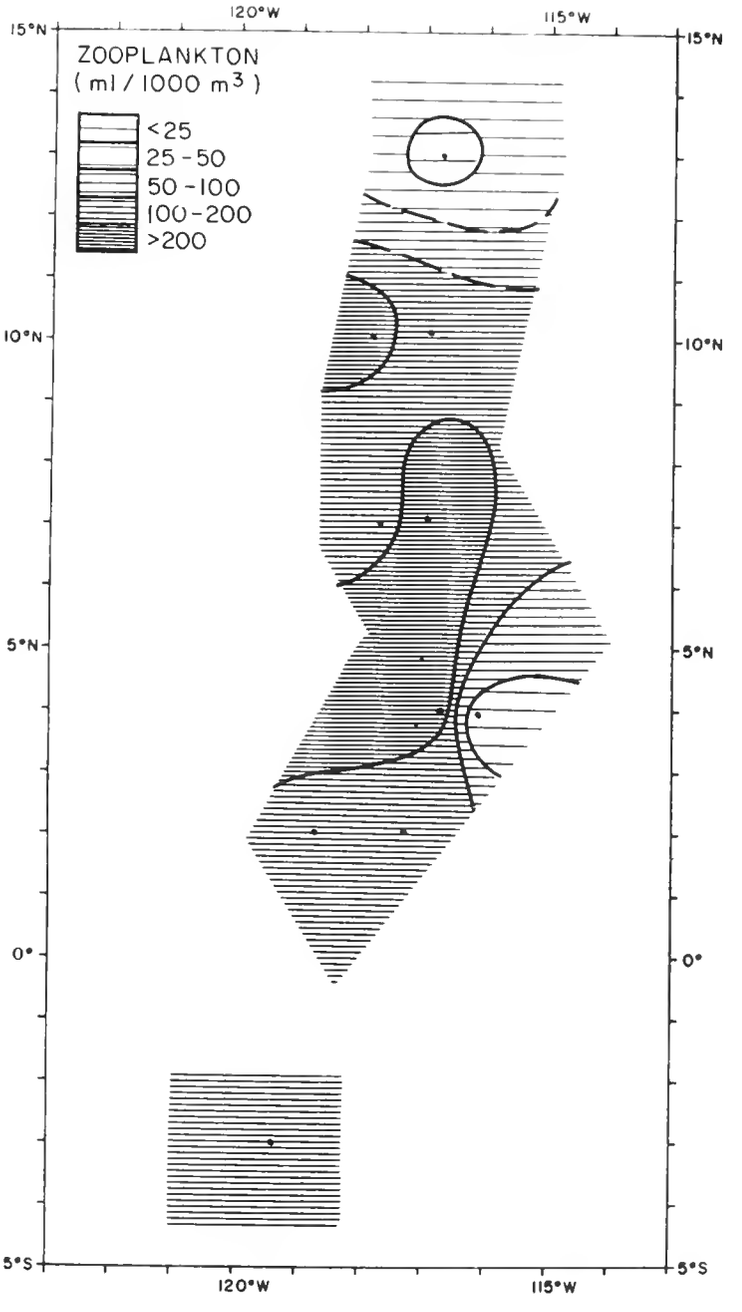


FIGURE 22.—Night standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruise *Jordan* 60, March-April 1971.

centration and related measurements with skipjack availability for all data from the study area. Table 11 gives the results of the tests using concentrations of day forage, day zooplankton, and their arithmetic product. Table 12 gives similar results using night concentrations. All variables were transformed to logarithms in order to bring distributions closer to normal, before correlation coefficients were calculated. A distinction is made between all skipjack and large skipjack; the latter excludes skipjack < 45 cm, which seem to be a separate age-group and exhibited some segregation from the other skipjack in space and time. Zooplankton data are from hauls of the 1-m net only, as explained above.

None of the 72 correlations in Table 11, involving day concentrations of forage and zooplankton with skipjack, are significant. On the other hand 4 of the 48 correlations in Table 12, involving night concentrations of forage and zooplankton with skipjack, are significant by the usual criteria and positive: two coefficients are above the 5% level of probability and two are above the 1% level. They refer only to availability of large November-December skipjack measured as catch per line-hour or schools per hour, in relation to night forage and to the product of night forage and night zooplankton, with both variables averaged over

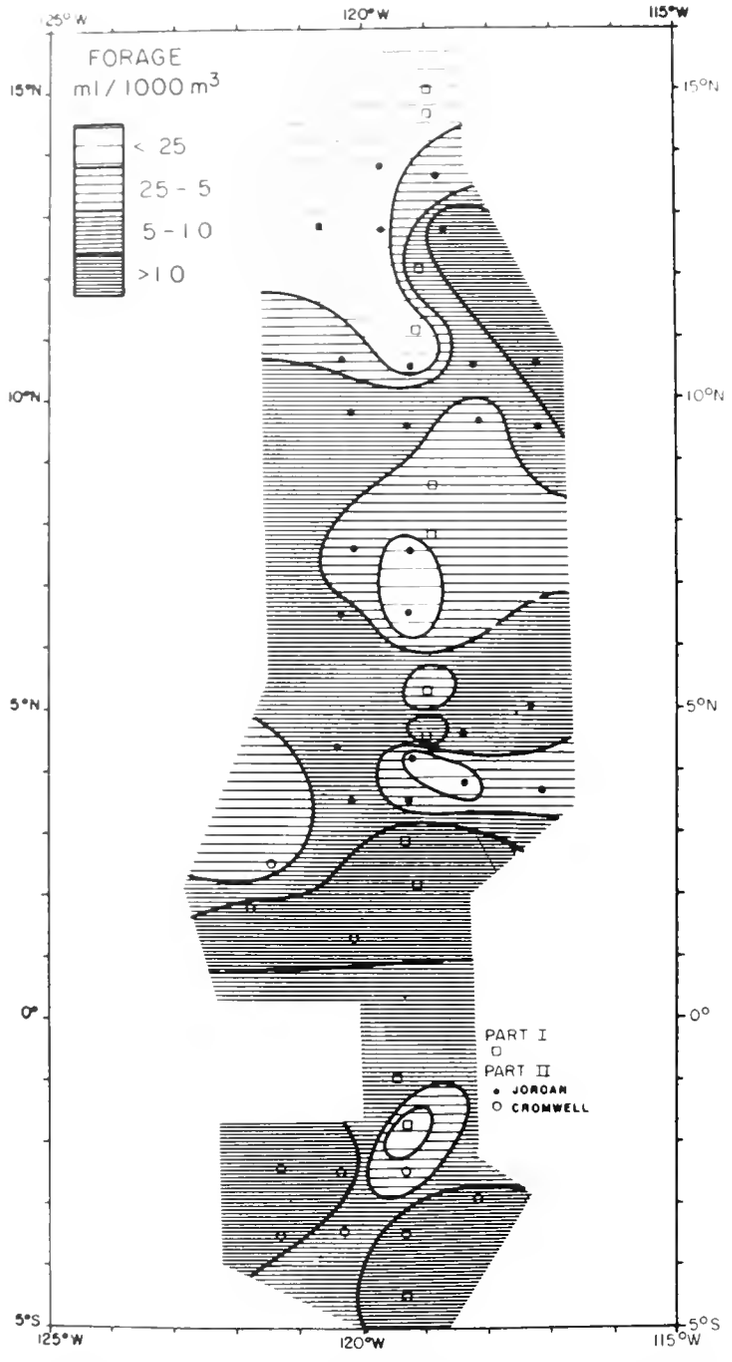


FIGURE 23.—Day standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

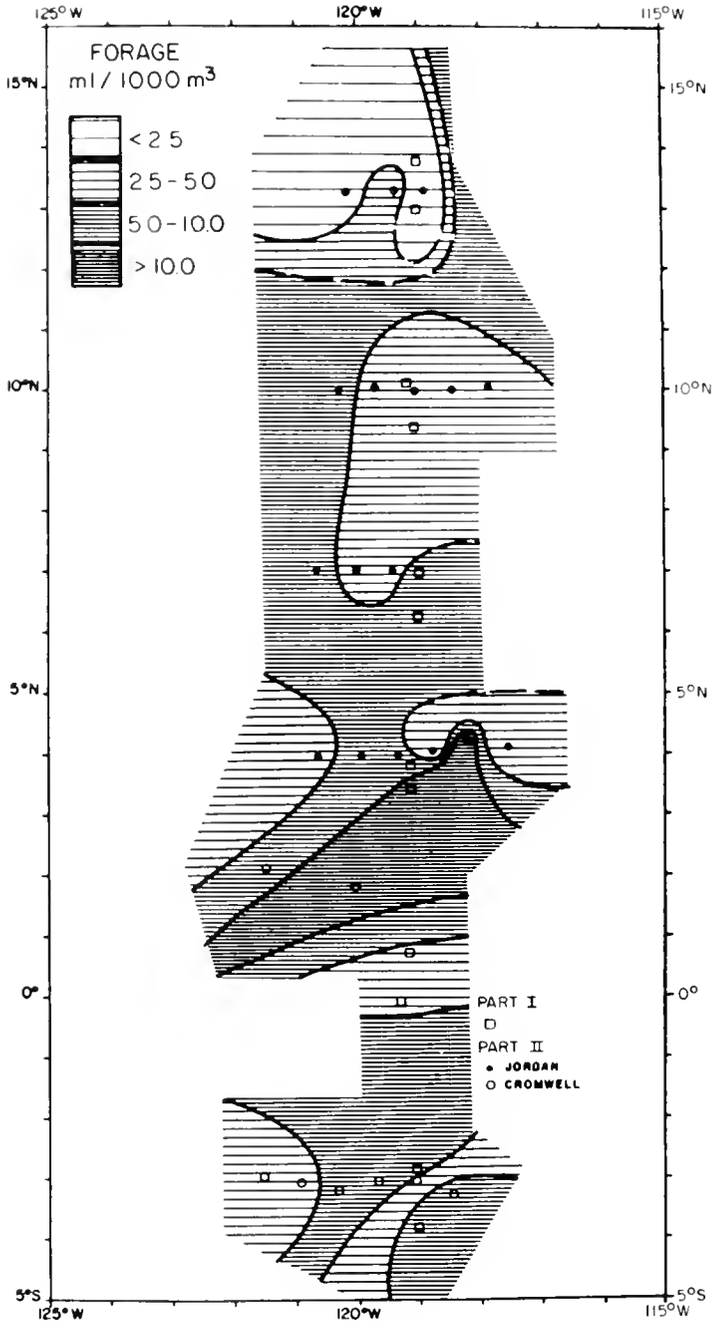


FIGURE 24.—Night standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

zones about 2° of latitude wide. There is no difference in the significance of coefficients depending on whether forage or forage × zooplankton was the variable, and no significant coefficients are obtained with zooplankton alone.

Table 13 gives the data that yielded the significant correlations between large skipjack and forage. The correlation coefficients are +0.947 with catch per line-hour and +0.886 with number of schools per hour, significant at the 0.5 and 2.0% probability levels respectively. The corresponding Spearman rank correlation coefficients are +0.952 and +0.905, both significant at the 5% level. No other grouping of 2°-latitude zones would have given so many zones with so much data in each (see Figure 3).

The significance of the four correlation coefficients in Table 12 has been disputed because of the much larger number of nonsignificant correlations in Tables 11 and 12 combined. It has also been pointed out that the two coefficients involving forage × zooplankton are not independent of the two coefficients involving forage alone. In our following comments we ignore all coefficients with forage × zooplankton, whether apparently significant or otherwise. We then have two possibly significant coefficients in a total of 80 for Tables 11 and 12, i.e., one in 40. From the previous paragraph, there is a chance of about one in 50 that

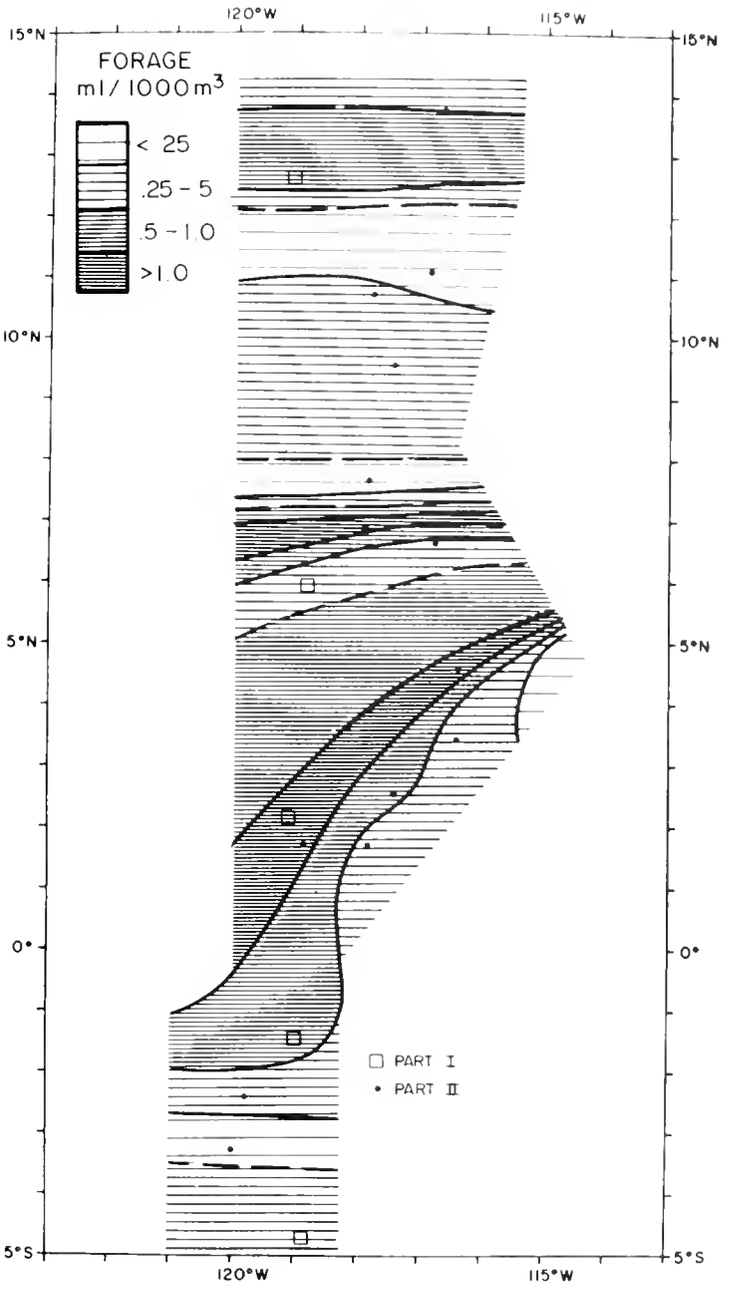


FIGURE 25.—Day standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruise *Jordan* 60, March-April 1971.

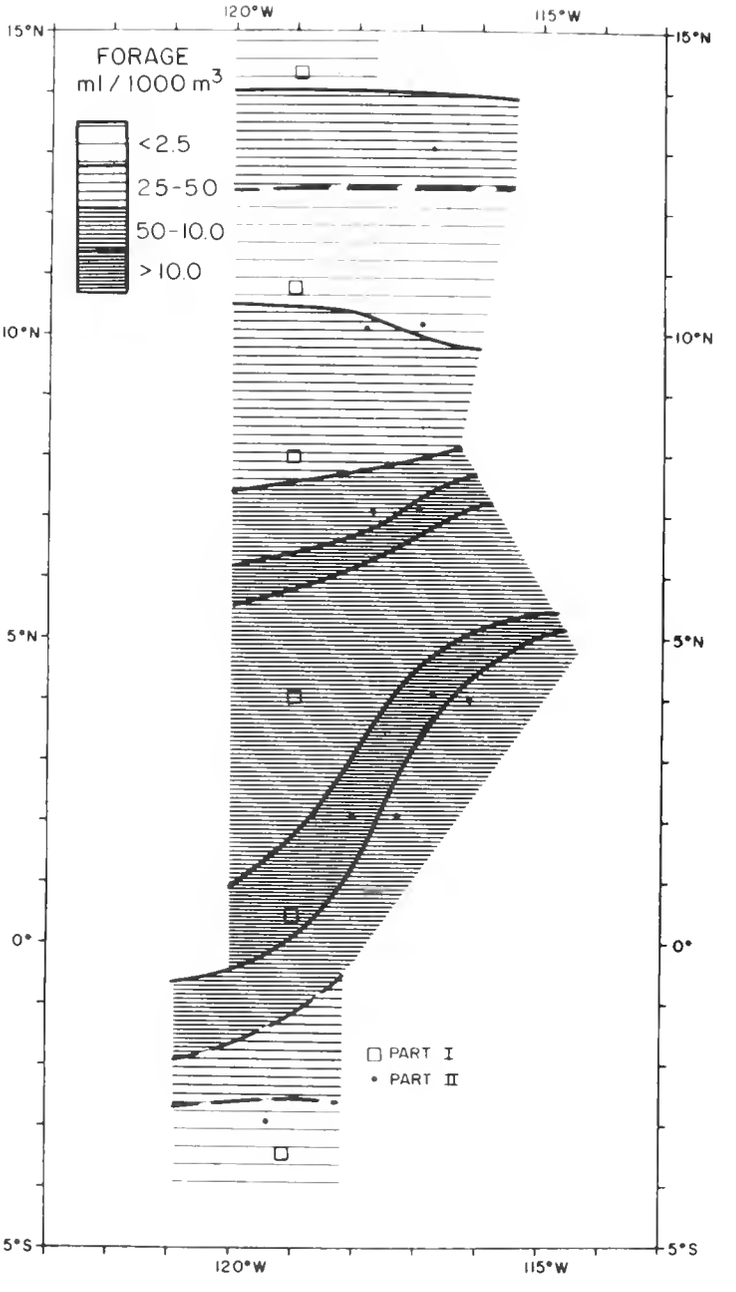


FIGURE 26.—Night standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruise *Jordan* 60, March-April 1971.

the lower coefficient could have been so high with no correlation, and a corresponding chance of only about one in 200 for the higher coefficient. There seems no reason to presume nonsignificance, at least for the higher coefficient.

Significant correlations were not obtained for any data from the March-April cruise. Only two degrees of freedom are available to test the significance of correlations corresponding to the significant correlations in the November-December data. In any case the meager forage data for March-April seem not to have adequately depicted the actual conditions, as noted above. Relations of skipjack to forage are discussed later.

CRUISE 116 OF RV *CHARLES H. GILBERT*, OCTOBER-NOVEMBER 1969

In October-November 1969, the RV *Charles H. Gilbert* of the Honolulu Laboratory of the National Marine Fisheries Service made a cruise to collect samples of skipjack and other tunas for a subpopulation study. The main fishing operations were located in the same area as the combined cruise *Jordan* 57-*Cromwell* 51, though approximately 1 yr earlier. The fishing and environmental data are analyzed here in more detail than by Hida (1970). Figure 27 shows the cruise track of

TABLE 11.—Measures of daytime availability of skipjack correlated with day concentrations (ml/1,000 m³) of skipjack forage, zooplankton, and their arithmetic product. All tests were made with the variables transformed to logarithms. Numbers are pairs of observations from which correlation coefficients were calculated. No coefficients were significant. "All" means all skipjack; "large" means skipjack ≥45 cm.

Skipjack availability		Period	Data grouping[1]	Forage (F)	Zooplankton (Z)	F × Z
Catch/line-hour	All	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6
	Large	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6
Schools/hour	All	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6
	Large	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6

[1]A. Numbers to the right of this letter are numbers of 1° × 1° quadrants. For each quadrant skipjack availability is based on all observations for the day, and F and Z are each based on a single observation made in the quadrant during the day.
B. Numbers to the right of this letter are numbers of 1° zonal rows of quadrants with ≥2 quadrants per row. For each row skipjack availability, F and Z are means of the data for the individual quadrants.
C. Numbers to the right of this letter are numbers of 2° zonal rows of quadrants. For each row skipjack availability, F and Z are means of the data for the individual quadrants.

TABLE 12.—Measures of daytime availability of skipjack correlated with night concentrations (ml/1,000 m³) of skipjack forage, zooplankton, and their arithmetic product. All tests were made with the variables transformed to logarithms. Numbers are pairs of observations from which correlation coefficients were calculated. Significant correlations occurred as shown by * (5% level of probability) or ** (1% level) and were positive. "All" means all skipjack; "large" means skipjack ≥45 cm.

Skipjack availability		Period	Data grouping[1]	Forage (F)	Zooplankton (Z)	F × Z
Catch/line-hour	All	Nov.-Dec.	A	25	25	25
			B	6	6	6
		Mar.-Apr.	A	11	11	11
			B	4	4	4
	Large	Nov.-Dec.	A	25	25	25
			B	6**	6	6**
		Mar.-Apr.	A	11	11	11
			B	4	4	4
Schools/hour	All	Nov.-Dec.	A	25	25	25
			B	6	6	6
		Mar.-Apr.	A	11	11	11
			B	4	4	4
	Large	Nov.-Dec.	A	25	25	25
			B	6*	6	6*
		Mar.-Apr.	A	11	11	11
			B	4	4	4

[1]A. Numbers to the right of this letter are numbers of night stations, one station per night, at which observations of F and Z were made. F, Z, and F × Z for a night station were paired for correlation purposes with the mean of skipjack availability for the daytime periods immediately before and after the night on which the station was occupied, in closely adjacent 1° × 1° quadrants.
B. Numbers to the right of this letter are numbers of 2° zonal rows of quadrants and night stations. For each row skipjack availability is the mean of the data for the individual quadrants, and F and Z are the means of the data for the individual night stations.

TABLE 13.–Means of night skipjack forage and availability of large skipjack for 2° zonal rows of quadrants and night stations in November-December 1970, on which significant correlations in Table 12 are based.

Zone latitude	A Forage (ml/1,000 m³)	B Skipjack (catch/line-hour)	C Skipjack (schools/hour)
12°-14°N	1.54	0.020	0.060
9°-11°N	3.62	0.036	0.111
6°-8°N	3.98	0.044	0.070
3°-5°N	12.07	0.118	0.161
1°-3°N	10.23	0.189	0.235
2°-4°S	4.89	0.080	0.112

the *Gilbert* in relation to the area of the present investigations. Observations on tuna forage were not made.

Temperature and Surface Currents

Data from bathythermograph (BT) records have been used to make the two temperature sections shown in Figures 28 and 29. Surface temperatures everywhere were optimal for skipjack. The lowest temperatures on both sections occurred at lat. 0°30′S in the equatorial upwelling, namely < 24°C at long. 118°W and < 26°C at long. 137°W.

The approximate boundaries of the surface NECC during the cruise have been determined from the slope of the thermocline in Figures 28 and 29. On the outward track from Honolulu, the northern boundary of the NECC was lat. 10°N at long. 147°30′W, and the southern boundary, lat. 5°N at long. 142°15′W. On the south-north transect of the survey area, the southern boundary of the NECC was about lat. 6°N at about long. 120°45′W, and the northern boundary, lat. 9°N at about long. 129°30′W. The location of the surface NECC is shown in Figure 27.

Distribution and Relative Abundance of Troll-caught Tuna

Relative abundance of troll-caught tuna has been calculated as previously. The data are considered for: the area equivalent to the present study area plus the area fished by *Gilbert* south of lat. 5°S within long. 115°-125°W; the outward track from Honolulu to the area; and the inward track from the area to Honolulu. Total fishing effort in line-hours is given in Table 14.

The relative abundance of troll-caught skipjack and other tuna as catch/line-hour in the study area is shown in Table 15 by 1° latitudinal zones and

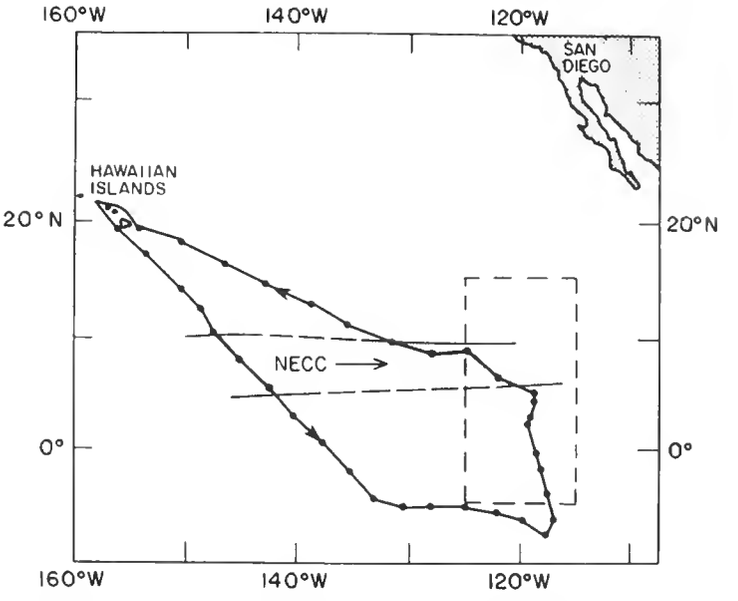


FIGURE 27.–Track of cruise *Charles H. Gilbert* 116, October-November 1969. Noon positions are indicated. Area of present investigations is outlined by dashed lines. NECC is surface North Equatorial Countercurrent.

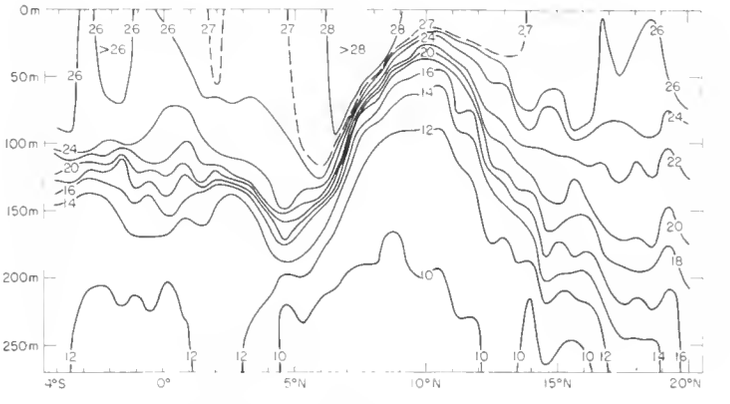


FIGURE 28.–Temperature (°C) section from lat. 19°55′N, long. 156°36′W to lat. 4°08′S, long. 133°40′W, cruise *Gilbert* 116, 3-13 October 1969.

surface currents. There was relatively little fishing effort (< 50 line-hours) in some latitudinal zones, which makes it difficult to define limits of maxima of skipjack abundance. However, the area from lat. 6° to 8°10′N is a maximum, with indices comparable with the highest ones in Table 3. Moderately high indices are seen at lat. 5° to 6°S and in the area lat. 0°-6°N, alternating with areas fished for less than 50 line-hours. Catch indices of other tunas were moderately high in the two zones where they occurred.

Relative abundance of skipjack as schools/hour in the area is given in Table 16 in two ways: firstly, as in previous sections of this report based on troll catches, and secondly, based on schools encountered during trolling and pole-and-line fishing. Usually, pole-and-line fishing was carried out subsequent to a jig strike, but occasionally not. The

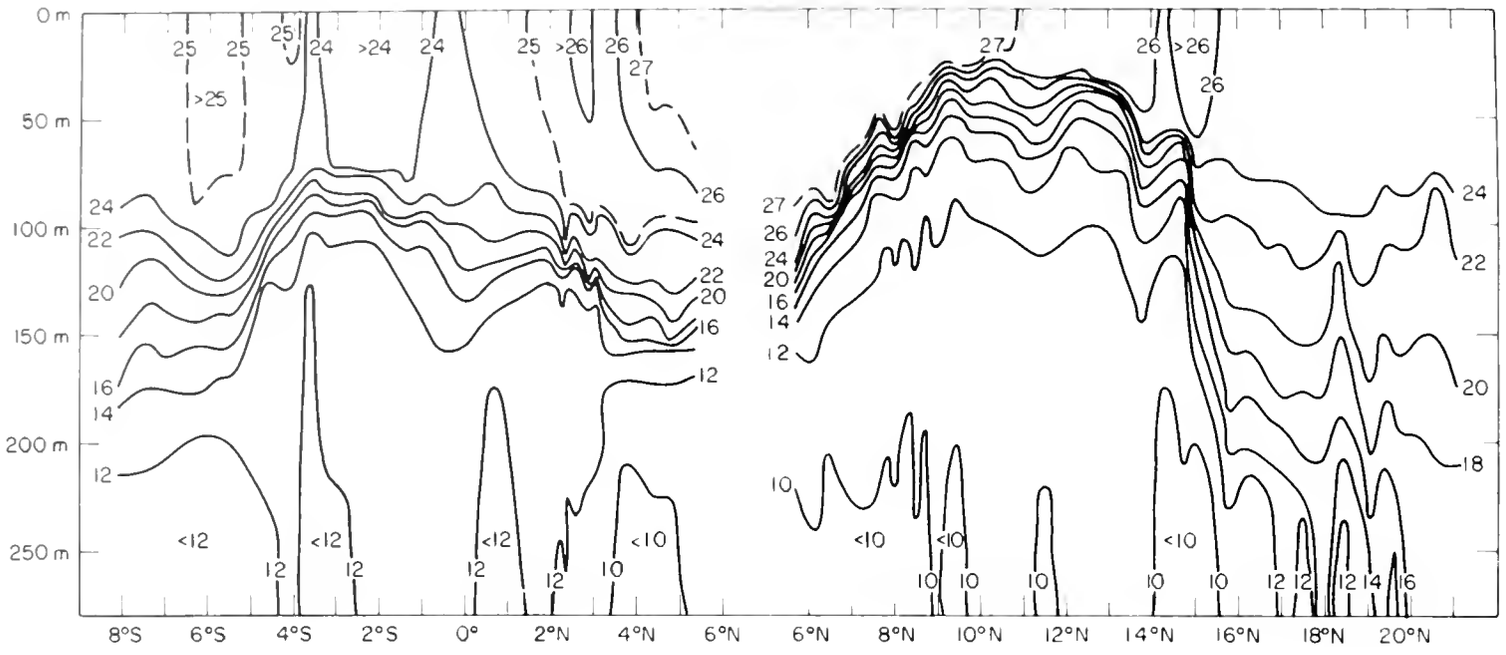


FIGURE 29.—Temperature (°C) sections from lat. 8°05′S to 5°21′N along long. 117° to 120°W, and from lat. 5°45′N, long. 120°14′W to lat. 21°03′N, long. 157°14′W, cruise *Gilbert* 116, 19 October-7 November 1969.

TABLE 14.—Total fishing effort Cruise *Gilbert* 116, October 1969.

Locality	Line-hours fished	
Study area		963
Outward track	382	788
Inward track	406	
Total		1,851

TABLE 15.—Relative abundance (catch/line-hour) of troll-caught skipjack and other tuna in the study area, Cruise *Gilbert* 116, October 1969. YF and BE mean yellowfin and bigeye. * means <50 line-h.

Zone latitude	Current system	Skipjack catch/ line-hour	Other tuna catch/line-hour
7°-8°10′N	NECC	0.240	0
6°-7°	NECC	0.342	0
5°-6°	SEC	0*	0
4°-5°	SEC	0.065	0
3°-4°	SEC	0*	0
2°-3°	SEC	0.087	0.138 (YF)
1°-2°	SEC	0*	0
0°-1°N	SEC	0.095	0
0°-1°S	SEC	0*	0
1°-2°	SEC	0*	0
2°-3°	SEC	0*	0
3°-4°	SEC	0*	0
4°-5°	SEC	0	0.093 (YF or BE)
5°-6°	SEC	0.097	0
6°-7°	SEC	0.017	0
7°-8°S	SEC	0.017	0

correlation between catch/line-hour and schools/hour was significant at the 1% level (r = 0.908, data of Tables 15 and 16), as on the cruises made in 1970 and 1971. The covariance analysis in Table 17 shows that the regressions of schools/hour on catch/line-hour for the three cruises did not differ significantly in slope, but differed in elevation.

TABLE 16.—Relative abundance (schools/hour) of skipjack in the study area, Cruise *Gilbert* 116, October 1969. *means <9 h of observations

Zone latitude	Current system	Schools/hour	
		Based on troll catch	Based on total catch (troll plus pole-and-line)
7°-8°10′N	NECC	0.42	0.42
6°-7°	NECC	0.50	0.50
5°-6°	SEC	0*	0*
4°-5°	SEC	0.31	0.39
3°-4°	SEC	0*	0*
2°-3°	SEC	0.21	0.26
1°-2°	SEC	0*	0*
0°-1°N	SEC	0.34	0.34
0°-1°S	SEC	0*	0
1°-2°	SEC	0*	0*
2°-3°	SEC	0*	0*
3°-4°	SEC	0*	0*
4°-5°	SEC	0	0.22
5°-6°	SEC	0.15	0.15
6°-7°	SEC	0.05	0.05
7°-8°S	SEC	0.08	0.08

Table 16 shows the maximum at lat. 6° to 8°10′N, as in Table 15. Inclusion of the pole-and-line data increases the indices in other zones, i.e. lat. 4° to 5°N, 2° to 3°N, and 4° to 5°S. The range of the indices for schools/hour is about the same as for the other cruises.

Considerable catches of skipjack and other tuna were made on passage to and from the area. Data on relative abundance (catch/line-hour) are given in Table 18. Results should be used with care as fishing effort never exceeded 50 line-hours per day. There were moderate to high catch rates between lat. 4°45′ and 8°30′N (long. 148° to 138°W), with indices at about the same level as at lat. 6° to 8°10′N in the study area (Table 15). Catch indices for other tuna were low.

TABLE 17.—Analysis of covariance: schools/hour (Y) on catch/line-hour (X) for the 1969, 1970, and 1971 cruises, data of Tables 3, 4, 15, and 16.

Year	df	Σx^2	Σxy	Σy^2	b	df	Σd^2	M.S.
1969	7	0.0905	0.1144	0.1754	1.264	6	0.0308	0.0051
1970	11	0.0936	0.0904	0.1060	0.965	10	0.0187	0.0019
1971	11	0.0187	0.0402	0.1684	2.147	10	0.0822	0.0082
Within						26	0.1317	0.0051
Reg. Coef.						2	0.0223	0.0112
Common	29	0.2028	0.2450	0.4498		28	0.1540	0.0055
Adj. Means						2	0.0410	0.0205
Total	31	0.2286	0.2807	0.5394		30	0.1950	

F (slope) = 2.196, nonsignificant.
F (elevation) = 3.727, significant at 5%.

TABLE 18.—Relative abundance (catch/line-hour) of troll-caught skipjack and other tuna, on track to and from the study area, Cruise *Gilbert* 116, October-November 1969. YF and BE mean yellowfin and bigeye.

Date	Approximate position (start and finish of day's trolling) Latitude	Longitude	Current system	Fishing effort (line-hour)	Catch/line-hour Skipjack	Other tuna
Outward track:						
4 Oct.	16°15′ -17°30′N	153° -154°15′W	NEC	24	0	0
5	14° -15°15′N	150°30′-151°45′W	NEC	24	0.043	0.043 (YF)
6	12° -13°15′N	148°30′-149°30′W	NEC	23	0	0
7	9°30′ -10°45′N	147° -147°45′W	NEC/NECC	23	0.088	0
8	7°15′ - 8°30′N	144°30′-145°45′W	NECC	23	0.216	0
9	4°45′ - 6°15′N	142°15′-143°30′W	NECC/SEC	24	0.336	0
10	2°15′ - 3°30′N	139°45′-141°W	SEC	24	0.083	0.042 (YF)
11	1°15′N- 0°15′S	137°15′-138°15′W	SEC	24	0.083	0
12	1°30′ - 2°30′S	134°45′-136°W	SEC	24	0	0
13	3°45′ - 5°S	133° -133°45′W	SEC	48	0.042	0
14	5°S	130°15′-131°45′W	SEC	50	0.040	0
15	5°S	127°15′-128°45′W	SEC	48	0.063	0
Inward track:						
30 Oct.	8° - 9°N	127°15′-129°W	NECC	48	0	0
31	9° -10°N	130°45′-132°45′W	NEC	48	0	0
1 Nov.	10°45′ -11°45′N	134°30′-136°30′W	NEC	48	0.021	0
2	12°30′ -13°30′N	138°15′-140°15′W	NEC	48	0.042	0.063 (BE)
3	14°30′ -15°15′N	142° -144°W	NEC	48	0	0
4	16° -17°N	145°45′-147°45′W	NEC	48	0	0
5	17°30′ -18°30′N	149°30′-151°30′W	NEC	48	0	0

Pole-and-Line Fishing

Hida (1970) recorded 109 schools of fish sighted during cruise *Gilbert* 116: 27 skipjack, 1 bigeye tuna, 1 yellowfin tuna, 2 mixed tunas (skipjack-bigeye-yellowfin), 13 of nontuna species, and 65 unidentified. On the outward track and in the southern part of the study area (from lat. 4°27′S, long. 133°22′W, to lat. 6°25′S, long. 117°47′W: 13 to 20 October 1969), at least 13 tuna schools were sighted or discovered by jig strikes. They were chummed, but did not respond to live bait. From 21 to 27 October in the study area (between lat. 4°09′S, long. 117°47′W and lat. 5°04′N, long. 118°50′W), at least 11 schools of tuna were chummed with live bait and of these 6 were successfully fished by pole-and-line (these schools were sighted and pursued, not discovered by jig strikes). Details are given in Table 19. All schools fished successfully by pole-and-line were located in the South Equatorial Current. These results are of special interest because they were obtained by a commercial fishing method. Trolling is not a commercial fishing method for skipjack in U.S. fisheries.

Size of Skipjack and Other Tuna

Table 20 shows the percent of skipjack in three broad size categories by fishing method and area. Only one skipjack (45 cm) was taken on the inward track to Honolulu. In the study area the percentages in size groups are similar for the two fishing methods. The percentage of fish < 45 cm, namely 8 to 11%, is much the same as that in the area in November-December 1970. The smallest skipjack measured 34 cm. The largest skipjack (mean lengths > 75 cm) were taken in the extreme south of the area. Elsewhere mean sizes of skipjack ranged from 46 to 67 cm, with two exceptions: 34 cm (trolling) and 40 cm (pole-and-line). On the outward track to the area, troll-caught skipjack

TABLE 19.—Details of successful live-bait pole-and-line fishing of tuna schools in the study area, Cruise *Gilbert* 116, October 1969. SJ, YF, and BE mean skipjack, yellowfin, and bigeye.

Date	School data[1]	No. birds	Approximate position Lat.	Long.	Time successful fishing commenced	Species	No. taken	Size (cm) Range	Mean	No. measured	Approximate weight (lb) Range	(Mean)
Oct.												
21	—	15 birds	4°S,	118°W	0710[2]	SJ	13	37-52	40	13	—	(3)
						YF	8	37-43	39	8	—	(3)
						BE	7	37-43	41	7	—	(3)
24	—	Flock, 50	2°N,	119°W	1220[3]	SJ	213	64-70	68	50	15-18	(17)
26	Breezer	Flock, 150	4°N,	119°W	1125[4]	SJ	519	41-56	47	60	3-8	(5)
						YF	28	40-58	47	28	4-8	(4)
						BE	13	41-46	43	13	3-4	(4)
	Boiler	Flock, 500	4°N,	119°W	1707[3]	BE	97	50-81	69	33	10-20	(—)
27	Boiler	Flock, 300	4°50′N,	118°25′W	0650[2,3]	SJ	49	47-67	59	49	—	(10)
	Breezer	Flock, 250	5°N,	118°49′W	1031[3]	SJ	110	48-61	52	54	—	(—)

[1] After Scott (1969).
[2] Poor biting school.
[3] School abandoned when sample complete.
[4] Very large school still around ship at 1500 h.

TABLE 20.—Skipjack by size categories as percent of total, and by fishing method and area, Cruise *Gilbert* 116, October 1969.

Size (cm)	Study area Troll	Study area Pole-and-line	Outward track to study area Troll
<45	8.0	11.2	80.0
45-59.9	52.0	57.0	15.0
≥60	40.0	31.8	5.0
Total skipjack	25	223	20

ranged from 29 to 78 cm, mean 41 cm. Although very few were caught, the high percentage of fish < 45 cm is of interest.

In the study area all small fish (< 45 cm) were from areas of the South Equatorial Current. In the area west of long. 125°W, small fish were found in all three current systems (NEC, NECC and SEC), approximately from lat. 15°15′N, long. 151°45′W to lat. 0°25′S, long. 137°15′W.

Skipjack percent length frequency distribution by 2-cm classes is given in Figure 30 for the study area in October 1969. There appear to be three

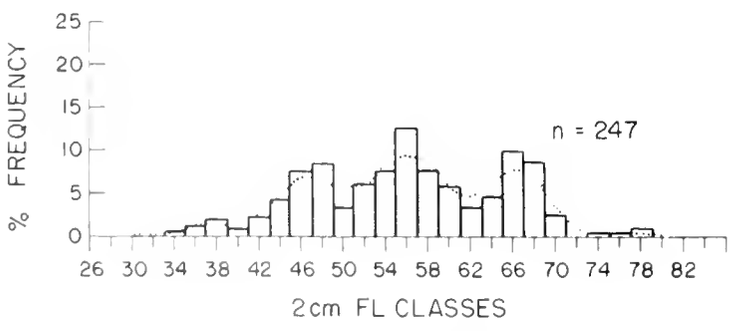


FIGURE 30.—Skipjack percent length frequency distribution (study area only), cruise *Gilbert* 116, October 1969. Smoothed curves are from 3-figure moving average. Stated length indicates midpoint of class.

modes at 46, 56, and 66 cm. Inclusion of data from the outward track would increase the probability of another mode at 36 to 38 cm. The November-December 1970 length data for the study area were similar and showed modes at 36, 48, and 58 cm; only the 66-cm mode was absent (Figure 9). The similarity suggests that the modes of 1969 (October-November) and 1970 (November-December) represent age-classes.

On the outward track yellowfin were small, mean lengths 37 and 32 cm, and on the return track bigeye had a mean length of 57 cm (Table 18). In the study area mean lengths of yellowfin ranged from 39 to 47 cm and those of bigeye from 41 to 69 cm (Table 19).

Sex and Maturity of Skipjack and Other Tuna

The sex ratio of skipjack in the study area was males to females 1:0.89 (n = 249), and on the outward track 1:1 (n = 20).

Tuna gonads taken on cruise *Gilbert* 116 were recorded as immature, maturing, mature, or spent and can be roughly compared with those for the other two cruises. The number of skipjack gonads in each maturity stage by size of fish is given in Tables 21 and 22 for the study area and outward track.

Apart from three females, all immature fish (19% of total in the study area and 80% of total on outward track) were <50 cm. The principal difference between fish caught on this cruise and the other two is the virtual absence of spent fish. Most fish (> 74%) were classed as maturing, and

this could indicate that they were southern spawners. All troll-caught yellowfin tuna were immature, sex indeterminate, as were the bigeye except for one immature male of 59 cm.

DISCUSSION AND CONCLUSIONS

Gulland (1971) reviewed research findings which indicate that skipjack is the most abundant tuna in the Pacific, except possibly for frigate mackerel which is a small and presently valueless species. Our results and those of Hida (1970) show that each of the three cruises yielded many more skipjack than all other species of fish combined, including nontunas and unidentified fish (Tables 2, 15, 18, 19). On each cruise some skipjack were obtained in almost every part of the area in which fishing was done. Occurrences of other tunas (yellowfin, bigeye, and frigate mackerel) were much fewer and more localized (Tables 2, 3, 4, 15, 18, 19).

Our results also support the general hypothesis of Rothschild (1965), Williams (1972), and others that skipjack migrate as juveniles from central Pacific spawning areas towards the American coast, spend part of their adolescent life near the coast, and then return to the central Pacific. The present study area lies between the spawning areas and the coast. Thus one would expect the skipjack in that area to include, at times, individuals both smaller and larger than those typical of coastal waters. We have demonstrated their occurrence (Tables 6, 7, 20; Figures 9, 30).

Matsumoto (1966), Ueyanagi (1969), and Love (1970, 1971a, in prep.: EASTROPAC data) indicate that skipjack larvae are rare east of long. 130°W in the tropical Pacific, but increase rapidly west of that meridian. Thus our study area is close to a spawning region. One would then expect some of the large skipjack in the study area to have maturing, spent, or spent-recovering gonads at times, and this condition was found (Tables 8, 9, 10, 21, 22). The occurrence of spent-recovering and resting gonads in November-December suggest principally northern summer spawning, especially since no spawned-out fish were taken south of lat. 3°N. The presence of spent-recovering fish in March-April perhaps indicates southern summer spawners (northern winter); however, the occurrence of skipjack with maturing gonads at this time may also signify northern summer spawners. Fish taken on the two cruises may be of two spawning groups, northern and southern (see Williams 1972).

The juvenile skipjack (< 45 cm) constituted a small proportion, 13% or less on each cruise, of the total skipjack caught in the study area. Their distribution varied spatially and temporally (Tables 6, 7, 20; text p. 389). On the cruise of October-November 1969 they were found only in the South Equatorial Current, but the North Equatorial Current was not sampled. In November-December 1970 they were found principally in the North Equatorial Current and sparsely in the South Equatorial Current. In March-April 1971 they were very scarce or absent in all parts of the study area. West of long. 125°W in October-November 1969, some juveniles were taken in the North Equatorial Countercurrent as well as in the other two currents. It does not seem possible from these data to make a choice among any of the three models of coastward migration of juveniles proposed by Williams (1972), or to eliminate any of them from consideration. Data from other periods of the year are desirable.

From previous studies by Williams (1970), adult skipjack (> 45 cm) were expected to occur in waters of surface temperature 20° to 29°C, but not preferentially at particular temperatures within that range. All waters of the study area had such temperatures on all cruises (Figures 10, 11, 12, 13, 28, 29). Thus they were all suitable for skipjack as far as temperature was concerned, and skipjack occurred to some extent in most of them (Figures

TABLE 21.—Number of skipjack gonads in each maturity stage by size of fish, study area, Cruise *Gilbert* 116, October-November 1969.

Size class (cm)	Immature		Maturing		Mature	
	M	F	M	F	M	F
30-39.9	2	6	1			
40-49.9	16	21	21	4		
50-59.9		3	48	38	3	6
60-69.9			38	34	1	2
70-79.9				1	2	2

Totals: males (M) 132, females (F) 117.

TABLE 22.—Number of skipjack gonads in each maturity stage by size of fish, outward track, Cruise *Gilbert* 116, October 1969.

Size class (cm)	Immature		Maturing		Mature		Spent	
	M	F	M	F	M	F	M	F
20-29.9	2							
30-39.9	3	4						
40-49.9	4	3						
50-59.9			1			1		1
60-69.9								
70-79.9						1		

Totals: males (M) 10; females (F) 10.

5, 6, 7, 8; Tables 15, 16, 19). No relation appears between skipjack distribution and particular temperatures within the 20° to 29°C range.

Blackburn and Laurs (1972) expected adult skipjack to be distributed like their forage in offshore areas where all surface temperatures are suitable. This was because Blackburn (1969) found such a relation for skipjack in waters of suitable temperature near the coast, and Magnuson (1969) found that skipjack eat the equivalent of 15% of their body weight per day when fed to saturation. Thus adult skipjack would probably be most numerous in the latitudinally oriented zones of abundant forage which occur offshore, with forage concentrations comparable to those in coastal waters, during their westward movement from the coast to the spawning areas (Blackburn and Laurs 1972). They would probably migrate slowly through forage-rich zones or areas and quickly through those poor in forage, and thus be more abundant per unit area in the forage-rich situations.

Blackburn and Laurs (1972) showed from EASTROPAC data that the richest and most persistent zones of skipjack forage in our study area occurred a few degrees north and sometimes south of the equatorial upwelling. They also recognized a less conspicuous zonal forage maximum near the northern boundary of the North Equatorial Countercurrent, probably associated with high biological production over the shoal pycnocline. Data from the November-December cruise show the expected maxima of forage and skipjack near the Equator, but do not clearly show a maximum of either on the north side of the Countercurrent (Figures 23, 24; Table 3). Tables 12 and 13 show two statistically significant positive correlations between availability of large skipjack and their forage on the same cruise, although only for night concentrations of forage and for data averaged over a 2° zone of latitude. As mentioned earlier the actual significance may be disputable for the lower of these correlation coefficients, but not for the higher one, taking the total number of correlations in Tables 11 and 12 into account. Correlations between skipjack and day forage were not significant (Table 11).

Skipjack probably do much of their feeding in the daytime (Nakamura 1962) although forage is much scarcer in the upper water layers by day than by night. Thus the lack of relation between skipjack and day forage may seem surprising. One could however interpret these results as follows. Spatial distributions of day and night forage broadly coincide (Blackburn and Laurs 1972) because they are determined by the same physicochemical and basic biological features of the environment. Skipjack tend to occur in broad zones where both kinds of forage are initially abundant, for reasons suggested above. Within these zones they aggregate in the richer patches of day forage and eat them down, whereby their relation with the day forage will be sometimes direct and sometimes inverse. If they eat the much more abundant night forage they probably do not so frequently reduce it to a point at which the relation becomes inverse.

The significant November-December correlations become nonsignificant when data for skipjack < 45 cm are included (Table 12). Thus juvenile skipjack may be distributed in relation to a different kind of forage, or possibly to other environmental properties excluding forage. Blackburn and Laurs (1972) made no statement about ecology of juveniles.

The relatively sparse data for the March-April cruise of 1971 show a forage maximum near the Equator but not clearly elsewhere (Figures 25 and 26), although one may nevertheless have been present near the northern edge of the Countercurrent, as mentioned previously. The principal maximum of skipjack in March-April 1971 was located slightly north of the North Equatorial Countercurrent, and there was a secondary maximum near the Equator (Table 4). Data on skipjack and forage yielded no significant correlations. They were probably too sparse to do so (Table 12).

Tables 3 and 4 show that skipjack were less abundant in the North Equatorial Countercurrent than in either of the adjacent currents, on both the 1970 and 1971 cruises. This was expected because neither Blackburn and Laurs (1972) nor we found much forage in the Countercurrent. However skipjack availability was much higher in the Countercurrent (lat. 6° to 8°N) than in the South Equatorial Current on the 1969 cruise (Tables 15, 16). Forage data are lacking for the cruise, but it is not likely that forage was highly abundant in the North Equatorial Countercurrent. We note that the large skipjack taken in October-November 1969 had sexually maturing or mature gonads (Table 21), whereas most of those taken on the other cruises had spent, spent-recovering, or resting gonads (Tables 8, 9). Possibly the October-November fish were close to spawning, and thus

becoming distributed in accordance with the requirements of their larvae. There is evidence that skipjack larvae occur only at sea temperatures from 23° to 31°C and are most common at about 29° to 30°C (Inter-American Tropical Tuna Commission 1971). Maximum surface temperatures in the study area in October-November 1969 were between 27° and 28°C and occurred from about lat. 4° to 11°N (Figure 29). Thus the Countercurrent waters at lat. 6° to 8°N could have been particularly suitable for the survival of skipjack larvae, and the parent fish may have been becoming distributed accordingly.

We found no direct relations between skipjack and mixed layer depth, dissolved oxygen, surface currents, chlorophyll, or zooplankton although some of these properties and features should have indirect effects on skipjack through their effects on temperature and forage. Some of them could also have direct effects upon larval or juvenile skipjack. Significant correlations between skipjack and zooplankton were not found (Tables 11, 12). Significant correlations between large skipjack and forage are also significant between skipjack and the arithmetic product of forage and zooplankton, but not between skipjack and zooplankton alone.

Although this paper has contributed to our knowledge of the distribution and relative abundance of skipjack in the offshore eastern tropical Pacific, where little information was previously available, the prospects for commercial fishing remain unknown. Our simple experimental fishing procedures served to identify zones of maximum occurrence of skipjack, but commercial trials will be needed to show if those zones can be exploited profitably. Ideally there should be trials by live-bait boats as well as purse seiners, in view of the fact that live-bait fishing gave good results on an experimental scale during the 1969 cruise. Our data and interpretations should be useful as a guide to those who make these tests.

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REPRODUCTION AND RECRUITMENT OF THE BRACKISH WATER CLAM *RANGIA CUNEATA* IN THE JAMES RIVER, VIRGINIA[1,2]

THOMAS D. CAIN[3]

ABSTRACT

Reproduction and recruitment of the brackish water clam *Rangia cuneata* were investigated in the James River, Va., from February 1970 to January 1972. Histological examinations of gonads were made, newly set clams were collected, and temperature and salinity measurements were taken from three populations living in different salinity regimes.

Gametogenesis began in April and ripe gonads were found from May to late November with no inactive period. From observations of set abundance, two periods of spawning were determined: one in early through midsummer, coinciding with the beginning of spawning as determined from gonadal examinations; and a second and longer period in late fall and early winter, with an increased percentage of partially spawned and spent clams. Gametogenesis ceased in December through March as residual gametes were cytolyzed. Sex was not detected during this last phase. More females than males were found in the upstream (lower salinity) populations. Temperature was important in initiating gametogenesis in the spring and midsummer. Spawning correlated best with changes in salinity to approximately 5 $^{o}/_{oo}$.

Over its estuarine range, salinity has a controlling effect on *Rangia* spawning and recruitment. Seasonal reduction in input of freshwater (increased seawater intrusion) is needed to induce spawning and recruitment in upstream populations. Best recruitment occurred to the middle of the habitat range which has an annual salinity change from fresh to $5^{o}/_{oo}$.

A southern species of clam, *Rangia cuneata* (Gray) has in the last 15 yr extended its range into Chesapeake Bay estuaries (Hopkins and Andrews 1970). This clam occupies an otherwise "open niche" in the oligohaline region of these estuaries. Although species diversity is usually low, there may be large numbers of individuals of species adapted to this environment. In the upper James River estuary, *Rangia* accounts for nearly 95% of the benthic biomass.

Rangia is important both ecologically and commercially (Hopkins 1970). It provides a substantial food source for several species of fish and crabs (Darnell 1958), and waterfowl (Wass and Wright 1969). It is ecologically significant because it converts detritus into biomass that can be utilized by these organisms (Odum and Copeland 1969).

Not only is *R. cuneata* a species for which low salinity, 1-15$^{o}/_{oo}$, is optimal; it is also a species which evidently cannot maintain a population outside this range (Hopkins 1970). That *Rangia* thrives in a zone unfavorable for most animals indicates it has some unusual adaptations. Despite its abundance in favorable environments and long history on the Gulf Coast, this clam has received little attention.

The study reported here concerns the reproductive cycle and recruitment of *Rangia cuneata* in the James River. The major objectives were to: (a) study the gametogenic cycle of *Rangia* from histological sections; (b) determine differences in gametogenesis or spawning of clams over the species range in the estuary; (c) investigate, from analysis of field data, the influence of temperature and salinity on initiation of gametogenesis and spawning; (d) corroborate gametogenic findings by collecting newly set clams; and (e) determine the duration of the larval period and differences in set abundance in the estuary.

Fairbanks (1963) studied the spawning cycle of *Rangia* in Lake Pontchartrain, La., but it is known that physiologically different races of bivalves can occur at different latitudes (Loosanoff 1969). Cain

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(1973, 1974) reported on the laboratory spawning of *Rangia* and the combined effects of salinity and temperature on embryos and larvae.

The impending action (at the time the work was initiated) of discharge of waste heat into the *Rangia* community by the Virginia Electric and Power Company's (VEPCO) Nuclear Generating Station at Surry, Va., was a further impetus to the study of the reproductive cycle, especially those factors that initiate gametogenesis and spawning.

DESCRIPTIONS OF THE STUDY AREA

The study area in the James River is a transition region between freshwater and salt water. The area has a seasonably variable salinity that ranges between about 0 and 15‰, depending on the volume of freshwater input. In the spring, high river flow covers most of this region (except station A) with freshwater (Figure 1). Occasionally, in late summer and fall the study area may exhibit measurable salinity as far upstream as station C. The mean annual discharge of the James River is approximately 212 m^3/s (7,500 cfs).

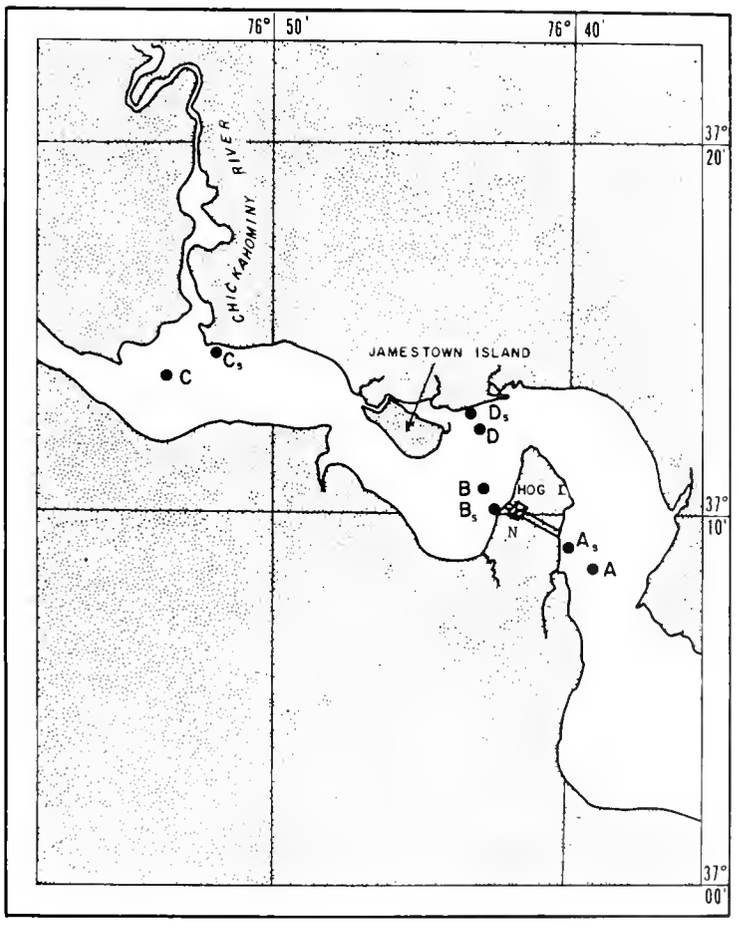

FIGURE 1.—Location of sampling stations for *Rangia cuneata* in the James River, Va. (N = nuclear generating station).

Field and hydraulic model studies of the James River estuary have shown a two-layer density flow pattern, in which the deep, more saline water has a net upstream flow and the surface, fresher water has a net downstream flow. The net sediment transport of the two-layer section averaged over many tidal cycles is upstream (Pritchard 1952). The transition section of the James River is characterized by high natural turbidity and sedimentation from the flocculation of river-borne sediments.

The distribution of bottom sediment types in the James River estuary has been studied by Nichols (1972). His survey indicates silt-clay substrates at stations A, B, C, and D and sand substrates at locations As, Bs, Cs, and Ds.

The distribution of *Rangia* in the James River was found to be approximately from nautical mile 25 to 55 above the river mouth (Figure 2). The downriver extent of its range overlaps the habitat of typical estuarine organisms such as the oyster; at the upriver limit *Rangia* is associated with completely freshwater forms such as freshwater mussels. In the oligohaline portion of its range it is typically associated with the polychaetes *Scolecolepides viridis* and *Laeonereis culveri;* the crustaceans *Cyathura polita*, *Corophium lacustre*, and *Gammarus* sp.; and the bivalves *Macoma balthica*, *Brachidontes recurvus*, and *Congeria leucophaeta*.

METHODS AND MATERIALS

The reproductive cycle was investigated by collecting clams at stations A, B, and C (Figure 1). Station A was near the downstream range of the clam. Station B was 18.5 km above station A. Station C was located (18.5 km above station B) near the mouth of the Chickahominy River in order to include part of the clam's range which seldom experiences salinity changes. All stations were located at approximately the same depth (3-4 m). The clams used in this study were collected from a predominantly silt-clay substrate. Although Tenore et al. (1968) indicated that such sediments were detrimental to *Rangia*, the clams at the various stations appeared to be thriving over the 2-yr study.

Beginning in February 1970 approximately 20 clams, 30-40 mm long, were collected at stations A and B using a modified oyster dredge. Attempts were made to collect clams at these stations every

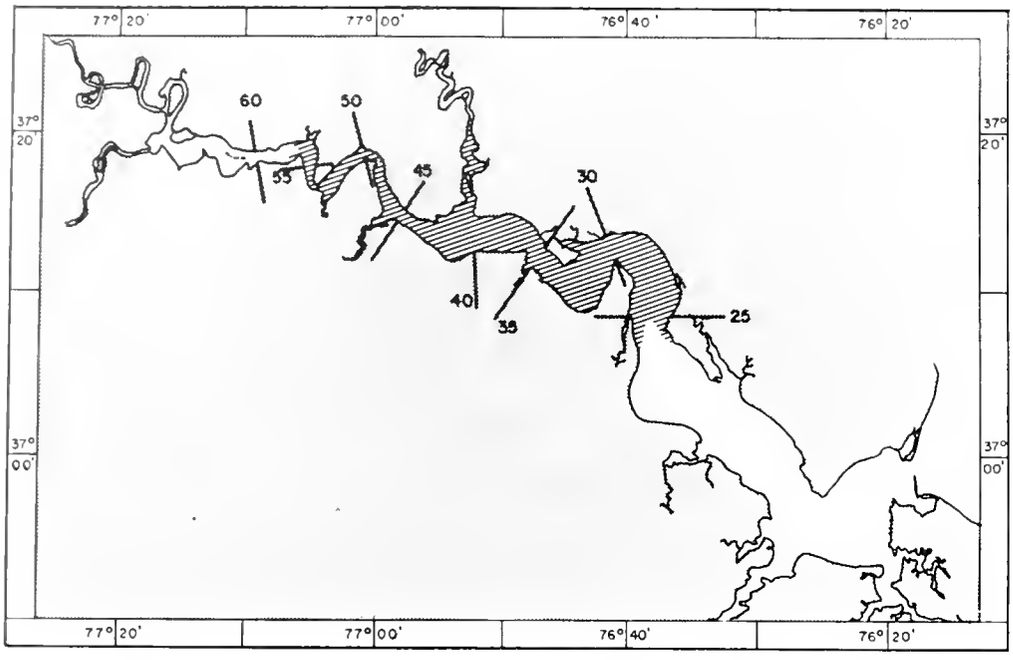

FIGURE 2.—The distribution of *Rangia cuneata* in the James River, Va. Segments are at 5-nautical mile intervals.

2 wk, but bad weather and boat failures occasionally delayed this to 3 wk. Beginning 22 September 1970 collections at station C commenced. Collections at all stations were terminated in January 1972.

In the laboratory these clams were measured, weighed, shucked, and the gonads dissected out and placed in a solution of alcohol, Formalin,[1] and acetic acid (AFA) for fixation. Gonad tissues were sectioned at 7-10 μm with a rotary microtome, stained with Delafield's hematoxylin, and counterstained with eosin. Gonad tissue stage of development was determined following the scheme of Ropes (1968) who categorized the seasonal gametogenic cycle of *Spisula solidissima* as: early active, late active, mature, partially spawned, or spent. Similar stages of development were first described by Ropes and Stickney (1965) for *Mya arenaria* and have subsequently been used for two other members of the family Mactridae; *Mulinia lateralis* (Calabrese 1970), and *Tresus capax* (Machell and De Martini 1971). The number of clams in each category, regardless of their sex, was recorded for each sample.

The sex ratio of clams from each station was calculated and a chi-square test used to establish goodness of fit to a 1:1 ratio.

During June 1970, clams collected at stations A and B were placed in four groups (5-10, 11-20, 21-30, and 41-50 mm). These clams were sectioned and stained to determine the size at which they contain reproductive products.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Set Collectors

Collectors used to determine the time and intensity of setting were placed at stations A, B, C, and D and inshore from these areas in shallow, sandy areas (Figure 1). These stations were designated as As, Bs, Cs, and Ds. Stations A, As, B, Bs, and Ds were examined from June 1970 and C, Cs, and D from September 1970, at approximately 2-wk intervals until January 1972.

The set collector was a plastic gallon jar with an 8.7 cm diameter mouth. The mouth was covered with a plastic 5 mm mesh to prevent the entry of predators. The jar rested on the bottom, fastened to a concrete block.

Water flowed across the mouth of the jar and suspended sediments, detritus, and metamorphosing clams settled to the bottom. In the field, the contents of the jar were washed through a 0.174 mm mesh screen. In the laboratory each sample was elutriated to remove most of the detritus (Coffin and Welch 1964). The material remaining after elutriation was examined for clams under a dissecting microscope. All bivalves were counted and some were measured. Set of bivalve species other than *Rangia* was also identified and counted.

Environmental Data

Water samples for salinity, dissolved oxygen, and temperature measurements were taken whenever biological collections were made. A Kemmerer bottle was used to obtain bottom water samples at the deep stations. Samples at shallow

stations were collected about 0.3 m below the surface. Temperature measurements were taken immediately with a stem thermometer. Bottom temperatures recorded at VEPCO instrument towers 1 and 6 (near stations A and B, respectively) were also used in this study. Salinity samples were analyzed in the laboratory with a Beckman RS7B induction salinometer. Dissolved oxygen samples were fixed immediately after collection and analyzed in the laboratory by a modified Winkler method.

Freshwater input was compiled from records taken at gauging stations on the James River near Richmond, the Appomattox River near Matoaca, and the Chickahominy River near Providence Forge. Combined, these three rivers are the major sources of freshwater for the James River in the study region.

RESULTS

Histological Study of the Reproductive Cycle

A histological basis for classifying the gonadal condition was used because the external appearance of gonads did not accurately reflect phase of development. The appearance of gonads of both sexes is superficially the same during each phase.

No evidence of gonadal parasitism was found in any of the tissue sections, nor were hermaphroditic individuals found.

There was little difference in the time of initiation of gametogenesis and ripening between the sexes so the number of males and females in each stage was combined for analyses. Figures 3 to 6 show the phases in the development of the female and male gonads.

Station A

The reproductive cycle of clams at station A (Figure 7) was more complex than at the other stations. From early February to late March 1970 most clams were in the spent phase, although a few male clams contained ripe sperm with sperm balls. In early April 1970, 40% of the sample were in the early active phase. By May, 40% were ripe, with 10% partially spawned. From May through September clams were found in all gonadal phases. Evidently some spawning and rematuration occurred during the summer months. In early October 1970, all clams examined were ripe. The volume of eggs and sperm at the second ripening was much greater than that in the early spring and summer. Partially spawned clams were numerous at the end of October and by mid-November 85% of the sample were partially spawned or spent. Throughout the rest of the winter most clams were in the spent stage, although some males retained sperm and slight gonadal activity was noted in some females.

The reproductive cycle for 1971 was basically the same as the previous year. In early June 1971, 65% of the clams were ripe. Spawning was indicated during the next 2-wk period because 60% were spent or partially spent. The fall spawning season was very similar to that of 1970, with 95% ripe by late September. Spawning was completed by early November and, again, some ripe males were observed during the winter.

Station B

Clams in the spent or inactive phase were found from February to early April 1970 (Figure 8). Some males still contained sperm in various stages of cytolysis. By late April 1970, half of those collected had begun gametogenesis, resulting in 80% being ripe by early June 1970. Clams remained in the ripe phase throughout the summer with some spawning occurring during July. During August there was a second development, resulting in all clams observed being ripe in early September 1970. Spawning commenced in early October and was completed by mid-November 1970. Immediately after spawning some clams were in the early active phase, but development did not proceed further during the winter.

The reproductive cycle for 1971 was similar to that of 1970. Gametogenesis commenced in early May. Fewer ripe clams were observed during the summer months than in 1970. The second cycle began in early July and by early September all clams were ripe. Spawning began in late October and was completed by late November. As found at station A, the second seasonal cycle for station B was more intensive; more ripe clams were found and their gonads contained far more sperm and eggs. Spawning was more intensive during the fall, with gonads progressing from ripe to spent in a month.

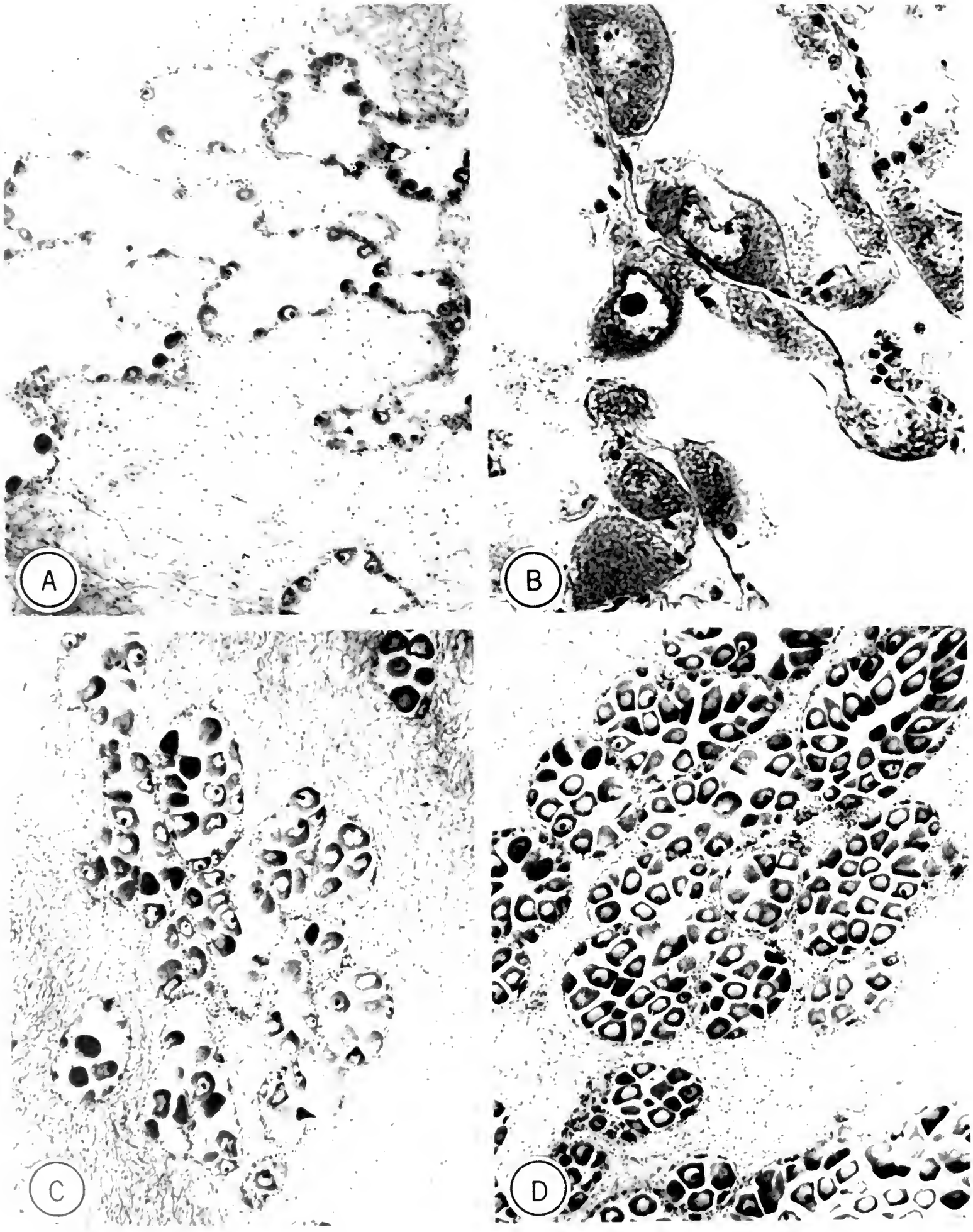

FIGURE 3.—A, section of *Rangia* ovary in the early active phase of oogenesis (× 120); B, ovary in early active phase (× 500); C, ovary in late active phase (× 120); D, ripe ovary (× 120).

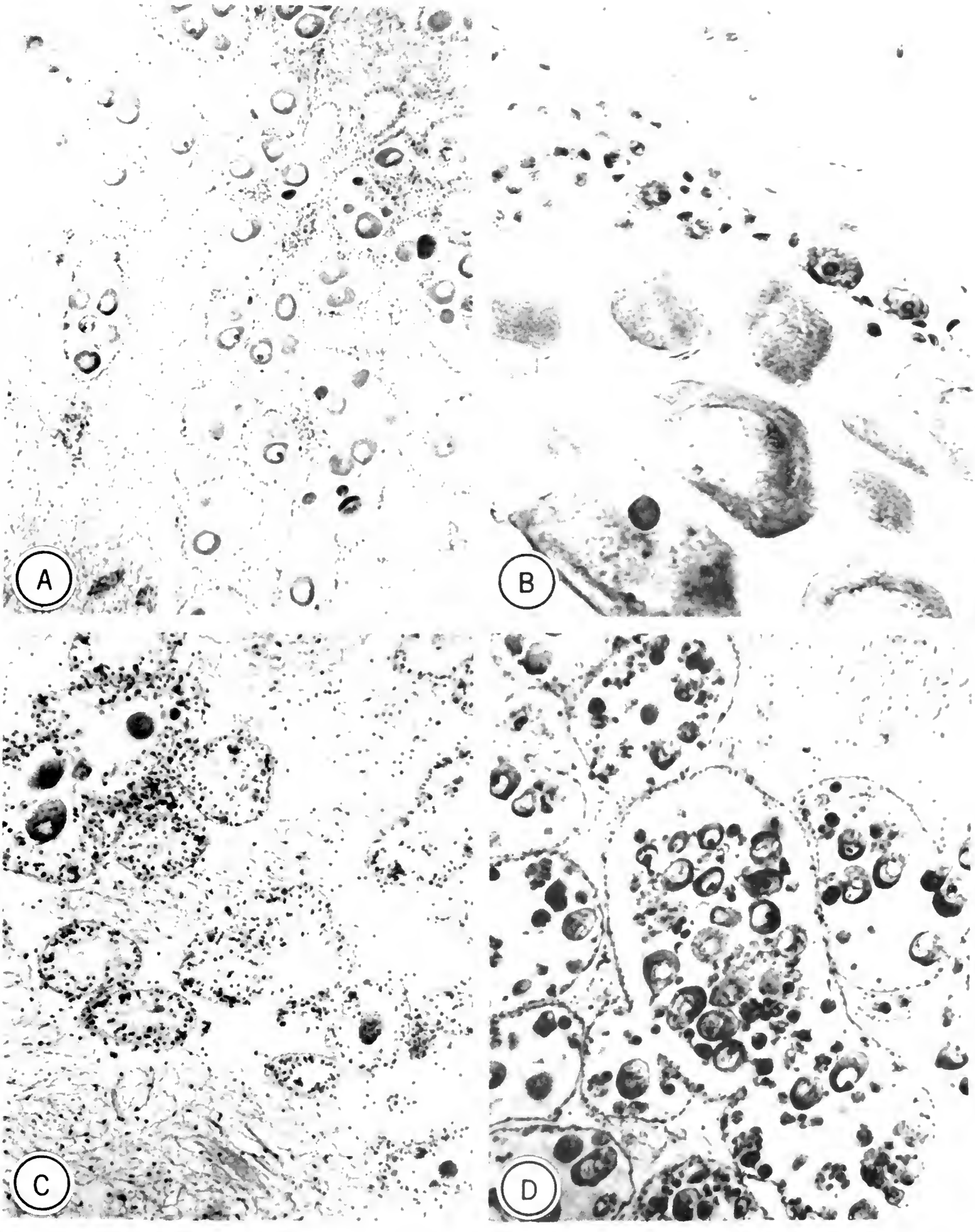

FIGURE 4.—A, *Rangia* ovary in the partially spawned phase (×120); B, partially spawned ovary (×500); C, spent ovary with few ova retained (×120); D, cytolysis of unspawned eggs (×120).

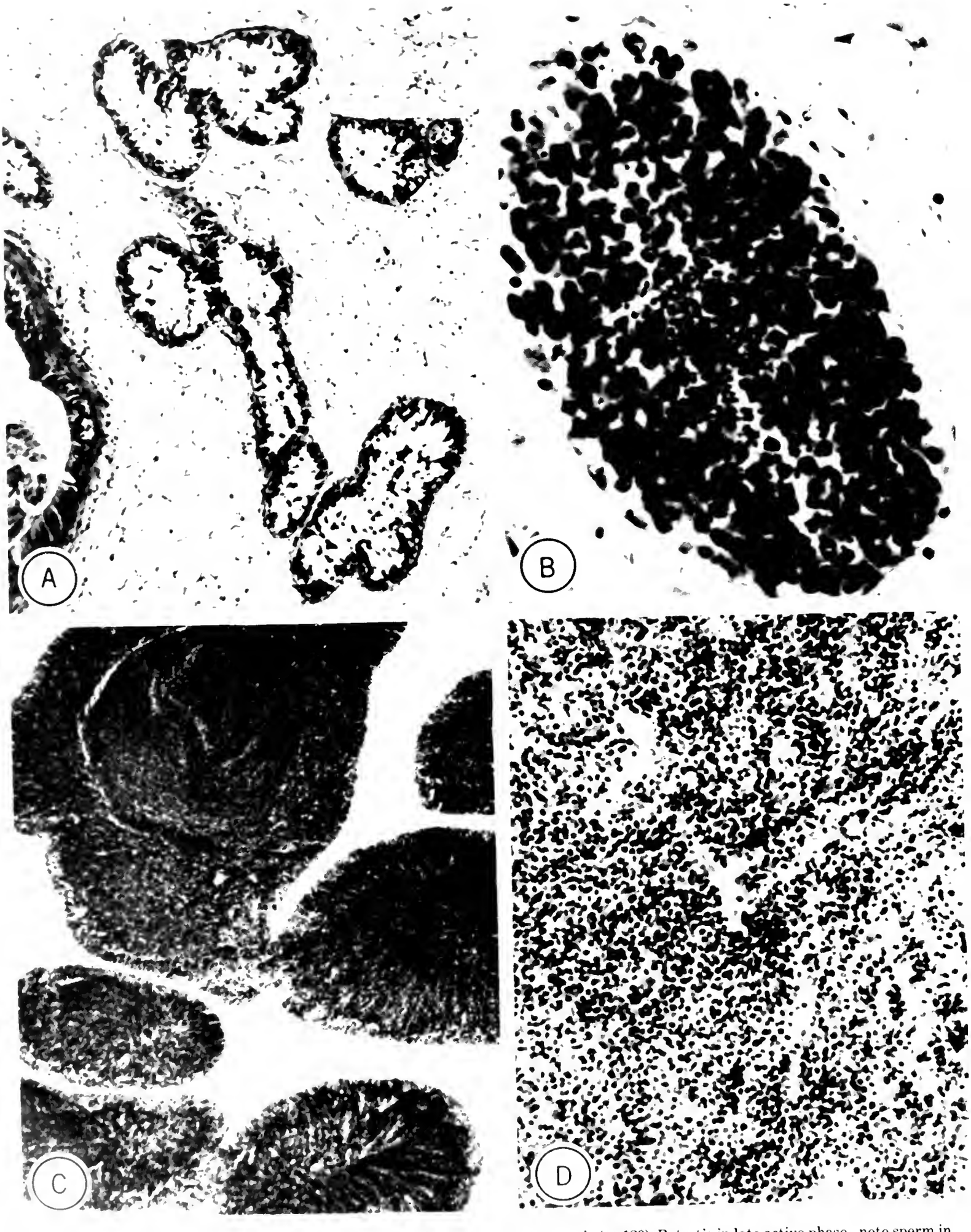

FIGURE 5.—A, Section of testis of *Rangia* in early active phase of spermatogenesis (× 120); B, testis in late active phase–note sperm in center (× 500); C, ripe male (× 120); D, ripe male (× 500).

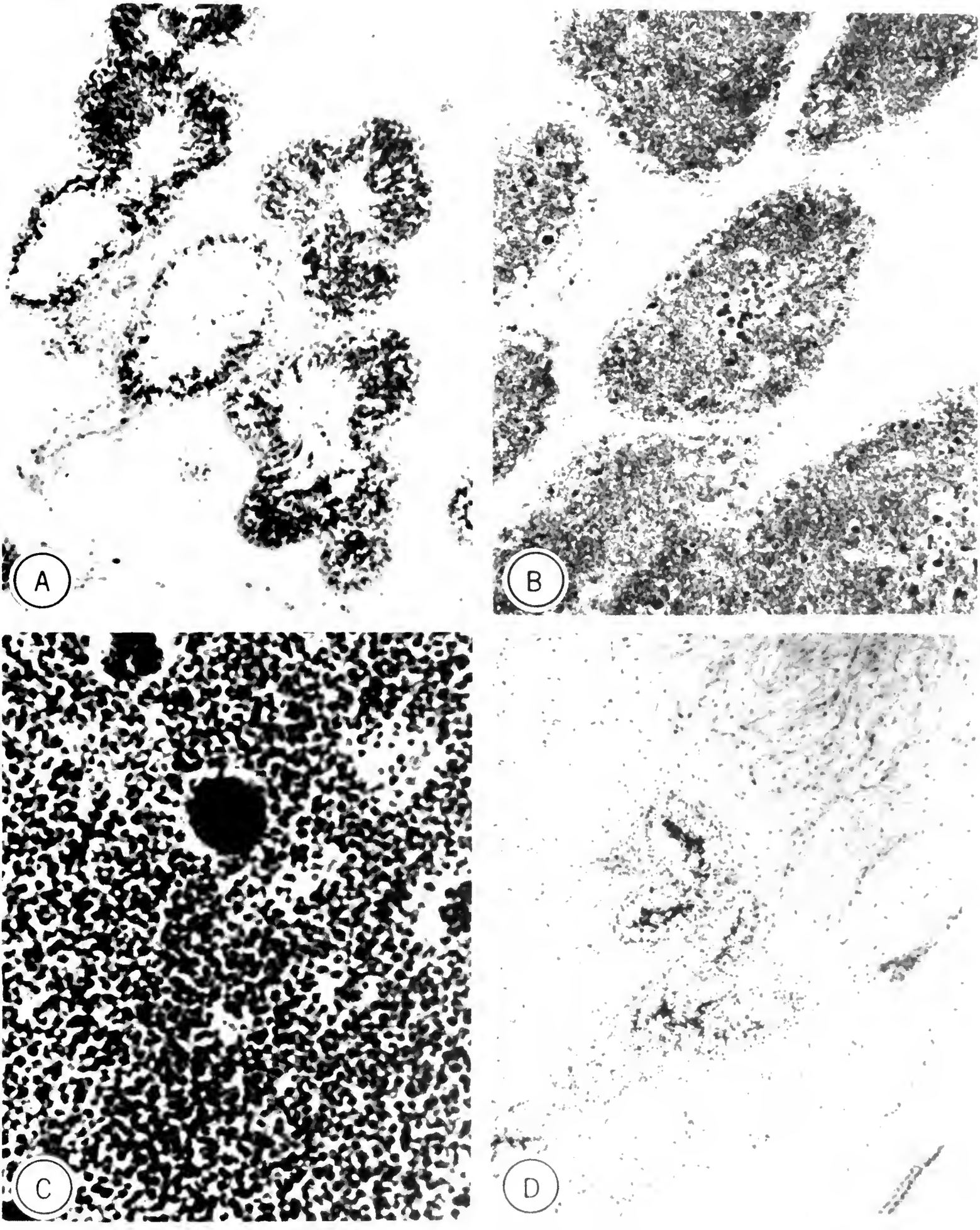

FIGURE 6.—A, Section of testis of *Rangia* in partially spawned phase (×120); B, testis with retained sperm and sperm balls (×120); C, testis with sperm balls (×500); D, spent testis with few sperm retained (×120).

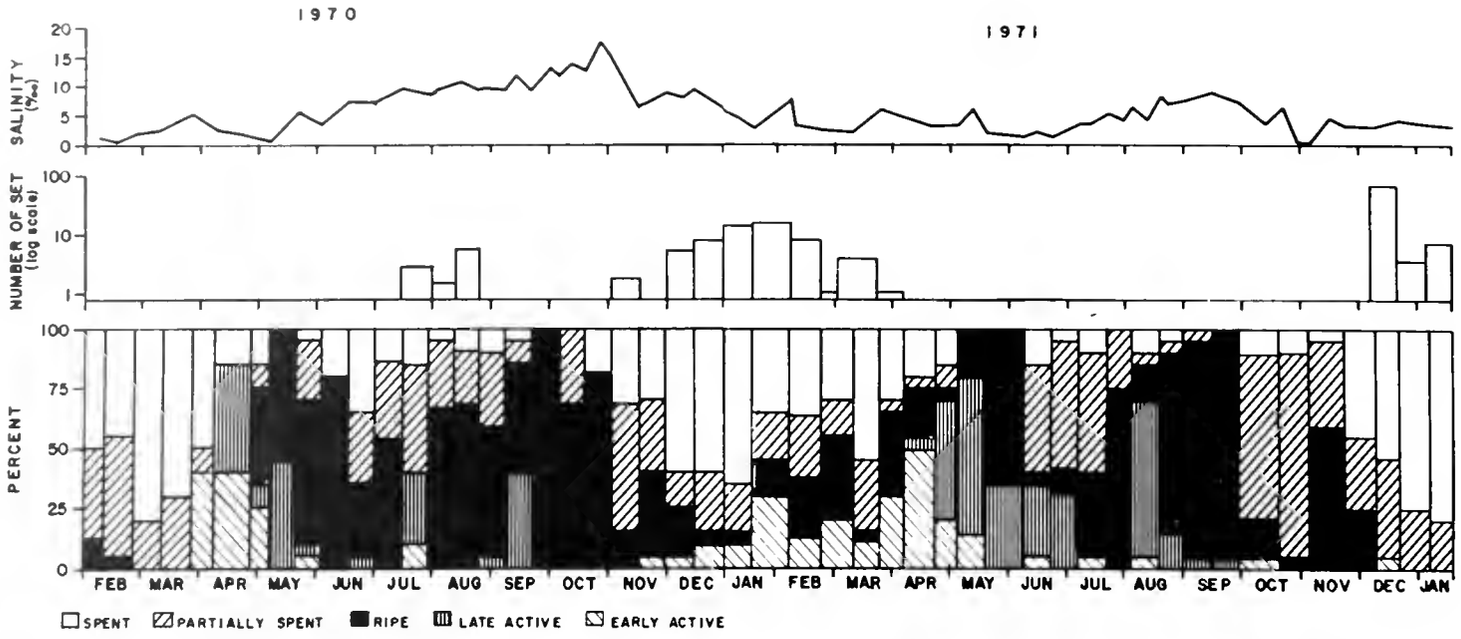

FIGURE 7.—Gonadal phases and setting of *Rangia* at station A in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

Station C

The reproductive cycle at station C was similar to that at station B during 1970. However, earlier spawning was indicated by 88% of the clams being either partially spawned or spent in early October (Figure 9). Clams remained in the spent phase until early May 1971, when gametogenesis began. Few ripe clams were found at this upstream station during the late spring and summer. Clams in the early active phase were found during July and by the end of August all clams were ripe. From September to November 1971 clams were predominantly ripe, but there was no spawning. Cytolysis of the eggs began in November, resulting in a spawned-out appearance (Figure 4D). No spawning occurred at station C during 1971, in marked contrast to stations A and B where the fall spawning was intense.

Sex Ratio

The data were divided into summer-fall and winter-spring seasons, because many clams contained no discernible gonads during the winter

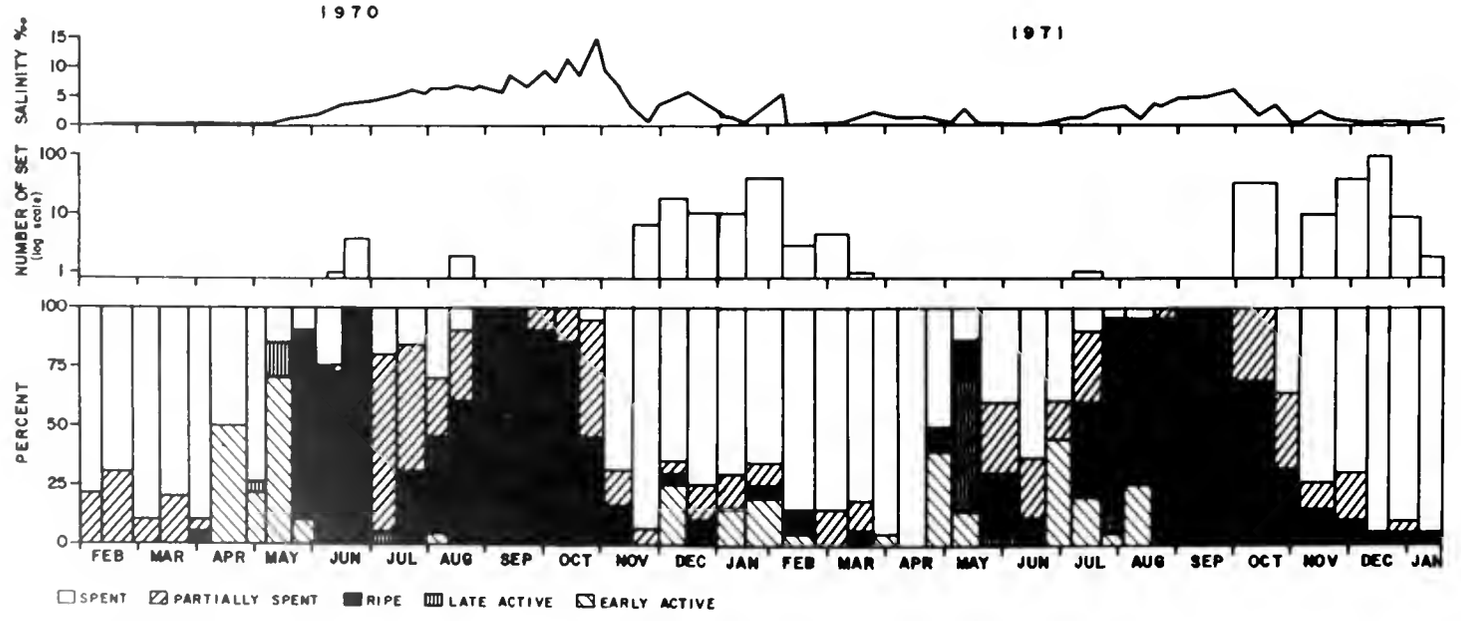

FIGURE 8.—Gonadal phases and setting of *Rangia* at station B in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

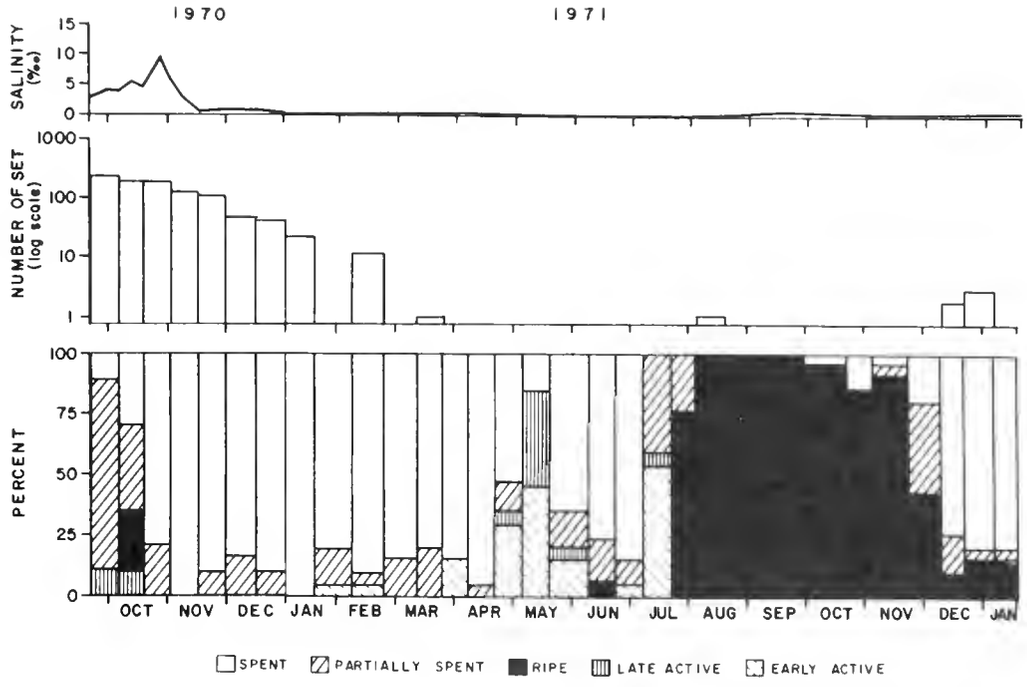

FIGURE 9.—Gonadal phases and setting of *Rangia* at station C in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

and early spring. During summer and fall the gonads of most clams could be recognized (Table 1). The ratio of females to males at station A was not significantly different from 1:1. Females predominated at stations B, D, and C during the summer and fall months of 1970 and 1971. When the clams of non-determinable sex are added to the male group, there are still significantly more females.

Of the clams collected in late June 1970 at station A, none measuring 5-10 mm contained gonads. In the second group 50% showed signs of gametogenesis and had recognizable sex products; 70% of the third group had discernible gonads; and most clams in the fourth group contained gonads. Most small clams were males, but too few were examined to test the significance of sex ratios.

Larval Setting

The number of *Rangia* clams setting at each station is shown in Figures 7 to 14. This number does not provide an estimate of survival because predators were excluded by the screen cover. The number of set clams at both deep and shallow stations by season is shown in Table 2. At stations A and As a small number (< 7) set during late July and August 1970. In December 1970 through March 1971 set clams were common but not very abundant at these two downriver stations. Only one setting period (29 individuals) was recorded during the summer months at station As. Larvae began setting again during the third week of December 1971 with 70 at station A. Collectors at both stations continued receiving set until sampling was terminated on 18 January 1972.

TABLE 1.—The ratio of females to males and the number of clams with non-determinable (ND) gonads at each station. Summer and fall seasons were tested with the ND clams added to the male group.

	Station A				Station B				Station D				Station C			
Seasons	F	ND	M		F	ND	M		F	ND	M		F	ND	M	
Summer and fall 1970	140	0	153	ns	209	3	57	**					166	9	70	**
Winter and spring	61	53	83		46	128	35		13	44	13		29	118	66	
Summer and fall 1971	127	7	102	ns	178	22	34	**	41	5	11	**	138	38	54	**

ns = not significant.
** = highly significant.

Setting at stations B and Bs was sporadic during the spring and summer of 1970, with no more than four clams in any jar. Setting began at station B in mid-November 1970 and continued there until late March 1971. A maximum of 42 individuals was collected on 8 February 1971. Set clams were found on only one sampling date during the next summer. Setting in the fall began in late October 1971, with very large numbers during late November and early December.

Setting at station D was similar to that at station B except more individuals were found during the fall and winter of 1970-71. One hundred eighty-five were collected in the station D bottle in mid-December 1971.

Only data beginning in September 1970 were available from station C. As noted in the tissue sections, spawning had commenced earlier. Setting from early September 1970 to March 1971 was very heavy, with 257 clams collected at this station

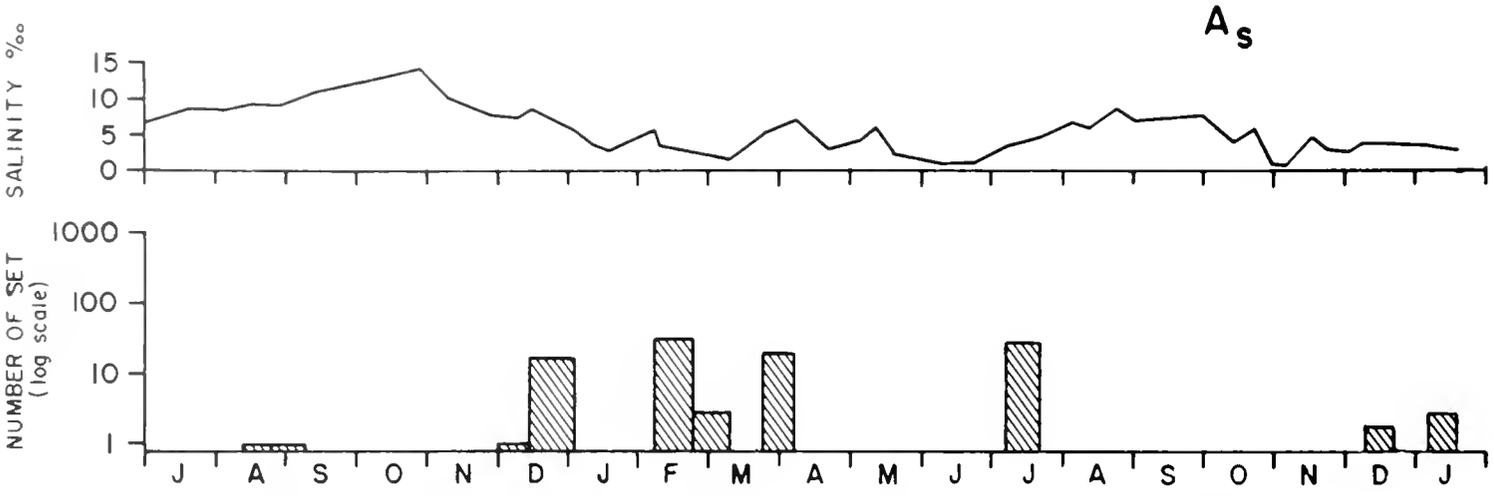

FIGURE 10.—Number of *Rangia* set and salinity at station A_S from July 1970 to January 1972.

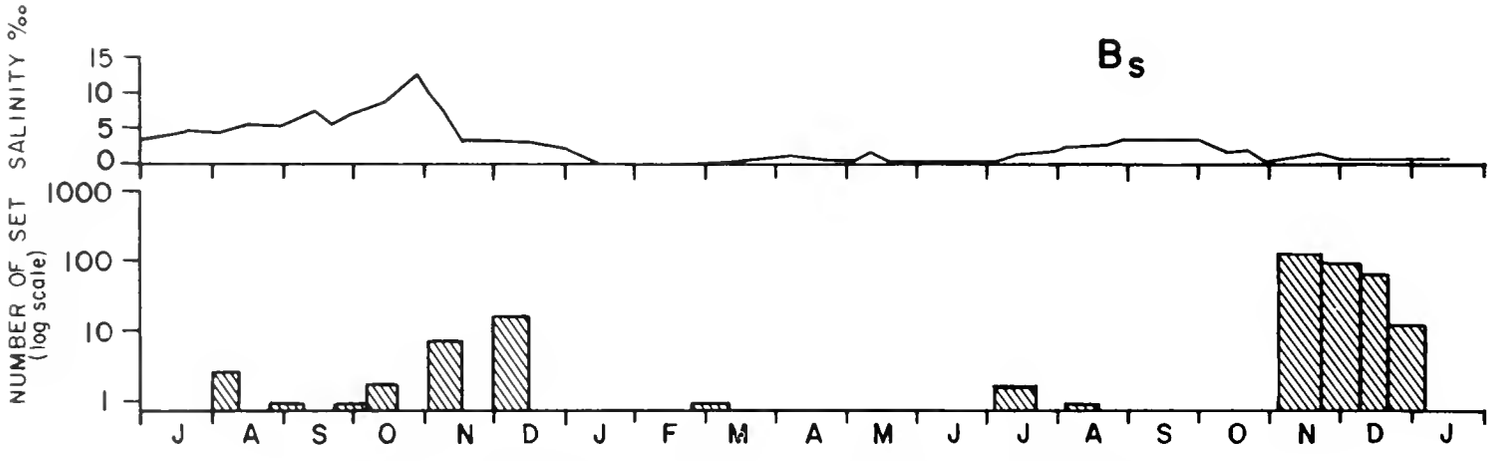

FIGURE 11.—Number of *Rangia* set and salinity at station B_S from July 1970 to January 1972.

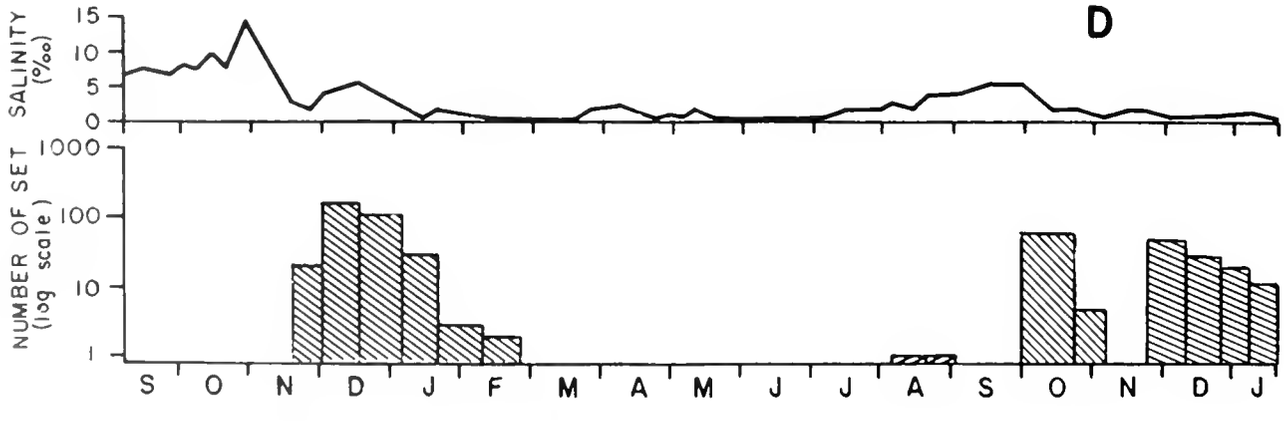

FIGURE 12.—Number of *Rangia* set at station D in relation to salinity for September 1970 to January 1972.

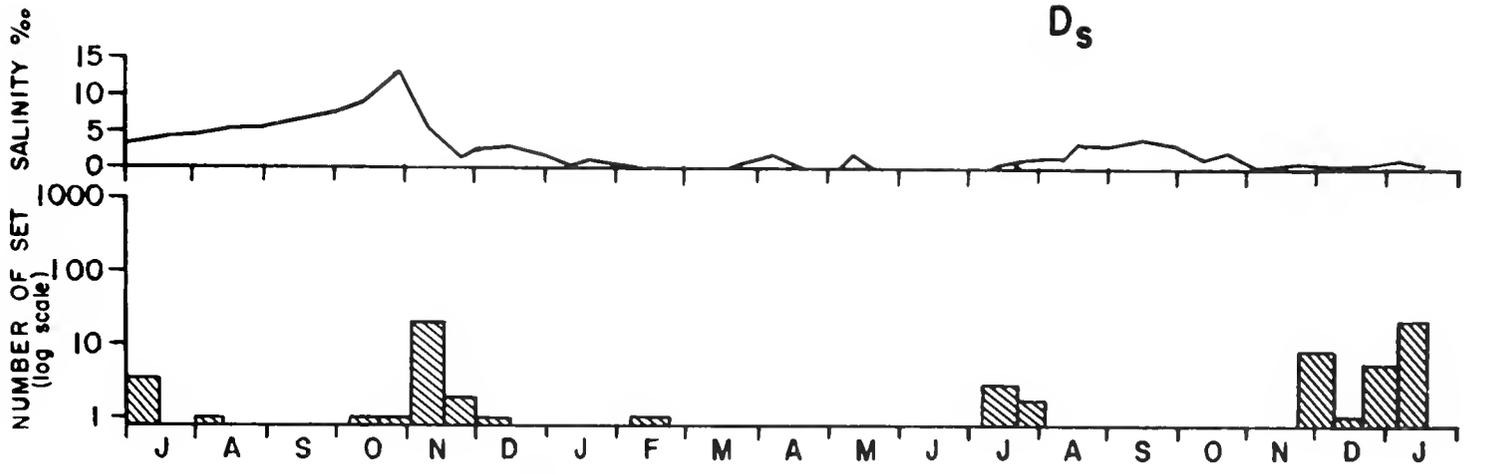

FIGURE 13.–Number of *Rangia* set and salinity at station D_S from July 1970 to January 1972.

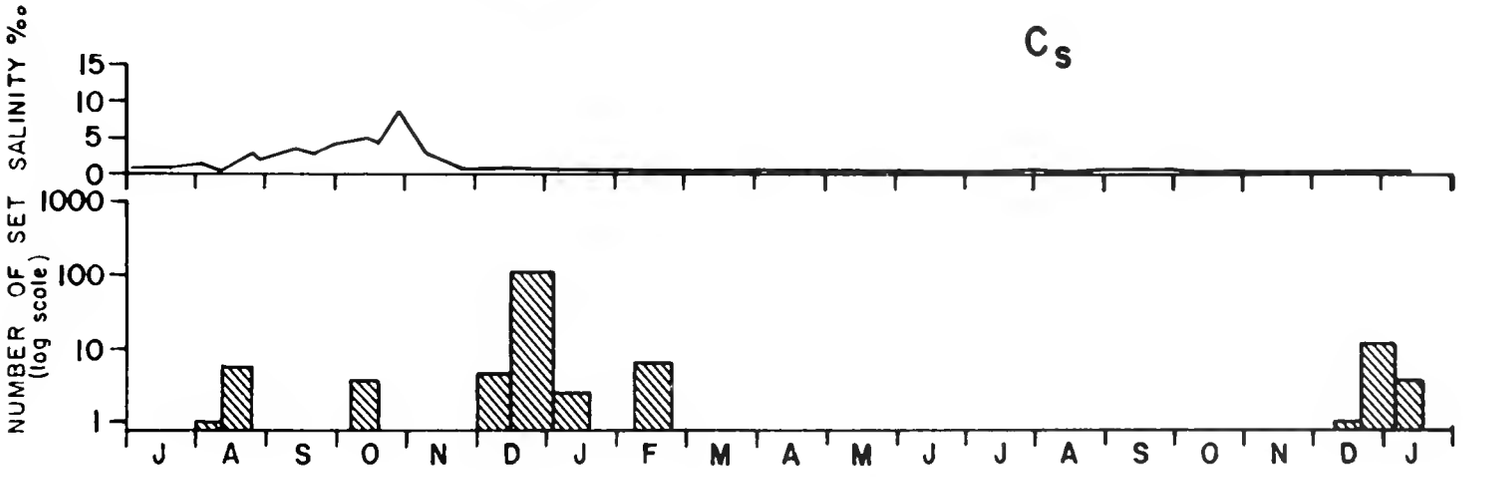

FIGURE 14.–Number of *Rangia* set and salinity at station C_S from July 1970 to January 1972.

TABLE 2.–Average number of *Rangia* set (per collector) at both deep and shallow stations by season.

Season	Station			
	A	B	D	C
Summer (1970)	0.7	0.7	0.7	–
Fall-winter	3.6	6.1	25.5	74.3
Summer (1971)	1.6	0.2	0.4	0.1
Fall-winter	6.2	44.9	15.4	2.5

by early October 1970. This was the highest number collected at any time or place during the study. No set was collected at stations C or Cs from late March to late December 1971. The fall setting was very small with only 5 collected at station C and 18 at station Cs during December 1971 and January 1972.

Rangia set ranged in length from 230 to 500 μm, but averaged about 300 μm. Larger individuals were generally collected at the shallow stations but may have been members of an earlier set washed in by wave action.

The setting patterns of the other bivalves are presented in Figure 15. Station A received more set of all three species than the other stations because of its proximity to their adult populations. *Brachidontes recurvus* and *Macoma mitchelli* were collected farther upriver than *M. balthica*. The first two species were common at stations A, B, and D. *Brachidontes recurvus* and *M. mitchelli* are evidently more tolerant of low salinities as they were the only set found during the low salinity conditions of fall 1971. All three species have a nearly year long spawning season with minor spring peaks and a major peak in the fall.

The three most common organisms found on the bottles were *Rhithropanopeus harrisii*, *Callinectes sapidus*, and the blenny, *Chasmodes bosquianus*. These three potential set predators were typically found at stations A, B, and D during the fall and winter months. During high salinity periods, *R. harrisii* was found at station C.

Hydrographic Data

Freshwater input levels were usually high in late winter and spring, declining to low levels in late summer and fall (Figure 16). Flow during the

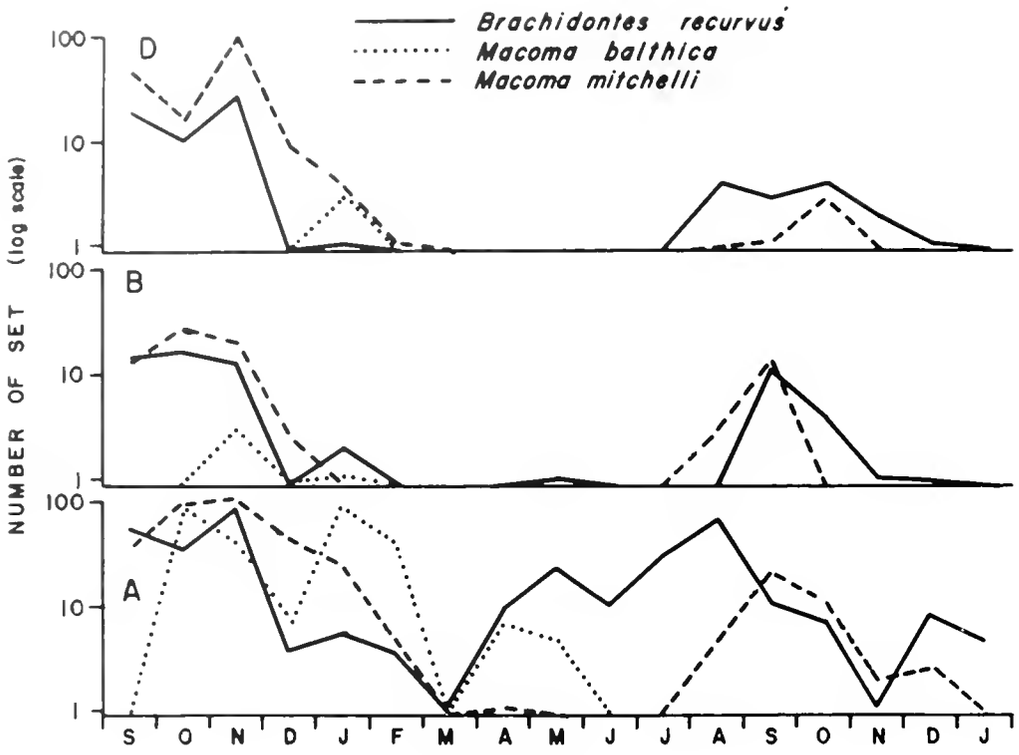

FIGURE 15.—Setting patterns of other bivalves at stations A, B, and D from September 1970 to January 1972. Data combined at deep and shallow stations.

fall of 1970 was very low, with about 28.32 m^3/s (1,000 cfs) input in September and October. This low input allowed measurable-salinity water to extend as far upstream as mile 45. Input was high and variable during the winter and early spring of 1971. The peak for the 2-yr period of 2,747 m^3/s (97,000 cfs) was recorded on 1 June 1971. The summer input was fairly low but quite variable and river flow during September and October was considerably higher than the previous fall. The salinity was rarely measurable at station B throughout the fall and winter months of 1971.

The annual temperature pattern for station B (Figure 17) is representative of the study area. Within relatively narrow limits, all deep stations exhibited similar temperature profiles. Lowest temperatures were measured during late January and early February, followed by a relatively smooth increase to a maximum of 29°C during early August. A period of stable high temperatures was recorded from June through September.

Dissolved oxygen concentrations in this region

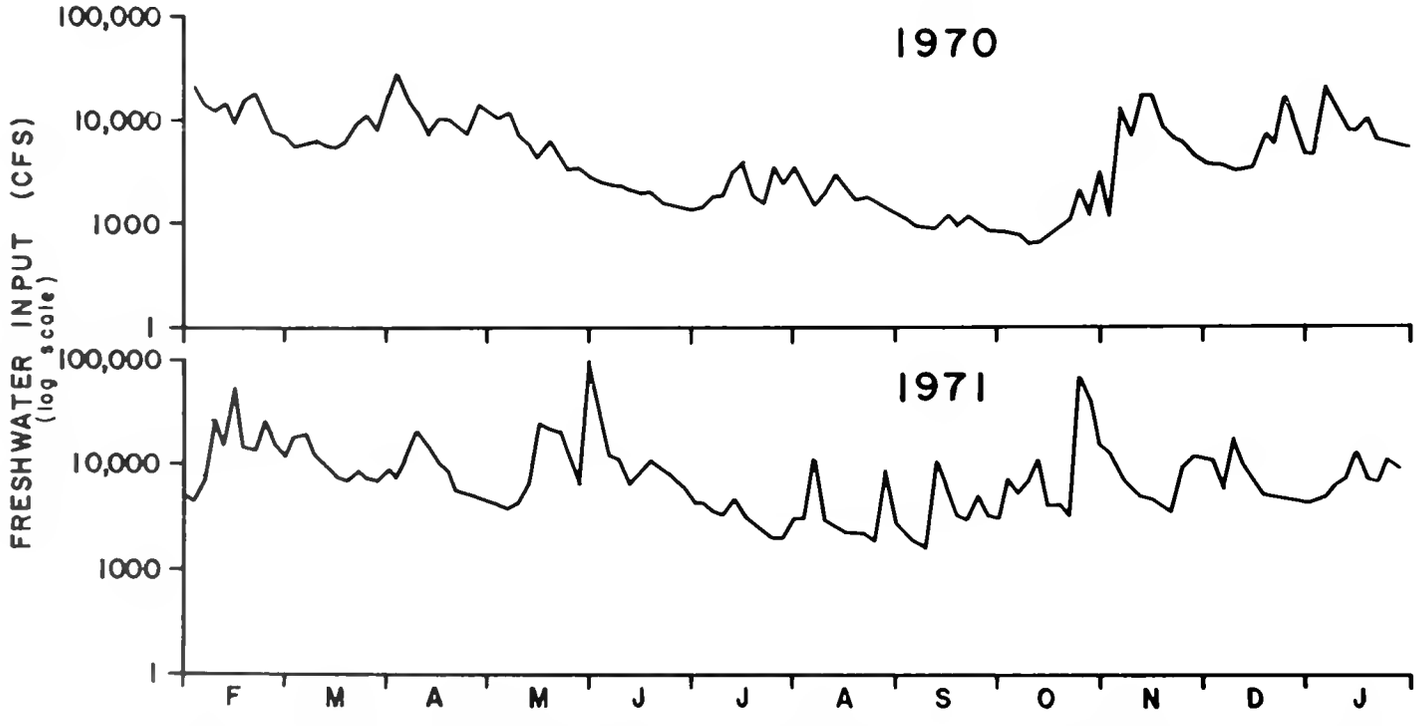

FIGURE 16.—Freshwater input into the James River at 4-day intervals. The data include input from the Appomattox and Chickahominy Rivers.

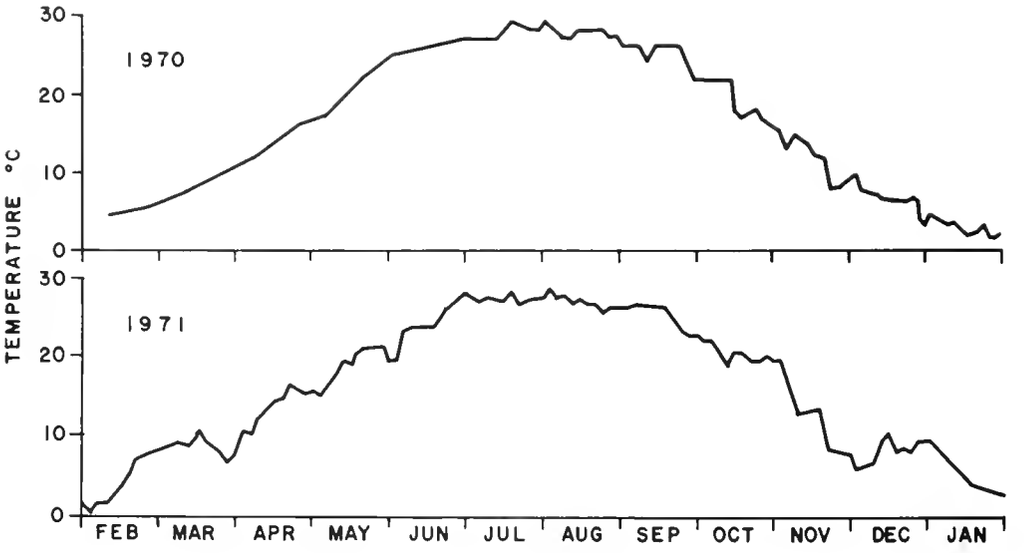

FIGURE 17.—Bottom water temperature at station B in the James River, Va. Values taken from VEPCO instrument tower (#6) and bottom water samples.

showed the normal seasonal variation, with the highest concentrations in the early part of the year during the low-water-temperature period. Low values (6-8 mg/liter) were recorded for deep stations during the summer months.

Relationship of the Reproductive Cycle to Environmental Data

At station A, gametogenesis started when the water temperature was near 10°C in the spring of 1970 (Figure 7). Ripe clams were first observed when the water temperature was 16°C and spawning was first noted when the salinity was between 3 and 5‰. Gametogenesis and spawning occurred through the summer period of high salinities and high temperatures. The fall spawning started at the highest salinities of the year with a definite major spawning after the salinity dropped 10‰ (Figure 7). The temperature during the fall spawning was 13°-15°C. Set first appeared the second week in November and occurred throughout the winter months. Fall and winter sets generally were accompanied by temperatures below 10°C and occasionally to 1°C. Gametogenesis was in progress again by the time the water temperature reached 15°C. No set clams were collected during the summer of 1971, although the histological sections showed all stages of development. Salinities and temperatures approximated those of the previous year, although salinity was more variable. Renewed gametogenesis coincided with the highest temperature of the summer and rising salinities. Some spawning took place with the declining salinity, but the major spawning occurred near 5‰.

Gametogenesis at station B started almost 2 wk later than at station A in the spring of 1970, with the temperature above 13°C (Figure 8). Ripe clams were similarly noted nearly 3 wk later than at station A. The salinity during the summer months was near 5‰ and gradually rising. There was little agreement between spawning times as noted in the histological sections and setting in the collectors during the summer. The progression of gonads in the fall from ripe to spent was clearer and more defined at station B than at station A. Spawning commenced when the salinity reached the yearly high and peaked when the salinity fell rapidly from 15 to 1‰. Setting took place 2 wk later and continued into the winter. Temperatures during spawning ranged from 22° to 12°C. Fewer clams were in the ripe phase throughout the summer of 1971 when the water was nearly fresh. More clams became ripe as the salinity increased, but few set were collected all summer at this station. Fall spawning commenced at 22°C and 6‰ and continued until the salinity reached approximately zero and the temperature dropped to 17°C. Some set were collected immediately after salinity decline and setting continued into January 1972.

Spawning was completed at station C by the end of October 1970, after salinity had fluctuated from 0 to 5‰ for the previous 2 mo. Setting began at temperatures above 25°C and continued throughout the winter at low water temperatures and low salinities (Figure 9). The salinity at station C remained below 1‰ until the termination of the study in January 1972. There was very little spawning and setting at station C during the low salinity period even though gametogenesis took place normally.

DISCUSSION

The histological examination of gonads indicates several generalizations about the reproductive cycle of *R. cuneata*. Gametogenesis began in early April and continued throughout the summer months. Ripe gametes were observed from May to late November. A slight spawning peak was noted during the summer, but a major spawn occurred in the fall. This was probably not a second cycle because gametogenesis in most cases had not terminated during the summer; instead, it appeared to be a continuation of gamete development at an increased rate.

The gametogenic cycle of *Rangia* in high and low salinities was basically the same. Temperature appeared to be the more important stimulus in initiating gametogenesis in the spring and summer. A temperature of approximately 15°C coincided with initiation of gametogenesis at all stations. Gametogenesis in clams from freshwater occurred at a slower rate during the spring and summer with more clams in the spent phase than at the other localities.

The reproductive cycle as determined in this study is similar to that reported for *Rangia* in other geographic areas. Fairbanks (1963) indicated that in Lake Pontchartrain, La., ripe clams could be found during March, April, May, and in the late summer and fall. A prolonged spawning season would seem reasonable as the rise in water temperature to 15°C in the spring is nearly 2 mo earlier at that location than in the James River. In addition, the drop in water temperature to 15°C in the fall is later. He also indicated a postspawning recovery phase during midsummer. The very high temperature (near 33°C) during the summer may have inhibited gametogenesis, but in the James River population a renewed surge occurred at the high midsummer temperatures of 28°-29°C. Tenore (1970) studying the macrobenthos of the Pamlico River, N.C., found *Rangia* containing mature gametes only in the fall. This observation was probably based on visual inspection of the viscera. The spring and summer ripening may have been missed because the gonads are not nearly as distended and colored as in the fall ripening. Pfitzenmeyer and Drobeck (1964) collected *Rangia* in August and September from the Potomac River. Clams at this time contained mature gametes, indicating that spawning was imminent.

The correlation of the environmental data to gonadal conditions suggests that temperature and salinity are important factors in spawning. Salinity, however, was more important than temperature. Clams upstream at station C spawned in fall 1970 following a 5‰ rise in salinity, but failed to spawn in 1971 when the salinity remained low. Spawning at station B was apparently related to salinity decreases. The correlation of salinity to spawning was not as clear at station A. The salinity variation at this station was very large over a tidal cycle and may have prevented complete synchrony of spawning.

Cain (1973) found that a salinity change was necessary for *Rangia* spawning in the laboratory. Spawning was accomplished by placing ripe clams from low salinities (< 1‰) into 5‰, 28°C flowing water. Evidently clams in upstream areas require a rise in salinity to spawn, while downstream populations require a reduction in salinity from the 10 to 15‰ levels at which they live.

There is little additional evidence in the literature on the importance of salinity to *Rangia* spawning. Fairbanks (1963) could not induce spawning. Chanley (1965) induced spawning at 15 ‰ by rapidly increasing the water temperature 7°C and adding sperm stripped from a ripe male. However, spawning was poor and he did not study the survival of the eggs. Such strong stimuli may cause premature release of immature eggs, with subsequent poor fertilization and survival. The only data suggesting the importance of salinity to *Rangia* spawning is that from the Bureau of Sport Fisheries and Wildlife (1965) in connection with a study on the food habits of ducks in Back Bay, Va., and Currituck Sound, N.C. These two bodies of water normally have a salinity of less than 1‰. During that study, a storm forced ocean water into the bay and raised the salinity to about 4.5‰. This intrusion of salt water must have caused spawning and successful setting since the following year nearly 9% of the diet of dabbling and diving ducks consisted of small *Rangia*, an amount estimated to be 83,000 lb (dry weight) for the year. During the previous 3 yr no *Rangia* were consumed by these ducks.

Two periods of setting occurred in the James River. The first was in early and midsummer, which coincided with the beginning of spawning as inferred from tissue sections. The second period was much longer, with a greater number of collected set, and took place in the late fall and winter, coinciding with the increased percentage

of partially spawned and spent clams, as identified by histological preparations. The second peak of spawning appeared to be the major one for the normal reproductive period (Table 1). Fairbanks (1963) found set (>0.375 μm) from October to April. A longer and more intense setting period was found in the area with the more variable salinity. Tenore (1970) collected set in bottom grabs only during the fall and winter months. The spring and summer spawning was either so light in these areas that no set were found or an abundance of predators at this time quickly consumed the sparse set.

Sex Ratio

There are at least two possible explanations for the unusual sex ratios in *Rangia*. *Rangia* may be protandric with a higher ratio of females to males in the older stages. If so, the clams at stations B, D, and C would have had to be older than those at station A; however, there were no consistent differences in the lengths of the clams at the various stations. This does not preclude the possibility that the ages of clams at the stations are different, but masked by varying growth rates resulting from substrate effects or nutrient levels.

The second possibility is that the environmental conditions upriver differ enough from those downriver at station A to affect the sex ratios. Changes in environmental factors could affect either juveniles or adults during the undifferentiated period. There is no proof of this type of sex alteration. None of the other mactrids studied, *M. lateralis*, *S. solidissima*, or *T. capax* have been found to have a ratio other than 1:1.

Relationship of Larval Studies to Setting

Cain (1973), on the basis of laboratory results, indicated that best survival and growth of larvae would be expected in the summer. Higher temperatures and generally high salinities are expected to provide for rapid growth to setting. But setting is very poor in summer (Table 1). A number of factors may account for this: clams are in all stages of gametogenesis, the gonads of ripe clams are not as full, and even though the stimulus to spawn may exist there is probably poor synchrony of spawning.

In the James River, fall and winter were the times of greatest setting activity. Fall spawning occurred as the temperature dropped from 29° to 15°C. This temperature range would provide good survival of eggs to straight-hinge larvae, but the larvae are exposed to declining fall temperatures. Larvae at low temperatures (and low salinity) should survive well, but grow slowly. Consequently, set in the late fall and winter come from a fall spawning after the delay in growth and metamorphosis expected from low temperatures. Some set in the jars could have come from previously set, slow-growing clams washed in by turbulence. This set, which is fairly active, tends to crawl over the bottom by use of the muscular foot and therefore is affected by currents (Carriker 1961).

Distribution and Recruitment of *Rangia* in the James River

Rangia extends to nautical mile 60 in the James River. In the upper reaches of its distribution it has been in freshwater for the last 4 or 5 yr. Since the embryos and early straight-hinge larvae cannot tolerate freshwater (Cain 1973) and a salinity rise is needed to induce spawning, there must be little recruitment to this population. No set or small clams have been found in this area, which raises the similar question of how *Rangia* spread into this region initially. The upriver population consisted of clams ranging in length from 53 to 63 mm in the spring of 1971. Using the von Bertalanffy growth curve constructed for *Rangia* by Wolfe and Petteway (1968), these clams were estimated to be from 5 to 7 yr old. The water records for the James River basin were analyzed from 1963 to 1966 (Anonymous 1966, 1970b). These records show yearly lows in the late summer and fall when the input dropped below 22.66 m^3/s (800 cfs), and in 1966 the input dropped to an average of 13.59 m^3/s (480 cfs) during the first half of September. These very low flow periods allowed measurable-salinity water to extend 63.5 miles upstream in December 1965 (Brehmer and Haltiwanger 1966).

To reach these upstream areas larvae must be transported in the more saline bottom water which has a net upstream movement (Pritchard 1952; Nichols 1972). Although the mechanism of such transport has not been deduced for *Rangia*, work done on the eastern oyster may indicate some possible mechanisms. Wood and Hargis (1971), who studied the lower James estuary, found a definite upstream transport of oyster larvae and

also of small coal particles. They indicated that the larvae move upstream by selectively swimming in more saline water associated with the flood tide. They further indicated that Korringa's (1952) idea of passive transport could not be denied, as the coal particles also had a net upstream motion. *Rangia* could be carried into upstream areas both by selective swimming or by passive transport under low flow conditions, and a series of dry years would allow set to progressively move upriver. Set from one year should be able to spawn the next year and certainly within 2 yr. Gonads occurred in clams 14 mm long, a length easily reached by the end of the first year (Fairbanks 1963; Wolfe and Petteway 1968). Rapid early growth and a relatively short larval life (above 20°C) should allow for the fast spread of set into areas uninhabited by adults. As *Rangia* has an 8-yr average life span (Fairbanks 1963) and a maximum life of 14 yr (Wolfe and Petteway 1968), recruitment to the population could occur at fairly long intervals. The Virginia Division of Water Resources (Anonymous 1970a) statistically predicts that low flows of less than 1,000 cfs for 7 days will occur at 5-yr intervals. This situation could allow minimum recruitment to maintain the upstream population, assuming good survival of set and adults in this region.

The downstream extent of *Rangia* could be determined by the adults approaching their high-salinity limit. This may not be the case as the larvae can survive higher salinities than normally occur at the downstream limit—and the adults may also do so. The downstream extent likely represents a multifactor barrier involving biological competition for space and food, and increased predation of the set.

Recruitment to the downstream population was at a low level but more regular, with more set collected in the summer months than at the upstream stations (Table 1). Probably the best recruitment would be expected in the population at station B near the lower middle of the habitat range. The fall set there was high and fairly consistent over the 2-yr period. Averaged over many years, this segment would likely receive more set, as this part of the estuary usually has an annual salinity change from fresh to 5‰.

General Discussion

The adults can utilize the high levels of detritus in this oligohaline sector (Darnell 1958) and convert it into growth and reproductive materials. *Rangia* is ripe for at least 7 mo of the year so it can spawn whenever favorable changes in salinity allow successful reproduction. Although adults are euryhaline, embryos are much more sensitive. Spawning at a salinity near 5‰ allows for the survival of the sensitive stages to the more eurytopic later larval stages. The increased tolerance of the larvae permits good survival during its more stressful pelagic existence.

The planktonic existence of *Rangia* larvae is greatly extended by low temperatures. Thorson (1946) indicated that prolonged low temperatures exposed larvae to increased mortality from disease, starvation, predation, dispersion, and environmental stress. *Rangia* larvae evidently are well adapted to a prolonged exposure because many set were collected during the coldest months. This increase in dispersal may allow *Rangia* to consume the unexploited resources of the species-poor environment in low salinity. Increased dispersal may also provide genetic interchange between populations distributed over a relatively extended habitat in the estuary. Pfitzenmeyer and Drobeck (1964) found the rate of increase of *Rangia* over a 4-yr period in the Potomac River to be very great. Pfitzenmeyer (1970) also recorded this clam in the upper Chesapeake Bay when its numbers increased from 0 to 10,000 per square meter in 2 yr.

Spawning of *Rangia* apparently is controlled by salinity change. The mechanism of this control, however, has not been examined. The exogenous factor of salinity may activate an endogenous control system of osmoregulation and serve as a signal to induce synchronous spawning of the population. The concept of "critical salinity" reviewed by Khlebovich (1969) appears operative for *Rangia* which spawns near 5‰. Khlebovich concluded that the salinity range of 5-8‰ is a faunal boundary defining the distribution of marine and freshwater species. Characteristic differences in physiological performances (adaptation, growth, activity and, especially, osmoregulation) are revealed at this salinity range.

The latitudinal distribution of *Rangia* is important because of its spread northward in the last decade. In the present study, gametogenesis and spawning were observed to occur over a wide range of temperatures. Although larval growth was best at high temperatures, survival and growth apparently take place even at low temperatures. Consequently, it appears that the

northward limit of *Rangia* is not controlled by low temperature effects on reproduction or larval tolerance. Reports on populations in upper Chesapeake Bay (Gallagher and Wells 1969; Pfitzenmeyer 1970) infer large adult mortalities from low temperature and low salinity. The only mortality of adults (freshly gaped clams) in this study was seen in the dredge hauls during the winter and early spring. Long periods of low temperature and freshwater may combine to increase the mortality of adults and thereby limit the northward range.

The possibility that widely separated populations may belong to different physiological races cannot be excluded (Loosanoff 1969). Populations of marine animals exposed to different environments within their geographical range may have different physiological properties (Sastry 1970), suggesting that more research should be conducted on the tolerances of embryos, larvae, and adults from different geographical areas.

The key to the welfare of a *Rangia* population over its normal distribution is probably not the physiology of the adult individual but successful reproduction and recruitment. Adults may live for years in habitats where reproduction is impossible. Spawning will not occur unless salinity changes, up from low salinity or down from high salinity. If spawning does occur, embryos and early larvae will have poor survival unless salinity is between 2 and 10‰ (Cain 1973). Once the larvae have developed past the swimming stage and settled to the bottom as juvenile clams, salinity is probably not as critical (except in combination with low temperatures).

The influence of salinity on reproduction and recruitment indicate that some changes in its environment may restrict the distribution of *Rangia* in the estuary. *Rangia*'s estuarine distribution is maintained by changes in salinity related to variations in the freshwater input. Any overall reduction in freshwater input or reductions in the seasonal variations of salinity will limit its range. These characteristics of this species should be considered before dams are constructed, freshwater is diverted for other uses, or other changes in the hydrography of the estuary are approved.

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HORMONAL-INDUCED OVULATION OF THE WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*

ALPHONSE S. SMIGIELSKI[1]

ABSTRACT

The response of winter flounder, *Pseudopleuronectes americanus*, to human chorionic gonadotropin (HCG), oxytocin, pregnant mare serum gonadotropin (PMSG), deoxycorticosterone (DOCA), and freeze-dried carp pituitary is described. HCG and PMS were successful in some instances in producing viable eggs and larvae while carp pituitary was successful in all instances. These were the first known successful attempts to induce maturation and spawning of winter flounder artificially in the laboratory.

Larvae obtained from these hormonal-induced spawnings were normal in all respects and were reared in the laboratory through metamorphosis. Wild plankton obtained from Narragansett Bay, brine shrimp nauplii, and chopped clams were fed as food. The early life history of this flatfish can, for the first time, be completed under controlled laboratory conditions.

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), an important species in local New England commercial and sport fishing industries, occurs from Chesapeake Bay to the northern shore of the Gulf of St. Lawrence (Bigelow and Schroeder 1953). Winter flounder spawn from January through April in Rhode Island estuaries with a peak spawning period in February. Demersal eggs are produced which range from 0.74 to 0.85 mm in diameter.

Investigations to evaluate methods of inducing spawning of winter flounder with the aid of hormones under controlled laboratory conditions were undertaken at the National Marine Fisheries Service, Northeast Fisheries Center, Narragansett Laboratory in 1970 and continued over a 3-yr period. The use of hormone injections for inducing spawning in other species of fish has been well documented by Pickford and Atz (1957). The induction of spawning in winter flounder in the laboratory provides a practical method of supplying viable eggs and larvae for physiological studies. By controlling water temperatures, photoperiods, and injecting hormones, the research time for this species can be extended. As far as is known, these were the first reported successful attempts to artificially mature and spawn the winter flounder in the laboratory.

MATERIALS AND METHODS

Adult winter flounder were captured by otter trawling in Narragansett Bay in the autumn of 1970, 1971, and 1972, and were brought to the Narragansett Laboratory in a 380-liter live car equipped with an aerator. In the laboratory, the fish were held in 1,890-liter circular aquaria (1.2 m in diameter; water depth, 0.8 m). A continual supply of filtered seawater was pumped to the aquaria from Narragansett Bay.

After acclimating in the laboratory, the fish were segregated by sex, measured and weighed, and tagged with numbered plastic pennants secured through the caudal peduncle with a double barbed stainless steel wire. Winter flounder adults may be sexed easily by placing the fish on its back and running a hand down the white underside. Females are quite smooth while the males are very rough to the touch. Winter flounder lend themselves quite readily to handling and have proven to be a durable fish. No anesthesia was required prior to injecting hormones as the fish rarely struggled.

An artificial photoperiod of 9 h light and 15 h darkness (9L:15D) simulating seasonal light conditions was maintained for all experiments by time clocks controlling four banks of 80-W cool white fluorescent lights suspended 1.2 m above the tanks.

Since winter flounder fast during the spawning season, as many other fish do, their food regimen was not difficult to maintain. A varied diet of clams, squid, chopped menhaden, and silversides

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was provided. Very few females fed actively. However the males, a majority of which were running ripe, fed throughout the experiments.

Hormone injections were carried out with 0-2 cc syringes fitted with 20 gauge, 3.85 cm (1.5 inch) needles. All injections were intramuscular. Intraperitoneal injections were ruled out for fear of injuring or killing the experimental fish. Injections were made into the back muscle below the dorsal fin. Inserting and withdrawing the needle slowly aided in retaining most of the fluid in the fish (Figure 1). After injection, the flesh of the fish was massaged to diffuse the fluid into the muscles. A saline solution of isotonic sodium chloride was used as a carrier for all hormone injections except with deoxycorticosterone, which was mixed with sesame oil and injected as a slurry. Hormones tested in the various studies were: human chorionic gonadotropin (HCG), oxytocin, deoxycorticosterone (DOCA), pregnant mare serum gonadotropin (PMSG) and carp pituitary (freeze-dried powder). The criteria chosen to test the effectiveness of the hormones were gonad index, spawning, fertilization of eggs, and hatching success. Hormones were prepared on the day of injection, and dosages were established by the weight of each individual fish.

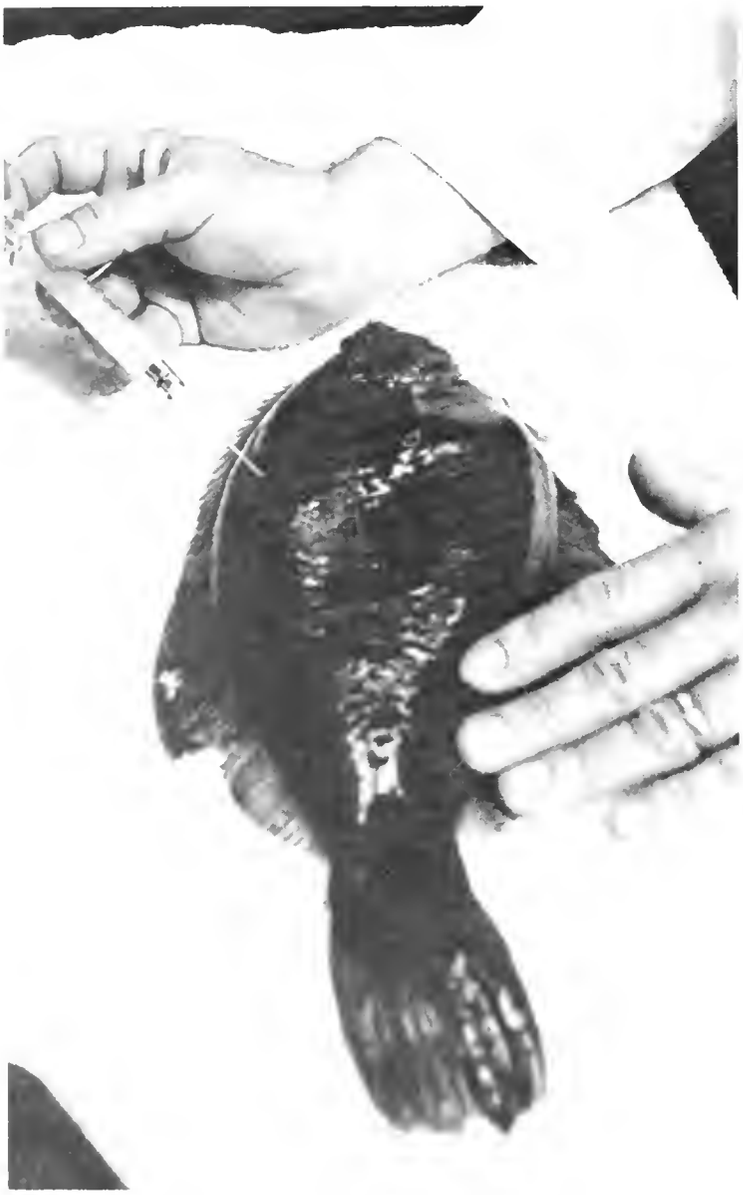

FIGURE 1.—Winter flounder receiving hormone injection.

Running ripe fish were stripped by hand. Winter flounder spawn adhesive demersal eggs which form clumps under experimental conditions. Spawned and fertilized eggs were handled and treated according to the separation techniques of Smigielski and Arnold (1972).

Human chorionic gonadotropin was the first hormone selected for evaluation. Stevens (1966) reported successful spawnings of striped bass with dosage levels of this hormone ranging from 31 through 403 IU/pound fish. Two hormone dosage levels and two time sequences of injecting were administered to three groups of test fish numbering five per group at dosage levels of 150 IU/454 g fish injected daily, 300 IU/454 g fish injected daily, and 300 IU/454 g fish injected every other day. A fourth group served as controls. Water temperatures during the first testing trial ranged between 5° and 7°C with a mean of 6.2°C.

A second series of experiments was initiated when the water temperature fell to 4°C. Water temperatures during these trials ranged between 3° and 5°C with a mean of 3.2°C. A test group numbering 15 fish was established and held in three 1,890-liter aquaria. Dosage levels of 150 IU/454 g fish were dispensed daily and administered over a time period of 12 days.

Further experiments were initiated to evaluate oxytocin, DOCA, and PMSG at the two water temperature ranges of 6°-7.5°C and 3°-5°C. Mean water temperatures during the trials were 7.2° and 3.2°C. Because of variable results obtained with the hormone HCG in prior experiments, HCG was included in these trials for further testing. Three dosage levels of each hormone were evaluated and a total of five injections administered over a period of 10 days. The dosage levels were: oxytocin at 10, 20, and 40 IU/454 g fish; DOCA at 5, 10, and 20 mg/454 g fish; PMSG at 55, 110, and 220 IU/454 g fish; and HCG at 100, 200, and 400 IU/454 g fish. Female test fish were measured, weighed, tagged, and placed into four 1,890-liter circular tanks supplied with a continual supply of seawater. Each tank contained a total of

16 fish. The three differing dosage levels of each test hormone were injected into groups consisting of four fish per group, and the remaining four fish in each tank served as uninjected controls. At the termination of the trial, test fish were sacrificed, ovaries examined, and gonosomatic index (GSI) levels recorded.

A final series of experiments was initiated to evaluate the effectiveness of carp pituitary (freeze-dried powder) at the dosage levels of 5.0 mg and 0.5 mg/454 g fish injected daily. Two groups of test fish with each group consisting of three trial fish and three uninjected controls were established and held in two 1,890-liter tanks. During the trials, water temperatures ranged between 1.5° and 3.5°C with a mean at 2.5°C.

RESULTS AND DISCUSSION

In the group of test fish that received HCG injections at 300 IU daily, one fish hydrated after a single injection (Table 1). Hydration, an increase in total body weight due to water uptake by the ovaries resulting in higher GSI levels, was rapid, and the following morning this fish was grossly bloated. Externally, hydrated fish may become slightly swollen or grossly bloated. The majority of the eggs stripped were opaque and misshapen, and approximately 5% of the total egg mass in the ovaries were viable. These eggs, numbering approximately 10,000, were fertilized but embryonic development ceased in the blastula stage and none survived to hatch. This rapid hydration may have been responsible for the poor quality of the eggs. A long development period for oocytes with a minimum of 2 or 3 yr from the time oocytes become histologically recognizable until they are spawned has been suggested for winter flounder by Dunn and Tyler (1969). Our observations in the past have noted that the natural hydration and ovulation process of winter flounder can occupy a lengthy period of time (unpubl. data). The remaining fish in this test group were refractory after receiving a total of 12 injections.

The group of five test fish that received injections of 300 IU every other day (for a total of seven injections in 13 days) contained three fish which were refractory at the conclusion of the trial; one fish displayed signs of slight hydration, but did not ovulate. The remaining fish in the group ovulated and was spawned 10 days after the last injection. Approximately 95% of the eggs were fertilized but development ceased at the blastula stage and none survived to hatch.

The group of test fish which received daily injections of 150 IU for 12 days contained three fish which were refractory and two which hydrated slightly but did not ovulate. Of the six fish that served as uninjected controls, five displayed no signs of hydration, and the remaining fish hydrated slightly but did not ovulate.

At the termination of the trials, the fish were not sacrificed. The only criterion for evaluating the success of the hormone was obtaining viable eggs. It was reasoned that the relatively warm-water temperatures (5°-7°C) coupled with suspected low GSI levels inhibited the effectiveness of the hormones. Observations made in the inner parts of the Gulf of Maine, (Bigelow and Schroeder 1953) have shown that extensive spawning of winter flounder does not occur in water temperatures above 6°C.

At the conclusion of the second series of experiments, four fish hydrated and ovulated after receiving from two to nine injections (Table 2). Fertilization was high for all fish but embryonic mortalities were high in the blastula and gastrula stages, and hatches were poor, ranging from 2 to 20%. Larvae obtained from these spawnings appeared to be normal in all respects and several were reared through metamorphosis. Three additional test fish became grossly bloated after receiving a total of 10 injections in 10 days and hydrated to the point of dying. Membranous plugs formed in their oviducts and the eggs were water hardened. The formation of these plugs is not understood as prior to receiving their last injection they were hydrating at a normal rate. Shehadeh and Ellis (1970) reported plugs forming in striped

TABLE 1.—Effects of human chorionic gonadotropin (HCG) on *Pseudopleuronectes americanus*, temperature range 5°-7°C ($\bar{x}$ 6.2°C). Photoperiod 9L/15D.

Hormone and dosage	No. of fish	No. of injections	Number hydrated	Number ovulated	Fertilization (%)	Hatch (%)
300 IU HCG/454 g fish daily	1	1	1	1	[1]5	0
300 IU HCG/454 g fish daily	4	12	0	0	—	—
300 IU HCG/454 g fish every 48 h	5	7	1	[2]1	95	0
150 IU HCG/454 g fish daily	5	12	2	0	—	—
Controls	6	0	1	0	—	—

[1]Approximate.
[2]Ovulated and spawned 10 days after last injection.

TABLE 2.—Effects of hormones on *Pseudopleuronectes americanus*. Temperature range 3°-5°C ($\bar{x}$ 3.2°C). Photoperiod 9L/15D. Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	Number of injections	Total length (mm)	Initial body weight (g)	Weight change at termination (% initial wt.)	GSI[1] (% final wt.)	Hydrated	Ovulated	Fertilization (%)	Hatch (%)
[2]HCG 150 IU/454 g fish daily	2	271	271	−3.32	1.29	+	+	80	2
	4	316	792	+0.76	1.08	+	+	90	5
	8	349	640	+0.63	1.24	+	+	80	10
	9	370	692	+0.58	1.15	+	+	80	20
	10	360	545	+3.67	32.74	+	[3]0	—	—
	10	290	275	+5.45	30.34	+	[3]0	—	—
	10	421	982	+2.75	30.13	+	[3]0	—	—
	12	391	670	+0.60	16.02	+	0	—	—
	12	334	571	−0.35	8.08	0	0	—	—
	12	377	486	+0.62	7.57	0	0	—	—
	12	317	562	+1.60	16.46	+	0	—	—
	12	342	454	+0.44	10.13	0	0	—	—
	12	280	352	+1.42	15.13	+	0	—	—
	12	336	599	+0.33	9.48	0	0	—	—
	12	352	800	+0.50	20.15	+	0	—	—
Control	0	341	721	+1.05	1.14	+	+	85	75
	0	330	540	+1.11	19.60	+	0	—	—
	0	321	449	+1.56	19.08	+	0	—	—
	0	337	497	+1.01	18.73	+	0	—	—
	0	271	299	−0.67	10.24	0	0	—	—
	0	269	356	+2.25	12.09	0	0	—	—

[1]Gonadosomatic index.
[2]Human chorionic gonadotropin.
[3]Plug formed, fish became grossly bloated and died, eggs were water hardened in ovaries.

mullet, *Mugil cephalus*, while attempting induced spawning.

The findings at the conclusion of the second series of experiments indicated that the injection of HCG, although more effective at the lower water temperatures, resulted in poor egg quality and egg survival, the formation of membranous plugs, and gross hydration causing death.

Oxytocin at all three dosage levels tested had little effect when water temperatures were above 5°C. Three fish hydrated but none ovulated or contained matured eggs (Table 3).

DOCA administered at the lower dosage levels of 5 and 10 mg/454 g fish and at water temperatures above 5°C, resulted in several fish hydrating but none ovulating. At the higher dosage level of 20 mg/454 g fish, two test fish hydrated, and although their GSI levels were high, no ovulation occurred and no mature eggs were present in their ovaries.

PMSG at the three dosage levels of 55, 110, and 220 IU/454 g fish showed low activity when administered at water temperatures above 5°C. Although some fish had hydrated, none ovulated and GSI levels were low in all of the test groups.

HCG was ineffective at the dosage levels of 100 and 200 IU. Dosage levels of 400 IU resulted in three fish hydrating at low GSI levels. Another fish ovulated and was stripped 3 days after the last injection. Egg fertilization was high and approximately 80% of the eggs hatched. The larvae obtained from this induced spawning appeared to be normal in all respects and several were reared through metamorphosis.

The data gleaned from this trial at water temperatures in the 6°-7.5°C range substantiated results derived from earlier experiments, suggesting that water temperatures above 6°C inhibit maturation of winter flounder, and for the most part hormones are ineffective. The manner in which hormones exert their effects on fish is poorly understood, and dosage levels are probably meaningless as the largest fish may not necessarily be the most sexually mature and may differ in receptibility to hormone injections.

Haydock (1971) has observed a temperature threshold of 17°C below which the gulf croaker, *Bairdiella icistia*, would not hydrate or ovulate. It is very probable that a similar temperature threshold exists for winter flounder above 6°C. Observations in the past at our laboratory have noted that gravid female flounder perished in water temperatures of 10°C, and ova from these fish were stunted and misshapen. Male flounder held under the same conditions suffered no apparent ill effects.

In the lower temperature range tested (range 3°-5°C, mean 3.2°C), oxytocin produced slightly better results (Table 4). Three fish hydrated but none ovulated nor contained mature eggs. GSI levels were higher at the lower temperatures at all dosage levels tested. No abnormal hydration was

TABLE 3.—Effects of hormones on *Pseudopleuronectes americanus* given five injections over a 10-day period. All fish experienced a 9L:15D photoperiod, water temperature range 6°-7.5°C ($\bar{x}$ 7.2°C). Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	Total length (mm)	Initial body weight (g)	Weight change (% initial wt.)	GSI[1] (% final wt.)	Hydrated	Ovulated	Fertilization (%)	Hatch (%)
Oxytocin	386	716	+3.91	13.87	+	0		
10 IU/454	336	495	0	15.25	0	0		
g fish daily	308	344	+0.87	17.87	0	0		
	333	504	−0.79	14.00	0	0		
Oxytocin	323	453	+2.21	17.17	+	0		
20 IU/454	305	350	−0.29	14.90	0	0		
g fish	345	477	−1.68	9.81	0	0		
	370	662	−0.30	12.00	0	0		
Oxytocin	306	409	+0.98	14.53	+	0		
40 IU/454	338	377	−1.06	13.94	0	0		
g fish	308	404	−0.50	8.83	0	0		
	349	471	0	16.99	0	0		
Control	346	443	+0.45	13.82	0	0		
	296	327	+1.22	13.14	0	0		
	302	389	+3.08	13.19	+	0		
	370	634	+1.58	16.61	0	0		
[2]DOCA 5 mg/454	340	456	+2.63	1.39	0	0		
g fish	345	549	+3.10	15.37	+	0		
	372	540	+5.74	14.97	+	0		
	299	310	+9.68	13.09	+	0		
[2]DOCA 10 mg/454	287	270	+13.70	11.24	+	0		
g fish	283	272	+7.35	8.39	+	0		
	300	354	−0.28	12.75	+	0		
	345	525	+5.71	15.05	+	0		
[2]DOCA 20 mg/454	392	726	+1.38	4.08	0	0		
g fish	306	338	+4.73	7.20	0	0		
	376	726	+5.79	19.79	+	0		
	375	516	+15.70	28.14	+	0		
Control	295	327	+1.22	12.24	0	0		
	323	408	+3.67	14.07	+	0		
	356	526	+1.71	24.58	+	[3]0		
	342	480	+2.92	17.21	+	0		
[4]PMSG 55 IU/454	315	448	+1.79	11.84	+	0		
g fish	321	420	−0.24	9.07	0	0		
	381	652	+0.46	10.23	0	0		
	358	582	+6.19	16.34	+	0		
[4]PMSG 110 IU/454	294	318	+1.57	0.93	[5]0	0		
g fish	349	546	−0.92	12.29	0	0		
	349	219	+1.83	9.42	0	0		
	303	341	+4.69	13.45	+	0		
[4]PMSG 220 IU/454	335	488	+2.46	18.00	+	0		
g fish	321	389	−1.03	3.64	0	0		
	315	390	+5.64	13.23	+	0		
	342	480	−0.21	6.26	0	0		
Control	357	474	+0.63	1.23	0	0		
	424	989	+1.01	16.52	0	0		
	310	351	+1.14	0.70	0	0		
	265	263	+1.90	1.12	0	0		
[6]HCG 100 IU/454	321	326	−1.23	6.83	0	0		
g fish	323	455	−0.22	13.00	0	0		
	358	517	0	10.35	0	0		
	350	530	+1.89	12.50	+	0		
[6]HCG 200 IU/454	315	300	−0.33	13.55	0	0		
g fish	316	345	+2.03	9.09	0	0		
	282	247	+4.05	11.67	0	0		
	292	275	+4.36	11.32	0	0		
[6]HCG 400 IU/454	337	549	−1.82	0.74	+	+	98	80
g fish	330	323	+3.10	2.25	+	0		
	388	706	+4.39	8.07	+	0		
	330	391	+2.30	9.75	+	0		
Control	301	309	−0.65	10.75	0	0		
	296	339	−0.88	14.14	0	0		
	282	346	−0.29	8.41	0	0		
	281	229	+6.99	18.57	+	[3]0		

[1]Gonadosomatic index.
[2]Deoxycorticosterone.
[3]Matured eggs in ovaries.
[4]Pregnant mare serum gonadotropin.
[5]Sexually immature.
[6]Human chorionic gonadotropin.

TABLE 4.—Effects of hormones on *Pseudopleuronectes americanus* given five injections over a 10-day period. All fish experienced a 9L:15D photoperiod, water temperature range 3°-5°C ($\bar{x}$ 3.2°C). Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	Total length (mm)	Initial body weight (g)	Weight change (% initial wt.)	GSI[1] (% final wt.)	Hydrated	Ovulated	Fertilization (%)	Hatch (%)
Oxytocin	378	578	−0.35	19.36	0	0		
10 IU/454	306	321	−1.25	13.72	0	0		
g fish	412	752	−3.32	20.50	0	0		
	340	488	+0.41	13.76	0	0		
Oxytocin	335	481	−1.66	12.90	0	0		
20 IU/454	373	654	+0.92	24.62	+	0		
g fish	308	356	−1.69	16.29	0	0		
	391	774	−0.65	18.66	0	0		
Oxytocin	305	352	+4.83	17.21	+	0		
40 IU/454	284	290	−4.92	14.88	0	0		
g fish	338	440	+3.30	20.34	+	0		
	352	478	−0.42	11.40	0	0		
Control	292	327	−1.21	12.08	0	0		
	235	184	+0.54	22.55	+	[2]0		
	316	360	0	17.92	+	0		
	300	399	−0.50	16.67	+	0		
[3]DOCA 5 mg/454	320	430	+3.49	11.24	0	0		
g fish	332	419	+0.48	16.79	+	0		
	360	619	+2.75	23.58	+	0		
	335	517	+0.77	23.03	+	0		
[3]DOCA 10 mg/454	314	270	−3.70	10.96	0	0		
g fish	374	649	+4.31	16.84	+	0		
	323	460	+4.35	24.79	+	[2]0		
	271	225	+8.44	11.07	0	0		
[3]DOCA 20 mg/454	333	528	+7.39	19.22	+	0		
g fish	402	1,003	+9.07	32.45	+	[2]0		
	337	468	+2.78	12.68	0	0		
	340	546	+2.01	23.07	+	0		
Control	284	314	+5.37	11.78	0	0		
	295	279	+2.20	11.83	0	0		
	396	800	+2.30	13.25	0	0		
	347	579	+0.35	24.27	+	0		
[4]PMSG 55 IU/454	334	693	+5.34	18.36	+	0		
g fish	336	435	+2.30	18.71	+	0		
	425	1,105	−0.09	18.98	+	0		
	321	539	+7.98	25.17	+	+[5]	[6]0	0
[4]PMSG 110 IU/454	327	467	+5.14	14.97	+	0		
g fish	340	498	+1.20	14.58	+	0		
	324	411	−2.92	14.44	0	0		
	303	372	−4.30	13.34	0	0		
[4]PMSG 220 IU/454	360	593	0	13.07	0	0		
g fish	261	207	−8.70	20.11	0	+[5]	0	0
	350	541	+0.74	17.61	+	0		
	437	1,173	+6.05	41.52	+	+[5]	20	18
Control	295	334	−6.59	14.74	0	0		
	329	500	+1.00	13.74	+	0		
	287	346	+1.45	15.10	+	0		
	310	350	−1.71	1.16	+	+	98	70
[7]HCG 100 IU/454	400	722	+2.08	11.13	0	0		
g fish	343	462	−5.19	18.04	0	0		
	335	446	−6.95	12.29	0	0		
	402	812	+2.83	20.12	+	0		
[7]HCG 200 IU/454	340	519	+0.39	19.67	+	0		
g fish	352	500	−4.20	18.58	0	0		
	331	462	+6.93	23.99	+	0		
	290	320	+9.69	1.21	+	+	98	80
[7]HCG 400 IU/454	285	298	−1.34	17.01	0	0		
g fish	348	516	+5.04	18.91	+	0		
	330	513	+3.12	27.03	+	+[5]	15	0
	296	336	−5.65	14.67	0	0		
Control	362	249	+1.20	14.48	0	0		
	324	548	+2.24	21.81	+	0		
	397	943	+1.18	24.13	+	0		
	318	500	+4.82	13.10	0	0		

[1]Gonadosomatic index.
[2]Matured ova in ovaries.
[3]Deoxycorticosterone.
[4]Pregnant mare serum gonadotropin.
[5]Plug formed in oviduct.
[6]Eggs water hardened.
[7]Human chorionic gonadotropin.

noted nor did any plugs form in the test fish. A weight loss occurred in almost all of the test fish at the lower temperatures.

Administering DOCA at lower temperatures resulted in GSI levels being higher in test fish at all three dosage levels. Several fish hydrated and although no ovulation occurred, some matured eggs were present in the ovaries of two test fish that received injections at the higher levels of 10 and 20 mg. No plugs were present in any of the test fish and no abnormal hydrations were observed.

Tests with PMSG in the lower temperature range resulted in some fish at all three dosage levels hydrating but not spawning. Plugs formed in the oviducts in two of the fish that received dosage levels of 55 and 220 IU respectively. Eggs were water hardened in one and were nonfertilizable. Approximately 20% of the total eggs obtained from the second fish were fertilized. These eggs were normal in size and the majority of them developed and hatched. The larvae obtained from this induced spawning appeared to be normal in all respects and several were reared through metamorphosis.

HCG administered at the level of 200 IU at lower temperatures produced ovulation in one fish, and 4 days after the last planned injection it was spawned. The eggs obtained were normal in size and appearance. Approximately 95% were fertilized and approximately 80% developed and hatched. The larvae obtained from this hormone-induced spawning appeared normal in all respects and many were reared through metamorphosis. One other fish that received the higher dosage level of 400 IU had a plug form in the oviduct and approximately 15% of the eggs present in the ovaries were mature. These eggs were spawned and fertilization was successful. All development halted at the blastula stage and none survived to hatch.

The limited success that was obtained with the hormones oxytocin, DOCA, PMSG, and HCG administered alone is apparent. It is hoped future studies will evaluate the synergistic actions of various hormone combinations administered to winter flounder.

Two test fish that received injections of carp pituitary at the level of 5.0 mg ovulated and were stripped (Table 5). The eggs obtained from these induced spawnings were in the normal size range of winter flounder eggs and approximately 90-95% were fertilized. The majority of them developed normally and approximately 85% hatched. The larvae appeared normal in all respects and many were reared through metamorphosis. At the dosage level of 0.5 mg, three fish ovulated and were spawned after receiving three to six injections. During the time of injecting these fish hydrated normally. The eggs obtained from these induced spawnings were normal in size and approximately 95% were fertilized. Their development was normal and approximately 70-85% survived to hatch. Larvae obtained appeared normal in all respects and several were reared through metamorphosis.

All of the uninjected controls at the conclusion of the trials displayed signs of hydrating. Four out of the six fish were sacrificed and GSI levels recorded. The remaining two fish that displayed the best signs of hydration were spared and

TABLE 5.—Effects of carp pituitary on *Pseudopleuronectes americanus*. All fish experienced a 9L:15D photoperiod, water temperature range 1.5°-3.5°C ($\bar{x}$ 2.5°C). Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	No. of injections	Total length (mm)	Initial body weight (g)	Weight change (% final wt.)	GSI[1] (% final wt.)	Hydrate	Ovulate	Fertilization (%)	Hatch (%)
Carp pituitary	3	410	830	+1.20	1.11	+	+	90	85
5.0 mg/454	3	415	1,069	+2.99	1.06	+	+	95	85
g fish	3	316	453	−0.04	1.60	[2]0	0		
Carp pituitary	3	325	509	+2.55	1.11	+	+	95	75
0.5 mg/454	6	357	556	+2.16	1.10	+	+	95	80
g fish	6	345	509	+3.54	1.32	+	+	95	70
Control	0	360	494	+3.64	20.04	+	0		
	0	347	462	+4.11	21.21	+	0		
	0	339	510	+4.31	21.37	+	0		
	0	310	381	+6.04	20.47	+	0		
	0	298	321	+2.18	2.18	+	+[3]	95	30
	0	359	492	+2.64	1.11	+	+[3]	95	90

[1]Gonadosomatic index.
[2]Sexually immature.
[3]Ovulated and spawned 46 days after termination of testing trials.

allowed to continue to develop without interruption. After 46 days they ovulated and were stripped.

The ability of carp pituitary as an aid in inducing spawning in winter flounder was dramatically shown in these trials. At least six additional weeks of research time was able to be realized when carp pituitary was administered in conjunction with low water temperatures (1.5°-2.5°C). It is hoped that future tests will be initiated to evaluate the effectiveness of various dosage levels and at warmer water temperatures. By controlling photoperiods and water temperatures and injecting carp pituitary it may be possible to extend the research time on the eggs and larvae of this species of flatfish in the laboratory for several additional months through induced spawnings.

In conclusion, it would appear that water temperature may be the most critical factor in producing ovulation; and while the administering of hormones was effective in producing hydration, hydration alone is not sufficient to initiate ovulation. Low GSI levels below 12% in conjunction with water temperatures above 6°C resulted in the majority of test fish not hydrating regardless of the hormone administered.

Hormone treatments had a range of effects depending on the degree of ovarian maturation; test fish in the later stages of development responded while less mature fish developed higher GSI levels but did not ovulate and spawn. No evidence was discovered indicating that spawning induced by hormones produced abnormal larvae.

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NOTES

DISTRIBUTION OF MELANIN IN THE COLOR PATTERN OF *DELPHINUS DELPHIS* (CETACEA; DELPHINIDAE)

Previous studies of cetacean pigmentation have been concerned with the description of color patterns and the possibilities for their evolutionary production and their adaptive significance. Mitchell (1970) identified four basic color patterns among the Delphinidae: saddled, as exemplified by some species of *Stenella*; spotted, as seen in *Stenella plagiodon*; striped, as seen in *Stenella coeruleoalba*; and crisscross, as seen in *Delphinus delphis*. Naming the crisscross pattern as the most complex, Mitchell used it to establish a terminology for elements of the color patterns. One of his conclusions concerning the evolutionary development of the patterns was that the saddled pattern is most primitive, since it is closest to generalized countershading and because one may hypothetically derive the other three patterns from it by addition of certain features, emphasis of some features, and de-emphasis of others.

Perrin (1972) compared the color pattern of a partially albinistic whitebelly spinner (*S. longirostris*) with that of a normally pigmented individual and showed that the normal color pattern may be described in terms of two independently produced but interacting pigmentation systems or components, only one of which had developed in the partially albinistic individual. Using the two-component approach, he analyzed the color patterns of other delphinids, including *Delphinus* spp., and proposed pattern homologies among the species. He suggested that the more generalized of the two pigmentation systems involves the cape (terminology of Perrin 1970) and its accessory stripes, eye and gape marks, and dorsal fin and fluke colorations. This is overlaid by a second component system that he named the "dorsal overlay system." He proposed that partial overlapping of the two produces the four-part crisscross pattern in *Delphinus*.

If two discrete interacting pigmentation systems are involved in the color pattern of *Delphinus*, that fact should be evidenced in the microstructure of the skin. Previous histological study of *Delphinus* skin provides only a description of the general microscopic anatomy. Stiglbauer (1913) described the microstructure of the skin of *Delphinus delphis* in great detail, including the existence of large dermal papillae and epidermal pegs with granular inclusions of pigment that he identified as melanin. His sample, however, was from the back of a single animal, and he did not have the opportunity to compare the distributions of pigment in different parts of the color pattern. Sokolov (1962) commented very briefly on the pigmentation of two specimens of *Delphinus*, stating that the epidermis on the back and below the dorsal fin was moderately pigmented, on the side of one animal was lightly pigmented, and along the side of the other animal and on the bellies of both was unpigmented. This paper reports the results of comparative microscopic examination of skin samples taken from various areas of the color pattern.

Materials and Methods

Skin samples, each about 5 cm square, were taken from various areas of the bodies of two animals as shown in Figure 1. The porpoise were collected at San Diego, Calif. One animal (field no. WFP 125, adult female, 176 cm, 61 kg) had been frozen for several months before dissection, and the other (WFP 221, adult male, 185 cm, 83 kg, Figure 2) was sampled about 1 h after death.

One centimeter-square specimens were fixed in 10% Formalin,[1] and imbedded in paraffin. Sections were cut 8 μm thick and stained with Schmorl's ferricyanide for malinin. This method stains melanins a dark blue or blue-green, while other epidermal and dermal tissue is stained light green.

The prepared sections were examined under a light microscope. Pigment densities were scored at 125 diameters magnification.

Results

General microscopic anatomy of the skin of *Delphinus* is simple when compared with that of terrestrial mammals and fits the description of cetacean skin given by Simpson and Gardner

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

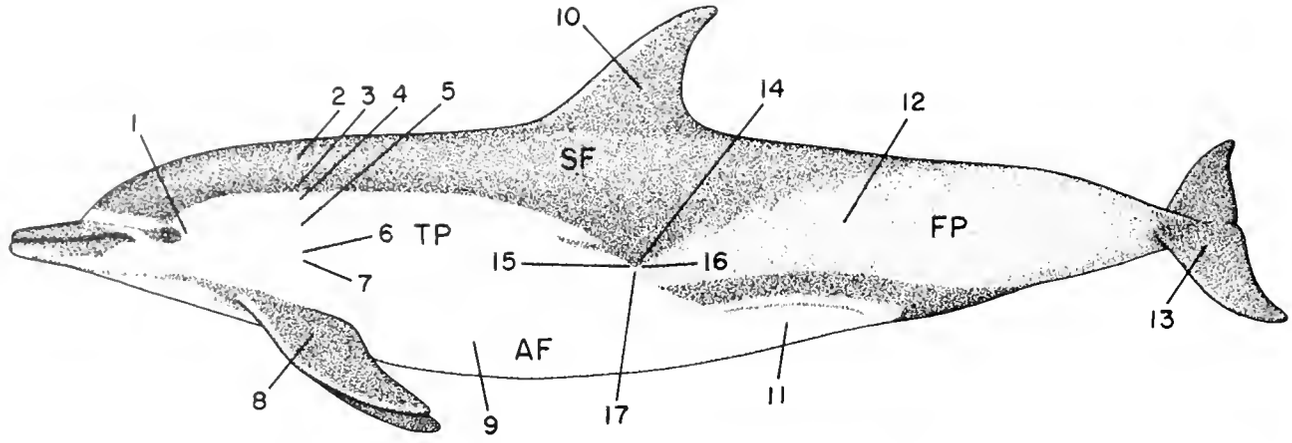

FIGURE 1.–Major pattern features (terminology of Mitchell 1970) and locations from which skin samples were taken: SF = spinal field (black), TP = thoracic patch (buff), FP = flank patch (gray), AF = abdominal field (white).

(1972). The epidermis generally lacks hair (a few hairs are present on the snout in early development but disappear before or shortly after birth), cuticular keratin, and accessory glands. Its thickness varies, being greatest in the ventral region and least on the flippers, dorsal fin, and flukes. The superficial layer of the epidermis, about 10 cells thick, shows considerable flattening of cells. The epidermis consists almost entirely of polyhedral prickle cells, many of which show clear, distended infranuclear cytoplasm. This clear cytoplasm at first appears as holes in the tissue when it is viewed in section, but upon closer examination one may identify the nucleoli inside the clear areas. The epidermis interlocks with the dermis by interdigitation of epidermal rete pegs and dermal papillae (Figure 3), and the dermis grades into the subcutaneous blubber layer. The dermis varies in thickness and density and is composed largely of collagen fibers. The dermal papillae contain blood vessels, blood cells, and other loosely organized connective tissue.

Melanin pigmentation is restricted to the epidermis and is consistently more concentrated at the edges of the epidermis than elsewhere. It is usually most concentrated around the bases of the dermal papillae (at the apices of the epidermal rete pegs) and extending in bands from the apices of the dermal papillae. The pigment has been classified here into three groups for purposes of quantification. "Diffuse" pigment appeared simply as an area which stained darker green than the background and in which pigment grains could not be discerned even at 1,250 diameters magnification. In addition to diffuse pigment, there were granules ranging from less than 0.1 μm to over 5 μm in diameter. Most were spherical or ellipsoid. Granules less than 5 μm in greatest diameter were termed "small grains." These seemed to be actually aggregations of even smaller granules. Those termed "large grains" were larger than 5 μm in diameter and were so dense as to appear as single entities even at high power. Diffuse pigment was characteristically situated peripheral to the nuclei of the prickle cells. This was particularly evident in the central areas of the epidermis. Pigment granules were in general most concentrated at the edges of the epidermis and appeared to extend toward the surface in diffuse bands. In the more lightly colored skin specimens these bands extended only from the apices of the dermal papillae, but in more densely pigmented skin they were more numerous and tended to blend together, resulting in uniform density of pigment throughout the epidermis.

The density of pigment was noted in three regions in each sample: around the bases and edges of the dermal papillae and in the bands described above (Table 1). The observations were each coded from 0 to 4 as follows: for diffuse pigment, 0 = none, 1 = very small amount, 2 = small amount, 3 = medium amount, 4 = large amount; for small grains, 0 = $<$ 1 grain per mm^2, 1 = 1-3 grains per mm^2, 2 = 4-7 grains per mm^2, 3 = 8-11 grains per mm^2, 4 = $>$ 12 grains per mm^2; for large grains, 0 = 0 grains per 4 mm^2, 1 = 1 grain per 4 mm^2, 2 = 2-3 grains per 4 mm^2, 3 = 3-6 grains per 4 mm^2, 4 = $>$ 6 grains per 4 mm^2. Skin samples which appeared white were completely unpigmented or showed very small amounts of diffuse and/or small grains. The buff color characteristic of the thoracic patch (terminology of Mitchell 1970) was associated with either equal prominence of diffuse and granular pigment or

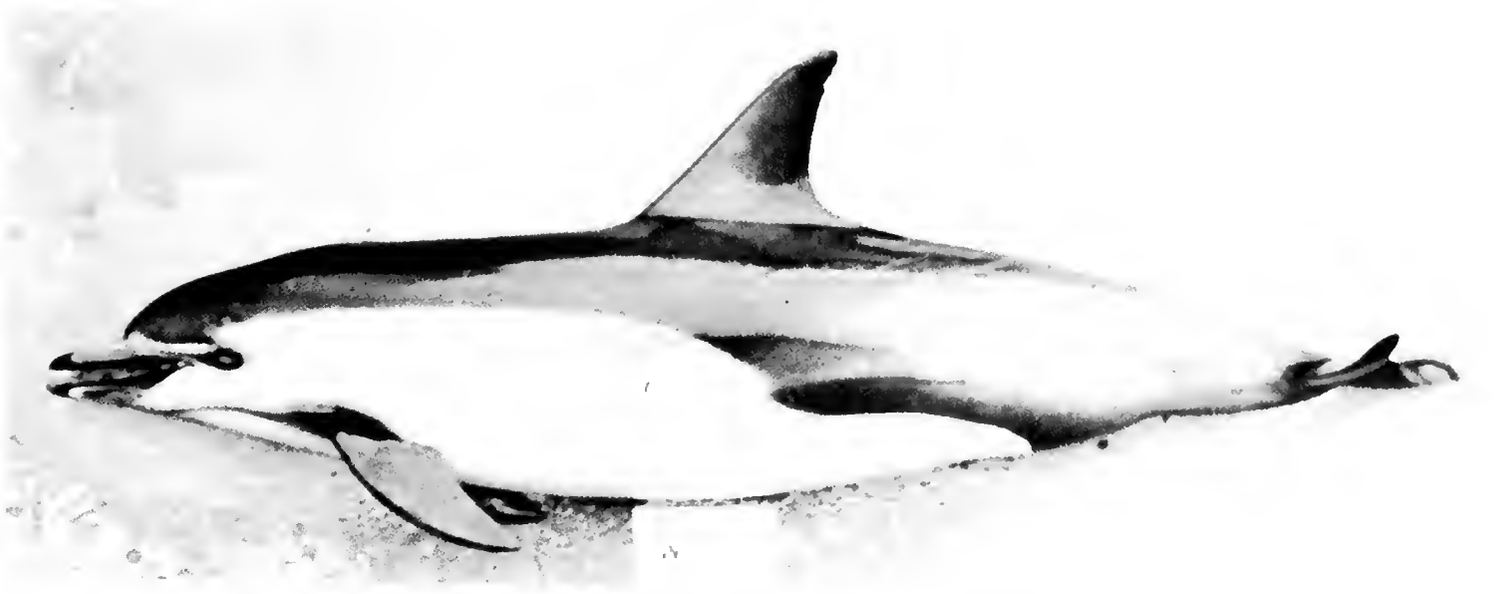

FIGURE 2.—*Delphinus delphis*: Specimen no. WFP 221.

FIGURE 3.—Typical appearance of dermal-epidermal boundary of skin of *Delphinus delphis* (WFP 221 sample no. 10 in Table 1). Note concentration of pigment granules around bases of dermal papillae and in bands extending from ends of papillae. Magnification 1,250 diameters.

greater prominence of diffuse pigment. In gray samples from the flank patch, large grains were present, but the small grains were most prominent. Samples of black skin from flippers and flukes showed the highest densities of large grains, which were more prominent than the small grains.

The histological evidence (summarized in Table 2) supports the concept of interacting color pattern components. As indicated previously, the spinal field may be described as a result of the interaction of the pigmentation of the cape and the dorsal field. The buff colored thoracic patch (i.e., the cape) contains relatively high concentrations of diffuse pigment, while in the grey flank patch (i.e., the dorsal overlay) granular pigment is more prominent. The spinal field is characterized by a larger amount of diffuse pigment than is present in the flank patch, and a larger amount of granular pigment than is present in the thoracic patch. The high concentration of grains in the spinal field indicates a possible synergistic effect of the two component systems.

Perrin (1972) suggested that the flukes are pigmented only as part of the cape system. The skin of the flukes (sample no. 13) contained large amounts of all three types of pigment, indicating that pigmentation of the flukes involves both the cape system and the dorsal overlay system. The skin of the flipper (sample no. 8) also contained large amounts of all three types of pigment.

The major difference between samples taken from WFP 125 (female) and those taken from WFP 221 (male) was that the epidermis was thicker (0.75-1.70 mm as opposed to 0.50-0.95 mm) in the latter animal. Thus a lower density of pigment was required to produce the same color. Also, the samples taken from the buff-colored area of WFP 221 showed conspicuously less diffuse pigment.

TABLE 1.—Results of microscopic examination of pigment distribution in skin of two *Delphinus delphis*. Codes explained in text.

	Pigment density (coded)									
	Diffuse			Small grains			Large grains			
Sample no.	Bases	Edges	Bands	Bases	Edges	Bands	Bases	Edges	Bands	Color
WFP 125♀										
1	4	3	2	2	2	2	0	0	0	buff
2	4	3	1	4	4	2	4	3	3	black
3	3	3	1	4	3	2	4	3	2	black
4	3	3	2	2	2	1	1	0	0	buff
5	3	3	2	2	2	1	1	0	0	buff
6	3	3	1	2	2	1	0	0	0	buff
7	2	2	1	3	2	1	0	0	0	white
8	3	2	1	4	3	3	4	3	2	black
9	2	2	0	1	1	0	0	0	0	white
10	4	3	0	3	3	2	2	1	0	gray
11	2	2	1	1	1	0	0	0	0	white
12	2	1	0	3	2	2	1	0	0	gray
13	4	3	2	4	3	2	4	3	2	black
14	3	3	1	4	2	2	3	2	1	black
15	3	3	2	2	2	1	0	0	0	buff
16	2	2	0	3	2	2	1	0	0	gray
17	2	2	1	1	1	0	0	0	0	white
WFP 221♂										
1	2	2	1	2	2	1	0	0	0	buff
2	2	2	2	4	4	3	3	3	3	black
3	3	2	2	4	4	2	3	2	2	black
4	1	1	1	2	2	2	0	0	0	buff
5	2	2	1	2	2	1	0	0	0	buff
6	2	2	1	2	2	0	0	0	0	buff
7	0	0	0	1	1	0	0	0	0	white
8	3	2	1	4	4	3	3	2	2	black
9	0	0	0	0	0	0	0	0	0	white
10	3	2	1	3	3	2	2	2	2	gray
11	1	1	0	0	0	0	0	0	0	white
12	0	0	0	2	2	1	0	0	0	gray
13	3	2	2	4	4	2	3	2	2	black
14	3	3	2	3	3	2	3	2	2	black
15	2	2	1	1	1	0	0	0	0	buff
16	2	1	1	2	2	1	1	1	1	gray
17	1	1	0	1	1	0	0	0	0	white

TABLE 2.—Average pigment density values for four major features of the color pattern of *Delphinus delphis*. Coded values in Table 1 are averaged over bases, edges, and bands, over all relevant samples, and over both animals. Number of samples included for each animal is in parentheses.

	Pigment density		
Feature	Diffuse	Small grains	Large grains
Ventral field: white (4)	0.96	0.67	0
Thoracic patch: buff (5)	2.37	1.60	0.07
Flank patch: gray (2)	0.92	2.00	0.42
Spinal field: black (4)	2.46	3.08	2.67

Discussion

The color pattern of *Delphinus* evidently consists of two overlapping and interacting pigmentation components that differ mainly in the density and size of pigment particles. The pigment exhibits a continuum of grain size, with the very smallest particles being associated with a buff color. It seems likely that the diffuse pigment is also composed of particles too small for resolution with the light microscope. This evidence suggests that there may be a developmental progression in grain size from the unpigmented or truly white condition through buff and gray to black. This result is consistent with Mitchell's (1970) proposal of the "saddled" pattern as most primitive in recent cetaceans. Inhibition of pigment aggregation could result in the high concentration of diffuse pigment which is typical of buff regions in *Delphinus*. Fox (1953) and others have stated that there are different types of melanins, possibly characterized by different chemical compositions or structures, although none have been adequately described chemically, due to their insolubility and their general lack of adaptability to most physicochemical methods. From the previously described evidence it may be suggested that the type of malanin which produces the buff color is of a composition which does not allow its further polymerization, but may well favor its combination with a protein, as phaeomelanin, instead of aggregation into granules. One might also hypothesize control by dispersing or concentrating

hormones, although this would be physiologically and developmentally more complex. In gray and black areas, aggregation of pigment seems to continue, and melanocytes migrate toward the surface from the base of the epidermis until diffuse pigment is largely replaced by granular pigment. The process is apparently stopped at some point, after which increase in thickness of the epidermis may result in a lower average density of pigment.

Acknowledgments

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OCCURRENCE OF TWO CONGRIDAE LEPTOCEPHALI IN AN ESTUARY

During the night of 23-24 August 1971, I caught two congrid leptocephali in Montsweag Bay, part of the Sheepscot River-Back River estuary, Wiscasset, on the southern Maine coast. These larvae were identified as conger eel, *Conger oceanicus* (D. G. Smith, pers. commun., 15 April 1974). The estuary was described by Stickney (1959). Recksiek and McCleave (1973) provide additional information about the estuary and Montsweag Bay. The leptocephali were collected near their sampling station G3 (lat. 43°56′N, long. 69°42′W). Briefly, Montsweag Bay is a shallow (1 m at mean low water) and wide (2.4 km) basin, but it has a narrow channel (9 m deep at mean low water) through most of its length. Narrow openings at its northern and southern ends allow tidal flow. Mean tidal difference is approximately 3 m. Seasonally, water temperature extremes in Montsweag Bay range from 0.0° to 18.5°C. Salinity ranges from 7 to 30‰. Gear used was essentially that described by Graham and Venno (1968).

One larva (98 mm TL) was captured during the flooding tide 1 m below the surface; the other (91 mm TL) during the ebbing tide within 3 m of the bottom. Water depth at this location was approximately 9 m at mean low water. During this period, the average salinity was 26.0‰ and the average water temperature was 17.7°C.

Conger eel adults and leptocephali have been reported from the Gulf of Maine (Bigelow and Schroeder 1953), but apparently most leptocephali are found in the western North Atlantic (Schmidt 1931). Conger eel leptocephali, however, have never been reported from such low-salinity water. Bigelow and Schroeder (1953) illustrated one 84 mm long from Chesapeake Bay, but they do not give the salinity at the collection site. They also state that conger eel leptocephali grow to 150-160 mm. Smith (pers. commun., 15 April 1974) commented that my specimens were beginning to metamorphose since the gut of each had shortened noticeably. Conger eel leptocephali apparently are able to tolerate this low-salinity water at least during metamorphosis.

If conger eel leptocephali typically grow to the size reported by Bigelow and Schroeder (1953), then they must shrink tremendously in length during metamorphosis. My specimens probably shrank during storage, but probably not enough to account for that much size difference.

Acknowledgments

David G. Smith, Marine Research, Inc., Woods Hole, Mass., identified the specimens. Equipment and facilities were furnished by the University of Maine, Orono, Maine. P. C. Jensen operated the RV *Cypris*. Research funds for this and associated research were provided by the Maine Yankee Atomic Power Company.

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CHLORINATED HYDROCARBONS IN SEA-SURFACE FILMS AND SUBSURFACE WATERS AT NEARSHORE STATIONS AND IN THE NORTH CENTRAL PACIFIC GYRE

Chlorinated hydrocarbons, DDT residues, and polychlorinated biphenyls (PCB's) entering the oceans via atmospheric transport, runoff, and outfalls (National Academy of Sciences 1971) may be concentrated in the lipid constituents (Garrett 1967; Duce et al. 1972) found in surface films. The chlorinated hydrocarbons can then enter marine food chains, most probably by association with particulate detritus and subsequent ingestion by filter-feeding organisms. Further concentration in higher trophic levels is well documented (see, for example, Harvey et al. 1971) and will not be discussed here.

There have been only two reported studies on the concentration of DDT residues and PCB's in surface films. Seba and Corcoran (1969) found high concentrations of *p,p'*DDT, *p,p'*DDE, *o,p*DDT, aldrin, and dieldrin in the surface microlayer collected at locations in Biscayne Bay, Fla., and 10 miles offshore in the Florida Strait. Duce et al. (1972) found that PCB's (but no DDT residues) were concentrated in surface films from Narragansett Bay, R.I. Seawater collected at 1-2 m in the California Current was analyzed for DDT residues (Cox 1971) and these results will be taken as subsurface water concentrations in California coastal waters.

This note reports on the content of *p,p'*DDT, *p,p'*DDE, and PCB's in surface films collected at coastal stations off southern California and Mexico; and in surface films, subsurface waters, and particulate matter from the North Central Pacific Gyre (Table 1).

Methodology

All surface films were collected with a Monel[1] or stainless steel screen (Garrett 1965) into 2.5-liter glass bottles. The coastal samples (SIO 1-2; M 1-4) were poisoned with mercuric chloride. The Cato samples were filtered on shipboard through solvent-extracted and ignited GF/C glass-fiber filters. The filters were frozen in glass vials at -20°C, and the filtrate preserved with 75 ml of hexane. Subsurface samples were collected in 2.5-liter glass bottles 10-15 cm below the surface and treated as above. In all operations the surface films were collected from a skiff at least 0.5 mile upwind from the ship. All glassware, screens, filters, etc., were scrupulously freed of organic matter by ignition at 550°C, rinsing with double distilled solvents, or both.

In the laboratory, the filtrates were acidified to pH 2 with distilled 6N HCl and extracted with three 60-ml portions of hexane. The hexane extracts were dried by passage through anhydrous Na_2SO_4, and then concentrated to 10-15 ml in a Kuderna-Danish evaporator. This extract was further reduced to 50 μl in vacuo, put onto an alumina microcolumn (McClure 1972), and eluted with 3.5 ml of hexane. The eluate was dried in vacuo and taken up in 50 μl of isooctane. The filters were extracted in a soxhlet overnight with 20 ml of

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sample locations, collection dates, and sea conditions.

Sample number and description		Sample location	Collection date	Sea conditions
[1]SIO-1	Surface film	Off SIO Pier	7-July-71	Calm. Moderate film
SIO-2	Surface film	Off SIO Pier	7-July-71	Calm. Moderate film
[2]M-1	Surface film	Lat. 21°30'N, long. 108°30'W Mouth of Gulf of Calif.	23-Oct.-71	Calm. No visible film
M-2	Surface film	Lat. 19°10'N, long. 104°30'W 4 mi. off Manzanillo	25-Oct.-71	Calm. Well-developed film
M-3	Surface film	Lat. 17°37.2'N, long. 101°33'W Zihuatenejo Harbor	28-Oct.-71	Calm. Slight film
M-4	Surface film	Lat. 16°49'N, long. 99°53'W 1 mile off Acapulco	30-Oct.-71	Calm. Slight film
Cato I-4	Surface film filtrate and filter	Lat. 31°51.9'N, long. 127°25.0'W	10-June-72	Calm. No visible film
	Subsurface water filtrate and filter	California Current		
Cato I-A1	Surface film filtrate and filter	Lat. 30°59.1'N, long. 155°24.0'W	27-June-72	Choppy. No visible film
	Subsurface water filtrate and filter	North Central Pacific Gyre		
Cato I-A2	Surface film filtrate and filter	Lat. 31°1.8'N, long. 155°25.8'W	29-June-72	Choppy. No visible film
	Subsurface water filtrate and filter	North Central Pacific Gyre		

[1]Scripps Institution of Oceanography.
[2]Mexico.

a 50:50 acetone-hexane solution, the extracts dried over anhydrous Na_2SO_4, and dried in vacuo. The residues were taken up in 50 μl of hexane and treated identically as the above water samples.

Aliquots of the isooctane solutions were injected into a Hewlett-Packard model 5750B gas chromatograph equipped with a Ni^{63} electron capture detector and a 6-foot glass column packed with either 1.5% OV-17 and 1.95% QF-1 or 5% SP2401 on 100/200 mesh Supelcoport. Column temperature was 195°C. An alkaline (KOH, NaOH) precolumn for saponification of DDT residues was used to give confirmatory identification (Miller and Wells 1969). Retention times and peak heights were compared with standard mixtures of *p,p'*DDT, *p,p'*DDE, and Aroclor 1254. Reagent and apparatus blanks were essentially zero, and reextraction of the water sample with hexane showed no additional traces of DDT residues or PCB's. The minimum detectable amounts of *p,p'*DDT, *p,p'*DDE, and PCB's (as Aroclor 1254) are 5×10^{-12} g, 3×10^{-12} g, and 1×10^{-10} g, respectively.

Results and Discussion

In the North Central Pacific Gyre (Table 2), the concentration of DDT residues in surface films and subsurface waters was less than 0.03 ng/liter for all samples, while the PCB content was two orders of magnitude higher, and PCB's were always present. A higher concentration of PCB's in the surface films as compared to the subsurface waters was significant but not striking, largely because well-defined surface films were not present at the time of sampling.

TABLE 2.—Concentrations of PCB's, *p,p'*DDT, and *p,p'*DDE in surface films and subsurface waters. All values in nanograms per liter.

Station	Sample	PCB's	*p,p'*DDT	*p,p'*DDE
SIO-1	Surface film	11	15	0.4
SIO-2	Surface film	50	12	0.2
M-1	Surface film	90	[1]<0.02	[1]<0.01
M-2	Surface film	12	6.8	0.4
M-3	Surface film	24	8.3	1.8
M-4	Surface film	13	2.1	0.1
Cato I-4	Surface film	4.9	0.3	0.1
	filtrate and filter	3.1	0.1	<0.01
	Subsurface water	1.6	<0.02	<0.01
	filtrate and filter	0.9	<0.02	<0.01
Cato I-A1	Surface film	3.3	<0.02	<0.01
	filtrate and filter	2.9	<0.02	<0.01
	Subsurface water	3.6.	<0.02	<0.01
	filtrate and filter	1.1	<0.02	<0.01
Cato I-A2	Surface film	3.5	<0.02	<0.01
	filtrate and filter	1.7	<0.02	<0.01
	Subsurface water	(contaminated)		
	filtrate and filter	0.7	<0.02	<0.01

[1]These lower limits are greater than the absolute minimum amounts detectable due to sample splitting during analysis.

In the California and Mexican coastal waters, both PCB and DDT residue concentrations in the surface films were slightly higher (as would be expected) than in the 1-2 m subsurface waters of the nearshore California Current (Cox 1971).

The available data in the literature pertaining to the chlorinated hydrocarbon content of surface films and subsurface waters is collected in Table 3. This table does not include a considerable amount of unpublished data taken in conjunction with outfall studies and pollution problems in general.

TABLE 3.—Comparison of this work with literature values for the concentration of PCB's and DDT residues in surface films and subsurface waters. All values in nanograms per liter, and are the sum of filtrate and filter from Table 2 where applicable.

Reference	Location	PCB's		DDT residues	
		Surface films	Subsurface waters	Surface films	Subsurface waters
Seba and Corcoran (1969)	Biscayne Bay	ND[1]	ND	185-13,710	<1
	Florida Strait	ND	ND	70	<1
Duce et al. (1972)	Narragansett Bay	450-4,200	<50-150	undetected	undetected
Cox (1971)	Nearshore California Current	ND	ND	ND	2.3-5.6 (1-2 m depths)
This work	California coastal	11-50	ND	12.2-15.4	ND
	Mexican coastal	12-90	ND	<0.03-11.2	ND
	Offshore California Current	8.0	2.5	0.4	0.1
	North Central Pacific Gyre	5.2-6.2	4.7	<0.02	<0.01

[1]Not determined.

The primary aim of this work has been to establish open ocean concentrations of PCB's and DDT residues in surface films and subsurface waters in oligotrophic regions of the ocean such as the North Central Pacific Gyre. The PCB content of open ocean waters are significantly lower relative to inshore waters, and represent the first such numbers for an open ocean environment in the Northeast Pacific.

Acknowledgments

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HATCHING SURVIVAL OF HYBRIDS OF *ONCORHYNCHUS MASOU* WITH *SALMO GAIRDNERI* AND WITH NORTH AMERICAN SPECIES OF *ONCORHYNCHUS*

The cherry salmon, *Oncorhynchus masou*, which is native only to Asian watersheds discharging into the northwestern Pacific Ocean, is a recent introduction to North America. While cherry salmon have been crossed with some Asian salmonids, information on their ability to hybridize with North American salmonids has not been reported in the literature. The primary purpose of these experiments was to determine hatching survival of some interspecific crosses involving cherry salmon, leading to a sound basis for predicting their effects on indigenous salmonid species and their potential value in salmon management.

Materials and Methods

From 10 October to 12 November 1972, hybridization experiments were carried out between 1-yr-old male cherry salmon parr from anadromous stock and female rainbow trout, *Salmo gairdneri*; pink salmon, *O. gorbuscha;* chum salmon, *O. keta;* coho salmon, *O. kisutch;* sockeye salmon, *O. nerka;* and chinook salmon, *O. tshawytscha*. Our cherry salmon were reared at the Washington State Department of Fisheries' Minter Creek Hatchery from eyed eggs sent in 1971 by the Hokkaido Salmon Hatchery, Sapporo, Japan. Incubation facilities were located at the Northwest Fisheries Center, National Marine Fisheries Service, Seattle, Wash. The standard dry fertilization technique was used in conjunction with delayed fertilization techniques described by Poon and Johnson (1970). All fertilization took place within 3 h of collection, with the exception of pink salmon eggs (14 h). There were no apparent effects from delayed fertilization. Numbers of eggs incubated ranged from 1,700 to 8,400; survival was based on the total eggs in each lot.

Discussion

Oshima (1957) reported that cherry salmon have successfully hybridized with redspot salmon, *O. rhodurus*, for many years. Other than hybrids of cherry salmon with redspot or Asian pink salmon, hybrids of cherry salmon with other salmon and trout are rare or unreported (Schwartz 1972; Dangel et al. 1973). Results of our own experiments, as shown in Table 1, show that crosses of cherry salmon with chum, chinook, and pink salmon and with rainbow trout were highly successful, each yielding higher hatching percentages than their respective controls. The reason for this phenomenon is not presently understood but it does indicate an area for further research. Only crosses of coho and sockeye salmon with cherry salmon showed poorer survival than their controls (Table 1). It is interesting to note that though there was no hatch of the cherry × sockeye cross, virtually all of the eggs were fertilized and developed to notochord formation. Each of the successful hybrid crosses yielded surviving fry to a 1 g or larger size accounting for over 85% of the hatch, except for the rainbow and coho crosses where survival to this size was less than 10%.

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TABLE 1.—Hatching success of eggs of hybrid crosses and controls.

Species[1]	Number of degree-days incubated	Percentage hatched	Previously reported results	Reference
Salmo gairdneri × *O. masou*	396	39.5	85% hatch	Suzuki and Fukuda 1971a, b
Salmo gairdneri (control)	321	34.7		
Oncorhynchus gorbuscha × *O. masou*	512	71.6	37-46% hatch	Smirnov 1969
Oncorhynchus gorbuscha (control)	593	62.5		
Oncorhynchus keta × *O. masou*	436	94.1	77% hatch	Sano and Eguchi 1936
			0-96% hatch	Smirnov 1969
			0-69% hatch	Terao and Hayashinaka 1961
Oncorhynchus keta (control)	504	90.9		
Oncorhynchus kisutch × *O. masou*	300	26.5	None	
Oncorhynchus kisutch (control)	333	90.9		
Oncorhynchus nerka × *O. masou*	660	0.0	0% hatch	Suzuki and Fukuda 1971a, b
			0-3.3% hatch	Terao and Hayashinaka 1961
Oncorhynchus nerka (control)	642	96.0		
Oncorhynchus tshawytscha × *O. masou*	426	97.4	None	
Oncorhynchus tshawytscha (control)	486	72.9		

[1]Female listed first and male last.

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TRAP CONTRIBUTIONS TO LOSSES IN THE AMERICAN LOBSTER FISHERY

Studies to evaluate the impact of unbuoyed traps on American lobster, *Homarus americanus*, survival were conducted in Maine waters from July 1971 to June 1973.

Materials

On 22 July 1971, 98 tagged lobsters of various legal and illegal sizes and both sexes were placed in 35 unbaited conventional square traps, with 30-mm lath spacing, without buoy lines, on the sea bottom near Jonesport, Maine, in depths ranging from about 10 to 20 m (Table 1). On 29 July 1971, four tagged lobsters were added to one trap from which the previous occupants had escaped by 24 July.

The 84-m^2 study site, considered by fishermen not to be a good lobster habitat, having a muddy bottom and no rocks which could be utilized as cover, was purposely selected because its use would not interfere with commercial fishing and traps would be protected from storm damage.

Methods

Traps were checked on nine occasions before 15 October 1971, by scuba diving. When traps were checked by diving, it was possible to count the lobsters and observe evidence of cannibalism, but tagged lobsters could not readily be distinguished from others that entered the traps. In order to differentiate tagged from untagged lobsters, all traps were brought to the surface for more thorough examination. This practice was commenced on 15 October 1971 and continued throughout the remaining period of the study.

Traps were retrieved 16 times between 15 October 1971 and 26 June 1973, making a total of 25 checks during the investigation. The length of time between observations of the 2-yr period ranged from 1 to 161 days, with a median interval of 13 days and a mean of 28 days. Observations were curtailed during the low temperature months because of the inactivity of lobsters in relatively shallow water.

Results

During the first summer-fall season, 43% of the tagged lobsters cannot be accounted for; 25% remained captive; 20% escaped and were recaptured; and 12% were cannibalized. During the second summer-fall season, 126% recruitment occurred; 22% cannot be accounted for; 18% of both tagged and recruited lobsters were cannibalized; 55% remained in the traps; and 5% of tagged lobsters escaped and were recaptured.

A minimum 67 "wild" lobsters were recruited by the traps, of which 24 still remained captive when the study was terminated. Two tagged lobsters that departed their original traps entered other experimental traps which they in turn left before entering two of the commercial traps surrounding the study site. A tagged male lobster missing from trap no. 6 was caught in a commercial trap 0.4 km from the study area on 28 April 1973, after having remained in trap no. 6 for 22 mo and having moulted once in October 1971 from sublegal to legal size. Four traps failed to recruit any lobsters; 9 recruited one each; 13, two each; 6, three each; 2, four each; and 1, six. Only five traps recruited more lobsters than were initially placed in them, six recruited a like number.

TABLE 1.—Numbers of lobsters observed in 35 unbaited conventional square traps from 22 July 1971 to 26 June 1973.

	1971											1972													1973	
Trap no.	7/22	7/23	7/24	7/27	7/29	8/1	8/2	8/9	8/25	9/21	10/15	2/15	7/25	8/25	9/12	9/18	9/25	10/2	10/12	10/26	11/2	11/15	11/28	12/5	4/24	6/26
1	2	2	2	2	2	2	2	2	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
2	2	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	2	2	2	2	2	2	2	2	2	2	[1]1	[1]1	[1]1	[1]1	[1]2	[1]2	1	1	1	1	1	1	1	1	1	0
4	4	4	4	4	4	4	4	2	2	2	[2]2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]2
5	4	4	3	2	2	3	2	1	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
6	4	4	3	3	3	2	2	2	1	1	[1]1	[1]1	[1]2	[1]3	[1]3	[1]2	[1]2	[1]2	[1]2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	0
7	2	2	2	2	2	2	2	2	2	2	[2]2	[1]1	[1]2	[1]2	[1]2	[1]2	[1]2	[1]2	2	[1]2	1	1	1	1	1	1
8	2	2	2	2	2	2	2	2	1	1	[1]1	1	2	2	3	3	3	3	3	3	3	3	3	3	1	1
9	2	2	1	1	1	1	1	1	1	1	[1]1	[1]1	[1]1	[1]2	0	[4]1	0	0	0	0	0	0	0	0	0	2
10	4	4	4	3	2	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
11	4	4	4	3	2	2	2	2	1	1	[1]1	[1]1	[1]1	[1][4]2	0	[4]1	0	0	0	0	0	0	0	0	0	0
12	4	4	4	3	3	3	3	3	3	1	[1]1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13	2	2	2	2	2	2	2	2	2	2	[2]2	[1]1	[1]1	0	0	0	0	0	0	0	0	0	0	0	0	0
14	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
15	2	2	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	4	—	0	0	[5]4	4	4	3	2	1	0	0	1	1	2	2	2	[4]2	1	1	1	1	1	1	1	1
17	4	4	4	4	4	4	5	5	3	2	[2]2	[1]1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2	3	2	2	2	2	2	1	1	2	2	3
19	2	2	2	2	2	2	2	2	1	1	[1]1	[1]1	[1]2	[1]1	[1]2	[4]3	3	1	1	1	1	1	1	1	1	1
20	2	2	2	2	2	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0
21	2	2	2	2	2	2	2	1	1	1	[1]1	[1]1	2	[1]2	[1]3	1	1	0	0	0	0	0	0	0	0	1
22	4	4	4	2	2	2	2	2	2	1	[1]1	[1]1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
23	4	4	4	4	1	1	1	1	1	2	[1]1	[1]1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
24	4	4	4	4	3	4	3	3	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
25	2	2	2	1	1	1	1	1	1	1	[1]1	[1]1	[1]1	2	1	2	2	[4]2	1	1	1	1	1	1	1	1
26	2	—	—	1	1	1	1	1	1	0	0	0	0	2	2	3	3	3	3	3	3	2	2	2	1	1
27	2	2	2	2	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	4	—	—	3	3	3	3	2	2	2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	0	0	0	0	0	0	0	0	0
29	4	4	4	4	4	4	4	4	2	2	[2]2	[1]1	[1]1	[1]1	[1]1	[4]3	1	1	1	1	1	1	1	1	1	1
30	2	2	2	2	2	2	2	2	2	2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]2
31	2	—	—	4	4	4	4	3	2	1	[1]1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	2	2	2	2	2	2	2	2	1	1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	2	[1]2	2	[1]2	1	1	1	1	1
33	2	2	2	2	2	2	2	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1
34	4	—	—	3	3	3	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
35	4	4	4	4	3	3	3	4	2	4	[1]2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	1	[1]1
Total lobsters	98			80	77	75	74	66	47	40	29	19	28	38	33	38	33	30	30	28	26	23	23	24	18	27
Total tagged	98										26	18	14	13	11	8	7	5	5	4	4	4	4	4	3	3
Cannibalized											1971 cumulative total = 12			1		4		2			1					

[1] One tagged lobster.
[2] Two tagged lobsters.
[3] One dead lobster.
[4] One lobster cannibalized.
[5] Four tagged lobsters added.
- Not checked.

Discussion

In the three most recent years, gross fishing effort in the Maine lobster fishery has, perhaps temporarily, stabilized at approximately 1.25 million traps, a 67% increase over the 0.75 million level of the preceding 12-yr period.

Annual loss of traps has varied markedly since the mid-1940's. In major late summer-fall storm years, fishermen have reported losses of up to 100% in many fishing areas; at other times less than 10% in other areas. An average annual loss of 20 to 25% has been estimated from interviews with fishermen and counts made by departmental scientific and enforcement personnel of traps stranded intertidally by storms. This estimate would indicate that about 200,000 traps have been lost annually during the past decade from storms, accidents, or vandalism, with each trap containing an average of 3.1 lobsters (Dow 1961). Storm-lost traps are the most consistently damaged and when they are washed ashore, they usually contain dead lobsters.

Cannibalism occurs principally from July to early November, coincident with the greatest concentration of traps, fishermen, and catch. Within this period, 70 to 75% of the annual catch is made, which for the last 30 yr has averaged 9,000 metric tons, consisting of approximately 18 million lobsters. Previous studies (Dow 1961, 1966) also demonstrated a 2½-fold increase in the total number of lobsters entering traps of the summer-fall fishery in comparison with the winter and spring fisheries.

During the 2-yr period of this investigation, in which only 12% of the traps used were sufficiently damaged by lobster chelipeds to permit escape, the annual Maine lobster catch was 7,670 metric tons, consisting of 14.2 million lobsters caught in 1.25 million traps. Between July and November when the peak of cannibalism occurs, 77% of the annual catch was made and consisted of 10.9 million lobsters.

Conclusions

1. Unbaited, unbuoyed traps continue to catch lobsters for an indefinite time, with most of the catch being made between June and September.
2. Cannibalism occurs during the summer and fall coincident with moult.
3. Approximately one-third or more of all lobsters in or entering unbuoyed traps will be lost to the fishery from cannibalism or retention.

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Vol. 73, No. 3 July 1975

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(Continued on back cover)

Seattle, Washington

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FIELD CRITERIA FOR SURVIVAL OF ANCHOVY LARVAE: THE RELATION BETWEEN INSHORE CHLOROPHYLL MAXIMUM LAYERS AND SUCCESSFUL FIRST FEEDING[1]

REUBEN LASKER[2]

ABSTRACT

Northern anchovy larvae, *Engraulis mordax*, produced by laboratory-spawned fish, have been used to detect concentrations of larval fish food in situ along the California coast. First-feeding larval anchovies, whose development was controlled by temperature manipulation aboard ship, were placed in samples of Los Angeles Bight water taken from the surface and from chlorophyll maximum layers. Feeding by larvae in water from the surface was minimal in all experiments but extensive feeding occurred in water from the chlorophyll maximum layers when these contained phytoplankters having minimum diameters of approximately 40 μm and which occurred in densities of 20 to 40 particles/ml. In March and April 1974, the chlorophyll maximum layer along the California coast from Malibu to San Onofre (a distance of about 100 km) consisted chiefly of a bloom of the naked dinoflagellate *Gymnodinium splendens*, a food organism known to support growth in anchovy larvae. Copepod nauplii and nonliving particles were never in high enough concentration or of the proper size to be eaten by the larvae. A storm which caused extensive mixing of the top 20 m of water obliterated the chlorophyll maximum layer and effectively destroyed this feeding ground of the larval anchovy.

Probably the major problem confounding fishery scientists interested in rational management of fisheries is an inability to predict recruitment failure (Gulland 1973) despite the vast amount of laboratory and field work on food chain analysis leading to fish production which has occupied many workers in marine studies for the past two decades (Steele 1970). Gulland (1973) asks the most pressing question, "Can a study of stock and recruitment aid management decisions?" and in the same article answers "No." This pessimistic reply is given because, as he says, "there is no method which is likely to be generally successful, [because] the most promising depends on lengthy and costly collection of data, probably extending over a long period." The work reported in this paper suggests an approach which has not been previously used in fishery research as far as I am aware, and which, I believe, makes the answer Gulland has given somewhat less pessimistic than when he made it.

However, it is generally agreed among fishery biologists that large spawning populations of fish do not ensure subsequent large year classes, and conversely, small spawning populations occasionally give rise to exceptionally large classes (Hjort 1926). Hjort (1914) postulated that these variations in year class strength are probably due to differential mortality of the larvae. He believed, for example, that the larvae of the Norwegian herring, *Clupea harengus*, suffered huge mortalities resulting in small year classes when there was a lack of food for the first-feeding larvae. The attractiveness of this hypothesis has generated a number of laboratory studies (see, for example, Lasker et al. 1970) which have shown that the density of larval food must be higher than that usually found at sea in order to obtain even moderate larval growth and survival. For an in-depth discussion of the larval "critical period" as affected by food see May (1974), and for a review of laboratory attempts to rear fish larvae, refer to May (1971). The conclusion that the mean density of larval food organisms in the ocean is generally too low to support reasonable survival of fish larvae through metamorphosis, is also substantiated by data from field surveys (Beers and Stewart 1967, 1969). Thus, despite extensive efforts in quantitative marine food chain analysis, it is yet to be demonstrated whether, where, and to what extent there are rich feeding areas in the sea for larval fishes.

[1]MARMAP (Marine Resources Monitoring, Assessment, and Prediction) Contribution No. 17.

[2]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

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As a new approach to this problem it is the purpose of this study to show how laboratory-spawned fish larvae can be used to detect larval feeding grounds at sea and to point out some of the ways this technique might be used to provide the link between marine food chain research and stock and recruitment predictions in fisheries; the latter by determining what the environmental conditions at sea must be with respect to larval fish food to result in a good or bad survival year for particular species of fish larvae.

Because it is essential to the general methodology of using larval fishes as assay organisms for the fitness of seawater as larval fish feeding grounds, in the following I describe some background information on maturation and spawning of anchovies in the laboratory; the methods used for feeding larval anchovies; and the laboratory-determined criteria for feeding already known for the larva of this species. A description of the field work is then given, concluding with a discussion of the criteria which can be used to judge the fitness of the larval anchovy's environment.

THE NORTHERN ANCHOVY

In the California Current, the major pelagic fish population at present is that of the clupeoid *Engraulis mordax*, the northern anchovy. This species is found from British Columbia, Canada to Cape San Lucas, Baja California and extending west about 600 km. Although the anchovy has a protracted spawning season from December to August, about three-quarters of its spawning occurs in the winter and spring months of January, February, March, and April. The factors affecting larval mortality of clupeoids have been investigated in a number of laboratories throughout the world (Holliday and Blaxter 1963) including my own. Recently, it has been possible to intensify laboratory research at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service because of the continuous availability of anchovy larvae. This has been made possible by inducing sexual maturation of adults in the laboratory resulting in daily spawning and fertilization of anchovy eggs throughout the year. Details of this maturation and spawning technique are given by Leong (1971) and Lasker (in press). The availability of first-feeding larvae hatched from laboratory-spawned eggs has made possible the development of a technique whereby specific areas of the ocean could be examined for their potential as larval feeding grounds, and criteria established to characterize parts of the ocean as good or bad areas for larval survival.

LABORATORY-DETERMINED CRITERIA FOR SUCCESSFUL LARVAL ANCHOVY FEEDING

A background of information on larval anchovy feeding is available from a number of studies and was used to guide this investigation.

1. *Particle size at first feeding appears to be critical.* First-feeding anchovy larvae (standard length 3.5 mm) have small mouths and require a food particle about 50 μm in diameter, although particles larger than 100 μm may be taken (Berner 1959). Smaller particles may not be visible to the larvae. Berner (1959) reported that anchovy larvae smaller than 4 mm long taken in plankton tows had eaten particles ranging in length from 24 to 186 μm. However, over 70% of the food in their intestines was between 60 and 80 μm long.

2. *The number of particles per unit volume in the anchovy larva's environment must be above a minimum concentration.* O'Connell and Raymond (1970), using natural plankton as food, showed that the survival of first-feeding anchovy larvae was dependent, in their experiments, on the number of micronauplii per unit volume available to the larvae. Successful first feeding, as pointed out by Hunter (1972), also depends on a sufficiently high density of food particles to compensate for the low capture efficiency (about 10%) exhibited by anchovy larvae when they begin to feed.

3. *The kind of food organism determines survival and growth.* Lasker et al. (1970) fed a variety of phytoplankters and zooplankters to first-feeding anchovy larvae. Only one phytoplankter of those tested, *Gymnodinium splendens*, supported growth and gave relatively good results in survival experiments when compared with larvae fed natural plankton. The rotifer *Brachionus plicatilis*, although not found in the anchovy's normal habitat, also could be used as a laboratory food for older anchovy larvae and a small proportion of first-feeding larvae (Theilacker and McMaster 1971; Hunter 1972).

4. *The greater the concentration of food particles, the more frequent are the feeding strikes made by anchovy larvae; consequently the greater the success in capturing food.* Although examination of field-caught anchovy larvae reveal very few with

any food in their intestine (Arthur 1956; Berner 1959), this seems to be a result of rough handling due to capture in a plankton net and subsequent preservation with Formalin[3] which causes almost all anchovy larvae to defecate (Kjelson et al. 1975). In the laboratory a high proportion of anchovy larvae which had never seen a food particle will strike at and ingest them provided there is a high enough concentration of the right size food particles. Hunter and Thomas (1974) have shown that the rate of larval anchovy feeding increases with increasing food density.

Despite the success of O'Connell and Raymond (1970) and Kramer and Zweifel (1970) who were able to rear anchovy larvae using micronauplii concentrated in wild plankton samples, the quantities needed by the larvae seemed inordinately higher than the concentration of nauplii reported by Beers and Stewart (1967) for the euphotic zone of the California Current. It was possible, of course, that concentrations of nauplii exist in dense aggregations. Beers and Stewart (1970a) reported that nauplii concentrate in or immediately above chlorophyll maximum layers off the California coast. However, no concentrations have been identified which are high enough to support anchovy larvae (e.g., 1/ml). On the other hand, Lasker et al. (1970) showed that anchovy larvae would feed and grow on a diet of the dinoflagellate *G. splendens*. The fact that blooms of a variety of phytoplankters are known to occur in the California Current, particularly in the spring, suggested that phytoplankton cells were more likely to provide the particle size and cell density essential to survival and growth of first-feeding anchovy larvae. For these reasons, inshore chlorophyll maximum layers were selected as possible fruitful areas to investigate for larval feeding.

METHODS

To determine areas in the sea where high concentrations of living particles might be present, a pump was used to bring water on board from known depths. The hose from the pump was lowered below the surface by means of a metered winch. The water was pumped through a Turner fluorometer in the ship's laboratory to measure chlorophyll *a* and other fluorescing substances. Chlorophyll *a* was extracted from water samples taken at each station from different depths and the fluorescence profile adjusted to reflect only chlorophyll *a* (Kiefer and Lasker 1975).

A school of approximately 700 sexually mature northern anchovies, maintained in the aquarium of the Southwest Fisheries Center, La Jolla Laboratory, produce about 1,000 fertilized eggs per day. The number of eggs can be increased by injections of gonadotrophins to stimulate massive spawning in individual fish (Leong 1971). With temperature control of development (Lasker 1964), larvae in first-feeding condition can be made available whenever desired. Thus, preliminary to a cruise, development of embryos and larvae can be accelerated or retarded by temperature manipulation to ensure that on each day of the cruise there will be at least several hundred larvae ready to feed.

Prior to each of the cruises described here, fertilized eggs at the same stage of development were sorted into liter jars containing seawater previously filtered through a 5-μm pore size Cuno Aquapure filter, and the jars were immersed in water baths at suitable temperatures. For transport to the ship insulated chests were used, and on board a temperature-controlled room was continually adjusted between 13° and 18°C to insure that feeding larvae would be available on specific days. Recent studies have shown that newly feeding larvae have only about 2½ days after the yolk sac is absorbed to get sufficient food or they will die (Lasker et al. 1970).

Experiments to determine if samples of seawater contained suitable food for anchovy larvae were done in cylindrical, 8-liter jars wrapped with dull black cardboard and set on black plastic. Above the jars a bank of four "daylight" fluorescent lights were suspended which illuminated the surface of the jars at approximately 2,152 lux. When a sample of seawater was brought into the ship's laboratory it was permitted to warm slowly to room temperature. Larvae were added to 5 liters of seawater by pouring them from the incubation jars. Dilution of the 5 liters by the larval incubation water was corrected by concentrating the contents of an additional liter of seawater to a few milliliters with fine mesh netting and by adding the concentrate to the whole.

A gentle air stream was directed onto the surface of the water in each experimental vessel to ensure mixing of the water. Control experiments on shipboard with cultured organisms indicated that this had little effect on the larvae.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Two cultured food organisms, *G. splendens* and *B. plicatilis*, were used aboard ship to determine if any particular batch of test larvae was in good condition and would feed. Details on the culture of these organisms are given by Thomas et al. (1973) for *G. splendens*, and Theilacker and McMaster (1971) for *B. plicatilis*. Usually a control 5-liter seawater sample was seeded with one or the other cultured organism and a feeding experiment with larvae run concurrently with samples of natural seawater.

Larvae were permitted to feed for 8 h then siphoned out and sucked down onto a membrane filter (pore size 0.8 μm) using a vacuum pump. This rapid removal of larvae from the experimental containers and their fast immobilization on the filters prevented defecation. After air drying, microscopic examination of the transparent larvae permitted counts to be made of larvae which had been feeding and those which had not. The relative proportion of feeding to nonfeeding larvae was subsequently correlated with sizes of the food particles, chlorophyll content, species composition, and the number of particles available to the larvae.

A 1-liter subsample of each seawater sample was preserved with Formalin (final concentration 5%) (Beers and Stewart 1970b). Later the particles in the preserved seawater were settled out and the species enumerated. The method of Utermöhl (as described by Lund et al. 1958) was used to concentrate organisms from known volumes of preserved seawater, usually 100 ml. At least 100 cells larger than 20 μm in diameter were counted from each settled water sample.

On a cruise of the NOAA RV *David Starr Jordan*, 18-21 March 1974, a 16-channel electronic particle counter with a 280-μm pore, Coulter Counter Model Ta, was used to determine the size distribution and numbers of sized particles in seawater samples used for feeding experiments. Only particles 20 μm and larger were counted. Very good agreement was obtained between the electronic counter particle counts and those obtained with the inverted microscope. A comparison is shown in Figure 1. The speed of counting and sizing particles makes the multichannel particle sizing instrument desirable for rapid field assessment of larval fish food organisms. Because the electronic counter was unavailable for two subsequent cruises. 8-12 and 22-23 April 1974, the results for these are given from microscope counts only.

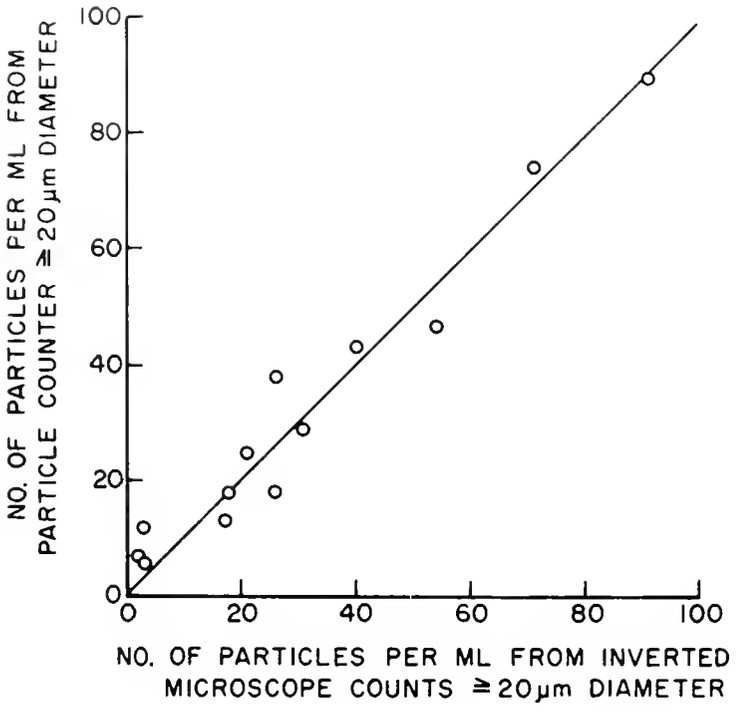

FIGURE 1.—Comparison between instantaneous particle counts per milliliter taken with Model Ta Coulter Counter and mean particle count per milliliter observed through an inverted microscope. A 100-ml sample was concentrated and at least 100 particles of the dominant organism were counted in any visual field. Only particles larger than 20 μm were counted.

To ascertain if anchovy larvae were present at particular depths, plankton tows were taken with a 0.333-mm mesh, 0.5-m mouth diameter net. Because an opening and closing net was unavailable for this work, an open net was dropped rapidly to the desired depth, towed for 10 min at a maintained wire angle of 45°, then pulled up rapidly. The total proportion of time the net spent in water other than in the desired stratum never exceeded 5% of the total towing time. All larvae captured were measured, sorted to species, and counted. Larval counts were corrected to a comparative volume of 1,000 m^3 (Kramer et al. 1972). A flowmeter in the mouth of the net provided a record of the volume of water filtered.

The shipboard experiments were ordinariy done at temperatures of between 15° and 19°C, whereas concentrations of larval fish food organisms and anchovy larvae were occasionally found between 14° and 15°C. It was desirable, therefore, to determine the feeding response of first-feeding anchovy larvae at different environmental temperatures. Experiments to determine this were identical to those done at sea except that the concentration of the cultured organism *G. splendens* was varied from 5 to 200 cells/ml, and the water temperature was controlled within $\pm$0.2°C.

AREA OF STUDY

This investigation was conducted in the Los Angeles Bight along the southern California coastline from Malibu to San Onofre, between 18 and 21 March 1974. All the stations occupied were over the 20-fathom line except for the Laguna Beach station which was over the 270-fathom contour. Table 1 gives the coordinate positions and Figure 2 shows the relative location of the stations. The San Onofre station was reoccupied on 8 April 1974 to determine the persistence of the chlorophyll maximum layer which earlier had contained relatively large numbers of *G. splendens*. The station was occupied again on 10 April, after a violent wind storm and later on 22-23 April after a period of no storms.

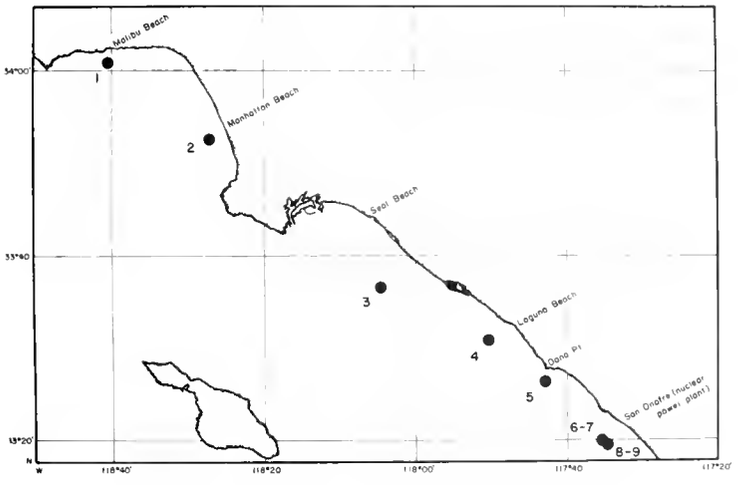

FIGURE 2.—Stations in the Los Angeles Bight.

RESULTS AND DISCUSSION

Shipboard Experiments with First-Feeding Anchovy Larvae

Table 1 provides a summary of the results of feeding experiments with first-feeding anchovy larvae in water from the surface and from the chlorophyll maximum layer or from a depth of about 15 m if no clear chlorophyll maximum was observed. The dominant phytoplankter in the chlorophyll maximum layers was *G. splendens*. For details about *G. splendens* blooms from Baja California, Mexico, and the Los Angeles Bight see Kiefer and Lasker (1975); as reported earlier, Lasker et al. (1970) had demonstrated that anchovy larvae will grow when fed on *G. splendens*.

Also given in Table 1 are the results of a feeding experiment at the San Onofre station on 8 April 1974, 18 days after a chlorophyll maximum layer containing *G. splendens* as the dominant phytoplankter was found. The chlorophyll maximum layer was still present and heavily populated with *G. splendens*. A violent wind storm on 9 April obliterated the chlorophyll maximum layer and no *G. splendens* were seen at this station when it was reoccupied on 10 and 11 April. A comparison of chlorophyll *a* profiles taken before and after the 9 April storm is shown in Figure 3. The results of control feeding experiments are given in Table 2.

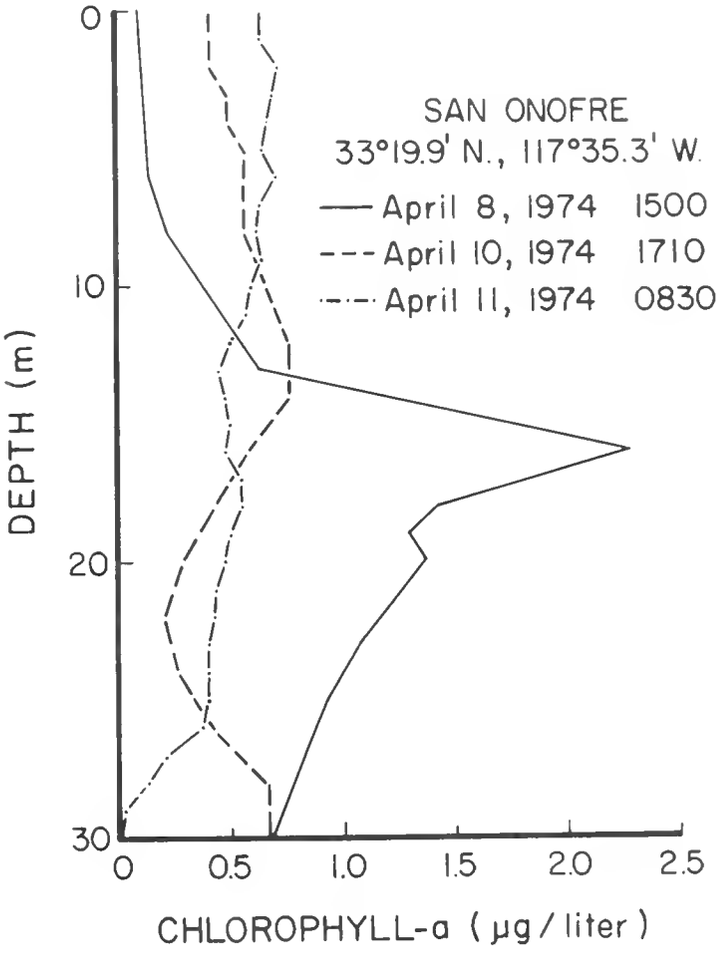

FIGURE 3.—Chlorophyll maximum layers before (8 April 1974) and after (10 and 11 April 1974) a violent wind storm near San Onofre, Calif.

Some anchovy larvae capture a few particles in any concentration of 20- to 100-μm particles over an 8-h period, but experience in the laboratory has shown that feeding on less than 1 particle/h will not sustain a first-feeding larva which becomes weak and dies. Thus, in Tables 1 and 2, two feeding categories are indicated: larvae observed with food organisms packed into the intestine, and

TABLE 1.–Summary of results of 8-h on-board feeding experiments with first-feeding anchovy larvae. *Gymnodinium splendens* appeared in the chlorophyll maximum layers (chl. max.) from Malibu to San Onofre, a distance of approximately 130 km. The subsurface bloom of *G. splendens* at San Onofre persisted until 8 April 1974 (see no. 7 below). A storm on 9 April obliterated the maximum and evidently dispersed the *G. splendens* by wind mixing (see Figure 3).

No.	Date and time A. Surf. temp. B. Chl. max., temp. and depth	Position (lat. N-long. W)	Total number particles/ml		μg Chl. *a* per liter	Feeding by anchovy larvae		
			23-37 μm diameter	>37-299 μm diameter		Percent of larvae with: ¼ to full gut	Percent of larvae with: 1-8 particles in gut	Number of larvae per experiment
1	20 March 1974, 1250							
	A. 15°C	34°00.8′-118°40.6′	14.2	[1]4.1 (< 1)	[2]1.0	2	15	69
	B. 14.2°C, 12 m	(Malibu)	37.3	38.0 (12)	1.8	23	46	93
2	20 March 1974, 1745							
	A. 15.2°C	33°52.5′-118 27.0′	23.1	6.1 (6)	0.4	0	11	94
	B. 14.5°C, 13.5 m	(Manhattan Beach)	29.8	19.7 (12)	1.3	0	18	49
3	21 March 1974, 0900							
	A. 15.8°C	33°36.5′-118°04.3′	217.9	33.2 (< 1)	0.3	0	12	42
	B. 14.2°C, 16.5 m	(Seal Beach)	53.8	352.0 (380)	42.0	22	24	104
4	21 March 1974, 1340							
	A. -	33°30.8′-117°50.3′	34.0	9.0 (0)	0.6	0	10	20
	B. -, 15 m (no chl. max.)	(Laguna Beach)	29.0	5.7 (0)	0.7	0	11	46
5	21 March 1974, 1715							
	A. 15.5°C	33°26.3′-117°42.8′	18.7	5.9 (< 1)	0.5	[3]5	16	19
	B. -, 15 m	(Dana Point)	55.2	23.2 (5)	1.3	0	69	26
6	21 March 1974, 1900							
	A. 15.2°C	33°19.9′-117°35.3′	9.3	4.0 (< 1)	0.2	0	8	49
	B. -, 19.5 m	(San Onofre)	42.4	47.7 (34)	2.3	9	25	32
7	8 April 1974, 1500							
	A. 17.1°C	33°19.9′-117°35.3′	5.7	9.1 (< 1)	0.2	0	13	23
	B. 14.8°C, 16 m	(San Onofre)	14.0	81.3 (64)	2.3	9	40	58
8	10 April 1974, 1710							
	A. 14°C	33°19.4′-117°34.6′	8.4	14.1 (0)	—	0	12	33
	B. 13.5°C, 14 m (no chl. max.)	(San Onofre)	10.5	23.2 (0)	0.8	0	15	20
9	11 April 1974, 0915							
	A. 13.0°C, 5 m (no chl. max.)	33°19.5′-117°34.6′ (San Onofre)	6.4	10.5 (0)	0.6	0	4	50

[1]( ) = number of *G. splendens* per milliliter.
[2]Particles smaller than 20 μm may have contributed to the elevated chlorophyll a at this station.
[3]This 5% figure represents only one larva which filled its intestine ¼ full.

TABLE 2.–Controls for the experiments reported in Table 1. Surface water was seeded with *Gymnodinium splendens* or *Brachionus plicatilis*. In each instance the results showed that the larvae on shipboard were competent to feed. Feeding time was 8 h.

Date	Species seeded	Number particles/ml	Feeding by anchovy larvae		
			Percent of larvae with: ¼ to full gut	Percent of larvae with: 1-8 particles in gut	Number of larvae per experiment
20 March 1974	*B. plicatilis*	40	29	45	72
8 April 1974	*G. splendens*	100	27	13	30
10 April 1974	*G. splendens*	100	32	22	46

those with eight or fewer particles in the intestine after an 8-h feeding period. The largest proportion of larvae did not feed at all, a result common to laboratory experiments as well. The feeding intensity at Malibu, Seal Beach, and San Onofre is typical of first-feeding anchovy larvae in laboratory experiments seeded with a like number of suitable size particles, e.g., *G. splendens*.

The data presented in Table 1 show that the criteria for larval anchovy feeding determined by laboratory experiments are the same when freshly obtained seawater is tested as a source of larval anchovy food. Large numbers of particles smaller than 37 μm in diameter did not stimulate feeding in anchovy larvae. This was particularly apparent at Seal Beach on 21 March; surface water having 218 particles/ml smaller than 37 μm in diameter but with low chlorophyll *a* did not stimulate anchovy larvae to feed. Conversely, the bloom of *G. splendens* in the chlorophyll maximum layer produced heavy feeding larvae tested in shipboard experiments. Furthermore, even with particles

having the right diameter for feeding, a minimum concentration of perhaps between 25 and 50 cells/ml was needed.

The Effect of Temperature on Feeding

The chlorophyll maximum layers along the coast were characterized by temperatures between 14° and 15°C, which is lower than the optimum temperature for feeding and growth in anchovy larvae (16°C). Because shipboard experiments were done at temperatures higher than those found in the chlorophyll maximum layers it was desirable to determine if the minimum particle count at which first-feeding larvae were stimulated to feed was in any way reduced by lower temperatures. Figure 4 illustrates the results of experiments which show that at 14°C, the food particle count must be higher than 20 cells/ml before significant feeding can occur over an 8-h period. At the higher temperature tested, 18°-19°C, food particle counts of between 5 and 20 particles/ml may stimulate feeding. However,

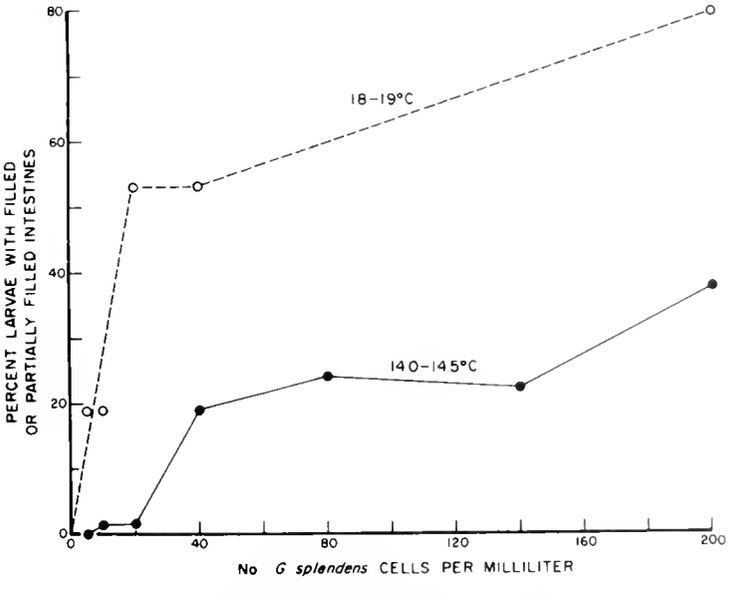

FIGURE 4.—The effect on larval anchovy feeding of different concentrations of food at two temperatures. Each experiment began with 100 larval anchovies which were in first-feeding condition and was terminated after 8 h. See text for details.

during the shipboard experiments, particle counts of 5-20 cells/ml did not stimulate larval feeding even at the higher temperatures (15°-19°C) of the ship's laboratory (Table 1). This discrepancy may be due to the different kinds of food particles available to the larvae, as well as to other factors related to a larva's inability to capture certain particles as opposed to others. For example, when *Chaetoceros* sp. was present in any of the samples, anchovy larvae did not feed on this phytoplankter, owing probably to the spiny nature of this chain-forming diatom, despite the considerable lengths (longer than 37 μm) of the chains. In the Seal Beach surface sample taken on 21 March 1974, *Chaetoceros* sp. and other chain-forming diatoms made up over 30% of the longer than 37-μm category. This result was confirmed at a station off Imperial Beach, Calif. (lat. 32°34.0′ N; long. 117°10.5′ W) on 11 April where a dense bloom dominated by *Thalassiosira* sp. (37 chains/ml) was found. Chlorophyll *a* at the surface was 4.8 μg/liter and slightly higher, 5.1 μg/liter, at a depth of 7 m. Feeding by anchovy larvae on this organism was virtually nil. Thus, the composition of the stock of phytoplankton appears to be an important factor in the initial feeding of anchovy larvae.

The observations described above indicate that chlorophyll measurements alone, and the indication of a strong chlorophyll maximum layer are not by themselves sufficient criteria for establishing the existence of good conditions for the feeding of anchovy larvae. A cruise of the RV *David Starr Jordan* was made back to the San Onofre station on 22 and 23 April 1974. A sharp chlorophyll maximum layer was discovered there once again and was found to extend seaward for at least 14 km (Figure 5), yet shipboard larval anchovy feeding was negative. Subsequent microscopic examination of the water from these layers indicated that cryptomonads of about 10 μm in diameter dominated the samples in concentrations of 3,400-7,200 cells/ml, a size too small to be fed upon by anchovy larvae.

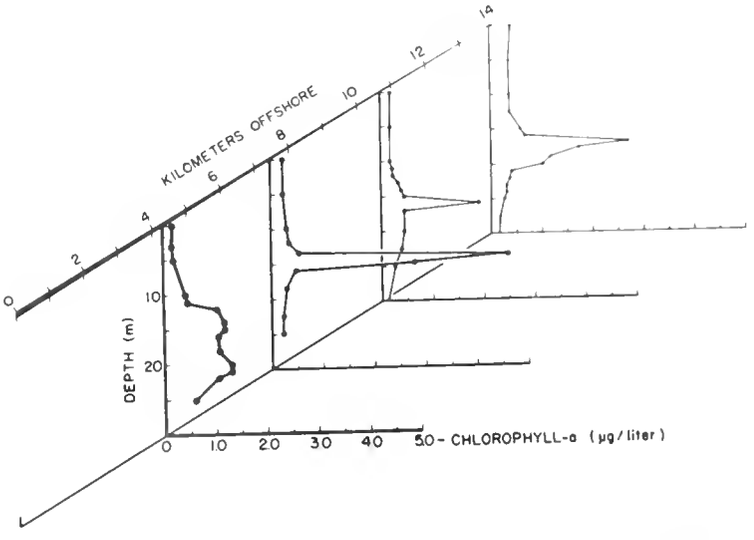

FIGURE 5.—Chlorophyll maximum layers off San Onofre, Calif., 22-23 April 1974.

Vertical Distribution of Anchovy Larvae

At San Onofre on 8 April the chlorophyll maximum layer was due, in part, to a high density of *G. splendens*. Larvae on board ship fed freely in the water from this layer. Judging from the larval feeding and the size and density of the food particles, this chlorophyll maximum layer should have been an ideal place for first-feeding larvae to be found. To test this, plankton tows were made at three depths: within the chlorophyll maximum layer at 16 m, just above the layer at 10 m, and at the surface (see Figure 3). The standard length of anchovy larvae from these tows was measured, and the degree of eye pigmentation noted (full pigmentation indicating a visually competent larva). The results, given in Table 3, show that there was a distinct difference in vertical distribution between the number of first-feeding larvae that could see as opposed to yolk-sac larvae which lack eye pigmentation and could not see.

The surface water contained 2,100 anchovy larve/1,000 m^3. Larvae without eye pigmentation outnumbered sighted larvae two to one. At the 10-m stratum above the chlorophyll maximum layer there were 40,000 anchovy larvae/1,000 m^3 with larvae capable of seeing outnumbered by eight to one. In the chlorophyll maximum layer 4,900 anchovy larvae/1,000 m^3 were present but larvae that could see were about as numerous as those which could not. Although it may be coincidental, the possibility that larvae were actively seeking out areas with food cannot be dismissed.

TABLE 3.—Distribution of anchovy eggs and larvae at three depths off San Onofre, Calif., 8 April 1974.

	Number of eggs or larvae per 1,000 m^3		
Stratum	Larvae with pigmented eyes	Larvae with unpigmented eyes	Eggs
Surface	756	1,344	67,200
10 m	4,610	35,804	151,965
16 m	2,004	2,941	60,034

Criteria for Successful First-Feeding by Anchovy Larvae

It is evident from the data presented in this report that the following environmental criteria must be met before first-feeding anchovy larvae can feed successfully in the ocean. Phytoplankton aggregations with over 20 cells/ml must be available at the same time or within 2½ days after the larvae are ready to feed. Individual phytoplankton cells must be about 40 μm in diameter. Successful feeding is dependent on food density so that the higher the concentration of cells, the better the feeding. Monotypic algal blooms are responsible for some chlorophyll maximum layers off the California coast and first-feeding anchovy larvae were found to be living within them. Only some phytoplankters stimulate feeding and support growth of anchovy larvae; for example *G. splendens* is known to support growth while anchovy larvae would not feed on *Chaetoceros* sp. or *Thalassiosira* sp., spiny and/or chain-forming diatoms. Finally, it could not be demonstrated that micronauplii or other microzooplankton contribute significantly to larval anchovy survival during the first week of larval life. Beers and Stewart (1967) reported that in December 1965, the inshore station off San Diego (their station I) contained a maximum of only 30 organisms/liter in the 35 to 103-μm size class. Of these organisms, copepod nauplii and post-nauplii together numbered 7-9/liter, two orders of magnitude lower than that required by anchovy larvae to survive, i.e., 1,000/liter (O'Connell and Raymond 1970). However, it is reasonable to assume that under special circumstances suitable concentrations of micronauplii might serve as a food source for first-feeding anchovy larvae. Nonliving particles larger than 37 μm were not seen and may be insignificant in the nutrition of first-feeding anchovy larvae because of their low concentration in anchovy spawning areas.

It is important to emphasize the transient nature of good feeding conditions. There was a large number of larvae present at depth at the San Onofre station on 8 April 1974, capable of taking advantage of the subsurface bloom of *Gymnodinium*. Furthermore, spawning had been extensive in the entire water column as indicated by the large number of anchovy eggs caught during the same tows (Table 3). Earlier I indicated that a wind storm obliterated the chlorophyll maximum layer at San Onofre on 9 April 1974, and that 8-h shipboard experiments showed the larvae were unable to capture enough food on 10 and 11 April to fill or partially fill their intestines. If my contention is correct, then a large proportion of the larvae which were present as eggs or yolk-sac larvae on 8 April were doomed to die from lack of food after the storm on 9 April because of the dilution and dispersion of suitable larval food organisms.

Although this investigation was confined to first-feeding anchovy larvae, the technique

described here, using laboratory-reared larvae for field tests of possible larval feeding areas, probably can be extended to older larvae and other species as well. An on-board electronic counter can give a rapid first evaluation of particle size and cell numbers. Microscopic examination of subsamples can be used to verify the shipboard counts and give additional information on species composition of phytoplankters. Chlorophyll profiles can be analyzed routinely on most oceanographic vessels. With information on the biology of the larvae being investigated, it may be possible to determine routinely the quality and extent of larval feeding grounds and with comprehensive temporal information on the food of the larvae, the degree of larval mortality due to inadequate food may be predictable.

ACKNOWLEDGMENTS

Thanks go to Eileen Setzler, Anne N. Dodson, Dale Kiefer, and the able crew of the NOAA RV *David Starr Jordan* for their invaluable assistance during this study, and to Richard Eppley for stimulating discussions which led to the examination of chlorophyll maximum layers as possible feeding grounds for larval fish. Roderick K. Leong provided the fish larvae on demand; without his help this study would not have been possible.

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SPERMATOPHORES AND THELYCA OF THE AMERICAN WHITE SHRIMPS, GENUS *PENAEUS*, SUBGENUS *LITOPENAEUS*

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The spermatophores of the five species of the American subgenus *Litopenaeus* of the genus *Penaeus*, three in the Pacific–*P.* (*L.*) *occidentalis*, *P.* (*L.*) *stylirostris*, and *P.* (*L.*) *vannamei*–and two in the Atlantic–*P.* (*L.*) *schmitti* and *P.* (*L.*) *setiferus*–are described in detail and illustrated. The spermatophore of *P. vannamei* uniquely lacks a wing and a lateral blade. That of *P. stylirostris* possesses a sac with overlapping walls, the free lateral margin not being attached to the underlying wall throughout most of its length; this spermatophore also exhibits the broadest wing, consisting of a rigid anterior region and a posterior membranous one. The spermatophore of *P. occidentalis* is the only one armed with an anterior lobe, a transverse anterior lamina, and a sclerotized flap. The spermatophores of the Atlantic species are very similar, both possessing moderately broad wings, large caudolateral flanges, and a lateral blade; however, in *P. schmitti* the blade is broad anteriorly, whereas in *P. setiferus* it is very narrow. During copulation, as the males deposit paired spermatophores on the females, the sperm masses are released through anterodorsal ruptures of the sperm sacs and become lodged on the thelycum, protected ventrally by the anterior part of the sacs. The open-type thelycum (sperm receptacle lacking), characteristic of the members of *Litopenaeus*, is unique within the genus *Penaeus*. The thelyca are described in order to facilitate understanding how the compound spermatophores are held in place. The thelycum of each species exhibits at least one obvious typical feature by which it may be easily recognized: that of *P. vannamei* is provided with an inverted troughlike median protuberance on sternite XIII; in *P. occidentalis* it possesses densely set setae over most of sternite XIV; in *P. stylirostris* it is armed with a strong, subpyramidal median protuberance on sternite XIV; in *P. schmitti*, on the other hand, it exhibits paired subparallel anterolateral ridges; and in *P. setiferus* paired crescentic anterolateral ridges are present which, although convergent, do not meet on the midline. In all but one species, thelycal concavities of sternite XIII serve to lodge the sperm masses which protrude from attached spermatophores; however, in *P. occidentalis* spoonlike coxal plates of the third pereopods receive the sperm masses.

The five species of *Penaeus*, subgenus *Litopenaeus*, commonly known as white shrimps, support some of the most intensive and valuable fisheries in American waters. Three species are limited to the eastern Pacific, *Penaeus occidentalis*, *P. stylirostris*, and *P. vannamei*, and two occur in the western Atlantic, *P. schmitti* and *P. setiferus*. Mass rearing experiments to discover methods for artificial cultivation on a commercial scale are being conducted on all five species, and spermatophore-bearing or "impregnated" females are needed for this undertaking. Despite these efforts, and the considerable interest of biologists in the reproduction of these species (including mating, spawning, and fertilization), descriptions of the spermatophores of only two of them and brief notes on a third are available. General features of the spermatophore of *P. setiferus* were presented by both Burkenroad (1934) and King (1948), and an account of that of *P. stylirostris* was given by Cárdenas Figueroa (1952). Subsequently, Ewald (1965) and Pérez Farfante (1969) recorded a few observations on the spermatophore of *P. schmitti*. The spermatophores of the remaining two species, *P. occidentalis* and *P. vannamei*, have not been mentioned previously.

Lack of information on spermatophores of the subgenus *Litopenaeus* is due, at least in part, to the fact that impregnated females are not readily found (Weymouth et al. 1933; Burkenroad 1939; Heegaard 1953). In this exclusively American group, the females possess an open-type thelycum (Burkenroad 1934; Pérez Farfante 1969), lacking a seminal receptacle and consisting, instead, of protuberances, ridges, concavities, or grooves and, occasionally, lamellae on sternites XII to XIV to which the spermatophore is attached. The latter is thus exposed to the surrounding water and might be dislodged during capture, as suggested by Burkenroad (1939), or retained for only a short period after copulation. In the females of all other

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subgenera of *Penaeus*, the thelycum exhibits a seminal receptacle where the spermatophores, deposited by the male, remain well protected until the time of spawning or until the succeeding molt.

Among the extensive collections of the subgenus *Litopenaeus* that I have examined, no females of either *P. occidentalis* of *P. vannamei* carrying spermatophores were found. Four impregnated females of *P. stylirostris* and two of *P. schmitti* in the National Museum of Natural History, Smithsonian Institution, constituted the only material at my disposal when this study was initiated. After several unfruitful attempts to collect spermatophore-bearing females in various localities throughout the range of the Pacific species, I obtained such specimens of the three in the Gulf of Panama in March 1973. I caught an additional one of *P. occidentalis* in the same month off Buenaventura, Colombia. In the fall of 1974, Billy R. Drummond sent me three impregnated females of *P. stylirostris* which had been collected off Costa Rica, and recently Harold H. Webber brought me eight spermatophore-bearing females of *P. stylirostris* and five of *P. vannamei* from the same area. The study of the spermatophore of the Atlantic *P. setiferus* was based largely on one female carrying a complete spermatophore and three additional ones in which paired masses of sperm embraced by winglike processes were present on sternite XIII; these specimens had been caught in the waters of North Carolina, and were made available to me by Austin B. Williams. Recently, further observations were made on four impregnated females, two from Apalachicola Bay, Fla., and two from off Texas, given to me by William H. Clark, Jr. and Kenneth N. Baxter.

The spermatophores of the various species are similar (herein described as when in position on the female), each consisting basically of a roughly semicylindrical hardened sperm sac enclosing a columnar sperm mass (spermatozoa within a viscous fluid) surrounded by a thick "sheath" (King 1948) of gelatinous substance (Figure 1A, B). The sac usually bears an anterolateral aliform process, the wing, and is produced caudally or caudolaterally, in a flange. A lateral flap, variable in width and consistency, extends both along the sac and the flange, or only along the latter, usually attached to a firm, elongate blade, and a hardened but plastic dorsal plate is present on the posterodorsal surface of the spermatophore. Finally, a glutinous material always lies against the flange, adhering to the mesial side of the flap. These various accessories associated with the sperm sac presumably help to anchor the spermatophores to the female.

The wall of the sperm sac consists of three somewhat distinct longitudinal regions: a thick, opaque ventral wall, a mostly thin and translucent lateral wall, and an entirely translucent dorsomesial wall. The heavy ventral wall is produced in a longitudinal mesial lapel, clearly delimited by a line along which the ventral and dorsomesial walls meet. The above terminology is consistently employed in the descriptions that follow.

During copulation, two closely attached spermatophores, which are here referred as the compound spermatophore, are transferred to the female (Figure 1C). Immediately after expulsion from the paired terminal ampullae of the male, each spermatophore joins its mate firmly along the dorsomesial walls of the sacs, thus forcing the mesial lapels to project ventrally from the contiguous ventral walls (Figure 1D). These walls, becoming strongly convex when the compound spermatophore is anchored to the thelycum, are responsible for the podlike appearance of the conjoined paired sacs, which constitute a median double structure referred to below as the geminate body.

If the posterior part of the thorax of live mature males is compressed, the spermatophores are readily expelled through the gonopores situated mesially on the coxae of the fifth pereopods. It then may be observed that the spermatophores leave the ampullae with the anterior end foremost, the surface facing the sternum of the male being the same as that which, through a rotation, comes to lie against the thelycum. Consequently, as Kishinouye (1900) first indicated, the right and left spermatophores on the female originate in the corresponding right and left terminal ampullae of the male. Observations by Hudinaga (1942) on *Penaeus* (*Marsupenaeus*) *japonicus* Bate 1888, demonstrated that copulation takes place in a head to head position, the sternum of the male pressing against that of the female. Previously, Burkenroad (1934) and later King (1948) presented hypotheses concerning the transfer of the spermatophores to the thelycum, taking into account the probable utilization of the petasma—apparently so well fitted to lodge the compound spermatophore—and the pereopods. No satisfactory explanation, however, has been advanced as to how a rotation of the spermatophore through 180° around its longitudinal axis, is accomplished.

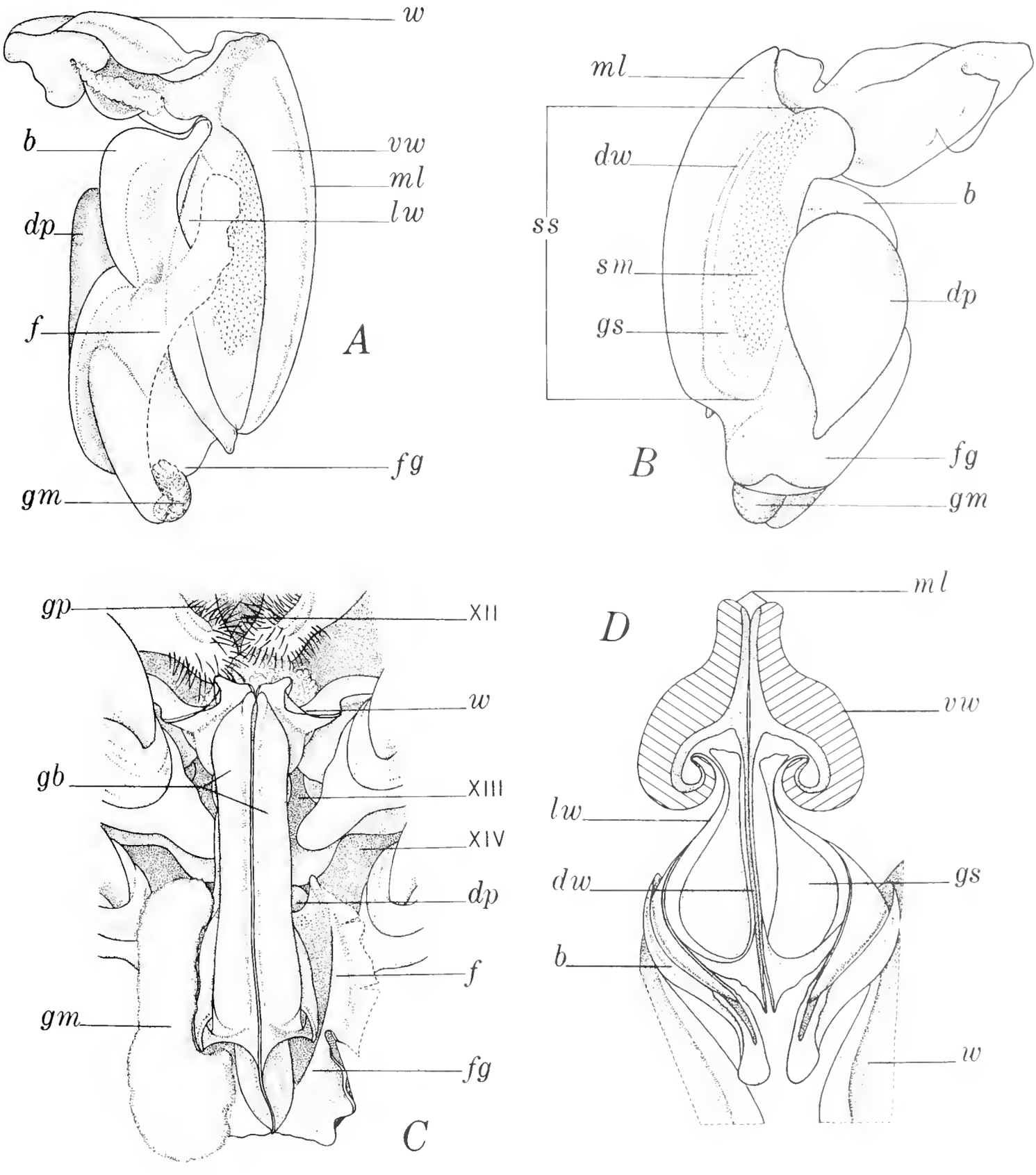

FIGURE 1.—The spermatophores of *Penaeus* (*Litopenaeus*) *schmitti* and *P.* (*L.*) *setiferus* illustrating terms used in the descriptive accounts. *A*, Ventrolateral view of *P.* (*L.*) *schmitti*. *B*, Dorsomesial view of same. *C*, Ventral view of a compound spermatophore of *P.* (*L.*) *setiferus* attached to female. *D*, Cross section of the geminate body of same, immediately posterior to the wings (in preparation of the section the blades together with the torn contiguous portion of the lateral walls have become displaced laterally). *b*, blade; *dp*, dorsal plate; *dw*, dorsomesial wall; *f*, flap; *fg*, flange; *gb*, geminate body; *gm*, glutinous material; *gp*, gonopore; *gs*, gelatinous substance; *lw*, lateral wall; *ml*, mesial lapel; *sm*, sperm mass; *ss*, sperm sac; *vw*, ventral wall; *w*, wing; XII, XIII, and XIV, sternites.

The intent of this paper is to present detailed descriptions of the spermatophores of the five species of *Litopenaeus*. Except for the close resemblance of the spermatophores of *P. schmitti* and *P. setiferus*, all of them, although structurally similar, are quite different in appearance; therefore I have emphasized apparent homologies. An effort has been made to explain the manner in which the spermatozoa egress from the spermatophores to fertilize the eggs. The association of the components of attached spermatophores with the corresponding thelycum in each species is indicated. Finally, the role played by the coxal plates of the third through the fifth pairs of pereopods of the females in keeping the compound spermatophore attached to the thelycum is briefly discussed.

The material examined is indicated in the treatment of each species. The following abbreviations are used for repositories of the specimens: ANSP - Academy of Natural Sciences of Philadelphia; INIBP - Instituto Nacional de Investigaciones Biológico-Pesqueras, México; UNC-IMS - Institute of Marine Sciences, University of North Carolina; USNM - National Museum of Natural History, Smithsonian Institution; and YPM - Peabody Museum of Natural History, Yale University. The carapace length (cl) is the linear distance between the orbital margin and the mid-posterior margin of the carapace. The illustrations have been made from preserved specimens; the accompanying scales are in millimeters.

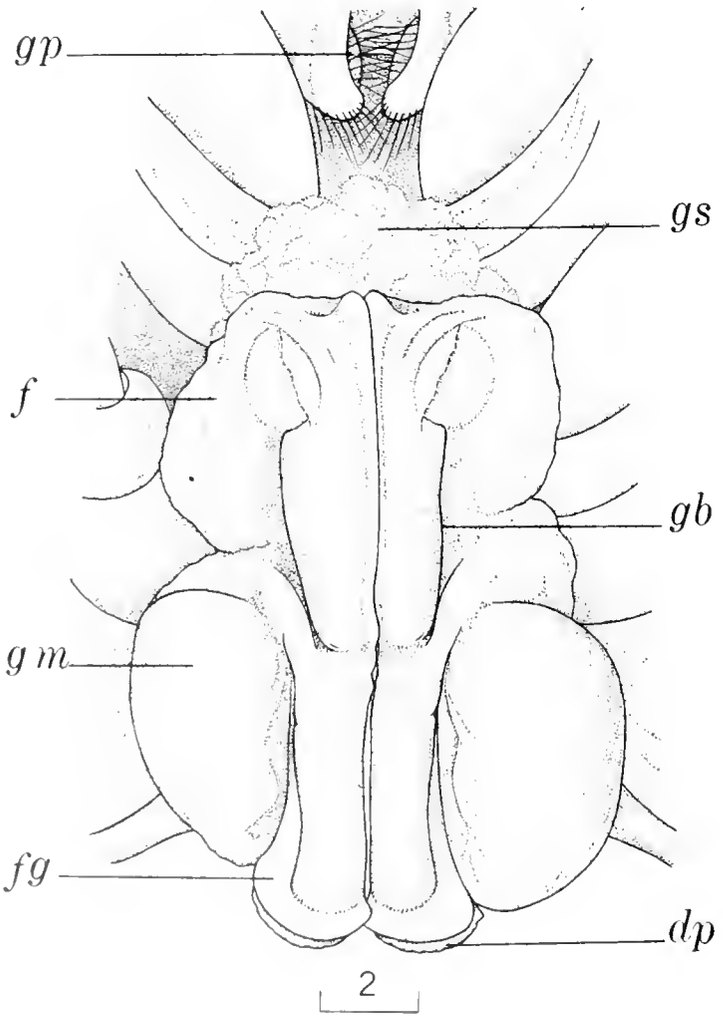

FIGURE 2.—*Penaeus* (*Litopenaeus*) *vannamei* Boone. Compound spermatophore attached to female, ♀ 43 mm cl, off Panamá Province, Panamá. Abbreviations as in Figure 1.

DESCRIPTIONS OF SPERMATOPHORES AND THELYCA

The descriptive accounts of the Pacific species are ordered according to the relative complexity of the respective spermatophores (*P. vannamei*, *P. occidentalis*, and *P. stylirostris*), and are followed by those of the Atlantic species (*P. schmitti* and *P. setiferus*), the spermatophores of which are markedly similar. The spermatophores of each species are described both as attached to the females, where they invariably occur in pairs, and as they appear when removed from the terminal ampullae of males. Next, detailed accounts of the thelyca are presented, which emphasize the main features for the support of the component parts of the spermatophores. A list of the material examined is given, including the numbers of impregnated females. Finally, the geographic range of each species is indicated.

Penaeus (*Litopenaeus*) *vannamei* Boone 1931 Figures 2-4

Spermatophore

The compound spermatophore (Figure 2) consists of a slender geminate body lacking wings and blades, and bearing thick, broad, lateral flaps, and a pair of long, caudal flanges.

Ventrally, each spermatophore (Figure 3A) exhibits a lateral furrow that roughly delimits a subovate anterior portion, bulging laterally, from an elongate, smoothly convex portion that extends to the flange; the thick, opaque ventral wall merges indistinctly with the lateral wall, which is mostly opaque and to which is loosely attached a conspicuous internal lamina; posteriorly, just before joining the flange, these walls turn strongly dorsad along an oblique line forming the fundus of the sac. The broad, mantlelike flap projecting from the lateral wall is thick, fleshy ventrally, and

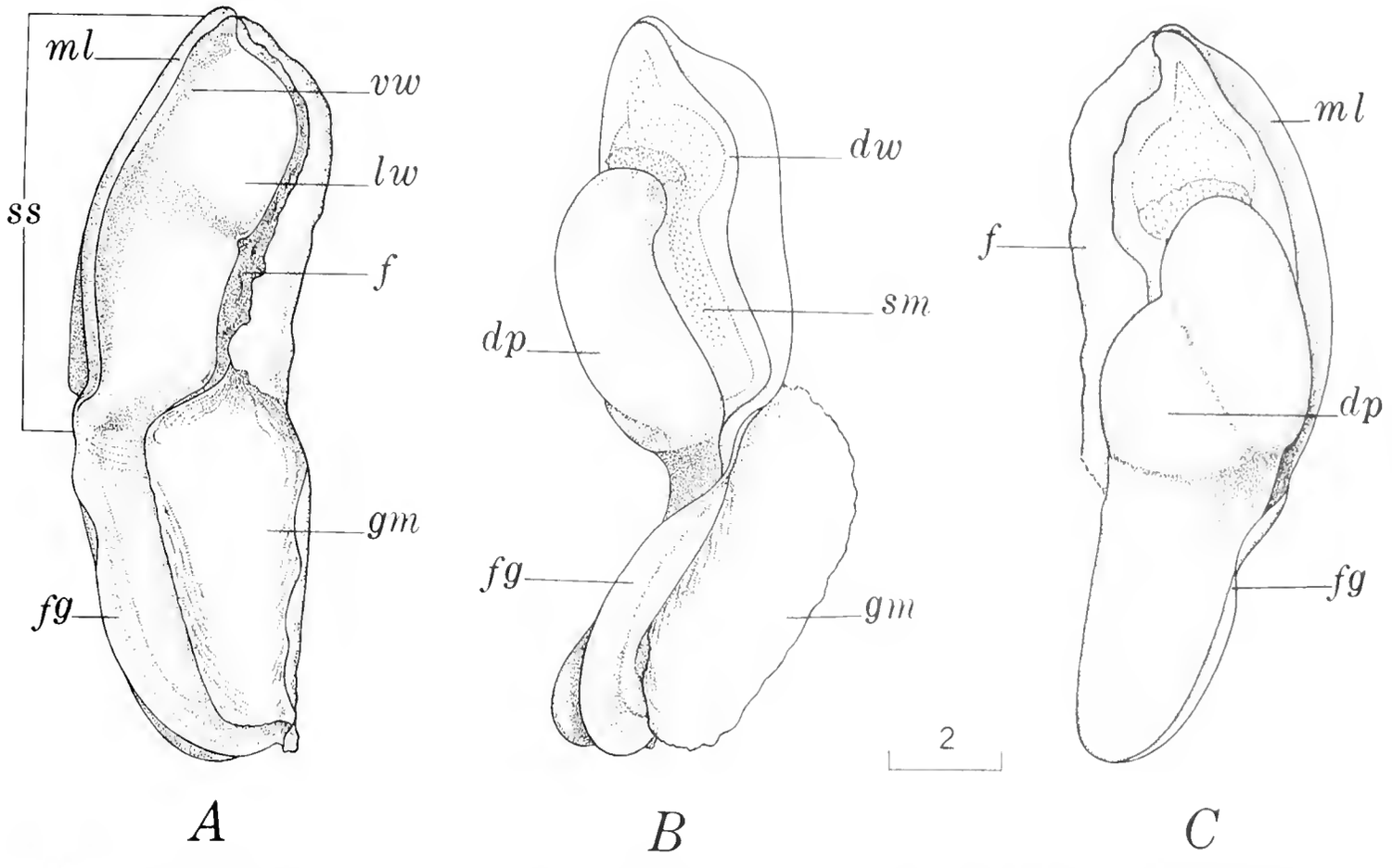

FIGURE 3.—*Penaeus* (*Litopenaeus*) *vannamei*. Left spermatophore dissected from terminal ampulla, ♂ off Juan Díaz, Panamá. *A*, Ventrolateral view. *B*, Mesial view. *C*, Dorsolateral view (glutinous material removed). Abbreviations as in Figure 1.

narrows anteromesially along the border of the sac; posteriorly along the flange, it continues as a flexible, but rather tough, narrow band. The flange is long, directed caudally, with the anterior portion marked by transverse wrinkles; a convex ridge runs parallel and contiguous to the free mesial margin along most of the entire length of the flange, and its lateral margin bears the narrow band from which a voluminous glutinous material is suspended. The thin but rigid dorsomesial wall (Figure 3B) is very broad basally and tapers anteriorly where it is produced in a subconical hood.

The dorsal plate is long (Figure 3C), the longest in the spermatophores of the five species, and at the base of the flange is bent strongly dorsally, the concavity thus formed delimiting two distinct parts. The anterior part, firmly attached to the dorsomesial wall, is nearly triangular in outline and elevated in a blunt mesial ridge which terminates anteriorly in a convex border at about the level of the lateral furrow; the posterior part is mostly flattened, and extends over the flange reaching, or almost reaching, its posterior margin.

The sperm mass, together with the gelatinous substance, is concentrated anteriorly in a large subspherical protuberance filling the lateral bulge and extends as a column in the posterior portion of the sac.

Thelycum (Figure 4A, B)

Sternite XIV bears a pair of setose, sigmoid, obliquely oriented anterolateral ridges, the lateral portions of which are low and rounded and the posteromesial portions high and sharp; the latter are continuous caudally with short elevations flanking a shallow central depression; sculpture is lacking on the posterior part of the sternite. Extending ventrally from the platelike posterior part of sternite XIII is a large, inverted, troughlike median protuberance which forms the anterior wall of a concavity bounded posteriorly by ridges of sternite XIV; the posterior part of the sternite XIII is also provided with a pair of small teeth, subjacent to the base of the median protuberance, and a pair of hornlike marginal projections lateral to the protuberance. The anterior part of sternite XIII bears two small setose lateral prominences, located close to the margin which is overhung

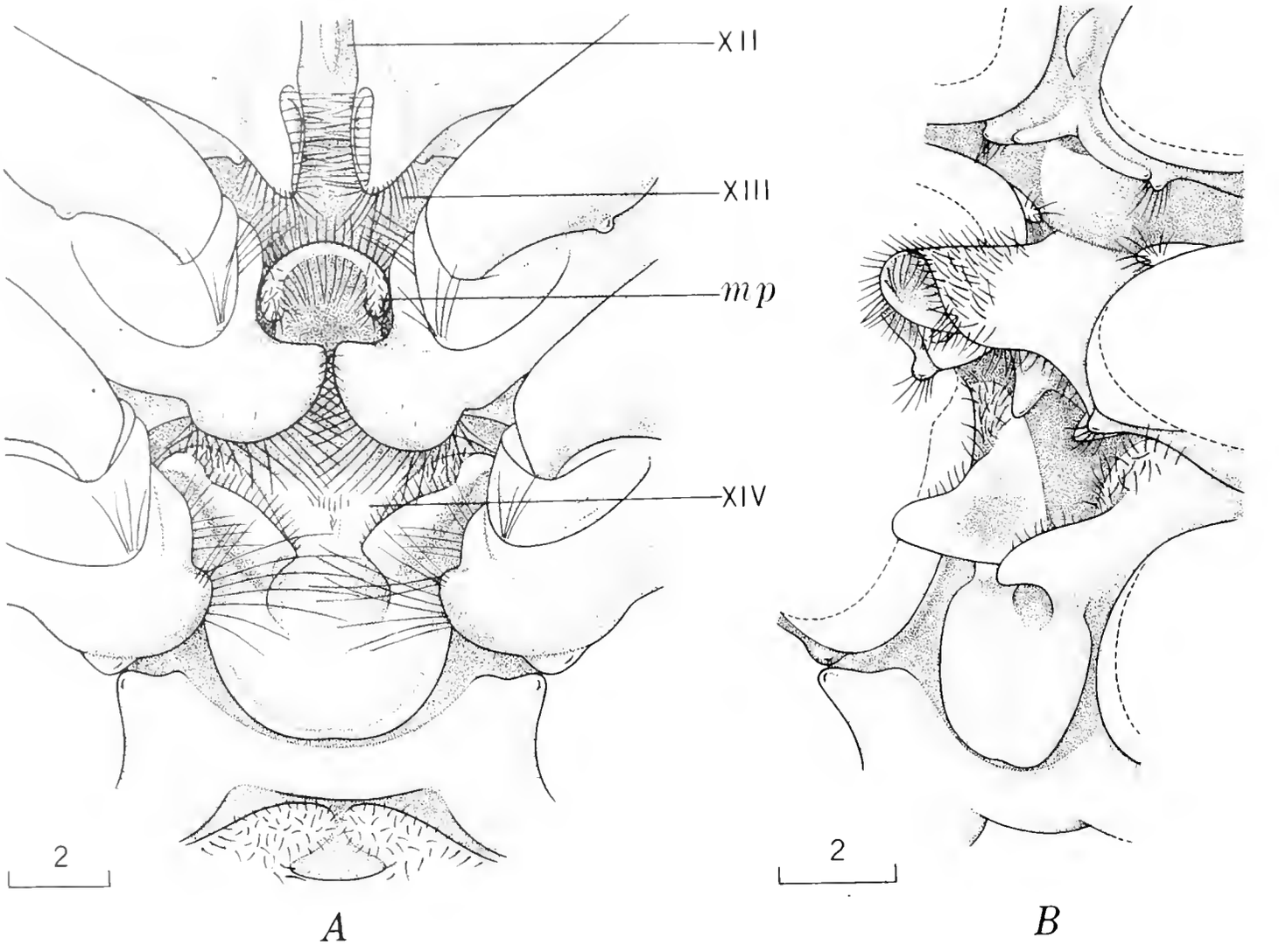

FIGURE 4.—*Penaeus* (*Litopenaeus*) *vannamei*. *A*, Thelycum, ♀51 mm cl, NW Península de Azuero, Panamá. B, Ventrolateral view of thelycum, ♀48 mm cl, same locality, *mp*, median protuberance; XII, XIII, and XIV, sternites.

ventrally by the short posteromesial extensions (protecting the gonopores) of the coxae of the third pereopods.

Disposition of the Compound Spermatophore on the Thelycum

When attached to the female, the compound spermatophore forms a distinct arc, the fundus of the sperm sacs being elevated (ventrally) well above the sternum. The sacs are thus directed anterodorsally with the anteriormost portions of their ventral walls resting on the border of the median protuberance of sternite XIII, and the contiguous lateral flaps extending over the coxae of the fourth pereopods; these flaps seem to serve as stabilizers for the rather compressed, vertically extended sacs. Anteriorly, the bulges of the sacs become very conspicuous, and the practically fused dorsomesial walls lie almost perpendicular to the horizontal coxal plates of the fourth pereopods. The sperm is released at the level of the median protuberance of the female, thus not as close to the gonopores as in the remaining species of the group. In opposition to the paired sacs, the flanges are directed posterodorsally reaching the first pleonic sternite; they cover the dorsal plates ventrally, embrace them mesially, and are flanked laterally by the glutinous material suspended from their narrow flaps. The anterior parts of the dorsal plates, which seem to be the principal elements of attachment of the spermatophores in this species, become fused along their mesial ridges, and are basally affixed to sternite XIV (pressing against the thelycal ridges) as well as to the coxae of the fifth pereopods. The posterior parts of the dorsal plates, in turn, lie on the transverse setose patch of the first pleonic sternite. Finally, the gelatinous substance, protruding through the anterodorsal extremity of the spermatophore, spreads over and beyond the thelycal protuberance of sternite XIII, while the paired

masses of glutinous material somewhat support the flanges.

Material

MEXICO. 6 ♂ 3♀, USNM, 6 km S of Bahía de Guaymas, Sonora, 23 November 1939, M. J. Lindner.- 10♂9♀, USNM, off San Simón, Chiapas, 24 m, I. Edén-Reyna.- 8♂3♀, INIBP, off Barra de Soconusco, Chiapas, 11 June 1960, F. Aguilar.

NICARAGUA. 2♂ 2♀, USNM, ex. Galveston Laboratory, National Marine Fisheries Service.

COSTA RICA. 1♀ [impregnated], USNM, off Parrita, 11 m, 8 March 1975, B. R. Drummond.- 4♀ [impregnated], USNM, off Dominical, 27 m, 8 March 1975, B. R. Drummond.

PANAMA. 18 ♂ 8♀, YPM, off Bella Vista, 8 February 1934, Bingham Oceanogr. Exped.- 2♂8♀, USNM, off Juan Díaz, 12 m, 16 February 1973, *Patricia*.- 2♂1♀,off Juan Díaz, 4 February 1969, L. G. Abele.- 4♂, USNM, off Juan Díaz, 8 m, 5 March 1973.- 4♀ [impregnated], USNM, off Panamá Prov., *Patricia*, 6 March 1973.- 1♀ [impregnated], Golfo de Panamá, ex. Instituto Nacional de Pesca de Panamá.- 3♀, USNM, NW Península de Azuero, 18 m, 14 December 1963, *Pelican* stn. 1614.

ECUADOR. 2♂ 1♀, USNM, Puerto Bolívar, 2 January 1964, Ortiz.

PERU. 2♀, USNM, Caleta Cruz, January 1969, E. M. del Solar.

Species Range

Gulf of California to Tumbes, Perú.

Penaeus (*Litopenaeus*) *occidentalis* Streets 1871
Figures 5-7

Spermatophore

The compound spermatophore is rather bizarre in appearance (Figure 5A, B), its geminate body bearing a pair of small anterolateral wings and a

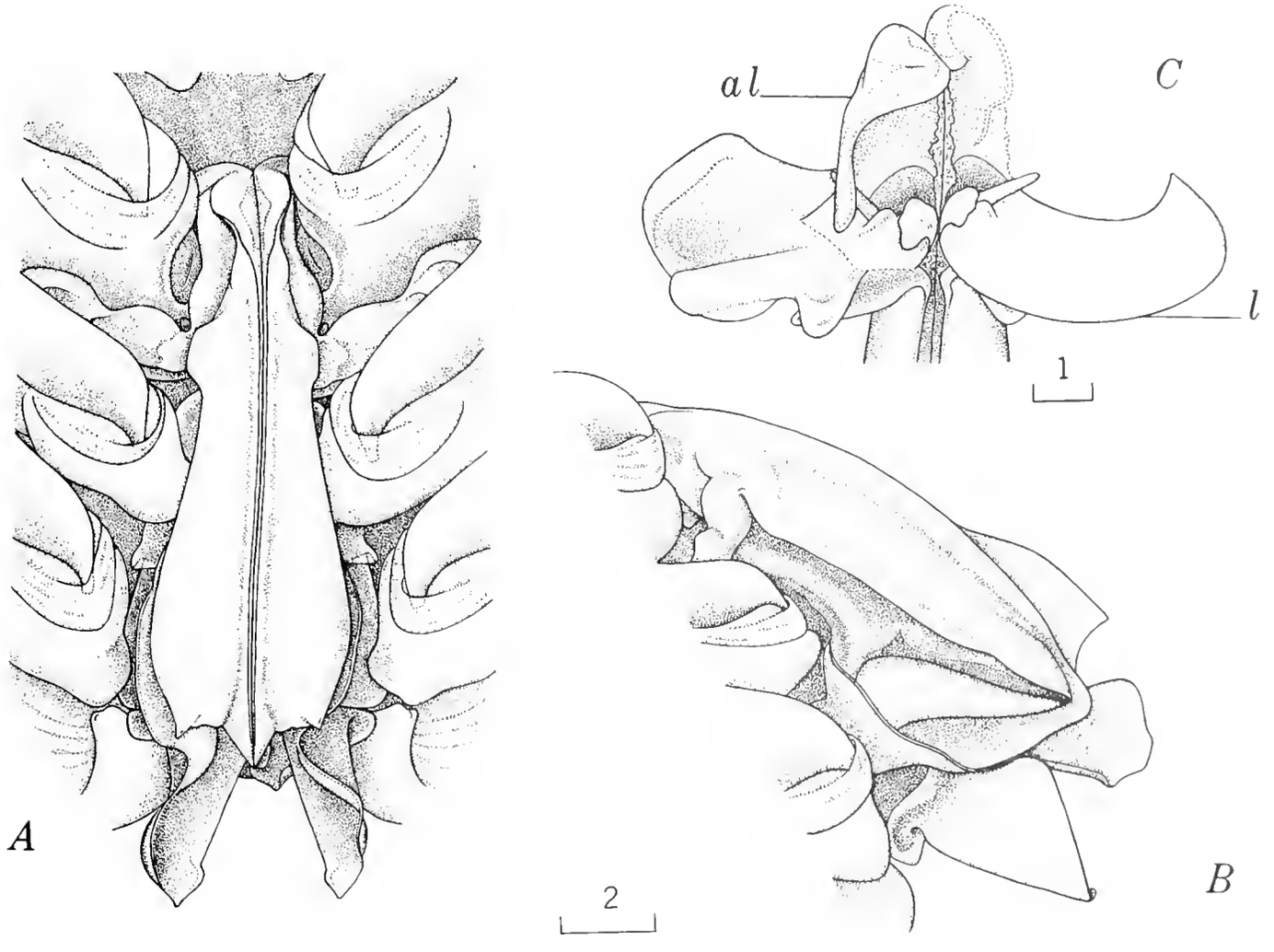

FIGURE 5.—***Penaeus* (*Litopenaeus*) *occidentalis*** Streets. ***A***, Compound spermatophore attached to female, ♀ 35.5 mm cl, off Panamá Province, Panamá. ***B***, Lateral view of same specimen. *C*, Dorsal view of anterior part of compound spermatophore removed from female, ♀ 40 mm cl, same locality. *al*, anterior lobe; *l*, lamina.

pair of long, broad lateral blades; the posterior parts of the blades are continuous with rigid ventromesial extensions or flaps flanking the posterolateral portions of the geminate body, and terminate in large caudal lobes. The flanges, extremely short and extending caudolaterally, are hidden by the ventromesial extensions.

The thick ventral wall of each spermatophore broadens at the level of the wing and from there tapers anteriorly continuing as a bridge (marked by a dorsal concavity) joining a firm, fanlike anterior lobe (Figure 6A). This lobe is bordered anteromesially by a rib that is produced laterally in a small projection, and its lateral margin bears a shallow emargination which demarks two lateral convexities, the posterior one is hollow. The ventral wall and the thick caudal portion of the lateral wall join in an acute angle, and continue in a short, heavily sclerotized, caudal flange. A dorsolateral rib marks the junction of the mostly thin and translucent lateral wall with the dorsomesial wall, and serves as the base of the blade. The blade exhibits two lateral constrictions that mark three sections: the anterior one is broad, roughly subelliptical, and delimited posteriorly by a transverse rib; the median section, also broad, is subtrapezoidal, and the posterior one narrow and bends around the apex of the caudal lobe, finally turning mesially to join the posterior border of the flange. The caudal lobe is the rather flexible extremity of the rigid ventromesial extension projecting from the line along which the flange and corresponding blade meet. A narrow, iridescent membrane runs along the margin of the ventromesial extension, which sustains a glutinous material on its inner surface (the membrane is not represented in Figure 6A, D for the sake of clarity). The rigid and translucent dorsomesial wall (Figure 6B) completes the sperm sac, which terminates and opens anteriorly at the base of the anterior lobe, mesial to the base of the wing.

The small wing (Figure 6C) is roughly subelliptical in ventral view, but bears a proximodorsal lobular process and is produced distally and posteriorly in a ventrally turned fold continuous with a small shelf at the base of the process (Figure 5C). A rigid but fragile lamina (Figures 5C, 6A, B) lies at the base of, and perpendicular to the anterior lobe; it extends from the mesial part of the sperm sac laterally almost to the tip of the wing. This peculiar lamina bears on its mesial border two conspicuous projections with a small ridge between them; one of the projections is dorsally located, flattened and strongly curved

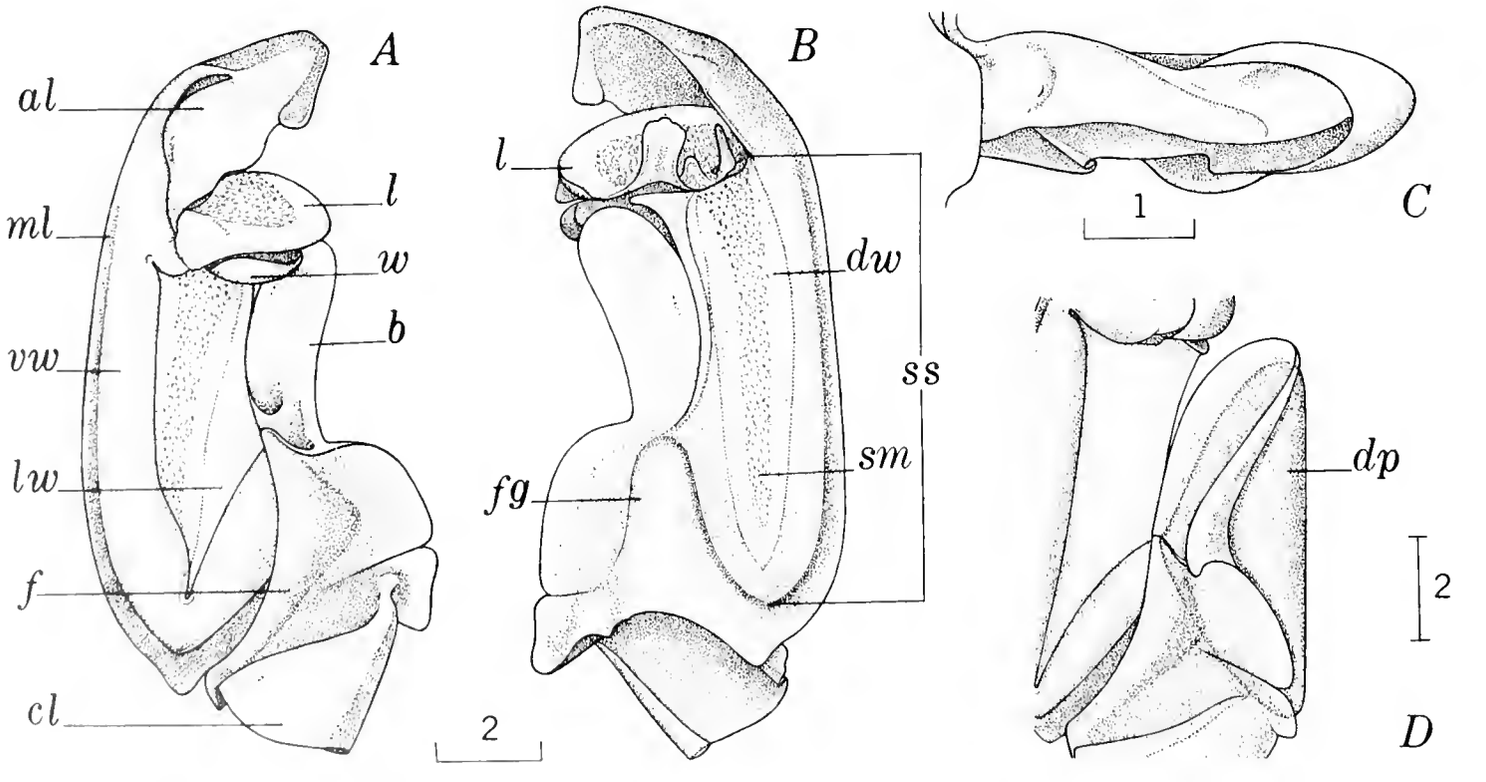

FIGURE 6.—*Penaeus* (*Litopenaeus*) *occidentalis*. *A*, Ventrolateral view of left spermatophore (dorsal plate removed) dissected from terminal ampulla, ♂ off Bella Vista, Panamá. *B*, Dorsomesial view of same specimen. *C*, Ventral view of wing as attached to female, ♀ 35.5 mm cl, off Panamá Province, Panamá. *D*, Lateral view of dorsal plate, ♂ off Punta Soldado, Buenaventura, Colombia. *al*, anterior lobe; *cl*, caudal lobe; *l*, lámina. Other abbreviations as in Figure 1.

laterally, whereas the other is spiniform—the tip of the latter projection shows in Figure 5A at the vertex of the emargination between anterior lobe and the base of wing.

The dorsal plate (Figure 6D) is almost as long as, and lies against the dorsal surface of the blade; it is produced in a central prominence that fits into the concavity on the posterior extremity of the anterior section of the blade.

Thelycum (Figure 7)

Sternite XIV is densely covered with setae except over a pair of posterolateral crescentic elevations separated by a short, sharp posteromedian ridge; this ridge is hidden in the adult by the bulging surrounding area. The posterior portions of the elevations are parallel to the thoracic ridge which typically bears a pair of lateral prominences provided with a brush of setae. Sternite XIII is heavily sclerotized posteriorly forming a plate with a broadly concave posteromedian margin not overlapping sternite XIV, but with lateral extremities produced into hornlike projections freely overhanging sternite XIV. The central region of the plate bears a strong rounded to subconical knob and the posterior margin occasionally is armed with a small median tooth. The anterior part of sternite XIII is provided with a pair of transverse folds, the mesial portions of which are produced into sharply pointed conical projections covered by minute setae. The strong posterior ridge of sternite XII is divided by a median depression, and its lateral extremities are produced caudally in a pair of convexities hidden by the scooplike coxal plates of the third pereopods. These uniquely shaped coxal plates support the sperm sacs anteriorly and seem to retain, at least briefly, the sperm masses immediately after their release. It should be remembered that the coxal plates are covered ventrally by the bases of the anterior lobes of the spermatophores.

Disposition of the Compound Spermatophore on the Thelycum

When the compound spermatophore is in position on the female, the fanlike anterior lobes become affixed to sternite XII with the lateral portions lying beneath the coxae of the third pereopods while their basal portions extend over (ventrally) the coxal plates. The angular junctions between the anterior lobes and the wings embrace

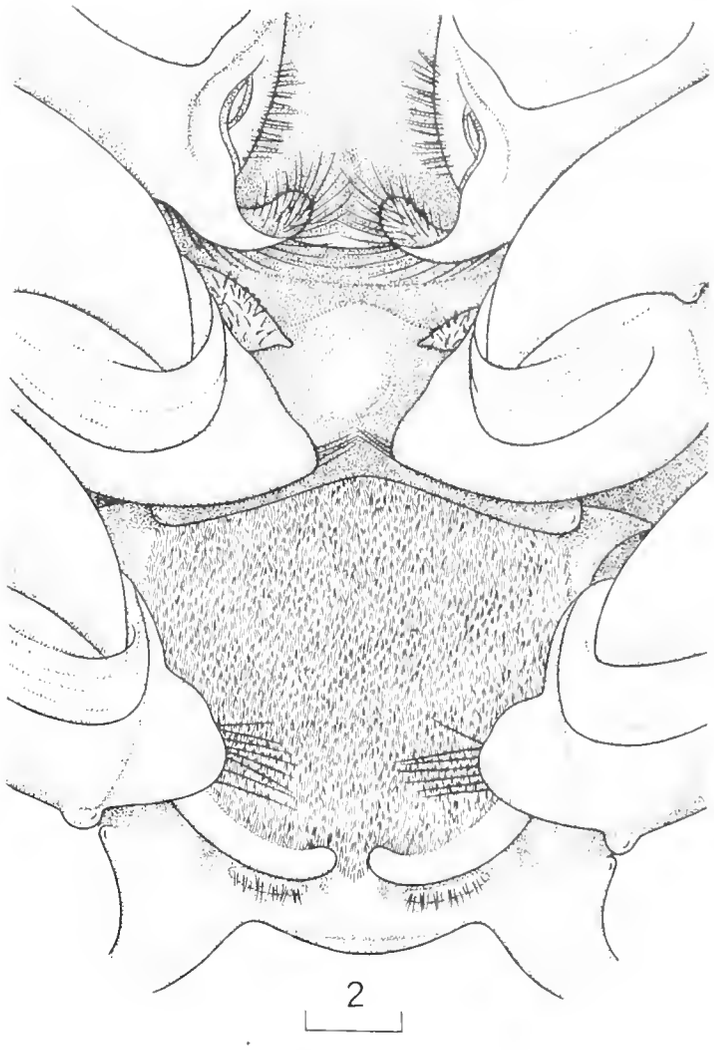

FIGURE 7.—*Penaeus* (*Litopenaeus*) *occidentalis*. Thelycum, ♀53.5 mm, cl, Golfo de Panamá, Panamá.

the posterior extremity of the corresponding female gonopore. The mesial borders of the laminae, in turn, form supporting rims along the lateral borders of the apertures of the respective sperm sacs, and the flattened projections of the laminae meet in the sagittal plane, while the spiniform projections lie contiguous to the posterior convexities of the anterior lobes (Figure 5C). The laminae extend laterally, adhering to the posteroventral surface of the coxae of the third pereopods, and the wings rest ventrally over and against the laminae, both processes helping to anchor the spermatophores to the thelycum. The position assumed by the anterior part of the spermatophore on the female brings the apertures of the sperm sacs to the coxal plates of the third pereopods and thus close to the gonopores; consequently, it seems that the sperm might well accumulate on these spoonlike coxal plates. Whether or not the opening of each sac is permanent, or results from a rupture, has not been ascertained.

Posterior to the wings, the lateral blades press

against the subjacent dorsal plates which come together, meeting mesially, and adhere to sternites XIII and XIV. The narrow posterior portions of the blades meet on the midline, forcing the geminate body ventrally and causing the caudal lobes to project posteroventrally, resembling paired rudders.

Material

MEXICO. 1♀, USNM, between Monte Alto and San José, Chiapas, 25 m, 8 August 1970, D. Palacios.

PANAMA. 6 ♂ 2♀, syntypes, ANSP No. 73, "Isthmus of Panama," J. A. McNeil.- 6♂ 12♀, YPM, off Bella Vista, 9 February 1934, Bingham Oceanogr. Exped.- 7♂, USNM, off Juan Díaz, 4.5-7 m, 26 February 1973, *Patricia*.-2♀ [impregnated], USNM, off Panamá Prov., 6 March 1973, *Patricia*.- 1♂ 1♀, USNM, E of Panamá City, 7 m, 5 November 1971, D. E. Sweat.

COLOMBIA. 12♂ 12♀ [1♀ impregnated], USNM, off Punta Soldado, Buenaventura, 4.5 m, 1 March 1973, *Santanderino*.- 6 ♂ 13♀, USNM, Tortugas Grounds, Buenaventura, 9 m, 19 September 1969, *Cacique* stn. 69-24.

ECUADOR. 6 ♂ 3♀, USNM, off Playas, 1963, commercial catches.

PERU. 1♀, USNM, Caleta Cruz, Tumbes, 18 m, January 1969, E. M. del Solar.

Species Range

Chiapas, México, to Tumbes, Perú, and Islas Galápagos.

Penaeus (*Litopenaeus*) *stylirostris* Stimpson 1871 Figures 8-12

Spermatophore

The compound spermatophore consists of a slender, geminate body produced into large anterolateral wings, broad posterolateral flanges, and bearing paired elongate blades (Figure 8).

The ventral wall of each spermatophore is truncate anteriorly; posteriorly it continues indistinctly with the thick posterior portion of the lateral wall, both walls then turning abruptly dorsad forming the fundus of the sac just before joining the flange (Figure 9A). The lateral wall, mostly thin, is bounded by a very fine dorsolateral rib. This rib serves as the base of a long, moderately broad blade, which extends from the base of the wing (there fused to its posterior ridge) to the anterior extremity of the flange, and continues along the entire border of the latter. The blade is somewhat arched over its attachment to the rib, which delimits two longitudinal parts. One part is directed dorsomesially to the base of the flange, where it twists laterally, the other part projects ventromesially throughout its entire length, and bears anteriorly an iridescent, rather membranous broad flap to which adheres (dorsally) a mass of viscous material; along the flange the ventromesially projecting part becomes flexible and sustains a narrow extension of the flap, supporting a mass of glutinous material on its mesial surface. The flange is somewhat broadly ovate, and is covered by a large dorsal plate which occupies its entire surface and extends beyond the flange

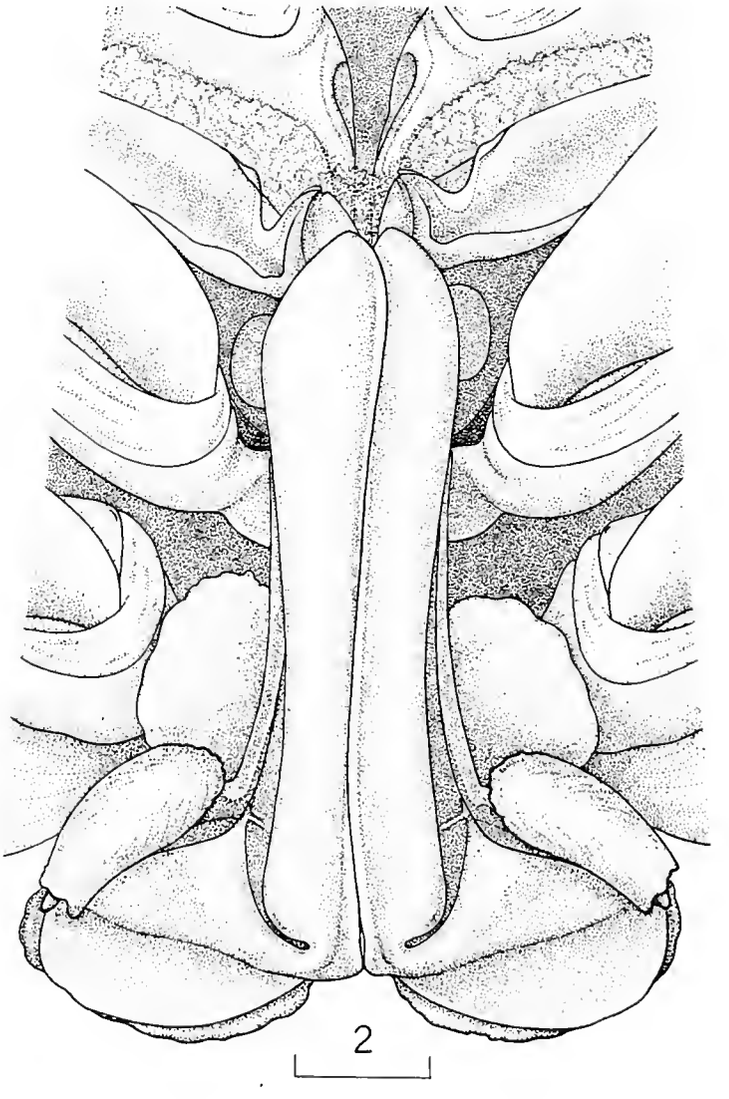

FIGURE 8.—*Penaeus* (*Litopenaeus*) *stylirostris* Stimpson. Compound spermatophore attached to female (geminate body slightly displaced posteriorly to show bases of wings),♀38 mm cl, off Panamá Province, Panamá.

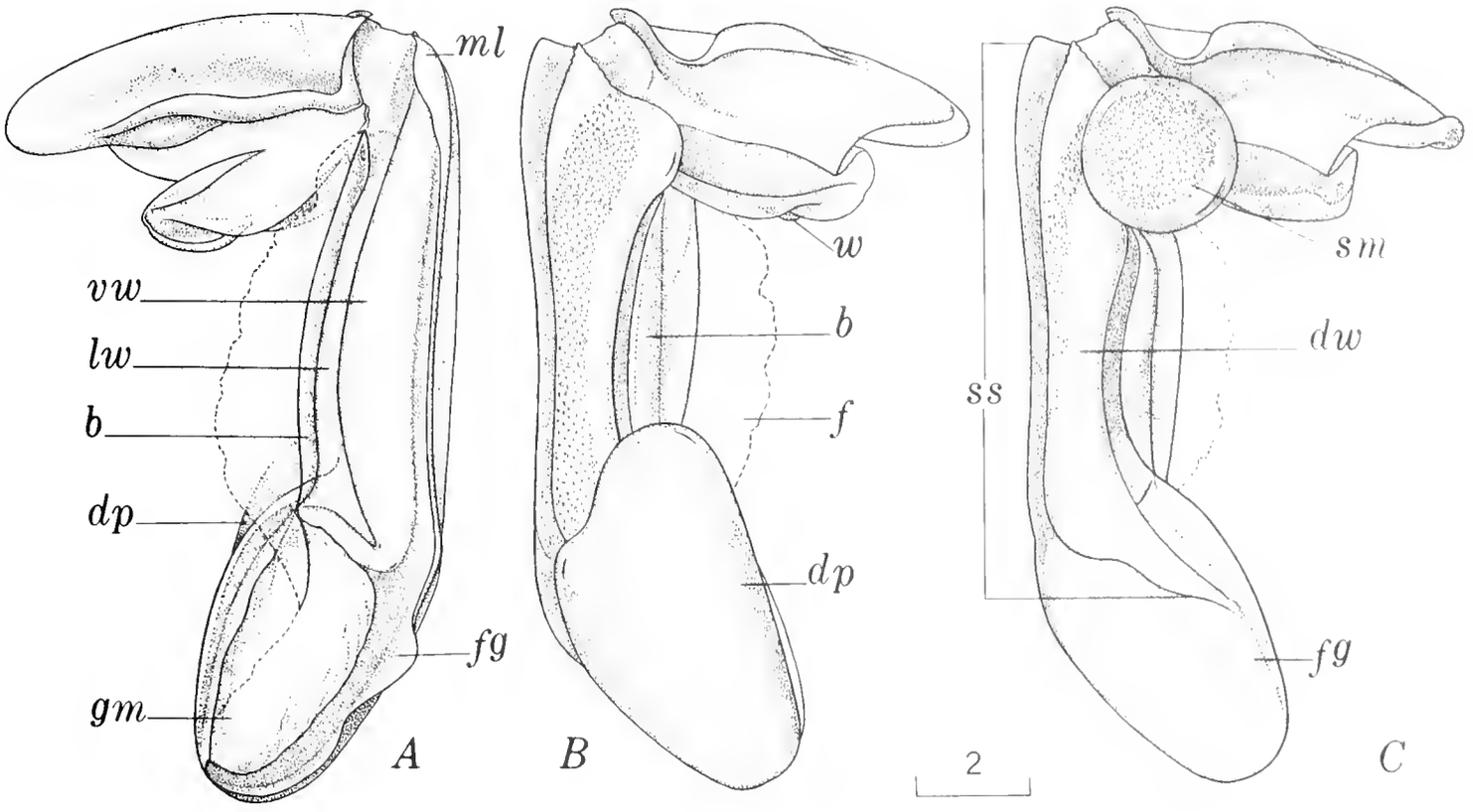

FIGURE 9.—*Penaeus* (*Litopenaeus*) *stylirostris*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂ off Juan Díaz, Panamá. *B*, Dorsomesial view of same specimen. *C*, Dorsomesial view of right spermatophore forcefully expelled from terminal ampulla, ♂ off Panamá Province, Panamá. (For the purpose of illustration the anterior ventromesially directed part of the blade has been turned laterally and the viscous material removed.) Abbreviations as in Figure 1.

anteriorly in a rounded portion affixed to the dorsomesial wall.

In this spermatophore, the dorsomesial wall (Figure 9B, C) is turned upon itself and attached to the mesial lapel of the ventral wall, but not joining the lateral wall—except posteriorly, where they become fused. Consequently, the lateral wall and part of the ventral wall overlap the sac (largely formed by the dorsomesial wall) as a protecting shield. The sac is subconical anteriorly; it expands in a conspicuous rounded bulge at the base of the wing, and continues into the elongate posterior portion affixed to the base of the flange and firmly attached to the dorsal plate.

The wing (Figure 10A, B) consists of a transversely elongate, mostly sclerotized anterior region, and a subrectangular, membranous posterior region. The anterior region bears a long, sharp, ventral ridge, joining a short, pointed, basal rib at almost a 90° angle; the area laterally contiguous to the basal rib is membranous, whereas that mesial to it is thick, but soft, and meets the ventral wall of the sac. Dorsally, the wing is produced in a broad, rounded lobe, situated close to its anteroproximal margin. The membranous region of the wing bears a posterior rib that ends

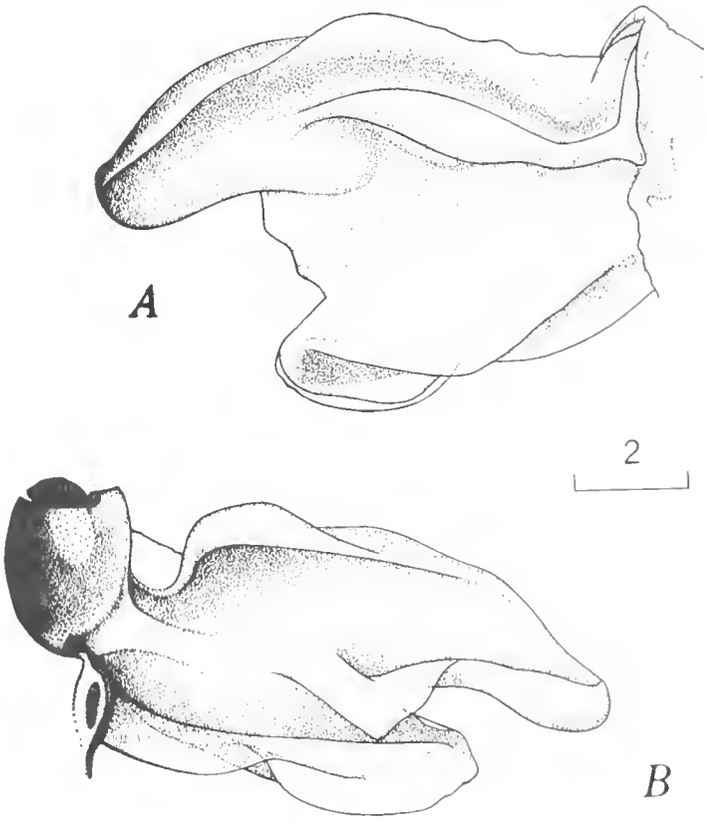

FIGURE 10.—*Penaeus* (*Litopenaeus*) *stylirostris*. Wing severed from geminate body of right spermatophore, ♂ off Playas, Ecuador. *A*, Ventral view, posterior membranous region extended. *B*, Dorsal view of same specimen.

premarginally. The posterolateral membranous extension is reflexed and attached to the rib dorsally, thus forming a shallow pocket. After the compound spermatophore is deposited on the thelycum, the pockets of the paired wings come to lie posteromesially and are quite conspicuous on those impregnated females in which the geminate body has been lost.

Thelycum (Figure 11)

Sternite XIV bears a large median subpyramidal prominence with a subtriangular base (broad anteriorly, tapering posteriorly), its sharp midlongitudinal carina armed with a row of very minute setae. The highly sclerotized posterior part of sternite XIII is produced into a rigid, subvertical shelf overhanging sternite XIV; this shelf constitutes the posterior wall of a pair of concavities which are separated by a sharp median ridge and are delimited anteriorly and laterally by strong angular paired ridges, the posterior bases of which extend laterally and bear toothlike projections. The anterolateral part of sternite XIII bears paired transverse rigid elevations covered by long setae. Heavily sclerotized sternite XII is nearly straight along its posteromedian margin, and produced caudally in a pair of lateral projections armed with tufts of setae. The conspicuous concavities of sternite XIII serve to lodge the sperm masses which emerge from the ruptured anterodorsal bulges of the compound spermatophore.

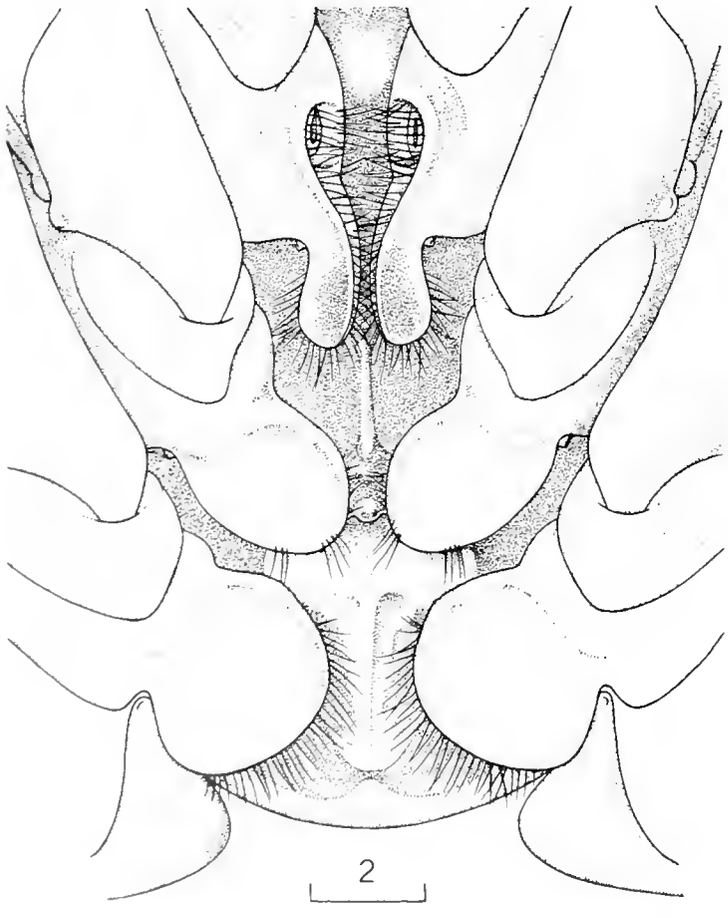

FIGURE 11.—*Penaeus* (*Litopenaeus*) *stylirostris*. Thelycum, ♀46 mm cl, off Bella Vista, Panamá.

Disposition of the Compound Spermatophore on the Thelycum

When the compound spermatophore is in position on the female, the anterior extremity of the geminate body lies on the ventrally turned mesial borders of the coxal plates of the third pereopods, with the sperm masses (projecting through the anterodorsal bulges) lodged in paired thelycal concavities of sternite XIII, near the gonopores (Figure 12). The wings contribute to anchoring the spermatophore: their anterior regions are attached to the posteroventral surfaces of the coxae of the third pereopods, the mesial portions following the contour of the strongly curved coxal plates; lobes borne on the dorsal side of the anterior regions certainly function as adhesive elements. The posterior region of each wing is extended

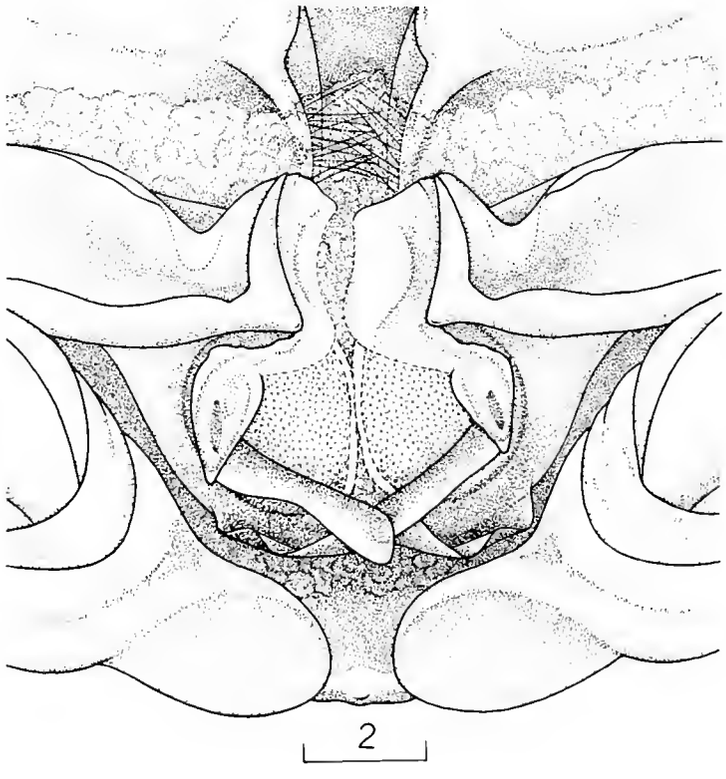

FIGURE 12.—*Penaeus* (*Litopenaeus*) *stylirostris*. Sternites XII and XIII bearing paired masses of sperm and wings of a compound spermatophore, the geminate body of which has been lost (see explanation in text), ♀48 mm cl, off Guaymas, México.

mesially, each with its marginal rib embracing the sperm mass protruding through the corresponding sac; the adjacent membranous portions cover each mass laterally and from there extend tightly attached to sternite XIII.

From the bases of the wings posteriorly, the lateral portions of the ventral walls together with the lateral walls are turned mesially in a spiral thus reducing the lumen of the sacs; at the same time, each blade comes to occupy a position deep within a fold so that the dorsomesial part of the blade abuts against the respective sac, and the other part, together with its flap, projects somewhat laterally. Caudally, the geminate body reaches the first pleonic sternite, and the thick portions of the lateral walls are turned sharply anterolaterad resulting in the elevation of paired ridges. These are continuous with the flanges which posteriorly extend laterally from the geminate body and either embrace or enfold the dorsal plates. These plates are attached in such a way that their smaller anterior parts rest against the coxal plates of the fifth pereopods, and their broad posterior parts (extending across the corresponding flange) lie almost entirely on the first pleonic sternite. Finally, the glutinous material, resting along the anterior borders of the flanges, become almost perpendicular to the median body.

As the compound spermatophore is anchored to the female, gelatinous substance extends over the coxae of the third pereopods and under the wings, penetrates the area between the coxal plates of those pereopods and covers the posterior portion of sternite XII.

In *Penaeus stylirostris* the spermatozoa are apparently released by the rupture of the attached spermatophore. By some unknown means, the geminate body with adjoining flanges breaks away, leaving the wings, together with paired rounded masses of sperm surrounded by gelatinous substance, on the female. It seems that when the spermatophores are expelled, the spermatozoa and the gelatinous substance, which were previously within the sacs, are forced into, and then break through, the anterolateral bulges, finally becoming lodged in the thelycal concavities of sternite XIII. In the extruded spermatophores that I have examined—removed from impregnated females or obtained by forcing their expulsion from the terminal ampullae of males—the sacs retained but little sperm. The wings are torn from the geminate body along the line of union between their mesial extensions and the corresponding ventral wall, and the break continues across the lateral wall to the posterior ridge of the respective wing. The rupture does not occur along definite sutures, but it follows the pattern described. Once the geminate body breaks away, the spermatozoa are exposed to the surrounding water, in close proximity to the female gonopores.

On one of the females examined there was an entire spermatophore superimposed upon the remains of another, the latter represented by a pair of wings and remnants of a sperm mass. This indicates that the animal had copulated twice within a short period of time.

Material

MEXICO. 1 ♂ 2 ♀ [impregnated], USNM, off Guaymas, Sonora, 8 April 1940, Capt. Corona.- 2 ♀ [impregnated], USNM, off Guaymas, Sonora, 9 April 1940, E. F. Ricketts.- 2 ♂ 2 ♀, INIBP, Bahía de Altata, Sinaloa, 14 April 1959, commercial catches.- 4 ♂ 3 ♀, USNM, between Monte Alto and San José, Chiapas, 25 m, 8 August 1970, D. Palacios.

COSTA RICA. 3 ♀ [impregnated], USNM, Parrita, SE of Puntarenas, 27 m, 4 July 1974, B. R. Drummond.- 1♀ [impregnated], USNM, off Parrita, 11 m, 8 March 1975, B. R. Drummond. 2♀ [impregnated], USNM, off Parrita, 18 m, 8 March 1975, B. R. Drummond. 5♀, [impregnated], USNM, off mouth Río Coronado, 16 m, 10 March 1975, *María del Pilar*.

PANAMA. 4♂ 9♀, USNM, off Panamá Prov., 12-24 m, 16 February 1973, *Patricia*.- 14 ♂ 1♀, USNM, 4.5-7.5 m, of Juan Díaz, 26 February 1973.- 6♂, USNM, off Panamá Prov., 5 March 1973.- 4 ♀ [impregnated], USNM, off Panamá Prov., 6 March 1973, *Patricia*.- 1♂ 3♀, USNM, Isla Gorgona, 1 m, March 1973, fishermen.

ECUADOR. 1 ♂ 1♀, USNM, off Playas, 3 December 1963, San Andrés.- 1 ♂, USNM, Ensenada de Valdivia, December 1934, S. Camino.

PERU. 2 ♂ 2♀, USNM, off Puerto Pizarro, 11 May 1941.

Species Range

Punta Abreojos, Territorio de Baja California, and Gulf of California, México, to Tumbes, Perú.

Penaeus (*Litopenaeus*) *schmitti*
Burkenroad 1936
Figures 1A, B, 13-15

Spermatophore

The compound spermatophore consists of a geminate body produced in a pair of anterolateral wings, flanked caudolaterally by flanges broadened posteriorly and bearing wide lateral flaps (Figure 13A, B).

Anteriorly, the thick, opaque ventral wall of each spermatophore is truncate and strongly inclined dorsally (Figure 14A); posteriorly, it is imperceptibly continuous with the thick portion of the lateral wall, both turning abruptly dorsad forming the fundus of the sac. The lateral wall bears a small, blunt to acute caudal projection, just before joining the flange. The flange is narrow and horizontal anteriorly, it becomes progressively broader posteriorly, and turning mesially is deflected ventrally becoming almost perpendicular to its anterior portion. The lateral wall is bounded dorsolaterally by a fine rib that serves as base for the anterior part of a long blade. The blade is divided by a deep horizontal incision. The anterior part is narrow and convex at its cephalic extremity, then broadens abruptly and reaches the flange where its free caudal margin overhangs (ventrally) the cephalic margin of the posterior part. The posterior part, in turn, is narrow and runs along the lateral border of the flange, tapering caudally. The flange bears a broad, lateral flap which is produced anteriorly in a narrow strip running laterally along the sac; the broad portion of the flap is strengthened by a subtriangular

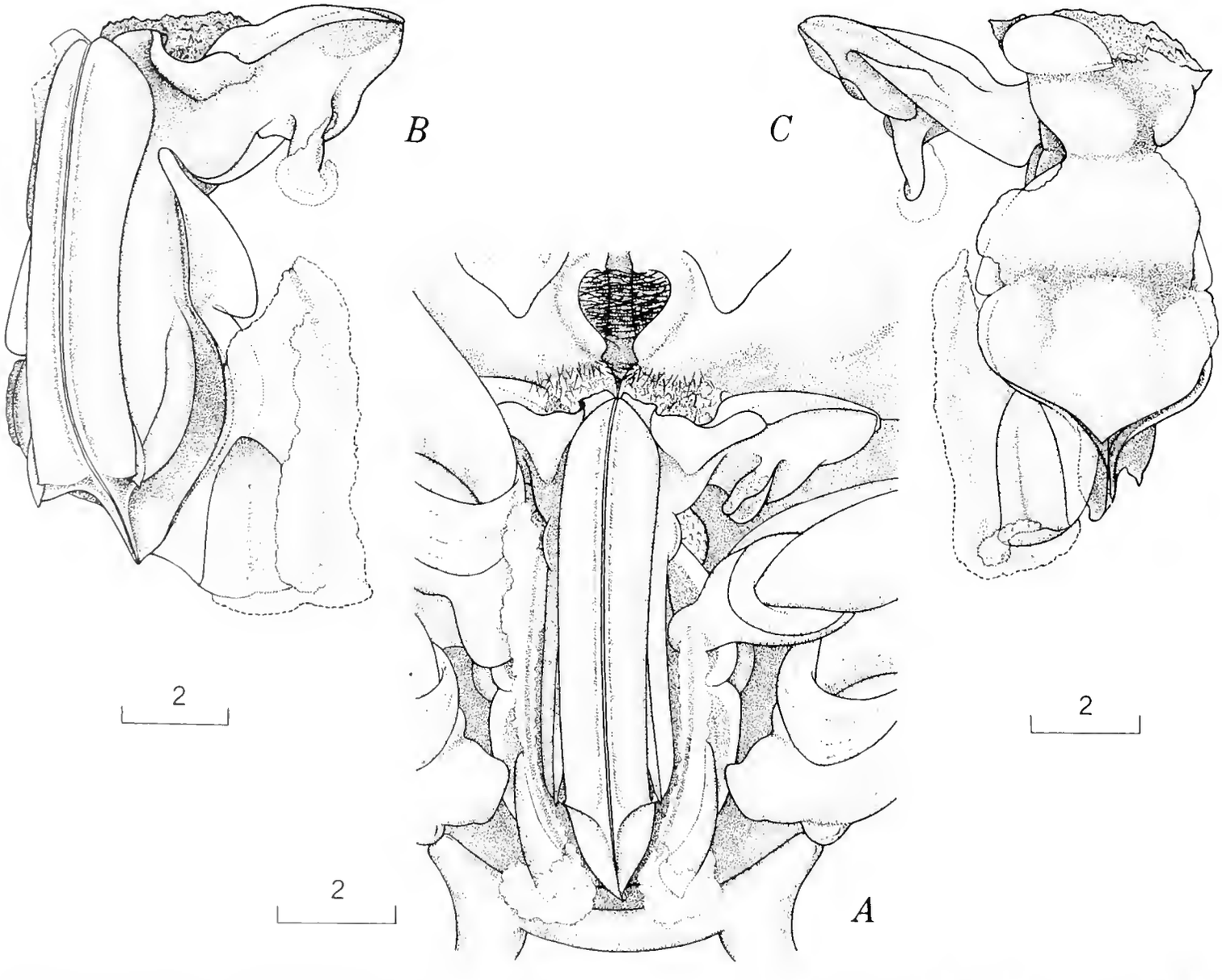

FIGURE 13.—*Penaeus* (*Litopenaeus*) *schmitti* Burkenroad. *A*, Compound spermatophore attached to female, ♀ 34 mm cl, off Tucuracas, Península de la Guajira, Colombia. *B*, Ventrolateral view of compound spermatophore dislodged from female, ♀ off Honduras. *C*, Dorsal view of same specimen (anterodorsal extremity missing).

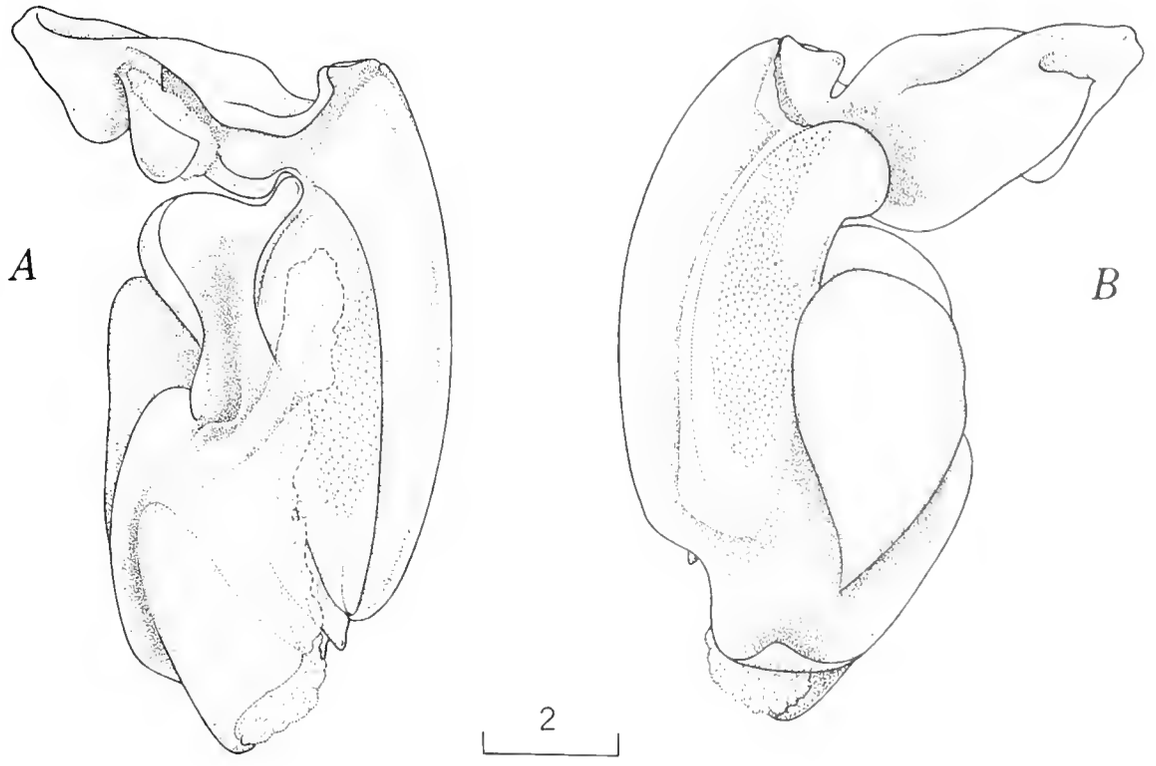

FIGURE 14.—*Penaeus* (*Litopenaeus*) *schmitti*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂ off Ubatuba, São Paulo, Brasil, *B*, Dorsomesial view of same specimen.

plate and a submarginal thickness somewhat stiffens the entire flap. A glutinous material rests against the flange, and adheres to the mesial surface of the flap.

The thin, translucent dorsomesial wall bulges conspicuously beyond its attachment along an oblique line extending from the anterior extremity of the mesial lapel to the posteroproximal end of the wing (Figure 14B; this bulge, occupied by the extremity of the sperm mass enclosed in the spermatophore, bears a triangular crest, rather similar to the subconical anterior extremity of the sperm sac in *P. stylirostris*. Posterior to the bulge, the dorsomesial wall, as in all the other spermatophores, is attached to the mesial lapel along its entire length, extending laterally to join the blade, and caudally to become affixed to the base of the flange.

The wing is long and irregular in contour, produced caudally in a broad proximal lobe, and tapers to a rounded excavated tip. The ventral surface is scabrous, bearing several projections: a rigid, rounded prominence on the anterior rib; an elongate, twisted process (its base situated slightly distal to midlength) that extends mesially in the form of a subovate to nearly semicircular lobule; and a distal shelf, obliquely flanking the process posterolaterally.

The dorsal plate (Figure 14B) is roughly tear-shaped, rounded anteriorly, tapering posteriorly, and relatively long, extending from the anterior end of the blade (at the base of the wing) almost to its posterior tip. The plate is intimately associated with the blade anteriorly, and practically fused to the flange posteriorly.

Thelycum (Figure 15)

Sternite XIV bears a pair of subparallel anterolateral ridges which extend posteriorly without turning mesially, to reach two rigid rounded or subconical prominences; a narrow median sulcus often divided by a slender longitudinal rib is present anterior to the prominences. Sternite XIII is rigidly sclerotized forming a strong plate produced posteriorly as an emarginate soft shelf overhanging sternite XIV; the anterior part of this sternite bears a pair of soft and naked transverse elevations flanking a tonguelike lamella bordered by setae. The lamella forms the roof of a concavity floored by a strong ridge from sternite XII. The ridge (a marginal thickening of platelike sternite XII and mostly hidden by setose, rounded, and relatively short coxal plates of the third pereopods) is produced into two pairs of convex projections, a small median pair and considerably larger lateral ones armed with long setae. The concavity of sternite

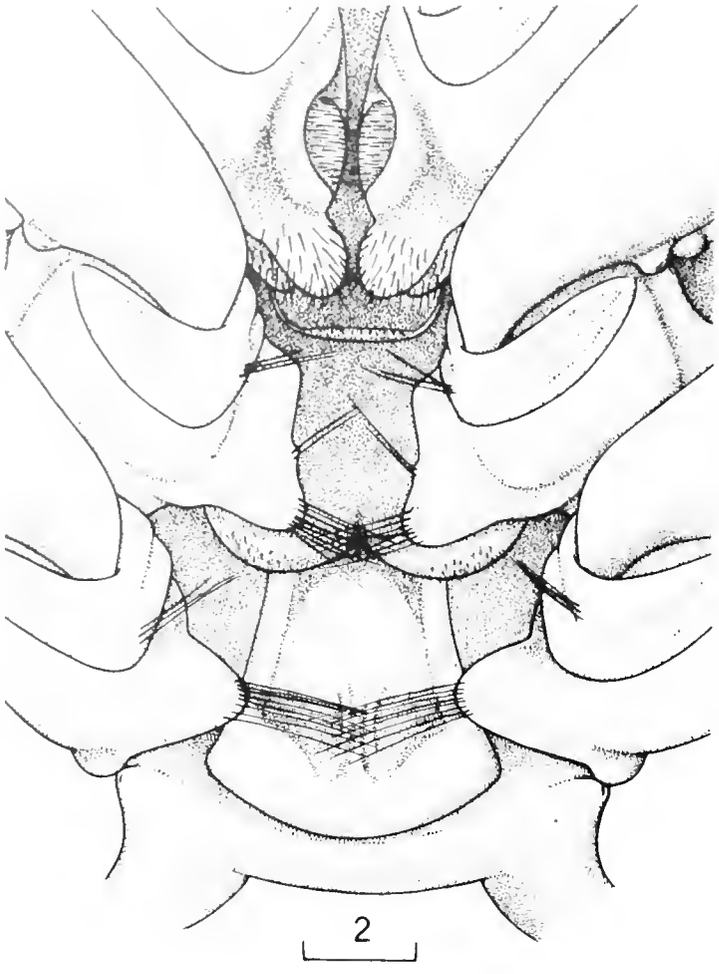

FIGURE 15.—*Penaeus* (*Litopenaeus*) *schmitti*. Thelycum, ♀50 mm cl, off Paramaribo, Surinam.

XIII serves to receive the sperm masses projecting through the ruptured anterodorsal bulges of the compound spermatophore, a function similar to that of paired concavities present on the same sternite in *P. stylirostris*.

Disposition of the Compound Spermatophore on the Thelycum

At mating, the compound spermatophore is applied to the thelycum with the anterior part of the geminate body lying on the mesial margins of the coxal plates of the third pereopods, in close proximity to the gonopores (Figure 13A). Basally, the wings extend over (ventrally) the coxal plates, their posterior lobes embrace laterally the sperm masses emerging from the sacs, and are attached caudal to the tonguelike lamella of sternite XIII, where they are almost contiguous; the anteromesial margins of the wings, however, are free, leaving a passageway between them and the body of the female, through which protrudes gelatinous substance. The wings are affixed distally to sternite XIII, with the twisted processes turned strongly posteromesiad and hidden by the articular (dorsal) membranes of the corresponding fourth pereopod. The sperm masses which emerge through the ruptured anterodorsal bulges of the spermatophore are lodged within the concavity roofed by the lamella of sternite XIII and floored by the strong ridge projecting from sternite XII. The sperm-filled concavity is lined by the gelatinous substance which surrounded the sperm while in the sac. Caudally, the geminate body extends to the posterior part of sternite XIV, where the posteromesial portions of the flanges meet on the sagittal plane and form a vertical shelf that is situated between the two thelycal protuberances. The broad anterior parts of the paired blades and the lateral (anterior) portions of the flanges are attached to sternite XIII and XIV successively, pressing against the dorsal plates. The broad flaps borne by the flanges conspicuously flank the geminate body, and the glutinous material—adhering to their mesial surfaces—enlarge, extending along the sides of the geminate body. The dorsal plates fuse in a single mass which is directly applied to sternites XIII and XIV, and which anteriorly abuts the indurate gelatinous substance enveloping the sperm masses within the concavity of sternite XIII (Figure 13C).

Several years ago, during the course of field work in Caribbean waters, I examined a few females carrying complete spermatophores as well as a few others bearing only those elements of the spermatophores which become affixed to sternite XIII. The latter specimens indicate that after the compound spermatophore is attached to the female, the geminate body is severed leaving behind only the wings and paired masses of sperm. Remarks on the rupture of the spermatophore in *P. setiferus*, which occurs in about the same manner as it does in *P. schmitti*, are presented on p. 481.

Material

Many specimens examined by me are recorded in Pérez Farfante (1969). Two females with spermatophores attached studied during the course of this investigation are in the lots listed below.

COLOMBIA. 6 ♂ 10♀, USNM, off Tucuracas, Península de la Guajira, 22 m, 6 October 1965, *Oregon* stn. 5674.

SURINAM. 1♀, USNM, E of Braams Point, 22 m, 30 May 1957, *Coquette* stn. 155.

A complete spermatophore dislodged from a female caught off Honduras was also examined. It is deposited in the USNM, and was presented by Eric J. Heald.

Species Range

Cuba to Guadeloupe, and along the continental coast from Belize (British Honduras) to Laguna, Santa Catarina.

Penaeus (*Litopenaeus*) *setiferus* (Linnaeus 1767)
Figures 1C, D, 16-19

Spermatophore

The compound spermatophore consists of a geminate body which bears a pair of anterolateral wings, and is flanked posterolaterally by a pair of flanges which broaden posteriorly and bear broad flaps (Figure 16A, B).

Anteriorly, the thick, opaque ventral wall of each spermatophore is truncate and strongly inclined dorsally (Figure 17A); posteriorly, it turns abruptly dorsad, and merges indistinctly with the thick posterior portion of the lateral wall, which bears a small, acute or blunt caudal projection. The thin and translucent portion of the lateral wall is bounded dorsolaterally by a rib that serves as a base for the narrow, scalloped blade which extends caudally along the lateral margin of the flange. The flange is narrow and horizontal anteriorly, becomes progressively broad posteriorly, and turning mesially is deflected ventrally becoming almost perpendicular to its anterior portion. Laterally, the flange sustains a broad, ventromesially directed firm flap, produced anteriorly in a narrow, subrectangular projection; the flap is strengthened by a subtriangular thickening, and is continuous with a milky white, iridescent, resistant membrane. An extremely sticky, glutinous material lies against the flange and adheres to the mesial surface of the flap.

The thin, translucent dorsomesial wall, like that in the spermatophore of *P. schmitti*, bulges anteriorly beyond its attachment to the ventral and lateral walls along an oblique fine rib extending from the mesial lapel to the posteroproximal end of the wing (Figure 17B). The bulge, occupied by the extremity of the sperm mass enclosed in the sac, bears a triangular crest which abuts on the

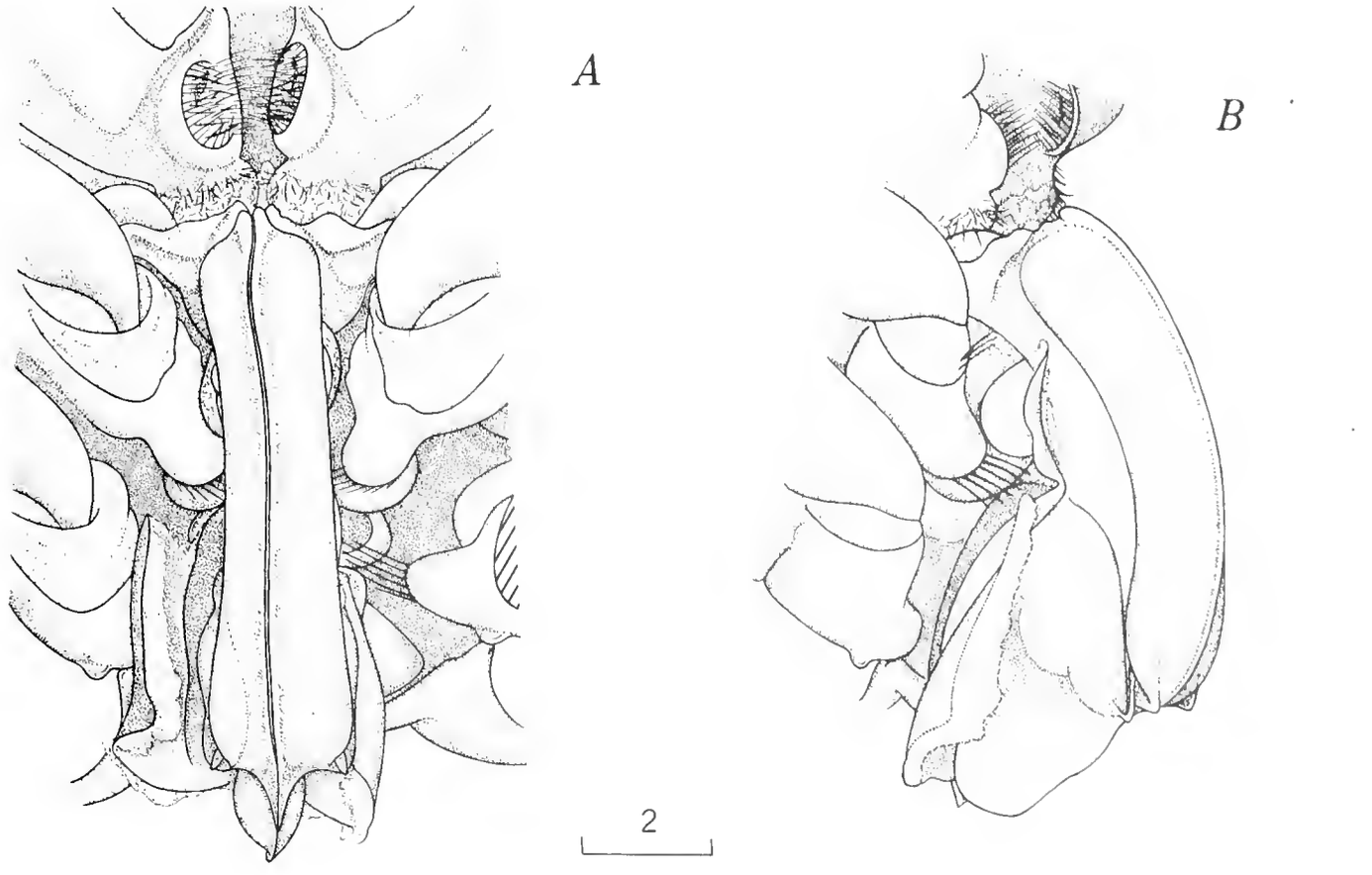

FIGURE 16.—*Penaeus* (*Litopenaeus*) *setiferus* (Linnaeus). *A*, Compound spermatophore attached to female, ♀32 mm cl, 0.8 km off Long Beach, N.C. *B*, Lateral view of same specimen.

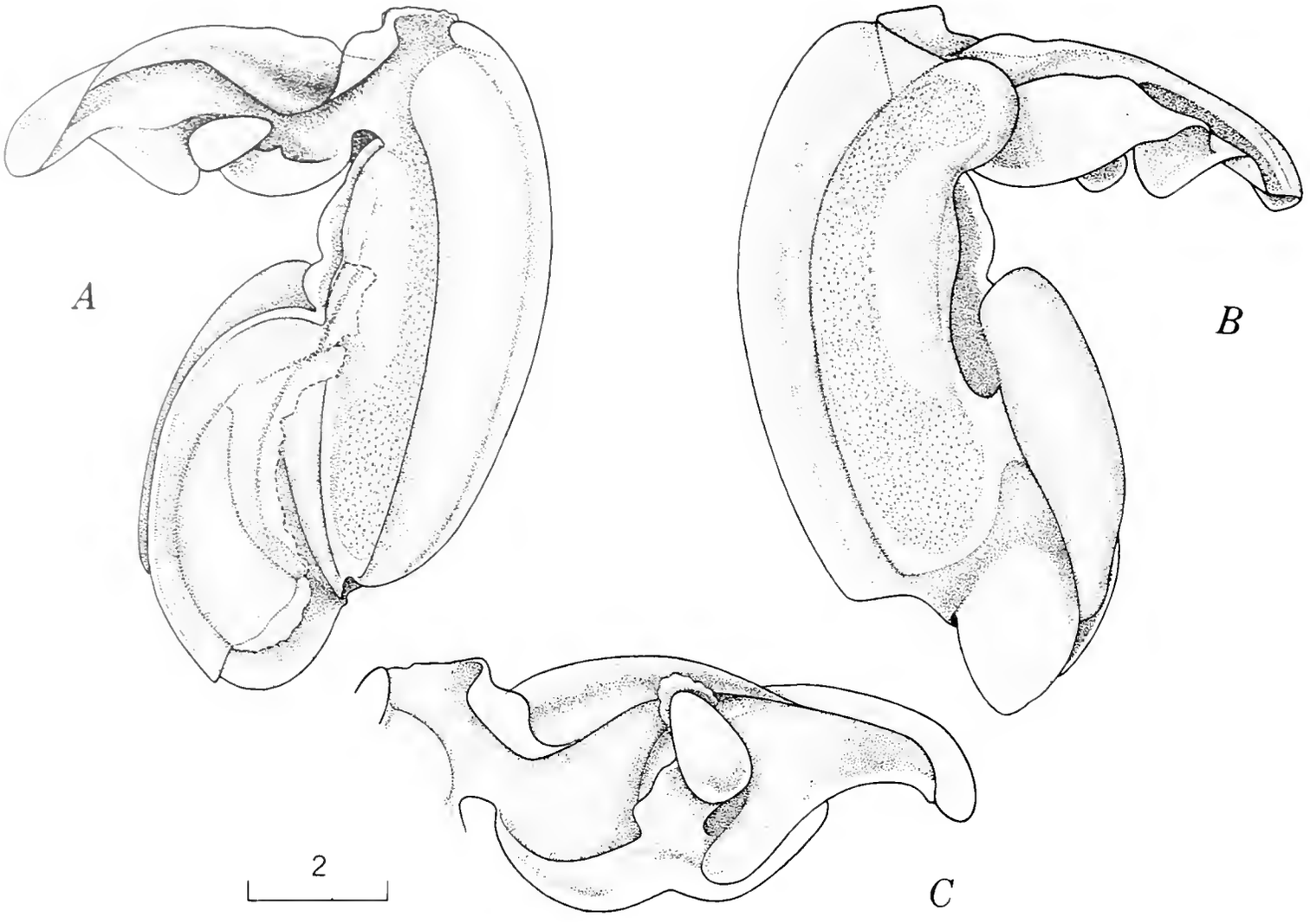

FIGURE 17.–*Penaeus* (*Litopenaeus*) *setiferus*. *A*, Ventrolateral view of right spermatophore dissected from terminal ampulla, ♂SW of mouth of Sabine River, Tex. *B*, Dorsomesial view of same specimen. *C*, Ventral view of wing, left spermatophore, ♂off Melbourne Beach, Fla.

mesial lapel; posterior to the bulge, the dorsomesial wall extends laterally to join the lateral wall (along the base of the blade), and posteriorly merges with the flange.

The wing, long and irregular in contour, is produced posteriorly in a broad proximal lobe, tapering laterally to a rounded, excavated, short tip (Figure 17C). The ventral surface is very irregular, bearing several projections: a rigid subtriangular or rounded prominence on an anterior rib; an elongate twisted process, its base continuous with a posterior fold of the proximal lobe situated about midlength, extending mesially into a subovate to semicircular flap; and a subdistal shelf obliquely flanking the twisted process.

The dorsal plate is tear-shaped in outline, rounded anteriorly, tapering posteriorly, and moderately long, extending from slightly beyond the anterior margin of the flange to its posterolateral corner.

Thelycum (Figure 18)

Sternite XIV bears a pair of sharp crescentic anterolateral ridges the posterior portions of which converge mesially but do not meet, and are often separated by a median longitudinal rib; the posterior part of this sternite is provided with a pair of closely set fleshy lobes, usually separated by a fine median rib which may be continuous with the anterior one. Sternite XIII is heavily sclerotized, forming a strong plate produced posteriorly as a soft emarginate shelf overhanging sternite XIV; the anterior part of this sternite bears a pair of soft, naked, transverse elevations flanking a tonguelike lamella bordered by setae. The lamella forms the roof of a concavity floored by a strong ridge of sternite XII. The ridge (a marginal thickening of heavily sclerotized sternite XII, mostly hidden by setose, rounded and relatively short coxal plates of the third pereopods) is almost

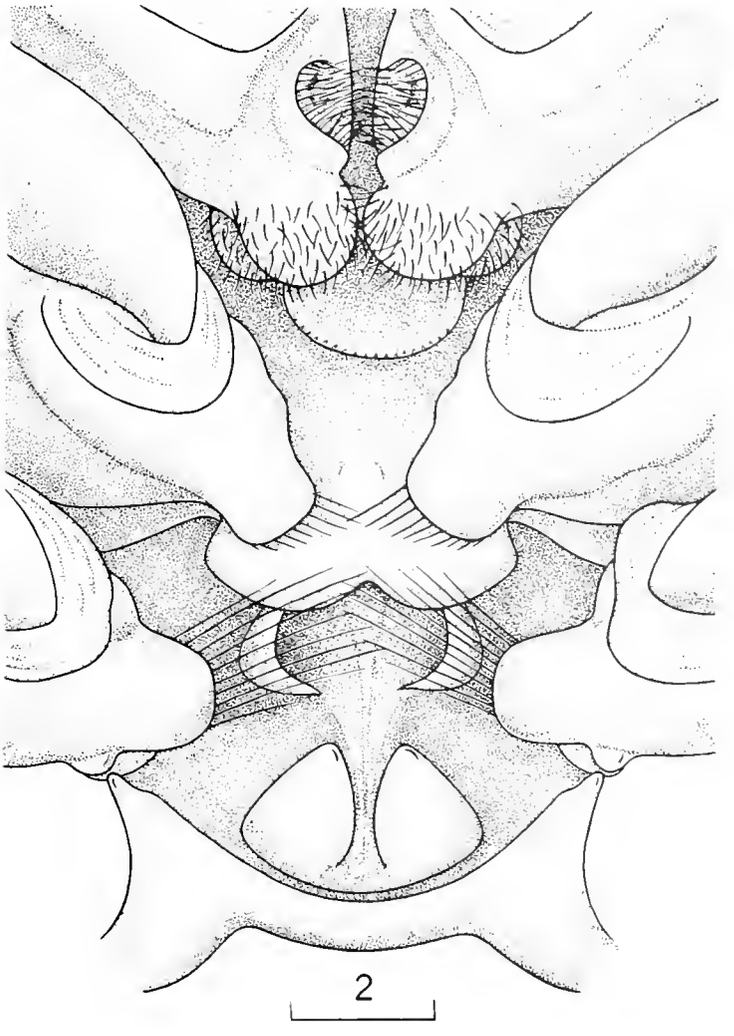

FIGURE 18.—*Penaeus* (*Litopenaeus*) *setiferus*. Thelycum, ♀40 mm cl, off Galveston, Tex.

straight or slightly emarginate along its median portion, and produced laterally in a pair of convex projections armed with long setae. The concavity of sternite XIII is most important in that it serves to lodge the sperm masses protruding anterodorsally from attached spermatophores.

Disposition of the Compound Spermatophore on the Thelycum

The compound spermatophore is anchored to the female much as it in *P. schmitti*. Anteriorly, the geminate body lies on the mesial portions of the coxal plates of the third pereopods (immediately posteroventral to the gonopores), with the sperm masses projecting anterodorsally through the ruptured bulges of the sacs, to lie in a gelatinous envelope fitting into the concavity of sternite XIII. The wings embrace the sperm masses and then extend over the coxal plates, leaving a passageway between them and the body of the animal. The wings are proximally attached to sternite XIII (just caudal to the thelycal lamella) by their posterior lobes, which are in close proximity, and distally affixed to the sternite, or partly to the latter and partly to the articular membranes of the third pereopods. Posterior to the wings, the lateral portions of the ventral walls are turned strongly mesially thus reducing somewhat the lumen of the sacs (Figure 1D). This action may be responsible in part for the transfer of the sperm masses from the sacs to the concavity of sternite XIII at the time of mating. The geminate body is elevated above the sternum so that between the wings and flanges it sometimes does not touch the animal, nor even do the accompanying paired blades, which become almost perpendicular to the sternum. Caudally, the geminate body reaches sternite XIV, where the vertical shelf formed by mesial portions of the flanges lies between the thelycal lobes, or farther beyond on the first pleonic sternite. The firm elongate flaps project ventromesially in conspicuous fashion on each side of the geminate body, whereas anterolateral portions of the flanges are horizontally applied to the dorsal plates, in turn attached to sternite XIV.

I have examined a few females carrying only those parts of the compound spermatophore which are firmly anchored to sternite XIII; the geminate body and adjoining structures have been lost. In all of them, parts remaining affixed to the thelycum (Figure 19) are almost identical: paired masses of sperm lie exposed in the concavity of sternite XIII, where each is contained in an indurate gelatinous substance which, in turn, is tightly embraced by the wings. It appears that in this species, as in *P. stylirostris*, when the spermatophores are released from the terminal ampullae of the male, the masses of sperm and jelly are transferred from the posterior parts of the sacs to the anterodorsal bulges which break under pressure allowing sperm, surrounded by jelly, to reach the thelycal concavity of sternite XIII. This gelatinous substance is directly applied to the concavity, there forming an envelope containing sperm. Eventually, the compound spermatophore splits, the geminate body falls, or is torn away, and the sperm is exposed.

In the impregnated females mentioned above, the compound spermatophore had split in the same fashion, leaving the sperm masses exposed to the surrounding water, suggesting that this rupture might be the means by which spermatozoa are

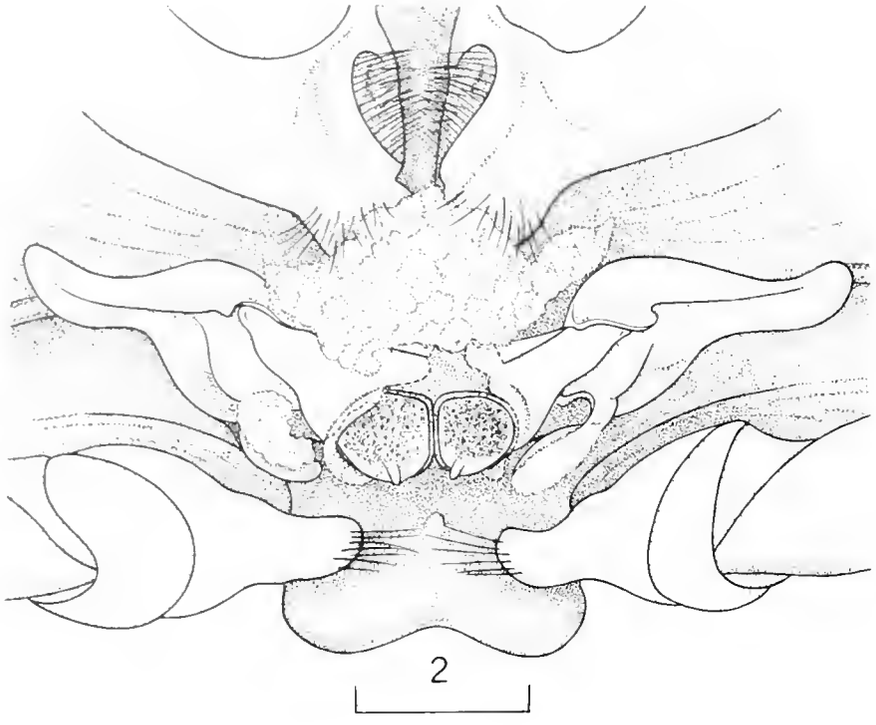

FIGURE 19.—*Penaeus* (*Litopenaeus*) *setiferus*. Sternites XII and XIII bearing wings and paired masses of sperm from a compound spermatophore the geminate body of which has been lost, ♀32.5 mm cl, off Long Beach, N.C.

released at the time of spawning. In some of these females, however, as well as in others with complete spermatophores, a part of each sperm mass protrudes anteriorly from the passageway between the wings and the body of the animal, and even extends onto sternite XII. This indicates that the spermatozoa might disperse anteriorly from the gelatinous envelops surrounding the paired sperm masses while the compound spermatophore is still attached to the female and otherwise intact. Thus, which of these methods is employed in the release of the sperm must await observations of live females immediately after copulation.

Material

The specimens examined by me are listed in Pérez Farfante (1969). Additional specimens follow.

UNITED STATES. 4 ♂ 3 ♀ [1♀ impregnated], UNC-IMS, 0.8 km off Long Beach, (3.2 km E of Lockwood's Folly), N.C., 6 m, 6 May 1949.- 3♂ 2♀ [impregnated], UNC-IMS, 0.8 km off Long Beach, N.C., 6 m, 6 May 1949.- 1♂ 2♀, [1♀ impregnated], UNC-IMS, Beaufort Bar (between Sea Buoy and Bar Buoy No. 1), N.C., 13-16 m, 6 July 1949, *Penny*.- 2♀[impregnated], USNM, Apalachicola Bay, Fla., June 1974.- 1♀ [impregnated], USNM, SE of Freeport, Tex., 15 m, 26 July 1973.- 1♀ [impregnated], USNM, off Galveston, Tex., 1973.- 20♂, USNM, off Galveston, Tex., 25 June 1974.

Species Range

Fire Island, N.Y., to Saint Lucie Inlet, Fla.; in the Gulf of Mexico, from west Florida to the vicinity of Ciudad Campeche, Campeche.

ROLE OF COXAL PLATES IN RETENTION OF COMPOUND SPERMATOPHORE

In the females of the various species of *Litopenaeus*, the coxal plates of the last three pairs of pereopods exhibit specific variations which seem to be associated with the position of the affixed compound spermatophore and the function they serve in holding it in place. In *P. vannamei*, in which the spermatophore reaches anteriorly only to the median protuberance of sternite XIII, the coxae of the third pereopods are not produced posteriorly into well-defined coxal plates. In contrast, the fourth pereopods bear large, flattened coxal plates offering extensive support to the anterior parts of the sperm sacs. The coxal plates of the fifth pereopods are rather short, but prominent, and directed mesially providing a base of attachment for the ventrally elevated lateral portions of the dorsal plates; thus, they are responsible in part for keeping the posterior parts of the sacs raised well above the sternum.

In *P. occidentalis*, the coxal plates of the third pereopods are very elongate and strongly curved anteromesially and dorsally in scooplike fashion,

serving to receive the sperm immediately after its release through the openings of the sperm sacs which lie immediately posteroventral to them; the enclosure for the freed sperm is completed ventrally by the bases of the anterior lobes of the spermatophores which are applied to sternite XII. The coxal plates of the fourth and fifth pereopods are relatively short but are directed mesially, helping to keep the compound spermatophore in position by supporting its lateral blades which lie dorsal to them and which are firmly applied to the thelycum.

In *P. schmitti*, *P. setiferus*, and, particularly in *P. stylirostris*, the coxal plates of the third pereopods are large and directed posteriorly; thus, they appear to aid in keeping the sperm masses (projecting dorsally through the compound spermatophore) within the thelycal concavity of sternite XIII. This is suggested by the fact that in the former two species, in which the concavity lies on the anterior part of sternite XIII, the coxal plates are much shorter than in *P. stylirostris* in which the double concavity is located on the posterior part of the sternite. In *P. schmitti* and *P. setiferus*, the coxal plates of the fourth and fifth pereopods (longer in the latter) are directed mesially, supporting the lateral components of the spermatophore and pressing them against the thelycum. In *P. stylirostris*, these coxal plates are larger than in any of the other species, those of the fifth pereopods offering a broad base for the attachment of the anterior portions of the dorsal plates of the spermatophore to their ventral surfaces. The coxal plates of the fourth pereopods are directed posteromesially, lying ventrad to the subvertical shelf of sternite XIII, thus helping in holding the sperm masses within the thelycal concavities of the latter sternite.

Finally, in all five species, the coxal plates are provided with numerous long, mesially directed setae which, in impregnated females, become embedded in the dorsal plates or extend over the blades and flanges, thus contributing to maintaining the spermatophore in position.

COMPARISONS OF SPERMATOPHORES

The morphology of the spermatophores of two species of the subgenus *Melicertus* have been studied in rather considerable detail: that of *P.* (*M.*) *kerathurus* (Forskål 1775) by Mouchet (1931) and Heldt (1938a, b), and that of *P.* (*M.*) *japonicus* Bate 1888, by Kishinouye (1900), Hudinaga (1942) and, later, more meticulously by Tirmizi (1958). A brief illustrated account of the spermatophore of *P.* (*Farfantepenaeus*)[2] *duorarum duorarum* Burkenroad 1939, was presented by Eldred (1958). Recently, Malek and Bawab (1974a, b), conducted a thorough study of the formation of the spermatophore within the vas deferens in *P.* (*M.*) *kerathurus*; the hardened cover of the spermatophore that is contributed by the ampulla is now being investigated by them. The above studies, as well as those on the subgenus *Litopenaeus*, have revealed that in spermatophores of *Penaeus* the sperm mass is surrounded by a gelatinous, multilayered (Malek and Bawab 1974b) sheath which, in turn, is enclosed in a sperm sac; this usually bears an aliform process, and in members of *Litopenaeus* additional attachment structures are present.

The principal characteristics of the spermatophores of the five species of *Litopenaeus* are presented in Table 1 to facilitate a comparison of them.

The spermatophore of *P. vannamei* is the simplest. It lacks an anterolateral wing, is not produced into an anterior lobe, and does not bear a lateral blade.The fact that the ventral and lateral walls are both opaque and thus almost indistinguishable, contributes to the relatively simple appearance of this spermatophore. However, it exhibits by far the thickest lateral flap and the largest dorsal plate. Apart from the seemingly firm affixation of the anterior part of the sacs to the thelycum, the attachment of the compound spermatophore to the female is accomplished by the very elongate dorsal plates, which support the geminate body and the paired flanges. Finally, the compound spermatophore when applied to the female extends only to about the midlength of sternite XIII, instead of reaching sternite XII as do those of the other species. The short anterior extensions of the ventral walls are applied to the median protuberance of sternite XIII, and the prominent bulges of the sacs, where the sperm masses are concentrated, lie at the anterior part of sternite XIV. Consequently, the sperm is released farther away from the gonopores of the female than in the remaining species.

[2]The subgenus *Farfantepenaeus* was recently established by Burukovskii (1972) to include the grooved species of *Penaeus* (those with adrostral sulci extending posteriorly beyond midlength of carapace) from American waters, one of them also occurring off West Africa. These shrimps were previously placed by Pérez Farfante (1969) in the subgenus *Melicertus* Rafinesque 1814, together with the grooved *Penaeus* occurring from the eastern Atlantic eastward to the waters of Hawaii.

TABLE 1.—Characteristics of the spermatophores of five species of *Penaeus (Litopenaeus)*.

Species	Sperm sac	Wing	Anterior lobe	Flange	Blade	Lateral flap		Anterior lamina	Dorsal plate	Position on female
						Along sac	Along flange			
P. vannamei	Simple[1]	Lacking	Lacking	Long, caudal	Lacking	Broad, fleshy	Narrow, flexible	Lacking	Long, underlying most of sac and flange	Reaching about mid-length of sternite XIII
P. occidentalis	Simple	Small	Present	Short, caudal	Attached at edge, extending laterally; broad	Lacking	Broad, highly sclerotized	Present	Moderately long, underlying blade	Reaching posterior part of sternite XII, and embracing gonopore
P. stylirostris	Complex[2]	Large	Lacking	Long, caudolateral	Attached along midline, extending dorsomesially and ventromesially	Broad, membranous	Narrow, flexible	Lacking	Moderately long, underlying base of sac and flange	Reaching anteriormost part of sternite XIII
P. schmitti	Simple	Moderately large	Lacking	Long, caudolateral	Attached at edge, extending laterally; broad anteriorly	Narrow, firm	Broad, firm	Lacking	Long, underlying blade and flange	Reaching anteriormost part of sternite XIII
P. setiferus	Simple	Moderately large	Lacking	Long, caudolateral	Attached at edge, extending laterally; narrow throughout	Narrow, firm	Broad, firm	Lacking	Moderately long, underlying flange	Reaching anteriormost part of sternite XIII

[1]Lateral wall continuous with dorsomesial.
[2]Lateral wall overlapping dorsomesial wall laterally, forming free shield (see p. 473).

It seems noteworthy that *P. vannamei* is the only species of the subgenus *Litopenaeus* in which a strongly developed median protuberance (projecting from sternite XIII) is present on the thelycum. Females of the remaining species of *Litopenaeus* lack a median protuberance, unlike all of the other species of *Penaeus*. In the former females, the midposterior part of sternite XIII bears instead a simple, relatively small knob—in *P. occidentalis*—or is produced into a shelf which overhangs sternite XIII. This shelf is horizontal in *P. schmitti* and *P. setiferus*, and subvertical in *P. stylirostris*.

The spermatophore of *P. occidentalis* is considerably more elaborate than that of *P. vannamei*, although the sac is structurally similar in the two and simpler than that of *P. stylirostris*. The spermatophore of *P. occidentalis*, unlike that of *P. vannamei*, possesses a wing and, unlike all other species of *Litopenaeus*, bears an anterior lobe, and is produced caudally in a very short flange. Also, it bears the largest lateral blade to be found in any of them, the blade being divided in several sections and continuous with the typical stiffened ventromesial extension, ending in a rather flexible caudal lobe; that extension seems to correspond to the flap borne by spermatophores of the other species. In addition, the spermatophore of *P. occidentalis* possesses a unique transverse lamina on the anterior extremity of the sac, which is not intimately associated or even firmly attached to it or to the other contiguous components, i.e., the anterior lobe and the wing. In this spermatophore, however, the flange is inconspicuous, consisting of a short rigid shelf at the posterior end of the sac. Finally, the compound spermatophore of *P. occidentalis* is affixed to the female farther anteriorly than in the other species, the anterior lobes extending over (ventrally) the coxae of the third pereopods to become attached to sternite XII; this brings the openings of the sacs to the scooplike coxal plates of the third pereopods, almost directly opposite the female gonopores.

The spermatophore of *P. stylirostris* differs from all the others chiefly in the structure of the sperm sac, which is largely formed by the dorsomesial wall. This wall, after extending laterally, is bent mesially in such a way as to reach, ventrally, the base of the mesial flap; as a result, part of the ventral and lateral walls, apart from giving support to the sac, serve as a protecting shield. The spermatophore of *P. stylirostris* also possesses the broadest wing to be found within the subgenus,

and is armed with a blade, the anterior portion of which is directed both dorsomesially and ventromesially instead of laterally, in specimens removed from males. Along the sac, the lateral flap is almost as broad as that in *P. vannamei*, but thinner and not fleshy. Furthermore, in *P. stylirostris*, the paired dorsal plates affix only the posterior part of the spermatophore to the females, not directly supporting the midportion. The flanges become attached to the female almost perpendicular to the geminate body, instead of extending entirely caudad as in *P. vannamei* or somewhat caudad as in *P. schmitti* and *P. setiferus*.

The spermatophores of *P. schmitti* and *P. setiferus* are almost identical. They may be distinguished by the width of the lateral blade, the anterior portion of which is broad (except for a narrow portion at the base of the wing) in *P. schmitti* and very narrow in *P. setiferus*. Sperm sacs of both species are similar to those of *P. vannamei* and *P. occidentalis*; however, they bear wings, which are lacking in *P. vannamei*, and the wings are moderately large and scabrous, with various projections on the ventral surface, thus very different from the small wing with the margins extensively folded found in *P. occidentalis*.Also, the flanges extend considerably anteriad along the lateral walls of the sacs, whereas those in *P. vannamei* are virtually caudal and, unlike *P. occidentalis*, are produced posteriorly much beyond the sac instead of barely overreaching the fundus. Finally, flaps borne by the flanges are broad in the two Atlantic species, instead of narrow as in *P. vannamei*, and, although firm, are different in texture from the heavy sclerotized shelf sustained by the flange in *P. occidentalis*.

Despite the similarities of the various sacs, the mode of dehiscence varies—differences among the spermatophores are due more to the elements associated with the sac than to the sac itself. It seems that in *P. occidentalis*, the sperm is released through anterior openings of the sacs which become applied to the coxal plates of the third pereopods, and are well protected by the anterior lobes of the spermatophores. In *P. stylirostris* as well as in *P. schmitti* and *P. setiferus*, it seems that the compound spermatophore attached to the female splits longitudinally into two parts, the geminate body breaks away leaving paired masses of sperm on the thelycum freely exposed to the surrounding water. In *P. schmitti* and *P. setiferus*, however, there are certain indications that the sperm reaches the water through a passageway between the wings and the body of the female, the geminate body persisting. On the basis of the available material of *P. vannamei*, there is no indication as to how the sperm escapes from the spermatophore. Understanding of the precise manner in which spermatozoa are freed from spermatophores in all of the species must await direct observations.

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DYNAMICS OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, RUNS IN THE DELAWARE RIVER[1]

MARK E. CHITTENDEN, JR.[2]

ABSTRACT

Adult American shad were collected by haul seining at regular intervals during the spring migrations from 1963 to 1965 and by collecting specimens from a fishkill in spring 1965. Supplementary sex and size composition data were obtained from summer rotenone sampling in 1961 and 1962.

Males tended to precede females in the spring run. Annual sex compositions were strongly male dominated from 1961 to 1963 and were strongly female dominated in 1964 and 1965. Repeat spawners composed 2.6% of 729 fish examined from 1963 to 1965. Age I and II fish were absent or virtually absent from the run. Males migrated upstream primarily at age IV and females at age V. Large runs during the early 1960's were based on the 1958 and 1959 year classes as defined which were much larger than other year classes produced in the period 1957-64. Delaware River American shad runs now have little buffering against fluctuations in abundance because few year classes are successful, few age groups support the run, and there are essentially no repeat spawners. Larger runs in the Delaware since 1925 and probably somewhat earlier, in general, were apparently based on one large year class and essentially no repeat spawners.

The American shad, *Alosa sapidissima*, formerly was one of the most abundant anadromous fishes in the United States where more than 50 million pounds were landed in 1896. In contrast, only 8 million pounds were caught in 1960 (Walburg and Nichols 1967). Much of this decline is due to the collapse of the Delaware River Basin fisheries which once supported larger landings of American shad than any other river system (Stevenson 1899). Estimates of the 1896 Delaware Basin catch are about 16.5 to 19.2 million pounds (Smith 1898; Sykes and Lehman 1957; Walburg and Nichols 1967)—about a third of the national total. Annual Delaware Basin catches about that time varied from 14 to 17 million pounds and were probably primarily fish of Delaware River origin (Chittenden 1974). In contrast, annual Delaware Basin landings since 1920 have consistently been much less than 0.5 million pounds (Sykes and Lehman 1957; Chittenden 1974).

Trends in abundance of Delaware Basin stocks have been described by Sykes and Lehman (1957) and Chittenden (1974), and causes of these fluctuations have been described by Ellis et al. (1947), Sykes and Lehman (1957), Walburg and Nichols (1967), and Chittenden (1969). The dominant factor affecting abundance during the past 60 yr, at least, has been pollution near Philadelphia, Pa. Complete understanding of the causes of fluctuations in abundance, however, depends on detailed knowledge of the population dynamics of this species. Many workers have described certain aspects of the population dynamics of American shad in other river systems. Little work has been published for the Delaware, in part because Delaware River American shad stocks have been so low that it has been difficult to collect large numbers of fish.

The present paper describes data collected on sex, size, age, and repeat spawner composition; comparative magnitudes of American shad runs; and year-class strengths in the Delaware River during the late 1950's and the 1960's.

MATERIALS AND METHODS

Adult fish were collected 22.5 km (14 miles) above tidal water in the years 1963 to 1965 at the site of the Lewis Fishery in Lambertville, N.J., using a 76-mm (3-inch) stretch-mesh, 107-m (350-foot) long and 3.6-m (12-foot) deep (4.3 m = 14 feet in 1963) haul seine that was paid out from a boat and landed about 396 m (1,300 feet) downstream. Sampling occurred at 4-day intervals after a randomly selected date in 1963 but at fixed intervals

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twice weekly in later years. Sampling occurred from 5 April to 19 May in 1963, from 20 March to 18 May in 1964 and from 26 March to 7 May in 1965. In 1964 and 1965, at least, several collections were made both before and after the first and last American shad were captured, but a few fish were captured on the first and last sampling dates in 1963. My sampling in 1963 essentially ended when the run did at Lambertville. I captured 1 fish after 15 May, and the Lewis Fishery captured 5 fish after that date of a total catch of about 4,000 fish (Chittenden 1969). The number of seine hauls and time of sampling varied each day during 1963. After 1963 two seine hauls were made from 1100 to 1300 EST on each sampling day after the first American shad was landed. In spring 1965, low dissolved oxygen levels near Philadelphia blocked upstream passage of part of the spawning run, and few fish were captured at Lambertville (Chittenden 1969). Hundreds of dead fish were collected during a fishkill seaward of Philadelphia in the area from Paulsboro, N.J., to Marcus Hook, Pa., during the period from 21 May to 10 June. Sex and size composition data for 1961 and 1962 were obtained from cooperative surveys (hereinafter referred to as the Tri-state Surveys) using rotenone during July and August by the states of New Jersey, New York, and Pennsylvania in conjunction with the U.S. Fish and Wildlife Service. I personally examined many of the American shad collected.

Each fish collected after 1962 was measured and was sexed by examination of the gonads, and scales were taken from the midline of the left side below the dorsal fin following Cating (1953) or from the same area on the right side. Many fish collected near Marcus Hook during 1965 had lost all or nearly all their scales, so scales were taken where available on these fish. Scales selected for age determination were cleaned and were dry-mounted between glass slides. Aging was done with a microprojector using Cating's (1953) method which was verified by La Pointe (1958) and Judy (1961). Scales were examined in the time sequence 1963, 1964, and 1965 for an initial determination. Many of the large fish were known to have been misaged when the sequence was completed. Scales were next thoroughly mixed to remove bias due to knowledge of the collection year and were reread. The first two readings disagreed on 31 of 301 fish (10%) from 1963, 38 of 199 (19%) from 1964, and 3 of 184 (2%) from 1965. Of these, 32 disagreements were on females reassigned from age-group V to VI (9 from 1963 and 23 from 1964). A third examination of the misaged scales agreed with the second on 67 of the 72 fish. The remaining 5 were discarded.

RESULTS AND DISCUSSION

Sex Composition of the Spawning Runs

Many American shad were captured at Lambertville during 1963 (301 fish) and 1964 (199 fish). Figure 1 shows trends in the cumulative percentage of males as these spawning runs progressed. Trends were similar during each year although the 1963 run contained a much higher percentage of males than the 1964 run. The cumulative proportion of males decreased as the run progressed in agreement with the observations or statements of many workers including Stevenson (1899), Prince (1907), Leach (1925), Hildebrand and Schroeder (1928), Nichols and Tagatz (1960), and Walburg and Nichols (1967).

Annual sex compositions of the runs from 1961 to 1965 are presented in Table 1 with 95% confidence limits for the proportion of males based upon normal approximations except for 1962 when a Poisson approximation to the binomial was used (Cochran 1953). Annual sex composition varied greatly from 1961 to 1965. It was male dominated from 1961 to 1963 and female dominated thereafter.

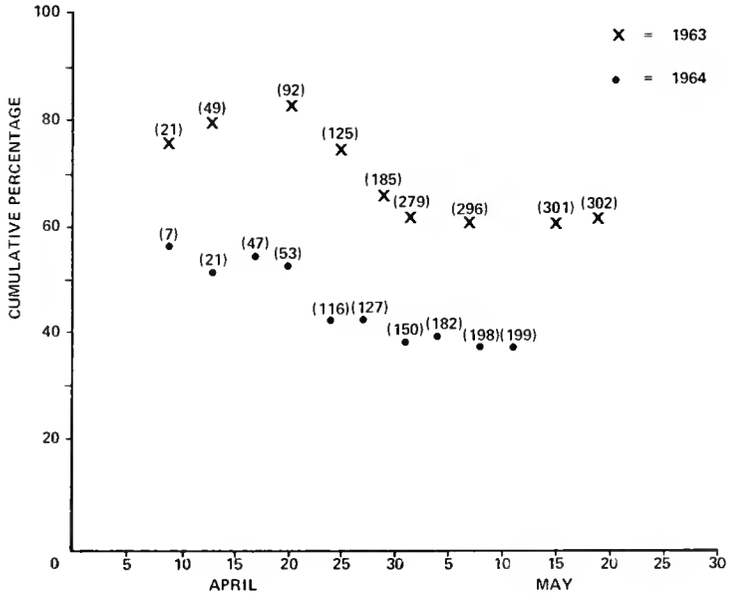

FIGURE 1.—Trends in the cumulative percentage of male American shad. Numbers in parentheses represent cumulative numbers of fish captured.

TABLE 1.–Annual sex compositions of American shad runs, 1961-65.

Year	Sample size (n)	Proportion male (p)	95% CL about p[1]
1961	198	0.86	0.81-0.94
1962	220	0.99	0.96-1.00
1963	302	0.62	0.57-0.67
1964	199	0.38	0.31-0.45
1965 Lambertville	23	0.52	0.32-0.72
1965 Tidal area	190	0.23	0.17-0.29

[1]Confidence limit for proportion of males.

Size Composition

Mean fork lengths, numbers of fish, 95% confidence limits for means, and 99% limits for individuals collected at Lambertville or the tidal area and during the Tri-state Surveys are summarized in Table 2. Data were originally expressed in total or fork length depending on year of collection. Means and confidence limits were transformed to fork lengths in inches using the regression of fork on total length presented by Chittenden (1969) and were then transformed to metric units. Females from Marcus Hook and Lambertville did not appear significantly different in size and were pooled. Males from Marcus Hook were significantly smaller (t = 4.67) than those from Lambertville, and they were not combined.

Fish were smaller in 1961 and 1962 than in later years, and this probably reflects the presence of very young individuals of the strong 1958 and 1959 year classes (see section "Comparative Year-Class Strengths"). Females averaged about 50 mm (2 inches) longer than males each year. Confidence limits for individuals indicate that there were few females longer than 545 mm (21.5 inches) and few males longer than 505 mm (19.9 inches). Maximum observed sizes were 559 and 495 mm (22.0 and 19.5 inches) for females and males, respectively. Small fish did not migrate upstream. The smallest female was about 64 mm (2.5 inches) longer than the smallest male each year. There were few females shorter than 416 mm (16.4 inches) in 1963, 1964, and 1965, the smallest being 406 mm (16.0 inches). The smallest female observed was 376 mm (14.8 inches) and 391 mm (15.4 inches) in 1961 and 1962, respectively. Confidence limits indicate that there were few males shorter than about 337 mm (13.2 inches) from 1962 to 1965. There were few males shorter than 289 mm (11.4 inches) in 1961, the smallest fish measured being 269 mm (10.6 inches).

Age and Repeat Spawner Comsposition

There were only 2.6% repeat spawners in 729 fish examined from 1963 to 1965. Annual occurrences were 1 of 299 fish (0.3%) in 1963, 3 of 199 (1.5%) in 1964, and 15 of 231 (6.5%) in 1965. Confidence limits for the annual percentages are 0.0 to 1.9% (1963) and 0.03 to 4.4% (1964) based upon Poisson approximations and 3.5 to 9.5% (1965) based upon the normal approximation.

Table 3 summarizes male and female age-class structures of the 1963 and 1964 runs at Lambertville, pooled data for 1965 from Lambertville and Marcus Hook, and data pooled over all years. Fluctuations in age composition due to variable year-class recruitment are apparent, but certain general features of the age composition stand out.

TABLE 2.–Summary of fork lengths of American shad, 1961-65. Lengths are in millimeters (top rows) and inches (bottom rows).

	Males				Females			
Year	n	Mean ($\bar{x}$)	95% CL $\bar{x}$	[2]99% CL x	n	Mean ($\bar{x}$)	[1]95% CL $\bar{x}$	[2]99% CL x
1961	170	401	394-407	289-512	28	452	441-463	371-533
		15.8	15.5-16.0	11.4-20.1		17.8	17.4-18.2	14.6-21.0
1962	217	415	414-415	362-467	3	451	322-579	—
		16.3	16.3-16.3	14.2-18.4		17.8	12.7-22.8	—
1963	186	428	425-431	371-485	115	472	468-476	416-529
		16.9	16.7-17.0	14.6-19.1		18.6	18.4-18.8	16.4-20.8
1964	76	427	420-434	350-504	122	480	477-484	428-533
		16.8	16.6-17.1	13.8-19.8		18.9	18.8-19.1	16.9-21.0
1965 Lambertville	12	436	417-455	342-530	11	483	472-495	431-536
		17.2	16.4-17.9	13.5-20.9		19.0	18.6-19.5	17.0-21.1
1965 Tidal area	43	417	408-426	337-498	147	484	480-488	422-546
		16.4	16.1-16.8	13.2-19.6		19.1	18.9-19.2	16.6-21.5
1965 Combined	—	—	—	—	158	484	481-488	423-545
		—	—	—		19.1	18.9-19.2	16.7-21.5

[1]Confidence limit for mean fork length.
[2]Confidence limit for indivdual fish collected.

TABLE 3.—Age-class structures of American shad, 1963-65.

Age	1963		1964		1965		Total	
	n	%	*n*	%	*n*	%	*n*	%
				Males				
II	0	0	1	1	0	0	1	0.00
III	4	2	1	1	3	6	8	2.58
IV	149	82	51	68	36	68	236	76.13
V	27	15	21	28	14	26	62	20.00
VI	2	1	1	1	0	0	3	0.01
				Females				
IV	31	27	9	7	10	8	50	13.70
V	63	56	77	64	85	65	225	61.64
VI	19	17	35	29	34	26	88	24.11
VII	0	0	0	0	2	2	2	0.01

The following comments essentially apply to virgin fish because the percentage of repeat spawners was negligible.

Age I and II males did not migrate upstream, although one age II male was captured in 1964. Few age III males migrated upstream, the percentage based on pooled data over all years being less than 3%. Males migrated upstream primarily at age IV (76%), but age V (20%) was also important. Few males survived to age VI, and all were virgin. No males older than age VI were captured. No females younger than age IV or older than age VII were observed. Only two age VII females (less than 1% of the pooled total) were captured, and one of these was a virgin. Females were primarily age V (62%) when they first entered the fishery, but ages IV (14%) and VI (24%) were also important.

Comparative Magnitudes of American Shad Runs, 1961-68

I here define magnitude of American shad runs as the numbers of adults reaching Lambertville on their upstream migration. The magnitude of runs as defined is influenced by year-class strength as later defined herein and by dissolved oxygen levels that the adults encounter during migration upstream past the Philadelphia area (Chittenden 1969). Chittenden examined in detail the annual effects of oxygen upon passage of adults and young. In general, dissolved oxygen is sufficiently high that the earlier stages, at least, of the adult run successfully migrate upstream.

Reasonably precise estimates of the comparative magnitudes of American shad runs in the 1960's are available from three sources of evidence: 1) catches of the Lewis Fishery at Lambertville presented by Chittenden (1974), 2) my own catches at Lambertville, and 3) sex compositions of the runs presented in Table 1.

Lewis Fishery annual catch/seine haul records indicate the comparative magnitudes of runs in descending size order were: 1963 (56.1 fish), 1964 (18.3), 1962 (13.9), 1965 (6.6), 1967 (3.7) = 1961 (3.5), and 1966 (1.8) = 1968 (1.2). Values in parentheses represent catch/seine haul. My annual catch/seine haul at Lambertville for the time period between capture of the first and last fish was 17.4 fish in 1963, 9.0 in 1964, and 3.0 in 1965, a pattern in agreement with the Lewis Fishery records. My general impressions derived from angling experience, interviews with other anglers, and visual observations of the abundance of adult American shad during extensive float trips each year from 1961 to 1974 are in general agreement with the patterns suggested by the Lewis Fishery records. Runs were much smaller from 1966 to 1968 than from 1962 to 1964. The size of the run in 1965 (and possibly 1961 based on my general impressions) was intermediate between the sizes in these two periods.

The relative magnitudes of runs estimated from sex composition data (Table 1) agree with patterns indicated by catch records at Lambertville. The sex ratio shift from 1963 to 1964 suggests passage through the fishery of a year class stronger than the one immediately following because males tend to enter the run a year earlier than females. This indicates the 1963 run was larger than that in 1964.

The male proportion at Lambertville in 1965 (0.52) is biased towards the high side because the later part of the run was blocked by low dissolved oxygen near Philadelphia. The male run was much greater in 1963 than in 1964. Confidence limits for the male proportion of fish collected at Marcus Hook in 1965 were much lower than any single daily male proportion in 1963 (Figure 1) but were similar to the lowest daily male proportion in 1964. Therefore, the 1965 run was probably similar in sex composition to that of 1964. Females enter the run a year older than males. Unless females suffer a much lower annual mortality, similarity of sex compositions suggests that the 1965 run was smaller than the 1964 run—even before the fish reached the Philadelphia area. The high female proportion in 1965 suggests an even smaller run was due in 1966, another year when low oxygen levels blocked part of the run (Chittenden 1969). Dissolved oxygen was sufficiently high throughout the 1967 run to permit large numbers of fish to reach Lambertville (Chittenden 1969). The Lewis Fishery in 1967 did not make large catches to reflect 1968 males or females associated with the

1966 males, suggesting that the 1966 and 1968 runs were small—even before the fish reached the Philadelphia area.

The higher proportion of males in 1962 than in 1961 indicates that the 1962 run was larger than the 1961 run.

Comparative Year-Class Strengths, 1956-64

I here define year-class strength as the numbers of young which exist at some constant point in time—say 1 January—after the entire year class has "passed" seaward through the grossly polluted Philadelphia area. Year-class strength is influenced by spawning success. However, the dominant factor, by far, in setting year-class strength in the Delaware River is the success with which the young pass seaward through the Philadelphia area in summer and fall (Chittenden 1969).

Comparative year-class strengths can be estimated from the age and sex compositions from 1963 to 1965 (Tables 1, 3) supported by estimates of comparative run sizes. Males usually first migrate upstream at age IV and females at age V, so that the size of a run chiefly reflects the strength of year classes produced 4 and 5 yr earlier assuming constant survival at sea. Therefore, American shad runs from 1961 to 1968 chiefly reflect year-class strengths from 1956 to 1964. The largest year classes as defined were produced from 1957 to 1960 because the largest runs were from 1962 to 1964.

The 1963 American shad run was the largest in this period and primarily reflects the 1958 and 1959 year classes. I captured 90 age V fish at Lambertville in 1963 and 98 in 1964 with approximately equal effort, suggesting that the 1958 and 1959 year classes were similar. This agrees with comparative magnitude estimates for the 1962 and 1963 runs. The 1963 run was based on two large year classes and was larger than the 1962 run which was based on one large and one smaller year class.

The 1960 and 1959 year classes can be compared. I collected 180 age IV fish at Lambertville in 1963 but only 60 age IV's in 1964. This suggests that the 1959 and, by inference, 1958 year classes were much larger than that of 1960. This deduction is supported by the shift in sex composition from 1963 to 1964, which indicates the age V year class from 1959 was much stronger than the age IV year class from 1960. The 1963 run was based on two large year classes and was larger than the 1964 run which was based on one large and one smaller year class.

The 1957 and 1958 year classes can be compared. At Lambertville, 36 and 21 age VI fish were captured in 1964 and 1963, respectively, suggesting that the 1958 and, by inference, 1959 year classes were stronger than that of 1957. This is supported by mean sizes of males collected during the Tri-state Surveys of 1961 and 1962 (Table 2). The 1961 fish (mean = 401 mm = 15.8 inches) were significantly smaller than the 1962 fish (mean = 414 mm = 16.3 inches). The observed mean fork length of age IV males in 1963 and 1964 was about 422 mm (16.6 inches) (Chittenden 1969, table 17), suggesting that age III fish from 1958 were important in the 1961 run.

The 1961 and 1960 year classes can be compared. Sex composition and catch data show that the 1964 run was smaller than the 1965 run. Age structures were almost identical, however, and this indicates that the 1961 year class was smaller than that of 1960.

The strength of the 1962, 1963, and 1964 year classes as defined must have been small, probably being no larger than the 1961 year class, because the 1966 to 1968 runs were very small.

In summary, the 1958 and 1959 year classes were extremely large in comparison to the year classes produced in the period 1961-64. The 1957 and 1960 year classes were much smaller than those of 1958 and 1959, but were larger than the 1962, 1963, and 1964 year classes.

GENERAL DISCUSSION

Delaware River American shad runs in the 1960's showed great shifts in the proportion of male fish. This variation was due, in large part, to fluctuations in year-class strength. The proportions in 1961 (0.86) and 1962 (0.99) are extreme. They are based upon summer collections and are biased if females tend to return seaward earlier than males do. However, these proportions also probably primarily reflect the temporary resurgence of the Delaware River American shad runs in the early 1960's reported by Chittenden (1974). The magnitude of American shad runs in the Delaware River was at a very low level prior to 1961, increased in 1961 and 1962, and in 1963 the magnitude was such that it ranked among the largest runs in the last 45 yr or more. Because Delaware River males tend to undertake their first

spawning migration at age IV and females at age V, the strongly male dominated runs of 1961 and 1962 reflect the entry of unusually large year classes into the fishery. The magnitude of the spawning runs declined greatly after 1963, and the shift towards female dominance reflects the failure of new year classes to be recruited. The strength of the 1962, 1963, and 1964 year classes as defined was small because the 1966 to 1968 runs were very small. Yet, from visual observations and collections of young during the summer, Chittenden (1969) concluded that strong year classes were produced throughout the period 1962-66. I presented dissolved oxygen data for the periods when the young passed the Philadelphia area each year and ascribed the failure of these strong year classes to later recruit to the fishery to catastrophic destruction of the young as they passed through the grossly polluted area.

There was a negligible percentage of repeat spawners in the Delaware River American shad runs from 1963 to 1965, and there were no repeat spawners among 245 American shad collected from the 1961 run (J. Malcolm, pers. commun.). The existence of numerically few repeat spawners must have continued to be the case after 1965 because the runs from 1966 to 1968 were very small. Delaware River runs apparently have included few repeat spawners for at least some 25 yr because Sykes and Lehman (1957) reported that less than 2% of 423 fish captured in 1944, 1945, 1947, and 1952 were repeat spawners. Even the production of very large year classes appears to have little effect on the percentage of repeat spawners in the Delaware River. The percentage was only 6.5% in 1965, a year when the very strong 1958 and 1959 year classes should have increased the percentage greatly rather than by only a few points. As Sykes and Lehman (1957) pointed out, the virtual absence of repeat spawners in the Delaware River is very unlike that in other middle-North Atlantic coast rivers where repeat spawner percentages have been: St. Johns River, N.B., Canada, 22-81% (Leggett 1969); Connecticut River, 14-60% (Moss 1946; Nichols and Tagatz 1960; Leggett 1969); Hudson River, 51% (Talbot 1954); Susquehanna River, 37% (La Pointe 1958); Potomac River, 17% (Walburg and Sykes 1957); York River, 21-27% (Nichols and Massmann 1963; Leggett 1969); James River, 27%, (Walburg and Sykes 1957). Some of the higher percentages of repeat spawners in these rivers are undoubtedly biased towards the high side because they are based on collections of fish from hightly selective commercial gill nets. However, it appears that the Delaware River has a much lower percentage of repeat spawners. The Delaware River seems most like rivers south of Cape Hatteras, N.C., where few repeat spawners have been reported: Neuse River, less than 3% (La Pointe 1958; Walburg 1957); Edisto River, 0% (Walburg 1956); Ogeechee River, 0% (Sykes 1956); Altamaha River, 0% (Godwin and McBay 1967; Godwin 1968); St. Jones River, Fla., 0% (Walburg 1960; Leggett 1969).

Age-class structures of American shad runs have been reported by many workers including Talbot (1954), Fredin (1954), Walburg (1956, 1957, 1960, 1961), Walburg and Sykes (1957), Sykes (1956), La Pointe (1958), Nichols and Tagatz (1960), Nichols and Massmann (1963), Godwin (1968), and Leggett (1969). Walburg and Nichols (1967) summarized the available information by stating that age IV and V fish make up the bulk of the catch in South Atlantic rivers and Chesapeake Bay tributaries while the catch is primarily composed of age IV to VII fish in middle Atlantic rivers. Delaware River runs in the 1960's were primarily supported by age IV and V fish, although age VI females were also important. Sykes and Lehman (1957) reported similar findings for fish collected in the 1940's and 1952 except that they gave more weight to age VI fish, possibly due to sampling with commercial gill nets.

Because of the absence of repeat spawners, which tend to be older fish, few age-groups support American shad runs in the Delaware River. This is similar to the situation in South Atlantic rivers but unlike that in North Atlantic rivers. The apparent similarity of Delaware River American shad to those of southern rivers rather than to geographically more closely related fish from northern rivers is an artifact caused by man. Howell (1837) reported that American shad captured in the Delaware River averaged about 3,175 g (7.00 pounds). In contrast, Chittenden (1969) reported that males averaged 1,107 g (2.44 pounds) with 95% confidence limits about the mean being 1,080-1,134 g (2.38-2.50 pounds) and females averaged 1,737 g (3.83 pounds) with the 95% confidence limits being 1,701-1,774 g (3.75-3.91 pounds). The older age-classes obviously present in Howell's time are now absent, primarily due to pollution and fishing activities. Sykes and Lehman (1957) and Chittenden (1969) attributed the virtual absence of repeat spawners to mortality of adults in low oxygen water near Philadelphia as they

migrate seaward after spawning. Added to this is a large postspawning mortality in nontidal water (Chittenden 1969). Fishing, in general, decreases the age of the stock exploited. The historical and recent effect of fishing on Delaware River stocks is not completely clear, but this was probably a much more important factor before 1910 when commercial landings were as high as 14 to 17 million pounds annually (Sykes and Lehman 1957; Chittenden 1974). White et al. (1969) tagging studies suggested that in recent years the fishing rate was probably 20%.

The larger runs in the Delaware River in the early 1960's appear to have been primarily based upon one large year class except in 1963, when two large year classes were involved. Because few age-classes and only one year class support the run each year, Delaware River American shad stocks have little buffering against fluctuations in abundance due to adverse natural or man-made environmental factors. Large fluctuations, in fact, do appear in the catch records of the Lewis Fishery since 1925 (Chittenden 1974, fig. 3). The Lewis Fishery records show large runs over a 1- or 2-yr period intermixed with stable periods when the run was of small magnitude. This is the pattern which would be expected when the fishery is supported by one year class in which males tend to enter the fishery a year before the females and there are essentially no repeat spawners. Therefore, it appears probable that sine 1925, at least, larger runs in the Delaware River have been based upon one large year class and essentially no repeat spawners.

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SELECTIVE AND UNSELECTIVE EXPLOITATION OF EXPERIMENTAL POPULATIONS OF *TILAPIA MOSSAMBICA*

RALPH P. SILLIMAN[1]

ABSTRACT

Two populations of *Tilapia mossambica* were grown under controlled conditions. After a period of growth and stabilization at about 10 kg and 200 fish, exploitation was started; about 50 fish of outside stock were added to each population to increase genetic variability.

Initial exploitation at 10% (later 20%) per 2 mo encompassed all sizes above fry in the unselectively fished population. In the selectively fished population, exploitation was practiced only on fish that could not pass through 25-mm (later 22-mm) vertical slots between glass bars.

Recruitment was estimated from data of stock, mortality, and catch. Parabolas fitted to the stock-recruitment relation suggested greater recruitment in the selectively fished stock than in the unselectively fished one.

Rectilinear thickness-length regressions were calculated for immature and male fish and separately for females.

The exploitation-yield relation was assessed by fitting Fox surplus-yield models to both populations. These revealed a greater maximum sustainable yield in weight from the unselectively fished population than from the selectively fished one. Efficiency of food conversion was 29-36%.

To test for genetic effect of selection, a group of 46 fish, matched as closely as possible in size and sex composition, was selected from each population. Growth in length over a period of 150 days was significantly greater among males from the unselectively fished population than among those from the selectively fished one. Growth in length of females was practically identical for both groups. Growth in total weight was distinctly greater for the group from the unselectively fished population than from the selectively fished one.

As applied to commercial fisheries, the experimental results suggested fishing as wide a range of sizes as possible. If economic gains from selection are indicated, they should be balanced against possible costs in reduced yield and retarded growth rate.

Controlled selective breeding for desirable attributes in plants and animals is a well-recognized technique in agriculture. This technique has also had limited application in fish culture, particularly with trout. Claimed achievements have included increased size and earlier age at maturity. Fishery biologists have speculated whether the reverse process, attainment of undesirable attributes, may have occurred in some fished populations because of inadvertent imposition of selection by the fishery. Although gill nets and trawls are perhaps the most obvious gear elements causing selection, the phenomenon is probably present to some extent with practically all fishing gears. It thus becomes a matter of considerable economic importance to determine if gear selectivity has adversely affected fish stocks.

The general subject of selection for slow growth by fishing was briefly reviewed by Miller (1957). He adduced no data, however, and drew no firm conclusions, merely noting that he knew of no instances where changed growth rates in fish could not be attributed to some cause other than genetic change. It seems entirely possible, nevertheless, that such a change could occur, if selection were of sufficient strength and continued during a sufficient number of generations. Such a possibility is indicated by the success of artificial selection in altering quantitative characters in a wide variety of organisms.

The purpose of the work reported herein was to test experimentally whether selective fishing could produce a genetic change in the growth pattern of the fish in the fished stock. This problem was approached by growing two populations of Mozambique tilapia, *Tilapia mossambica*, under as nearly identical conditions as possible. One of these was then fished selectively from only those fish above a fixed thickness. The other was fished over the entire range of sizes, except the small "fry."

A secondary purpose was to compare amount and size composition of the yields under selective

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and unselective fishing. To achieve this comparison, records of weight and size composition were kept for each catch made during the experiments.

MATERIALS AND METHODS

For the experimental animal, *Tilapia mossambica* was chosen. This species is hardy and will grow readily in experimental tanks. It also is used widely in tropical pond culture and thus has some economic importance. Since it is a mouth breeder, handling and exploitation were done only at approximately 2-mo intervals.

Tanks, feeding, etc. were as reported in Silliman (1970) and represented a modification of the methods of Uchida and King (1962). Briefly summarized, the procedures were to raise the two populations in hatchery-type troughs of 850-liter (225-gallon) capacity. Water condition was maintained either by changing it biweekly or by a continuous dribbling flow into the head of each trough plus bimonthly partial changing. Temperature was maintained at 80° ± 5°F or 26.7°C (weekly means). Illumination was by fluorescent light 12 h per day. Feeding schedules and water condition are detailed in Tables 1 and 2.

Rectangular enclosures at the standpipe ends were separated from the rest of the troughs by plates with 3-mm holes through which the newly expectorated "fry" could escape, thus furnishing them refuges from cannibalism by the adults. After each counting, all fish in the refuges were placed in the main part of the tanks.

Fishing was done at approximately 2-mo intervals by removing each nth fish for fishing rate $1/n$ (n was always an integer). For the selectively fished population, all fish were placed on one side of a grid consisting of 25-mm diameter vertical glass rods spaced 25 mm (22 mm in latter part of experiment) apart. All fish were provided an opportunity to swim through the spaces between the rods; only those which could not do so were fished. In the unselectively fished population all sizes were fished except the fry (under 4-mm thickness).

Counting was done simply by netting fish from one container to another. For weighing, fish were drained in a net and then placed in a previously weighed container of water. Fish weight was obtained by subtracting the tare from the total.

All caught fish and the preexploitation stocks were measured for thickness and length. They were categorized as immature (where sex could not be determined by external inspection), male, and female. Sex determination was based on the characteristics set forth by St. Amant (1966). Length (total length to outermost tip of caudal fin) was measured on a board with millimeter scale and head block. Thickness was measured on the same device, plus a sliding block; the fish were held upright between the sliding block and the head block with firm pressure for the thickness measurement. Fish for the pretest measurements

TABLE 1.—Food placed in tanks, grams.

Date[1]	Month	Day of week	Trout pellets		Tropical fish food		Total
			Moist	Dry	A[2]	B[2]	
15 Aug. 1966	0.5-40.2	Sun.	30	10	4	5	49
to		Mon.	40	10	4	10	64
6 Dec. 1969		Tues.	40	10	4	10	64
		Wed.	40	10	4	10	64
		Thurs.	40	10	4	10	64
		Fri.	40	10	4	10	64
		Sat.	40	10	4	10	64
		Total	270	70	28	65	433
7 Dec. 1969	40.2-82.2	Sun.	30	10	4	5	49
to		Mon.	40	10	4	10	64
5 June 1973		Tues.	40	10	4	10	64
		Wed.	40	10	4	10	64
		Thurs.	40	10	4	10	64
		Fri. A.M.	40	10	4	10	64
		Fri. P.M.[3]	40	10	4	10	64
		Total	270	70	28	65	433

[1]Diet was varied initially to achieve optimal reproduction and growth; it was stabilized at the listed amounts on 18 June 1967, month 10.6.
[2]Commercal makes of dry food.
[3]This feeding was combined with the Friday A.M. feeding in 37 out of 183 wk. and with the Sunday feeding once.

TABLE 2.—Water condition on selected dates.[1]

Date	Month	O_2 (ppm.) Test[2]	O_2 (ppm.) Control[3]	CO_2 (ppm.) Test[2]	CO_2 (ppm.) Control[3]	pH Test[2]	pH Control[3]
1968:							
9 Aug.	24.3	5.2	5.0	—	—	—	—
16	24.5	4.6	4.4	—	—	—	—
29	24.9	4.8	4.8	10	10	6.9	6.9
6 Sept.	25.2	3.6	3.8	—	—	—	—
13	25.4	3.6	3.6	—	—	—	—
20	25.7	4.0	4.4	10	10	—	—
27	25.9	4.0	4.0	—	—	—	—
4 Oct.	26.1	4.0	4.4	—	—	—	—
11	26.4	3.8	4.0	—	—	—	—
18	26.6	3.0	3.8	—	—	—	—
25	26.8	3.0	4.0	—	—	—	—
8 Nov.	27.3	3.6	4.0	—	—	—	—
15	27.5	3.4	4.0	—	—	—	—
28	27.9	4.2	4.4	—	—	—	—
6 Dec.	28.2	3.8	4.0	—	—	—	—
13	28.4	3.4	4.0	—	—	—	—
26	28.8	3.0	3.4	—	—	—	—
1969:							
2 Jan.	29.1	3.4	3.6	—	—	—	—
17 Sept.	37.6	5.2	4.8	10	10	6.5	6.7
2 Oct.	38.1	5.4	5.4	—	—	—	—
9	38.3	5.0	4.8	—	—	—	—
23	38.7	5.0	4.8	—	—	—	—
30	39.0	5.4	5.0	—	—	—	—
1971:							
25-26 Feb.	54.9	4.6	4.4	20	20	6.0	6.0
1972:							
23 Mar.	67.7	3.4	[4]2.6	20	25	6.5	6.5
1973:							
29 May	81.9	3.4	3.2	15	15	7.0	7.0

[1]With the exception noted in footnote 4, all values were within (or above for oxygen) the ranges stated to be suitable for warm-water fishes by Lewis (1963). These were: oxygen, 3-5 ppm.; carbon dioxide, below 30 ppm.; pH, 5-9.
[2]Selectively fished.
[3]Unselectively fished.
[4]Aeration was increased and O_2 had risen to 3.8 ppm. by the next day.

were anesthetized with MS-222 [2] (tricaine methanesulfonate) in a 1:2,500 solution. Caught fish were measured some time after removal. They were usually alive or freshly dead, and rigor mortis was rare. The group selected for growth study at the end of the experiment was measured alive without an anesthetic.

COURSE OF POPULATIONS

A single population was started on 15 August 1966, but this was divided into two populations as nearly equal as possible after 2 mo. A period of population growth then ensued (Table 3, Figures 1, 2). This growth was extensively discussed by Silliman (1970), who found growth in biomass of the two populations to be practically identical. He therefore combined the two populations for growth analysis. A Gompertz curve fitted to the total biomass of both populations had the formula $W_t = 1.337 \exp[2.85 - 2.85 \exp(-0.2\,(t-3.6))]$, where W_t is biomass in kilograms at the time t in months. The asymptote of this curve was 23.1 kg or 11.55 kg per population. An accidental interruption to population growth (Figures 1, 2) resulted from temporary relocation of the fish during refinishing of the laboratory floor. After recovery and re-equalization, the populations did not approach the asymptote predicted by the Gompertz curve but leveled off at about 10 kg each.

Because the fish were descendants of an original three males and three females, I felt that in-

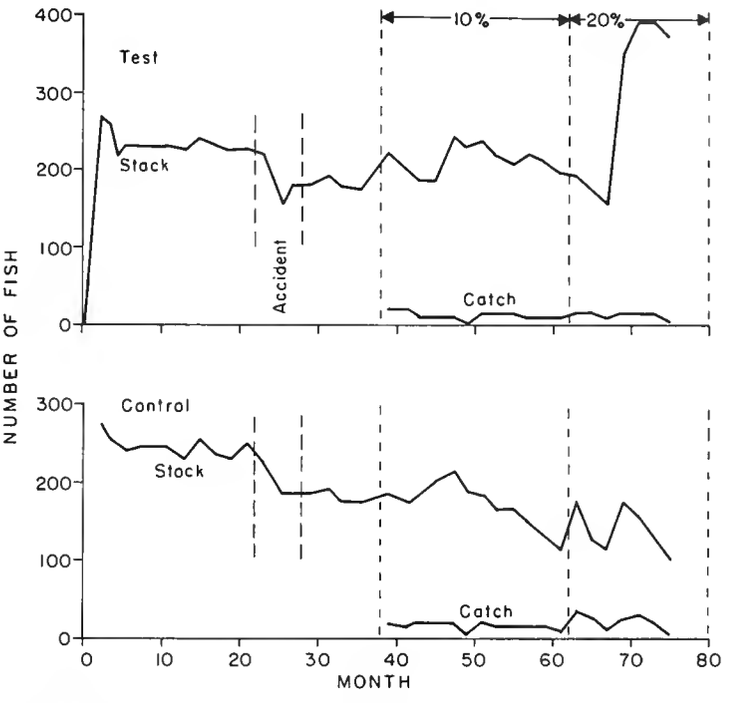

FIGURE 1.—Population size and catch, numbers. Percentages indicate target exploitation rates. Test population was selectively fished; control, unselectively.

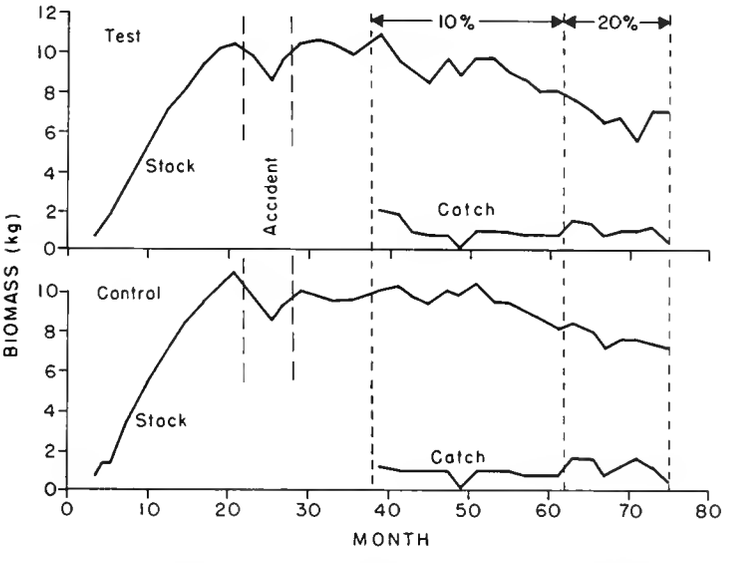

FIGURE 2.—Population size and catch, weight. Percentages indicate target exploitation rates. Test population was selectively fished; control, unselectively.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.—Population and catch, *Tilapia mossambica*.

Month[1]	Target expl. rate[2]	Test (selectively fished) population				Control (unselectively fished) population			
		Number		Weight (g)		Number		Weight (g)	
		Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.5	0.00	6	—	—	—	—	—	—	—
2.5		272	—	—	—	273	—	—	—
3.6		258	—	856	—	253	—	825	—
4.5		220	—	1,318	—	251	—	1,325	—
5.5		231	—	1,924	—	239	—	1,447	—
7.5		228	—	3,306	—	247	—	3,303	—
10.5		228	—	5,614	—	246	—	5,749	—
13.0		224	—	7,420	—	232	—	7,313	—
15.0		239	—	8,275	—	253	—	8,692	—
17.1		228	—	9,346	—	237	—	9,448	—
19.2		226	—	10,174	—	232	—	10,244	—
21.1		224	—	10,459	—	251	—	10,907	—
23.2		[3]221	—	[3]9,859	—	[3]226	—	[3]9,826	—
25.4		[3]156	—	[3]8,567	—	[3]186	—	[3]8,561	—
27.2		181	—	9,560	—	184	—	9,431	—
29.1		180	—	10,415	—	183	—	9,967	—
31.3		189	—	10,525	—	189	—	9,791	—
33.1		181	—	10,348	—	177	—	9,622	—
35.3		177	—	9,881	—	173	—	9,661	—
39.2	0.10	218	19	10,760	2,023	183	18	10,009	1,168
41.3		201	18	9,468	1,714	174	17	10,139	1,033
43.2		187	8	8,984	906	187	18	9,743	974
45.2		187	8	8,311	794	199	19	9,300	956
47.3		[4]240	8	[4]9,534	883	[4]217	22	[4]9,917	909
48.9		231	2	8,860	182	191	4	9,843	191
51.2		233	14	9,690	960	186	18	10,368	1,057
53.2		217	14	9,575	991	163	16	9,532	927
55.1		207	14	9,037	929	165	16	9,315	951
57.2		221	12	8,542	848	148	15	8,956	895
59.0		210	10	8,056	806	131	13	8,507	827
61.1		196	10	7,935	853	117	12	8,287	824
63.2	0.20	191	17	7,687	1,575	177	35	8,322	1,681
65.4		172	17	6,944	1,377	124	25	7,965	1,531
67.1		157	11	6,382	738	114	12	7,261	840
69.1		345	15	6,684	1,050	176	26	7,592	1,217
71.2		388	14	5,465	1,061	155	31	7,664	1,574
73.2		389	14	7,046	1,170	123	21	7,389	1,272
75.1		371	6	6,901	438	101	6	7,280	459

[1]0 = 1 August 1966.
[2]Because of selection problems, actual rates varied considerably from these. In analyses, effective rates in terms of weight were used.
[3]Populations re-equalized after accidental mortality from temporary relocation of fish.
[4]New fish added for genetic variability.

sufficient genetic variability might exist in the populations to permit a genetic effect of selection. Since one of the major objectives of the experiment was to detect such an effect, I decided to add outside stock. During the 2-mo period preceding month 47.3 (Table 3), I added 45-47 (2 fish uncertainty due to counting difficulties) immature *Tilapia mossambica* from Arizona to each population. These fish were descendants of ones from Malacca.

Exploitation was started at month 39.2 (Table 3, Figures 1, 2) at a conservative 10% per 2 mo. This exploitation period included 1.0 to 2.6 of the brood intervals reported by various authors (Kelly 1957, 30-40 days; Swingle 1960, 30-40 days; Uchida and King 1962, 23-61 days). Because of irregularities in recruitment, population numbers (Figure 1) reflected population responses less well than population biomasses (Figure 2). The latter, however, generally reflected the expected population decrease from imposition of the 10% exploitation rate. When the rate was increased to 20% at month 63.2 (Table 3, Figure 2), further declines in population biomasses occurred.

BASIC RELATIONS

Recruitment was estimated from changes (R_{INT}) in stock number and data of mortality and catch (Table 4), using the approach of Silliman (1972). Because of variations in length of period between counts, values of R_{INT} were adjusted to a standard 2-mo interval (Table 4). Observation of large numbers of fry in the refuges, followed by the later appearance of peaks of recruitment (Table 4), indicated that the "reproductive lag" was about 2

TABLE 4.–Recruitment and stock. $R_{INT} = P_{n+1} - P_n + M_{INT} + C_{INT}$, where P is stock, INT is interval between counts n and $n+1$, R is net change[1], M is recorded mortality and C is catch, all in numbers. $\bar{S}$ is mean stock in kilograms for previous interval.

Interval (months)	Interval length (months)	Selectively fished population			Unselectively fished population		
		R_{INT}	[2]R_{INT}	$\bar{S}$	R_{INT}	[2]R_{INT}	$\bar{S}$
5.5- 7.5	2.0	−3	−3.0	1.4	+9	+9.0	1.1
7.5-10.5	3.0	+1	+0.7	2.6	+1	+0.7	2.4
10.5-13.0	2.5	+4	+3.2	4.4	−13	−10.4	4.5
13.0-15.0	2.0	+15	+15.0	6.5	+21	+21.0	6.5
15.0-17.1	2.1	−5	−4.8	7.8	−5	−4.8	8.0
17.1-19.2	2.1	−2	−1.9	8.8	−5	−4.8	9.0
19.2-21.1	1.9	0	.0	9.8	+19	+20.0	9.8
25.4-27.2	1.8	+25	+27.8	—[3]	−1	−1.1	—[3]
27.2-29.1	1.9	−1	−1.1	9.1	−1	−1.1	9.0
29.1-31.3	2.2	+9	+8.2	10.0	+6	+5.5	9.7
31.3-33.1	1.8	−6	−6.7	10.4	−12	−13.3	9.9
33.1-35.3	2.2	−2	−1.8	10.4	−2	−1.8	9.7
35.3-39.2	3.9	+44	+22.6	10.1	+16	+8.2	9.6
39.2-41.3	2.1	+7	+6.7	10.8	+10	+9.5	9.8
41.3-43.2	1.9	+4	+4.2	9.1	+30	+31.6	9.4
43.2-45.2	2.0	+8	+8.0	8.4	+30	+30.0	9.4
45.2-47.3	2.1	[4]+16	+15.2	8.2	[4]−6	−5.7	9.0
47.3-48.9	1.6	+2	+2.5	8.5	0	.0	9.1
48.9-51.2	2.3	+4	+3.5	8.8	−1	−0.9	9.4
51.2-53.2	2.0	−1	−1.0	9.2	−3	−3.0	10.0
53.2-55.1	1.9	+5	+5.3	9.2	+18	+18.9	9.4
55.1-57.2	2.1	+31	+29.5	8.8	0	.0	9.0
57.2-59.0	1.8	+3	+3.3	8.3	−1	−1.1	8.7
59.0-61.1	2.1	−2	−1.9	7.9	+2	+1.9	8.3
61.1-63.2	2.1	+5	+4.8	7.6	+73	+69.5	8.0
63.2-65.4	2.2	−1	−0.9	7.4	−16	−14.5	7.9
65.4-67.1	1.7	+3	+3.5	6.5	+15	+17.6	7.3
67.1-69.1	2.0	+199	+199.0	6.0	+75	+75.0	6.8
69.1-71.2	2.1	+62	+59.0	6.2	+6	+5.7	7.0
71.2-73.2	2.0	+16	+16.0	5.6	−1	−1.0	7.0
73.2-75.1	1.9	−2	−2.1	5.7	+1	+1.1	6.8

[1]$R_{INT} > 0$ indicates recruitment of at least the indicated number of fish; $R_{INT} < 0$ indicates unrecorded mortality of at least the indicated number and $R_{INT} = 0$ indicates either no recruitment and unrecorded mortality or the two exactly balanced.
[2]Adjusted to a standard 2-mo interval length.
[3]Indicated intervals omitted because of re-equalization of stocks.
[4]Exclusive of 46 new fish added for genetic variability.

mo. Each value of R_{INT} was therefore compared with the mean stock ($\bar{S}$) for the preceding 2-mo interval (Table 4).

The stock-recruitment data were highly variable and were, therefore, treated as group means based on 5-kg intervals of $\bar{S}$, considering negative values of R_{INT} to be equal to zero. Although the data indicated no regular relation (Figure 3), they were fitted with parabolas to indicate central tendency, even though fits were poor. These, based on 30 pairs of observations each, were:

Selectively fished stock

$$R_{N+1} = 6.163\ \bar{S}_N - 0.5209\ \bar{S}_N^2.$$

Unselectively fished stock

$$R_{N+1} = 3.304\ \bar{S}_N - 0.2158\ \bar{S}_N^2,$$

where N is number of the 2-mo interval, R is in

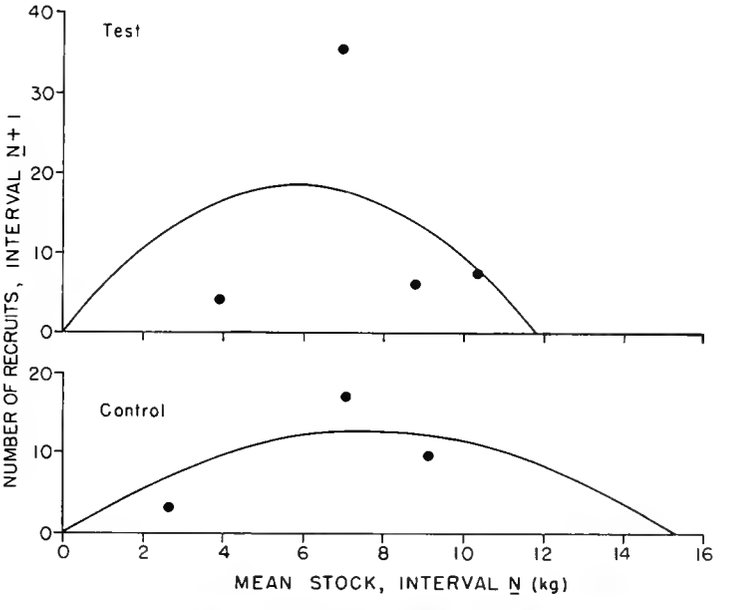

FIGURE 3.–Stock and recruitment. Test population was selectively fished; control, unselectively. Parabolas shown were fitted by least squares.

numbers, and S is in kilograms. The somewhat higher maximum for the selectively fished stock may have resulted from its changed size composition; it included fewer extremely large males than the unselectively fished population.

Since selection reflected the ability of fish to escape through vertical slots between glass bars, thickness was the controlling dimension. Most of the fish-size data in this report are therefore in thickness. However, to reduce fish handling to a minimum, the growth measurements of live fish during the final part of the experiment were in lengths. Because of this, and because other biologists may wish to compare their length data with my thickness data, I calculated thickness-length relations.

Measurements for the relation were from the caught fish, for which both thickness and length were recorded. Preliminary analysis showed that data for immature and male fish could be combined into a single rectilinear regression of length on thickness. The regression for females was also rectilinear but had a gentler slope, probably because of the distention of mature fish carrying eggs. It was therefore calculated separately. The regression equations, numbers of pairs of observations in parentheses, and correlation coefficients were (fitting was by least squares):

Immature and male

$$L = 7.027\ T \qquad (368) \qquad r = 0.987 \qquad r^2 = 0.974.$$

Female

$$L = 26.89 + 5.037\ T \qquad (207) \qquad r = 0.866$$
$$r^2 = 0.750,$$

where L is length and T is thickness, both in millimeters. The squared coefficients suggest that 97 and 75% of variations in length were associated with variations in thickness.

RESULTS

Exploitation and Response

Before selective exploitation could be started, it was necessary to determine the selection point. To aid in this the thickness of all of the fish in both populations was measured at month 33.5. At this time the population to be selectively fished (pretest) consisted of 85 males and 95 females—that to be unselectively fished (precontrol), 77 and 98, respectively. The thickness frequencies (Figure 4) revealed a low point in the pretest population between males and females at about 25 mm. This was used as the initial selection point and it meant, of course, that the early catches were mostly males. It will be shown below, however, that later catches were composed of roughly equal proportions of males and females.

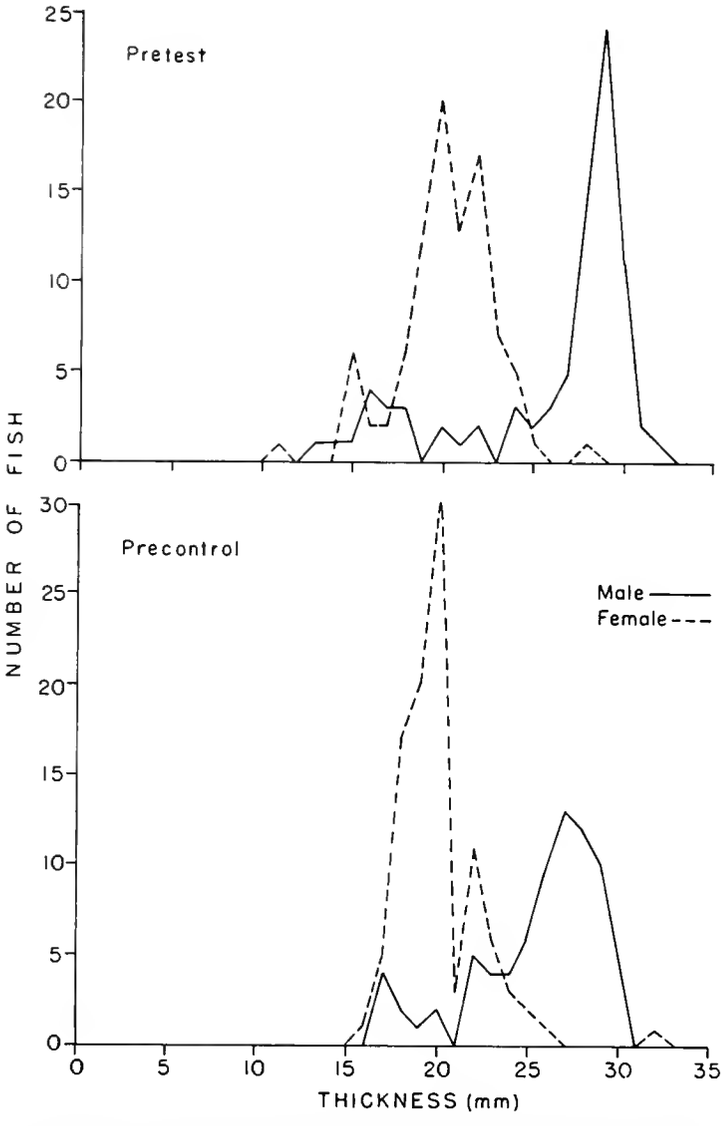

FIGURE 4.—Thickness frequencies at month 33.5. Test population was to be selectively fished; control, unselectively.

Changes from exploitation, in addition to those described under "Course of Populations," were reflected in the size composition of the catches (Figures 5, 6). In the test population, the catches were roughly the target percentage of the selected group; the percentages in the control population were adjusted to take the same proportion of the entire population as taken in the test population. Percentages were by number at months 39.2 and 41.3, but it became evident that this procedure took too large a proportion of the biomass. At months 43.2-75.1, the percentages were by weight

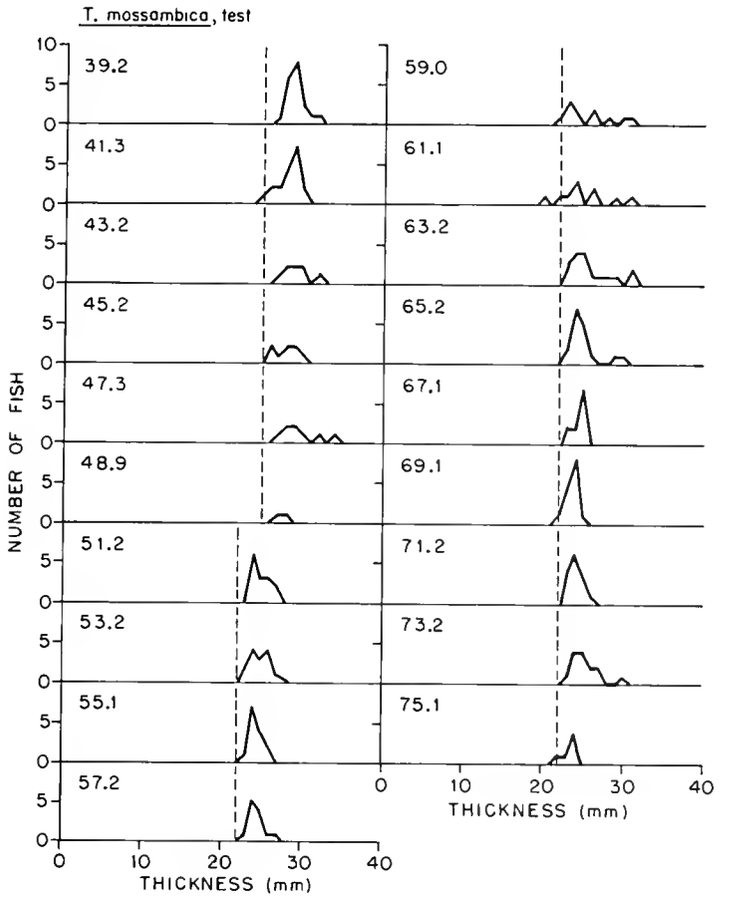

FIGURE 5.—Bimonthly thickness frequencies of catches, test (selectively fished) population. Vertical broken lines indicate selection points. Numbers in panels indicate months from start.

(Table 3). Numbers of fish growing above the selection point rapidly diminished in the test population (Figure 5) so that insufficient numbers were available from which to catch the target percentage. To continue exploitation, it was necessary to lower the selection point to 22 mm as shown. With few exceptions, all fish caught from the test population were above the selection point.

Catches from the control population were taken representatively over all sizes larger than fry and, therefore, represented the size composition of the stock above the fry size (Figure 6). Significant amounts of recruitment at months 43.2, 45.2, 55.1, 63.2, 67.1, and 69.1 (Table 4) appear as modes of small fish in the size frequencies, and the more prominent ones can be traced through succeeding frequencies.

A summary of catch size frequencies (Figure 7) clearly reveals the differences between catches from test and control populations. It is evident that the selection device employed was almost completely effective. The appearance of roughly equal proportions of males and females in the test catches, after lowering the selection point, is also apparent. It can be seen that a selection curve was at work, such that fish were not fully retained until they had reached a thickness of about 2-4 mm above the selection point.

The relation of yield to exploitation was assessed by fitting a Fox (1970) exponential surplus-yield model to data of catches and stock (Figure 8). The method of fitting used requires equilibrium yields. Although absolute equilibrium obviously was not attained, it was considered that the biomass and catch levels (Figure 2) at months 29-35 (zero exploitation), 59-61 (10% target rate), and 69-73 (20% target rate) represented sufficiently close approximations to equilibrium for fitting the model. The calculated maximum sustainable yield (1.39 kg per 2 mo) from the selectively fished test population was substantially lower than that for the unselectively fished control (2.36 kg). If we wish to consider a comparable commercial fishery, however, we might assume that only the fish above the selection point are commercially desirable. Catch thickness frequencies for the 22-mm selection point (Figure 7) showed that 97% of the fish in test catches were above the selection point as compared with 40% for the control catches. Although these data cannot be

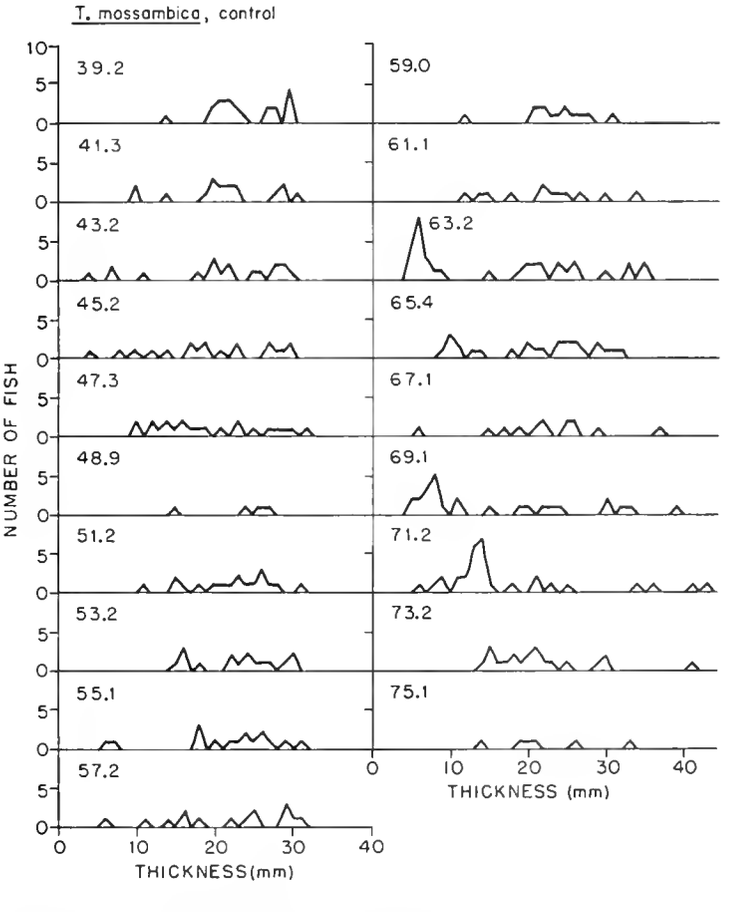

FIGURE 6.—Bimonthly thickness frequencies of catches, control (unselectively fished) population. Numbers in panels indicate months from start.

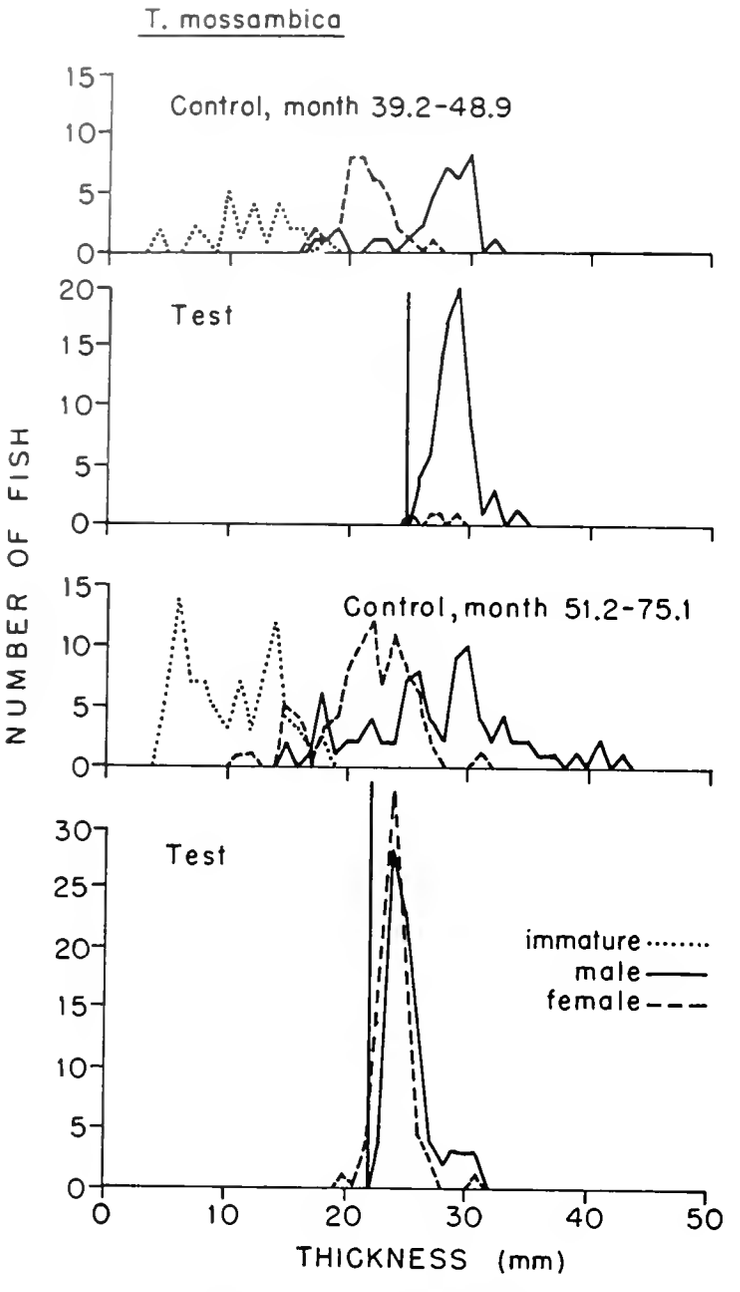

FIGURE 7.—Summary of catch thickness frequencies. Test population was fished selectively; control, unselectively. Vertical lines indicate selection points.

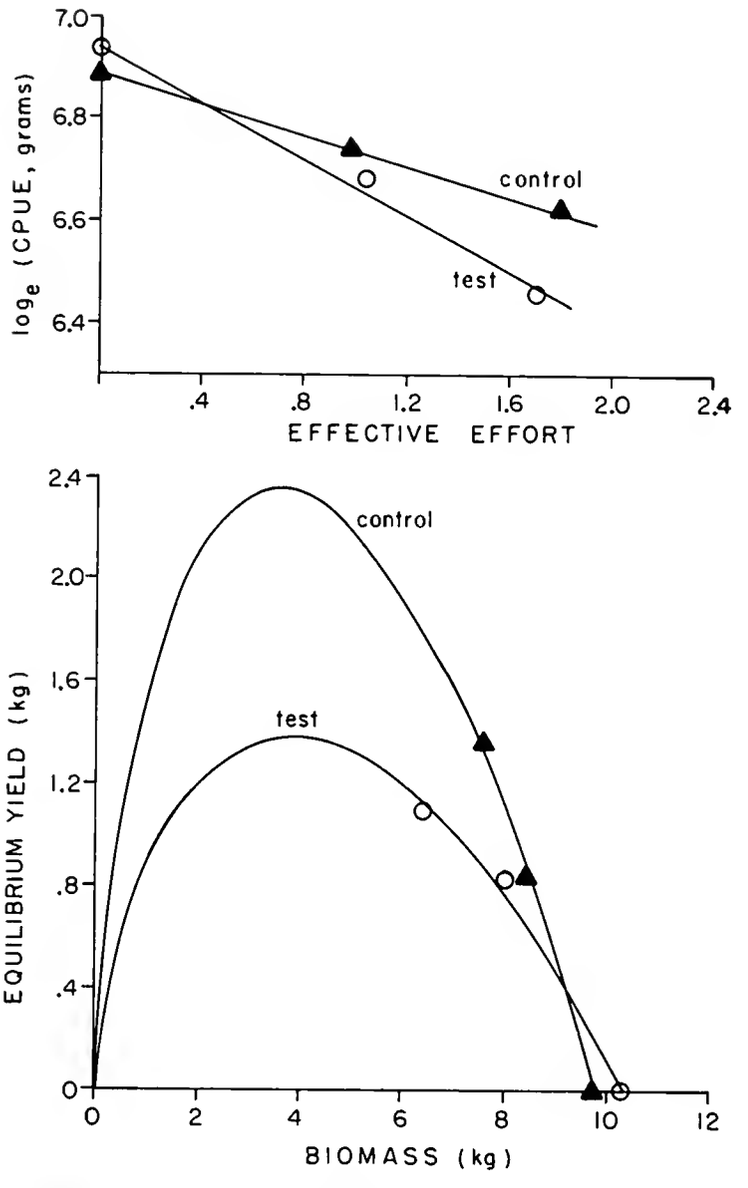

FIGURE 8.—Fitting of Fox (1970) model. Catch-per-unit-effort (CPUE) is considered proportional to biomass; effort is in arbitrary units. Regression lines shown are least-squares fits. Target exploitation rates were 0, 10%, and 20% per 2 mo, left-to-right in upper panel, reversed in lower panel.

converted to weights, it is certain that the comparison for fish above the selection point would be more favorable to the test catches than was true for all sizes of fish.

It is possible to calculate the efficiency of conversion of food to fish flesh under both types of fishing. The amount fed per 2-mo period was 3.75 kg (433 g per week from Table 1, for 8⅔ wk). Maximum sustainable yields (MSY's) of 1.39 kg and 2.36 kg indicate 37 and 63% conversion efficiencies for selective and unselective fishing, respectively. Since the theoretical MSY's represent a considerable extrapolation (Figure 8), it is of interest to calculate from equilibrium yields actually attained during the experiment. The largest yields were under the 20% per 2-mo target rate for both populations. Effective exploitation rates and corresponding yields were: selectively fished, 17.1% and 1.09 kg; unselectively fished, 17.9% and 1.35 kg. These yields indicate 29 and 36% efficiency, respectively. The values are in fair agreement with the 33% calculated by Silliman (1970) for the initial growth of the populations.

Genetic Response

Knowledge of the number of generations involved is essential to any genetic experiment. Progression of the two most prominent thickness frequency modes (months 63.2 and 69.1) in the unselectively fished population (Figure 6) gave an indication of the growth rate of the fish. Frequen-

cies of thickness for immature and mature fish (Figure 7) suggested a thickness at maturity of about 15-20 mm. The two prominent modes in the frequencies seemed to require about 4 mo (63.2-67.1, 69.1-73.2) to reach this size. To this must be added the 2-mo "reproductive lag" mentioned above under "Basic Relations," suggesting a generation length of about 6 mo. The 36-mo period of selective fishing would thus include about six potential generations. Because of irregularities in recruitment, however, the effective number of generations was less, and it was necessary to make an estimate.

Such an estimate can be derived from the record of recruitment numbers (R_{INT}, Table 4, Figure 9). An arbitrary criterion for significant recruitment was established, requiring at least 15 recruits per 2 mo. A generation was considered to be such a peak separated from the previous filial generation by a period of at least 6 mo (the parental generation for the test group had been fished selectively at month 40). Under the arbitrary criterion the estimated generations (Figure 9) during the selection period were only three for the selectively fished test and four for the unselectively fished control population. Experiments with other animals, such as those of Robertson with thorax length of *Drosophila* cited by Falconer (1960), have shown that measurable change in a size character can occur in as few as three generations of selection.

To test whether genetic response to selection did occur, groups of 46 mature fish as similar in sex and length composition as possible were selected from test and control populations on 5 January 1973 at month 77.2 (Table 5). It was not possible to match these fish as closely as desired by total weight, and that of the control group exceeded that of the test group by 19%. These fish were fed the standard diet (Table 1) which furnished them, even at the end of the growth period, with 1.5% (test) or 1.3% (control) of body weight of food per day. This was 2.5 (test) or 2.1 (control) times as much as was received by the 10 kg preexploitation stocks. Any offspring that appeared were removed as soon as possible.

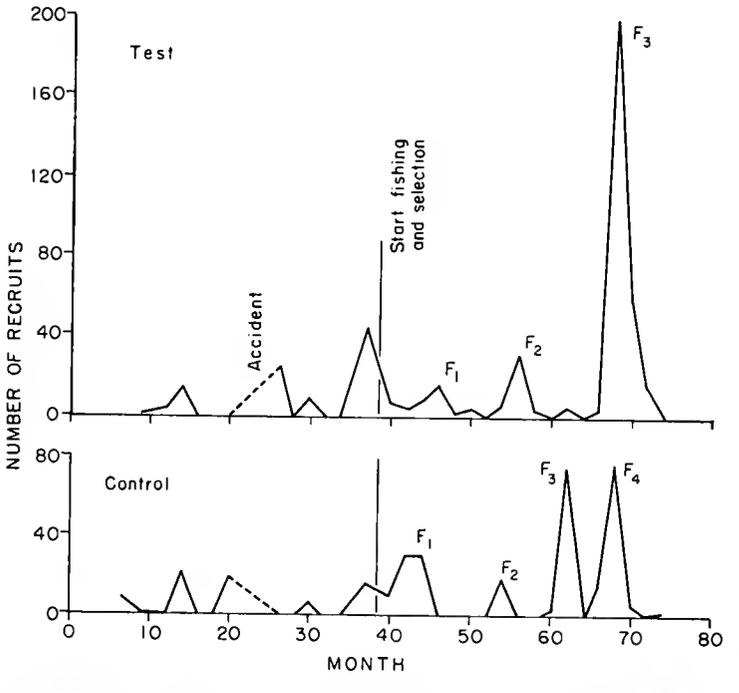

FIGURE 9.–Recruitment numbers from R_{INT} in Table 4, with negative values considered zero. Test population was selectively fished; control, unselectively.

TABLE 5.–Growth of selected groups of fish. Lengths are from snout to tip of tail.

Group	Day[1]	Male No.	Male Mean length (mm)	Female No.	Female Mean length (mm)	Total No.	Total Wt. (g)
Test	0	10	152.0	36	140.6	46	2,158
	56	[2]9	180.0	[2,3]36	155.0	45	3,199
	118	9	197.8	[4]34	165.0	43	3,794
	150	9	207.2	[3]33	169.8	42	4,078
Control	0	10	148.0	36	141.4	46	2,561
	55	[5]8	195.0	[3,5]37	153.4	45	3,504
	119	8	235.6	[6]35	164.4	43	4,455
	151	8	253.1	[7]34	169.1	42	4,819

[1]0 = 5 January 1973.
[2]One female misclassified as male on day 0.
[3]One female died.
[4]Two females died.
[5]Two females misclassified as males on day 0.
[6]Two females removed to match mortalities in test group.
[7]One female removed to match mortality in test group.

Growth of the selected fish was measured by determining the lengths of individual fish and the total weight of each group at 55-56, 118-119, and 150-151 days after the start of the growth period (Table 5, Figures 10, 11). The length frequencies reveal the general correspondence of the groups at the beginning of the period, in addition to the expected more rapid growth of the males than the females in each group. They also reveal that the males in the unselectively fished control group grew more rapidly than those in the selectively fished test group.

Growth was further studied by curves based on mean lengths and total weights of the selected groups. Gompertz curves fitted to lengths had the equation:

$$L_{t'} = L_0 \exp[G - G \exp(-gt')],$$

where L is mean length in millimeters, t' is time in days, and G and g are empirical constants. This curve and all other Gompertz curves were fitted by

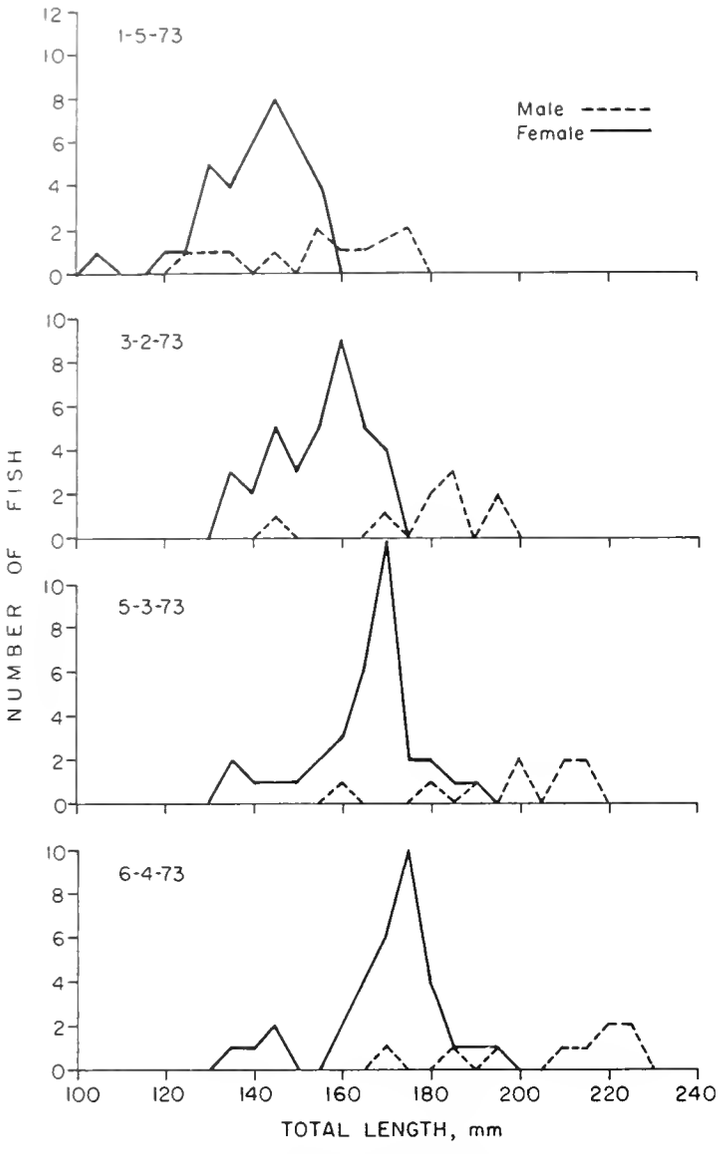

FIGURE 10.—Length frequencies of group selected from selectively fished test population. Lengths are from snout to tip of tail.

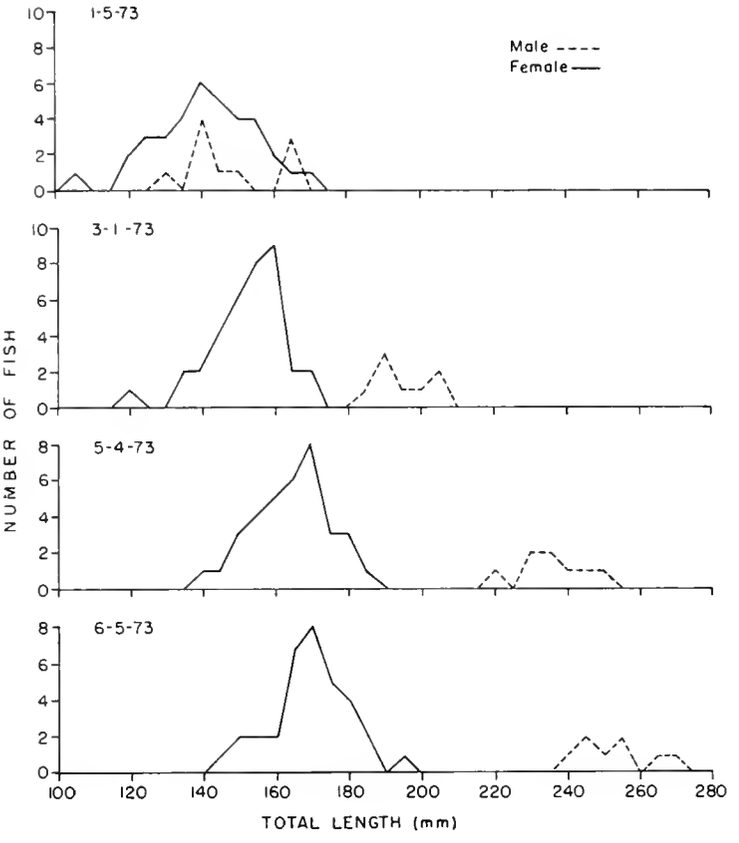

FIGURE 11.—Length frequencies of group selected from unselectively fished control population. Lengths are from snout to tip of tail.

the analog computer method of Silliman (1967). Growth in length was essentially identical in the two groups for the females (Table 5, Figure 12), and a single curve was fitted. Constants are given in Table 6. For males, however, growth was significantly greater in the unselectively fished control group than in the selectively fished test group.

The sexual misclassification of one fish in the test group and two in the control group (Table 5) must be considered in relation to possible effects on the results. These fish were misclassified at the beginning of the growth period, when the fish were relatively small (chosen so to provide room for growth) and sex determination was difficult. As the fish grew and determination became easier, the errors were discovered and corrected. To test the effect of the errors it was assumed that they occurred in the manner most contrary to the conclusion adopted—that growth was greater among males in the control than in the test group.

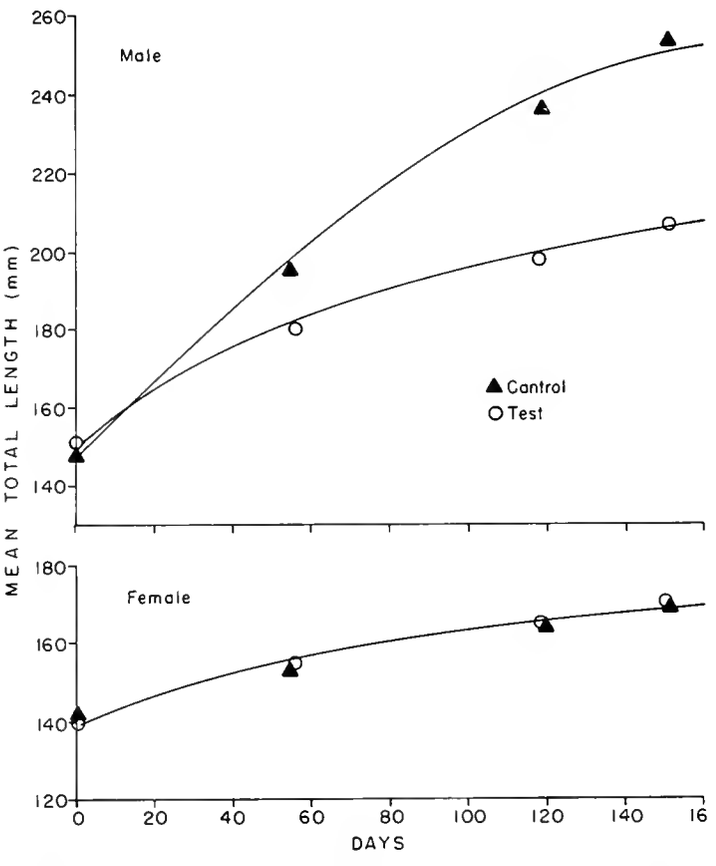

FIGURE 12.—Gompertz curves fitted to mean lengths in group selected from selectively fished test population and unselectively fished control population.

TABLE 6.—Constants of Gompertz curves for growth of selected groups of fish.

Sex	Variable	Population	L_0 (mm)	L_∞ (mm)	W_0 (kg)	W_∞ (kg)	g	G
♂	Length	Test	148	214	—	—	0.0150	0.367
		Control	146	274	—	—	0.0127	0.630
♀	Length	Both	141	174	—	—	0.0128	0.211
Both	Weight	Test	—	—	2.23	4.45	0.0130	0.692
		Control	—	—	2.49	5.65	0.0105	0.819

Note: L_0 = Length at time zero.
L_∞ = Asymptotic limit of length.
W_0 = Weight at time zero.
W_∞ = Asymptotic limit of weight.
g and G = Empirical constants of the Gompertz curve.

Thus it was assumed that at day 0 one of the two males at maximum length in the test group was misclassified as a female and, similarly, for the two smallest males in the control group. Resulting mean lengths in millimeters comparable to those for day 0 in Table 5 are: test male, 149.4; test female, 141.5; control male, 151.2; control female, 141.1. Percentage differences are 1.7, 0.6, 2.2, and 0.2, respectively. The means under the "most contrary assumption" are indistinguishable from the values used on the scale of Figure 12. It is evident that substitution of the most contrary values would not change the conclusion of greater male growth in the controls.

Gompertz curves were also fitted to biomasses of the two groups (Table 5, Figure 13). Here the equation was:

$$W_{t'} = W_0 \exp[G - G \exp(-gt')],$$

where W is total weight in kilograms, t' is time in days, and G and g are empirical constants. Constants are given in Table 6. In weighings, fish were not separated as to sex, and only a single growth curve was available for each population. Because of the initial difference in total weight, the curve for the control population is shown moved over to the time when weight of the test group had grown to the initial weight of the control group. Even so treated, the control group exhibits markedly greater growth than the test group, reflecting greater growth of the males in it. This is even more striking when it is considered that the amount of food per weight of fish was somewhat less in the control than in the test group. The observed growth in biomass supports the conclusion of diminished genetic growth in males as a result of selective fishing.

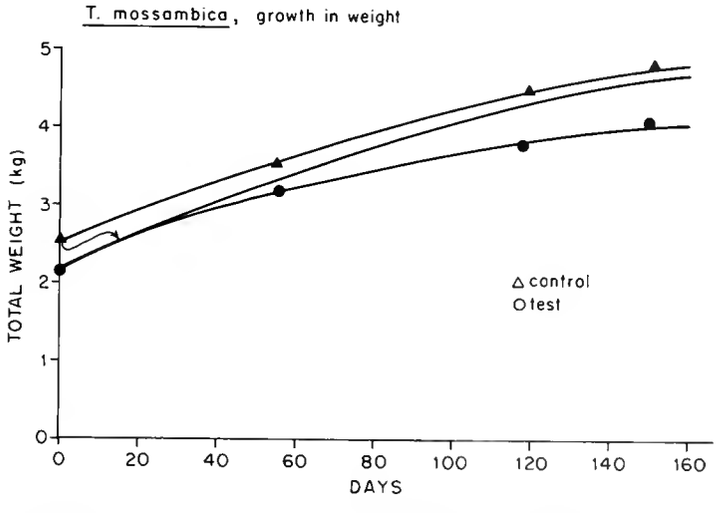

FIGURE 13.—Gompertz curves fitted to total weights of groups from selectively fished test population and unselectively fished control population. Line branching upward from test curve indicates control curve moved over to same starting point as test curve.

CONCLUSIONS

Analyses presented above have revealed significant differences of responses to exploitation between the selectively fished test population and the unselectively fished control population. These differences were demonstrated both in catches obtained and in genetic growth patterns.

Yield models fitted demonstrated marked differences in the catches obtained under selective and unselective fishing. It is clear that, with the particular populations studied and under the assumptions of stability made, weight of yield under unselective fishing was greater than that under selection. This yield included a large proportion of fish below the selection point, however. To the extent that one may generalize from this experiment, it appears that unselective fishing would be preferable if maximum physical yield were the sole objective. If selection is required to secure fish that are of appropriate size for the market, the objective may be achieved only at the sacrifice of part of the weight of the catch.

That three generations of selective fishing caused a change in the genetic growth pattern of males, resulting in slower growth than in the controls, seems certain from the results. It is necessary to explain, however, why a similar change did not occur in the females. This may have resulted from the phenomenon of epistasis. In this it is considered that a single gene may control the hormone which permits males to grow to larger ultimate size than females. Since females have less of this hormone than males, they are unable to

express genotypic differences which otherwise might cause changed growth patterns. In other words, the degree of selection imposed did not work against females because they were unable to achieve extra large size in any event. This hypothesis cannot be tested with data from the present experiment.

Fishing in the experiment was similar to that in a commercial fishery, with the vertical slots in the apparatus corresponding to the meshes of commercial gear. Results may, therefore, be of some significance in fishery management. They suggest that as wide a range of sizes as possible be included in the catch. An appropriate balance should be struck between the possible higher market value of large fish and the lesser yields that may be achieved under selection. Also, the possibility of a genetic change in growth pattern under selection should not be overlooked.

SUMMARY

1. Two populations of *Tilapia mossambica* were grown with as nearly identical space, water condition, and food as possible.
2. After a period of initial growth each population stabilized at a weight of about 10 kg. Numbers were less stable at this time and ranged from 173 to 218 fish.
3. To increase genetic variability, 45-47 immature fish of Malacca descent were added to each population at month 47.3.
4. Exploitation was started at month 39.2, at 10% per 2 mo (1.0-2.6 brood intervals) and increased to 20% at month 63.2. Selective fishing was from fish which could not pass through 25-mm (later 22-mm) vertical slots between glass rods. Unselective fishing was from all fish except fry (under 4-mm thickness).
5. Recruitment was estimated from data of stock number, mortality, and catch. Reproductive lag was 2 mo. The stock-recruitment relations, roughly fitted with parabolas, suggested greater recruitment in the selectively fished stock than in the unselectively fished one.
6. Two rectilinear thickness-length relations were calculated, one for immature and male fish and another for females.
7. Catch thickness frequencies for the unselectively fish population revealed modes corresponding to peaks of recruitment.
8. Catch thickness frequencies for the selectively fished population, compared with those for the unselectively fished population, demonstrated that the device for selection at 25 and 22 mm was almost completely effective.
9. The exploitation-yield relation was assessed by fitting Fox exponential surplus-yield models to data from both populations. Fitted models indicated a higher maximum sustainable yield in weight for the unselectively fished population than for the selectively fished one. Efficiency of food conversion was 29-36%.
10. Growth rates from catch thickness frequencies, together with the 2-mo reproductive lag, suggested a generation length of 6 mo. Recruitment records indicated three generations under exploitation for the selectively fished population and four during the same period for the unselectively fished one.
11. To test for genetic effect of selection, a group of 46 fish was selected from each population. These were matched as closely as possible by size and sex composition and grown under previously established standard conditions.
12. Growth in length over a period of 150 days was significantly greater among males from the unselectively fished population than among males from the selectively fished one. Growth for females in the two groups was practically identical.
13. Growth in total weight was distinctly greater for the group from the unselectively fished population than in that from the selectively fished one.
14. It was concluded that these experiments demonstrated diminished total yield and retarded male growth in the selectively fished population compared with the unselectively fished one. An hypothesis based on epistasis was advanced to explain lack of growth response among females.
15. As applied to commercial fisheries, the experimental results suggest fishing as wide a range of sizes as possible. If economic gains from selection are indicated, they should be balanced against possible costs in reduced total yield and retarded growth rate.

ACKNOWLEDGMENTS

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Utter, Harold O. Hodgins, and Donald D. Worlund, all of the Northwest Fisheries Center, National Marine Fisheries Service, NOAA. The plan of the experiment was reviewed by them and by Joseph Felsenstein of the University of Washington, Seattle, Wash. It is pertinent to note, however, that some changes were made in the plan due to developments during the experiment.

My special thanks are due Alban R. Essbach of the Arizona Game and Fish Department. He generously shipped stocks of fish on two different occasions.

Experimental populations were maintained during various periods by George F. Slusser, Christopher E. Mathews, Martin G. Beam, Jimmy R. Chrnaoski, and Judy A. Trauth. I also thank George F. Slusser for furnishing the initial stock of fish. All of these persons are present or former members of the National Marine Fisheries Service, NOAA (formerly Bureau of Commercial Fisheries).

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UPTAKE AND LOSS OF PETROLEUM HYDROCARBONS BY THE MUSSEL, *MYTILUS EDULIS,* IN LABORATORY EXPERIMENTS

ROBERT C. CLARK, JR., AND JOHN S. FINLEY[1]

ABSTRACT

Petroleum paraffin hydrocarbons (n-$C_{14}H_{30}$ to n-$C_{37}H_{76}$) from No. 2 and No. 5 fuel oils were rapidly incorporated into the mussel, *Mytilus edulis*, in a laboratory system that simulated tides. The mussels were exposed to levels of petroleum hydrocarbons from a surface slick similar to those encountered in the environment after an oil spill. After 14 days in clean seawater, the mussels had lost most of the hydrocarbons from the fuel oils; however, detectable traces of the No. 2 fuel oil still remained after 35 days. Preliminary results from these laboratory studies confirm previous studies of pollutant uptake and loss following actual oil spills.

Petroleum hydrocarbon uptake by the common bay mussel, *Mytilus edulis*, can be readily determined in the laboratory with the analytical chemical methods of solvent extraction, liquid-solid, and gas-liquid chromatography. Mussels lend themselves well to such studies because of 1) their worldwide distribution and ready availability (Davies 1969; Becker et al. 1973); 2) the considerable amount of physiological base line data available (Field 1922); 3) their hardiness as an experimental test organism (Gilfillan 1973); 4) their convenient size, which is small enough to sample adequately and use in the laboratory experimentally but large enough for specific organ dissection (Lee, Sauerheber, and Benson 1972); 5) their position in the intertidal ecosystem as a major pathway for energy transfer utilizing phytoplankton and debris (Ricketts and Calvin 1962); and 6) their known capacity for concentrating various pollutants from their environment (Greffard and Meury 1967; Modin 1969; Zitko 1970; Clark and Finley 1973a).

Earlier studies of hydrocarbon uptake and its effects on marine organisms include those by Griffith (1970) who determined the toxicity of Arabian light crude oil and oil-dispersant mixtures on mussels under tidal conditions, and Lee, Sauerheber, and Benson (1972) who used mineral oil and radio-labeled [^{14}C] heptadecane to study the laboratory uptake, body distribution, and loss of hydrocarbons in mussels. We previously reported on uptake of petroleum hydrocarbons by aquatic organisms from several oil spills (Clark and Finley 1973a). This paper reports the findings of a preliminary laboratory study using two refined petroleum products, a No. 2 fuel oil and a No. 5 fuel oil, in a laboratory system that simulates tidal action.

EXPERIMENTAL METHODS

A tidal aquarium for laboratory studies of the uptake and loss of petroleum by intertidal organisms has been described (Clark and Finley in press) (Figure 1). This system consists of two aquaria set at a 25° angle to represent a beach surface. The first aquarium contained the organisms being exposed to the pollutant, and the second aquarium, where all procedures were duplicated except for the pollutant exposure, contained control organisms. These control organisms served as the base line comparison for mortality studies and hydrocarbon analysis. The flood tide was simulated twice a day by pumping an artificial seawater medium (LaRoche et al. 1970) from a carboy using a timer-equipped, variable-speed pump. The ebb tide was accomplished by siphoning the seawater medium back into the carboys from beneath the surface oil slick in the test tank. Prior to exposure, the mussels (collected in an area distant from known sources of petroleum pollution) were acclimated to the tidal system for 24 h following a previous 48- to 96-h conditioning in the laboratory in an aerated aquarium (Table 1).

In practice, usually two sets of test organisms were used; one set was placed in the intertidal zone, held by glass rods placed horizontally across

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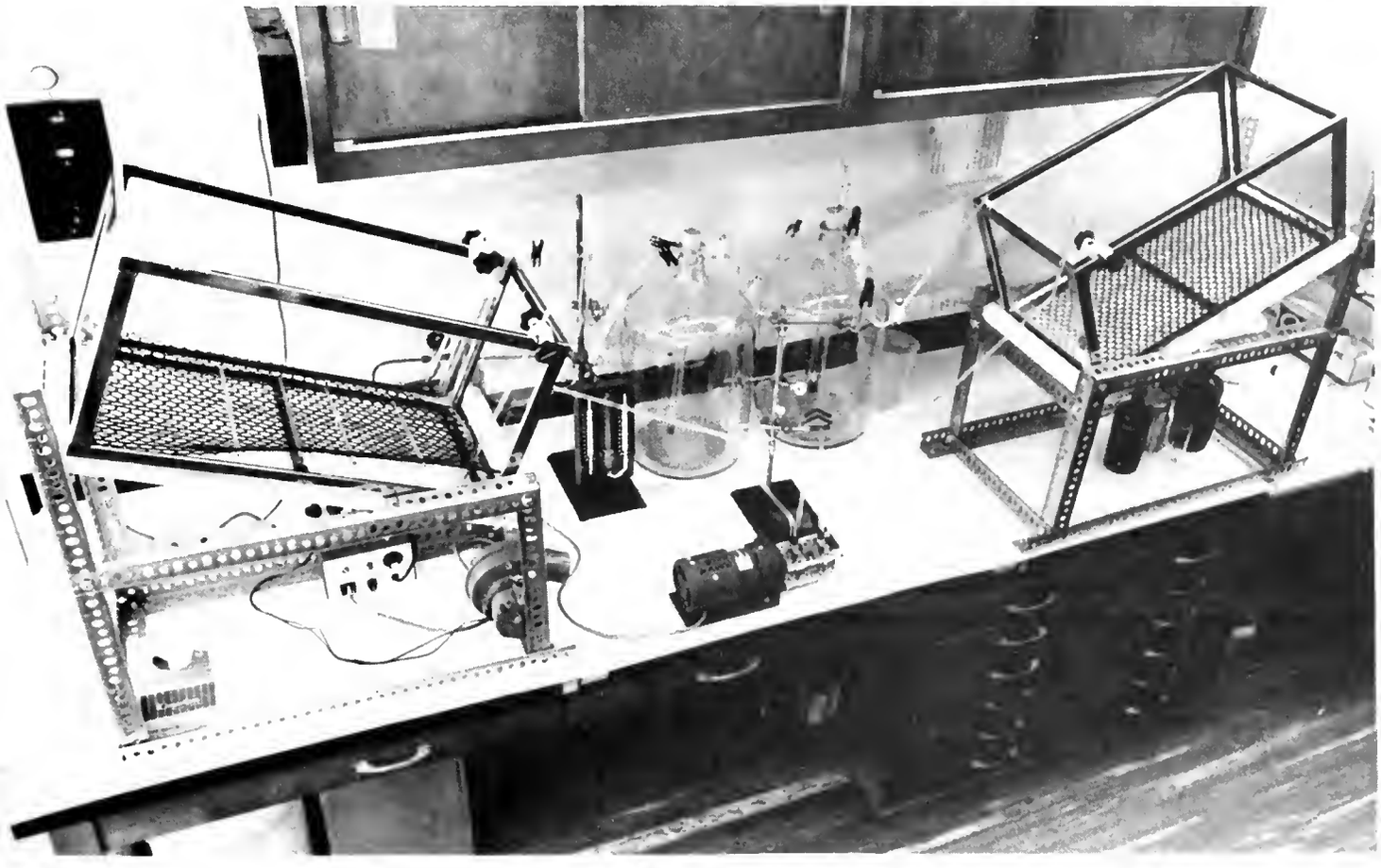

FIGURE 1.—Tidal aquarium system showing the test and control tanks.

the bottom of the sloping aquarium bottom, and exposed to the tidal sweep of the oil floating on the water surface. The second set was placed below the extreme lower level of the tidal sweep so that the organisms were continuously immersed in the medium where they were exposed to dissolved and emulsified fractions of the pollutant but never physically covered with oil.

During the experiment, a known volume of oil was layered onto the 1,700 cm^2 surface of the test aquarium at "high" tide. The system was then allowed to run through several complete tidal cycles in an attempt to simulate the conditions which might be found under a pier or along a beach following a significant oil spill. Two types of refined products were used in the uptake studies, a No. 2 heating fuel oil and a No. 5 heavy burner fuel oil.

TABLE 1.—Data on size of mussels, number of specimens, and experimental conditions.

Item	No. 2 fuel oil	No. 5 fuel oil
Average shell length	56.7 mm	54.7 mm
Number of specimens:		
Controls	36	16
Exposed — Surface slick	18	18
Exposed — Submerged	18	6
Exposure time	48 h	32 h
Complete tidal cycles	4	2.7
Water/air temperature	21°C	20°-22°C
Actual volume of oil applied	100 ml	97 ml
Slick thickness calculated:		
"High tide"	0.55 mm	0.53 mm
"Low tide"	1.53 mm	1.49 mm

At the end of the exposure, the bulk oil was skimmed from the surface at "high" tide, and the organisms were immediately placed in aerated aquaria containing seawater medium. The water was changed daily and the mussels fed a clam-based diet three times a day (LaRoche et al. 1970). Groups of the two sets of mussels were removed from these aquaria for analysis 1, 7, 14, and 35 days after the end of the exposure experiments.

The paraffin hydrocarbon analysis techniques for marine organisms have been described by Clark and Finley (1973b). Mussels were sampled and analyzed in groups of two to six individuals; analysis was run on the combined tissue and body fluids. No hydrocarbon content of the test seawater medium nor of the clean seawater was determined. Care was taken to minimize contamination of the shucked meats from oil that might have adhered to the shell, particularly in the early samples (1 and 7 days). All results have been reduced to "parts-per-million (ppm) dry extract-

ed-weight" basis (10^{-6} g of *n*-paraffin hydrocarbon per gram of the sum of the dried residue plus the solvent extractables).

RESULTS

Mortality Studies

Acute toxicity studies were not intended to be a major portion of this investigation since our paraffin hydrocarbon analysis techniques are used primarily on surviving organisms that have taken up oil pollutants at levels below that detectable by sight or smell.

The percentage of cumulative mortality (Figures 2 and 3) shows an approximate doubling for mussels exposed to the No. 2 fuel oil compared with the mussels exposed to the No. 5 fuel oil, although the duration of exposure was also greater for the No. 2 fuel oil (46 h vs. 32 h). Both the slick-exposed and the submerged specimens in the No. 5 fuel oil had a slightly higher mortality than the controls, but these differences might not be significant because of the small number of organisms used. The No. 2 fuel oil slick-exposed specimens, however, showed a mortality over twice that of the controls. The submerged specimens had a low initial mortality, but after 2 wk mortality had increased to the level of the slick-exposed specimens.

These mortality data provide a comparison of the two petroleum pollutants and of the test and control groups but were not further utilized to compute median tolerance limits which were beyond the scope and objective of these preliminary qualitative studies.

Griffith (1970) reported no mortalities in mussels exposed to aged crude oil for four tidal cycles over a total of 120 h. When the same mussels were placed in clean seawater, their rate of recovery was assessed by noting that byssal reattachment required 18 h for 50% of the exposed organisms but less than 12 h for the controls. No observations beyond 120 h (5 days) were reported.

No. 2 Fuel Oil Studies

Groups of mussels were collected 1, 7, 14, and 35 days after their removal to clean seawater medium. The *n*-paraffin hydrocarbon patterns for one set are presented as an example (Figure 4). If one assumes that the hydrocarbon pattern of the "controls" represents the natural or biogenic paraffin hydrocarbons and that the pattern of the "test" specimens represents the biogenic plus the pollutant, then by subtracting the former from the latter the resulting "residual" pattern might be expected to depict the pollution hydrocarbon pattern of the petroleum product tested. The "residual" paraffin patterns are shown for the No. 2 fuel oil bioassay study for mussels sampled 1 and 7 days (Figure 5) and 14 and 35 days (Figure 6) after removal from the pollutant.

The shape of the residual paraffin patterns for all four sampling periods approximates that of the pollutant below n-$C_{27}H_{56}$ and above a residual content level of 0.050 ppm., although individual paraffin hydrocarbons may show variation from the smooth, nearly bell-shaped curve for the No. 2 fuel oil. The quantities of uptake and loss of *n*-paraffin hydrocarbons from the No. 2 fuel oil by the mussels are shown in Figure 7. The uptake after

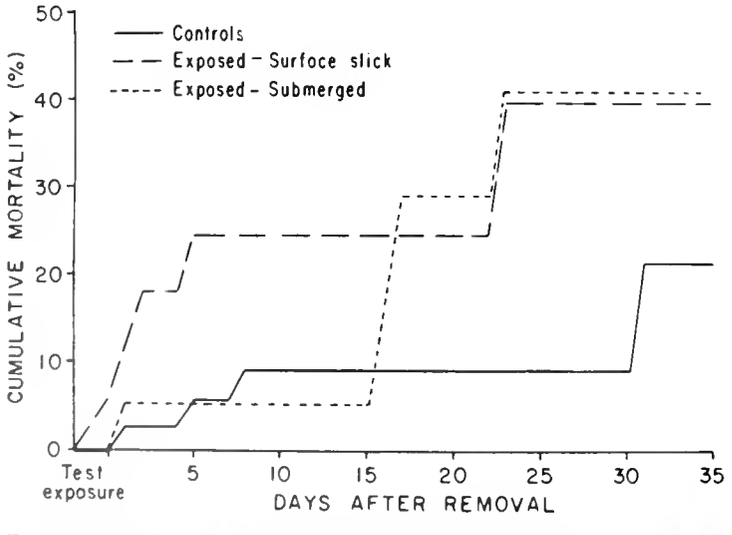

FIGURE 2.—Cumulative mortalities of mussels for 35 days following a 48-h exposure to a No. 2 fuel oil.

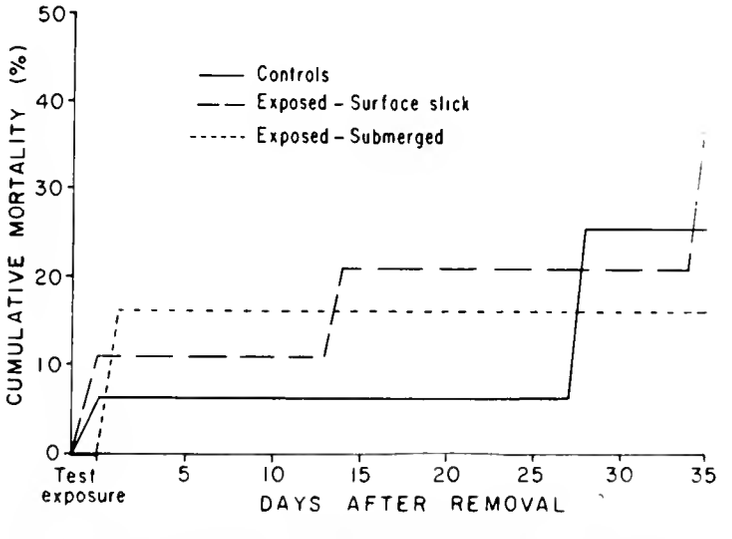

FIGURE 3.—Cumulative mortalities of mussels for 35 days following a 32-h exposure to a No. 5 fuel oil.

48-h exposure plus 1 day in clean medium was 110 ppm. for the slick-exposed specimens compared with only 29 ppm. for the submerged specimens. Within 7 days the residual content had dropped by nearly 75%, after which it declined at a slower rate but was still significantly above background (8 ppm.) after 35 days in the slick-exposed specimens.

No. 5 Fuel Oil Studies

The residual paraffin hydrocarbon pattern (Figure 8) for mussels exposed to a No. 5 fuel oil revealed a definite uptake of pollutant hydrocarbons at the end of the 32-h exposure, and the specimens collected 7 days later from clean seawater medium contained less than 1 ppm. total residual paraffin hydrocarbons attributable to the pollutant (Figure 7).

Gas-liquid chromatography of the saturated hydrocarbon fraction of the exposed mussels revealed a series of branched-chain hydrocarbons from below C_{14} to C_{26}, but of this series only pristane was quantified and included in the calculations. Most unsaturated and aromatic compounds were separated from the saturated fraction at the silica gel/alumina column chromatography stage without further analysis.

DISCUSSION AND CONCLUSIONS

These experiments, although preliminary in nature, provide four basic conclusions: 1) mussels rapidly took up pollution hydrocarbons during exposure; 2) mussels lost pollution hydrocarbons when removed from the test tanks and held in clean seawater (depuration), but significant quantities of No. 2 fuel oil remained for 35 days; 3) the *n*-paraffin residual pattern (exposed levels minus control levels) established for the exposed mussels nearly duplicated the shape of the pollutant hydrocarbon pattern; and 4) these laboratory results confirmed analyses made on shellfish following actual oil spills in the marine environment.

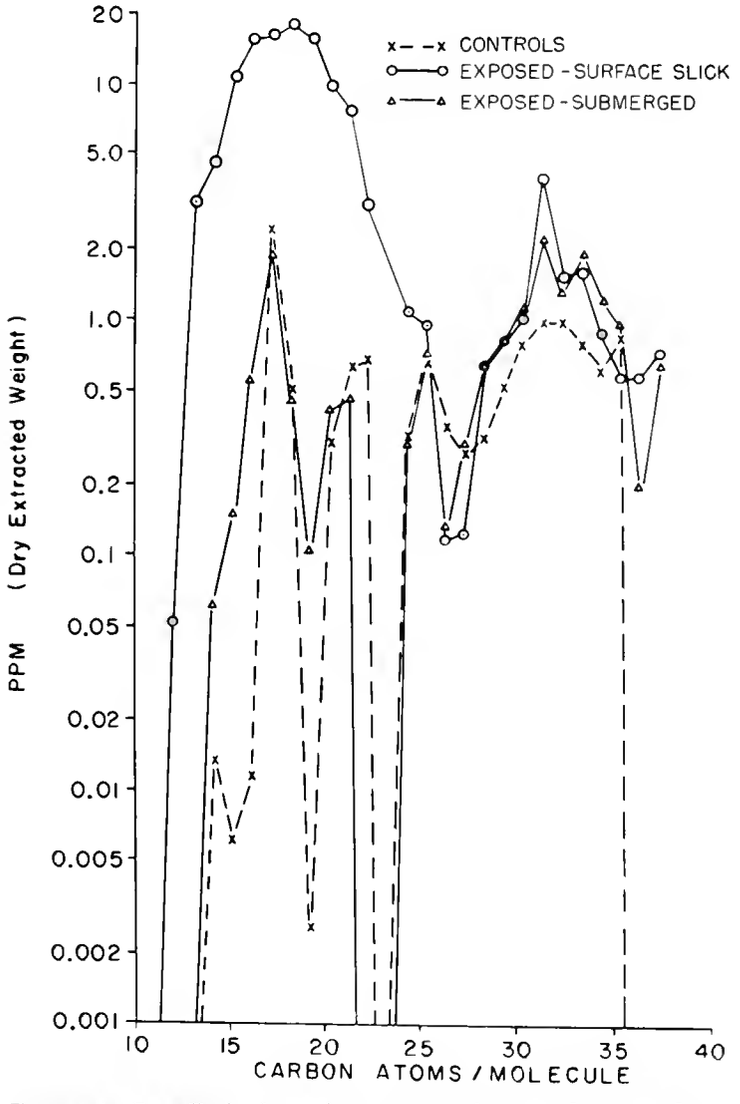

FIGURE 4.—Paraffin hydrocarbon patterns in mussels exposed to a No. 2 fuel oil: 1 day after removal.

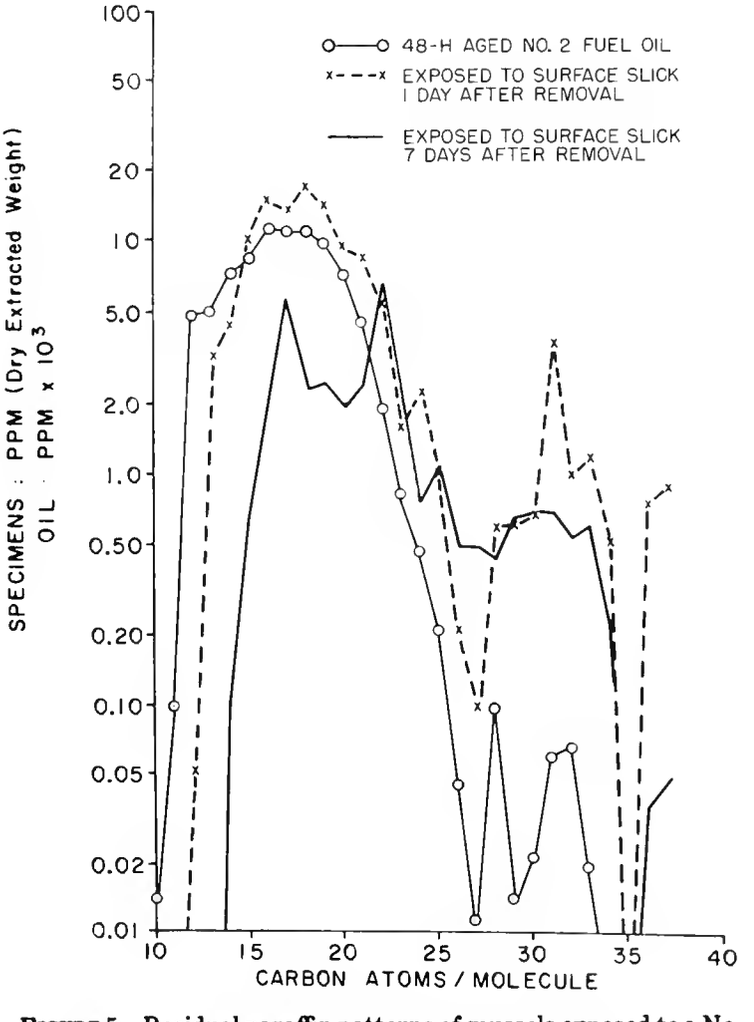

FIGURE 5.—Residual paraffin patterns of mussels exposed to a No. 2 fuel oil: 1 and 7 days after removal.

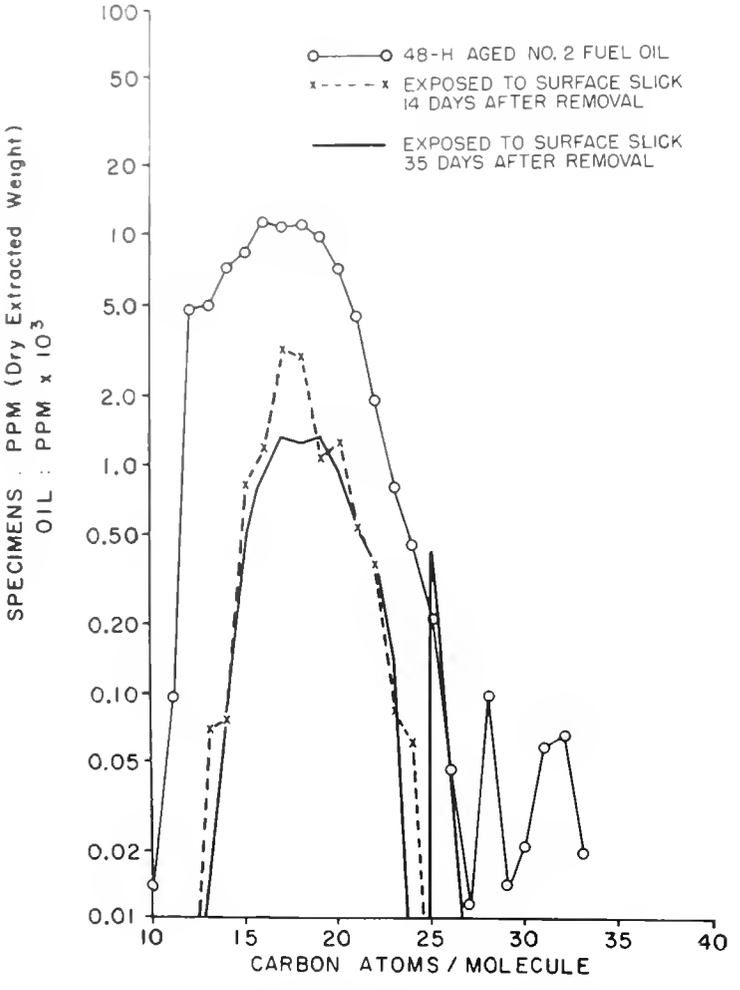

FIGURE 6.—Residual paraffin patterns for mussels exposed to a No. 2 fuel oil: 14 and 35 days after removal.

The mussels rapidly took up a wide range of petroleum paraffin hydrocarbons. Lee, Sauerheber, and Benson (1972) had found this to be the case for mussels where [^{14}C] heptadecane was detected within 15 min. The level of hydrocarbons we found in our mussels exposed to No. 2 fuel oil represents less than maximum uptake because after exposure they were held 24 h in clean seawater before sampling. The No. 5 fuel oil specimens were collected immediately after their 32-h exposure to the oil, and extreme care was exercised to avoid contaminating the tissue with any oil adhering to the outside of the shell when shucking prior to extraction.

Griffith (1970) suggests that the attachment of the byssal threads by the mussel could be affected by the exposure to petroleum. The byssal attachment is made by means of a grooved foot, which is extended from the shell and placed in contact with the substratum. Glandular secretions of collagen mixed with phenolic protein run from the foot groove, become attached to the substratum, and during withdrawal of the foot undergo tanning by the action of polyphenoloxidase (Pujol 1967). It is

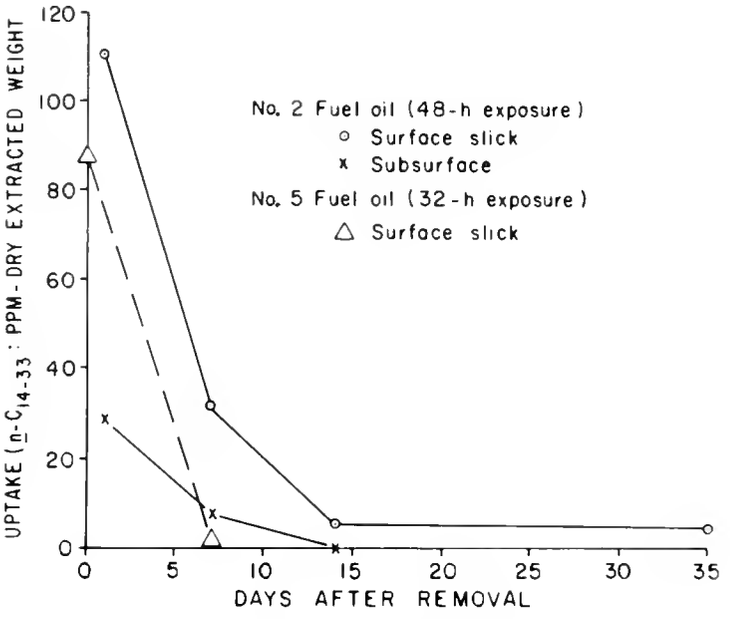

FIGURE 7.—*n*-Paraffin hydrocarbon uptake and loss of fuel oil by mussels.

not certain whether the oil upsets this chemical process or inhibits the muscular actions of the foot necessary to anchor the byssal thread.

When other mollusks such as the American oyster, *Crassostrea virginica*, were exposed to an

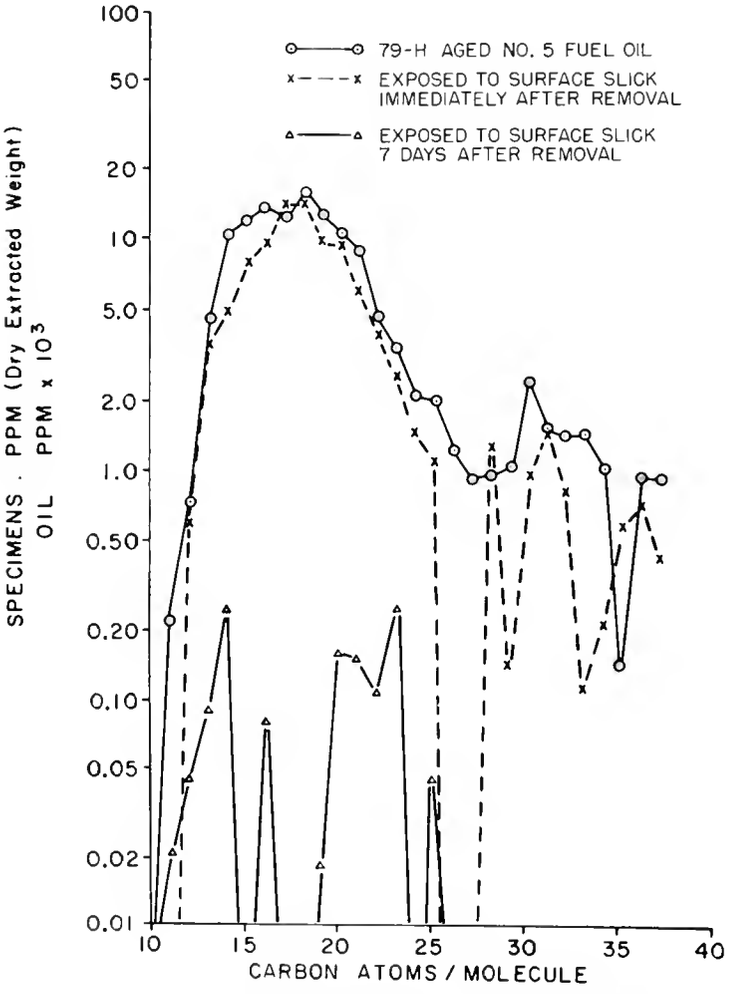

FIGURE 8.—Residual paraffin patterns for mussels exposed to a No. 5 fuel oil.

oil-water mixture, as distinct from our nonagitated surface oil slick under tidal conditions, they also showed rapid uptake. Anderson (1973) found uptake of No. 2 fuel oil to be greatest in the first 24 h with lower uptake at longer periods. By comparison, he found uptake in clams, *Rangia cuneata*, reached a maximum in 72 h, and greater concentrations in the clam tissue were reached than for oysters. Aromatic hydrocarbons showed a greater uptake in the mollusk tissue than saturated forms.

Stegeman and Teal (1973), using a flow-through exposure system, showed that oysters initially took up a No. 2 fuel oil-water mixture in direct relation to the hydrocarbon concentration in the water up to at least 450 μg/liter, above which they remained closed. They also found an enrichment in aromatic fractions compared to the saturated fraction, and under long-term exposure (49 days) the latter fraction showed a progressive decrease in amount with increasing length of exposure.

Under our conditions the No. 5 fuel oil-exposed specimens took up less *n*-paraffin hydrocarbons than the No. 2 fuel oil-exposed mussels, and the former also lost them faster. Both sets of specimens had depurated their residual hydrocarbons by 75% within 1 week, but the No. 2 fuel oil-exposed mussels still contained detectable amounts at the end of 35 days. Lee, Sauerheber, and Benson (1972) found that mussels would discharge over 90% of the incorporated mineral oil after several days, a result they confirmed with labelled *n*-heptadecane.

Anderson (1973) found that oysters lost 94% of the saturated hydrocarbon uptake but only 82% of their aromatics after 13 days when exposed to a No. 2 fuel oil; after 52 days no residual pollutant hydrocarbons were detected at the 0.5-ppm. level (wet weight). Exposure to South Louisiana crude oil showed detectable but low levels of saturates but no detectable aromatics after 27 days depuration. Stegeman and Teal (1973) also found a rapid loss of hydrocarbons from oysters exposed to No. 2 fuel oil-water mixture, but a persistent portion (34 ppm. wet weight above background) remained.

These preliminary experiments did not provide results as to the mechanisms or pathways of petroleum hydrocarbon uptake by the contaminated mussels. The mechanisms of uptake and transport of pollutant hydrocarbons from the environment into organisms may have a very important effect on the degree to which the subsequent depuration is reversible. For instance, hydrocarbons transported across gill membranes in solution or as emulsified droplets enter the bloodstream of fishes very rapidly and can be rapidly depleted on removal of the pollutant (Roubal 1974). On the other hand, hydrocarbons in food sources are resorbed at a different site, which, for the basking shark occurs in the spiral valve where they are transferred to the liver and remain highly persistent (Blumer 1967).

The residual paraffin hydrocarbon patterns showed a strikingly similar pattern to the aged pollutant, yet the organisms appeared healthy and had no visible contamination or oily odor. Lee, Sauerheber, and Benson (1972) indicated that gas-liquid chromatograms of mineral oil in mussels were like the original mineral oil except for some loss of the short-chain paraffin hydrocarbons. Blumer et al.(1970) used gas chromatograms of oysters and scallops contaminated by a No. 2 fuel oil to show that the patterns had the same general features as the chromatogram of the fuel oil.

Anderson (1973) found an *n*-paraffin hydrocarbon pattern in clams similar to the high-aromatic No. 2 fuel oil; however, the maximum hydrocarbon in the clam (*n*-C_{17}: approximately 1.6 times more than *n*-C_{16} and 1.9 times *n*-C_{18}) was one carbon number higher than the pollutant maximum (*n*-C_{16}: 1.1-1.2 times the adjacent paraffins). Stegeman and Teal (1973) showed gas chromatograms of contaminated oysters having a pattern similar to the pollutant and a maximum *n*-paraffin concentration of C_{18} or C_{19}.

Our presentation of petroleum hydrocarbon uptake as evidenced by *n*-paraffin analyses is not a complete picture of petroleum contamination since it reflects only a portion of the total hydrocarbons and non-hydrocarbons in the oil. Also, the various hydrocarbon components of the petroleum are not necessarily available to the organisms in the water in the same proportion as they exist in the original petroleum. Vaughan (1973) reported an enrichment of methylnaphthalenes compared to *n*-$C_{12\text{-}20}$ paraffins of 15:1 in oysters exposed to a South Louisiana crude oil (50 μg/ml) in a seven-day bioassay experiment and an enrichment in the water extracts of about 3:1. Further, the *n*-paraffin content of petroleum pollutants in shellfish is often depleted with time relative to that of the source (Stegeman and Teal 1973). Therefore, while our values for pollutant uptake based on *n*-paraffin hydrocarbon analyses yield conservative estimates, they demonstrate that these experimentally simple methods can be

useful. Aromatic hydrocarbons, which are a biogenic rarity yet often a major component of petroleum and its refined products found to be rapidly taken up by marine organisms, may be rapidly lost from contaminated organisms (Lee, Sauerheber and Dobbs 1972; Stegeman and Teal 1973; Anderson 1973). Consequently, the utility of these compounds in marine pollution monitoring programs and in long-term bioassay experiments may be somewhat limited.

We previously reported (Clark and Finley 1973b) uptake by mussels, *M. edulis* and *M. californianus*, of petroleum *n*-paraffins following oil spills in the marine environment. A No. 2 fuel oil spill resulted in considerably greater uptake (10 ppm. of n-C_{17}) than for mussels exposed to Navy Special fuel oil residue (nearly 1 ppm. of n.-C_{17}); however, in both cases it was obvious that the apparently healthy mussels had acquired an *n*-paraffin hydrocarbon pattern like that of the pollutant. By creating an oil slick and a tidal system within an aquarium under laboratory conditions, it is possible to show that these earlier findings can be reproduced. These results add further support to the data of other investigators who used different approaches and analytical techniques.

We did not analyze hydrocarbon levels in specific organs, conduct metabolic studies, or determine aromatic content. Stegeman and Teal (1973) and Anderson (1973) found that aromatic hydrocarbons were often enriched in oysters in preference to the *n*-paraffins.

While we have given percentage loss of pollutant paraffin hydrocarbons in our presentation as well as actual concentration levels (Figure 7), the percentage value is very dependent on both the level of initial pollution exposure and on the lower limit of sensitivity of the experimental method for detecting pollutant uptake near biogenic background concentrations in marine organisms. Thus, one might have two sets of organisms showing similar concentrations of residual pollutant after considerable depuration but with a dramatically different percentage loss as a result of different exposure levels.

The variation of uptake and loss of petroleum hydrocarbons in marine organisms most certainly is related to the magnitude of the exposure—the amount of the pollutant and the duration, as well as physical and chemical properties of the pollutant.

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SYSTEMATICS AND MORPHOLOGY OF THE BONITOS (*SARDA*) AND THEIR RELATIVES (SCOMBRIDAE, SARDINI)[1]

BRUCE B. COLLETTE[2] AND LABBISH N. CHAO[3]

ABSTRACT

The bonitos constitute the scombrid tribe Sardini, consisting of eight species placed in five genera. They differ from the more primitive mackerels and Spanish mackerels in lacking a notch in the hypural plate and in having a bony lateral keel on the posterior caudal vertebrae. From the higher tunas, they differ in having the bony keel only incompletely developed and in lacking a specialized subcutaneous vascular system. The monotypic Australian endemic *Cybiosarda elegans* shares several characters with the monotypic eastern Atlantic endemic *Orcynopsis unicolor* (structure of the bony caudal keel; relative lengths of liver lobes; position and size of spleen) that distinguish them from *Gymnosarda unicolor* and the species of *Sarda*. *Sarda* contains four allopatric species, which differ from each other in such characters as numbers of fin rays, gill rakers, vertebrae, and teeth: the Atlantic *S. sarda*; the southeastern Australian *S. australis*; the tropical Indo-Pacific *S. orientalis*; and the eastern temperate Pacific *S. chiliensis*. The monotypic Indo-West Pacific reef species *Gymnosarda unicolor* is the only member of the Sardini that has a swim bladder and lacks intermuscular bones on the back of the skull. The monotypic Southern Ocean *Allothunnus fallai* differs from all other scombrids in having laterally extended prootic wings. It is more closely related to the bonitos than to any other scombrids. *Allothunnus* resembles the higher tunas in having a prootic pit but lacks the subcutaneous vascular system. Tables of meristic characters, diagrams of the soft anatomy, and drawings of most bones are included in the first part of the paper. The second part of the paper includes sections on synonymy, comparative diagnosis, types of nominal species, and distribution for each species.

The purpose of this paper is to clarify the relationships of the Sardini at the generic and specific level. This work is part of a continuing study of the systematics of the Scombridae. The methods used are similar to those used by Gibbs and Collette (1967) in a revision of *Thunnus* and rely heavily on the classic work of Kishinouye (1923) and Godsil (1954, 1955).

The bonitos (*Sarda*) and their relatives form a tribe (Sardini) of the subfamily Scombrinae intermediate between the primitive mackerels (Scombrini) and Spanish mackerels (Scomberomorini), and the more advanced tunas (Thunnini) (see Collette and Gibbs 1963a; Gibbs and Collette 1967). Five genera are treated in this paper. The status of the related monotypic genera *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* has been unclear; for example, Fraser-Brunner (1950) placed *Cybiosarda* in the synonymy of *Gymnosarda*. The systematic position of the monotypic *Allothunnus* has been still more confused—whether it is closer to *Thunnus* (Fraser-Brunner 1950), to *Sarda* (Fitch and Craig 1964), or strikingly different from all other scombrids (Nakamura and Mori 1966). There has been no agreement on the number of species of *Sarda*. Fraser-Brunner (1950) recognized three species: *chiliensis*, *orientalis*, and *sarda*. Godsil (1955) believed that there were two basic groups of species—*sarda-chiliensis* and *orientalis-velox*. Some authors have considered *S. australis* as a valid species, others as a subspecies of *S. chiliensis*.

This project was initiated at the request of the FAO (Food and Agriculture Organization of the United Nations) panel of Experts for the Facilitation of Tuna Research at its Fourth Session in La Jolla, Calif. in November 1971, and should be considered as a report from the Working Party on Tuna and Billfish Taxonomy. Bonitos, as a group, are one of the few underexploited groups of tunalike fishes; therefore, research on their systematics is a necessary predecessor of successful management.

According to the FAO Yearbook of Fishery Statistics for 1972 (Food and Agriculture Or-

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ganization of the United Nations 1973), the two species of bonitos that are presently of economic importance are *Sarda chiliensis* and *S. sarda*. Peruvian fishermen landed 54,000-73,000 metric tons per year of the southeast population of *S. chiliensis* in 1965-1972. Smaller catches by Chile and of the northeast Pacific population by Mexico and the United States made the total 65,000-94,000 metric tons per year during that period. *Sarda sarda* is fished particularly by Turkey in the Mediterranean and the Black Sea where 11,700-55,200 metric tons per year were landed in 1965-1972. Other catches of *S. sarda* by Spain, Portugal, Greece, Angola, Argentina, and Brazil made the total 25,000-65,000 metric tons per year in 1965-1972. Both the Japanese and the Koreans fish for *S. orientalis* and there are smaller catches elsewhere throughout its range. *Sarda australis* comes into the markets in Sydney and probably elsewhere in southeastern Australia. In 1971, Morocco was reported to have landed 600 metric tons of *Orcynopsis* and we have seen *Orcynopsis* in the markets in Tunis. We have seen specimens of *Cybiosarda* in the Sydney fish market mixed with *S. australis*. The only commercial catch of *Allothunnus* was the 230 tons taken with purse seines off eastern Tasmania in June 1974 (Webb and Wolfe 1974). *Gymnosarda* occurs around coral reefs where it is taken by fishermen on hook and line.

Emphasis was placed on obtaining fresh or frozen specimens from each population of each species for dissection. Standard counts and measurements were taken, color pattern was recorded, and a search was made for parasitic copepods. Results of the copepod study will be reported on later by Roger F. Cressey (United States National Museum, USNM). The viscera were examined and drawn in situ following removal of an oval portion of the ventral body wall. The viscera were then removed and drawings were made of the liver and other selected organs. The kidneys and anterior parts of the arterial system were then drawn. Counts of ribs and intermuscular bones were made and the specimen was then skeletonized. Specimens were immersed in hot water to assist removal of the flesh.

For morphometric comparisons, the base measurement used for fresh, frozen, and preserved specimens was millimeters fork length (mm FL). Skeletal material was measured in millimeters skeletal length, the distance from the anterior margin of the ethmoid to the posterior tip of the hypural plate, a distance somewhat shorter than fork length. Skulls were measured from the anterior margin of the ethmoid to the posteroventral junction of the skull with the first vertebral centrum.

This paper is divided into two major sections. The first part describes and illustrates the squamation, morphometry, meristic characters, soft anatomy, and osteology of the Sardini. The second part treats the genera and species separately including synonymy, diagnosis (based on characters from the first section), types of nominal species, geographical distribution, and, for some species, geographic variation.

MATERIAL

Abbreviations used for the institutions cited herein are as follows:

AB - Northwest Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, Alaska.
AMS - Australian Museum, Sydney.
ANSP - Academy of Natural Sciences, Philadelphia, Pa.
BMNH - British Museum (Natural History), London.
BPBM - Bernice P. Bishop Museum, Honolulu, Hawaii.
CAS - California Academy of Sciences, San Francisco.
CBL - Chesapeake Biological Laboratory, Solomons, Md.
CSIRO - CSIRO Marine Biological Laboratory, Cronulla, N.S.W., Australia.
DM - Dominion Museum, Wellington, New Zealand.
FMNH - Field Museum of Natural History, Chicago, Ill.
HUJ - Hebrew University, Jerusalem.
LACM - Los Angeles County Museum of Natural History, Los Angeles, Calif.
MACN - Museo Argentina de Ciencias Naturales, Buenos Aires.
MCZ - Museum of Comparative Zoology, Harvard.
MNHN - Muséum National d'Histoire Naturelle, Paris.
MSNG - Museo di Storia Naturale, Genoa.
MSUF - Museo de La Specola, Universita di Firenze, Florence.

NHMV - Naturhistorisches Museum, Vienna.
NMC - National Museum of Natural Sciences, Ottawa.
QM - Queensland Museum, Brisbane.
RMNH - Rijksmuseum van Natuurlijke Historie, Leiden.
RUSI - J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown.
SAM - South African Museum, Capetown.
SFRS - Sea Fisheries Research Station, Haifa, Israel.
SIO - Scripps Institution of Oceanography, La Jolla, Calif.
SMF - Senckenberg Museum, Frankfurt-am-Main.
TABL - Southeast Fisheries Center, National Marine Fisheries Service, NOAA (formerly Tropical Atlantic Biological Laboratory), Miami, Fla.
UBC - Institute of Fisheries, University of British Columbia, Vancouver.
UCLA - University of California, Los Angeles.
UMML - Rosenstiel School of Marine and Atmospheric Science, Miami, Fla.
UMMZ - University of Michigan Museum of Zoology, Ann Arbor.
USNM - United States National Museum, Washington, D.C.
WAM - Western Australia Museum, Perth.
WHOI - Woods Hole Oceanographic Institution, Woods Hole, Mass.
ZMK - Zoological Museum, Copenhagen.
ZMO - Zoological Museum, Oslo.

The material examined is listed by general locality under four or five headings for each species (except *Sarda chiliensis*, *S. orientalis*, and *S. sarda* which are subdivided into two populations each). The numbers in each category are not additive but are included to give some degree of confidence in the morphological data presented in the body of the paper. "Total specimens" is the total number of individuals examined whether preserved, dissected, or skeletons. "Measured and counted" includes specimens that were subsequently dissected and the preserved museum specimens used for detailed morphometric and meristic examination. "Counts only" are the additional museum specimens used only for meristic examination. "Skeletons" refer to all the skeletal material examined, specimens that were dissected plus skeletal museum material.

Allothunnus fallai. Total 8 specimens (451-787 mm FL).

Dissected 4 (680-778). Tasmania (3); California (1).

Measured and counted 7 (642-787). Tasmania (4); California (1); New Zealand (2).

Skeletons 5 (451-778). Tasmania (3); California (1); South Africa (1).

Cybiosarda elegans. Total 22 specimens (250-422 mm FL).

Dissected 5 (355-422). Perth, Western Australia (1); Macleay River, New South Wales (4).

Measured and counted 21 (250-422). New South Wales (11); E. Queensland (7, including holotype of *Scomberomorus* (*Cybiosarda*) *elegans* Whitley); Gulf of Carpentaria (1); Western Australia (2).

Examined 1 (380). New South Wales.

Skeletons 5 (355-422). Western Australia (1); New South Wales (4).

Gymnosarda unicolor. Total 38 specimens (71.6-1,080 mm FL).

Dissected 6 (522-787). Amirante Islands (2); Truk Islands, Caroline Islands (3); Bikini, Marshall Islands (1, partial).

Measured and counted 31 (71.6-1,040). Red Sea (5, including holotype of *Thynnus unicolor* Rüppell); Comoro Islands (1); Amirante Islands (2); Madagascar (1); New Britain (1); Solomon Islands (2); Gilbert Islands (1); Japan (3); Palau Islands (1); Caroline Islands (7); Marshall Islands (5); Society Islands (1); Marquesas Islands (1).

Examined 1 (267-mm head of 1,080-mm specimen). Pitcairn Group.

Skeletons 11 (about 625-1,013). Amirante Islands (2); Marshall Islands (4); Truk Islands (3); unknown locality (2).

Orcynopsis unicolor. Total 55 specimens (164-960 mm FL).

Dissected 11 (332-645). Israel (5, partial); Tunisia (6, complete).

Measured and counted 43 (164-960). Lebanon (12, 242-325); Israel (12, 285-735); Egypt (5, 164-280); Tunisia (7, 312-645); Nice (1, 553); Mauritania (2, 400-410); Senegal (2, 405-960); Norway (2, 565-570, types of *Thynnus peregrinus* Collett).

Counts only 12 (417-950). Pizza (1, ca. 950); Elba (1, ca. 790); Gulf of Genoa (1, 670); Rimini, Adriatic (1, ca. 600); Egypt (6, 417-556); locality unknown (2).

Skeletons 11 (332-645). Israel (5); Tunisia (6).

Sarda australis. Total 21 specimens (195-495 mm FL).

Dissected 3 (360-495). New South Wales, Australia.

Measured and counted 21 (195-495). Norfolk Island (1); New South Wales (20, including holotype of *Pelamys australis* Macleay).

Skeletons 3 (360-495). New South Wales.

Sarda chiliensis—northeast Pacific. Total 91 specimens (207-643 mm FL).

Dissected 4 (401-472). La Jolla, Calif.

Measured and counted 24 (207-587). California: La Jolla; San Diego (including holotype of *Pelamys lineolatus* Girard); Los Angeles; San Pedro; Santa Barbara; Oceanside. Baja California: Coronados Island; Natividad Island; Cedros Island; Blanca Bay.

Counts only 21 (220-625). Vancouver, British Columbia (1); Alaska (2); S. California (17); Revillagigedos Island (1).

Skeletons 50 (310-643). S. California (including holotype of *Sarda stockii* (David)).

Sarda chiliensis—southeast Pacific. Total 44 specimens (57.2-672 mm FL).

Dissected 7 (437-571). Callao, Peru.

Measured and counted 23 (94.1-672). Valparaiso, Chile (holotype of *Pelamys chiliensis* Cuvier). Arica Bay, Chile. Peru: Callao; Foca Island; San Lorenzo Island; Pachacamac Island; Guañape Island; San Gallán Island.

Counts only 9 (57.2-636). Peru: San Lorenzo Island; San Gallán Island; Foca Island; Callao.

Skeletons 18 (437-571). Callao, Peru.

Sarda orientalis—Indo-West and central Pacific. Total 31 specimens (150-645 mm FL).

Dissected 5 (341-500). Tokyo (3); Hawaii (2).

Measured and counted 27 (150-645). South Africa (2); Seychelles Islands (1); Red Sea (2); Cochin, India (1); Western Australia (paratype of *Sarda orientalis serventyi* Whitley); China (4); Japan (12, including types of *Pelamys orientalis* Temminck and Schlegel); Hawaii (4).

Counts only 3 (223-370). Muscat (2); Ceylon (1).

Skeletons 6 (341-500). Muscat (1); Tokyo (3); Hawaii (2).

Sarda orientalis—eastern Pacific. Total 21 specimens (354-447 mm FL).

Dissected 4 (354-447). Navidad Bay, Mexico (1); Piñas Bay, Panama (2); Pearl Islands, Panama (1).

Measured and counted 12 (354-447). Mexico (1); Panama (8, including holotype of *Sarda velox* Meek and Hildebrand); Galapagos Islands (2); Gulf of Guayaquil (1).

Counts only 7 (429-650). Cabo San Lucas and Las Tres Marias Islands, Mexico (4); Galapagos Islands (3).

Skeletons 6 (354-447). Mexico (2); Panama (3); unknown locality (1).

Sarda sarda—western Atlantic. Total 86 specimens (118-637 mm FL).

Dissected 2 (333). New Jersey (1); Miami, Fla. (1).

Measured 29 (228-637). North America 12 (257-637): Massachusetts (4); New York (3); Chesapeake Bay (2); Florida (1); Cuba (1). Gulf of Mexico 5 (228-321): Florida (1); Texas (4). South America 12 (202-450): Gulf of Carioca, Venezuela (6); Brazil (5); Mar del Plata (1).

Counts only 51 (118-572). North America 39 (118-572): Massachusetts (24); Rhode Island (3); New York (3); New Jersey (1); Chesapeake Bay (2); Maryland (3); Florida (1). Gulf of Mexico 11 (103-400): Florida (3); Mississippi delta (3); Texas (1). South America 5 (214-570): Venezuela (1); Brazil (3); Mar del Plata (1).

Skeletons 9 (333-577). Massachusetts (2); Connecticut (1); New York (1); New Jersey (1); Florida (1); exact locality unknown (3).

Sarda sarda—eastern Atlantic. Total 62 specimens (104-680 mm FL).

Dissected 5 (363-504). Azores (3); Tunisia (1); Gulf of Guinea (1).

Measured and counted 30 (260-600). Atlantic Europe 9 (418-600): Norway (5); Spain (1); Azores (3). Mediterranean 8 (260-564). Black Sea 1 (550). Gulf of Guinea 10 (305-478). Port Elizabeth, South Africa 2 (447-517).

Counts only 31 (104-680). Europe 2 (482-670). Mediterranean 18 (187-487). Black Sea 9 (104-680). Gulf of Guinea 2 (366-375).

Skeletons 6 (363-504). Azores (3), Tunisia (1); Gulf of Guinea (2).

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KEY TO THE SPECIES OF SARDINI

1a. Jaw teeth tiny, 40-55 on each side of upper and lower jaws; gill rakers fine and numerous, total of 70-80 on first arch; body elongate, snout to second dorsal 610-654 thousandths of fork length; maxilla short, 354-379 thousandths of head length ..... *Allothunnus fallai* Serventy

1b. Jaw teeth larger and more prominent, 10-30 on each side of upper and lower jaws; total gill rakers on first arch 8-27; body less elongate, snout to second dorsal 481-610 thousandths of fork length; maxilla longer, 431-557 thousandths of head length 2

2a. Five to ten narrow, dark, longitudinal stripes on upper part of body; no teeth on the tongue; spleen prominent in posterior third of body cavity in ventral view ..... *Sarda* 3
2b. Body either without stripes or with dark spots above the lateral line and longitudinal dark stripes below; two patches of teeth present on tongue; spleen either concealed or located in anterior third of body cavity in ventral view 6
3a. Spines in first dorsal fin 20-23; total vertebrae 50-55 ..... *S. sarda* (Bloch)
3b. Spines in first dorsal fin 17-19; total vertebrae 43-46 4
4a. Total gill rakers on first arch 8-13; supramaxilla narrow (see Figure 32e) ..... *S. orientalis* (Temminck and Schlegel)
4b. Total gill rakers on first arch 19-27; supramaxilla wider (see Figure 32c-d) 5
5a. Total gill rakers on first arch 19-21; pectoral rays 25-27, modally 26; teeth sometimes present on vomer; length of first dorsal base 315-343 thousandths of fork length; maxilla 503-539 thousandths of head length ..... *S. australis* (Macleay)
5b. Total gill rakers on first arch 23-27; pectoral rays 22-26, modally 24 or 25; teeth never present on vomer; length of first dorsal base 267-314 thousandths of fork length; maxilla 460-503 thousandths of head length ..... *S. chiliensis* (Cuvier)
6a. Body with dark spots above lateral line and dark longitudinal stripes below (see Figure 1a); spines in first dorsal fin 16-18 ..... *Cybiosarda elegans* (Whitley)
6b. Body without a prominent pattern of stripes or spots (see Figure 2); spines in first dorsal fin 12-15 .....
7a. Pectoral rays 21-23; small conical teeth in jaws; total gill rakers on first arch usually 14 or more; interpelvic process bifid; spleen not visible in ventral view; laminae in olfactory rosette 25-28; interorbital width 239-310 thousandths of head length ..... *Orcynopsis unicolor* (Geoffroy St. Hilaire)
7b. Pectoral rays 25-28; jaw teeth very large and conspicuous; total gill rakers on first arch usually 13 or fewer; interpelvic process single; spleen visible on right side of body cavity in ventral view; laminae in olfactory rosette 48-56; interorbital width 321-400 thousandths of head length ..... *Gymnosarda unicolor* (Rüppell)

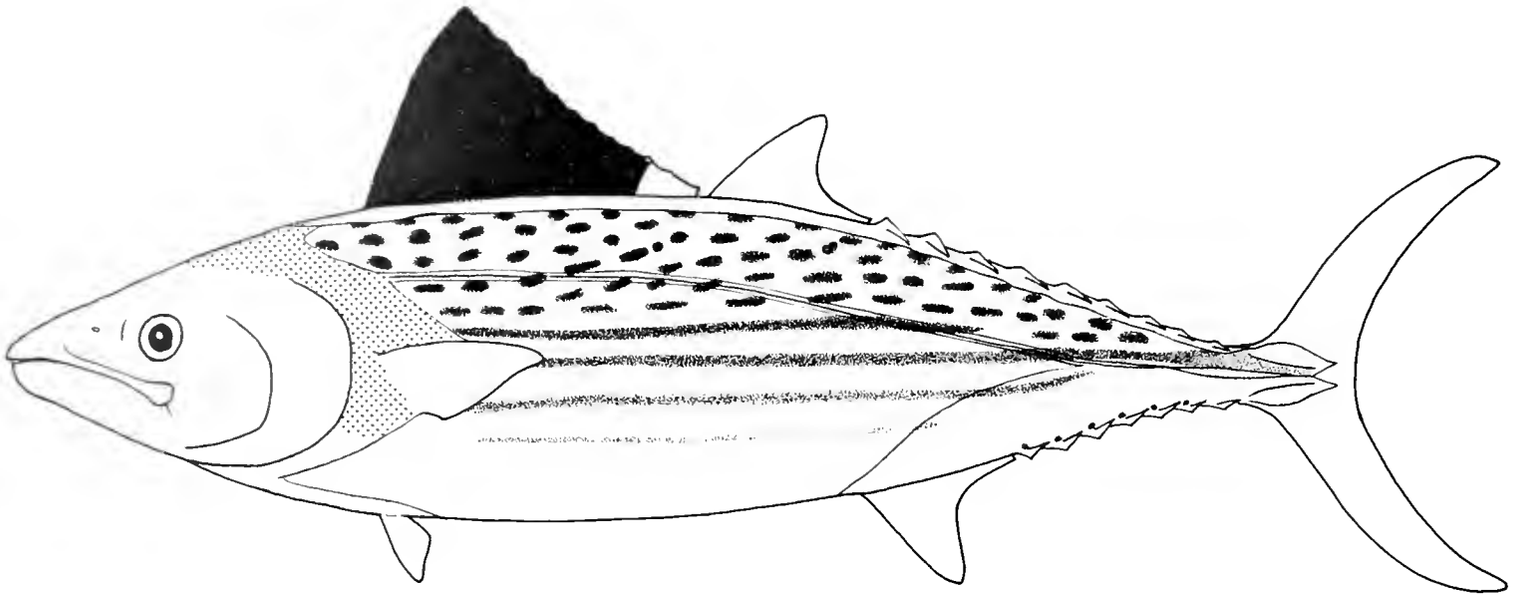
PART 1. COMPARATIVE MORPHOLOGY

The morphological characters useful for distinguishing the species of bonitos and for evaluating their phylogenetic relationships are divided into six categories: color pattern, scales, morphometry, meristics, soft anatomy, and osteology.

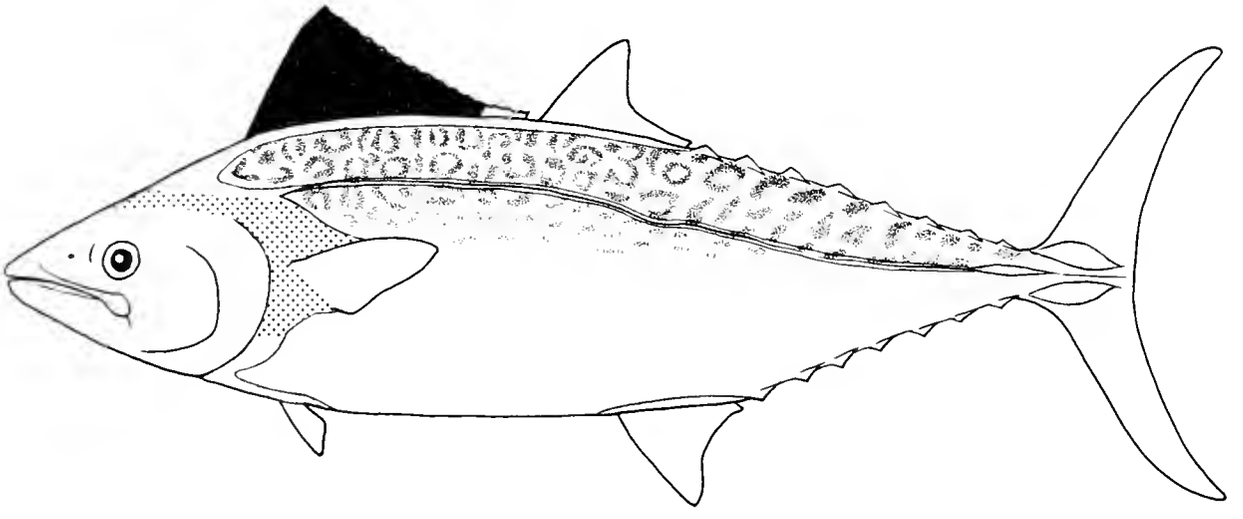
Color Pattern

The most strikingly colored species of the Sardini, and perhaps the entire family Scombridae, is clearly *Cybiosarda elegans* (Figure 1a). The light venter has several stripes reminiscent of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus). The dorsum is covered with black spots over a deep blue background. The high first dorsal fin is jet black anteriorly and white posteriorly. The anal and second dorsal fins are yellow. *Orcynopsis unicolor* (Figure 1b) has a high black first dorsal fin as in *Cybiosarda*, but there the similarity ends because adult *Orcynopsis* have only a faint mottled pattern that has been deliberately exaggerated in the figure. All species of *Sarda* (Figure 1c) have stripes along their backs but the number of stripes and their alignment varies both interspecifically and intraspecifically. *Sarda australis* has stripes on the venter as well as on the dorsum. *Sarda* also has a black first dorsal fin but it is lower and longer than in *Cybiosarda* and *Orcynopsis*. *Gymnosarda unicolor* (Figure 2a) is deep blue without any distinct pattern; *Allothunnus fallai* (Figure 2b) also lacks distinctive markings.

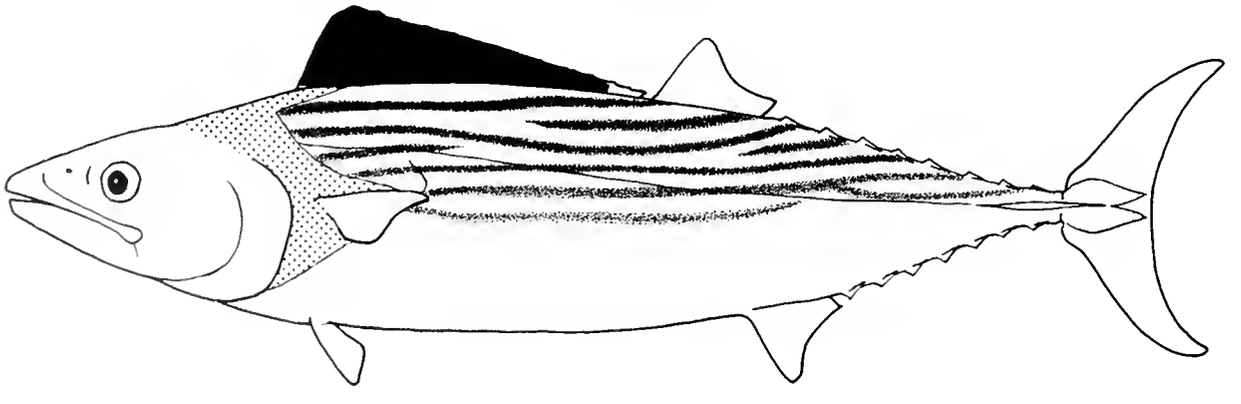
Color plates have been published of all the species of bonitos except *Allothunnus*. Paintings of three Australian species by George Coates were published by Marshall (1964, 1966): *Cybiosarda elegans* (fig. 345), *Sarda australis* (fig. 348), and *Gymnosarda unicolor* (fig. 342). Color illustrations of *Orcynopsis unicolor* were published by Lozano y Rey (1952, pl. 41, fig. 2—800-mm adult and fig. 3—150-mm juvenile) and by Bini (1968:39). *Sarda sarda* was illustrated by La Monte (1945, pl. 8; 1952, pl. 17), Lozano y Rey (1952, pl. 39, fig. 4—500-mm adult), and Bini (1968:37). Walford (1937, pl.



a



b



c

FIGURE 1.–Diagramatic lateral views of three species of Sardini to show general pigment pattern, extent of corselet (coarse stippling), and parts of the body covered by smaller scales (fine stippling). a. *Cybiosarda elegans*, New South Wales, 337 mm FL, USNM 259407-F2. b. *Orcynopsis unicolor*, Tunisia, 312 mm FL, USNM 206526. c. *Sarda sarda*, Gulf of Mexico, 287 mm FL, USNM 118646.

38) includes color photographs of a northeastern Pacific *Sarda chiliensis* and an eastern Pacific *S. orientalis*.

Scales

In bonitos, the body scales are cycloid and usually small. Those on the corselet, along the fin bases, and along the lateral line are larger and more elongate. The predorsal and opercular scales are larger and are embedded under the skin. No scales are present on the snout, the interorbital area, or on the fins. Posterior to the corselet, the distribution of scales differs among the genera of bonitos (Figures 1, 2). Species of *Sarda* have their body completely covered with small scales except for the distal portion of the caudal keels (Figure 1c). *Allothunnus* has the dorsal half of the body covered with scales (Figure 2b), but they do not extend onto the caudal keels, although they do cover the base of the caudal fin. Serventy (1948) described the type of *Allothunnus fallai* as having its whole body covered with scales. But later authors, Talbot (1960), Olsen (1962), and Nakamura and Mori (1966), all indicated that the minute scales of *Allothunnus* are present only on

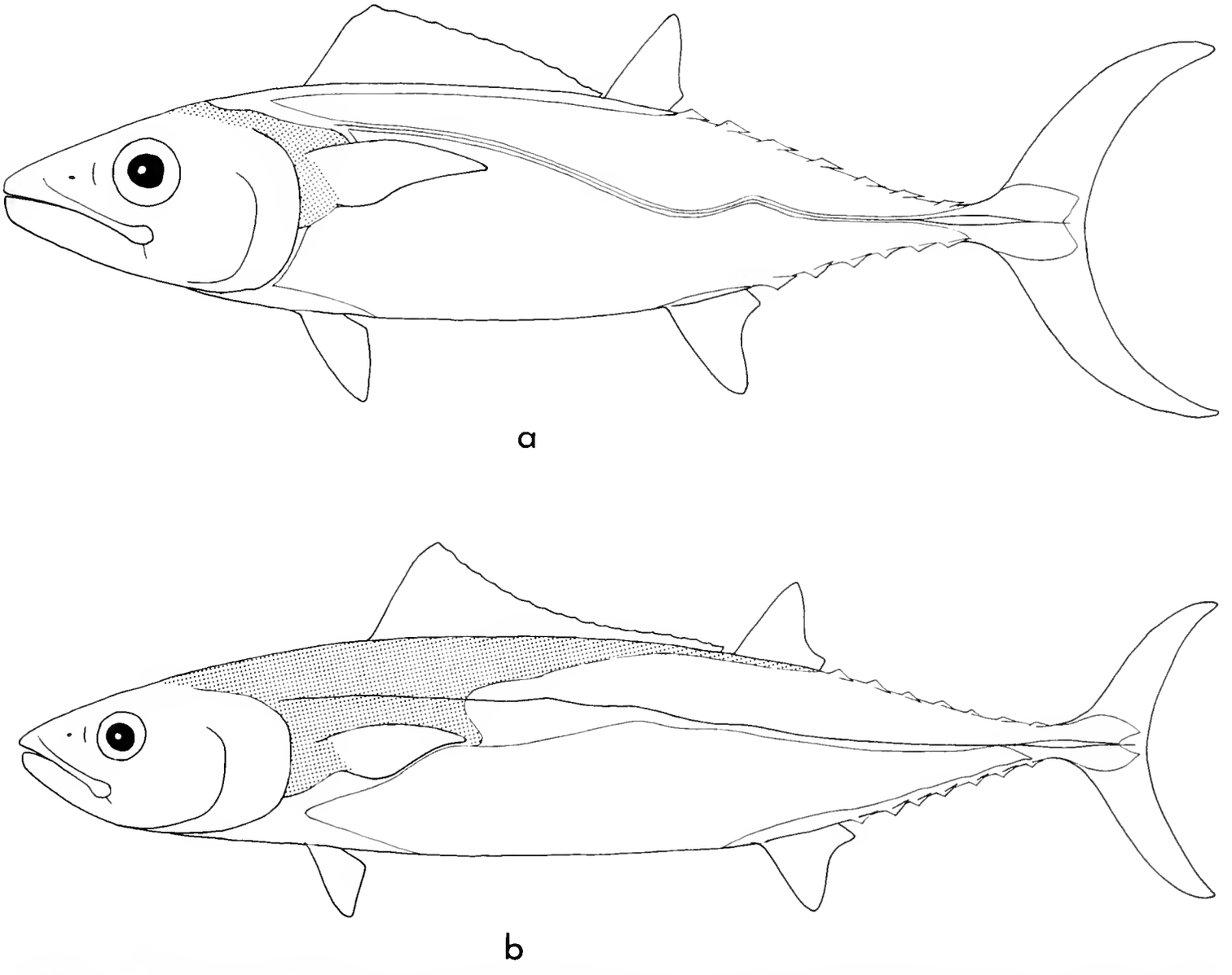


FIGURE 2.–Diagrammatic lateral views of two species of Sardini to show extent of corselet (coarse stippling) and parts of body covered by smaller scales (fine stippling). a. *Gymnosarda unicolor*, Tahiti, 446 mm FL, ANSP 93818. b. *Allothunnus fallai*, New Zealand, 642 mm FL.

the dorsal half of the fish. A patch of scales is also present around the base of the pelvic fins. *Cybiosarda* has a band of scales dorsally extending along the entire midline (Figure 1a). Ventrally, scales are present around the base of the pelvic fins and a broad band of scales extends from the anal fin origin posterodorsally to the caudal peduncle. The peduncular region is entirely covered with scales except for the distal margin of the caudal keel. *Orcynopsis* (Figure 1b) has fewer scales than *Cybiosarda*. The band of scales along the dorsal midline is narrower and ends at the dorsal finlets. Ventrally, *Orcynopsis* has scales around the bases of the pelvic and anal fins. The caudal peduncle is naked except for the caudal keel. *Gymnosarda* is completely naked posterior to the corselet except for the lateral line, dorsal fin base, and caudal keel (Figure 2a).

The corselet, composed of enlarged scales, is well defined in the pectoral region of bonitos. It extends from the dorsal end of the gill slit to the tip of the pectoral fin, except in *Sarda* and *Allothunnus*. Anterior and ventral to the pectoral fin base, the scales are smaller than on other parts of the corselet in bonitos. In *Sarda*, an extra wing of the corselet extends dorsally toward the origin of the first dorsal fin. *Allothunnus* has the most extensive corselet, covering most of the area between the first dorsal fin base and the pectoral fin.

Morphometric Characters

Twenty-six measurements, in addition to fork length, were routinely made on all specimens destined to be dissected to insure that these data would be available if needed. Preserved material was also measured until an adequate sample was obtained. Measurements follow the methods of Marr and Schaefer (1949) as modified by Gibbs and Collette (1967). Morphometric characters can be used to separate genera, species, and populations within species. Tables showing the 26 characters as thousandths of fork length and 8 characters as thousandths of head length are presented in the systematic section of the paper. Most of the characters are best used at the species level; therefore, only a summary table of the means of proportions (Table 1) is presented in this section.

Orcynopsis is short-bodied and short-headed. It has shorter snout-anal and snout-second dorsal distances than do the other bonitos. *Cybiosarda* is also relatively short-bodied. *Allothunnus* is the most elongate of the bonitos and has the greatest distances between the snout and the origins of the anal and second dorsal fins. *Cybiosarda* and *Orcynopsis* both have high first dorsal, second dorsal, and anal fins compared to other bonitos. *Gymnosarda* has a differently shaped head than do other bonitos: the interorbital distance is much wider, the eyes are larger, the postorbital distance is shorter, and the distance between the origins of the pectoral and pelvic fins is much larger. In addition, *Allothunnus* has large eyes and a very short snout and maxilla.

Because of small sample size, restricted geographical distribution, or both, morphometric data were combined for each of four species: *Cybiosarda elegans*, *Sarda australis*, *Gymnosarda unicolor*, and *Allothunnus fallai*. Three populations of *Orcynopsis unicolor* are compared: Israel, Lebanon, and Tunisia. The southeast Pacific population of *Sarda chiliensis* (nominal *S. c. chiliensis*) is compared with the northeast Pacific population (*S. c. lineolata*). The population of *Sarda orientalis* in the eastern tropical Pacific (nominal *S. o. velox*) is compared with the only other sufficiently large sample, northwest Pacific. Three populations of *S. sarda* are compared: western Atlantic, Mediterranean Sea (including the Black Sea), and the Gulf of Guinea.

Meristic Characters

Countable structures are of special value systematically because they are relatively easy to record unambiguously and because they are easy to summarize in tabular fashion. Meristic characters that have proved valuable systematically in the Sardini include numbers of fin rays (first dorsal spines, second dorsal rays, dorsal finlets, anal rays, anal finlets, pectoral rays), gill rakers, teeth (especially on the upper and lower jaws), vertebrae, and laminae in the olfactory rosettes. Olfactory laminae are discussed as the last section under soft anatomy. The other meristic characters are discussed in the relevant osteological sections of the paper.

Soft Anatomy

The relative position, shape, and size of the various internal organs provide valuable diagnostic characters. Within the genus *Sarda*, these characters are useful at the species level. For purposes of discussion, the characters in the soft anatomy are divided into five sections: viscera, vas-

TABLE 1.—Morphometric comparison of species and populations of Sardini. Means as thousandths of fork length or head length.

Character	*Cybiosarda elegans*	*Orcynopsis unicolor* Israel	Lebanon	Tunisia	*Sarda australis*	*Sarda chiliensis* NE Pacific	SE Pacific	*Sarda orientalis* NW Pacific	E Pacific	*Sarda sarda* NW Atlantic	Mediterranean	Gulf of Guinea	*Gymnosarda unicolor*	*Allothunnus fallai*
Fork length														
Snout — A	652	577	587	578	674	665	654	694	678	668	660	657	629	676
Snout — 2D	531	499	511	481	586	566	569	606	582	582	579	578	557	628
Snout — 1D	273	247	253	246	263	269	279	286	288	270	266	298	285	306
Snout — P_2	299	273	284	270	296	295	303	303	310	296	288	275	285	284
Snout — P_1	267	238	247	229	267	266	275	281	290	269	263	265	264	269
P_1 — P_2	125	113	122	—	116	123	118	113	114	111	104	111	139	110
Head length	266	235	243	231	267	263	272	278	284	264	259	271	261	258
Max. body depth	227	246	255	240	231	210	210	234	213	214	205	217	224	223
Max. body width	133	124	123	130	141	131	134	146	144	135	131	—	151	164
P_1 length	138	138	135	142	121	116	—	115	127	115	116	130	160	129
P_2 length	82	63	61	64	85	78	84	76	86	79	82	83	103	78
P_2 insertion-vent	327	294	288	300	390	353	341	392	367	366	370	357	332	371
P_2 tip-vent	262	230	228	233	290	276	269	311	280	282	285	266	229	293
Base 1D	254	246	248	241	326	297	286	306	292	311	311	311	262	319
Height 2D	108	128	117	126	86	83	97	78	94	80	95	91	102	93
Base 2D	121	117	133	120	103	93	94	93	95	96	104	107	77	72
Height anal	107	126	118	125	81	74	92	73	89	77	79	85	99	90
Base anal	91	114	111	106	78	71	74	73	79	73	78	80	62	72
Caudal spread	251	261	270	213	259	246	258	214	236	222	247	253	304	226
Snout (fleshy)	98	89	94	91	96	94	95	96	101	94	93	96	107	75
Snout (bony)	82	76	80	83	81	78	81	86	86	82	78	82	98	65
Maxilla length	130	113	123	112	139	126	130	145	150	136	131	138	138	93
Post orbital	136	112	117	—	130	139	142	139	146	136	132	138	101	139
Orbit (fleshy)	29	28	31	31	39	31	31	42	37	35	31	34	51	45
Orbit (bony)	58	51	57	52	66	57	56	56	64	57	57	60	73	63
Interorbital width	73	68	66	72	66	63	70	71	71	64	62	63	92	—
Head length														
Snout (fleshy)	367	381	387	396	361	357	348	344	357	358	358	353	410	292
Snout (bony)	308	326	328	358	305	297	299	308	303	309	303	301	374	252
Maxilla length	489	483	505	483	518	481	477	522	528	514	505	509	527	361
Post orbital	511	478	484	—	492	526	523	503	512	516	511	506	381	545
Orbit (fleshy)	109	121	129	107	137	119	115	136	130	133	118	122	196	175
Orbit (bony)	218	218	236	211	246	218	205	220	226	217	220	220	279	244
Interorbital width	273	289	272	297	249	239	257	256	251	242	238	231	353	224

cular system, pharyngeal muscles, urogenital system, and olfactory organ.

VISCERA

Emphasis was placed on the appearance of the viscera in ventral view, after removal of an oval segment of the belly wall (Figure 3). Important papers on the viscera of bonitos include Kishinouye (1923 - *Sarda* and *Gymnosarda*), Godsil (1954, 1955 - *Sarda*), Postel (1954 - *Orcynopsis*), Blanc and Postel (1958 - *Gymnosarda*), Silas (1963 - *Gymnosarda*), and Nakamura and Mori (1966 - *Allothunnus*).

General Description. —The anterior end of the liver abuts against the transverse septum anteriorly in the body cavity. There are usually three lobes to the liver: the middle lobe is conspicuous in ventral view in all bonitos, whereas one or both lateral lobes are visible only in *Gymnosarda* and *Sarda*. No striations are present on the surface of the liver as they are in four species of *Thunnus* (see Gibbs and Collette 1967). Two efferent (venous) vessels lead directly from the anterior surface of the liver into the sinus venosus in all species. The short esophagus leads into the stomach. The intestine arises from the anterior end of the stomach which extends posteriorly as a blind sac. The caecal mass covers 22-81% of the anterior part of the body cavity and opens into the intestine immediately posterior to the junction of intestine and stomach. The intestine forms a loop anteriorly. The remainder of the digestive tract is straight in *Sarda*, but two additional loops are present in the mid-intestine of *Cybiosarda*, *Gymnosarda*, and *Orcynopsis*.

The spleen is prominent in ventral view in *Gymnosarda* and *Sarda*, but is hidden by the liver and caecal mass in *Allothunnus*, *Cybiosarda*, and

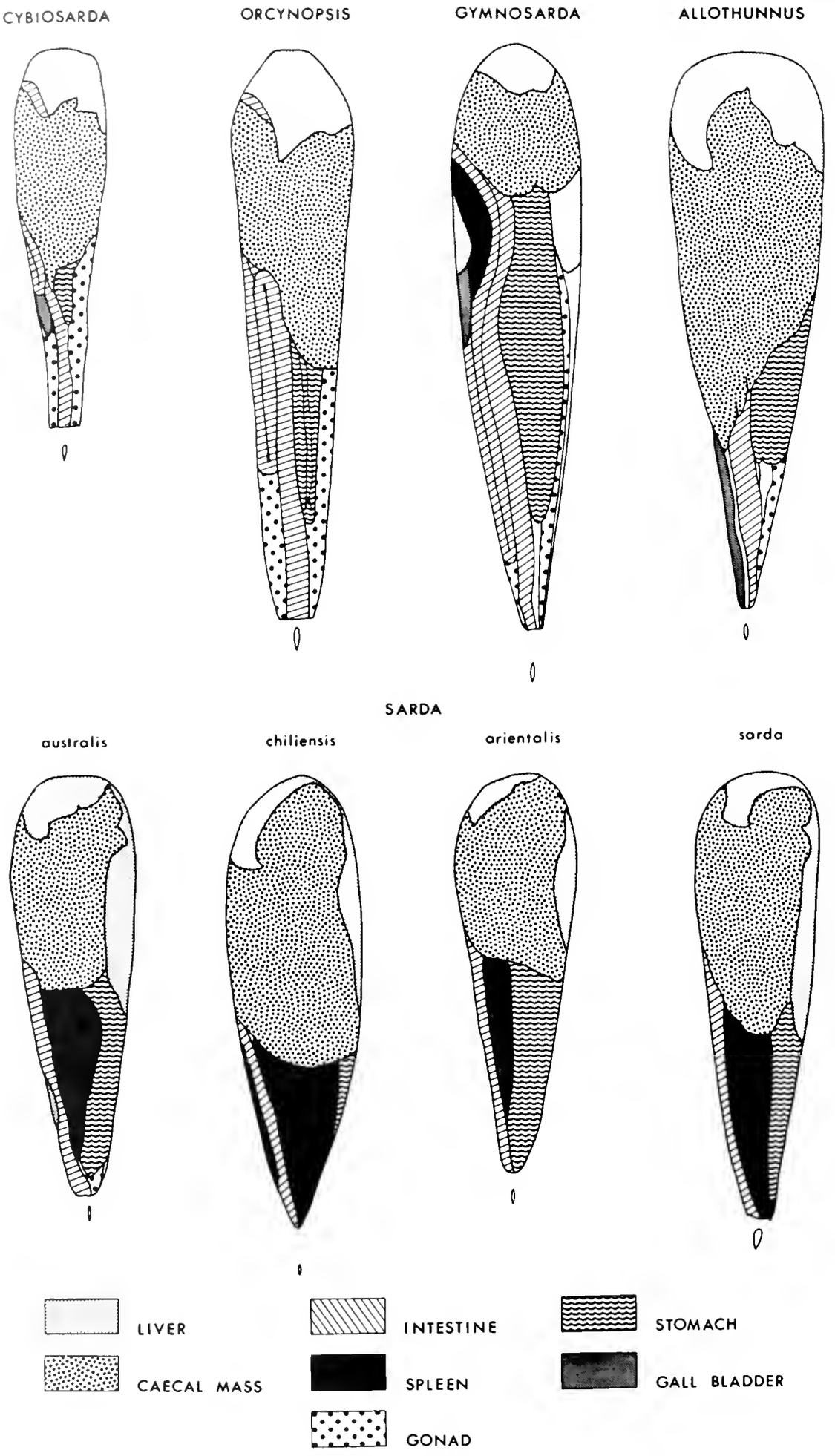


FIGURE 3.—Viscera, in ventral view, of the eight species of Sardini.

Orcynopsis. The gall bladder, an elongate tubular sac which is usually green in color, arises from the right lobe of the liver and usually lies along the intestine on the right hand side. The stomach extends further posteriorly and is more prominent in ventral view when it is full. The mature ovary is sometimes large enough to cover the stomach ventrally. A swim bladder is absent in all bonitos except *Gymnosarda*.

Specific Characters.—The bonitos are divided into three groups based on the shape of the liver (Figure 4). *Sarda* and *Gymnosarda* have three distinct liver lobes; both lateral lobes are elongate and much longer than the middle lobe; the right lateral lobe is always longer than the left lateral lobe. All three lobes in *Gymnosarda* are visible ventrally if the dissection extends far enough laterally. In addition, the connection of middle and left lobes is visible anteroventrally in *Sarda*. *Orcynopsis* and *Cybiosarda* have an elongate right lateral lobe and a very short left lateral lobe which tends to fuse with the middle lobe. *Allothunnus* differs from the other genera in having three subequal lobes, as in the bluefin tuna group of species of *Thunnus*.

The bonitos can be divided into three groups based on the relative length of the caecal mass. *Allothunnus* has the longest caecal mass (71-81% of body cavity length, $\bar{x}$ 76.4%) of any of the bonitos followed by *Cybiosarda* (65-72%, $\bar{x}$ 69.2%) and *Orcynopsis* (46-59%, $\bar{x}$ 56.3%). *Gymnosarda* has the shortest caecal mass (22-30%, $\bar{x}$ 25.2%). The species of *Sarda* are intermediate between these two groups, most having the caecal mass about half the length of the body cavity (*S. australis* 44-55%, $\bar{x}$ 49.7; *S. sarda* 38-58%, $\bar{x}$ 48.3; and *S. orientalis* 41-50%, $\bar{x}$ 46.7). There is significant geographic variation in the fourth species, *S. chiliensis*. Three northeast Pacific specimens have a distinctly longer caecal mass (61-65%, $\bar{x}$ 62.3) than six southeast Pacific specimens (40-53%, $\bar{x}$ 48.5). This

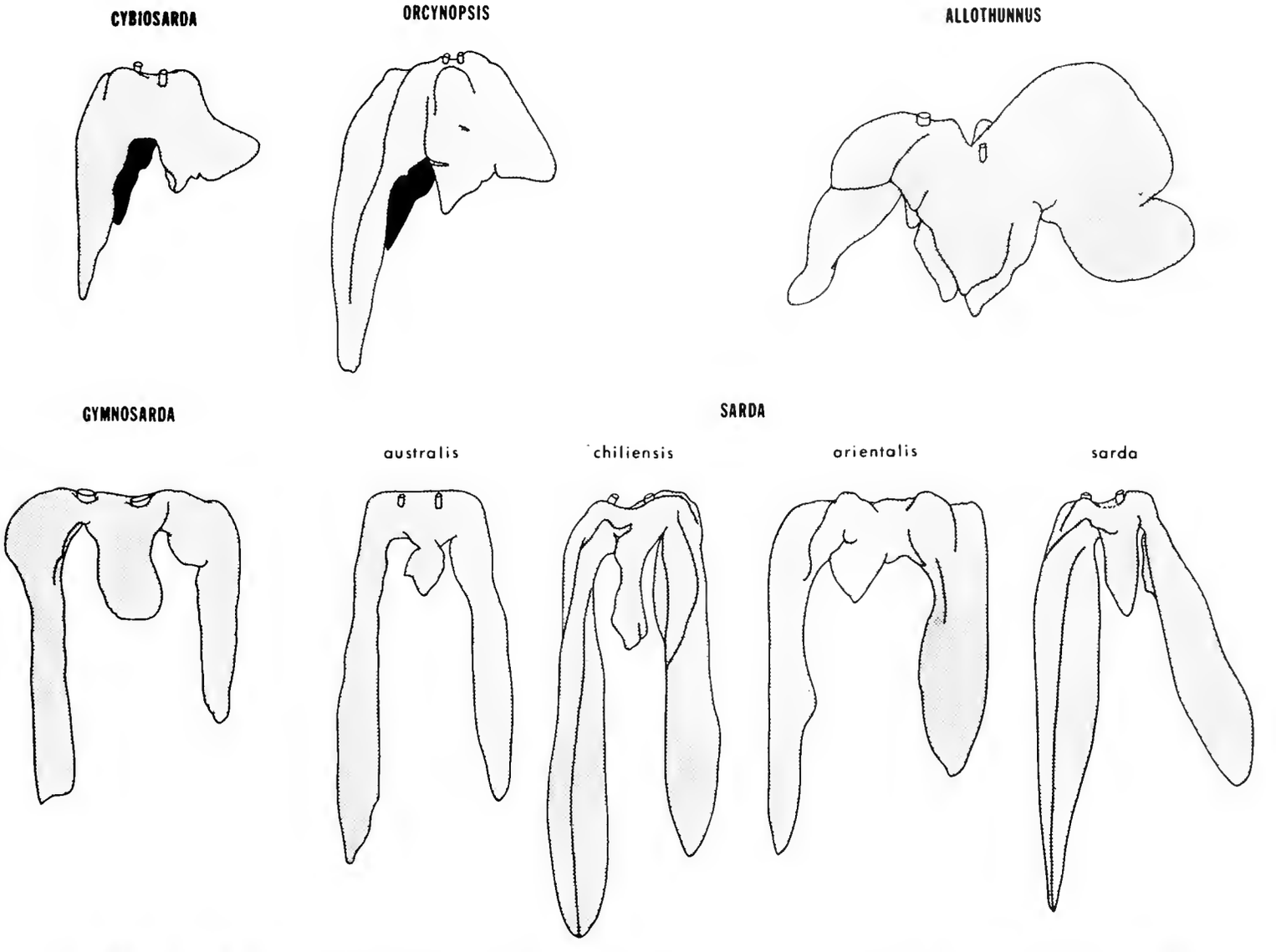


FIGURE 4.—Ventral view of excised livers of eight species of Sardini. Spleen shown in black for *Cybiosarda* and *Orcynopsis*.

tendency supports the findings of Godsil (1955). However, a seventh southeast Pacific specimen had a considerably longer caecal mass (70%) than our other six specimens.

The position and size of the spleen are distinctive among the genera. Species of *Sarda* have a large spleen, the major portion of which is located in the posterior half of the body cavity between the intestine and the stomach in ventral view. The spleen of *Gymnosarda* is also visible ventrally, but it is smaller than in *Sarda* and located in the anterior half of the body cavity. In *Orcynopsis* and *Cybiosarda*, the spleen is hidden by the right lobe of the liver and caecal mass. The spleen was visible in ventral view in one specimen of the four *Allothunnus* examined.

The number of loops in the intestine separates *Sarda* and *Allothunnus* from the other three genera of bonitos. In *Sarda* and *Allothunnus*, the intestine leaves the stomach and then moves posteriorly along the right side of the body cavity straight to the anus (Figure 5a). In the other genera, the intestine makes a loop at about the level of the posterior end of the stomach, runs anteriorly almost to where it came off the stomach, forms another loop, and then goes straight posteriorly to the anus (Figure 5b).

The caecal mass is connected to the anterior part of the intestine by 6-9 ducts as shown diagrammatically in Figure 5. Each of the main ducts branches into numerous smaller ducts within a short distance from the intestine. We did not count the number of ducts often enough to determine the systematic value of this character and so merely present the results for six specimens: *Cybiosarda*—3 anterior and 5 posterior ducts in one specimen, 3 anterior and 6 posterior in another; *Sarda australis*—3 anterior and 4 posterior; *S. chiliensis*—2 anterior and 4 posterior; *S. orientalis*—3 anterior and 4 posterior; and *Gymnosarda*—a total of 6 ducts.

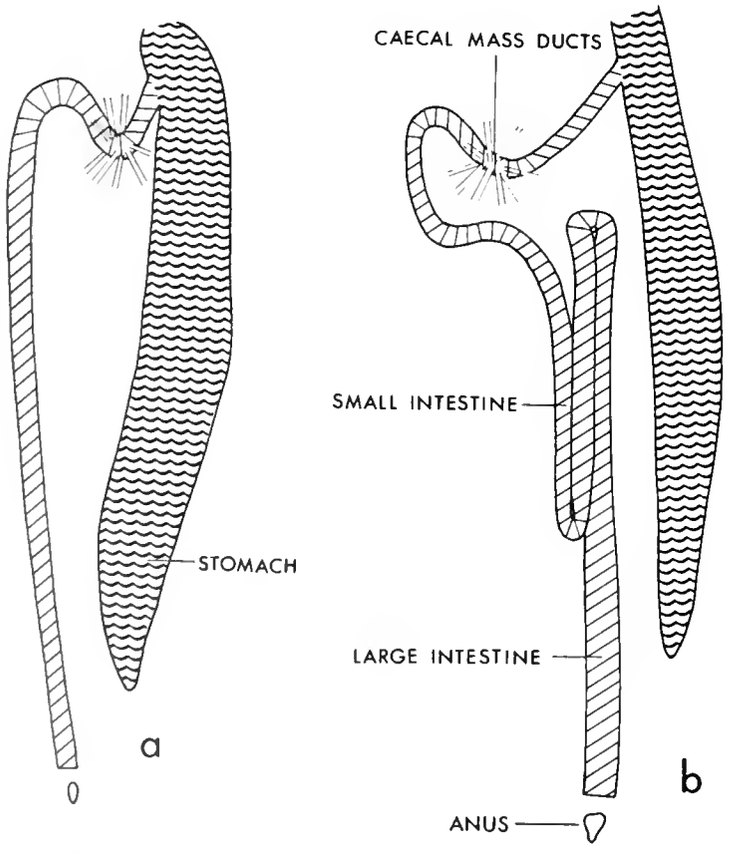


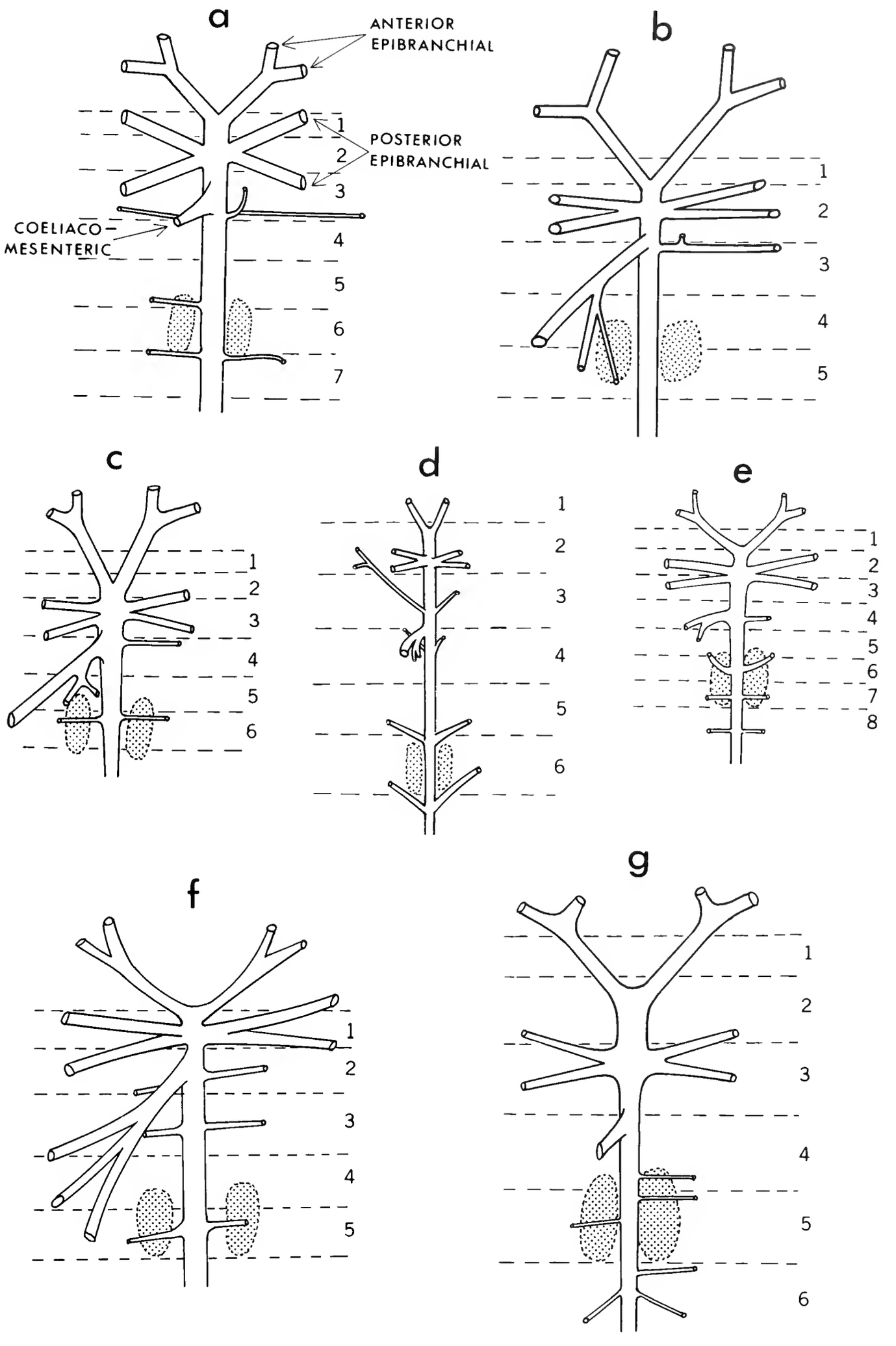
FIGURE 5.—Course of intestine from stomach, through area where the ducts of the caecal mass empty into the intestine, to the anus in two species of Sardini, ventral view (diagrammatic). a. *Sarda orientalis*, Tokyo, 341 mm FL. b. *Cybiosarda elegans*, New South Wales, 365 mm FL.

VASCULAR SYSTEM

The only published work on the vascular system of the bonitos is on the Pacific species *Sarda orientalis* by Kishinouye (1923) and Godsil (1954, 1955) and on *S. chiliensis* by Godsil (1954, 1955). No specialized subcutaneous vascular system and no cutaneous arteries or veins are present as they are in the higher tunas, *Auxis* to *Thunnus*. Therefore, this description will be confined to the anterior portion of the dorsal aorta and the postcardinal vein.

General Description.—The efferent branchial (epibranchial) arteries and coeliaco-mesenteric artery form a unit at the anterior end of the dorsal aorta (Figure 6). Two anterior epibranchials on each side unite to form a common trunk, and these trunks join as the "Y" of the aorta beneath the first or second vertebra. The posterior two epibranchials of each side unite immediately before they join the aorta, usually ventral to the second or third vertebra. As the aorta proceeds posteriorly it gives rise to the large coeliaco-mesenteric artery on the right side ventral to the second to fourth vertebra. The coeliaco-mesenteric

FIGURE 6.—Anterior part of arterial system in seven species of Sardini. Numbers indicate vertebral centra; stippled areas show where pharyngeal muscles originate. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 543 mm FL. c. *Sarda australis*, New South Wales, 408 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Sarda sarda*, eastern United States, 388 mm FL. f. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. g. *Allothunnus fallai*, Tasmania, 764 mm FL.


a
ANTERIOR EPIBRANCHIAL
POSTERIOR EPIBRANCHIAL
COELIACO-MESENTERIC
1
2
3
4
5
6
7
b
1
2
3
4
5
c
1
2
3
4
5
6
d
1
2
3
4
5
6
e
1
2
3
4
5
6
7
8
f
1
2
3
4
5
g
1
2
3
4
5
6

has two or three main branches which lead to the liver and other viscera. Godsil (1954, 1955) illustrated and described the branches of the coeliaco-mesenteric in great detail.

The postcardinal vein runs along the ventral surface of the kidney (Figure 7) from the vicinity of the first complete haemal arch anteriorly in the median line to the pectoral region. There it curves to the right and discharges into the right Cuvierian duct. Posteriorly, the postcardinal receives a pair of small veins at the level of each vertebra. The postcardinal is composed of two main branches that join anterior to the Y of the ureter. The main branch leaves the haemal arch dorsally and the small branch runs under the surface of the kidney from the urogenital area.

Specific Characters.—Variation was found in the location of the components of the anterior part of the arterial system (Table 2). *Orcynopsis* and *Gymnosarda* tend to have both the epibranchials and coeliaco-mesenteric more anterior than in the other bonitos (ventral to first vertebra vs. second, second vs. third, respectively).

To locate which haemal arch the dorsal branch of the postcardinal enters, a pin was forced into the vertebral column at the point where the postcardinal came up to the surface of the kidney. The number of the vertebra bearing this haemal arch was then determined at the end of the dissection. The number of the vertebra varied as follows:

Cybiosarda 15, 16, 17, 17
Orcynopsis 16
Sarda australis 17, 18
S. chiliensis 16, 17, 17, 19, 21
S. orientalis 15, 16, 18, 19
S. sarda 18, 19, 20
Gymnosarda 16, 16, 17
Allothunnus 21

PHARYNGEAL MUSCLES

The paired pharyngeal (retractor dorsalis) muscles are included on the figures of the anterior part of the arterial system (Figure 6). The muscles originate on the ventral surface of one to three vertebrae between the fourth and the seventh and insert on the upper pharyngeal bones.

The pharyngeal muscles insert on the fourth and fifth vertebra in *Gymnosarda* and are mostly on the fifth or sixth vertebra in the other bonitos. The data are as follows: *Cybiosarda* 6 (3 specimens), 5 (1 specimen), 7 (1 specimen); *Orcynopsis* 5 extending onto 4 (4 specimens); *Sarda australis* 6 (3 specimens, extending onto 7 in 1 specimen); *S. chiliensis* NE Pacific 6 and 7 (2 specimens); *S. chiliensis* SE Pacific 5 (5 specimens, extending onto 6 in 3); *S. orientalis* Indo-West Pacific 6 (2 specimens), 5 extending onto 4 (1 specimen), 6 extending onto 7 and 5 (1 specimen); *S. orientalis* eastern Pacific 6 (4 specimens, extending onto 7 in all 4, onto 5 in 1); *S. sarda* 6 (3 specimens, extending onto 7 in 2 specimens, onto 5 in 1); *Gymnosarda* 4 extending onto 5 (3 specimens); and *Allothunnus* 5 extending onto 4 (1 specimen).

TABLE 2.—Location of "Y" of aorta, posterior epibranchials, and the coeliaco-mesenteric artery, in the eight species of Sardini.

Structure under vertebra no.	*Cybiosarda elegans*	*Orcynopsis unicolor*	*Sarda australis*	*Sarda chiliensis* SE Pac.	*Sarda chiliensis* NE Pac.	*Sarda orientalis* Indo-W Pac.	*Sarda orientalis* E Pac.	*Sarda sarda*	*Gymnosarda unicolor*	*Allothunnus fallai*
Y of aorta										
skull									1	
skull-1	3	1		2					2	
1	2	5	1	1	1	2	1	2	1	1
1-2		2	—	2	2	—	2	1	—	1
2			2			3	1	2	1	2
2-3										
Posterior epibranchials										
1		2		1					2	
1-2		3		1					2	
2	3	2		2	2	3	2	2	1	
2-3	1		1	1		1	1	1		2
3	1		2			1	1	1		1
Coeliaco-mesenteric										
1-2		1								
2		1							3	
2-3		3		1					1	
3	2	3		2	3	2	1		1	1
3-4	2		1	—		1	1	1		1
4	1		2	2		2	2	3		1

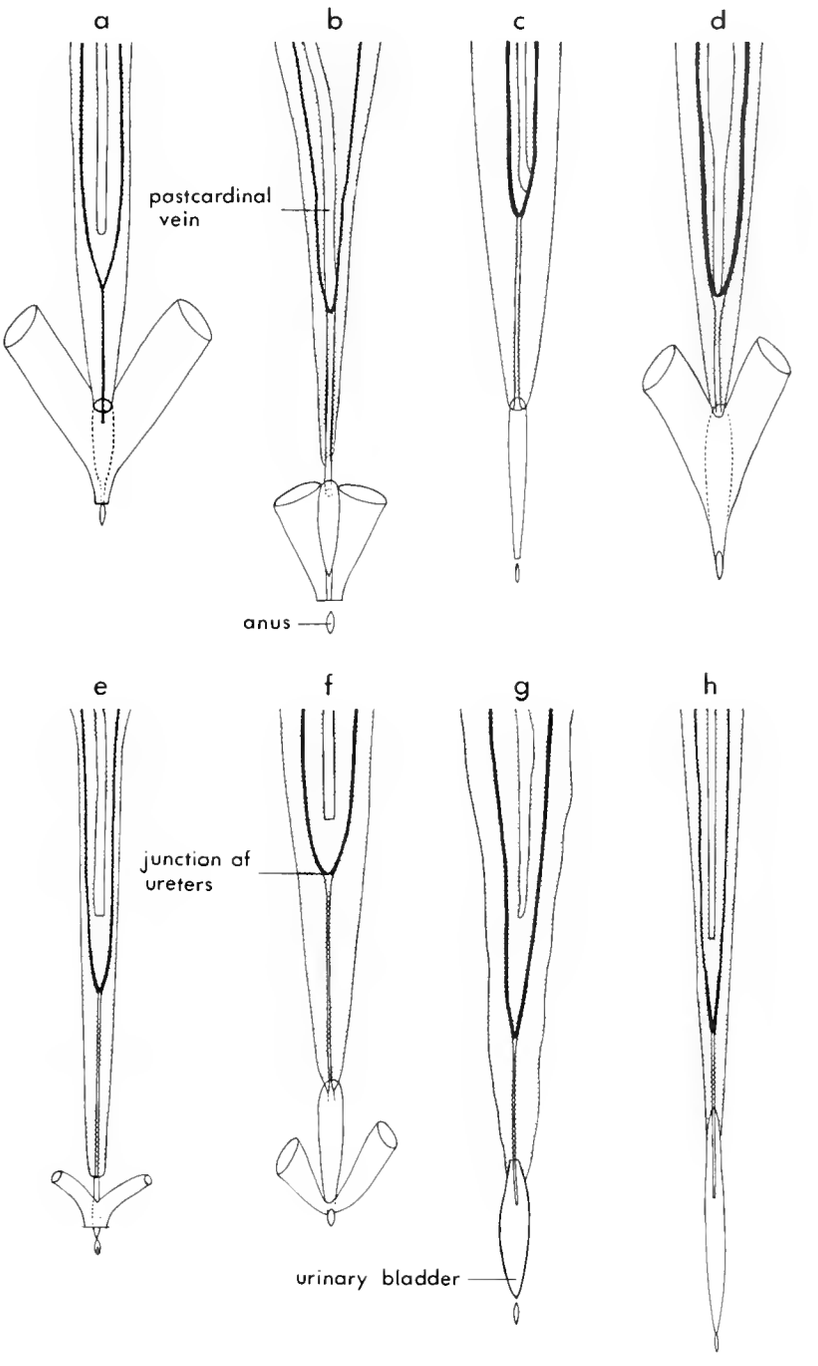


FIGURE 7.—Ventral view of posterior part of kidney showing postcardinal vein, junction of ureters, and urinary bladder in eight species of Sardini. Posterior ends of gonads shown in some figures. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Cybiosarda elegans*, New South Wales, 360 mm FL. c. *Orcynopsis unicolor*, Tunisia, 567 mm FL. d. *Orcynopsis unicolor*, Tunisia, 593 mm FL. e. *Sarda australis*, New South Wales, 355 mm FL. f. *Sarda chiliensis*, La Jolla, Calif., 472 mm FL. g. *Sarda orientalis*, Tokyo, 500 mm FL. h. *Sarda sarda*, Tunisia, 504 mm FL. i. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. j. *Allothunnus fallai*, Tasmania, 764 mm FL.

UROGENITAL SYSTEM

The only references to the anatomy of the urogenital system are those of Kishinouye (1923) on *Sarda orientalis* and Godsil (1954, 1955) on *S. orientalis* and *S. chiliensis*.

General Description.—The paired gonads lie along the dorsolateral body wall and are visible in ventral view in mature adults. The kidney lies dorsal to the layer of fibrous connective tissue which forms the dorsal layer of the peritoneum. Anteriorly, the kidney divides into a pair of narrow projections which extend along the sides of the parasphenoid and usually reach the posterior end of the "mid-ridge" of the prootic. The anterior ends of the kidney surround the origins of the pharyngeal muscles on the vertebral column and usually separate along the middle of the vertebral column. The kidney may be absent in the area between the vertebrae and where the epibranchial arteries join to form the aorta. In some cases in each species, the kidney is well developed dorsal to this area and even covers the posterior end of the parasphenoid. In the vicinity of the esophagus, the kidney expands laterally and forms two projections which may reach anteriorly to the upper end of the gill slits. Posteriorly, near the posterior fifth of the body cavity, the kidney narrows to an elongate triangle (Figure 7). The branches of the ureter join to form a common trunk which leads to the urinary bladder between the gonads. The distance between the junction of the ureters and the urinary bladder and the size of ureters varies intraspecifically. The urinary bladders appear similar in all the bonitos, but no detailed study was made of them.

OLFACTORY ORGAN

General Description.—Kishinouye (1923) provided a generalized account of the olfactory organ of several scombrids. More detailed studies have been made on *Scomber scombrus* (Burne 1909), *Sarda sarda* (Tretiakov 1939), *Allothunnus fallai* (Nakamura and Mori 1966), *Katsuwonus pelamis* (Gooding 1963), and *Thunnus* (Iwai and Nakamura 1964b; Gibbs and Collette 1967). As in other scombrids, the olfactory cavity in bonitos has a small anterior naris and a slitlike posterior naris. No information on the supplementary sacs, or accessary olfactory cavity (Iwai and Nakamura 1964b), was obtained from the present study comparable to that of Tretiakov (1939), who described three supplementary sacs (middle, maxillary, and rostral sacs) in *S. sarda*. The central axis of the olfactory rosette is located beneath the anterior naris. Leaflike laminae radiate from the central axis and occupy the anterior dorsal third of the olfactory cavity. Gooding (1963) studied the morphology and histology of the olfactory organ of *Katsuwonus pelamis* and found olfactory cells on the olfactory epithelium of the laminae. Iwai and Nakamura (1964b) were the first to use the number of laminae to distinguish species of scombrids, but Gibbs and Collette (1967:91) felt additional material was necessary to validate the character in *Thunnus*.

We counted the number of olfactory laminae (by averaging both sides and rounding upward) in bonitos and found a rather wide range of variation (Table 3). Gooding (1963) also found a wide variation in *Katsuwonus*: 38-47 laminae per rosette in 38 skipjack olfactory rosettes. The number of laminae increases from small specimens to adults but does not appear to change after a certain size is reached. For example, 15 specimens of *Orcynopsis unicolor* (242-645 mm FL) had 25-28 laminae, a 178-mm specimen had 22, and a 164-mm specimen had 23. Twelve *Gymnosarda unicolor* (400-940 mm FL) had 48-56 laminae; a 306-mm specimen, 45; a 215-mm specimen, 43; and a 71.6-mm specimen, 27. Looking only at adults and subadults (Table 3), *Gymnosarda* has the highest number of olfactory laminae (48-56) and is completely separated from the other bonitos (21-39) in this character. *Orcynopsis*, *Cybiosarda*, and *Sarda australis* form a series with increasing numbers of laminae.

The pigmentation of the olfactory rosette varied in preserved specimens. In *S. australis* and *Orcynopsis* the dorsal margins of the olfactory laminae were pigmented and gave a radial pigmentation to the olfactory rosette. Black spots were found on the laminae of a specimen of *Cybiosarda* (Figure 8a). The fleshy ring of *S. sarda* showed grayish pigmentation in large specimens. No specific pigmentation was noted in other species of bonitos. The morphology of each olfactory lamina (Figure 8) is similar in each olfactory rosette, but decreased in size anteriorly. The olfactory cavity and accessary cavity are similar in all bonitos, except in *Cybiosarda* where the opening of the accessary sac was more dorsally located and led interiorly rather than interior-ventrally as in other bonitos.

TABLE 3.—Number of laminae in olfactory rosettes in species of Sardini. (Means based on original data not combined frequency distribution.)

Species	20-1	22-3	24-5	26-7	28-9	30-1	32-3	34-5	36-7	38-9	40-1	42-3	44-5	46-7	48-9	50-1	52-3	54-5	56-7	*N*	$\bar{x}$
Orcynopsis unicolor			2	8	5															15	26.9
Cybiosarda elegans					1	5	3													9	30.8
Sarda australis								1	1	4										6	37.2
S. chiliensis:																					
NE Pacific	1	2	8	7	1	1														20	25.4
SE Pacific		3	4	6	2															15	25.5
S. orientalis:																					
Red Sea - Indian Ocean			2	—	—	2	2	4												10	31.4
NW Pacific			2	—	1	1	1													5	28.0
Cent. Pacific			1	—	—	1	—	—	1											3	30.7
E Pacific						1	4	3	4											12	34.3
S. sarda:																					
North America		1	3	2	3	2	4													15	27.5
South America					2															2	28.5
Mediterranean - Black Sea		2	5	—	—	2														9	25.1
Gulf of Guinea - South Africa		1	3	1	2															7	25.4
Gymnosarda unicolor															4	1	3	3	1	12	51.6
Allothunnus fallai					2	1														3	29.0

Specific Characters.—A fleshy ring (Iwai and Nakamura 1964b) was found along the posterior margin of the olfactory rosettes in some bonitos. This fleshy ring is the continuation of the well-developed distal end of the olfactory laminae and forms a fleshy elevated area in species of *Sarda*. In *S. sarda* the fleshy ring usually develops in larger specimens (over 360 mm FL) as a folded fleshy pad (Figure 8h). Different developmental stages of the fleshy pad were found in all species of *Sarda* except in *S. c. chiliensis* which had no apparent rings. No fleshy ring or pad was found in *Cybiosarda* or *Orcynopsis* (Figure 8a, b). In *Gymnosarda*, a very definite fleshy ring surrounds all the olfactory laminae (Figure 8i) except in a juvenile specimen (71 mm FL), which had an elongated oval rosette with only 27 laminae. Nakamura and Mori (1966) found the olfactory rosette of *Allothunnus* to have labial fleshy rings around the olfactory laminae, similar to our observations (Figure 8j).

Osteology

Osteological characters proved to be very useful in determining how many genera of Sardini should be recognized. The osteological description is divided into five sections: skull, axial skeleton, dorsal and anal fins, pectoral girdle, and pelvic girdle. Osteological terminology generally follows de Sylva (1955) and Gibbs and Collette (1967) with a few changes to bring this nomenclature into closer agreement with more modern terminology.

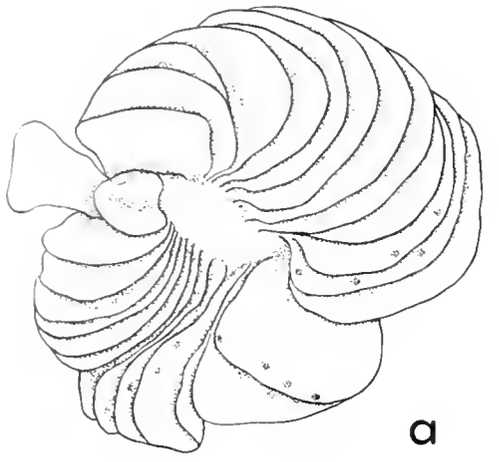
SKULL

Description of the skull is presented in two sections: neurocranium and branchiocranium. Figure 9 shows an articulated skull of *Gymnosarda unicolor* in lateral view to provide orientation for the descriptions of the individual bones.

Neurocranium

Following a general description of the neurocranium, the four major regions are discussed: ethmoid, orbital, otic, and basicranial. Descriptions of the otoliths are included at the end of this section.

General Characteristics.—In dorsal view, the neurocranium of bonitos is roughly triangular in shape. The interorbital and otic regions are not as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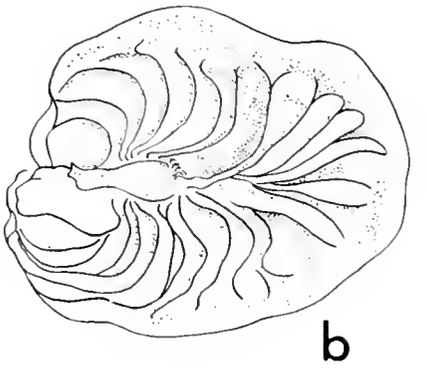
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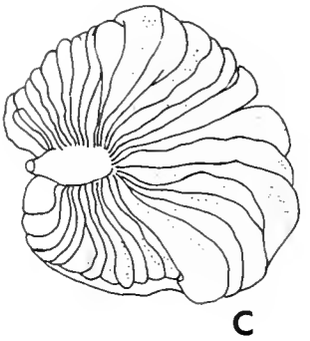
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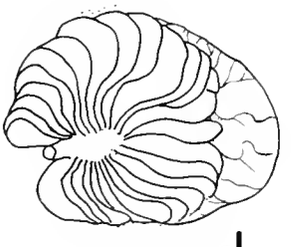
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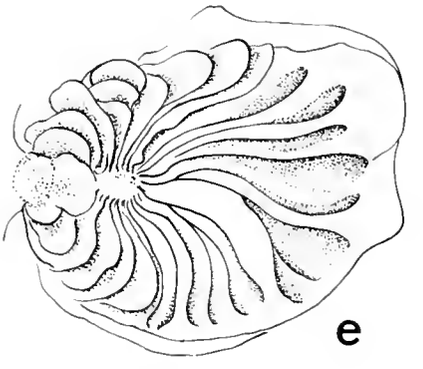
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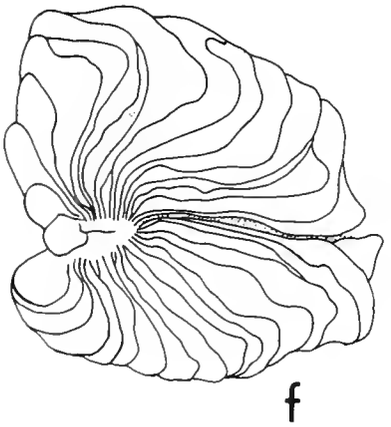
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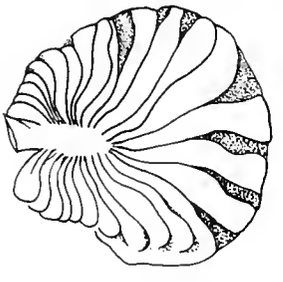
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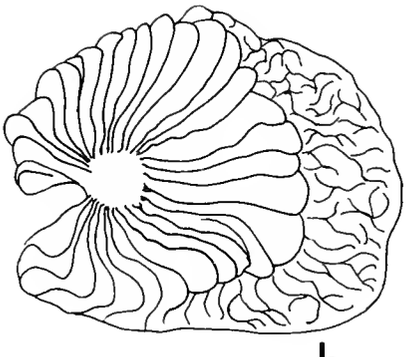
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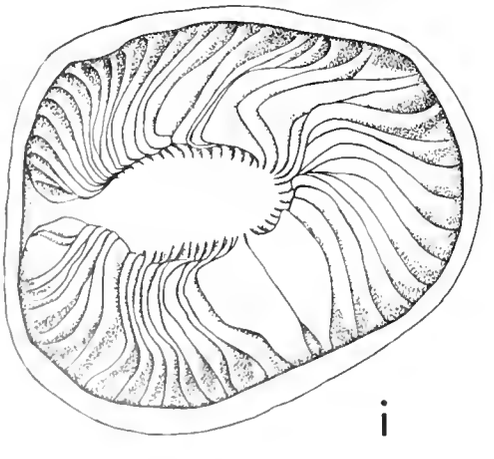
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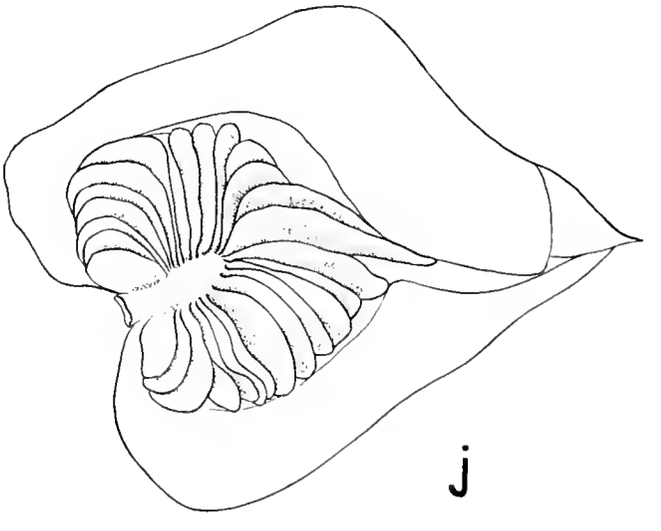
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FIGURE 8.–Olfactory rosettes (left) of eight species of Sardini. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, USNM 59881, 332 mm FL. d. *Sarda chiliensis*, Santa Barbara, Calif., USNM 31104, 335 mm FL. e. *Sarda chiliensis*, Callao, Peru, 571 mm FL. f. *Sarda orientalis*, Pearl Island, Panama, USNM 128644, 505 mm FL. g. *Sarda sarda*, Portuguese Guinea, 361 mm FL. h. *Sarda sarda*, Chesapeake Bay, 436 mm FL. i. *Gymnosarda unicolor*, Bikini, USNM 140980. j. *Allothunnus fallai*, New Zealand, DM 2472, 740 mm FL.

broad as in the most advanced scombrid genera–*Thunnus*, *Euthynnus*, *Katsuwonus*, and *Auxis* (Kishinouye 1923; de Sylva 1955; Gibbs and Collette 1967), but are broader than in the more primitive genera–*Scomber*, *Rastrelliger*, *Grammatorcynus*, *Scomberomorus*, and *Acanthocybium* (Allis 1903; Kishinouye 1923; Conrad 1938; Mago Leccia 1958; Gnanamuttu 1971), except in *Gymnosarda* which has a broad and short skull (Figure 10; Kishinouye 1923, fig. 38). *Allothunnus* has a more elongate and narrow skull (Figure 11) than do other bonitos. Bonitos lack the prominent frontoparietal foramen (Gibbs and Collette 1967) which is present on each side of the dorsal surface of the skull at (or near) the junction of the frontal, parietal, and supraoccipital bones of the three most advanced genera of Scombridae: *Euthynnus*, *Katsuwonus*, and *Thunnus*. The corresponding junction in bonitos does have a small hole and/or an area of very thin dermal bone (see Figure 12 of *Sarda sarda*). Two prominent dorsolateral crests are present on each side of the neurocranium (Figures 10-14). The inner crest arises at the anterolateral edge of the frontal bone, extends along the frontal and parietal bones, and terminates at the posterolateral corner of the epiotic bone. This crest is a thin bony process in all bonitos except *Allothunnus*, in which it arises from the posterior half of the frontal bones and has a much thicker and wider anterior half than do the other scombrid genera mentioned above. The primitive scombrid *Grammatorcynus* resembles *Allothunnus* in this character. The outer crest (Figure 11), which constitutes the posterolateral margins of the neurocranial roof, is formed by the edges of the frontal and pterotic bones. It originates at the posterolateral region of the frontal bones and extends posteriorly as a flat pterotic spine. The

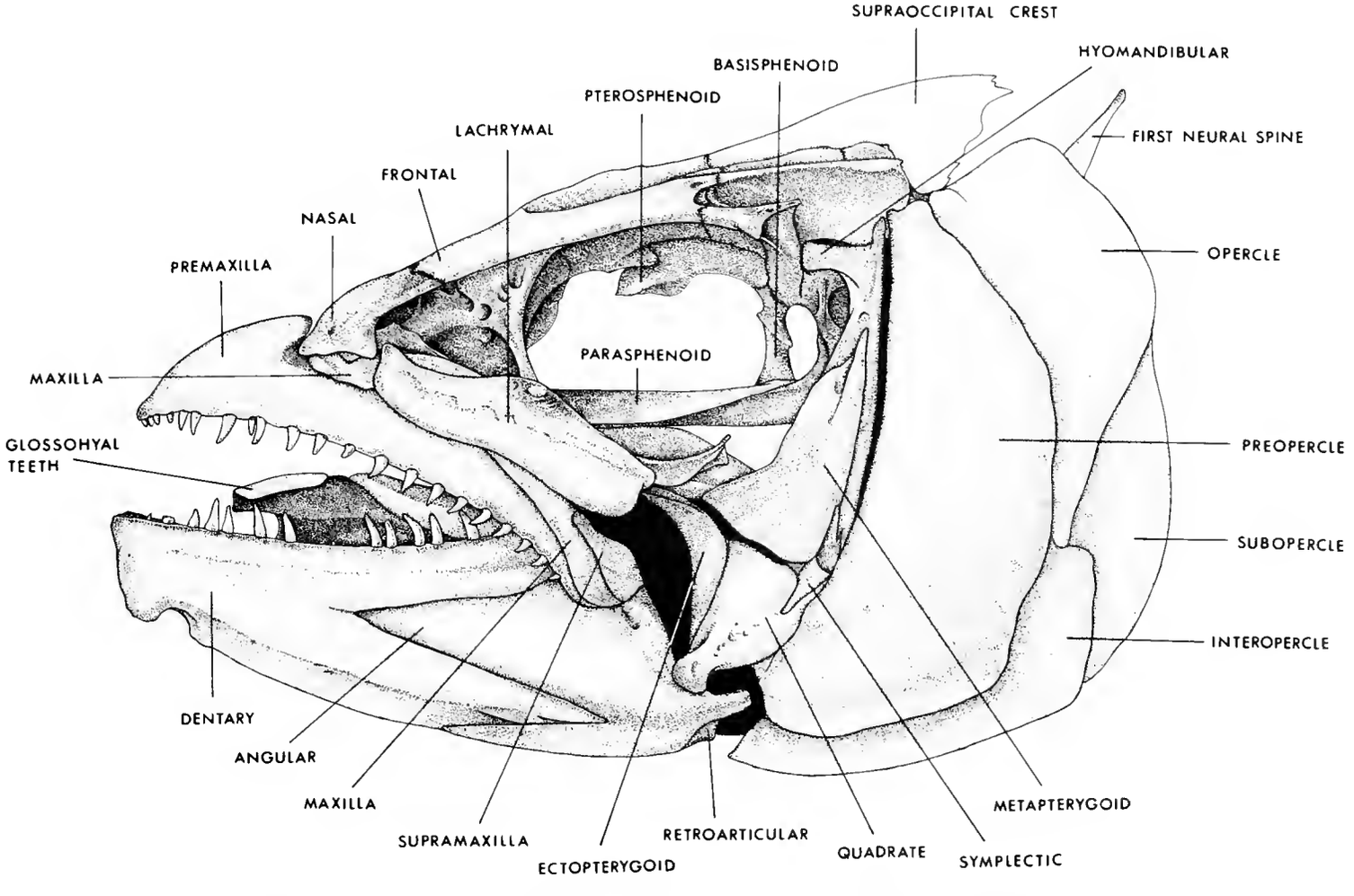


FIGURE 9.–Lateral view of head of *Gymnosarda unicolor*, Bikini, Marshall Islands, USNM 11478, 750 mm FL.

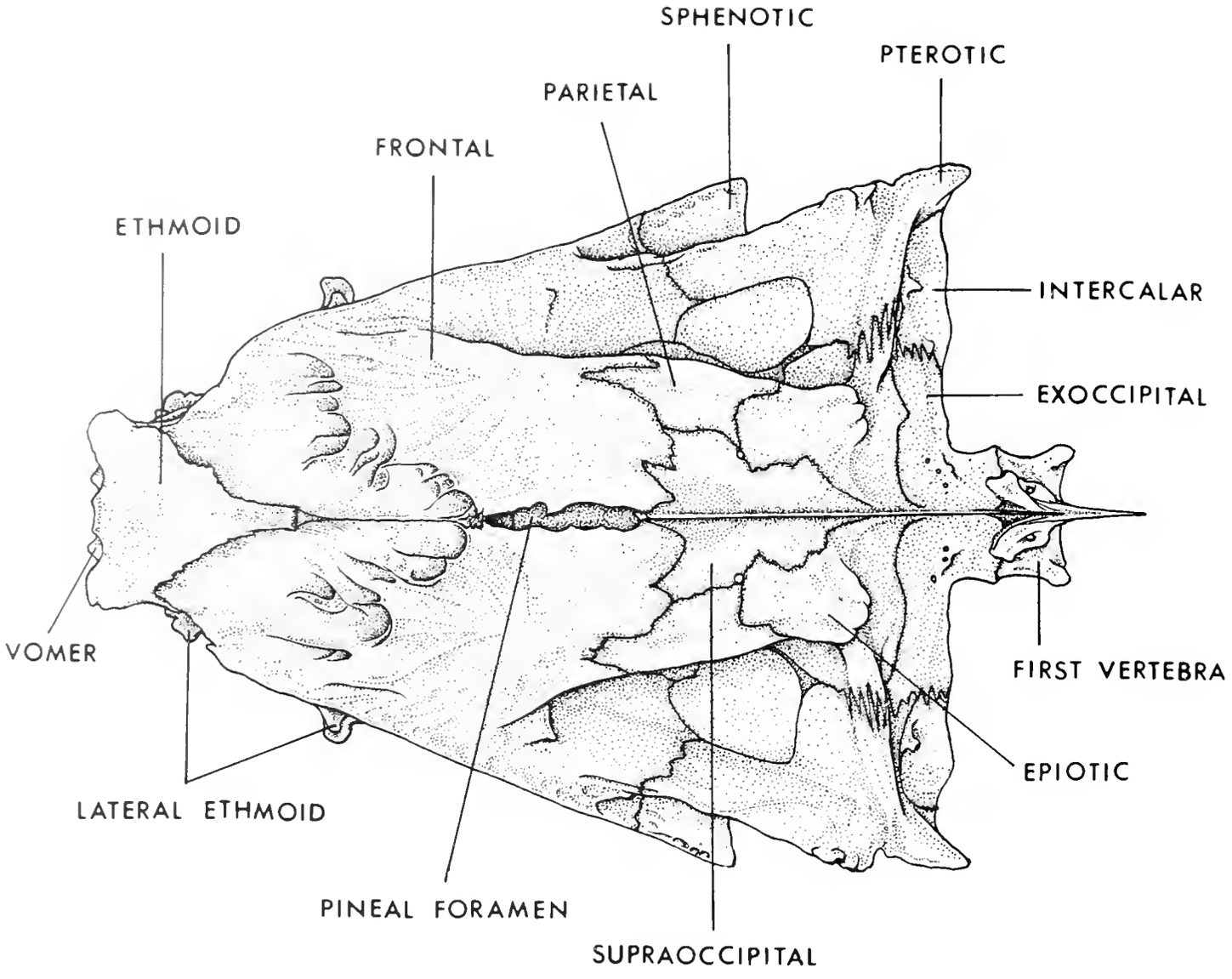


FIGURE 10.—Dorsal view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

supraoccipital crest is high and usually does not extend posteriorly past the tip of the first neural spine.

A prominent pineal foramen (Figures 10-14) is present anterior to the supraoccipital crest between the median edges of the frontal bones. Among the bonitos, it is most prominent in *Allothunnus*. Other scombrids either have a reduction in the thickness of the bone in this area (*Scomber*, *Rastrelliger*, and *Scomberomorus*) or a similar pineal foramen (*Grammatorcynus*, *Acanthocybium*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*). In life, the pineal foramen is filled with a translucent cartilaginous lens and is covered by a layer of skin usually having an unpigmented window dorsal to the cartilage. Rivas (1953) hypothesized that, by permitting light to reach the pineal body, the pineal apparatus in *Thunnus* could be instrumental in controlling phototactic movements involved in migration. Holmgren (1958) concluded that while there are morphological indications of light sensitivity in the pineal area of *T. thynnus*, there is not enough physiological evidence to be sure of possible hormonal control by this area.

Ventrally (Figures 15-19), the prelateral ethmoid region of bonitos is shorter and broader than in other scombrids. The ventral surface of the skull is formed by the vomer, lateral ethmoids, and parasphenoid and is broader than that of more advanced scombrids. The anterior three-fifths of the parasphenoid is almost flat, there is a medial, ventral keel in the next fifth, and posteriorly it is thin and smoothly curved into lateral flanges which enclose a parasphenoidal chamber (Kishinouye 1923). The lateral wings of the parasphenoid project dorsolaterally from the posterior half of the ventral keel to form the anteroventral part of the posterior myodome. The ventral surface of the brain case is formed by the frontal, pterosphenoid, sphenotic, prootic, basioccipital, exoccipital, intercalar, and pterotic bones.

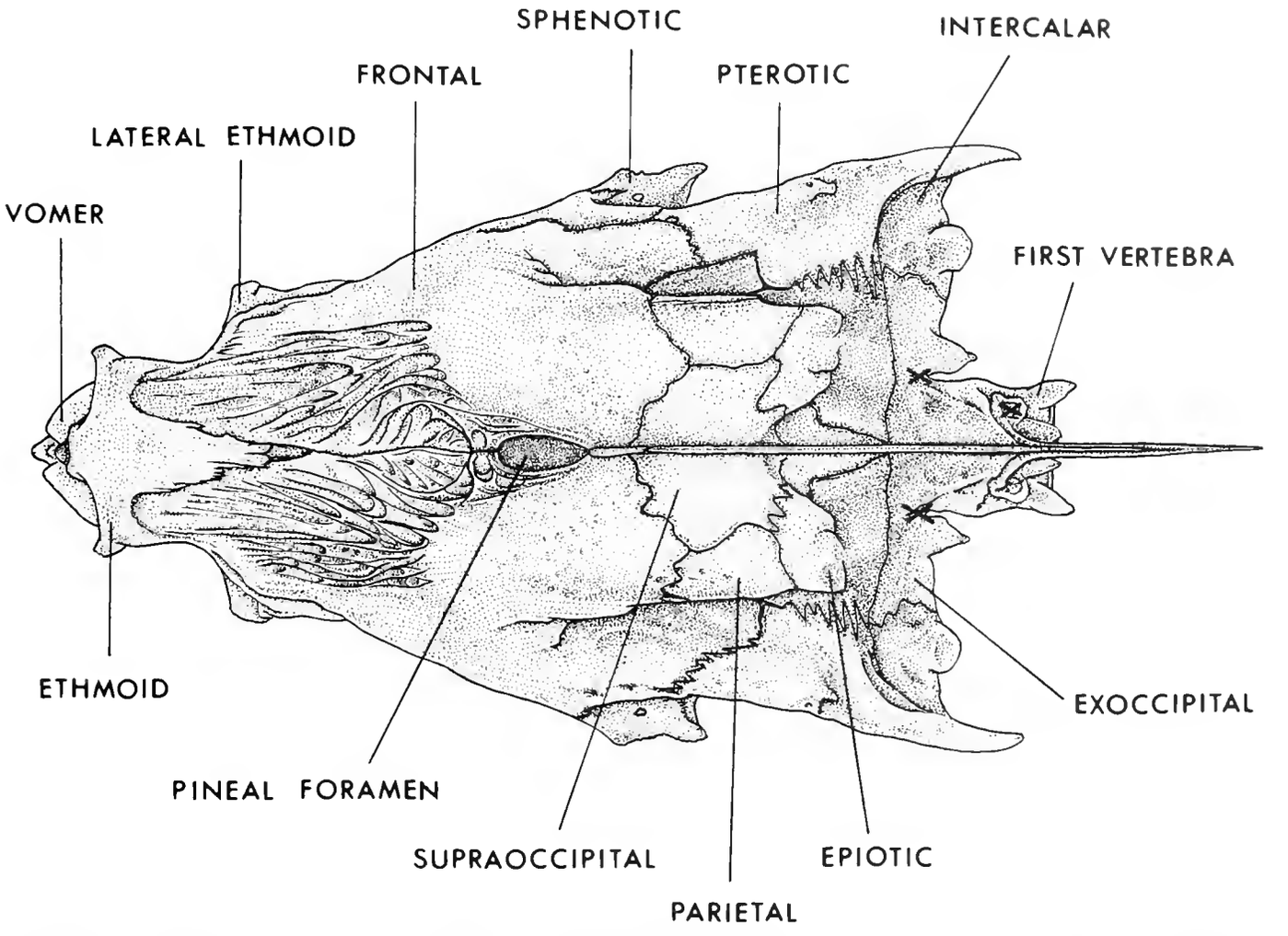


FIGURE 11.—Dorsal view of skull of *Allothunnus fallai*, California, 680 mm FL. X's indicate the points of attachment of intermuscular bones.

In lateral view (Figures 20-24), bonito skulls are similar to more advanced scombrids, but are more elongate and have the roof of the orbit less fully arched. *Allothunnus* (Figure 24) is most distinct in having a more pointed anterior end and a deeper posterior portion. The pterosphenoids project ventrally from the roof of the skull and form a partial interorbital septum which never fuses with the parasphenoid as in large *Thunnus thynnus* (see Gibbs and Collette 1967). In the posterior part of the orbit, the basisphenoid bisects the orbital capsule by connecting the pterosphenoids and prootic bones to the parasphenoid. The orbit is formed by the posterior edge of the lateral ethmoid, the ventral surface of the frontal and pterosphenoid, the parasphenoid, basisphenoid, and the anterior edge of the prootic. As expressed by the ratio of orbit height to length (see section on orbital region), the orbit is low and elongate in bonitos (Table 4); *Cybiosarda*, *Orcynopsis*, and *Sarda* have the lowest orbits as in *Scomberomorus* and *Acanthocybium*. *Gymnosarda* and *Allothunnus* each have a more highly arched orbit resembling that in *Scomber*, *Grammatorcynus*, *Rastrelliger*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* (Allis 1903; Kishinouye 1923; Mago Leccia 1958; Gibbs and Collette 1967; Gnanamuttu 1971).

TABLE 4.—Ratio of orbit height to length in species of Sardini.

Species	Range	$\bar{x}$	N	Skull length (mm)	Fork length (mm)
Orcynopsis unicolor	3.85-4.60	4.32	6	43.2-71.2	323-620
Cybiosarda elegans	3.83-5.37	4.49	4	48.6-64.3	355-422
Sarda australis	3.03-3.70	3.33	3	23.1-29.6	363-495
Sarda chiliensis:					
SE Pacific	3.78-6.69	5.12	17	26.7-86.7	437-571
NE Pacific	3.10-5.78	4.12	37	24.3-92.3	332-570
Sarda orientalis:					
Indo-W Pacific	3.67-4.30	4.06	3	47.8-68.8	340-500
E Pacific	3.20-5.09	4.03	7	50.9-68.0	354-497
Sarda sarda	3.42-5.00	3.92	7	45.6-66.1	333-504
Gymnosarda unicolor	2.26-2.68	2.45	5	102-120	625-772
Allothunnus fallai	2.94-3.40	3.19	4	72.4-114	406-778

The posterior part of the base of the cranium is formed by the lateral flanges of the parasphenoid (ventral profile) and basioccipital (posterior profile). Along the dorsal profile, a crest formed anteriorly by the joint between the frontals is most distinctive in *Sarda*, as in *Scomberomorus*

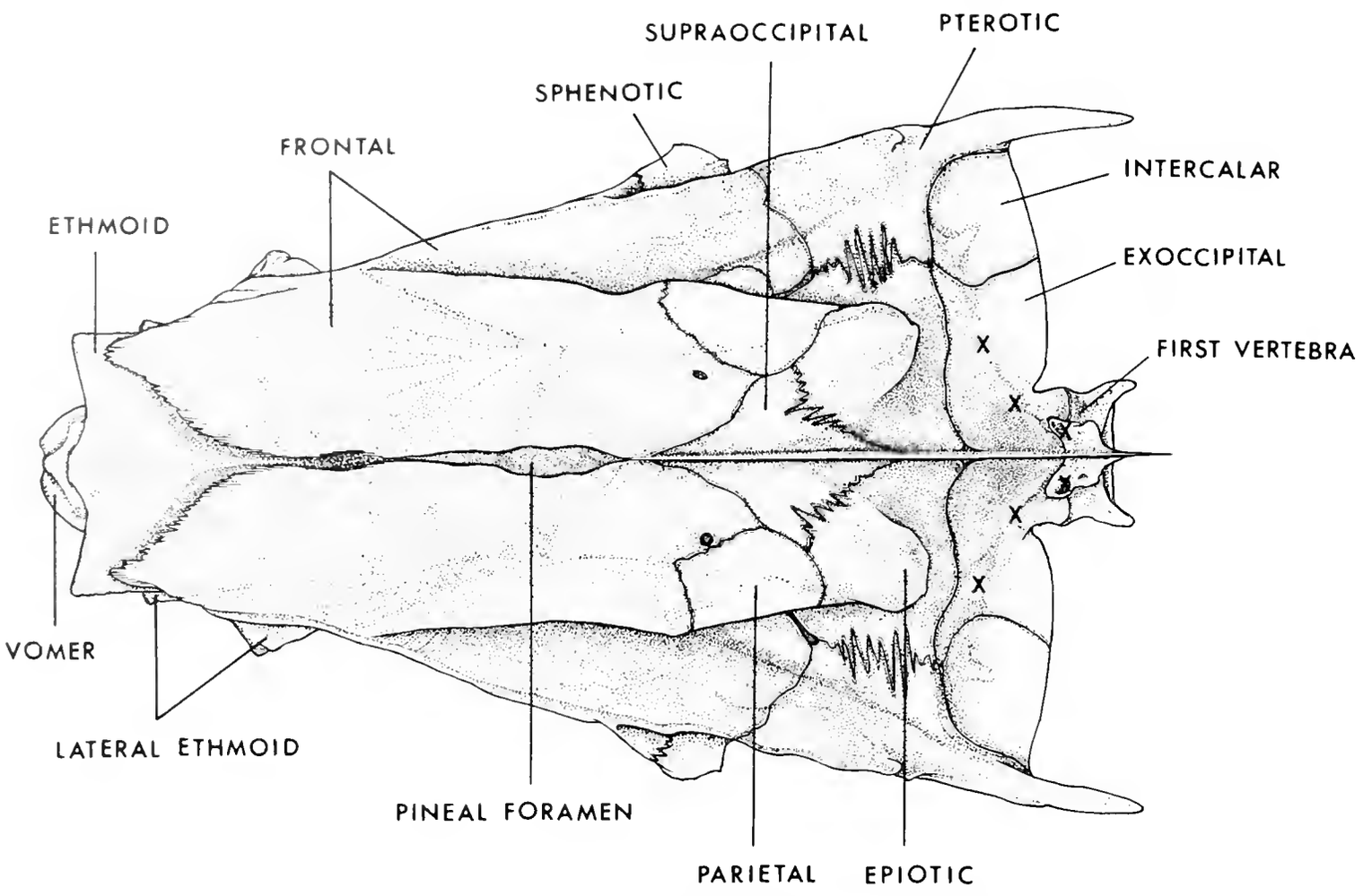


FIGURE 12.—Dorsal view of skull of *Sarda sarda*, eastern United States, 388 mm FL. X's indicate the points of attachment of intermuscular bones.

(Mago Leccia 1958), *Katsuwonus*, and *Thunnus*. In *Cybiosarda* and *Orcynopsis*, these anterofrontal crests are merely visible laterally as in *Auxis* and *Euthynnus*. No anterofrontal crest is present in *Gymnosarda* and *Allothunnus* (Figures 22, 24) and it is also absent in *Grammatorcynus* and *Acanthocybium*.

The first vertebral centrum has modified neural prezygapophyses (Figure 25) that firmly attach the first vertebra to the modified exoccipital and basioccipital region (Figure 26) of the skull. The anterior circular margin of the first centrum is smaller than its posterior margin and is in a forward oblique position to meet the posterior margin of the modified basioccipital which is in a backward oblique position. The strong first neural spine, with its tubular base, sits on the junction of the first centrum and exoccipital and it is not fused to the first centrum. No bony shelf is present in the neural canal (Figure 25a) to divide it into dorsal and ventral portions as is the case in *Auxis*, *Euthynnus*, and *Katsuwonus*. An intermuscular bone is attached to the center of each exoccipital in the bonitos (also see section on ribs and intermuscular bones) except in species of *Sarda* (Figure 26) which have an additional pair of intermuscular bones attached to the exoccipital just anterior to the first neural prezygapophyses and *Gymnosarda* which lacks cephalic intermuscular bones.

The prootic pits (Godsil 1954) of the more advanced scombrids are incipient in bonitos except in *Allothunnus*, which has a larger pouchlike concavity on each side of the ventral surface of the cranium. Part of the roof, floor, and sides of the prootic pit are formed by the prootic and pterotic bones. The branchial musculature originates in these pits in *Thunnus* (Gibbs and Collette 1967). The posterior end of the orbital region extends into a deep median depression, the posterior myodome, which is surrounded by the prootic anterodorsally, the parasphenoid ventrally, and the basioccipital postdorsally and postlaterally, and then opens at the back of the skull between the posterior flanges of the parasphenoid, or communicates with a posterior or parasphenoidal chamber (Kishinouye 1923). The rectus muscles of the eyes attach in the posterior myodome (Gibbs and Collette 1967).

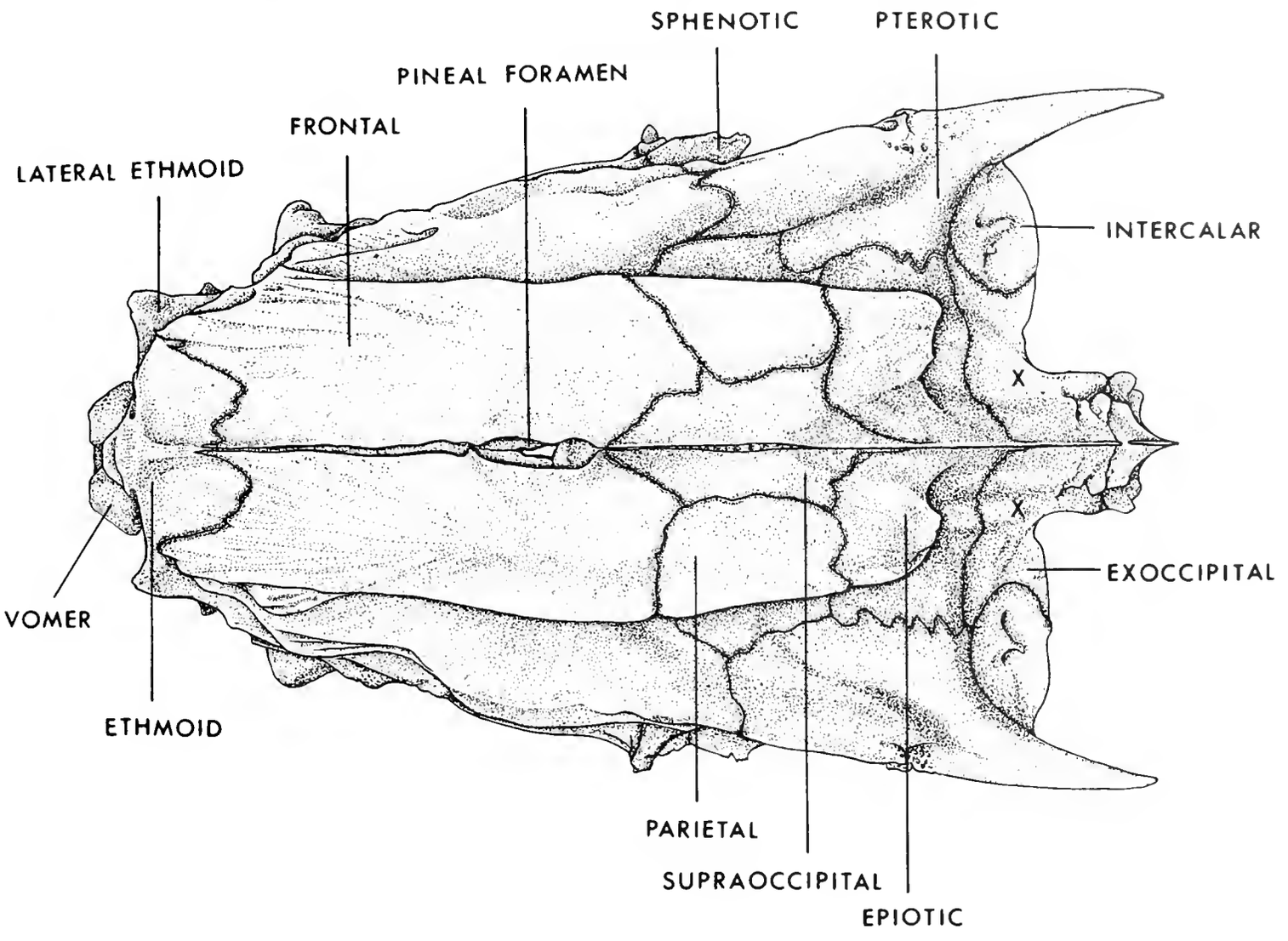


FIGURE 13.—Dorsal view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL. X's indicate the points of attachment of intermuscular bones.

ETHMOID REGION.—This region is composed of the ethmoid, lateral ethmoid, and vomer. The nasal bone lies lateral to the ethmoid and lateral ethmoid and, therefore, is included here.

Ethmoid.—The ethmoid (dermethmoid) is the most anterodorsally located bone of the neurocranium. It has a smooth flat dorsal surface, slightly convex at the median posterior end, to receive the frontal bones. It connects ventrally to the vomer and posteriorly to the lateral ethmoids with rough and porous sutures. The anterior border of the ethmoid is nearly straight in *Orcynopsis* (Figure 14), but is concave in the other genera with an anteromedian projection and an anterolateral horn on each side.

Lateral Ethmoid.—The paired lateral ethmoids (parethmoids) form the posterolateral wall of the ethmoid region and the anterior wall of the orbit with an olfactory foramen on each side. The lateral ethmoid articulates with the ethmoid anterodorsally, with the frontal bone posterodorsally, with the parasphenoid posteroventrally, and with the vomer anteroventrally. The posterolateral process of the lateral ethmoid serves as an articulating surface for the lachrymal, ectopterygoid, and the entopterygoid. In ventral view, this articulating surface area is small in *Cybiosarda*, slightly larger in *Allothunnus*, and most expanded in the species of *Sarda*, (Figures 15, 18, 19). In *Orcynopsis* and *Gymnosarda*, it is an elongate narrow strip (Figures 16, 17). The lateral expansions of the lateral ethmoids in bonitos resemble those of more primitive scombrids in being wider than in more advanced genera.

Vomer.—The vomer is the most anteroventrally located bone of the cranium. It is located beneath the ethmoid and the lateral ethmoids. Its pointed posterior end fits into the V-shaped anterior projection of the parasphenoid to form the sup-

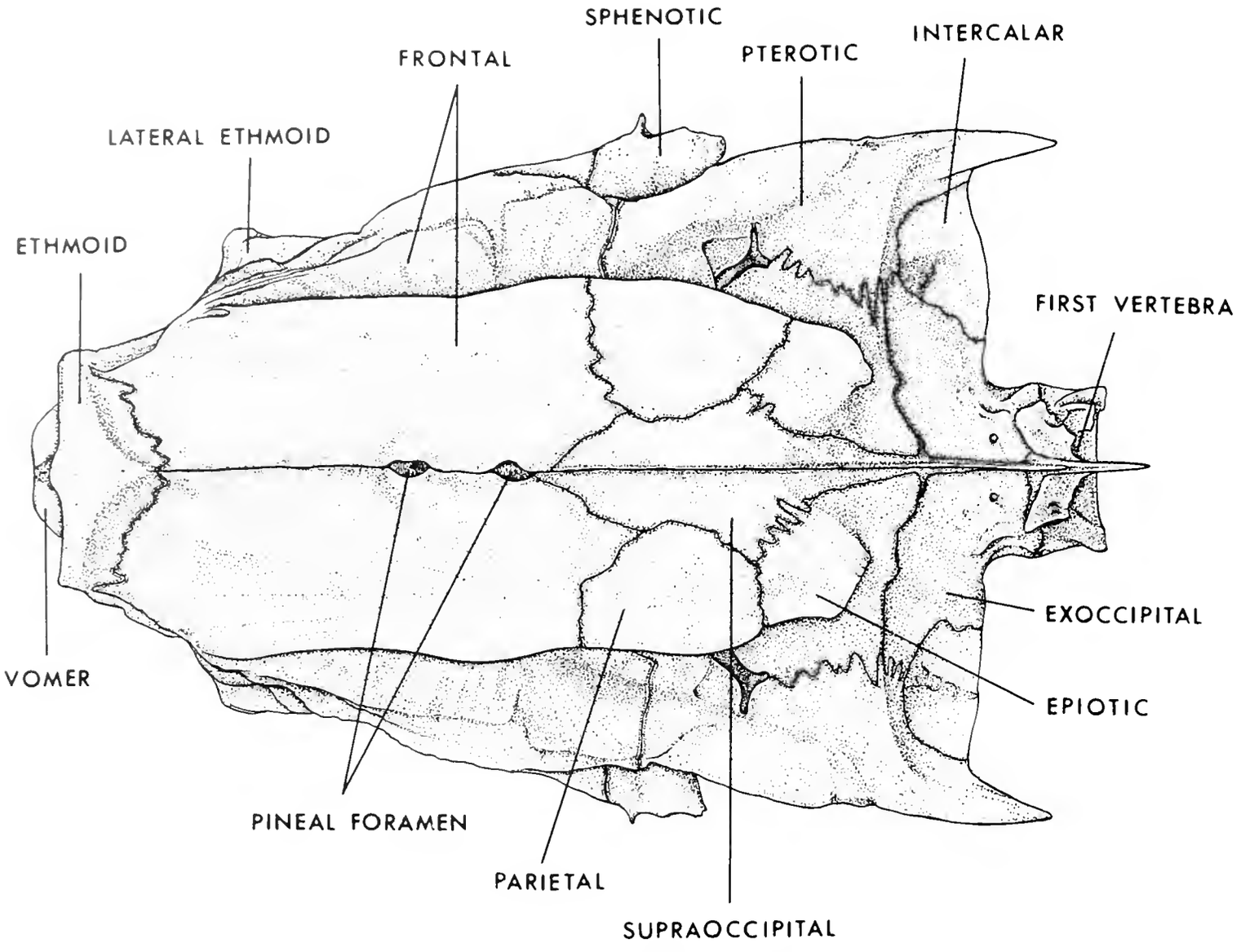


FIGURE 14.—Dorsal view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

porting axis of the roof of the mouth. Ventrally, the vomer of *Cybiosarda* and *Orcynopsis* (Figures 15, 16) has a blunt anterior edge and bears a patch of villiform teeth. *Sarda australis* and *S. sarda* frequently have a few small teeth on the middle of the expanded part of the vomer, but vomerine teeth are absent in the other bonitos. Some specimens of *S. chiliensis* have a ridge along the midline of the vomer but most have this area flat or convex. The variation is individual, not geographic: 3 of 12 southeastern specimens have a ridge; 6 of 26 northeastern specimens have a ridge. Godsil (1955) mentioned that the ventral surface of the expanded portion of the vomer was flat in Indo-West Pacific *S. orientalis* and that of eastern Pacific specimens was slightly cupped or concave ventrally. We found that this character is not consistent in our material. The anterolateral edges of the vomer are prominent and project ventrally in *Gymnosarda*. The anterior one-third of the vomer in *Allothunnus* projects ventrally with an axelike anterior end and is porous in the middle of the ventral surface. The pointed posterior end of the vomer is more elongate in *Sarda* than in other genera of bonitos.

The bonitos fall into three groups based on vomerine dentition. *Allothunnus*, *Sarda orientalis*, and *S. chiliensis* lack vomerine teeth. A few small teeth are frequently present on the head of the vomer in *S. sarda* and *S. australis* and sometimes in *Gymnosarda*. Both *Orcynopsis* and *Cybiosarda* have a small patch of teeth on the head of the vomer and a few teeth usually extend posteriorly a short distance on the shaft of the vomer.

Nasal.—The anterior end of the nasal, which reaches the premaxilla posterodorsally, is thickened in all bonitos and has an expanded hammerlike head except in the species of *Sarda* (Figure 27). The nasal gradually becomes thinner

towards its posterior margin which attaches to the frontal bone. *Gymnosarda* has the strongest nasal bone, with serrations along its anteroventral margin. The nasal in *Allothunnus* is more elongate than in other bonitos and its constricted midportion is more prominent.

ORBITAL REGION.—The orbit is surrounded by the posterior wall of the lateral ethmoid, the ventral side of the frontal, the pterosphenoid, sphenotic, prootic, suborbital, and lachrymal bones. The left and right orbits are partially separated by the basisphenoid. The sclerotic bones enclose the eyeballs.

Godsil (1955) found a difference in the ratio of orbit height to length between southeastern and northeastern populations of *Sarda chiliensis*. The ratio in his material varied from 5.83 to 6.83 in 5 southeastern specimens (606-659 mm FL) and from 3.40 to 4.50 in 6 northeastern specimens (439-563 mm FL). Following Godsil's definitions, length was measured along the shaft of the parasphenoid, from its juncture with the lateral ethmoid to the point where the lateral wing of the parasphenoid begins. Orbit height is the least distance between the anterior ventral projection of the pterosphenoid and the shaft of the parasphenoid. The range of variation in this ratio (Table 4) indicates that this is not a useful diagnostic character within the genus *Sarda*, although the means for the populations of *S. chiliensis* show the same trend that Godsil found. *Orcynopsis* and *Cybiosarda* have the highest ratios, which indicate the most elongate and narrow orbits and the most ventrally projecting pterosphenoids. *Allothunnus* and *Gymnosarda* have the lowest ratios due to their slightly higher arched orbits and the smooth ventral margins of the pterosphenoids.

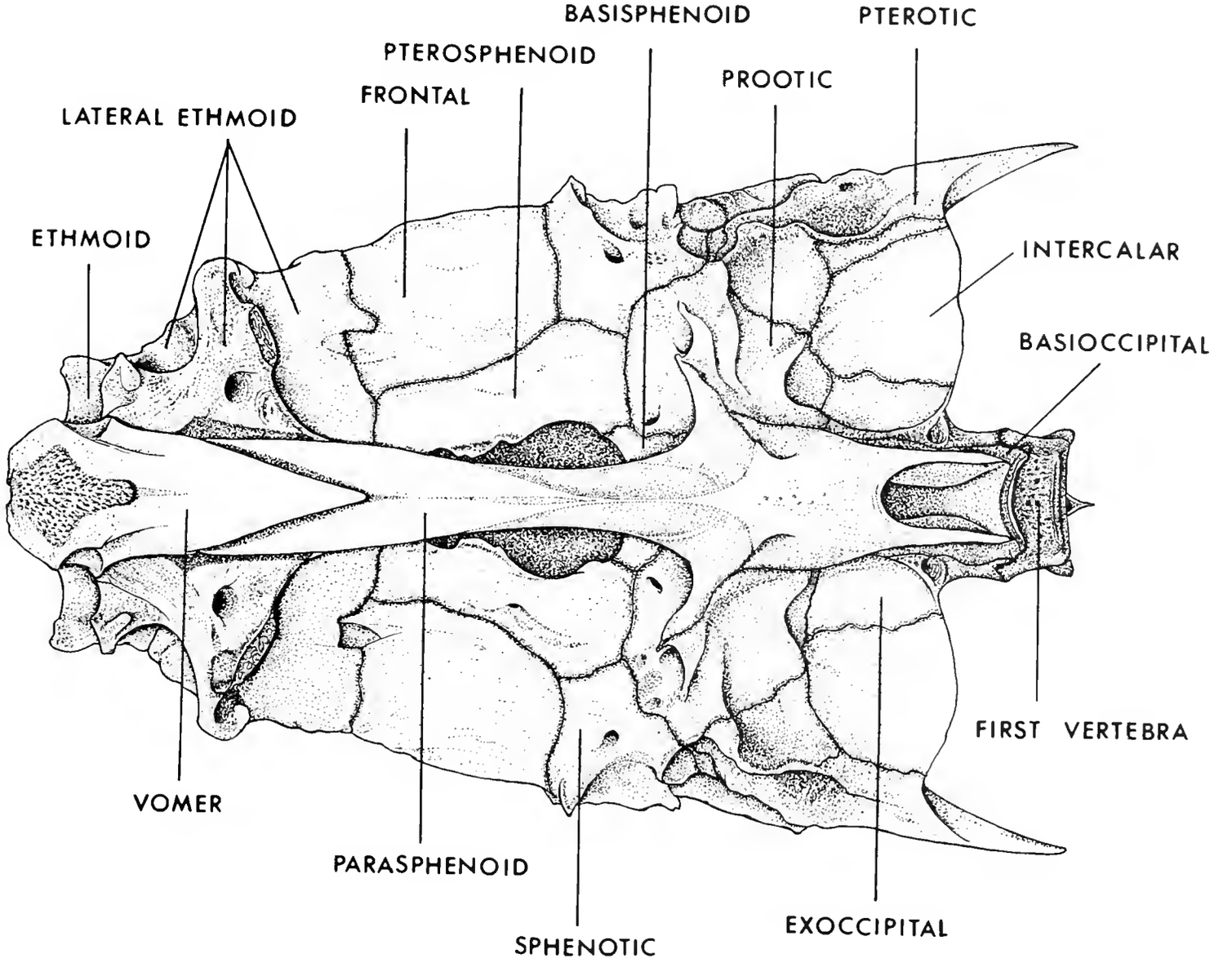


FIGURE 15.—Ventral view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL.

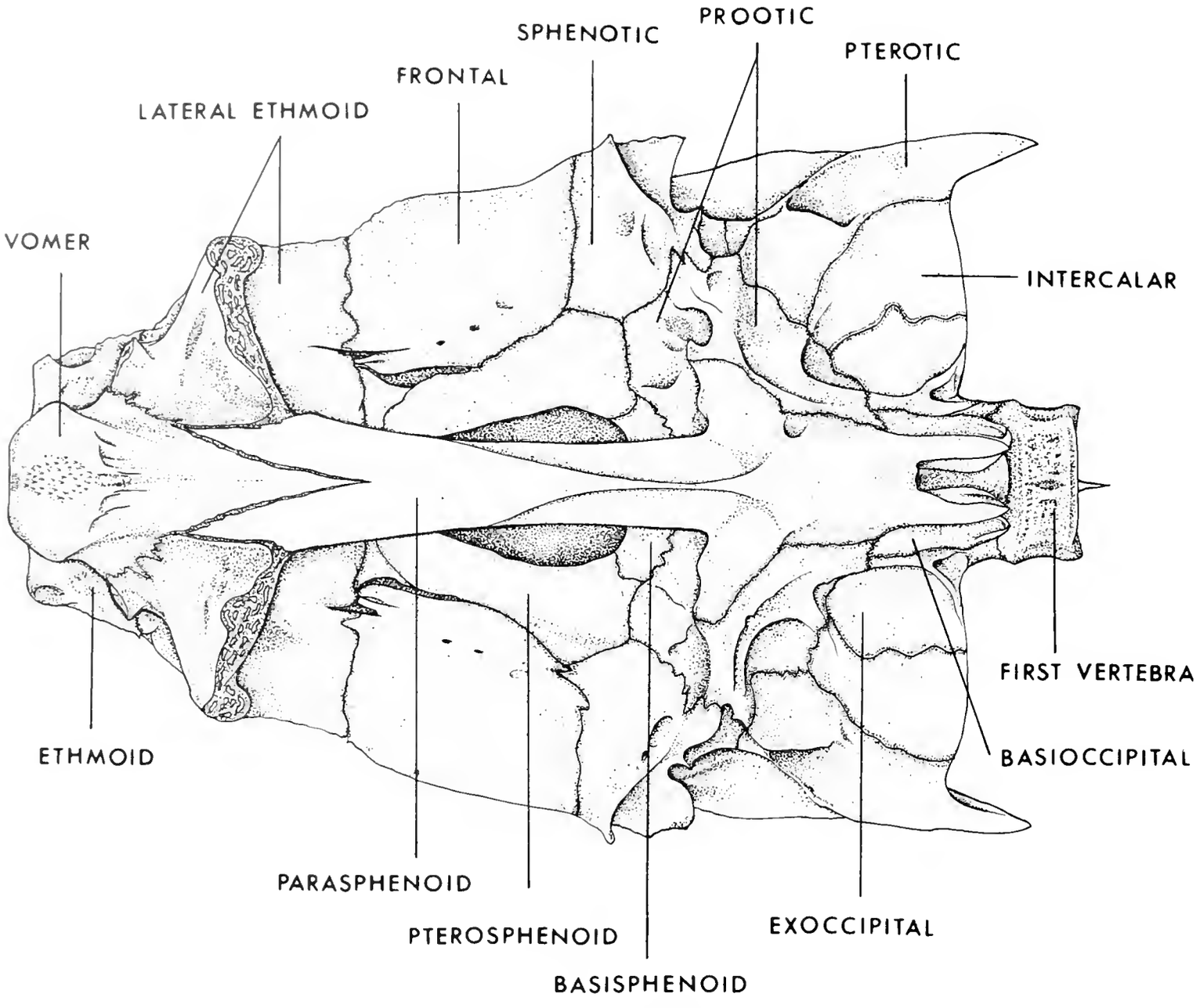


FIGURE 16.—Ventral view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

Frontal.—Most of the dorsal surface of the cranium is covered by large concave frontal bones. In dorsal view, the anterior ends of the frontals overlap the posterior part of the ethmoid. Posteriorly, they articulate with the sphenotic, pterotic, parietal, and supraoccipital bones. The frontal bones are thickened laterally to form the roof of the orbit; they become thinner where they meet along the median line of the skull and form a crest. A thin bony inner lateral crest begins at the middle of each frontal bone and continues along the parietal to the epiotic bone. A pineal foramen is present immediately anterior to the supraoccipital crest. The pineal foramen is slitlike and filled with cartilage in most bonitos. *Allothunnus* has the largest and thickest frontal bones; they are concave dorsally, with deep conspicuous radiating ridges and lack a frontal crest. A deep round depression, lined with bony ridges, is present anterior to the oval pineal foramen. This feature of *Allothunnus* is similar to that in *Acanthocybium* (Conrad 1938). *Grammatorcynus* also has many conspicuous shallow radiating ridges on the frontal bones. In ventral view, the frontal bone articulates with the lateral ethmoid anteriorly, the pterosphenoid medially, and the sphenotic posteriorly. The ratio of the length of the external edge of the frontal bone to the length of the skull (anterior edge of the vomer to the articulation of the first centrum) varies from 30.9 to 33.3% in *S. australis* (3 specimens 363-495 mm FL) and thus differs from other species of *Sarda*, whose ratios were less than 28%. Laterally, the frontal bone divides into two shelves posteriorly

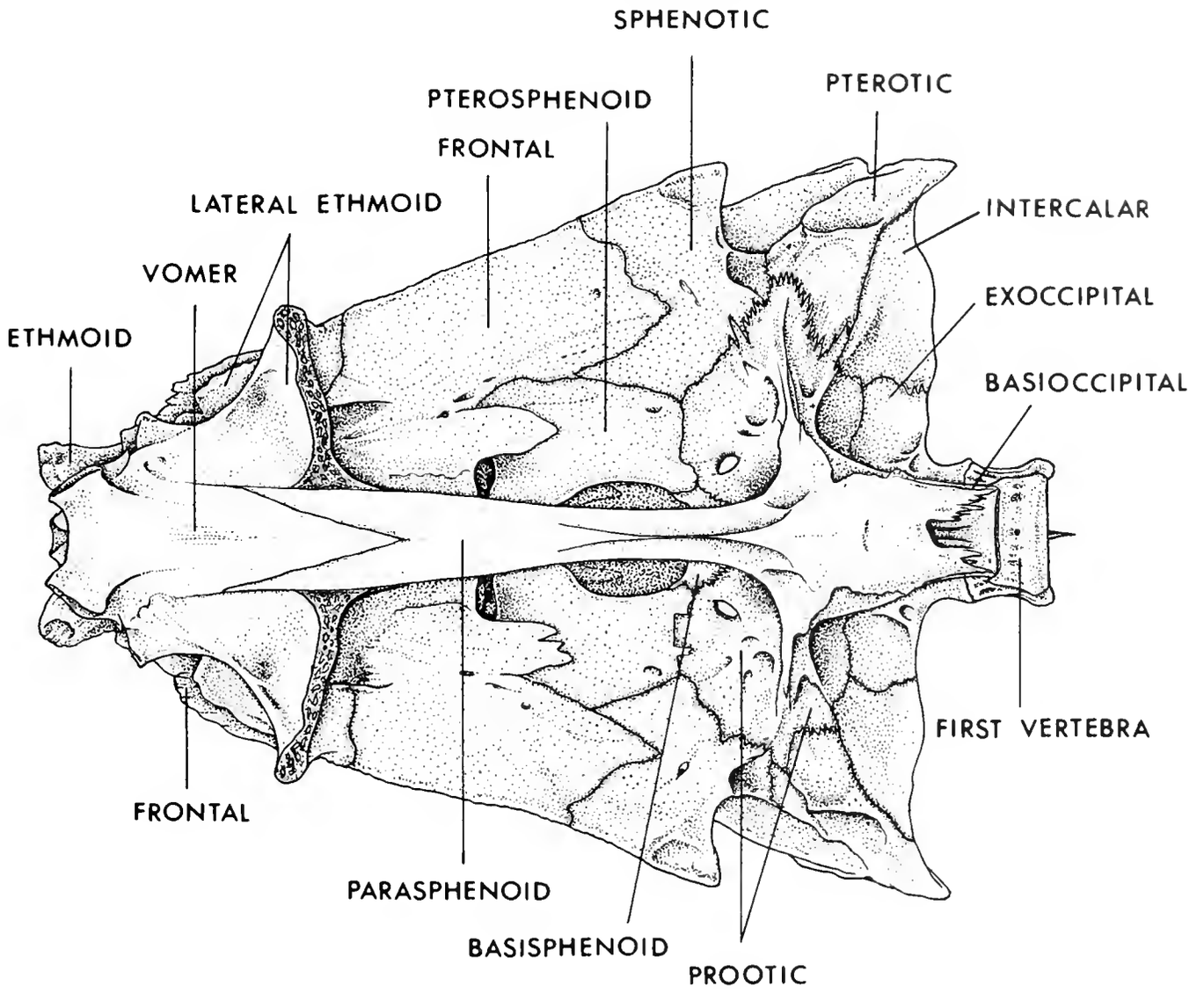


FIGURE 17.—Ventral view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

where the upper shelf meets the pterotic and the lower shelf meets the sphenotic. The frontal crest is absent in *Allothunnus* (Figure 24), indistinct in *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* (Figures 20-22), and is most prominent in the species of *Sarda* (Figure 23).

Basisphenoid.—The basisphenoid is a Y-shaped bone, connected dorsally to the prootics and the pterosphenoids. In anterior view, the basisphenoid bisects the entrance of the myodome, with an anteriorly and a posteriorly directed process in its upper half (Figures 20-24), except in *Allothunnus* (Figure 25). Ventrally, the basisphenoid extends toward the parasphenoid to which it is connected in all the bonitos except *Allothunnus*.

Godsil (1954) studied possible differences between the basisphenoids of eastern Pacific *Sarda chiliensis* and *S. orientalis*. He concluded that the lower portion of the basisphenoid in *S. chiliensis* is generally a narrow bone, only slightly expanded, and firmly ankylosed to the parasphenoid. In *S. orientalis*, the lower extremity of the basisphenoid is greatly expanded and it is apparently only loosely attached to the parasphenoid. We agree with his statements in part. In *S. orientalis* from the eastern Pacific and the Indo-West Pacific, the lower extremities of the basisphenoid are expanded and firmly attached to the parasphenoid. In northeast and southeast populations of *S. chiliensis*, the lower portions of the basisphenoid are narrow or slightly expanded and are either firmly or loosely ankylosed to the parasphenoid. In general, the lower extremities of the basisphenoid in *S. chiliensis* are less expanded and less firmly attached to the parasphenoid than in *S. orientalis*.

The angle of the long axis of the basisphenoid relative to the parasphenoid in bonitos is less variable than in *Thunnus* (Gibbs and Collette 1967), but no specific differences were found among the bonitos, except in *Allothunnus*. The

basisphenoid curves posteriorly as it approaches the parasphenoid and is not attached to the parasphenoid in *Allothunnus* (Figure 25). This may explain why the basisphenoid was lost in three of the four skulls that we prepared. The angle of the anterior basisphenotic process was used as a character in *Thunnus* by de Sylva (1955:32-35), but Gibbs and Collette (1967:73) found it too variable to be useful. In bonitos, the axes of the anterior and the posterior processes of the basisphenoid are straight, with the anterior process slightly directed downward in some specimens. *Allothunnus* has no basisphenotic process and the anterior process in *Orcynopsis* and *Cybiosarda* is not as prominent as in the other bonitos. The angle between the axis of the process and the vertical axis of the basisphenoid is similar in all bonitos except for *Gymnosarda* (Figure 19). In *Gymnosarda*, a ridge is present along the axis of the process and the posterior process is more ventrally directed.

Among other scombrids, *Thunnus* and *Scomberomorus* lack a prominent posterior process on the basisphenoid (Gibbs and Collette 1967; Mago Leccia 1958, pl. 3), *Allothunnus* and *Rastrelliger* have no process on the basisphenoid (Nakamura and Mori 1966; Gnanamuttu 1971, fig. 1), *Acanthocybium*, *Auxis*, *Euthynnus*, and *Katsuwonus* have both the anterior and the posterior process. If the shape of the basisphenoid bone is used as a diagnostic character in scombrid classification (Kishinouye 1923; Godsil 1954; de Sylva 1955; Gibbs and Collette 1967), its high intraspecific variability must be taken into account.

Pterosphenoid.—The pterosphenoid (alisphenoid) articulates with the edges of the frontal, sphenotic, prootic, and basisphenoid on the ventral surface of the brain case. Anteriorly, the pterosphenoids are connected to the lateral ethmoids directly or indirectly by a cartilaginous membrane. The paired pterosphenoid bones meet each other anteriorly along the median ventral line forming a pterosphenotic window that differs

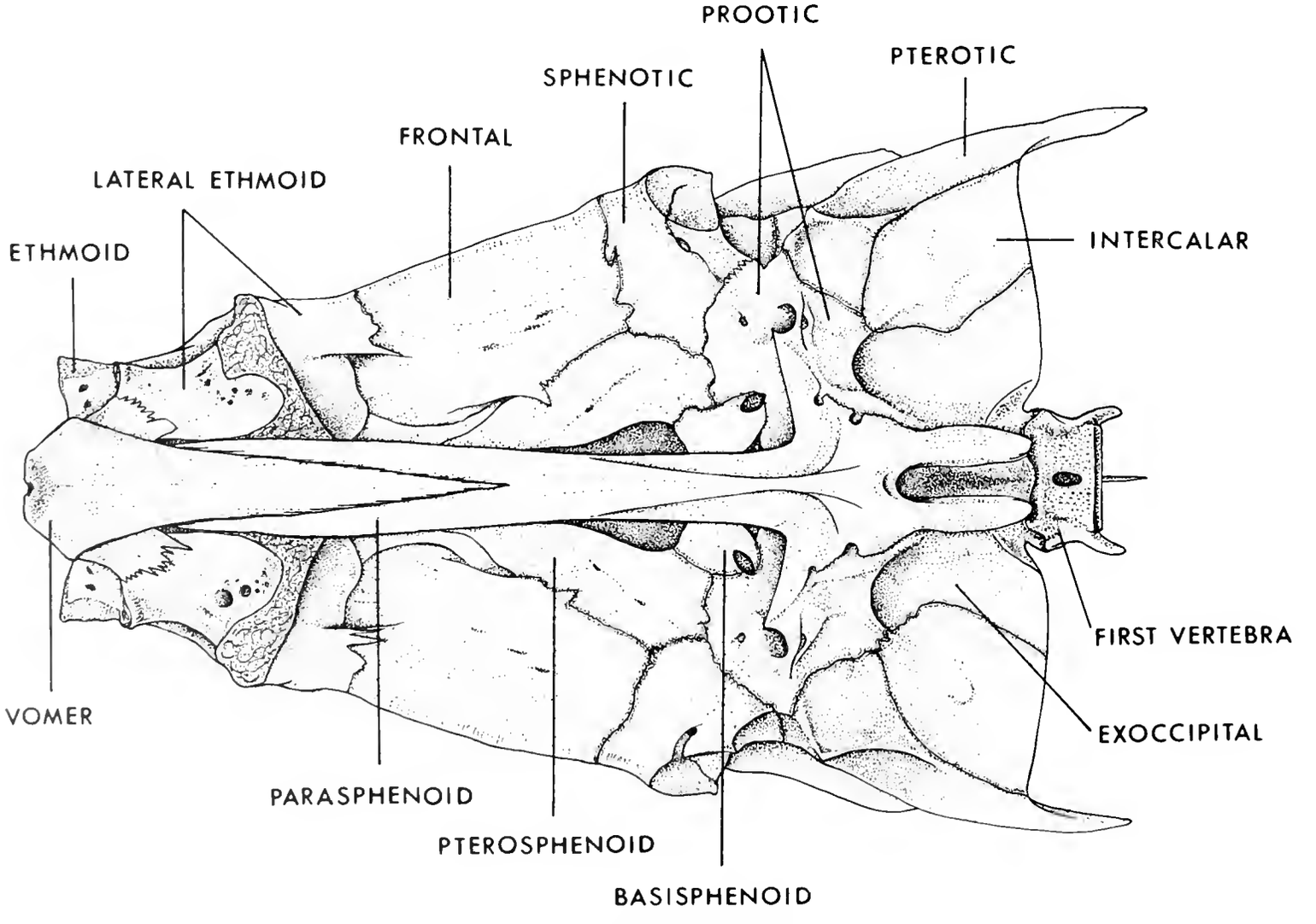


FIGURE 18.—Ventral view of skull of *Sarda sarda*, eastern United States, 388 mm FL.

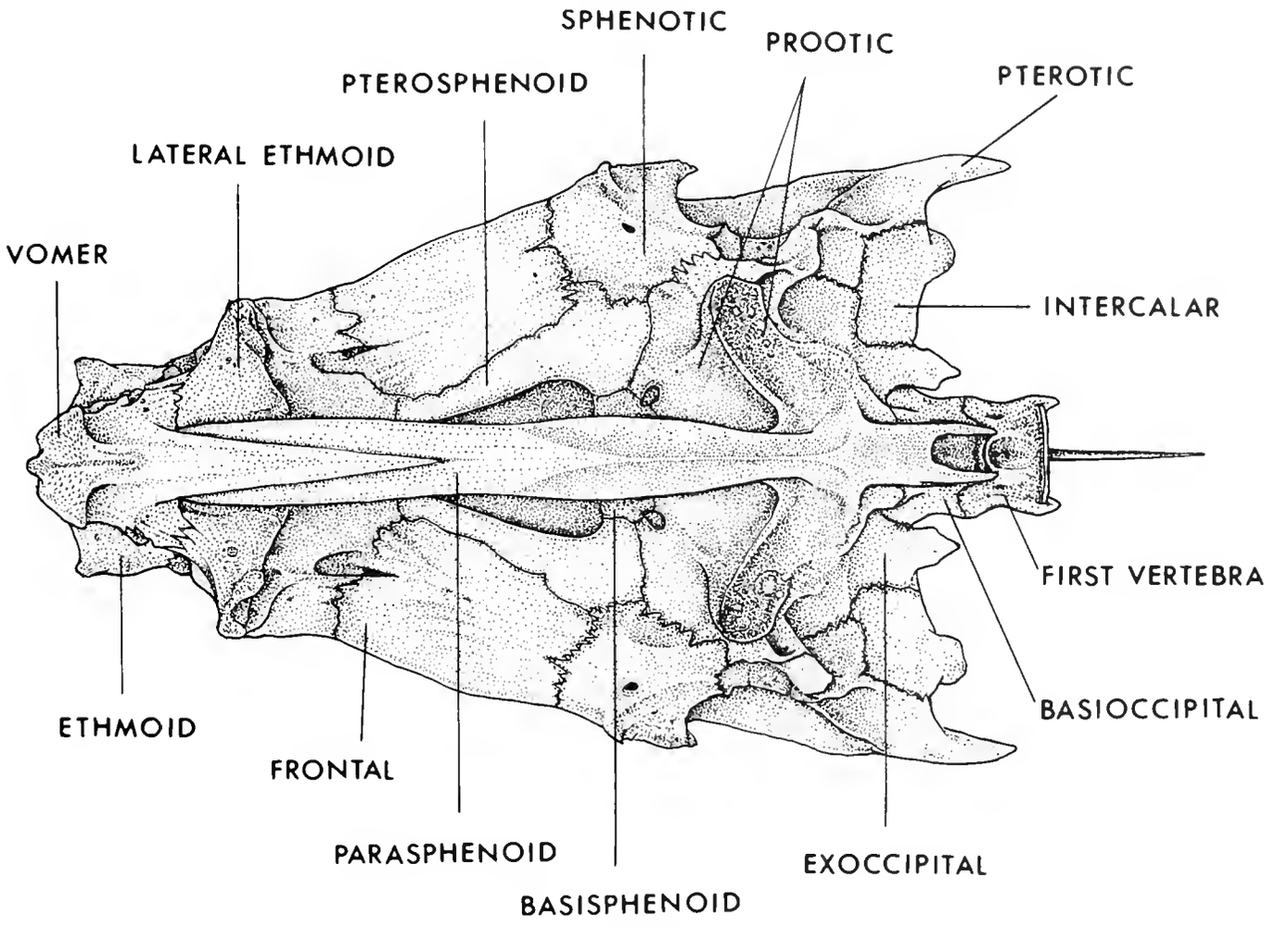


FIGURE 19.—Ventral view of skull of *Allothunnus fallai*, California, 680 mm FL.

slightly among the bonitos in shape. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have a beer bottle-shaped window; it is roughtly triangular with a broad arched posterior margin in *Sarda*. In *Allothunnus*, a thin bony membrane is present along the inner edge of the pterosphenoid toward the center of the window. The pterosphenoids do not fuse with the parasphenoid, as they frequently do in large specimens of *Thunnus thynnus* (Gibbs and Collette 1967).

Lachrymal.—The lachrymal is an elongate bone that covers up part of the maxilla and is attached to the lateral ethmoid by means of a dorsal projection on its inner surface (Figure 9). This process is most pronounced in *Gymnosarda* and most flattened in *Allothunnus*. The anterior margin of the lachrymal has an indentation with an anteriorly projecting process on the dorsal margin of the indentation (Figure 28). The margin is slightly concave in *Sarda* and *Gymnosarda* compared to the deep notch present in the other bonitos. *Cybiosarda* has the longest anterior process, much longer and thinner than in *Orcynopsis*. *Gymnosarda* has a wide blunt process. The lachrymal is relatively shorter and stronger in *Gymnosarda* and it is extremely heavy and sculptured at the dorsal projection and along the posterodorsal margin.

Suborbital bones.—Nakamura and Mori (1966) stated that the first and second suborbital bones are inconspicuously developed and not much differentiated from the scales on the cheek in *Allothunnus*. Suborbital bones are present in the bonitos, but we have made no special effort to study them.

Sclerotic.—The sclerotic bones consist of two thickened semicircular segments connected by cartilage on the inner lateral surface and by corneal membranes on the outside. The inner rim of the sclerotic bones appears elliptical externally in all bonitos as in *Thunnus atlanticus* (de Sylva 1955, fig. 7).

OTIC REGION.—This region encloses the otic chamber inside the skull, and is formed by the

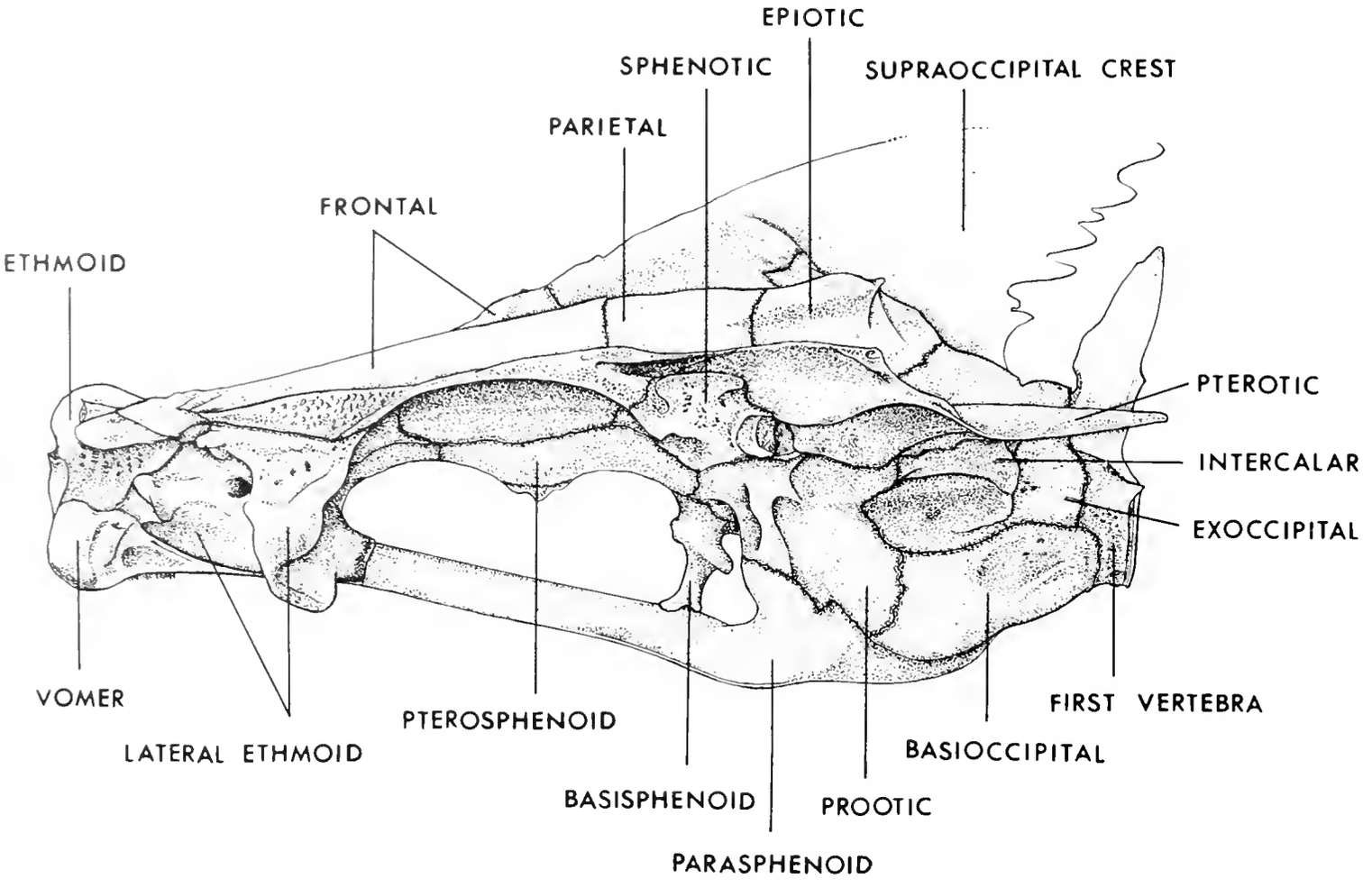


FIGURE 20.—Lateral view of skull of *Cybiosarda elegans*, Western Australia, 422 mm FL.

parietal, epiotic, supraoccipital, pterotic, prootic, sphenotic, and intercalar (opisthotic) bones.

Parietal.—The parietal articulates with the frontal anteriorly, the supraoccipital and the pterotic laterally, sphenotic ventrally, and epiotic posteriorly. The inner lateral crest that originates at the middle of the frontal bones continues through the parietals to terminate at the epiotics. This crest is typical of scombrids but is less developed in *Grammatorcynus* and in *Scomber* (Allis 1903).

Epiotic.—The epiotic is massive, irregular, and bounded by the parietal anteriorly, the supraoccipital mediolaterally, the exoccipital posteriorly, and the pterotic distolaterally. The inner lateral crest terminates at the posterior end of the epiotic. The medial process of the posttemporal bone is also attached here. The epiotic bones of all the bonitos are similar.

Supraoccipital.—The supraoccipital can be divided into two parts: a thin, elongate triangular crest and a roughly hexagonal shaped base. The supraoccipital crest arises just behind the pineal foramen and extends posterodorsally. In bonitos, the crest extends posteriorly over the first neural spine but usually not over the posterior margin of the first centrum. In *Allothunnus* the crest extends posteriorly over the second centrum. In dorsal view, the hexagonal base articulates with the frontal bones anterolaterally, the parietals laterally, and the epiotic posteriorly. *Cybiosarda* and *Orcynopsis* have the narrowest and most elongate supraoccipital base; *Allothunnus* has the shortest and widest.

Pterotic.—Dorsally, the pterotic is the most posterolaterally located bone. The pterotic articulates with the epiotic and parietal medially and with the exoccipital and intercalar posteriorly. A sharp posteriorly pointed process is characteristic of the pterotic bone of the bonitos as well as other scombrids. In ventral view, the pterotic articulates with the sphenotic anteriorly and the prootic and intercalar medially. Two fossae, one at the posterior half of the pterotic bone and one at its joint with the sphenotic, seat the dorsal and anterior condyles of the hyomandibula. A deep

depression continues from the interspace of the posterior frontal shelves and separates the pterotic from the sphenotic. In bonitos, the size of both fossae varies only slightly; they tend to be deeper and larger in *Gymnosarda* and *Allothunnus*.

Prootic.–In ventral view, the prootic connects with all ventral bones which compose the posterior part of the neurocranium (Figures 15-19). The prootic bones are irregular in shape and meet each other along the ventral median line of the brain case to form the anterior portion of the posterior myodome. A prootic foramen is present anterolaterally between the tip of the parasphenoid wing and the sphenotic. The strut forming the outer part of the foramen is absent in *Allothunnus* forming a deep groove. The prootic pit of the more advanced scombrids (Gibbs and Collette 1967) is present in *Allothunnus* and absent or incipient in the other bonitos. In addition to the distinct prootic pit in *Allothunnus*, there is a very peculiar thick bony wing which is developed laterally; this twisted wing has a smooth convex anterior surface and a concave posterior surface.

Sphenotic.–The sphenotic bone forms the most posterior dorsolateral part of the roof of the orbit. It forms a continuation of the outer lateral shelf from the frontal bones and articulates with the pterosphenoid medially and the prootic and pterotic posteriorly. The lateral process of the sphenotic serves as an attachment for the outer process of the supratemporal. This process is pointed in *Cybiosarda*, *Orcynopsis*, *Gymnosarda*, and *Allothunnus*, and is less sharp in the species of *Sarda*. There are differences in the outlines of the joints around the sphenotic bone with the adjacent bones, but these are probably individual variations.

Intercalar.–The intercalar (opisthotic) bone fits between the pterotic and exoccipital bones (Figures 10-14) and bears a dorsal protuberance which connects to the lateral process of the post-

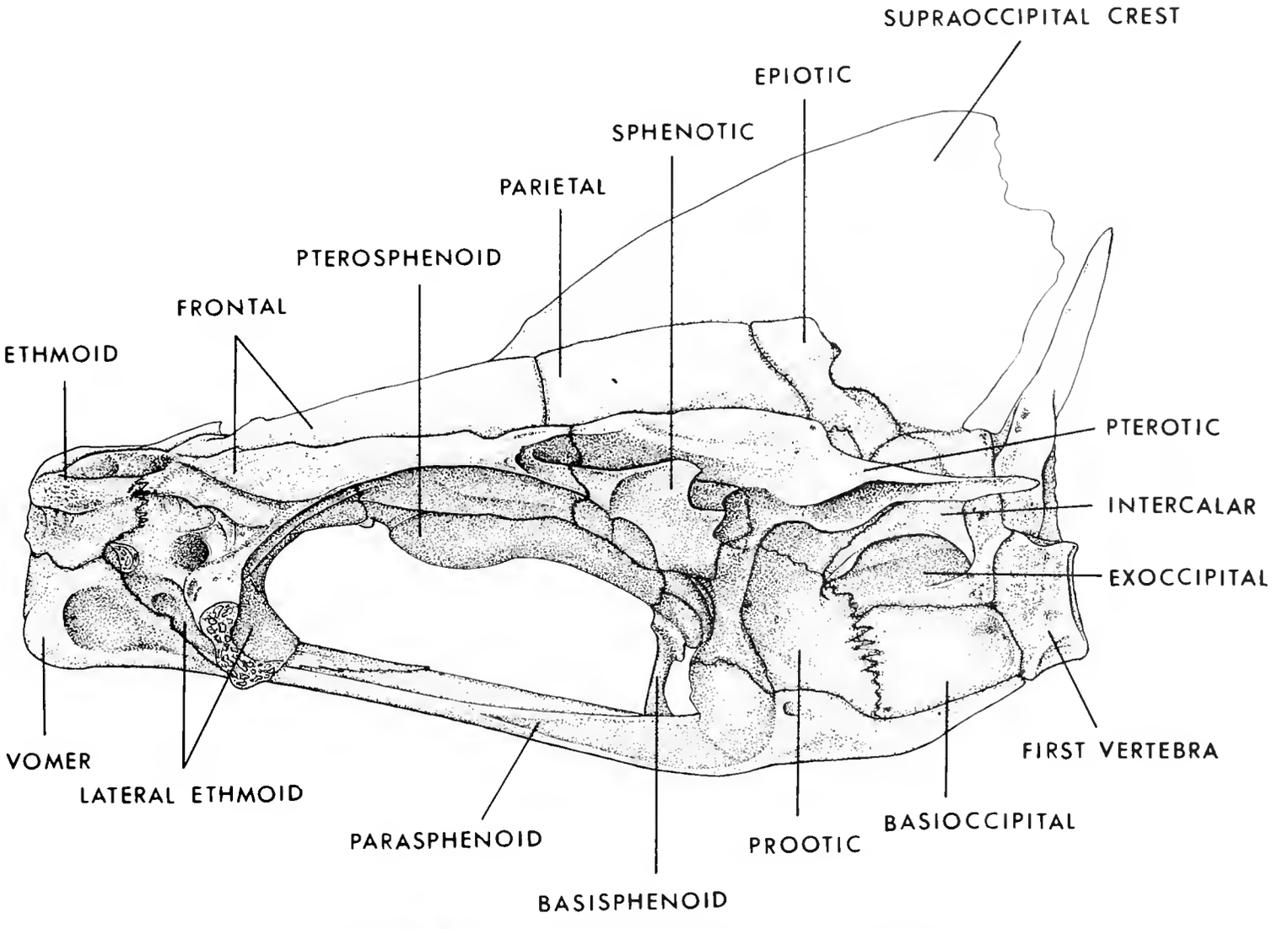


FIGURE 21.–Lateral view of skull of *Orcynopsis unicolor*, Tunisia, 543 mm FL.

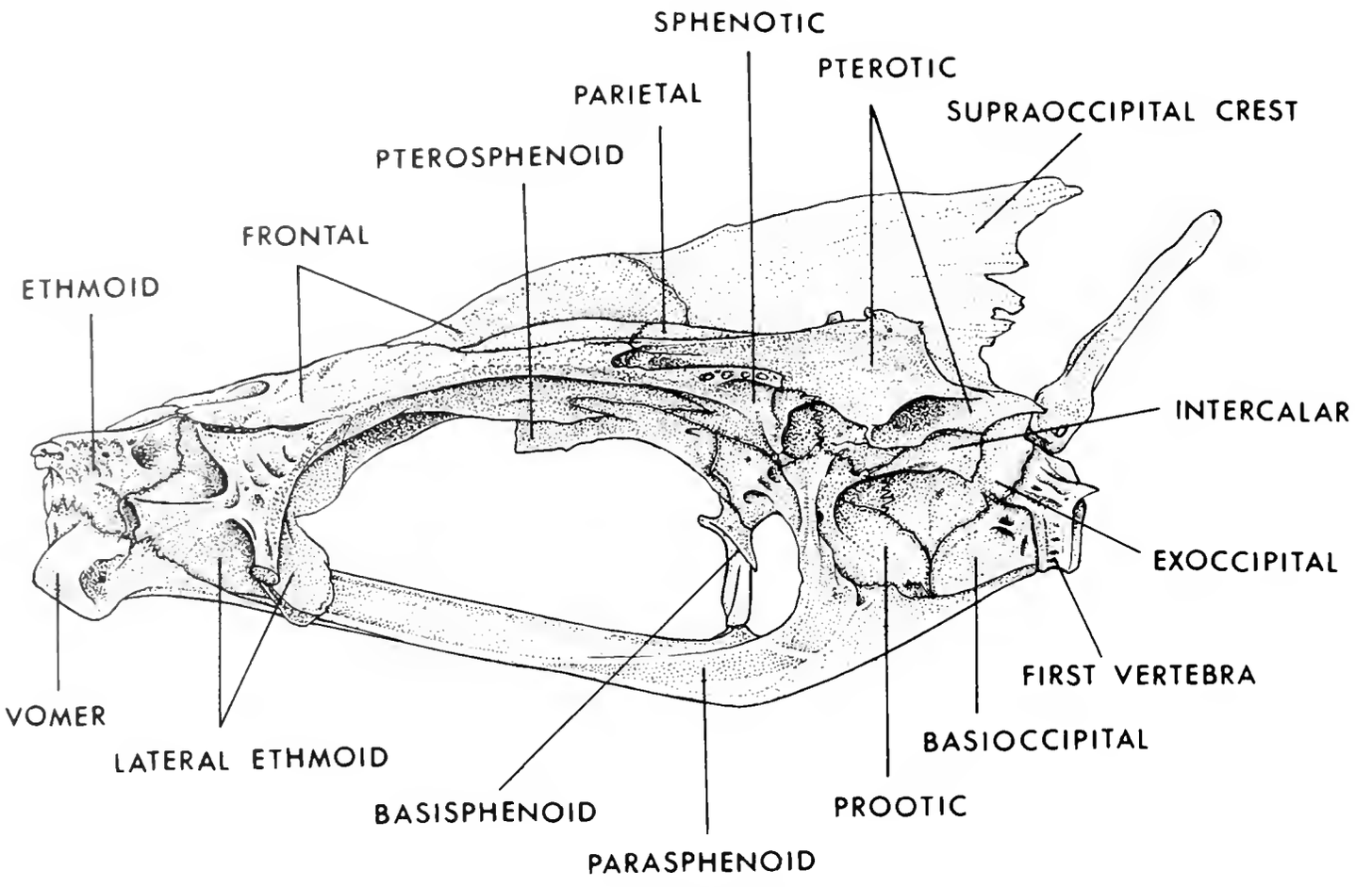


FIGURE 22.—Lateral view of skull of *Gymnosarda unicolor*, Truk Islands, 696 mm FL.

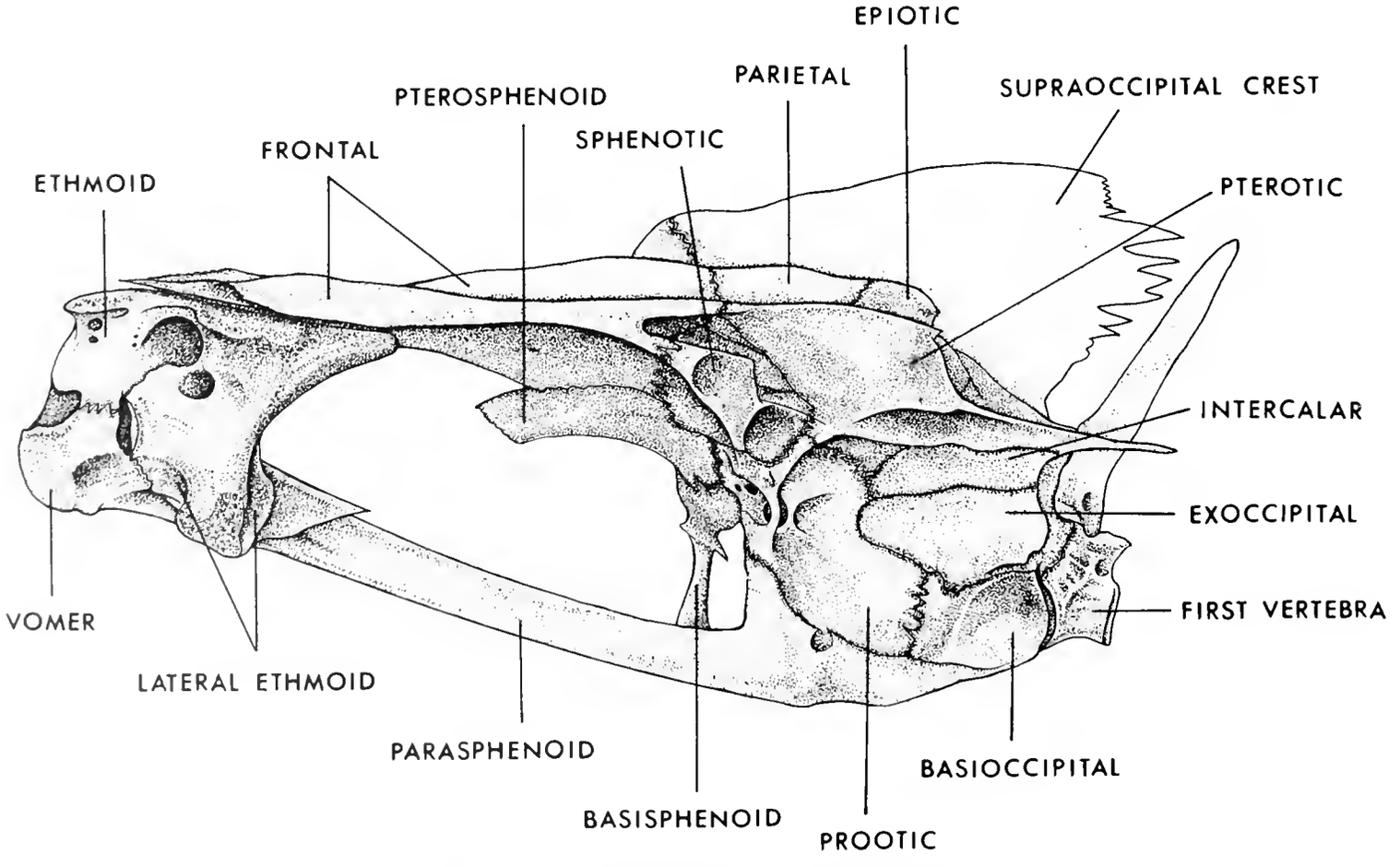


FIGURE 23.—Lateral view of skull of *Sarda sarda*, eastern United States, 388 mm FL.

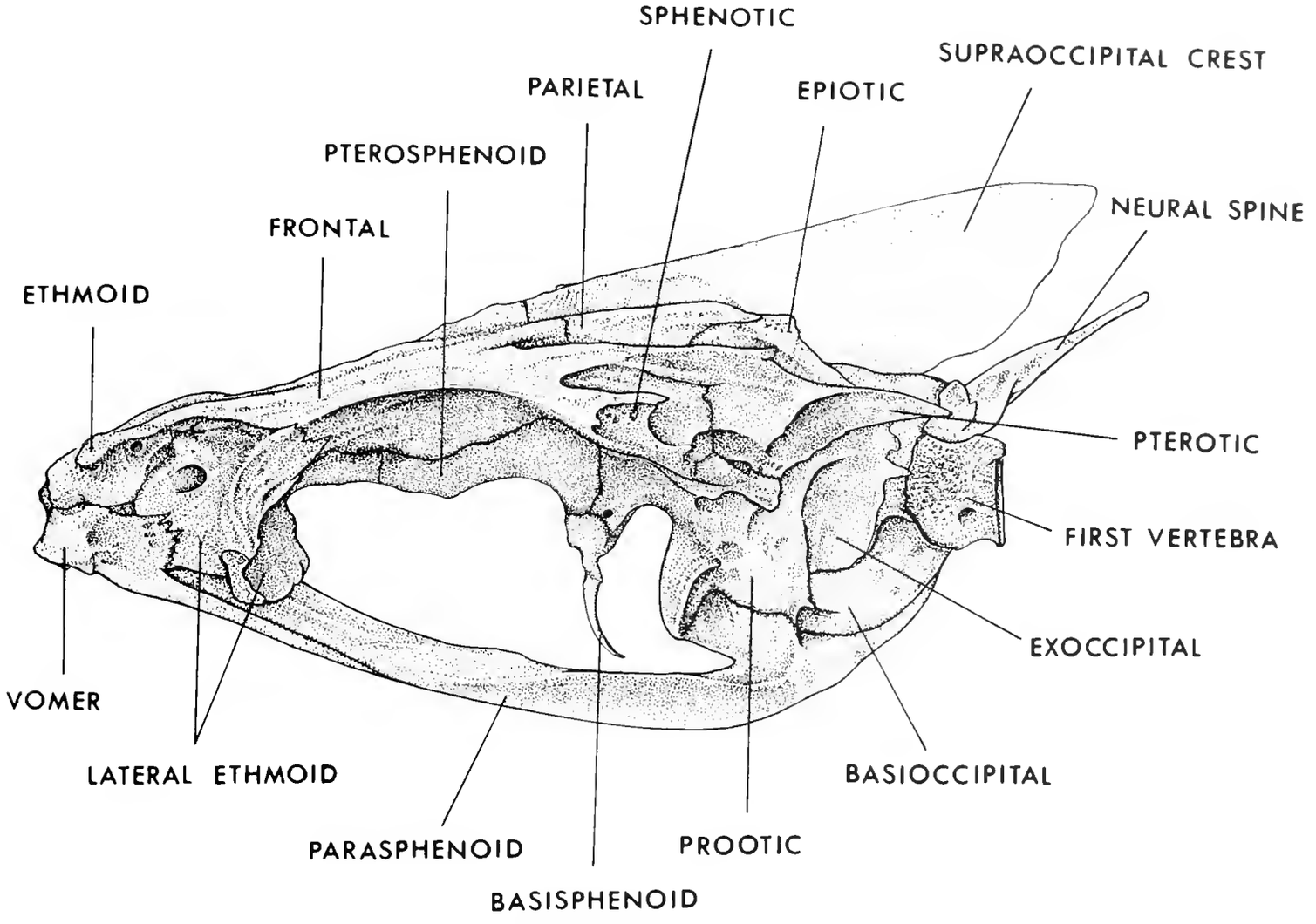


FIGURE 24.–Lateral view of skull of *Allothunnus fallai*, California, 680 mm FL.

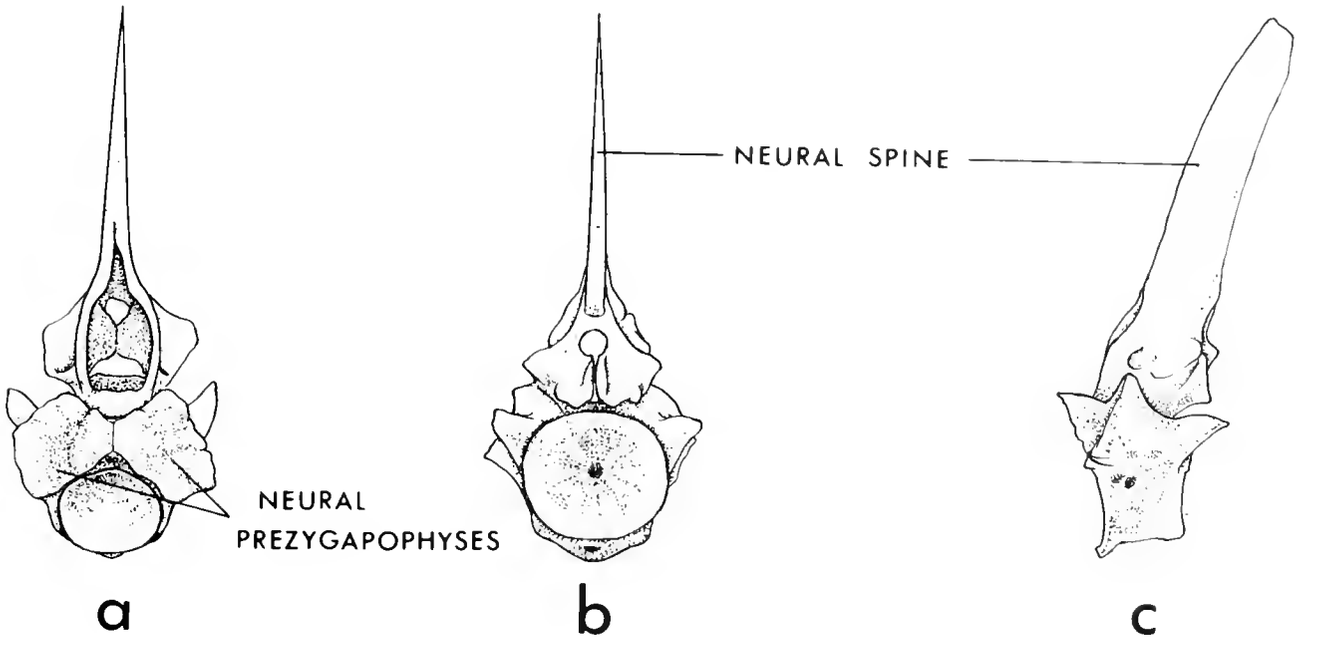


FIGURE 25.–First vertebra of *Sarda chiliensis*, Callao, Peru, 571 mm FL. a. Anterior view. b. Posterior view. c. Lateral view.

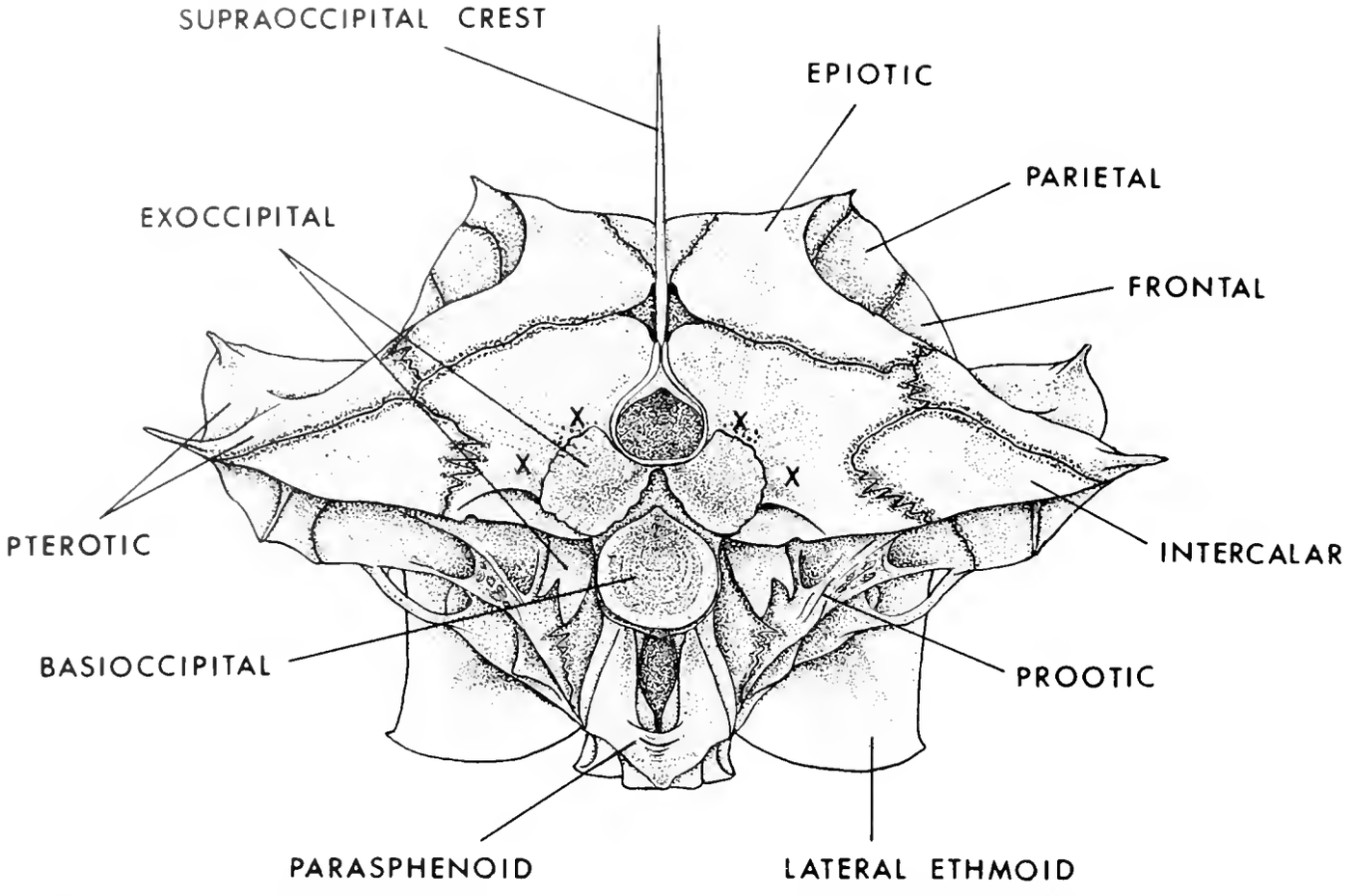


FIGURE 26.–Rear view of skull of *Sarda chiliensis*, Callao, Peru, 571 mm FL. X's indicate the points of attachment of intermuscular bones.

temporal. In *Allothunnus*, this protuberance projects out from the posterior outline of the skull, while in other bonitos this outline is smooth. Ventrally, the intercalar articulates with the prootic bone anteriorly and the exoccipital and pterotic bones laterally (Figures 15-19).

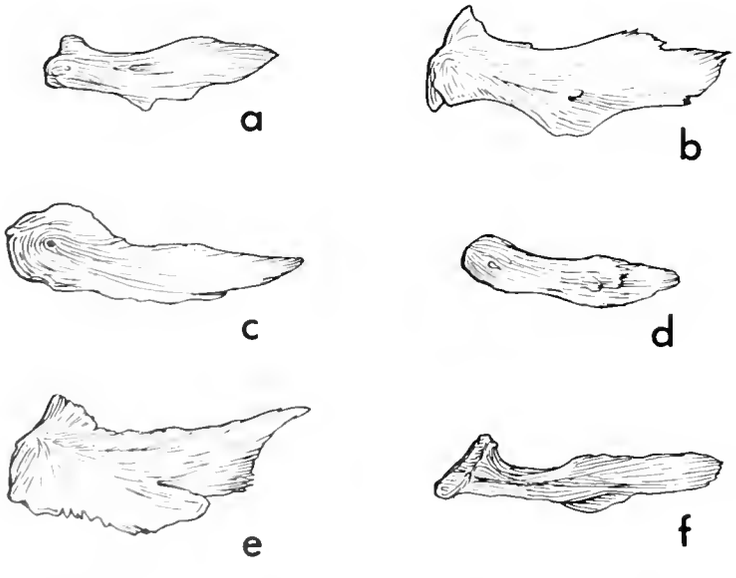


FIGURE 27.–Nasals of six species of Sardini, left external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 442 mm FL. d. *Sarda sarda*, Florida, 333 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a-d drawn twice as large as e and f.

BASICRANIAL REGION.–This region consists of the parasphenoid, basioccipital and exoccipital bones, and forms the posteroventral base of the skull.

Parasphenoid.–Ventrally, the parasphenoid is a long cross-shaped bone (Figures 15-19) which articulates with the vomer anteriorly and forms the ventral axis of the skull. The lateral wing of the parasphenoid extends dorsolaterally along the ventral ridge of the prootic bones on either side and has a pointed end, which forms part of the anteroventral wall of the posterior myodome. Posteriorly, the parasphenoid bifurcates into two lateral flanges which attach dorsally to the corresponding posteroventral flanges of the basioccipital bone and surround the posterior opening of the posterior myodome. A ventrally projecting keel is present along the posterior two-fifths of the parasphenoid. The V-shaped joint connecting the parasphenoid with the vomer anteriorly is most

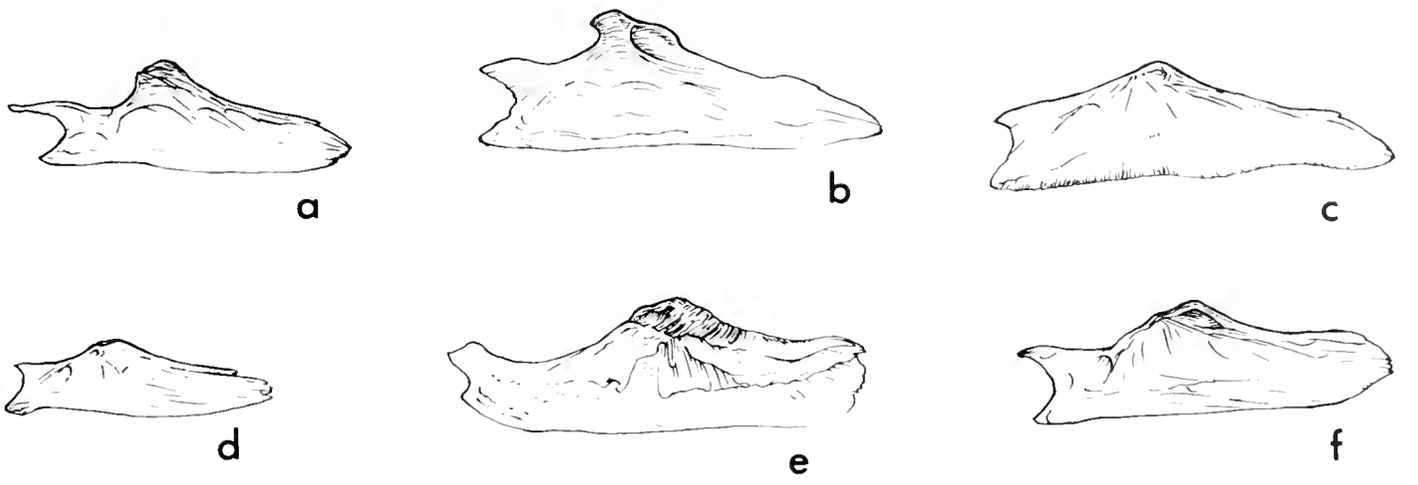


FIGURE 28.—Larchrymals of six species of Sardini, left lateral view. a. *Cybiosarda elegans*, New South Wales, 360 mm FL. b. *Orcynopsis unicolor*, Tunisia, 495 mm FL. c. *Sarda orientalis*, Tokyo, 350 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a, b, and c drawn twice as large as d, e, and f.

elongate in *Allothunnus* and the species of *Sarda* (also see vomer). In ventral view, the general characteristic of the parasphenoid is a gradual narrowing of the bone from anterior to posterior. *Orcynopsis* has the widest and strongest parasphenoid; species of *Sarda* have the weakest. Broad parasphenoids are also present in *Scomberomorus* and *Acanthocybium*; narrower parasphenoids in *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*. The broadest portion of the parasphenoid is usually located at or before the tip of the V-shaped joint with the vomer in all bonitos except *Allothunnus*. In five skulls (406-778 mm FL) of *Allothunnus*, the broadest portion of the parasphenoid is in the posterior half of the bone, about at the beginning of the ventral keel. This is in contradiction to Nakamura and Mori (1966, fig. 4B), whose illustration of a specimen (876 mm FL) shows the parasphenoid as similar to other bonitos.

The anterior edge of the lateral wings of the parsphenoid is smoothly concave forward and forms a dorsolaterally directed shelf, visible ventrally in all bonitos except *Allothunnus*. In *Allothunnus* (Figure 19), the anterior edge of the lateral wing is deeply concave and the wing projects vertically along the prootic wing toward the roof of the skull, as in the more advanced scombrids. The posterior opening, between the lateral flanges of the parasphenoid, is usually elongate and the lateral flange does not extend beyond the juncture of the skull with the first centrum (Figures 15-19). In our *Gymnosarda* skulls, this opening is much smaller than in the other bonitos (Figure 17). A thin layer of bone covers the anterior portion of the opening, perhaps indicating additional ossification in larger individuals of this particular species.

In lateral view (Figures 20-24), the parasphenoid forms the ventral border of the orbit and connects with the lateral ethmoid, basisphenoid, prootic, and basioccipital bones dorsally. The ventral keel projects further ventrally in *Gymnosarda* and *Allothunnus* than in *Orcynopsis* and *Cybiosarda*. The posterior one-third of the parasphenoid and its lateral flanges are strongly convex in *Allothunnus*, forming the unique posteroventral outline of its skull (Figure 24). A middorsal ridge is also present in all bonitos. This ridge arises from the juncture of the lateral ethmoids, where the ridge projects the most, and merges into the main axis of the parasphenoid posteriorly at about the beginning of the ventral keel. Usually, a triangular piece of cartilage, connecting with the lateral ethmoid, covers the most anterior end of the dorsal ridge. The middorsal ridge is least prominent in *Cybiosarda*.

Basioccipital.—The basioccipital is the most posteroventrally located bone of the skull. It is shaped like an inverted U with lateral flanges on either side of the skull and forms the roof and lateral walls of the posterior myodome. Anteriorly, the basioccipital is attached to the prootic bones and dorsally with the exoccipital bones. Its lateral flanges expand ventrally to meet the flat posterior flanges of the parasphenoid. Posteriorly, the lateral flanges fuse to form a circular margin in a slightly backward oblique position and attach to the margin of the first vertebral centrum (Figure 25). In lateral view, a distinct deep concave pit is

present at the posterodorsal corner of the basioccipital in all bonitos (Figures 20-24). Godsil (1954) first noted this feature, "a deep-rimmed, crater-like depression in the basioccipital," and stated that "This character is sufficient to separate *Sarda* from any species of the Plecostei." In 1955, Godsil modified this statement to ". . . it is not a positive diagnostic generic character." In comparing this basioccipital depression with other scombrids, we found it to be diagnostic of bonitos. In *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* only a shallow concave surface is present; *Scomberomorus* and *Acanthocybium* have small foramina on the corresponding position of the basioccipital. *Grammatorcynus* has a similar depression but it is much shallower.

Exoccipital.–The exoccipitals connect the skull to the first vertebra dorsally. The exoccipital articulates with the epiotic and supraoccipital bones anterodorsally, the intercalar laterally, and with the other exoccipital posterodorsally. In ventral view, the exoccipital articulates with the prootic anteriorly, basioccipital medioventrally, and intercalar laterally. In posterior view, the foramen magnum is framed by the exoccipitals. Dorsally, a small foramen is present at the medioposterior corner of the exoccipital and it opens into the brain cavity. The exoccipital bones are similar, with an intermuscular bone attached, in all bonitos except *Gymnosarda* which has none and *Sarda* which has two (Figure 12).

OTOLITHS.–The first figures of bonito otoliths were presented by Shepherd (1910a, b) who illustrated the asteriscus and sagitta of *Sarda sarda* along with other miscellaneous eastern Atlantic species, but his figures are too small and poorly defined to be of any comparative value. Chaine (1957) published good figures of the sagittae of *Sarda sarda* as well as two species of *Scomber*, two of *Thunnus*, and *Scomberomorus tritor*. Bauzá Rullán (1961:155-156, pl. 1, figs. 7-10) also illustrated the sagitta of *S. sarda*. Two studies include information about intraspecific variation in the shape of bonito sagittae. Chaine (1957) discussed variation in *S. sarda*; Kuo (1970:125, fig. 7) showed considerable variation with outline sketches of sagittae from the left and right sides of 47 *S. chiliensis* from California in an age and growth study. Fitch and Craig (1964) made the first comparative study of scombrid otoliths when they compared the sagittae of eastern Pacific scombrids in an attempt to assess the relationships of *Allothunnus fallai*. They found that scombrid sagittae, except for *Scomber japonicus*, have a long thin rostrum, finely serrate margins, and a deep sulcus on the inner face. Among bonitos, they compared the otoliths of *Allothunnus* and three species of *Sarda* (*chiliensis*, *orientalis*, and *sarda*). *Allothunnus* and *S. chiliensis* were illustrated.

Specific Characters.–We calculated proportions of the sagittae as percent of the otolith (sagitta) length (OL) in fork length and the greatest height (H) in length of sagitta and in length of rostrum (R).

	FL (mm)	*OL/FL* (%)	*H/OL* (%)	*H/R* (%)
Orcynopsis	576	1.54	48.3	1.3-1.4 ($n=3, \bar{x}=1.39$)
Cybiosarda	365	1.56	44.6	1.0-1.2 ($n=4, \bar{x}=1.09$)
Sarda sarda	418	1.17	35.7	0.9
S. orientalis	350	1.10	33.8	0.8
Gymnosarda	789	0.91	44.4	1.2
Allothunnus	775	0.92	44.8	1.2

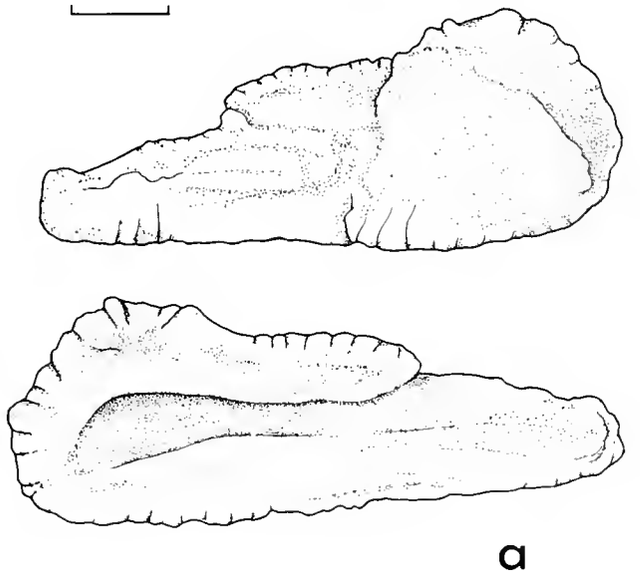
($n=1$ unless otherwise noted)

The sagitta of *Orcynopsis* is the largest among the bonitos relative to fork length. It has a ridge extending from the postdorsal part of the outer surface to the middle of the otolith. It also has the shortest and widest rostrum and the deepest sulcus of any bonito (Figure 29b).

The sagitta of *Cybiosarda* is larger and heavier than *Sarda*. It is similar in size to *Orcynopsis* but has a longer and thinner rostrum. *Cybiosarda* has two ridges extending from the middorsal and posteroventral parts of the sagittae toward the ventral and middorsal areas respectively (Figure 29a). The latter one seems to be weaker. Both *Cybiosarda* and *Orcynopsis* are distinct in having a winglike flange which extends outward and forms a small platform at the posterodorsal margin on the inner side.

The sagittae in the species of *Sarda* are small and have similar outlines (Figure 29c, d). A pyramidlike ridge is present in the middle of the posterior half of the sagitta. They also have the

FIGURE 29.–Sagittae of six species of Sardini, upper figure of each pair is the outer view, lower figure the inner view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 567 mm FL. c. *Sarda orientalis*, Tokyo, 350 mm FL. d. *Sarda sarda*, Azores, 418 mm FL. e. *Gymnosarda unicolor*, Marshall Islands. f. *Allothunnus fallai*, Tasmania, 775 mm FL. (Scale indicates 1 mm.)



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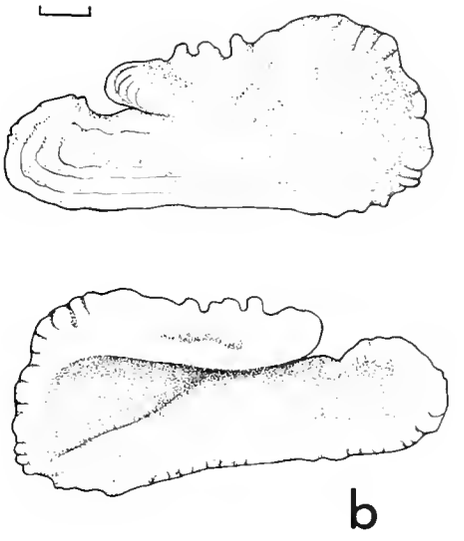

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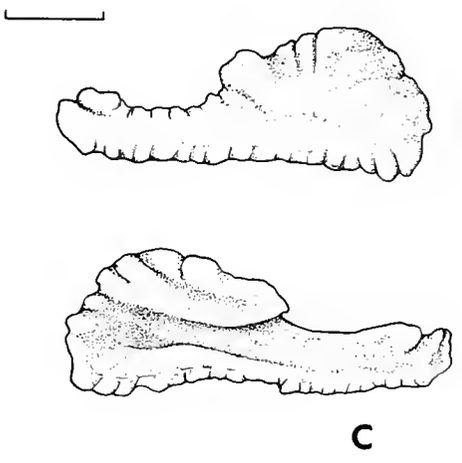

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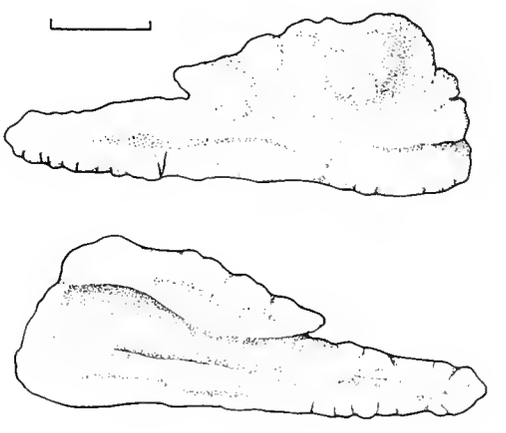

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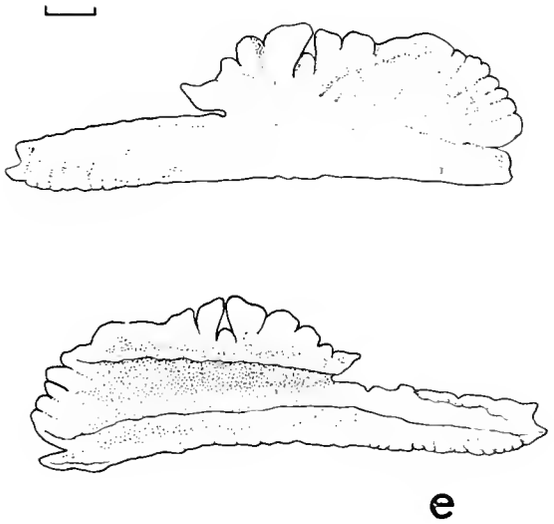
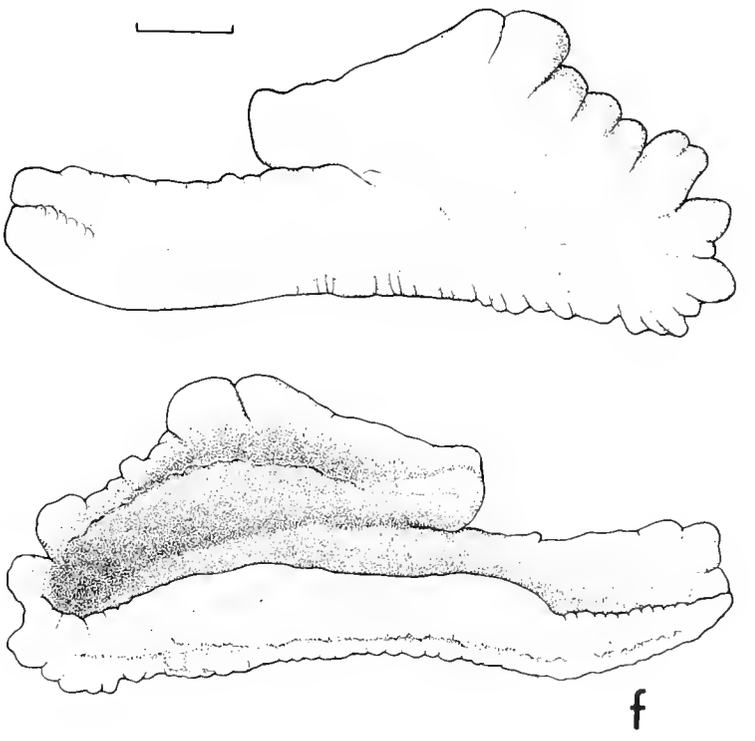


e



f

longest and narrowest rostra among bonitos. The dorsal process above the rostrum seems to vary considerably inter- and intraspecifically (see Kuo 1970, fig. 7).

The sagittae of *Gymnosarda* are distinct from those of all other bonitos by their extreme curvature when viewed in situ from above, by their concave ventral margin (sagittae of all other bonitos have relatively straight ventral margins), and by the fact that except for minor protuberances and other irregularities the dorsal margin, in the posterior half of the otolith, roughly parallels the ventral margin, giving a sameness of height to the otolith in this region. The sulcus is more distinctive on the inner surface. The posterior dorsal margin is deeply serrate. No pyramidlike ridge is present in the middle of the posterior half. Laterally, the deepest part of the sagitta is in front of the middle of the posterior half.

The sagitta of *Allothunnus* is small and similar in size to the species of *Sarda*. It has a very distinctive triangular outline; with an acute posteroventral angle and no prominent ridges on the outer surface. The inner surface of the sagitta has a deep sulcus with a very prominent dorsal ridge.

Branchiocranium

The branchiocranium is divided into five sections: mandibular arch, palatine arch, hyoid arch, opercular apparatus, and branchial arch.

MANDIBULAR ARCH.–The mandibular arch is composed of the upper jaw (premaxilla, maxilla, and supramaxilla) and the lower jaw (dentary, angular, and retroarticular). Teeth are borne on the premaxilla and dentary, and the number of teeth on these bones is a useful taxonomic character.

Dentition.–Conical teeth are present on the upper and lower jaws in all bonitos. These teeth differ from the laterally compressed teeth with serrate edges found in Spanish mackerels (Scomberomorini) and are generally larger than the tiny conical teeth of the higher tunas (Thunnini). In addition to jaw and palatine teeth,

TABLE 5.–Number of teeth in the upper jaw in species of Sardini. (Mean of left and right sides rounded off upwards to nearest whole number.)

Species	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	*N*	$\bar{x}$
Cybiosarda elegans		1	2	1	2	1	5	4	4	1	1										22	17.9
Orcynopsis unicolor:																						
E Mediterranean							2	3	2	5	5	5	6	3	2						33	22.2
Cent. Mediterranean								1	—	—	3	—	—	1	1	1					7	23.3
Atlantic										2	—	1	2								5	22.6
Total							2	4	2	7	8	6	8	4	3	1					45	22.4
Sarda australis					2	3	2	7	2	2	1										19	18.7
Sarda chiliensis:																						
NE Pacific									2	9	11	15	16	11	6	2	—	2	2		76	23.7
SE Pacific							3	3	3	—	5	9	7	2	6	2	1				41	23.0
Total							3	3	5	9	16	24	23	13	12	4	1	2	2		117	23.5
Sarda orientalis:																						
Indian Ocean		1	3	—	3	1	2	1													11	15.9
NW Pacific	1	2	2	4	4	1															14	14.8
Cent. Pacific	1	—	1	2																	4	14.0
E Pacific		2	3	1	4	4	3	1	1												19	16.2
Total	2	5	9	7	11	6	5	2	1												48	15.5
Sarda sarda:																						
North America						8	4	18	12	10	6										58	19.5
South America					1	—	—	1	2	2	6	3									15	21.2
NE Atlantic							2	1	—	—	—	—	5	1							9	22.2
Mediterranean-Black Sea					1	1	1	—	5	6	8	5	4								31	21.4
(Demir 1964, Turkey)			(1	2	2	4	17	18	19	12	14	11	11	5	2)						(118)	(20.6)
Gulf of Guinea-S. Africa						3	2	5	4	3	3	5	1								26	20.4
Total					2	12	9	25	23	21	23	13	10	1							139	20.5
Gymnosarda unicolor:																						
Indian Ocean				2	—	4	1	—	—	—	—	—	1	—	1						9	18.4
W Pacific			1	3	3	1	2	3	3	2	—	1	1	—	—	1	—	—	1	1	23	19.8
Total			1	5	3	5	3	3	3	2	—	1	2	—	1	1	—	—	1	1	32	19.4
Allothunnus fallai															(40-42-44-51-54-55)						6	47.7

patches of teeth are present on the vomer and tongue in some genera. *Allothunnus* has many very small teeth (40-55) on each of the upper and lower jaws, compared to a range of 12-31 on the upper jaw and 10-25 on the lower jaw in other bonitos (Tables 5, 6). *Orcynopsis* averages more teeth in both upper and lower jaws than does *Cybiosarda*. Both *Gymnosarda* and *Sarda australis* have a very wide range in the number of jaw teeth. In the eastern Pacific, the tropical *Sarda orientalis* differs from the south and north temperate *S. chiliensis* in having fewer upper (13-20, $\bar{x}$ 16.2 vs. 18-30, $\bar{x}$ 23.5) and lower (10-17, $\bar{x}$ 13.2 vs. 14-25, $\bar{x}$ 19.2) jaw teeth. Numbers of jaw teeth and gill rakers are correlated: note especially *Allothunnus* with 70-80 gill rakers and *Orcynopsis* with more gill rakers than *Cybiosarda* (Table 7).

Premaxilla.—The premaxilla (Figure 30) is a long curved bone with a stout arrowhead-shaped anterior end and teeth on the ventral margin. The angle between the oblique anterior and the ventral margin of the premaxilla is most acute in *Gymnosarda* and *Orcynopsis*, similar to *Scomberomorus*. It is almost perpendicular with a small anterior projection in *Allothunnus* (Figure 30f), as in *Thunnus*. The sharp anterior dorsal process of the premaxilla in the species of *Sarda* separates them from the other bonitos (Figure 30c, d). The posterior end of the premaxilla in *Allothunnus* is also similar to *Thunnus*, sharper and thinner than in the other bonitos. The main axis of the premaxilla is curved more in *Gymnosarda*, *Cybiosarda*, and *Orcynopsis* than in *Sarda* and *Allothunnus*.

Maxilla.—The maxilla (Figure 31) is a long curved bone with two irregularly shaped condyles which join the premaxilla anterodorsally. The main axis of the maxilla is most curved in *Orcynopsis* and most flattened in *Gymnosarda* and *Allothunnus* (as in *Thunnus*). A process from the lower condyle of the anterior portion of the maxilla protrudes ventrally in *Cybiosarda* and the species of *Sarda*. This projection is not present in *Scomberomorus* or *Thunnus*. The posterior ends of the maxillae of *Gymnosarda* and *Allothunnus* are broader than in other bonitos. The anterior ends of

TABLE 6.—Number of teeth in the lower jaw of species of Sardini. (Mean of left and right sides rounded off upwards to nearest whole number.)

Species	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	*N*	$\bar{x}$
Cybiosarda elegans	2	1	7	8	1	1	2	1									23	13.0
Orcynopsis unicolor:																		
E Mediterranean			1	1	2	3	6	3	9	5	1	2					33	17.1
Cent. Mediterranean							1	1	2	1							5	17.6
Atlantic						1	—	1	1	1	1						5	17.8
Total			1	1	2	4	7	5	12	7	2	2					43	17.2
Sarda australis		1	2	2	5	5	2	1	—	—	1						19	14.5
Sarda chiliensis:																		
NE Pacific						2	2	7	18	16	9	10	8	2	1	2	77	19.4
SE Pacific					1	3	4	5	8	7	4	2	5	4			43	18.9
Total					1	5	6	12	26	23	13	12	13	6	1	2	120	19.2
Sarda orientalis:																		
Indian Ocean		2	4	3	—	2											11	12.6
NW Pacific		2	3	5	3	1											14	12.9
Cent. Pacific				3	1												4	13.3
E Pacific	2	1	3	6	2	3	1	1									19	13.2
Total	2	5	10	17	6	6	1	1									48	13.0
Sarda sarda:																		
North America			3	4	12	18	15	3	2	1							58	15.0
South America					2	2	4	3	3								14	16.2
NE Atlantic						1	—	4	—	1	2	—	—	—	1		9	18.4
Mediterranean-Black Sea				1	2	4	6	3	10	4	1						31	16.9
(Demir 1964, Turkey)			(1	6	9	21	18	22	18	16	3	3	1)				(118)	(16.7)
Gulf of Guinea-S. Africa				1	5	3	7	6	2	2							26	16.0
Total			3	6	21	28	32	19	17	8	3	—	—	—	1		138	16.0
Gymnosarda unicolor:																		
Indian Ocean	1	—	2	4	—	—	—	1	—	1							9	13.5
W Pacific	2	5	4	3	4	1	1	1	—	—	—	1	1	—	1		24	13.9
Total	3	5	6	7	4	1	1	2	—	1	—	1	1	—	1		33	13.8
Allothunnus fallai													(41-42-49-53)				4	46.3

TABLE 7.–Total number of gill rakers on the first arch in species of Sardini.

Species	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	N	$\bar{x}$
Cybiosarda elegans					3	12	4	1													20	13.2
Orcynopsis unicolor:																						
E. Mediterranean						1	8	18	8	1											36	15.0
Cent. Mediterranean					1	—	1	3	1												6	14.5
(Postel 1956a, Tunisia)						(2	51	96	34	6)											(189)	(15.0)
Atlantic							1	4	1												6	15.0
Total					1	1	10	25	10	1											48	14.9
Sarda australis												3	10	5							18	20.1
Sarda chiliensis:																						
NE Pacific																3	9	12	10	6	40	25.2
(Kuo 1970)															(1	28	226	229	25	1)	(510)	(24.5)
SE Pacific																3	4	9	10	3	29	25.2
(Kuo 1970)																(6	41	44	1)		(92)	(24.4)
Total																6	13	21	20	9	69	25.2
Sarda orientalis																						
Indian Ocean			2	4	2	1															9	11.2
NW Pacific		2	4	3	1	1															11	10.0
Cent. Pacific			4																		4	10.0
E Pacific	1	—	2	7	4	3															17	11.3
Total	1	2	12	14	7	5															41	11.0
Sarda sarda:																						
North America									6	25	14	7	2	—	1						55	17.6
South America										2	6	2	2	2							14	18.7
NE Atlantic											3	—	4	4							11	19.8
Mediterranean-Black Sea											1	5	7	5	12	2					32	20.9
(Demir 1964, Turkey)									(1	2	31	172	427	247	112	7	1)				(1,000)	(20.3)
Gulf of Guinea-S. Africa											1	1	11	4	10	1					28	20.9
Total									6	27	25	15	26	15	23.	3					140	19.3
Gymnosarda unicolor:																						
Indian Ocean						3	4	1													8	12.7
W Pacific				1	7	13															21	12.6
Total				1	10	17	1														29	12.6
Allothunnus lallai																	(72-73-74-75-76-80)				6	75.0

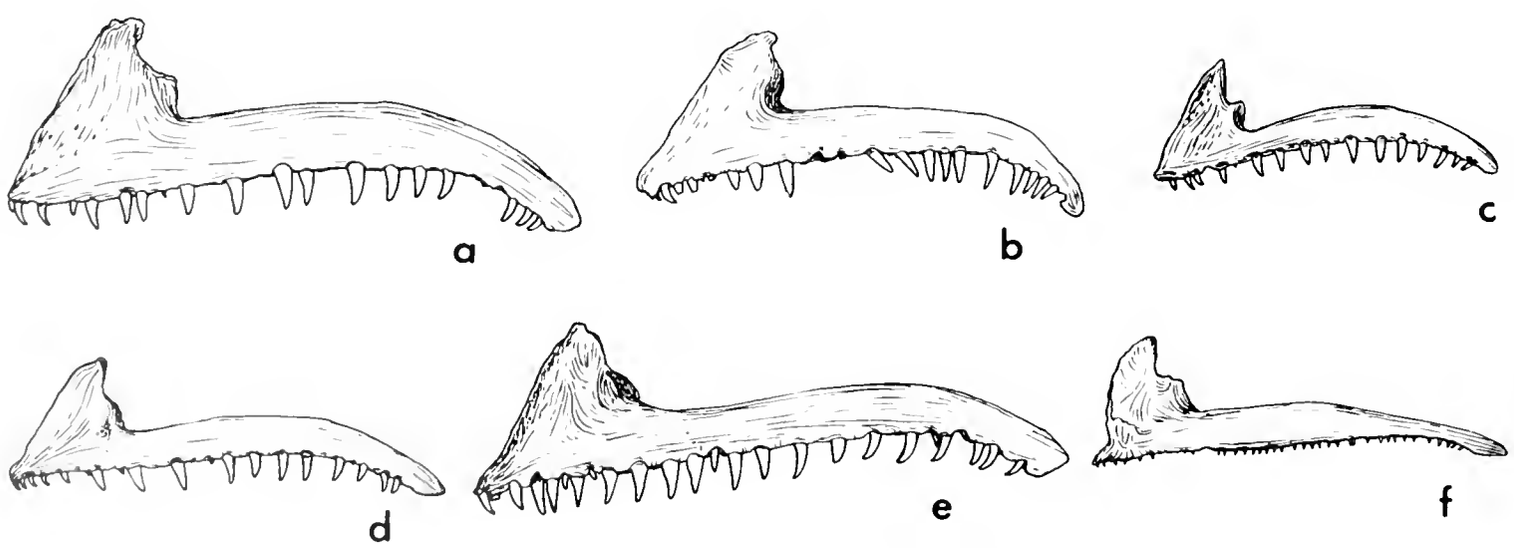


FIGURE 30.–Left premaxillae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

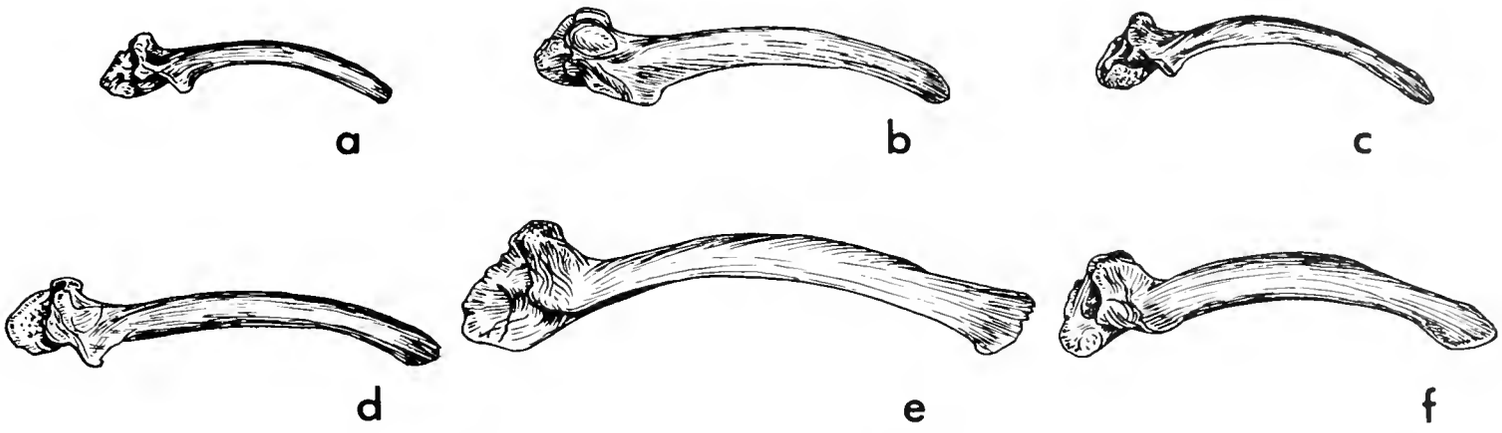


FIGURE 31.—Left maxillae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

the maxillae of *Cybiosarda* and *Orcynopsis* are more pointed than in the other bonitos.

Supramaxilla.—The supramaxilla covers the posterior part of the maxilla and is partly covered anteriorly by the lachrymal (see Figure 9). It has a flat oval posterior main body and an anterior process which forms a shelf on the inner surface of the bone that continues as a ridge posteriorly. *Allothunnus* has a smoother dorsal margin and a more gradual transition between the process and the body giving the bone a more triangular shape (Figure 32h). The posterior edge of the supramaxilla of *Gymnosarda* is more curved and the anterior process is blunter (Figure 32g). *Orcynopsis* has a much deeper main body than *Cybiosarda*. Godsil (1954) used the width of this bone (called auxiliary maxillary) to separate *Sarda chiliensis* from *S. orientalis* in the eastern Pacific. He found the bone to be much narrower in relation to length in *S. orientalis* (ratio of width to length 4.1-4.4) than in northeast Pacific *S. chiliensis* (ratio 3.0-3.1). We also found that the main body of the supramaxilla is broader in *S. chiliensis* and narrower in *S. orientalis*. There do not appear to be any significant differences between northeast and southeast Pacific populations of *S. chiliensis* or between Indo-West Pacific and eastern Pacific *S. orientalis* in this character. *Sarda sarda* and *S. australis* have the supramaxilla intermediate in width between the wide bone present in *S. chiliensis* and the narrow bone in *S. orientalis*.

Dentary.—The dentary divides posteriorly into a dorsal dentigerous branch and a ventral branch, which are usually about equal in length, although the ventral branch is slightly longer in *Gymnosarda* and *Allothunnus* and sometimes in *Sarda* (Figure 33e, f). *Allothunnus* has a row of numerous (40-50) tiny teeth on the dentary while the other genera have fewer (10-25) strong conical teeth. The number of teeth varies among genera and species (Table 6). The shape of the anterior margin of the dentary can be used to divide the bonitos into three distinct groups. The anterior margin of the bone forms an acute angle with the dentigerous dorsal margin in *Sarda*, and there is a notch present at the upper portion of the anterior margin. The notch is deeper and located in the middle of the margin in *Allothunnus* (Figure 33f). *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* lack an anterior notch (Figure 33a, b, e). Another notch is present in *Gymnosarda*, on the anterior part of the ventral margin; there is a slight depression in this position in the other genera of bonitos. In overall shape and size, the dentary of *Sarda* is more elongate, especially that of *S. orientalis*. The angle between the dorsal and ventral arms of the dentary is slightly greater in *Gymnosarda*. The dorsal branch is wider, flatter, and thinner in *Allothunnus*.

Angular and Retroarticular.—The triangular anterior end of the angular (frequently called articular) fits into the dentary anteriorly (Figure 9). *Allothunnus* has the most elongate angular (Figure 34f). The strongest angular is found in *Gymnosarda* (Figure 34e) followed by *Cybiosarda* and *Orcynopsis* (Figure 34a, b). An anteriorly projecting spine is present on the ventral edge of the angular. This spine is thin and weak in

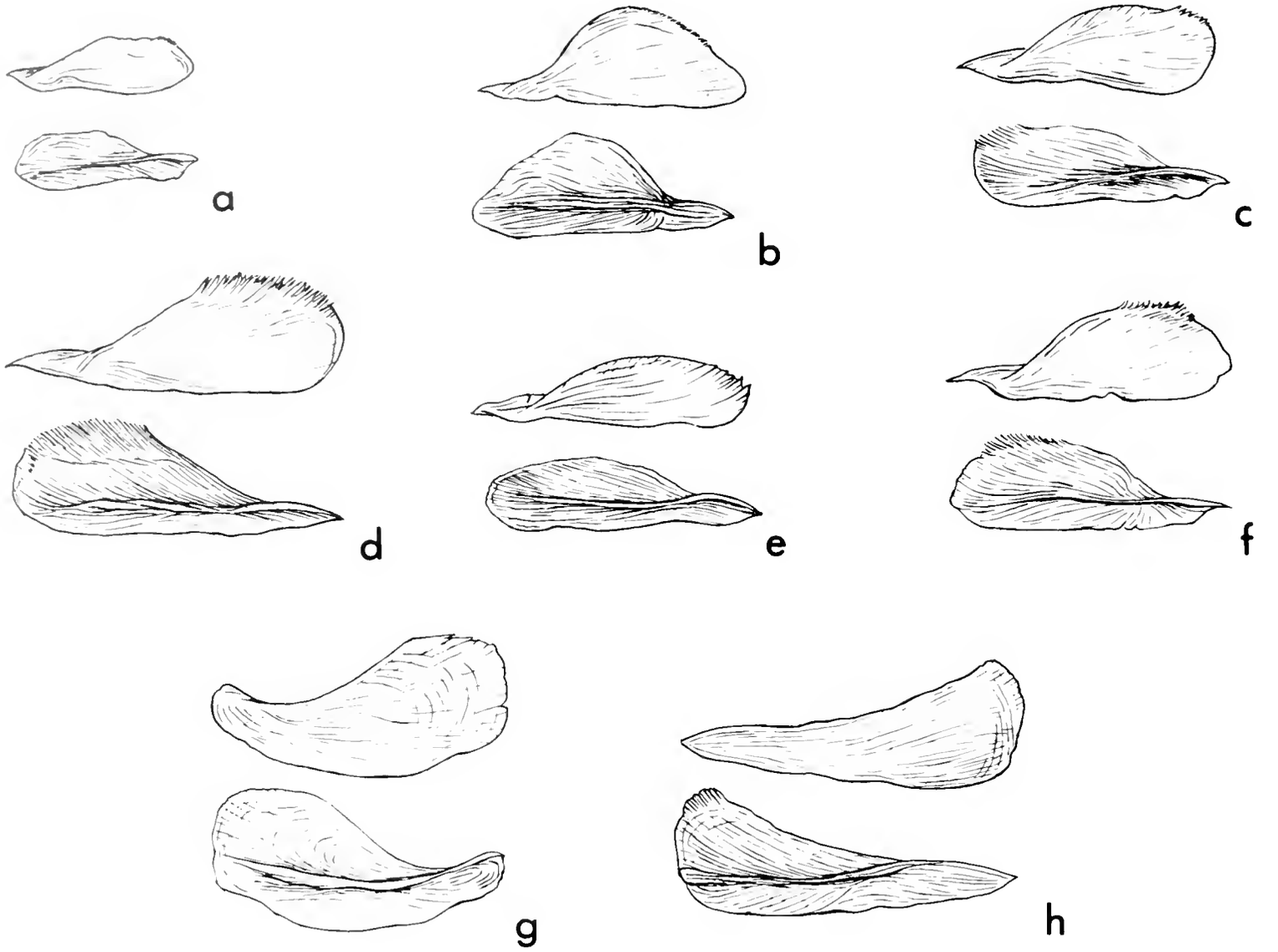
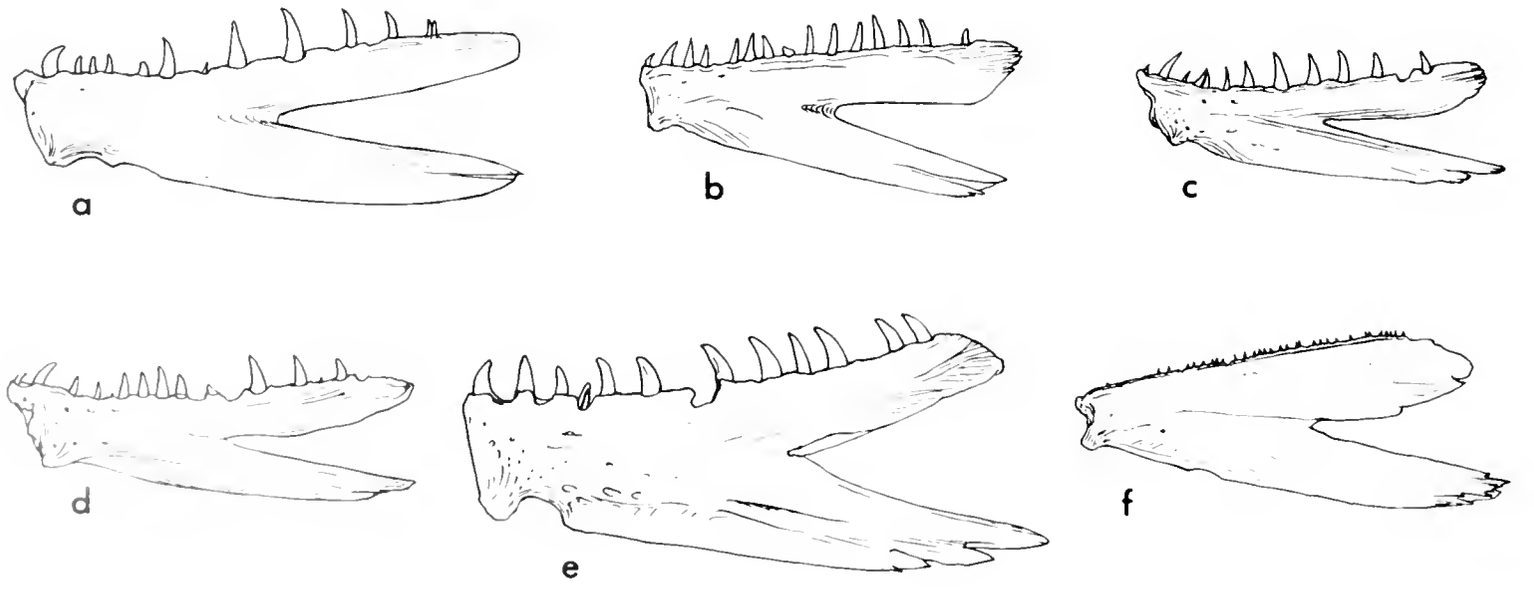


FIGURE 32.–Left supramaxillae of eight species of Sardini, upper figure of each pair is the external view, lower the internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 453 mm FL. d. *Sarda chiliensis*, Callao, Peru, 571 mm FL. e. *Sarda orientalis*, Jalisco, Mexico, 434 mm FL. f. *Sarda sarda*, Tunisia, 504 mm FL. g. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. h. *Allothunnus fallai*, Tasmania, 775 mm FL.



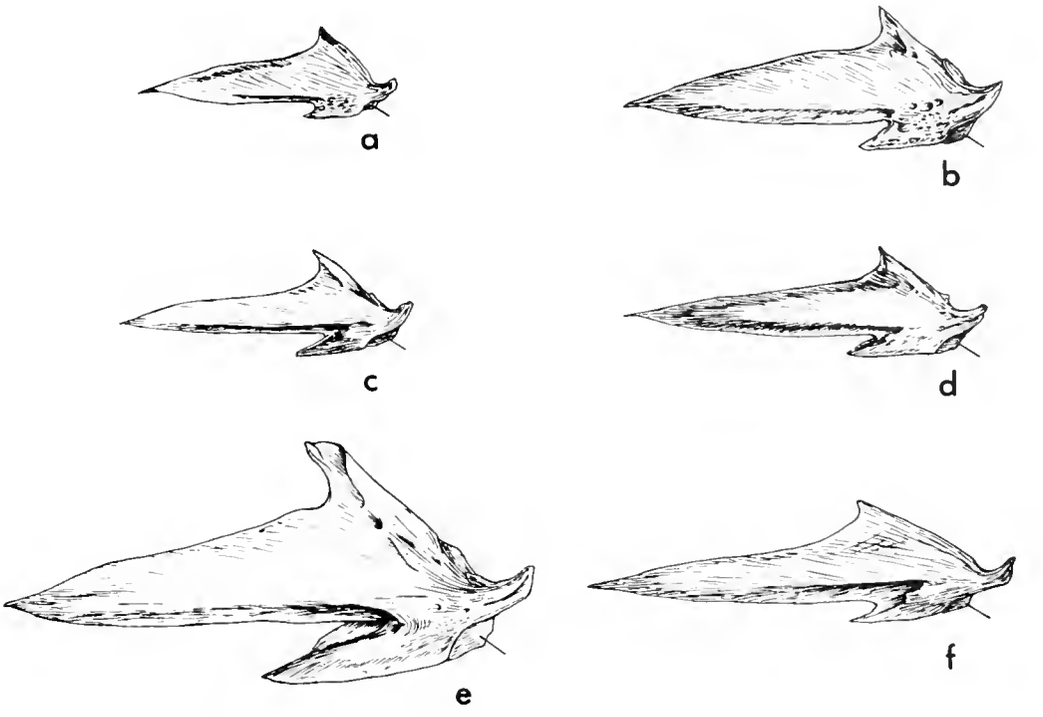


FIGURE 34.—Left angulars and retroarticulars of six species of Sardini, external view. Line indicates position of retroarticular. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

Allothunnus as in *Thunnus*. There is also an anterodorsally projecting spine on the dorsal edge of the angular. This spine has a sharp point in the bonitos, except in *Gymnosarda* where the spine is heavier and blunt as in *Scomberomorus*. The retroarticular bone (frequently called angular) is rhomboid and attached firmly to the posteroventral margin of the angular. No differences were found among the retroarticulars of the bonitos.

PALATINE ARCH.—The palatine arch consists of four pairs of bones in the roof of the mouth: palatine, ectopterygoid, entopterygoid, and metapterygoid.

Palatine.—For illustration (Figure 35), the palatine bones were placed flat with the external side up and tipped so that when viewed from above the palatine teeth and part of the anterior end of dorsal ridge were exposed. A longer ventral ridge and a shorter dorsal ridge are present as in *Thunnus*. *Cybiosarda*, *Orcynopsis*, *Gymnosarda*, and *Allothunnus* have slightly elongated dorsal ridges compared to *Sarda* (Figure 35c, d). The anterior process of the dorsal ridge is hooked in all bonitos except *Allothunnus* in which the distance between the process and the front of the ventral ridge is greater (Figure 35f).

Teeth are located along the inferior margin of the ventral ridge. Palatine teeth vary from a relatively few, large, conical teeth curved posteriorly and arranged in a single row to a broad roughened patch of tiny villiform teeth. Species of *Sarda* have one row of small conical teeth, the number of teeth varying from 7 to 22, usually 10-18. *Sarda chiliensis* has the most palatine teeth (9-22, $\bar{x}$ 15.2) but it broadly overlaps with the other three species: *S. sarda* (8-21, $\bar{x}$ 12.3), *S. orientalis* (8-19, $\bar{x}$ 11.9), and *S. australis* (7-14, $\bar{x}$ 10.7). *Cybiosarda* has about 50 small teeth in two or three rows; *Orcynopsis* about 75 tiny teeth in a patch one or two rows wide posteriorly and about five rows anteriorly; and *Gymnosarda* has an elongate oval tooth patch with hundreds of tiny teeth. There are even more and smaller teeth in *Allothunnus*, so small that Nakamura and Mori (1966) thought they were absent.

Ectopterygoid.—All bonitos have a slender T-shaped ectopterygoid (Figure 36). The ventral

FIGURE 33.—Left dentaries, external view, of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 775 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL.

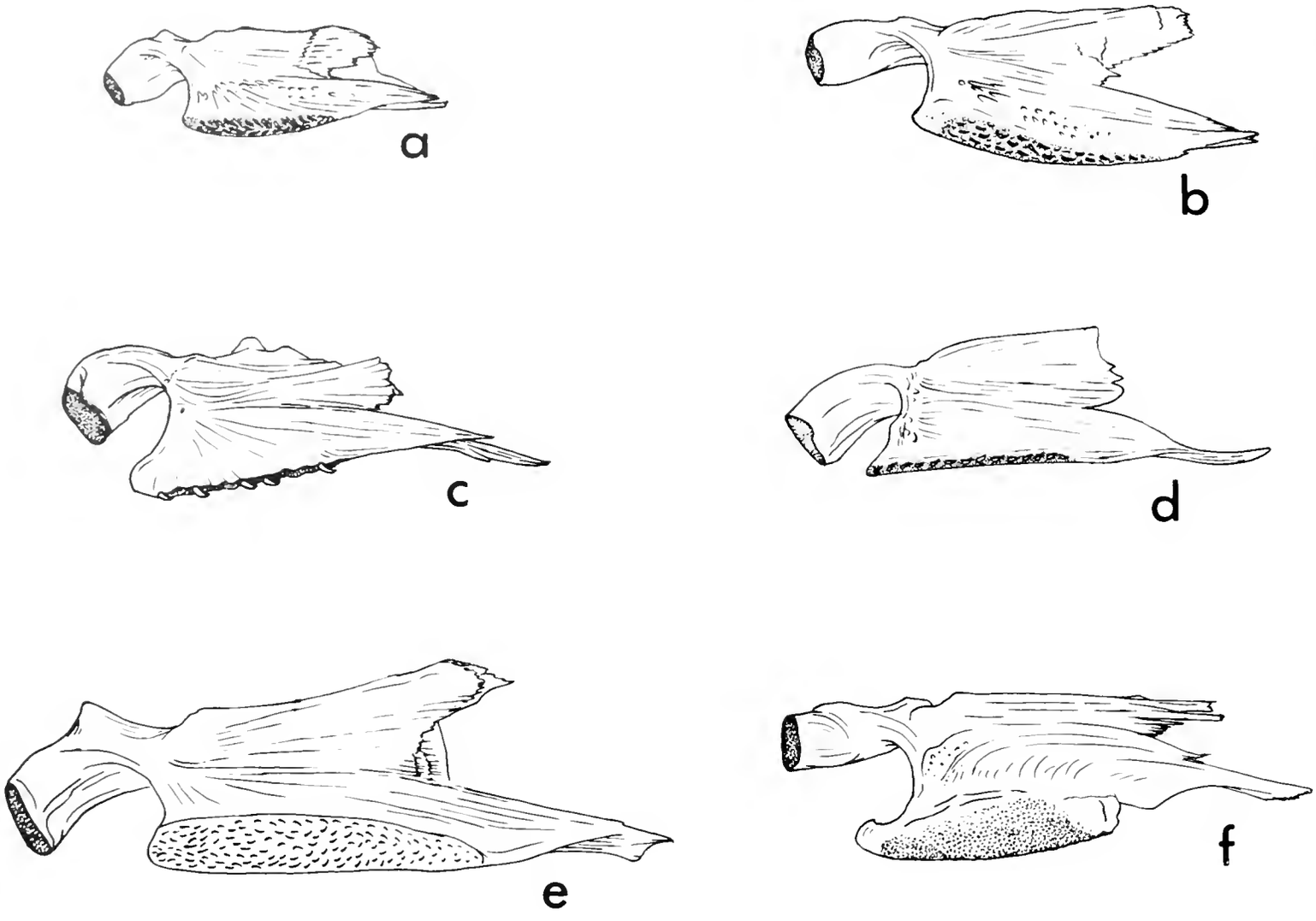


FIGURE 35.—Right palatines of six species of Sardini, internal view rotated slightly to better show palatine teeth. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

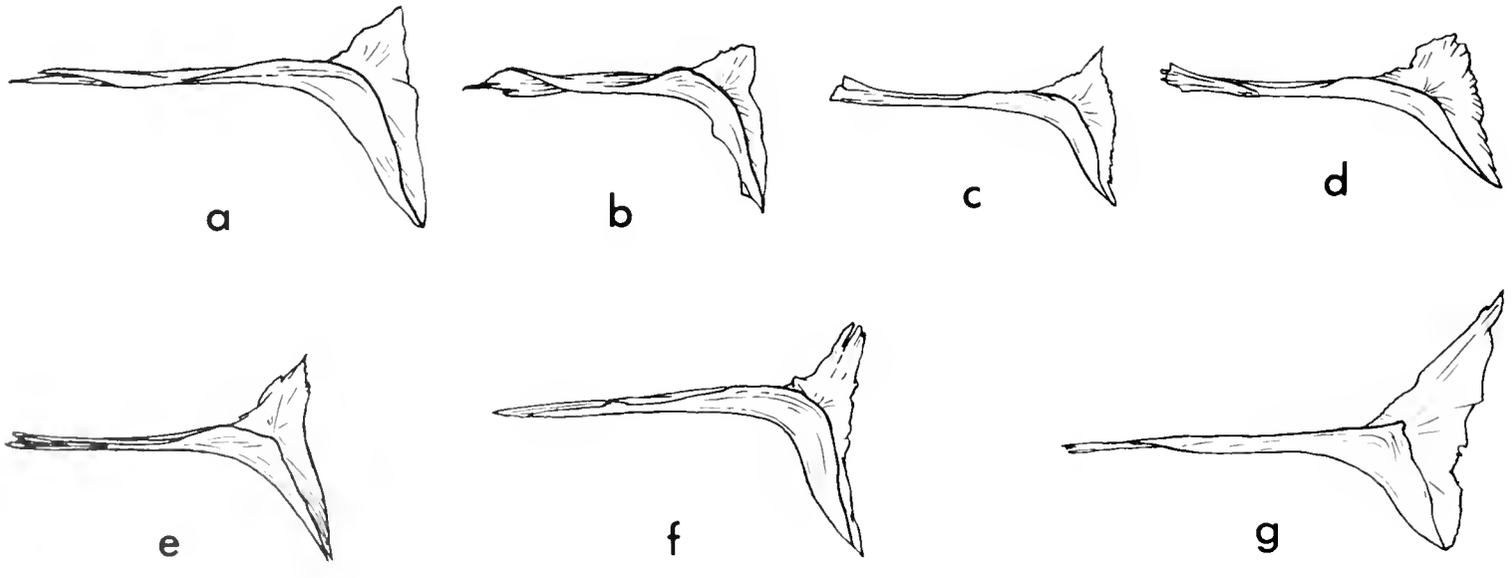


FIGURE 36.—Left ectopterygoids of seven species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda orientalis*, Tokyo, 500 mm FL. e. *Sarda chiliensis*, Callao, Peru, 549 mm FL. f. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. g. *Allothunnus fallai*, California, 680 mm FL.

projection of the ectopterygoid is longer than the dorsal projection except in *Allothunnus* which has a larger dorsal projection. The ridge extending from the main axis to the tip of the ventral projection has a sharper angle in *Allothunnus* compared to the smooth curve in the other bonitos. The main shaft of the ectopterygoid is thicker and higher in *Gymnosarda* than in the other bonitos. *Sarda orientalis* has the dorsal projection slightly expanded instead of pointed as in the other species of *Sarda*.

Entopterygoid.–The entopterygoid is elongate oval in shape in all the bonitos (Figure 37). The external margin of the entopterygoid is the strongest and thickest part of the bone, and there is a bent posterior end which attaches to the ectopterygoid externally. *Allothunnus* has a more elongate entopterygoid and *Gymnosarda* has a broader one than the other bonitos.

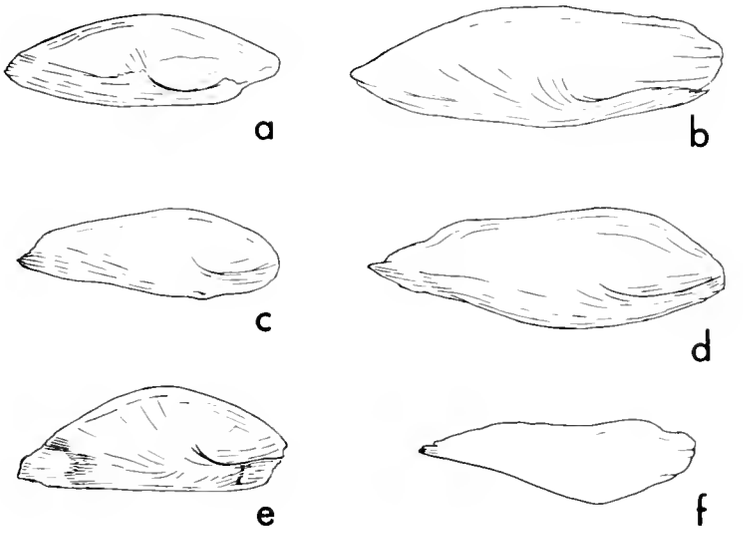


FIGURE 37.–Left entopterygoids of six species of Sardini, dorsal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 363 mm FL. d. *Sarda sarda*, Azores, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a-d drawn twice as large as e and f.

Metapterygoid.–The posterior and dorsal margins of the metapterygoid articulate with the hyomandibula (Figure 9). A groove is present on almost the entire posterior margin in all bonitos except *Allothunnus*, which has a deeper and wider groove on the upper half of the posterior margin, as in *Thunnus*. *Cybiosarda*, *Orcynopsis*, and *Sarda* have a thin projection along the upper half of the posterior margin extending from the internal surface of the metapterygoid (Figure 38). These three genera also have a posteroventral notch on the inner surface of the bone into which the anterodorsal process of the symplectic fits. The metapterygoid of *Gymnosarda* is more elongate and triangular in shape and has no projection along the posterior margin. In *Allothunnus*, the anteroventral and posteroventral margins are very similar to those in *Thunnus* (Gibbs and Collette 1967, fig. 7).

HYOID ARCH.–The hyoid arch is the chain of bones that connect the lower jaw and the opercular apparatus with the skull. The arch is composed of the hyomandibula, symplectic, quadrate, hyoid complex (basihyal, ceratohyal, epihyal, interhyal,

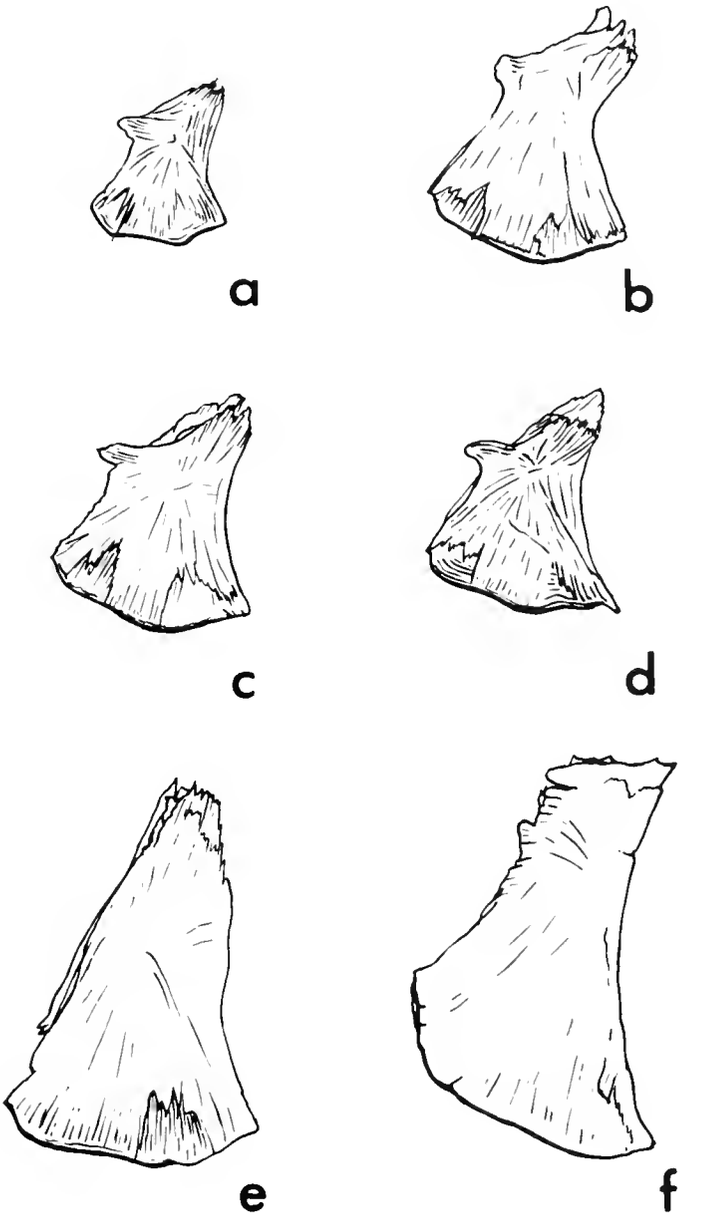


FIGURE 38.–Left metapterygoids of six species of Sardini, internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

and the seven branchiostegal rays), and two median unpaired bones, the glossohyal and urohyal.

Hyomandibula.—The hyomandibula is an inverted L-shaped bone that connects the mandibular suspensorium and opercular bones to the neurocranium (Figure 9). Dorsally, there are three prominent condyles. The longest and anteriormost forms the base of the L and fits into the fossa at the junction of the pterotic and sphenotic bones. The dorsal condyle articulates with the ventral fossa of the pterotic and the lateral process is attached to the inside of the opercle. Anterolaterally the hyomandibula joins the metapterygoid; posterolaterally it has a long articulation with the preopercle.

Godsil (1954, 1955) found two differences between the hyomandibula in *Sarda orientalis* and *S. chiliensis*. In both species a spine protrudes posteriorly from the center condyle. The spine forms an angle of 90° or less with the major axis of the hyomandibula in *S. orientalis* and greater than 90° in *S. chiliensis*. We confirm this difference and use the character to divide the bonitos into groups. *Sarda chiliensis*, *Cybiosarda* (Figure 39a), and *Orcynopsis* (Figure 39b) have the angle greater than 90°; *Gymnosarda* and *Allothunnus* probably belong in this group based on the angle, but the spines are greatly reduced in both genera. *Sarda orientalis* has the angle 90° or less. *Sarda sarda* (Figure 39c) and *S. australis* are intermediate between the two groups in having the angle about 90°.

Godsil used the length of the spine on the ridge of bone next to the groove into which the preopercle fits as a second character to distinguish *S. orientalis* from *S. chiliensis*. The spine is much longer in *S. orientalis* and projects beyond the center condyle when the spine is placed flat with the internal side down. Again we can confirm this difference and note that *S. sarda* agrees with Godsil's description of *S. orientalis*. *Sarda australis* and *S. chiliensis* have the spine short and not protruding. Godsil (1955:34) noted that on one

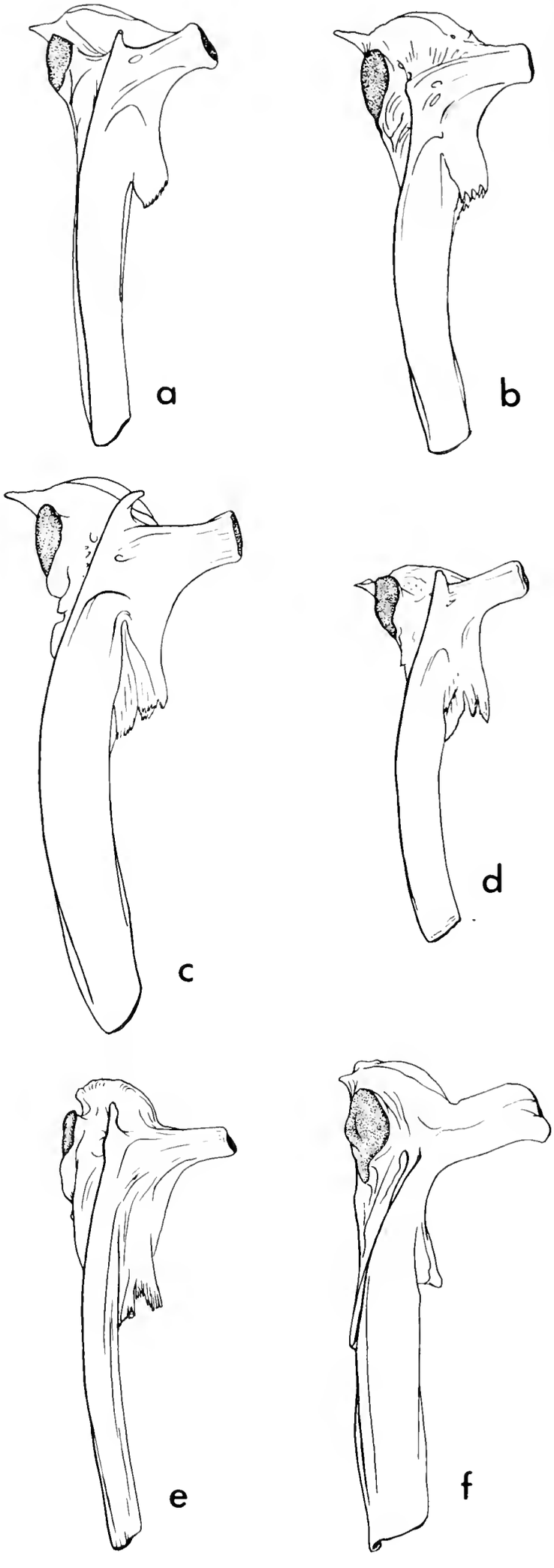


FIGURE 39.—Right hyomandibulae of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a and c drawn twice as large as e and f, b and d drawn 1.5 times as large.

side of one hyomandibula of a Tokyo specimen of *S. orientalis*, the spine was short as in *S. chiliensis*. We found one specimen of *S. chiliensis* from Callao, Peru in which the spine projected as in *S. orientalis*. Thus, this difference is not absolute but "corroboratory" as Godsil has noted. *Cybiosarda* (Figure 39a) and *Gymnosarda* (Figure 39e) resemble *S. chiliensis* but the spine is still shorter. The ridge forms an angle but no spine is present in *Orcynopsis* (Figure 39b) and *Allothunnus* (Figure 39f).

The lateral condyle is broader in *Allothunnus* than in other bonitos, and its lower anterior vertical margin, where the metapterygoid attaches, does not project as far (Figure 39f). Also, the groove into which the preopercle fits is more curved in *Allothunnus*.

Symplectic.–The symplectic is a small bone that fits into a groove in the quadrate (Figure 9). Bonitos fall into three groups based on the shape of the symplectic. *Orcynopsis*, *Cybiosarda*, and *Sarda* (Figure 40a-d) have a wider upper part with a pointed or "flared" anterodorsal projection as in *Thunnus*. *Gymnosarda* has a rather thick upper part and only a slight lateral expansion about the middle of the anterior margin (Figure 40e). The anterolateral expansion of the symplectic is better developed in *Allothunnus* (Figure 40f) than in *Gymnosarda*, but there is no anterior projection at the upper end.

In external view, there is a longitudinal axis to the symplectic which is shaped differently in the three groups. *Gymnosarda* has a much thicker upper end. The upper part is also thick but somewhat flattened in *Allothunnus* as also noted by Nakamura and Mori (1966). *Orcynopsis*, *Cybiosarda*, and *Sarda* all have a notch at about the middle of the axis on the external surface of the bone which is absent in *Gymnosarda* and *Allothunnus*.

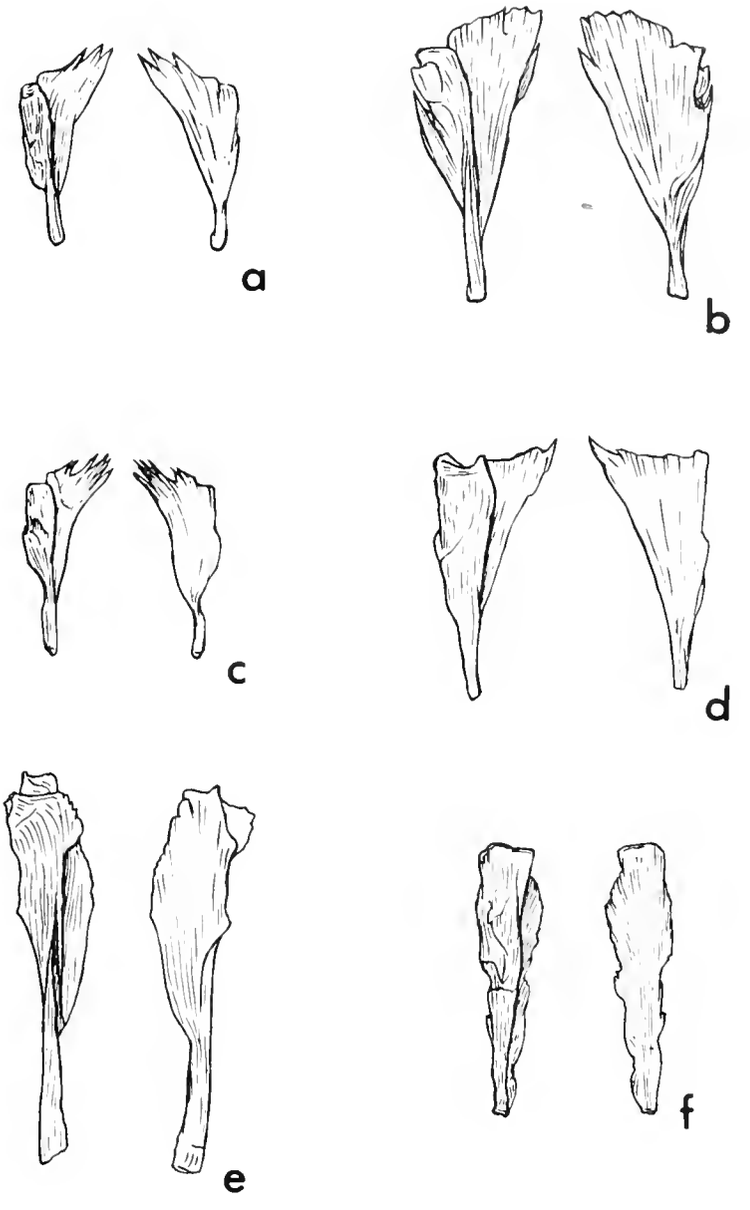


FIGURE 40.–Right symplectics of six species of Sardini, left figure of each pair is the external view, right the internal view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 363 mm FL. d. *Sarda chiliensis*, Callao, Peru, 437 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 775 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a-e drawn twice as large as f.

Quadrate.–The lower jaw is suspended from the cranium by means of the articulating facet of the ventral surface of the triangular quadrate (Figure 9). The quadrates are similar in all bonitos, with a deep groove where the symplectic fits along the inner posterior margin and a posterodorsal process (Figure 41). The quadrate of *Allothunnus* has a distinctly longer posterodorsal process resembling those in *Thunnus*. The process in *Gymnosarda* (Figure 41e) has a slightly broader tip and also its base is expanded more than in other genera of bonitos.

Hyoid Complex.–This complex, as discussed here, includes the hypohyal, ceratohyal, epihyal, and interhyal bones and the seven branchiostegal rays (Figure 42). The external view of the four bones in *Sarda orientalis* and *Gymnosarda unicolor* has been previously illustrated by Kishinouye (1923:326) along with the hyoid arches of six other genera of Scombridae.

The hypohyal is composed of a dorsal and a ventral segment fused longitudinally along a

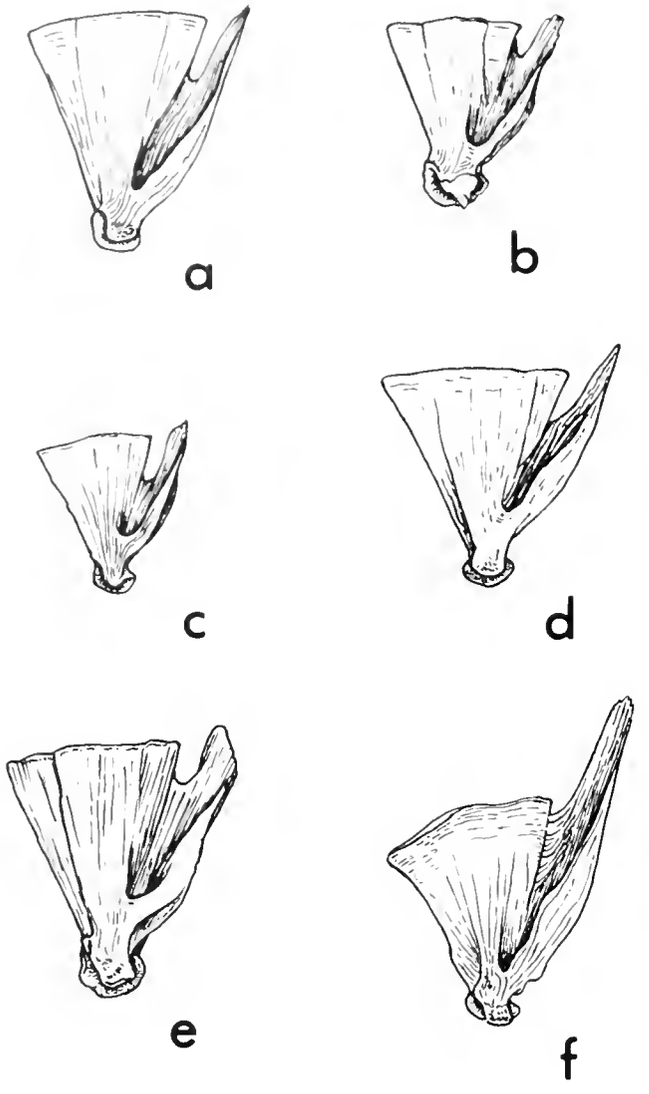


FIGURE 41.—Right quadrates of six species of Sardini, internal view to show groove for symplectic. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Florida, 333 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

serrated suture that is most prominent in *Gymnosarda* (Figure 42e). There is a depression on the outer surface at the posterior half of the suture in all bonitos, as in *Thunnus*. Internally, a lateral process at the anterodorsal end forms a symphysis with the glossohyal, urohyal, basibranchial, and the process of the hypohyal from the opposite side.

The ceratohyal is a long flat bone, broader at the posterior end and with an anteroventral projection that articulates with the posteroventral notch of the hypohyal. The middle portion of the ceratohyal is concave dorsally in all bonitos. There are three notches along the ventral margin where the anterior three branchiostegal rays attach. Bonitos have no notch at the site of attachment of the fourth branchiostegal ray. All bonitos have an elliptical ceratohyal window (Nakamura and Mori 1966, fig. 6), except for *Sarda orientalis* which has only a trace of a depression at the appropriate site (Figure 42d). A deep groove extends along the upper third of the ceratohyal from the depression of the hypohyal to the middle of the epihyal in *Gymnosarda*, but there is only a slight trace of this groove in the other bonitos.

The epihyal is a triangular bone which interlocks medially with the ceratohyal. This serrated interlocking suture is limited to the inner surface of the bone in *Cybiosarda*, *Orcynopsis*, and *Sarda* (Figure 42 a-d); there are only cartilaginous connections between these two bones on the outer surface, as in *Thunnus* (de Sylva 1955, fig. 36). *Gymnosarda* and *Allothunnus* also have well-developed interlocking sutures on the outer surface (Figure 42 e, f). The epihyal bears a small condyle on its posterior end that articulates with the inner surface of the interopercle. The fifth to seventh branchiostegal rays are attached to the outer surface of the ventral margin of the epihyal. The fifth branchiostegal is at the junction of the epihyal and ceratohyal in *Gymnosarda* and is a short distance behind the junction in other bonitos.

The interhyal is a small bone with an expanded ventral end that is attached to the epihyal dorsal to the epihyal condyle. The interhyal is attached, with connective tissue, to the symphysis of the hyomandibula, quadrate, symplectic, metapterygoid, and preopercle. The interhyal also articulates above the interopercular fossa posteriorly.

Glossohyal.—The glossohyal is a spatulate bone underlying the tongue and overlying the first basibranchial bone at the anterior end of the branchial arch (see Figure 49). *Cybiosarda* and *Orcynopsis* have a pair of oval tooth patches on the dorsal surface of the glossohyal (Figure 43a, b). *Gymnosarda* also has a pair of tooth patches on the tongue, but they are on plates over the glossohyal and are not fused to the bone (Figure 43f). The ventral surface of the tooth patches of *Gymnosarda* have a deep longitudinal ridge which fits the ventral ridge of the glossohyal laterally. On the dorsal surface of the glossohyal of *Gymnosarda*, there is a prominent longitudinal ridge on which the paired tooth patches meet. The size of the tooth patches may vary from one side to the other as in the specimen of *Orcynopsis unicolor* illustrated (Figure 43b). *Sarda* lacks tooth patches (Figure

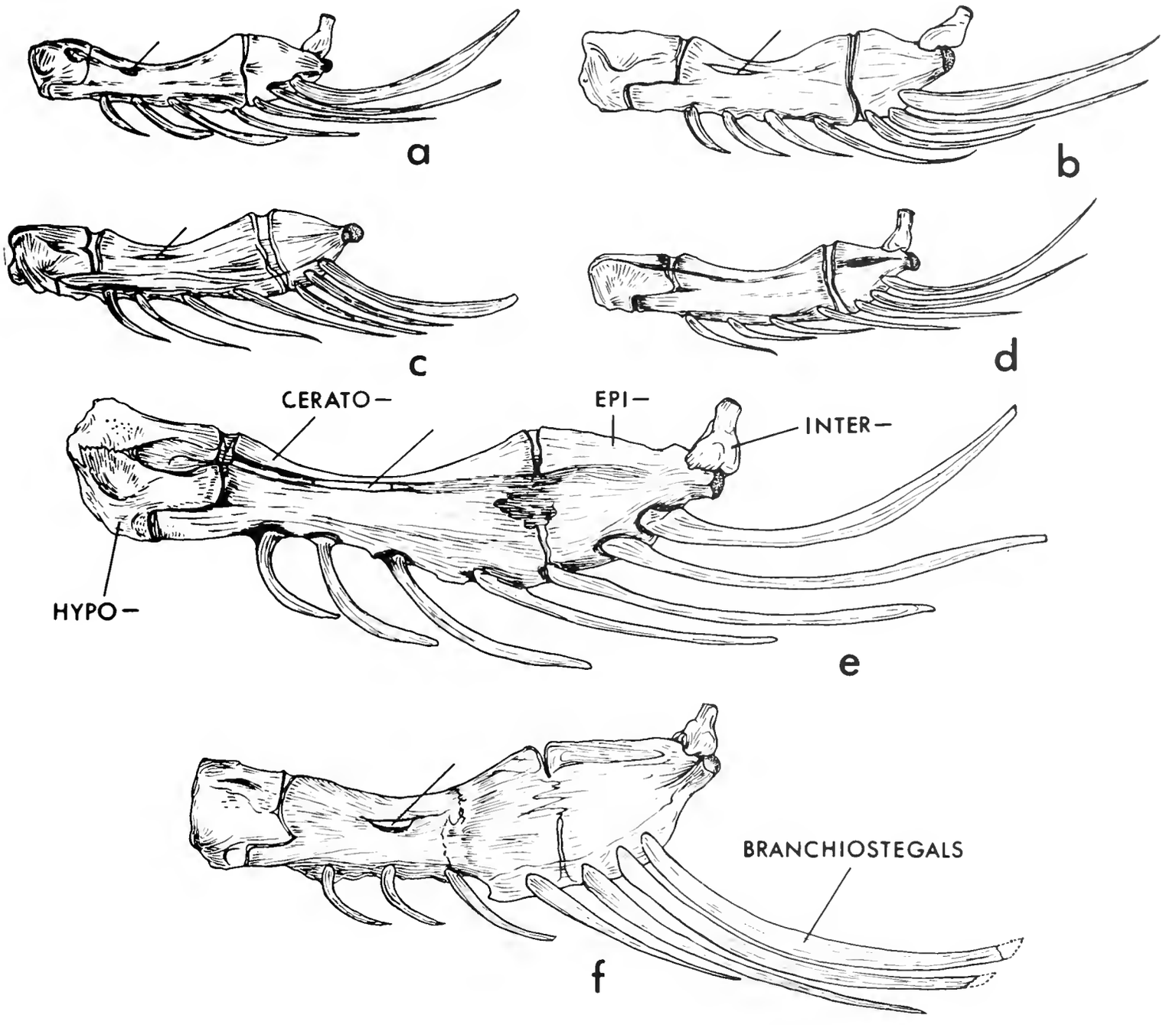


FIGURE 42.–Hyoid complex (hypohyal, ceratohyal, epihyal, and interhyal) and branchiostegal rays of six species of Sardini, external view of left side. Unlabelled line points to ceratohyal window. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 543 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda orientalis*, Panama, 415 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

43c-e) and the shape and proportions of the glossohyal is extremely variable both inter- and intraspecifically as Godsil (1955) has pointed out for *S. chiliensis* and *S. orientalis*. A slightly concave anterior margin is present on the glossohyal of *Allothunnus*. A depression on the ventral surface of the proximal portion of the glossohyal is present in most bonitos except for *Sarda orientalis* (Godsil 1954, 1955) and *Gymnosarda*.

Urohyal.–The urohyal is a median unpaired bone. The anterior end of this element lies between, and is connected with, the hypohyals of the left and right sides. The urohyals of the bonitos have a thickened anteroventral margin which gradually narrows posteriorly (Figure 44). *Gymnosarda* has a distinctive thickened posterodorsal margin, which starts at the anterior third of the bone and forms a flattened platform at the posterior end. A similar tendency was found occasionally in other bonitos, especially *Orcynopsis*, but the thickening was limited to the middle portion of the dorsal margin. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have relatively deep urohyals; *Sarda* and *Allothunnus* have relatively elongate urohyals.

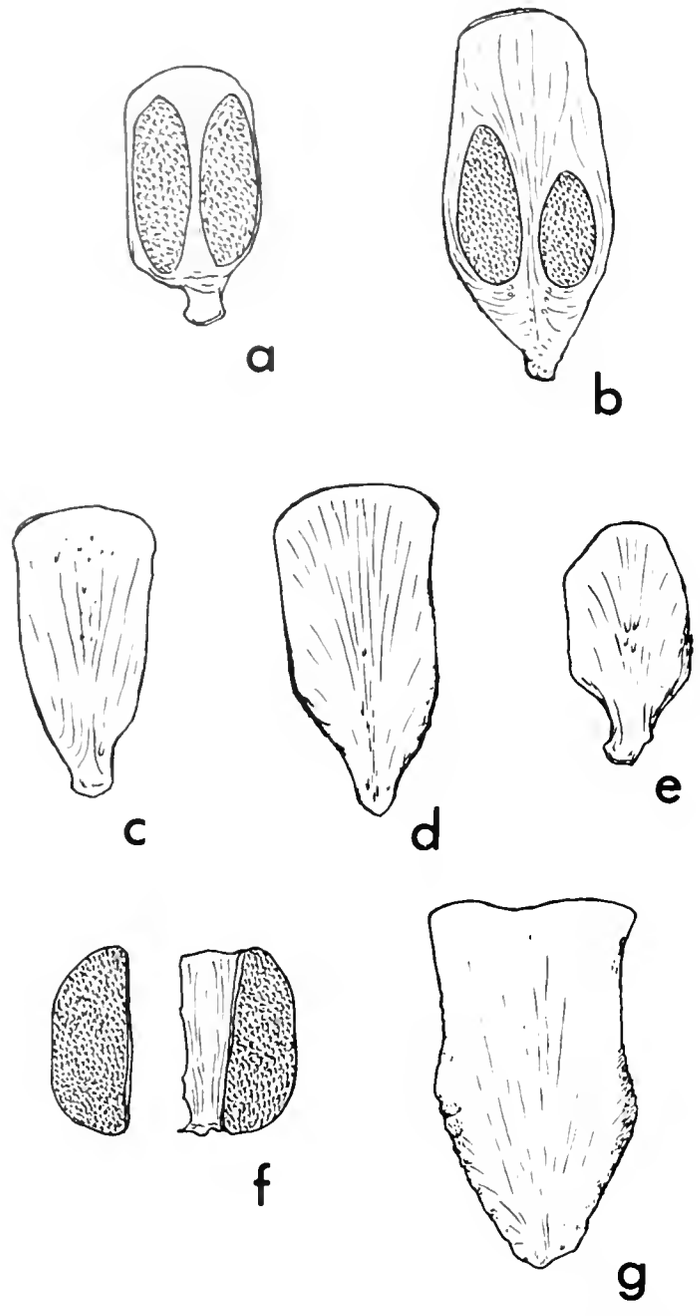


FIGURE 43.—Dorsal view of glossohyals of seven species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL, note unequally developed tooth patches. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Sarda sarda*, Tunisia, 504 mm FL. f. *Gymnosarda unicolor*, Truk Islands, superficial tooth plate removed from left side of bone. g. *Allothunnus fallai*, California, 680 mm FL. a-e and g drawn twice the size of f.

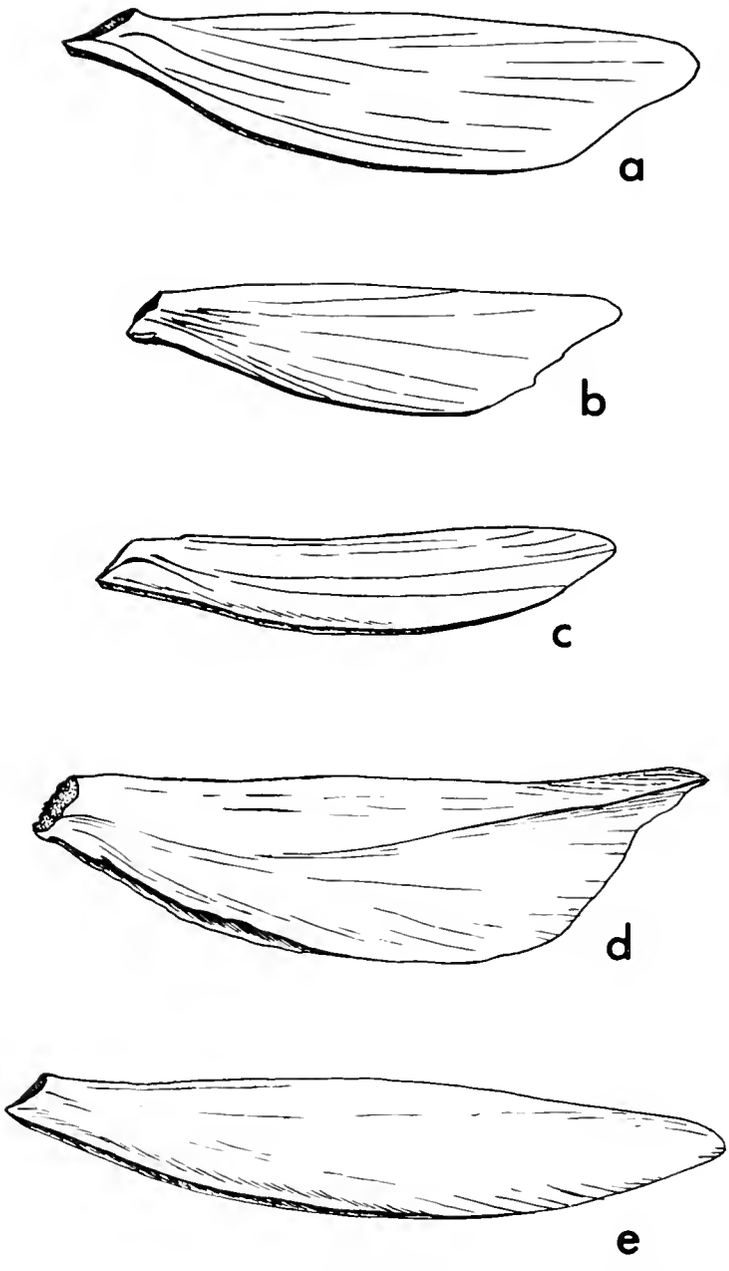


FIGURE 44.—Urohyals of five species of Sardini, in left lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 549 mm FL. d. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. e. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as b-e.

OPERCULAR APPARATUS.—Four wide flat bones fit together to form the gill cover which protects the underlying gill arches.

Opercle.—The opercle is broad and more or less rectangular in shape in all bonitos except *Gymnosarda*, in which it is narrower, elongate, and more triangular (Figure 45e). *Cybiosarda*, *Orcynopsis*, and *Sarda* have similar lower posterior projections which extend beyond the posterior notch and their dorsal margins are flat or slightly concave (Figure 45a-d). *Allothunnus* has no distinct lower projection (Figure 45f).

Subopercle.—The subopercle is similar among bonitos and generally resembles those of scombrids such as *Thunnus*. *Cybiosarda*, *Orcynopsis*, and *Sarda* (Figure 46a-d) have two ridges that converge posteriorly from the anterior projection. The upper ridge articulates with the lower posterior projection of the opercle and the lower ridge connects to the posterodorsal margin of the interopercle. The ridges are much stronger

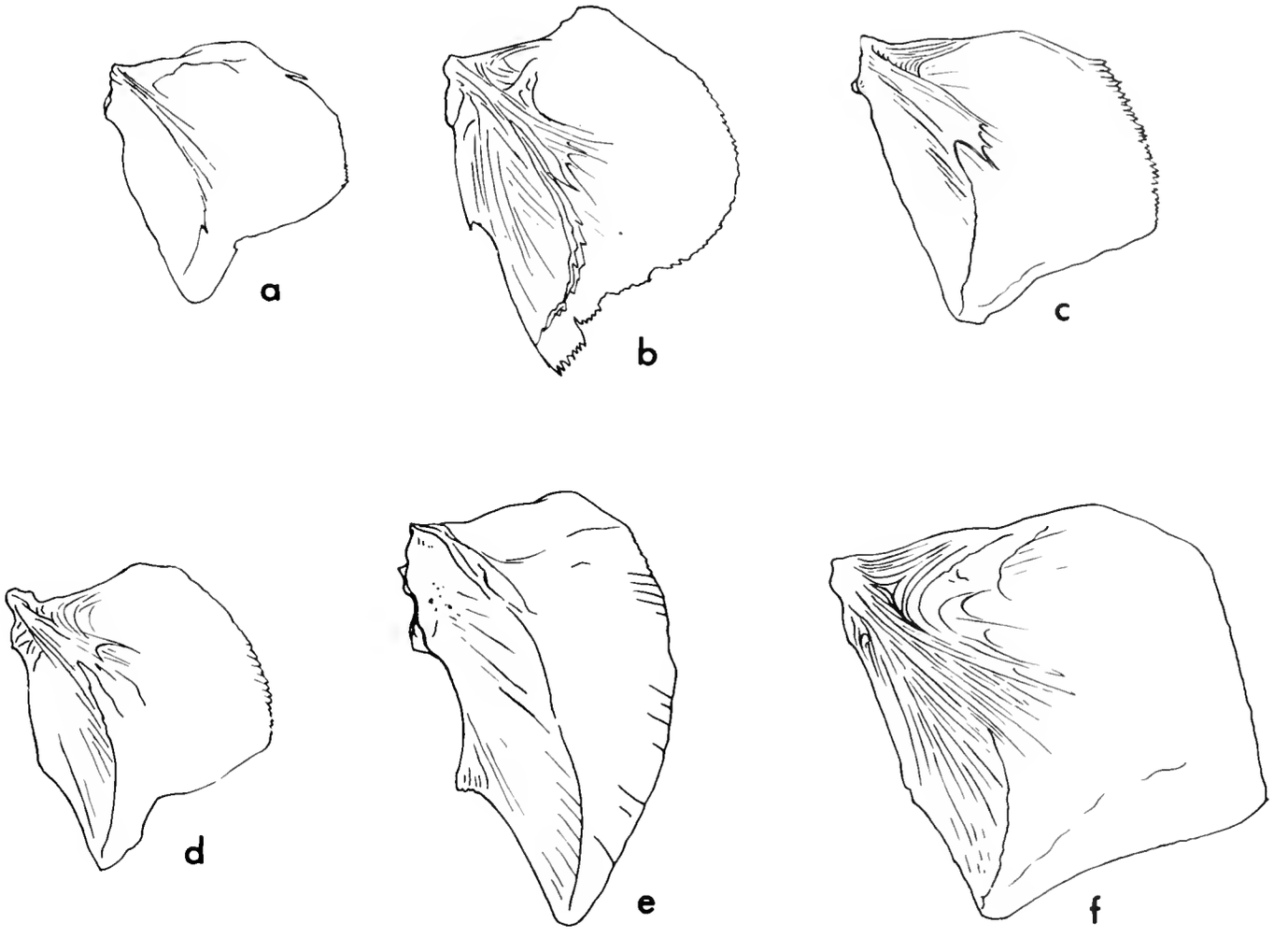


FIGURE 45.–Left opercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda orientalis*, Tokyo, 500 mm FL. d. *Sarda australis*, New South Wales, 495 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

in *Cybiosarda* and *Orcynopsis* than in the species of *Sarda*. A trace of these ridges is discernible in *Allothunnus* and the bone is much thinner than in other genera. *Gymnosarda* (Figure 46e) has no ridges and the entire subopercle is more elongate than in other bonitos.

Preopercle.–The elongate preopercle is thickened along its inner surface for attachment with the hyomandibula (see Figure 9). The preopercles are similar in *Cybiosarda*, *Orcynopsis*, and the species of *Sarda* (Figure 47a-d). The dorsal projecting arm is somewhat longer and narrower in the species of *Sarda* than in *Cybiosarda* and *Orcynopsis*. As is true of the subopercle, the preopercle of *Gymnosarda* (Figure 47e) is long and narrow compared to the previous three genera. *Allothunnus* (Figure 47f) has a preopercle much more similar to *Thunnus* (de Sylva 1955:17, fig. 28) than to other bonitos. It is divided into superior and inferior arms which are approximately equal in length instead of the superior arm being longer than the inferior arm.

Interopercle.–The interopercle is roughly shaped like an elongate triangle, with a narrow anterior end. Most of the outer surface of the anterodorsal portion of the interopercle is covered by the preopercle. On the inner surface, beneath the middle of the anterodorsal margin of the interopercle, there is a condyle, which articulates with the posterior end of the epihyal and the interhyal. The anterior and posterior ends of the interopercle are narrowest in *Allothunnus* and broadest in *Gymnosarda* (Figure 48). The thinnest part of the interopercle is along the ventral margin, and a weak fimbriate posterior margin is present in all the bonitos as in *Thunnus*.

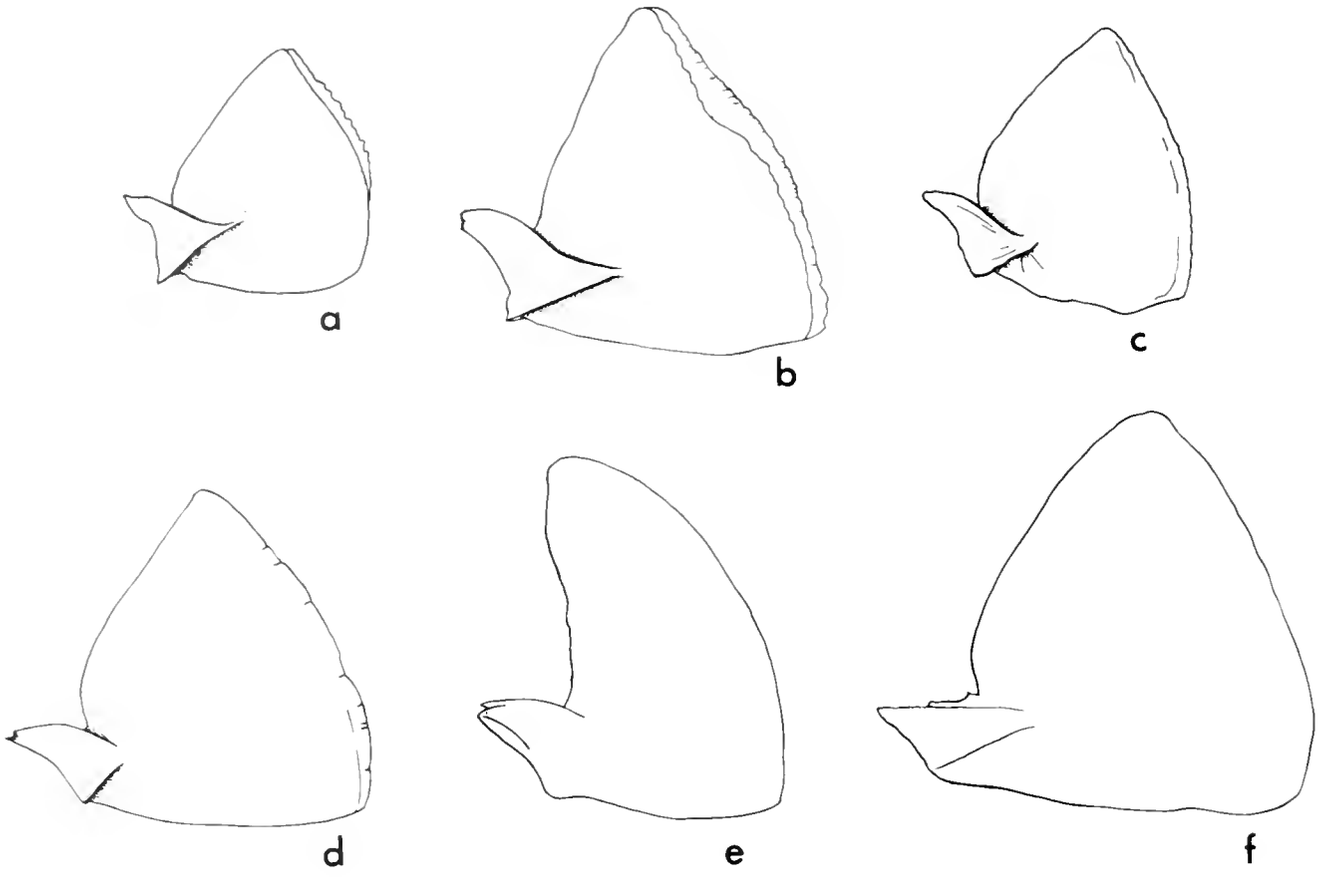


FIGURE 46.—Left subopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 405 mm FL. d. *Sarda chiliensis*, Callao, Peru, 549 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

BRANCHIAL ARCH.—The branchial arch is composed of the five pairs of gill arches: gill filaments, gill rakers, pharyngeal tooth patches, and supporting bones. The general arrangement in the Sardini (Figure 49) is similar to that found in other scombrids such as *Thunnus* (Iwai and Nakamura 1964a:22, fig. 1; de Sylva 1955:21, fig. 40), *Scomberomorus* (Mago Leccia 1958:327, pl. 12), and *Rastrelliger* (Gnanamuttu 1971:14, fig. 6). Within the Sardini, the most important generic and specific differences are in the number of gill rakers. All of the branchial bones bear patches of tiny teeth.

Basibranchials.—The three basibranchials form a chain from anterior to posterior. The first and second are about the same size and considerably shorter than the third. The first basibranchial is covered dorsally by the broad, flattened glossohyal which is dentigerous in *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* as described in the hyoid arch section.

In lateral view (Figure 50), the first basibranchial has an expanded anteroventral end and is curved downward except in *Allothunnus* (Figure 50f). The second basibranchial has a prominent notch in the ventral margin that is absent in *Allothunnus*. The third basibranchial has an expanded anterior end at its junction with the second basibranchial and then tapers posteriorly. A section of cartilage extends posteriorly to articulate with the fourth ceratobranchial and lower pharyngeal.

Hypobranchials.—The first three arches have hypobranchials which connect with the ceratobranchials. The first hypobranchial is attached to the second basibranchial; the second and third hypobranchials are attached to the third basibranchial. The first two hypobranchials are longer than the third.

Ceratobranchials.—The ceratobranchials are the longest bones in the branchial arch and support most of the gill filaments and gill rakers. The first three are morphologically similar and articulate

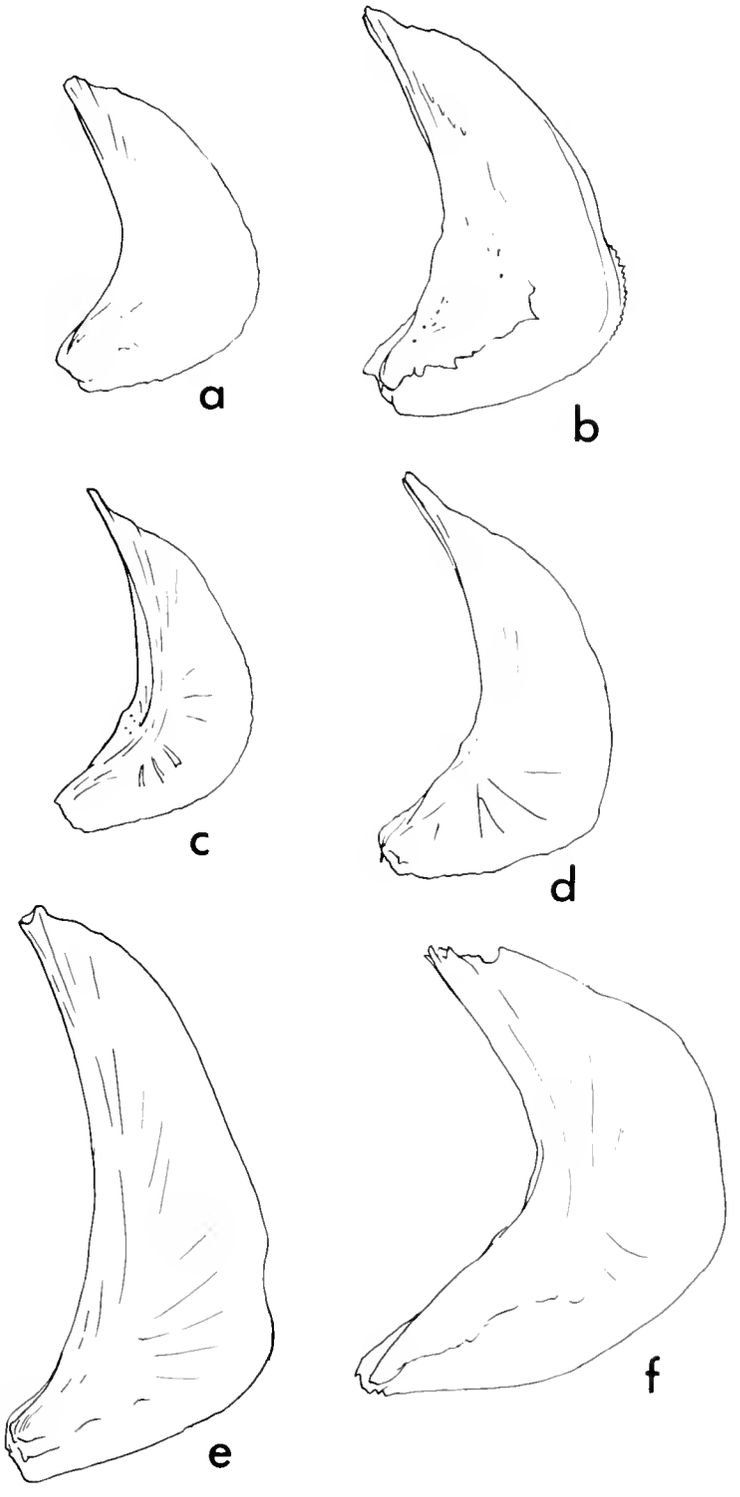


FIGURE 47.–Left preopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, Callao, Peru, 517 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

with the posterior ends of their respective hypobranchials. The fourth is more irregular and attaches to a cartilage posterior to the third basibranchial. The fifth ceratobranchial is also attached to the cartilage, has a dermal tooth plate fused to its dorsal surface, and the complex is termed the lower pharyngeal bone. It is covered

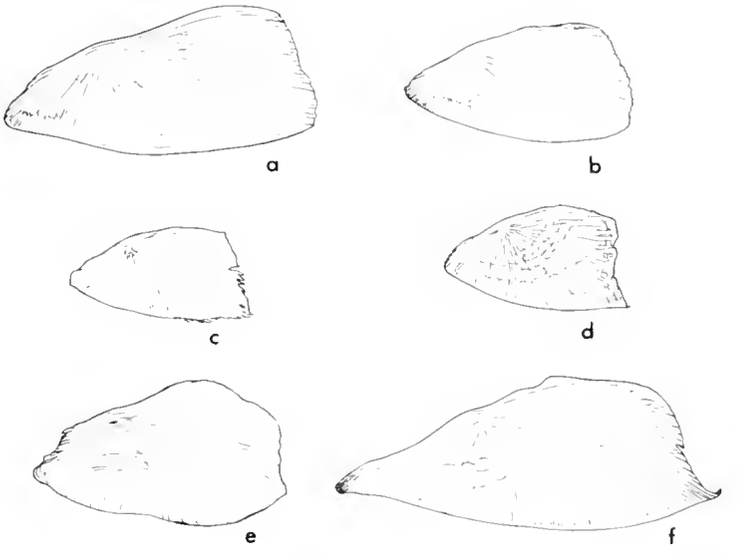


FIGURE 48.–Left interopercles of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda australis*, New South Wales, 475 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

with small conical teeth that are directed slightly posteriorly. *Allothunnus* has the smallest pharyngeal teeth among the bonitos.

Epibranchials.–The four epibranchials are attached basally to the ceratobranchial of their respective gill arch. They vary in shape with the first one being long and slender like a short ceratobranchial, the second and third shorter and stubbier, and the fourth one almost V-shaped.

Pharyngobranchials.–There are four pharyngobranchials attached basally to the epibranchial of their respective gill arch. The recurved first one articulates dorsally with the parasphenoid and is frequently referred to as the suspensory pharyngeal (Iwai and Nakamura 1964a). The triangular second pharyngobranchial bears a patch of small teeth. The third and fourth pharyngobranchials both have dermal tooth plates fused to them and are termed upper pharyngeal bones.

Gill Rakers.–The hypobranchial, ceratobranchial, and epibranchials of the first gill arch support a series of slender rigid gill rakers. The longest gill raker is at or near the junction of the upper and lower arches, between the ceratobranchial and epibranchial. Gill rakers prevent food loss through the opercular gap. There is a correlation between numbers of gill rakers, gap between gill rakers, and size of food items as

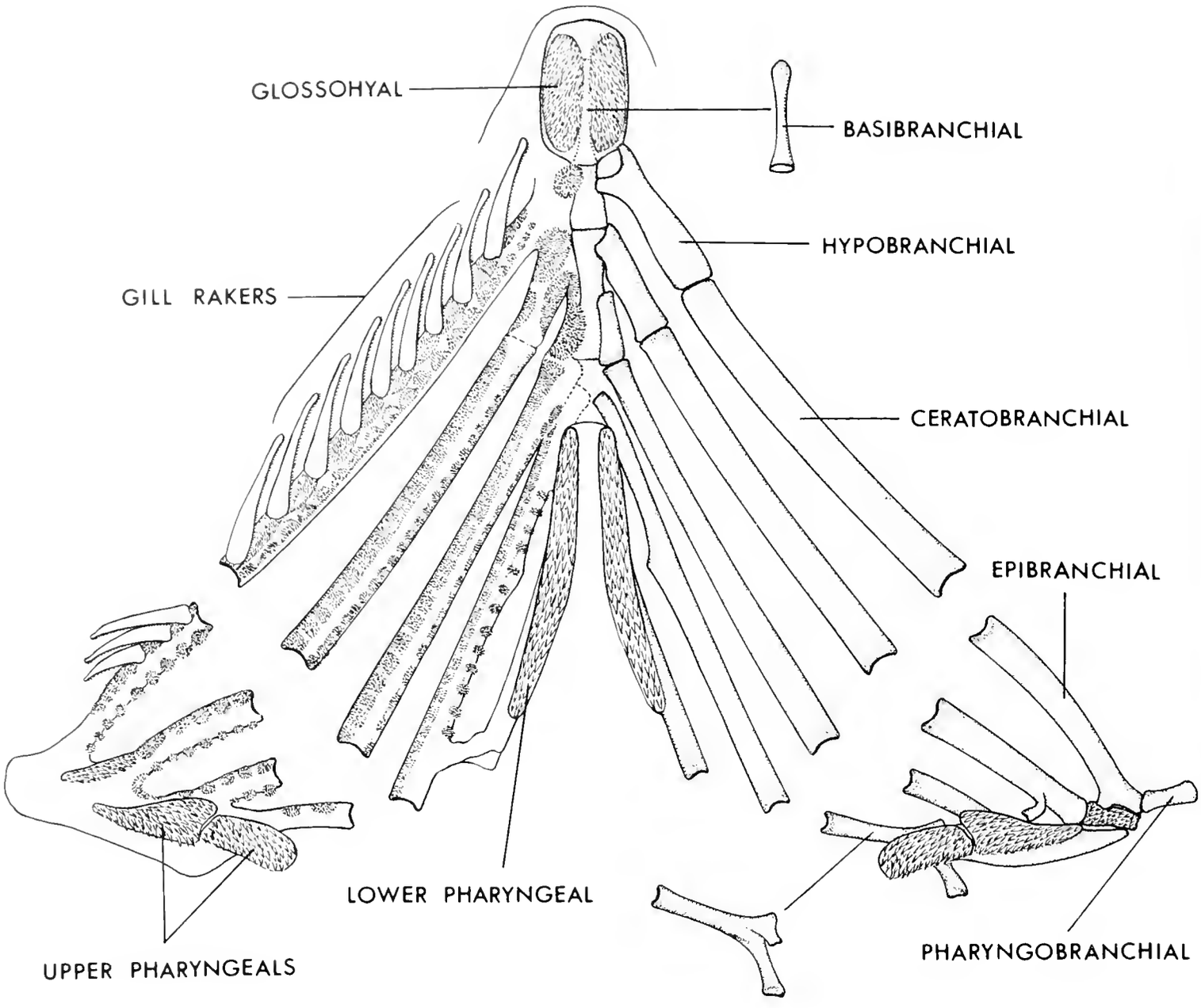


FIGURE 49.—**Branchial arch of *Cybiosarda elegans*.** Dorsal view of the gill arches with the dorsal halves folded back to show their ventral aspect. Epidermis removed from right hand side to reveal underlying bones.

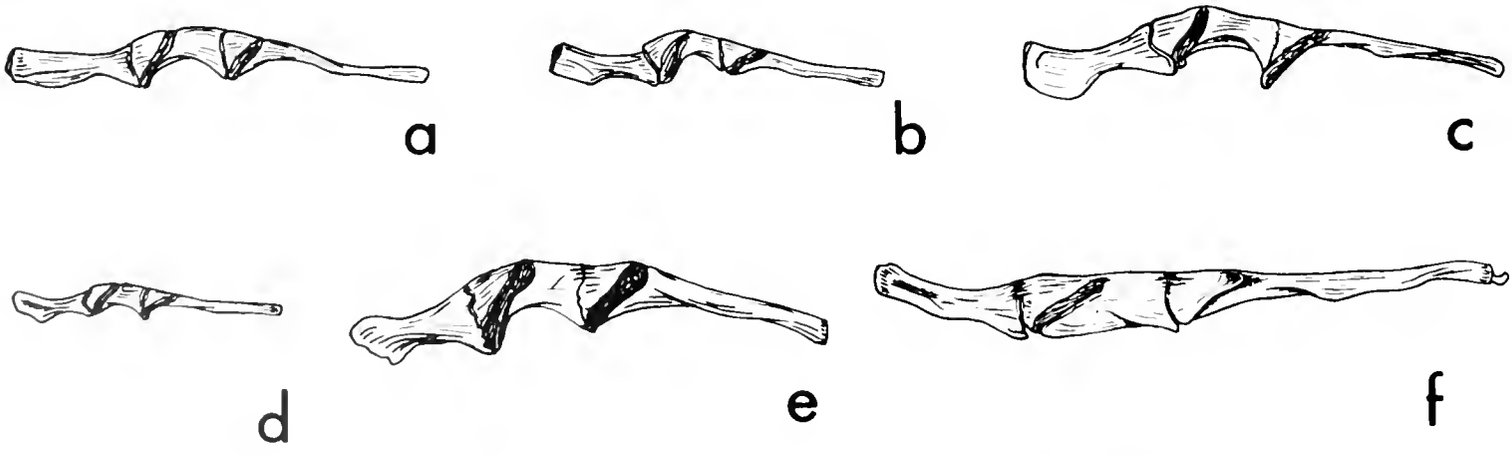


FIGURE 50.—Left lateral view of the three basibranchial bones in six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 593 mm FL. c. *Sarda sarda*, Azores, 418 mm FL. d. *Sarda australis*, New South Wales, 407 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL. a-c drawn twice as large as d-f.

Magnuson and Heitz (1971) have clearly shown for a number of species of Scombridae. The number of gill rakers is easily countable and is an important taxonomic character in the Sardini as well as among other groups of the Scombridae.

Allothunnus differs strikingly from other bonitos in having many more gill rakers on the first arch, 72-80 compared to 8-27 (Table 7). The only other scombrids that approach this high number of gill rakers are *Katsuwonus pelamis* with 53-63 and two species of the genus *Rastrelliger*, *R. kanagurta* (Cuvier) and *R. brachysoma* (Bleeker), with 48-68. As discussed under dentition, the high number of gill rakers in *Allothunnus* is correlated with a high number of teeth in both upper and lower jaws.

Cybiosarda, *Orcynopsis*, and *Gymnosarda* all have few gill rakers (11-17), fewer than any other bonitos except *Sarda orientalis* (8-13).

Number of gill rakers is a valuable character within the genus *Sarda*. The largest difference is between *S. orientalis* (8-13) and *S. chiliensis* (23-27), which is particularly useful in the eastern Pacific where the tropical *S. orientalis* can be separated from *S. chiliensis* to the north and south on the basis of fewer gill rakers (and, in a similar fashion, jaw teeth). *Sarda australis*, which has been considered a subspecies of *S. chiliensis* by many authors, is intermediate in number of gill rakers (19-21) between *S. chiliensis* and *S. orientalis* but completely separated from both. There are also differences below the species level: *Sarda sarda* in the western Atlantic averages fewer (North America, 17.6; South America, 18.7) gill rakers than the other four populations, especially the Mediterranean–Black Sea (20.9) and Gulf of Guinea (20.9).

Inner Gill Rakers.–The inner surface of the hypobranchial, ceratobranchial, and epibranchial bones of the first gill arch supports a series of tubercles, the inner gill rakers. The strongest tubercle usually occurs at or near the junction of the upper and lower arches on the lower arch. The number of inner gill rakers (Table 8) is correlated with the number of gill rakers on the first gill arch (Table 7). *Allothunnus* has the longest, thickest, and most numerous inner gill rakers (49-56). In many specimens of *Cybiosarda elegans* and *Sarda orientalis* the inner gill rakers are degenerate with only a few small tubercles present. We agree with Godsil (1954, 1955) that the counts are difficult to make in *Sarda* with any consistency. Godsil used the presence of the inner gill rakers ("gill teeth") as a character to distinguish *Sarda chiliensis* from *S. orientalis* in the eastern Pacific. *Gymnosarda* completely lacks inner gill rakers, but many small conical teeth are present around the base of the gill rakers. These small teeth are also present around the base of the gill rakers in the other bonitos but they are much smaller than in *Gymnosarda*.

AXIAL SKELETON

This section is divided into six parts: vertebral number, vetebral column, infracentral grooves, ribs and intermuscular bones, caudal peduncle keels, and caudal complex.

TABLE 8.–Total number of inner gill rakers on the first gill arch in species of Sardini.

Species	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
Cybiosarda elegans		1	1	—	—	1	—	—	—	—	2	1	—	—	1											7	10.6
Orcynopsis unicolor														2	3	2	1	3	—	2	2	—	—	—	1	16	19.8
Sarda australis											1	—	—	2	2	3	4	2	2	1	1					18	18.6
Sarda chiliensis:																											
NE Pacific														4	3	7	4	1	3	—	1					23	18.4
SE Pacific												1	1	1	2	1	2	3	2	4	1	1	1			20	19.9
Total												1	1	5	5	8	6	4	5	4	2	1	1			43	19.1
Sarda orientalis:																											
Indo-West Pacific	1	1	1	—	—	—	—	—	—	—	—	—	—	1	1											5	9.0
E Pacific		1	—	—	1	—	1	1	1	1	1	—	—	—	—	—	—	—	—	—	1					8	12.4
Total	1	2	1	—	1	—	1	1	1	1	1	—	—	1	1	—	—	—	—	—	1					13	10.8
Sarda sarda:																											
W Atlantic							3	—	3	1	4	1	9	3	—	3	2	1								30	14.3
E Atlantic											2	1	1	2	4	2	2	2	—	2						18	17.4
Total							3	—	3	1	6	2	10	5	4	5	4	3	—	2						48	15.5
Allothunnus fallai																						(49-52-54-55-56)				5	53.2

Vertebral Number

Vertebrae may be divided into precaudal (abdominal) and caudal. The first caudal vertebra is defined as the first vertebra that bears a notably elongated haemal spine and lacks pleural ribs. Vertebral counts include the ural centrum which bears the hypural plate.

As with dorsal spines, the bonitos fall into three groups based on total number of vertebrae (Table 9): few vertebrae (37-39) in *Orcynopsis*, *Gymnosarda*, and *Allothunnus*; moderate number (42-48) in *Cybiosarda* and three species of *Sarda*; and many (50-55) in *S. sarda*. These groups can be further subdivided by dividing the total count into precaudal plus caudal. *Orcynopsis* usually has 18+20=38; *Gymnosarda* 19+19=38; and *Allothunnus* 20+19=39. *Cybiosarda* has more, usually (22-23)+(24-25)=47, than the middle group of *Sarda* species, which usually have (23-25)+(20-22)=44-45. Precaudal, caudal, and total counts all vary more in *S. sarda* than in other species of bonitos.

Vertebral Column

The neural arches and spines are stout and laterally flattened on the first to fifth vertebrae in

TABLE 9.—Numbers of precaudal, caudal, and total vertebrae in species of Sardini.

Species	Precaudal vertebrae													
	17	18	19	20	21	22	23	24	25	26	27	28	*N*	$\bar{x}$
Orcynopsis unicolor	2	27											29	17.9
Cybiosarda elegans						5	6	2					13	22.8
Sarda australis							1	11					12	23.9
Sarda chiliensis:														
NE Pacific						2	34	9					45	23.2
SE Pacific						5	13	1					19	22.8
Total						7	47	10					64	23.0
Sarda orientalis:														
Indo-W Pacific							1	7	6				14	24.4
E Pacific							2	6	7				15	24.3
Total							3	13	13				29	24.3
Sarda sarda:														
W Atlantic										15	16	1	32	26.6
Mediterranean-Black Sea											11	4	15	27.3
Gulf of Guinea-S. Africa											8	9	17	27.5
Total										15	35	14	64	27.0
Gymnosarda unicolor			17										17	19.0
Allothunnus fallai				7									7	20.0

Species	Caudal vertebrae										
	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
Orcynopsis unicolor	1	26	2							29	20.0
Cybiosarda elegans					2	5	5	1		13	24.4
Sarda australis			10	2						12	21.2
Sarda chiliensis:											
NE Pacific		1	14	26	3					44	21.7
SE Pacific			10	8	1					19	21.5
Total		1	24	34	4					63	21.7
Sarda orientalis:											
Indo-W Pacific		9	4	1						14	20.4
E Pacific		8	4	2						14	20.6
Total		17	8	3						28	20.5
Sarda sarda:											
W. Atlantic					2	13	16	1		32	24.5
Mediterranean-Black Sea							3	9	3	15	26.0
Gulf of Guinea-S. Africa							11	6		17	25.4
Total					2	13	30	16	3	64	25.1
Gymnosarda unicolor	17									17	19.0
Allothunnus fallai	7									7	19.0

TABLE 9.—CONTINUED.

Species	Total vertebrae																			N	$\bar{x}$
	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55		
Orcynopsis unicolor	3	24	3																	30	38.0
Cybiosarda elegans											11	2								13	47.2
Sarda australis									11	1										12	45.1
Sarda chiliensis:																					
NE Pacific							1	8	34	4										47	44.9
(Kuo 1970)							(1	14	54	4)										(73)	(44.8)
SE Pacific							1	17	4	1										23	44.2
(Kuo 1970)						(9	29	23	4	1)										(66)	(43.4)
Total							2	25	38	5										70	44.7
Sarda orientalis:																					
Indo-W Pacific								2	12											14	44.9
E Pacific								1	14											15	44.9
Total								3	26											29	44.9
Sarda sarda:																					
W Atlantic														4	25	4	1			34	51.1
NE Atlantic															3					3	51.0
Mediterranean-Black Sea																	11	4		15	53.3
(Demir 1964, Turkey)																(6	71	34	1)	(112)	(53.3)
Gulf of Guinea-S. Africa																2	14	—	1	17	53.0
Total														4	28	6	26	4	1	69	52.0
Gymnosarda unicolor		17																		17	38.0
Allothunnus fallai			7																	7	39.0

all bonitos except *S. sarda* (first to seventh). Posteriorly, towards the caudal peduncular vertebrae and caudal complex, the neural spines bend abruptly backward and cover most of the neural groove; caudally they merge into the caudal complex as in *Thunnus* (Kishinouye 1923; Gibbs and Collette 1967). Neurapophyses are present on all centra. The neural prezygapophyses on the first vertebra are modified to articulate with the exoccipital where the vertebral axis is firmly articulated with the skull. They are stronger at the anterior portion of the vertebrae and are spurlike spines on the peduncular vertebrae and in the caudal complex. Neural postzygapophyses arise posterodorsally from the centrum and overlap with prezygapophyses posteriorly. The postzygapophyses progressively merge into the neural spine in the peduncular region. The basic structure and elements of the neural arches and neurapophyses are similar in bonitos (Figures 51-53) to those of other scombrids (Kishinouye

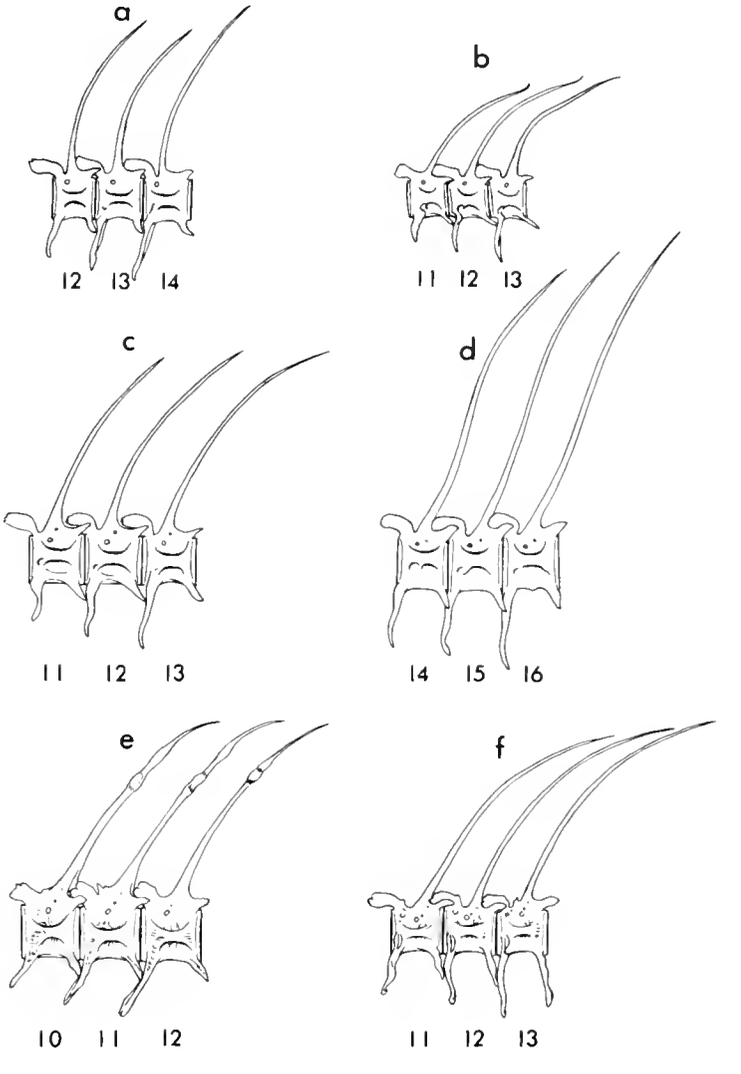


FIGURE 51.—Left lateral view of vertebra bearing first closed haemal arch (middle vertebra of each set of three) in six species of Sardini. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL (lumps on neural spines are anomalies). f. *Allothunnus fallai*, California, 680 mm FL.

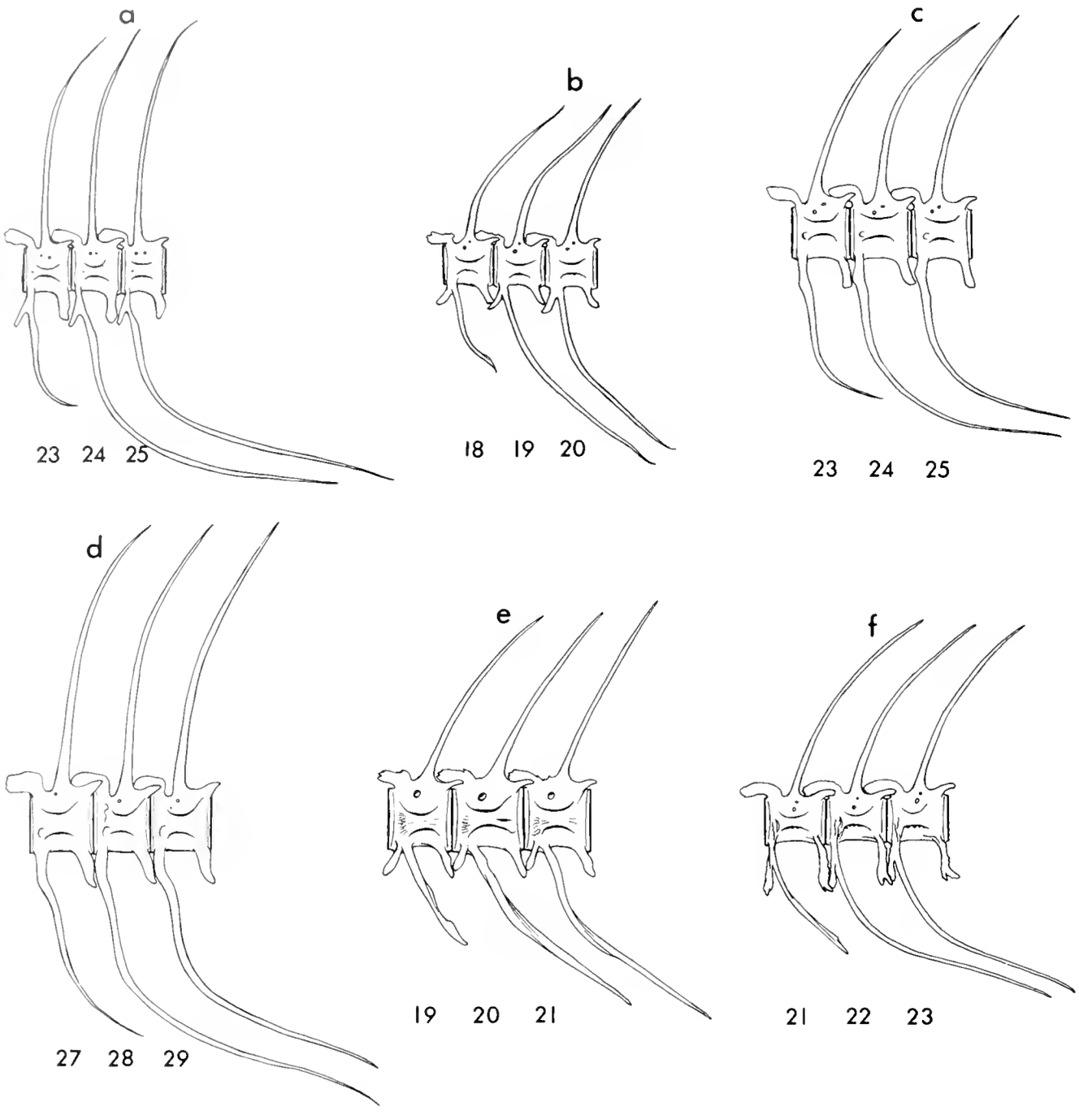


FIGURE 52.—Junction of precaudal and caudal vertebrae (middle vertebra of each set of three is first caudal vertebra) in six species of Sardini, left lateral view. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

1923; Conrad 1938; Mago Leccia 1958; Nakamura 1965; Gibbs and Collette 1967).

Variable characters are found on the haemal arches and haemapophyses in bonitos. Laterally directed parapophyses, arising from the middle of the centrum, appear distinctively on the third to fifth vertebrae, where the intermuscular bones and pleural ribs are encountered (see section on ribs and intermuscular bones). The parapophyses become broader and longer posteriorly and gradually shift to the anteroventral portion of the centra. In lateral view, the first ventrally visible parapophyses are found on the 8th to 10th vertebrae as described by Godsil (1954) for eastern Pacific *Sarda chiliensis* and *S. orientalis*. Posteriorly, the distal ends of the paired parapophyses meet on the 11th to 15th vertebrae forming the first closed haemal arch as Godsil (1954) found in eastern Pacific *S. chiliensis*. Nakamura (1965) suggested that the location of the first closed haemal arch can be used to assess relationships within the Thunnini. In the bonitos,

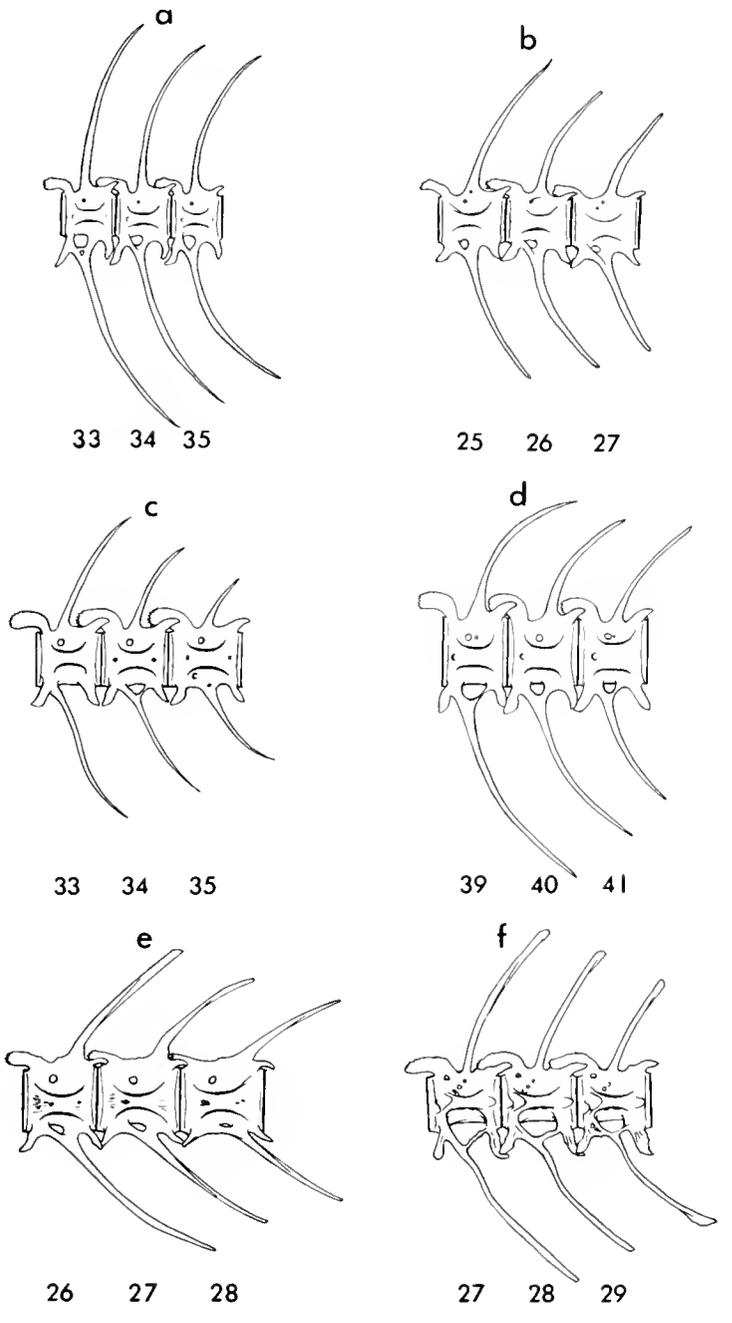


FIGURE 53.—Inferior foramina on caudal vertebrae in six species of Sardini, left lateral view. Vertebrae numbered from anterior. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 772 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

the first closed haemal arch is at the 11th to 13th vertebra in *Orcynopsis*, 13th in *Cybiosarda*, 13th to 15th in *Sarda sarda*, 12th to 14th in the other species of *Sarda*, 11th in *Gymnosarda*, and 12th in *Allothunnus*. This position is correlated with the number of vertebrae (Table 9). The first closed haemal arch is pointed anteriorly or posteriorly (Figure 51). The haemal spines become elongate and point posteriorly until they abruptly elongate on the first caudal vertebra. The paired pleural ribs (see section on ribs and intermuscular bones) attach to the distal end of the parapophyses and arches and extend posteriorly to the last precaudal vertebra. Symmetrically with the neural arches and spines on the caudal vertebrae, the haemal arches and spines bend posteriorly at the caudal peduncle and then merge into the caudal complex.

Haemapophyses include pre- and postzygapophyses but their relative positions are different from those of the neurapophyses, and they do not overlap in the bonitos. Haemal arches and haemapophyses are best developed in *Allothunnus*. The first haemal postzygapophyses arise posteroventrally from the eighth or ninth centrum, and they reach their maximum length at about the junction of the precaudal and caudal vertebrae (Figure 52). They begin at the fourth vertebra in *Thunnus* (Gibbs and Collette 1967) and the eighth vertebra in *Scomberomorus* and *Acanthocybium* (Mago Leccia 1958; Conrad 1938). The haemal postzygapophyses fuse with the haemal spine in the caudal peduncle region. The haemal prezygapophyses arise from the anterior base of the haemal arches on the 14th to 23rd vertebra, depending on the species. They begin at the 12th to 18th vertebra in "Thunninae" (Nakamura 1965; Gibbs and Collette 1967; Potthoff 1974) and at the 16th in *Acanthocybium* (Conrad 1938). As do their counterpart neural prezygapophyses, the haemal prezygapophyses persist symmetrically into the caudal complex.

The relative position and contacts between pre- and postzygapophyses of both neuro- and haemapophyses, especially the latter, vary in different regions of the vertebral column (Figures 51-53). Godsil (1954) compared haemal pre- and postzygapophyses of eastern Pacific *Sarda chiliensis* and *S. orientalis*. We believe that comparisons should be made within specific regions of the vertebral column. The haemal postzygapophysis of the last precaudal vertebra and the haemal prezygapophysis of the first caudal vertebra (Figure 52) abut each other in *Orcynopsis*, *Sarda orientalis*, and *Allothunnus*. A space between these two elements is present in other bonitos. The haemal prezygapophysis is longer than the postzygapophysis at the junction (Figure 52) of precaudal and caudal vertebrae in *Cybiosarda*, *Orcynopsis*, *S. chiliensis*, and *S. orientalis*. The opposite condition is found in *S. sarda*, *S. australis*, and *Allothunnus*.

Struts between the haemal arch and the centrum form the inferior foramina. These are variably developed on 3 to 12 vertebrae anterior to the

caudal peduncle, depending on the species (Figure 53). *Cybiosarda* has the most inferior foramina, on 10 to 12 vertebrae; *Orcynopsis* has 9 to 10; *Sarda* 3 to 7; and *Gymnosarda* 6 to 7. *Allothunnus* has the largest inferior foramina on 7 to 9 vertebrae.

Infracentral Grooves

Nakamura and Kikawa (1966) described three types of infracentral grooves on the ventral side of the vertebral centra in tunas. They placed *Sarda orientalis* in type C, with a single groove, and this is the category of all species of *Sarda*, *Cybiosarda*, and *Orcynopsis* (Figure 54). *Gymnosarda* (Figure 54e) has the type C infracentral grooves on the centra, but the grooves are much deeper and a shallow transverse septum is present in the middle of each groove. Nakamura and Kikawa (1966) did not place *Allothunnus* in any of the three categories. The precaudal vertebrae of *Allothunnus* have type A, with two separate infracentral grooves per centrum, but these are not distinct posteriorly as shown in Figure 54f. Some of the grooves may be covered with a layer of thin bone, especially on the anterior precaudal vertebrae. In all the bonitos, the grooves are very irregular on the first several vertebrae.

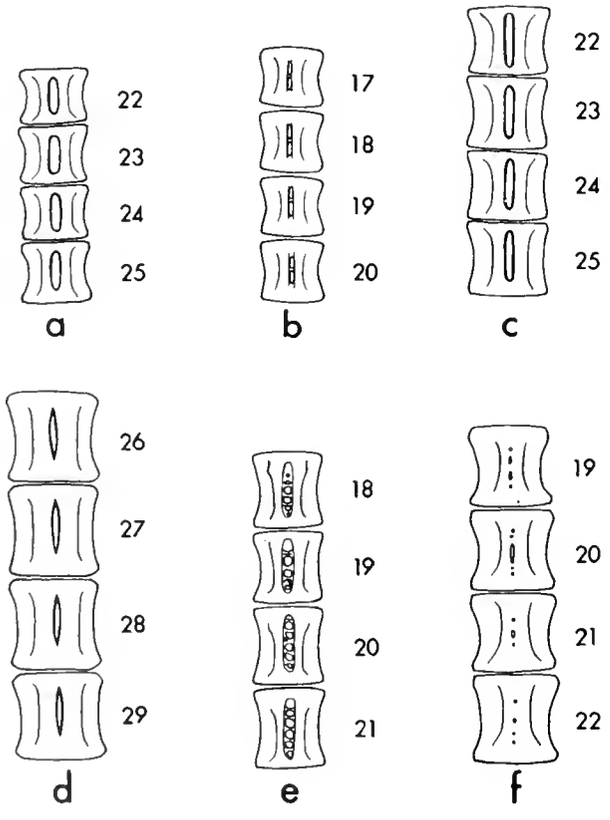


FIGURE 54.—Infracentral grooves on the ventral surface of four vertebrae including the last precaudal and first caudal vertebra in six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Israel, 545 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, Tasmania, 775 mm FL. a, c, and d drawn twice as large as b, e, and f.

Ribs and Intermuscular Bones

Pleural ribs are present from the third vertebra posterior to the 18-27th vertebra, depending on the species. Intermuscular bones start on the back of the skull and extend to the 19-39th vertebra.

Sarda differs from other bonitos in having two cephalic intermuscular bones attached to the exoccipital on each side of the skull (Figures 12, 26). One is attached to the center of the exoccipital. The other one is attached to the exoccipital just anterior to the first neural prezygapophysis close to the midline of the skull. *Orcynopsis*, *Cybiosarda*, and *Allothunnus* have the median cephalic intermuscular bone, but the lateral one is represented only by an unossified ligament. *Gymnosarda* completely lacks cephalic intermuscular bones and also lacks a ligament in the lateral position. A ligament is present in the comparable position of the median cephalic intermuscular bone.

Sarda has more pleural ribs than do other genera, 19-24 pair; *Cybiosarda* has 20, *Allothunnus* 18, *Gymnosarda* 17, and *Orcynopsis* 16. These numbers are well correlated with vertebral number except that *Cybiosarda* has fewer than would be predicted.

The same general trend is apparent in the number of intermuscular bones but several genera are not in corresponding order. *Sarda sarda* has the most (36-45 pair) followed by other species of the genus (32-36). Following are *Allothunnus* (28-29) and *Gymnosarda* (25-28) with more than expected; *Cybiosarda* (23-24) with fewer than expected; and *Orcynopsis* (19-20) with the fewest.

Caudal Peduncle Keels

We believe that there is a general evolutionary trend within the Scombridae in the relative development of keels on the caudal peduncle. The Gasterochismatinae and the primitive members of the Scombrinae (Scombrini—mackerels and Scomberomorini—Spanish mackerels) lack supporting bony keels and have only external fleshy keels on the caudal peduncle. Starting with the bonitos, bony keels are developed under the largest pair of fleshy keels to strengthen and support them. They are developed in two different ways in

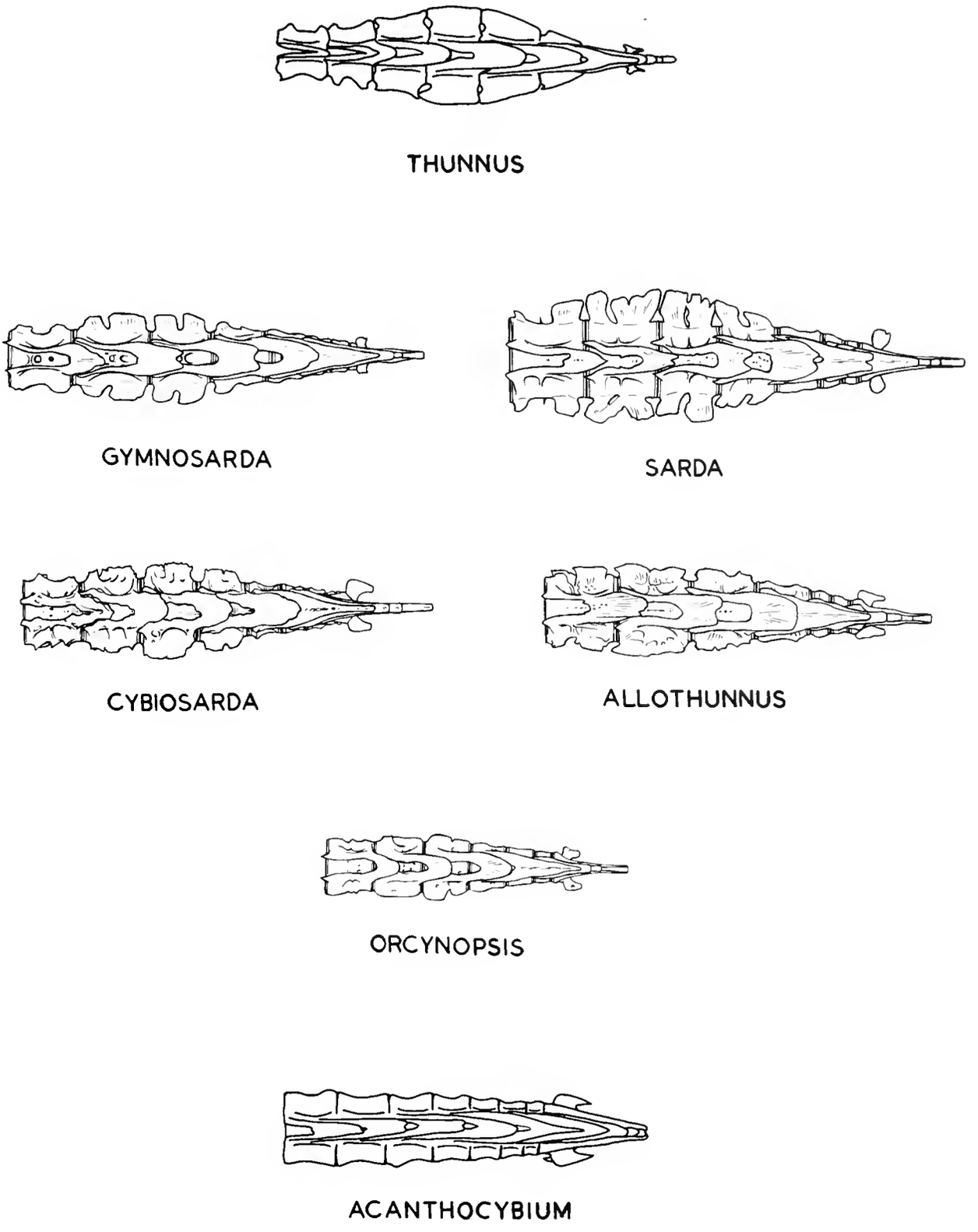


FIGURE 55.—Dorsal view of last seven or eight preural centra to show structure of bony caudal keels in the five genera of Sardini plus *Acanthocybium* and *Thunnus* representing a more primitive (Scomberomorini) and a more advanced tribe (Thunnini) respectively.

the bonitos. *Orcynopsis*, *Cybiosarda* (Figure 55), and *Allothunnus* have low keels running the entire length of the vertebrae involved. *Sarda* and *Gymnosarda* have wider keels, as in the higher tunas, but they are divided into two segments on each vertebra, one on the anterior part of the vertebra and one on the posterior part. The higher tunas (Thunnini—*Auxis* through *Thunnus*) have a wide flattened plate that acts as a single functional unit over several vertebrae.

Within the bonitos, there are minor differences as to which vertebrae bear the bony caudal keel. Counting anteriorly from preural centrum one, *Orcynopsis* differs from *Cybiosarda* in having keels concentrated on the fourth to sixth preural vertebrae instead of on the fifth to seventh.

Allothunnus has keels on the fourth to seventh; *Gymnosarda*, *Sarda australis*, *S. orientalis*, and *S. chiliensis* all have them on the four vertebrae between the fourth and eighth. Correlated with its greatly increased number of vertebrae (Table 9), *Sarda sarda* has keels on the 5th to 10th preural vertebrae.

Caudal Complex

Posterior to the peduncular vertebrae, the supporting bones of the caudal fin (Figure 56) consist of four preural centra. Preural centra four and three bear stout haemal and neural spines. Preural centrum two has a haemal spine and a fused epural. The urostyle represents a fusion of preural centrum one and the ural centrum (Potthoff 1975). The urostyle is fused with a triangular plate posteriorly and with the uroneural anteriorly. Dorsally, the urostyle bears an autogenous epural and ventrally, the autogenous parhypural. Preural centra two to four are compressed in all bonitos, as in *Thunnus*. Usually, two neural and three haemal spines bend abruptly away from the vertebral axis on these preural centra and parallel the dorsal and ventral edges of the hypural plate. Exceptions are found in some specimens of *S. sarda* and *S. chiliensis* (Figure 56c), which have an additional pair of neural and haemal spines from preural centrum five supporting caudal rays. The figure of *S. sarda* presented by Monod (1968, fig. 749) has two haemal spines on preural centrum three which is an anomaly. Other elements of the preural centra are described in the sections on the vertebral column and caudal peduncle keels.

The triangular hypural plate is composed of five fused hypural bones (Potthoff 1975). The dorsalmost (hypural 5) is not completely fused with the hypural plate in the bonitos (Figure 56c) or in the higher tunas, *Auxis* to *Thunnus*. The primitive hypural notch is absent from the middle of the posterior margin in all bonitos except for a vestige in *Gymnosarda*. The anterior epural (epural one) resembles the neural spine of the adjacent preural centrum three because it is secondarily fused to the neural arch of the second preural centrum. The posterior epural (epural two) is a free splint located between the anterodorsal margin of the hypural plate and the anterior epural in the Sardini (Figure 56b). It is absent (or may be secondarily fused to the anterior epural) in one Tunisian specimen of *S. sarda* (Figure 56d), which is an anomaly.

The parhypural has a strong hooked process, the parhypurapophysis, at its proximal end. As in *Thunnus*, it is located between the first haemal spine and the anteroventral margin of the hypural plate in all bonitos, except *Gymnosarda*. In *Gymnosarda* (Figure 56e), the parhypural is fused with the hypural plate as in *Acanthocybium* and some species of *Scomberomorus*. Kishinouye's (1923) figures of *Gymnosarda* (fig. 38) and *Acanthocybium* (fig. 39) are similar to our observations, but the caudal complex is upside down in his figure of *Gymnosarda*. Fusion of the parhypural with the hypural plate in *Acanthocybium* was also noted by Conrad (1938) and Fierstine and Walters (1968). In *Scomberomorus niphonius*, we also find this fusion, which is in agreement with Kishinouye's (1923) fig. 41. However, the parhypural is not fused with the hypural plate in *Scomberomorus chinense* (Kishinouye 1923, fig. 40) and the three western Atlantic species of *Scomberomorus* described by Mago Leccia (1958). The shape of the parhypurapophysis separates *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* from *Sarda* and *Allothunnus*. The former have a smooth oblique anterior margin and the latter are concave. The concentrations of tendons and muscular bands between the parhypurapophysis and caudal rays in scombroids were described by Fierstine and Walters (1968), but no specific study of this aspect was made during our work.

One of the diagnostic characters of the Scombridae is that the bases of the caudal rays cover the hypural plate (Figure 57), instead of only extending part way over the plate as is true of the Gempylidae and Trichiuridae. Another diagnostic character of the Scombridae is that four preural centra support the caudal rays (Figure 57). In the Gempylidae, Carangidae, and Coryphaenidae, only three preural centra support the caudal fin rays (Berry 1969; Potthoff 1975).

DORSAL AND ANAL FINS

Scombrids have two dorsal fins. The first dorsal fin is composed of stiff spines and is separated from the second dorsal by a short distance, except in *Rastrelliger*, *Scomber*, and *Auxis* which have a greater distance between the fins. The second dorsal fin is composed of soft rays and is followed by a series of free finlets, 6-10 in the Sardini. The anal fin is located approximately opposite the dorsal fin and is composed largely of soft rays

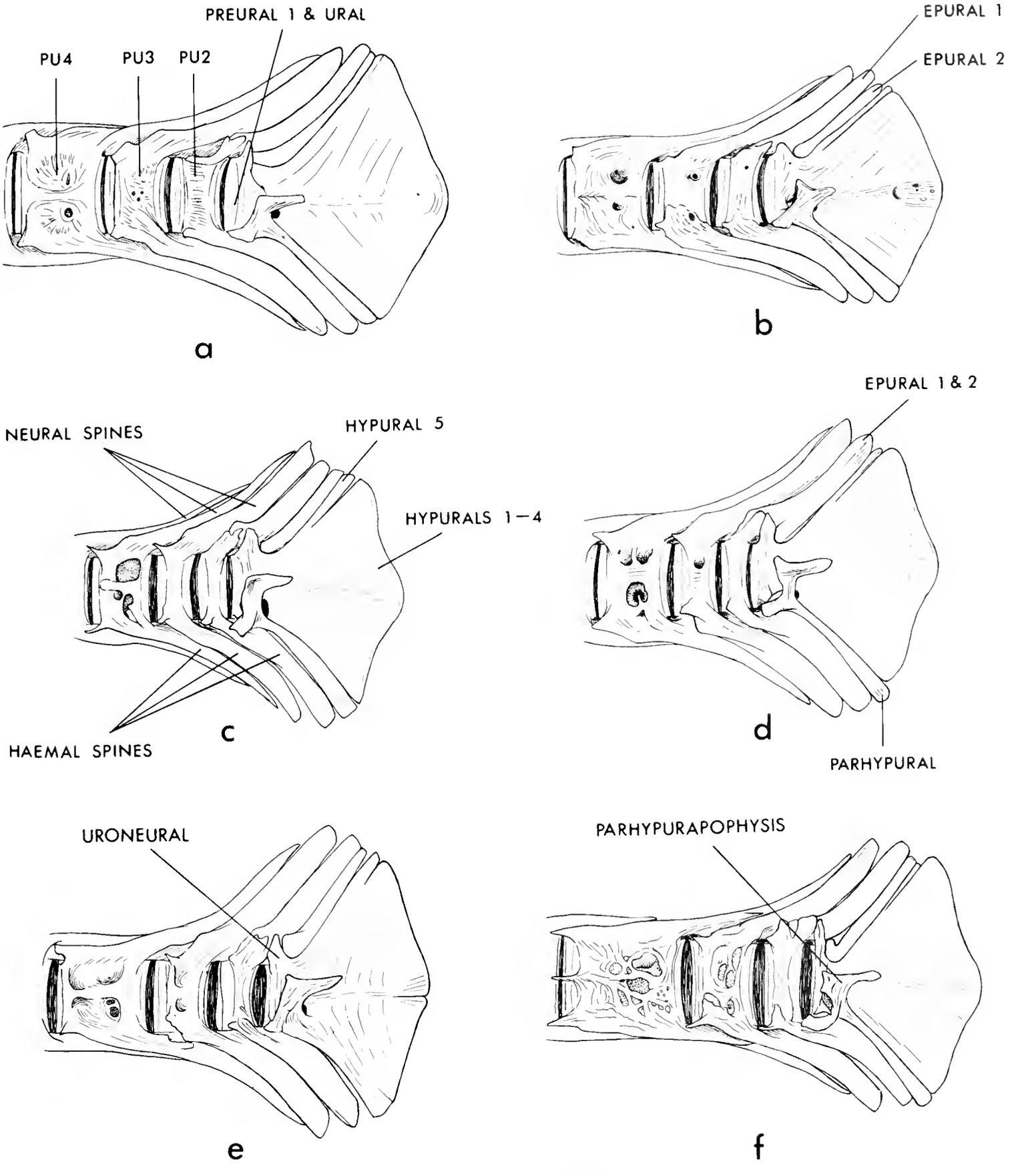


FIGURE 56.—Left lateral view of caudal complex of six species of Sardini. a. *Cybiosarda elegans*, Western Australia, 422 mm FL. b. *Orcynopsis unicolor*, Tunisia, 573 mm FL. c. *Sarda chiliensis*, Callao, Peru, 571 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL (with anomalous fusion of the two epurals). e. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a is drawn twice as large as b, e, and f, and c and d are 1.5 times as large as b, e, and f.

FIGURE 57.—Radiograph of the caudal complex with the bases of the caudal fin rays covering the hypural plate. *Orcynopsis unicolor*, Dakar, 960 mm FL.

followed by a series of anal finlets similar to the dorsal finlets. Some scombrids have a free or partially free spine preceding the anal fin, but in the Sardini it is difficult to tell if the anterior elements are spiny or soft rays so all are included as "anal rays." Numbers of fin rays are useful taxonomic characters in the Sardini.

Using the number of dorsal spines (Table 10), bonitos can be divided into three groups: few spines (12-15) in *Orcynopsis* and *Gymnosarda*; moderate numbers (16-19) in *Cybiosarda*, *Allothunnus*, and three species of *Sarda*; and many (20-23) in *S. sarda*. The difference between these groups is correlated with the number of vertebrae. Intraspecifically, eastern Atlantic specimens of *Sarda sarda* have modally higher counts (22) than western Atlantic specimens (21).

The most distinctive bonito in counts of second dorsal elements is *Cybiosarda*, with a high count of 17-19 rays (Table 11). *Orcynopsis*, *Gymnosarda*, and *Allothunnus* have low counts (15 or fewer). *Sarda australis* has, modally, one more second dorsal ray than do *S. orientalis* and *S. chiliensis*.

TABLE 10.—Number of spines in the first dorsal fin of species of Sardini.

Species	11	12	13	14	15	16	17	18	19	20	21	22	23	*N*	$\bar{x}$
Cybiosarda elegans						12	9	1						22	16.5
Orcynopsis unicolor:															
E Mediterranean		1	28	7										36	13.2
Cent. Mediterranean			10											10	13.0
(Postel 1956a, Tunisia)	(3	22	161	3)										(189)	(12.9)
Atlantic			4	2										6	13.3
Total		1	42	9										52	13.2
Sarda australis								7	12					19	18.0
Sarda chiliensis:															
NE Pacific								19	16					35	18.5
(Kuo 1970)							(20	420	69	2)				(511)	(18.1)
SE Pacific							5	19	7					31	18.1
(Kuo 1970)							(8	77	5)					(90)	(18.0)
Total							5	38	23					66	18.3
Sarda orientalis:															
Indian Ocean								10						10	18.0
NW Pacific								11	4					15	18.3
Cent. Pacific								2	2					4	18.5
E Pacific							4	11	1					16	17.8
Total							4	34	7					45	18.1
Sarda sarda:															
North America										6	46	8	1	61	21.1
South America										6	8			14	20.6
NE Atlantic										2	2	8		12	22.2
Mediterranean-Black Sea											5	21	4	30	22.0
(Demir 1964, Turkey)							(1	1	2	38	351	558	49)	(1,000)	(21.6)
Gulf of Guinea-S. Africa											6	22		28	21.8
Total										14	67	59	5	145	21.4
Gymnosarda unicolor:															
Indian Ocean			4	3	2									9	13.8
W Pacific			2	16	3									21	14.1
Total			6	19	5									30	13.9
Allothunnus fallai					1	4	1	1						7	16.3

TABLE 11.—Number of second dorsal rays, dorsal finlets, and total second dorsal rays in species of Sardini.

Species	Second dorsal rays										Dorsal finlets							Total second dorsal rays										
	12	13	14	15	16	17	18	19	*N*	$\bar{x}$	6	7	8	9	10	*N*	$\bar{x}$	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
Cybiosarda elegans						11	8	3	22	17.6			4	17	1	22	8.9							1	9	12	22	26.5
Orcynopsis unicolor:																												
E Mediterranean	1	6	16	7					30	14.0		3	22	11		36	8.2		1	4	16	7	1				29	22.1
Cent. Mediterranean		1	5	2					8	14.1			6	2		8	8.3			1	4	2	1				8	22.4
(Postel 1956a, Tunisia)												(7	140	42)		(189)	(8.2)											
Atlantic			3	2					5	14.4			6			6	8.0				3	2					5	22.4
Total	1	7	24	11					43	14.0		3	34	13		50	8.2		1	5	23	11	2				42	22.2
Sarda australis				5	11	3			19	15.9		15	4			19	7.2				4	9	6				19	23.1
Sarda chiliensis:																												
NE Pacific		4	10	15	6				35	14.7		5	28	2		35	7.9			5	10	14	6				35	22.6
(Kuo 1970)		(1	42	260	195	12)			(510)	(15.3)		(73	411	28)		(512)	(7.9)											
SE Pacific		3	18	9					30	14.2		12	18	1		31	7.6		1	8	14	7					30	21.9
(Kuo 1970)			(29	53	10)				(92)	(14.8)		(22	65	1)		(88)	(7.8)											
Total		7	28	24	6				65	14.4		17	46	3		66	7.8		1	13	24	21	6				65	22.3
Sarda orientalis:																												
Indian Ocean			1	5	4				10	15.3			9	1		10	8.1				1	4	5				10	23.4
NW Pacific			2	6	6	1			15	15.4		1	14			15	7.9				2	7	5	1			15	23.3
Cent. Pacific				2	2				4	15.5			3	1		4	8.3				1	2	—	1			4	23.3
E Pacific			1	7	8				16	15.4		1	12	3		16	8.1				2	3	11				16	23.6
Total			4	20	20	1			45	15.4		2	38	5		45	8.1				6	16	21	2			45	23.4
Sarda sarda:																												
North America		1	1	17	33	3	1		56	15.7		4	34	19		57	8.3				3	14	26	11	2		56	23.9
South America			1	3	8	2			14	15.8		1	9	4		14	8.2				1	2	7	4			14	24.0
NE Atlantic				1	7	2			10	16.1		1	6	4		11	8.3					1	5	3	1		10	24.4
Mediterranean-Black Sea				2	4	10	2		18	16.7		2	10	6		18	8.2					1	5	8	3	1	18	24.9
(Demir 1964, Turkey)		(2	4	17	87	114	25	1)	(250)	(16.5)	(1	15	530	439	15)	(1,000)	(8.5)											
Gulf of Guinea-S. Africa				2	7	13	5		27	16.8		7	18	2		27	7.8					3	7	15	2		27	24.6
Total		1	2	25	59	30	8		125	16.1		15	77	35		127	8.2				4	21	50	41	8	1	125	24.3
Gymnosarda unicolor:																												
Indian Ocean	1	7	1						9	13.0	1	8				9	6.9	2	6	1							9	19.9
W Pacific		13	9						22	13.4	2	20				22	7.0		15	7							22	20.3
Total	1	20	10						31	13.3	3	28				31	6.9	2	21	8							31	20.2
Allothunnus fallai	3	4							7	12.6	1	5	1			7	7.0	3	4								7	19.6

Cybiosarda has, modally, nine dorsal finlets; *Gymnosarda*, *Allothunnus*, and *S. australis* have seven; and the other four species have eight. Thus, in total number of second dorsal elements, *Cybiosarda* is high (25-27), *Gymnosarda* and *Allothunnus* are low (19-21), and the other species are intermediate.

Anal rays (Table 12) follow a similar trend to that of dorsal rays. *Cybiosarda* has many anal rays (15-17) and total anal elements (21-24). *Gymnosarda* has few anal rays (12-13) and total anal elements (18-19). Modally, *Cybiosarda*, *Orcynopsis*, *Allothunnus*, *Sarda chiliensis*, and *S. sarda* have seven anal finlets; *Gymnosarda*, *Sarda australis*, and *S. orientalis* have six finlets.

PECTORAL GIRDLE

The pectoral girdle consists of the girdle itself (cleithrum, scapula, and coracoid), the radials to which the pectoral fin rays attach and a chain of bones that connect the girdle onto the rear of the skull (posttemporal, supratemporal, supracleithrum, and two postcleithra).

Posttemporal

The posttemporal bones of the bonitos are generally similar with two anterior processes and a flat posterior body (Figure 58). The median process is thin and flat and articulates with the epiotic. The lateral process is rounded and rodlike and articulates with the intercalar anteroventrally. *Cybiosarda*, *Orcynopsis*, *Sarda*, and *Allothunnus* each have a well-developed shelf connecting the median and lateral processes while *Gymnosarda* (Figure 58e) has the shelf greatly reduced. The shelf extends posteriorly and forms a posteriorly directed spine beneath the body in all bonitos. *Cybiosarda*, *Orcynopsis*, and *Gymnosarda* have a shorter body than do *Sarda* and *Allothunnus*. There is a notch at the middle of the posterior edge of the body of the bone. The dorsal profile of the posttemporal is more or less flat in all the bonitos except in *Gymnosarda*, which has the margin convex posteriorly.

Supratemporal

The supratemporal bones of the bonitos are thin with two anterior processes and an elongated posterior body (Figure 59). The dorsal process lies free beneath the skin and the ventral process is firmly attached with connective tissue. The posterior body of the supratemporal overlaps externally the lateral process and part of the posterior body of the posttemporal. Lateral line canals are present on the internal surfaces of the

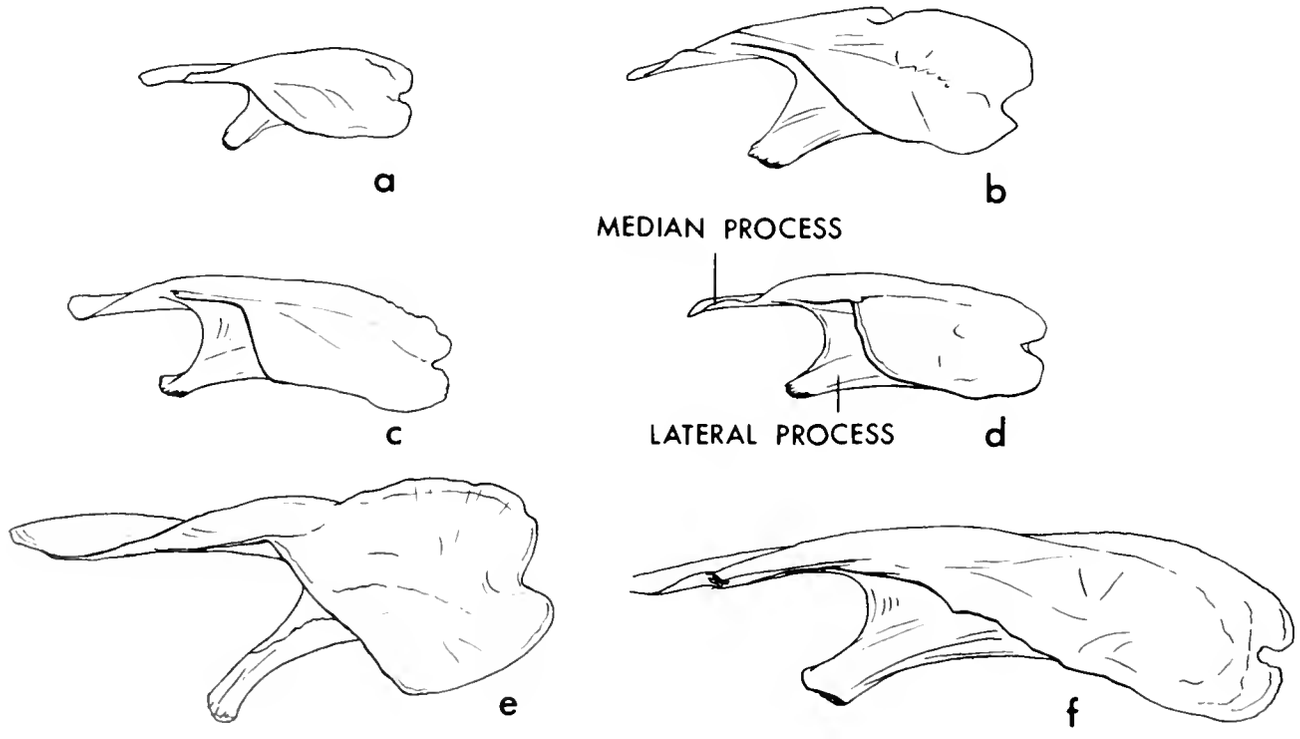


FIGURE 58.—External view of left posttemporals of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda sarda*, Tunisia, 504 mm FL. d. *Sarda australis*, New South Wales, 363 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 784 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

TABLE 12.—Number of anal rays, anal finlets, and total anal rays in species of Sardini.

Species	Anal rays										Anal finlets							Total anal rays								
	11	12	13	14	15	16	17	18	*N*	$\bar{x}$	5	6	7	8	9	*N*	$\bar{x}$	18	19	20	21	22	23	24	*N*	$\bar{x}$
Cybiosarda elegans					1	8	12		21	16.5		5	16			21	6.8				1	2	7	11	21	23.3
Orcynopsis unicolor:																										
E Mediterranean				1	17	9			27	15.3		9	23	2		34	6.8				1	25	1		27	22.0
Cent. Mediterranean				1	4	3			8	15.3		1	5	1		7	7.0					5	2		7	22.3
(Postel 1956a, Tunisia)												(16	150	23)		(189)	(7.0)									
Atlantic				1	3	1			5	15.0			5			5	7.0				1	3	1		5	22.0
Total				3	24	13			40	15.3		10	33	3		46	6.9				2	33	4		39	22.1
Sarda australis				1	14	4			19	15.2	1	17	1			19	6.0		1	—	13	5			19	21.2
Sarda chiliensis:																										
NE Pacific		2	11	17	5				35	13.7		10	23	2		35	6.8		3	16	12	4			35	20.5
(Kuo 1970)	(3	100	269	124	13)				(509)	(13.1)		(51	427	34)		(512)	(7.0)									
SE Pacific		2	10	17	2				31	13.6		18	12	1		31	6.4	1	5	14	10				30	20.1
(Kuo 1970)	(2	40	42	8)					(92)	(12.6)		(27	65)			(92)	(6.7)									
Total		4	21	34	7				66	13.7		28	35	3		66	6.6	1	8	30	22	4			65	20.3
Sarda orientalis:																										
Indian Ocean				3	7				10	14.7		8	2			10	6.2			1	9				10	20.9
NW Pacific				7	9				16	14.6		15	1			16	6.1			6	10				16	20.6
Cent. Pacific				2	2				4	14.5		4				4	6.0			2	2				4	20.5
E Pacific				4	10	2			16	14.9		12	4			16	6.3			1	12	3			16	21.1
Total				16	28	2			46	14.7		39	7			46	6.2			10	33	3			46	20.8
Sarda sarda:																										
North America				18	37	7			62	14.8		14	42	5		61	6.9			1	22	35	3		61	21.7
South America				2	10	2			14	15.0		3	11			14	6.8			1	2	10	1		14	21.8
NE Atlantic				1	9				10	14.9		2	7	1		10	6.9				3	6	1		10	21.8
Mediterranean-Black Sea				1	10	7			18	15.3		4	11	3		18	6.9				3	10	5		18	22.1
(Demir 1964, Turkey)			(2	8	66	88	24	5)	(193)	(15.7)	(2	98	730	164	6)	(1,000)	(7.1)									
Gulf of Guinea-S. Africa				2	9	14	2		27	15.6		8	19			27	6.7				5	9	13		27	22.3
Total				24	75	30	2		131	15.1		31	90	9		130	6.8			2	35	70	23		130	21.9
Gymnosarda unicolor:																										
Indian Ocean		6	3						9	12.4		9				9	6.0	6	3						9	18.4
W Pacific		4	17						21	12.8		21				21	6.0	4	17						21	18.8
Total		10	20						30	12.7		30				30	6.0	10	20						30	18.7
Allothunus fallai			3	4					7	13.6		2	5			7	6.7		1	3	3				7	20.3

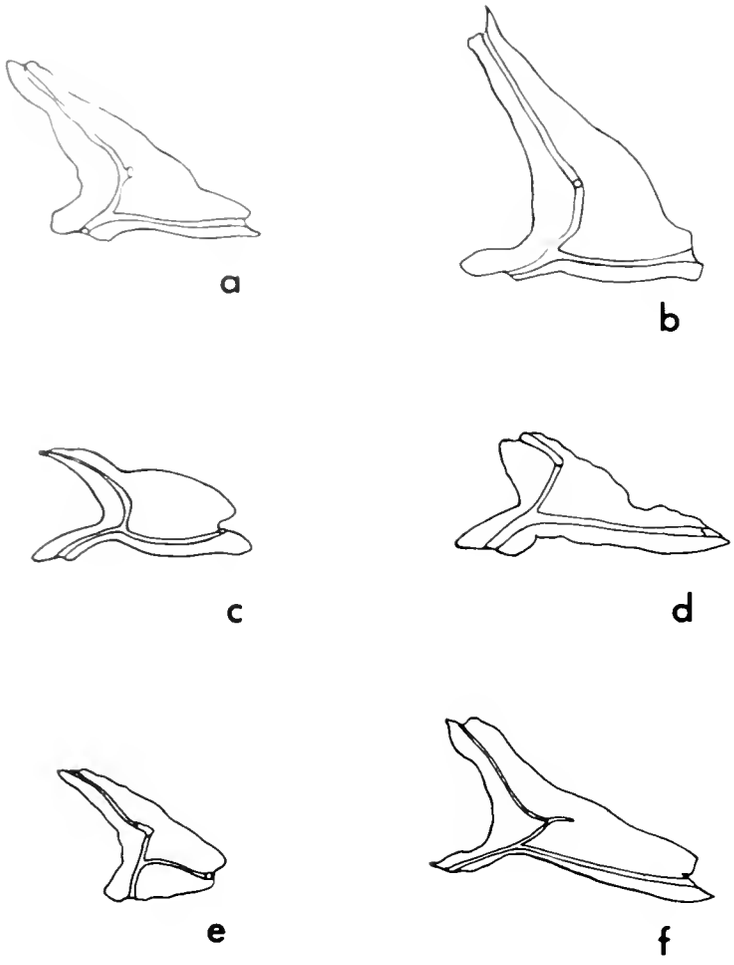


FIGURE 59.—Left supratemporals of six species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 365 mm FL. b. *Orcynopsis unicolor*, Tunisia, 503 mm FL. c. *Sarda sarda*, New Jersey, 375 mm FL. d. *Sarda chiliensis*, Peru, 473 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 607 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

supratemporal bones in all bonitos. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have a shorter posterior body than do *Sarda* and *Allothunnus*. The thin edges of the supratemporal vary slightly among species of *Sarda* (Figure 59) and within each species of bonito. *Allothunnus* has the most elongate posterior body.

Supracleithrum

The supracleithrum lies in between the posttemporal and the cleithrum. *Cybiosarda*, *Orcynopsis*, and *Sarda* have relatively narrow and elongate supracleithra compared to *Gymnosarda* and *Allothunnus*. A dorsally projecting process is set off from the main body of the supracleithrum by a notch or angle on the anterodorsal part of the outer surface of the bone. *Sarda australis* and *Allothunnus* have the notch almost right-angled (Figure 60f, h). The other species of *Sarda* have a more poorly developed notch with a wider angle.

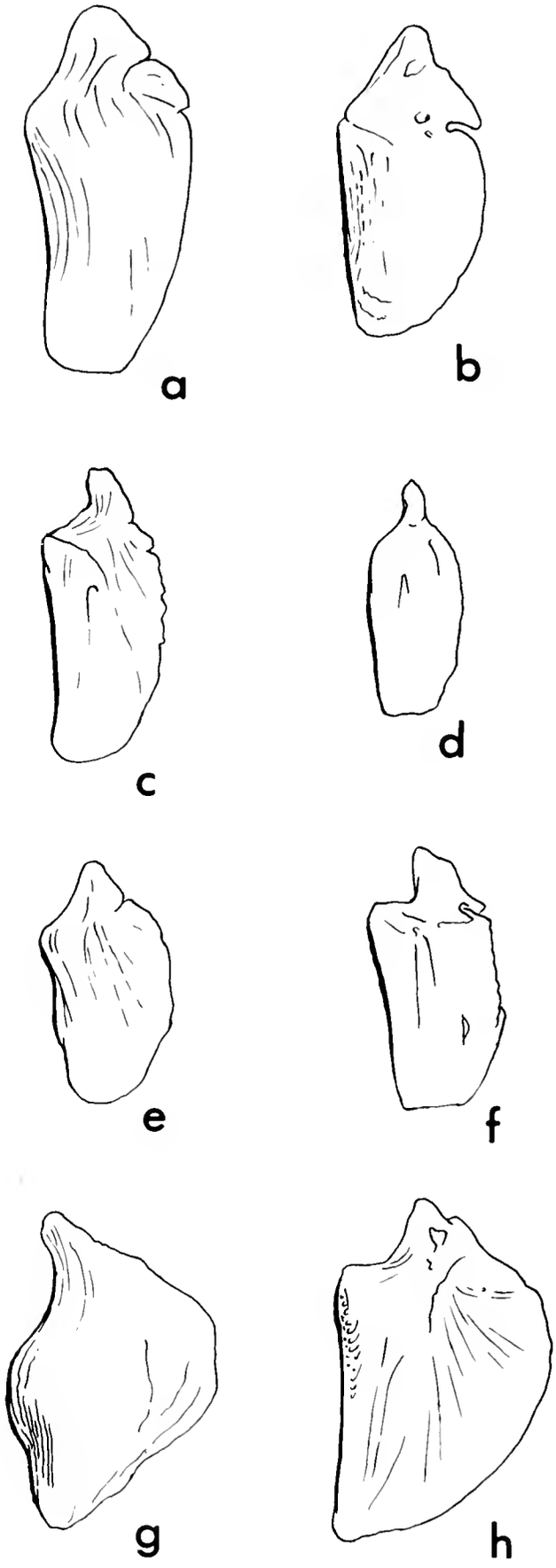


FIGURE 60.—Left supracleithra of eight species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, Callao, Peru, 549 mm FL. d. *Sarda orientalis*, Panama, 415 mm FL. e. *Sarda sarda*, Tunisia, 504 mm FL. f. *Sarda australis*, New South Wales, 495 mm FL. g. *Gymnosarda unicolor*, Amirante Islands, 713 mm FL. h. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as other figures.

Gymnosarda has a comparatively deep notch but the dorsally projecting process points more anteriorly than in any other bonito (Figure 60g). There is only a slight notch in *Cybiosarda* and no indentation at all on the anterodorsal edge of the bone in *Orcynopsis*. A ridge extends along the length of the inner surface of the supracleithrum. The ridge gradually merges into the main body of the bone dorsally. It stops abruptly about two-thirds of the way toward the dorsally projecting tip and is almost absent anteriorly in *Allothunnus*, as in *Thunnus*.

Cleithrum

The main body of the cleithrum in bonitos is crescent-shaped with an anterodorsal spine and a posteriorly projecting plate at the upper end, as in other scombrids (Figures 61, 62). The angle between the spine and the dorsal margin of the plate is smallest in *Gymnosarda* and widest, almost a right angle, in the species of *Sarda*. The angle is intermediate in *Cybiosarda*, *Orcynopsis*, and *Allothunnus*, similar to the condition in *Thunnus*. Godsil (1954) stated that the posteriorly projecting plate in *S. velox* (= *S. orientalis*) has a bluntly rounded distal end compared to *S. chiliensis*, which has the plate tapered distally. We found that this character is not consistent in *S. orientalis*, but *S. chiliensis* does have a more tapered distal portion than do the other species of *Sarda*. The main body of the cleithrum consists of an inner and an outer shelf, which join at the main axis, and a ridge at the anterior margin of the main axis on its inner surface. *Cybiosarda*, *Orcynopsis*, and *Sarda* have a poorly developed ridge along the anterior margin of the outer shelf (Figure 61a-d) as does *Thunnus* (de Sylva 1955, fig. 34). It is present only along the posterior edge of the upper two-thirds of the inner shelf of *Gymnosarda*. In *Allothunnus* (Figure 64f), the ridge becomes a broad well-developed inner shelf which extends internally from the outer shelf and at right angles to the inner shelf along the upper two-thirds of the main body. *Orcynopsis* has an expanded lower portion of the inner shelf; in

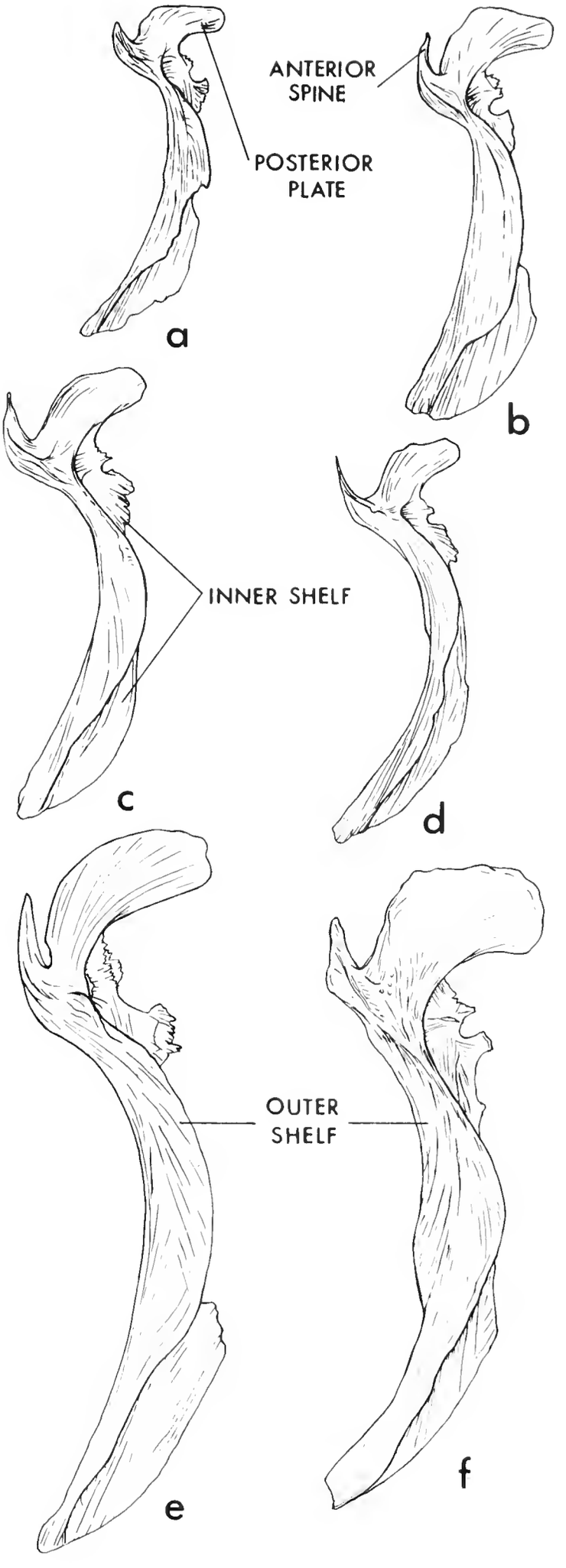


FIGURE 61.—Left cleithra of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 495 mm FL. c. *Sarda australis*, New South Wales, 495 mm FL. d. *Sarda chiliensis*, La Jolla, Calif., 453 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 680 mm FL.

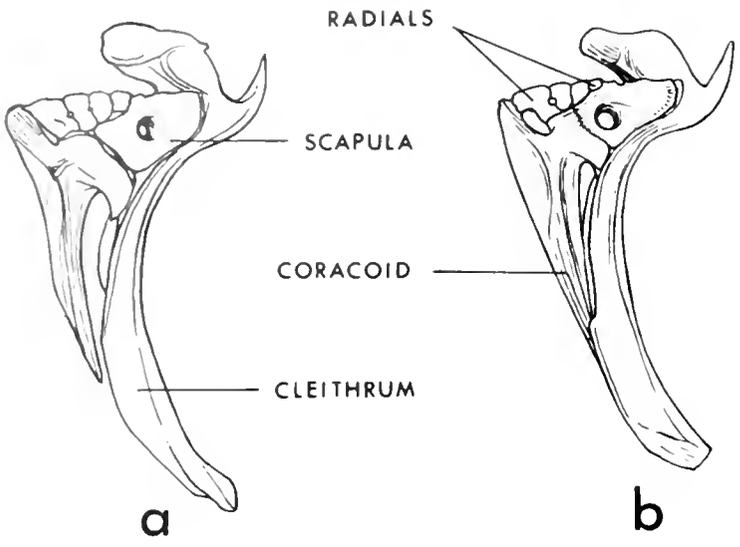


FIGURE 62.—Left pectoral girdles of two species of Sardini, internal view. a. *Sarda sarda*, Azores, 418 mm FL. b. *Cybiosarda elegans*, New South Wales, 360 mm FL.

Gymnosarda the inner shelf stops abruptly at the middle portion where the marginal ridge begins.

Scapula

The anterior margin of the scapula fits into the inner shelf of the cleithrum (Figure 62). This attachment extends to the posterior projecting plate anterodorsally. The scapula is attached with the coracoid posteriorly and dorsally it is attached with the first two and part of the third upper radials (Figure 63). The posterior margin of the scapula is drawn out into a facet which accepts the anterior ray of the pectoral fin. A suture bisects the scapula through the scapular fenestra. The general features of the scapula are similar among the bonitos. The scapular fenestra of *Gymnosarda* (Figure 63e) is relatively larger, and that of the species of *Sarda* (Figure 63c, d) is smaller, than the other bonitos.

Coracoid

The coracoid is elongated and more or less triangular in shape (Figure 63). It is connected with the scapula along its flat dorsal edge in *Allothunnus* (Figure 63f). In all other bonitos, this margin is interrupted ventral to the scapular fenestra and extends dorsally as an interdigitating suture. The ventral wing of the coracoid is xiphoid with a V-shaped depression along the midline. The coracoid has two points of attachment with the cleithrum, the first along the anterior margin near the scapula, and the second at the anterior end of the ventral wing. The margin of the coracoid, between its articulations with the cleithrum, is curved inward. This curvature is more pronounced in *Gymnosarda* (Figure 63e) than in the other bonitos, which resemble *Thunnus*.

Radials

The four radials differ in size and shape and are attached directly to the thickened posterior edges of the scapula and coracoid (Figures 62, 63). The size of the radials increases ventrally. Two small foramina are located between the second and third, and the third and fourth radials, counting downward. The first two radials and the upper half of the third radial attach to the coracoid; the ventral half of the third plus the fourth radial attach to the scapula. A fenestra is present between the dorsoposterior end of the coracoid and the largest radial, which has a prominent posteroventral process in all bonitos except *Sarda* and *Allothunnus*. In both characters, the fenestra and the last radial process, *Sarda* and *Allothunnus* resemble *Thunnus*; the other bonitos resemble *Acanthocybium*.

Pectoral Fin Rays

The first (and largest) pectoral ray articulates directly with a posterior process of the scapula. The other rays attach to the radials. Within the Scombridae, the number of pectoral fin rays increases from the more primitive members of the family to the more advanced: Scombrini 18-21, Scomberomorini 20-25, Sardini 21-28, Thunnini (except for *Thunnus*) 22-29, *Thunnus* 30-36. Within the Sardini (Table 13), *Orcynopsis* and *Cybiosarda* have the fewest pectoral fin rays (modes of 22 and 23, respectively). *Gymnosarda* has the most (25-28), followed by one species of *Sarda* (*S. australis*, 25-27), and *Allothunnus* (24-26). The other three species of *Sarda* are intermediate with species modes of 24 or 25.

Postcleithrum 1 and 2

The posterior projecting plate of the cleithrum has its posterior end attached to the curved first postcleithrum, which connects to another bone, the second postcleithrum. Both postcleithra are thin and bent. Postcleithrum 1 (the upper one) has a narrow anterodorsal end and a broad posteroventral body (Figure 64). *Gymnosarda* has a pointed

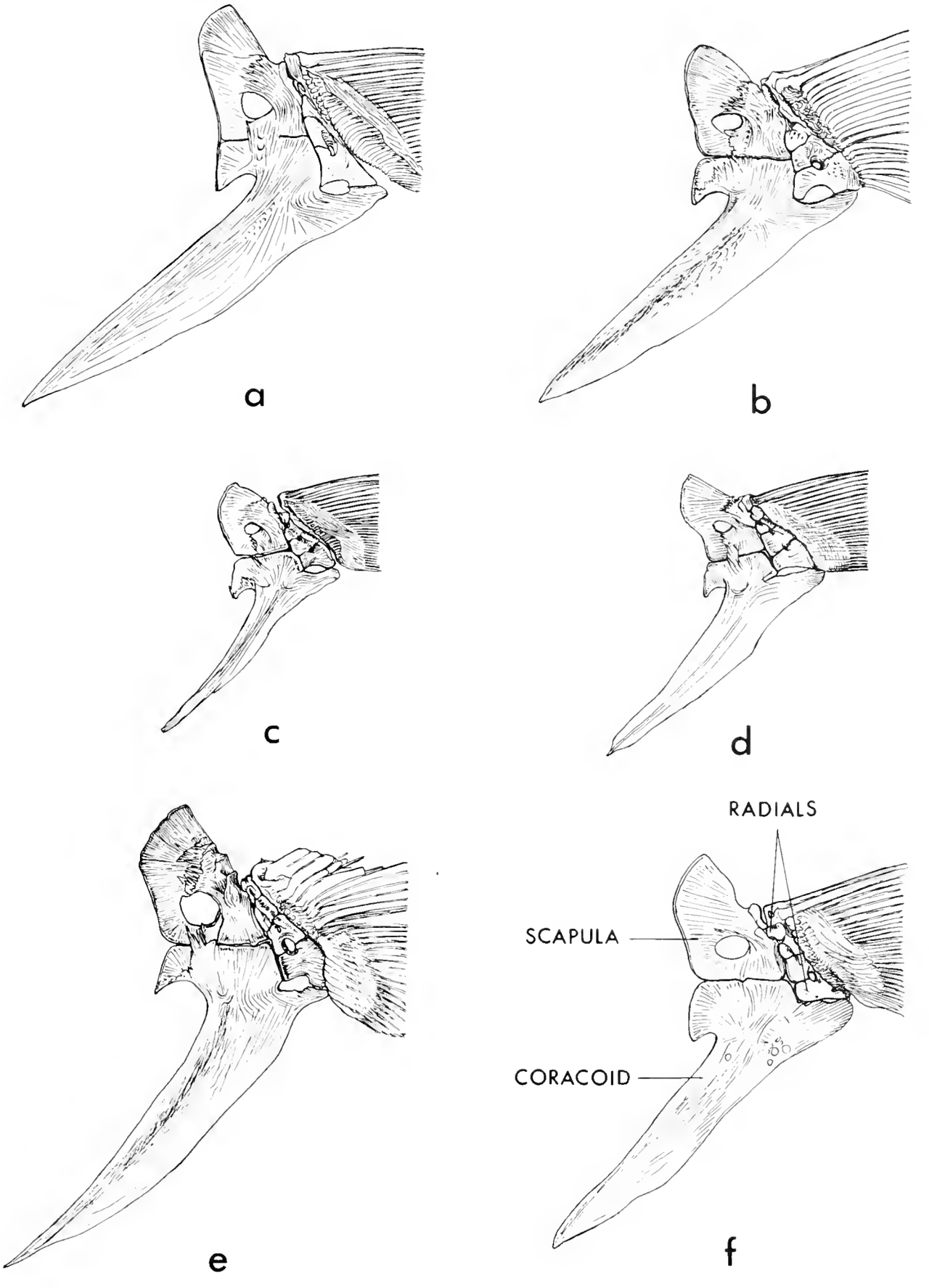


FIGURE 63.–Left pectoral girdles (minus cleithra) of six species of Sardini, external view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda chiliensis*, California, 472 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, California, 680 mm FL. a drawn twice as large as b-f.

TABLE 13.—Number of pectoral rays in species of Sardini.

Species	21	22	23	24	25	26	27	28	N	$\bar{x}$
Orcynopsis unicolor:										
E Mediterranean	6	17	7						30	22.0
Cent. Mediterranean		5	3						8	22.4
Atlantic		3	5						8	22.6
Total	6	25	15						46	22.2
Cybiosarda elegans		1	15	5					21	23.2
Sarda australis					6	9	4		19	25.9
Sarda chiliensis:										
NE Pacific		1	6	9	12	3			31	24.3
(Kuo 1970)		(1	28	226	229	25	1)		(510)	(24.5)
SE Pacific		2	4	13	10	3			32	24.2
(Kuo 1970)			(6	41	44	1)			(92)	(24.4)
Total		3	10	22	22	6			63	24.3
Sarda orientalis:										
Indian Ocean			2	4	2	1			9	24.2
NW Pacific			2	10	3				15	24.1
Cent. Pacific				2	2				4	24.5
E Pacific			2	6	6				14	24.3
Total			6	22	13	1			42	24.2
Sarda sarda:										
North America			9	27	21	4			61	24.3
South America			1	3	3	1			8	24.5
NE Atlantic				4	5	2			11	24.8
Mediterranean-Black Sea			2	11	5				18	24.2
(Demir 1964, Turkey)		(1	12	51	34	7)			(105)	(24.3)
Gulf of Guinea-S. Africa			6	13	7				26	24.0
Total			18	58	41	7			124	24.3
Gymnosarda unicolor:										
Indian Ocean					3	5	—	1	9	25.9
W Pacific					3	8	9	1	21	26.4
Total					6	13	9	2	30	26.2
Allothunnus fallai				2	1	3			6	25.2

anterodorsal end on postcleithrum 1, which is unique among bonitos. Postcleithrum 1 in *Orcynopsis* and *Cybiosarda* is elongate and broad at the upper end. The general features of postcleithrum 1 of *Sarda* species are similar to those of *Thunnus*. *Allothunnus* has the broadest postcleithrum 1. Postcleithrum 2 (the lower one) is a spinelike structure with both ends pointed and a broad upper process (Figure 65). These bones are similar in all bonitos except for minor variations. Postcleithrum 2 of *Gymnosarda* has an elongate upper end and a curved lower portion. The broad process of postcleithrum 2 is much enlarged in *Allothunnus* as in *Thunnus*.

PELVIC GIRDLE

The pelvic fin rays (I, 5) attach directly to the paired basipterygia which make up the pelvic girdle. The bones are fused together along the midline and are imbedded in the ventral abdominal wall free from connections with any other bones. Each basipterygium is composed of three main parts (Figure 66): a wide anterodorsal plate and two processes: an anterior process (anterior xiphoid process of de Sylva 1955) and a shorter, stronger, posteriorly directed styliform process (posterior xiphoid process of de Sylva 1955). There are three wings to the anterodorsal plate (Kishinouye 1923): external, internal, and vertical (ventral). Anteriorly, the external wing turns into the same vertical plane and merges into the vertical wing. The internal wing and the external wing meet in one plane posteriorly along a ridge. A "valleylike" depression is present in the posterior half of the anterodorsal plate in all the bonitos except *Allothunnus* (Figure 66f). The internal wing of *Allothunnus* attaches to the vertical wing horizontally at a right angle which is completely separate from the external wing, as in *Thunnus* (de Sylva 1955, figs. 50-52). The vertical wing is the largest and most variable character of the bonito basipterygium. The vertical wings of *Orcynopsis*, *Cybiosarda*, and *Sarda* are elongate and have pointed anterior ends. *Gymnosarda* and *Allothunnus* have vertical wings that are shorter

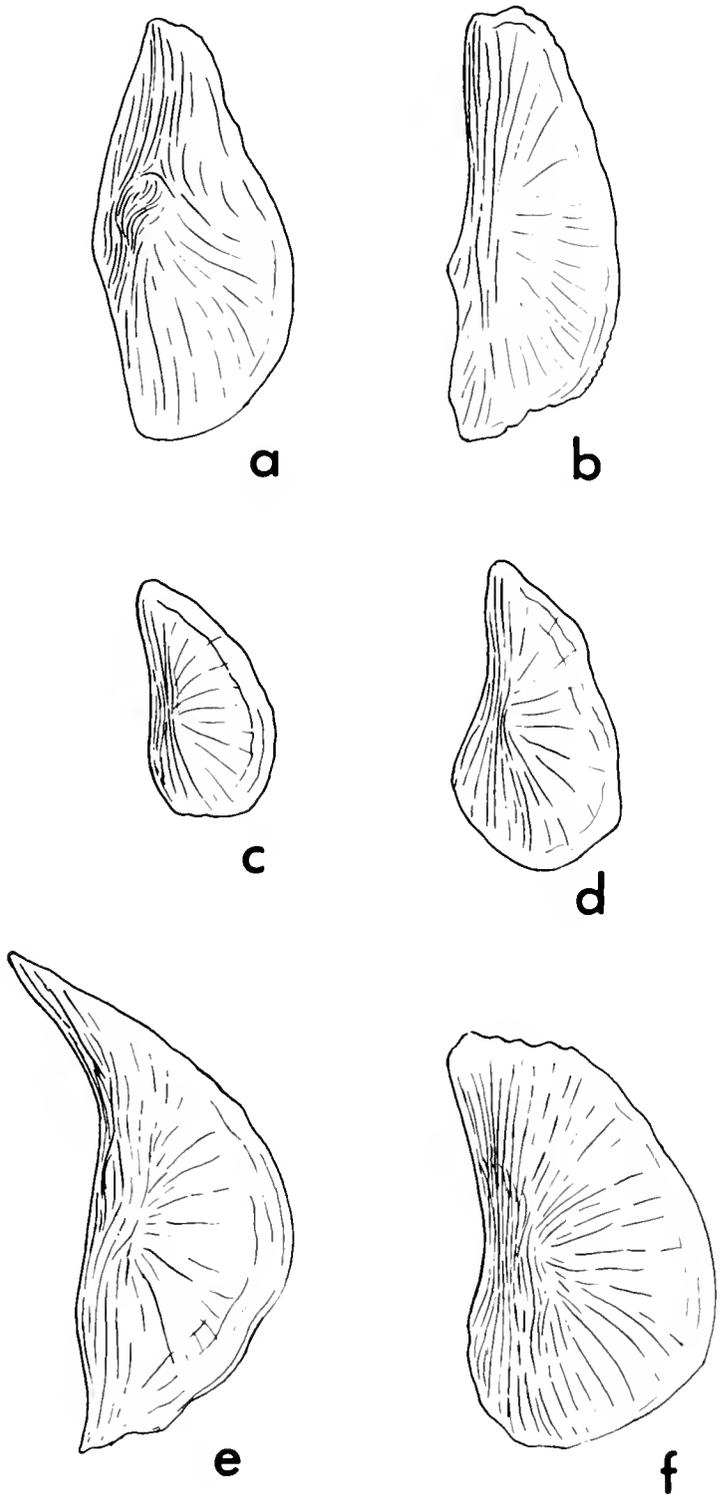


FIGURE 64.—Left first postcleithra of six species of Sardini. a. *Cybiosarda elegans*, New South Wales, 360 mm FL. b. *Orcynopsis unicolor*, Tunisia, 645 mm FL. c. *Sarda australis*, New South Wales, 407 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 774 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

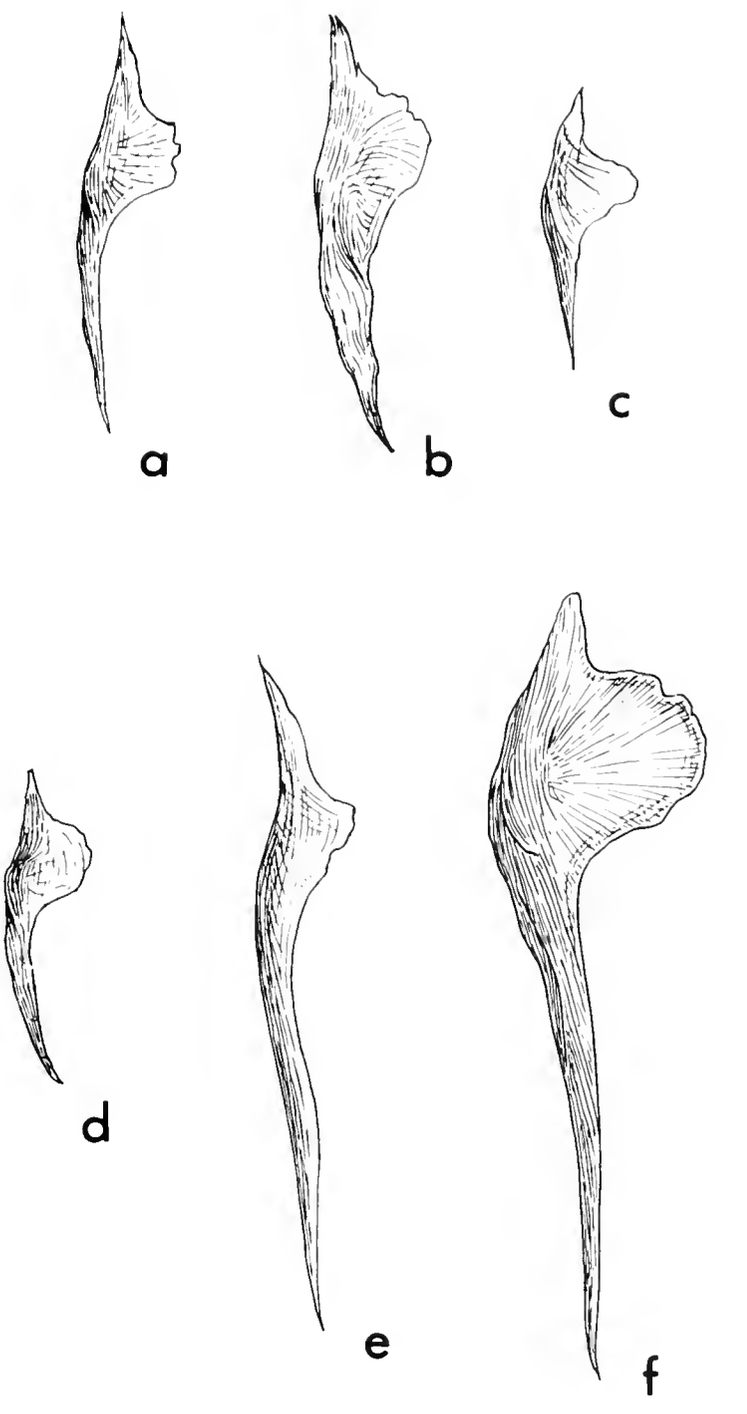


FIGURE 65.—Left second postcleithra of six species of Sardini, external lateral view. a. *Cybiosarda elegans*, New South Wales, 355 mm FL. b. *Orcynopsis unicolor*, Tunisia, 545 mm FL. c. *Sarda sarda*, New Jersey, 375 mm FL. d. *Sarda orientalis*, Jalisco, Mexico, 434 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 607 mm FL. f. *Allothunnus fallai*, California, 680 mm FL.

and broader in the midanterior portion. The portion above the internal wing is even better developed in *Allothunnus* than in *Thunnus* (de Sylva 1955, fig. 51). The internal and external wings of *Allothunnus* are less prominent than in the other bonitos. Among the species of *Sarda*, *S. orientalis* has a narrower and longer vertical wing.

The anterior process of the basipterygium extends anteriorly to about the middle of the anterodorsal plate. The posterior styliform process is shorter and stronger than the anterior process in the bonitos. Except for *Gymnosarda*, no differences were found among the bonitos in the fleshy bifid interpelvic process that is supported by the paired posterior styliform process of the basipterygia

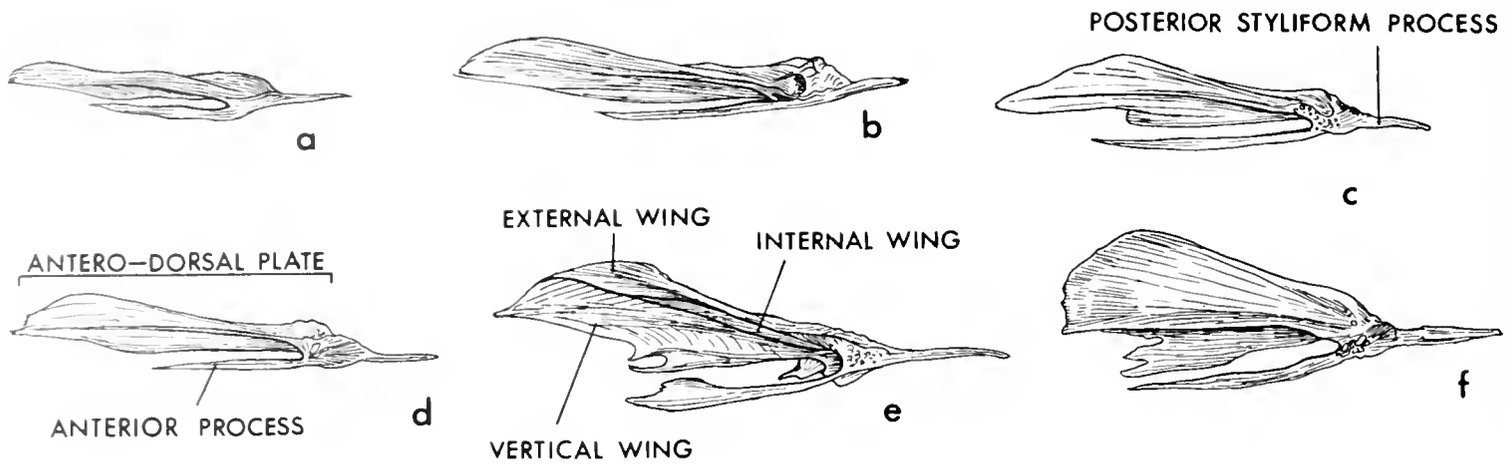


FIGURE 66.—Lateral view of inner surface of right basipterygium of pelvic girdles of six species of Sardini. a. *Cybiosarda elegans*, Western Australia, 442 mm FL. b. *Orcynopsis unicolor*, Tunisia, 620 mm FL. c. *Sarda chiliensis*, Callao, Peru, 437 mm FL. d. *Sarda sarda*, Tunisia, 504 mm FL. e. *Gymnosarda unicolor*, Truk Islands, 696 mm FL. f. *Allothunnus fallai*, Tasmania, 778 mm FL.

(Figure 67). *Gymnosarda* differs from the other bonitos in having a single interpelvic process. *Auxis* and *Grammatorcynus* also have a single interpelvic process, the former very large, the latter small. However, there is a posterior styliform process from each basipterygium regardless of whether the fleshy interpelvic process is single or bifid.

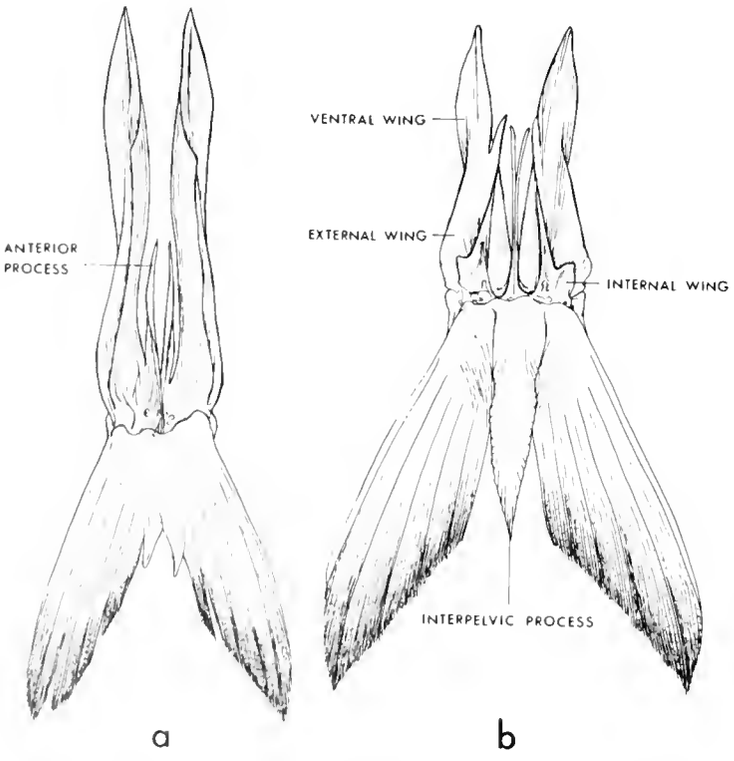


FIGURE 67.—Ventral view of pelvic girdles and fins of two species of Sardini. a. *Orcynopsis unicolor*, Tunisia, 495 mm FL. b. *Gymnosarda unicolor*, Truk Islands, 787 mm FL. a drawn twice as large as b.

PART 2. SYSTEMATICS

The family Scombridae can be divided into two subfamilies: the Gasterochismatinae, which contains only the aberrant *Gasterochisma melampus* Richardson, and the Scombrinae. The Scombrinae is composed of two groups of tribes (Figure 68). The more primitive mackerels (Scombrini – *Scomber* and *Rastrelliger*) and Spanish mackerels (Scomberomorini–*Grammatorcynus*, *Scomberomorus*, and *Acanthocybium*) have a distinct notch in the hypural plate, lack any bony support for the fleshy caudal peduncle keels (Figure 56), and do not have preural centra two and three greatly shortened. The bonitos comprise a tribe (Sardini, Starks 1910) of five genera and eight species. The bonitos differ from the higher tunas (Thunnini–*Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*) in lacking any trace of a specialized subcutaneous vascular system, in lacking dorsally projecting lateral cartilaginous ridges on the tongue, and in having the bony caudal keel only partially developed instead of complete. The Sardini lack the prominent paired frontoparietal foramina characteristic of the Thunnini (except *Auxis*). Except for *Allothunnus*, the Sardini also differ from the Thunnini in lacking prominent prootic pits. In this character, and in its tiny conical teeth, *Allothunnus* is similar to the Thunnini. The Sardini agree with *Thunnus* and with the Scombrini and Scomberomorini in lacking the bony shelf that divides the neural canal of the anterior six vertebrae into dorsal and ventral portions. This bony division is characteristic of the

other three genera of Thunnini—*Katsuwonus*, *Euthynnus*, and *Auxis*.

Five genera, four of them monotypic, are recognized as a result of analyzing the morphology described in the first part of this paper. A sample of some of the more important characters is summarized in Table 14. *Orcynopsis* and *Cybiosarda* form a pair of related genera in characters such as the poor development of the bony caudal keels, location of the spleen, presence of a pair of tooth patches fused to the glossohyal bone, and length of the liver lobes. They differ sharply in vertebral number; *Orcynopsis* usually has 18 precaudal plus 20 caudal vertebrae compared to (22-23) + (24-25)=47 in *Cybiosarda*. In some respects, *Sarda* and *Gymnosarda* also form a pair of related genera. However, characters of *Gymnosarda* such as the well-developed swim bladder, curved sagitta, large number of olfactory laminae, paired glossohyal tooth plates, location of the spleen, lack of cephalic intermuscular bones, and parhypural fused to the hypural plate demonstrate that *Gymnosarda* is very different from the other genera of Sardini. *Allothunnus* differs strongly from the other bonitos in liver shape, presence of prootic wings, and shape of pineal foramen, but shares more characters in common with the Sardini than with the Thunnini as previously noted.

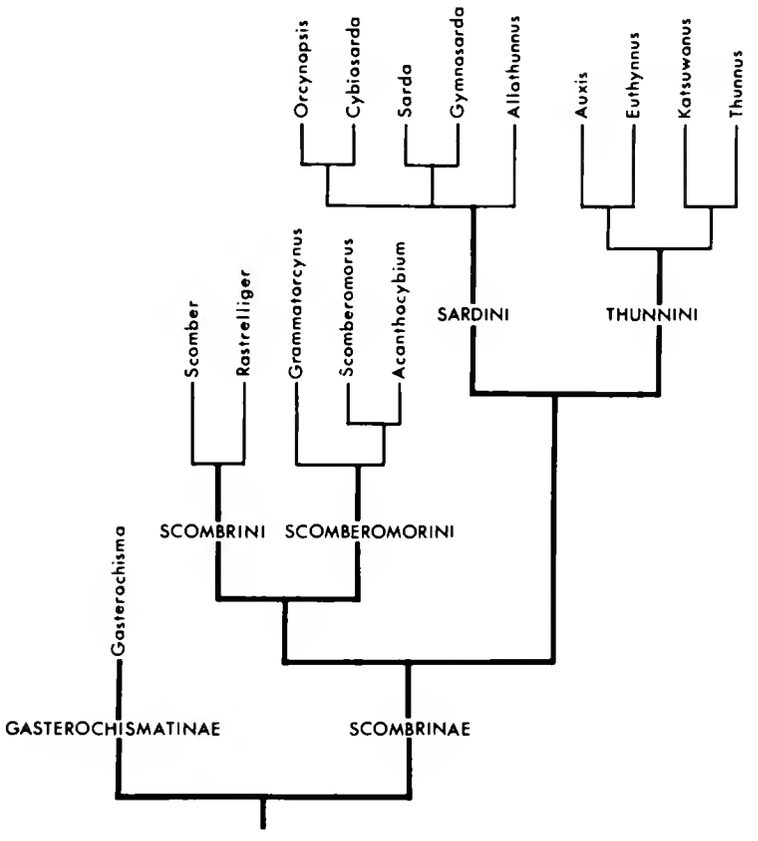


FIGURE 68.—The subfamilies, tribes, and genera of the Scombridae.

Orcynopsis Gill

Orcynopsis Gill 1862:125 (type-species *Scomber unicolor* Geoffroy St. Hilaire; misspelled *Orycnopsis*).

TABLE 14.—Summary of characters distinguishing the five genera of Sardini.

Character (reference)	*Orcynopsis*	*Cybiosarda*	*Sarda*	*Gymnosarda*	*Allothunnus*
Intestine (Fig. 5)	folded	folded	straight	folded	straight
Tongue teeth (Fig. 43)	2 patches fused to glossohyal	2 patches fused to glossohyal	none	2 patches free from glossohyal	none
Prootic pit	absent	absent	absent	absent	present
Prootic wings	absent	absent	absent	absent	present
Bony caudal keels (Fig. 55)	low and poorly developed	low and poorly developed	well-developed and divided into 2 parts	well-developed and divided into 2 parts	low and poorly developed
Length of liver lobes (Fig. 4)	right lobe longest	right lobe longest	right and left lobes equally long	right and left lobes equally long	3 subequal lobes
Spleen (in ventral view) (Fig. 3)	small and concealed under liver	small and concealed under liver	large and prominent posteriorly	present on right side anteriorly	not visible
Cephalic intermuscular bones	1 on each side of skull	1 on each side of skull	2	none	1
Pineal foramen (Fig. 10-14)	elongate and slit-shaped	elongate and slit-shaped	elongate and slit-shaped	elongate and slit-shaped	large and oval
Swim bladder	absent	absent	absent	well-developed	absent
Sagitta	flat	flat	flat	curved	flat
Opercular bones (Fig. 45-47)	not elongate	not elongate	not elongate	elongate	not elongate
Olfactory laminae (Table 3)	25-28	28-33	21-39	48-56	28-30
Vertebrae (Table 9)	18+20=38	(22-23)+(24-25)=47	43-46; 50-55	19+19=38	20+19=39
Pectoral rays (Table 13)	22-23	23-24	23-26	25-27	24-26
Dorsal spines (Table 10)	12-14	16-17	17-23	13-15	15-18
Parhypural (Fig. 56)	free from hypural plate	free from hypural plate	free from hypural plate	fused to hypural plate	free
Interpelvic process (Fig. 67)	small paired processes	small paired processes	small paired processes	single large process	small and paired
Total first arch gill rakers (Table 7)	12-17	12-15	8-27	11-14	72-80

Pelamichthys Giglioli 1880:25 (type-species *Scomber unicolor* Geoffroy St. Hilaire by original designation).

Comparative Diagnosis.—The monotypic genera *Orcynopsis* and *Cybiosarda* share several important characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal keels versus well-developed caudal keels divided into anterior and posterior sections; right lobe of liver longest versus right and left lobes much longer than the middle lobe; spleen small and not visible in ventral view versus large and prominent in ventral view. Both genera have high first dorsal fins (Figure 1a, b) and are relatively more compressed (almost like *Scomberomorus*) than fusiform. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have two patches of tongue teeth, but the patches are attached to the glossohyal bone in *Orcynopsis* and *Cybiosarda* and are on separate plates that fit over the glossohyal in *Gymnosarda*.

Orcynopsis differs from *Cybiosarda* most obviously in lacking the bold pattern of stripes and blotches on the body of the latter. *Orcynopsis* has lower counts than does *Cybiosarda*: vertebrae 37-39 vs. 47-48; dorsal spines 12-14 vs. 16-18; second dorsal rays 12-15 vs. 17-19; pleural ribs 16 vs. 20; and intermuscular bones 19-20 vs. 24-25.

Orcynopsis unicolor is a short-bodied and short-headed species (Table 15). It has a shorter snout-anal and snout-second dorsal distance than do other bonitos. The snout-first dorsal and snout-pelvic fin origin distances are shorter than in other bonitos except *Gymnosarda unicolor* and *Sarda australis*. The snout-pectoral fin origin, pelvic fin insertion-vent, and pelvic fin tip-vent distances are all shorter than in other bonitos except *Gymnosarda*. The fins are high compared to fork length, the second dorsal and anal fins are higher than in other bonitos except for the second dorsal in *Cybiosarda*. The bases of the second dorsal and

TABLE 15.—Comparison of morphometric characters of three populations of *Orcynopsis unicolor*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	Israel			Lebanon			Tunisia		
Character	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*
Fork length (mm)	285-735	404	12	242-325	287	11	312-645	539	7
Fork length									
Snout — A	555-597	577	12	573-598	587	11	556-597	578	7
Snout — 2D	481-522	499	12	496-530	511	11	400-503	481	7
Snout — 1D	239-253	247	12	248-262	253	11	229-257	246	7
Snout — P_2	265-282	273	12	276-293	284	11	263-285	270	7
Snout — P_1	231-243	238	12	240-257	247	11	219-239	229	7
P_1 — P_2	109-116	113	7	118-129	122	11			
Head length	226-246	235	12	239-251	243	11	224-241	231	7
Max. body depth	221-268	246	11	240-272	255	11	226-248	240	7
Max. body width	106-140	124	9	113-135	123	11	116-139	130	7
P_1 length	125-153	138	12	131-140	135	11	135-148	142	7
P_2 length	57- 68	63	12	55- 64	61	11	62- 66	64	6
P_2 insertion - vent	278-307	294	12	266-296	288	11	280-315	300	7
P_2 tip - vent	218-241	230	12	209-242	228	11	216-241	233	7
Base 1D	235-255	246	10	241-259	248	11	230-255	241	7
Height 2D	109-148	128	10	108-124	117	10	116-150	126	7
Base 2D	107-126	117	12	107-140	133	11	108-149	120	7
Height anal	111-148	126	10	107-126	118	11	119-131	125	7
Base anal	94-128	114	11	98-131	111	10	95-120	106	7
Caudal spread	236-275	261	6	249-297	270	10	239-259	244	5
Snout (fleshy)	76- 95	89	11	92- 98	94	11	90- 94	91	6
Snout (bony)	65- 80	76	11	77- 83	80	11	76-111	83	7
Maxilla length	101-118	113	11	116-129	123	11	104-119	112	6
Post orbital	109-115	112	7	113-122	117	11			
Orbit (fleshy)	24- 32	28	11	29- 34	31	11	23- 66	31	7
Orbit (bony)	46- 58	51	11	53- 61	57	11	44- 69	52	7
Interorbital width	65- 74	68	11	59- 70	66	11	67- 83	72	6
Head length									
Snout (fleshy)	327-405	381	11	376-392	387	11	385-406	396	6
Snout (bony)	280-353	326	11	316-335	328	11	329-480	358	7
Maxilla length	431-508	483	11	485-517	505	11	456-495	483	6
Post orbital	453-490	478	7	462-515	484	11			
Orbit (fleshy)	107-133	121	11	120-137	129	11	98-121	107	7
Orbit (bony)	204-249	218	11	221-254	236	11	192-222	211	6
Interorbital width	256-308	289	11	239-288	272	11	262-310	297	6

anal fins are longer than in any bonitos except *Cybiosarda*.

Orcynopsis unicolor Geoffroy St. Hilaire

Scomber unicolor E. Geoffroy St. Hilaire 1817: pl. 24, fig. 6 (original description). I. Geoffroy St. Hilaire 1827:331-332 (description; Alexandria, Egypt). Guichenot 1850:58-59 (description; Algeria).

Cybium commersoni (not of Lacépède, 1800). Bonaparte 1845:74 (listed after Verany; Italy).

Cybium Bonapartii Verany 1847:493 (original description; Genoa, Italy).

Pelamys Bonaparte. Filippi and Verany 1859:194 (description, comparison with *S. sarda*), fig. 4. Moreau 1881:434-436 (synonymy, description; very rare, Nice). Liebman 1934:325 (Israel).

Pelamys unicolor. Günther 1860:368 (synonymy, description). Canestrini 1870:103 (description, rare in Italian waters). Rochebrune 1882:95-96 (Senegal). Stassano 1890:32-33 (Spanish Sahara). Griffini 1903:398-399 (synonymy; description; Italy).

Cybium altipinne Guichenot in Duméril 1858:262 (nomen nudum, listed; Senegal).

Orycnopsis unicolor. Gill 1862:126 (original description of *Orcynopsis*, misspelled *Orycnopsis*).

Thynnus peregrinus Collett 1879a:20-30 (original description; Christiania (now Oslo) Norway), pl. 1.

Orcynopsis unicolor. Collett 1879b:1-3 (*Thynnus peregrinus* Collett a synonym of *O. unicolor*). Ninni 1882:264 (Adriatic). Dresslar and Fesler 1889:434-435 (description; synonymy). Vinciguerra 1890:98-100 (synonymy; Cabo Blanco, Spanish West Africa). Carus 1893:659-660 (synonymy; description). Gruvel and Bouyat 1906:150 (Cabo Yubi to Cabo Blanco, Spanish West Africa). Lozano 1916:298-302 (description; Melilla, Spanish Morocco). Parona 1919:91-95 (synonymy, description; Italy), pl. 10-11. Ehrenbaum 1924:12 (Alexandria). Chabanaud 1925:197-200 (comparison with *Sarda* and *Gymnosarda*), fig. 1 (lingual and pharyngeal teeth), 2 (vomerine teeth). Chabanaud and Monod 1927:278-279 (common; Port Étienne, Mauritania), fig. 30B. Buen 1930a:46-47 (description, synonymy), pl. 2, fig. 5. Dieuzeide 1930:141-144 (synonymy, description, Algeria). Buen and Frade 1932:72 (in key), fig. 5. Frade and Buen 1932:70 (in key). Le Gall 1934a:288 (description), fig. (after Smitt). Jensen 1937:11-12 (Collett's 1879 records from the Skagerak). Fraser-Brunner 1950:148-149 (description), fig. 14. Postel 1950:63-66 (description; reproduction; food; length-weight; Cape Verde), 64 (fig. of viscera). Lozano y Rey 1952:527-531 (description), pl. 40, fig. 1, col. pl. 41, figs. 2 and 3. Morice 1953a:37 (dentition; gill rakers), 41 (generic key). Postel 1954:357-358 (stomach contents), 359 (parasites), 361 (gonosomatic index). Dieuzeide et al. 1955:145-146 (description, fig.; Algeria). Dollfus 1955:55 (listed), 141 (references to occurrence in Atlantic Morocco; Rabat market). Frade and Postel 1955:35 (gonads; spawning season; Cape Verde), fig. 6 (ovary). A. Postel 1955:59-60, 65, table 2, fig. 2 (number of teeth on upper and lower jaws, 100 Tunisian specimens). Postel 1955b:31-32 (sex ratio by months, maximum size by sexes, number of eggs). Postel 1956a:1220-1248 (synonymy, relationships, distribution, morphometry, meristics, anatomy, reproduction, food, parasites), fig. 3 (distribution map), fig. 4 (drawing), figs. 9, 10 (viscera). Postel 1956b:52 (common names). Postel 1956c:67-68 (abundant in Gulf of Gabes, Tunisia). Tortonese 1956:7 (Mediterranean). Postel 1960:257 (distribution). Collette and Gibbs 1963a:26 (relationships). Šoljan 1963:147-148 (description; figs.; Adriatic Sea). George et al. 1964:21 (rare, Lebanon). Postel 1964:220 (listed, North Africa). Collette 1966:370 (*Cybium altipinne* a synonym of *O. unicolor*). Zharov 1967:220 (relationships of scombroids). Bini 1968:39-40 (synonymy; description), color plate. Williams 1968:436 (Ghana). Blache et al. 1970:375 (in key; fig. 961, not fig. 960 which is *Scomberomorus tritor*). Collette 1970:4 (Israel). Ben-Tuvia 1971:20 (Israel). De Groot and Nijssen 1971:8 (Arguin Bank, Mauritania). Lozano Cabo 1970:158 (North Africa). Economidis 1972:526 (Greece). Magnuson 1973:350 (maximum size, no swim bladder, short pectoral fin). Postel 1973:474-475 (range, synonymy).

Pelamichthys unicolor. Giglioli 1880:25 (original description of *Pelamichthys*, Italy).

Cybium Veranyi. Giglioli 1880:25 (description, Italy).

Sarda unicolor. Smitt 1892:102-104 (synonymy; description; rare in Scandinavia), fig. 29. Fowler 1936:625-626 (synonymy; description;

compiled), fig. 283 (after Smitt). Cadenat 1937:482 (Sénégal). Navarro 1943:131 (Arguin Bank, Mauritania), pl. 19, fig. B (photograph). Tortonese 1949:65 (permanent resident, Mediterranean Sea). Tortonese and Trotti 1949:87 (Ligurian Sea).

Types of Nominal Species.—*Scomber unicolor* E. Geoffroy St. Hilaire 1817: pl. 24, fig. 6. No type-specimens, text published by Isidore Geoffroy St. Hilaire in 1827 ". . . sont extraits des notes prises en Egypte par mon pére. Je n'ai pu me procurer ni cette especé, ni celle qui est figurée dans l'Atlas sous le nom de *Maquereau unicolore*; . . . trouvee dans le Méditerranée."

Cybium Bonapartii Verany 1847:493. The type was examined in the Museo della R. Universita di Genova by Collett (1879b) and the name placed in the synonymy of *O. unicolor* (along with *Thynnus peregrinus* Collett). The present whereabouts of the type, if extant, are unknown. It is not listed in the type catalog of the Museo Civico di Storia Naturale di Genova (Tortonese 1963) which absorbed the University collections. The original description was based on a specimen from the Genoa market taken on 31 May 1847. It had eight dorsal finlets, seven anal finlets, conical teeth, and lacked spots on the body.

Cybium altipinne Guichenot in Duméril 1858. Apparently a nomen nudum as there is no description and we cannot find a description by either Guichenot or Duméril elsewhere. Also considered a nomen nudum by Postel (1973). Previous authors (Fraser-Brunner 1950; Bauchot and Blanc 1961) have considered *C. altipinne* to be a synonym of *Scomberomorus tritor* (Cuvier) but the specimen labelled as type is clearly *O. unicolor* as Collette (1966) has shown.

Thynnus peregrinus Collett 1879a:20-30, pl. 1. Placed in the synonymy of *Orcynopsis unicolor* later in the same year (Collett 1879b). Lectotype (herein selected): ZMO J4632; 565 mm FL; Norway, Christianiafjord (Oslo), Naesøen; 26 Aug. 1876. Prof. Esmark. Paralectotype: ZMO J4631; 570 mm; same data as lectotype. The smaller syntype is selected as lectotype because the dorsal spine count of 13 matches the original description and because the two patches of teeth on the tongue are the usual size for *O. unicolor*. The paralectotype has two very small patches of tongue teeth. Counts for the lectotype (paralectotype in parentheses): dorsal fin rays XIII + 14 + VIII (XIV + 14 + VIII); anal fin rays 15 + VII (15 + VII); pectoral fin rays (left-right) 23-21 (23-22); gill rakers 3 + 1 + 11 = 15 in both; upper jaw teeth (left-right) 23-25 (20-22); lower jaw teeth 20-20 (16-17).

Distribution.—*Orcynopsis unicolor* is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Sénégal and north to Oslo, Norway (Figure 69). It was first described from Egypt by Geoffroy St. Hilaire (1817) and most subsequent records have come from the southern Mediterranean: Lebanon (George et al. 1964; 12 USNM specimens), Israel (Liebman 1934; Collette 1970; Ben-Tuvia 1971; 5 USNM specimens; SFRS 1686, 2009, BT-1767, BT-1582, BT-1986), Egypt (Ehrenbaum 1924; 10 NHMV specimens), Tunisia (Postel 1956c; 7 USNM specimens), Algeria (Guichenot 1850; Dieuzeide 1930; Dieuzeide et al. 1955), and Morocco (Lozano 1916). Records from the northern Mediterranean are scarcer: Genoa, Italy (Verany 1847; MSNG 1987); Ligurian Sea (Tortonese and Trotti 1949); Adriatic Sea (Ninni 1882; Šoljan 1963; MSUF 495D); Elba (MSUF coll. 1172); Nice, France (Moreau 1881; NHMV 1884.I.204). The Norwegian record is based on the two types of *Thynnus peregrinus* Collett, taken at Naesøen, Christianiafjord (= Oslofjord) in August 1876. There are several records for the Atlantic coast of North Africa south to Dakar, Sénégal: Rabat, Morocco (Dollfus 1955); Spanish West Africa (Stassano 1890; Vinciguerra 1890; Gruval and Bouyat 1906); Mauritania (Chabanaud and Monod 1927; Navarro 1943; de Groot and Nijssen 1971; USNM uncat.); and Cape Verde and Dakar, Sénégal (Duméril 1858; Rochebrune 1882; Postel 1950; Frade and Postel 1955; MNHN A.5797). There is one record from further south, in the Gulf of Guinea. Williams (1968:436) reported that a specimen was taken off Ghana during the Guinean Trawling Survey. The specimen was apparently not saved, the identification was probably based on the first draft of the illustrated key by Blache et al. (1970) which has the figures of *Scomberomorus tritor* and *Orcynopsis unicolor* transposed, and the record is well out of the normal range of the species. Therefore, the record must be considered highly questionable unless confirmed by additional specimens.

Cybiosarda Whitley

Scomberomorus (*Cybiosarda*) Whitley 1935:236 (type-species *S.* (*C.*) *elegans* Whitley by monotypy).

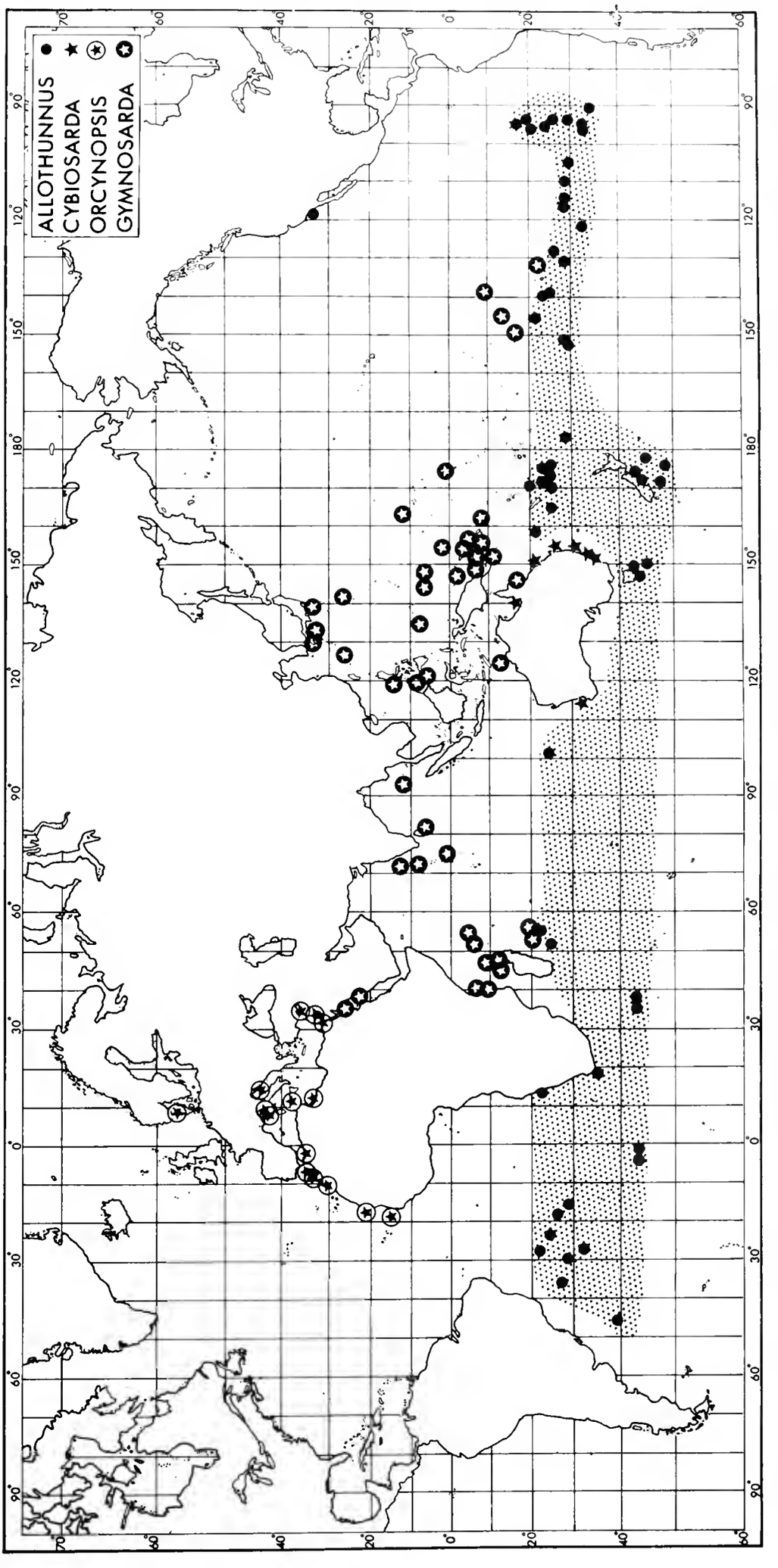


FIGURE 69.—Distribution of *Orcynopsis unicolor*, *Gymnosarda unicolor*, *Cybiosarda elegans*, and *Allothunnus fallai* based on specimens personally examined and literature records.

Comparative Diagnosis.—The monotypic genera *Cybiosarda* and *Orcynopsis* share several characters that distinguish them from *Sarda* and *Gymnosarda*: low and poorly developed bony caudal keels instead of well developed, but divided into anterior and posterior parts; right lobe of liver much longer than middle and left lobes instead of both right and left lobes elongate; spleen small and not visible in ventral view versus spleen large and prominent in ventral view. Both have one intermuscular bone on the back of the skull compared to none in *Gymnosarda* and two in *Sarda*. Both genera have high first dorsal fins and are relatively more compressed (almost like *Scomberomorus*) than fusiform. *Orcynopsis*, *Cybiosarda*, and *Gymnosarda* have a pair of tooth patches on the tongue, but these are attached to the glossohyal bone in the first two genera and are on separate plates that fit over the glossohyal in *Gymnosarda*. Osteologically, the two genera also show many similarities.

Cybiosarda differs from *Orcynopsis* most obviously in its prominent pattern of blotches above the lateral line and stripes below it (Figure 1a). *Cybiosarda* has higher counts than does *Orcynopsis*: vertebrae 47-48 vs. 37-39; dorsal spines 16-18 vs. 12-14; second dorsal rays 17-19 vs. 12-15; pleural ribs 19 vs. 16; and intermuscular bones 23-24 vs. 19-20. *Cybiosarda* has a smaller sagitta with a longer and thinner rostrum than does *Orcynopsis*.

Cybiosarda is a relatively short-bodied bonito (Table 16). The snout-second dorsal distance is shorter than in other bonitos except *Orcynopsis* and *Sarda chiliensis*, the first dorsal fin base is shorter than in the others except *Orcynopsis* and *Gymnosarda*. The second dorsal and anal fins are higher than in *Sarda* and *Allothunnus* and the second dorsal fin is also higher than in *Gymnosarda*.

TABLE 16.—Morphometric characters of *Cybiosarda elegans*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	250-422	347	19
Fork length			
Snout — A	638-678	652	19
Snout — 2D	509-547	531	18
Snout — 1D	260-284	273	19
Snout — P_2	289-317	299	18
Snout — P_1	258-291	267	18
P_1 — P_2	113-136	125	18
Head length	259-280	266	19
Max. body depth	199-252	227	16
Max. body width	105-168	133	17
P_1 length	128-148	138	19
P_2 length	76- 88	82	19
P_2 Insertion - vent	344-363	327	17
P_2 tip - vent	240-282	262	17
Base 1D	229-270	254	19
Height 2D	101-118	108	19
Base 2D	112-133	121	18
Height anal	97-118	107	18
Base anal	82-100	91	19
Caudal spread	219-275	251	16
Snout (fleshy)	94-104	98	19
Snout (bony)	79- 87	82	19
Maxilla length	125-140	130	19
Post orbital	128-146	136	19
Orbit (fleshy)	26- 34	29	19
Orbit (bony)	54- 61	58	9
Interorbital width	65- 78	73	19
Head length			
Snout (fleshy)	352-383	367	19
Snout (bony)	299-323	308	19
Maxilla length	475-501	489	19
Post orbital	489-551	511	19
Orbit (fleshy)	98-125	109	19
Orbit (bony)	204-232	218	9
Interorbital width	244-292	273	19

Cybiosarda elegans (Whitley)

Scomberomorus (*Cybiosarda*) *elegans* Whitley 1935:236-237 (original description; Moreton Bay, Queensland, Australia).

Cybiosarda elegans. Whitley 1936:42-45 (redescription of type; anatomy; pl. 4, fig. 1; text fig. 5; Queensland). Whitley 1939:274 (New South Wales). Serventy 1941a:43 (description, New South Wales and Western Australia), pl. 4, bottom fig. Whitley 1948:24 (listed; Western Australia). La Monte 1952:48, 50 (description). Munro 1958a:113-114 (description; Queensland, New South Wales, Western Australia), fig. 756 (after Serventy). Jones and Silas 1961:379 (compiled), fig. 5 (after Fraser-Brunner). Collette and Gibbs 1963b:28 (description), pl. 7 (after Fraser-Brunner). Jones and Silas 1963:1786-1787 (compiled). Jones and Silas 1964:24-25 (description). Marshall 1964:357-358 (summary), col. pl. 52, fig. 345. Whitley 1964a:228-229 (summary), pl. 2, fig. b (Western Australia specimen), text fig. 4c (distribution). Whitley 1964b:48 (listed). Marshall 1966:204, col. pl. 52. Grant 1972:113 (description; Queensland), fig. (after Serventy).

Gymnosarda elegans. Fraser-Brunner 1950:149 (description), fig. 15.

Types.—*Scomberomorus* (*Cybiosarda*) *elegans* Whitley 1935:236-237. Original description repeated with additional locality data and the QM catalog number for the type plus more information on the species by Whitley (1936). Holotype: QM

I.5413; 356 mm FL; Queensland, Moreton Bay, Goat Island; G. W. Watson. A second specimen (QM I.5142) is labelled as a paratype and is mentioned as having been collected with the first specimen by Whitley (1936:42). However, it is not mentioned in the original description where the statement is made "Described from a specimen in the Queensland Museum from Moreton Bay, Queensland"; therefore, it should not be considered as a paratype. Counts for the holotype: dorsal fin rays XVI+17+IX; anal fin rays 17+VII; pectoral fin rays (left-right) 24-24; gill rakers 4+10=14; upper jaw teeth (left-right) 17-20; lower jaw teeth 12-12.

Distribution.—*Cybiosarda elegans* is restricted to the northern three quarters of Australia (Figure 69). It was first described by Whitley (1935) from Moreton Bay, Queensland, and then reported from New South Wales by Whitley (1939) and from Western Australia by Serventy (1941a). We have examined specimens from near Perth, Western Australia, and several localities along the east coast (Shellharbour and Maclean, New South Wales, and Moreton Bay and Lindeman Island, Queensland). In addition, we have examined a 250-mm specimen (AMS I.15557-095) taken by the CSIRO shrimp survey in the Gulf of Carpentaria at lat. 16°40′S, long. 139°50′E.

Sarda Cuvier

Sarda Cuvier 1829:199 (type-species *Scomber sarda* Bloch 1793 by monotypy).

Pelamys Cuvier in Cuvier and Valenciennes 1831:149 (type-species *Scomber sarda* Bloch 1793 by original designation).

Palamita Bonaparte 1831:173 (substitute name for *Pelamys* Cuvier 1831 preoccupied by *Pelamys* Oken 1816 in Reptilia, Hydrophiidae; therefore, takes the same type-species *Scomber sarda* Bloch 1793).

Creotroctes Gistel 1848:p. x (type-species *Scomber sarda* Bloch 1793; substitute name for *Sarda* Cuvier 1829).

Comparative Diagnosis.—The species of *Sarda* all have several stripes dorsally, ranging from horizontal to oblique in orientation. *Sarda* (and *Allothunnus*) differ from the other genera of bonitos in having the intestine run straight from the stomach to the anus (versus having two additional loops, Figure 5) and two intermuscular bones on each side of the back of the skull (*Gymnosarda* has none, the other three genera have one on each side).

Sarda and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal peduncle keels are well developed as in higher tunas, but are divided into anterior and posterior sections on each vertebra; the spleen is large and prominent in ventral view versus small and not visible in ventral view; the right and left lobes of the liver are both much longer than the middle lobe versus only the right lobe elongate. Both *Sarda* and *Gymnosarda* are fusiform in body shape instead of being more laterally compressed.

Sarda (Figure 1c) differs from *Gymnosarda* (Figure 2a) in being completely covered with fine scales posterior to the corselet (instead of being naked posteriorly); in lacking a swim bladder; in having the spleen centrally located in the posterior half of the body cavity in ventral view (instead of on the right side of the anterior half); in having fewer lamellae in the olfactory rosettes (21-39 vs. 48-56); more vertebrae (42-55 vs. 38); and in lacking a pair of tooth patches on the glossohyal bone.

Species of *Sarda*.—Four allopatric species of *Sarda* are recognized based on the morphological characters described in the first part of this paper (a summary of 26 of these characters is presented in Table 17). *Sarda australis* is similar to the other three species in the genus in 11-15 characters. *Sarda chiliensis* and *S. orientalis* resemble each other in 12 characters. *Sarda sarda* stands out as being very different from *S. chiliensis* and *S. orientalis*, sharing only eight or nine characters with each. Many of the meristic differences between *S. sarda* and the other species of *Sarda* are correlated with its greater number of body segments as reflected by having 50-55 vertebrae (compared to 43-46). Thus, *S. sarda* also has more dorsal spines, pleural ribs, intermuscular bones, vertebral keels, and the first closed haemal arch is further posterior. *Sarda sarda* is most similar to *S. australis* in numbers of anal rays, gill rakers, upper and lower jaw teeth, occasional presence of vomerine teeth, angle of the hyomandibular spine and the condyle, width of the supramaxilla, and relative length of the haemal pre- and postzygapophyses on the first caudal vertebra. If the several differences between *S. australis* and *S. sarda* that are correlated with the higher number of body segments are considered as one character, the two species would appear even more similar.

TABLE 17.–Summary of characters distinguishing the four species of *Sarda*.

Character (reference)	*S. sarda*	*S. australis*	*S. chiliensis*	*S. orientalis*
Lamellae in nasal rosettes (Table 3)	22-33 ($\bar{x}$ 26.5)	34-39 ($\bar{x}$ 37.2)	21-30 ($\bar{x}$ 25.4)	25-36 ($\bar{x}$ 31.9)
Vomerine teeth present	sometimes	sometimes	never	never
Upper jaw teeth (Table 5)	16-26	16-26	18-30 ($\bar{x}$ 23.5)	12-20 ($\bar{x}$ 15.5)
Lower jaw teeth (Table 6)	12-24 ($\bar{x}$ 16.0)	11-20 ($\bar{x}$ 14.5)	14-25 ($\bar{x}$ 19.2)	10-17 ($\bar{x}$ 13.0)
Palatine teeth	8-21 ($\bar{x}$ 12.3)	7-14 ($\bar{x}$ 10.7)	9-22 ($\bar{x}$ 15.2)	8-19 ($\bar{x}$ 11.9)
Supramaxilla width (Fig. 32)	intermediate	intermediate	wide	narrow
Ectopterygoid-dorsal portion (Fig. 36)	pointed	pointed	pointed	slightly expanded
Hyomandibular spine-condyle (Fig. 39)	projects beyond condyle	short	short	projects beyond condyle
Angle of hyomandibular spine (Fig. 39)	about 90°	about 90°	greater than 90°	less than 90°
Elliptical ceratohyal window (Fig. 42)	present	present	present	only slight depression
Ventral surface of glossohyal (Fig. 43)	depression present	depression present	depression present	no depression
Gill rakers (Table 7)	16-23	19-21	23-27	8-13
Vertebrae (Table 9)	50-55	43-46	43-46	43-46
Pleural ribs	24	19-23	19-23	19-23
Intermuscular bones	31-45	32-36	32-36	32-36
Keels on vertebrae number	5-10	5-8	5-8	5-8
First closed haemal arch (Fig. 51)	13th-15th vertebra	13th-15th vertebra	12th-14th vertebra	12th-14th vertebra
Length of haemal prezygapophyses and postzygapophyses at precaudal-caudal junction (Fig. 52)	postzygapophyses longer than prezygapophyses	postzygapophyses longer than prezygapophyses	prezygapophyses longer than postzygapophyses	prezygapophyses longer than postzygapophyses
Dorsal spines (Table 10)	20-23	17-19	17-19	17-19
Dorsal finlets (Table 11)	modally 8	modally 7	modally 8	modally 8
Anal rays (Table 12)	14-17 (modally 15)	14-17 (modally 15)	12-15 (modally 14)	14-16 (modally 15)
Anal finlets (Table 12)	modally 7	modally 6	modally 7	modally 6
Total anal elements (Table 12)	19-23 (modally 21-22)	19-23 (modally 21-22)	18-22 (modally 20)	20-22 (modally 21)
Supracleithral notch (Fig. 60)	wide angle	almost 90°	wide angle	wide angle
Pectoral rays (Table 13)	23-26	25-27 (modally 26)	22-26 (modally 24-25)	22-26 (modally 24-25)
Vertical wing of pelvic girdle (Fig. 66)	shorter and wider	shorter and wider	narrower and longer	narrower and longer

Sarda australis (Macleay)

Pelamys australis Macleay 1880:557 (original description; Port Jackson, Sydney, Australia). Ogilby 1887:29 (listed, New South Wales; should be compared with *P. chilensis*). McCoy 1888:208 (compared with *P. schlegeli*). Stanbury 1969:206 (holotype in Macleay Museum, University of Sydney).

Pelamys schlegeli McCoy 1888:207-208 (original description from one specimen from Prince Phillip Bay, Victoria), col. pl. 155.

Pelamys chilensis (not of Cuvier, 1831). Ogilby 1893:97-98 (synonymy, description; New South Wales), pl. 26.

Sarda chilensis (not of Cuvier 1831). Waite 1904:42 (listed, New South Wales). Stead 1906:163-164 (New South Wales and Victoria), fig. 59. Stead 1908:94-95 (New South Wales), pl. 54.

Sarda chiliensis (not of Cuvier 1831). McCulloch 1922:105 (New South Wales), pl. 33, fig. 291a.

Sarda orientalis (not of Temminck and Schlegel 1844). Lord 1927:15 (listed, Tasmania).

Sarda australis. Walford 1936:9 (in key as valid species of *Sarda*). Serventy 1941a:42-43 (description; Eastern Australia), pl. 4, middle fig. Serventy 1941b:7 (summer visitor to Victoria). Laevastu and Rosa 1963:1844 (fig. 7, map of distribution and fishing areas, in part). Whitley 1964a:236 (common from the Capricorn Islands, Great Barrier Reef to Sydney), fig. 2 (distribution map). Whitley 1964b:48 (listed).

Sarda chiliensis australis. Roughley 1951:121-122 (description; Australia), plate 49b. Munro 1958a:113 (description; Queensland, New South Wales, and Victoria), fig. 754. Grant 1972:114 (description; Queensland), fig. (after McCoy).

Sarda chilensis australis. Silas 1964:296 (in key, map, *S. chilensis* divided into an eastern Pacific *S. c. chilensis* and an Australian *S. c. australis*).

Comparative Diagnosis.–*Sarda australis* shows 11-15 similarities each, among characters considered (Table 17), with *S. sarda*, *S. chiliensis*, and *S. orientalis*. It differs from all of them in having slightly fewer pectoral rays (25-27, modally 26 vs. 22-26, modally 24-25) and in having a 90° angle in

the supracleithral notch instead of a much wider angle. *Sarda australis* resembles *S. sarda* in characters such as the numbers of anal rays, gill rakers, and upper and lower jaw teeth, occasional presence of vomerine teeth (vs. never), having a 90° angle between the hyomandibular spine and condyle, having the haemal postzygapophyses longer than the prezygapophyses at the precaudal-caudal vertebral junction, and having a supramaxilla of intermediate width between the wide one in *S. chiliensis* and the narrow one in *S. orientalis*. *Sarda australis* resembles *S. chiliensis* in having a short hyomandibular spine that does not project beyond the condyle.

Morphometrically (Tables 1, 18), *Sarda australis* is very similar to the other species of *Sarda*. It has a longer first dorsal fin base (315-343 thousandths of FL) than either *S. chiliensis* (267-314) or eastern Pacific *S. orientalis* (282-302) but overlaps with Indo-West Pacific *S. orientalis* (285-327) and *S. sarda* (291-330). The maxilla is longer (503-539 thousandths of head length) than in *S. chiliensis* (460-503).

Types.—*Pelamys australis* Macleay 1880:557. Holotype: AMS Macleay Mus. F-333; 405 mm FL; Australia, New South Wales, Sydney, Port Jackson. Counts: dorsal fin rays XIX + 16 + VII; anal fin rays 15+VI; pectoral fin rays 25-25; gill rakers 6+1+13=20; upper jaw teeth (left-right) 14-19; lower jaw teeth 13-10; palatine teeth about 10 in one long row; vertebrae 24+21=45; head length 82.9 mm, maxilla length 43.2 mm.

Distribution.—*Sarda australis* has the most restricted range of any species of bonito: the east coast of Australia plus Norfolk Island (Figure 70). Munro (1958a) gave the range as Queensland, New South Wales, and Victoria. Whitley (1964a) stated that *S. australis* "... is common at practically all times off eastern Australia from about the Capricorns [Queensland] to Sydney or even Gabo Island ..." [just south of New South Wales–Victoria border]. There are specific literature reports from Victoria (McCoy 1888; Serventy 1941b) and Tasmania (Lord 1927), as well as from New South Wales. Except for one specimen from Norfolk Island (AMS I.10751), all the material we have examined has come from New South Wales (from north to south: Macleay River, Broughton Island off Port Stephens, Laurieton, New Castle, Sydney, Woolongong). Sherrin (1886) and others have reported *Sarda* from New Zealand, but it seems likely that these reports were based on misidentified specimens of *Allothunnus fallai* which was not described until 1948.

TABLE 18.—Morphometric characters of *Sarda australis*. First set of numbers are measurements expressed in thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	195-526	349	21
Fork length			
Snout — A	662-698	674	20
Snout — 2D	581-605	586	20
Snout — 1D	251-276	263	20
Snout — P_2	281-312	296	20
Snout — P_1	258-281	267	20
P_1 — P_2	104-125	116	19
Head length	259-279	267	20
Max. body depth	221-240	231	16
Max. body width	127-169	141	17
P_1 length	112-135	121	19
P_2 length	76-118	85	20
P_2 insertion - vent	340-393	374	18
P_2 tip - vent	260-311	290	18
Base 1D	315-343	326	20
Height 2D	77-95	86	19
Base 2D	88-118	103	20
Height anal	72- 92	81	20
Base anal	48- 88	78	20
Caudal spread	238-277	259	11
Snout (fleshy)	88-103	96	20
Snout (bony)	76- 88	81	20
Maxilla length	131-150	139	20
Post orbital	120-136	130	20
Orbit (fleshy)	32- 41	37	19
Orbit (bony)	56- 84	66	20
Interorbital width	58- 72	66	19
Head length			
Snout (fleshy)	342-381	361	20
Snout (bony)	291-324	305	20
Maxilla length	503-539	518	20
Post orbital	478-508	492	20
Orbit (fleshy)	134-148	137	19
Orbit (bony)	231-287	246	20
Interorbital width	226-266	249	19

Sarda chiliensis (Cuvier)

Two subspecies of *S. chiliensis* are recognized: *S. c. chiliensis* (Cuvier) for the southeastern Pacific population and *S. c. lineolata* (Girard) for the northeastern Pacific population.

Sarda chiliensis chiliensis (Cuvier)

Pelamys chiliensis Cuvier in Cuvier and Valenciennes 1831:163 (original description; Valparaiso, Chile).

Pelamys chilensis. Günther 1860:368 (in part; description).

Sarda chilensis. Starks 1906:784 (Callao, Peru). Meek and Hildebrand 1923:318-319 (in part; description; Peru). Hildebrand 1946:372-374 (description; 13 Peruvian

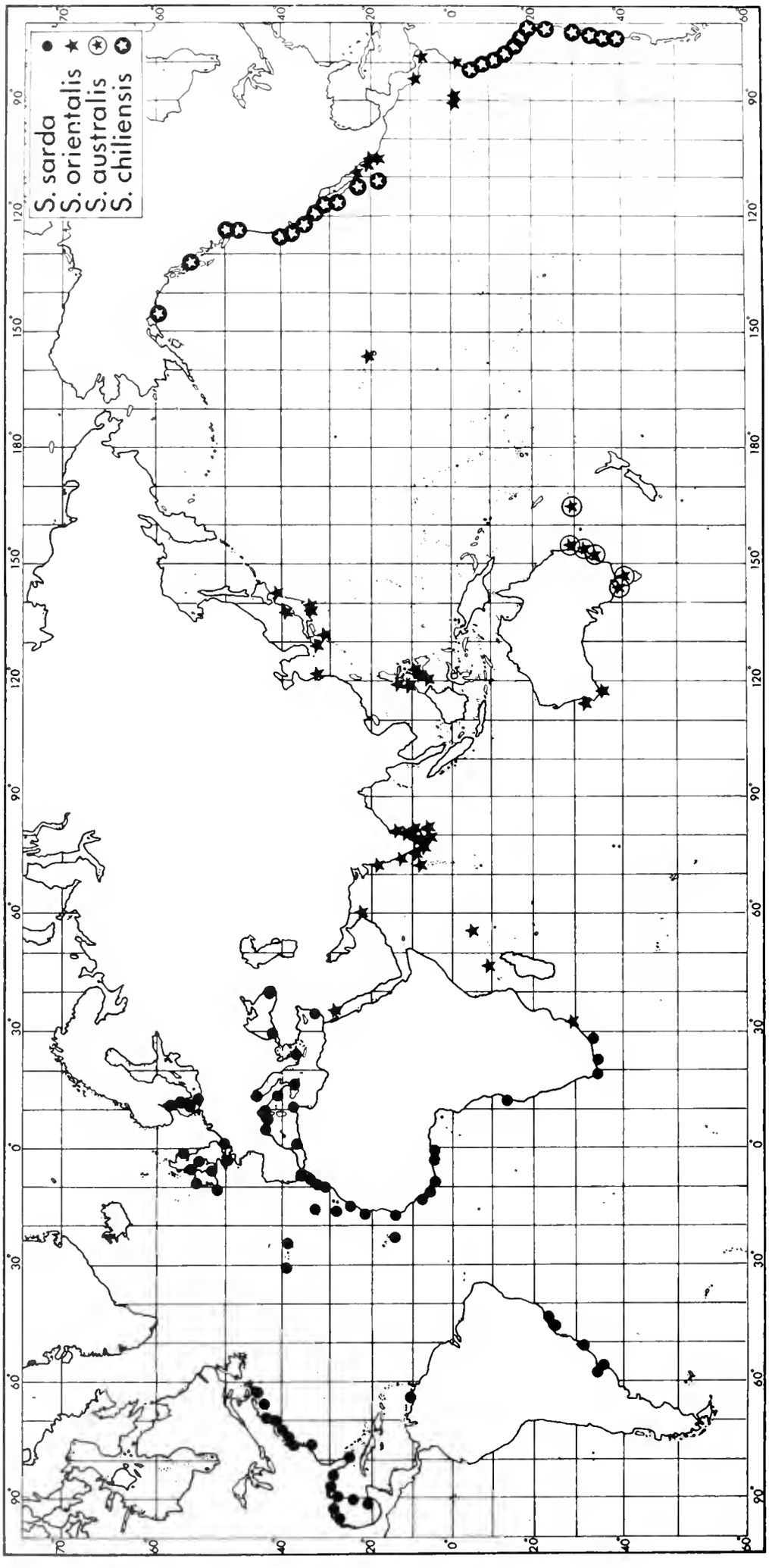


FIGURE 70.—Distribution of the four species of *Sarda* based on specimens personally examined and literature records.

specimens [USNM]). Fraser-Brunner 1950:146-147 (in part). La Monte 1952:44 (description), pl. 15. Mann 1954:298 (description, distribution; Chile). Vildoso 1960:1-75 (sexual maturity and reproduction; Peru). Bauchot and Blanc 1961:373 (type of *P. chiliensis*). Ancieta 1963:1607-1619 (fishery in Peru). Laevastu and Rosa 1963:1844, (fig. 7, in part; map of distribution and fishing areas). Vildoso 1963a:1143-1152 (reproduction; Peru). Blanc and Bauchot 1964:449, fig. 21 (type of *P. chiliensis*). Ancieta 1964:17-49 (species synopsis; Peru).

Sarda chiliensis. Walford 1936:8-10 (description; comparison with other species of *Sarda*). Chabanaud 1944:1-6 (in part; description; synonymy; all Indo-Pacific species considered synonyms of *S. chiliensis*). Godsil 1955:7-21, figs. 1-6, table 1-3 (description; anatomy; 5 Peruvian specimens). Pinkas 1961:175-188 (in part; 8 Peruvian juveniles, 38.0-201 mm). Klawe 1961b:487-493 (in part; juveniles from Peru and Chile), fig. 4 (160-mm Peruvian specimen).

Sarda sarda chiliensis. Buen 1958:12-17 (synonymy; description; fishery; range south to Talcahuano, Chile). Chirichigno 1969:75 (common name), 79 (fig. 147).

Sarda chilensis chilensis. Vildoso 1963b:1549-1556 (Peru; subspecifically distinct from *S. c. lineolata* based on vertebral number). Silas 1964:296-297 (in key, map, *S. chilensis* divided into an eastern Pacific *S. c. chilensis* and an Australian *S. c. australis*).

Sarda sarda chilensis. Sánchez and Lam 1970:42-43 (length-weight; weights of parts of body; fig. of vertebral column; photograph; Peru).

Sarda chiliensis chiliensis. Kuo 1970:2805-2806 (taxonomy, growth, maturation).

Sarda chiliensis lineolata (Girard)

Pelamys lineolata Girard 1859:106 (original description, San Diego, Calif.).

Pelamys chilensis. Günther 1860:368 (in part).

Sarda chilensis. Jordan and Gilbert 1882:428 (in part; description; synonymy). Jordan and Evermann 1896:872-873 (in part; description; synonymy). Starks 1910:91-93 (osteology; Puget Sound specimen). Meek and Hildebrand 1923:318-319 (in part; description; synonymy). Hildebrand 1946:374 (*S. lineolata* a synonym of *S. chilensis*). Fraser-Brunner 1950:146 (in part). Morice 1953a:37-39 (dentition; number of gill rakers and vertebrae). Ricker 1959b:6 (Revillagigedos Island, new record).

Sarda lineolata. Walford 1936:8-10 (key to species of *Sarda*; description). Walford 1937:22-23 (description). Clothier 1950:52-53 (vertebrae), pl. 10 (vertebral column). Godsil 1954:30-43, figs. 12-19, tables 4-5 (anatomy). Clemens and Wilby 1961:226-227 (description; north to northern end of Vancouver Island), fig. 131. Manzer 1965:853-855, fig. 1 (description; record from east coast of Vancouver Island).

Sarda stockii David 1943:31-33 (original description; Santa Monica Mountains, Calif.; Modelo formation, Upper Miocene), pl. 4 (holotype), 155 (additional specimen from Lompoc).

Sarda chiliensis. Chabanaud 1944:1-6 (description, in part; recognizes Atlantic *S. sarda* and Indo-Pacific *S. orientalis*). Fraser-Brunner 1950:146 (in part). Godsil 1955:38-42 (*S. lineolata* a synonym of *S. chiliensis*). Pinkas 1961:175-188 (in part; 27 juveniles 16.7-54.5 mm, from California and Baja California), fig. 4 (16.7-mm juvenile), fig. 5 (33.0-mm juvenile). Klawe 1961b:487-493 (in part; juveniles from California and Baja California), fig. 3 (42-mm juvenile). Radovich 1961:22, 31 (records north of Point Conception). Klawe 1962:180 (92-mm juvenile, Baja California). Laevastu and Rosa 1963:1844 (fig. 7, in part, map of distribution and fishing areas). Fitch and Craig 1964:201 (fig. 4, outline of sagitta), 202 (sagittae of three species of *Sarda* almost identical). Quast 1964:448 (11 specimens from coastal Alaska). Patten et al. 1965:298-299 (Puget Sound records). Magnuson and Prescott 1966:54-67 (courtship, locomotion, feeding). Fierstine and Walters 1968:1-31 (vertebral counts, myology, aspect ratio of caudal fin). Magnuson and Heitz 1971:363-365 (gill raker apparatus and filtering area). Pinkas et al. 1971:64-82 (food habits in southern California and Baja California). Hart 1973:373-374 (description, distribution, fig.).

Sarda chiliensis lineolata. Kuo 1970:2805-2806 (taxonomy, growth, maturation).

Comparative Diagnosis.—*Sarda chiliensis* is most similar to *S. orientalis* and *S. australis* and most different from *S. sarda* (Table 17). It differs from all three other species in having fewer anal fin rays (12-15, modally 14 vs. 14-17, modally 15)

and fewer total anal elements (18-22, modally 20 vs. 19-23, modally 21 or 22). *Sarda chiliensis* also has the greatest number of palatine teeth (9-22 vs. 7-14 in *S. australis*, 8-21 in *S. sarda* and *S. orientalis*) and the widest supramaxillary (slightly wider than in *S. sarda* and *S. australis*, much wider than in *S. orientalis*). *Sarda chiliensis* resembles *S. orientalis* and differs from *S. sarda* and *S. australis* in always lacking teeth on the vomer; *S. chiliensis* and *S. australis* both have a short hyomandibular spine that does not project beyond the condyle.

Morphometrically (Tables 1, 19), *Sarda chiliensis* has the shortest maxilla (463-489 thousandths of head length in the southeast Pacific population, 460-503 in the northeast Pacific), much shorter than *S. australis* (503-539) and *S. orientalis* (510-529) and the North American population of *S. sarda* (503-529), but overlapping with the eastern Atlantic populations of this species (497-511, 494-523). It has a shorter first dorsal base (267-314 thousandths of fork length) than *S. australis* (315-343) and differs from the northwest Pacific population of *S. orientalis* in snout-second dorsal and pelvic origin to vent distances.

TABLE 19.–Comparison of morphometric characters in two populations of *Sarda chiliensis*, northeast Pacific (*S. c. lineolata*) and southeast Pacific (*S. c. chiliensis*). First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	Northeast Pacific			Southeast Pacific		
Character	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*
Fork length (mm)	207-587	375	24	325-672	498	18
Fork length						
Snout — A	642-674	656	23	631-672	654	18
Snout — 2D	553-595	573	24	551-585	569	18
Snout — 1D	243-281	269	24	268-290	279	18
Snout — P_2	275-318	295	24	280-323	303	18
Snout — P_1	247-279	266	24	260-300	275	18
P_1 — P_2	106-121	112	21	105-131	118	16
Head length	248-275	263	24	259-292	272	18
Max. body depth	179-232	210	19	177-230	210	13
Max. body width	98-167	131	22	116-154	134	10
P_1 length	99-132	116	24	125-152	138	18
P_2 length	65- 87	78	24	65- 91	84	18
P_2 insertion - vent	329-367	353	24	327-368	346	16
P_2 tip - vent	248-331	276	24	237-352	269	17
Base 1D	278-314	297	24	267-303	286	16
Height 2D	64- 98	83	23	82-116	97	17
Base 2D	71-115	93	23	80-109	94	18
Height anal	58- 89	74	23	77-107	92	18
Base anal	61- 84	71	24	61- 88	74	18
Caudal spread	196-300	234	20	228-289	258	11
Snout (fleshy)	87-119	94	24	86-102	95	18
Snout (bony)	71- 83	78	24	75- 89	81	18
Maxilla length	115-136	126	24	121-143	130	18
Post orbital	125-144	139	21	131-150	142	16
Orbit (fleshy)	25- 44	31	24	27- 36	31	18
Orbit (bony)	47- 63	57	22	47- 63	56	18
Interorbital width	57- 69	63	24	62- 82	70	18
Head length						
Snout (fleshy)	339-368	353	23	331-363	348	18
Snout (bony)	283-308	297	24	279-329	299	18
Maxilla length	460-503	481	24	463-489	477	18
Post orbital	499-548	526	21	504-544	523	16
Orbit (fleshy)	102-168	119	24	102-141	115	18
Orbit (bony)	190-238	218	22	174-229	205	18
Interorbital width	213-278	239	24	233-302	257	18

Types of Nominal Species.–*Pelamys chiliensis* Cuvier in Cuvier and Valenciennes 1831:163. Holotype: MNHN A.5608; 672 mm FL; Chile, Valparaiso; d'Orbigny. Type previously considered by Bauchot and Blanc (1961), Blanc and Bauchot (1964, photograph-fig. 21), and Collette (1966). Counts: dorsal fin rays XVIII+14+VIII; anal fin rays 12+VI; pectoral fin rays 24; gill rakers missing; upper jaw teeth 23; lower jaw teeth (left-right) 16-19.

Pelamys lineolata Girard 1859:106. Holotype: USNM 688; 266 mm FL; California, San Diego; A. Cassidy. Counts: dorsal fin rays XIX+14+VIII; anal fin rays 12+VII; pectoral fin rays (left-right) 26-26; gill rakers 9+1+17=27; upper jaw teeth (left-right) 23-22; lower jaw teeth 18-19; palatine teeth 18-17; vertebrae 24+21=45; lamellae in nasal rosette 26.

Sarda stockii David 1943:31-33, pl. 4. Holotype: LACM 1035/1059A; originally Calif. Inst. Technol. 10039; ca. 522 mm FL; California, Santa Monica Mountains, quarry near Mulholland Drive, locality 1035; Modelo Formation; Upper Miocene. Counts from holotype: dorsal fin rays XVIII or XIX+13 or 14+VI; anal fin rays 12+VI; vertebrae 24 or 25+21-22=45 or 46. Caudal rays cover the hypural plate; teeth not visible; lower jaw with anteroventral notch similar to *Sarda*.

Distribution.–*Sarda chiliensis* is restricted to the eastern Pacific Ocean. Its range is divided into north and south temperate populations by a tropical population of *S. orientalis* (Figure 70). The southern *S. chiliensis chiliensis* was originally described from Valparaiso, Chile, and has been reported as far south as Talcahuano by Buen (1958) and Valdivia at lat. 39°48′S, long. 79°13′W by Kuo (1970). Its northern limit is at Mancora, Peru (Ancieta 1964), at lat. 4°09′S, long. 81°01′W, immediately south of the Gulf of Guayaquil, Ecuador. Most of our material comes from near Callao, Peru.

The northern subspecies, *S. c. lineolata* was originally described by Girard (1859) from San Diego, Calif. It regularly reaches south to Magdalena Bay, Baja California (Radovich 1961; CAS

SU 61662, Blanca Bay, lat. 24°46′30″N, long. 112°15′W), and occasionally to Cabo San Lucas at the tip of Baja California (lat. 22°20′N, long. 112°27′W). There is one specimen (Ricker 1959b; UBC 57-149) from Socorro Island in the Revillagigedos Islands 250 miles south of Cabo San Lucas. It is not common north of Point Conception, Calif., but there are several scattered records: off the Farallon Islands and off Eureka, Calif. (Radovich 1961); Puget Sound (Starks 1910, Patten et al. 1965); east coast of Vancouver Island, British Columbia (Manzer 1965; UBC 64-394); and coastal Alaska (Quast 1964) in Clarence Strait northwest of Ketchikan (USNM 213494) and off the Copper River at lat. 60°16′N, long. 145°32′W (USNM 213495).

Geographic Variation.—Although the temperate northeast (*c. lineolata*) and southeast (*c. chiliensis*) Pacific populations of *Sarda chiliensis* are completely separated from each other by the tropical eastern Pacific population of *S. orientalis* (Figure 70), there are few differences between the two populations; anatomically they are virtually identical. The caecal mass extends posteriorly for more than half the length of the body cavity in ventral view in the northeast population; less than half this distance in the southeast population.

Walford (1936) used the posterior extent of the corselet to distinguish the northeast *Sarda lineolata* (pectoral fin extends scarcely beyond corselet) from the southeast *S. chiliensis* (pectoral fin extends an eye diameter further). Hildebrand (1946) considered this character entirely unreliable in separating the two populations. Kuo (1970) measured the extent of the corselet in 380 specimens from southern California and 49 from Callao, Peru. He found that the corselet does extend further posteriorly in the southern population but that the interpopulational differences were not significant at the 5% level. He concluded that the character was not reliable even for subspecific separation of the two populations.

Morphometrically, there are some differences in the ranges and means between the two populations (Table 19), but these are smaller than those between some populations of *S. sarda* and *S. orientalis*. Kuo (1970) found, through covariance analyses and scatter diagrams, significant differences at the 1% level between the two populations in such morphometric characters as head length, predorsal length, prepelvic length, and the distance from the origin of the second dorsal and anal fins to the caudal base.

Among meristic characters, the total number of vertebrae is the best distinguishing character between the southeast and northeast populations of *Sarda chiliensis*. The northeast population has more vertebrae (Table 9) with means of 44.9 for our data, 44.8 for Kuo (1970), and 45 ± 0.47 for a sample of 19 reported by Vildoso (1963b). Our data for 23 southeast specimens ($\bar{x}$ 44.2) agrees with that reported by Vildoso (1963b) for two samples, 44.15 ± 0.40 for 38 specimens, and 44.21 ± 0.40 for a sample of 100. Kuo (1970), however, found even fewer: a range of 42-46 with a mode of 43 and a mean of 43.4 compared to our range of 43-46, mode 44, mean 44.2. The reasons for the discrepancies between our data and that of Vildoso on the one hand, and that of Kuo on the other are not known. We have reexamined seven of Kuo's southeastern specimens and find totals of 43 (1 specimen), 44 (5), and 45 (1).

There are also differences in the highly variable number of teeth in the upper and lower jaws (Tables 5, 6) with the northeast Pacific population having slightly more: upper jaw 20-30, $\bar{x}$ 23.7 vs. 18-28, $\bar{x}$ 23.0; lower jaw 15-25, $\bar{x}$ 19.4 vs. 14-23, $\bar{x}$ 18.9.

The available data does not convince us that the northeast and southeast Pacific populations are subspecies. However, as the populations are genetically isolated from each other and there are some significant differences, there is practical value in using the available subspecific names, and there is ample historical precedent for the name *lineolata* for the northeast population. Therefore, we have emphasized comparisons between the two geographic populations by labelling the populations northeast and southeast Pacific in the tables but have retained the subspecies designations in the formal synonomies.

Sarda orientalis (Temminck and Schlegel)
Indo-West Pacific

Pelamys orientalis Temminck and Schlegel 1844:99 (original description, Japan), pl. 52. Richardson 1846:268 (Sea of Japan). Günther 1860:368 (description). Tirant 1885:46 (Cambodia).

Pelamys chilensis (not of Cuvier 1831). Day 1878:253-254 (description; Bombay), pl. 56, fig. 1.

Sarda chilensis var. *orientalis*. Steindachner and Döderlein 1884:179 (description; Japan).

Sarda orientalis. Jordan and Snyder 1900:352 (Tokyo). Jordan and Snyder 1901:64 (Tokyo, Nagasaki). Kishinouye 1923:424-426 (description, anatomy; Japan, southern species abundant around Kyushu, juvenile from Aomori, Honshu), figs. 11, 17, 33, 42. Jordan and Hubbs 1925:215 (not uncommon in Japanese markets). Walford 1936:9 (*S. orientalis* separate species from *S. velox*). Tortonese 1939:323-324 (Yokohama, Japan). Boeseman 1947:94-95 (lectotype of *P. orientalis* selected). Smith 1949:299 (description; south to Durban, South Africa). Warfel 1950:18 (description; Philippine Islands), 21 (fig. 14, fish, gill arch, excised liver). Fraser-Brunner 1950:147-148 (description), fig. 12. Honma 1952:143 (Echigo Province, Honshu, Japan). Herre 1953:251 (Philippine Islands). Morice 1953a:37-39 (dentition; number of gill rakers and vertebrae), fig. 5 (after Warfel 1950). Godsil 1955:22-35, figs. 7-13, tables 4-6 (description, anatomy, five Japanese specimens). Smith 1956:721 (Aldabra). Munro 1958a:113 (Western Australia), fig. 755. Jones 1961:343,346, fig. 10 (158 mm. juvenile, fig. 11 (80 mm juvenile). Jones and Silas 1961:379-380 (Vizhingam and Cape Comorin, Western India), fig. 6 (juvenile and adult). Collette and Gibbs 1963b:30 (Indian Ocean), pl. 9, upper fig. Jones and Silas 1963:1787 (distribution in Indian Ocean). Kikawa et al. 1963:147-156 (species synopsis). Thomas and Kumaran 1963:1667 (diet in Indian waters mostly fish). Boeseman 1964:465, pl. 3, fig. 11 (lectotype of *P. orientalis*). Jones and Kumaran 1964:357-358, 360, fig. 60 (after Jones 1961). Jones and Silas 1964:26 (description), pl. 8A. Kumaran 1964:605 (diet 98% fish). Rao 1964:736 (ripe ovaries). Nakamura and Kikawa 1966:60-62 (infracentral grooves on vertebrae). Sivasubramaniam 1967:29 (catch in Ceylon), 44 (fig. 14, length-weight). Gnanamuttu 1968:365 (Madras). Sivasubramaniam 1969:73-77 (description, biology; Ceylon), pl. 1 (photos of juvenile and adult). Nair et al 1970:13-17 (biology, description; India). Nagabhushanam and Chandrasekhara Rao 1972:303 (Minicoy Atoll, Laccadive Archipelago).

Sarda chilensis (not of Cuvier 1831). Jordan and Snyder 1904:125 (description; Honolulu). Jordan et al. 1913:121 (Japan). Jordan and Jordan 1922:32 (occasional at Hawaii). Barnard 1927:801 (description; Natal coast, South Africa). Fowler 1928:134-135 (Hawaii). Chevey 1934:45-46 (Tirant's Cambodia record). Tinker 1944:160-161 (Hawaii). Brock 1949:275 (in key to Hawaiian scombrids).

Sarda chiliensis (not of Cuvier 1831). Fowler 1938:277 (Honolulu). Fowler 1949:73 (Honolulu).

Sarda orientalis serventyi Whitley 1945:41 (original description; Western Australia). Whitley 1947:146, pl. 11, fig. 4 (holotype). Whitley 1948:24 (range in Western Australia). Whitley 1964a:236, 242 (Western Australia). Whitley 1964b:48 (listed).

Sarda orientalis
Eastern Pacific

Sarda chilensis (not of Cuvier 1831). Gilbert and Starks 1904:68 (description; Panama City).

Sarda chiliensis (not of Cuvier 1831). Herre 1936:107 (Galapagos). Erdman 1971:68-69 (Gulf of Nicoya, Costa Rica).

Sarda velox Meek and Hildebrand 1923:320-321 (original description; Panama City), pl. 24. Walford 1936:8-10 (description; recognized as valid species). Walford 1937:23 (description), col. pl. 38a. Schmitt and Schultz 1940:3 (Galapagos Islands [USNM 107055]). Fowler 1944:342 (Galapagos Islands [ANSP 82007, 89065]). Hildebrand 1946:374-375 (description; Gulf of Guayaquil, Peru [USNM 127907]; Galapagos; Pearl Islands, Panama). La Monte 1952:44, 46 (description), pl. 15. Morice 1953a:37 (listed). Godsil 1954:44-59 (description; anatomy; 4 Galapagos specimens), tables 6, 7 (counts and measurements), figs. 21-27 (morphometrics), figs. 28-33 (anatomy), figs. 35-41 (osteology). Vildoso 1963b:1549-1556 (description; range). Laevastu and Rosa 1963:1844 (fig. 7, distribution map).

Sarda orientalis. Fraser-Brunner 1950:147 (*S. velox* a synonym of *S. orientalis*). de Sylva 1955:38, fig. 61 H (dorsal view of skull). Godsil 1955:36-42 (no significant anatomical differences between *S. velox* and *S. orientalis*). Ricker 1959a:13 (S. Baja California; Las Tres Marías Islands). Silas 1964:296 (in part; in key and on range map). Fitch and Craig 1964:202 (sagittae of three species of *Sarda* almost identical).

Comparative Diagnosis.—*Sarda orientalis* is similar to *S. australis* and *S. chiliensis* in an equal

number of characters (Table 17). It differs from the other species of *Sarda* in having the lowest number of gill rakers (8-13 vs. 16-27); a very narrow supramaxillary; the dorsal projection of the ectopterygoid slightly expanded versus pointed; only a trace of a depression in the position of the elliptical ceratohyal window; no depression on the ventral surface of the proximal portion of the glossohyal; the haemal postzygapophyses of the last precaudal vertebra and the haemal prezygapophyses of the first caudal vertebra abutting against each other; gall bladder not visible in ventral view between the intestine and spleen; and a narrower and longer vertical wing to the pelvic girdle. *Sarda orientalis* is similar to *S. sarda* in having a long hyomandibular spine that projects beyond the condyle and in having a low number of palatine teeth (8-19 vs. 8-21). *Sarda orientalis* is sharply differentiated from *S. chiliensis* in having fewer gill rakers, a much narrower supramaxillary, and also in having fewer larger teeth (upper jaw 12-20, $\bar{x}$ 15.5 vs. 18-30, $\bar{x}$ 23.5; lower jaw 10-17, $\bar{x}$ 13.0 vs. 14-25, $\bar{x}$ 19.2).

Morphometrically (Tables 1, 20), *Sarda orientalis* is generally similar to the other species of *Sarda*. It does have a longer maxilla (141-149 and 146-156 thousandths of fork length in the northwest and eastern Pacific populations, respectively) than *S. chiliensis* (115-143) and *S. sarda* (125-145). The base of the first dorsal fin (285-327, 282-302) is shorter than that of *S. australis* (315-343).

TABLE 20.–Comparison of morphometric characters in populations of *Sarda orientalis* from Japan and the eastern tropical Pacific. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	Japan			East tropical Pacific		
Character	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*
Fork length (mm)	342-560	432	7	354-613	472	10
Fork length						
Snout — A	674-703	694	5	662-703	678	10
Snout — 2D	596-614	606	5	569-596	582	10
Snout — 1D	273-308	286	7	274-311	288	10
Snout — P_2	293-316	303	5	299-321	310	10
Snout — P_1	272-292	281	7	277-299	290	10
P_1 — P_2	109-118	113	5	105-118	114	10
Head length	268-286	278	7	266-294	284	10
Max. body depth	221-244	234	4	193-236	213	10
Max. body width	143-151	146	4	127-153	144	10
P_1 length	104-125	115	7	119-134	127	10
P_2 length	70- 78	76	5	81- 91	86	10
P_2 insertion - vent	374-419	392	7	353-384	367	10
P_2 tip - vent	305-322	311	3	265-302	280	10
Base 1D	285-327	306	7	282-302	292	10
Height 2D	75- 82	78	7	89-101	94	8
Base 2D	85-111	93	7	88-107	95	9
Height anal	61- 85	73	7	84- 97	89	8
Base anal	66- 78	73	7	73- 83	79	9
Caudal spread	168-234	214	4	192-259	236	5
Snout (fleshy)	86-103	96	7	98-105	101	10
Snout (bony)	80- 97	86	7	83- 91	86	10
Maxilla length	141-149	145	6	146-156	150	10
Post orbital	128-147	139	5	141-151	146	10
Orbit (fleshy)	32- 60	42	7	34- 40	37	10
Orbit (bony)	29- 65	56	7	60- 68	64	10
Interorbital width	67- 73	71	6	65- 79	71	10
Head length						
Snout (fleshy)	306-368	344	7	348-369	357	10
Snout (bony)	288-344	308	7	291-317	303	10
Maxilla length	510-529	522	6	512-557	528	10
Post orbital	476-525	503	5	494-553	512	10
Orbit (fleshy)	102-152	136	7	120-147	130	10
Orbit (bony)	210-234	220	7	210-238	226	10
Interorbital width	251-263	256	6	230-283	251	10

Types of Nominal Species.–*Pelamys orientalis* Temminck and Schlegel 1844:99, pl. 52. There are three syntypes in Leiden of which Boeseman (1947:94-95; 1964:465, pl. 3, fig. 11) selected the largest as lectotype. Lectotype: RMNH 2286; about 560 mm FL, stuffed and mounted; Japan; 1830; Burger. Paralectotypes: RMNH 842; about 470 mm, stuffed and mounted; Japan; Burger. RMNH 1244; 451 mm, stuffed but preserved in alcohol; Japan; 1824-29. Counts for lectotype (paralectotypes in parentheses): dorsal fin rays XVIII+14+VIII (XVIII+14+VIII, XIX+15+VIII); anal fin rays ca. 14+VI (ca. 13+VI, 15+VI); pectoral fin rays 24 (23-23, 25-24); gills missing in all three; upper jaw teeth ca. 14 (ca. 13-11, 15-17); lower jaw teeth (left-right) 12-12 (?, 12-13).

Sarda velox Meek and Hildebrand 1923:320-321, pl. 24. Holotype: USNM 81060; 364 mm FL; Panama City market; 19 Jan. 1912; S. E. Meek and S. F. Hildebrand. Counts: dorsal fin rays XVIII+15+VIII; anal fin rays 15+VI; pectoral fin rays (left-right) 25-24; gill rakers 3+1+8=12; upper jaw teeth (left-right) 17-19; lower jaw teeth 13-11; vertebrae 25+20=45; lamellae in nasal rosette 34-32.

Sarda orientalis serventyi Whitley 1945:41. Holotype figured in Whitley (1947:pl. 11, fig. 4). Holotype: WAM P.3512; 265 mm FL; Western Australia, Perth. Paratype: WAM P.2568; 480 mm; Western Australia, Busselton. The holotype could not be located when Collette visited Perth in 1970. Counts for paratype: dorsal fin rays XVIII+14+VIII; anal fin rays 14+VI; pectoral fin rays 24-24; no gills; upper jaw teeth (left-right) 19-17; lower jaw teeth 15-14; palatine teeth 13.

Distribution.–*Sarda orientalis* is widespread in the Indo-Pacific but there are two reports from the Atlantic Ocean. Nichols and Breder (1927) record-

ed it (as *S. velox*) from Block Island, R.I., based on a drawing (Stillman 1921). We do not believe a positive identification of a species of *Sarda* can be based solely on a drawing. Fraser-Brunner (1950) "confirmed" the presence of *S. orientalis* in the Atlantic based on a specimen from the Gold Coast (Ghana), but reexamination of this specimen (BMNH 1939.7.12.31) shows it to be a perfectly normal *S. sarda*.

There appear to be large gaps between populations in the tropical Indo-West Pacific (Figure 70). In the western Indian Ocean, it is recorded from along the coast of Natal, South Africa (Barnard 1927; ANSP 91185), south to Durban (Smith 1949; BMNH 1920.7.23.59). It occurs at Aldabra (Smith 1956) and in the Seychelles Islands (Smith and Smith 1963; BMNH 1927.4.14.81). We have examined specimens from Eilat at the northern end of the Gulf of Aqaba in the Red Sea (SFRS 704/1-2) and from Muscat at the entrance to the Persian Gulf (BMNH 1888.12.129-131). Day (1878) gave an early report from Bombay. Silas (1964, fig. 7) mapped the occurrence and fishery areas for *Sarda orientalis* in the eastern Arabian Sea along the southwest coast of India and Nagabhushanam and Chandrasekhara Rao (1972) listed it among the fauna of Minicoy Atoll, Laccadive Archipelago. Sivasubramaniam (1967, 1969, 1970) recorded it as one of the least abundant tunas in the inshore water of Sri Lanka (Ceylon); we have examined a juvenile from there (UBC 57-183). Small quantities were taken in gill nets off Madras in 1966 (Gnanamuttu 1968). We have not seen any records or specimens from the eastern Indian Ocean except for the southwest tip of Australia from where Whitley (1945) described *S. orientalis serventyi* (Albany and Busselton, Western Australia; WAM P. 2568).

There appear to be no records or museum specimens of *Sarda orientalis* from Indonesia or elsewhere in the East Indies. There is an old published record for Cambodia (Tirant 1885), but we have seen no specimens from the Gulf of Thailand or South China Sea in any collections including the extensive series of scombrids collected by the George Vanderbilt Expedition. Warfel (1950) and Herre (1953) reported it from the Philippine Islands and there are specimens from Shanghai (MNHN 91-628; NHMV uncat.). Starting with its original description by Temminck and Schlegel in 1844, there have been numerous reports from Japan where it is not uncommon in many markets (Jordan and Hubbs 1925): Richardson 1846 (Sea of Japan); Jordan and Snyder 1900 (Tokyo); Jordan and Snyder 1901 (Tokyo and Nagasaki); Tortonese 1939 (Yokohama). Kishinouye (1923) reported *S. orientalis* as abundant around the island of Kyushu and he recorded a juvenile from north as far as Aomori Prefecture (about lat. 41°N) at the north end of Honshu. According to Kikawa et al. (1963), this remains the northernmost record of the species in Japan. Honma (1952) listed it from Sado Island (about lat. 38°N), Niigata Prefecture, in the Sea of Japan. Carl L. Hubbs obtained specimens (UMMZ uncat.) from Suruga Bay and Sagami Bay in 1923 and Collette purchased specimens in the Tokyo market in 1966. There appears to be a large gap in the range from Japan and China on the north and the Philippine Islands further south all the way east to the Hawaiian Islands where it is not common (Jordan and Snyder 1904; Jordan and Jordan 1922; Fowler 1928; Tinker 1944; Brock 1949); however, we have examined two preserved Hawaiian specimens (USNM 58527; ANSP 82258) and have dissected two recently collected specimens.

The eastern Pacific population is confined to the tropical coasts of Middle America and Ecuador and also occurs in the Galapagos Islands. This population was described as *Sarda velox* by Meek and Hildebrand in 1923 from Panama City specimens and several other records are also from Panama and the Pearl Islands (Gilbert and Starks 1904; Hildebrand 1946; CAS SU 12824; USNM 81060, 128643-5). The range extends south to the Galapagos (Herre 1936; Schmitt and Schultz 1940; Fowler 1944; Hildebrand 1946; Godsil 1954; ANSP 82007, 89065; CAS SU 4885; USNM 107055, 119781) and the Gulf of Guayaquil, Ecuador (Hildebrand 1946; USNM 127907). To the north, there are records from the Gulf of Nicoya, Costa Rica (Erdman 1971) and from the coast of Mexico at Banderas Bay, Las Tres Marías Islands, and Cape San Lucas (NMC 68-0710) at the southern tip of Baja California (Ricker 1959a).

Geographic Variation.—The distribution of *Sarda orientalis* (Figure 70) is disjunct and, therefore, subspecific or populational differences are possible. Two forms have been named—the population in southwestern Australia (*S. orientalis serventyi* Whitley) and the tropical eastern Pacific population (*S. velox* Meek and Hildebrand). Based on the scattered material available, there appear to be no significant anatomical or meristic

differences between any populations of the species. Morphometrically, there appear to be some differences between the small samples from Japan and the eastern Pacific (Table 20), in such characters as snout-second dorsal distance, pelvic fin tip to vent, height of anal and second dorsal fins. Until more material is examined, there does not seem to be adequate data to support recognition of subspecies in *S. orientalis*. However, to facilitate entry into the literature, the synonomies have been divided into Indo-West Pacific (including Hawaii) and tropical eastern Pacific.

Sarda sarda (Bloch)

Pelamis Belon 1553:177-179 (description).

Amia Rondelet 1554:238-241 (description, fig.).

Pelamyde vera Rondelet 1554:245-248 (description, fig.)

Pelamyde sarda Rondelet 1554:248 (description, fig.).

Thunnus authoris primus Aldrovandi 1613:313 (fig.).

Pelamys sarda Willughby 1686:179 (description).

Scomber pelamis Brünnich 1768:68-69 (original description; Adriatic Sea; preoccupied by *Scomber pelamis* Linnaeus, 1758 [= *Katsuwonus pelamis*]).

Bonite Duhamel du Monceau 1769: pl. 7, fig. 2.

Thonin sorte de pélamide Duhamel du Monceau 1769: pl. 7, fig. 5.

Scomber sarda Bloch 1793:44-48 (original description; pre-Linnean synonymy; Europe) pl. 334. Bloch and Schneider 1801:22-23 (description; Mediterranean and Atlantic). Risso 1810:168-169 (description; Nice).

Scomber mediterraneus Bloch and Schneider 1801:23 (substitute name for *Scomber pelamis* Brünnich; description). Delaroche 1809:336 (description; Balearic Islands and Mediterranean coast of Spain).

Scomber palamitus Rafinesque 1810:44-45 (original description; Palermo, Sicily), pl. II, fig. 2.

Scomber ponticus Pallas 1811:217 (original description; Crimea).

Thynnus pelamis. Risso 1826:415-416 (synonymy; description; Nice).

Thynnus sardus. Risso 1826:417 (synonymy; description; Nice).

Thynnus brachypterus Cuvier 1829:198 (original description based on the *pelamyde vera* of Rondelet (1554:245) and the thonin sorte de pélamide of Duhamel du Monceau (1769:pl. 7, fig. 5).

Sarda sarda. Cuvier 1829:199 (original description of *Sarda*). Dresslar and Fesler 1889:440-441 (synonymy; description; Woods Hole, Mass.), pl. 8. Berg 1895:41 (Mar del Plata, Argentina). Jordan and Evermann 1896:872 (description; synonymy). Ihering 1897:52 (Rio Grande do Sul, Brazil). Fowler 1915:532 (Trinidad). Miranda Ribeiro 1918:766 (Santos, Brazil). Schroeder 1924:6 (uncommon in Florida Keys). Chabanaud 1925:199-200 (vertebral number; West Africa), fig. (dentition). Fowler 1926:268 (Buenos Aires). Barnard 1927:800 (description; Cape Seas, South Africa). Chabanaud and Monod 1927:279 (Port Étienne, Mauritania). Nichols and Breder 1927:122-123 (description; Western Atlantic north to Casco Bay, Maine) fig. 169. Buen 1930a:40 (pl. 1, fig. 4), 46 (synonymy; description; Spain). Buen 1930b:1-32 (larvae and juveniles; Mediterranean Sea), figs. Dieuzeide 1930:134-140 (synonymy; description; Algeria), pl. 2. Le Gall 1934b:287 (description), fig. (after Smitt). Pozzi and Bordale 1935:162 (lat. 35-38°S, Argentina). Vladykov 1935:7-8 (Nova Scotia). Fowler 1936:626-627 (synonymy; description; Italian and New Jersey specimens). Walford 1936:9 (key to species of *Sarda*). Cadenat 1937:482 (Cape Verde, Sénégal). Lovén 1938:274-280 (Scandinavian records), 275 (fig. 1), 276 (fig. 2, map). McKenzie 1939:16 (St. Margaret's Bay, Nova Scotia). Baughman 1941:18 (Texas [USNM 118644-6]). Jensen 1941:201-202 (14 locality records from the Kattegat off Denmark). Redeke 1941:212-213 (description; Netherlands). Chabanaud 1944:3-6 (*S. sarda* a distinct species). La Monte 1945:20-21, col. pl. 8. Irvine 1947:185-186 (description; Accra, Ghana). Poll 1947:284-285 (description), fig. 183. Molteno 1948:23 (abundant off Angola and South West Africa; summer schools from Cape Point to Mosselbaai, South Africa). Smith 1949:299 (occasional at Cape Point, South Africa), col. pl. 66, fig. 833. Tortonese and Trotti 1949:86 (common in Ligurian Sea). Cadenat 1950:134 (Cape Verde Islands). Fraser-Brunner 1950:146-147 (key; range), fig. 11. Postel 1950:59-62 (description; length-frequency; biology; Cape Verde Islands). Rivas 1951:223 (synonymy; description; Western Atlantic). La Monte 1952:46 (description; range), col. pl.

17. Lozano y Rey 1952:523-527 (synonymy; description), col. pl. 39, fig. 4. Bigelow and Schroeder 1953:337-338 (description; habits; range in Gulf of Maine), fig. 180 (after Smitt). Morice 1953a:37-41 (anatomy), p. 58 (fig. 5 after Dresslar and Fesler 1889). Morice 1953b:72 (fig. 6, liver). Belloc 1954:297-310 (description; synonymy; Mediterranean distribution; biology; fishery). Collins 1954:27 (Azores). Mather and Day 1954:182 (Spanish Sahara). Pew 1954:28-30 (Texas), fig. 27. Postel 1954:357-358 (stomach contents); 359 (parasites), 361 (gonosomatic index). Dieuzeide et al. 1955:147-148 (description; range; fig.; Algeria). Dollfus 1955:55 (listed), 141 (references; Atlantic coast of Morocco). Frade and Postel 1955:34 (gonads; spawning season; Cape Verde Islands), 35 (fig. 5, ovary). Hildebrand 1955:206 (common sports fish in northwest Gulf of Mexico; 6 trawled west of Campeche). Nümann 1955:75-127 (migrations in the Black Sea and Sea of Marmara). A. Postel 1955:57-67 (number of teeth in 503 specimens; Tunisia). E. Postel 1955a:1-167 (summary of biology in the tropical eastern Atlantic). E. Postel 1955b:31-32 (sex ratio; maximum size). Springer and Bullis 1956:71 (Arcas Cay, off Campeche, Mexico). Mather and Gibbs 1957:243 (Shag Harbour, Nova Scotia). Ionescu et al. 1958:165-186 (biology; Roumania). Klawe and Shimada 1959:111 (2 juveniles, 64-67 mm; Gulf of Mexico), 112 (fig. 6, 67-mm juvenile). Gordon 1960:47-48 (summer visitor to Block Island Sound, R.I. Bauzá Rullán 1961:155-156 (otoliths), pl. 1 (figs. 7-10, sagittae). Klawe 1961a:154 (34-mm juvenile off Charleston, S.C.). Mansueti 1962:47-49 (description; Chesapeake Bay). Nunes-Ruivo 1962:17 (copepod *Caligus pelamydis* from Angolan specimen). Collette and Gibbs 1963a:26 (species of *Sarda*). Demir 1963:101-129 (description, synonymy; range; biology, especially in the Black Sea). Idyll and de Sylva 1963:755-760 (biology; western Atlantic). Laevastu and Rosa 1963:1844 (fig. 7, map of distribution and fishing areas). Bănărescu 1964:805-809 (synonymy; description; ecology; Roumania), fig. 355 (adult), fig. 356 (larvae). Demir 1964:455-457 (meristics of 1,000 specimens; Black Sea and Sea of Marmara). Fitch and Craig 1964:202 (sagittae of three species of *Sarda* almost identical). George et al. 1964:21 (Lebanon, rare). Postel 1964:220 (summary of biology, North Africa). Svetovidov 1964:389-395 (extensive synonymy; description; biology; Black Sea), fig. 125 (adult), fig. 126 (juvenile). Boschung 1966:227-228 (Gulf of Mexico records; stomach contents). Rodrígues-Roda 1966:269-279 (biology; Spanish trap net fishery 1958-1964). Jensen 1967:45-46 (central and western Gulf of Guinea). Padoa 1967:479-483 (eggs and larvae), figs. 308-312 (eggs and larvae). Bini 1968:37-38 (description; col. fig.). Granier 1968:325 (Golfe d'Aigues-Mortes, Golfe du Lion, France). Rae and Pirie 1968:212 (Montrose, east coast of Scotland). Went 1968:37-38 (Streedagh, near Grange, County of Sligo, Ireland; previous Irish records). Williams 1968:436 (Gulf of Guinea). Dornescu and Mişcalencu 1968:15 (perciform type of branchial apparatus). Muir 1969:168 (gill dimensions). Rae and Pirie 1969:279 (Garliesston, Scotland). Went 1969:149 (7 previous Irish records). Wheeler and Blacker 1969:327 (British seas 1966-67). Lozano Cabo 1970:158 (Spanish Morocco). Mago Leccia 1970:109 (Venezuela). Muir 1970:22 (measurements of branchial vessels of second gill arch). Carey et al. 1971:136 (body temperature). Dahl 1971:276-277 (Colombia). De Groot and Nijssen 1971:8 (Arguin Bank, Mauritania). Went 1971:44 (Irish records). Adamicka 1972:308-331 (functional anatomy of the head), figs. 1-4 (head muscles). Wheeler and Blacker 1972:162 (British seas, 1968-69). Postel 1973:475 (synonymy; distribution).

Pelamys sarda. Cuvier in Cuvier and Valenciennes 1831:149-162 (synonymy; description; Cape Verde Islands and Brazil); pl. 217. Rathke 1837:335 (*Scomber ponticus* Pallas a synonym of *P. sarda*). Bonaparte 1845:74 (synonymy). Guichenot 1850:58 (synonymy; Algeria). Lowe 1850:248 (Madeira). Storer 1855:141-143 (description; Massachusetts), pl. 11, fig. 5. Günther 1860:367 (synonymy; description). Duméril 1858:262 (Cape Verde Islands). Steindachner 1865:401 (Canary Islands). Steindachner 1868:358-360 (description; Iberian Peninsula and Canary Islands). Canestrini 1870:103 (description; Italy). Collett 1879a:19-20 (description; Christiana (= Oslo), Norway). Giglioli 1880:25 (Italy). Moreau 1881:430-434 (synonymy; description; France). Ninni 1882:264 (Adriatic). Rochebrune 1882:95

(Cap Vert). Hilgendorf 1888:208 (Azores Islands). Osorio 1890:56 (Angola). Vinciguerra 1893:93 (Canary Islands). Griffini 1903:398 (description; Italy). Pellegrin 1908:89-90 (Dakar), fig. 6. Shepherd 1910a:59, fig. 13 (asteriscus). Shepherd 1910b:293, fig. 1 (sagitta). Parona 1919:84-91 (synonymy; common names; description; distribution; Italy; col. pl. 8). Farran 1923:106 (Ireland). Sanzo 1932:3-9 (eggs and larvae; Italy; col. pl. with 7 figs. of egg and developing embryo). Athanassopoulos 1934:315-316 (Greece; Sea of Marmora). Liebman 1934:325 (Israel).

Palamita sarda. Bonaparte 1831:173 (original description of *Palamita*, substitute name for *Pelamys* Cuvier, preoccupied).

Pelamis sarda. Valenciennes 1844:49-50 (Canary Islands). Verany 1847:493 (Liguria, Italy). Ehrenbaum 1924:10-11 (vertebral counts; description of 7.2-mm larva from Oran, Algeria); fig. 3a (7.2-mm larva) and 3b (preopercle of larva).

Sarda pelamys. Gill 1862:126 (type-species of *Sarda*). Jones 1879:88 (Halifax, Nova Scotia).

Sarda mediterranea. Jordan and Gilbert 1882:427-428 (description; both sides of Atlantic; synonymy). Carus 1893:659 (Mediterranean). Šoljan 1963:147 (description; figs.; Adriatic Sea).

Sarda pelamis. Smitt 1892:105-107 (synonymy; description; occasional visitor to Scandinavia), fig. 30. Sanz Echeverría 1926:150 (sagitta). Jensen 1937:10-11 (a summer visitor to the Skagerak and Kattegat). Otterstrøm 1943:125-126 (summary of previous records from Denmark, photograph).

Comparative Diagnosis.—*Sarda sarda* is the most distinct species in the genus and can be distinguished from the other three species by higher counts in several characters (Table 17). Dorsal spines number 20-23 compared to 17-19; vertebrae 50-55 vs. 43-46; pleural ribs 24 vs. 19-23; intermuscular bones 31-45 vs. 32-36; keels on vertebrae number 5-10 (counting from hypural plate anteriorly) vs. 5-8. *Sarda sarda* is closest to *S. australis* in several characters: numbers of anal rays, gill rakers, upper and lower jaw teeth, occasional presence of vomerine teeth, angle of the hyomandibular spine and the condyle, width of the supramaxilla, and relative length of the haemal pre- and postzygapophyses on the first caudal vertebra. As in *S. australis*, the supramaxilla is intermediate in width, wider than in *S. orientalis*, but narrower than in *S. chiliensis*. *Sarda sarda* resembles *S. orientalis* in having a long hyomandibular spine, projecting beyond the condyle.

Morphometrically (Tables 1, 21), *Sarda sarda* is similar to the other species of *Sarda* but has a shorter first dorsal base (291-330 thousandths of fork length, $\bar{x}$ 311 vs. 315-343, $\bar{x}$ 326) and smaller orbit (35-64 vs. 60-80, $\bar{x}$ 66) than *S. australis*. The first dorsal fin base is longer than in *S. chiliensis* (329-368) as is also the maxilla (494-529 thousandths of head length vs. 463-503). *Sarda sarda* differs from *S. orientalis* in averaging a longer head and greater distances from snout to anal origin and snout to pelvic fin origin.

Types of Nominal Species.—*Scomber pelamis* Brünnich 1768:68-69. Adriatic Sea. No types known to be extant. Counts from the original description (dorsal fin rays XXIII + 15 + VIII; anal fin rays 15 + VII; pectoral fin rays 24) leave little doubt about the description being of *S. sarda*.

Scomber sarda Bloch 1793:44-48, pl. 334. Europe. No types known to be extant. The plate leaves little doubt as to the identity of the description. Counts from the original description: dorsal fin rays XXI + 15 + VII; anal fin rays 14 + VI.

Scomber palamitus Rafinesque 1810:44-45, pl. 2, fig. 2. Palermo, Sicily. No types known to be extant. Original description states that there are 20 spines in the first dorsal fin and the figure is of *S. sarda*.

Scomber ponticus Pallas 1811:217. Black Sea. No types known to be extant. Original description includes counts of dorsal fin rays XXII + 14 + IX; anal finlets VIII; and pectoral fin rays 25.

Thynnus brachypterus Cuvier 1829:198. The original description is not based on specimens but on pre-Linnean authors—the "pelamyde vera" of Rondelet (1554:245-248) and the "thonin sorte de pélamide" of Duhamel du Monceau (1769:pl. 7, fig. 5). The large teeth, general body shape, and broad vertical bands show both figures to be of juvenile *Sarda*. The specimens used by Cuvier (in Cuvier and Valenciennes 1831) in the redescription of *T. brachypterus* and considered by Bauchot and Blanc (1961) and Blanc and Bauchot (1964) as types are not types. (As Collette 1966, pointed out, four of these specimens are *Thunnus thynnus* and one is *Euthynnus alletteratus*).

Distribution.—*Sarda sarda* occurs along the tropical and temperate coasts of the Atlantic

TABLE 21.–Comparison of morphometric characters in populations of *Sarda sarda* from North America, the Mediterranean Sea, and the Gulf of Guinea. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

	North America			Mediterranean			Gulf of Guinea		
Character	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*	Range	$\bar{x}$	*N*
Fork length (mm)	228-500	362	17	260-504	376	7	305-443	379	9
Fork length									
Snout — A	646-690	668	13	641-685	660	7	648-666	657	9
Snout — 2D	570-594	582	13	563-593	579	7	570-585	578	9
Snout — 1D	262-275	270	13	257-284	266	7	262-306	298	9
Snout — P_2	286-304	296	12	280-302	288	6	267-284	275	9
Snout — P_1	259-284	269	13	255-274	263	7	253-273	267	9
P_1 — P_2	105-118	111	12	94-114	104	7	107-118	111	8
Head length	256-272	264	13	251-268	259	7	253-278	271	9
Max. body depth	200-224	214	8	197-216	205	5	195-228	217	8
Max. body width	96-171	135	10	115-148	131	6			
P_1 length	96-138	115	13	105-127	116	6	120-136	130	9
P_2 length	73- 84	79	12	76- 86	82	7	77- 87	83	9
P_2 insertion - vent	348-403	366	13	356-379	370	7	341-388	357	9
P_2 tip - vent	269-302	282	12	269-297	285	7	252-293	266	9
Base 1D	291-330	311	13	301-323	311	7	298-323	311	9
Height 2D	68- 90	80	10	85-117	95	5	81- 99	91	9
Base 2D	85-113	96	13	93-112	104	5	92-112	107	9
Height anal	68- 98	77	11	68- 85	79	6	77- 91	85	9
Base anal	63- 86	73	13	69- 90	78	7	66- 89	80	9
Caudal spread	204-235	222	5	226-270	247	4	223-289	253	3
Snout (fleshy)	76-100	94	13	88- 98	93	7	88-101	96	9
Snout (bony)	78- 93	82	13	74- 83	78	7	75- 85	82	9
Maxilla length	131-141	136	13	127-136	131	7	125-145	138	9
Post orbital	130-142	136	11	126-136	132	7	133-144	138	9
Orbit (fleshy)	27- 40	32	17	27- 34	31	7	31- 36	34	9
Orbit (bony)	35- 64	57	13	53- 62	57	6	53- 64	60	9
Interorbital width	59- 73	64	13	59- 64	62	7	58- 65	63	9
Head length									
Snout (fleshy)	354-374	360	17	346-367	358	7	346-366	353	9
Snout (bony)	289-342	309	13	289-312	303	7	293-308	301	9
Maxilla	503-529	514	13	497-511	505	7	494-523	509	9
Post orbital	494-541	516	11	503-521	511	7	489-519	506	9
Orbit (fleshy)	100-149	121	17	104-133	118	7	116-132	122	9
Orbit (bony)	203-248	222	16	210-232	220	6	204-228	220	9
Interorbital width	216-275	242	13	231-245	238	7	212-245	231	9

Ocean, including the Gulf of Mexico and the Mediterranean and Black seas (Figure 70). Its usual northern limit in the western North Atlantic is Cape Ann, Mass. (Bigelow and Schroeder 1953), but there are records north to Casco Bay, Maine (Nichols and Breder 1927) and to several localities along the outer coast of Nova Scotia (from north to south): Cape Breton Island (McKenzie 1939); Halifax (Jones 1879); Lunenberg (McKenzie 1939); Shag Harbour (Mather and Gibbs 1957); and Pubnico (Vladykov 1935). It is common along the east coast of the United States but becomes uncommon around Miami (D. P. de Sylva, pers. commun.) and the Florida Keys (Schroeder 1924). Although Rivas (1951) stated that there were no records of *S. sarda* from the Gulf of Mexico or Caribbean Sea, there are now several such reports; northern Gulf of Mexico (Boschung 1966) off Pensacola, Fla. (USNM 30692; CAS IU 7825), Dauphin Island, Ala. and the Mississippi Delta (USNM 188420; UMML 7745); Texas (Baughman 1941; Pew, 1954; Hildebrand 1955; USNM 118644-6; CAS SU 18003); the middle of the Gulf (Klawe and Shimada 1959); and Campeche, Mexico (Hildebrand 1955; Springer and Bullis 1956). We have also examined a specimen that was collected by Poey and labelled "Cuba" (MCZ 17047). *Sarda sarda* is apparently absent from most of the Caribbean Sea but is recorded from Colombia (Dahl 1971) and Venezuela (Röhl 1942; Mago Leccia 1970), and we have examined a series of specimens from the Gulf of Cariaco, Venezuela, collected by the RV *Geronimo* in 1966. Fowler (1915) stated that several were seen in the fish market of Port-of-Spain, Trinidad but none were preserved. Published records and museum specimens become more common south of the Amazon: Rio de Janeiro (BMNH 1903.6.9.77, 1923.7.30.303); Santos (Mirando Ribeiro 1918); Rio Grande do Sul (Ihering 1897; MCZ 4739); Argentina from lat. 35° to 38°S (Pozzi and Bordale 1935);

Buenos Aires (Fowler 1926); and Mar del Plata, Argentina (Berg 1895; MACN 5151; MSNG 27472).

Sarda sarda extends further north and south in the eastern than in the western Atlantic, from near Oslo, Norway to Port Elizabeth, South Africa. In Scandinavia it has been taken in Oslo Fjord (Collett 1879a; five ZMO specimens, 425-600 mm FL) and along the Swedish and Danish coasts of the Kattegat (Smitt 1892; Jensen 1937; Lovén 1938; Jensen 1941; Otterstrøm 1943). There is one record from the Netherlands (Hubrecht 1879; Redeke 1941) and there are records from Scotland (Montrose on the east coast, Rae and Pirie 1968; Wigtown on the west coast, Rae and Pirie 1969) and from many counties in Ireland (Farran 1923; Went 1968, 1969, 1971; Wheeler and Blacker 1969, 1972). It is common throughout most of the Mediterranean (Belloc 1954) including the Adriatic Sea (Brünnich 1768; Ninni 1882; Šoljan 1963), Aegean Sea, Sea of Marmora, and the Black Sea (Pallas 1811; Athanassopoulos 1934; Nümann 1955; Demir 1963, 1964; Bănărescu 1964; Svetovidov 1964; MNHN A.6870; USNM 199648; BMNH 1864.4.25.13, 1888.2.3.53). There are records from the four major groups of islands off Europe and Africa: the Azores (Hilgendorf 1888; Collins 1954; USNM skeletons), Madeira (Lowe 1850; BMNH uncat.), Canaries (Valenciennes 1844; Steindachner 1865, 1868; Vinciguerra 1893), and Cape Verdes (Cuvier and Valenciennes 1831; Duméril 1858; Cadenat 1950; Postel 1950). Along the coast of North Africa, there are records from Spanish Morocco (Lozano Cabo 1970), Morocco (Dollfus 1955); Spanish West Africa (Mather and Day 1954); Port Étienne and d'Arguin Bank, Mauritania (Chabanaud and Monod 1927; De Groot and Nijssen 1971); Cape Verde, Sénégal (Rochebrune 1882; Pellegrin 1908; Cadenat 1937; Frade and Postel 1955). *Sarda sarda* is also present in the Gulf of Guinea from Sénégal to Ghana (Irvine 1947; BMNH 1939.7.12.31; Jensen 1967; 23 USNM specimens from the Guinean Trawling Survey; Williams 1968); along the coasts of Angola (Osorio 1890) and South-West Africa (Molteno 1948) through the "Cape Seas" (Barnard 1927) to the Cape of Good Hope (Smith 1949), Mosselbaai (Molteno 1948), and Port Elizabeth, South Africa (SAM uncat.), in the southwestern corner of the Indian Ocean.

Geographic Variation.—For purposes of comparison, *Sarda sarda* was divided into five populations: North America, South America (no vertebral counts available), northeast Atlantic (Scandinavia, Atlantic Europe, and the Azores), Mediterranean Sea (including the Black and Adriatic seas), and Gulf of Guinea (extending south to South Africa). Comparison of meristic characters shows that the two western Atlantic populations are similar to each other as are the Mediterranean and Gulf of Guinea populations. There are differences in a number of characters between combined eastern and combined western Atlantic populations, mostly correlated with higher vertebral counts in the eastern Atlantic. The small northeast Atlantic sample is similar to the other two eastern Atlantic populations but resembles the western Atlantic populations in some characters.

The North American population has 50-53 vertebrae, mode 51, $\bar{x}$ 51.1, compared to a range of 52-55, mode 53, $\bar{x}$ 53.3, for the Mediterranean-Gulf of Guinea (Table 9). Three specimens from the Azores have 51 vertebrae, thus resembling the western Atlantic population. Correlated with vertebral counts, there are fewer fin rays in the western Atlantic (Tables 10-12): dorsal spines modally 21 vs. 22; second dorsal rays modally 16 vs. 17; total second dorsal elements 24 vs. 25; anal rays modally 15 vs. 15 or 16; total anal elements modally 22 skewed toward 21 vs. 22 or 23 skewed toward 22. Independently, there are also fewer gill rakers (Table 7) in the western Atlantic (North America modally 17, $\bar{x}$ 17.6, South America modally 18, $\bar{x}$ 18.7) compared to the eastern Atlantic (Mediterranean and Gulf of Guinea, $\bar{x}$ 20.9)

Based on admittedly small samples, there seems to be a difference between western and eastern Atlantic specimens of *S. sarda* in the size of the caecal mass. Western Atlantic specimens have the caecal mass extending posteriorly for more than half the length of the body cavity in ventral view; eastern Atlantic specimens less than half this distance.

Study material was adequate to compare three areas morphometrically: western Atlantic, Mediterranean Sea, and Gulf of Guinea. There appear to be differences in three characters (Table 21). The western Atlantic population has a lower second dorsal fin (68-90 thousandths of fork length, $\bar{x}$ 80) and a smaller caudal spread (204-235, $\bar{x}$ 222) than do the two eastern Atlantic populations (85-117, $\bar{x}$ 95 and 81-99, $\bar{x}$ 91 for the second dorsal height of the Mediterranean and Gulf of Guinea populations, respectively; 226-270, $\bar{x}$ 247 and 223-289, $\bar{x}$ 253 for the caudal spread). In the snout-

pelvic fin origin distance, the western Atlantic and Mediterranean populations have a longer distance (286-304, $\bar{x}$ 296 and 280-302, $\bar{x}$ 288 respectively) than does the Gulf of Guinea population (267-284, $\bar{x}$ 275).

Of the three widespread species of *Sarda*, there is at least as much justification for recognition of subspecies in *S. sarda* as in *S. chiliensis*. However, there appears to be no available name for the western Atlantic population, the Azores specimens appear intermediate in some characters, and the differences are not great enough to warrant recognition of this population as a distinct subspecies at this time. Additional study is needed on this problem.

Gymnosarda Gill

Gymnosarda Gill 1862:125 (type-species *Thynnus unicolor* Rüppell 1838 by original designation).

Comparative Diagnosis.–The monotypic genus *Gymnosarda* differs from other bonitos in having a well-developed swim bladder, in lacking any intermuscular bones on the back of the skull, and in having more olfactory lamellae (48-56 vs. 21-39 in the other Sardini). It is the only bonito with 19 precaudal and 19 caudal vertebrae. *Gymnosarda* has a differently shaped head than do other bonitos (Tables 1, 22); the interorbital distance is much wider, the eyes are larger, the postorbital distance is shorter, and the distance between the origins of the pectoral and pelvic fins is much larger. The opercular bones are more elongate in *Gymnosarda* than in other bonitos.

Gymnosarda and *Sarda* share characters that distinguish them from *Orcynopsis* and *Cybiosarda*: the bony caudal peduncle keels are well developed, but each keel is divided into anterior and posterior portions on each vertebrae; the spleen is large and prominent in ventral view versus small and not visible in ventral view; the right and left lobes of the liver are both much longer than the middle lobe versus only the right lobe being greatly elongate.

The two genera also differ in several characters. *Gymnosarda* has a pair of glossohyal tooth plates which are absent in *Sarda*. *Gymnosarda* has a naked body; *Sarda* is covered with tiny scales behind the anterior corselet. *Gymnosarda* lacks the horizontal stripes characteristic of *Sarda*. The intestine makes a loop before reaching the anus in *Gymnosarda*; the intestine runs straight from the stomach to the anus in *Sarda*. In ventral view, the spleen is visible on the right side in *Gymnosarda*; it is centrally located in the posterior half of the body cavity in *Sarda*.

TABLE 22.–Morphometric characters of Pacific *Gymnosarda unicolor*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	*N*	Kapingamarangi specimens	
Fork length (mm)	240-1040	597	18	875	930
Fork length					
Snout — A	612-651	632	18	650	651
Snout — 2D	545-580	560	18	554	554
Snout — 1D	267-303	292	18	292	303
Snout — P_2	276-306	292	18	298	278
Snout — P_1	251-283	270	18	276	278
P_1 — P_2	123-154	139	16	151	154
Head length	251-275	267	18	297	271
Max. body depth	200-254	222	15	~231	~217
Max. body width	139-176	153	14	—	—
P_1 length	127-188	163	18	180	182
P_2 length	97-120	107	18	120	120
P_2 insertion - vent	321-358	320	18	348	349
P_2 tip - vent	219-251	233	17	—	—
Base 1D	234-284	265	18	258	234
Height 2D	76-121	105	15	120	121
Base 2D	64-102	77	18	73	75
Height anal	76-128	102	17	128	120
Base anal	56- 68	63	18	59	62
Caudal spread	272-344	318	12	328	344
Snout (fleshy)	104-118	109	18	108	108
Snout (bony)	96-106	100	18	98	97
Maxilla length	133-151	140	18	139	136
Post orbital	92-110	101	17	103	103
Orbit (fleshy)	41- 64	53	18	57	57
Orbit (bony)	63- 88	75	16	82	84
Interorbital width	88-110	96	18	104	110
Head length					
Snout (fleshy)	385-430	409	18	403	393
Snout (bony)	355-397	374	18	368	355
Maxilla length	496-550	526	18	524	496
Post orbital	360-409	380	17	388	375
Orbit (fleshy)	161-231	197	18	212	209
Orbit (bony)	232-320	281	16	307	307
Interorbital width	321-400	359	18	391	400

Remarks.–There has been a question as to the valid name for the species in this monotypic genus–*unicolor* Rüppell or *nuda* Günther. The problem arose when Günther placed both *Scomber unicolor* Geoffroy St. Hilaire 1817 and *Thynnus* (*Pelamis*) *unicolor* Rüppell 1838 in the genus *Pelamys* Cuvier 1831. This action made *P. unicolor* Rüppell a junior secondary homonym of *P. unicolor* Geoffroy St. Hilaire so Günther replaced the former name with *P. nuda* Günther. Gill (1862) eliminated the homonomy by describing new genera for both *unicolor* Geoffroy St. Hilaire (*Orcynopsis*) and *unicolor* Rüppell (*Gymnosarda*). We recognize *unicolor* Rüppell as the valid name for the type-species of *Gymnosarda*. Review of the following synonymy shows equal usage of the

names *unicolor* (22 references) and *nuda* (23 references) so there is no reason to favor either name on the grounds of stability.

Gymnosarda unicolor (Rüppell)
Dogtooth Tuna

Thynnus (*Pelamis*) *unicolor* Rüppell 1838:40-41 (original description; Jiddah, Red Sea; pl. 12, fig. 1).

Pelamys nuda Günther 1860:368 (replacement name for *Thynnus unicolor* Rüppell 1838 preoccupied in *Pelamys* by *Scomber unicolor* Geoffroy St. Hilaire 1817). Klunzinger 1871:443-444 (description; Koseir, Red Sea).

Gymnosarda unicolor. Gill 1862:125 (original description of *Gymnosarda*). Chabanaud 1925:198-200 (comparison with *Sarda* and *Orcynopsis*). Fraser-Brunner 1950:149-150 (description), fig. 16. Smith 1956:721 (Aldabra Island), 722 (photograph). Blanc and Postel 1958:370-371 (description, Réunion Island), fig. 1 (viscera), fig. 2 (excised liver). Jones and Silas 1961:380-381 (Port Blair, Andaman Islands; Minicoy Island, Laccadive Archipelago), fig. 7 (after Fraser-Brunner). Jones et al. 1960:136 (Port Blair, Andaman Islands). Postel et al. 1960:392-393 (description; Réunion Island). Collette and Gibbs 1963a:26 (relationships). Collette and Gibbs 1963b:29 (compiled). Gorbunova 1963:87-89, fig. 13, table 11 (19 larvae 8.0-14.0 mm, Indian Ocean). Silas 1963:877-899 (synonymy, description, range, anatomy, biology). Smith and Smith 1963:41 (Seychelles), pl. 31H. Baissac 1964:185-186 (Mascarene waters). Williams 1964:122-124 (Mafia Island, Tanganyika). Talbot 1965:469 (Tutia Reef, Tanganyika). Merrett and Thorp 1966:375 (St. Lazarus Bank, East Africa). Jonklaas 1967:1134 (Maldive Islands), pl. 1 (underwater photo). Jones 1969:26 (Laccadive Archipelago). Nagabhushanam and Chandrasekhara Rao 1972:299, 317, 321 (Laccadive Archipelago). Fukusho and Fujita 1972:32-33 (description, 27 juveniles; Tsushima Island, Korea Straits), fig. 1 (42.9 cm FL juvenile).

Gymnosarda nuda. Kishinouye 1923:426-428 (anatomy; Ryukyu and Ogasawara [Bonin] Islands). Chabanaud 1925:198-199 (comparison with *Sarda* and *Orcynopsis*). Jordan and Hubbs 1925:215 (description; Tokyo market). Fowler 1938:139-140 (description; Tahiti [ANSP 93818]). Marshall 1941:61-62 (first Australian record, Townsville, Queensland). Herre 1945:148 (several records from Philippine Islands). Coates 1950:22 (Barrier Reef), fig. Serventy 1950:19 (Cartier Island and Woodbine Bank, Timor Sea). Warfel 1950:11, 14 (description, Philippine Islands), 15 (fig. 9, lateral view of fish, gill arch, excised liver), 16 (fig. 10, distribution map). La Monte 1952:40 (description), pl. 12. Dung and Royce 1953:tables 93-96 (morphometric data for specimens from Japan, Marshall Islands, Caroline Islands, and Philippine Islands). Herre 1953:248-249 (Philippine records). Fourmanoir 1957:224 (Madagascar, Mauritius, and Comoro Islands), pl. 14, fig. B. Munro 1958b:264 (new records for the New Guinea region: Louisiade Archipelago, Solomon Islands, Woodlark Island, Laughlan Island, Carteret Island, New Ireland, New Britain, Admiralty Islands). Schultz 1960:416-417 (description; Marshall Islands [USNM 140980]). Ronquillo 1963:1723, 1725, 1738, 1739 (length-weight; Philippine Islands), 1732-1733 (gonad index). Marshall 1964:355-356 (description, N. Queensland, Australia), col. pl. 51, fig. 342. Marshall 1966:204, col. pl. 51, fig. 342. Munro 1967:203 (description; New Guinea), pl. 17 (fig. 344). Kami et al. 1968:123 (Guam). Lewis 1968:56 (copepod *Caligus pseudokalumai* described from Eniwetok specimen). Fourmanoir and Griessinger 1971:484 (Rangiroa, Tuamotus). Grant 1972:112 (description; Barrier Reef), col. pl. 17. Bablet 1972:62, 87 (Tuamotu Archipelago).

Misidentification.—*Sarda orientalis*. Smith and Pope 1907:464-465 (77-mm specimen from Urado, Japan [USNM 59638]).

Types.—*Thynnus* (*Pelamis*) *unicolor* Rüppell 1838:40-41, pl. 12, fig. 1. Holotype: SMF 2739; 473 mm FL stuffed specimen; Red Sea, Jiddah; 1834; E. Rüppell. Counts: dorsal fin rays XIII + 13 + VI, but there is probably one more spine concealed in the groove to make the count XIV + 13 + VI; anal fin rays 12 + VI; pectoral fin rays 26; gill rakers cannot be counted (if still present); upper jaw teeth 18; lower jaw teeth (left-right) 14-12.

Distribution.–*Gymnosarda unicolor* is a coral reef species of the tropical Indo-West Pacific (Figure 69). It was originally described by Rüppell (1838) from Jiddah in the Red Sea and was reported by Klunzinger (1871) from Koseir, also in the Red Sea. Western Indian Ocean records include: Tanzania (Mafia Island, Williams 1964; Tutia Reef, Talbot 1965; St. Lazarus Bank, Merrett and Thorp 1966); the Seychelles Islands (Smith and Smith 1963); Amirante Islands (USNM uncat.); Aldabra Island (Smith 1956); Madagascar, Mauritius, and the Comoro Islands (NMC 73-244; Fourmanoir 1957); Réunion Island (Blanc and Postel 1958; Postel et al. 1960) and Mascarene waters (Réunion, Mauritius, and Rodrigues; Baissac 1964). There are records from the Laccadive Archipelago (Jones and Silas 1961; Jones 1969; Nagabhushanam and Chandrasekhara Rao 1972), the Maldive Islands (Jonklaas 1967), Sri Lanka (Ceylon) (Sivasubramaniam 1970), and the Andaman Islands (Jones and Silas 1961; Jones et al. 1960). The only records from the Indonesian area appear to be from Cartier Island and Woodbine Reef in the Timor Sea (Serventy 1950). *Gymnosarda unicolor* is known from several localities in the Philippine Islands (Herre 1945, 1953; Warfel 1950; Dung and Royce 1953; Ronquillo 1963); the New Guinea region–Louisiade Archipelago, Solomon Islands, Woodlark Island, Laughlan Island, Carteret Island, New Ireland, New Britain, and the Admiralty Islands (Munro 1958b); and the northern part of Australia's Great Barrier Reef (Townsville, Marshall 1941; Coates 1950; Marshall 1964). (The record from off Scotland Island, New South Wales (Whitley 1964a) is based on a specimen (AMS IB. 4291) of *Scomberomorus*.) The northern limit of the range is the Sagami Sea (CAS SU 24080, 97 mm FL) and Urado, near Kochi, Shikoku, Japan (USNM 59638, 72 mm FL), the Ryukyu and Bonin islands south of Japan (Kishinouye 1923), and the Straits of Korea (Fukusho and Fujita 1972). To the southeast, there are records or specimens from Guam in the Mariana Islands (Kami et al. 1968), the Palau Islands (CAS GVF), the Carolines (Kapingamarangi and Ifalik, CAS GVF; Pikelot Island in the Truk Islands group, 5 uncataloged USNM specimens; Dung and Royce 1953; Marshalls (Dung and Royce 1953; Schultz 1960; USNM 140980); Gilberts (AMS IB. 5660); Society Islands (Tahiti–Fowler 1938; ANSP 93818); Marquesas Islands (SIO 59-282-43a); Rangiroa Atoll, Tuamotu Archipelago (Fourmanoir and Griessinger 1971; Bablet 1972); and Oeno Island in the Pitcairn Group (BPBM 16966).

Remarks.–Two large specimens from Kapingamarangi Atoll (CAS GVF, 930 and 875 mm FL) require special mention. They have a higher number of very small teeth on the upper (left side, right side 31-29+, 31-30) and lower jaws 22-22, 25-22) than other *Gymnosarda* (Tables 5, 6). Morphometrically, these two Kapingamarangi specimens have distinctly greater snout-anal origin, pectoral to pelvic origin, pelvic fin length, height of second dorsal, height of anal fin, and greater interorbital widths than 18 *Gymnosarda* (240-1,040 mm FL) from throughout the range. The specimens are not very well preserved, but we feel confident that the morphometric differences are real. The differences are not great enough to require the description of a new species, but we cannot fully account for the differences that exist. Additional material, over a wider size range, from Kapingamarangi will be necessary to solve this problem.

Allothunnus Serventy

Allothunnus Serventy 1948:132 (type-species: *Allothunnus fallai* Serventy 1948, by monotypy).

Comparative Diagnosis.–The monotypic genus *Allothunnus* differs from all other scombrids in its very high number of gill rakers. It is the most elongate species of bonito and so has the greatest distances between the snout and the origins of the dorsal and anal fins (Tables 1, 23). The snout and maxilla are shorter than in any other bonito.

Allothunnus differs from all other scombrid genera in having the prootics remarkably extended laterally as wings that frame the posterior margin of the orbit. A pair of dorsolateral processes extend from the parasphenoid up to the prootic wing. *Allothunnus* resembles the Thunnini and differs from all other bonitos in having a prootic pit. Only *Gymnosarda* has a trace of the prominent ridges present on the frontals of *Allothunnus*. The pineal foramen is large and oval in *Allothunnus*, elongate and slit-shaped in all other Sardini and Thunnini. The otoliths are more similar to those of *Sarda* than to those of other bonitos.

The liver has three subequal lobes like *Thunnus*; other bonitos have the right lobe or both right and

left lobes longer than the middle lobe. The nasal rosettes are also more similar to those of *Thunnus* than to those of other bonitos.

Allothunnus fallai Serventy

Allothunnus fallai Serventy 1948:132-135 (original description; Timaru, South Island, New Zealand), fig. 1 (photograph of holotype), fig. 2 (internal gill rakers), fig. 3 (ventral view of liver). Fraser-Brunner 1950:148 (description), fig. 13. Parrott 1958:30-31 (after Serventy). Moreland 1959:30 (New Zealand endemic). Talbot 1960:258-259 (description; Cape Peninsula, South Africa). Olsen 1962:95-96 (description; 4 specimens from southern Tasmania). Collette and Gibbs 1963a:26 (relationships). Collette and Gibbs 1963b:31 (compiled), pl. 9 (after Fraser-Brunner). Jones and Silas 1963:1795 (compiled). Jones and Silas 1964:43-44 (compiled), fig. 8 (after Serventy). Talbot 1964:191-192 (description; anatomy; relationships), pl. 1, fig. 1. Fitch and Craig 1964:199-201 (description; relationships based on otoliths; figs. 3, 5A; California). Whitley 1964a:227 (compiled). Whitley 1964b:48 (listed; Australia). Smith 1965:23 (description; 4 specimens off Walvis Bay, South West Africa), pl. 3, figs. A-B. Nakamura and Kikawa 1966:59-62 (comparison of vertebrae with other scombrids). Nakamura and Mori 1966:67-83 (anatomy, relationships, figs. 1-14; Tasman Sea). Watanabe et al. 1966:85-94 (description of larvae; 100 specimens, 3.2-10.5 mm TL; Indian and South Pacific oceans), figs. 1-5 (larvae 4.0-10.5 mm TL), fig. 6 (distribution map). Tominaga 1966:44-46 (description; specimens from Uruguay and Tasmania), fig. 1B (photo of 870-mm Tasmanian specimen), fig. 2B (first gill arch). Mori 1967a:105-111 (description of 36 larvae from South Atlantic Ocean), figs. 1, 2 (larvae 5.5-13.3 mm TL). Mori 1967b:113-120 (description of 40 juveniles, 96-290 mm FL from stomachs of tunas and marlins from South Pacific), fig. 1 (distribution map). Zharov 1967:220 (*Allothunnus* included in Sardidae). Fierstine and Walters 1968:12 (aspect ratio of caudal fin). Whitley 1968:72 (listed; New Zealand). Ueyanagi 1969:193 (fig. 16e, relationship between occurrence of larvae and ocean structure near New Caledonia). Magnuson 1973:350 (maximum size, no swim bladder, short pectoral fins). Mori 1972:29-31 (juveniles from istiophorid stomach contents; SE of Palau Islands and off South-West Africa), fig. 1 (219-mm juvenile). Warashina and Hisada 1972:51-75 (adults found south of lat. 38°S in the Atlantic, Indian, and Pacific oceans; larvae between lat. 20° and 30°S; juveniles between lat. 25° and 35°S; length-frequency data on 652 specimens 650-960 mm FL). Webb and Wolfe 1974:5-7 (230 tons taken with purse seines off eastern Tasmania, June 1974; fig.).

TABLE 23.–Morphometric characters of *Allothunnus fallai*. First set of numbers are measurements expressed as thousandths of fork length, second set as thousandths of head length.

Character	Range	$\bar{x}$	N
Fork length (mm)	642-787	734	6
Fork length			
Snout — A	654-688	676	6
Snout — 2D	607-654	628	6
Snout — 1D	291-315	306	6
Snout — P_2	274-294	284	6
Snout — P_1	257-285	269	6
P_1 — P_2	102-116	110	4
Head length	248-272	258	6
Max. body depth	199-239	223	6
Max. body width	159-172	164	4
P_1 length	119-142	129	6
P_2 length	69- 83	78	6
P_2 insertion - vent	356-382	371	6
P_2 tip - vent	276-306	293	6
Base 1D	305-341	319	6
Height 2D	88- 97	93	6
Base 2D	59- 88	72	6
Height anal	82- 98	90	6
Base anal	66- 77	72	6
Caudal spread	210-246	226	3
Snout (fleshy)	70- 79	75	6
Snout (bony)	60- 69	65	6
Maxilla length	91- 96	93	6
Post orbital	136-144	139	4
Orbit (fleshy)	40- 67	45	6
Orbit (bony)	61- 65	63	6
Interorbital width	29- 66	57	6
Head length			
Snout (fleshy)	283-301	292	6
Snout (bony)	242-263	252	6
Maxilla length	354-379	361	6
Post orbital	540-554	545	4
Orbit (fleshy)	153-246	175	6
Orbit (bony)	232-252	244	6
Interorbital width	108-255	224	6

Types.–*Allothunnus fallai* Serventy 1948:132-135. Holotype: Canterbury Museum; 616 mm FL female; New Zealand, South Island, Timaru; 17 July 1916. Two other specimens from the Canterbury Museum are mentioned in the original description and so may be considered paratypes: a cast of a specimen from Kaiapoi, north of Christchurch, dated 4 October 1911 and measuring 920 mm TL and a specimen, 840 mm FL, from Akaroa, Banks Peninsula, dated 4

February 1938. We have not examined any of these and report the counts of the holotype from Serventy's original description: dorsal fin rays XVII + 12 + VII; anal fin rays 14 + VII; pectoral fin rays 25; gill rakers (left-right) 25 + 48 = 73, 24 + 51 = 75.

Distribution.—*Allothunnus fallai* is found around the world in the Southern Ocean (Figure 69). It was originally described from the South Island of New Zealand in 1948, then reported from Cape Peninsula, South Africa, by Talbot (1960), South-West Africa by Smith (1965), and from Tasmania by Olsen (1962). Fitch and Craig (1964) reported the most unusual record, a 680-mm FL specimen from the Los Angeles-Long Beach harbor complex, the only adult specimen that had been taken north of lat. 35°S. Subsequent to this, Nakamura and Mori (1966) studied several specimens from the Tasman Sea and a series of Japanese authors (Watanabe et al. 1966; Mori 1967a, b; Ueyanagi 1969; Mori 1972) reported juveniles from the southern parts of the Atlantic, Indian, and Pacific oceans to complete our present knowledge of the range of the species. Another scombrid, *Gasterochisma melampus*, and probably also *Thunnus maccoyii*, has a similar distribution in the northern part of the South Ocean around the world.

Food.—One of the Tasmanian specimens reported on by Webb and Wolfe (1974) had its stomach filled with euphausiids. Edward Brinton (SIO) has kindly identified these as *Nyctiphanes australis*, a species endemic to eastern Australian and New Zealand neritic and slope waters.

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VELOCITY AND TRANSPORT OF THE ANTILLES CURRENT NORTHEAST OF THE BAHAMA ISLANDS

MERTON C. INGHAM[1]

ABSTRACT

Meridional geostrophic velocities and volume transports were computed from data collected on six occupations of Standard Section A-7 by U.S. Coast Guard cutters. The section extends offshore from Cape Canaveral, Fla., along lat. 28°35'N for about 520 nautical miles (960 km), but this study involved only that portion seaward of the 800-m isobath (situated at about long. 79° 30'W), a portion which would transect the Antilles Current just before it merges with the Gulf Stream. The velocity sections did not reveal a broad northward flowing Antilles Current in the surface layer as has been shown on many average current charts in the past. Instead, the sections revealed a generally sluggish (≤10 cm/s) surface flow, either northward or southward. Imbedded in the low speed surface flow were two bands of higher speed (10-40 cm/s), one northward and the other southward, usually located in the vicinity of the 1,000-fathom (1,830-m) isobath. Computed net transport for the sections ranged from 30.4×10^6 m^3/s northward to 6.4×10^6 m^3/s southward, with an average of 8.6×10^6 m^3/s northward, which is considerably less than customarily hypothesized in the past to provide for the observed downstream increase in Gulf Stream transport between the Straits of Florida and Cape Hatteras, N.C.

The position of the band of relatively rapid southward flow corresponded approximately with the position suggested by Kort for the southward flowing Antilles-Guiana Countercurrent. A comparison of temperature-salinity properties in the bands showed them to be identical with each other but different from Florida Current water, making it highly unlikely that the bands are manifestations of two continuous currents, the Antilles Current and Antilles-Guiana Countercurrent, from different source areas. The identical temperature-salinity properties of the bands indicate that they are manifestations of eddies or a countercurrent formed by recurving of an adjacent current; the former alternative appears more likely.

The importance of the Antilles Current as a means of transporting significant quantities of pelagic ichthyoplankton into the Gulf Stream system is doubtful. The current speeds and transports appear to be substantially less than hypothesized and highly variable. An alternate means of transport of ichthyoplankton in the surface layer which may be in operation is Ekman drift generated by local winds, yielding a flow which may not be reflected in the field of mass and geostrophic computations.

One of the objectives of the initial ichthyoplankton cruises of the MARMAP (Marine Resources Monitoring Assessment and Prediction) program of the National Marine Fisheries Service was to estimate the transport of eggs and larvae of pelagic fishes into the Gulf Stream system by the Antilles Current. Scientists in the program began gathering information and data from various sources in an attempt to characterize the Antilles Current and other currents in the area of interest, the western North Atlantic and northern Caribbean Sea. These attempts revealed that the portion of the Antilles Current east of the Bahama Islands and northward has been little investigated and is only sketchily described, even though frequently mentioned in general works and shown on charts of "average" or "permanent" surface currents. Descriptions based on ship-drift data (U.S. Naval Oceanographic Office 1965; Boisvert 1967) portray the surface current in this region as having a prevailing direction of flow toward the north-northwest with a modal speed of about 0.5 knot (25 cm/s), an average speed of about 0.7 knot (35 cm/s), and a directional persistence of 40-55% in most of the area, except immediately north of the Bahama Islands, where a pair of eddies are shown (Figure 1). The strongest currents were found in a narrow band 10-30 nautical miles (18-55 km) wide near the Bahama Banks.

The junction of the Antilles Current with the Gulf Stream generally has been thought to occur over about 8° of latitude south of Cape Hatteras, N.C., (about lat. 28°-36°N) with the current supposedly adding about 60×10^6 m^3/s to the transport of the Gulf Stream, approximately tripling its flow (Stommel 1965). Knauss (1969) concluded from direct and indirect measurements of Gulf Stream transport in the Florida Straits-Cape Hatteras area that there is a gradual, uniform addition of

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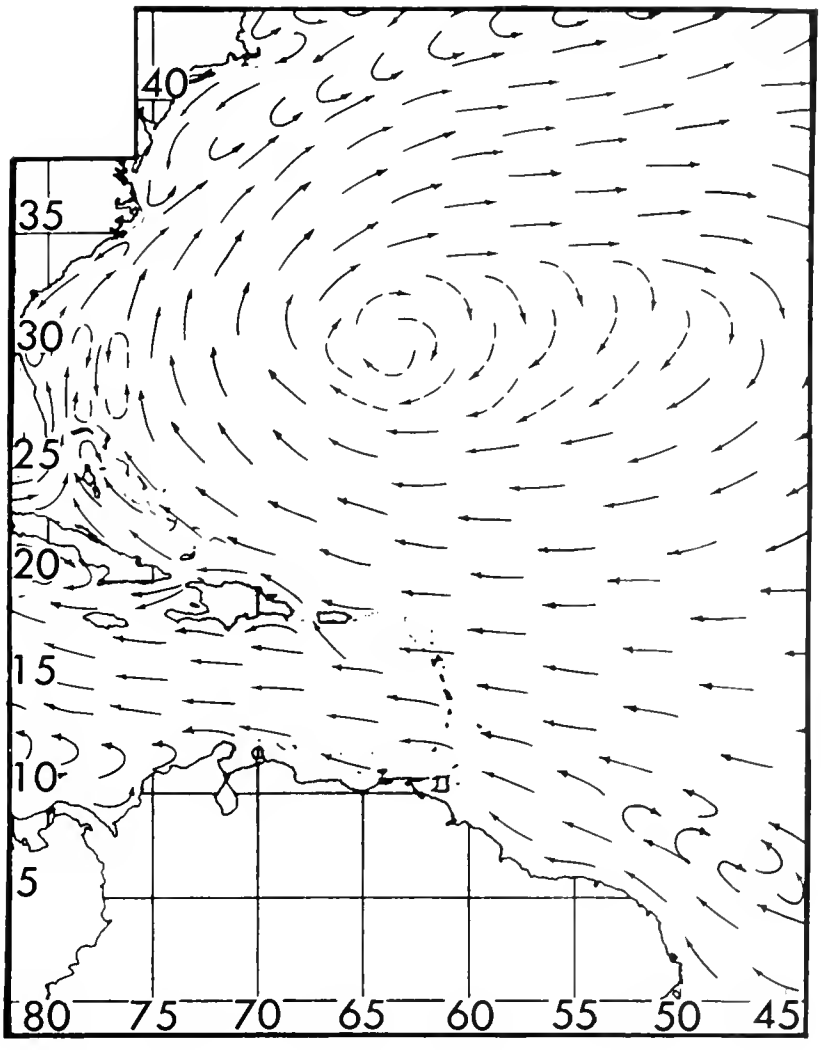

FIGURE 1.—Surface currents in the western North Atlantic and Caribbean during the winter months (from Oceanographic Atlas of the North Atlantic Ocean. Section I. Tides and currents. U.S. Nav. Oceanogr. Off. Publ. 700).

volume to the Gulf Stream at the rate of 7% per 100 km of its path leading to total values off Cape Hatteras of about 60×10^6 m^3/s. Knauss did not speculate on the source of the water added to the Gulf Stream. More recent direct measurements of the transport of the Gulf Stream off Cape Hatteras (Richardson and Knauss 1971) yielded an average value of 63×10^6 m^3/s which means that the addition to the Gulf Stream between the Florida Straits and Cape Hatteras, assumedly from the Antilles Current, amounts to about 30×10^6 m^3/s, approximately doubling its flow.

Some doubt has been cast on the existence of the hypothesized junction of the Antilles Current with the Gulf Stream and even on the existence of the current itself. A study by Day (1954) of drift bottle data and hydrographic data then available from the region northeast of the Bahama Islands revealed little evidence of a surface current with the characteristics attributed to the Antilles Current. Instead of surface flow to the northwest, he found that "... the surface waters in the region tend to move with a pronounced southerly component of direction rather than to the northwest, and that the Antilles Current appears at depth, varies markedly in its transport from one time to another, and should not be considered a permanent, clearly defined tributary to the Gulf Stream current." A hydrographic section occupied between Bermuda and Elbow Cay in the northern Bahamas in February 1933 showed a northwestward transport of 20.3×10^6 m^3/s in a 140-nautical mile band off Elbow Cay (lat. 26° 30'N) which Day identified as the Antilles Current.

Earlier, Iselin (1936) commented on this same section of stations, pointing out that: 1) the temperature field was nearly horizontal except near the Bahamas (within 40 nautical miles) where it indicated southward flow in the upper 400 m and northward flow beneath that; 2) the temperature observations showed no evidence of a "... broad or powerful Antilles Current, readily distinguishable from the general westerly movement continuing from the Northern Equatorial Current . . ."; 3) salinity observations agreed with the thermal trends and afforded little further evidence for the Antilles Current; and 4) at other times of the year, when the trade winds are stronger, the Antilles Current may be better developed.

Day (1954) also points out that a dynamic

topography based on a grid of stations occupied northeast of the Bahama Islands in April 1947 showed no general manifestations of the Antilles Current in the upper 150 m, showing southeastward flow instead. In a 330-nautical mile (610-km) section from this grid off Great Abaco Island (about lat. 27° to 28°N), a southeastward flow of 2.8×10^6 m^3/s was found in the upper 250 m, and a weak northwestward flow of 0.7×10^6 m^3/s was found in the 250- to 1,000-m layer, yielding a net transport through the section of 2.1×10^6 m^3/s southeastward.

A similar conclusion can be drawn concerning a much earlier investigation. Although Bigelow (1917), in his pioneer analysis of the *Bache* data, regarded the northward extension of warm water in the surface layer east and north of the Bahama Islands to be an expression of the Antilles Current, his pertinent vertical section of temperature just north of the Bahamas collected in March 1914 doesn't support that contention. The slope of the temperature isopleths northeast of the Bahama Islands indicated the presence of a southward flowing surface current in the upper 200 m or so, with a northward current at greater depth. Wüst (1924) computed geostrophic current speeds and volume transports from the *Bache* data including the transect of eight stations, from Jupiter Inlet to the Sargasso Sea (SW-NE) crossing just north of the Bahamas. He found an 80-km band of northwestward flow, which he called the Antilles Current, contiguous with southeastward flowing countercurrents on both sides. The transport of the Antilles Current he computed, 12.0×10^6 m^3/s, was approximately balanced by the transport of the two countercurrents, 12.4×10^6 m^3/s, yielding a net transport through the portion of the section seaward of the Gulf Stream (depths>800-900 m) of 0.4×10^6 m^3/s to the southeast.

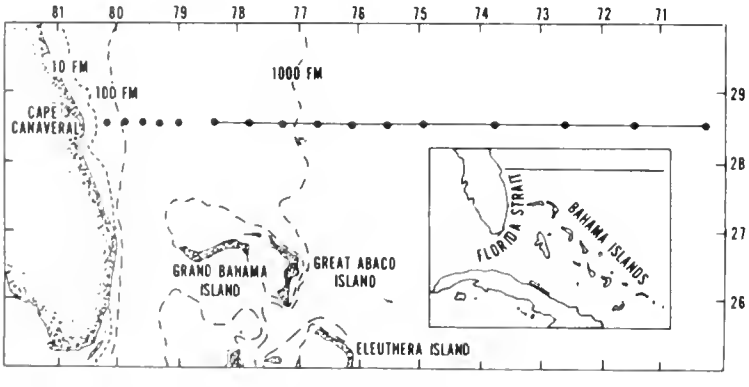

FIGURE 2.—Location of stations occupied by U.S. Coast Guard cutters along Standard Section A-7. The stations connected by the solid line are those generally used in this study.

During 1967-72, vessels of the U.S. Coast Guard made nine occupations of Standard Section A-7, each consisting of 16 oceanographic stations along 28°35′N from near Cape Canaveral at long. 80°10′W to a point about 520 nautical miles (960 km) offshore at long. 70° 15′W (Figure 2). Temperature and salinity data were collected on each station from casts of Nansen bottles located at or near NODC (U.S. National Oceanographic Data Center) standard depths or from lowerings of STD (Salinity Temperature Depth) sensors calibrated against data collected by Nansen bottles and reversing thermometers. Contoured profiles of temperature, salinity, and density are to be published along with lists of the data in the Coast Guard Oceanographic Report series (Robe in press). This section transects the Antilles Current where it is supposed to begin merging with the Gulf Stream, thus providing a portrayal of its potential contribution to the Gulf Stream system. Unfortunately, the occupations are not distributed uniformly throughout the seasons; five are in winter, two in fall, and two in summer, so seasonal variations cannot be discerned from the data.

Geostrophic velocities were computed from the temperature and salinity data utilizing a standard computer program employed by the Coast Guard Oceanographic Unit (Hislop[2]). The velocities were computed relative to the 1,000-decibar surface which was consistently reasonably level, as indicated by the small variation of density at 1,000 m (mean σ_t = 27.547, standard deviation = 0.098, sample size = 52). No attempt was made to carry the computation into water shallower than about 800 m because of the considerable errors introduced by extrapolation of water properties into the bottom and by close approach to the Gulf Stream.

Vertical sections of geostrophic velocity were hand drawn from lists of the computed values by assigning the values to midpoints between stations at middepths between depths of temperature and salinity observations. Interpolations necessary for contouring were based on an assumption of linear variation in properties horizontally and vertically between data points. This procedure was followed for six of the nine occupations of Standard Section A-7. Three occupations were rejected because they contained too many short casts in critical areas.

[2]Hislop, A. S. 1973. Coast Guard Oceanographic Unit DDP-516 programs. Oceanogr. Unit Tech. Rep. 73-2, p. 16-17. Unpubl. manuscr.

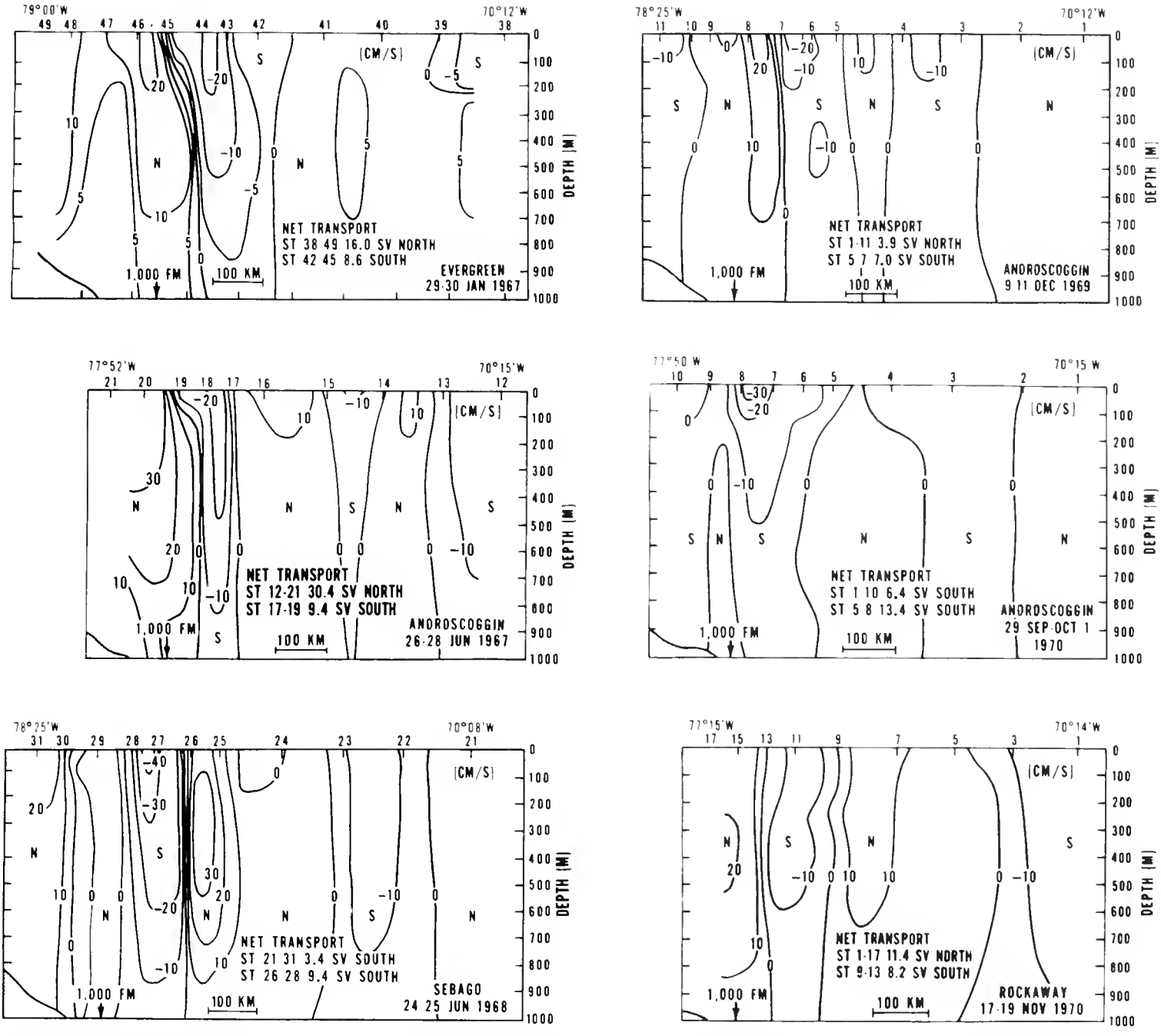

FIGURE 3.—Vertical distributions of meridional geostrophic velocity (cm/s) through Standard Section A-7 computed relative to the 1,000-decibar surface. Net transport values given in Sverdrups (1 SV = 10^6 m^3/s). Station numbers are arrayed along the upper horizontal boundary. Positive velocities are northward.

The vertical sections of geostrophic velocity (Figure 3) revealed a fairly consistent pattern of alternate bands of weak ($\leq$10 cm/s) northward and southward flow in the offshore half of the transect (seaward 400-500 km). West of this, a narrow band of stronger (10-40 cm/s) northward current was found in five of the sections, located generally just seaward of the 1,000-fathom isobath, about where the band of stronger northward Antilles Current was shown by Boisvert (1967). However, a band of southward flow of about the same speed was found nearby in each of the transects. Net transport through the section was northward in four of the occupations and southward in two, ranging from 3.9 to 30.4×10^6 m^3/s northward and 3.4 to 6.4×10^6 m^3/s southward. The mean net transport for the six sections was 8.6×10^6 m^3/s northward. In five of the sections, the northward transport values fall far short of the 30×10^6 m^3/s or more which the Antilles Current is supposed to add to the Gulf Stream, indicating that sources other than the Antilles Current must contribute to the observed increase.

Although it is difficult to make a direct comparison with Kort's findings (Kort 1972), because of the small size of his charts, paucity of data portrayed, and the fact that all of his data were collected south of lat. 28° 35'N, the locations of the

bands of relatively strong southward current corresponded reasonably well with the location of the southward flowing Antilles-Guiana Countercurrent that he hypothesized (Figure 4). Estimates of transport in the major southward band in each of the Coast Guard sections varied from 7.0 to 13.4×10^6 m^3/s, with an average of 9.3×10^6 m^3/s, which is only about one-third of the southward transport Kort (1972) reported for the Antilles-Guiana Countercurrent. However, Kort's value, computed for the transect near the coast of South America at about lat. 8°N, was based on data throughout the entire water column, not just the upper 1,000 m.

Kort's discussion includes some speculation concerning the source of his hypothesized Antilles-Guiana Countercurrent as follows: "One may suppose that a branch of the Florida or North Tradewind Currents is a source of the Antilles-Guiana Countercurrent. On the other hand, the studies made by Swallow and Worthington (1961) in the Gulf Stream in 1961 enable one to consider that the Antilles-Guiana Countercurrent can be traced far to the north flowing as a southward countercurrent on the oceanward side of the Gulf Stream." His portrayal of the general current pattern (Figure 4), however, shows recurving of the Florida Current, "North Tradewind Current,"

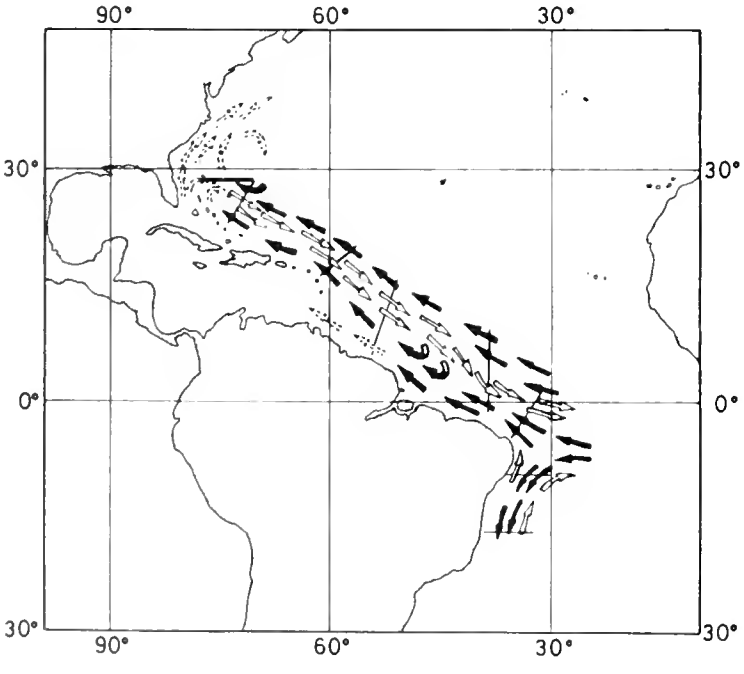

FIGURE 4.—Location of hypothesized Antilles-Guiana Countercurrent (open arrows) according to Kort (1972). Solid lines crossing the arrow field indicate locations of oceanographic transects. The northernmost, broad line represents the portion of the U.S. Coast Guard Standard Section used in this study; the others are sections cited by Kort.

and possibly the Antilles Current, as sources of the countercurrent.

If the bands of southward flowing water found in the Coast Guard transects are manifestations of the Antilles-Guiana Countercurrent and if, as Kort suggested, the source of the hypothesized Antilles-Guiana Countercurrent is (1) the recurving of the Florida Current, (2) the recurving of the North Tradewind Current, or (3) a countercurrent seaward of the Gulf Stream, then the properties of the water masses in the Antilles Current (northward band) and Antilles-Guiana Countercurrent (southward band) should be different. A plot of observed temperature and salinity values (Figure 5) from the bands of northward and southward flowing water detected in the Coast Guard transects shows that the bands have identical temperature-salinity (T-S) characteristics, implying that none of the three sources suggested is valid. Further, the comparison of the T-S characteristics of the southward band with those of the Florida Current (Figure 5) shows them to be significantly different, substantiating the contention that the recurving of the Florida Current is not a source for southward flowing water.

The identical T-S properties of the water in the southward and northward flowing bands leads to the conclusion that one flow is formed by a recurving of the other. Such recurving would lead to the formation of either a countercurrent, such as the hypothetical Antilles-Guiana Countercurrent, or an eddy. On the basis of the Coast Guard transect data it is impossible to determine which feature was present, but the direct measurement of large scale eddies farther south in the Antilles Current performed by satellite tracking of drogue buoys (Hansen[3]) suggests that eddies are more likely. The nearly constant position of the bands of northward and southward flow (eddies) in the transects would suggest that they are formed as a consequence of interaction of the Antilles Current with the Bahama Islands and surrounding banks.

The significance of these findings in relation to the distribution of ichthyoplankton in the area of the northern Antilles Current is difficult to state positively. However, it is clear that eggs and larvae in the upper 200 m in this area cannot be

[3]Hansen, D. V. Mesoscale motions in the Sargasso Sea: A result from the EOLE Complementary Program. Presented to the 54th meeting of the American Geophysical Union, April 18, 1973.

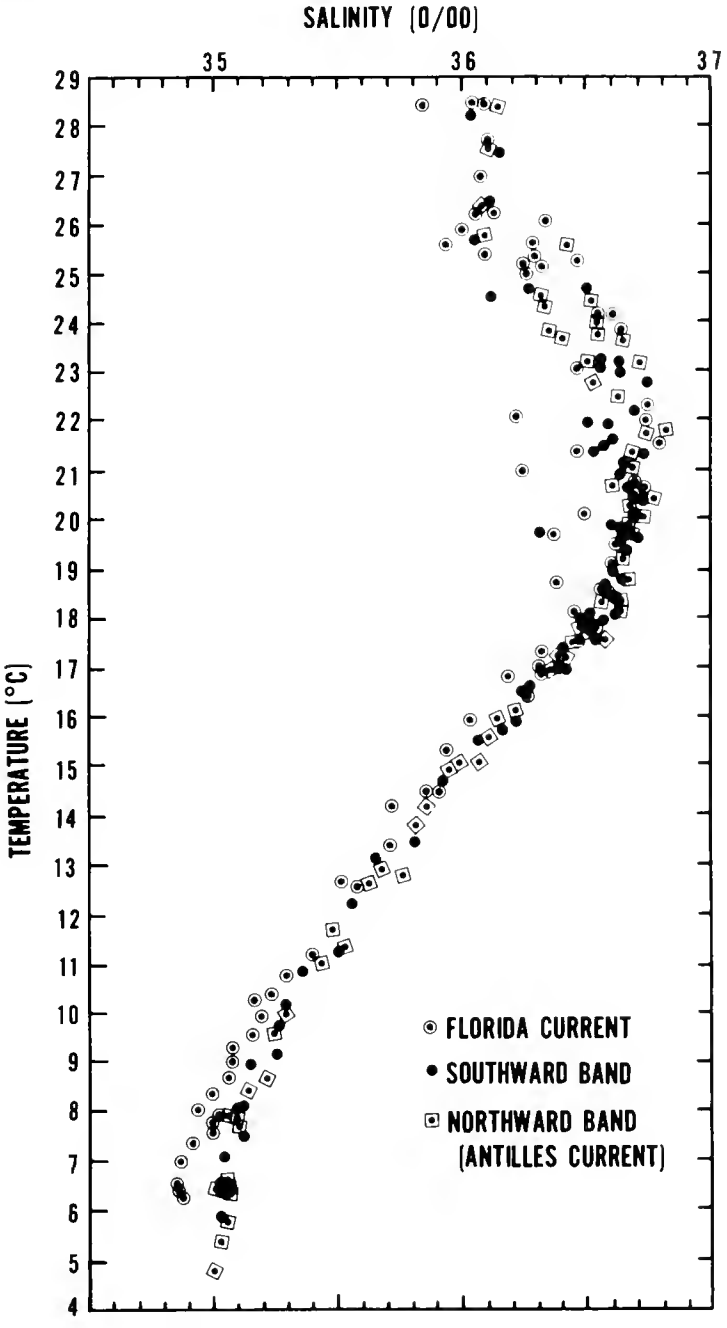

FIGURE 5.—Observed temperature (°C) - salinity (°/oo) points in the northward and southward bands and the Florida Current from six occupations of Standard Section A-7.

assumed to be moving steadily toward the northwest along the path traditionally assigned to the Antilles Current. Planktonic organisms located in water just seaward of the continental shelf at this latitude (28.5°N) are likely to have a northward compoent of velocity of about 10-30 cm/s, while those in deeper water 100-200 km farther offshore are likely to have a southward component of about the same magnitude. Seaward of that, plankton are likely to move either northward or southward at relatively slow speeds, in the range of 5-10 cm/s. If the higher speeds in the northward and southward bands are manifestations of a quasi-permanent eddy or transient eddies passing through, the net northward transport of plankton would be small, even in the area of higher current speeds near the continental shelf. Instead, planktonic organisms may be caught up in eddies or slowly moving water for long periods of time. Since the waters east of the northern Bahama Islands contain a relatively small plankton biomass and are thought to yield low rates of primary and secondary production, pelagic fish larvae held in the area for an extended period of time would have little likelihood of growth and survival.

A clearer resolution of quasi steady-state currents should be realized when analysis of data and geostrophic computations are complete for two MARMAP cruises (July-August 1972 and January-March 1973), which included the area east of the Bahama Islands. However, the transport of planktonic organisms in the surface layer may be governed by local wind-driven currents which may not be manifested as geostrophic currents computed from the density field. Average monthly wind roses (U.S. Naval Oceanographic Office 1963) for the area off the northern Bahamas shows that the winds from the east or northeast occur with greater frequency than those from any other quadrant every month, except June, July, and August, when winds from the south and southeast are more frequent. Such easterly and northeasterly winds would yield northward and northwestward Ekman (wind-driven) transports in the surface layer coinciding with the direction assumed for the Antilles Current. The net Ekman transport in the surface layer depends on the frequency distribution of wind direction and speed during the time period of interest, the subject of further research.

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THE DISTRIBUTION OF MYCTOPHID FISHES ACROSS THE CENTRAL EQUATORIAL PACIFIC

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ABSTRACT

Analysis of myctophid fishes collected in the upper 50-75 m at night along long. 145°W between lat. 12°N and 3°30′S indicated three faunal groups. Warmwater species ocurred across the entire transect and were most abundant at or just north of the equator. A second group of species occurred only in the North Equatorial Current or the Counter Current, but most are known to be more widely distributed. A third group occurred only at or just north of the equator; all are apparently found within a small latitudinal range between about long. 130° and 170°W. Certain species which are abundant in the central water mass were absent from the present samples. The faunal change within the equatorial water mass is likely a response to the increased primary production and food supply resulting from upwelling near the equator and northward transport of enriched surface waters. Some of the faunal changes observed appear to be replacements of one species by a congener or morphologically similar species.

The geographic ranges of oceanic organisms frequently conform with the boundaries of the major water masses (Johnson and Brinton 1963). The water masses are, however, large-scale, subsurface features defined by the temperature-salinity profiles of the deeper water (Sverdrup et al. 1942). In the surface layers of a given water mass there are variations in temperature and salinity as well as in other biologically relevant factors. Thus it is not surprising that, within major water masses, subpatterns of abundance and distribution have been reported for species which might likely respond to such variations in the upper layers. There are numerous reports of subpatterns in epipelagic zooplankton, e.g., Fager and McGowan (1963) and McGowan (1971); and Ebeling (1962) and Backus et al. (1969) have noted similar changes within water masses for mesopelagic fishes. Backus et al. related these to shallow thermal fronts, and Ebeling suggested that, where species' ranges deviated from water-mass boundaries, they were related to variation in primary productivity in the surface layers.

Within the Pacific equatorial water mass, major and presumably biologically relevant changes are observed in the upper layers. Grandperrin and Rivaton (1966), studying the mesopelagic fishes along the equator, found four longitudinal faunal zones which appeared related to the depth of the Cromwell Current or Equatorial Undercurrent, variations in primary productivity, and concentrations of dissolved oxygen and nutrients in the upper layers. Latitudinally, one encounters four separate current regimes in the upper layers (Cromwell 1951) with associated changes in thermocline depths. Marked changes in primary productivity (Koblentz-Mishke et al. 1970), zooplankton volume (King and Hida 1957), and tuna abundance (Murphy and Shomura 1972) also occur across the water mass.

This study considers the distribution and abundance of myctophid fishes collected by shallow night trawl tows across a latitudinal transect of the Pacific equatorial water mass. It was expected that any patterns observed might be related to available data on differences in surface layer features.

MATERIALS AND METHODS

Most data were collected during cruise 43 of the U.S. Fish and Wildlife Service RV *Townsend Cromwell* (29 April-11 June 1969). Pelagic trawl collections were made along long. 145°W at five latitudes: approximately 12°N, 7°30′N, 3°30′N, 0°, and 3°30′S. Five tows were made with a modified Cobb pelagic trawl (CT) described by Higgins

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(1970) at each latitude except lat. 3°30'S (four tows). Towing speed was about 2 knots (ca. 1 m/s). All tows were made at night; the trawl was at depth for about 6 h each tow (2000-0200 h). Depths of tows were estimated from amount of wire out, wire angle, and depth determinations made on later cruises with a time-depth recorder. Two depth zones were sampled—20-30 m and 50-75 m. These will be referred to as "shallow" and "deep" tows, respectively. Depth of tow was alternated nightly except at the equator where all tows were deep. Station numbers, exact positions, depths, and dates are given in Table 1.

TABLE 1.—Station numbers, positions, towing depths, and dates of mid-water trawl collections taken May-June 1969 on cruise 43 of the RV *Townsend Cromwell*.

Station number	Position		Depth (m)	Date
	Lat.	Long.		
8	12°04' N,	144°54' W	20-30	7 May
10	12°03' N,	144°55' W	50-75	8 May
12	12°11' N,	145°11' W	20-30	9 May
14	11°56' N,	144°54' W	50-75	10 May
16	11°58' N,	144°57' W	20-30	11 May
22	07°41' N,	145°01' W	50-75	13 May
24	07°27' N,	145°05' W	20-30	14 May
26	07°33' N,	144°50' W	50-75	15 May
28	07°33' N,	144°48' W	20-30	16 May
30	07°19' N,	145°09' W	50-75	17 May
36	03°29' N,	145°03' W	20-30	19 May
38	03°30' N,	145°06' W	50-75	20 May
40	03°31' N,	145°00' W	20-30	21 May
42	03°32' N,	144°59' W	50-75	22 May
44	03°40' N,	144°54' W	20-30	23 May
46	00°01' N,	144°50' W	50-75	25 May
48	00°04' N,	145°07' W	50-75	26 May
50	00°03' N,	145°05' W	50-75	27 May
52	00°01' N,	145°03' W	50-75	28 May
54	00°04' N,	144°59' W	50-75	29 May
55	02°59' S,	144°53' W	20-30	30 May
57	03°31' S,	145°11' W	50-75	31 May
59	03°34' S,	145°00' W	20-30	1 June
61	03°35' S,	145°11' W	50-75	2 June

Except for very large samples, the entire collection was preserved and counted. When total volume of the sample exceeded ca. 4 gallons (ca. 15 liters), 1-gallon (ca. 4 liters) subsamples were preserved, and counts were adjusted according to the original total volume. Specimens were identified primarily from Nafpaktitis (1968), Nafpaktitis and Nafpaktitis (1969), and an unpublished manuscript kindly provided by R. L. Wisner.[3]

During cruise 43, bathythermograph casts to 300 m were made at approximately 50-km intervals between lat. 14° and 3°N and at approximately 16-km intervals between lat. 3°N and 3°S. Salinity-temperature-depth casts to 500 m were made every degree from lat. 14° to 3°N and every 32 km from lat. 3°N to 3°S.

We have also counted the myctophids from 12 tows with a 10-foot (3 m) Isaacs-Kidd mid-water trawl (IK) taken 5-11 February 1970 at lat. 3°30'N, long. 145°W during cruise 47 of the *Townsend Cromwell*. These tows were all taken at night. Towing depths were 50-500 m; each tow spent about 2 h at depth (Table 2). The data from these tows along with data on vertical distribution of myctophids near Hawaii, somewhat north and west of the sampling area (Clarke 1973), allow us to estimate whether the absence of certain species from Cobb trawl tows in some zones was due to the species' simply occurring deeper than the Cobb trawl sampled.

TABLE 2.—Station numbers, towing depths, and dates of mid-water trawl collections taken near lat. 3°30'N, long. 145°W, February 1970 on cruise 47 of the RV *Townsend Cromwell*.

Station number	Depth (m)	Date
48	50	5 Feb.
49	50	5 Feb.
52	450	6 Feb.
57	200	7 Feb.
58	100	7 Feb.
60	500	7 Feb.
61	300	8 Feb.
67	300	9 Feb.
68	100	10 Feb.
69	200	10 Feb.
76	450	10 Feb.
78	500	11 Feb.

RESULTS AND DISCUSSION

The slope of the isotherms on the temperature profile of the transect (Figure 1) indicate the locations of the major currents of the area. The North Equatorial Current (NEC) extended to about lat. 9°N, the Equatorial Counter Current (ECC) from about lat. 4° to 9°N, and the South Equatorial Current (SEC) southward from about lat. 4°N. The Cromwell Current or Equatorial Undercurrent (EUC) was centered about on the equator. Thus the lat. 12°N samples were taken within the NEC, the lat. 7°30'N samples just south of the boundary between the NEC and the ECC, and the other samples in the SEC, the lat 0° samples actually being in the upper layers of the EUC.

A total of 32 species of myctophids were taken by the CT collections. The catches per tow are given in Table 3. Failure to catch a given species at

[3]Wisner, R. L. Annotated and illustrated key to the identification of fishes of the family Myctophidae of the eastern Pacific Ocean, eastward of 160° West Longitude. Unpubl. manuscr., Scripps Institution of Oceanography, La Jolla, CA 92037.

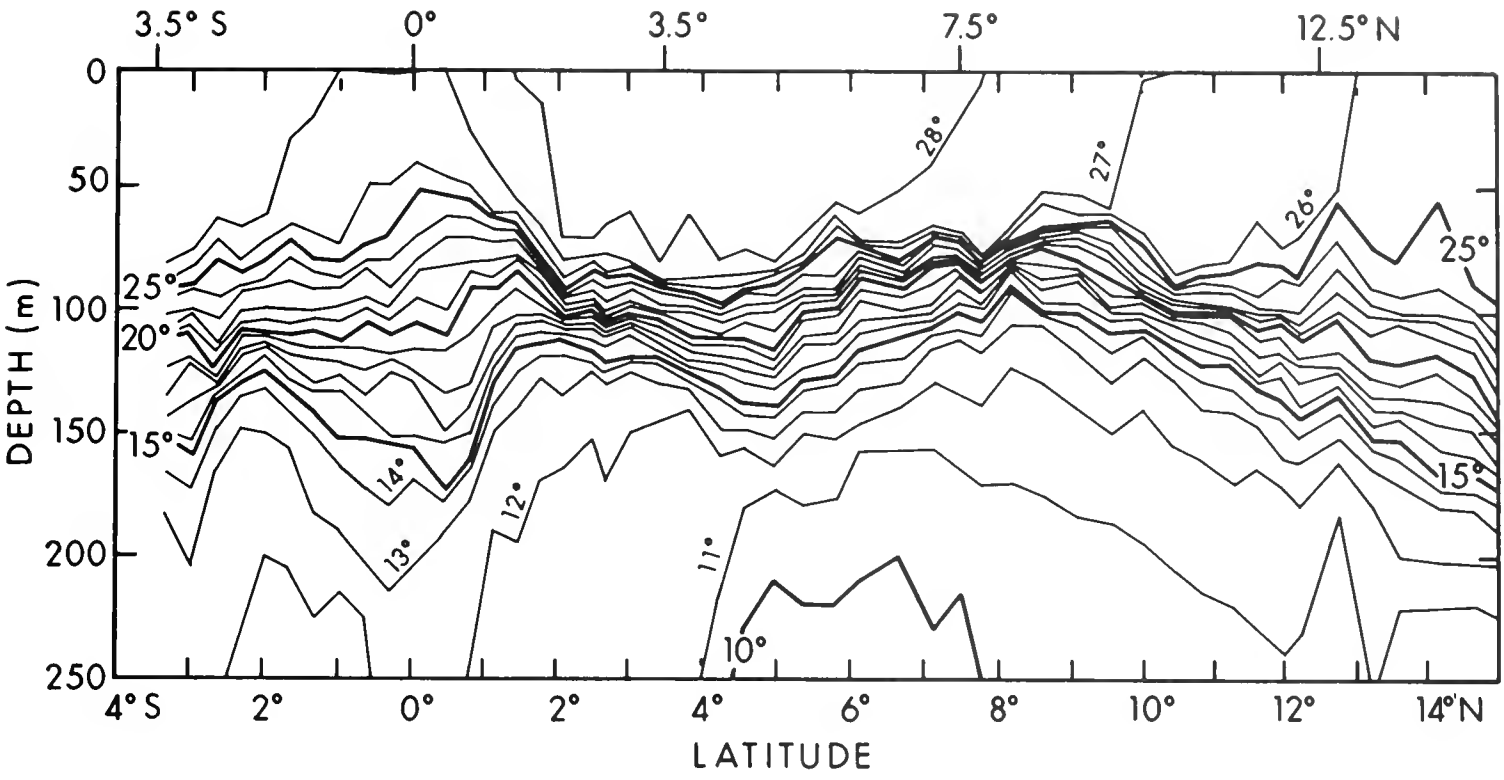

FIGURE 1.–Temperature (in degrees Celsius) profile along long. 145°W. (Compiled by R. A. Barkley from data collected on cruise 43 of the RV *Townsend Cromwell*.)

all stations at a given latitude does not, of course, necessarily mean the species was not present. It may have been present at low abundance and missed by the collections or may have occurred at depths greater than 75 m. With respect to the first possibility, we have ignored zero values in a few cases below, e.g., for very rare species and for the data from lat. 3°30′S where total catches were so much lower than elsewhere that it is likely some fraction of the total species present were not caught. With respect to the second possible source of error, we exclude from further consideration six species for which the upper limit of the depth range is close to the depth of the deep CT tows. Based on vertical distribution data from near Hawaii (Clarke 1973), only slight changes in the depth ranges of *Diaphus brachycephalus*, *Notolychnus valdiviae*, and *Lampanyctus steinbecki* would determine presence or absence in the CT collections. The IK data from lat. 3°30′N (Table 4) indicates that the same may be true for *D. jenseni*, *D. longleyi*, and *D. splendidus*. In the absence of data to the contrary and in some cases with reasonable evidence (see below), we assume that the remaining 26 species have shallow nighttime depth ranges wherever they occur in any abundance and that zero catches were not the result of changes in depth ranges with latitude.

In the presentation below, we attempt to relate patterns of distribution in the study area to other data on the species. Unfortunately, we have felt it necessary to disregard data from certain earlier studies where species identifications are doubtful. We have relied heavily on data from recent studies by Clarke (1973) near Hawaii, by M. A. Barnett (pers. commun.) near the center of the eastern central Pacific gyre (ca. lat. 29°N, long. 155°W), and by Ahlstrom (1971, 1972) in the eastern equatorial Pacific. For convenience, these will not be cited formally each time; unless otherwise cited, "near Hawaii," "gyre center," and "eastern equatorial," respectively, refer to the above three studies.

Eight species occurred across the entire sampling area. These were: *Hygophum proximum*, *Diogenichthys atlanticus*, *Myctophum aurolaternatum*, *M. spinosum*, *Symbolophorus evermanni*, *Diaphus fragilis*, *Triphoturus nigrescens*, and *Ceratoscopelus warmingi*. Other records of these species and of *M. nitidulum* and *Bolinichthys longipes*, which were taken at all latitudes except 3°30′S, indicate that all 10 occur widely throughout central water masses of the Indo-Pacific and, in most cases, the world (Bekker 1965; Nafpaktitis 1968; Nafpaktitis and Nafpaktitis 1969; Gibbs et al. 1971; Wisner footnote 3). All but *M. aurolaternatum* are taken consistently near Hawaii and all have been taken at the gyre center.

TABLE 3.–Species of myctophids and number taken per tow for stations given in Table 1. Stations are grouped by latitude and by depth (Shallow = 20-30 m, Deep = 50-75 m). Species are grouped in roughly the order considered in the text.

Species	Lat. 12°N					Lat 7°30'N					Lat. 3°30'N					Lat. 0°					Lat. 3 30'S			
	Shallow			Deep		Shallow		Deep			Shallow			Deep		Deep					Shallow		Deep	
	Stn. 8	12	16	10	14	24	28	22	26	30	36	40	44	38	42	46	48	50	52	54	55	59	57	61
Diaphus brachycephalus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	21	2	1
Diaphus jenseni	—	—	—	—	—	—	—	—	—	—	—	—	—	53	46	7	5	11	4	60	—	—	—	—
Diaphus longleyi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—
Diaphus splendidus	—	—	—	—	—	—	—	—	1	106	—	—	11	—	—	—	—	—	—	—	—	—	—	—
Notolychnus valdiviae	—	—	—	—	—	—	—	—	—	—	—	—	—	4	2	312	4	—	12	144	—	—	—	13
Lampanycytus steinbecki	—	—	—	—	20	—	—	—	—	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hygophum proximum	8	—	3	170	30	111	51	206	274	98	17	58	52	35	26	91	40	176	64	196	55	117	175	157
Diogenichthys atlanticus	—	—	—	9	1	—	—	5	7	12	1	—	14	60	52	26	4	22	12	32	—	2	27	19
Myctophum aurolaternatum	4	1	1	1	1	3	1	10	18	14	8	5	8	20	16	12	14	20	6	8	1	1	0	0
Myctophum spinosum	1	—	—	—	—	12	1	14	4	10	4	24	6	3	5	5	7	55	48	20	—	1	—	—
Symbolophorus evermanni	1,491	334	270	62	75	446	745	514	359	927	92	141	161	220	92	1,216	819	968	1,984	1,244	43	4	75	62
Diaphus fragilis	—	—	—	—	1	—	—	15	66	259	14	—	—	—	90	13	81	99	20	168	—	—	40	54
Triphoturus nigrescens	—	2	—	—	—	7	7	1	9	18	2	4	3	259	82	1,670	1,526	1,232	1,308	1,824	—	—	—	21
Ceratoscopelus warmingi	—	—	—	—	8	—	—	96	192	2,289	2	—	6	5,103	1,907	1,391	1,764	1,232	2,024	4,016	—	—	71	186
Myctophum nitidulum	6	2	12	4	1	13	3	10	11	3	2	—	3	2	1	2	1	—	24	20	—	—	—	—
Bolinichthys longipes	—	—	—	—	2	—	—	2	15	333	2	—	—	108	11	566	158	99	148	136	—	—	—	—
Diogenichthys laternatus	—	2	—	1,139	173	3	—	214	150	168	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gonichthys teniculus	2	4	4	1	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaphus garmani	—	—	—	114	63	—	—	1,085	359	485	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaphus problematicus	—	—	—	—	—	—	—	1	15	382	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lampanyctus nobilis	—	—	1	193	520	—	2	177	105	126	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lampanyctus omostigma	12	127	17	83	39	2	20	34	17	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Notoscopelus resplendens	—	—	—	9	26	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diaphus malayanus	—	—	—	—	—	—	—	—	1	19	—	—	7	1,190	638	156	270	1,694	112	800	—	—	—	—
Diaphus regani	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	65	18	—	32	64	—	—	—	—
Diaphus signatus	—	—	—	—	—	—	—	—	—	—	—	—	—	112	97	604	2,025	2,299	4,400	3,804	—	—	—	—
Diaphus sp. (near *mollis*)	—	—	—	—	—	—	—	—	—	—	—	—	—	46	37	91	495	154	212	280	—	—	—	—
Lampanyctus hubbsi	—	—	—	—	—	—	1	1	1	1	—	—	1	259	43	175	45	33	44	—				
Myctophum asperum	—	—	—	—	—	2	13	13	26	77	3	3	7	1	16	3	43	253	236	26	—	—	2	3
Myctophum obtusirostrum	—	—	—	—	—	—	—	—	—	—	—	2	—	—	3	—	—	11	32	24	—	—	—	—
Diaphus elucens	—	—	—	—	—	—	—	—	—	—	34	—	—	39	32	—	—	—	—	—	—	—	—	—
Centrobranchus choerocephalus	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Total	1,524	472	308	1,785	960	599	845	2,403	1,631	5,356	181	237	279	7,515	3,197	6,408	7,319	8,358	10,722	12,866	100	146	392	516
Average, shallow or deep		768		1,372		722		3,130			232			5,356				9,134			123		454	

TABLE 4.–Species of myctophids and number taken per tow for stations given in Table 2.

Species	50 m		100 m		200 m		300 m		450 m		500 m	
Stn.	48	49	58	68	57	69	61	67	52	76	60	78
Electrona rissoi	—	—	—	—	—	—	—	1	—	—	—	—
Hygophum proximum	1	2	5	3	4	6	3	1	—	1	2	16
Diogenichthys atlanticus	3	3	4	—	—	1	1	—	—	1	—	5
Myctophum aurolaternatum	—	—	—	—	—	1	—	—	—	—	—	—
Myctophum asperum	3	—	—	1	—	—	—	—	—	—	—	—
Myctophum nitidulum	—	2	1	1	1	—	—	—	1	—	—	—
Myctophum obtusirostrum	1	—	—	1	—	—	2	—	—	—	1	—
Myctophum selenoides	—	—	3	—	—	—	1	—	—	—	—	—
Myctophum spinosum	—	2	2	—	1	1	1	—	—	—	—	—
Symbolophorus evermanni	5	8	9	8	3	—	1	2	—	1	—	1
Diaphus drachmani	—	—	—	—	—	—	1	—	—	1	—	—
Diaphus elucens	7	17	1	—	1	—	—	3	1	1	—	—
Diaphus fragilis	5	6	1	2	2	—	2	2	—	—	—	—
Diaphus jenseni	—	—	56	5	2	4	2	1	—	—	—	—
Diaphus longleyi	—	—	31	6	4	10	1	1	4	—	3	2
Diaphus lucidus	—	—	4	4	—	—	—	—	—	—	—	—
Diaphus luetkeni	2	—	4	—	3	4	1	—	2	2	2	1
Diaphus malayanus	67	10	1	2	1	1	—	2	—	—	—	—
Diaphus problematicus	—	—	2	—	—	—	—	—	—	—	—	—
Diaphus regani	—	—	1	—	—	—	—	—	—	—	—	—
Diaphus splendidus	7	—	46	14	6	2	5	3	—	2	5	1
Diaphus termophilus	—	—	—	1	—	7	3	3	6	1	—	1
Diaphus sp. (near *mollis*)	25	—	5	—	2	3	1	1	—	5	2	—
Notolychnus valdiviae	—	—	25	3	4	25	3	1	1	—	8	—
Lampadena luminosa	—	—	7	—	—	2	—	1	—	—	1	—
Triphoturus nigrescens	8	3	14	—	5	27	8	2	3	12	11	7
Lampanyctus hubbsi	78	66	7	4	4	8	—	2	1	4	—	2
Lampanyctus "niger"	—	—	43	23	34	127	13	31	42	11	1	28
Lampanyctus nobilis	—	—	—	—	—	—	1	—	—	1	—	—
Lampanyctus omostigma	—	—	—	—	—	—	—	—	—	1	—	—
Lampanyctus steinbecki	1	—	1	3	1	4	—	—	—	—	—	—
Bolinichthys sp.[1]	—	—	1	—	—	—	1	2	1	—	—	—
Bolinichthys longipes	12	10	1	2	2	1	1	—	3	1	—	1
Bolinichthys photothorax	—	—	2	—	—	—	2	2	1	—	—	—
Ceratoscopelus warmingi	90	123	25	2	10	12	11	14	1	8	5	3

[1]*Bolinichthys* sp. is similar to *B. supralateralis*, but is apparently distinct and undescribed (R. K. Johnson, Field Museum of Natural History, Chicago, Ill., pers. commun.).

Several of these species are truly warmwater cosmopolites (McGowan 1971). *Hygophum proximum*, *M. aurolaternatum*, *M. nitidulum*, and *B. longipes* occur in equatorial waters not only in the study area, but widely throughout the eastern equatorial Pacific. Others, *C. warmingi*, *Diogenichthys atlanticus*, and *Diaphus fragilis*, apparently occur in equatorial waters only west of ca. long. 130°W.

Most of the 10 above species showed similar trends in abundance with latitude; peak abundance was at either lat. 3°30′N or at the equator. The same trend is evident in the total numbers of myctophids taken in deep tows (Table 3). (The total catches of the shallow tows tended to decrease southward. This trend is not marked, and the absence of data from the equator is perhaps critical.) A trend similar to that of the deep catches and of the wide-ranging species has been noted in zooplankton standing crop (King and Hida 1957). The increases in abundance are probably related to the higher primary productivity resulting from the upwelling and subsequent northward transport of enriched waters near the equator (Cromwell 1953; Murphy and Shomura 1972).

Three species of myctophids which are abundant at night in the upper layers near Hawaii and also taken at the gyre center were conspicuously absent from the present samples. *Benthosema suborbitale*, *Diaphus schmidti*, and a *Diaphus* sp. similar to *D. mollis* (called *Diaphus* sp. A by Clarke 1973) are apparently restricted to the central water mass–at least to the east of long. 145°W.

Seven species occurred only or principally at the northern two stations. *Diogenichthys laternatus*, *Gonichthys teniculus*, *Diaphus garmani*, *Lampanyctus omostigma*, *L. nobilis*, and *Notoscopelus resplendens* were taken only at lat. 12°N and 7°30′N. *Diaphus problematicus* was taken only at lat. 7°30′N. Three of these species, *D. problematicus*, *L. omostigma*, and *L. nobilis*, were captured in the IK series at lat. 3°30′N, but in low numbers (Table 4). It is clear that none of these species occurred at lat. 3°30′N in abundance.

Of these seven species, one appears to be widely distributed in the central water masses and four

are widely distributed in the eastern equatorial Pacific. *Lampanyctus nobilis* is taken at the gyre center and consistently near Hawaii. Its distribution pattern at long. 145°W is thus intermediate between that of the three strictly central water-mass species mentioned above and that of the species which were taken all the way across the transect. *Diogenichthys laternatus*, *G. teniculus*, *L. omostigma*, and *N. resplendens* occur over a broad latitudinal range in the eastern equatorial Pacific and in a narrower tongue extending into the central equatorial Pacific (Wisner 1963, footnote 3; Bekker 1966). None of these species are taken near Hawaii, and only *G. teniculus* and *N. resplendens* are taken near the gyre center, neither very frequently.

Little is known of the distribution of *Diaphus garmani* and *D. problematicus* in the Pacific. *Diaphus garmani* has been reported from Johnson Island (Nakamura 1970). Wisner (footnote 3) reports it from near Hawaii but it was not taken there by Clarke (1973) nor does it occur at the gyre center. Ahlstrom (1972) recorded *D. garmani* in "an offshore equatorial belt" but mentions neither species as present in the eastern equatorial Pacific. In the Atlantic, both species occur in equatorial waters, but also occupy a broad latitudinal range in the west (Nafpaktitis 1968).

Five species were taken principally at lat. 3°30′N or the equator. *Diaphus signatus* and *D.* sp. (near *mollis* but apparently distinct from either of the *mollis*-like forms recorded from near Hawaii by Clarke) were taken in abundance at both stations, while *D. regani* was taken almost exclusively at the equator. A few *D. malayanus* and *Lampanyctus hubbsi* were taken at lat. 7°30′N, but these species were clearly more common at lat. 3°30′N and the equator. All of these species are found only in the Pacific. There are no reports of any from either the eastern equatorial Pacific or the eastern section of the central water mass. *Lampanyctus hubbsi* is restricted to the offshore equatorial water mass (Wisner 1963). The same is apparently true of the undescribed species of *Diaphus* (Wisner footnote 3). The other three species of *Diaphus* were originally described from farther south or west and near island groups (Gilbert 1908; Weber 1913; Tåning 1932), and a few were collected in the western Pacific by Kulikova (1961). Wisner (footnote 3) indicates that they occur, like *L. hubbsi*, in the narrow offshore equatorial region between ca. long. 130-170°W.

Diaphus elucens was taken only at lat. 3°30′N, and *Myctophum obtusirostrum* at lat. 3°30′N and the equator. Their distributions are however, much broader than the present data indicates (Nafpaktitis 1968, 1973). Both are taken consistently near Hawaii. It seems likely that their capture only at the above latitudes was due more to their greater abundance there as opposed to their absence from the other latitudes sampled. *Centrobranchus choerocephalus* was taken only twice (lat. 7°30′N and 3°30′N). Bekker (1966) suggests it is a central water-mass species, and it is taken regularly near Hawaii. No real significance can be attached to the capture of only two specimens in the equatorial water mass.

The remaining species, *Myctophum asperum*, was taken at all latitudes except lat. 12°N. Its distribution in the Pacific is poorly known. Ahlstrom (1972) records it from lat. 7°N to 2°S between long. 98° and 119°W. It is not taken at the gyre center or near Hawaii. It is apparently, like *Diaphus garmani* and *D. problematicus*, neither a central nor eastern equatorial species, but may have a broader distribution to the west.

Although the data from both the present study and the literature are admittedly fragmentary and we know nearly nothing about distributions south and west of the study area, the evidence indicates that there is no distinct or abrupt change between the shallow-water myctophid faunas of the central and equatorial water masses as defined by Sverdrup et al (1942). While there are at least three abundant central species which did not occur in our equatorial samples, there were more which occurred throughout the sampling area and, in most cases, are also widely distributed in equatorial waters farther east. In between are several central species which occur in the equatorial water mass to a limited extent—both latitudinally (*L. nobilis*) and longitudinally (*Ceratoscopelus warmingi*, *Diogenichthys atlanticus*, and *Diaphus fragilis*).

Within the equatorial water mass, however, there is a distinct and rather abrupt change in fauna. Four species which occur throughout equatorial waters farther east were taken only at the northern two stations, while five other species which do not occur east of ca. long. 120-130°W were taken at lat. 3°30′N and the equator. There is thus little or no overlap between the ranges of the strictly offshore and those of the eastern equatorial species whose ranges extend into the study area.

The change in fauna is close to the northern

boundary of the SEC and may be related to the upwelling and northward transport of surface waters near the equator. In Figure 1, the latter are indicated by the shallow 27°C isotherm between about lat. 1°S and 0°30′N—somewhat south of the indicated faunal change. However, King and Hida (1957) and Murphy and Shomura (1972) point out that, while strength of upwelling and extent of northward surface transport vary irregularly over short periods depending on strength and direction of winds, the area between about lat. 1°S and about lat. 4°N can be regarded as a zone of high primary production and high zooplankton standing crop over most of the year.

The central equatorial Pacific is thus somewhat unique in that it is the only major offshore and truly oceanic area in the world where upwelling and high primary production are not strongly seasonal. Other areas of upwelling are either relatively close to land or, e.g., the Antarctic, are light-limited over part of the year. Thus it is not surprising that the fauna of the zone is different from both that of the oceanic, but relative sterile central water mass and that of the highly productive, but less oceanic eastern equatorial Pacific. Nor is it surprising that five of the species which occur in the zone are either endemic or restricted to it at least in the eastern part of the Pacific.

The faunal change observed in the data here could in part be a consequence of the change in primary production and availability of food. Ebeling (1962) has suggested that distributions of even deep-living, nonmigrating fishes are associated with differences in surface primary production, and Backus et al. (1969) have suggested that faunal changes associated with thermal fronts are more directly related to differences in primary production which result from differences in thermal structure on either side of the front. It is not unreasonable to suggest that the five species which were found only near the equator are unable to survive in the less productive waters north of about lat. 4°N.

This is, of course, insufficient to explain other features of the faunal change. It is not clear why some species, many which occur also in sterile central waters, not only occur in the equatorial zone of high production but are markedly more abundant there, while other species, which occur in the highly productive eastern equatorial Pacific, are apparently excluded from the offshore zone near the equator. More knowledge, e.g., the reproductive potential and food requirements, of the species concerned and of environmental characteristics of the areas, e.g., types and rates of predation, is needed before even speculation is warranted.

There are several examples where dominant species are "replaced" by congeners or morphologically similar species. *Lampanyctus omostigma* and *L. hubbsi* are very similar congeners which both occur in the equatorial water mass but with separate distributions. *Diaphus schmidti*, a central water-mass species, is replaced by *D. garmani* and *D. problematicus* in the northern section of the equatorial water mass, and these in turn are replaced by *D. malayanus*, *D. signatus*, and *D. regani* in the zone near the equator. All these *Diaphus* species are similar morphologically. *Diaphus schmidti*, *D. garmani*, and *D. malayanus* are of similar size at maturity while the others are somewhat larger. In addition to differences in placement of body photophores and development of sexually dimorphic head organs, these species are all distinguished by slightly different gill raker counts, suggesting differences in feeding habits. The *Diaphus mollis*-like forms also show a replacement series of sorts. The central water-mass species (*Diaphus* sp. A of Clarke 1973) is very similar in size and morphology to the *Diaphus* sp. taken near the equator; however, no similar form was present in the northern section of the equatorial water mass.

It is not implausible to suggest that *Benthosema suborbitale* and the *Diogenichthys* species form a replacement series. *Benthosema suborbitale* is a diminutive species of *Benthosema* and very similar to the *Diogenichthys*; the two genera are closely related (Moser and Ahlstrom 1970; Paxton 1972). It is apparently replaced by *D. laternatus* in the northern section of the equatorial water mass. *Diogenichthys atlanticus* occurs in all three zones, but is an abundant and dominant species only near the equator—where neither *B. suborbitale* nor *D. laternatus* occur.

Clarke (1973) has shown that, at a single location, closely related species have different nighttime depth ranges. The data here suggest that within a given depth range, closely related species are frequently separated geographically. Investigations of the biology of such closely related, but separated species, particularly near their geographic boundaries, would be a promising approach toward understanding the factors determining zoogeographic distribution in the open ocean.

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YEAR-TO-YEAR VARIATIONS IN THE PLANKTOLOGY OF THE OREGON UPWELLING ZONE

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ABSTRACT

Sampling results from Oregon coastal waters show that plankton abundance in 1971, a year of reduced coastal upwelling, was lower than in 1969 or 1970. This was correlated with greater frequency and abundance in 1971 for species usually found more offshore and with a general reduction in the number and density of the most strictly neritic species. It is proposed that these changes are related to changes in nearshore fisheries which, therefore, appear to depend upon the general stimulation of production by upwelling.

In this paper we describe the nearshore zooplankton community found off the Oregon coast during the upwelling seasons of 1969, 1970, and 1971. Differences in species composition and abundance between the individual upwelling seasons will be described and related to differences in upwelling strength, hydrographic conditions, and wind patterns. Our research on coastal zooplankton is centered upon understanding the dynamics of the nearshore community found within 18 km of the beach. We have concentrated our efforts in this area because it has been shown to be the location of the most intense coastal upwelling. Effects of upwelling are present farther offshore, but the phenomenon is most pronounced within 10 km of shore (Huyer 1974). The importance of understanding coastal upwelling and its effect upon biological production is well established.

PREVIOUS ZOOPLANKTON STUDIES IN THE OREGON AREA

Distribution and abundance of Oregon coastal zooplankton has been the subject of several theses at Oregon State University. Seasonal variations in distribution and abundance along a single line of latitude have been studied by Hebard (1966) off Newport (Figure 1) and by Laurs (1967) off Brookings. Both seasonal and spatial variations were considered by Cross (1964) from data collected off Astoria, Newport, Coos Bay, and Brookings. Lee (1971) looked at samples collected from a grid of stations during one brief interval in August 1963. Both Hebard and Laurs employed plankton nets with a mesh size of 570 μm while Cross and Lee used nets with 240-μm mesh. Since the larger mesh retained only very large forms, some very different conclusions about the relative importance of zooplankton species were reached by the different authors. Hebard found that the euphausiid *Euphausia pacifica* was numerically dominant, and Laurs found that this animal dominated the zooplankton biomass. Copepods were unimportant in their studies. Conversely, Cross and Lee found that the copepods *Oithona similis*, *Pseudocalanus*, and *Acartia longiremis* were numerically dominant. A forthcoming paper by Pearcy (in litt.) will summarize the results of a

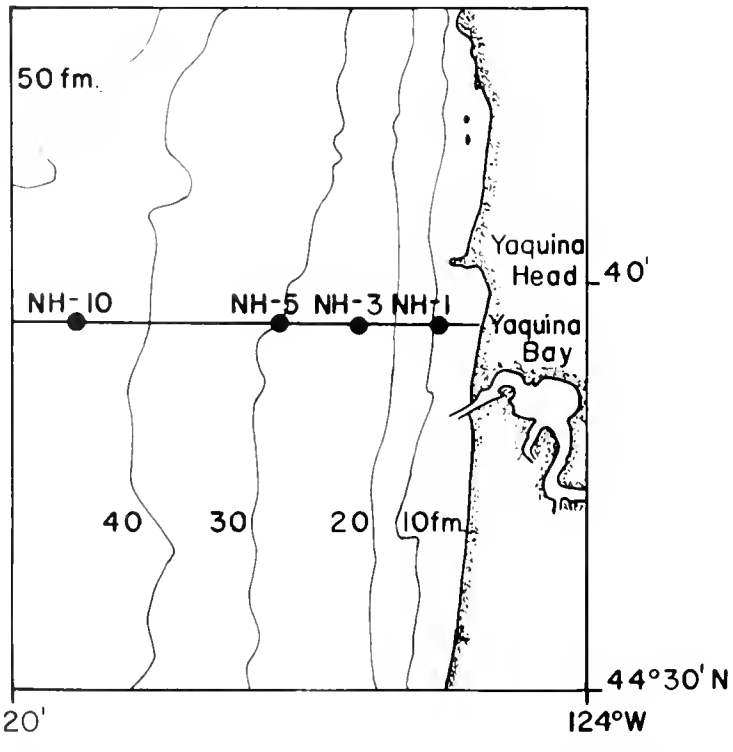

FIGURE 1.—Map of the study area showing the Newport hydrographic line (solid dark line) and the sampling positions.

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4-yr study of seasonal biomass cycles at distances of 28 km from shore and beyond, which employed mid-water trawls and 570-μm plankton nets.

Peterson (1972) summarized the results of 434 zooplankton samples collected off Oregon and Washington with 110-μm mesh Clarke-Bumpus nets at an irregular set of stations in 1961 and 1962. Most of the samples were taken beyond the continental shelf break. His conclusion that copepods attain larger inshore populations in winter than in summer is not in agreement with our results for the Oregon nearshore zone. We have found winter densities to be several orders of magnitude lower than summer densities. This discrepancy makes his work difficult to evaluate.

All of these studies share two shortcomings: First, few or no samples were collected within 10 km of the coast. Second, the time intervals between samplings were large, ranging from monthly (Hebard 1966) to quarterly and longer (Cross 1964; Laurs 1967; Peterson 1972). Under such sampling programs the authors could only document large scale phenomena, such as faunal changes associated with seasonal hydrographic changes, and faunal differences between nearshore and offshore stations.

THE COASTAL ENVIRONMENT OF OREGON

Aspects of descriptive physical oceanography of Oregon coastal waters can be found in Burt and Wyatt 1964; Pattullo and Denner 1965; Cross and Small 1967; Collins et al. 1968; Bourke 1972; Pillsbury 1972; Huyer 1974; and Smith 1974.

Circulation Patterns

The California Current is a slow, southward-flowing current situated within a band 300 to 800 km off the Oregon coast. Inshore of this permanent feature the circulation changes with season. During spring and summer months nearshore flow is southward, driven by northerly winds. During fall and winter months, after cessation of upwelling, flow is northward. This flow is called the Davidson Current.

Wind and Coastal Upwelling

Northerly winds predominate from April to September. They produce a generally southward transport of surface water with a component to the right of the wind away from the coastline. This offshore, near-surface transport is balanced by northward and onshore transport at depth of cool, high salinity, nutrient rich water. When northerly winds are strong and/or persistent, cold, high salinity water appears on the beach and throughout the entire water column out to about 10 km. This condition is called active or intense upwelling. When north wind stress is weak or nonexistent, this onshore deep transport is weakened and nearshore waters are warmed by solar radiation.

Intense upwelling is not a continuous process during summer, but occurs sporadically. If northerly winds blow for a day or two, upwelling will develop. If wind ceases or changes direction, upwelling ceases. During July and August northerly winds are often persistent, so that intense upwelling may continue for several weeks without interruption.

Waters offshore of 10-20 km do not experience these rapid changes. In these deeper waters, upwelling is indicated in hydrographic sections by upward sloping isolines of temperature, salinity, and density (see Smith 1974). The upward slope develops in April or May and persists until cessation of upwelling in September or October. Offshore surface waters are warm (as high as 17°C) and a mixed layer is well developed. Salinities are reduced as a result of the Columbia River plume.

Temperature and Salinity Relationships

Pillsbury (1972) has summarized all temperature and salinity data collected within the top 10 m of the water column at stations 5 and 9 km from shore during the April-September upwelling seasons of 1960 through 1970, a total of 188 observations. Pillsbury used the modal cell technique of Pattullo and Denner (1965) to summarize the data. The portion of a temperature-salinity plot containing the most data points was one bounded by 8.1°-9.0°C and 33.1-34.0‰. That "cell" accounted for 28% of the data. Pillsbury identified two general water types that occur at the two stations: 1) cold-upwelled water (7.5°-8.5°C and 33.5-34‰) and 2) warm, low salinity water (11.0°-12.0°C and 30.5-31.5 ‰) which is a mixture of Columbia River plume water and surface oceanic water.

MATERIALS AND METHODS

Zooplankton were collected along the Newport Hydrographic (NH) line, lat. 44°40′N. We chose this line because extensive hydrographic data are available from cruises made since 1960. Station labels NH 1, NH 3, NH 5, and NH 10 refer to distances in nautical miles from shore and are approximately 2, 5, 9, and 18 km from the beach. Figure 1 is a map of the study area.

Zooplankton samples were collected with 20-cm "Bongo" nets without an opening-closing mechanism. To construct the net frame, two 20-cm diameter × 30-cm PVC (polyvinyl chloride) cylinders were bolted to either side of a pivoting wire clamp. When mounted on the towing cable the net frame was free to move in the vertical plane about 120° of arc, and it could rotate horizontally about the towing cable.

The two plankton nets were 145 cm long and were constructed of NITEX[2] nylon with mesh aperatures of 505 and 240 μm. The ratio of net mesh area to net mouth area was about 11.5:1 for the 240-μm net. The cod ends were 9-cm diameter × 16-cm PVC buckets with stainless steel mesh screens cemented to laterally positioned filtering windows. The two cod ends were fastened about 15 cm apart with a stainless steel strap which kept the nets from wrapping about the cable while being towed. Tsurumi-Seiki Kosakusho flowmeters were mounted off-center in each net mouth. Tows were made obliquely over the entire water column using either a V-fin or Kite-Otter depressor. A time-depth recorder was used to record the towing track. Samples were preserved with 10% buffered formaldehyde solution.

In the laboratory, samples were poured into 500-ml pharmaceutical graduates and allowed to settle. Several hours later the settled volume was read. Water was then decanted off or added to make a diluted volume of five times the settled volume. Aliquots for counting were removed from this volume with a 1-ml Stempel pipette, after the animals were suspended by agitation with a small spatula.

Animals were enumerated with the aid of a binocular dissecting microscope at 25× magnification. Five aliquots were drawn from each sample. Taxa were counted in the first and successive aliquots until 50 in a category were enumerated. These counts were multiplied by appropriate factors to arrive at a number of individuals in a category per five aliquots. A computer was used to convert these raw data into number of individuals per cubic meter and to carry out much of the summary data analysis.

All adult copepods were divided by sex and identified to species. Two morphs of the genus *Metridia* were seen and were separated on the basis of shape of the prosome in lateral view. The *Metridia pacifica* type is more robust and has a steeply sloping forehead, while the *M. lucens* type has a much less sloping forehead. Detailed morphological study of the two types has not been done. Copepodite stages were identified for all species except those of *Clausocalanus*. Only the nauplii of *Calanus* sp. were distinguished. Both euphausiids and cladocerans were identified to species. All other holoplanktonic taxa were grouped (e.g., amphipods, ostracods, medusae, ctenophores, chaetognaths, etc.). Meroplankton were counted as general categories: barnacle nauplii, crab zoea, bivalve veligers, etc. The crab larvae were not counted because they are being studied by R. Gregory Lough, School of Oceanography, Oregon State University.

Surface temperature was measured at all stations and a surface salinity sample was gathered at nearly all stations. Bottom salinity samples were taken on many cruises. Bathythermograph traces were taken at most stations.

Hourly wind data were supplied by William Gilbert, School of Oceanography, Oregon State University. They were gathered by the National Weather Service, NOAA (National Oceanic and Atmospheric Administration) from a recording anemometer located on the south jetty off Newport, Ore., and are stored on magnetic tapes as north-south and east-west components. We determined the resultant vector from the daily mean components and constructed progressive vector diagrams (PVD's) for each upwelling season.

RESULTS

Hydrography and Wind Data

We have compared our surface temperature and salinity data to Pillsbury's modal cell. Data collected during the upwelling seasons 1969-71, from NH 1, NH 3, and NH 5 are shown in Figure 2. None of our observations were part of Pillsbury's data. Striking differences between upwelling

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

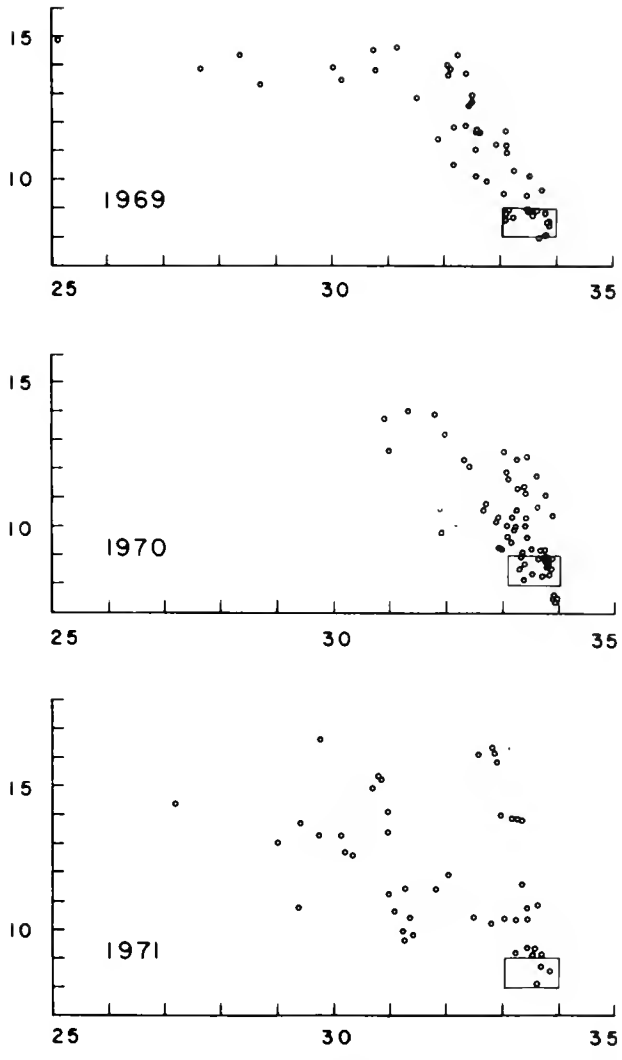


FIGURE 2.—Temperature-salinity diagrams for NH 1, NH 3, and NH 5 in 1969, 1970, and 1971 between April and September.

seasons are seen. About 26% of the 1969 and 1970 data fell within the limits of the modal cell (8.1°-9.0°C and 33.1-34.0 °/∞). Only 6% of the 1971 data fell within the limits. Water was generally warmer and of a lower salinity during most of the 1971 upwelling season. Higher temperatures and lower salinities indicate the presence of mixed Columbia River plume water and surface oceanic water. Both the modal cell and surface temperature observations indicate that upwelling was weaker in 1971 than in 1969 or 1970.

Wind data supports the conclusion that the upwelling season of 1971 was a weak one. The PVD's (Figure 3) illustrate the pattern of the wind from 1 May through 30 September for the years 1969-71. They give an indication of amounts of upwelling-inducing northerly winds during a given season, and are useful for comparing different seasons. The axes of the PVD's are wind-miles (i.e., miles per hour multiplied by hours). The northerly component of the wind extends positively down the ordinate and westerly component extends positively along the abscissa. The seasonal pattern for 1971 is quite different from 1969 and 1970. Northerly wind miles are low while westerly wind miles are exceptionally high. Therefore, upwelling should have been relatively weak. This explains the low frequency of temperature and salinity observations in the modal cell in 1971, compared to 1969 or 1970. The 1969 and 1970 wind patterns are similar; 1969 had about 2½ mo of persistent northerlies, while 1970 had about 4 mo of persistent northerlies. A higher total northerly component was achieved in 1970 than in 1969.

The upwelling index data of Bakun (1973) show 1969 and 1970 to have been close to average years compared with the years 1946 to 1971, while 1971 was far below average. These monthly indices estimate the magnitude of the offshore component of the Ekman transport and are calculated from an estimate of the mean monthly sea surface wind stress, which is based in turn on a geostrophic wind calculation from pressure field data. The anomalies of the index at lat. 45°N, long. 125°W for the periods of interest in our study are:

Month	*25 yr mean index for month*	*1969*	*1970*	*1971*
May	34	-22	- 1	+32
June	48	+13	- 2	-36
July	74	+32	- 3	- 9
Aug.	51	- 5	+23	-27
Sept.	17	-11	- 5	- 8
Total		+ 7	+12	-48

Bakun's indices were derived from different data than the PVD's and comparisons between years would not be expected to be in exact agreement.

Total Zooplankton

Table 1 is a list of the sampling dates and total zooplankton abundance at stations NH 1, 3, 5, and 10. The 1972 data set is shown, but since so few samples were taken relative to the number gathered in other years, we have eliminated these data from comparative discussions. One can see several patterns in Table 1. Abundances are usually highest at the station nearest the shore (2 km from the beach). Abundances grade to lows at the station 18 km from shore. They continue to decrease farther from shore (Cross 1964). There is

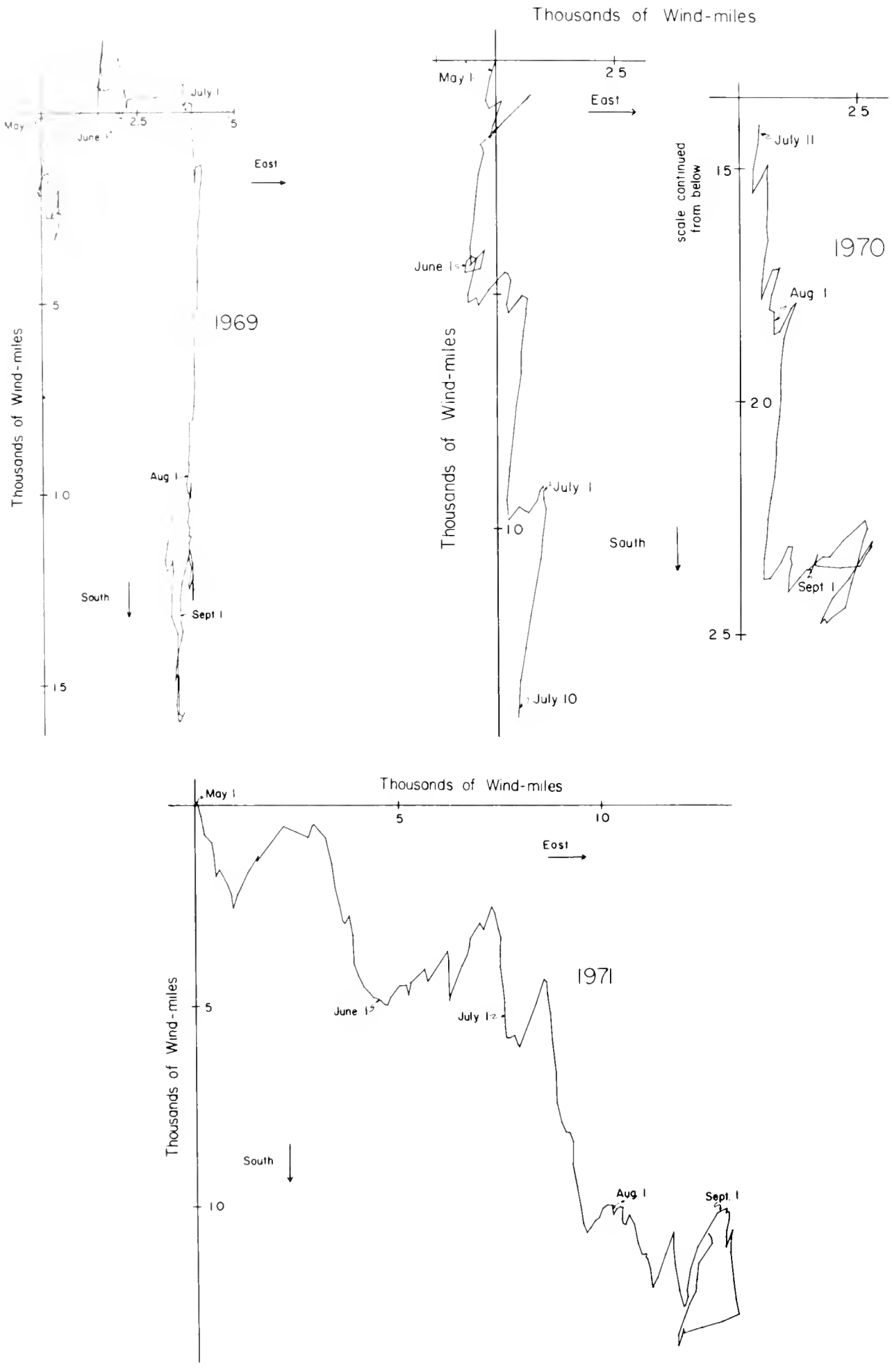


FIGURE 3.–Progressive vector diagrams for the wind at the Newport jetty between May 1 and September 30 in 1969, 1970, and 1971.

TABLE 1.—A list of sampling dates and total zooplankton catch (individuals/m³) at stations NH 1, 3, 5, and 10. These stations are approximately 2, 5, 9, and 18 km from shore.

Date	NH 1	NH 3	NH 5	NH 10
1969:				
22 June	15,305	2,780	2,375	553
29 June	—	3,712	—	3,895
10 July	15,097	—	8,016	—
18 July	44,782	3,442	10,131	766
25 July	16,277	30,633	1,042	1,334
6 Aug.	9,531	7,482	2,940	—
26 Aug.	—	—	1,721	90
30 Aug.	9,069	6,150	3,141	998
3 Sept.	4,344	3,051	4,756	3,058
14 Sept.	—	5,707	4,447	—
28 Sept.	—	3,457	3,368	—
1970:				
27 Apr.	105	606	767	797
6 May	1,393	872	—	158
22 May	1,166	1,793	1,739	178
4 June	5,375	614	1,185	—
23 June	51,372	1,118	59	434
2 July	30,952	3,633	3,172	2,136
16 July	6,495	4,195	1,935	1,508
29 July	—	4,198	3,179	1,833
13 Aug.	4,135	—	2,202	108
23 Aug.	5,846	4,070	1,264	1,846
11 Sept.	3,121	9,307	322	2,406
25 Sept.	11,450	5,806	6,263	4,349
1971:				
3 May	1,153	1,820	933	927
14 May	967	1,660	1,292	1,679
29 May	4,691	741	1,410	1,715
2 June	—	2,721	—	—
12 July	8,276	4,075	2,086	2,385
28 July	6,737	973	765	—
6 July	3,638	313	674	1,482
21 July	9,577	1,236	1,069	760
2 Aug.	4,276	1,370	2,940	886
19 Aug.	1,559	1,165	531	388
23 Sept.	1,023	896	565	613
1972:				
20 Apr.	1,123	—	1,131	1,057
22 May	2,553	1,652	164	194
11 June	1,242	952	2,578	913
28 June	3,108	1,293	1,090	1,606
21 July	1,372	886	1,071	1,835
5 Aug.	2,589	—	338	575

a seasonal pattern in total zooplankton abundance. Low abundances always occur in April, May, and early June. Low abundances occur at various times during summer and fall as well. Peak abundances occurred in late June and July during 1969 and 1970. No such peak developed in 1971. As a result, standing stocks in 1971 were much lower than other years. There is some indication that 1972 may have had low standing stocks as well.

Table 2 shows the average catch at each station for three seasons. The 1969 data are biased since there are no samples for spring months. To make the average catch data comparable, samples averaged for 1970 began with 23 June and for 1971 began with 12 June. As with temperature-salinity and wind data, 1971 is markedly different from 1969 and 1970, particularly close to shore. This inference was tested by the Kruskal-Wallis sum of

TABLE 2.—Average catch of zooplankton at stations NH 1, 3, 5, and 10 for each upwelling season. Not all sampling dates are included in the mean because the 1969 data are biased since the first samples were collected on 22 June. Therefore, to make all data sets comparable, only samples taken from 23 June through September 1970 and 12 June through September 1971 were used.

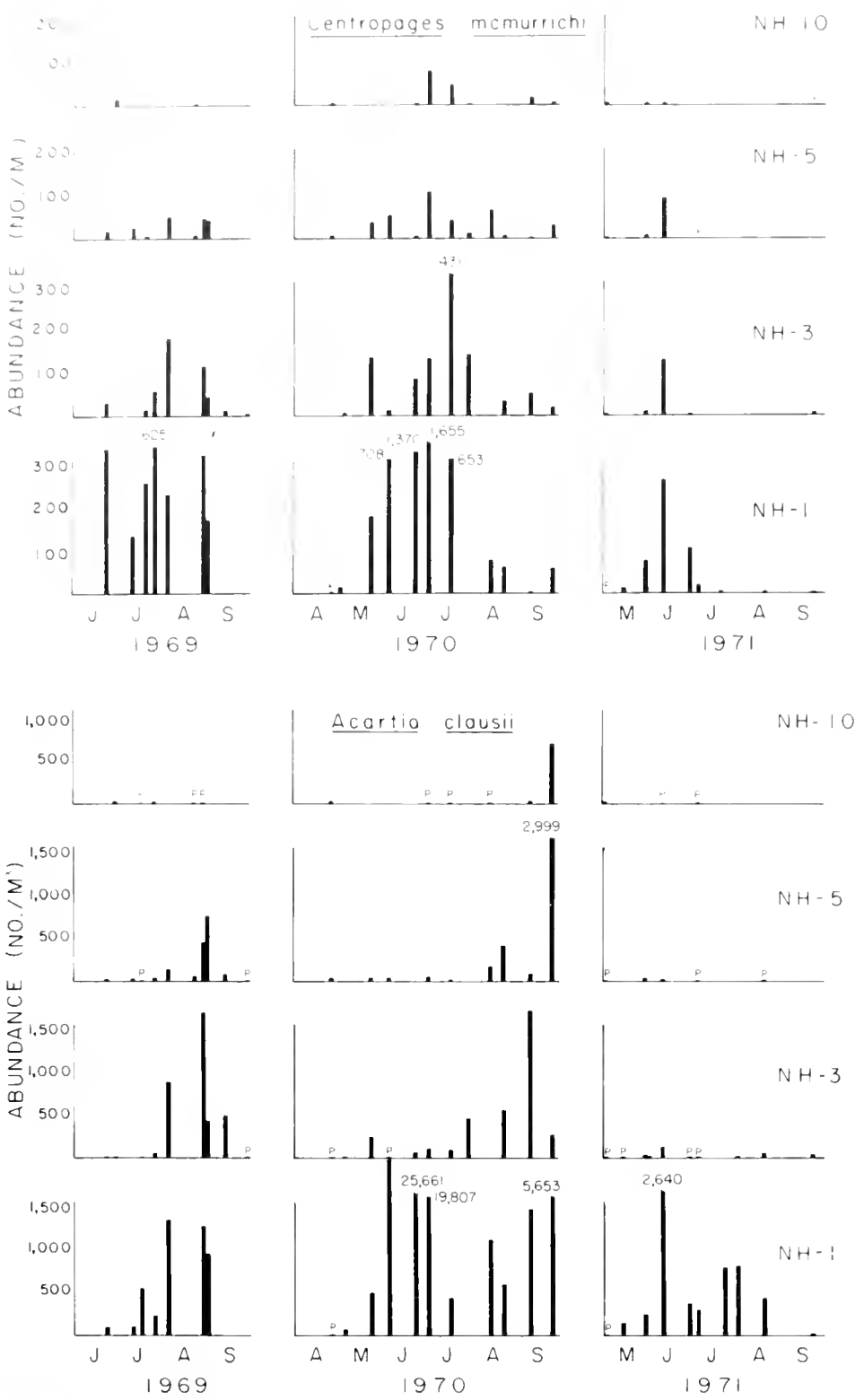
Year	NH 1	NH 3	NH 5	NH 10
1969	16,344	7,379	4,090	1,528
1970	16,196	4,618	2,300	1,828
1971	5,012	1,433	1,233	1,086

ranks test. Medians for the 3 yr were found to be significantly ($P < 0.05$) nonhomogeneous at all of the stations except NH 10.

Zooplankton Species

Copepods are the dominant zooplankters in our samples. In 100 of 137 samples collected 1969-72, they account for more than 90% of the total catch. In the remaining samples they made up at least 50%. Several species of copepods were individually dominant or shared dominance: *Calanus marshallae* Frost (1974), *Pseudocalanus* sp., *Centropages abdominalis* Sato (= *C. mcmurrichi* Willey), *Acartia clausii* Giesbrecht, *A. longiremis* Lilljeborg, and *Oithona similis* Claus. These copepods are responsible for the patterns of seasonal and spatial abundance seen in Table 1. Individual species patterns are illustrated in Figures 4 and 5. *Pseudocalanus* sp., *A. clausii*, and *C. abdominalis* are grouped in Figure 4 because they are most abundant at the station nearest the beach. Figure 5 contains *A. longiremis* and *Calanus* sp. because they are usually more abundant farther offshore. *Oithona similis* abundance has no certain relationship to distance offshore within 18 km of the coast. Other species exhibit similar abundance gradients but they will not be discussed in this paper.

Table 3 lists relative density and frequency of occurrence of all copepod species. Relative density is the average number of individuals in samples in which the species occurred. The values in the table are sums of relative densities at the four stations for individual years. Table 4 lists relative density and frequency of occurrence of other holoplanktonic taxa and of the meroplankton. The taxa that occurred most frequently or were abundant include chaetognaths (*Sagitta elegans* Verrill predominantly), bivalve veligers, barnacle nauplii, euphausiid eggs, and small round eggs which are probably *Calanus* eggs.



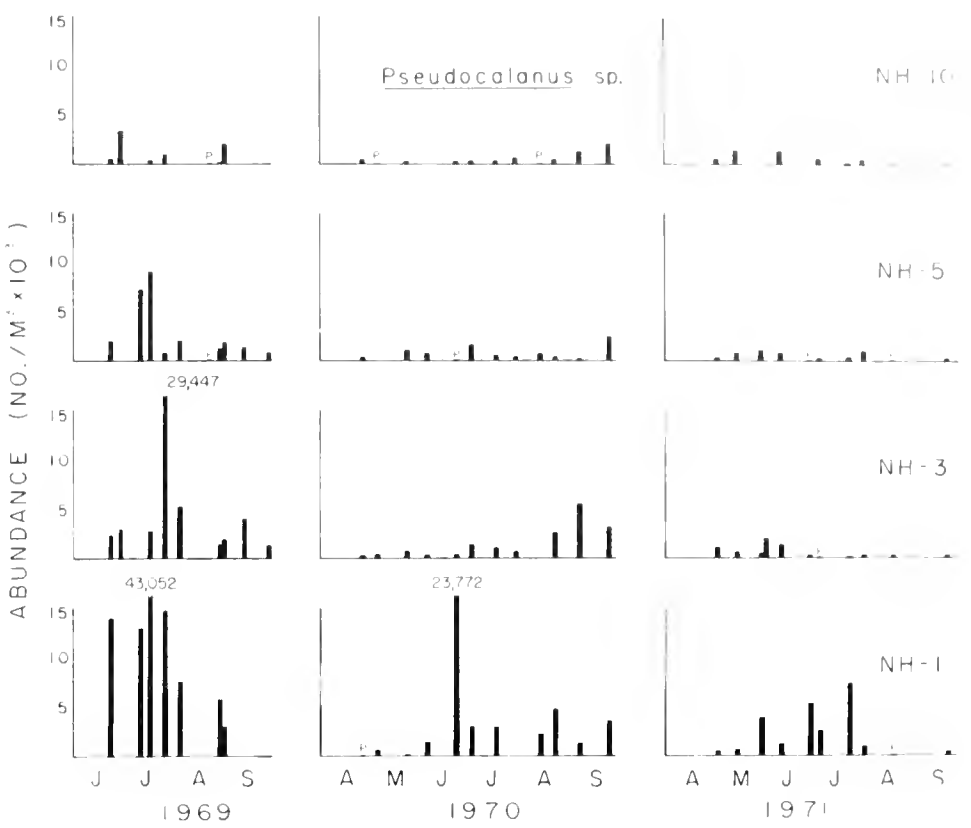


FIGURE 4.–Density of *Pseudocalanus* sp., *Acartia clausii*, and *Centropages mcmurrichi* (= *C. abdominalis*) at NH 1, NH 3, NH 5, and NH 10 in the upwelling seasons of 1969, 1970, and 1971.

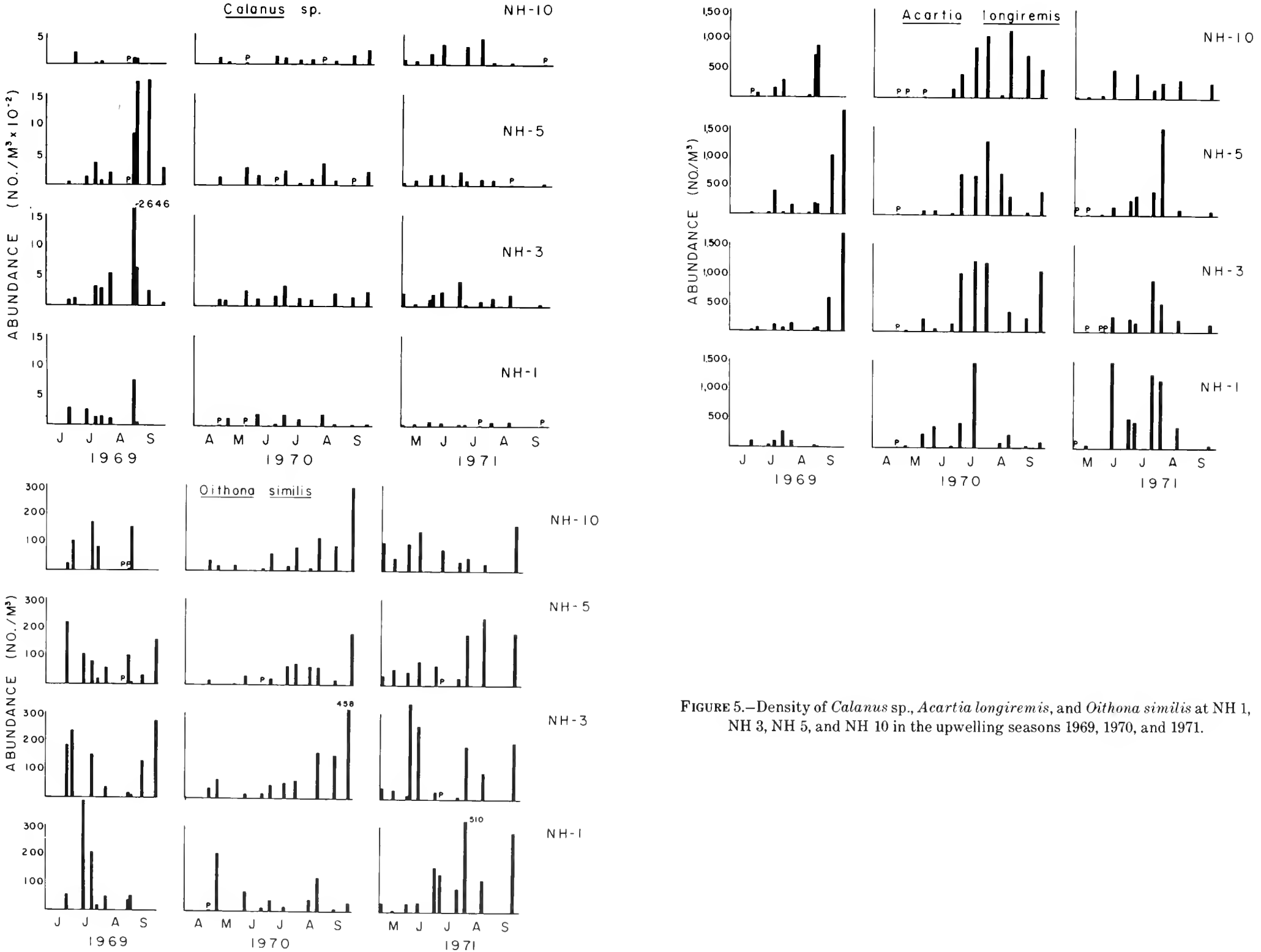


FIGURE 5.—Density of *Calanus* sp., *Acartia longiremis*, and *Oithona similis* at NH 1, NH 3, NH 5, and NH 10 in the upwelling seasons 1969, 1970, and 1971.

TABLE 3.—Total relative density and frequency of occurrence of the copepod species taken within 18 km of the Oregon coast, during 1969, 1970, and 1971. Relative density is average number of individuals per cubic meter in samples in which the species occurred. The table entries represent the sums of relative density at each of four stations. A total of 33 samples were collected in 1969, 44 in 1970, and 40 in 1971.

	Total relative density			Frequency		
Species[1]	1969	1970	1971	1969	1970	1971
Calanus sp.	1,475.2	482.5	436.1	32	44	40
C. tenuicornis	1.3	5.1	7.9	1	4	14
Eucalanus bungii	21.1	3.1	9.0	13	10	15
Paracalanus parvus	80.7	147.3	16.8	29	21	20
Pseudocalanus sp.	23,776.3	6,682.4	3,994.5	33	44	40
Microcalanus pusillus	2.2	18.5	1.8	4	17	2
Clausocalanus arcuicornis	0	1.4	4.0	0	3	7
C. pergens	20.2	5.9	6.6	5	5	9
Clausocalanus immatures	0	0.5	2.1	0	5	2
Ctenocalanus vanus	4.8	31.0	11.0	5	7	16
Aetideus pacificus	1.5	2.3	2.7	4	4	1
Gaidius immatures	2.5	3.4	3.7	3	3	2
Racovitzanus antarcticas	0.6	2.1	1.3	1	2	2
Scolecithricella minor	9.3	4.6	16.0	7	14	16
Metridia lucens	21.4	16.3	48.6	18	29	26
M. pacifica	6.7	2.9	3.7	2	5	6
Lucicutia flavicornis	0	0.4	2.0	0	1	9
Centropages abdominalis	371.8	686.2	110.7	29	42	23
Epilabidocera longipedata	2.9	10.8	0	5	6	0
Acartia clausii	1,178.1	6,045.1	414.9	31	37	29
A. longiremis	1,078.2	1,509.2	1,331.1	33	44	38
A. tonsa	130.7	27.5	0	31	19	0
Tortanus discaudatus	17.5	12.3	0	3	10	0
Oithona similis	369.9	275.0	416.2	32	42	40
O. spinirostris	19.9	16.0	55.5	19	28	31
Corycaeus anglicus	2.8	8.0	3.6	2	10	3

[1]The following species were found in less than five samples: *Calanus plumchrus*, *Gaetanus* immatures, *Paraeuchaeta japonica* immatures, *Candacia bipinnata*, *Eurytemora thompsoni*, *Rhincalanus nasutus*, *Oncaea borealis*, *O. tenella*, *O. media hymena*, *O. mediterranea*, *Sapphirina* sp., and *Microsetella* sp.

TABLE 4.—Total relative density and frequency of occurrence of other holoplanktonic taxa and meroplankton taken within 18 km of the coast during 1969, 1970 and 1971 upwelling seasons. Entries are sums of average abundances at each of four stations.

	Total relative density			Frequency		
Species	1969	1970	1971	1969	1970	1971
Calanus nauplii	119.5	695.5	172.7	21	40	28
Other Copepod nauplii	43.1	68.1	52.3	10	20	20
Amphipods	8.5	18.5	15.7	5	15	14
Euphausiid nauplii	46.3	85.9	84.0	5	26	18
Euphausiid calyptopis	13.3	14.5	17.2	4	17	11
Euphausiid furcilia	30.2	13.6	17.7	14	20	10
Thysanoessa spinilera	35.4	4.0	87.3	2	7	11
Evadne nordmanni	73.7	58.9	9.8	17	26	2
Podon leukarti	2.8	115.3	5.2	2	12	1
Pteropods	10.2	24.6	60.6	11	22	35
Chaetognaths	89.4	50.3	30.8	25	33	34
Oikopleura	69.2	85.7	66.5	11	15	21
Ctenophores	6.0	2.5	34.9	7	5	19
Scyphomedusae	22.9	70.9	22.8	13	28	22
Decapod shrimp mysis	142.7	52.6	45.3	16	24	22
Barnacle nauplii	59.3	168.3	231.4	8	32	23
Barnacle cypris	4.4	64.0	8.3	2	19	10
Polychaete post-trochophores	16.2	20.1	21.4	5	23	15
Bivalve veligers	170.5	258.9	68.3	20	40	27
Gastropod veligers	28.9	79.2	42.2	16	33	23
Hydromedusae	6.1	3.2	10.3	2	2	11
Unidentified annelid without parapodia	8.2	23.1	35.8	3	3	16
Pluteus	0	16.0	117.6	0	5	11
Large round eggs (fish)	36.8	25.0	17.8	11	13	12
Small round eggs	[1]870.1	168.7	226.1	10	28	25
Euphausiid eggs, early	55.0	686.1	449.6	11	29	24
Euphausiid eggs, late	70.0	57.5	39.6	2	16	14
Other fish eggs	19.1	35.1	34.3	12	18	18

[1]Biased by a single observation of 760 individuals/m^3.

Only a few of the taxa in these tables had similar average abundances in each season. Some of the taxa can be assigned "good" and "bad" years on the basis of either their abundance or frequency of occurrence in samples. Others cannot be assigned with much confidence. Accordingly, on the basis of frequency of occurrence, 1971 was the "best" year for the following copepods: *Calanus tenuicornis* Dana, *Clausocalanus arcuicornis* Dana, *Ctenocalanus vanus* Giesbrecht s.l. and *Lucicutia flavicornis* Claus. On the basis of abundance, the following categories can be added to the list: *Metridia lucens* Boeck, *O. spinirostris* Claus, the euphausiid *Thysanoessa spinifera* Holmes, the pteropod *Limacina helicina* (Phipps), ctenophores, hydromedusae, echinoderm pluteus larvae, and unidentified annelids. Using the same criteria, 1971 was the poorest year for the copepods *Paracalanus parvus* Claus, *Pseudocalanus*, *Aetideus pacificus* Brodskii, *Centropages abdominalis*, *Acartia clausii*, *A. tonsa* Dana, *Tortanus discaudatus* Thompson and Scott, and *Epilabidocera longipedata* Sato (= *E. amphitrites* McMurrich). Also poorly represented in 1971 were the cladoceran *Evadne normanni* (Loven) and bivalve mollusc veligers.

A definite pattern emerges from the above classifications. All of the copepod species having their best year in 1971 are basically offshore, warmwater species that can always be found well off the Oregon coast (Peterson and Anderson 1966; Peterson 1972) and which seem to have their highest abundances to the south (Fleminger 1967). Those species which had their poorest year in 1971 are all nearshore, coastal species. In fact, some of the neritic species which had their "best" years in 1969 or 1970 did not even occur in 1971 (*Epilabidocera longipedata*, *T. discaudatus*, and *A. tonsa*; see Figure 6). Fleminger (1967) listed *Paracalanus parvus* and *A. tonsa* as temperate-subtropical neritic, and *Pseudocalanus*, *A. clausii*, *T. discaudatus*, and *E. longipedata* as boreal-temperate neritic. *Centropages mcmurrichi* is also a boreal neritic species (Cameron 1957). The attribute shared by each of the animals having a "poor" year in 1971, is restriction to the neritic zone. Warmwater or cold-water affinities seem unimportant. Even though surface temperatures were much higher in 1971, two important animals with norther affinities and not narrowly restricted to the neritic zone, maintained the same level of abundance as they had in 1969 and 1970: *A. longiremis* and *O. similis*.

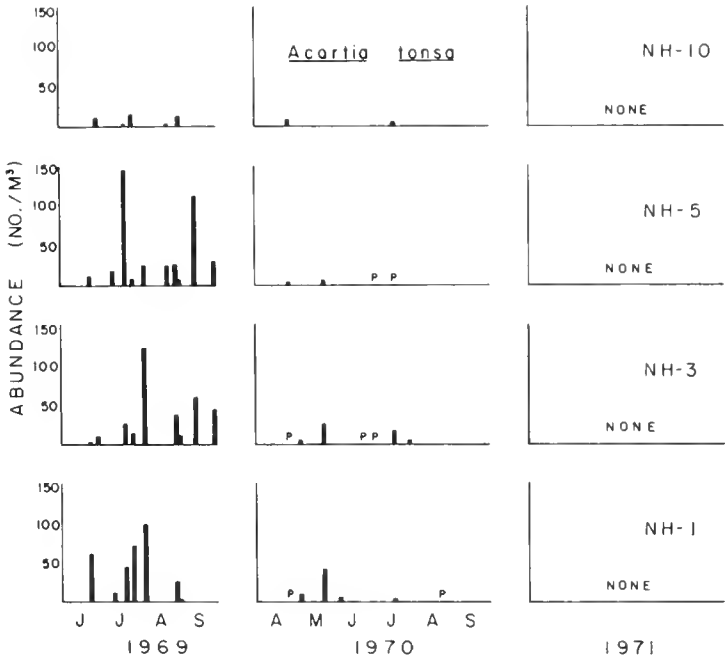


FIGURE 6.—Density of *Acartia tonsa* at NH 1, NH 3, NH 5, and NH 10 in the upwelling seasons of 1969, 1970, and 1971.

There are important differences between the good upwelling years of 1969 and 1970. A number of taxa were very abundant only in 1970: the copepods *Microcalanus pusillus* Sars and *A. clausii*, *Calanus* nauplii, the cladoceran *Podon leukarti* (Sars), barnacle cypris, and gastropod veligers. The year 1969 was the better year for two dominant copepod species (*Calanus* sp. and *Pseudocalanus* sp.), for the copepods *Eucalanus bungii* Giesbrecht and *A. tonsa*, and for shrimp larvae. We do not fully understand these observations.

The greatest share of the taxa listed in Tables 3 and 4 seem to be either equally abundant over all three upwelling seasons (copepod nauplii, euphausiid life history stages, *Oikopleura* sp., polychaete post-trochophores, small round eggs, euphausiid eggs, and fish eggs), or have uncertain or no relationship to the upwelling seasons. These animals include the copepods *Clausocalanus pergens* Ferran, *Scolecithricella minor* Brady, *Metridia pacifica* Brodskii, *Racovitzanus antarcticus* Giesbrecht s.l., *Gaidius* sp., and chaetognaths, barnacle nauplii, and scyphomedusae.

DISCUSSION

Upwelling along the Oregon coast was relatively weak in 1971. It was seldom strong enough to create the low temperature-high salinity conditions close to the beach that are characteristic of the process. This occurred because there were no

sustained periods of southward wind in 1971. There were only four "upwelling events": 2-10 May, 16-25 May, 20 June-2 July, and 10-24 July. Each of these events was unusual compared to those of other years in that the wind also had a substantial eastward component. There were also four storms from the southwest of the sort that characterize the winter period on the Oregon coast: 11-15 May, 16-23 June, 7-9 July, and 27-31 August. It is expected that under these conditions surface waters from offshore would have been more prevalent in the nearshore zone in 1971 than in other years. The composition of the plankton observed in 1971 within 18 km from shore is in agreement with that hypothesis.

Comparison of onshore-offshore hydrographic sections for upwelling events and for intervals of low southward winds (Smith 1974) suggests an explanation for the fact that NH 10 does not show the same degree of year-to-year variations as stations nearer shore. During the upwelling season all isopycnals below 15 m slope upward toward the shore at least as far seaward as 30 km. Upward sloping extends to the shore during upwelling events, but during lapses of the southward wind the isopycnals come to slope downward toward shore from 10 km seaward to the beach. Seaward of 10 km they continue to slope upward despite prolonged lapses. It seems likely that coastal upwelling only takes the form of pulsed events in this most inshore zone. Thus it is reasonable that the low frequency and amplitude of upwelling events in 1971 only had a pronounced effect on the planktology at stations less than 10 km from shore. On the other hand, Hubbard and Pearcy (1971) demonstrated marked changes in the species composition of the salp fauna off Oregon at distances beyond 28 km from shore in 1963, another year of anomalously low coastal upwelling (Bakun 1973). The detailed relationship between inshore and offshore plankton changes as correlated with year-to-year weather variations cannot yet be deduced. The length, frequency, and spatial extent of the data set necessary to deal with this problem probably puts it beyond our reach.

There is a suggestion in the data that intense upwelling events rather immediately result in high zooplankton abundance at the NH 1 and NH 3 stations. Huge population peaks on 10, 18, and 25 July 1969 and 23 June and 2 July 1970 were associated with periods of intense upwelling. The high density found on 22 June 1969, however, followed a 41-day period of little or no north wind. It seems most likely that peak densities are simply reached at about the same time each year, namely late June and early July. We do not as yet know the relationship between copepod developmental schedules and the seasons in this area well enough to decide this issue with any certainty. Further analysis of our data as it bears on this point is planned.

Summers of below average upwelling like 1971, together with the resultant reductions in primary and secondary production, probably have important effects upon nearshore fisheries. A statistical link exists between summer upwelling strength and Dungeness crab production (Peterson, 1973). A strong upwelling season results in a heavy crab catch 1½ yr later. The Dungeness crab catch for the 1972-1973 season was one of the lowest on record.

Other fisheries seem to have been similarly affected. The Fish Commission of Oregon has documented 1971 as a poor growth year for the shrimp *Pandalus jordani* (Robert L. Demory, Oregon Fish Commission, Newport, Ore., pers. commun.), coho salmon, *Oncorynchus kisutch* (Paul H. Reed, Oregon Fish Commission, Newport, Ore., pers. commun.), and razor clams *Siliqua patula* (C. Dale Snow, Oregon Fish Commission, Newport, Ore., pers. commun.). The shrimp data are mean carapace length of Age I animals from the Coos Bay, Ore. area (lat. 43°15'N) and are as follows: 1969, 16.45 cm; 1970, 16.76 cm; and 1971, 15.87 cm. Averaged dressed weights of coho salmon were 2.59 kg in 1969, 3.41 kg in 1970, and 2.68 kg in 1971. Razor clam lengths averaged 75.4 mm in 1969, (no data for 1970), 69.4 mm in 1971, 78.5 mm in 1972, and 83.5 mm in 1973. Some of these data may be better interpreted in terms of good growth years. As shown by the wind data (Figure 3), 1970 had many more days of upwelling inducing winds than 1969. Primary and secondary production should have been greater in 1970. Both shrimp and coho salmon were larger in 1970. Unfortunately no razor clam data were taken in 1970, but data for other years support the conclusion that 1971 was a poor growth year.

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USE OF OTOLITHS TO SEPARATE JUVENILE STEELHEAD TROUT FROM JUVENILE RAINBOW TROUT[1]

J. T. RYBOCK[2], H. F. HORTON[2], AND J. L. FESSLER[3]

ABSTRACT

Otolith nuclei were investigated as a means of separating juvenile steelhead trout, *Salmo gairdneri*, from juvenile rainbrow trout, *S. gairdneri*, in the lower Deschutes River, Oreg. An intensive recreational fishery necessitated development of a technique for differentiation so that impact of the fishery on each race could be assessed independently.

Investigations of adults and hatchery-reared young of *S. gairdneri* revealed that otolith nuclei of steelhead are significantly larger than those of rainbow, size of otolith nuclei does not change with growth of either race, and there are no differences in size of otolith nuclei due to sex or origin (wild vs. hatchery). Thus, size of otolith nuclei provides a means to differentiate effectively juvenile steelhead trout and juvenile rainbow trout regardless of sex or origin. Resuits also indicated that steelhead mature at a larger size than rainbow, egg size is directly related to body size of dam in both races, and size of otolith nuclei is likely determined by egg size.

This paper reports on an investigation of growth characteristics of the sagittae, the largest of the otoliths, as a means to separate juvenile steelhead trout, *Salmo gairdneri*, from juvenile rainbow trout, *S. gairdneri*. The technology for such differentiation is presently lacking but is necessary for independent management of the two races in streams where they coexist. In the lower Deschutes River, Oreg., for example, the most intensive fishery for rainbow trout occurs during the first week in May when most steelhead smolts migrate; consequently, the catch may be composed of 22-80% juvenile steelhead (King 1966; Wagner and Haxton 1968). Precise knowledge of this catch composition at various locations and times would allow fisheries managers to manipulate fishing pressure so that most steelhead smolts escape capture during migration.

Previously, otoliths have been used to differentiate stocks and races of salmonids. Kim (1963) found differences in the appearance and size of growth rings between spawning groups of sockeye salmon, *Oncorhynchus nerka*. The study most relevant to our investigation demonstrated that winter and summer races of steelhead trout can be separated on the basis of differences in size of the otolith nucleus (ON) (McKern et al. 1974).

The latter authors found that the otolith nucleus is formed early in steelhead trout embryos when all or a great part of nutrition comes from the yolk, and that ON size appears to be directly related to egg size. Also, egg size and fish length of salmonids are often directly related (McFadden et al. 1965; Bulkley 1967; Galkina 1970), and steelhead trout are generally larger than rainbow trout at maturity. Therefore, we hypothesized that steelhead ON are sufficiently larger than rainbow ON to permit separation of juveniles of both races.

We investigated this hypothesis via two series of observations. In the first, an indirect test of validity of the hypothesis, we compared measurements of ON of fish of known race and then determined whether these measurements changed with growth of fish or whether they were related to sex or origin. In the second series, we measured body size of adult fish, egg size of ripe dam, and ON size of fry hatched from these eggs, to determine if correlations between these variables logically accounted for differences in ON sizes. All investigations were conducted on adults and hatchery-reared fingerlings of summer steelhead trout and resident rainbow trout captured in 1971-73 from the lower Deschutes River.

METHODS AND MATERIALS

Study Area

The study area was the lower 100 miles of the

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Deschutes River in north central Oregon (Figure 1). The Deschutes River drains approximately 10,400 square miles, or nearly 11% of the land area of Oregon. Its western tributaries stem from the Cascade Mountains, while eastern tributaries drain Oregon's high plateau. Regulated river flows below Pelton Dam average from 3,000 to 7,100 cfs. Important sport fish in the area include resident rainbow trout, summer steelhead trout, and chinook salmon, *O. tshawytscha*, (Montgomery 1971).

Collection of Samples

Otoliths were obtained from adult (≥200 mm fork length [FL]) rainbow and steelhead (n = 101) sampled during routine Oregon Wildlife Commission creel censuses at Webb's access road (at Buck Hollow Creek) and near Maupin (Figure 1) during August and September 1971 and 1972. Otoliths were removed with a punch described by McKern and Horton (1970). Each fish was measured (FL) and scales (ca. 20) were removed from an area below the origin of the dorsal fin and just above the lateral line. Race was determined from a combination of coloration, relative size, and analysis of scales (Maher and Larkin 1954). In most cases sex was determined from jaw conformation and opercular coloration (steelhead only), and occasionally from fisherman's observations if the fish had been cleaned. To determine origin, we examined steelhead for hatchery marks; hatchery-reared rainbows were distinguished by worn or rounded fins, excessive number of missing scales, and other abnormalities.

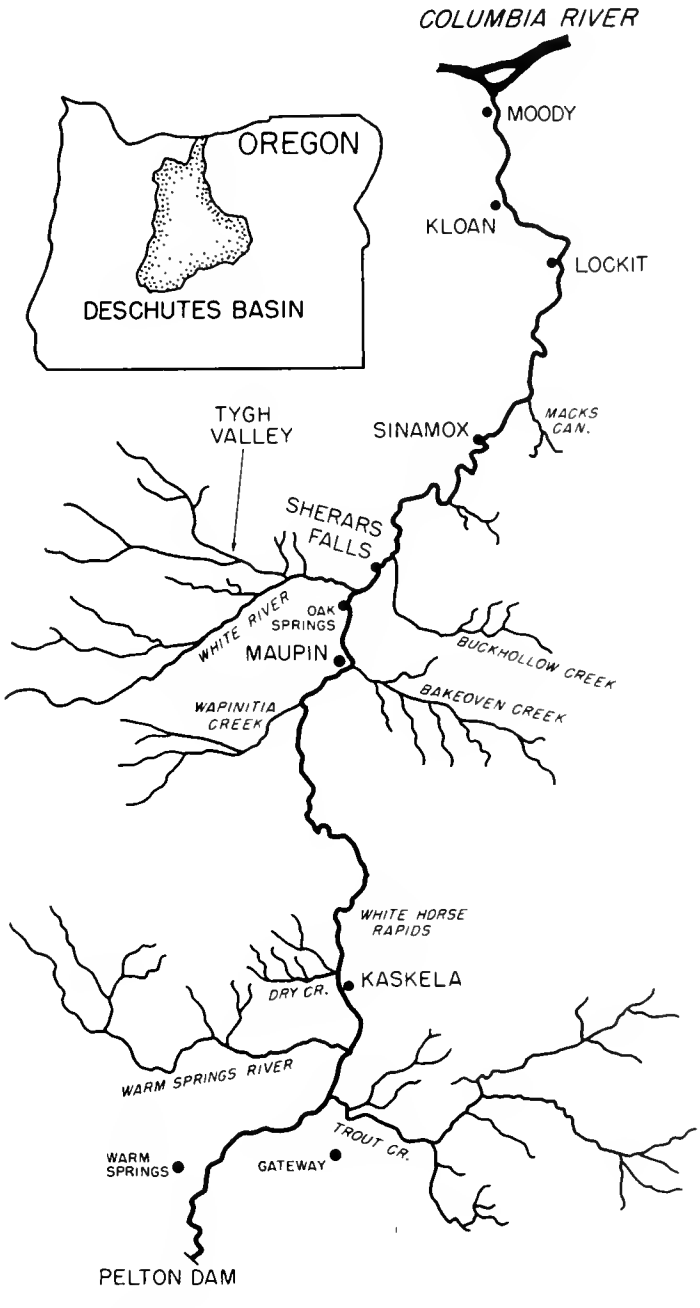

FIGURE 1.—Map of study area on the lower 100 miles of the Deschutes River, Oreg.

Other adult fish (n = 92) were collected by electrofishing near Maupin, below Pelton Dam, and in Bakeoven and Trout creeks (Figure 1) in April-June 1971 and August 1972. Each fish was measured (FL), and race, sex, and origin were determined as above. Otoliths were removed by dissection.

In January 1973, 52 steelhead fingerlings were obtained from the stock of Deschutes River steelhead reared at Wizard Falls Hatchery (Oregon Wildlife Commission) on the Metolius River. These fish represented a random assortment of the offspring of ca. 150 females captured below Pelton Dam. Fork lengths were measured, and otoliths were removed by dissection.

To determine body lengths of mature steelhead trout and rainbow trout, specimens were obtained by electrofishing in the lower Deschutes River in 1972. Fork lengths were measured, and race was determined from hatchery marks or coloration (migrating summer steelhead are more silvery than resident rainbow).

For determination of ova size, adult steelhead were captured in late winter 1972 by trapping below Pelton Dam and were held in tanks until ripe. Twenty-two females were measured (FL), and a sample of eggs (ca. 100) was collected from each fish, fertilized, and allowed to water harden 8-22 h. From 20 to 60 eggs from each pairing were then measured volumetrically (10^{-2} ml) in a 25-ml burette.

Rainbow trout were captured in spring 1972 by electrofishing in the main stem of the Deschutes River. Male-female pairs were individually

spawned, and, after water hardening, the eggs were transported to a laboratory in Corvallis to be hatched. Shortly after arrival, 20 eggs from each of 13 matings were measured as above. Fork lengths were later determined from the frozen dams and sires.

To obtain samples for determination of possible correlation between egg size and ON size of the hatched fry, we randomly selected 10 fingerlings from each of eight available matings of rainbow trout individually hatched and reared in Corvallis (above). Fork lengths were measured, and otoliths were removed by dissection.

Storage and Treatment of Otoliths

The enveloping membrane (sacculus) was removed from each otolith prior to storage. Initially, otoliths were stored dry in coin envelopes before transfer to a clearing solution. Because this method led to breakage of otoliths, later samples were placed in a clearing solution immediately after removal from the fish. Otoliths were cleared from 1 to 21 mo before examination; there was no apparent relationship between clearing time and readableness of the otolith.

Samples were initially cleared in methyl salicylate. Because some otoliths did not clear sufficiently, a 50:50 mixture of glycerin and water (McKern et al. 1974) was used for the remainder of the samples, but this solution tended to increase the opacity of the entire otolith. Neither burning these otoliths on an asbestos pad over a bunsen burner nor clearing the otoliths in oil of cloves increased contrast between the opaque and hyaline parts. Consequently, it was difficult to discern the nucleus.

Improved readings were obtained by applying drops of HCl to the medial surface of otoliths preserved in glycerin and water; this resulted in a dissolution of the medial lobes, a consequent thinning of the otolith, and clearer definition of density patterns. This method is quick (a few milliliters of HCl applied for 2-4 min for a large otolith) and is easily controlled by periodic inspection of the otolith during treatment. Because the edges of the otolith are dissolved, this method should not be used when age determinations are required.

Terminology and Examination of Otoliths

When viewed under reflected light on a black background, the ON of *S. gairdneri* is hyaline with a narrow opaque ring around the border (Figure 2). The metamorphic check is a narrow hyaline ring delineating the nucleus (Kim and Koo 1963). For examination, otoliths were placed lateral surface up on black Plexiglas[4] depression plates, illuminated with a beam of light at 45° and photographed on 35-mm film through a microscope at 50×. Panatomic-X film (ASA 32) was used, and the negatives were enlarged to 4×5 or 5×7 inches onto grade 3 or 4 (high contrast) paper. A stage micrometer was also photographed and enlarged at the same magnifications so that otolith measurements could be determined from the photographs. The length and width of the nucleus (Figure 2) was measured from the photographs by using a compass and the corresponding photograph of the micrometer.

RESULTS AND DISCUSSION

Size of Otolith Nucleus

The linear correlation between ON length and width was strong in both rainbow trout (r = 0.838)

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

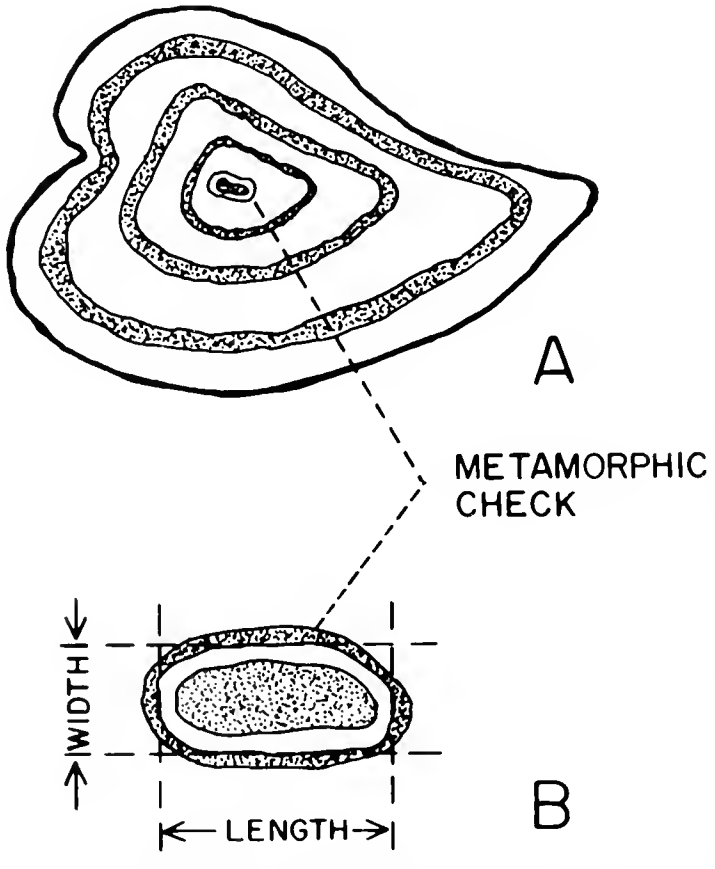

FIGURE 2.—Illustration of (A) otolith and (B) otolith nucleus of *Salmo gairdneri*, with notation of measurements and terminology used.

and steelhead trout (r = 0.916). Neither seemed easier to read. Primarily due to problems of developing methodology, 189 ON (29% of 641 examined) were not sufficiently distinct to permit measurement. Usually, the hyaline center of the nucleus was visible, but the metamorphic check could not be distinguished. Because measurement of the larger dimension would likely be more precise than widths, ON length was used in the following analyses.

The mean ON lengths of steelhead trout (0.354 mm; n = 114) and rainbow trout (0.245 mm; n = 145) differed significantly ($P \leq 0.001$). The length-frequency plot of these data (Figure 3A) demonstrates an overlap of lengths. Most unexpected in this plot are the nucleus lengths for steelhead less than 0.26 mm. These values occur in direct proportion to the values for rainbow; also, these steelhead are from Wizard Falls Hatchery, where both rainbow and steelhead are reared. Perhaps these fish are rainbow offspring which were inadvertently mixed with steelhead during hatchery operations or hybrids of the two species. The length-frequency plot of steelhead ON excluding those from Wizard Falls Hatchery increased the normality of the histogram (Figure 3B); the nadir

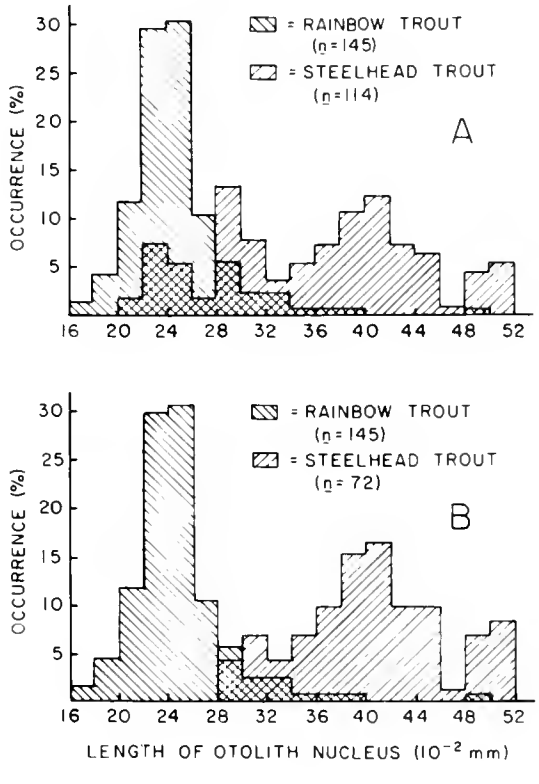

FIGURE 3.—Length-frequency distribution of otolith nuclei of (A) rainbow trout and all steelhead trout and (B) rainbow trout and steelhead trout excluding those from Wizard Falls Hatchery. All fish were captured from the lower Deschutes River, Oreg., 1971-73.

at 0.46-0.48 mm is probably due to the small sample size of each interval. Therefore, although overlap of ON size of the two races occurs between 0.28 mm and 0.34 mm, the race of most juvenile *S. gairdneri* from the Deschutes River can be determined reliably on the basis of this measurement.

The histogram for rainbow more closely approximates a normal distribution, probably the result of a larger sample size and of the many sources of variation operating within a more narrow size range of spawning fish. The ON length of one adult rainbow was 0.48 mm. Although no hatchery marks were noticed, scale characteristics suggested a hatchery origin; because we have observed that almost all hatchery-reared rainbow succumb to *Ceratomyxa* before reaching maturity in the lower Deschutes River, this may have been a nonmigratory steelhead. In general, though, data from our samples do not support the suggestion of Wagner and Haxton (1968) that there may be a great number of such nonmigrants in the Deschutes River.

To determine whether size of ON changes during growth of fish, we regressed length of ON against FL of fish: For rainbow, r = 0.060. For all steelhead, r = 0.694; however, if Wizard Falls fish are excluded, r = 0.018. Even with this exclusion, a wide range of steelhead FL (504-762 mm) was tested; and if the relationship was strong it should have been noticeable in these data.

Mean length of ON was 0.339 mm for all females and 0.317 mm for all males; they are not significantly different ($P \geq 0.20$). Also, the data suggest no significant male-female difference within either race.

Mean length of ON of wild steelhead (0.395 mm; n = 52) was not significantly different ($P \geq 0.20$) from that of hatchery-reared steelhead excluding those from Wizard Falls Hatchery (0.405 mm; n = 20). A similar comparison between adult hatchery-reared and wild rainbow cannot be made since there are few, if any, adult hatchery-reared rainbow in the lower Deschutes River (as mentioned earlier, hatchery fish released in spring succumb to *Ceratomyxa* by summer).

Fish, Egg, and ON Size Relationships

The lengths of rainbow trout and steelhead trout from the lower Deschutes River are distributed into discrete size ranges (Figure 4). Although these fish are not necessarily ready to

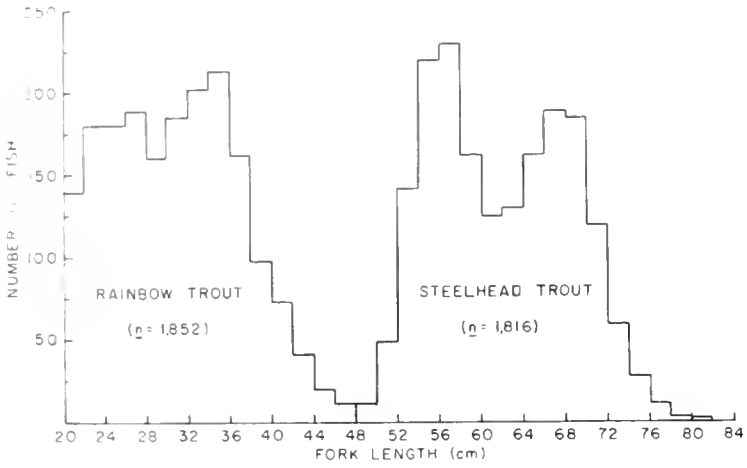

FIGURE 4.—Length-frequency distribution of mature (>20 cm) rainbow trout and steelhead trout from the lower Deschutes River, Oreg., 1972.

spawn, the data indicate low likelihood of significant overlap in length of mature rainbow and steelhead trout.

The mean egg size of steelhead (0.0936 ml) was significantly greater ($P \leq 0.001$) than that of rainbow (0.0727 ml). Also, mean egg size was strongly correlated with length of female (r = 0.829 and 0.791 for rainbow and steelhead trout, respectively) (Figure 5), although there was much variability of mean egg sizes between fish of a similar length and of egg sizes from any one female. For some fish, the largest egg was twice the size of the smallest.

The above r values between body size of dam and egg size are higher than those reported in many other investigations. Scott (1962) measured FL and egg weight of rainbow trout and found no significant correlation. Considering the narrow range of FL (231-264 mm) and the great variability of egg size within length classes, his

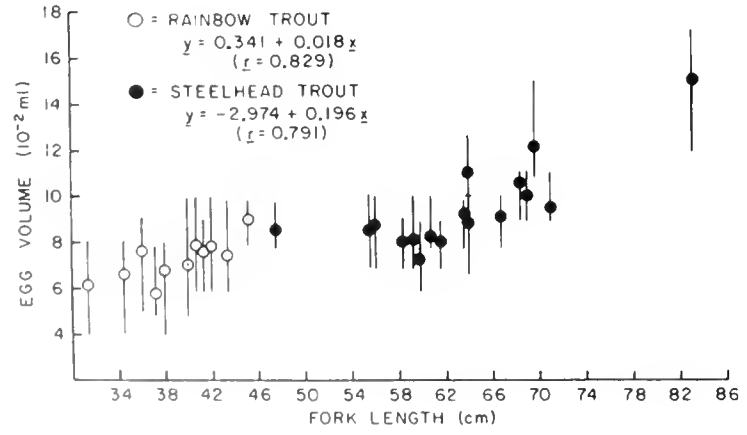

FIGURE 5.—Means and ranges of egg size plotted against length of dam for rainbow trout and steelhead trout from the lower Deschutes River, Oreg., 1972.

results are not surprising. Galkina (1970) found that length of rainbow trout, *S. irideus*, was not highly correlated with mean egg weight (r = 0.48). Although eggs of average size were found in all his females, the smallest eggs were obtained only from smaller females and vice versa. McFadden et al. (1965) found a higher correlation (r = 0.73) between egg size and length of brown trout, *S. trutta*. Blaxter (1969), Galkina (1970), and Lindsey and Ali (1971) cited numerous authors who examined this relationship in many species of fish; although most authors reported a wide range of egg sizes in females of similar length, there is general agreement that a direct, and often high, correlation exists between egg size and dam size.

The presence or absence of any correlation between egg size and ON size of the hatched fish could not be determined directly for the rainbow trout groups reared in Corvallis (egg size had been measured for only four of the eight females whose offspring were available, and we considered this sample size too small). However, since there was a high correlation between egg size and length of dam (r = 0.829), this latter measurement was regressed against ON size of offspring from the eight matings (Figure 6). The r value of 0.489 and the overlap of ranges indicate the relationship is not strong; however, it is a positive correlation. Also, the small sample size (8), the narrow range of dam lengths (295-415 mm), the variation of egg size within any dam, and the substitution of FL for egg size are factors which may have obscured the real extent of the relationship of fish size to ON size.

In summary, we found that because steelhead ON are larger than rainbow ON, size of ON does not change with growth of either race, and correlations of ON size between dams and sires and between wild and hatchery-reared fish of either race are insignificant, ON size is an effective means of differentiating juvenile steelhead trout and juvenile rainbow trout regardless of sex or origin. We also concluded that because steelhead trout are larger at maturity than rainbow trout and because egg size is a direct function of body size, eggs of steelhead trout are larger than those of rainbow trout; and although we did not conclusively demonstrate that ON size is directly related to egg size, other evidence was offered to support the hypothesis that larger egg size was the mechanism responsible for larger ON size in steelhead trout as compared to rainbow trout.

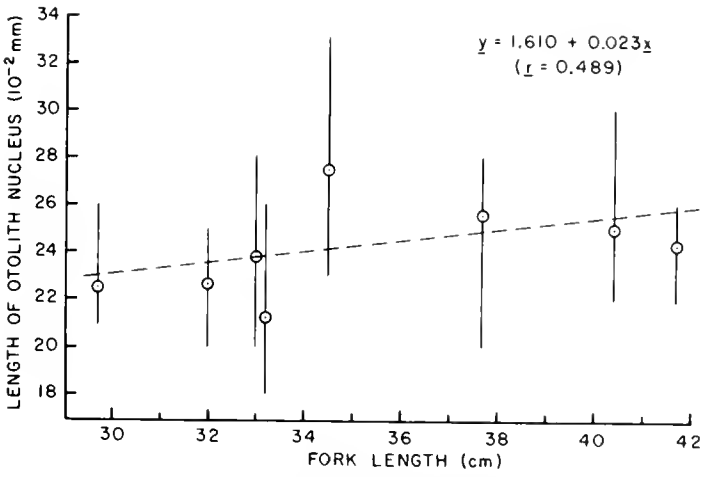

FIGURE 6.—Regression of length of rainbow trout dam from the Deschutes River on length of otolith nucleus of offspring cultured in Corvallis, Oreg., 1972. (Circles are means, and vertical bars are ranges of observation.)

ACKNOWLEDGMENTS

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DESCRIPTION OF EGGS AND LARVAE OF YELLOWFIN MENHADEN, *BREVOORTIA SMITHI*[1]

EDWARD D. HOUDE[2] AND L. J. SWANSON, JR.[3]

ABSTRACT

Development of yellowfin menhaden, *Brevoortia smithi*, is described from eggs and larvae reared in the laboratory. Eggs were collected during November 1972 in Biscayne Bay, Florida. Eight embryos and 66 larvae and juveniles ranging from 3.7 to 36.2 mm standard length were used to describe development. Mean egg diameter was 1.27 mm, mean oil globule diameter was 0.15 mm, and mean yolk diameter was 1.07 mm. The perivitelline space averaged 16% of the egg diameter. Length at hatching was about 3.0 mm standard length. Larvae were fed on zooplankton and grew about 0.45 mm per day from the 4th until the 20th day after hatching at 26°C. Morphology, meristics, osteology, and pigmentation are described. Transformation from larvae to juveniles apparently was completed at 20 to 23 mm standard length. During transformation full complements of fin rays were developed, the dorsal fin moved forward, the gut shortened, and the anal fin moved forward. Yellowfin menhaden larvae have some characteristics that serve to distinguish them from larvae of other clupeid genera occupying the same geographic range, and also have some characters that may be helpful to distinguish them from other species in the genus *Brevoortia*.

The yellowfin menhaden, *Brevoortia smithi* Hidelbrand, is one of four species of *Brevoortia* that occur along the Atlantic and Gulf of Mexico coasts of the United States. The biology and systematics of yellowfin menhaden were discussed in detail by Hildebrand (1963) and most recently by Dahlberg (1970). Dahlberg reported that *B. smithi* occurs from North Carolina to Louisiana. Atlantic and Gulf of Mexico populations exist, which apparently are distinct, and the species is uncommon south of West Palm Beach on the Florida Atlantic coast and north of Tampa Bay on the Florida west coast. Although common in parts of its range, yellowfin menhaden are not abundant enough to contribute substantially to commercial menhaden catches (Dahlberg 1970). Reproducing populations apparently are confined to coastal areas of the United States, but Levi (1973) reported some juveniles from the Bahamas. Hybrids of *B. smithi* × *B. tyrannus* on the Atlantic coast and *B. smithi* × *B. patronus* on the Gulf coast commonly occur (Turner 1969; Dahlberg 1970).

Reintjes (1962) artificially fertilized eggs of yellowfin menhaden from Indian River, Fla. He presented a series of photographs and described developing embryos and yolk-sac larvae. Hybrid embryos and yolk-sac larvae of yellowfin menhaden and Gulf menhaden, *B. patronus*, were produced artificially (Hettler 1968), and photographs of these embryos and larvae were published. More recently, Hettler (1970a) reared some yellowfin menhaden larvae from artificially fertilized eggs to 14.9 mm. He illustrated larvae of 7.6 and 11.9 mm total length (TL). Despite the literature on yellowfin menhaden development, no complete series from egg through transformation of larvae to the juvenile stage is available, nor have detailed illustrations been published that would be helpful to distinguish yellowfin menhaden from other similar clupeid larvae. We have reared yellowfin menhaden from naturally spawned planktonic eggs to advanced juveniles and we describe development of these stages in this paper.

Eggs and larvae of other *Brevoortia* species have been described, but only those of the Atlantic menhaden, *Brevoortia tyrannus*, are well known. Mansueti and Hardy (1967) have reviewed published information on Atlantic menhaden development. Suttkus (1956) described larvae of Gulf menhaden 18.9 mm and longer, but smaller specimens are undescribed. The eggs and larvae of finescale menhaden, *Brevoortia gunteri*, have not

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been described. DeCiechomski (1968) has discussed occurrence and photographed eggs and yolk-sac larvae of *Brevoortia aurea* from Argentina.

Using our rearing techniques (Houde 1973b), it was relatively simple to rear yellowfin menhaden from eggs to advanced juveniles. Presumably the other species, including Atlantic and Gulf menhaden, can be reared by similar methods if their eggs can be obtained. It should now be possible to conduct experiments under laboratory conditions, testing environmental factors on development of eggs and larvae of these important commercial species.

METHODS

Collecting Eggs

Naturally fertilized eggs from Biscayne Bay, Miami, Fla. were collected in 1-m diameter, 505-μm mesh plankton nets suspended from the dock of the Rosenstiel School of Marine and Atmospheric Science on 3 November and 26 November 1972. Surface temperatures were 25.4° and 22.7°C on the respective collecting days and salinity was 32-33‰. Yellowfin menhaden eggs were sorted by pipette from the other plankton organisms. The eggs that were sorted were known to be yellowfin menhaden because some of the same type had been hatched and the larvae reared during rearing trials in 1971. A total of 90 eggs on 3 November and 170 eggs on 26 November were placed in rectangular tanks of 38-liter capacity for rearing.

Rearing and Preserving Methods

Rearing techniques were similar to those described by Houde (1973b) and Houde and Palko (1970). For the first 20 days of culture, temperature was controlled at 26° ± 1.0°C. Salinities ranged from 33.5 to 37.0‰ and light was provided by fluorescent fixtures at an intensity of 2,500 lx. Zooplankton, consisting mostly of copepod nauplii and copepodites, collected in a 35-μm mesh plankton net, was fed to larvae for the first 12 days; subsequently *Artemia salina* nauplii were fed in addition to zooplankton. A total of 8 embryos and 66 surviving larvae were preserved in 5% buffered Formalin[4] during the culture period to provide the series used to describe development. Specimens from 3.7 mm to 36.2 mm SL (standard length) were included in the developmental series (Table 1), but many juveniles continued to survive and were reared to lengths of 50-60 mm before experiments were terminated.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Meristics and Morphometrics

Methods for counting and measuring are identical to those used by Houde et al. (1974) for *Harengula jaguana* Poey larvae.

Fin rays were counted in each of the developing fins of unstained larvae (Table 2). Myomeres were counted (Table 3) and examined in relation to the dorsal fin and anus. The following myomere counts were made:

Total myomeres: all myomeres; does not include the triangular area preceding the first myoseptum.
Preanus myomeres: number anterior to the anus.
Postanus myomeres: number posterior to the anus.
Predorsal myomeres: number anterior to the dorsal fin origin.
Postdorsal-preanus myomeres: number between the posterior insertion of the dorsal fin and the anus.

The following measurements were made (Table 1): total length, standard length, preanus length, predorsal length, prepelvic length, head length, snout length, eye diameter, and body depth. All references to lengths of larvae in text are to standard length unless otherwise noted.

Osteology

Sequence of ossification was determined from 10 specimens ranging from 5.2 to 25.3 mm SL. They were cleared with trypsin and stained with alizarin, using the method of Taylor (1967).

DESCRIPTION

Embryos

Eight fertilized eggs from the plankton collections were preserved. The embryos were approximately at the midstage of development at the time of collection. Eggs were spherical, the

TABLE 1.—Specimens of laboratory-reared *Brevoortia smithi* used to describe development. Measurements in millimeters.

Total length	Standard length	Preanus length	Predorsal length	Prepelvic length	Head length	Snout length	Eye diameter	Body depth
4.0	3.7	3.1	—	—	0.46	0.08	0.22	—
4.2	4.0	3.4	—	—	0.60	0.11	0.22	0.38
4.2	4.1	3.3	—	—	0.56	0.09	0.20	0.39
4.3	4.1	3.4	—	—	0.52	0.10	0.24	—
4.3	4.2	3.4	—	—	0.52	0.09	0.24	—
4.4	4.2	3.4	—	—	0.56	0.10	0.19	0.40
4.4	4.2	3.4	—	—	0.54	0.06	0.20	0.37
4.4	4.2	3.5	—	—	0.60	0.08	0.26	—
4.4	4.2	3.6	—	—	0.54	0.08	0.26	—
4.5	4.3	3.5	—	—	0.56	0.07	0.22	0.39
4.6	4.4	3.5	—	—	0.55	0.08	0.22	0.34
4.6	4.4	3.6	—	—	0.56	0.08	0.20	0.40
4.6	4.4	3.6	—	—	0.57	0.08	0.23	0.34
4.6	4.4	3.6	—	—	0.60	0.08	0.22	0.38
4.6	4.4	3.6	—	—	0.61	0.10	0.21	0.42
4.7	4.5	3.7	—	—	0.56	0.06	0.24	—
4.7	4.5	3.8	—	—	0.62	0.09	0.24	0.34
4.7	4.5	3.7	—	—	0.56	0.07	0.24	0.40
4.8	4.6	3.8	—	—	0.56	0.08	0.24	0.36
4.8	4.6	3.8	—	—	0.55	0.08	0.22	0.36
4.8	4.6	3.7	—	—	0.56	0.10	0.24	0.36
4.9	4.7	3.7	—	—	0.60	0.09	0.24	0.42
5.4	5.2	4.3	—	—	0.69	0.11	0.25	0.43
5.5	5.2	4.2	—	—	0.74	0.16	0.24	0.43
5.9	5.7	4.8	—	—	0.72	0.10	0.26	0.43
6.3	6.1	5.0	—	—	0.86	0.16	0.26	0.48
6.7	6.4	5.5	—	—	0.84	0.18	0.27	0.47
7.3	7.0	5.9	—	—	0.93	0.18	0.28	0.50
7.5	7.3	6.1	5.0	—	0.88	0.16	0.34	0.58
7.5	7.2	6.0	4.9	—	0.82	0.12	0.26	0.50
7.7	7.4	6.1	5.0	—	1.04	0.26	0.32	0.56
7.7	7.5	6.2	5.1	—	1.08	0.18	0.36	0.65
7.8	7.4	6.3	4.8	—	1.14	0.20	0.26	0.64
8.8	8.6	7.2	5.7	—	1.28	0.22	0.36	0.72
8.8	8.6	7.1	5.5	—	1.42	0.30	0.42	0.70
8.9	8.6	7.1	5.8	—	1.04	0.23	0.28	0.60
8.9	8.6	7.2	5.0	—	1.16	0.28	0.32	0.56
9.3	8.8	7.6	5.8	—	1.42	0.32	0.40	0.74
9.6	9.2	7.8	6.1	—	1.20	0.34	0.38	0.72
10.0	9.5	8.0	6.2	—	1.36	0.22	0.42	0.73
10.2	9.6	8.1	6.3	—	1.56	0.36	0.42	0.72
10.6	10.2	8.6	6.9	—	1.48	0.32	0.42	0.84
10.7	9.9	8.4	6.4	—	1.68	0.30	0.46	0.80
10.8	10.0	8.4	6.5	—	1.64	0.30	0.44	0.80
11.0	10.1	8.5	6.4	—	1.72	0.34	0.48	0.86
11.1	10.3	8.7	6.8	—	1.80	0.38	0.48	0.92
11.2	10.5	8.9	6.7	—	1.64	0.34	0.48	0.80
11.3	10.3	8.7	6.6	—	1.80	0.34	0.48	0.88
11.8	10.9	9.3	6.8	—	2.04	0.40	0.59	0.94
12.3	11.2	9.5	7.0	—	2.24	0.52	0.64	1.04
12.8	11.3	9.3	6.8	5.5	2.14	0.47	0.60	1.00
13.6	12.1	10.3	7.9	—	2.32	0.47	0.60	1.12
13.7	12.3	10.6	7.7	5.8	2.32	0.48	0.76	1.18
14.2	12.6	10.3	7.7	6.1	2.76	0.56	0.84	1.42
15.2	13.5	10.9	8.4	6.6	3.00	0.66	0.80	1.48
15.6	13.8	11.4	8.4	6.2	2.68	0.52	0.82	1.54
18.0	15.5	12.5	9.2	7.9	4.00	0.83	1.32	2.60
18.0	15.9	13.0	9.2	6.9	3.12	0.68	0.90	1.80
19.1	16.2	12.6	9.2	7.9	4.12	0.86	1.24	2.66
19.5	16.9	13.0	9.3	8.8	4.83	1.00	1.50	3.42
21.1	17.8	13.3	9.4	9.1	5.25	1.20	1.56	3.92
21.2	18.0	14.2	9.5	9.1	5.17	1.25	1.62	4.25
27.1	22.7	16.8	11.7	11.8	7.46	1.67	2.50	6.58
30.1	25.3	18.3	12.5	13.2	7.92	1.90	2.50	7.50
41.2	33.3	23.9	15.7	17.4	11.10	2.31	3.42	10.60
43.9	36.2	26.7	18.0	20.0	12.05	2.74	3.42	11.96

chorion was thin and unsculptured, and they had a single yellowish oil globule. Egg diameters ranged from 1.21 to 1.34 mm (mean = 1.27 mm), and oil globule diameters ranged from 0.12 to 0.17 mm (mean = 0.15 mm). Yolk diameters ranged from 0.80 to 1.19 mm (mean = 1.07 mm) and were large relative to egg diameter. Our egg diameters and oil globule diameters are much like those reported

TABLE 2.—Some meristic characters of laboratory-reared specimens of *Brevoortia smithi*.

Standard length (mm)	Days after hatching	Principal caudal rays	Procurrent caudal rays		Dorsal rays	Anal rays	Pectoral rays	Pelvic rays
			Dorsal	Ventral				
3.7-7.2	0-5	No elements present on 29 specimens in this size range.						
7.3	5	—	—	—	6	—	—	—
7.4	7	—	—	—	7	—	—	—
7.4	5	—	—	—	4	—	—	—
7.5	9	2	—	—	7	—	—	—
8.6	6	2	—	—	6	—	—	—
8.6	5	2	—	—	6	—	—	—
8.6	7	4	—	—	8	—	—	—
8.6	15	3	—	—	12	—	—	—
8.8	9	18	—	—	14	7	—	—
9.2	7	3	—	—	9	—	—	—
9.5	8	17	—	—	11	—	—	—
9.6	9	19	—	—	13	?	—	—
9.9	11	19	—	—	15	10	—	—
10.0	10	19	—	—	14	—	—	—
10.1	16	19	—	—	17	7	—	—
10.2	7	17	—	—	13	—	—	—
10.3	13	19	—	—	16	12	—	—
10.3	11	19	—	—	14	8	—	—
10.5	11	19	—	—	15	9	—	—
10.9	18	19	—	—	16	16	—	—
11.2	18	19	3	2	18	14	—	—
11.3	15	19	2	1	18	18	—	—
12.1	15	19	3	2	17	14	—	—
12.3	20	19	3	2	19	18	—	—
12.6	29	19	4	3	18	20	—	6
13.5	24	19	5	3	18	19	—	6
13.8	24	19	4	3	19	19	—	6
15.5	43	19	7	6	20	21	13	7
15.9	18	19	6	5	17	18	5	4
16.2	28	19	8	6	19	20	13	7
16.9	43	19	7	6	19	20	14	7
17.8	31	19	8	7	20	21	15	7
18.0	38	19	9	8	20	20	14	7
22.7	60	19	8	6	21	21	14	7
25.3	50	19	8	7	20	21	14	7
33.3	176	19	8	7	20	21	16	7
36.2	102	19	8	7	20	20	15	7

TABLE 3.—Distribution of myomeres relative to other body parts for *Brevoortia smithi* larvae.

Length class (mm, SL)	Preanus myomeres			Postanus myomeres			Predorsal myomeres			Postdorsal-preanus myomeres		
	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Number of specimens	Range	Mean
3.7- 6.0	24	36-39	37.58	24	7- 9	7.96	—	—	—	—	—	—
6.1- 8.0	8	36-38	37.25	8	7- 9	8.12	4	27-29	28.00	4	5-6	5.25
8.1-10.0	10	35-37	36.20	10	8-11	9.70	10	24-28	26.20	10	4-5	4.60
10.1-12.0	8	33-37	35.38	8	10-13	10.75	8	22-25	24.00	8	3-5	4.00
12.1-14.0	5	33-35	33.40	5	11-13	12.20	5	21-22	21.40	5	3-4	3.40
14.1-16.0	2	30-33	31.50	2	13-15	14.00	2	19-21	20.00	2	2-4	3.00
16.1-18.0	4	29-31	29.75	4	15-16	15.50	4	18-22	19.50	4	2	2.00
>22.7	4	28-29	28.50	4	16-18	17.00	4	15-17	15.75	4	2-3	2.25

by Reintjes (1962) for yellowfin menhaden, but yolk diameters differ greatly. In his specimens the perivitelline space averaged more than 30% of the egg diameter, but in our specimens it averaged only 16%. The difference might be partly accounted for by the incubation salinities. Salinities at Indian River where Reintjes did his study were relatively low, ranging from 20.5 to 27.2‰, while those in Biscayne Bay during our study exceeded 32‰. Hettler (1968) also reported narrow perivitelline spaces in hybrid eggs from *B. smithi* × *B. patronus* that he artificially fertilized at the collection site where salinities were 33-34‰. Previtelline spaces in his embryos ranged from 7 to 17% of the egg diameters, and he attributed the narrow spaces to possible effects of high salinity. Yellowfin menhaden eggs have been collected by us from Biscayne Bay on many occasions in 1971 to 1973, and they always are characterized by a relatively narrow perivitelline space, which is unusual

for clupeid species that spawn in South Florida marine waters.

Developing embryos resembled those described and photographically illustrated by Reintjes (1962). On our preserved specimens, tiny melanophores were present only on the dorsal surface of the developing embryo. The yolk mass was segmented, but this was observed with difficulty in preserved material. No pigment was observed on the yolk sac or oil globule of our preserved eggs.

Spawning by yellowfin menhaden in Biscayne Bay occurred at least between November and February. Spawning by this species has not been reported previously in Biscayne Bay, but eggs were common during 1971-73. We do not know the time of day at which spawning took place or the total incubation time at 22° to 26°C. Hettler (1970b) collected planktonic eggs of yellowfin menhaden in the Indian River and observed that they spawned at dusk. Reintjes (1962) reported hatching in 46 h at 19°C. Since we have collected embryos only in a single stage of development when temperatures were above 22°C, incubation time might be 24 h or less at these temperatures. Eggs were collected between 0900 and 1400 h; hatching in our aquaria was complete before 2400 h.

Description of Larvae

Body Shape and Growth

Larvae were about 3.0 mm SL at hatching. They averaged 4.2 mm SL at 20 h after hatching (Figure 2A) when the body axis had straightened. During the first 2 days after hatching they were similar to yellowfin menhaden larvae described by Reintjes (1962). Larvae resemble those of other clupeid fishes. They are elongate, rod-shaped larvae after the yolk has been absorbed. At transformation they become deeper bodied and more laterally compressed. Proportional measurements of larvae in relation to standard length are summarized in Table 4.

Most larvae did not grow in length from the 1st until the 4th day after hatching at 26°C. Growth was rapid from the 4th until the 10th day (Figure 1), averaging about 0.80 mm/day. Growth was slower and more variable on subsequent days, but averaged about 0.45 mm/day from the 4th until the 20th day after hatching. Our 36.2-mm specimen was preserved 102 days after hatching,

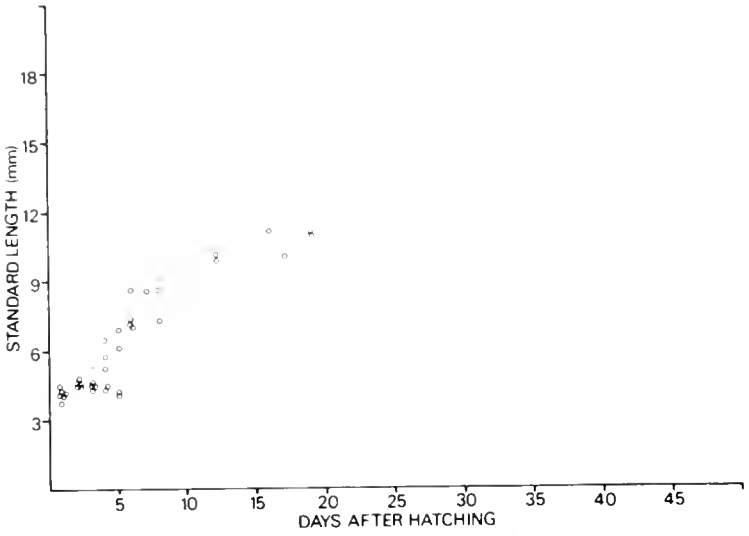

FIGURE 1.—Growth of laboratory-reared larvae of *Brevoortia smithi*.

but growth rate of juveniles was almost certainly lower than might be expected under better feeding conditions because we did not maintain a careful feeding schedule after larvae transformed to the juvenile stage. Several juveniles from 50 to 60 mm were preserved when the experiments were terminated at 235 days after hatching. At 20°C, Hettler (1970a) reported growth rates of about 0.27 mm/day for yellowfin menhaden larvae that he reared for 27 days. The four smallest larvae that we preserved on the 4th and 5th days after hatching were smaller than larvae preserved on previous days (Figure 1). It is probable that those larvae had not begun to feed and that they were starving at the time of preservation.

Yolk Absorption and Gut Differentiation

The yolk sac is broadly ellipsoid in newly hatched larvae with the oil globule located ventrally and just posterior to the middle of the yolk mass (Figure 2A; see also Reintjes 1962). The yolk was nearly absorbed in specimens preserved 1 day after hatching (Figure 2B). All visible yolk remains, including the oil globule, had disappeared by 60 h after hatching at 26°C. Many larvae were observed to begin feeding before all of the yolk had been absorbed. At that time the gut was a straight tube, but within 24 h (at about 5.0 to 5.5 mm SL) it had developed into distinct fore and hind sections, the latter characterized by the bands of muscle common to all clupeid larvae.

Preanus Length

Preanus length averaged 82 to 84% SL from hatching until larvae were 15.0 mm SL (Table 4).

TABLE 4.—Summary of the measurements of various body parts of *Brevoortia smithi* larvae and juveniles in relation to standard length. Tabulated measurements are means for measurements from 1-mm length classes.

Length class (mm, SL)	Number of specimens	Preanus length:SL	Predorsal length:SL	Prepelvic length:SL	Body depth:SL	Head length:SL	Snout length:SL	Eye diameter:SL
3.1- 4.0	2	0.84	—	—	0.09	0.14	0.02	0.06
4.1- 5.0	20	0.82	—	—	0.09	0.13	0.02	0.05
5.1- 6.0	3	0.82	—	—	0.08	0.13	0.02	0.05
6.1- 7.0	3	0.84	—	—	0.08	0.14	0.03	0.04
7.1- 8.0	5	0.84	0.67	—	0.08	0.13	0.03	0.04
8.1- 9.0	5	0.84	0.66	—	0.08	0.15	0.03	0.04
9.1-10.0	5	0.84	0.65	—	0.08	0.15	0.03	0.04
10.1-11.0	6	0.84	0.64	—	0.08	0.17	0.03	0.05
11.1-12.0	2	0.84	0.62	0.49	0.09	0.20	0.04	0.06
12.1-13.0	3	0.84	0.63	0.47	0.10	0.20	0.04	0.06
13.1-14.0	2	0.82	0.62	0.47	0.11	0.21	0.04	0.06
15.1-16.0	2	0.81	0.59	0.47	0.14	0.23	0.05	0.07
16.1-17.0	2	0.77	0.56	0.50	0.18	0.27	0.06	0.08
17.1-18.0	2	0.77	0.53	0.51	0.23	0.29	0.07	0.09
22.7	1	0.74	0.52	0.52	0.29	0.33	0.07	0.11
25.3	1	0.72	0.49	0.52	0.30	0.31	0.08	0.10
33.3	1	0.72	0.47	0.52	0.32	0.33	0.07	0.10
36.2	1	0.73	0.49	0.55	0.33	0.33	0.08	0.09

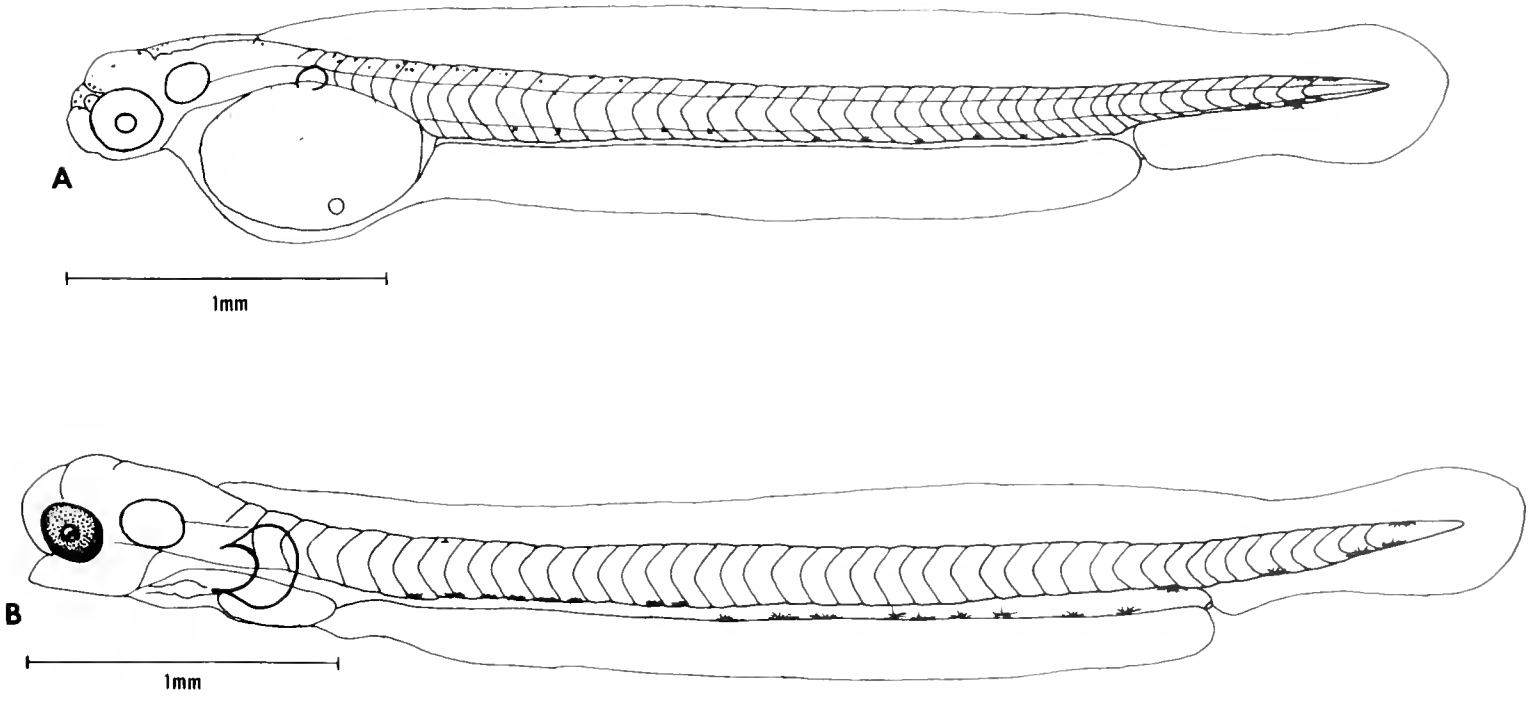

FIGURE 2.—4.2-mm SL (20 h posthatching) and 4.6-mm SL (41 h posthatching) larvae of *Brevoortia smithi*.

As the gut shortened during transformation, preanus length was reduced to 77% SL at 16.0 to 18.0 mm and averaged 72 to 74% for juveniles 22.7 mm and longer.

Head Length

Head length averaged 13 to 14% SL for larvae from 3.0 to 8.0 mm (Table 4). It then increased gradually to 29% at 18.0 mm and stabilized at 31 to 33% SL for juvenile specimens. Hildebrand (1963) and Dahlberg (1970) recorded head lengths ranging from 29 to 32.5% SL for large juvenile and adult yellowfin menhaden.

Eye Diameter

Eye diameter averaged 6% SL on newly hatched larvae but gradually decreased to 4% SL at about 6.0 mm and was stable until larvae grew to 10.0 mm (Table 4). Eye diameter then increased to 9% SL at 18.0 mm and averaged 9 to 11% SL for juveniles 22.7 to 36.2 mm. A relative decrease in eye diameter must occur in older juveniles because

Hildebrand (1963) reported eye diameters ranging from 6.1 to 7.5% SL for specimens 91 mm and longer.

Snout Length

Snout length increased gradually throughout development. It averaged 2% SL at hatching and increased to 7 to 8% SL in our juveniles (Table 4). Snout lengths of large juvenile and adult yellowfin menhaden range from 6.8 to 8.0% SL (Hildebrand 1963).

Body Depth

Body depth, measured at the pectoral symphysis, averaged 8 to 9% SL from hatching until larvae were 12.0 mm (Table 4). A rapid increase in body depth then occurred; it was 23% SL at 18.0 mm and apparently was still increasing in juvenile specimens 22.7 mm and longer. Our 36.2-mm specimen had a body depth of 33% SL. Hildebrand (1963) did not measure body depth by the same method that we used, but he noted that yellowfin menhaden juveniles are deep bodied, more so than adults of this species.

Predorsal Length

Predorsal lengths were measured on larvae that had dorsal fin rays developing. No dorsal fin development was observed on any specimens less than 7.3 mm. Predorsal length decreased gradually from 67 to 62% SL for larvae from 7.3 to 14.0 mm and then decreased more rapidly for larger specimens (Table 4). It was 52% SL for our 22.7-mm specimen and ranged from 47 to 49% SL for larger individuals. The decrease in predorsal length from 67 to 62% for 7.3- to 14.0-mm larvae may be partly due to measuring predorsal length on specimens with incompletely developed dorsal fins. The marked decrease in predorsal length on larger larvae resulted from forward movement of the dorsal fin as larvae began to transform to the juvenile stage.

Prepelvic Length

Prepelvic lengths were measured on larvae that had pelvic fin buds or fins. From 11.1 to 16.0 mm, prepelvic lengths ranged from 47 to 49% SL (Table 4). In larger specimens, prepelvic lengths increased to 51% SL at 18.0 mm and to about 52% SL for 22.7- to 33.3-mm individuals. Our 36.2-mm specimen had a prepelvic length of 55% SL. Pelvic fins moved posteriorly during growth of yellowfin menhaden larvae, causing the observed increase in prepelvic length.

Meristics

Myomeres

The number of myomeres in fishes corresponds approximately to the number of vertebrae. Dahlberg (1970) reported 43 to 46 vertebrae (mean = 45) for juvenile and adult *B. smithi*. Myomeres can be counted on larvae before development of vertebrae and are a valuable meristic character. Total numbers of myomeres in our specimens ranged from 45 to 47 on the 63 individuals for which accurate counts were obtained. There was no correlation between the number of myomeres and standard length, indicating that the full complement was present at hatching. The frequencies of occurrence were as follows:

Number of myomeres	*45*	*46*	*47*
Frequency	26	32	5

The mean number of myomeres was 45.67 ($S_{\bar{x}}$ = 0.1109).

The distribution of myomeres in relation to other body parts can be useful for identifying clupeid larvae (Ahlstrom 1968). We examined the distribution of myomeres for yellowfin menhaden larvae relative to the dorsal fin and anus (Table 3). Preanus myomeres decreased from a mean number of 37.6 in newly hatched larvae to 28.5 in juveniles that were 22.7 mm and longer. Postanus myomeres increased accordingly, from 8.0 in newly hatched larvae to 17.0 for juveniles. Shortening of the gut during development caused the change in distribution of preanus and postanus myomeres. Predorsal myomeres decreased in numbers as larvae developed, because the dorsal fin moved forward. Larvae of 6.1 to 8.0 mm had a mean number of 28.0 predorsal myomeres, but juveniles had only 15.8. Numbers of predorsal myomeres were variable for specimens within any given size class (Table 3). The number of postdorsal-preanus myomeres decreased as larvae grew. Larvae 6.1 to 8.0 mm had a mean number of 5.3 postdorsal-preanus myomeres, but advanced larvae and juveniles always had 4 or fewer (usually 2

or 3). Larvae of *Opisthonema oglinum* and *Harengula jaguana* always had 5 or more post-dorsal-preanus myomeres during all developmental stages (Richards et al. 1974; Houde et al. 1974).

Fin Development

A finfold surrounded the trunk and caudal area of newly hatched yellowfin menhaden larvae. Some parts of it remained along the ventral body margin until larvae were approximately 16.0 mm. Pectoral fin buds were already present when larvae hatched (Figure 2A), but the pelvic and median fins were not formed. Rays first appeared in fins in the following sequence: dorsal, caudal, anal, pelvics, and pectorals. Because rays first develop as cartilaginous structures, the size at which full complements were present was not necessarily the size at which all rays were ossified (Tables 2, 5). Although the beginning and completion of fin ray development were best correlated with length of larvae, age was also a factor, especially for anal fin development (Table 2).

Median fins had full complements of rays when larvae were 17.0 mm (Table 5). Dorsal rays first appeared at 7.3 mm, although an opaque area was present in the dorsal finfold, near the future dorsal fin, in some larvae as small as 6.4 mm. Full complements of 20 or 21 dorsal rays usually were attained when larvae were 15.5 to 17.0 mm. Principal caudal rays first appeared at 7.5 to 8.6 mm and the full complement of 19 principal rays was present when larvae were 9.6 to 10.3 mm. The notochord began to flex while principal caudal rays and other caudal fin structures were developing. Procurrent caudal rays began to develop at 11.2 mm, and full complements of 8 or 9 dorsal and 6 or 7 ventral rays were present at 16.2 to 17.8 mm. Anal rays first developed at 8.8 to 10.3 mm. A full complement of 20 or 21 rays was present on all larvae 16.2 mm or longer, although one specimen only 12.6 mm had 20 anal rays. Hildebrand (1963) and Miller and Jorgenson (1973) reported from 21 to 24 anal rays in yellowfin menhaden specimens longer than 72 mm that they examined. We examined six juveniles from our rearing experiment that were 40-50 mm in length. Two of these specimens had 22 anal rays, two had 21 rays, and two had 20 rays.

Rays in paired fins began to develop later than in median fins. Pectoral fins without rays were present soon after hatching, but no rays developed until larvae had attained approximately 15.5 mm. A full complement of 14 to 16 pectoral rays was present on larvae 16.9 mm and longer. Pelvic fins appeared as tiny buds when larvae were 10.9 to 11.3 mm, but rays did not develop until larvae were about 13.0 mm. A full complement of 7 pelvic rays was attained at 15.5 to 16.2 mm.

Scales and Scutes

Scales and ventral scutes were observed in specimens 17.8 mm and longer. Scales first developed anterior to the dorsal fin and in the region of the caudal peduncle. Specimens 22.7 mm or longer were fully scaled. Ventral scutes first developed anterior to the pelvic fins when larvae were 16.9 mm. Full complements of 30 to 32 (18 to 20 anterior to the pelvic fins and 11 to 13 posterior to the pelvic fins) were present on specimens 22.7 mm and longer. These counts are the same as those given for adult *B. smithi* by Dahlberg (1970).

Osteology

Ten specimens of yellowfin menhaden were cleared and stained to determine sequence of development of skeletal structures. Ossification was similar to that described for larvae of Atlantic thread herring (Richards et al. 1974) and of scaled sardine (Houde et al. 1974). Consequently,

TABLE 5.–Summary of fin development sequence in larvae of *Brevoortia smithi*.

Fin	Standard length (mm)			Number of rays in fully developed fin
	Buds first appear	Rays first appear	Full complement of rays	
Dorsal	—	7.3	15.5 to ~17.0	19 to 21
Caudal:				
Principal	—	7.5 to 8.6	9.6 to 10.3	19
Procurrent	—	11.2	16.2 to 17.8	8 or 9 dorsal 6 or 7 ventral
Anal	—	8.8 to 10.3	12.6 to 16.2	20 or 21
Pelvic	10.9 to 11.3	~12.6	15.5 to 16.2	7
Pectoral	<4.0	~15.5 mm	16.9	14 to 16

[1]Rays were present at the tabulated lengths, but not necessarily ossified at those sizes.

osteology of yellowfin menhaden larvae is treated rather briefly in this paper. Ossification of most structures occurred at a smaller size in yellowfin menhaden than in either Atlantic thread herring or scaled sardines, but the sequence of development was similar in all of the species.

No bones were ossified in our 5.2-mm specimen, but the cleithra were lightly stained in 6.1- and 7.2-mm specimens. Cleithra were well stained in a 7.4-mm specimen, but no other bones were ossified. Slight ossification of the maxillaries and dentaries, in addition to the cleithra, was observed in our 8.6-mm larva. At 10.5 mm, the caudal fin complex began to ossify, cranial bones were lightly stained, and 8 maxillary and 3 dentary teeth were present. Vertebral centra were beginning to stain at 12.3 mm; neural and hemal arches were developing, but were unstained. Dorsal fin rays were ossifying at 12.3 mm. Also, cranial bones were ossifying, the hyoid apparatus was stained, 11 teeth were present on the maxillaries, and 4 were present on the dentaries. At 16.2 mm, most of the major skeletal structures were at least partly ossified. Rays in median and paired fins were stained as were neural and hemal spines along the vertebral column. Premaxillaries and posterior supramaxillaries were ossified in this specimen. At 18.0 mm, the degree of stain uptake increased in most bones. Also, ribs were stained, anterior supramaxillaries were stained, and 16 maxillary teeth were present, but the dentary bore no teeth. Ossification was complete in our 25.3-mm specimen. A total of 25 maxillary teeth but no dentary teeth were present. Dentary teeth are a transient larval character in *B. smithi*. One large, erect tooth was present on the basihyal of our 18.0-mm specimen, and two were present on the 25.3-mm specimen. Basihyal teeth also were reported from Atlantic thread herring and scaled sardine larvae (Richards et al. 1974; Houde et al. 1974).

The caudal fin complex of yellowfin menhaden developed much like that of scaled sardine, and we give a brief description here, using the terminology of Houde et al. (1974) in their description of scaled sardine. Some cartilaginous, principal caudal rays developed in specimens as small as 7.5 mm. Flexure of the notochord and appearance of cartilaginous hypural plate elements occurred at about 8.5 to 9.0 mm. Our 10.5-mm specimen had stain uptake in the proximal parts of the 19 principal caudal rays, and the first uroneural was slightly stained. Hypural elements were present but unstained. At 12.3 mm, the 19 principal caudal rays were fully stained, the second ural vertebra was stained as were the first and second uroneurals, and the parhypural was lightly stained. The hypurals were present but unstained as were two epural bones. Ossification was progressing in our 16.2-mm specimen. Both the first and second ural vertebrae were stained, the six hypurals were stained, the parhypural was well stained, and all three uroneurals were now stained. In addition to the 19 principal caudal rays, 8 dorsal procurrent caudal rays and 6 ventral procurrent caudal rays were stained. Two epurals were present on this specimen but were unstained. At 18.0 mm, all of the bones in the caudal fin area were at least partly ossified. The two epurals were now slightly stained, and 9 dorsal plus 8 ventral procurrent caudal rays were present and stained. The 25.3-mm specimen had all caudal fin bones ossified. The two epurals were well stained on this specimen, these bones being the last to ossify in the caudal fin complex.

Pigmentation

Melanophore distribution on yellowfin menhaden larvae is similar to other clupeid larvae, but there are some distinctive characteristics which may serve to distinguish them from other clupeid larvae with which they can occur. Melanophores were contracted on some specimens and expanded on others, accounting for some of the apparent variability among individuals. Our illustrated specimens (Figures 2-5) have pigment that is typical of most specimens of those lengths.

Head Region

Newly hatched yellowfin menhaden larvae have several tiny melanophores on the snout and a few over the brain. Within 1 day after hatching those melanophores have migrated or disappeared, because no pigment is present on the heads until larvae attain about 9.0 mm. The eyes became pigmented at about 4.5 mm, at 1 day after hatching. Typical pigmentation on the pectoral symphysis and over the heart developed at 4.5 to 6.0 mm. One or two melanophores appeared on the pectoral symphysis after yolk absorption when larvae were 4.5 to 5.0 mm. Those melanophores developed into two distinct pairs by 7.0 mm. Either one or two melanophores developed over the heart at about 6.0 mm. A single melanophore occurred at the

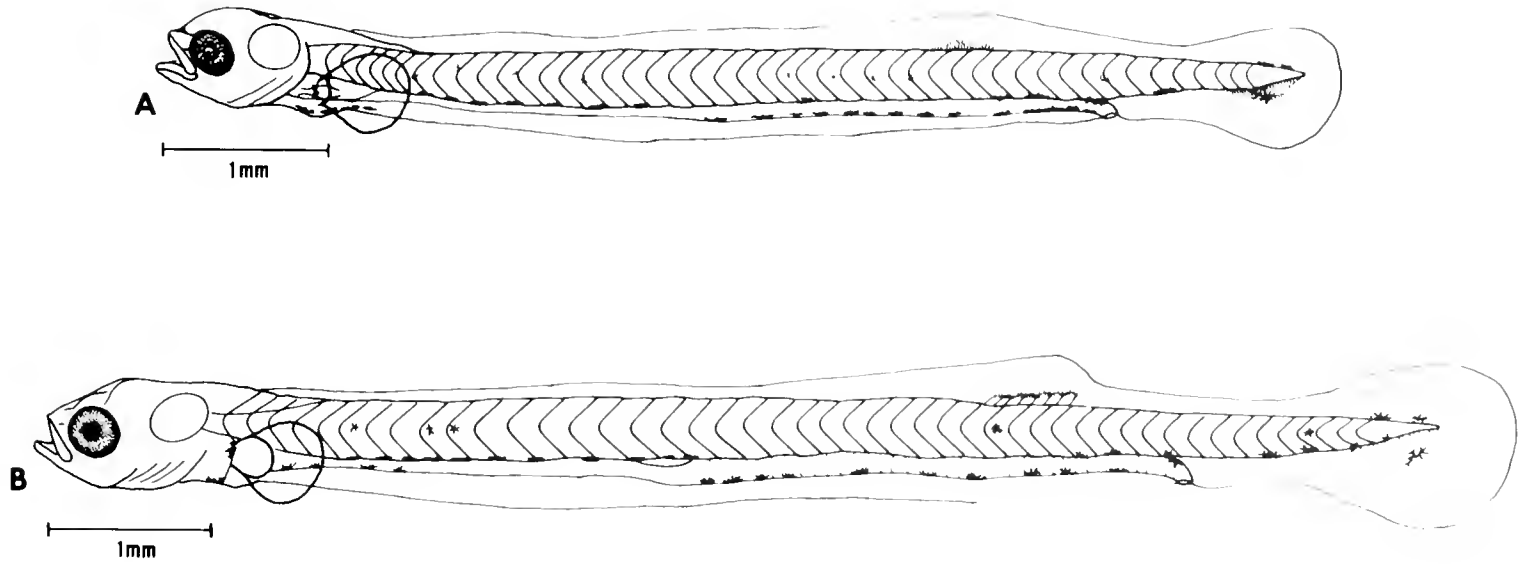

FIGURE 3.—7.0-mm SL (4 days posthatching) and 8.6-mm SL (6 days posthatching) larvae of *Brevoortia smithi*.

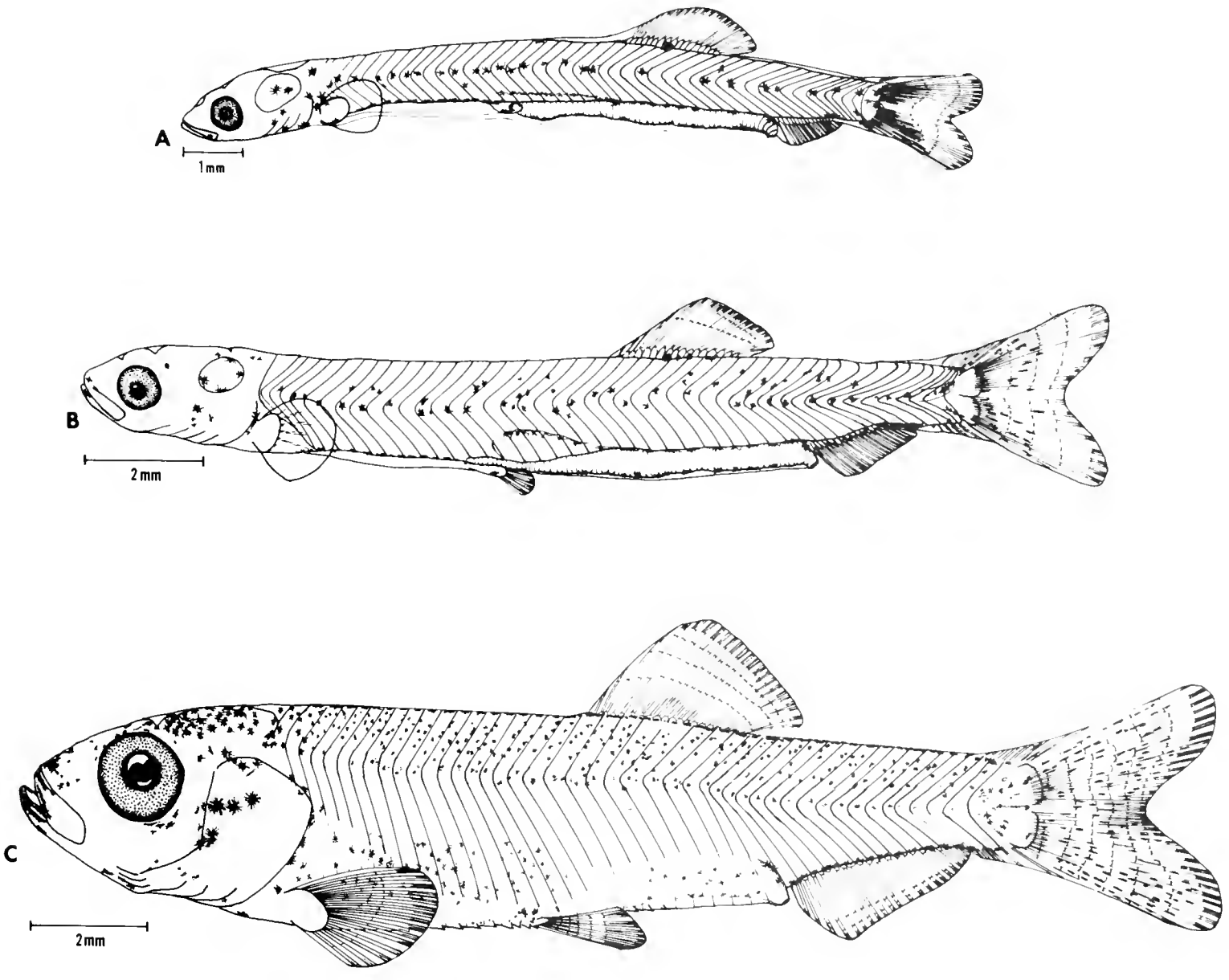

FIGURE 4.—12.1-mm SL (15 days posthatching), 15.9-mm SL (18 days posthatching), and 17.8-mm SL (31 days posthatching) larvae of *Brevoortia smithi*.

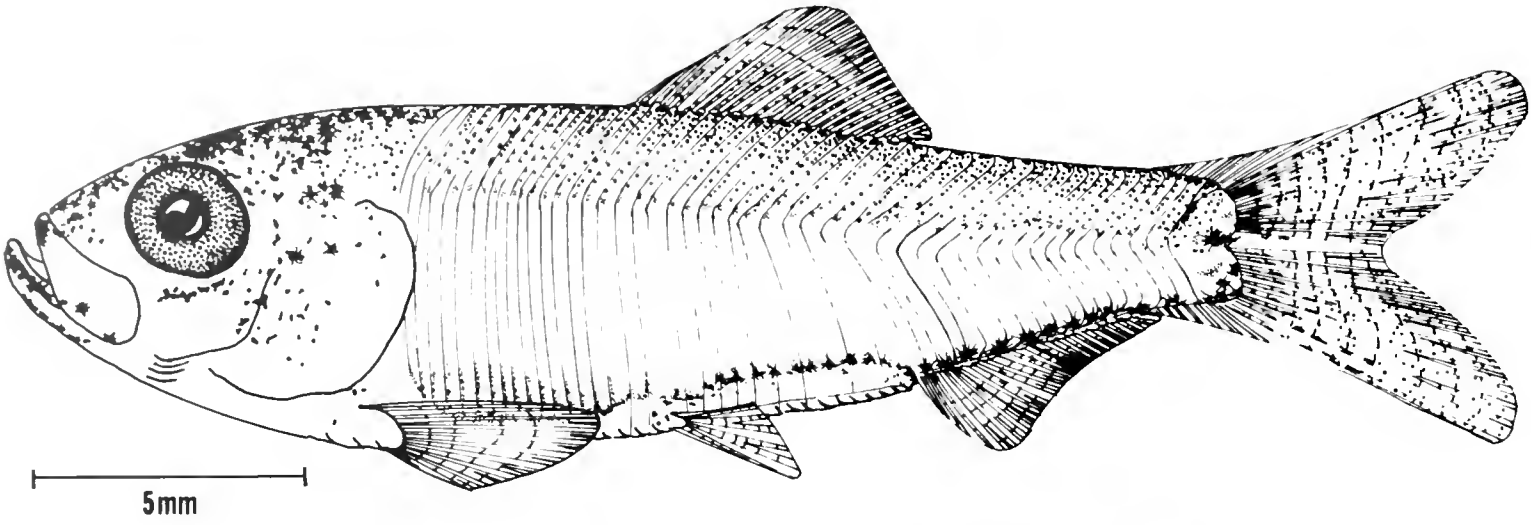

FIGURE 5.—22.7-mm SL (60 days posthatching) juvenile of *Brevoortia smithi*.

pectoral fin base in some larvae as small as 4.5 mm and was present in all larvae at 7.0 mm. The pigment pattern associated with the pectoral symphysis, heart area, and pectoral fin base was retained until larvae were about 16.5 mm.

At 9.0 mm, from one to three stellate melanophores had developed internally and could be seen through the otic capsules. A single, stellate melanophore frequently was present over the hindbrain at 10.0 mm, and some specimens had a small melanophore just posterior to and dorsal to the eye at that length. At about 12.0 mm, the pigmentation on the head began to increase substantially. Melanophores appeared on both jaws, on the side of the head, and over both midbrain and hindbrain regions. The number of melanophores increased as larvae grew, and numerous stellate melanophores were present on the heads of the larvae at 16.5 mm. Melanophores were especially concentrated on the jaws and over the brain in larvae larger than 16.5 mm.

Gut and Trunk Region

Newly hatched yellowfin menhaden had a few tiny melanophores on the dorsal surface of the trunk along the forebody. Within 12 h of hatching, these melanophores apparently migrated ventrally because they disappeared on the dorsal surface, but a series of malanophores was developing along the gut region of larvae.

Paired series of melanophores along the gut margin, which are typical of clupeid larvae, were present on yellowfin menhaden larvae of 4.5 mm and longer. Distinct pairs, numbering from 8 to 16, developed along the dorsolateral margin of the foregut and less distinct pairs, numbering 9 to 14, occurred along the ventral margin of the hindgut. These series were clearly visible until larvae were about 17.0 mm; they were not present on specimens longer than 18.0 mm. From one to three stellate melanophores usually occurred near the anus along the dorsal surface of the gut on larvae longer than 4.5 mm. These were continuous with an internal series of melanophores that were visible over the hindgut on most specimens longer than 8.5 mm. The number in this series increased from 6 to about 17 at 10.5 mm. Three or four melanophores were associated with the developing swim bladder in 10.0- to 12.0-mm larvae. A second internal series of melanophores was associated with developing vertebrae, but these were too indistinct to count accurately.

Pigment developed along the sides of the trunk of some yellowfin menhaden as small as 5.2 mm. From 1 to 3 stellate melanophores were present on some larvae between 5.5 and 7.0 mm, and this number usually increased to as many as 10 for 7.0- to 10.0-mm larvae. Some larvae up to 8.6 mm had no lateral pigment on the trunk, but most specimens, when examined closely, were observed to have these melanophores. The number of lateral melanophores increased greatly when larvae were between 10.0 and 12.0 mm; some specimens of those lengths had as many as 25 lateral melanophores. When larvae were 14.0 mm or longer, these melanophores became very numerous, and most were located above the lateral midline. A paired series of melanophores developed along the dorsal midline, both anterior and posterior to the dorsal fin, on specimens longer than 16.5 mm.

There are melanophores associated with the developing fins. From 1 to 3 stellate melanophores

were present at the dorsal fin base of 9.5- to 11.0-mm larvae. They numbered from 3 to 8 at about 14.0 mm and then as many as 15 at 18.0 mm. Two or three stellate melanophores were present at the anal fin base on 11.0- to 12.0-mm larvae; these numbers increased rapidly to 11 or 12 at 18.0 mm. Numbers of melanophores at the dorsal and anal fin bases were variable among individuals of the same length. A single stellate melanophore developed at the pelvic fin base on specimens as small as 12.3 mm. Some tiny melanophores began to occur in the pectoral, dorsal, and anal fins at 16.2 mm.

Caudal Region

Newly hatched larvae have melanophores on both the dorsal and ventral sides of the notochord tip. Numbers on the dorsal tip range from one to two, while those on the ventral tip range from one to three. In addition, one or two melanophores are located along the ventral midline posterior to the anus. Pigment along the ventral tip of the notochord began to migrate into the caudal finfold at 7.0 to 7.2 mm. This pigment was associated with developing caudal rays in larger larvae. Pigment in the caudal fin increased rapidly when larvae exceeded 10.0 mm. Internal melanophores were first present in the hypural plate region on larvae 10.3 mm and longer. Larvae longer than 16.5 mm invariably had many melanophores among the rays of the caudal fin.

Transformation

Transformation of larvae to juveniles apparently was complete between 20 and 23 mm. Unfortunately, we preserved no specimens that were between 18.0 and 22.7 mm. However, our specimens of 17.8 and 18.0 mm were not completely transformed while the 22.7-mm specimen had acquired nearly all of the juvenile characteristics. Larvae began transforming at about 14.0 mm. At that time, proportional measurements relating preanal length, predorsal length, body depth, head length, snout length, and eye diameter to standard length (Table 4) began to change rapidly. Except for body depth, which continued to increase, the proportional measurements became nearly constant at 22.7 mm. The distribution of myomeres relative to other body parts became stable for specimens 22.7 to 36.2 mm (Table 3). Fin rays were completely ossified at 18.0 mm (Table 5), but the epural bones of the caudal skeleton were still unossified at that size. Although some scales were present on our 17.8- and 18.0-mm specimens, the 22.7-mm specimen was the smallest that was fully scaled. The slender, rodlike shape of the larva was replaced by the deeper bodied, laterally compressed form of the juvenile between 17.8 and 22.7 mm. The silvery coloration of juveniles was present on our specimens from 22.7 to 36.2 mm. Transformation included the following features: forward movement of the dorsal fin; shortening of the gut; forward movement of the anal fin; and relative increases in head length, snout length, eye diameter, and body depth. The same features were noted for transforming larvae of Atlantic thread herring (Richards et al. 1974) and scaled sardine (Houde et al. 1974).

COMPARISONS

Eggs and larvae of the genus *Brevoortia* almost always can be distinguished from those of other clupeid genera that spawn in marine waters of the south Florida and Gulf of Mexico region. Members of the genera *Alosa* and *Dorosoma* have demersal eggs, unlike those of *Brevoortia* which are pelagic. *Dorosoma* spawns in fresh waters and *Alosa* in fresh or nearly fresh waters, so that occurrence of their larvae with those of *Brevoortia* is unlikely. Larvae of *Alosa* spp. have more total myomeres than any species of *Brevoortia*, and the genera can be easily distinguished. Dwarf herrings (*Jenkinsia* spp.) might occur with *B. smithi* at the southern extreme of their range in Florida. Neither spawning habits nor eggs and larvae of *Jenkinsia* have been described, but the total myomeres of *Jenkinsia* did not exceed 42 (Miller and Jorgenson 1973), making it unlikely that larvae could be confused with *Brevoortia* which have higher myomere numbers (*Brevoortia*, 44-48). Since *B. smithi* may occur with either *B. tyrannus* or *B. patronus* and because hybrids are known (Dahlberg 1970), the specific identification of menhaden eggs and larvae from plankton collections is still in doubt where the species' ranges overlap.

Eggs of *B. smithi* are smaller than those of *Harengula jaguana* which range from 1.55 to 1.78 mm in diameter (Houde et al. 1974), and they cannot be confused with those of *Etrumeus teres* because eggs of that species have no oil globule. Our *B. smithi* eggs were similar to those of *Opisthonema oglinum* (Richards et al. 1974) and to

those of western Atlantic *Sardinella* sp. (Simpson and Gonzales 1967; Matsuura 1971; Houde and Fore 1973), but their average diameter was greater than for those species. Our *B. smithi* eggs ranged from 1.21 to 1.34 mm in diameter (mean = 1.27 mm) while those of *O. oglinum* are 1.10 to 1.28 mm (mean = 1.19 mm) (Richards et al. 1974) and those of western Atlantic *Sardinella* sp. are 1.00 to 1.32 mm (mean = 1.12-1.18 mm) (Simpson and Gonzales 1967; Matsuura 1971; Houde and Fore 1973). Reintjes (1962) reported *B. smithi* eggs ranging from 1.15 to 1.48 mm, including both planktonic and artificially fertilized eggs. The eggs of *O. oglinum* would not usually occur with those of *B. smithi* because *Opisthonema* spawns during spring and summer (Fuss et al 1969; Houde 1973a; Richards et al. 1974), while members of the genus *Brevoortia* are winter spawners (e.g., Turner 1969; Dahlberg 1970) in waters of south Florida and the Gulf of Mexico. *Sardinella* eggs could conceivably occur with those of *B. smithi*, but *Sardinella* probably spawns farther offshore than does *B. smithi*. Eggs of *B. tyrannus* apparently are larger than those of *B. smithi*, the reported diameters ranging from 1.30 to 1.95 mm (Mansueti and Hardy 1967). *Brevoortia patronus* eggs usually are slightly smaller than *B. smithi* eggs, the diameters ranging from 1.04 to 1.30 mm (Houde and Fore 1973). Hybrid embryos from artificial fertilization of *B. smithi* × *B. patronus* ranged from 1.05 to 1.18 mm (Hettler 1968).

Larvae of *Brevoortia* spp. have some distinctive characters that serve to distinguish them from other clupeid larvae with which they may occur. Newly hatched larvae of *B. smithi* have been photographed by Reintjes (1962), but these photographs fail to show distinguishing characters of larvae in that size range. Hettler (1970a) presented illustrations of 7.6- and 11.9-mm TL larvae of *B. smithi*, but only the 11.9-mm specimen has some characteristics illustrated that help to identify it as a *Brevoortia* sp.

Myomere numbers ranged from 45 to 47 in *B. smithi*, thus separating it from *H. jaguana* (42 or fewer) (Houde et al. 1974) and *E. teres* (48 or more) (Houde and Fore 1973). Total myomere counts of *B. smithi* overlap those of *O. oglinum* (45 to 49), *Sardinella* sp. (45 to 47) (Houde and Fore 1973), and the other species of *Brevoortia*. Numbers of postdorsal-preanus myomeres always were fewer than 5 in *B. smithi* larvae longer than 10 mm and never exceeded 6 in smaller larvae (usually 4 or 5). The other identified clupeid genera from this region, excepting *Etrumeus*, have 5 or more (usually 6 to 9) postdorsal-preanus myomeres in all length classes, thus serving to distinguish them from *Brevoortia* larvae.

Pigmentation of newly hatched *Brevoortia* larvae apparently differs from that of other clupeid genera in its details. Recently hatched *B. smithi* larvae have pigment on both the dorsal and ventral sides of the notochord tip (Figures 2A-3B), distinguishing them from other co-occurring clupeid genera, except for some specimens of *Harengula* (see Houde et al. 1974). *Brevoortia tyrannus* has pigmentation similar to *B. smithi* at the notochord tip (Mansueti and Hardy 1967), and we suspect that *B. patronus* also has this pigment characteristic based on our observations of *Brevoortia* larvae that were collected in the northern Gulf of Mexico, where *B. patronus* is known to spawn. Recently hatched larvae of *O. oglinum*, *Sardinella* sp., and *E. teres* have pigment only on the ventral side of the notochord tip.

Lateral pigmentation is present on *B. smithi* larvae as small as 5.2 mm—which is smaller than other clupeids found in their geographical range. At 10 to 12 mm, most of our *B. smithi* larvae had more than 5 melanophores on their sides, and some had as many as 25. No larvae of *Harengula*, *Opisthonema*, *Sardinella*, or *Etrumeus* that we have observed have had pigment on the sides until they were at least 15 mm in length. We do not know if *B. tyrannus* or *B. patronus* develop lateral pigmentation at sizes as small as *B. smithi*, but illustrations of *B. tyrannus* larvae (Mansueti and Hardy 1967) from 8 to 23 mm do not show any such pigment, nor is it mentioned in their text.

Size at transformation varies among clupeid species. *Brevoortia smithi* had completed transformation at about the same size as *H. jaguana* (Houde et al. 1974) and *O. oglinum* (Richards et al. 1974), at lengths from 20 to 24 mm. However, other species of *Brevoortia* apparently do not transform until they are of larger size. *Brevoortia tyrannus* exceeds 30 mm before having a typical juvenile form (Mansueti and Hardy 1967), and the observations and morphological data of Suttkus (1956) suggest that *B. patronus* does not transform until 28 mm or longer. It is possible that our tank-reared *B. smithi* transformed at smaller sizes than in nature, but the seemingly good growth rate and the selection of normal appearing larvae to describe development lead us to believe that *B. smithi* is transformed at approximately 22 mm.

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NOTES

TWO BLOOMS OF *GYMNODINIUM SPLENDENS*, AN UNARMORED DINOFLAGELLATE

Little is known about the ecology and physiology of an unarmored dinoflagellate (30 to 50 μm), *Gymnodinium splendens* Lebour, although feeding experiments have shown it to be an important food source for certain marine herbivores. Lasker et al. (1970) found that anchovy larvae may be reared the first week upon unialgal suspensions of *G. splendens* while Paffenhöfer (1970, 1971) and Barnett (1974) showed it to be a preferred food for *Calanus finmarchicus* and larval stages of *Labidocera trispinosa*. Pokorny and Gold (1973) reported on cell ultrastructure of *G. splendens*, Sweeney (1954) observed vitamin B_{12} requirements, and Thomas et al. (1973) described optimal light and temperature requirements. In addition to these laboratory studies, Loftus et al. (1972) have noted *G. splendens* in a bloom of diverse dinoflagellate species in Chesapeake Bay.

This note reports upon two field studies of blooms of *G. splendens*. The first observation was made in Coyote Bay of Bahia Concepción, Gulf of California, where *G. splendens* was the dominant phytoplankter in March 1971. The second observation was made in March 1974, when large concentrations were observed in coastal waters of the Southern California Bight. In both occurrences *G. splendens* dominated the phytoplankton crop so that measurements of primary production and the chemical composition of suspended particles allowed a reasonable description of this species.

Gymnodinium splendens in Coyote Bay

Coyote Bay (lat. 26°43.0'N, long. 111°53.0'W) of Bahia Concepción is well protected and shallow. Chemical and physical observations were made while the ship (RV *E. B. Scripps*) was at anchor in 20 m of water and included measurements of particulate adenosine triphosphate (Holm-Hansen and Booth 1966) and chlorophyll (Yentsch and Menzel 1963; Holm-Hansen et al. 1965), microscopic examination of water samples preserved in 5% (V/V) buffered Formalin[1] (Utermöhl 1958), and determinations of primary production based upon rates of incorporation of radioactive carbon (Steemann Nielsen 1952). The depth distribution of phytoplankton was recorded at regular intervals by continuous vertical profiles to the bottom with both a submersible transmissometer (Petzold and Austin 1968) and a fluorometer attached to a hose and submersible pump (Lorenzen 1966; Kiefer and Austin 1974). The continuous profiles of in situ fluorescence were translated into chlorophyll *a* concentrations by frequent calibration with discrete samples which were analyzed fluorometrically for chlorophyll and phaeophytin concentration (Kiefer 1973).

The five phytoplankters which occurred together and were numerically most abundant in Coyote Bay were: *G. splendens* (1.0×10^5/liter), *Leptocylindrus danicus* (3.4×10^4/liter), *Skeletonema costatum* (1.4×10^3/liter), *Cerataulina bergonii* (1.4×10^3/liter), and *Thalassiothrix frauenfeldii* (4.0×10^3/liter). Chlorophyll concentration varied with depth and ranged from 4.4 μg/liter to 13 μg/liter for numerous samplings of the 20-m water column. Figure 1 shows a time sequence of profiles of in situ fluorescence of chlorophyll. Profiles of light transmission displayed a similar stratified structure. The increase in depth of the upper chlorophyll maximum between 1845 and 2300 and the decrease in depth between 2300 and 0720 the following day indicated a diel migration of *G. splendens*. This suggestion was supported by the predominance of *G. splendens* in the maxima and by the improbability of physical factors such as advection or internal waves affecting such variations. Conditions were calm at the sea surface and the water column was isothermal with depth.

The upper chlorophyll maximum (Figure 1) moved downward at sunset with a velocity of approximately 1.7 m/h. Such velocities are similar to those of other dinoflagellates. For example, a natural bloom of *Ceratium furca* occurring off the southern California coast was observed to migrate downward at 2 m/h and mass cultures of *Cachonina niei* and *Gonyaulax polyedra* displayed migratory rates of 1 to 2 m/h (Eppley et al. 1968). Our observations suggested that a portion of the *G. splendens* population moved upward between 2300 and 0400 the following day. Since sunrise was

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

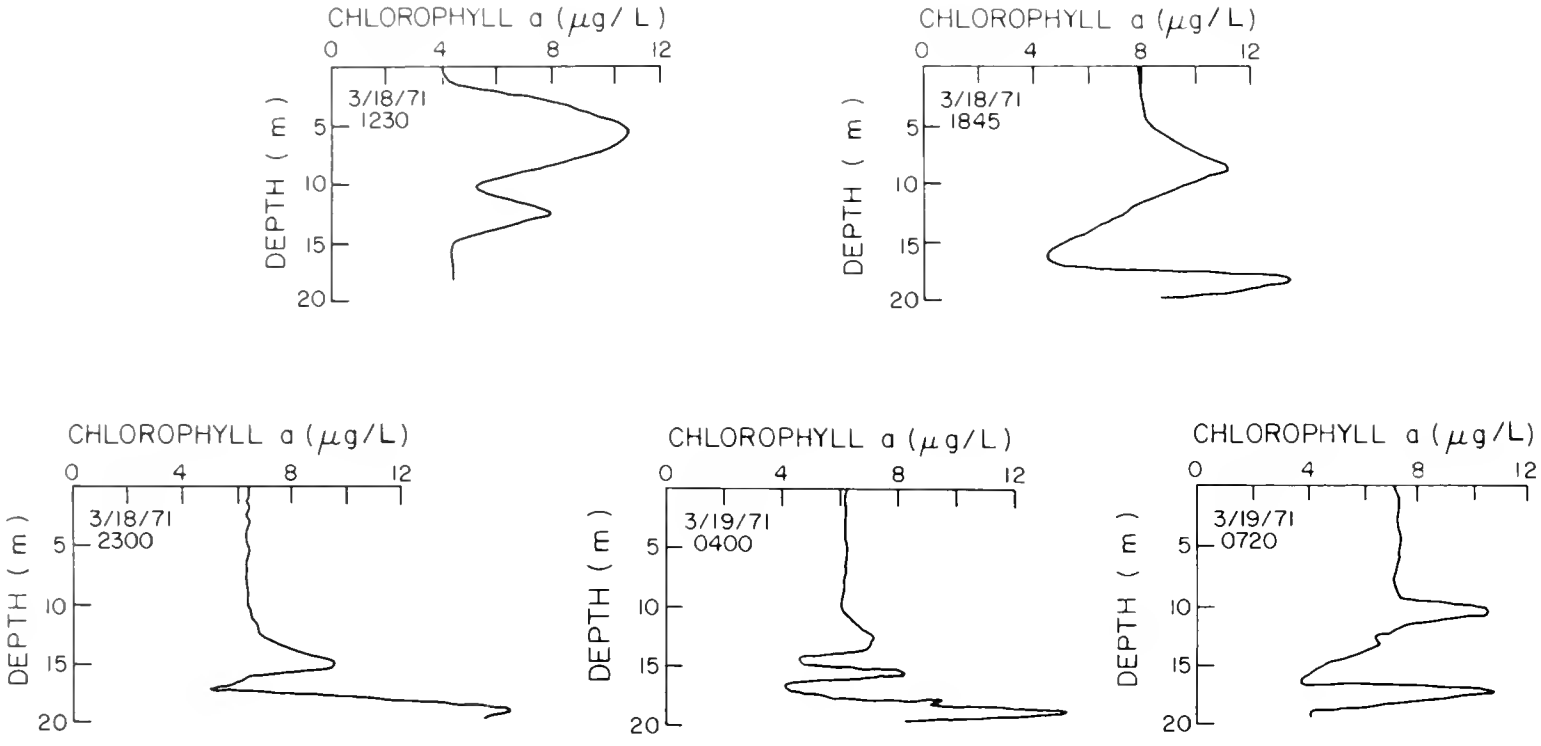

FIGURE 1.—Profiles of the concentration of chlorophyll *a* based upon fluorescence profiles. The upper layer of *Gymnodinium splendens* at 1230 h was concentrated at 6 m; by 1845 it had moved to 8 m and reached 15 m by 2300. Movement upward commenced at 0200 reaching 10 m by 0720. The lower layer remained relatively close to the bottom during this time.

around 0600, this movement may originate from a biological clock rather than from a phototactic response. These observations partially conflict with laboratory studies of phototaxis in *G. splendens* (Forward 1974). He found that not only was the cell strongly phototactic but that the strength of the response was subject to a circadian rhythm, being strongest at the end of the entrained dark period.

By assuming that *G. splendens* dominated the production as well as the standing crop of phytoplankton in Coyote Bay, we obtain information on the steady state doubling time for the species. Water samples were collected from four depths, 0, 5, 10, and 18 m, inoculated with $NaH^{14}CO_3$, and incubated from sunrise to sunset in situ. Primary production was then determined from rates of light-induced incorporation of ^{14}C into particles removed by filtration. The water samples were also analyzed for concentrations of chlorophyll *a* and adenosine triphosphate (ATP). By multiplying the concentration of ATP by 250, we obtained an estimate of "living-carbon" (Holm-Hansen and Booth 1966); this estimate allowed a crude determination of doubling time t_d from the steady-state equation:

$$t_d = \frac{\ln 2}{\mu} = \frac{C \cdot \ln 2}{\Delta C/\Delta t}$$

where μ is the specific growth rate and equal to the rate of carbon assimilation, $\Delta C/\Delta t$, divided by C, the concentration of cell carbon. On this basis, the doubling time for *G. splendens* at 0, 5, 10, and 18 m was 2.3, 2.6, 2.7, and 62 days, respectively (Table 1). These estimates of doubling time for a natural population of *G. splendens* may be compared with a maximal doubling time of 1.6 days for cells grown in the laboratory (Thomas et al. 1973). We also note that our estimates of the chlorophyll *a* concentration per cell yielded a value of approximately 100 pg/cell, typical for laboratory cultures (Bailey 1974).

TABLE 1.—Production, chlorophyll *a*, ATP, and doubling time for a *Gymnodinium splendens* bloom in Coyote Bay, Gulf of California.

Depth (m)	Production (μg C/liter•day)	Chlorophyll *a* concentration (μg/liter)	ATP (μg/liter)	Doubling time (days)
0	125	5.8	1.7	2.3
5	108	5.3	1.6	2.6
10	126	6.2	1.9	2.6
18	35	4.7	1.3	62

Gynmodinium splendens in the Southern California Bight

A second bloom of *G. splendens* was observed in March 1974, along the southern coast of California,

during a cruise on RV *David Starr Jordan*. Stations in the sampling program extended along the 20-fathom contour from Malibu (lat. 34°00.8′N, long. 118°40.6′W) south to San Onofre (lat. 32°56.0′N, long. 117°17.4′W). Intermediate stations included Manhattan Beach (lat. 33°52.5′N, long. 118°27.0′W), Seal Beach (lat. 33°36.5′N, long. 119°04.3′W), and Dana Point (lat. 33°26.3′N, long. 117°42.8′W). A sixth station was on the 270-fathom contour off Laguna Beach (lat. 33°30.8′N, long. 117°50.3′W).

Continuous vertical profiles of in situ chlorophyll fluorescence were made to a depth of 35 m. Water from the outflow of the fluorometer was collected at the surface and within the fluorescence maximum. Three analyses were made on subsamples of water from the two depths. First, the size distribution of suspended particles was immediately determined with an electronic particle counter (model T_a Coulter Counter). We accumulated counts in the upper nine channels which gave us a frequency distribution for particles with equivalent diameters ranging from 20 to 128 μm. Second, subsamples were preserved in 5% Formalin for species determination. Third, the chlorophyll *a* concentration in each subsample was determined fluorometrically for acetone extracts of filtered particles.

Vertical profiles made at various times of the day and night at each of the six stations on the 20-fathom contour were characterized by a unimodal distribution of chlorophyll. The chlorophyll maximum varied little in depth from 15 to 20 m within a moderately developed thermocline, and was most often less than 4 m thick. At these stations, *G. splendens* contributed most of the phytoplankton crop within the maxima. However, in surface waters it contributed a much smaller fraction of the crop. The highest concentration (Figure 2) of *G. splendens* was within the well-defined maximum at Seal Beach where its concentration reached 4×10^5 cells/liter (chlorophyll a = 42.0 μg/liter). The lowest concentration within a maximum was at Manhattan Beach, 1.2×10^4 cells/liter (chlorophyll a = 1.3 μg/liter.

The predominance of *G. splendens* in the chlorophyll maximum was also evident from the particle size distributions obtained with the electronic particle counter. Within the maximum, particles with equivalent diameters between 36 and 57 μm far outnumbered smaller- and larger-sized particles. In surface waters the smaller-sized

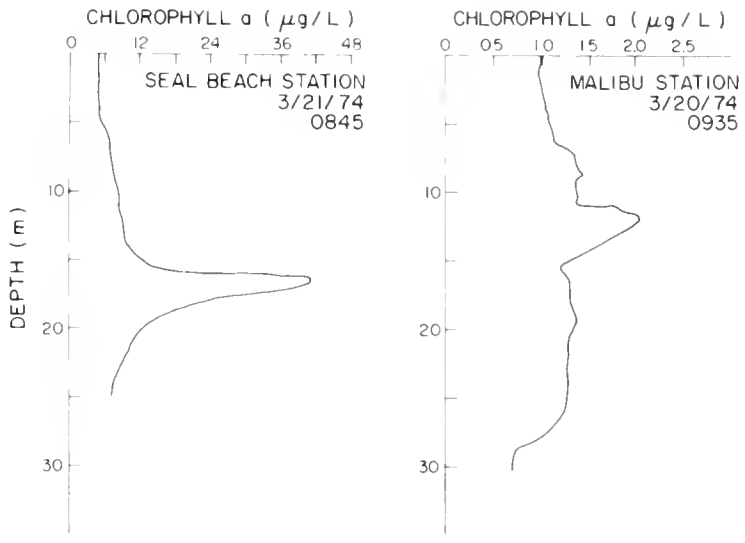

FIGURE 2.—Profiles of the concentration of chlorophyll *a* based upon fluorescence profiles at two stations along the 20-fathom contour of the Southern California Bight. The subsurface maxima are predominantly composed of *Gymnodinium splendens*.

particles outnumbered particles of the size of *G. splendens*. The other phytoplankton in surface waters included *Ceratium furca* and *C. kofoidii*, *Dinophysis acuminata*, and a species of *Gyrodinium*. Very few diatoms were present.

It appeared that the bloom of *G. splendens* dissipated seaward since the subsurface chlorophyll maximum was poorly developed at the Laguna Beach station which was on the 270-fathom contour. Here the concentration of chlorophyll in the maximum was only 0.76 μg/liter, while the concentration at the surface was 0.63 μg/liter. In addition, both the particle size distribution and microscopic counts indicated a more diverse assemblage of dinoflagellate species at this station, with the unarmored dinoflagellate *Cochlodinium catenatum* being most abundant.

Thus, the bloom of *G. splendens* appeared to be limited to nearshore waters, in a band extending as far as 100 km along the coast. This subsurface bloom was presumed to be a large food source for planktonic herbivores, but more field sampling is necessary to determine whether the bloom is a seasonal occurrence. In another paper, Lasker (1975) describes the feeding responses of anchovy larvae to these natural concentrations of *G. splendens*.

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ENHANCED SURVIVAL OF LARVAL GRASS SHRIMP IN DILUTE SOLUTIONS OF THE SYNTHETIC POLYMER, POLYETHYLENE OXIDE[1]

Small amounts of linear, high molecular weight synthetic polymers when added to liquids can significantly reduce frictional resistance in turbulent pipe and channel flow (Castro and Squire 1967; Peterson et al. 1974). These drag-reducing agents have potential for improving efficiency of sewer, water, and fire-fighting systems (Castro 1972); reducing friction around ships' hulls (Wade 1973); and perhaps increasing water flow and circulation in mariculture operations (Zielinski et al. in press). Such uses may result in the introduction of relatively large quantities of polymers into nearshore marine and estuarine waters or culture tanks.

We report here experiments to evaluate effects of chronic exposure to polyethylene oxide, a very effective friction-reducing additive, on larvae of estuarine grass shrimp, *Palaemonetes vulgaris* and *P. pugio*. This polymer exhibits a very low

[1]Contribution No. 22 from the South Carolina Marine Resources Center. This work is a result of research sponsored by NOAA Office of Sea Grant, under Grant #NG-33-72.

degree of toxicity and is approved for food contact applications and as an additive to some foods (Smyth et al. 1970). *Palaemonetes* shrimp were chosen for this study because of their importance in estuarine food chains (Hedgpeth 1947; Welsh 1973), the ease with which their larvae may be cultured in the laboratory, the general similarity of their larvae to those of *Macrobrachium* shrimp being evaluated for commercial culture, and the known sensitivity of these carideans to a variety of toxic agents (Lowe et al. 1971; Hansen et al. 1973; Redmann 1973; Sandifer and Shealy 1974[2]).

Methods and Materials

Two experiments were conducted with *P. vulgaris*, one with *P. pugio*. Effects of three polyethylene oxide concentrations (25, 50, and 100 wppm—weight parts per million) were tested versus controls in all experiments. Forty *Palaemonetes vulgaris* larvae were reared at each condition in experiments I (10 replicates of 4 animals each in 10.5-cm finger bowls) and II (4 replicates of 10 animals each in 19.1-cm bowls), while 72 *P. pugio* zoeae (4 replicates of 18 each) were maintained at each concentration in experiment III. The *P. pugio* larvae were isolated in compartments of covered plastic boxes. The culture containers were placed in a Percival Model I-35VL incubator[3] (Percival Manufacturing Co., Boone, Iowa) where temperature was held at approximately 25°C in experiment I and 28°C in the subsequent trials. A 14-h light – 10-h dark schedule was maintained in all studies. All animals were transferred to clean containers with fresh, filtered seawater (30‰ salinity) and fed newly hatched nauplii of *Artemia salina* daily.

Fresh stock solutions (200 wppm) of polyethylene oxide (Polyox Coagulant, molecular weight approximately 5×10^6 [Union Carbide Corp.]) in seawater were prepared every 3 or 4 days. Test solutions were prepared by diluting the stock with appropriate volumes of seawater.

Results and Discussion

Addition of small amounts of polyethylene oxide to the culture water significantly enhanced the survival of grass shrimp larvae in static water culture (Figure 1). The polymer affected neither the number of molts to the postlarval stage nor the size of postlarvae produced. However, a slight but definite trend toward increasing development time with increasing polyethylene oxide concentration was apparent in all experiments (Table 1).

Stranding of larvae above the waterline on the walls of the culture containers was a significant cause of mortality in all control cultures, but addition of ≥25-wppm polyethylene oxide virtually eliminated stranding deaths (Figure 1). This effect was probably the result of the reduced surface tension and increased viscosity, lubricity, and stringiness of the treatment solutions. Of course, this type of effect would not be manifested in

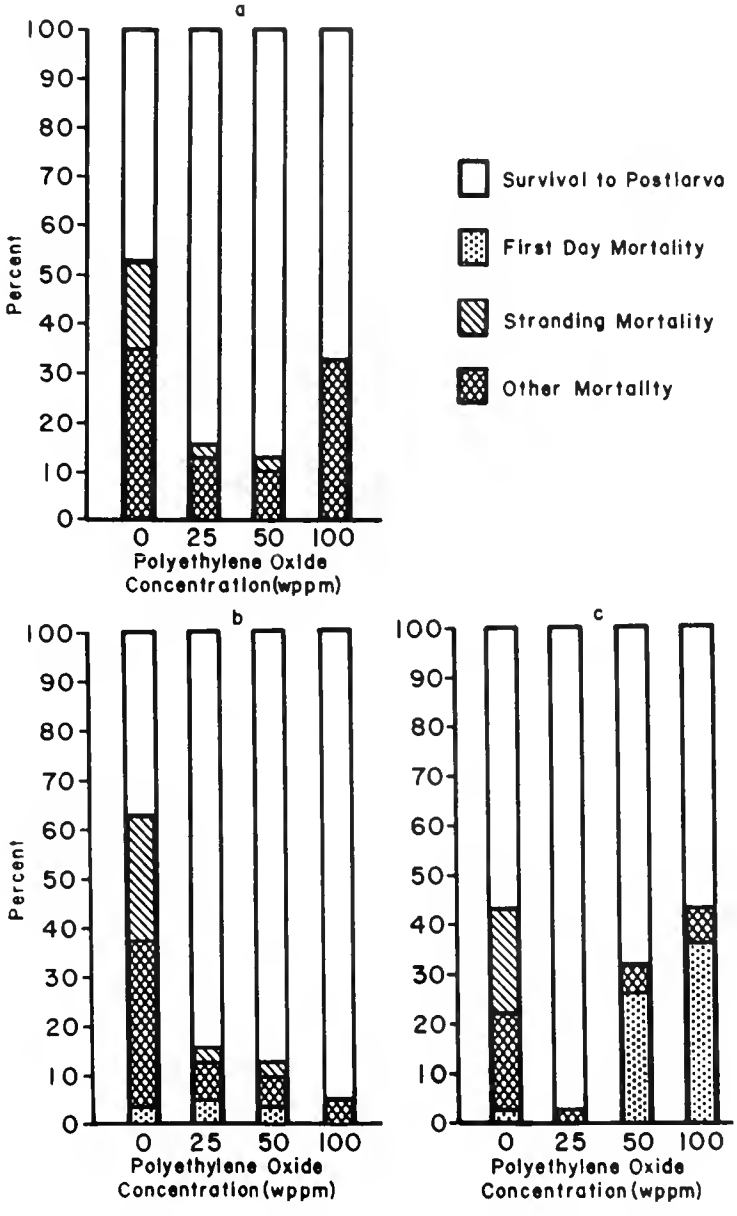

FIGURE 1.—Percentage survival and mortality of *Palaemonetes* larvae reared in polymer and control solutions. (a) *P. vulgaris* experiment I, (b) *P. vulgaris* experiment II, (c) *P. pugio*.

[2]Sandifer, P. A., and M. H. Shealy, Jr. 1974. Some effects of mercury on survival and development of larval grass shrimp, *Palaemonetes vulgaris* (Say). (Unpubl. manuscr.)

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA; NOAA Office of Sea Grant; or the State of South Carolina.

TABLE 1.—Development of *Palaemonetes* larvae exposed to polyethylene oxide solutions (Mean with standard deviation).

Experiment	Species	Polyethylene oxide concentration (wppm) 0	25	50	100
		Development time (days)			
I	*Palaemonetes vulgaris*	19.1 ± 1.5	20.9 ± 2.0	21.3 ± 2.5	22.1 ± 2.8
II	*P. vulgaris*	14.3 ± 0.9	14.6 ± 0.8	14.9 ± 0.9	15.6 ± 1.4
III	*P. pugio*	15.5 ± 1.6	15.5 ± 1.5	16.2 ± 1.4	16.2 ± 2.1
		Molts to postlarva			
III	*P. pugio*	8.0 ± 0.8	8.1 ± 0.9	8.5 ± 0.8	8.3 ± 1.4
		Length of postlarvae (mm)			
II	*P. vulgaris*	6.5 ± 0.6	6.4 ± 0.5	6.4 ± 0.5	6.1 ± 0.5
III	*P. pugio*	6.6 ± 0.6	6.6 ± 0.6	6.6 ± 0.6	6.6 ± 0.5

natural waters, but it may appear in tank culture operations.

First-day mortalities were significant only in the higher treatment concentrations when *P. pugio* larvae were reared in covered plastic boxes (Figure 1c). These deaths apparently were the result of oxygen depletion in the culture water caused by overfeeding and the relatively high biochemical oxygen demand of the polymer solutions (Wade 1973). Other mortalities totaled only 5.6 and 6.9% in the 50- and 100-wppm concentrations, respectively, after the first day.

In all but one instance, larvae in the polymer solutions exhibited a marked reduction in other mortalities (i.e., "natural" deaths) over the controls. Thus, in addition to eliminating stranding, the polyethylene oxide somehow acted to reduce other causes of mortality. The reason for this beneficial effect is unknown, but it is unlikely to be nutritional since, in vertebrates at least, the polymer is poorly absorbed from the gut (Smyth et al. 1970). Further study is needed to examine the reasons for this effect and to evaluate the potential of polyethylene oxide for use in mariculture operations.

Acknowledgments

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A COMPUTER PROGRAM FOR ANALYSIS OF POLYMODAL FREQUENCY DISTRIBUTIONS (ENORMSEP), FORTRAN IV

Program ENORMSEP (Extended Normal Separator Program) separates a polymodal frequency distribution into its component groups where aging studies have not been or cannot be performed. The program calculates preliminary estimates of the number of size groups and their points of overlap using probit analysis and polynomial regression techniques. These preliminary estimates are then entered into NORMSEP (Normal Separator Program) (Hasselblad 1966), used as a subroutine, in order to complete the analysis.

Output data are generated both as listings and punched cards. Listings include at the option of the user: 1) table of values of the standardized normal distribution; 2) table of values of probabilities, standardized normal variables, and probits; 3) polynomial regressions and analyses of variance of probits; 4) table of residuals for the final regression; 5) table of roots corresponding to all regressions after taking second derivative; 6) tables for analyses for the separation of modes; 7) plots of observed and predicted values for the final regression; and 8) plot of the original frequency distribution. Punched card output includes the number of observed frequency distributions with their intervals and probits and regression coefficients for the polynomials.

Input data require the observed size frequency together with values for identification and control purposes. No more than nine size groups may be separated because of limits on the efficiency of parameter estimate in the polynomial regression.

This computer program was developed on an IBM 360/65I computer[1] using release 20.7 MVT/HASP system at the Statistical and Computing Center at the University of Hawaii. This computer program is capable of processing multiple sets of data. For a "typical" problem, the program takes about 1 min of central processing unit time and a total machine unit time of 1.5 min to run a single problem "individually." The requirement for core storage is 168K, where K is 1,024 bytes and where a byte is an address collection consisting of eight binary bits or binary digits.

A description of the program, including program listing as well as input and output for two examples, is available from the authors upon request.

[1]Reference to this particular computer system does not imply endorsement of the product by the National Marine Fisheries Service, NOAA, but is given to provide the reader with a base for determining the cost of performing jobs with the particular computer system at his disposal.

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RECORDS OF LARVAL, TRANSFORMING, AND ADULT SPECIMENS OF THE QUILLFISH, *PTILICHTHYS GOODEI*, FROM WATERS OFF OREGON

This report extends the southern range of the quillfish, *Ptilichthys goodei* Bean 1881, in the northeast Pacific to waters off the central coast of Oregon where larval, transforming, and adult specimens have been collected. The previously reported range of this species in the North Pacific was from the Okhotsk and Bering seas to northern Washington and Puget Sound (DeLacy et al. 1972; Quast and Hall 1972; Hart 1973). The life history of the quillfish is poorly understood and nothing is known of the early stages (Walker 1953; Makushok 1958; Grinols 1965; Hart 1973).

Materials and Methods

Three larvae (20.3, 24.7, 36.0 mm SL—standard length) and one transforming specimen (114 mm SL) of *P. goodei* came from plankton collections made with large-mouth (0.7 m) bongos having 0.571-mm mesh nets. Tows were made in a step-oblique or oblique manner from near the bottom or 150 m (at deeper stations) to the surface at a vessel speed of 2 knots. Tow times were 16 to 25 min. The specimens were fixed in 10% and stored in 5% buffered Formalin.[1]

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Two adults (272, 309 mm SL) of *P. goodei* came from otter trawl (5-m headrope, 4-cm stretch mesh body, 1.25-cm mesh cod end liner) collections. The trawl was towed on the bottom for 15 min at a speed of 2 to 3 knots. The specimens were fixed in 10% Formalin and stored in 40% isopropyl alcohol.

Body measurements were made as described by Hubbs and Lagler (1958). For larvae, standard length was measured from snout tip to notochord tip. The point of reference used to determine notochord tip in larvae of *P. goodei* is indicated by an arrow in Figure 1. It is the point near the end of the tail, at the posterior edge of the region having no pigment on the ventral margin. This point was determined from the tail tip of the 114-mm specimen which had been stained with alizarin red S.

Meristic counts were made on unstained larval and transforming specimens and radiographs of the adults.

Results

Descriptions

The larvae of *P. goodei* are characterized by their slender, elongate form; gut length (35-40% SL, decreasing with growth); myomere numbers, (55 to 57) + (170 to 174) = 225 to 229; and pigment pattern (Figure 1). Morphometrics and meristics are in Table 1. Compared with adults, the larvae have a short snout (17-18% HL—head length) and no fleshy protrusion of the lower jaw. The mouth is oblique. Dorsal and anal fin rays are evident in the 36-mm specimen but the adult numbers have not been attained. The spines of the first dorsal and the rays of the second dorsal begin to form at the posterior and anterior ends of the fins respectively. Development then proceeds anteriorly in the first dorsal fin and posteriorly in the second dorsal. The anal fin rays begin to form slightly anterior to the center of the fin with development proceeding anteriorly and posteriorly. Pectoral fin rays were not formed and pelvic fins were absent in the size range examined.

Pigmentation (Figure 1) on the three larval specimens is similar. Head pigmentation consists of that on the lower jaw, anterior part of the upper jaw, throat, and internally at the base of the hindbrain. Gut pigmentation is mostly restricted to the dorsal and ventral surface with some additional melanophores scattered over the anterior region. The melanophores on the ventral gut sur-

FIGURE 1.—Larva of *Ptilichthys goodei* from waters off Oregon (arrow indicates point of reference for SL).

TABLE 1.—Morphometrics (mm) and meristics of *Ptilichthys goodei* from Oregon waters.

Morphometrics										Meristics								
													P_1			Myomeres		
SL	TL[1]	Snout length	Eye diameter	Head length	Upper jaw length	Lower jaw length	Snout to anus	Depth at pectoral base	Depth at anus	DI	DII[2]	A[2]	Left	Right	Branchiostegals	Preanal	Postanal	Total
Larvae:																		
20.3	21.0	0.4	0.7	2.3	0.8	1.1	8.0	0.9	0.9	—	—	—	—	—	—	55	174	229
24.7	25.5	0.4	0.6	2.2	0.7	1.1	9.3	1.1	1.1	—	—	—	—	—	—	55	170	225
36.0	36.9	0.5	0.7	2.7	0.9	1.1	12.5	1.1	1.1	40	~80	~113	—	—	5	57	170	227
Transforming:																		
114	117	1.6	1.1	6.1	1.8	2.6	32.2	2.0	2.0	83	148	179	13	13	5	55	172	227
																	Vertebrae	
Adults:																Abdominal	Caudal[3]	Total
272	276	5.2	2.8	17.0	3.8	5.0	81	5.5	7.0	83	144	180	13	13	5	53	174	227
309	313	6.3	3.0	19.0	4.2	6.0	91	6.0	7.7	88	142	181	13	13	5	53	174	227

[1]Total length is given for comparison with other publications, although the long caudal filament was not intact.
[2]Dorsal and anal fin ray counts include possible caudal fin elements dorsal and ventral to the fleshy caudal extension respectively.
[3]One fused caudal vertebra found in each adult specimen was counted as one vertebra.

face form a single row on the anterior one-fourth to one-half the length of the gut and a double row along the remaining length. Body pigmentation is concentrated dorsally and ventrally. From a dorsal view, the dorsal melanophores appear somewhat as a double row, one on each side of the dorsal midline, extending from a point over the middle of the gut to near the tail tip (arrow in Figure 1). These dorsal melanophores are larger than the ventral ones. Ventrally, a heavy concentration of melanophores lines the body margin from the hindgut to near the tail tip. Posterior to this ventral body pigment is a small unpigmented area. Posterior to the ventral unpigmented area (arrow in Figure 1) is the fleshy caudal extension characteristic of the species. Pigment on this extension is distinct from that on the rest of the body. It is scattered rather evenly dorsally and ventrally on the body and out on to the finfolds. The lateral midline of this area remains unpigmented.

Identification of the larvae was possible because of the link to the adults provided by the 114-mm SL transforming specimen captured in the same area. The 114-mm specimen has meristics (Table 2), hooked dorsal spines, and a fleshy protrusion of the lower jaw characteristic of adult *P. goodei* and pigmentation similar to the larvae described above. The fleshy caudal extension is more distinct than in the larvae. Gut length (28% SL) is proportionately shorter and snout length (26% HL) proportionately longer. Additional pigment occurs on the dorsal surface of the head posterior to the eye, on the snout, and in a line along the margin of the preopercle extending posteriorly from the angle of the lower jaw. The ventral gut melanophores are in a single row along the entire gut length. Body pigmentation is less pronounced than in the larvae but still distinct.

Adults of *P. goodei* are characterized by their extremely elongate body, the absence of a distinct caudal fin, and the presence of a fleshy protrusion at the tip of the lower jaw. When alive, the two Oregon specimens were brightly colored. The body was light green dorsally shading to yellow ventrally and orange on the throat. Two dark maroon, horizontal stripes were present laterally with maroon spots scattered over the entire dorsal surface. Several dashed maroon lines radiated posteriorly from the snout. A distinct maroon-colored, horizontal bar extended anteriorly from the margin of each eye half the distance to the snout tip. Morphometrics and meristics appear in Table 1. Gut length (29% SL) is similar to that for the transforming specimen, but the snout length (31-33% HL) is greater. Both specimens exhibited a vertebral anomaly in which the centra of two adjacent vertebrae were fused to form a single element with two neural and two hemal spines. In the 309-mm SL specimen the 160th vertebra was fused and in the 272-mm SL specimen it was the 169th element.

Occurrence

Collection data for *P. goodei* from Oregon waters is presented in Table 2. All specimens came from waters off the central coast of Oregon between March and August. All but one was captured during daylight. All but one was taken in water greater than 120 m deep on the continental shelf 18 km or closer to shore where the bottom was primarily gray sand.

TABLE 2.–Collection data for *Ptilichthys goodei* from Oregon waters.

SL (mm)	Date	Location		Km from coast	Coastal reference	Time	Bottom depth (m)	Tow depth (m)	Gear	Bottom type[1]	Surface temp. (°C)
		Lat. N	Long. W								
Larvae:											
20.3	25 Mar. 1973	44°00′	124°22.1′	18	Siuslaw River	1526-1542	117	100-0	Bongos	Gray sand-green mud	11.0
24.7	20 Apr. 1973	44°00′	124°22.1′	18	Siuslaw River	0235-0300	109	75-0	Bongos	Gray sand-green mud	10.4
36.0	14 May 1971	44°39.1′	124°17.7′	18	Newport	1621-1641	80	75-0	Bongos	Gray sand	11.2
Transforming:											
114	29 June 1971	44°39.1′	124°52.7′	65	Newport	1128-1153	340	150-0	Bongos	(Slope)	14.5
Adults:											
272	7 Aug. 1973	44°42′	124°7′	5	Moolach Beach	0945-1007	52	52	Otter trawl	Gray sand	9
309	3 July 1973	44°45′	124°14′	13	Cape Foulweather	1010-1028	80	80	Otter trawl	Gray sand	10

[1]From USC&GS Charts No. 5702 and No. 5802.

The larval and transforming specimens reported here are the only representatives of *P. goodei* found in 847 small-mouth (0.2 m) bongo and 413 large-mouth (0.7 m) bongo samples analyzed to date from waters off Oregon. The samples are part of an ongoing project to study seasonal and annual variations in distribution and abundance of larval fishes. Other studies of larval fishes off Oregon (Richardson 1973; Pearcy and Myers 1974) yielded no *P. goodei*.

The two adult specimens are the only ones recovered from 23 trawl samples taken during the summer of 1973 in conjunction with an ecological baseline study of the nearshore region of the mid-Oregon coast in the vicinity of Yaquina Head. Although they were taken with a bottom trawl, it is possible that the specimens entered the net shortly before it was brought on board. Thus, they may have been in near surface water rather than on the bottom as their presence in trawl samples would suggest.

Discussion

Vertebral counts, (53 to 55) + (172 to 174) = 227, of the transforming and adult Oregon specimens are lower than those, (58 to 59) + (179 to 182) = 238 to 240, reported by Makushok (1958), presumably for Bering Sea specimens. The counts are also lower than those, 236 to 240, given by Hart (1973), presumably for British Columbia specimens. This could indicate clinal variation with the southern specimens having fewer vertebrae. On the other hand, the lower number of both abdominal and caudal vertebrae of the Oregon specimens could indicate the presence of an undescribed species. Additional Oregon specimens are needed to determine the range of variation in vertebral number and to compare with northern specimens to see if they are actually the same species.

Reasons why quillfish have not previously been reported from Oregon waters are speculative. A partial explanation may be the lack of major sampling efforts in Oregon's coastal zone until recent years. Rarity (Makushok 1958; Hart 1973), inaccessibility, avoidance, and escapement also offer explanations. It is possible the adults bury themselves in the bottom (Makushok 1958) and are thus inaccessible to conventional types of gear. Behavior exhibited by one of the adults taken off Oregon suggests the quillfish may readily avoid and/or escape from trawl gear. Immediately after the trawl was brought aboard, the slender fish wriggled through the meshes of the net onto the deck of the vessel. It demonstrated great agility with snakelike undulations. The larvae may remain on or near the bottom, or they may spend all or part of the time in the neuston. Either situation would make them inaccessible to most plankton gear. The large size of the larvae indicates good avoidance capabilities.

Acknowledgments

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EFFECT OF CROWDING ON STOCK AND CATCH IN *TILAPIA MOSSAMBICA*

In a previous report (Silliman 1972) I described the effect of crowding on the relation between exploitation and yield in *Tilapia macrocephala*. Subsequently I performed a similar experiment with *T. mossambica*. Since the results were somewhat different for the latter species and because of its wide use in pond culture, a brief report of the second experiment seems justifiable.

Apparatus and Procedures

Most of the procedures and apparatus were identical with those reported by Silliman (1972). Essentially the approach was to raise the populations in two conventional aquariums, one (L) with a volume of 155.2 liters and the other (S) with 77.6 liters so that S had exactly one-half the capacity of L. Aeration was by airstones and illumination by overhead fluorescent lamps. Rectangular spaces at the ends of the aquariums were fenced off with rods placed 3 mm apart, providing refuges for the young. Further shelter was provided by floats with suspended cords and by fiber brush shelters. Covering part of the aquarium walls with black plastic furnished shaded areas for spawning. Water condition was maintained by filtration and weekly partial water changes. Water temperature was 24° ± 2°C to month 5.7 and 30° ± 2°C thereafter. Feeding details are given in Table 1.

Populations were counted and weighed at approximately 2-mo intervals. Since *T. mossambica* is a mouthbreeder, it was desirable not to handle the fish more often than this. The 2-mo period includes 1.0 to 2.6 of the brood intervals reported by various authors (Kelly 1957, 30-40 days; Swingle 1960, 30-40 days; Uchida and King 1962, 23-61 days). Exploitation consisted of removing each 10th fish. In weighing, fish were drained in a net and placed in a previously weighed container of water; fish weight was total weight less the tare.

Table 1.—Food (in g) placed in tanks.

Day of week	Trout pellets		Tropical fish food		Total
	Moist	Dry	A[1]	B[1]	
Sun.	4.0	1.5	0.5	1.0	7.0
Mon.	5.5	1.5	0.5	1.5	9.0
Tues.	5.5	1.5	0.5	1.5	9.0
Wed.	5.5	1.5	0.5	1.5	9.0
Thurs.	5.5	1.5	0.5	1.5	9.0
Fri. A.M.	5.5	1.5	0.5	1.5	9.0
Fri. P.M.[2]	5.5	1.5	0.5	1.5	9.0
Total	37.0	10.5	3.5	10.0	61.0

[1]Commercial makes of dry food.
[2]This was combined with the Friday A.M. feeding in 35 out of 131 wk and with the Sunday feeding once.

Results and Conclusions

The two populations were started 10 July 1970 (Table 2, Figure 1). Recruitment (estimated from counts as in Silliman 1972) occurred after the temperature increase at month 5.7 and readjustment of the sex ratios at month 6.9 (Table 2). As was true for *T. macrocephala*, recruitment was greater in tank L (62) than in tank S (20). Some

TABLE 2.–Population and catch, *Tilapia mossambica*, in two sizes of tanks. Target exploitation rate was 10% per 2 mo.

	S—77.6-liter tank				L—155.2-liter tank			
	Number		Weight (g)		Number		Weight (g)	
Month[1]	Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.3	[2]11	—	—	—	[2]11	—	—	—
0.5	[3]16	—	—	—	[3]16	—	—	—
4.1	[4]9	—	650	—	[4]9	—	593	—
6.9	[5]4	—	282	—	[5]4	—	303	—
9.2	20	—	372	—	50	—	529	—
11.1	20	—	641	—	49	—	571	—
13.1	20	—	831	—	46	—	754	—
15.2	20	—	983	—	44	—	900	—
17.0	20	—	1,088	—	46	—	1,006	—
19.1	20	2	1,154	119	46	5	1,081	115
21.2	18	2	1,121	108	41	4	1,047	113
23.0	16	1	1,120	146	36	4	1,071	100
25.1	14	1	987	89	34	3	1,070	100
27.1	12	1	912	90	31	3	1,083	198
29.2	10	1	861	114	29	3	1,043	119

[1]0 = 1 July 1970.
[2]Initial stocks were: S-6 immatures, 2 males, 3 females; L-4 immatures, 4 males, 3 females.
[3]To each stock, 5 immatures were added.
[4]Stocks were adjusted to 3 immatures, 2 males, and 4 females each.
[5]Stocks readjusted to 1 male and 3 females each. Temperature was increased from 24° to 30°C at month 5.7.

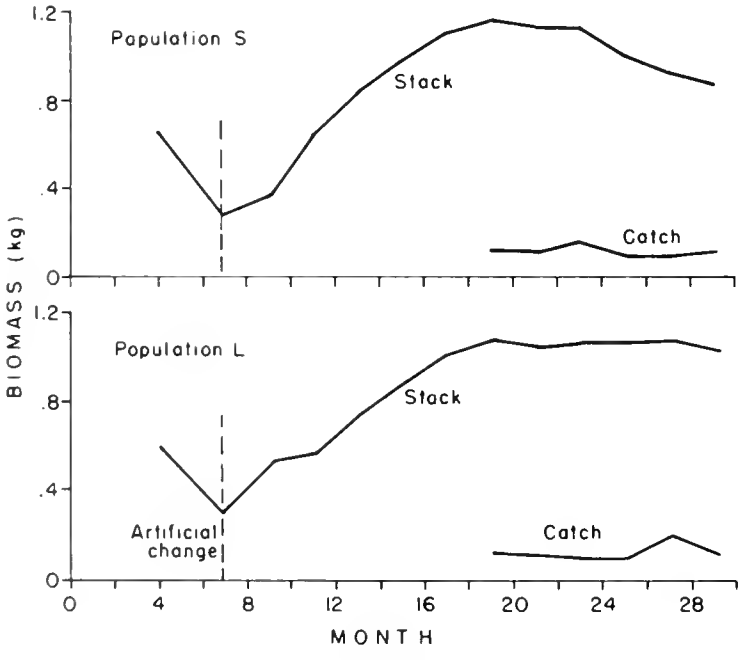

FIGURE 1.–Course of biomass and catch.

recruitment occurred throughout the experiment after month 6.9 in L but was limited to 2-mo period 6.9-9.2 in S.

Exploitation began at month 19.1 for both populations, at a target rate of 10% per 2 mo. Because of the small numbers of fish in the populations, actual percentages removed (Table 2) varied considerably from 10%. Populations differed in their response, S declining while L remained almost constant (Figure 1). Mean values of catch were S, 111 g; L, 124 g. Although the exploitation data were too few for firm conclusions, they suggest a greater yield from the larger tank, under the same catch rate and food amount. Here the response for *T. mossambica* was reversed from that found by Silliman (1972) for *T. macrocephala*. If significant, this difference may be due to the fact that *T. mossanbica* reaches larger ultimate size than *T. macrocephala*. The presence of a few large individuals in a population of small numbers (Table 2) could lead to a different response of the population to space available.

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THE OCCURRENCE OF ELVERS OF *SYNAPHOBRANCHUS AFFINIS* ON THE CONTINENTAL SLOPE OFF NORTH CAROLINA[1]

Members of the family Synaphobranchidae are demersal eels which are widely distributed in the Atlantic and Indo-Pacific oceans (Castle 1964). Data from a June 1973 cruise in the Norfolk Canyon area indicate that they are an important part of the fish community in both numbers and biomass in depths around 1,000 m (Virginia Institute of Marine Science unpubl. data). Bruun (1937) reported on the life histories and larval development of several synaphobranchids, and Castle (1964) listed synonomies in addition to keys to genera and species. Robins (1971) gave osteological, meristic, and morphometric data and also discussed the life history and ecology (Robins 1968).

Although Robins (1971) intensively examined 46 *Synaphobranchus affinis* Günter 1877 greater than 193 mm in total length, the occurrence of elvers or unpigmented juveniles of this species is unreported. The purpose of this report is to provide a record of capture, meristic and morphometric data, and some observations in food habits of *S. affinis* elvers.

Materials and Methods

A total of 89 elvers of *S. affinis* (Figure 1) were collected during a ½-h otter trawl haul from 1745 to 1815 h EST aboard the RV *Eastward* on 29 April 1973 at Eastward station 22039, lat. 34°03.2′N, long. 75°52.0′W at depths from 550 to 600 m. The gear used was a 30-foot shrimp trawl with a ¼-inch stretch-mesh cod end liner.

Total length of all specimens was measured to the nearest millimeter. A subsample of 40 elvers was taken for meristic analysis using a table of random numbers (Rohlf and Sokal 1969). Elvers were cleared in 2% potassium hydroxide, stained with alizarin red-S in 2% KOH, passed through a graded series of glycerine, and stored in 100% glycerine to which thymol was added. Three replicate counts were made of the following meristic characters: total vertebrae; dorsal, anal, caudal, and left and right pectoral fin rays; left and right branchiostegals. The presence and position of vertebral deformities (fused or partially fused vertebral centra; extra, fused, or distorted neural or hemal spines) were noted and representative types were drawn with the aid of a camera lucida.

To determine if osteological deformities might result in differential mortality of *S. affinis* during later life, 40 additional specimens ($\bar{x}$ total length = 220 mm, extremes 173-305 mm) collected on 13 June 1973 aboard the RV *Columbus Iselin* in 630 m of water with a 45-foot otter trawl at lat. 37°03.2′N, long. 74°34.1′W were examined. These fishes were X-rayed, vertebrae counted, and the presence or absence of deformities noted. Frequency of occurrence of deformities in elvers and larger fish were compared by χ^2 analysis (Sokal and Rohlf 1969).

Morphometric measurements were taken following the method of Robins (1971) with either dividers and dial calipers or a binocular microscope fitted with a calibrated ocular micrometer.

Results and Discussion

Eels of the genus *Synaphobranchus* are characterized by confluent branchial apertures with a slitlike opening on the midline of the throat (Robins 1971). Synaphobranchid eels commonly encountered in trawls on the continental slope near Cape Hatteras, N.C. are *Synaphobranchus kaupi*, *S. affinis*, and *Ilyophis brunneus* (Markle 1972; Virginia Institute of Marine Science unpubl. trawl records). Members of this group show varying degrees of plasticity and overlap in morphometric characters but also show mean differences (Robins 1971). The specific identification of these elvers as *S. affinis*, therefore, was based on vertebral counts.

Mean, 95% confidence interval, and the frequency distribution of vertebral counts are shown in Figure 2. Vertebral counts of the 40 specimens had extremes of 130 and 136 with a mode of 134. This is within the range of values for 44 *S. affinis* given by Robins (1971) ($\bar{x}$ = 133.1, extremes 128-139) and outside the range of the other species of synaphobranchids common to this region (*S. kaupi*: $\bar{x}$ = 148.0, extremes 146-150; *Ilyophis brunneus*: $\bar{x}$ = 147.5, extremes 144-151). Means, 95% confidence intervals, and frequency distributions of other meristic characters are found in Figure 2. Paired t tests (Sokal and Rohlf 1969) showed no significant differences between the number of left and right pectoral fin rays (t = 1.00, df = 39) or the number of left and right branchiostegals (t = 0.42, df = 39). Dorsal and

[1]Virginia Institute of Marine Science contribution no. 652.

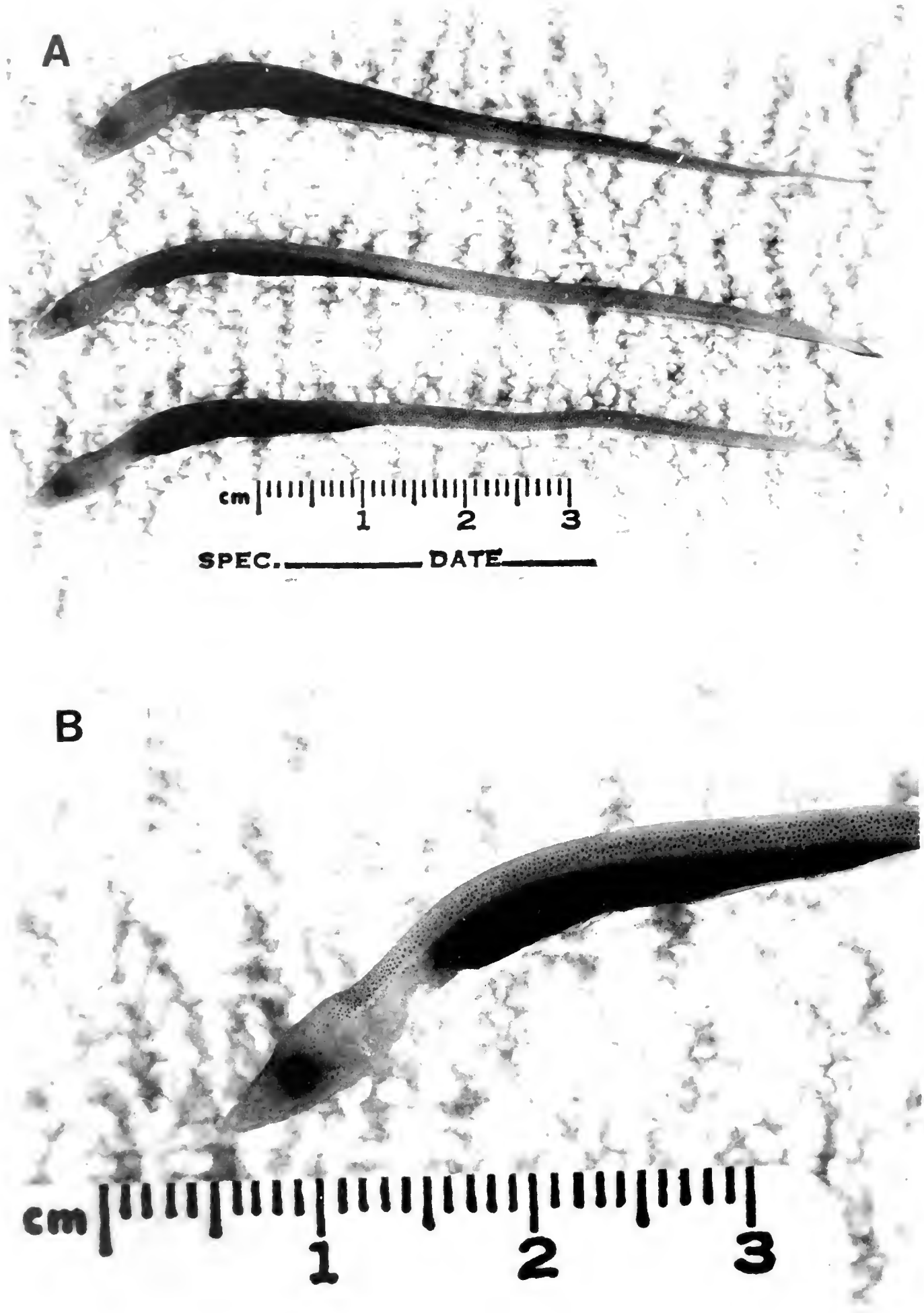

FIGURE 1.–(A) Photograph of a series of *Synaphobranchus affinis* elvers. (B) close-up view of anterior region of one elver of *S. affinis* showing dark, bluish-black peritoneum and slight pigmentation above lateral line.

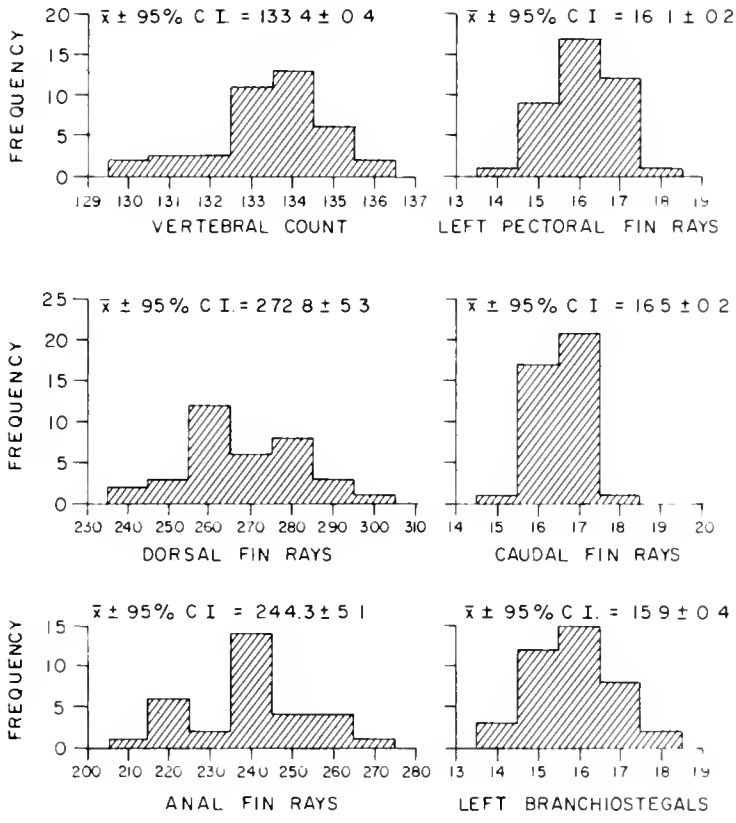

FIGURE 2.–Means, 95% confidence intervals (C.I.), and frequency distributions of various meristic characters of *Synaphobranchus affinis* elvers.

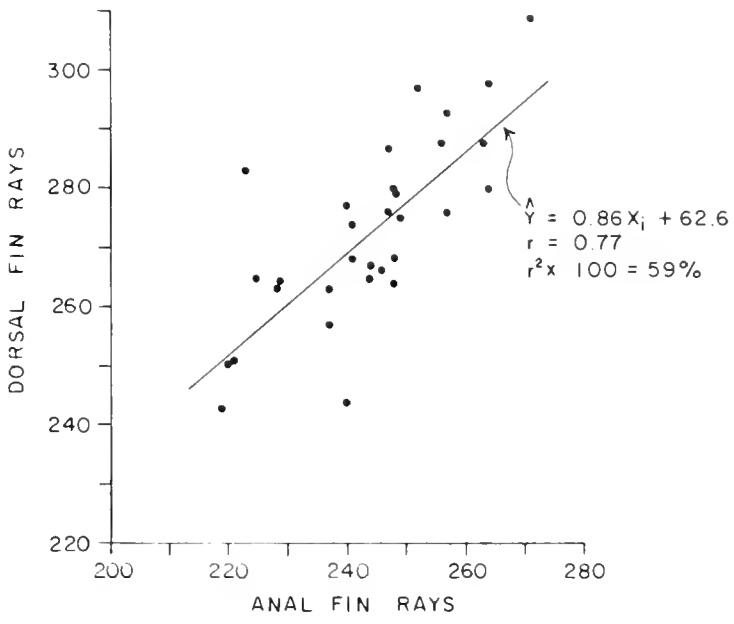

FIGURE 3.–Regression relationship between dorsal and anal fin rays of *Synaphobranchus affinis* elvers, where y = dorsal fin rays, x = anal fin rays, r = correlation coefficient, and $r^2 \times 100\%$ = coefficient of determination.

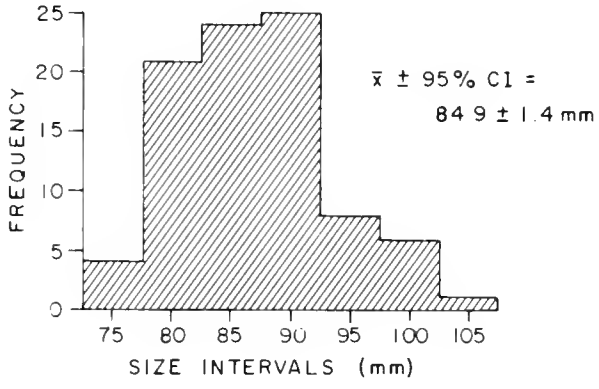

FIGURE 4.–Frequency distribution, mean, and 95% confidence interval (C.I.) of total length of *Synaphobranchus affinis* elvers.

anal fin rays showed a great degree of variability which is also characteristic of the American eel, *Anguilla rostrata* (Wenner 1972), and the snake eel, *Pisodonophis cruentifer* (Wenner unpubl. observations). Dorsal fin rays had extremes of 243 and 309 whereas anal fin rays had extremes of 219 and 271. Plots of dorsal against anal fin rays suggested a correlation and therefore the linear regression equation, correlation coefficient, and coefficient of determination were calculated (Figure 3). Fifty-nine percent of the variation in the number of dorsal fin rays was associated with the number of anal fin rays.

Mean length of the *S. affinis* elvers was 89 mm with extremes of 72 and 105 mm. Length-frequency distribution is found in Figure 4. Means, 95% confidence intervals, and extremes for morphometrical measurements are given in Table 1. All values fell within the ranges of those of *S. affinis* presented by Robins (1971).

Osteological deformities associated with the vertebral column were found in 72.5% of the 40 elvers and in 60% of the larger *S. affinis* examined. In both instances, most deformities were in the caudal part of the vertebral column, generally in the last 30 vertebrae. Illustrations of some representative deformities are shown in Figure 5

TABLE 1.–Summary of morphometric characters of elvers of *Synaphobranchus affinis*. C. I. refers to confidence interval.

Morphometric character	Mean ± 95% C.I.	Extremes	*n*
% total length			
Preanal length	27.7 ± 0.5	25.6-32.0	39
Predorsal length	30.0 ± 0.7	25.6-34.7	39
Head length	13.0 ± 0.2	11.3-14.2	40
% head length			
Gape length	66.9 ± 1.1	58.3-74.5	40
Horizontal eye diameter	16.8 ± 0.4	14.8-21.0	40

and a summary of the major types is in Table 2. X^2 analysis showed that there was no significant difference between elvers and larger immature fish (X^2 = 1.72, df = 39), suggesting that these deformities do not result in differential mortality in fishes possessing them.

It is conjectural whether these specimens

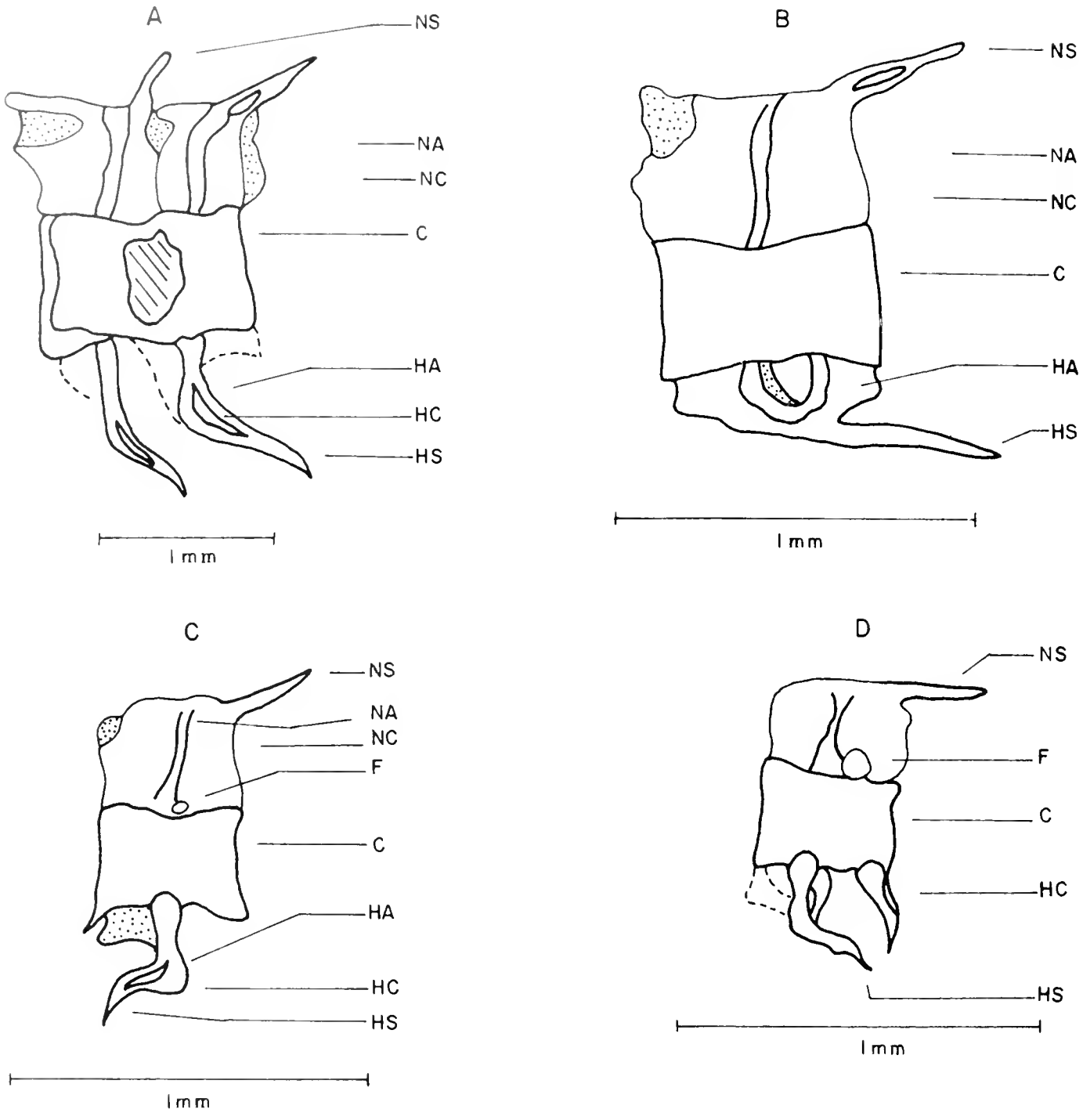

FIGURE 5.—Lateral views of various osteological deformities associated with the caudal vertebrae of *Synaphobranchus affinis*. Dashed lines in figures represent areas of incomplete ossification. NS = neural spine; NA = neural arch; NC = neural canal; C = centrum; F = foramen; HA = hemal arch; HC = hemal canal; HS = hemal spine; TL = total length in millimeters. (A) Fused centra with a bony knob projecting laterally; TL = 92. (B) Two sets of hemal spines which are fused together forming an arch; TL = 102. (C) Hemal spines projecting anteriorad rather than posteriorad; TL = 91. (D) Extra unfused set of hemal spines with one set projecting anteriorad and one set posteriorad; TL = 79.

represent the size at which the elvers descend to the bottom from the pelagic realm, where they pass their larval existence, because closing and mid-water nets were not used.

Of the 40 cleared and stained specimens, 12 had material in the gut cavity. Three contained crustacean appendages whereas nine had discernable fish remains such as disarticulated vertebrae. One elver contained an intact gonostomatid which had been swallowed head first. Gonostomatids are mesopelagic but the elver could have ingested it while in the trawl.

Acknowledgments

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TABLE 2.–Summary of the types of vertebral anomalies in *Synaphobranchus affinis* elvers expressed as percent of specimens with anomalies. The sum of the percentages is greater than 100% because some individuals had more than one type.

Item	Elvers	Larger immature fish
Sample size	29	24
Abnormal hemal spines	81.6	83.3
Abnormal neural spines	3.4	0.0
Fused or partially fused vertebrae	13.6	16.7
Multiple anomalies	57.8	16.7

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CATCHES OF ALBACORE AT DIFFERENT TIMES OF THE DAY

The purpose of this study is to examine the hypothesis that diel variations occur in the catches of albacore by boats trolling surface jigs off Oregon. Although albacore fishermen talk of "morning bites" and "evening bites," no published data exist, to our knowledge, confirming these trends.

Studies on the feeding habits of tunas, however, provide evidence for intense feeding activity during certain periods of the day. Based on the quantity of food in stomachs, Iverson (1962) concluded that major feeding periods of albacore occurred in early morning and late afternoon-evening. Similarly, Nakamura (1965) and Dragovich (1970) found evidence for morning and late afternoon peaks in the stomach fullness of skipjack and yellowfin tunas. Food consumption of captive skipjack was greatest between 0630 and 0830 h, and skipjack tuna in only one of three tanks fed intensively in late afternoon (Magnuson 1969). This was in agreement with Uda (1940) who reported that catches of skipjack tuna with pole and live bait peaked in early morning hours and were usually followed by successively lower peaks later in the day.

Fishermen were solicited to record data on 1969 and 1970 albacore catches in special logbooks. Several entries per day were requested. The records of five boats fishing off Oregon during July, August, and September 1969 were used for this study. These five skippers kept detailed records averaging eight entries per day. In 1970 the records of 12 boats were used that recorded catches at least every 4 h during the fishing day for 20 July-2 August 1970. All boats were 45-60 feet in length.

Average catches per boat were calculated for each hour fished, usually 0500-2200 h or 2300 PDT, for 3 mo in 1969 and 2 wk in 1970. When the interval between logged catches was greater than 1 h, the catch for the interval was divided by the number of hours fished, and this average number was distributed uniformly within the interval. Because the selected boats did not necessarily fish in the same locality or during the same days of the months, the data provide only an estimate of the general trends in hourly catches of albacore off Oregon.

The catches of albacore versus hours of the day are shown in Figure 1. Chi-square tests of the

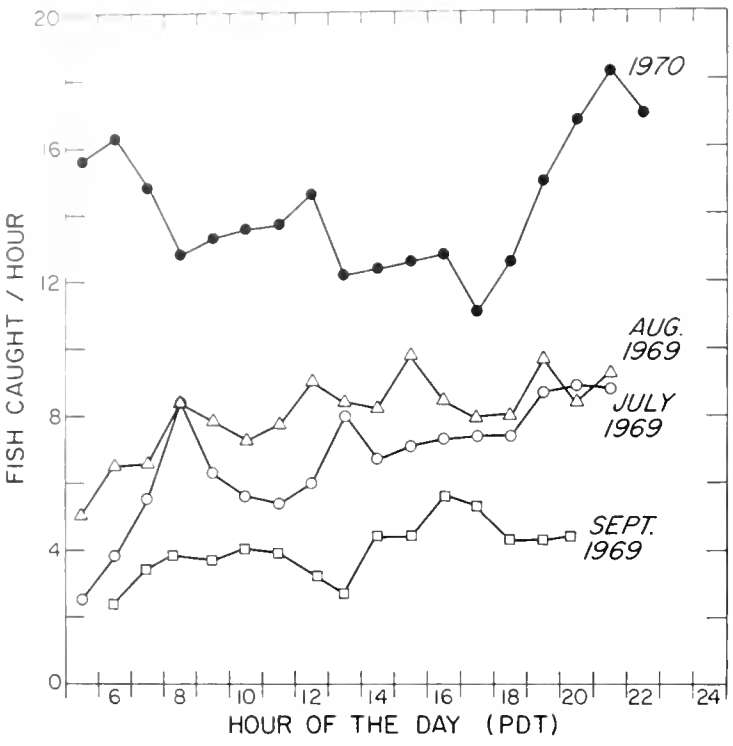

FIGURE 1.—Average catch of albacore per boat for each hour of the day from 0500 to 2200 for 3 mo in 1969 and for 20 July-2 August 1970. The numbers for hours of the day refer to the time at the beginning of the interval.

heterogeneity of catches for all four of the data sets are significant ($P<0.05$), indicating that catch rates were not constant with time but varied throughout the day. Consistent trends for diel periodicity in catches, however, are not apparent.

Only during 1970 was there an obvious trend for peak catch rates to occur early in the morning and in the evening. These peaks coincided with the local mean times of sunrise and sunset (about 0600 and 2100 PDT).

The separate months of 1969 show a variable pattern with peaks occurring at different times during different months. There is no evidence for a pronounced early morning "bite," except perhaps 0800-0900 in July. Catch rates generally increased with time during the day. Most 1969 afternoon catch rates were above the median for each of the 3 mo, but they were not markedly higher in the evening as was found for 1970.

The catches during 1970 were exceptionally high. Even the lowest 1970 catch rate was higher than any of the peak 1969 catches (Figure 1). The 1970 jig-boat season for albacore off Oregon was unusually short (most fish were caught between 22 and 29 July) and the fleet was localized in a small area (Pearcy 1973; Keene 1974). For those reasons, the spatiotemporal variability for the 1970 data is probably much less than for the separate months of 1969.

From our limited data we conclude that albacore feed throughout the day. Catch rates averaged over several weeks do not always indicate morning and evening periods of intense feeding. Obviously this does not preclude the occurrence of morning and/or evening bites in some areas on some days.

Although stomach fullness and catch rates are both related to feeding behavior, they may provide different results on feeding periodicity because of the influence of such factors as changes in depth distributions, vulnerability to fishing methods, and the times required for accumulation and digestion of food in the fish's stomach. For example, the especially high rates of capture of albacore on surface jigs during sunrise-sunset periods of 1970 may be related to the vertical migration of Pacific saury, *Cololabis saira*, their major prey during this time (Pearcy 1973). Saury migrate to surface waters at sunset and descend into deeper waters at sunrise (Hotta and Odate 1956; Hughes and Gill 1970). Relatively low catch rates during the day may therefore be the result of either albacore pursuing saury into deeper water where albacore are less vulnerable to surface lures or to reduced feeding activity.

Acknowledgments

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UNITED STATES OF AMERICA

Fishery Bulletin

National Oceanic and Atmospheric Administration • National Marine Fisheries Service

Vol. 73, No. 4 October 1975

(Continued on back cover)

Seattle, Washington

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Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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Fishery Bulletin

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MARINE TROPHIC INTERACTIONS BY DYNAMIC SIMULATION OF FISH SPECIES

JAMES D. PARRISH[1]

ABSTRACT

A mathematical model was developed for performing dynamic simulations of groups of interacting animal species. The energy balance of the individual animal was modeled so that growth and reproduction respond to food consumption after metabolic expenses are met. Populations change in response to recruitment (based on parental spawning) and mortality from natural causes, predation, starvation, and (where applicable) human exploitation. The forms of the various component mathematical functions were derived from the available ecological sources. Functions and parameters are especially applicable to marine fish species. Trophic webs of any size or form can be constructed using this basic species model. Computer solution of the essentially continuous differential model gives a time history of trophic and population variables for all species in the web.

Models of trophic webs of 2, 3, and 4 levels were constructed and exercised. These were used to examine effects of age class structure, reproductive time lag, and population regulation by starvation mortality and fecundity control. Competition between species and the effects of a top predator on competitors, with and without human exploitation, were studied.

Thus far in the history of trophic ecology there has been little effort to bring together the important results of the diverse studies which provide the components of the total trophic system into a construct that will permit analyzing the effects of metabolism, food consumption, reproductive effort, and the structure of the trophic web upon the weight, population, and biomass of the various species involved. Perhaps the most complete and useful approaches in the literature are those of Menshutkin and Kislyakov (1967, 1968), Menshutkin (1968), Menshutkin and Prikhodko (1968, 1969, 1970), Karpov et al. (1969), Krogius et al. (1969), Menshutkin and Umnov (1970), Lassiter and Hayne (1971). The present work is an attempt to create a complete model for fish in the natural environment and to employ it for the stated type of total trophic analysis.

The mathematical "trophic anatomy" of the generalized species modeled contains certain functions which represent trophic interactions with other species. The trophic web consists of an arbitrary number of such interacting species, coupled in this way into any arbitrary design; e.g., with any number of trophic "levels" (or coupled across levels), any number of species at each level, any number of predator species on a single prey species, etc. The trophic properties of the generalized, modular species are established by specifying a set of equations which define its various ecological functions, such as respiratory metabolism, feeding, natural mortality, and reproduction. The composite nature of the model species' trophic anatomy permits considerable structural flexibility in model development. A particular ecological function, such as feeding rate as a function of prey abundance, may be expressed differently in different simulation runs by changing a single component equation. The separate identity of each species is determined primarily by the numerical values of the parameters in its component functions, but the form of functions may be different in different species where the data dictate.

The model approach used allows a number of different levels of approximation. In the simulations performed here, no differentiation is made between sexes in the populations. The sexes could easily be represented separately at the cost of more computing time and a larger data base. A common and convenient simplification that is used in most of the present simulations is construction of an entire species population of identical individuals. Thus, the individual must be given a set of characteristics and parameter values that are in some sense representative of the entire life history after recruitment. A population with separate age classes has also been created explicitly with the present model.

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The model was employed in a number of simulations for a variety of trophic webs. There were not sufficient data at hand for all the species of a real trophic web to permit simulation of such a web in this way. The parameters and initial values used in these simulations are, therefore, reasonable illustrative values for fish in the natural environment, based mostly on the literature.

Despite the scarcity of the real data that would be required to use the model effectively for quantitative prediction of real systems at present, models of this sort have considerable immediate value. Representing and interrelating animal functions analytically enforces a discipline in thinking which tends to clarify perceptions of the trophic relations. Formulation of a system in mathematical functions makes clear the nature of the data required, so that effort in gathering data can be applied efficiently. Component functions for a single species can be collected from a variety of sources and fused. The trophic behavior of the resulting model species can be studied, at least qualitatively, to see if the model behaves as the animal appears to behave. If the species model appears to represent the animal reasonably well, and if a trophic web is constructed from such animals, some confidence may be placed in its predictions of the behavior of the real system—a system which may be much more difficult to evaluate independently of the model.

THE MODEL

The basic model used for each species in every trophic web was developed from an energy balance of the individual and a formulation of the population dynamics of the species. Table 1 contains a glossary of symbolic notation used in the model.

(A) The Energy Balance

The energy balance was written by equating assimilated food intake, kC, to the sum of the three physiological uses of the assimilated food: respiratory metabolism, Q, reproductive material produced for spawning, S, and growth, G.

$$kC = Q + S + G \tag{1}$$

Similar expressions are found in Winberg (1956:210, 1962), Ivlev (1961a), Warren and Davis (1967), Mann (1967, 1969), Davis and Warren (1971), and elsewhere. Mann (1965) has made one of the very few attempts to include the S term quantitatively in the balance. Most workers (e.g., Winberg 1956:209; Mann 1967, 1969) find that to a very acceptable ecological approximation, most fish under most circumstances assimilate a fairly constant fraction, $k \approx 0.8$, of the food, C, consumed (C, the feeding rate, is commonly called the ration and will be so designated herein). Ten (1967) should be consulted for a minority opinion on the effective constancy of k. Kostitzin (1939:180) and Beverton and Holt (1957:113) also deal with the form of possible variation.

All the above terms are time rates. In the present simulations, the time unit used is the year. Since G is dW/dt, the instantaneous value of body weight, W, can be found by integration of G. Each term in Equation (1) can be expressed as energy or as the equivalent weight of body tissue, wet (live) or dry. In these simulations, all terms for all species are expressed in wet weight of tissue, based on a standard conversion factor of 1 kcal/g wet weight (Winberg 1956; Mann 1969). Recent results (Davis 1968; Kausch 1968; Brett et al. 1969) on changes in water content of fish tissues at various nutritional states suggest that a dry weight basis may be noticeably more accurate where data are available. The use of different conversion factors for different species or conditions, when known, introduces no conceptual problems. That Equation (1) can be balanced using experimental values of k, C, Q, and G determined simultaneously in the laboratory for a group of fish over a range of sizes, ambient temperatures, and nutritional states, has been demonstrated by Kausch (1968), using the carp, *Cyprinus carpio*.

The results of many investigations indicate that respiratory metabolism can be expressed approximately as a function of body weight, W, by the relation

$$Q = \alpha W^{\gamma}, \tag{2}$$

where γ is some fractional power. For most fish species a value of $\gamma = 0.8$ appears to be sufficiently reliable for ecological purposes (Winberg 1956:149, 1962; Mann 1965, 1969; Paloheimo and Dickie 1966). Where a more accurate value of γ is known for a particular species, the model will accept it readily.

For the purpose of the present simulations, a level of α for a constant (or long-term average) temperature of 10°C is used. Based on a large

TABLE 1.—Glossary of symbolic notation used in the model. [Notation defined in referenced literature, when different from that of the present model, is not repeated here.]

Symbol	Definition	Symbol	Definition
a	Numerical parameter in the Beverton and Holt reproductive function	m_{mc}	Numerical predation parameter in the Holling feeding function
B	Species biomass	N	Species population
B_i	Biomass of the ith species	N_{Fish}	Population of a fish species
B_1	Biomass of the food base	N_i	Population of the ith species or age class
b	Numerical parameter in the Beverton and Holt reproductive function	N_m	Sexually mature species population
C	Actual ration; actual rate of food consumption by an individual	N_0	Initial population
C_{max}	Maximum ration when feeding to satiation	N_p	Predator population
$C_P = C_{P_{Total}}$	Ration of a predator	N_s	Standard equilibrium value of species population
C_{P_i}	Consumption of the ith prey species by a predator	n	Numerical parameter in the starvation mortality function
c_{s1}	Numerical predation parameter in the linear feeding function	P	Prey abundance
c_1	Instantaneous coefficient of natural increase of an "exponential growth" type food base	P_1	Rate of food base biomass input to the system in a "constant input" model
D_{FISH}	Rate of change of population due to fishing mortality	Q	Rate of respiratory metabolism of an individual
D_{NAT}	Rate of change of population due to natural mortality	Q_{max}	Rate of respiratory metabolism of an individual at maximum ration
D_{PRED}	Rate of change of population due to predatory mortality	R	Rate of reproductive recruitment
D_{STARV}	Rate of change of population due to starvation mortality	R_s	Standard equilibrium recruitment rate
E	Total egg production rate of a population	r	Fraction of the maximum ration actually consumed
e	Base of natural logarithms	S	Fecundity: actual rate of production of reproductive material by an individual
F	Coefficient of instantaneous fishing mortality	S_{max}	Maximum fecundity at current body weight
G	Actual growth rate of an individual	s	Computed numerical parameter in the starvation mortality function
G_{max}	Maximum growth rate; growth rate when C = C_{max}	t	Time
G_{VB}	Growth rate predicted by the von Bertalanffy growth function	t_c	Critical time to 100% starvation mortality
g_m	Fraction of the species population that is sexually mature	u	Fecundity coefficient of an individual
g_1, g_2	Numerical parameters in the linear sexual maturity function for g_m	v_i	Coefficient of predator preference for the ith prey
I_1	Constant of integration for critical starvation mortality time	W	Body weight of an individual
j	Convenience combination of variables in Equation (A-2), Appendix	W_{Fish}	Body weight of an individual fish
K_1	Recruit body weight coefficent	W_i	Body weight of an individual of the ith species or age class
k	Ration assimilation coefficient; fraction of the ration assimilated	W_0	Initial body weight of an individual
L_∞	Numerical parameter (theoretical maximum body length) in the von Bertalanffy growth function for length	W_{prey}	Body weight of a prey individual
M	Coefficient of instantaneous natural mortality	W_s	Standard equilibrium body weight of an individual
m	Numerical parameter in the starvation mortality function	W_∞	Numerical parameter (theoretical maximum body weight) in the von Bertalanffy growth function
		α	Respiratory metabolism coefficient
		α_{max}	Respiratory metabolism coefficient at maximum ration
		α_{starv}	Respiratory metabolism coefficient at zero ration
		γ	Numerical parameter (weight exponent) in the respiratory metabolism function
		κ	Numerical parameter in the von Bertalanffy growth function
		ξ	Numerical predation parameter in the Ivlev feeding function

collection of data from the experimental literature, a level of α appropriate to an average spontaneous activity level was chosen. The instantaneous value of α is allowed to vary in response to ration according to the equation

$$\alpha = \alpha_{starv} + (\alpha_{max} - \alpha_{starv}) \frac{C}{C_{max}}, \qquad (3)$$

where C is the actual instantaneous ration, α_{starv} is the value corresponding to minimum metabolic rate at complete starvation, and α_{max} corresponds to the maximum metabolic rate when feeding to satiation at ration C_{max}. Equation (3) is a linear expression that generally approximates the best results from the few applicable long-term fish feeding and growth experiments (Davis and Warren 1965, 1971; Paloheimo and Dickie 1965, 1966; Beamish and Dickie 1967; Warren and Davis 1967; Brett et al. 1969). Use of Equation (3) in Equation (2) gives Q for any size fish at any feeding level.

Fecundity of fish must be dependent on size and, at least in some limiting sense, on nutrition. A number of workers have noted reduced fecundity in overcrowded, undernourished fish populations and have speculated on how this reduced fecundity might tend to regulate the population (Woodhead 1960; Nikolskii 1961, 1962; Scott 1962; Bagenal 1967; Mackay and Mann 1969). There is good

evidence (Simpson 1951; Bagenal 1957, 1967; Beverton 1962; Pitt 1964; LeCren 1965; Bagenal and Braum 1971) that in most fish with adequate food supply above metabolic demands, fecundity is strongly dependent upon body weight. Regressions on weight usually fit better than regressions on length or age (Bagenal 1957, 1967; Nikolskii 1962). It seems reasonable to represent the rate of production of reproductive material, S, (or accumulation of body stores for that purpose) as a simple function of weight. Although more general functions have been proposed (Bagenal and Braum 1971), apparently most regressions so far fitted using data from specimens have been quite close to the linear expression.

$$S = uW, \tag{4}$$

where u is a constant. In the present simulations, u = 0.1 in all cases, based on average values for several species and both sexes (Bagenal 1957, 1967; LeCren 1958, 1962; Mann 1965; Norden 1967; Phillips 1969). The linear function is truncated near its lower end at a weight corresponding to sexual maturity. This is consistent with the general observation that the onset of sexual maturity in fish appears to be a function of size rather than age (Beverton and Holt 1959; LeCren 1965). Exceptions for individual species are noted in Bagenal (1957).

Trophic factors regulate the animal's fecundity through their effect on body weight. Also, when food intake becomes sufficiently low, there must not be enough energy above metabolic demands for normal fecundity. The scanty field data available suggest that usually fish sacrifice growth for reproduction, so that as food intake decreases, fecundity stays at or near normal (with decreased growth) until the net energy above metabolic expenditures is less than the normal fecundity requirements, after which fecundity decreases (Mackay and Mann 1969). The model operates in this way.

The ration, C, under any instantaneous set of conditions, is obtained from the maximum ration, C_{max}, and the current abundance of the prey which constitutes the food supply. C_{max} is dependent on body weight, and its current value can be determined from Equation (1) if the maximum growth rate, G_{max}, is known. Since G_{max} is a function of the current size of the individual, this function is required. Data from appropriate ad libitum feeding experiments with a particular species of interest could be fitted to the appropriate function to give continuous values of G_{max}. The von Bertalanffy growth function is a convenient one to which growth data from a large number of fish species have been fitted (e.g., Beverton and Holt 1959; Ursin 1967). In its differential form it expresses growth

$$G_{VB} = \kappa(W_\infty{}^{1/3}W^{2/3} - W), \tag{5}$$

where κ and W_∞ are numerical fitting parameters (κ corresponds to the ${}_1k$ of Ursin 1967, and to 3 times the K of Beverton and Holt 1959). W_∞ corresponds to a theoretical maximum weight, asymptotically approached. Values of κ and W_∞ for the present simulations are taken for certain illustrative species from Beverton and Holt (1959) and Ursin (1967:2421-2423). Equation (5) is employed in the model with a constant coefficient of 4.0 as an arbitrary standard adjustment to represent the highest feeding conditions. This gives a relationship between values over the full feeding range (e.g., zero, maintenance, and maximum ration) consistent with those observed in long-term feeding and growth experiments. With the C_{max} term thus expressed, the Q_{max} term is simply Equation (2) with $\alpha = \alpha_{max}$ and using the current weight, W. The S_{max} term comes from Equation (4). Thus

$$C_{max} = \frac{Q_{max} + S_{max} + G_{max}}{k}. \tag{6}$$

There is a considerable and developing body of theory, for which evidence continues to accumulate, that where environmental conditions are fairly stable, a predator's ration may be expressed as a fraction, r, of its maximum ration, r being a simple function of the abundance of prey, P. This approach is taken as a useful long-term ecological approximation, in which short-term behavioral factors, factors affecting the accessibility of the prey, etc. are smoothed out. Several expressions for this relationship have been proposed.

Three alternative expressions for simple predation with no explicit competitive effect between predator individuals were used in the model in different simulation runs. These are:

$$\text{Linear:} \quad r = c_{s1}P \tag{7A}$$

$$\text{Ivlev:} \quad r = 1 - e^{-\xi P} \text{(Ivlev 1961b)} \tag{7B}$$

$$\text{Holling:} \quad r = \frac{P}{m_{mc} + P} \text{(Holling 1959)} \tag{7C}$$

where c_{s1}, ξ, m_{mc} are numerical parameters. For prey species modeled as described here, expressing P in terms of prey numbers rather than biomass seems to have system stability advantages. It is through Equation (7) that this species interacts with the next lower species in the trophic chain (web).

The instantaneous rate of production of reproductive material and growth at the current body weight and prey abundance can be determined by use of the above terms in Equation (1). Using $r = \frac{C}{C_{\max}}$ from Equation (7) in Equation (3) gives the current value of α to be used in Equation (2) to give the current value of Q. When food supply is adequate; i.e., when $kC - Q > S_{\max}$, "fecundity" is

$$S = S_{\max},$$

and, from Equation (1), positive growth is

$$\frac{dW}{dt} = G = kC - Q - S_{\max}. \quad (8)$$

When food supply is so low that $0 < kC - Q < S_{\max}$, growth is zero and fecundity is

$$S = kC - Q. \quad (9)$$

In more extreme food shortage, when $kC - Q < 0$, fecundity is zero and growth is

$$\frac{dW}{dt} = G = kC - Q. \quad (10)$$

(Note that in the last case, growth is negative; i.e., dystrophy occurs). Equations (8) and (10) are in differential form, representing rates of change of body weight. Numerical integration of these equations gives "continuous" values of body weight over the entire time span of the simulations. Figure 1 shows the relationships between the component equations which describe a single species.

(B) Population Dynamics

Numerical changes in the population of any species are the net result of gains through reproduction (recruitment) and losses through the various sources of mortality. Therefore, the dynamics of any species population can be summarized in the expression

$$\frac{dN}{dt} = R + D_{\text{NAT}} + D_{\text{PRED}} + D_{\text{STARV}}. \quad (11)$$

The rate of change of population is the algebraic sum of four terms: reproductive recruitment, R, natural mortality, D_{NAT}, mortality due to predation, D_{PRED}, and starvation mortality, D_{STARV} (the sign of the reproductive term is positive; all the other terms have negative signs). Equation (11) is used in essentially this form for the representative individual model. For the age class model, the last three terms appear for all age classes. Instead of including the first term, the appropriate number of recruits is simply introduced as a pulse into the youngest age class at the appropriate times in the simulation.

The recruitment rate, R, is expressed as a function of the rate of egg production, E, by the Beverton and Holt (1957:49) reproductive function

$$R = \frac{1}{a + \frac{b}{E}}, \quad (12)$$

where a and b are numerical parameters. A simple relationship such as Equation (12) is appropriate for the present model where the response of a system of essentially adult populations to purely trophic variables is of interest. The egg production rate, E, is the cumulative spawn of the entire mature population, N_m; i.e.,

$$E = N_m S. \quad (13)$$

For the age class model, this involves summing over all mature age classes and over the entire year. All real species have some reproductive time lag or "generation time." In all except the simplest animals, this lag is significant and can have important influence on the dynamics of the population. Such lags of any desired length are introduced in the simulations by properly coding the programs so that the E produced in 1 yr is stored and used in Equation (12) to compute the R for the appropriate later year.

Except for fishing mortality, natural mortality is the only kind expressed in most fishery models. The position taken is that all mortality not due to fishing is "natural" and may be measurable in an unexploited stock or by eliminating the fishing mortality from statistics on an exploited stock by some analytical technique. Thus defined, natural mortality is almost invariably represented in

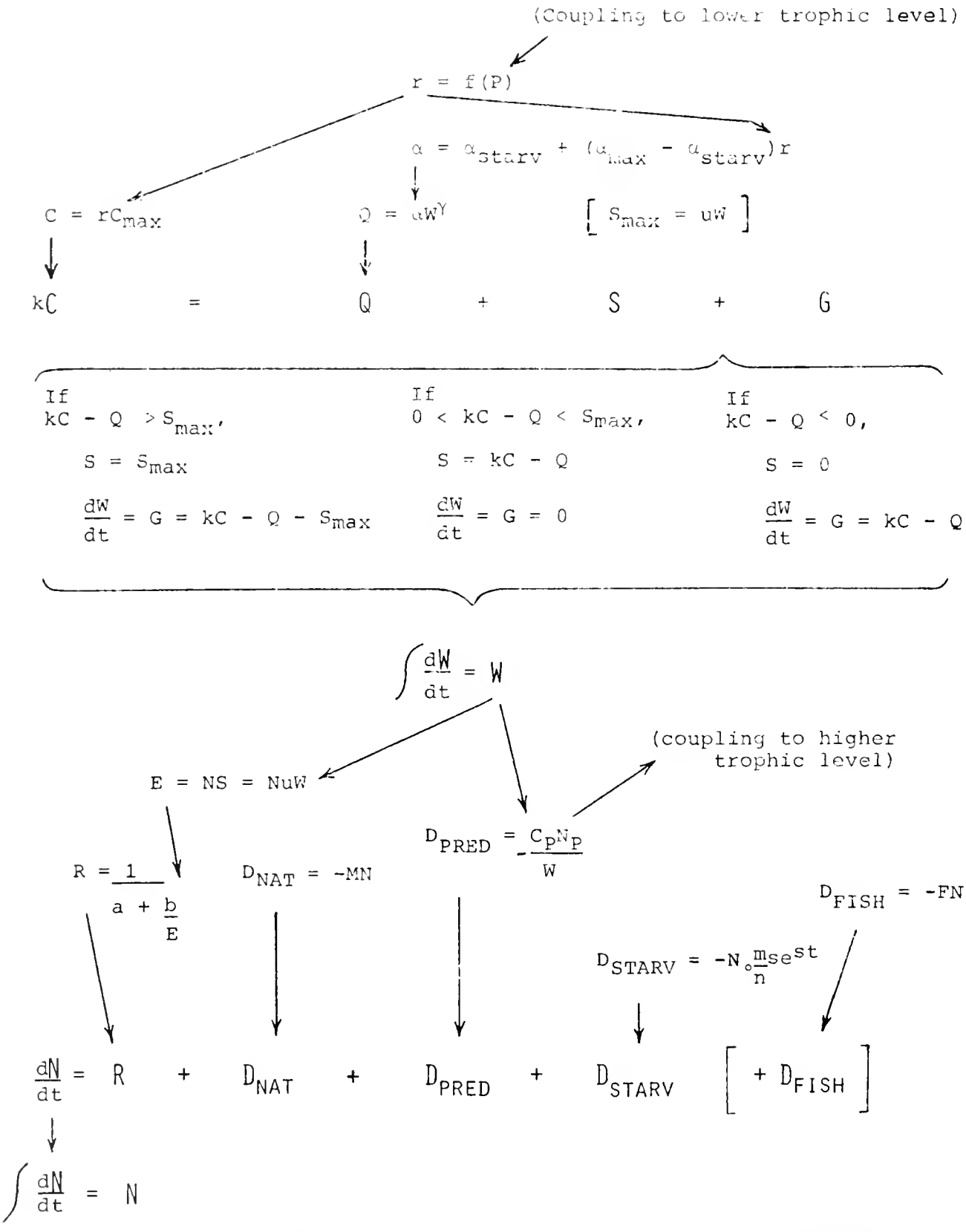

FIGURE 1.—Relationships between principal component equations describing a single species.

fishery works by the simple decaying exponential function

$$D_{NAT} = -MN, \tag{14}$$

where M is a numerical parameter, the "coefficient of instantaneous natural mortality." The function has been applied very widely, whatever the predation rate may be (even where it is zero) and in situations where starvation probably does not occur. Lacking data to support another assumption, it seems reasonable to use Equation (14) to express the more limited category of natural mortality of the present model also. In the model, then, natural mortality is all mortality not due to predation or starvation (the trophic controls) or

fishing, and would include death due to disease, senility, accident, environmental stress, etc. Field data for this limited class of mortality are rather scarce. For the hypothetical species in these simulations, approximate conventional M values were taken from Beverton and Holt's (1959) tables, and for species under predation, these were at times modified. In the age class models, different values of M are used for different age classes. Beverton and Holt (1959) discussed the variation of mortality with age more fully.

The expression for mortality due to predation, D_{PRED}, comes directly from the ration of the predator species, C_P, modeled as described in the preceding discussion of energy balance. Thus, the rate of change of prey population due to predation, D_{PRED}, is

$$D_{\text{PRED}} = -\sum \frac{C_P N_P}{W_{\text{prey}}}, \qquad (15)$$

where N_P is the number of predators, each with ration, C_P, W_{prey} is the weight of a prey individual, and the summation is over all predator species which consume the particular prey. Equations (15) and (7) provide the coupling between each model species and the other species with which it interacts in the trophic web.

Despite the scarcity of knowledge on starvation in fish, it would seem that a complete model for a system controlled by trophic variables should include some reasonable attempt at a formulation of this source of mortality. An expression was developed that can approximate the general form of the survival versus time curves from Ivlev's (1961b:266) starvation experiments with fish. This expression states that under pressure of starvation alone, the surviving number, N, of an initial population, N_0, after time, t, will be

$$N = N_0 \frac{1}{n}(m + n - me^{st}). \qquad (16)$$

The m and n are numerical parameters, and the parameter, s, comes from the boundary condition at 100% mortality, after the critical time, t_c, to extinction has been found from the integrated form of the energy balance equation under starvation conditions (see Appendix). The form of the function of Equation (16) is plotted in Figure 2. Use of Equation (1) in computing t_c and s provides an appropriate curve for any ration. The model uses the differential form of Equation (16),

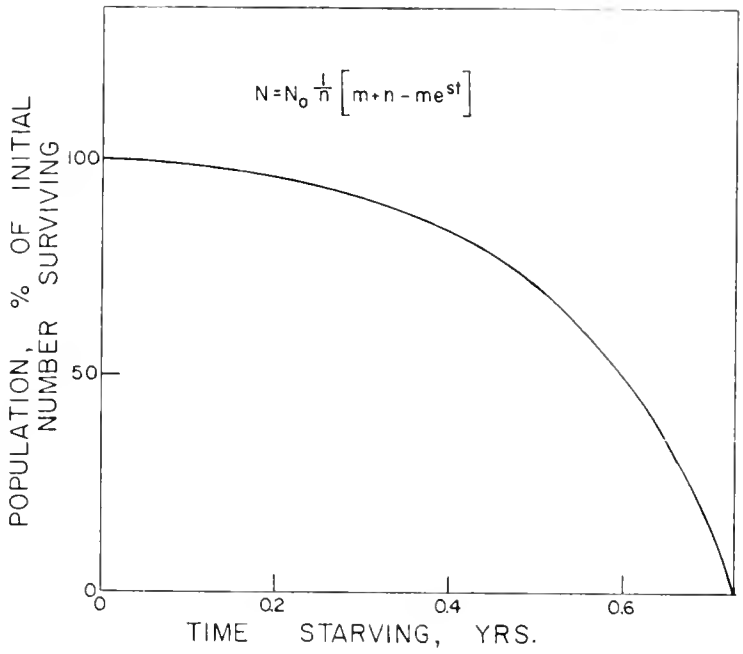

FIGURE 2.–Survival curve of a population undergoing only starvation mortality at zero ration.

$$D_{\text{STARV}} = -N_0 \frac{m}{n} s e^{st}, \qquad (17)$$

as the fourth term in Equation (11).

When exploitation by man is included in the system, the only modification is the addition of another term to Equation (11). In accordance with conventional fishery theory and the concept of chance encounter between fish and fishing gear, this term is exactly like Equation (14); i.e., fishing mortality, D_{FISH}, is

$$D_{\text{FISH}} = -FN. \qquad (18)$$

The numerical parameter, F, is an expression of the intensity of fishing effort and the vulnerability of the prey to the fishing gear.

Equations (12), (14), (15), (17)–and (18) where appropriate–provide all the terms for determining rate of change of population from Equation (11). (Figure 1 summarizes their relationships.) Numerical integration of Equation (11)–less the first term for the age class model–gives "continuous" values of population of the species over the entire time span of the simulation. Biomass of an entire species population at any instant is the product of instantaneous values of W and N (summation of a group of such products in age class models). Production over any desired period is obtained by integrating the incremental growth rates, G, and reproductive products, S (if desired), over that period.

(C) The Trophic Web

All the fish species in a trophic web can be modeled more or less as described above. Many invertebrates that serve as fish food can be modeled in much the same way, with some appropriate changes in individual component functions and by use of the proper parameter values (see Winberg 1962, and Mann 1969 for discussion relative to invertebrates). Since this model uses feeding functions based on prey abundance, an operational limitation is imposed that the ultimate resource base—the lowest item in the food chain—cannot be modeled fully in this way. In terms of total ecosystems, this is natural enough. Although the ultimate autotroph might be thought to "prey" upon inorganic nutrients, and models for plant growth as a function of nutrient abundance exist, the present model is obviously not appropriate for autotrophs.

Thus, any trophic web modeled in this way must have at its base an arbitrarily defined species or group of species. The purpose of this first exercise with the model is to explore trophic interactions among fishes. Therefore, the cause of clarity seems best served by modeling all the species of interest as fishes. The level(s) below the lowest fish species—the food base for the fish community—is then given only the simplest representation.

Two types of food base have been used in these simulations: 1) the "constant input", and 2) the "exponential growth." Properties of the constant input base are that biomass, B_1, enters the system at a constant rate, P_1, and is reduced only through predation by the higher level, fully modeled species. Thus, the rate of change of food base biomass is

$$\frac{dB_1}{dt} = P_1 - \Sigma C_P N_P, \tag{19}$$

where the summation is over all predators with their individual rations, C_P, and populations, N_P. Ecologically, this system might correspond to a fish community whose base prey enters the community feeding area at a constant rate; e.g., as brought in by water circulation or by migration as prey individuals continuously reach a particular life stage. Because of its extreme simplicity, this type food base model is preferred for studying the trophic relationships of fishes higher in the web.

Properties of the exponential growth food base are that biomass is produced at a rate directly proportional to the current standing crop of biomass and is reduced only through predation by the higher level species. Thus

$$\frac{dB_1}{d_t} = c_1 B_1 - \Sigma C_P N_P, \tag{20}$$

where c_1 is a numerical parameter corresponding to the "instantaneous coefficient of natural increase" of classical population growth theory. Again the summation is over all predator species preying on the food base. Without predation, B_1 would of course increase exponentially and indefinitely. This makes stability of such a system precarious, a fact borne out by experimentation with the model.

For these simulations, numerical values of P_1 and c_1 were selected arbitrarily to be compatible with the standard equilibrium state of the trophic webs constructed.

SIMULATION TECHNIQUE

Combination of the previously described functions produces the basic species model. A single such model species, with one of the food base models described above as prey, was exercised over a range of conditions and with some variety in certain component functions, in an effort to become familiar with some of the dynamic properties of the basic species model. Groups of such model species were then interconnected in various ways to explore the behavior of various trophic webs. Interactions between species occur through Equations (7) and (15). Where a predator feeds on more than one prey species, P in Equation (7) for that predator is the total abundance of all the n species. For each of the n prey species, the predation mortality imposed by that predator is given by Equation (15) in which the C_P upon the ith prey is

$$C_{P_i} = C_{P_{\text{TOTAL}}} \frac{v_i N_i}{\sum_n v_i N_i}, \tag{21}$$

where N_i is the current population of the ith species, and v_i is a coefficient expressing predator preference and availability (vulnerability) of the prey. The two (or more) elements contained in v can be separately expressed by making v a product of separate coefficients. By Equation (21), the predator tends to adjust the makeup of its diet

proportionately to the abundance of the various prey, but bias is allowed for known preferences or differences in the ease with which various prey can be taken. These features, together with the basic structure of the age class model, allow that predators and prey interacting with any species may be different for different age classes of the species or may change in their degree of importance.

All the model species created for these simulations are hypothetical. To avoid resorting to pure fantasy and to get some consistency among certain species properties, each model fish species was based on a real fish species (see Table 2). Real species were selected which are sympatric, and in fact, each of the predator/prey relationships modeled has been reported in the literature in a nonquantitative way. A major simplification in

TABLE 2.—Values of parameters and of basic variables at standard equilibrium state as used in simulations. [Values shown in parentheses are alternate values used in some simulations.]

Parameter or standard equilibrium variable	Units	Source	Namesake species: *Clupea sprattus*	*Clupea sprattus*	*Clupea sprattus*	*Scomber scombrus*	*Sarda sarda*
			Model species: E	A	B	C	D
α_{starv}	$g^{0.2}$-$yr^{-1.0}$	See MODEL	1.0	1.0	0.7	1.0	1.0
α_{max}	$g^{0.2}$-$yr^{-1.0}$	section (A)	7.0	7.0	4.9	7.0	7.0
u	yr^{-1}	See MODEL section (A)	0.1	0.1	0.1	0.1	0.1
γ		See MODEL section (A)	0.8	0.8	0.8	0.8	0.8
k		See MODEL section (A)	0.8	0.8	0.8	0.8	0.8
κ	yr^{-1}	Ursin (1967): 2421-2423	1.75	1.75	1.75	1.2	0.539
W_∞	g	Ursin (1967): 2421-2423	30.6	30.6	30.6	516.0	9,400.0
M	yr^{-1}	Beverton and Holt (1959)	1.0	1.076 [0.1169]	1.076 [0.1169]	0.9 [0.0325]	0.9
W_s^*	g		10.0	15.16106	15.16106	150.0	600.0
N_s^*			1.0×10^5	0.61032×10^5 (1.22064×10^5)	0.61032×10^5 (1.22064×10^5)	5,000	500
R_s^*			1.0×10^5	0.65680×10^5 (1.31360×10^5)	0.65680×10^5 (1.31360×10^5)	4,500	450
a		Computed based on R_s	0.66667×10^{-5}	1.09232×10^{-5} (0.54616×10^{-5})	1.09232×10^{-5} (0.54616×10^{-5})	0.13333×10^{-3}	0.13333×10^{-2}
b	$g\text{-}yr^{-1}$	Computed based on R_s	0.33333	0.39808	0.39808	6.66667	26.66667
ζ		See	0.49584×10^{-7}	0.60178×10^{-7}	0.60178×10^{-7}	0.37902×10^{-5}	0.79657×10^{-4}
c_{sl}		SIMULATION		0.45217×10^{-7}	0.45217×10^{-7}	3.03435×10^{-6}	0.65706×10^{-4}
m_{mc}		TECHNIQUE section.		1.21158×10^7	1.21158×10^7	0.20750×10^6	0.10219×10^5
m		Selected to fit form of	1.0	1.0	1.0	1.0	1.0
n		Ivlev (1961b: 266)	40.0	40.0	40.0	40.0	40.0
v		See SIMULATION TECHNIQUE section		1.0	1.0		
g_1		See RESULTS section (A)		−1.02147	−1.02147	−1.00000	−0.71428
g_2	g^{-1}	See RESULTS section (A)		0.13333	0.13333	0.013333	0.00286
F	yr^{-1}	See RESULTS section (D)		0.05 to 0.90	0.05 to 0.90	0.05 to 0.20	

*Values of variables at standard equilibrium state.

the simulations is the extremely limited range of diet of the model species; their factual namesakes have rather catholic tastes.

For these hypothetical species, a set of values for an arbitrary standard equilibrium condition was established as follows. Populations for all species were arbitrarily set at values that seemed reasonable relative to each other and in respect to the various body weights and reproductive rates. Using the various parameters selected, for each species, the r value corresponding to the standard equilibrium state was then computed. From this r and the equilibrium population of the prey, the predation parameters of Equation (7) were computed. Using this procedure for each fish species, working up the trophic chain, a complete set of equilibrium values for all species became available. A compatible trophic web was thus created arbitrarily, having at least static stability; i.e., dN/dt and dW/dt were zero for all species. Table 2 provides the values of parameters and of basic variables at standard equilibrium state for the model species used in these simulations. Where a consistent set of laboratory and field data on species in a real trophic web were available to be used in the model for predictive purposes, some of these procedures would be unnecessary.

Like all simulations, those run with the model require that initial conditions be specified. Typically in these runs, the initial conditions were those of the standard equilibrium state with the exception of some single variable value which was displaced so as to perturb the system. For example, a simulation run started with all variables at equilibrium except B_1 might be analogous to the natural occurrence of sudden catastrophic mortality in a prey species. Initial conditions are discussed further under RESULTS. In each case, the simulation was allowed to run for an arbitrary length of time, or until automatically terminated when some variable reached a prescribed limiting value. Usually runs were continued until a stable state (the original standard equilibrium or otherwise) was approached, or until a distinct monotonic trend with a predictable outcome was detected.

All the simulations were programmed using the IBM[2] System/360 CSMP (Continuous System Modeling Program) (International Business Machines Corporation 1969, 1971) and run on an IBM 360/50 Data Processing System.

RESULTS

A limitation of the approach taken here, as with any simulation model for numerical solution, is that mathematically exact and general solutions are not obtainable. A full solution of the system represents a very complex multidimensional response surface. In the very simplest case of one modeled fish species and a food base species, there are three basic dependent variables whose integrated values appear in the solution; viz., N_{Fish}, W_{Fish}, and B_1. In a "representative individual" model with n fish species and the food base, there are $2n + 1$ basic dependent variables, and in a similar model with x explicit age classes per species, there are $2nx + 1$ basic dependent variables.

A system with the complexity and nonlinearities of this type of model is capable of behaving quite differently in different regions of the state space. Since it is impossible to explore the entire response surface thoroughly, measures must be taken to limit simulation effort to regions of interest. Eventually a detailed and systematic exploration of regions of known interest using established optimization techniques (e.g., Box et al. 1953; Box 1954; Box and Hunter 1957) may be useful with the model.

For the present, the scope of simulation effort has been limited by selecting parameter values that seem reasonable and compatible for each of a small group of rather common fish species and by building out from a system already investigated to a larger system of which the original is a subset. In a number of cases where moderate changes to values of parameters or even to the form of component functions have been made, system dynamics have been somewhat altered or the system has even moved toward a new stable state. Usually, however, in a system with any regulatory capacity (stability) at all, the change has not been drastic. Rather large perturbations in initial values of the basic dependent trophic variables of such a system have not usually displaced the system to a distant stable region or resulted in breaking the trophic web (eliminating one or more species). This behavior of most of the systems simulated gives evidence that there is at least one region of some useful size in the total state space—i.e., the region in which the arbitrary

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

equilibrium state has been placed—in which the system models are fairly stable. For these reasons, it is believed that the basic form of the behavior of systems demonstrated in these simulations has some generality beyond the specific cases tested. However, in all cases, the results shown here are simply examples of interest from an infinite number of possibilities.

The simulation technique used here is amenable to use in sensitivity analyses; i.e., for determination by a systematic program of successive trials how sensitive the result is to the numerical value of a parameter or an initial variable value. Such analyses not only help define useful regions for particular results; they also give an indication of how accurately particular parameters must be measured in the field or laboratory, so that effort is applied where it is important to the system result.

In describing the following results, the shorthand notation used to reference the trophic webs has the following form:

P	1	2	1	0	0
	1st	2nd	3rd	4th	5th

Trophic level

The digit in each column indicates the number of species at that trophic level. Where two species appear at a common level, they compete for prey at the next lower trophic level and are preyed upon equally by the next higher trophic level. The lowest level is always occupied by the food base with biomass B_1.

(A) Regulation of Body Weight and Population

The basic species model seems to have a considerable capacity for self-regulation; i.e., it can return to an equilibrium state after sizable displacements of some of the variables in the system. The return usually involves a series of oscillations above and below the equilibrium values, with the degree of damping depending on the exact structure and parameter values.

One of the most common and interesting perturbations involves displacement of prey abundance. Figure 3 illustrates a P11000 trophic web with a representative individual model of a species A fish preying on an exponential growth type food base with an Ivlev feeding function. The system

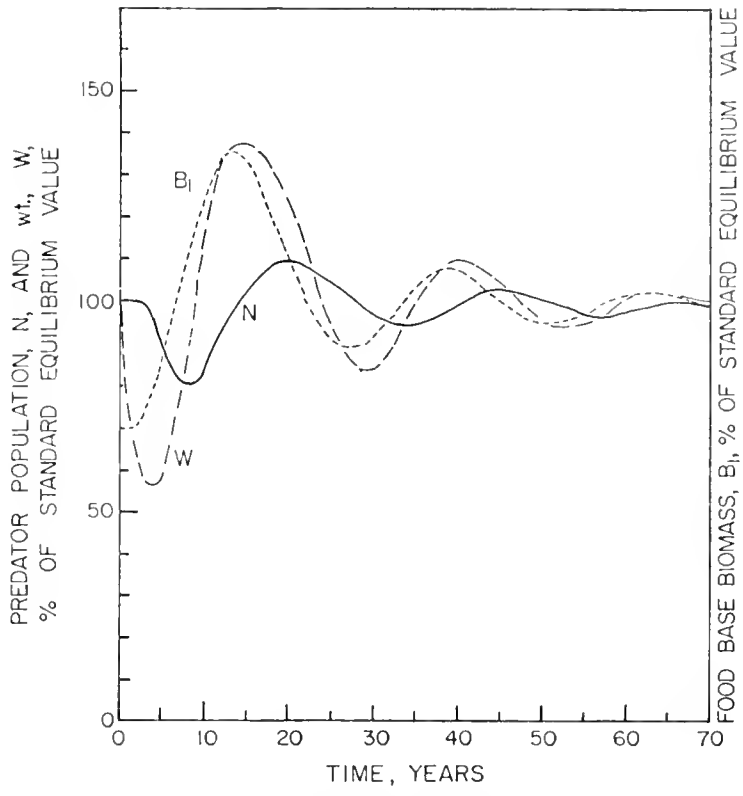

FIGURE 3.—Response of a single species to an initial perturbation in the abundance of its prey. N = predator population; W = predator body weight; B_1 = prey (food base) biomass.

responded to an initial condition in which the fish population was at the standard equilibrium value and the prey abundance was initially about 71.4% of the standard equilibrium value. The system returned to the standard equilibrium state with damped oscillations. The purely population controls, natural mortality and reproduction (D_{NAT} vs. R), were satisfied initially, but the system was unbalanced trophically because of the scarcity of prey. Regulation resulted from the response of body weight and resulting fecundity to food consumption, balanced by natural mortality responding to the changing population level.

Similar stable responses were demonstrated with the model for cases of initial perturbation due to high prey abundance, B_1, high predator population, N, and high predator body weight, W.

At sufficiently low values of prey abundance and production, substantial starvation mortality can occur. This is particularly true when the prey abundance decreases suddenly, since the normal population response of the predator through reduced fecundity is delayed by the reproductive time lag. Figure 4 shows such mortality for a population for four age classes modeled explicitly. The abundance of each year class decreased with time until those which had become 4-yr-olds were decimated at about 1.6 yr after the start. The

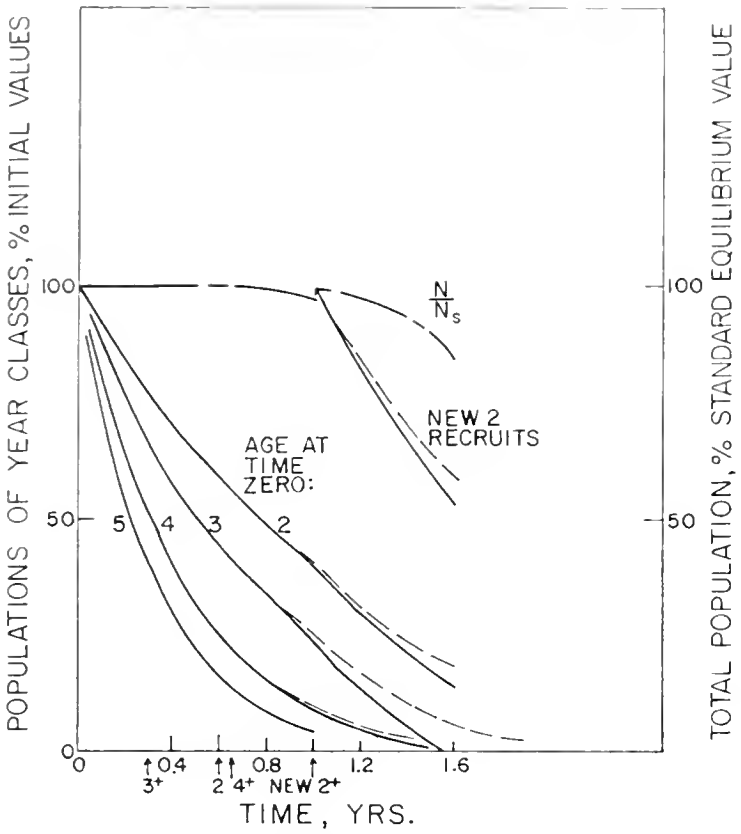

FIGURE 4.—Effects of starvation mortality on the 4 age classes of a species population and on the total population. A new class of recruits entered one year after the start of the simulation. Arrows indicate when starvation mortality began for each year class. (___ actual population of an age class; _ _ _ _ population of an age class in the absence of starvation mortality; ___ _ _ _ N/N_S, where N = total species population, N_S = standard equilibrium value of total species population.)

dashed lines indicate the course of natural mortality. As interesting as the fate of individual year classes is the substantial effect on the total population (shown by the upper broken line in Figure 4).

Theoretically, starvation mortality should be capable of regulating the population. However, based on a considerable range of simulation runs, it appears that with the usual sets of reasonable parameter values for the species considered here, body weight and fecundity normally respond to produce regulation so that a starvation condition is not reached. With longlived, slowly growing species, starvation would tend to become a more important factor. In some of the cases simulated, where trophic conditions were sufficiently extreme to produce heavy starvation mortality, total extinction occurred. Figure 4 represents such a case, in which the food base biomass, B_1, was initially 20% of the standard equilibrium value and c_1 was 10%. Extinction occurred during the initial 2-yr reproductive time lag before fecundity changes could be reflected in recruitment. Some simulations were run in which fecundity was made unresponsive to actual body weight so that the effects of starvation could be better observed. With the nutritional control on fecundity thus removed, starvation occurred for some systems and started with B_1 at 50% of standard equilibrium and c_1 at 90%. With normal nutritional control on fecundity, these systems had survived.

Experience with the model indicates that for the types of species used, where extreme trophic conditions exist, disruption of the system is more likely to result from excessive stunting of growth and resultant failure of spawning than from starvation mortality. In age class models, the stunting can be observed directly in the failure of individuals of a year class to grow normally while in the recruited population. Where food supply is extremely low, actual weight loss by an individual can also be observed. In representative individual models, these separate effects are combined in the single continuous variable, W. A smaller-than-standard W represents a population that, on the whole, is undersize. If the population as a whole becomes sufficiently stunted, at some point, egg production will be reduced to zero. This corresponds to a population unable to reach sexual maturity. If the entire population fails to spawn for enough successive years, extinction of the local species population must result. It is difficult to see how a species could persist if it failed to spawn for a continuous period as long as its lifespan.

In most of the results shown here, no effort has been made to impose a sexual maturity limit on fecundity; i.e., Equations (4) and (13) with $N_m = N$ determine the egg production, E, at any body weight.

$$E = N_m u W = N u W. \tag{22}$$

For exploring the limits of stability of systems against perturbations, it seems useful to represent the attainment of sexual maturity in the model. A "knife-edge" representation—one in which fecundity has a substantial positive value or functional form above some age, length or weight, and zero below it—has been used for simplicity in much fishery work. This may be a justifiable approximation of nature for some species, especially those with short lives, fast growth, and infrequent spawning. However, a smoother and more realistic representation seems desirable. For some species, data exist on the fraction of all in-

dividuals mature as a function of age, length, or weight. In some cases (e.g., Bagenal 1957) the weight function appears reasonably linear. This means that in Equations (13) and (22) the mature spawning population, N_m, can be expressed as

$$N_m = g_m N, \tag{23}$$

and

$$g_m = g_1 + g_2 W, \tag{24}$$

where g_1 and g_2 are numerical parameters, for all values of W between that which gives $g_m = 0$ and that which gives $g_m = 1.0$. At lower and higher values of W, g_m is 0 and 1.0 respectively.

For species A and C, information from Bigelow and Schroeder (1953) permitted a rough fitting of this function. The length corresponding to the body weight at which all were mature agreed reasonably well with the ratio: length at maturity/theoretical maximum length (L_∞) of Beverton and Holt (1959) for both species. The same sort of weight limits for the function were assumed for species D, in the absence of better data. The standard equilibrium weight and the 100% sexual maturity weight were made to coincide in each species. This means that in this particular modified model, any reduction below standard equilibrium weight decreases the number of mature spawners. The effect of the linear sexual maturity of Equation (24) on the total population egg production is shown in Figure 5.

Figure 6 illustrates the response of a single P11000 trophic web with sexual maturity of species A modeled in this way. For the first 4 yr of the simulation run, input production at the food base level was about 20% of the standard equilibrium value; subsequently it was always at the standard equilibrium value. The reduced food supply resulted in stunting the population so much that from year 6 through 9 there was no recruitment. The subsequent reduced total food consumption by the greatly reduced population tended to bring the system into balance. If it survived, it would eventually return to standard equilibrium conditions. However, for this species with a lifespan of 6 yr or less, an interruption of recruitment for 4 yr is very dangerous. This, combined with a minimum population of about 1.4% of the standard at one point in the simulation, suggests that the condition reached here was very near a critical one for survival of the local species population. This

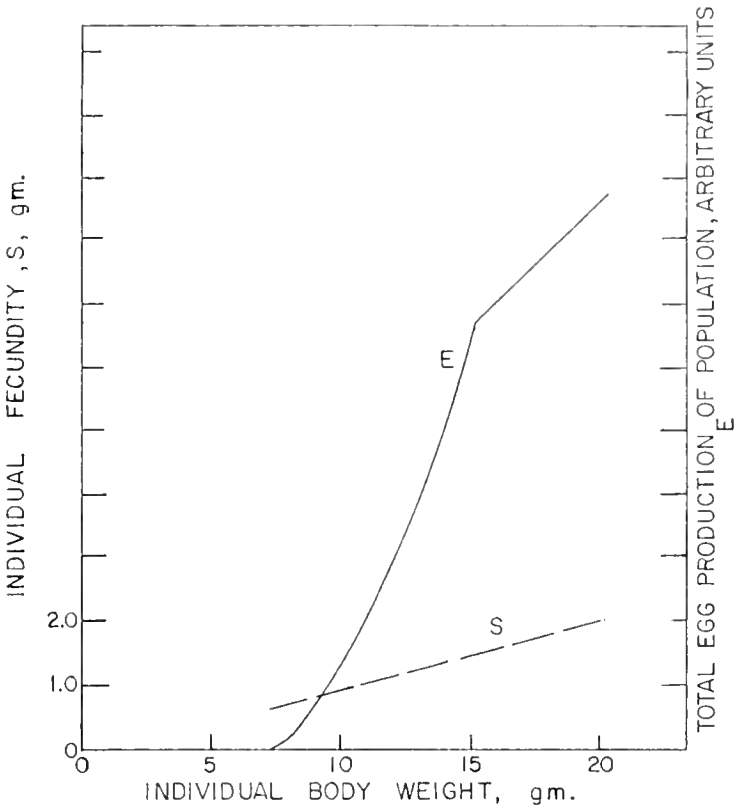

FIGURE 5.—Relationship between individual fecundity, S, and body weight and between total population egg production, E, and body weight. Sexual maturity is a linear function of body weight.

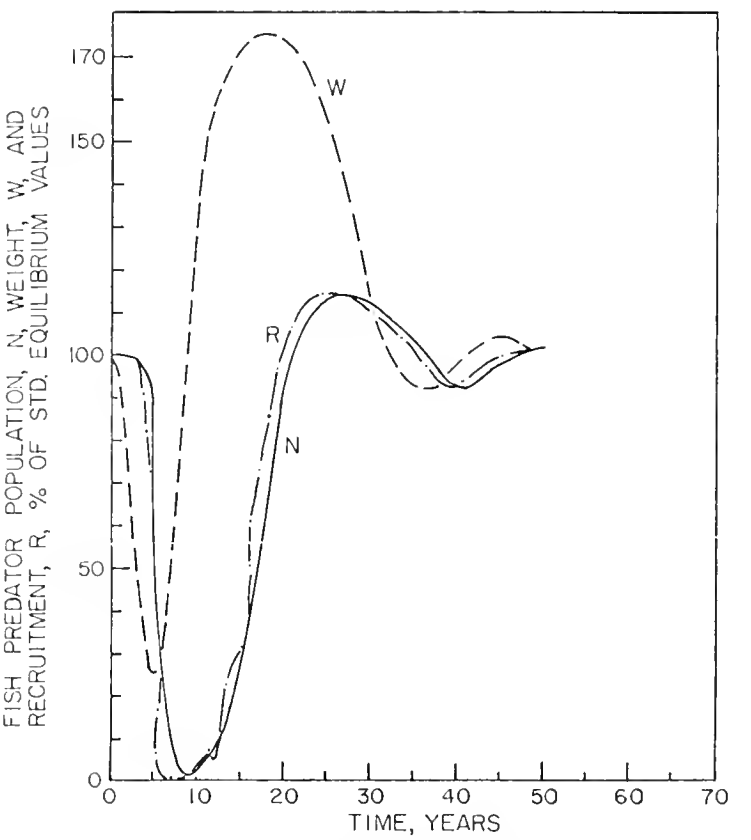

FIGURE 6.—Response of a single species, with sexual maturity a linear function of weight, to an initial 4-yr perturbation of low production by its prey. (P_1 = 20% of standard equilibrium value for the first four years.) Reproduction ceased between years 6 and 9. N = predator population; W = predator body weight; R = predator recruitment.

approach seems to offer a means of predicting the limits of stability of trophic webs against perturbation.

(B) Reproductive Time Lag

A limited study of the effects of the length of reproductive time lag was made using a representative individual model of the simplest trophic web, P11000 (a food base and the fish predator, species E). The food base was of the exponential growth type and the predator employed an Ivlev feeding function. Reproductive lags of 0, 2.50, and 6.25 yr were tried with a model that was otherwise basically the same. These three alternatives correspond respectively to the assumptions: 1) that offspring are mature when spawned, 2) that they take 2.50 yr to reach the "representative" stage, 3) that they take 6.25 yr to reach this stage. The second assumption is reasonable for species E.

The system was initially perturbed by starting with species E at 20% above its standard equilibrium population. The results for the biomass of species E are shown in Figure 7. It is clear that with increasing reproductive lag, the regulation of the system about its standard equilibrium becomes weaker; i.e., the biomass of species E, and other variables (not shown), reach more extreme oscillatory amplitudes. Larger amplitudes always incur greater risk of disaster. For example, in the runs shown here, a different sexual maturity criterion was used—knife-edge maturity at 80% of the standard equilibrium body weight. In the 6.25-yr lag run, this weight was reached at about 59 yr into the simulation, and after the 6.25-yr lag, it so reduced recruitment and the species E population that the system became unstable. This instability, which did not occur in the other runs, was due to the long lag in recruitment response to change in fecundity with changing food availability.

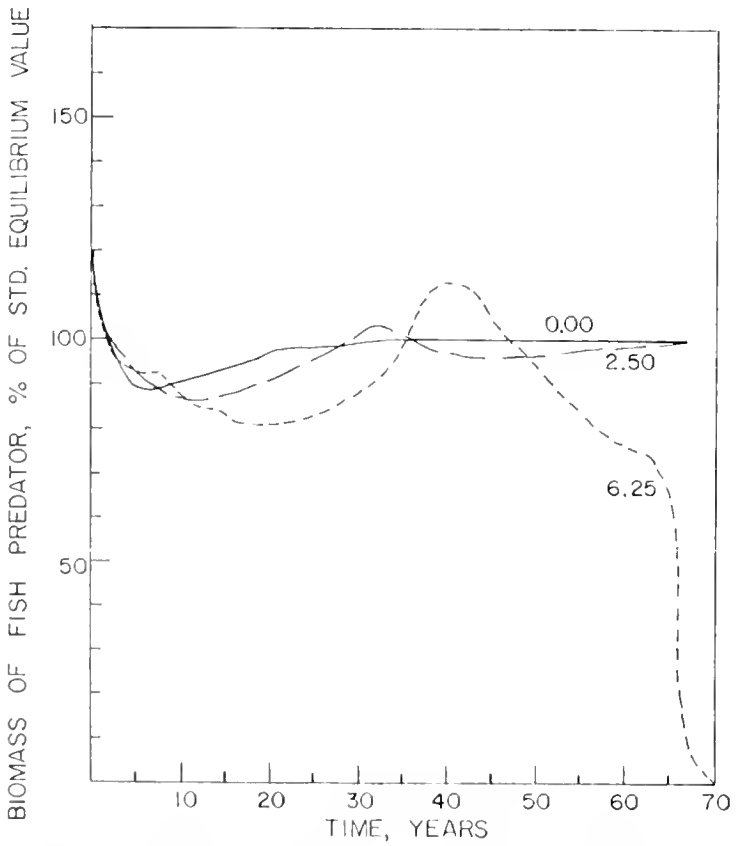

FIGURE 7.—Effects of reproductive time lag on the response of a single species to an initial perturbation in its population. The three cases illustrated have reproductive time lags of 0.00, 2.50, and 6.25 yr, respectively.

Except where otherwise stated, all the results presented here are for representative individual models having 2.50-yr lag and age class models having 2.00-yr lag. These are reasonable for the species involved. They are mutually consistent because in the age class model, reproductive products are summed over a full year and produce recruits 2.00 yr after the end of the year. Thus the average lag is about 2½ yr for the age class model also.

(C) Age Class Effects

A number of simulations were run with an explicit 4-age class model. Some results involving starvation have been shown above. Other exercises investigated the capabilities of this more accurate type of population model to regulate in the normal manner. Figure 8 illustrates the response of a simple food base-fish predator P11000 system with Ivlev feeding function to an initial perturbation of the fish predator population. The "mean total population" is a variable obtained by summing the populations of all the age classes, $\sum_{i=1}^{4} N_i$, during each computational increment of the year and taking the arithmetic average of these values. "Population mean annual biomass" is obtained by similarly summing and averaging the biomass values, $\sum_{i=1}^{4} N_i W_i$. These variables are shown in Figure 8 as percents of their standard equilibrium

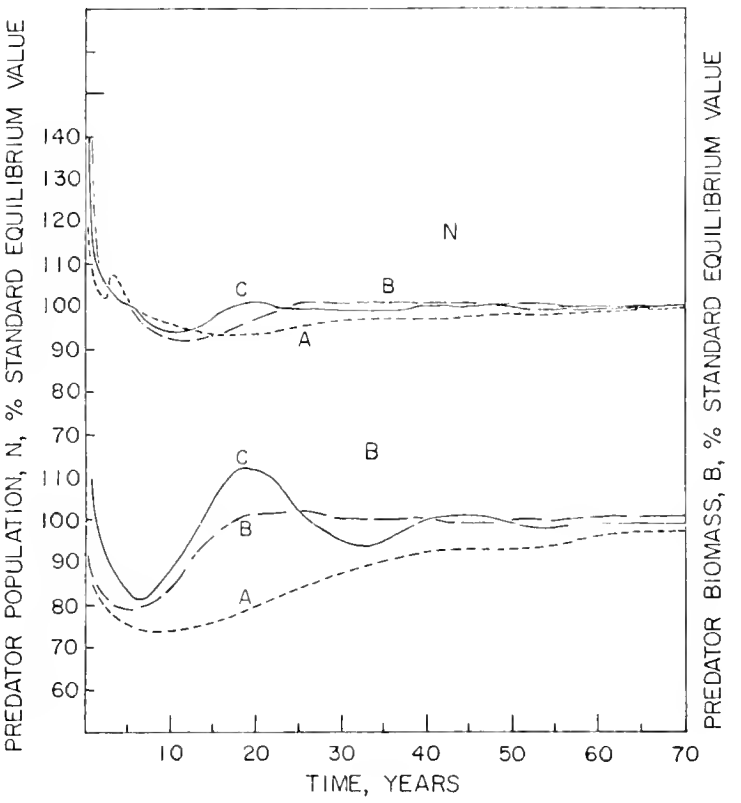

FIGURE 8.—Effects of age class structure and condition of recruits on the response of a single species to an initial overpopulation. (Curve A - 4-age class model with recruitment at standard recruit weight; curve B - 4-age class model with K_1 recruitment; curve C - representative individual model.) The three upper curves represent total species population, N; the three lower curves represent total species biomass, B.

values. In curve A, the system was represented by an explicit 4-age class model in which recruitment occurred at "standard recruit weight" (standard equilibrium weight for recruitment age). In curve B the model was identical except that recruitment occurred at K_1 times "standard recruit weight." The coefficient, K_1, is the ratio of the weight of the class ending its first recruited year to its standard equilibrium weight. Its use makes recruitment weight more consistent with current conditions. In curve C the system was represented by the corresponding representative individual model. Because of the way weight at recruitment is expressed, curves B and C are most directly comparable.

It is clear that there are some real differences in dynamics among all three models. These simulations and others indicate that for some detailed studies of the dynamics of trophic systems, age class models can provide additional information not available through representative individual models. However, much of the information of basic interest is contained in the representative individual solution. The final stable state is predicted accurately. Because of its lower damping, this model gives a conservative (maximum) estimate of the time required for the system to return to within any given range of this state, and this maximum is close enough to the actual time to be useful. For most variables and most perturbations, the maximum amplitudes of the age class model tend to be less than those of the representative individual model, so that the latter tends to predict an envelope of reasonable size within which the actual values will lie. These characteristics make the representative individual model especially useful for predicting stability.

The results shown and others suggest that the representative individual model can be used to approximate the behavior of the much more difficult and expensive age class model sufficiently well to justify use of the simpler model for many purposes. However, the quality of the approximation depends upon the characteristics of the particular system to be simulated. Where species are included that display a large range of sizes and ecological differences among the age classes of the recruited population, the representative individual approximation is likely to be less acceptable.

(D) Competition and Predation in More Complex Webs

A major purpose of the model developed here is to serve as a tool for study of more complex trophic systems. A few examples of particular interest are presented below.

In Figure 9 the trophic chain is extended by one link in the simplest possible manner to make a P11100 web. Species C preys on species A which preys on a constant input food base. Both interactions employ Holling feeding functions. The populations of all three trophic levels oscillated as the system returned from the initial perturbation of low food base biomass. Within about 3½ to 4 cycles (≈35 to 40 yr), all variables were within about 1% of standard equilibrium values again. The phase sequence of population and biomass rapidly became level 1, level 2, level 3 as would be expected. The population phase displacement was complicated by the 2½-yr reproductive lags and the effect of predation on the species A population (as species A lost weight, species C ate more species A individuals to meet its energy demands).

Such an extremely simple trophic web would be

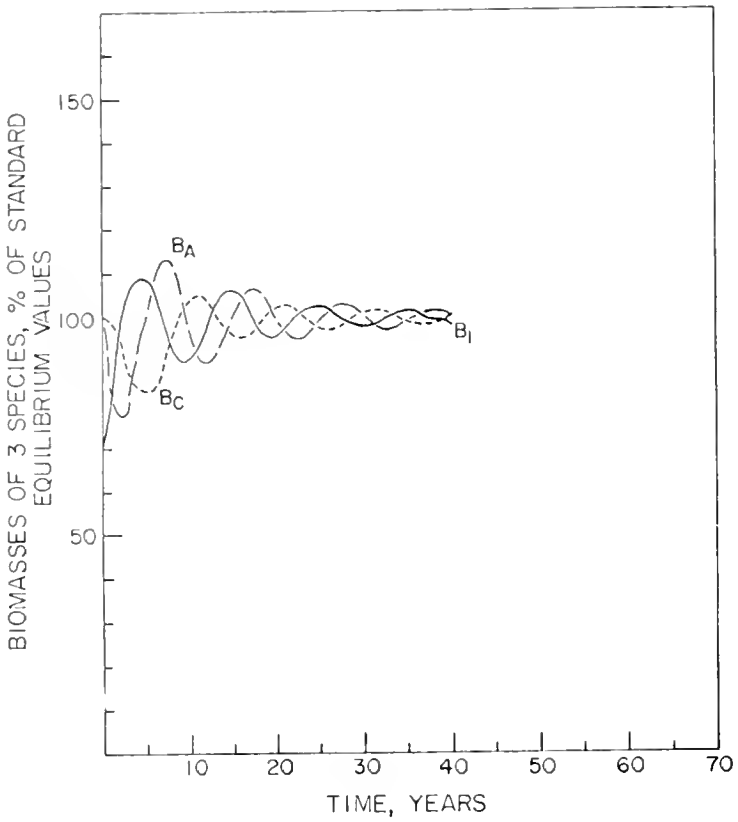

FIGURE 9.—Response of a simple 3-level trophic web (P11100) to an initial low prey abundance. (___ food base; ___ ___ 2nd level fish species; ----3rd level fish species.)

rare indeed in nature, but it is interesting for at least two reasons. The various species might be thought of as representing in some sense whole trophic levels of more extensive natural systems, each level consisting of a rather homogeneous group of species. If all the species at a single level have identical trophic parameters, this simple web in fact represents them exactly. This follows logically and has also been verified in simulation. Thus, the P11100 web model provides a base line for comparison for later unequal competition runs in a 3-level system. It represents the behavior of any n equally competing species at a trophic level, each with a population of $1/n$th the total population. The P11000 web model provides the same kind of base line for competition in 2-level systems.

Figure 10 illustrates the simplest web, P11110, with four trophic levels: the food base and three fully modeled fish species. It consists of the P11100 web with species D added as a top predator. Again, an initial perturbation of low food base biomass caused oscillation of trophic variables of all species. After about 8 to 9 cycles (≈70 yr), all were within a very few percent of standard equilibrium values again. The same population and biomass phase sequence appears. Predation by species D caused quicker response of the species C population, reducing the phase displacement between species A and species C. The large phase displacement now occurred between species C and species D. The basic period of oscillation was also shortened from about 10 yr to about 8 yr. In all the above cases, maximum oscillation amplitudes of variables were less than the initial perturbation, and they rapidly became substantially less.

Effects produced on the system by feeding competition between species were of particular interest in these studies. No attempt was made to formulate explicit (interference) competition. Implicit competition was studied by constructing models with two predator species utilizing a common prey species. The P11000 and P11100 models above represent exactly equal competition at the second level in 2- and 3-level webs respectively.

The abstraction of exactly equal competition is not likely nor very interesting ecologically. A simple type of unequal competition is modeled by replacing one of the two species A-type competitors with species B, which is identical except that it has the advantage that its α_{starv} and α_{max} are 70% of the species A values. Thus it has lower metabolic requirements and grows more for a given food intake. Figure 11 illustrates a simulation of this

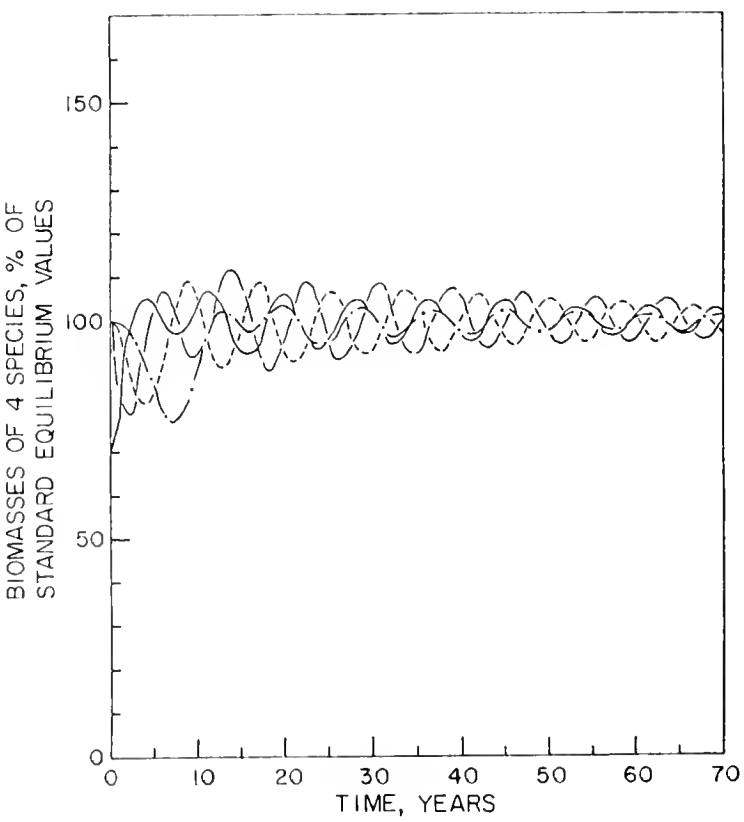

FIGURE 10.—Response of a simple 4-level trophic web (P11110) to an initial low prey abundance. (___ food base; ___ ___ 2nd level fish species; ----- 3rd level fish species; ___.___4th level fish species.)

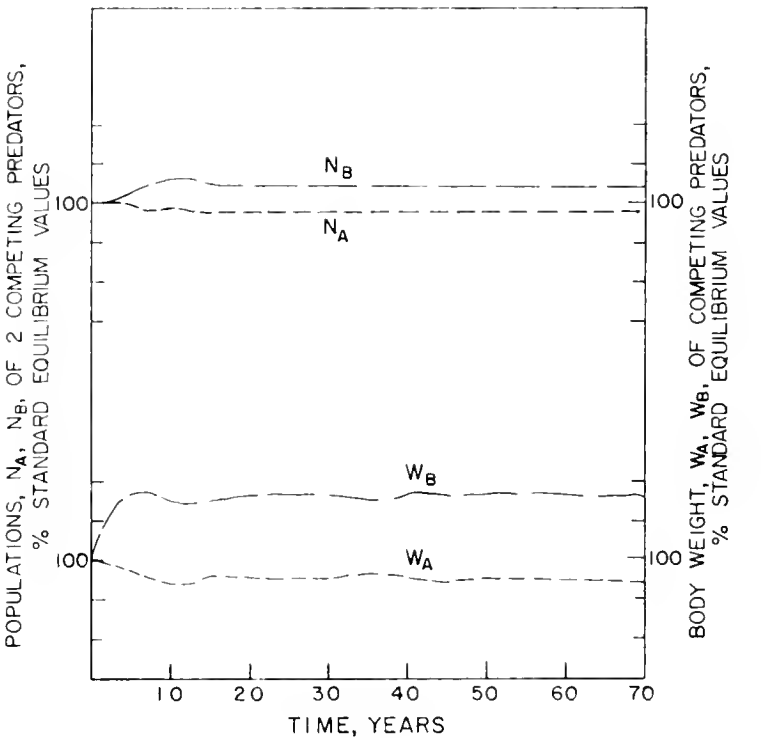

FIGURE 11.–Course of competition between two fish species with unequal metabolic demands, competing for a common food base. Species B is favored, since $\alpha_B = 0.7\,\alpha_A$. N_A = population of species A; N_B = population of species B; W_A = body weight of species A; W_B = body weight of species B.

2-level P12000 web started without initial perturbation, with identical body weights and populations of the two species. This situation is somewhat analogous to the simultaneous entry of the two competitors into an environment where the prey biomass and input are fairly close to the standard equilibrium values. The system moved away from the even start with oscillations which were firmly damped toward an apparent new steady state. In this state, the population and weight of the more capable competitor were increased relative to those of the less able contender. Their final relative positions might be characterized by the biomass ratio $B_B/B_A = 1.30$.

It is interesting to compare this prediction with that derived from the simpler graph theory analysis (Saila and Parrish 1972). This was accomplished by using the variable values from the present model for Q, B, and M to calculate the parameters q, h, a, b, and m for the graph theory model. These parameter values were then used in Equation (18) of Saila and Parrish (1972) to compute the biomass ratio $B_2/B_3 = 1.56$ of the competitors. This ratio is directly comparable with the ratio $B_B/B_A = 1.30$ from Figure 11. In view of the considerable differences in the two approaches, the agreement seems too good to be entirely fortuitous.

The above simulation represents simple unequal competition with the competitors' populations controlled by natural mortality and fecundity. Considerable theoretical and practical interest attaches to the influence of predatory mortality on such a system. Questions arise concerning whether more competing species can coexist, or whether competitors can coexist on a more even basis, where they are utilized by a common predator than in an otherwise similar environment without such top predation. Paine (1966) dealt with these questions by observation and field experiment and suggested that some intertidal systems seemed able to support more competing species when a top predator was present. Parrish and Saila (1970) explored a small number of cases by dynamic simulation of systems using Lotka-Volterra type interactions. Some competitive situations were found in which two unequally competing species persisted longer in more equal numbers when utilized by a top predator. Subsequently, May (1971) did a neighborhood stability analysis of the same systems and determined stability criteria in terms of competitive and predatory coefficients. Using coefficient values picked on this basis, Cramer and May (1972) used the Parrish and Saila model to demonstrate a case where an unstable two-species competition became stable when a common top predator was added to the system.

Figure 12 illustrates the behavior of a system with species C added as a top predator on the P12000 web of Figure 11. After some oscillation, the system moved to a new stable state with species C reduced to a level such that the competitors could support the total mortality. The stable relative biomasses of the competitors still reflect the competitive advantage of species B, but the ratio $B_B/B_A = 1.23$ is less than in the comparable 2-level system; i.e., the competitors occur in more nearly equal numbers. The result obtained by using the graph theory parameter values in Equation (19) of Saila and Parrish (1972) is $B_2/B_3 = 1.39$. When compared with the $B_2/B_3 = 1.56$ for the P12000 web, this also represents a more even standing among the competitors. Table 3 summarizes the B_B/B_A values obtained by dynamic simulation and by graph theory.

The same trend toward more equal biomasses of two species competing in the q coefficient when a common predator was present was found (Saila and Parrish 1972) using an independent set of "rough coefficients" provided by Menshutkin (1969). These comparisons of biomass ratios are

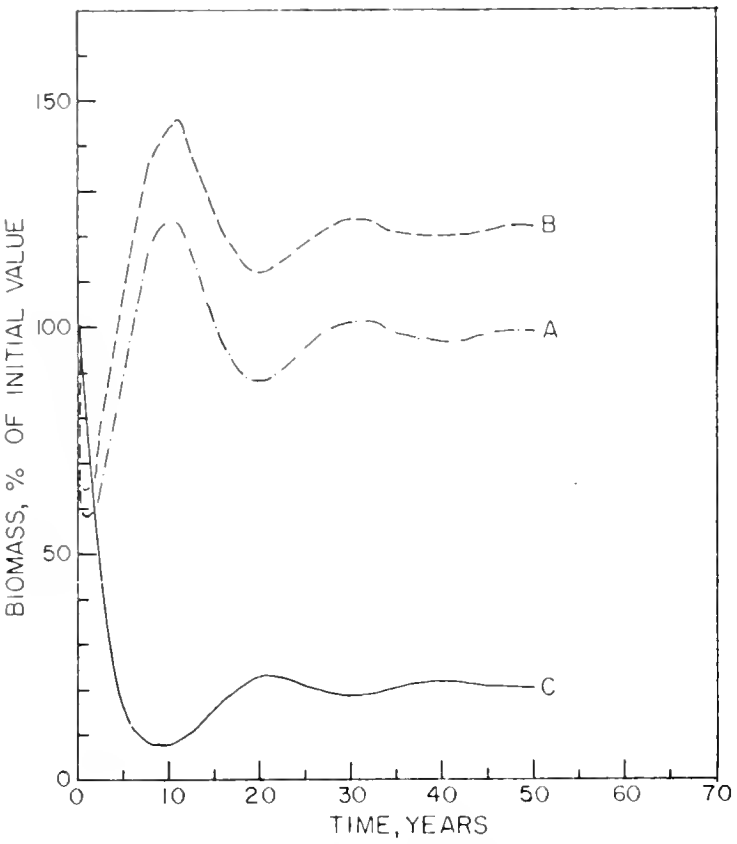

FIGURE 12.—Course of competition between two fish species, A and B, with unequal metabolic demands, competing for a common food base and utilized equally by a common predator, C. ($\alpha_B = 0.7\alpha_A$).

TABLE 3.—Biomass ratios for competing species.

Trophic system	Biomass of species with lower α / Biomass of species with higher α	
	Dynamic model prediction, B_B/B_A	Graph theory prediction, B_2/B_3
P12000 web	1.30	1.56
P12100 web	1.23	1.39

related to the concept of equitability diversity (Lloyd and Ghelardi 1964).

Some effects of human exploitation on systems of this kind have been briefly examined. Human exploitation on any species in any trophic web is expressed by the addition of Equation (18) to Equation (11) for that species (see MODEL section). Exploitation has been applied to two identical competitors in simple P12000 webs which were initially at standard equilibrium. It has produced the expected result of reducing both populations. Since the system is energy-controlled, there is always an accompanying increase in the competitors' body weights (which are always equal), and an increase in food base biomass, B_1. The total biomass of the competitor trophic level remains essentially constant. Differential exploitation of the two competitors affects the ratio of

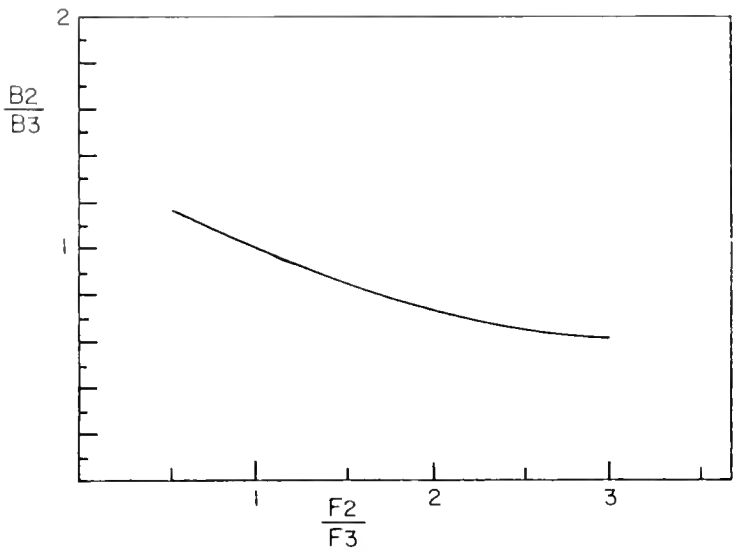

FIGURE 13.—Effect of differential exploitation on the biomass ratio, B_2/B_3, of two equally competing fish species: dynamic simulation prediction. The coefficient of instantaneous fishing mortality for species 3 is always $F_3 = 0.3$.

their numbers, and therefore also their biomass ratio. Figure 13 shows an example, using identical species A-type competitors that have arbitrarily been designated species 2 and species 3. This is the kind of curve produced by graph theory analysis for exploitation situations by Saila and Parrish (1972); e.g., their Figure 6, curve B. Parameter relationships are considerably different in the two papers. Natural mortality, M, in the present case is about 10 times its value in the Saila and Parrish paper. For another set of parameter values and a particular series of values of the exploitation coefficient, F, the stable B_2/B_3 ratio was predicted by both the dynamic simulation and the linear graph theory technique, as shown in Figure 14.

Exploitation of a comparable 3-level trophic web has also been simulated. A common predator, similar to species C except smaller, was added preying equally on two competitors almost identical with species A. A stable state for this unexploited system was found. Exploitation was applied to the competitors at various F values that had been used previously with the P12000 web. At sufficiently low values of F (in the range of Figure 14), in the new exploited steady state, the food base biomass, B_1, increased with exploitation of the competitors. The competitor with the lower F value increased in absolute population and biomass, while the more heavily exploited competitor decreased in both. Again, total biomass at the second trophic level remained essentially constant. In all cases, population and body weight of the predator decreased markedly when the competi-

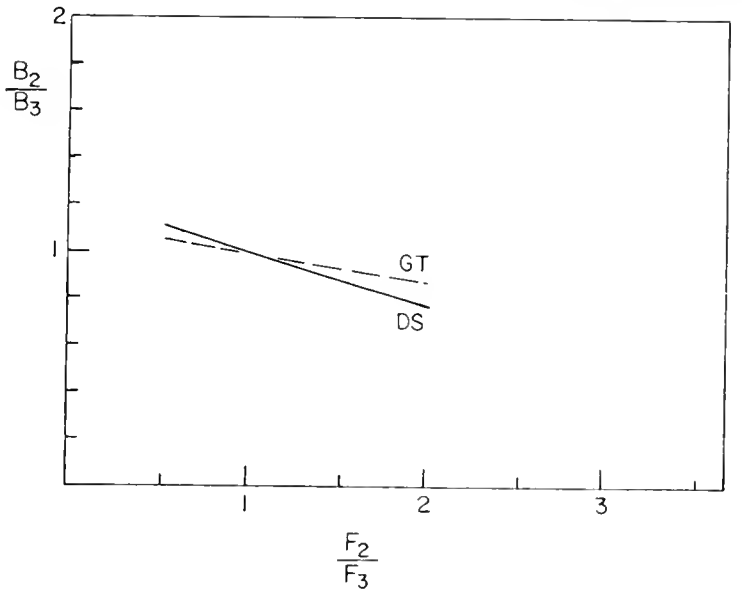

FIGURE 14.—Effect of differential exploitation on the biomass ratio, B_2/B_3, of two equally competing fish species: predictions of dynamic simulation (DS) and graph theory (GT). The coefficient of instantaneous fishing mortality for species 3 is always F_3 = 0.1.

tors were exploited. The ratio B_2/B_3 from the simulation at a given F_2/F_3 ratio was slightly less extreme than in the P12000 web. However, the difference was too slight to permit a meaningful check against graph theory calculations.

The top predator in this system could also be exploited using low values of F. The results were qualitatively similar to the last case above. The B_2/B_3 ratio changed only very slightly in this particular system to values intermediate between those of the last case above and those obtained with the P12000 web. At even the lowest F values for the competitors in Figure 14, if exploitation of the top predator was carried above about F = 0.2, the top predator was lost from the system. The same result occurred with $F \leq 0.2$ on the top predator if slightly higher F values than those in Figure 14 were applied to the competitors. The two lower trophic levels persisted stably. This vulnerability of the top predator represents another limit to the stability of the larger system. Although it has not been explored, it appears to have implications for possible effects of exploiting real multispecies fisheries.

The particular combinations used in this brief investigation were far from optimum for exploring a large range of exploitation intensities in multilevel webs (The choices were made primarily for similarity to other cases studied previously). The low permissible levels of predation and exploitation that the 3-level system would tolerate, together with the high natural mortality, made for difficulty in comparing results with those of trophic systems previously examined; e.g., by graph theory. However, the considerable similarity of the predictions in Figure 14 and Table 3 by these very different approaches seems highly suggestive.

AVAILABILITY OF MODEL AND COMPUTING DETAILS

Written descriptions of various portions of the model and their sources in somewhat more detail are available from the author. The basic computer software package used (IBM 1969) and a more advanced version (IBM 1971) are described in the manufacturer's literature with enough detail in the former case for ready use by the reader. The CSMP package is sufficiently user-oriented that no further interface program is required; the model is written directly into the CSMP structure using simplified FORTRAN-like statements. Program listings and card decks for sample trophic models are available from the author, together with tables of input values used and a glossary of code names of variables and parameters.

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APPENDIX

The parameter, s, in the starvation mortality Equations (16) and (17) is found as follows:

During starvation, since $kC < Q$ and $S = 0$, Equation (1) simplifies to

$$G = \frac{dW}{dt} = kC - Q = kC - \alpha W^{\gamma} \qquad \text{(A-1)}$$

At any constant level of ration, C, this integrates to give

$$t = \frac{5j}{4\alpha}\left[\ln\left|\frac{j + W^{0.20}}{j - W^{0.20}}\right| + 2\tan^{-1}\frac{W^{0.20}}{j}\right] - \frac{5W^{0.20}}{\alpha} - I_1, \qquad \text{(A-2)}$$

where: $j = \left(\frac{kC}{\alpha}\right)^{0.25}$,

I_1 is a constant of integration. Taking the boundary condition that $W = W_0$; i.e., the initial weight of each original N_0 individual, at time $t = 0$, the constant I_1 can be evaluated any any level of ration.

The boundary condition at 100% mortality is taken to correspond with a critical fraction—0.6—of the body weight of a normal, well-fed individual (the critical fraction is estimated from a variety of sources, including: Dawes 1930; Lawrence 1940; Phillips 1954; Adelman et al. 1955; Brett 1962; Brett et al. 1969). Using this critical lethal body weight for W, Equation (A-2) can be solved to give the critical time, t_c, to 100% mortality. Using this t_c in Equation (16) when $N/N_0 = 0$ gives the value of s.

HOMING BEHAVIOR AND CONTRIBUTION TO COLUMBIA RIVER FISHERIES OF MARKED COHO SALMON RELEASED AT TWO LOCATIONS

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ABSTRACT

This study was initiated to determine the feasibility of creating or enhancing fisheries in specific areas by releasing salmon smolts into those areas. In 1970, two groups each of approximately 100,000 1968-brood coho salmon, *Oncorhynchus kisutch*, were marked with a right ventral (RV) or a left ventral (LV) finclip at Little White Salmon National Fish Hatchery near Cooks, Wash. The LV-marked group was transported by truck to Youngs Bay, 19 km (12 miles) from the mouth of the Columbia River near Astoria, Oreg., and released in April 1970. The RV-marked group was released in May 1970 at Little White Salmon Hatchery, 242 km (150 miles) from the mouth of the Columbia River. The Youngs Bay and Columbia River gill-net fisheries were sampled for these marks in the fall of 1970 and 1971. The two groups homed to their respective areas of release with very little straying. The LV-marked group contributed 7.7 fish to the fisheries sampled for each 1,000 fish released, and the RV-marked group contributed 11.7 fish to the fisheries sampled per 1,000 fish released. However, a fair comparison of the contribution of the two groups is inhibited by 1) incomplete sampling for these marks in the ocean fisheries, 2) the difference in time and size of release of the groups, 3) the unknown effect of delayed mortality due to hauling the LV-marked group, and 4) duplication of these marks in the ocean fisheries.

The Pacific salmon, *Oncorhynchus* spp., hatchery program has undergone considerable evolution in the past 10 yr. The escapement of adult fish to hatcheries is often more than sufficient to supply egg needs. In many cases, hatcheries receive sizable excesses of returning adults. These fish must be disposed of either by releases into streams, burial, donations, or sales. The sale of salmon carcasses has caused considerable friction between commercial fishermen and fishery agencies. Salmon returning to hatcheries often arrive in a condition which makes them unsuitable for donation or release into streams. Burial of the excess salmon is an obvious waste of a valuable resource.

Taft and Shapovalov (1938) found the homing instinct of coho salmon, *O. kisutch*, to the parent stream to be fairly exact. Hasler and Wisby (1951), Wisby and Hasler (1954), and Groves et al. (1968) reported the importance of olfaction in homing of adult salmon. Hasler (1966) and Wagner (1969) felt that the organic odor of the parent stream was imprinted rapidly in juvenile salmon, possibly at the time of downstream migration. We felt that if the homing instinct was exact and the homestream imprint was acquired quickly during parr-smolt transformation, then the homing site could be altered by transportation and release of coho salmon smolts.

The purpose of this study was to determine the feasibility of creating or enhancing fisheries in specific areas by releasing salmon smolts in those areas. If salmon returned to the area of release, the problem of excess hatchery returns could be reduced. This homing behavior would provide local fisheries with larger catches of salmon and a longer fishing season.

Youngs Bay was the site picked for testing the homing behavior of salmon. It is about 19 km (12 miles) upstream from the mouth of the Columbia River near Astoria, Oreg. The Lewis and Clark, Walluski, Youngs, and Klaskanine rivers empty into Youngs Bay (Figure 1). All are small rivers with low summer flows and greatly fluctuating winter flows. The Klaskanine Salmon Hatchery, operated by the Fish Commission of Oregon, is located on the North Fork of the Klaskanine River (Weiss 1966).

A commercial salmon fishery began on Youngs Bay in the early 1900's. The bay was closed to commercial fishing from 1931 to 1962, but has remained open from 1962 to present. From 1962 to

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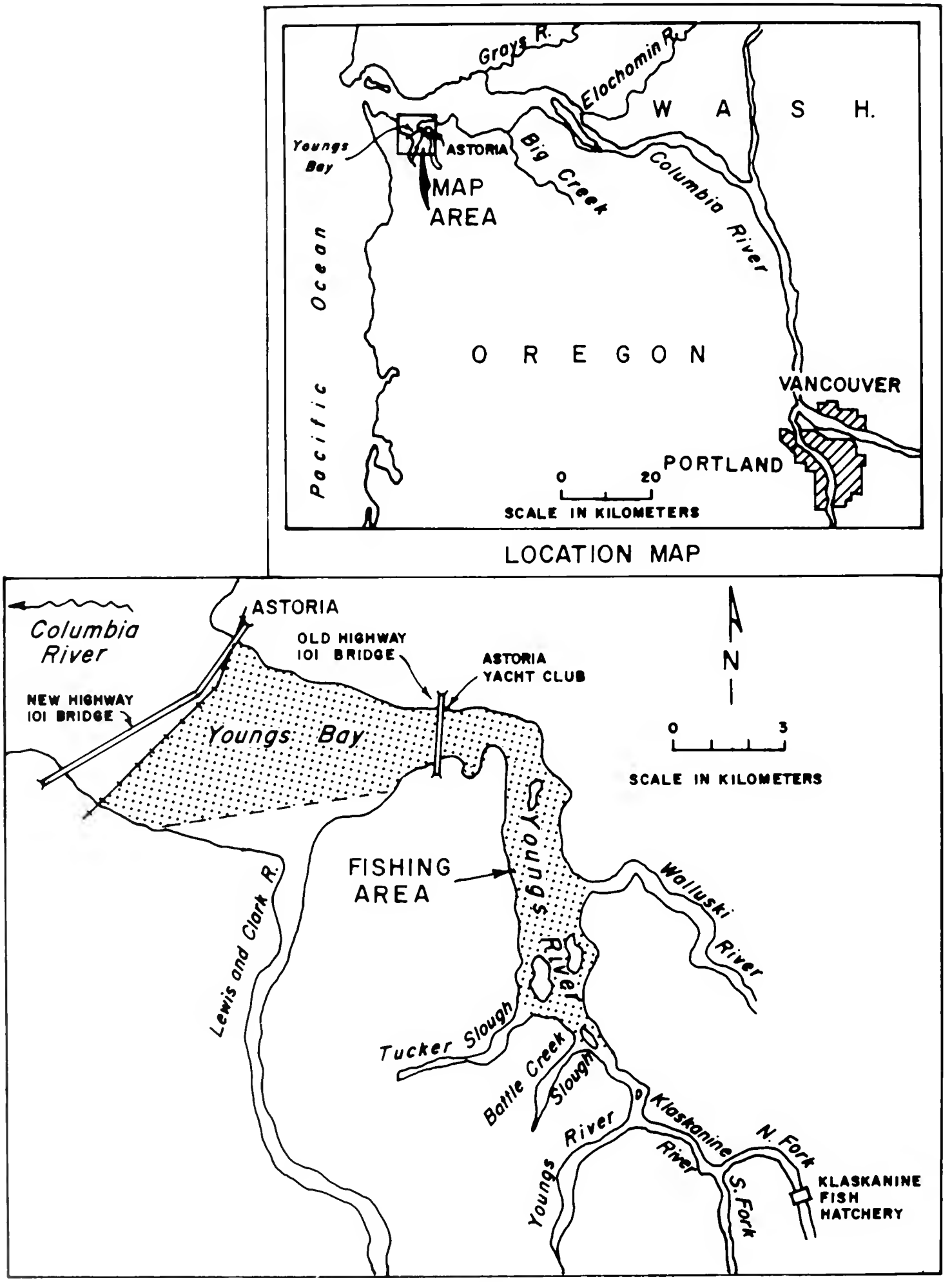

FIGURE 1.—Youngs Bay, Oreg.

1965, the fishing area extended from Battle Creek slough to the old Highway 101 bridge (Figure 1). The open area was extended to the new Highway 101 bridge in 1965. Coho salmon is the main species caught, but some chum salmon, *O. keta*, chinook salmon, *O. tshawytscha*, and steelhead trout, *Salmo gairdneri*, are also taken (Weiss 1966). The coho fishery has fluctuated from a low of 2,100 adults in 1962 to a high of 31,600 adults in 1967.[3]

The sport fishery in Youngs Bay itself is very limited. A majority of the sport fishing occurs from the confluence of the North and South forks of the Klaskanine River upstream to the Klaskanine Salmon Hatchery. A minor sport fishery for coho salmon exists on the Youngs River. It is limited by an impassable falls a short distance upstream from the river's confluence with Youngs Bay. There is little or no sport fishing for salmon on the Lewis and Clark or Walluski rivers. Sport fishing for coho in Youngs Bay and its tributaries starts after the first fall rains, from mid-September to the first of October.[4]

METHODS AND MATERIALS

Source of Fish

Coho salmon were selected as the test species for this study because of the success of hatchery coho culture exhibited by large hatchery returns. The coho for this experiment were obtained from Little White Salmon National Fish Hatchery. The eggs were taken in 1968 at Klaskanine Salmon Hatchery, and 926,300 were shipped to Little White Salmon Hatchery for hatching and rearing. Eggs from coho returning to Little White Salmon Hatchery were not reared at the station because the stock was considered undesirable. This stock had inadvertently been selected to commingle with the hatcheries fall chinook returns. This made it difficult to retain coho in good condition until spawning time. The Klaskanine coho were a later returning stock and would presumably eliminate the conflict with fall chinook.

Little White Salmon Hatchery is located near Cooks, Wash. on the Little White Salmon River approximately 1.5 km (1 mile) upstream from its confluence with the Columbia River and is about 242 km (150 river miles) from the Pacific Ocean. The hatchery is operated by the U.S. Fish and Wildlife Service and is funded primarily by the National Marine Fisheries Service.

Marking

The marking portion of the study took place in March 1970. A total of 201,700 1968-brood coho salmon were marked with a finclip at Little White Salmon Hatchery. The right ventral (RV) fin was removed from 100,809 coho which were to be released in the Little White Salmon River. The left ventral (LV) fin was removed from 100,914 fish which were to be released into Youngs Bay. Fish were 55-62/kg (25-28/pound) at time of marking.

Release Procedures

Youngs Bay was selected as a release site for three reasons. First, the bay is within the Columbia River system and yet a great enough distance from the Little White Salmon Hatchery to examine homing characteristics of coho salmon. Second, the bay provides a specific area separate from the Columbia River to which the salmon could home. Finally, the intensive commercial fishery in the bay was somewhat separate from the Columbia River fishery and would be relatively easy to sample.

A total of 100,662 LV-marked coho salmon weighing 2,019 kg (4,451 pounds) or 49.8 fish/kg (22.6/pound) were transported from the Little White Salmon Hatchery to Youngs Bay on 23, 27, and 29 April 1970. This was the normal historical coho release time at the hatchery. Two hatchery tank trucks, each making one trip per day, were used to transport the fish. On the first trip the water in the trucks was iced to maintain a constant temperature during transportation. The weather was rainy and cold, and the result was 2°C lower water temperature in the trucks than in the bay. Bay water was added to the tanks to equalize the two temperatures. The weather was the same on ensuing trips so icing was discontinued. The dates and water temperatures at the time of release are as follows:

		Temperature (°C)	
Date	*Time*	*Bay*	*Truck*
23 April	1930	11.1	10.6
27 April	2000	10.0	10.6
30 April	2000	11.1	10.6

[3]James L. Galbreath. 1968. Youngs Bay commercial coho fishery in 1967. Fish Comm. Oreg., Fish Comm. Res. Lab., Clackamas, Oreg. (Unpubl. manuscr., 10 p.)

[4]Franklin R. Young. Fish Comm. Manage. Res. Hdqrs., Clackamas, Oreg. (Pers. commun.).

The Astoria Yacht Club boat launching ramp (Figure 1) was chosen as the release site in Youngs Bay. It provided easy access and no spawning gravel or stream mouths occurred near the site. We hoped that returning adult coho salmon would mill around the bay in search of a stream. This would provide ample opportunity for commercial fishermen to harvest the fish.

All releases were made at dusk to reduce predation by gulls, grebes, ducks, and resident fish. The smolts dispersed rapidly upon release, most of them swimming toward deeper water. Movements could be seen as far as 100 m from shore shortly after releases. Only one instance of predation by birds was observed, and initial transportation losses were negligible. All the fish appeared health and active upon release.

The RV-marked coho salmon were released directly from the Little White Salmon Hatchery rearing ponds into the Little White Salmon River on the evening of 12 May 1970. A total of 100,367 fish weighing 2,504 kg (5,520 pounds) or 40.1 fish/kg (18.2/pound) were liberated. The RV-marked group was released 2 wk later than the Youngs Bay group. The reason for this difference in release dates is unknown.

Sampling

In the fall of 1970, we sampled the Youngs Bay commercial fishery for marked 2-yr-old coho salmon. The sampling was concentrated at The New England Fish Company. A fish buyer, Lawrence Peterson, was contracted by New England Fish Company to purchase fish from Youngs Bay commercial fishermen and deliver them to the processing plant. We also did some sampling of the Youngs and Klaskanine rivers sport fisheries. The Columbia River commercial fishery was sampled by the Fish Commission of Oregon. The California ocean fisheries were not sampled for single fin marks and the British Columbia and Alaska ocean fisheries and Columbia River sport fisheries were not sampled for marked fish.

Returns to hatcheries near Youngs Bay were examined for stray LV- or RV-marked coho salmon. The major effort was concentrated at the Klaskanine Salmon Hatchery since it is the only hatchery on a tributary of Youngs Bay. Returns to Big Creek Salmon Hatchery on Big Creek near Knappa, Oreg., the Elokomin Salmon Hatchery on the Elochomin River near Cathlamet, Wash., and the Grays River Salmon Hatchery on the Grays River near Grays River, Wash., were examined for LV- and RV-marked coho (Figure 1). The coho returning to Little White Salmon National Fish Hatchery were also checked for marks.

The sampling in the fall of 1971 was similar to that done in 1970. The only differences being that the sampling effort was concentrated at Barbey Packing Corporation in Astoria, and there was no sampling of the Youngs and Klaskanine River sport fisheries.

RESULTS

1970 Sampling Season

The Youngs Bay gill-net season began on 13 September 1970 and ended on 31 October 1970, a total season of 49 days. Sampling for marked 1968-brood coho jack salmon at the New England Fish Company took place on 13 of the 49 days (jack salmon are predominately males that mature early and that on the average are considerably smaller than the normal adult fish). The entire catch of coho jacks was examined on the days sampled. The total catch of jacks was estimated at 2,300 in the Youngs Bay fishery in 1970.[5] Of these, 952 were examined for marks for a 41.4% sample. Only two LV-marked and no RV-marked coho were found. This is to be expected since most fishermen use nets of 15.9-cm (6¼-inch) stretched mesh size for adult coho because of the higher price paid for adults. Table 1 shows the days sampled, the total weight and number of coho examined by day, and the marks found.

The Klaskanine River sport fishery was sampled on 23, 24, 25, 26, and 30 September. No marks were found on 18 coho jacks examined.

The Fish Commission of Oregon sampled the Columbia River commercial fishery in 1970. Only two marked coho jacks were found, one LV and one RV. This was again due to the use of 15.9-cm or larger mesh size gill nets for adult chinook and coho.

There was no concentrated sampling effort for the LV- and RV-marked coho salmon in the Columbia River sport fishery or the California, British Columbia, or Alaska ocean commercial and sport fisheries. Also, duplication of these marks in the ocean fisheries precluded their assignment to specific experiments. Table 2 lists the number of

[5]James L. Galbreath. Fish Comm. Manage. Res. Hdqrs., Clackamas, Oreg. (Pers. commun.).

TABLE 1.–Weight, number, and marks of 1968-brood coho salmon examined by sample day during the 1970 Youngs Bay gill-net season.[1]

Date 1970	Weight (kg)	Number	Marks			
			LV	Ad-LV	Ad-RV	Ad
9/17	—	14	—	1	—	—
18	—	7	—	—	—	—
22	147	125	—	—	—	—
23	82	77	—	—	—	—
24	147	126	1	—	—	—
25	186	137	—	—	—	—
26	108	90	—	—	—	—
27	87	70	—	—	—	—
28	—	68	—	—	—	—
30	104	118	1	—	1	—
10/ 6	—	12	—	—	—	—
7	69	58	—	—	—	1
8	—	50	—	—	—	—
Total	930	952	2	1	1	1

[1]The sampling was done at New England Fish Co. unloading dock.

1968-brood LV- and RV-marked coho recovered by year, area, and fishery.

The returns of Klaskanine, Big Creek, Grays River, Elokomin, and Little White Salmon hatcheries were examined for LV- and RV-marked 1968-brood coho salmon. A total of 9,039 jacks returned to Klaskanine Hatchery and 8,705 were examined for marks. Only three LV and no RV marks were observed. No LV or RV marks were found in the returns to the other three hatcheries. At Little White Salmon Hatchery, 1 LV-marked and 55 RV-marked coho were observed. Table 3 lists the number of marked 1968-brood coho returning to the five previously mentioned hatcheries by hatchery, year, and mark.

1971 Sampling Season

In 1971 the sampling for marks was done at Barbey Packing Corporation, Astoria, Oreg. The entire catch of coho salmon was examined on 27 days of the 49-day season. The catch of 1968-brood coho was estimated to be 8,110 fish. Of these, 5,477 were examined for marks for a 67.5% sample. Table 4 shows the days sampled, the weight and numbers of coho sampled, and the marks found. A total of 355 marked coho were observed, of which 336 were LV marked and 8 were RV marked (Table 4). Length and weight data were collected from 320 of the marked 1968-brood coho examined. These data are presented in Table 5.

The sport fisheries of Youngs Bay and its tributaries were not sampled in 1971, but the Fish Commission of Oregon again sampled the Columbia River gill-net fishery for marks. A total of 17

TABLE 2.–Number of 1968-brood LV- and RV-marked coho salmon recovered by year, area, and fishery, 1970 and 1971.[1]

Area and fishery	1970		1971	
	LV	RV	LV	RV
Youngs Bay gill net	2	0	336	8
Youngs Bay sport	0	0	—	—
Columbia River gill net	1	1	17	74
Total	3	1	353	82

[1]Columbia River and ocean sport and ocean commercial fisheries were not sampled for these marks.

TABLE 3.–Number of 1968-brood LV- and RV-marked coho salmon recovered at five Columbia River hatcheries by year, 1970 and 1971.

Hatchery	1970		1971	
	LV	RV	LV	RV
Klaskanine	3	0	1	0
Big Creek	0	0	1	0
Grays River	0	0	0	1
Elokomin	0	0	0	0
Little White Salmon	1	55	3	300
Total	4	55	5	301

LV-marked and 74 RV-marked 1968-brood coho salmon were recovered. As in 1970, the Columbia River sport, California, British Columbia, and Alaska ocean sport, and ocean commercial fisheries were not sampled for LV- or RV-marked coho.

Hatchery returns examined in 1970 were again examined in 1971. Klaskanine Hatchery had an adult coho return of 5,476 fish. Only one LV-marked and no RV-marked fish were found. No RV- or LV-marked adults were seen at Big Creek or Elokomin hatcheries, and only one RV mark was recovered at Grays River Hatchery. At Little White Salmon Hatchery, 300 RV-marked and only 3 LV-marked 1968-brood coho were recovered. (See Table 3.)

The estimated catches of marked 1968-brood coho salmon by fishery, year, and mark are presented in Table 6. These values were obtained by multiplying the total 1968-brood coho catch for a fishery by the rate of occurrence of a mark in that fishery. Columbia River gill-net estimates were calculated for weekly periods and summed for the season. The Youngs Bay marked fish estimates were made for the entire fall season. For example, it was estimated that 8,110 1968-brood coho were caught in Youngs Bay in 1971 (Table 4). Of these fish 5,477 were sampled for marks and 336 LV marks were observed. Thus the estimated catch of LV marks was $8,110 \times 336/5,477 = 498$.

TABLE 4.—Weight, number, and marks of 1968-brood coho salmon caught each day during the 1971 Youngs Bay gill-net season.[1]

Date 1971	Weight (kg)	Number	Marks						
			LV	RV	Ad	Ad-LV	Ad-RV	Ad-LM	Ad-RM
9/17	1,007	236	—	—	—	—	—	—	—
18	1,204	282	—	—	—	—	—	—	—
19	1,427	334	—	—	—	—	—	—	—
20	929	217	—	—	—	—	—	—	—
21*	1,457	305	12	—	—	—	—	—	—
22*	1,132	260	12	—	—	—	—	—	—
23*	910	210	9	1	1	—	—	—	—
24	835	195	—	—	—	—	—	—	—
25*	1,084	240	14	—	—	—	—	—	—
26*	1,289	296	17	—	—	—	—	—	—
27*	434	98	4	—	—	—	—	—	—
28*	408	99	3	1	—	—	—	—	—
29	650	152	—	—	—	—	—	—	—
30*	978	225	6	—	—	—	—	—	—
10/ 1*	1,341	305	8	—	—	—	—	—	—
2*	1,135	265	14	—	—	—	—	—	—
3*	1,289	307	17	1	—	—	—	—	—
4*	552	128	7	—	—	—	—	—	—
5*	2,085	503	31	1	—	—	—	—	—
6*	1,084	271	18	—	—	1	—	—	—
7*	980	222	29	1	—	—	—	3	—
8*	627	144	14	1	—	—	2	—	1
9*	766	185	6	1	—	—	—	—	—
10*	725	173	12	—	1	—	1	—	—
11*	668	152	14	—	1	—	—	—	—
12*	563	137	5	—	—	—	—	—	—
13	477	112	—	—	—	—	—	—	—
14	901	211	—	—	—	—	—	—	—
15*	716	172	12	—	—	—	—	—	—
16*	615	147	8	—	—	—	—	—	—
17*	660	161	13	—	—	—	—	—	—
18	689	115	—	—	—	—	—	—	—
19	494	116	—	—	—	—	—	—	—
20	811	190	—	—	—	—	—	—	—
21	1,070	250	—	—	—	—	—	—	—
22*	786	186	18	1	—	—	—	—	—
23*	528	132	21	—	—	—	—	—	—
24*	353	91	10	—	—	—	—	—	—
25*	252	62	2	—	—	—	—	—	—
26	57	13	—	—	—	—	—	—	—
27	312	73	—	—	—	—	—	—	—
28	245	57	—	—	—	—	—	—	—
29	83	20	—	—	—	—	—	—	—
30	31	7	—	—	—	—	—	—	—
31	33	8	—	—	—	—	—	—	—
Total	34,672	8,110	336	8	3	1	3	3	1

[1]The sampling was done at Barbey Packing Corp. unloading dock. The days sampled are denoted by an asterisk. The entire catch was sampled for those days. The number of fish landed at Barbey on the days not sampled was estimated by using an average weight of 4.28 kg/fish which was calculated by dividing 23,417 kg sampled by 5,477 fish sampled.

TABLE 5.—Sex composition and average size of LV- and RV-marked 1968-brood coho salmon sampled during the 1971 Youngs Bay gill-net season.

Mark	Number of fish	Average size		Sex of fish	
		Length (cm)	Weight (kg)	Male	Female
LV	303	67	3.9	120	183
RV	7	70	4.2	5	2
Total	310	67	3.9	125	185

TABLE 6.—Estimated catch of 1968-brood LV- and RV-marked coho salmon by year, area, and fishery, 1970 and 1971.[1]

Area and fishery	1970		1971	
	LV	RV	LV	RV
Youngs Bay gill net	5	0	498	12
Youngs Bay sport	0	0	—	—
Columbia River gill net	8	2	267	1,162
Total	13	2	765	1,174

[1]Columbia River and ocean sport and ocean commercial fisheries were not sampled for these marks.

DISCUSSION

Hatchery returns (see Table 3) indicate that there is little straying of the LV-marked coho salmon released in Youngs Bay to hatcheries in the area or back to the parent hatchery (Little White Salmon). Only five LV-marked fish were recovered at the four hatcheries near Youngs Bay. Only 4 LV-marked coho returned to Little White Salmon Hatchery in 1970 and 1971, while 355 RV-marked fish returned to the hatchery.

Catches of marked coho also suggest that they home to the area of release (Table 6). An estimated 504 LV-marked coho were caught in the Youngs Bay gill-net fishery in 1970 and 1971. Only 12 RV-marked fish were estimated to have been caught in the bay. For 1970 and 1971 combined, the estimated Columbia River gill-net catch of LV- and RV-marked coho was 267 and 1,162, respectively. Of the 267 LV coho caught, about 45% were taken in Zone 1; 30% in Zone 2; and 25% in Zones 3 through 5. This means that about 75% of the LV-marked coho caught in the Columbia River were caught in waters adjacent to Youngs Bay. Since few LV-marked fish returned to Little White Salmon Hatchery or hatcheries in the area, it is reasonable to assume that these fish were bound or searching for the area of release.

These catches and hatchery returns gave an indication that the coho homed to the area of release with little straying. With few exceptions, the LV-marked coho released in Youngs Bay returned to the Youngs Bay area, and the RV-marked coho released at Little White Salmon Hatchery were bound for or returned to the hatchery.

Other investigators have reported various degrees of straying and homing tendencies of transported fish. Ellis and Noble (1960) reported returning fall chinook salmon from Klickitat Salmon Hatchery released in the lower Columbia River showed a greater tendency to stray than chinook released at the hatchery. Few of the transported chinook returned to the hatchery.

Wagner (1969) found that steelhead trout smolts trapped on the Alsea River and transported downstream returned as adults to an upstream trap in fewer numbers than untransported steelhead trout. This was probably due to the transported steelhead straying into tributaries as they moved upstream. From this and other studies (Wagner 1967), he concluded that the homing imprint in definitely influenced by stocking site and that capturing and transferring smolts during their downstream migration may cause gaps in imprinting. These gaps could result in delayed adult upstream migration. The duration of the delay probably depends on the strength of upstream stimuli.

Experiments conducted at hatcheries in Oregon, Washington, and California have shown that a majority of the chinook salmon, coho salmon, or steelhead trout released as smolts in an area with no downstream migration prior to hauling return to the area of release as adults. Studies at Ice Harbor Dam on the Snake River, 538 km above the Columbia River mouth (334 miles), indicated that chinook transported from Ice Harbor to below Bonneville Dam, a distance of 304 km (189 miles), returned as adults to Ice Harbor with little straying (Ebel et al. 1972).

These studies and our data suggest that coho salmon released in an area to create or enhance a fishery would home back to that area.

When examining the contribution of the RV- and LV-marked coho salmon to the fisheries sampled, it appears that the RV group released at Little White Salmon Hatchery had better survival than the LV group released at Youngs Bay. The total catch of RV-marked 1968-brood coho in 1970 and 1971 was 1,176 or 11.7 per 1,000 released compared to 778 LV coho caught or 7.7 per 1,000 released. However, a good comparison between the recoveries of the two groups cannot be made because of incomplete sampling. The ocean fisheries and Columbia River sport fishery were not sampled for LV- or RV-marked coho, and the Youngs Bay sport fishery was sampled only sparsely in 1970. Catches of LV- and RV-marked fish in these fisheries could alter the contribution of either or both groups significantly.

A good comparison of the contribution of the two groups is also hampered by the difference in size and time of release of the groups. The LV-marked coho were released in Youngs Bay on 23, 27, and 29 April 1970, at 49.9 fish/kg (22.6/pound). The RV-marked coho were released at Little White Salmon Hatchery 2 wk later on 12 May and at a larger size, 40.1 fish/kg (18.2/pound). This later release of larger fish could have improved the survival of the RV-marked coho.

A third factor inhibiting comparisons of the contributions of the RV and LV groups is hauling mortality. Tests have indicated that post-transport mortality may have a noteworthy effect on transported fish (Ebel et al. 1972). It is not known if the procedures used in this study to transport

fish to Youngs Bay were more or less detrimental than the more natural migration pattern from the hatchery through Bonneville Dam and downstream to the ocean. If the employed transportation method caused significant mortalities and if changes in the method can be made to improve survival, then a better contribution from this type of release procedure could be obtained.

Other researchers have had similar difficulties in evaluating groups of fish released at different sites. Ellis and Noble (1960) had difficulty comparing the contribution and survival of groups of chinook salmon released at Klickitat Hatchery and Skamokawa, Wash., 354 km (220) and 53 km (33 miles), respectively, from the Columbia River mouth. Differences in the size of fish at release and marks used on each group as well as generally poor nutrition and survival during the hatchery rearing period influenced the results. However, the catch data indicate that contribution to the Columbia River fisheries was increased by release site manipulation. If straying could have been evaluated, total survival for the transported group may have been greater than the nontransported fish.

Wagner (1967, 1969) noted in studies with various release sites for steelhead on the Sandy, Alsea, and Wilson rivers that, in general, the contribution of hatchery reared steelhead to the sport fisheries was increased by releasing smolts in the lower stream areas. Here again, different mark types on the groups and variations in fishing effort on different stream sections may have influenced the results.

More recently Ebel et al. (1972) transported chinook salmon around Snake and Columbia River dams. They found that the contribution ratio of transported versus nontransported fish in the lower Columbia River sport and commercial fisheries was 1.4 to 1. Passage of chinook smolts through Snake and Columbia River dams certainly had an influence on survival differences between transported and nontransported groups.

SUMMARY AND CONCLUSIONS

This study was initiated to determine the feasibility of creating or enhancing a fishery in a specific area by releasing hatchery salmon smolts into that area. The plan was to release hatchery coho salmon smolts into an area and sample the fisheries in the area to determine if the fish returned in great enough numbers to warrant expansion of this practice.

Two groups of approximately 100,000 1968-brood coho at Little White Salmon National Fish Hatchery were marked—one with a right ventral finclip and the other with a left ventral finclip. Youngs Bay near Astoria, Oreg., was selected as the release site for the LV-marked group. The RV-marked coho were released at the hatchery. The releases were made in April and May of 1970.

The Youngs Bay and Columbia River gill-net fisheries were sampled for these marks in the fall of 1970 and 1971. A comparison of the catches and hatchery returns of the two groups showed that the two groups homed back to their respective areas of release with very little straying. The contribution of these two groups to the fisheries sampled was 7.7 fish per 1,000 released for the LV-marked Youngs Bay release and 11.7 fish per 1,000 released for the RV-marked Little White Salmon Hatchery release.

These statistics appear to favor the Little White Salmon Hatchery release, but there are several factors which prevent an accurate comparison of the two groups. First, the LV-marked coho were released in Youngs Bay 2 wk prior to and at a smaller size than the RV-marked coho released at the hatchery. Second, no evaluation was made of the possible effects of delayed mortalities of the LV coho due to hauling. Third, incomplete sampling for these marks was carried out in the ocean sport and commercial fisheries. Finally, duplication of single fin marks in the ocean fisheries prevented assignments to specific experiments. These four factors could have a significant influence on the contribution of either or both groups of coho.

Conclusions as to the practicality of transporting fish to an area to create or enhance local fisheries cannot be reached because of the four unknown factors influencing contribution. However, catches, hatchery returns, and the lack of straying indicate that this practice is biologically feasible. A study structured to evaluate the total contribution of two releases similar to those in this investigation and to eliminate the unknowns is presently underway.

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MESOPELAGIC MICRONEKTON IN HAWAIIAN WATERS: FAUNAL COMPOSITION, STANDING STOCK, AND DIEL VERTICAL MIGRATION

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ABSTRACT

On one cruise off leeward Oahu, Hawaii, micronekton from 9 deep-oblique mid-water trawl tows (0-1,200 m) and a 24-h series of 14 consecutive shallow-oblique tows (0-400 m) were sorted into 16 faunal groups, enumerated, and weighed. Diel-related trawl avoidance was not significant in deep tows. Mean total micronekton standing stocks for the deep tows were 898 organisms/100 m^2 ocean surface and 494 g (wet weight)/100 m^2 ocean surface. Fishes comprised half of the total numbers and biomass, while crustaceans contributed one-third of the total numbers and one-fifth of the biomass. Of the micronekton deeper than 400 m during the day, 43% of the number of organisms with 47% of the biomass migrated into the upper 400 m at night.

Micronekton play important roles in the oceanic ecosystem, yet few studies have examined the whole fauna in one area to measure standing stock, percent standing stock involved in diel vertical migration, or the relative contributions of major groups to the standing stock. This study considers such data taken on one cruise off Hawaii in the fall of 1972.

Samples were taken over 2,500-m deep waters 10-25 km off the leeward (west) coast of Oahu, in the Hawaiian Archipelago (approximately between lat. 21°15′N, long. 158°15′W and lat. 21°30′N, long. 158°22′W). Physical, chemical, and microbiological data are available for the sampling area (Schuert 1970; Gundersen et al. 1972) and nearby Station Gollum (lat. 22°10′N, long. 158°00′W) (Gordon 1970, 1971). A broad thermocline about 50-500 m deep is present throughout the year (Figure 1). A salinity minimum of 34.0‰ occurs at 400-500 m and a maximum of about 35.2‰ occurs around 100 m (Gordon 1970). The oxygen concentration varies from a minimum of 0.7 ml O_2/liter at 600-800 m to a maximum of about 5.3 ml O_2/liter at the surface (Gordon 1970). Water transparency is very high. In August 1972, noon irradiance measurements at a nearby station, lat. 28°29′N, long. 155°14′W, dropped from a surface level of 7×10^{2} $\mu W/cm^2$ (at 471 nm) to 1.8×10^{-3} $\mu W/cm^2$) at 471 nm) 400 m deep, k = 0.029 below 200 m (E. M. Kampa, pers. commun.) (cf. G. L. Clarke 1971:43). Primary productivity in this area has been estimated at 50 g C/m^2·yr (S. A. Cattell, pers. commun.). The mean seasonal standing stock of zooplankton in the upper 200-m layer off Oahu is about 2.6 g (wet weight)/m^2 (Nakamura 1967).

GEAR AND METHODS

Trawl

All samples were taken with a 10-foot (3-m) Isaacs-Kidd Mid-water Trawl (IKMT) of standard design (Devereaux and Winsett 1953). The anterior portion of the net was lined with 6.35-mm (stretch) knotless nylon mesh; the middle portion was lined with 4.75-mm knotless nylon mesh; and the cod end was a 1.0-m diameter plankton net of 0.333-mm Nitex[2] mesh. Water flow was measured with a flowmeter (General Oceanics 2030) suspended near the center of the mouth, about 1 m inside the net. A time-depth recorder (TDR) (Benthos 1170-1000 or -2500) provided data on the sampling path.

Trawling Method

All samples were taken on cruise TEUTHIS-18

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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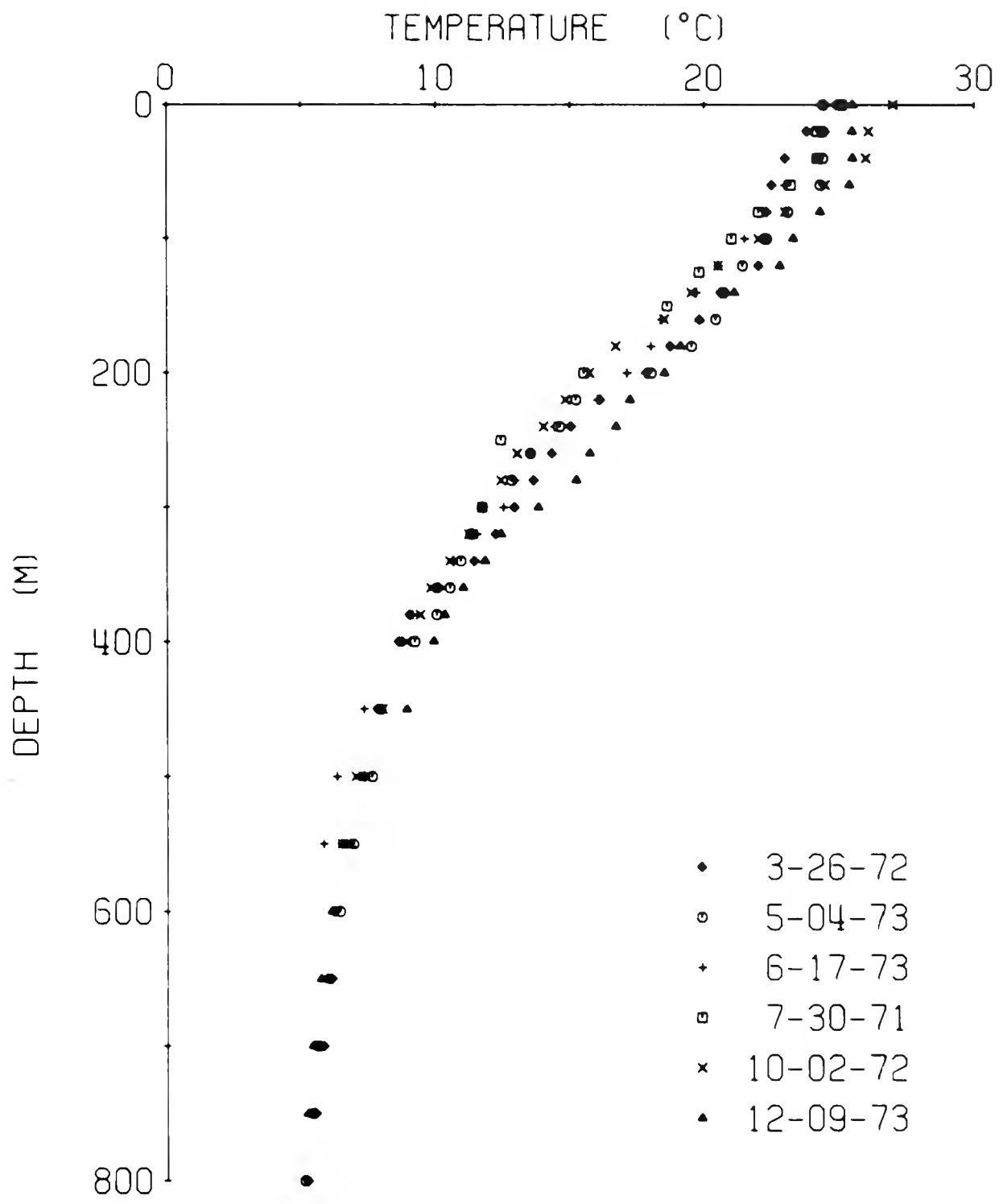

FIGURE 1.—Temperature-depth profiles taken by expendable bathythermographs in the sampling area.

on the University of Hawaii RV *Teritu*, 29 September to 3 October 1972 (Table 1). Sunrise occurred at about 0630 h, sunset at 1830. The moon was in its last quarter; on the last day of the cruise it rose at 0330 and set at about 1530.

All hauls were oblique and sampled primarily during descent. Two types of tows were made: deep tows 0-ca. 1,200 m (Figure 2a) and shallow tows 0-ca. 400 m (Figure 2b). Two deep-tow series (four day tows, five night tows total) were separated by a 24-h shallow-tow series (six day tows, six night tows); three twilight tows (no. 180, 184, 197) were also made, but the data were not included in computations of mean standing stocks. The two types of tows were designed to complement each other and provide data on diel vertical migrations; the two deep series were intended to examine day-to-day catch variability. The sampling depths were based on the results of previous horizontal sampling which indicated that nearly all micronekton resided between 400 and 1,200 m during the day.

TABLE 1.–Tow data for TEUTHIS-18.

Tow number	Date	Local time Begin	Local time End	Number flowmeter revolutions	Max. depth (m)
180	9/29	1703	2025	517,814	1,350
181		2040	0213	998,460	1,500
182	9/30	0235	0408	290,325	365
183		0657	1203	1,061,855	1,160
184		1221	1710	841,941	1,250
185		1912	0002	884,407	1,320
186	10/1	0015	0500	872,342	1,350
187		0522	0657	399,056	390
188		0716	0851	307,434	400
189		0904	1040	336,306	400
190		1051	1220	284,953	400
191		1236	1408	346,136	500
192		1429	1607	307,172	405
193		1620	1751	306,759	410
194		1758	1928	275,434	400
195		1937	2110	295,355	400
196		2117	2250	284,199	395
197		2257	0029	293,163	440
198	10/2	0036	0210	274,276	415
199		0232	0409	308,441	420
200		0421	0554	305,249	400
201		0630	1117	935,456	1,200
202		1134	1612	844,093	1,240
203		1856	2330	857,374	1,310
204		2340	0434	935,631	1,210

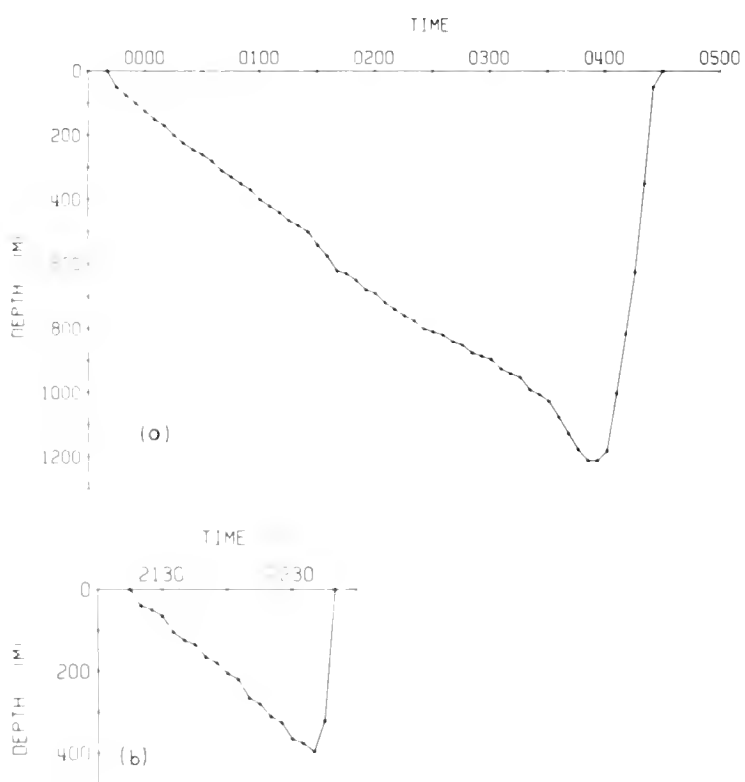

FIGURE 2.–Time-depth records for typical tows, depth plotted every 5 min. a. Deep tow, no. 204. b. Shallow tow, no. 196.

A stepped sampling strategy was adopted. The ship speed was 100 m/min (3.5 knots) for all sampling except during retrieval when the ship was nearly stopped. For the shallow tows, 100 m of cable were let out at 50 m/min every 5 min until 1,100 m of cable were out. This placed the trawl at about the 400-m depth. After 5 min at this depth, the trawl was retrieved as fast as possible. Total duration of shallow tows was about 1.5 h, that of the retrieval phase about 0.3 h. For deep tows, the first 1,100 m of cable were let out in the same manner as for the shallow tows. Beyond 1,100 m, 200 m of cable were let out at 50 m/min every 10 min until 3,400 m of cable were out. After 10 min at this depth (about 1,200 m), the trawl was retrieved as fast as possible. Total duration of deep tows was about 5 h; retrieval took about 1 h. The distribution of mean sampling times in each 100-m depth interval is shown in Table 2. By inspection, the variability seemed small enough to treat all tows within each type equally.

TABLE 2.–Distribution of mean sampling time per tow (minutes) and standard deviation (SD) with depth.

Sample depth interval (m)	Shallow Day (6 tows) Mean time/ tow (min)	SD	Shallow Night (7 tows) Mean time/ tow (min)	SD	Deep Day (4 tows) Mean time/ tow (min)	SD	Deep Night (5 tows) Mean time/ tow (min)	SD
0-100	21.0	0.0	21.3	1.4	19.3	4.9	17.4	3.2
101-200	22.0	1.4	21.3	1.0	20.3	6.7	17.8	2.8
201-300	21.5	1.7	22.2	2.4	24.3	0.6	21.4	3.9
301-400	26.0	1.4	25.2	3.1	26.0	4.6	28.4	3.8
>400	3.5	0.5	2.7	4.6				
0-400	94.7	2.7	92.9	2.3	90.0	7.9	89.0	4.5
401-500					24.7	3.1	25.0	2.1
501-600					24.7	11.6	18.8	4.4
601-700					23.0	1.7	29.6	4.4
701-800					22.3	2.8	21.8	2.7
801-900					39.7	7.1	34.0	5.6
901-1,000					23.7	7.8	20.6	5.6
1,001-1,100					17.7	8.6	14.8	2.4
1,101-1,200					19.7	14.4	13.4	3.5
1,201-1,300					10.7	9.7	11.0	2.0
1,301-1,400					0.0		10.6	7.2
1,401-1,500					0.0		7.4	16.6
Total					291.0	13.7	292.0	23.3

Sample Processing

For this study, micronekton was defined as the pelagic marine animals longer than 1 cm caught by the 10-foot IKMT with the trawling methods described above. Each catch was preserved in buffered 7% seawater-Formalin. The animals were originally sorted to family or genus but subsequently were lumped into larger groups chosen to roughly discriminate between vertical migrators and non-migrators, as well as among trophic groups (Table 3). Group names are capitalized in the text. All micronekton except siphonophores were counted, and all groups were weighed (blotted wet weight ±0.01 g). Siphonophore biomass was included in the Cnidaria group, but the

TABLE 3.—Group composition used to sort each catch.

1. Myctophidae.
2. *Cyclothone* (Gonostomatidae).
3. Other Gonostomatidae.
4. Sternoptychidae.
5. Other Stomiatoidei: Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiatidae, Stomiatidae.
6. Anguilliformes: Cyemidae, Eurypharyngidae, leptocephali, Nemichthyidae, Serrivomeridae.
7. Miscellaneous fishes: Alepisauridae, Apogonidae, Bathylagidae, Bregmacerotidae, Brotulidae, Ceratioidei, Cetomimidae, Chiasmodontidae, Evermanellidae, Giganturidae, Macrouridae, Melamphaeidae, Neoscopelidae, Omosudidae, Opisthoproctidae, Paralepididae, Scorpaenidae, Trachipteridae, Zeidae, Zoarcidae, larval neritic, unidentified larval midwater.
8. Caridea: Oplophoridae, Pandalidae, Pasaphaeidae.
9. Penaeidae: Penaeidae, Sergestidae.
10. Euphausiacea: Bentheuphausidae, Euphausiidae.
11. Mysidacea: Eucopeidae, Lophogastridae.
12. Miscellaneous Crustacea: Amphipoda, Isopoda, Ostracoda.
13. Cephalopoda.
14. Tunicata: Pyrosomidae, Salpidae.
15. Cnidaria: Hydrozoa, Scyphozoa, Siphonophora.
16. Miscellaneous invertebrates: Annelida, Ctenophora, Heteropoda, Pteropoda, Nemertea.
17. Zooplankton: Copepoda, larval Stomatopoda, other meroplankton, organisms ≤ 1 cm, residue.

Pooled classifications
Total fishes = Groups 1-7.
Total Crustacea = Groups 8-12.
Other invertebrates = Groups 14-16.
Total micronekton = Groups 1-16.

number of siphonophores could not be determined from the assorted zooids (Pugh 1974), and the numerical standing stock of Cnidaria is thus slightly underestimated. Organisms larger than 10 g/individual were weighed separately, but their weights and abundance were included in group totals. Most animals with greatest linear dimensions of about 1 cm or less, such as the euphausiid *Stylocheiron* spp., were placed into the zooplankton group although some sergestids in this size range were included in Penaeidea. Standing stocks of zooplankton shrimps were calculated from subsamples (Folsom splitter) of one deep tow.

Calculations

The volume of water filtered by each tow was determined by multiplying the distance travelled (as determined by the flowmeter) by the area of the net mouth. Mouth areas from 7.08 to 8.19 m^2 have been reported for the 10-foot IKMT (Brooks et al. 1974). We used 7.7 m^2 for our trawl. Zooplankton biomass was calculated for a mouth area of 7.7 m^2, the full IKMT mouth, and 0.785 m^2, the area of the cod end mouth. The true zooplankton concentration probably lies somewhere between these values because the anterior portions of the trawl funnel some zooplankton into the cod end while others pass through the meshes (Banse and Semon 1963; Hopkins 1966; Friedl 1971).

To calculate the number of organisms or biomass of each group per 100 m^2 of ocean surface, the catch was divided by the volume of water filtered; this quotient was multiplied by the maximum depth of the tow and the product was then multiplied by 100. This computation assumes all depths were sampled equally.

RESULTS

Standing Stock

The standing stocks from deep-day and deep-night tows were not significantly different (t-test, $P<0.05$) in either number of organisms or biomass for most groups, including total micronekton. Only the numbers of miscellaneous fishes and Mysidacea showed significant diel differences. Likewise there were no significant differences ($P<0.05$) between the two series of deep tows (tows 183-186 vs. 201-204). Consequently we treated all deep tows as replicates and pooled the data to compute mean micronekton standing stocks for the 0- to 1,200-m deep water column (Tables 4, 5). Shallow-day (tows 188-193) and shallow-night (tows 182, 195-200) data were obviously different and were treated separately in these tables. The percentage composition of the fauna by group is illustrated in Figure 3 for each of the three classes of tows.

The mean standing stocks of total micronekton for the 0- to 1,200-m water column are about 900 organisms and 500 g wet weight/100 m^2 of ocean surface (Tables 4, 5). Fishes comprised over one-half of both the total numbers and biomass; crustaceans constituted about one-third of the numbers and one-fifth of the biomass, while the cephalopods contributed only one-hundredth of the numbers but one-tenth of the biomass (Tables 4, 5). *Cyclothone* were more than twice as numerous as any of the other 15 groups, totalling almost 35% of the individuals caught (Figure 3a). The distribution of biomass among the groups varied less than the distribution of the abundance. No group contributed more than the Myctophidae which comprised 13% of total biomass (Figure 3a). A comparison of group rank by biomass with rank by abundance indicates that most of the more

TABLE 4.—Micronekton standing stock, mean number of organisms per 100 m^2 ocean surface. Standard deviation in parentheses.

Group	0-1,200 m		Day 0-400 m		Night 0-400 m	
Myctophidae	108.13	(45.71)	1.02	(1.15)	80.72	(22.65)
Cyclothone	308.29	(103.34)	6.07	(8.84)	19.48	(39.01)
Other Gonostomatidae	25.77	(3.70)	3.25	(3.84)	22.13	(8.56)
Sternoptychidae	22.97	(5.98)	0.42	(0.78)	4.36	(1.47)
Other Stomiatoidei	3.92	(2.04)	0.00		2.68	(1.70)
Anguilliformes	11.43	(4.46)	2.64	(1.04)	2.96	(2.23)
Misc. fishes	27.49	(7.64)	16.31	(5.68)	21.08	(5.83)
Caridea	40.18	(5.93)	1.70	(2.21)	27.52	(11.18)
Penaeidea	137.90	(34.99)	6.83	(3.74)	132.90	(21.69)
Euphausiacea	97.79	(28.16)	6.79	(5.77)	69.01	(11.50)
Mysidacea	9.89	(3.02)	0.00		8.73	(6.67)
Misc. Crustacea	4.08	(6.72)	0.00		1.88	(1.54)
Cephalopoda	8.44	(2.04)	3.60	(1.98)	5.95	(1.81)
Tunicata	28.05	(14.10)	50.26	(24.73)	25.01	(10.97)
Cnidaria	10.80	(9.41)	11.82	(2.49)	11.47	(8.81)
Misc. invertebrates	52.93	(25.02)	55.55	(7.73)	42.04	(10.03)
Total micronekton	898.07	(149.50)	166.27	(16.45)	477.94	(69.27)
Total fishes	508.00	(133.50)	29.71	(7.48)	153.41	(60.43)
Total Crustacea	289.84	(54.25)	15.32	(4.92)	240.04	(13.91)
Cepholopoda	8.44	(2.04)	3.60	(1.98)	5.95	(1.81)
Other invertebrates	91.78	(25.22)	117.63	(19.26)	78.52	(22.71)
No. organisms caught	12,037		1,576		5,136	
No. tows	9		6		7	

TABLE 5.—Micronekton standing stock, mean biomass, grams wet weight per 100 m^2 ocean surface. Standard deviation in parentheses.

Group	0-1,200 m		Day 0-400 m		Night 0-400 m	
Myctophidae	65.71	(20.36)	0.19	(0.17)	69.85	(12.26)
Cyclothone	45.91	(11.26)	0.46	(0.75)	1.20	(2.92)
Other Gonostomatidae	14.92	(8.48)	0.41	(0.49)	29.24	(25.22)
Sternoptychidae	25.05	(14.02)	0.39	(0.91)	7.45	(2.75)
Other Stomiatoidei	15.56	(12.53)	0.00		13.36	(14.73)
Anguilliformes	48.18	(43.65)	2.40	(3.04)	1.53	(1.63)
Misc. fishes	41.37	(40.16)	2.65	(0.93)	9.46	(6.35)
Caridea	50.49	(21.07)	0.15	(0.28)	30.27	(13.11)
Penaeidea	31.59	(10.61)	0.13	(0.10)	22.71	(3.88)
Euphausiacea	18.52	(3.98)	0.86	(0.80)	12.28	(1.57)
Mysidacea	8.80	(9.76)	0.00		4.42	(3.45)
Misc. Crustacea	1.09	(1.92)	0.00		1.09	(0.78)
Cephalopoda	48.71	(47.46)	2.02	(2.02)	13.84	(16.28)
Tunicata	34.07	(42.52)	5.90	(3.50)	21.68	(15.00)
Cnidaria	40.86	(46.86)	10.50	(5.50)	11.34	(12.87)
Misc. invertebrates	3.38	(3.49)	6.61	(2.35)	1.39	(0.33)
Total micronekton	494.20	(99.30)	32.68	(6.58)	251.11	(53.46)
Total fishes	256.70	(81.30)	6.50	(2.99)	132.09	(39.33)
Total Crustacea	110.49	(36.15)	1.14	(1.06)	70.77	(12.30)
Cephalopoda	48.71	(47.46)	2.02	(2.02)	13.84	(16.28)
Other invertebrates	78.31	(53.50)	23.01	(8.34)	34.41	(21.93)
Zooplankton[1]	48.12	(21.64)	15.24	(4.07)	49.20	(12.30)
Zooplankton[2]	471.95	(212.26)	149.45	(39.94)	482.57	(120.91)

[1]Calculated assuming 7.7 m^2 net mouth, full 10-foot IKMT mouth.
[2]Calculated assuming 0.785 m^2 net mouth, cod end mouth area.

abundant groups are comprised of small individuals (Figure 3a). Biomass estimates for zooplankton in deep tows ranged from about 10 to 100% of the total micronekton, depending on which mouth area was used for calculation (Table 5).

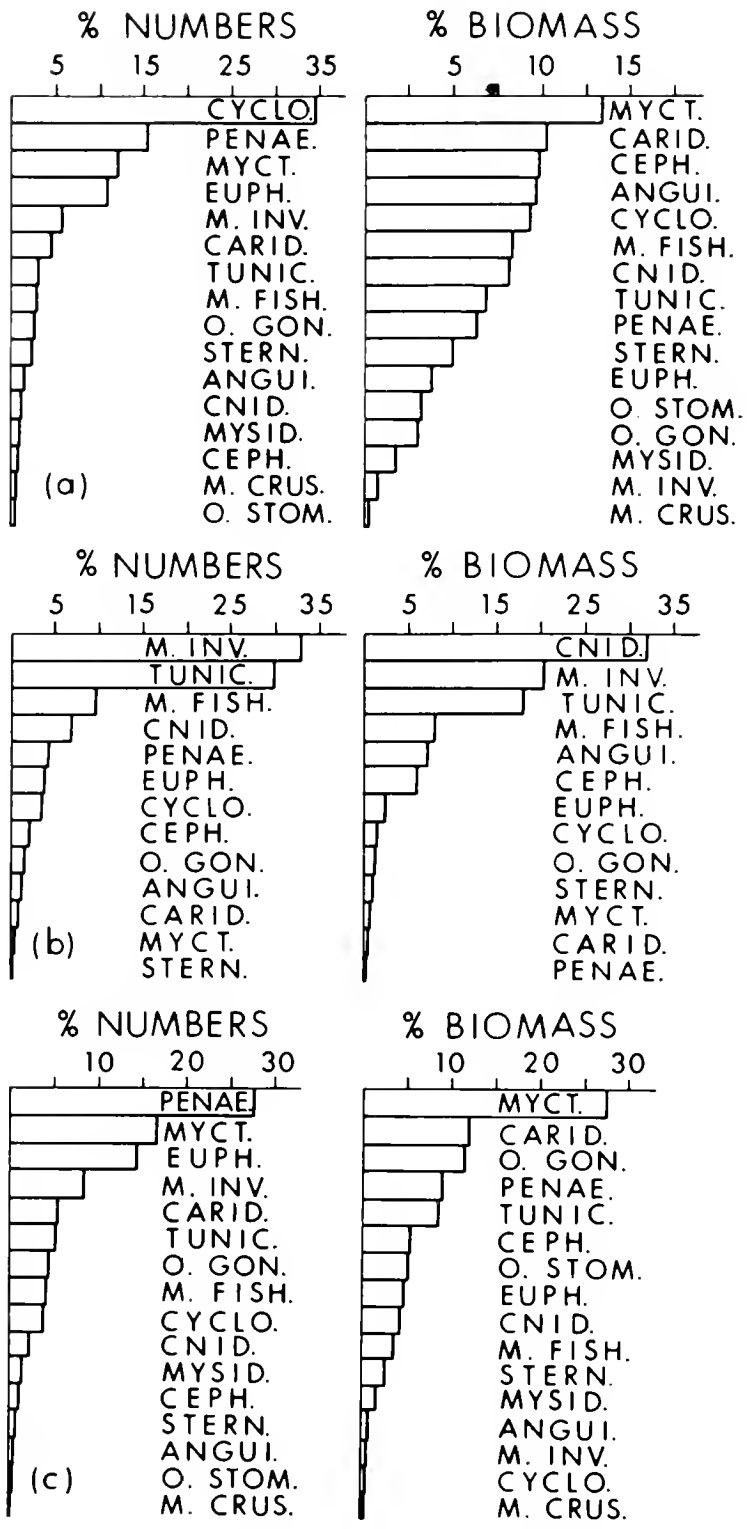

FIGURE 3.—Mean faunal composition by group as percent of total micronekton standing stock, number of organisms and wet-weight biomass. a. Deep-tows, 0-1,200 m. b. Shallow-day tows, 0-400 m. c. Shallow-night tows, 0-400 m. ANGUI. = Anguilliformes, CARID. = Caridea, CEPH. = Cephalopoda, CNID. = Cnidaria, CYCLO. = *Cyclothone*, EUPH. = Euphausiacea, M. CRUS. = Miscellaneous Crustacea, M. FISH. = Miscellaneous fishes, M. INV. = Miscellaneous invertebrates, MYCT. = Myctophidae, MYSID. = Mysidacea, O. GON. = Other Gonostomatidae, O. STOM. = Other Stomiatoidei, PENAE. = Penaeidea, STERN. = Sternoptychidae, TUNIC. = Tunicata.

The small euphausiids (<1 cm) which were sorted into the zooplankton group constituted 3.9 g wet weight and 831 individuals/100 m^2 ocean surface

for one deep tow (no. 183). This is about nine times the mean abundance of micronektonic euphausiids, but only one-fifth of the mean euphausiid biomass.

To establish a rough index of the contribution of neritic and meroplanktonic animals to the pelagic catch for future comparison, the standing stock of stomatopod larvae (otherwise included in the zooplankton group (Table 5)) was compared to the total micronekton stock (Table 6). The stomatopod concentration is large relative to shallow-day micronekton catches but quite small with respect to shallow-night and especially to deep-tow catches.

TABLE 6.—Mean standing stock of stomatopod larvae expressed as percent of total micronekton standing stock per 100 m^2 of ocean surface, number of organisms and wet-weight biomass.

Item	Day 0-1,200 m	Day 0-400 m	Night 0-400 m
Number (%)	4.3	58.3	11.4
Biomass (%)	0.6	12.9	2.9

Diel Vertical Migration

Because there were no significant differences between standing stock estimates of deep-day and deep-night tows, we concluded that any trawl avoidance was not due to diel factors and that increased shallow-night catches were primarily the result of vertical migration. Thus, the amount of vertically migrating micronekton was the difference between the shallow-day stock and the shallow-night stock (Tables 4, 5, 7). The percent migrating was then computed by dividing the amount migrating by the amount of micronekton deeper than 400 m during the day (deep-tow standing stock minus shallow-day stock). Percentages larger than 100 are considered sampling artifacts.

Of the total micronekton which resided deeper than 400 m during the day, 43% of the individuals with 47% of the biomass migrated into the upper 400 m at night (Table 7). This dramatic diel change in the catch rates of shallow tows is illustrated in Figures 4 and 5. The most numerous migrators were crustaceans, but most of the biomass was fishes. Between day and night tows the difference in composition of the 0- to 400-m layer of fauna is quite pronounced (Figure 3b, c).

The average weight per organism in each group for the 0- to 1,200-m deep water column was computed by dividing the mean group biomass in Table 5 by the mean number of organisms in the group shown in Table 4. The results are presented in Table 8 along with computations of the average biomass of individual migrators and non-migrators, based on the data in Table 7 and assuming that the non-migrator standing stock was the

TABLE 7.—Mean standing stock of vertically migrating micronekton, grams wet-weight biomass and number of organisms per 100 m^2 of ocean surface between 0 and 1,200 m, groups ranked by biomass and abundance. Percent migrating represents the portion of the group residing deeper than 400 m during the day which migrated into the 0- to 400-m layer at night.

Biomass				Abundance	
Group	g / 100 m^2	% migr.	Group	No./ 100 m^2	% migr.
Myctophidae	69.66	106	Penaeidea	126.07	96
Caridea	30.12	60	Myctophidae	79.70	74
Other Gonostomatidae	28.83	199	Euphausiacea	62.22	68
Penaeidea	22.58	72	Caridea	25.82	67
Tunicata	15.78	56	Other Gonostomatidae	18.88	84
Other Stomiatoidei	13.36	86	Cyclothone	13.41	4
Cephalopoda	11.82	25	Mysidacea	8.73	88
Euphausiacea	11.42	65	Misc. fishes	4.77	43
Sternoptychidae	7.06	29	Sternoptychidae	3.94	17
Misc. fishes	6.81	18	Other Stomiatoidei	2.68	68
Mysidacea	4.42	50	Cephalopoda	2.35	49
Misc. Crustacea	1.09	100	Misc. Crustacea	1.88	46
Cnidaria	0.84	3	Anguilliformes	0.32	4
Cyclothone	0.74	2	Cnidaria	[1]	
Misc. invertebrates	[1]		Misc. invertebrates	[1]	
Anguilliformes	[1]		Tunicata	[1]	
Total fishes	125.59	50	Total Crustacea	224.72	82
Total Crustacea	69.63	64	Total fishes	123.70	26
Cephalopoda	11.82	25	Cephalopoda	2.35	49
Other invertebrates	11.40	21	Other invertebrates	[1]	
Total micronekton	218.43	47	Total micronekton	311.67	43

[1] 0-400-m day stock > 0-400-m night stock.

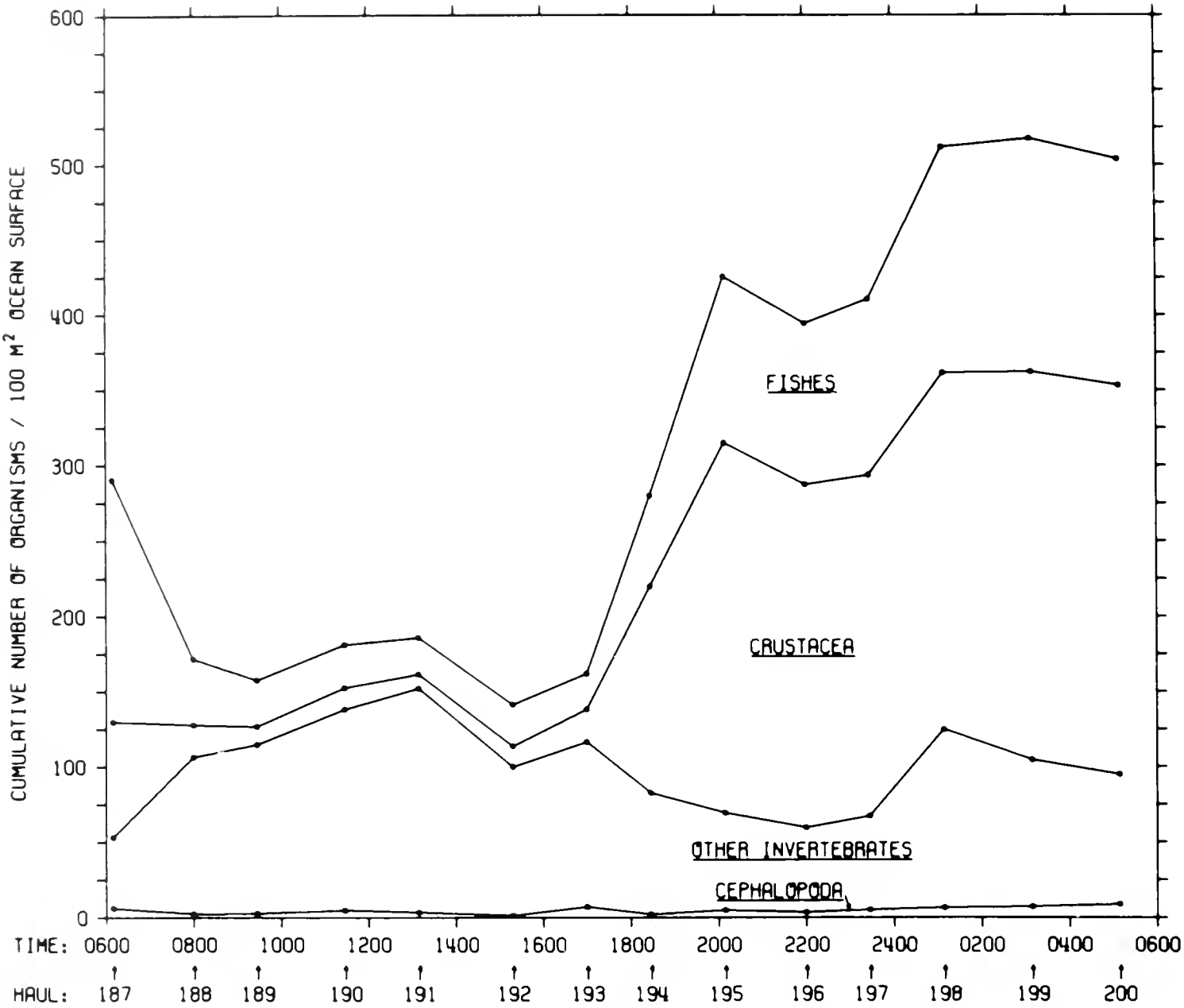

FIGURE 4.—Shallow-tow (0-400 m) standing stock of micronekton abundance over 24 h. Time is plotted for midpoint of each tow.

difference between the deep-tow stock and the migrator stock. In general, the average weight per migrating fish is greater than the weight of the non-migrators, while the opposite holds for the crustaceans and cephalopods, that is, the smaller-sized members of the groups migrate.

The occurrence of organisms larger than 10 g (wet weight) per individual was highly variable both with respect to abundance and biomass (Table 9). None occurred in the groups of *Cyclothone*, Sternoptychidae, Penaeidea, Euphausiacea, miscellaneous Crustacea, or miscellaneous invertebrates. The only large organism in shallow-day tows was one tunicate. In deep tows, large animals were less than 1% of the number of total micronekton but 30% of the biomass. With respect to biomass, about one-quarter of the total fishes, one-eighth of the total crustacea, four-fifths of the Cephalopoda and one-half of the other invertebrates were made up of individuals larger than 10 g each. In shallow-night tows these proportions are smaller for all groups except other invertebrates which is about the same.

DISCUSSION

Restrictions

The interpretation of our data must be considered with several restrictions. Larger, highly mobile micronekton, especially fishes and cephalopods, probably avoid or escape the trawl (Pearcy and Laurs 1966; M. R. Clarke 1969; T. A. Clarke 1973, 1974) resulting in underestimation of

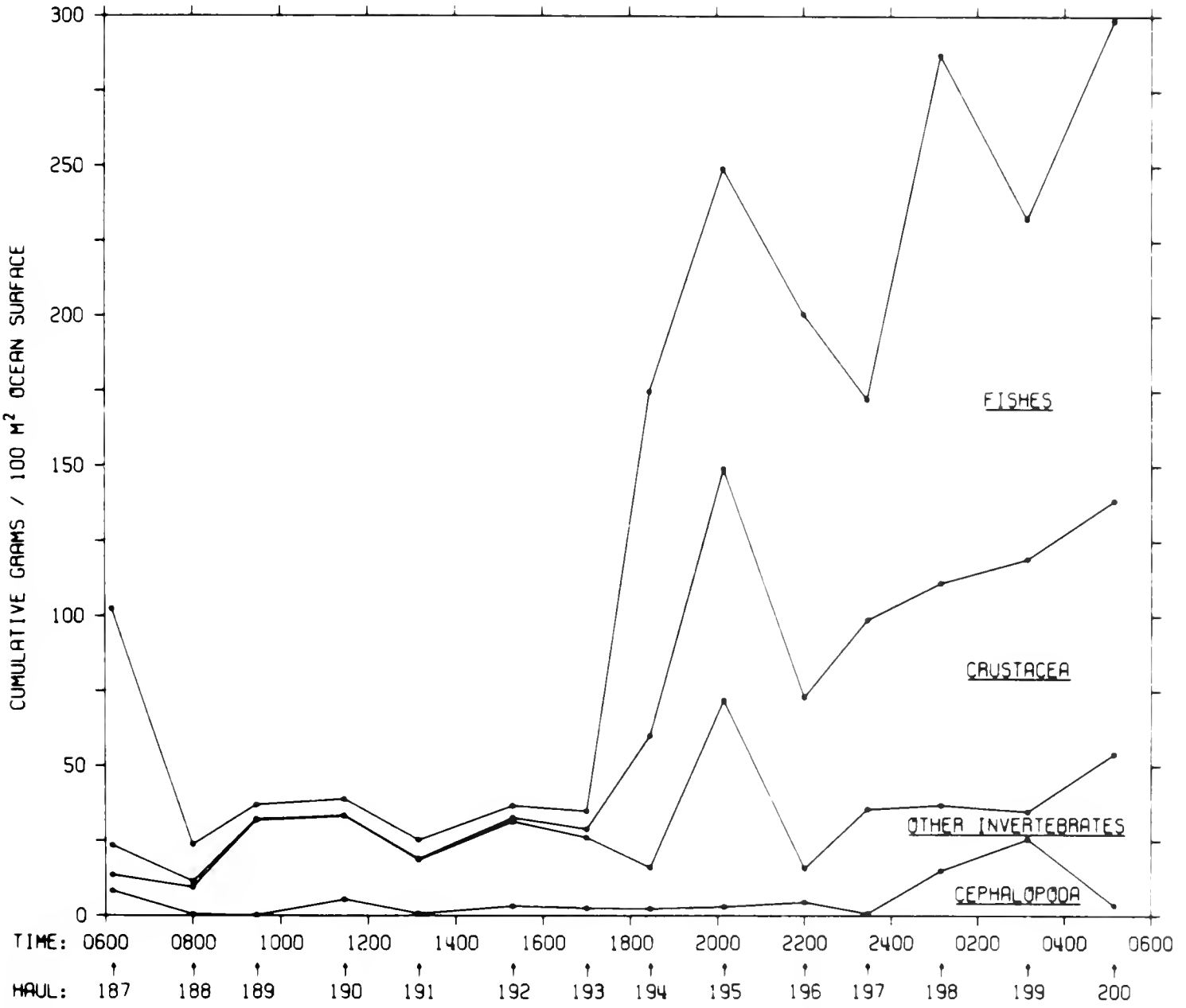

FIGURE 5.—Shallow-tow (0-400 m) standing stock of micronekton biomass (wet weight) over 24 h. Time is plotted for midpoint of each tow.

the numbers and especially biomass. In addition, pooling species into the 16 groups of Table 3 sometimes lumps vertical migrators with non-migrators, and primary carnivores with higher predators, blurring a precise ecological definition for a group. We feel, however, that our groups are adequate for a first overview of the micronekton fauna off Hawaii.

Our data may not represent standing stocks characteristic of the open ocean, and the possibility of an island effect should be considered. Oahu affects surface circulation up to 1,500 km downstream (Barkley 1971), but effects on plankton and micronekton standing stocks are not clear. An island mass effect has been observed off Oahu for phytoplankton (Gilmartin and Revelante 1974). King and Hida (1954, 1957a, b) found little correlation between distance from Oahu and zooplankton standing stock, whereas other workers have found a decreasing standing stock with increasing distance from the island (Sette 1955; McGary 1955; Doty and Oguri 1956). Nakamura (1967) could detect no differences in mean zooplankton standing stock between windward and leeward Oahu samples, but windward samples consistently contained more decapods. We are not certain what island effects, if any, influence the leeward Oahu micronekton other than the occasional occurrence of some larvae of reef and benthic animals (e.g., stomatopods, crabs, fishes) which fall into the size range of micronekton as defined here.

Temporal fluctuations in micronekton standing stock pose an important caveat in evaluating our

TABLE 8.—Mean biomass per animal, grams wet weight, for the 0- to 1,200-m water column, vertical migrators (Table 7), and non-migrators (animals residing deeper than 400 m at night).

Group	0-1,200 m	Migrators	Non-migrators
Myctophidae	0.61	0.87	[1]
Cyclothone	0.15	0.06	0.16
Other Gonostomatidae	0.58	1.53	[1]
Sternoptychidae	1.09	1.79	0.95
Other Stomiatoidei	3.97	4.99	1.77
Anguilliformes	4.22	[2]	[2]
Misc. fishes	1.50	1.43	2.12
Caridea	1.26	1.17	1.42
Penaeidea	0.23	0.18	0.76
Euphausiacea	0.19	0.18	0.20
Mysidacea	0.89	0.51	3.77
Misc. Crustacea	0.27	0.58	[1]
Cephalopoda	5.77	5.03	6.06
Tunicata	1.21	[2]	[2]
Cnidaria	[3]	[3]	[3]
Misc. invertebrates	0.06	[2]	[2]
Total micronekton	0.55	0.70	0.47
Total fishes	0.51	1.01	0.34
Total Crustacea	0.38	0.31	0.63
Other invertebrates	[2, 3]	[2, 3]	[2, 3]

[1]0- to 400-m night stock minus 0- to 400-m day stock ≥0- to 1,200-m stock.
[2]0- to 400-m day stock >0- to 400-m night stock.
[3]Siphonophores were not enumerated.

single-cruise data. In other parts of the world, investigators have reported seasonal biomass fluctuations of two- to sevenfold for some micronekton groups (Legand 1969; Blackburn et al. 1970; Tranter 1973), and abundance fluctuations of some species up to fifteen- to fortyfold (Pearcy 1964; Legand et al. 1970). Previous work in Hawaiian waters has demonstrated temporal variability in primary productivity (Gordon 1971:1132), epipelagic zooplankton standing stock (Nakamura 1967; Shomura and Nakamura 1969), and such mesopelagic micronekton as myctophids (T. A. Clarke 1973) and stomiatoids (T. A. Clarke 1974). The limited data available suggest at least twofold temporal fluctuations in micronekton standing stocks might be expected in Hawaiian waters. At this time we cannot predict seasonal oscillations in standing stock. Thus, until better seasonal data are available, our reported standing stock and faunal composition values should only tentatively be considered characteristic for Hawaii.

Standing Stock

On the basis of fish distributions, Amesbury (1975) has definied the 400- to 1,200-m depth range off Hawaii as the mesopelagic zone. Very few animals have been taken deeper than 1,200 m in opening-closing tows. Thus, standing stock values determined from our deep tows are probably reliable estimates for the micronekton of the whole water column except near-bottom waters.

In spite of the shortcomings, the data add considerably to our knowledge of micronekton especially because we sampled nearly the whole depth range of the fauna, used a fully lined net with small mesh, towed at a relatively high speed, sampled when the moon had a minimal effect on avoidance (cf. T. A. Clarke 1973), took several sample replicates, monitored sampling volume and depth, and determined standing stocks for all components of the catch. The general lack of diel-related avoidance agrees with the findings of T. A. Clarke (1973) and Atsatt and Seapy (1974) but is in contrast to the results of Pearcy and Laurs (1966).

TABLE 9.—Mean standing stock of micronekton larger than 10 g (wet weight)/individual, by group. *a*. No. organisms/100 m² ocean surface. *b*. Grams biomass/100 m² ocean surface. Standard deviation in parentheses.

a. Number. Group	0-1,200 m	Day 0-400 m	Night 0-400 m
Myctophidae	0.08 (0.22)	0.00	0.10 (0.26)
Other Gonostomatidae	0.15 (0.28)	0.00	0.38 (0.55)
Other Stomiatoidei	0.31 (0.36)	0.00	0.18 (0.32)
Anguilliformes	0.81 (0.83)	0.00	0.00
Misc. fishes	0.56 (0.88)	0.00	0.00
Caridea	0.53 (0.56)	0.00	0.09 (0.25)
Mysidacea	0.22 (0.49)	0.00	0.00
Cephalopoda	0.54 (0.47)	0.00	0.27 (0.51)
Tunicata	0.83 (1.57)	0.10 (0.23)	0.54 (0.45)
Cnidaria	0.52 (1.16)	0.00	0.18 (0.49)
Total micronekton	4.62 (2.27)	0.10 (0.23)	1.76 (0.65)
Total fishes	1.97 (1.21)	0.00	0.67 (0.41)
Total Crustacea	0.76 (2.76)	0.00	0.09 (0.25)
Cephalopoda	0.54 (0.47)	0.00	0.27 (0.51)
Other invertebrates	1.35 (1.74)	0.10 (0.23)	0.73 (0.77)
No. organisms	61	1	19
No. tows	9	6	7

b. Biomass, grams/100 m². Group	0-1,200 m	Day 0-400 m	Night 0-400 m
Myctophidae	1.08 (3.25)	0.00	1.06 (2.82)
Other Gonostomatidae	2.99 (6.41)	0.00	13.24 (20.52)
Other Stomiatoidei	9.38 (11.25)	0.00	7.77 (16.46)
Anguilliformes	26.60 (36.06)	0.00	0.00
Misc. fishes	19.25 (37.84)	0.00	0.00
Caridea	10.93 (12.41)	0.00	1.14 (3.01)
Mysidacea	3.06 (6.71)	0.00	0.00
Cephalopoda	40.03 (49.24)	0.00	8.15 (15.80)
Tunicata	26.28 (12.95)	1.39 (11.54)	15.29 (14.92)
Cnidaria	14.58 (35.30)	0.00	2.69 (7.11)
Total micronekton	153.98 (54.80)	1.39 (11.54)	49.34 (14.81)
Total fishes	59.31 (58.50)	0.00	22.08 (20.18)
Total Crustacea	13.77 (17.36)	0.00	1.14 (3.01)
Cephalopoda	40.03 (49.24)	0.00	8.15 (15.80)
Other invertebrates	40.86 (44.70)	1.39 (11.54)	17.98 (18.57)

We searched the literature for data to compare the standing stock and composition of micronekton off Hawaii with that of other regions. Few studies provided data from more than one sampling period; each used different gear and techniques, and all are subject to most of the restrictions cited previously. We feel that meaningful regional comparisons are premature until data on the temporal variability of the fauna are available from samples covering the entire depth range of the fauna.

Diel Vertical Migration

About one-half of the total micronekton wet-weight biomass in our study area appeared to migrate from day-depths greater than 400 m to night-depths shallower than 400 m. During the day, about 90% of the mean total micronekton standing stock biomass lived deeper than 400 m (Tables 5, 7). Because most vertically migrating fishes have a lower water content than non-migrators (Childress and Nygaard 1973) the percent of total micronekton dry weight which migrates would be even higher. The same probably holds for cephalopods. If migrators have shorter life spans and higher metabolic rates than non-migrators (cf. Childress and Nygaard 1973; T. A. Clarke 1973; Meek and Childress 1973), then the percent of the annual micronekton production represented by migrating animals would be especially high.

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DESCRIPTION AND BIOLOGY OF A NEW SPECIES OF PELAGIC PENAEID SHRIMP, *BENTHEOGENNEMA BURKENROADI*, FROM THE NORTHEASTERN PACIFIC[1]

EARL E. KRYGIER[2] AND ROBERT A. WASMER[3]

ABSTRACT

The new species of pelagic penaeid shrimp lacks the richly plumose arthrobranch described for the genus and has a single pair of terminal spines on the telson. It is found mainly in transitional water of the North Pacific between 500 and 1,000 m by day and 150 and 1,000 m at night. Examination of testes and ovaries, and the structures of the petasma and thelycum, indicates a 4-5 mo spawning season and an equal male to female sex ratio. Generation time was estimated to be 2 yr.

This paper describes the systematics and biology of a new species of pelagic penaeid shrimp of the genus *Bentheogennema*. Since 1961, studies of the fauna and ecology of the mesopelagic waters off the coast of Oregon have been conducted by members of the School of Oceanography, Oregon State University. Several unusual species of macrurous decapod Crustacea have been obtained. The discovery and identification of this new species of *Bentheogennema* was by Carl Forss, who entrusted his material to the authors. Subsequent sampling with mid-water trawls has provided detailed information on the distribution and biologyof this shrimp, as well as abundant material for taxonomic description.

METHODS AND MATERIALS

Material for the zoogeographic distribution was collected in Isaacs-Kidd Mid-water Trawls (IKMT) from the research vessels *Yaquina*, *Endeavor*, *John R. Manning*, and *Hugh M. Smith* in the northeastern Pacific, normally within 320 m of the surface (Wasmer 1972). Information on vertical distribution, reproductive biology, and growth of this species was obtained from samples taken on five cruises aboard RV *Yaquina* at a single sampling station 65 nautical miles (120 km) off the central Oregon coast (NH 65–lat. 44°35′N, long. 125°25′W) in 1972-73. Samples at this station were taken both day and night, using an 8-foot IKMT with a five net opening-closing cod end section similar to the one described by Pearcy and Mesecar (1971).

All samples were preserved at sea in 10% buffered Formalin.[4] The samples were later sorted, identified, sexed when possible, and measured. Carapace length (measured from the postorbital margin to the median posterior edge of the carapace) was used as an indication of size. All figures were drawn with the aid of a camera lucida.

In males, sexual maturity was based on three characteristics: 1) petasmata joined; 2) well-developed accessory lobe on anterior surface of the petasma; 3) and dilated vas deferens with large terminal ampoule (indicative of developed spermatophore) at the base of the fifth pereiopod. The combined characteristics of fully developed thelycum and the posterior lateral lobe of the ovary swollen with eggs at the base of the fifth pereiopod were used as signs of sexual maturity in females. Estimates of growth are presented from analysis of length-frequency data.

Section Penaeidea
Family Penaeidae Bate
Subfamily Aristaeinae Alcock
Series Benthesicymae Bouvier
Bentheogennema burkenroadi n. sp.

Types.—Holotype (USNM 150835), male, carapace length (c.l.) 18 mm, from Station lat.

[1]Research supported by the Office of Naval Research (Contract N000-14-67-A-0369-0007 under project NR 083-102) and the Atomic Energy Commission (Contract AT[45-1] 2227, Task Agreement 12). Publication number RL0-2227-T12-51.

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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51°26′N and long. 138°28′W, Mid-water Trawl No. 857 (MT 857); Allotype (USNM 150836), female, 14.5 mm c.l., station Newport Hydrographic Line 65 nautical miles (120 km) offshore (NH 65), MT 2130; Paratypes: 1 male (USNM 150837), 15 mm c.l., from NH 265, MT604; 2 males (USNM 150838), 8 and 6.5 mm c.l., NH 65, MT 2088; 1 male (USNM 150839), 14 mm c.l., NH 65, MT 2131; 1 male (USNM 150840), 13.5 mm c.l., NH 65, MT 2130; 4 females (USNM 150841), 14.5, 14, 10, 18 mm c.l., NH 65, MT 2130; 4 males (USNM 150842), 12.5 13.0, 13.2, 17.5 mm c.l., NH 65, MT 2130; 1 male (USNM 150843), 9.0 mm c.l., NH 50, MT 570; 1 male (USNM 150844), 9.5 mm c.l., lat. 40°28′, long. 133°46′, MT 613; 3 females (USNM 150845), 13.3, 14.0, 15 mm c.l., NH 65, MT 2121 Net #5; 1 female (USNM 150846), 20.0 mm c.l., NH 65, MT 2133 Net #1; 2 females (USNM 150847), 7 and 10 mm c.l., NH 65, MT 2070 Net #5; 2 males, 1 female (BMNH 1975:10), 14.2, 16.4, 13.2 mm c.l., NH 65, MT 2175 Net #5; 1 female (BMNH 1975:10), 15.7 mm c.l., NH 65, MT 2178 Net #4; 1 female (BMNH 1975:10), 12.6 mm c.l., NH 65, MT 2302 Net #4; 1 male (BMNH 1975:10), 11.5 mm c.l., NH 65, MT 2301 Net #1. Other, nonparatype, material deposited at Los Angeles County Museum; Fisheries Research Board of Canada Biological Station, Nanaimo, British Columbia; and School of Oceanography, Oregon State University, Corvallis, Oreg.

Diagnosis.—Benthesicymae with podobranch on second maxilliped to third pereiopod inclusive; first maxilliped with single rudimentary arthrobranch; only sixth abdominal somite with middorsal carina; telson distally truncate, usually with single pair of mobile terminal lateral spinules. Accessory lobe of petasma characterized by large upturned terminal hook. Plate of thelycum on sixth thoracic sternite triangular and elevated, projecting ventrally in strong ridge; plate on eighth thoracic sternite pentagonal with anteriormost angle concave and anterolateral margins bearing spines.

Description.—Rostrum extending to level of eye tubercle, well elevated above middorsal carina of carapace (Figure 1). Margin between rostral tip (apex) and dorsal spine with usual setal fringe (although broken in type). Middorsal carina of carapace bearing minute tubercle posterior to

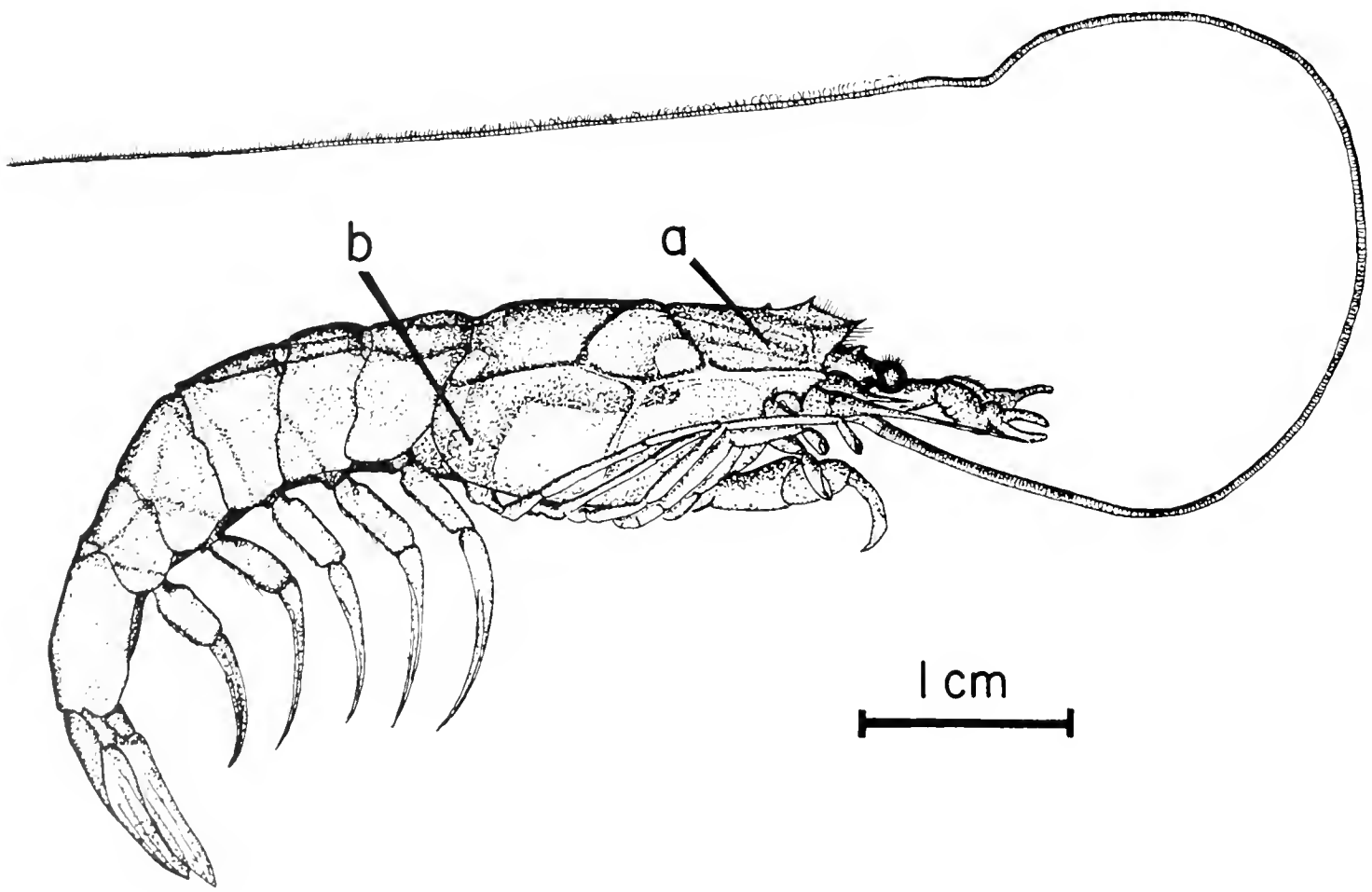

FIGURE 1.—Mature female *Bentheogennema burkenroadi* n. sp. illustrating the (a) anterior and (b) posterolateral lobes of the ovary.

dorsal spine; carina absent between well-defined cervical and postercervical sulci and on posteriormost portion of the carapace. Mid-lateral longitudinal carina consisting of strong antennal carina continuous with hepatic and branchial carinae. Branchiostegal spine small and branchiostegal carina distinct; hepatic sulci continuous from branchiostegal spine towards lower margin of carapace; post-hepatic carina orientated dorsoventrally from longitudinal hepatic carina toward inferior margin of carapace. Antennal angle obtuse and infra-antennal angle acute (Figure 2a).

Only sixth abdominal somite with middorsal carina; second through fifth abdominal somites with weak lateral ridges in approximately dorsoventral position extending from mid-lateral to ventrolateral edge of the pleuron. Fourth, fifth, and sixth abdominal somites with prominent, roughly transversal, lateral ridges which together form "half moon" area (Figure 1). Fourth and fifth abdominal somites bearing small mid-lateral tooth on posterior margins.

Antennal flagellum (Figure 1) similar to *Gennadas* (Foxton 1969), having proximal and distal sections divided by short series of annuli forming kink in flagellum; proximal section rigid, bearing scattered short nonplumose setae; distal section bearing paired arched plumose setae with small plumose setae perpendicular to flagellum at irregular intervals between bases of some arched pairs. Second element of antennular peduncle, along dorsal midline, 0.7 ultimate element (Figure 2b). Antennal scale (Figure 2c) little less than 3 times as long as greatest width; distinct spine (outer margin of scale), slightly convex, terminal end free, not extending beyond narrow apex of blade.

Mandible (Figure 2d) with two segmented palp; palp thickly covered with setae on medial and lateral margins, distal element not quite as long as widest portion of basal element. Endopod of first maxilla (Figure 2e) distally narrow, with tip rounded; proximal gnathobasic lacinia (endite of coxa) subequal in width to distal lacinia (endite of basis), both terminating in strong spines among setae fringe. Anterior lobe of proximal lacinia (endite of coxa) of second maxilla (Figure 2f) strongly constricted behind apex, not broader than posterior lobe of distal lacinia (endite of basis); anterior lobe of distal lacinia very broad; endopod distally long and narrow, with two (sometimes three) curved spines at base of apical portion.

Endopod of first maxilliped (Figure 2g) reaching beyond endite of basis but falling short of exopod; endopod of four elements, third less than twice second; fourth extremely minute; first element bearing usual compliment of three curved spines on distomesial margin. Exopod bladelike, without constricted, segmented distal portion. Merus of second maxilliped (Figure 2h), including anterior prolongation, 1.9 times as long as wide; dactylus with single strong apical spine surrounded by medium and small spines back to proximal end of propodus; merus and carpus with numerous spines and setae; podobranch present. Third maxilliped (Figure 2i) reaching to, or beyond, middle of ultimate joint of antennal peduncle; ischium nearly 3 times as long as greatest width; merus usually twice as long as greatest width; carpus slightly longer than propodus; dactylus with long slender terminal spine; podobranch present.

Merus of first pereiopod (Figure 3a) 1.4 times length of carpus and 1.7 ischium; fingers slightly setose. In second pereiopod (Figure 3b), carpus 1.2 times length of propodus; merus 1.2 carpus and 1.5 propodus; chela with heavy tufts of bristles. Merus and carpus of third pereiopod (Figure 3c) of equal length, each twice ischium; fingers of chela similar to those of second pereiopod. Carpus and propodus of fourth pereiopod nearly equal, each approximating two-thirds of merus which is 2.4 times ischium. Propodus of fifth pereiopod subequal to carpus which is subequal to merus; ischium slightly more than one-third of merus.

Outer scale of appendix masculina (Figure 3d) longer than inner; proximal half of lateral margin expanding slightly then tapering toward base. Inner scale broadly rounded distally; spines on distomesial margin (few to many) long and thin, spines on distal margin smaller, stronger, and of uniform length.

Telson with single pair of mobile terminal-lateral spines (Figure 3e) fringed with setae on terminal and distal two-thirds of lateral margins (of the large number of specimens inspected, only two mature males had any indication of more than one pair of mobile spines (USNM 150839, 150840), each with two pair of mobile spines on terminal edge of telson). No mobile nonterminal-lateral spines present on telson. Lateral margins of lateral rami of uropods (Figure 3f) bearing spine at 0.78 total length. Mesial rami about 0.73 lateral rami.

Each half of petasma (Figure 3g, h), distally divided into three lobes (external, median, and in-

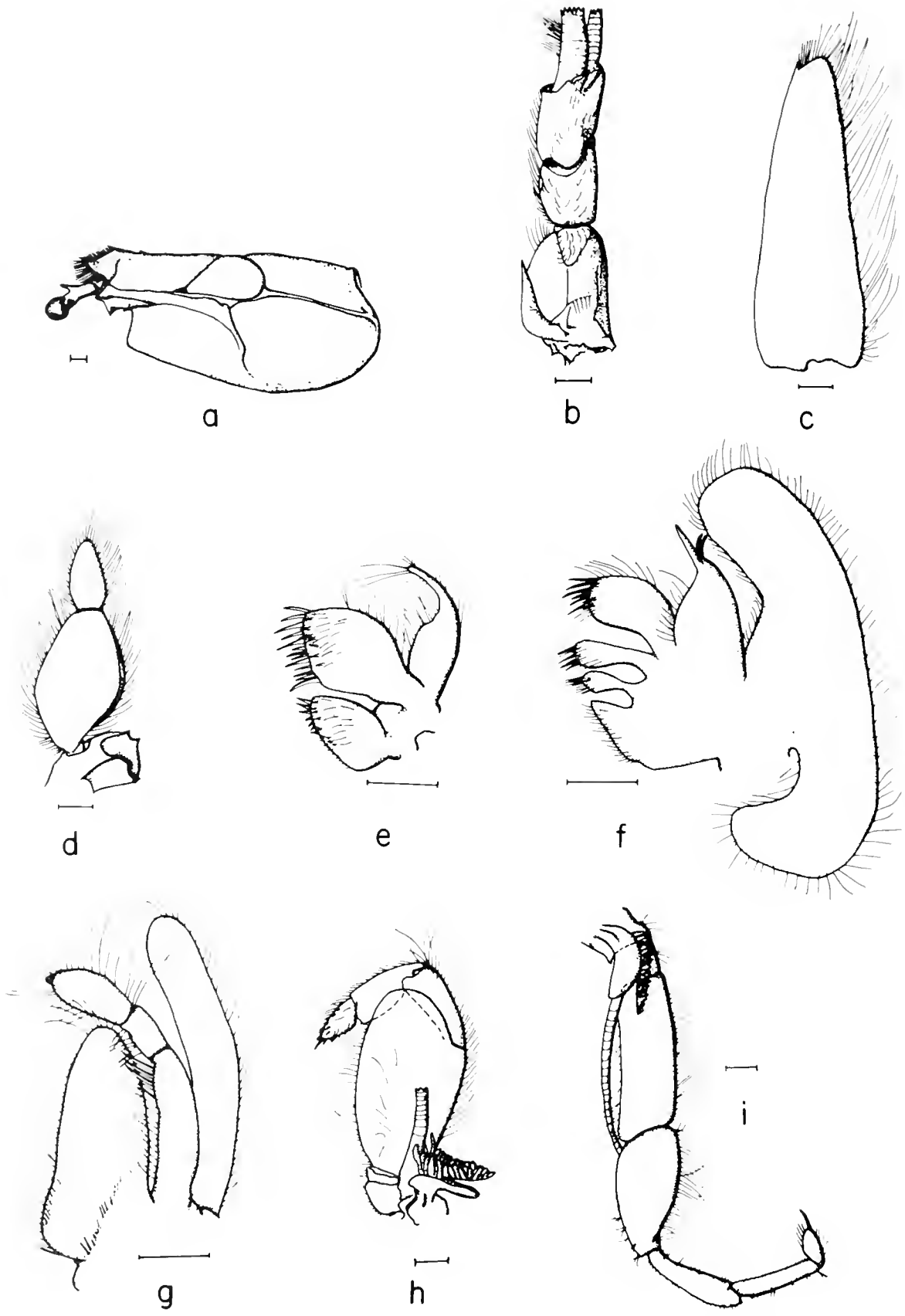

FIGURE 2.—*Bentheogennema burkenroadi* n. sp. (Holotype, male 18 mm carapace length) a, carapace; b, antennular peduncle; c, antennal scale; d, mandible; e, first maxilla; f, second maxilla; g, first maxilliped; h, second maxilliped; i, third maxilliped. Scale equals 1 mm.

ternal (Balss 1927) which are equivalent to Burkenroad's (1936) distoventral, distolateral, and distomedian lobes). External lobe bipartite; lateral part elongate projection with minute terminal teethlike protuberances distally; mesial part curving inward with apex directed toward median lobe. Median lobe broadly rounded; subdistally, accessory lobe on anterior face of petasma, characterized by large upturned terminal hook (Figure 3g) with free margin attaching to base of

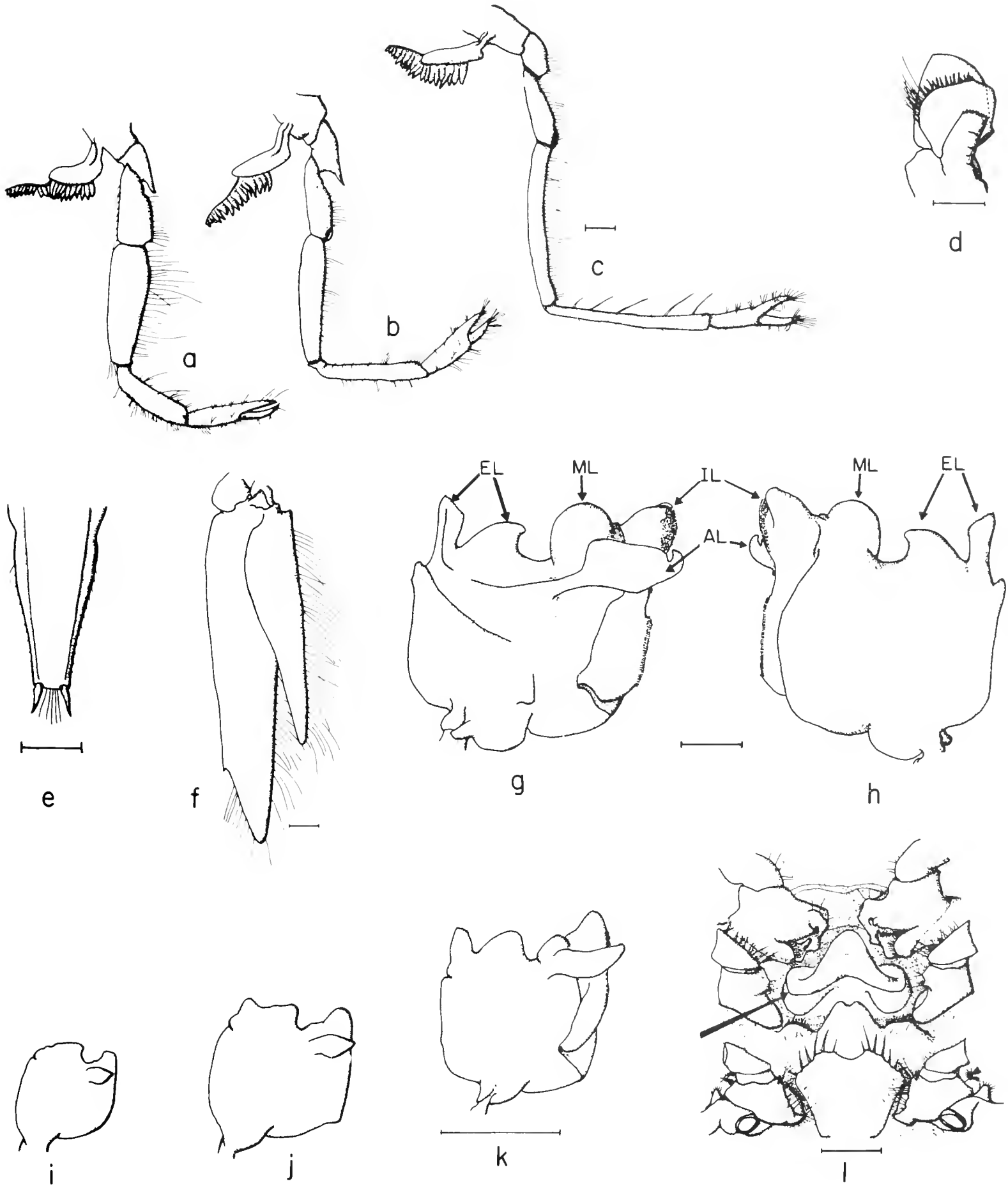

FIGURE 3.—*Bentheogennema burkenroadi* n. sp. (Holotype, male 18 mm carapace length) a, first pereiopod; b, second pereiopod; c, third pereiopod; d, appendix masculina; e, distal half of telson; f, uropod; g, anterior view of petasma (EL = external lobe, ML = median lobe, IL = internal lobe, AL = accessory lobe); h, posterior view of petasma; i, anterior view of petasma from young male (8.0 mm c.l.); j, anterior view of petasma from young male (9.0 mm c.l.); k, anterior view of petasma from young male (9.5 mm c.l.); l, thelycum of female (17 mm c.l.), arrow pointing to right sperm receptacle. Scale equals 1 mm.

median lobe, attachment area distinguishable to level of elongate projection of external lobe. Internal lobe undivided, bearing rigid hooks continuous with row of cincinnuni, holding two halves of petasma together. The accessory lobe develops early in the juvenile stage (Figure 3i, j, k) and together with characteristic spination of telson and presence of podobranchs behind second maxilliped, young of this species were discernable to a size of 6 mm c.l. (the smallest size captured).

Thelycum (Figure 3l) with plate on eighth thoracic sternite pentagonal, with anteriormost angle concave, anterolateral margin bearing long spines (this plate exhibits greatest variation during growth, being more rectangular in young females, changing to the pentagonal shape of maturity but becoming almost bilobed in very large females). Plate of seventh thoracic sternite bearing three anterior directed projections; lateral pair, shortest, bearing short spines; center projection exhibits varying amount of concavity after maturity such that distolateral margins may appear as raised wings. Elevated plate on sixth thoracic sternite triangular and inverted "V" shaped, with apex pointing anteriorly; apex not reaching anterior limit of sternite. Sperm receptacles located toward lateral edges near bases of inverted V.

Coloration at time of capture varying from deep red over entire body to medium red on cephalothorax and lighter on abdomen. Black pigment fleck on distolateral edge of ocular peduncle just below corneal region (Figure 2a). Other small flecks of purple pigmentation often observed on carpus and propodus of third maxilliped and first and second pereiopods, on carpus of third pereiopod, and on ventral surface of abdominal somites just anterior to lateral edge of base of each pleopod.

Remarks.–Burkenroad (1936) proposed the genus *Bentheogennema* for those species of *Gennadas* Bate which possesses podobranchs on the second maxilliped to third pereiopods inclusive. Other generic characters he included were: arthrobranch of first maxilliped large and richly plumose; exopod of first maxilliped without a constricted, segmented distal portion; dorsal carina on sixth abdominal somite only; telson with truncated apex and more than a single pair of mobile lateral spinules.

As is often the case, the addition of a new species changes the generic formula for that group. The new species is similar to *Gennadas* in the armature of the telson but more closely resembles *Bentheogennema* with podobranchs on the second maxilliped through third pereiopod. We agree with Kemp (1909) and Burkenroad (1936) that the presence of podobranchs, a primitive characteristic, is a more important generic trait than the number of pairs of spines on the telson.

We found that the two species of *Bentheogennema*–*B. borealis* (Rathbun) and *B. burkenroadi* n. sp.–from the Oregon coast lack the large, richly plumose arthrobranch on the first maxilliped that Burkenroad (1936) included as a generic characteristic. Both have small rudimentary arthrobranchs similar to *Gennadas*. We assume that Burkenroad (1936) did not have samples of *B. borealis* but included this arthrobranch structure as a generic characteristic from samples of *B. intermedium* (Bate) and *B. pasithea* (Man).

Although Tirmizi (1959) stated that the endopod of the first maxilliped is five-segmented in *Gennadas* and apparently only four-segmented in *Bentheogennema*, we have found that *Gennadas propinquus* Rathbun off the Oregon coast has a four-segmented endopod. Hence these characters are not reliable to distinguish these two genera.

Bentheogennema burkenroadi can be separated from *B. borealis*, *B. intermedium*, *B. pasithea*, and *B. stephenseni* (Burkenroad) by the armature of the telson, and the structures of the petasma and thelycum. The telson of *B. burkenroadi* typically possesses only a single pair of terminal-lateral spines, whereas the other members of this genus possess two or more pairs of lateral spines: *B. borealis* and *B. stephenseni* two pairs; *B. pasithea* three pairs; *B. intermedium* (as described by Tirmizi 1959) four pairs. The number of spines present on the telson should not be held as an invariable characteristic, there is undoubtedly a small percentage of variation as exemplified by the two males of *B. burkenroadi* (USNM 150839, 150840) which possess two pairs of terminal spines. It is possible that one of the two specimens of *Gennadas calmani* (Kemp) (synonymy: *B. borealis*), which Kemp (1909) illustrated with two pairs of terminal spines is also an example of such variation.

The petasma of this new species is unique and easily distinguishable from that of other members of the genus. The combined structures of the accessory lobe with its mode of attachment, its large

size, and its terminal hook (present in mature individuals) and the shape of the bipartate external lobes make identification, even of the juvenile stages (Figure 3g-k), possible.

The thelycum differs from that seen in other species by the pentagonal shape of the plate on the eighth thoracic sternite and the elevated triangular plate on the sixth sternite (Figure 3l).

We have named *B. burkenroadi* after Martin D. Burkenroad, whose work on Crustacea, especially the Penaeidae, is well known.

GEOGRAPHICAL AND VERTICAL DISTRIBUTION

Shrimps were examined from mid-water trawl collections taken over much of the North Pacific (Figure 4). *Bentheogennema burkenroadi* was found only in collections from the northeastern sectors (lat. 52-34°N and east of long. 142°W) (Wasmer 1972). Pearcy and Forss (1966, 1969) observed *B. burkenroadi* off the coast of Oregon, as close as 28 km to the northern end of the coast and occurring ≥92 km off the central and south coast. Wasmer (1972) found the greatest concentration in the Transitional Water Mass (Figure 5), with a few individuals occurring in the Pacific Subarctic and eastern North Pacific Central Water Masses. It is assumed to be a transitional species, although as is the case for many shrimps, it is not totally confined to a single physicochemically definited water mass (Wasmer 1972). Since *B. burkenroadi* is a deep mesopelagic species and most of the available geographical collections were from shallow depths, the known geographic range will undoubtedly be increased by more systematic deep trawls in the eastern Pacific.

This species was captured in opening-closing nets from the surface to 1,000-m depth. It apparently demonstrates a diel vertical migration. The depth distribution is, with few exceptions, below 500 m during the day and below 100 m at night (Table 1). Neither day nor night distributions are confined to a narrow depth stratum but are diffused in concentration over a broad range. The nocturnal migration into the upper waters appears to entail only a small segment of the population with the main concentration remaining at depth. Those migrating above 500 m included both sexes, though the immature shrimp (<11-mm

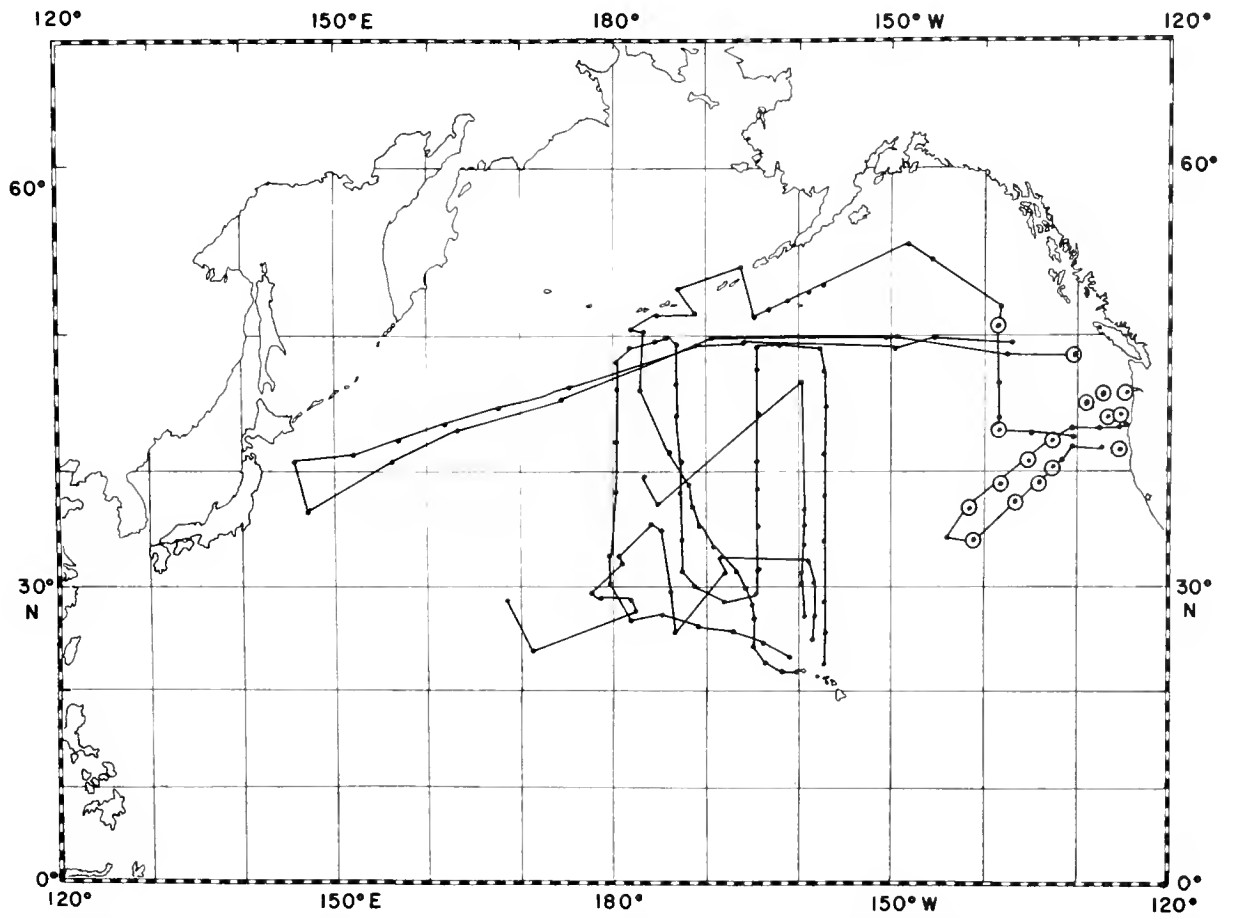

FIGURE 4.—Cruise tracks of the North Pacific from which shrimp were enumerated, indicating mid-water trawl stations (solid dots). *Bentheogennema burkenroadi* n. sp. was collected at stations where dot is encircled.

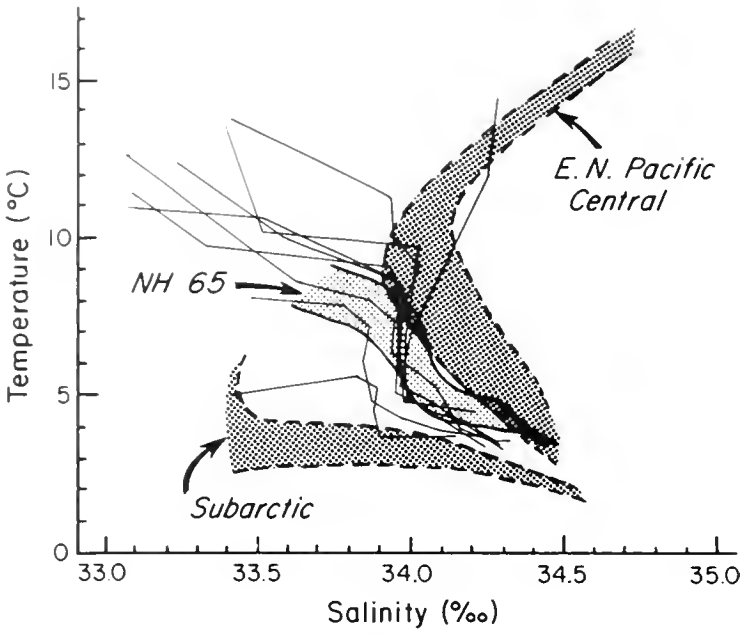

FIGURE 5.—Zoogeographical temperature-salinity (T-S) capture diagram for *Bentheogennema burkenroadi* n. sp. Relevant water masses in darkest bands; medium band in T-S envelope for the station 65 nautical miles off Newport, Oreg. (NH 65); single lines indicate T-S diagram for sampling stations other than NH 65 where this shrimp was captured.

males and <12-mm females) were not observed to migrate as high in the water column as adults. Vinogradov (1968) earlier stated that the intensity of diurnal migration of zooplankters increases with age, and migration may be absent in early stages of development, and our observations concur with this.

More shrimp were caught in nighttime than daytime tows. This may be explained by enhanced visual avoidance of the net during the day (Pearcy and Laurs 1966). However, the lack of obvious differences in size structure between day and night caught shrimp (Figure 6) argues against increased daytime avoidance, as larger more mobile animals should be preferentially sampled at night. Another explanation for the increased nighttime catch, as suggested for *Acanthephyra purpurea* Milne-Edwards and *Gennadas valens* (Smith) by Foxton (1970a, b), is migration up from below our maximum sampling depth of 1,000 m. Such a migration is indicated by the high concentrations between 600 and 1,000 m both day and

TABLE 1.—Seasonal diel vertical distribution to a depth of 1,000 m of mature males (≥11 mm c.l.), mature females (≥12 mm c.l.), and sexually immature male and female *Bentheogennema burkenroadi* at a sampling location 65 nautical miles (120 km) off Newport, Oreg. (lat. 44°35'N—long. 125°30'W).

Time of year	Size group	Depth (m) 0-50	50-100	100-150	150-200	200-300	300-400	400-500	500-600	600-700	700-800	800-900	900-1,000
							DAY						
June 1972	Mature males									3	4	2	2
	Mature females									3	2	3	2
	Immatures								1	5	6	2	2
Sept. 1972	Mature males								1	2	6	4	1
	Mature females								2		8	2	4
	Immatures										2	1	1
Nov. 1972	Mature males			1				1	2	2	4	5	
	Mature females				1				2	3	3		1
	Immatures									1	1		1
Mar. 1973	Mature males										[1]3		
	Mature females										[1]1		
	Immatures						1		1		[1]1		
Total number				1	1		1	1	9	19	41	19	14
Total volume in 1,000 m³		103.5	149.9	103.2	94.7	474.7	497.9	310.9	259.6	132.6	182.3	183.3	162.4
Number/1,000 m³ (day)		0	0	0.0097	0.0106	0	0.0020	0.0032	0.0347	0.1433	0.2249	0.1037	0.0862
							NIGHT						
June 1972	Mature males	1				1	3				1		
	Mature females						1	3		1			
	Immatures						2	2					
Sept. 1972	Mature males	[2]2			1	1	1	4	5	[2]1	2	1	1
	Mature females			1	2		5	2	2		3	1	4
	Immatures						3	1	1	1	5		
Nov. 1972	Mature males					1	5	2		7	3		5
	Mature females				[2]1	4	7	2	1	5	1	1	4
	Immatures					1		1		1	3		1
Mar. 1973	Mature males				3	3	1	1	1	1	1		
	Mature females			1	1	4	2	1	1	2			
	Immatures					2			1	1			
Total number		3		2	8	17	30	19	12	20	19	3	15
Total volume in 1,000 m³		111.8	530.6	184.8	292.8	251.0	435.9	288.6	261.6	147.2	170.7	132.3	129.3
Number/1,000 m³ (night)		0.0268	0	0.0108	0.0273	0.0677	0.0688	0.0658	0.0459	0.1359	0.1113	0.0227	0.1160

[1]Twilight 1 h after sunset.
[2]Twilight 1 h before sunrise.

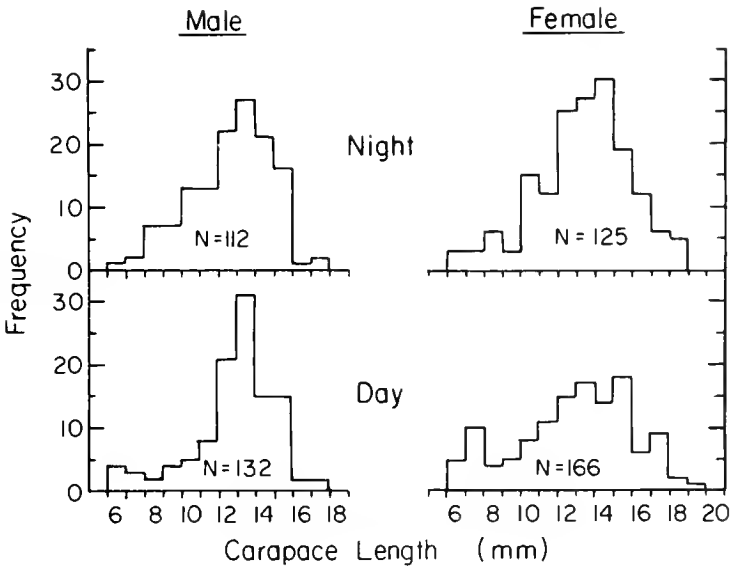

FIGURE 6.—Day and night length-frequency distributions of male and female *Bentheogennema burkenroadi* n. sp.

night with no progressive drop in concentration with increased depth to 1,000 m (Table 1).

The slight upward movement of this species may be related to its morphology. Vinogradov (1968) considers reduced musculature and a thin integument, which we observed in *Bentheogennema burkenroadi*, to be a means of achieving buoyancy. Because of weak swimming musculature, they may swim too slowly to keep pace with the upward movement of the stimulating isolume, resulting in broad day and night distributions (Donaldson 1973).

REPRODUCTION

Since penaeid shrimp do not brood their eggs, a description of the breeding cycle must rely on anatomical changes, especially in the development of the ovary and ova. The female reproductive system consists of a bilaterally symmetrical ovary and paired oviducts internally, and externally of a thelycum. Each half of the mature ovary has an anterior lobe angling from the cervical sulcus and almost reaching the base of the eye, and then folding back along itself (Figure 1a). The anterolateral lobe lies over the hepatopancreas extending approximately one-half the way down the body wall. The posterolateral lobe, of such a mature ovary, will have visible distinct ova, measuring up to 240-288 μm crossectional diameter, and will extend ventrally, making a pouchlike structure at the base of each of the fifth pereiopods (Figure 1b). The posterior lobes extend beneath the dorsal abdominal muscle bands, becoming swollen in the first abdominal segment and then extending on toward the end of the third segment. Females were considered to have reached maturity after attaining a size of 12 mm c.l. and males at a size of 11 mm c.l.

The reproductive cycle, as judged from the sexual condition of the testis and ovary, appears to consist of a 4- to 6-mo spawning season and a 6- to 8-mo resting phase. Based on samples collected in 1972 and 1973, the carapace of females in June is fairly rigid, though the ovaries are not ripe. Some males, from external observation, appear to be ready to release sperm, though most display only partial swelling of the terminal ampoule and vas deferens or lack swelling at all. By fall, females exhibit developing ovaries (two females were in spawning condition), and the carapace is correspondingly rigid. Most males have full, ripe looking testes and dilated terminal ampoules. By the end of November, spawning is in evidence. Most females are mature with readily distinct ova; some mature females have evidently spawned as the thoracic cavity appears empty; the carapace is correspondingly nonrigid, due to the spent ovary which had crowded much of the other organs; others have developing ovaries distended by small diameter ova. All males at this time have ripe testes and dilated terminal ampoules. By February, 50% of all females exhibit signs of spawning activity; the rest have probably spawned because their thoracic cavities appear empty and the carapace nonrigid due to the flaccid ovary. Most males still exhibit ripe testes and enlarged terminal ampoules.

The sex ratio for adult males to females (N = 440), when all tows are included, was: 1:1, 1:1.08, 1:1, 1:1.02, and 1.03:1 for the respective cruises. This approximate 1:1 sex ratio, if it applies to all ages, indicates that there is no selective mortality by sex for this species (Geise 1959).

GROWTH

If spawning occurs from November through February and young (6-7 mm c.l.) enter the population April through June (Figure 7), the intervening egg and larval stages must take 3 to 5 mo. Based on size frequency diagnosis, about 12 additional months are required to reach maturity (11-12 mm c.l.) and another 5 to 6 mo are required before spawning commences Thus the generation time is estimated to be about 2 yr. The largest

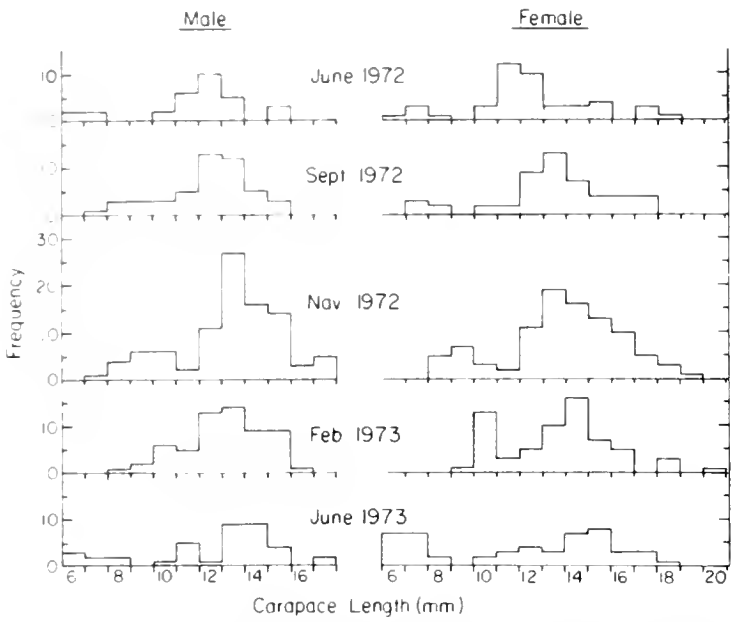

FIGURE 7.—Length-frequency histograms of *Bentheogennema burkenroadi* n. sp., from the five cruises (1972-73) off the Oregon coast.

shrimp captured were a 17-mm c.l. male and a 20-mm c.l. female.

Since the mesh size of the net liner was small enough to retain the young (6-7 mm c.l.) and we assume equal chance of capture of young and adults, then adults apparently live more than a year or two after first spawning because the number of adults captured is greater than the number of immature. In fact, the 12- to 15-mm mode must consist of greater than one age class since by itself it exceeds the juveniles in number. This overlap of age classes at >12 mm c.l. indicates that growth slows after maturity is reached.

ACKNOWLEDGMENTS

We thank R. J. LeBrasseur (Fisheries Research Board of Canada, Nanaimo, B.C. [POG]) and E. C. Jones (Hawaii Area Fishery Research Center in Honolulu [POFI]) for providing us with shrimp specimens collected during their oceanographic exploration. We thank Robert Carney for his aid and instruction in the illustrations, and W. G. Pearcy for his critical review and financial support.

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THE AMERICAN SAMOA LONGLINE FISHERY, 1966-71

HOWARD O. YOSHIDA[1]

ABSTRACT

Aspects of the longline fishery based at American Samoa covering the period from 1966 to 1971 are described. The fishery is discussed primarily as it relates to the albacore, *Thunnus alalunga*, and to a small extent the yellowfin tuna, *T. albacares*. The landings of albacore fluctuated between 17,722 and 28,310 metric tons from 1966 to 1971. Although no downward trend was evident in the relation between total landings and total effort, the relation between CPUE (catch per unit of effort) and effort showed a definite downward trend. Generally, fishing effort was confined to the north of lat. 20°S in the first and fourth quarters. In the second and third quarters large amounts of effort were also expended south of lat. 20°S. The length-frequency distribution of albacore showed that albacore sizes were stratified by latitude. North of lat. 20°S the size of albacore was rather uniform, in that only a single mode was evident in the length-frequency distributions. South of lat. 20°S two or more modes were evident.

The Honolulu Laboratory of NMFS (National Marine Fisheries Service) has been involved in assessing and monitoring the fisheries resources and developing the high seas fishing industry of the territories and island possessions of the United States in the Pacific Ocean. Part of this work included an investigation of the longline fishery based in American Samoa, which resulted in a report describing the history of the fishery and the distribution, apparent abundance, and size composition of albacore, *Thunnus alalunga*, landed from 1954 to 1965 (Otsu and Sumida 1968). The present report describes the status of the American Samoa longline fishery from 1966 to 1971; it is timely because the fishery has changed considerably since 1965, particularly with regard to the apparent abundance of albacore. Data published by Otsu and Sumida will also be used, especially where they are useful in illustrating certain continuing trends.

The earlier report included a rationale for confining the study to the albacore, the principal species of tuna taken in the fishery. The data were reliable only with respect to albacore because the catches of the other species were often not sold in their entirety to the canneries and, therefore, were not included in the catch reports by the vessel operators. However, as will be discussed later, the vessel operators have expended a considerable amount of effort to catch yellowfin tuna, *T. albacares*, in recent years. It is believed that most of the yellowfin tuna are now included in the catch reports and this species has become an important factor in the American Samoa longline fishery, and can no longer be ignored.

The tuna canneries, operated by Star-Kist Samoa, Inc. and the Van Camp Sea Food Company, depend entirely upon deliveries made by foreign flag vessels and fishermen. One of the most notable changes in the fishery over the years has been in terms of vessel nationality. The fishery began in 1954 with seven Japanese vessels. Vessels from Korea entered the fishery in 1958, and from the Republic of China (Taiwan) in 1964. The Japanese continued to increase their participation until 1963, but thereafter began a gradual withdrawal. On the other hand, the vessels from Korea and Taiwan greatly increased in number until the fleet reached a peak in 1967. Due largely to the withdrawal of the Japanese, the fleet has decreased since 1967. During the last quarter of 1971 there were 209 vessels in the fleet, consisting of 4 from Japan, 90 from Korea, and 115 from Taiwan.

SOURCES OF DATA

The data in this report were obtained through the operation of a field station in American Samoa, established in 1963, and manned continuously through December 1970 by personnel from NMFS, Honolulu. In January 1971 the field station was taken over by the Office of Marine Resources, Government of American Samoa. In the begining, the length, weight, and sex of 50 albacore, randomly chosen, were obtained from each trip landing. For various reasons, e.g.,

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changes in cannery operating procedures, changes in the sampling procedures were necessitated in subsequent years. The collection of sex and weight data was discontinued in early 1971. Catch and effort data have been provided voluntarily by the fishing vessel operators from about 75% of the fishing trips.

The longliners on some occasions fish widely scattered areas on a single fishing voyage. Since there is no way to determine the origin of each fish in the catch and because the fish are sampled at random at the docks, it is probable that some samples included fish from several different locations. This problem was minimized by summarizing the length data by large geographical areas.

ANNUAL LANDINGS OF ALBACORE AND YELLOWFIN TUNA

Except for dips in 1961 and 1964, the albacore landings increased steadily from 1954 to 1965 (Otsu and Sumida 1968). In the 6 yr that followed, the landings fluctuated between 17,722 and 28,310 metric tons (Table 1).

The gain in importance of yellowfin tuna can be seen in the increased landings in the later years (Table 1). After a period (1954 to 1964) of reported landings of less than 2,500 metric tons, the reported landings increased substantially and fluctuated between 4,514 and 8,567 metric tons from 1965 to 1971.

TABLE 1.–Total annual albacore and yellowfin tuna landings in American Samoa, 1954-71.

Year	Landings (metric tons)	
	Albacore	Yellowfin tuna
1954	338	597
1955	1,760	1,628
1956	3,680	2,113
1957	5,873	1,537
1958	9,869	2,458
1959	10,292	1,780
1960	10,852	1,134
1961	9,740	1,331
1962	13,326	1,406
1963	13,972	2,057
1964	10,652	2,452
1965	15,591	4,514
1966	25,278	6,531
1967	28,310	5,326
1968	17,722	7,337
1969	18,767	8,207
1970	23,875	7,689
1971	22,193	8,567

APPARENT ABUNDANCE OF ALBACORE AND YELLOWFIN TUNA

Otsu and Sumida (1968) used various indices of apparent abundance in discussing the status of the fishery for albacore during 1954 to 1965. These indices included catch per trip, catch per day, and catch per 100 hooks. However, because data on number of hooks fished per day were not available for the entire period of their study, they elected to use the fishing trip as the basic measure of effort in analyzing the apparent abundance of albacore. They also examined the relation between catch and effort, and CPUE (catch per unit of effort) and effort, in evaluating the effect of fishing on the stock.

Ideally, in considering the mean annual CPUE as an index of apparent abundance, the fishery should affect all portions of the stock(s) under consideration equally throughout the years. However, since the geographical limits of the fishery have been expanding each year, the situation is almost certainly not ideal. In this section I will extend some of the analyses of Otsu and Sumida to determine if any changes have occurred in the apparent abundance of albacore from 1966 to 1971. Since there are now 9 yr of effort data in terms of the number of hooks fished, I will make greater use of the catch per 100 hooks to determine the apparent abundance of albacore. It is assumed that fishing efficiency is not influenced by the nationality of the vessels, for Skillman (1975) found no evidence to suggest that any gear modification or change in the nationality of the fleet has caused any change in the catchability coefficient of albacore in the Samoan fishery.

Apparent Abundance of Albacore

Otsu and Sumida (1968) analyzed the mean annual CPUE of albacore from 1954 to 1965 in terms of the catch per trip. They believed that the catch per trip was a satisfactory measure of apparent abundance because their analysis showed a close relationship between the monthly average catch per trip and the monthly average catch per day. However, there are some basic shortcomings in the catch per trip. One is that the catch per trip of any vessel is limited by its fish-holding capacity. Also, as indicated by Otsu and Sumida (1968), the catch per trip is influenced by changes in the number of days fished per trip and by changes in the size composition of the vessels in the fleet. Changes in the number of hooks fished per day can also affect

the catch per trip. The data do indeed show that the mean number of days fished per trip has increased during recent years (Table 2). The increase in the mean number of days fished per trip may also, in part, indicate change in the size of the vessels. That is, larger vessels, which presumably have larger fish-holding capacities, probably fish more days to obtain a full load of fish.

TABLE 2.–Total trip length, days spent fishing, and traveling time per trip by longline vessels based at American Samoa.

Year	Mean number of days		
	Total trip length	Fishing time per trip	Traveling time per trip
1963	42.35	26.12	16.23
1964	41.26	27.39	13.87
1965	48.79	32.09	16.60
1966	50.58	33.74	17.05
1967	62.13	38.03	23.50
1968	68.02	43.20	24.82
1969	67.34	44.25	23.08
1970	70.74	45.03	25.72
1971	84.16	52.03	32.13

In their analysis of the apparent abundance of albacore from 1954 to 1965, Otsu and Sumida (1968) indicated that the mean catch per trip increased from 1954 through 1960 and then fell slightly and stabilized at a lower level in 1963-64. A continuation of this analysis (Figure 1) showed that the mean catch per trip continued to fluctuate around this lower level with no definite upward or downward trend. It is possible that the mean catch per trip is fluctuating near the mean fish-holding capacity of the vessels or near a level that is related to the profitability of the fishing trip. That is, a vessel may fish as many days as are needed to obtain a full load or until a catch that is at least profitable is obtained. The trip, as an index of effort, does not take this factor into consideration, and, therefore, the catch per trip is not an accurate indicator of the apparent abundance.

It would be useful then, to compare the catch per trip with the catch per day, which is not affected by as many variables as the catch per trip. The mean annual catch per trip from 1959 to 1971 fluctuated between 29.9 and 38.2 metric tons (Figure 2) and, as noted earlier, did not reveal any obvious trends. The mean annual catch per day during the same period fluctuated between 0.7 and 1.7 metric tons, and, contrary to the catch per trip, declined after 1962 suggesting that the longline vessels are fishing more days to compensate for the reduced catch per day. The mean total length of a fishing

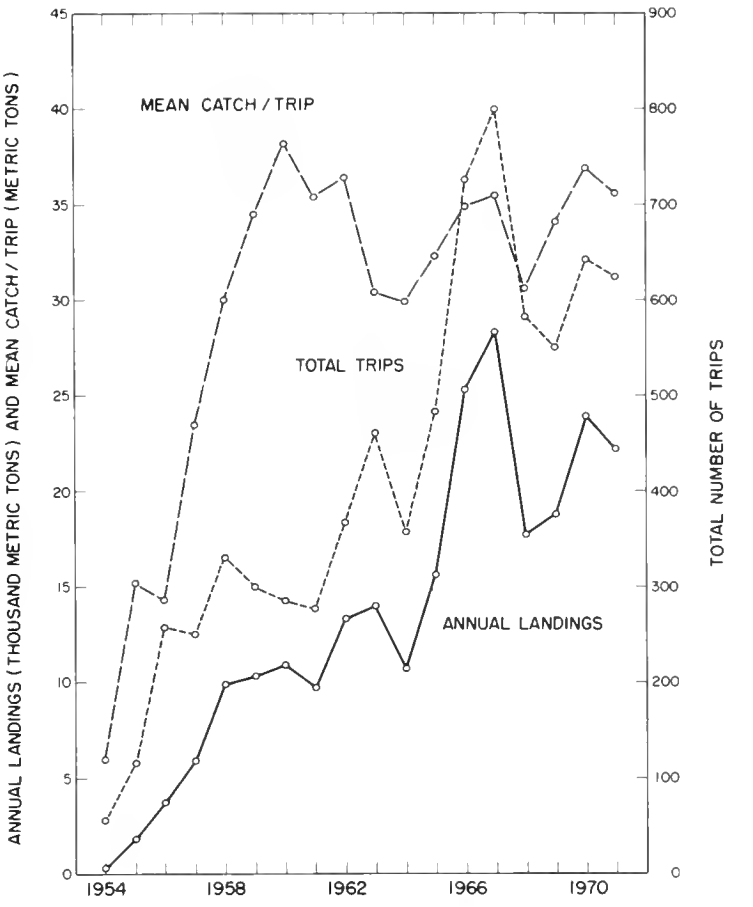

FIGURE 1.–Total number of fishing trips, mean catch of albacore per trip, and annual albacore landings, 1954-71.

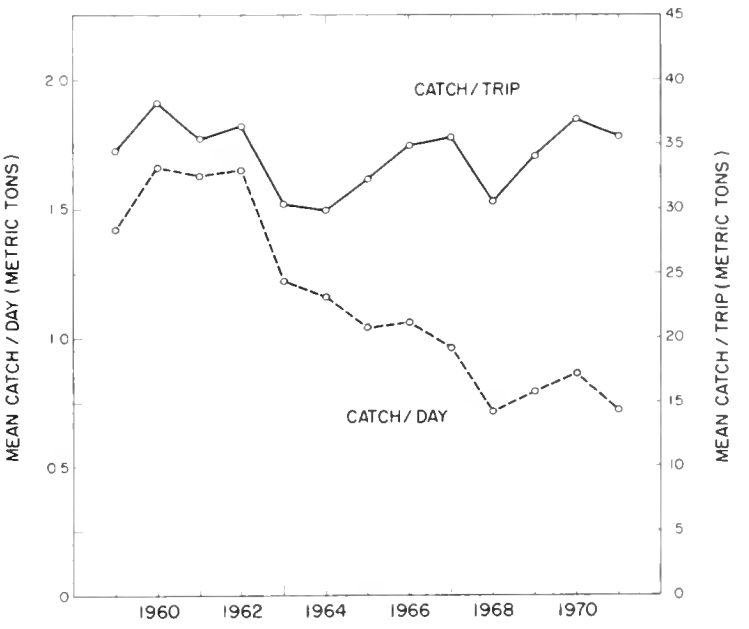

FIGURE 2.–Comparison of the mean catch per day and mean catch per trip of albacore, 1959-71.

trip, number of days spent fishing, and number of days spent traveling on each trip (Table 2) all showed an increasing trend from 1963 to 1971, which indicates that, in general, the vessels are traveling farther away from the home base to fish and are fishing more days per trip.

The relation between the annual total landings of albacore and the total fishing effort (number of fishing trips) indicated that the annual landings increased with increasing fishing effort from 1954 to 1965. Based on this analysis, Otsu and Sumida (1968) concluded that the point of maximum yield of albacore had not been reached in the American Samoa-based fishery. The fishing effort continued to increase subsequent to 1965, and reached a peak of close to 800 fishing trips in 1967. The albacore landings also continued to increase with the increased effort. The relation between the annual landings and the effort, in total number of days fished, from 1959 to 1967 also showed that the landings increased with increasing fishing effort (Figure 3). The mean catch per day plotted against effort in total number of days fished, however, shows a decline in the CPUE from 1959 to 1971 with increasing effort (Figure 4).

As noted earlier, our laboratory has been obtaining, from the vessel operators, effort data in terms of number of hooks fished since 1963. Using these data, the mean monthly catch per 100 hooks of albacore from 1963 to 1971 was computed (Figure 5). A salient feature of Figure 5 is that the mean monthly CPUE fluctuated much more from 1966 to 1971 than they did from 1963 to 1965. It is not clear what caused this change in trends in the monthly CPUE after 1965. One possibility is that it is related to a geographical change in fishing effort. As will be discussed in more detail in another section, in the years after 1965 more fishing effort has been expended in latitudes south of lat.20°S where good CPUE's of albacore are obtained in the second and third quarters of the year. This fact could also account for the definite peak in abundance of albacore in June or July during 1966 to 1971. It is also evident, however, that there is a slightly declining trend in the CPUE from 1963 to 1971.

A plot of the total annual catch of albacore against the estimated total annual effort in number of hooks fished from 1963 to 1971 is shown in Figure 6. During this period the estimated total effort ranged from about 13,165,000 to 51,092,000 hooks and the annual albacore catch from 10,652 to 28,310 metric tons. With some minor exceptions, there was a strong positive relation between the annual catch and effort for the 1963-71 period. Generally, the catches increased with increased fishing effort. Suda (1971) also found a similar relationship between albacore catch and fishing effort in the South Pacific from 1952 to 1968.

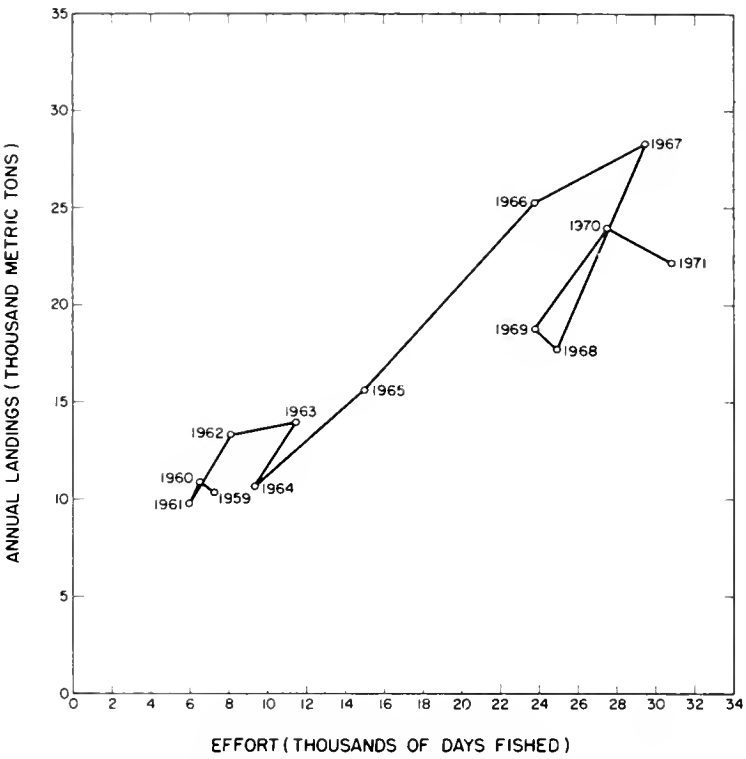

FIGURE 3.—Relation between annual landings of albacore and effort.

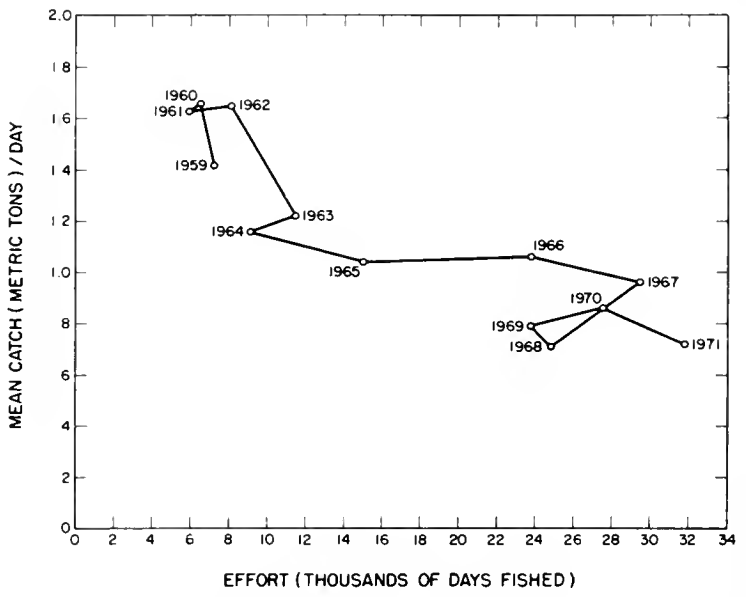

FIGURE 4.—Relation between mean catch of albacore per day and effort.

In Figure 7 is plotted the CPUE in number of fish and in weight per 100 hooks fished against the estimated total annual number of hooks fished from 1963 to 1971. Both plots show a negative relation between CPUE and effort; the CPUE decreased with increased fishing effort. Thus, although the catch has been increasing with increasing effort, it appears that the fishery has had some effect on the stock size in that the CPUE has been declining with increasing effort.

The analyses above reflect average conditions of

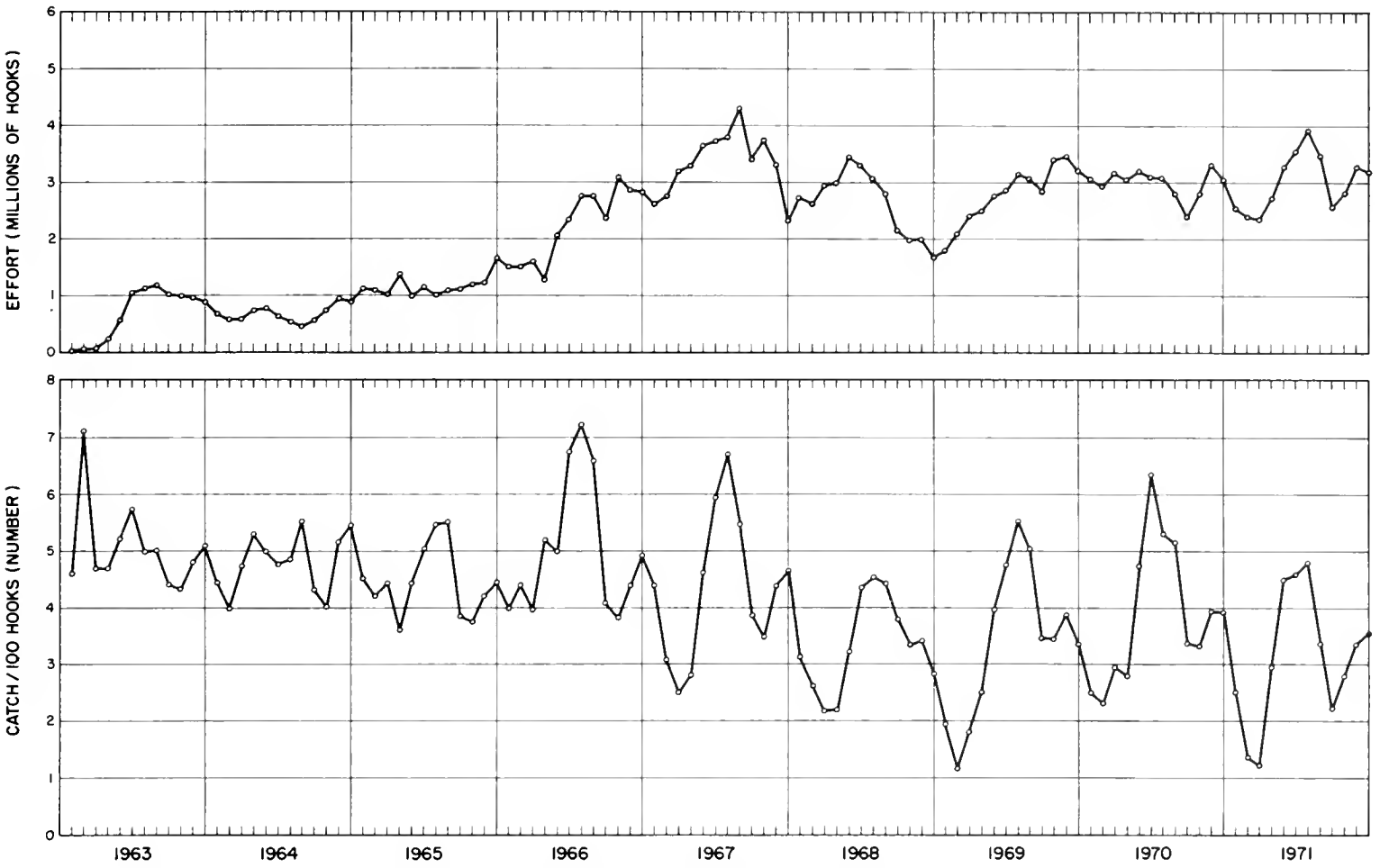

FIGURE 5.—Monthly mean albacore CPUE and effort, 1963-71.

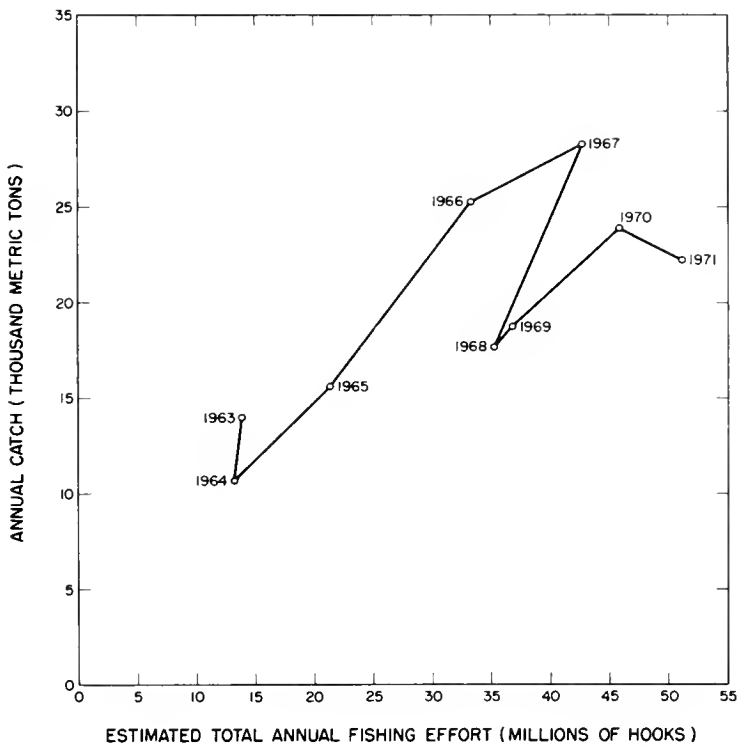

FIGURE 6.—Relation between total catch of albacore and total effort, 1963-71.

the fishery taken as a whole. It is of interest to compare the conditions north and south of lat. 20°S, especially since the geographic boundaries of the fishery have been expanding over the years. That is, it would be useful to see how the CPUE in the older fishing grounds north of lat. 20°S compares with that in the more recently exploited grounds south of lat. 20°S. The annual mean CPUE was computed for the area north of lat. 20°S, which represents the older fishing ground, and the area south of lat. 20°S, which represents the newer grounds (Figure 8). This analysis must be viewed with some caution, however, since total effort expended south of lat. 20°S is less than that expended in the north. Southern waters are fished heavily only in certain quarters of the year and these are the quarters when good catch rates are obtained. The mean catch rates in the southern waters therefore, may be overly weighted by the catch rates obtained in these quarters. However, the mean annual CPUE is higher in the newer grounds than in the old. The mean annual CPUE's

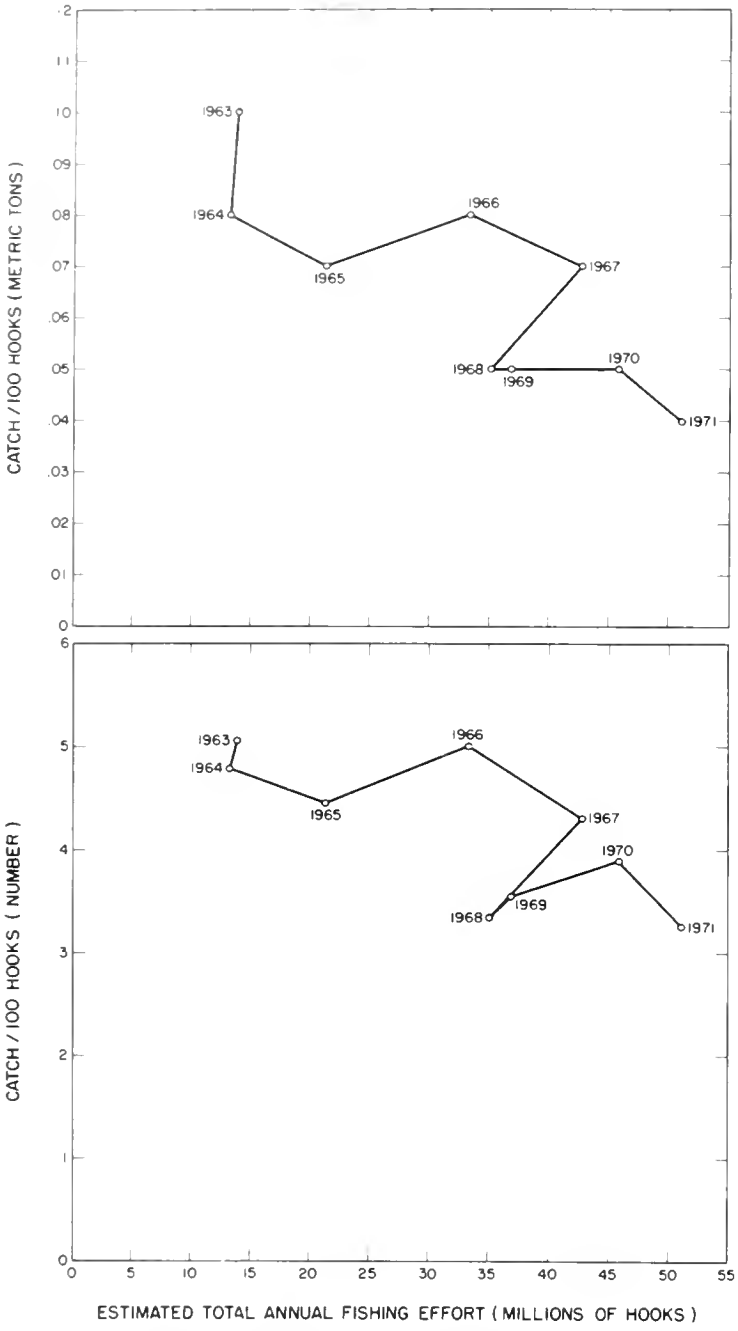

FIGURE 7.–Relation between CPUE of albacore in weight and numbers and total effort, 1963-71.

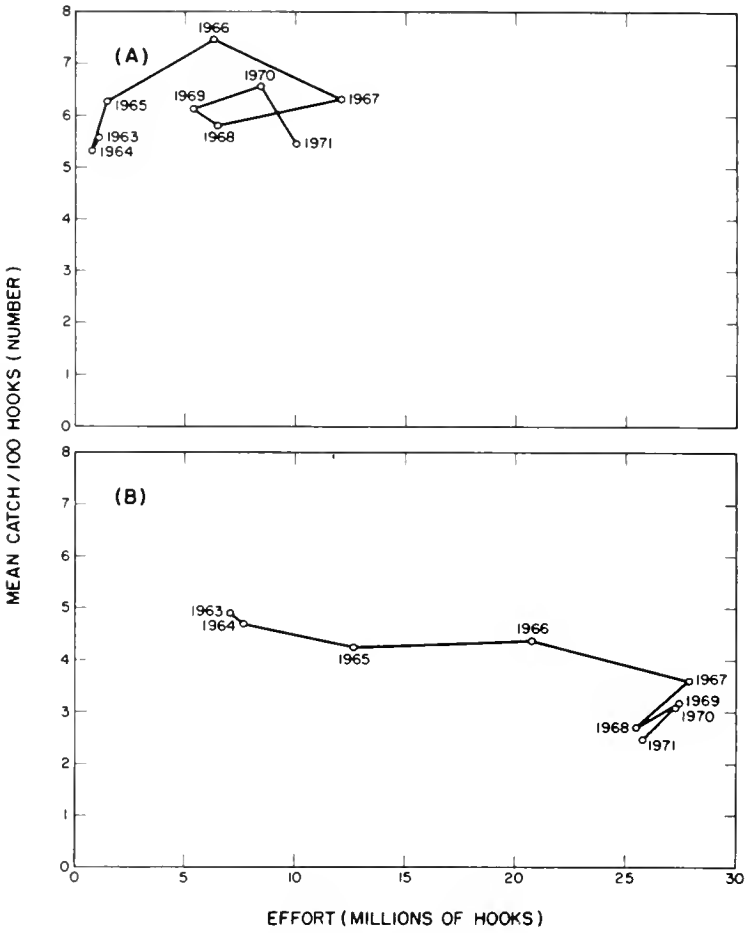

FIGURE 8.–Relation between CPUE of albacore and effort in areas south (A) of lat. 20°S and north (B) of lat. 20°S.

from 1963 to 1971 in the old grounds were all less than five albacore per 100 hooks, whereas in the new grounds they were all greater than five per 100 hooks during the same period. Another difference is that in the old grounds the mean CPUE has been declining with increasing effort. In the new grounds the CPUE increased with increasing effort from 1963 to 1966. In 1967, the CPUE declined slightly and from that year to 1971 the CPUE appears to have stabilized around six albacore per 100 hooks. These facts suggest that the albacore fishery has been able to maintain itself by continuously expanding geographically to take advantage of better CPUE in newer areas. It should be repeated here, however, that despite the expansion into new fishing grounds the overall trend for the fishery has been a decline in CPUE (Figure 5). Furthermore, in the southern grounds to which the fishery has expanded, the albacore catches, as will be shown in a later section, are composed of a large proportion of smaller fish. These smaller albacore may not be the optimum size at which to harvest the stock.

Apparent Abundance of Yellowfin Tuna

The discussion of the apparent abundance of yellowfin tuna will be primarily in terms of how it relates to the apparent abundance of albacore in the Samoan longline fishery. For one thing, although albacore are selectively fished for by the fleet, yellowfin tuna (and small numbers of other species) are also caught by the longlines, and the CPUE for one species may affect the CPUE of another (Rothschild 1967). The CPUE for one species may affect that for another species because, in computing the CPUE, the total effort expended was applied to the catch of each species without regard to the competition of the species

for space on the gear. Furthermore, there is another complicating variable: the fishermen apparently seek out yellowfin tuna when the catches of albacore are poor. They do this by modifying the longlines to fish shallower and by fishing closer to the equator where yellowfin tuna catches are known to be better. The fact that the price of yellowfin tuna increased from an average of $270 a ton in 1965 to $394 a ton in 1970 may also have been a factor.

As noted earlier, the CPUE of albacore in relation to increased fishing effort has been declining, especially in the years subsequent to 1967. During 1968 to 1971, the yellowfin tuna CPUE was relatively good. It is apparent that as albacore fishing deteriorated, the vessels expended more effort to catch yellowfin tuna. The relation between albacore and yellowfin tuna CPUE in the Samoan longline fishery from 1963 to 1971 is shown in Figure 9. It appears that an inverse relation existed between albacore and yellowfin tuna CPUE: When yellowfin tuna CPUE was high, albacore CPUE was low, and vice versa. The correlation coefficient (r = -0.6636; df = 7), however, was not significant.

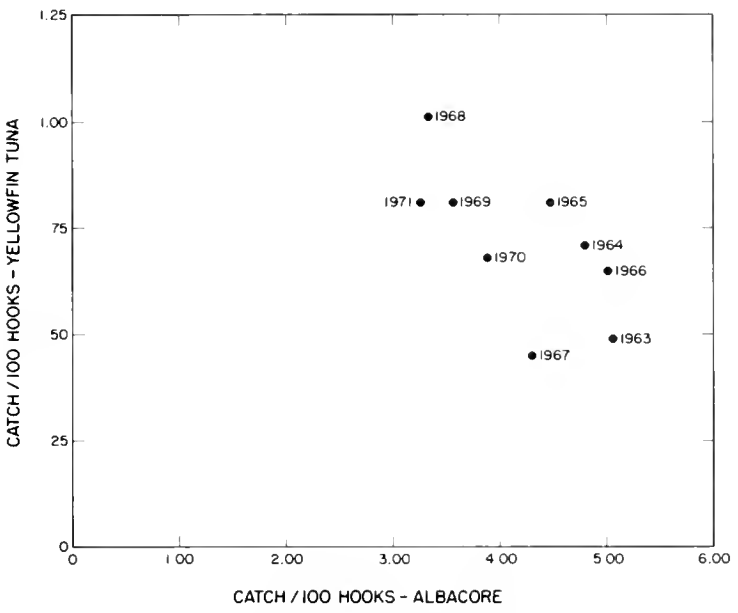

FIGURE 9.—Relation between albacore and yellowfin tuna CPUE.

SPATIAL AND TEMPORAL CONSIDERATIONS

Observations on the American Samoa fishery during the period from 1954 to 1965 indicated that the longline vessels shifted fishing grounds with season (Otsu and Sumida 1968). Seasonal and geographical differences in CPUE, however, were not readily apparent in the early years. In the following sections I will examine the spatial and temporal distribution of effort and CPUE in the fishery from 1966 through 1971.

Effort

In the early years of the fishery, the longliners confined their fishing largely to the vicinity of the Samoa Islands. Over the years, the vessels gradually extended their operations to more distant waters, and by 1965 the fishing grounds reached from about long. 175°E to about long. 120°W between the equator and lat. 30°S (Otsu and Sumida 1968). From 1966 to 1971 there was a further extension of the fishing grounds; the vessels fished from off the east coast of Australia to long. 100°W and from about lat. 10°N to about lat. 40°S. The fishing effort, however, was not uniformly distributed throughout the geographical limits of the fishery. Rather, there were distinct seasonal patterns in the spatial distribution of fishing effort.

A composite geographic distribution of the fishing effort on a quarterly basis for 1966 to 1971 summarized by 2° squares between the equator and lat. 40°S and east of long. 150°E is shown in Figure 10. As composite charts they can reflect only "average" conditions.

In the first and fourth quarters, the vessels generally fished to the north of lat. 20°S, and areas of concentrated fishing effort developed in about the same area each year. In the second and third quarters, the vessels expanded their operations to the south of lat. 20°S and, in addition to the usual area of concentrated effort to the north, an area of high fishing effort also developed to the south of lat. 20°S. However, there apparently has been a change from earlier years in the operations of the fleet because prior to 1966 the vessels fished in the north during both the first and second quarters (Otsu and Sumida 1968). These figures indicate that the vessels are moving south in the second quarter, earlier than previously. In any event, these seasonal changes in the concentration of fishing effort have been interpreted to reflect the movement of albacore in the South Pacific Ocean (Suzuki 1961; Otsu and Sumida 1968).

Catch Per Unit of Effort

The mean quarterly CPUE for 1966-71 plotted by 2° square areas is shown in Figure 11. In a

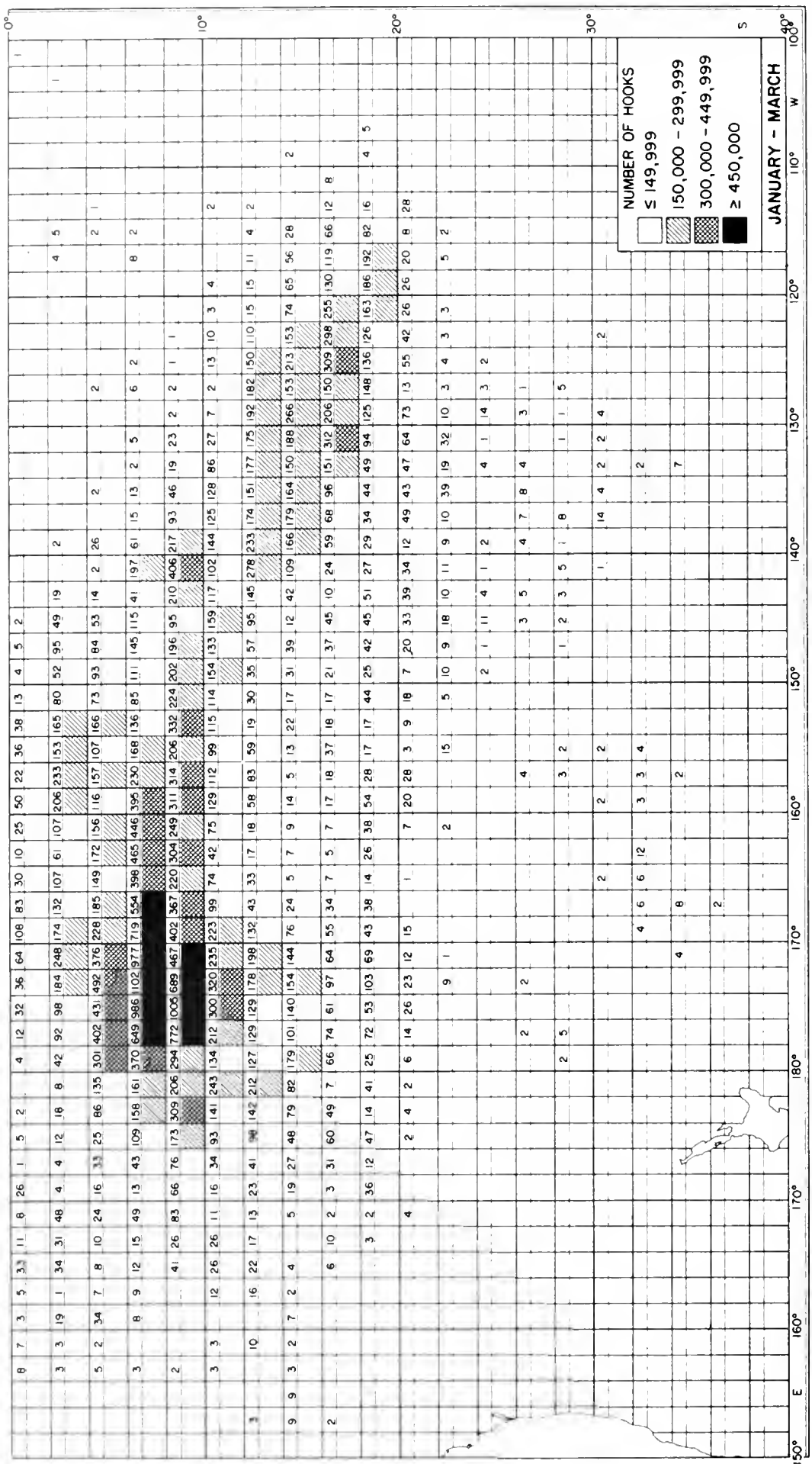

FIGURE 10.–Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.

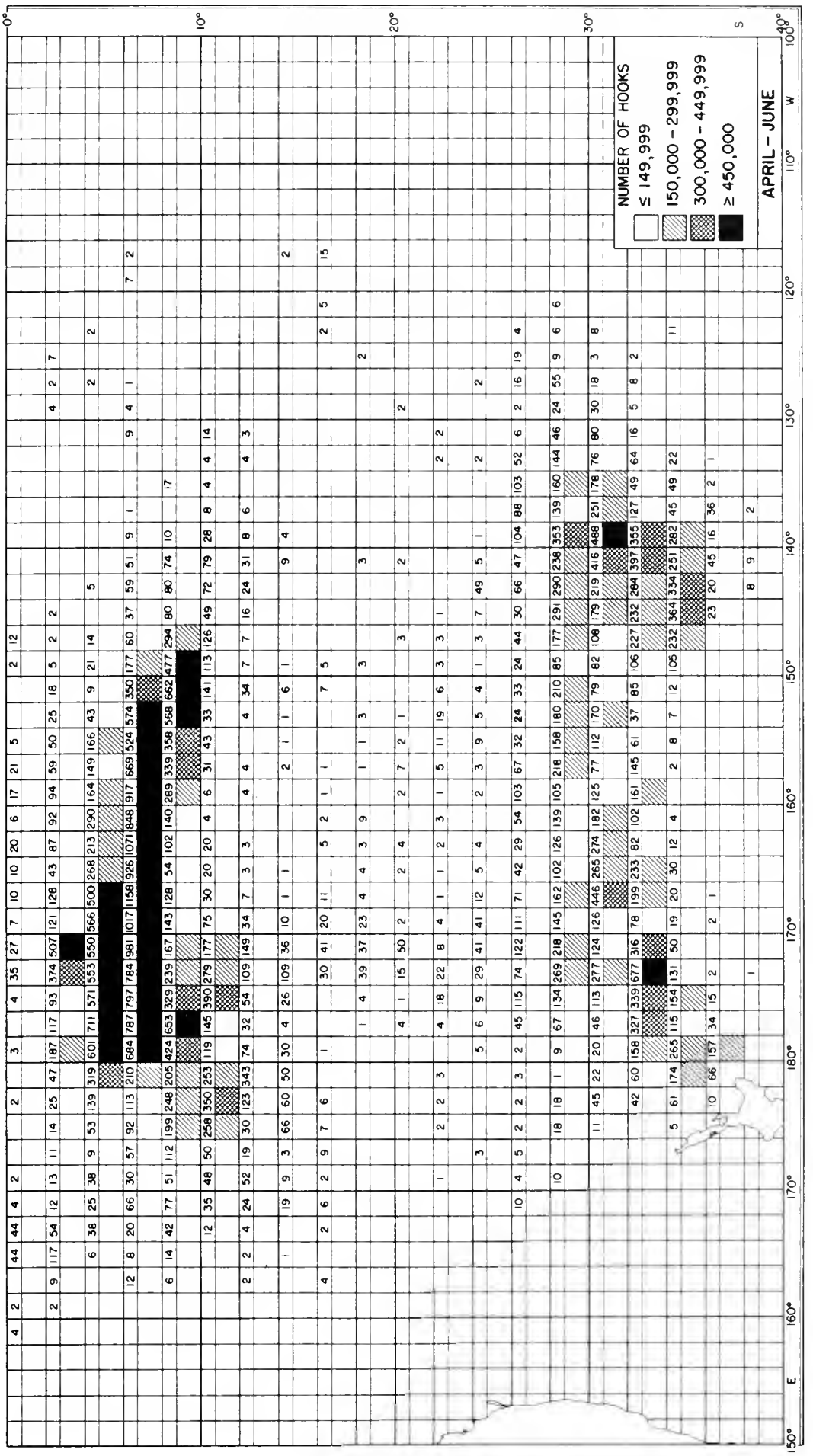

FIGURE 10.–Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.–Continued.

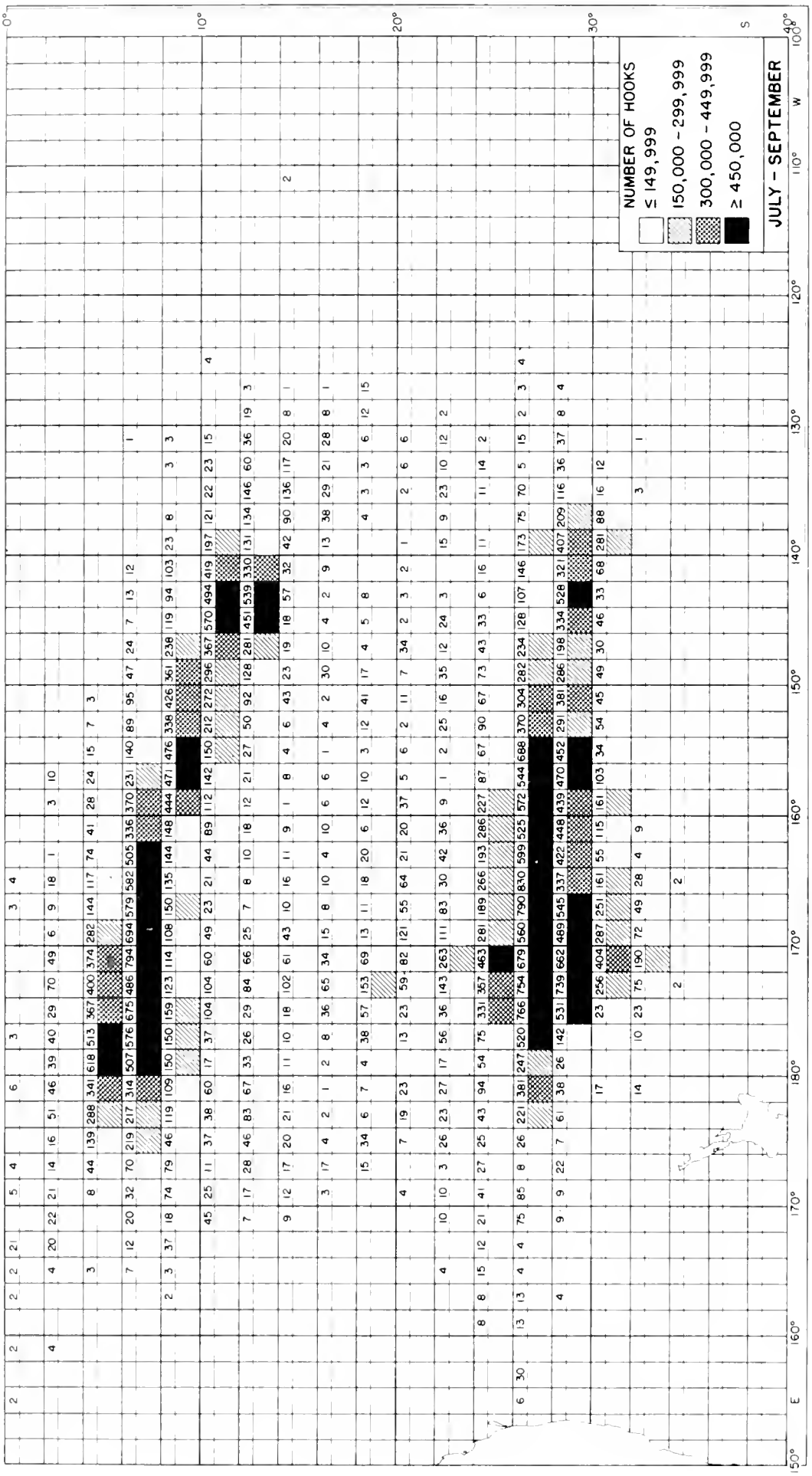

FIGURE 10.—Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.—Continued.

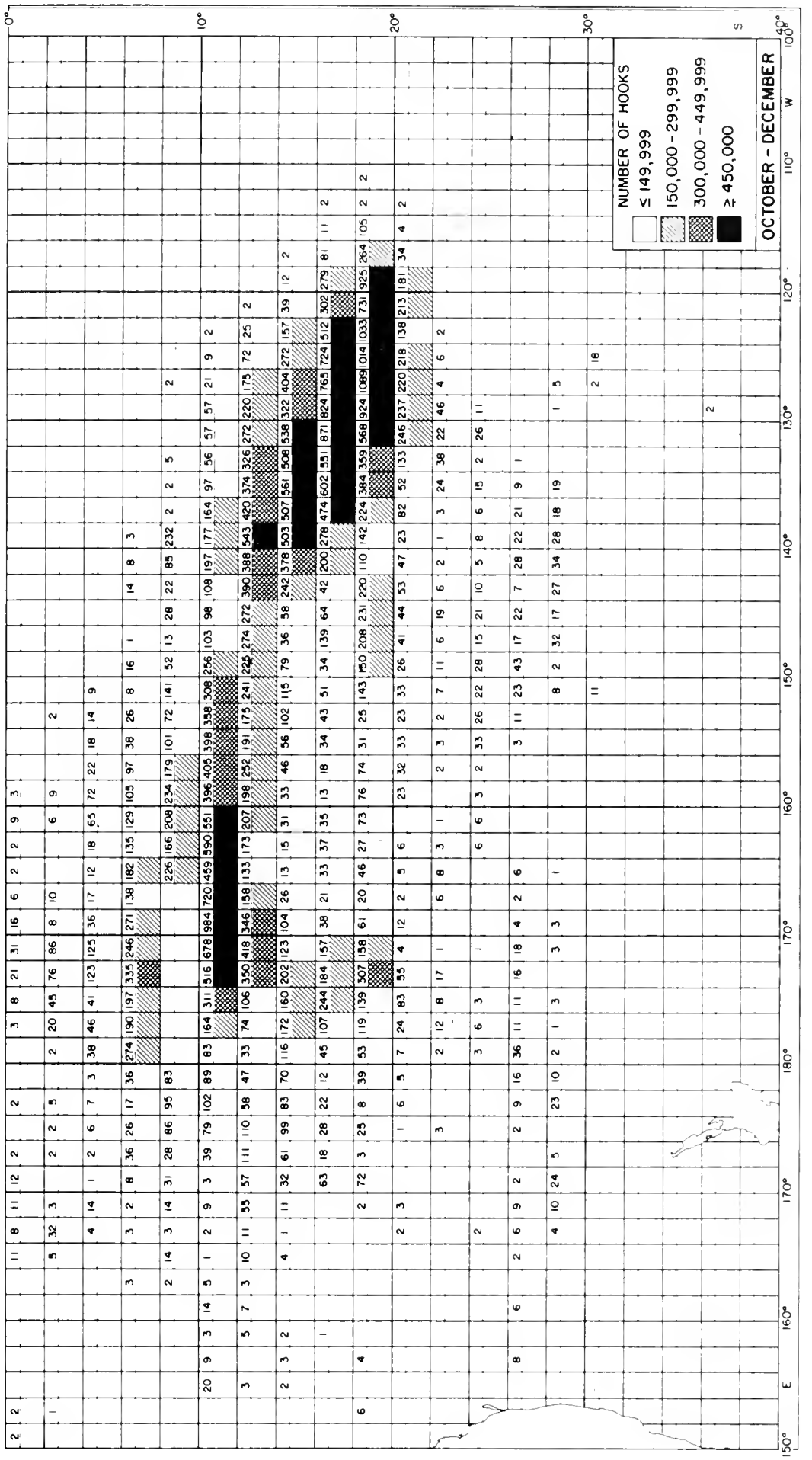

FIGURE 10.–Quarterly geographic distribution of effort, 1966-71. The numbers in the figures are in thousands.–Continued.

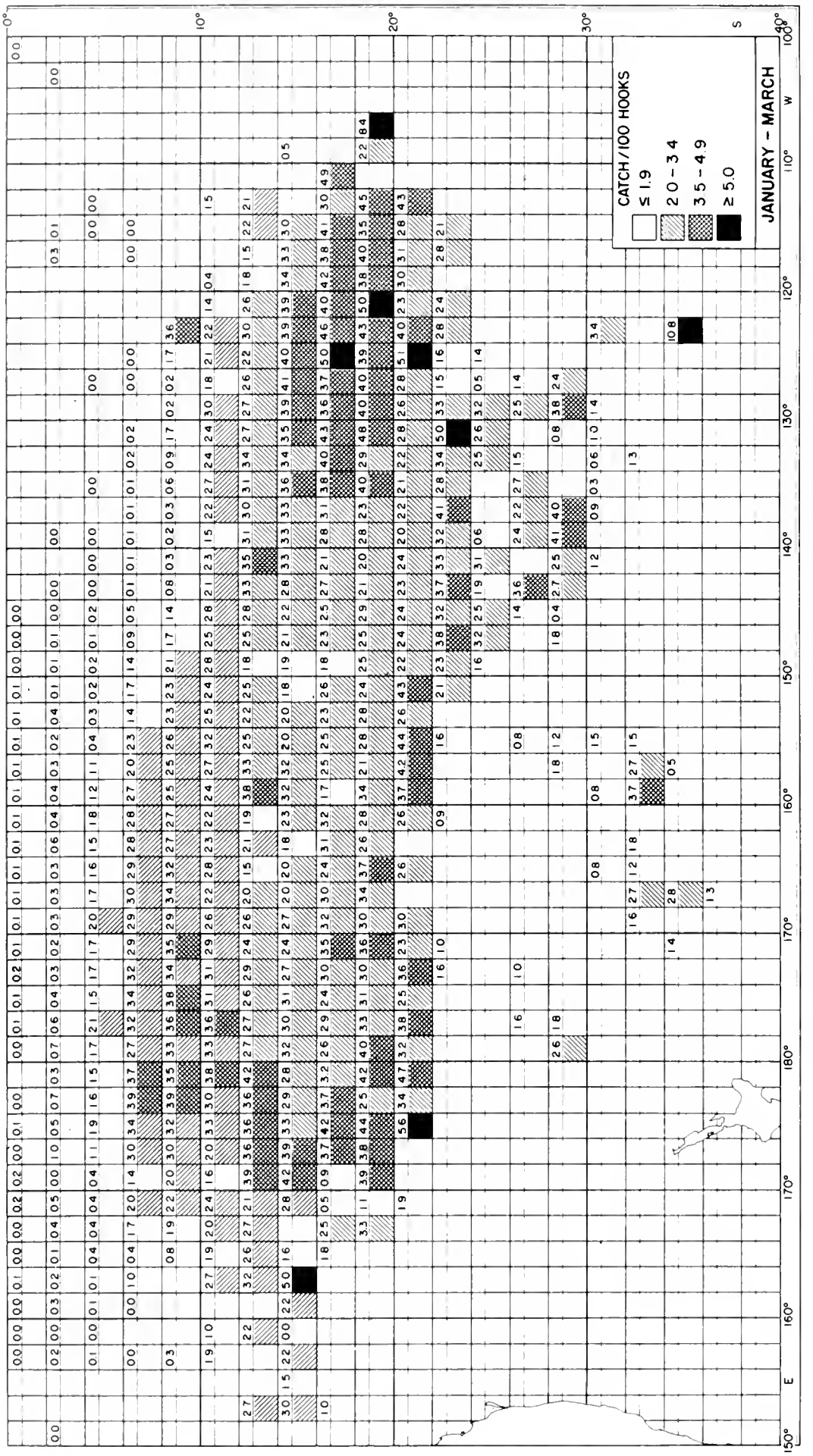

FIGURE 11.–Seasonal and geographic distributions of albacore CPUE, 1966-71.

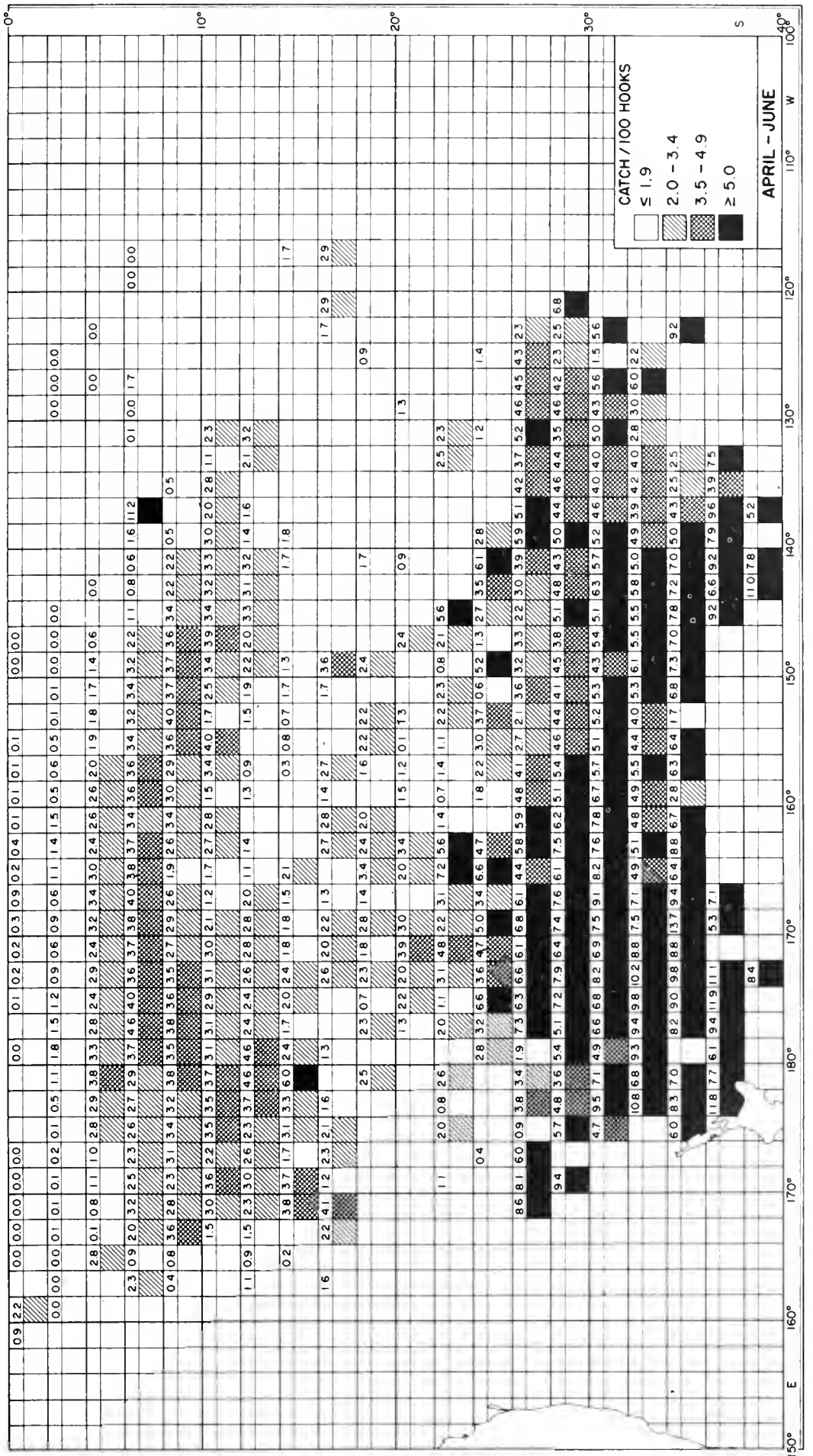

FIGURE 11.–Seasonal and geographic distributions of albacore CPUE, 1966-71.–Continued.

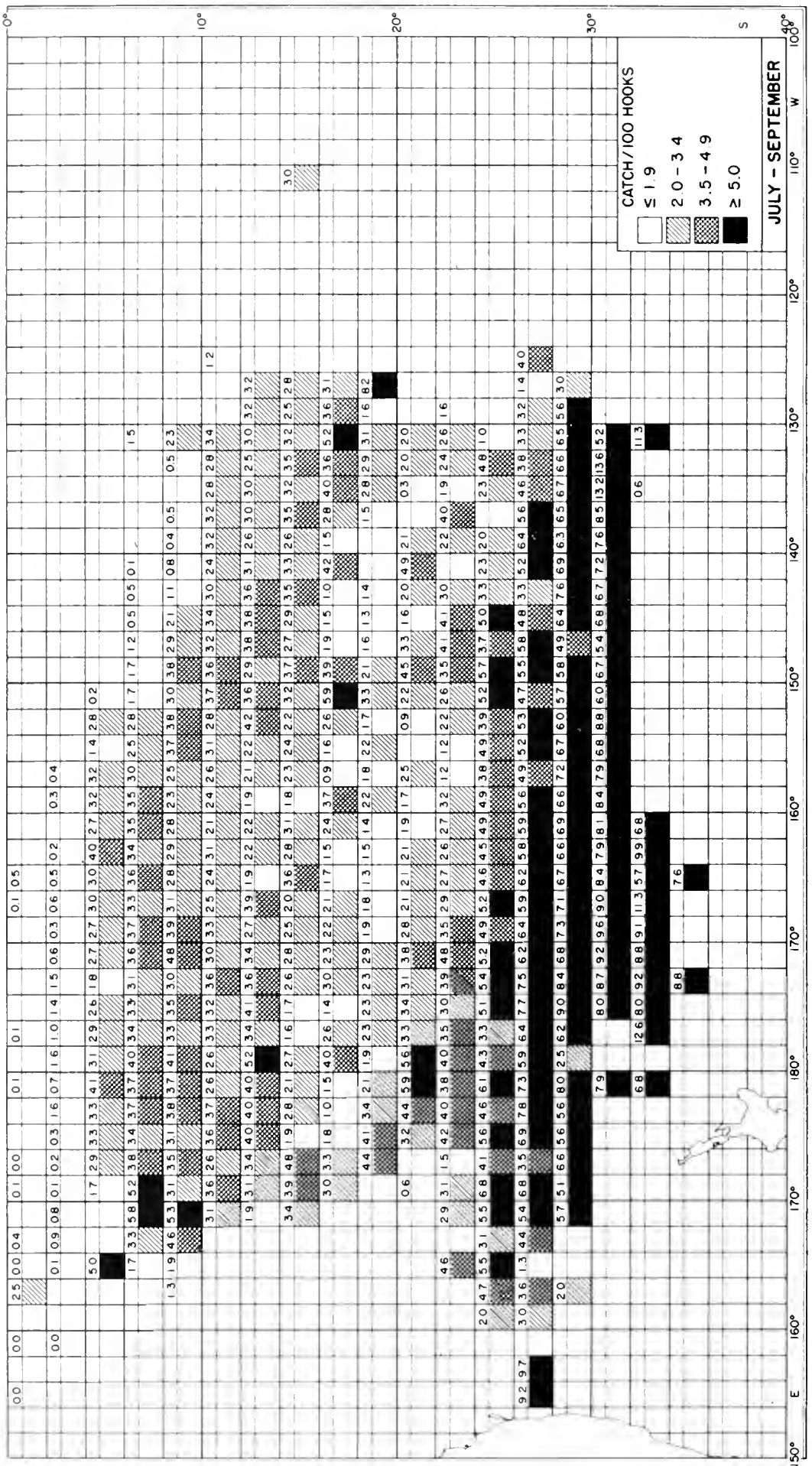

FIGURE 11.–Seasonal and geographic distributions of albacore CPUE, 1966-71.–Continued.

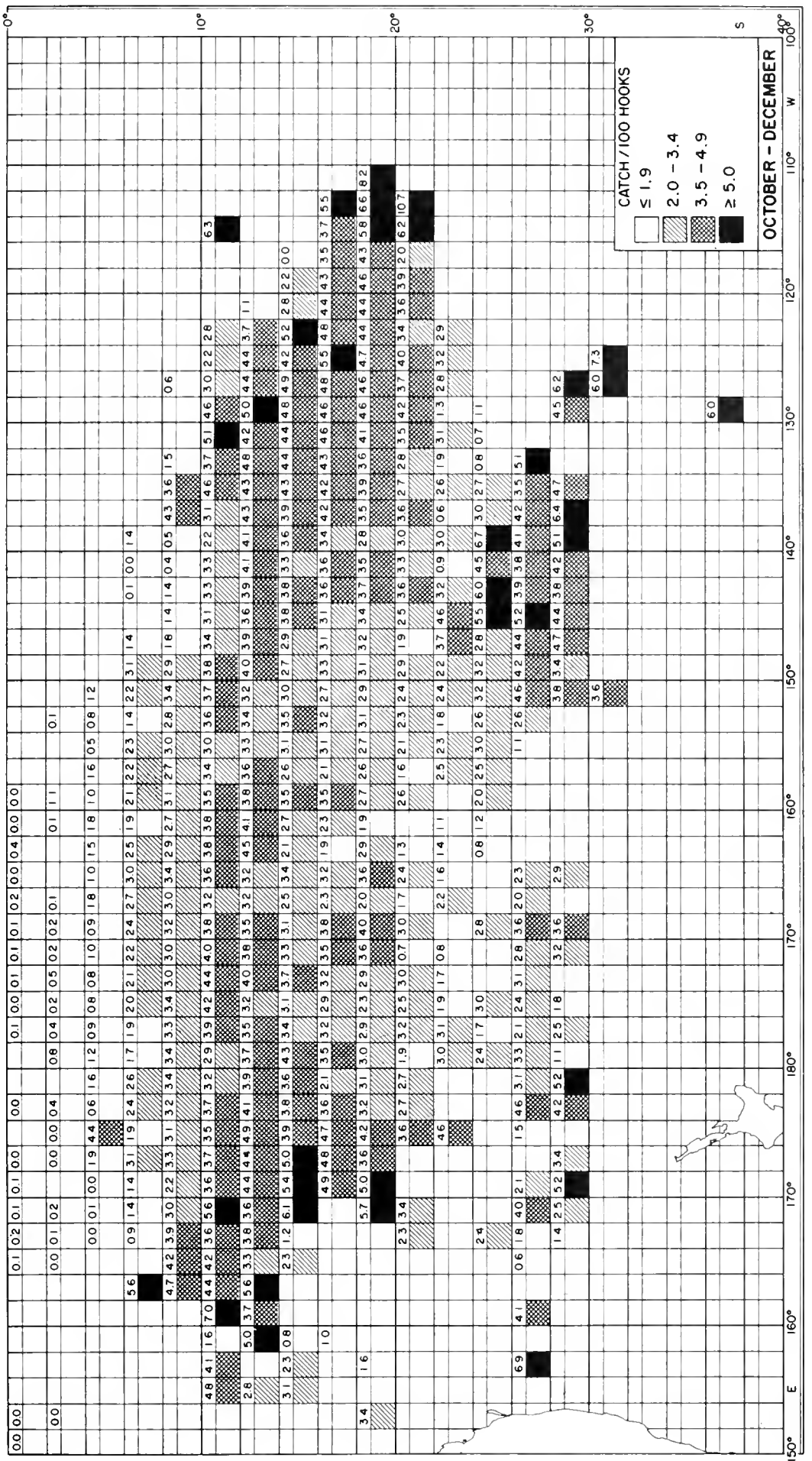

FIGURE 11.–Seasonal and geographic distributions of albacore CPUE, 1966-71.–Continued.

similar analysis covering a period from 1963 to 1965, seasonal and geographical differences in CPUE were not readily apparent (Otsu and Sumida 1968). For some reason that is not immediately clear, a distinct seasonal pattern in geographical differences in CPUE has developed in recent years. In the first quarter, there appeared to be no pattern in the distribution of areas with high CPUE (greater than five albacore per 100 hooks). However, the CPUE was better in the east-west extremes of the fishery. In the second and third quarters, an area of high CPUE developed between lat. 25° and 40°S. The fishery was also well developed north of lat. 20°S in the second and third quarters but as in the first quarter there were no well-defined areas of high CPUE. The situation in the fourth quarter reverted to approximately what it was in the first quarter. However, in some years there was a tendency for an area of high CPUE to develop in the eastern extreme of the area fished between lat. 10° and 20°S.

Because of geographical and temporal variations in the distribution of the fishing effort, the description of the geographical and temporal changes in CPUE as given above is incomplete. As noted earlier, very little fishing effort was expended south of lat. 20°S in the first and fourth quarters. It would be of interest to determine whether a high CPUE could be obtained south of lat. 20°S also in the first and fourth quarters. The possibility exists, of course, that very little effort was expended south lat. 20°S in the first and fourth quarters because the fishermen know from past experience that poor catch rates are obtained during those periods. Honma and Kamimura (1957) suggested that albacore in the South Pacific make north-south migrations and that the fishing vessels follow the movements of the albacore. In the eastern Pacific tuna fishery, Griffiths (1960) showed that the bait boat fishermen were able, on the average, to concentrate their effort on high densities of yellowfin tuna about 70% better than if their effort had been random. The data indicate that the fishermen may be able to predict the movements of the albacore with some degree of success in that areas of high fishing effort were usually associated with areas of high CPUE. There were quarters, however, in which areas of high fishing effort did not coincide with areas of high CPUE. Then, too, the fishermen may avoid fishing south of lat. 20°S in the first and fourth quarters because of bad weather or unfavorable conditions.

One other interesting observation is the division of the fishery at lat. 20°S. As noted above, the fishery develops north or south of lat. 20°S but seldom straddles it. This appears to be a well-established phenomenon, for Koto (1966) has made the same observation. Koto mentioned belts of high catch rates in the area between lat. 10° and 20°S and between lat. 20° and 30°S, and a belt of low catch rates centered at lat. 20°S. The data also indicate that the latitudinal belt centered at lat. 20°S is also a low-effort area. The causes of this phenomenon are not clear.

SIZE OF ALBACORE

Because the canneries have changed the method of handling the fish, the albacore that are sampled for length are no longer being sexed. Consequently, in the analysis of the length distribution of albacore only the data collected from 1966 to 1970, when sex data were available, are presented.

A composite length-frequency distribution of male and female albacore taken by the fishery from 1966 to 1969 is shown in Figure 12. The fish

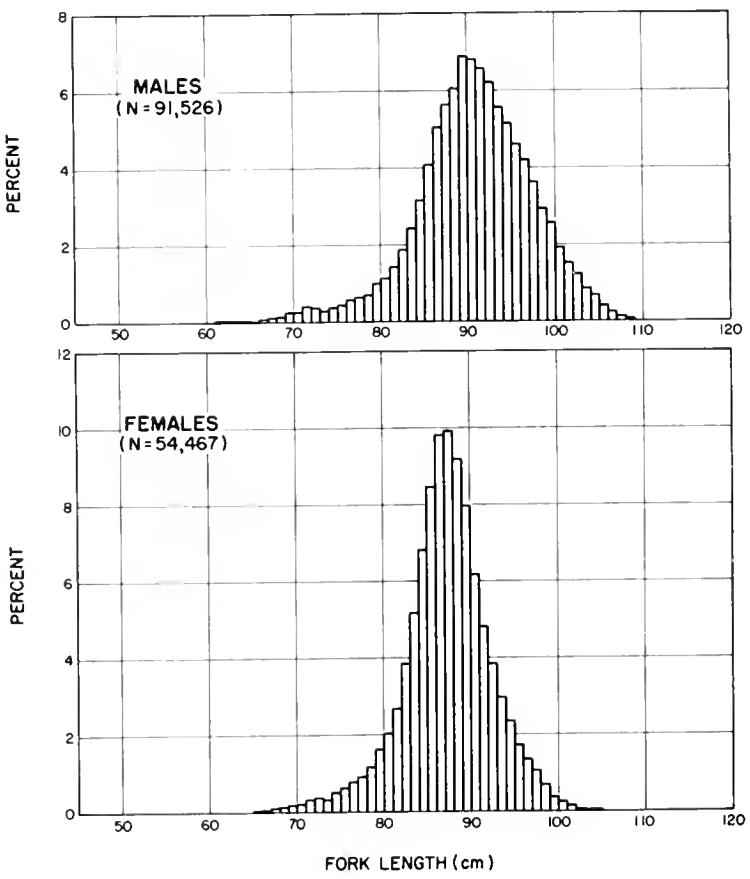

FIGURE 12.—Composite length-frequency distributions of albacore, 1966-69.

ranged in length from 50 to 120 cm. A single prominent mode was present in both the male and female distributions. For the males the mode was located at 91 cm and for the females at 88 cm.

The albacore size data were also summarized into smaller units of time and area to detect any variations which might exist. Initially the geographical area of the fishery was divided longitudinally at long. 150°W and by 10° of latitude from the equator to lat. 40°S. This was done on a quarterly basis, keeping all the years separate. This analysis did not indicate any obvious differences in the length-frequency distributions of albacore east and west of long. 150°W, nor did it show any consistent annual and seasonal differences within each geographical unit. There were, however, differences in the length-frequency distributions between the latitudinal subdivisions of the fishery. Therefore, the length data were rearranged by 10° of latitude but without regard to longitude, seasons, and year (Figure 13).

Almost without exception, the modal sizes of male albacore were larger than those of female

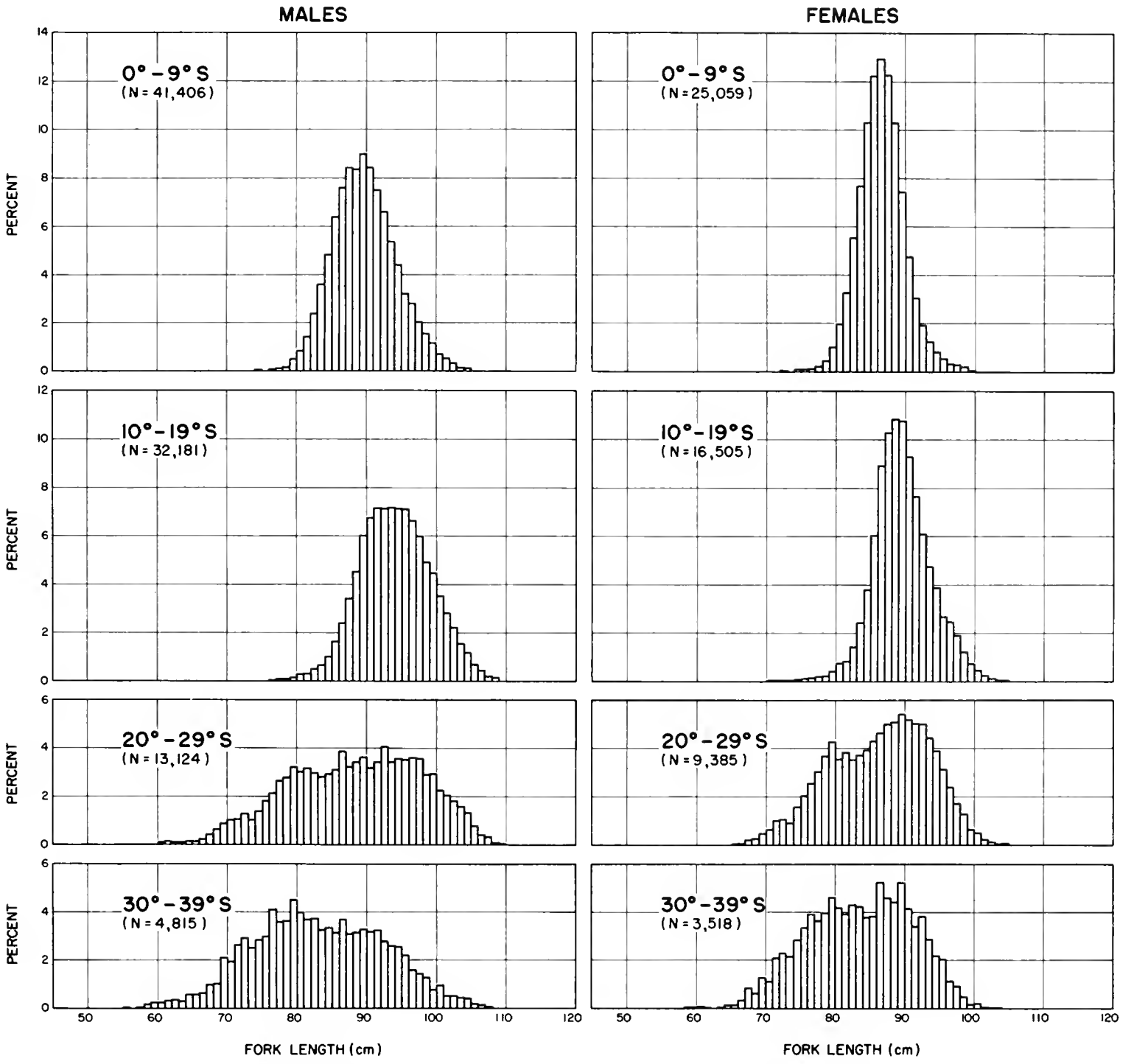

FIGURE 13.—Length-frequency distributions of albacore arranged by sex and 10° bands of latitude, 1966-70.

albacore in each of the latitudinal subdivisions. In the areas north of lat. 20°S, both male and female length-frequency distributions had a single well-defined mode. In the areas south of lat. 20°S the modes were less well defined. Koto and Hisada (1967) found a similar pattern in the length-frequency distribution of albacore in the South Pacific in 1961.

Otsu and Sumida (1968) computed the mean length of albacore in the fishery during the period from 1962 to 1965. They divided the fishery into 5° bands of latitude and noted that the fish were smallest near the equator, largest at lat. 20° to 25°S and tended to be smaller again south of lat. 25°S. The results agree in general with those of Otsu and Sumida; however, as seen above, the length-frequency distributions indicate a more complex situation than do the mean sizes. North of lat. 20°S the mean sizes may be good indicators of the general size of albacore because the length-frequency distributions showed that the fish were composed of single uniform size groups. South of lat. 20°S, the catches were composed of several size groups of fish and the mean does not indicate the presence of different size groups of fish. For example, although Otsu and Sumida stated that albacore south of lat. 25°S tended to be smaller, my data show that large fish were also present in these latitudes.

Although it is not readily apparent in the length-frequency distributions, there appears to be a declining trend in the mean size of albacore in the fishery. Otsu and Sumida (1968) noted that albacore taken in 1964 and 1965 were shorter on the average than those caught in 1963. My data show that the declining trend in the mean length of albacore has continued (Table 3).

TABLE 3.—Mean lengths of albacore, sexes combined, 1963-71.

Year	Mean length (cm)	Year	Mean length (cm)
1963	95.0	1968	89.8
1964	91.6	1969	90.4
1965	91.3	1970	88.6
1966	91.7	1971	91.5
1967	90.8		

The mechanisms that produced such a pattern in the distribution of sizes in the fishery are probably complex. The unique character of the length-frequency distributions among the four latitudinal bands must have resulted from some nonrandom distributional process. The larger numbers of smaller albacore in the more southern waters suggest that albacore are initially recruited into the fishery in the area south of lat. 20°S. The high CPUE experienced in the second and third quarters south of lat. 20°S may be an indication of this. Also, it has been shown that juvenile albacore which originate from spawning that takes place north of lat. 20°S migrate south as they grow larger (Yoshida 1971).

SUMMARY

A comparison of various indices of apparent abundance of albacore indicated that catch per day and catch per 100 hooks were better indicators of apparent abundance than catch per trip. The mean catch per day and catch per 100 hooks of albacore have generally declined over the years, which suggests that the apparent abundance of albacore has declined in the American Samoa longline fishery. To compensate for the reduced CPUE, the longliners fished more days per trip and traveled farther from the home base seeking areas of good catch rates.

The fishery apparently has had an effect on the albacore stock. Although the annual landings have continued to increase with increased fishing effort, the CPUE has declined. That the apparent overall effect was not greater was due to the fact that the fishing grounds have expanded, especially into areas south of lat. 20°S where good catch rates were obtained. The mean annual CPUE plotted against fishing effort for selected, discrete areas north and south of lat. 20°S indicated that the fishery has not as yet had as great an effect in the south as it has to the north. There are at least two possible reasons for the better condition of the fishery to the south. First, the area south of lat. 20°S has not been exploited as long as the area to the north. Second, it was shown that the albacore are first recruited into the fishery in the latitudes south of lat. 20°S, which may account in part for the higher apparent abundance.

There was some indication that there were temporal changes in apparent abundance of albacore south of lat. 20°S. Because of poor weather conditions or because the fishermen have learned through experience that catch rates are better during certain seasons, or a combination of these and other reasons, fishing effort expended south

of lat. 20°S fluctuates seasonally. Areas of concentrated fishing effort were evident in the second and third quarters in the area south of lat. 20°S. Very little effort was expended in these waters in the first and fourth quarters. Good CPUE's were experienced in these areas of high fishing effort in the second and third quarters. Although there were some indications that the apparent abundance of albacore was low in the southern waters in the first and fourth quarters, more data are needed to show this conclusively.

The apparent temporal changes in CPUE in the southern waters may be related to seasonal changes in recruitment of albacore into the fishery. The length-frequency distribution of albacore in waters south of lat. 20°S showed that several size groups of fish were represented in the catches, including groups of small fish not found north of lat. 20°S. The good CPUE in the second and third quarters may indicate periods of active recruitment. Generally, the albacore were stratified by size latitudinally; however, no such stratification was evident longitudinally. North of lat. 20°S the catches were composed of fish of a single size group. South of this latitude, as already indicated, the catches were composed of several size groups of fish.

ACKNOWLEDGMENTS

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EFFECTS OF PHOTOPERIOD-TEMPERATURE REGIMES AND PINEALECTOMY ON BODY FAT RESERVES IN THE GOLDEN SHINER, *NOTEMIGONUS CRYSOLEUCAS*

VICTOR L. DE VLAMING[1]

ABSTRACT

Various photoperiod-temperature regimes were examined for their effects on total fat content (excluding gonads) in *Notemigonus crysoleucas*; experiments were conducted during several different phases of the reproductive cycle. In *Notemigonus*, fattening normally occurs in fall and early winter concomitant with the early phases of gonadal development. Body fat stores are progressively depleted during the prespawning and spawning seasons. Warm temperature (25°C) normally favored body fat depletion in *Notemigonus*. Short photoperiod (9L/15D) accentuated the lipid depleting effects of warm temperatures. Low temperatures (12°-15°C) usually promoted lipid deposition. Short photoperiods complimented the lipid anabolic effects of low temperatures. Thus, a given photoperiod can have opposite effects on body fat levels depending on temperature. A long photoperiod, in combination with warm temperatures, is required for final gonadal maturation and results in a reduction of lipid reserves. Short photoperiod-warm temperature regimes have similar effects on fat levels, but bring about gonadal regression. Thus, the effects of photoperiod-temperature regimes on lipid metabolism are apparently not totally dependent on the effects of these environmental factors on reproduction.

The effects of pinealectomy on lipid reserves varied depending on the phase of the natural reproductive cycle when the organ was removed, as well as, with the photoperiod-temperature regime under which the experimental animals were maintained. At 25°C and under a 15.5L/8.5D photoperiod, fat levels were frequently lower in pinealectomized than in sham animals. The opposite was usually true for fish exposed to a 9L/15D-25°C regime. Lipid reserves were normally greater in pinealectomized than in sham operated fish maintained on 15.5L/8.5D-12°C regime. Body fat composition was frequently less in pinealectomized than in sham operated animals exposed to a 9L/15D-12°C regime. Pinealectomy reverses the effects of photoperiod on lipid metabolism at a particular temperature. These results suggest that the pineal body is involved in regulating physiological functions and may serve as a photoreceptor and/or transducer of photoperiod information.

In most temperate-latitude aquatic environments food availability varies seasonally and annual cycles of growth, reproduction, and fattening are normally observed in teleost fishes. Lipid reserves may be used to meet the energy demands of reproduction, and seasonal fattening cycles in teleosts may be related to sexual cycling (Lovern 1934; Lühmann 1953; Love 1957; Idler and Bitners 1960; Woodhead 1960; Nikolsky 1963; Wilkins 1967; Lasker 1970; de Vlaming 1971). Environmental factors such as photoperiod and temperature are used as cues to maintain annual reproductive cycles in fishes (for reviews see de Vlaming 1972, 1974), but little is known about environmental control of fattening.

The pineal body of most fishes has sensory organ characteristics (e.g., Rüdeberg 1966, 1969; Omura and Oguri 1969; Owman and Rüdeberg 1970; Bergmann 1971; Oksche et al. 1971). Histological examination of the pineal in various teleosts also reveals secretory gland characteristics (e.g., Takahashi 1969; Chèze and Lahaye 1969; Chèze 1970; Rizkalla 1970; Hafeez 1971). In mammals the pineal appears to function as an endocrine gland and the indolamine, melatonin, may be one of the hormones of this organ (cf. Reiter 1973). Histochemical and biochemical data show that the teleost pineal has an active indolamine metabolism (Quay 1965; Hafeez and Quay 1969, 1970; Fenwick 1970; Owman and Rüdeberg 1970). Very little, however, is known about the physiological role of the pineal in teleost fishes.

De Vlaming, Sage, Charlton, and Tiegs (1974) showed that melatonin treatment results in body lipid depletion in *Fundulus similis* and *Cyprinodon variegatus* acclimated to a long photoperiod. In *F. similis* acclimated to a short photoperiod during May, melatonin therapy also resulted in fat depletion, but body fat deposition

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was observed in *F. similis* acclimated to a short photoperiod during July and treated with this indolamine (de Vlaming, Sage, Charlton, and Tiegs 1974). These investigators concluded that the pineal might be somehow involved in regulating body fat reserves in teleosts. The data of de Vlaming, Sage, Charlton, and Tiegs (1974) and others (Fenwick 1970; Urasaki 1972a, b, c) indicate that the influence of the pineal on physiological functions in teleosts may vary depending on season and photoperiod conditions.

The objectives of the present investigation were to examine the effects of various photoperiod-temperature regimes on body lipid reserves in the cyprinid teleost *Notemigonus crysoleucas* and to determine if pinealectomy altered the response of this fish to the experimental regimes. The possible relationship between reproductive activity and body fat reserves was also examined. That is, the effects of photoperiod-temperature regimes and pinealectomy on reproductive activity were determined and compared to the data on fat metabolism. The effects of pinealectomy on reproductive activity and fattening were examined during different phases of the natural sexual cycle (at various times of the year) to determine if physiological responses vary seasonally.

MATERIALS AND METHODS

Samples of *N. crysoleucas* were collected in ponds around the area of Menomonee Falls, Wis. (lat. 43°10′N) at several different times during the year. The reproductive cycle consists of a spawning season which extends from May through July. There is a postspawning season during August and September in which the gonads regress. From October through February there is a gonadal preparatory period, in which spermatogonia proliferate slowly and spermatocytes appear in the testes. Vitellogenesis is initiated during this period. March and April can be referred to as the prespawning period; during this time, final gonadal maturation occurs (i.e., spermatozoa fill the testes and ovaries are distended with mature oocytes). Several fish from each field sample were sacrificed, the gonads examined and body lipid levels determined at the time of collection; these fish served as a reference for the experiments that followed. In the following discussion the fish sacrificed at the time of collection will be identified as initial controls.

Sham operated and pinealectomized fish were maintained under various photoperiod and constant temperature regimes (see Results) in 114- or 285-liter tanks supplied with aerated and filtered dechlorinated tap water. Temperatures selected for these experiments are within the range normally experienced during the year in nature by this species. Illumination was a combination of incandescent and cool white fluorescent bulbs which gave a light intensity of 200 to 275 lx at the surface of each tank. Fish were fed ad libitum on a commercial fish food (Tetra-Min)[2]; animals maintained at warm temperatures were fed twice daily whereas fish at low temperatures were fed only once a day. All *Notemigonus* used in these studies weighed between 12 and 17 g.

For pinealectomies, fish were anesthetized in buffered tricaine methane-sulfonate (1:4,000). Each fish was then wrapped in cheesecloth and submerged in water so that only the top of the skull was emergent. The section of skin covering the pineal area was cut and folded back to reveal the parietal bone. Using a diamond-edged wheel saw (diameter = 2.2 cm) attached to a dental drill, three sides of a rectangle (5×4 mm) were cut in the parietal bone. This bone flap was then lifted forward toward the animal's mouth to expose parts of the cerebrum and midbrain. The pineal could then be easily removed using a gentle suction applied through a Pasteur pipette. After removal of the pineal, the parietal bone and the epithelial flaps were individually sealed into place with Eastman's 910 Adhesive. Sham operations consisted of raising the parietal bone flap without removing the pineal. Removal of the pineal can be completed within 2 min in this species.

The effects of pinealectomy on reproductive function were assessed by gravimetric and histological techniques. Fish were sacrificed by severing the spinal cord. Body weight and gonadal weight were recorded immediately after sacrifice. Gravimetric data are expressed in terms of the gonosomatic index (GSI) (gonadal weight/body weight × 100) since gonadal size in this species depends on body weight. After weighing, gonads were fixed in Bouin's solution and embedded in paraplast for histological examination. The data obtained on the effects of pinealectomy on reproductive function in *Notemigonus* are the subject of another report (de Vlaming 1975). GSI

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

data are presented here without statistical comparisons or extensive discussion so that comparisons can be made with the results on body lipid reserves. After removal of the gonads, the bodies of the fish were extracted to remove lipids. The procedure used to measure body fat content has been previously described (de Vlaming, Sage, Charlton, and Tiegs 1974; de Vlaming et al. in press). Basically this technique consists of extracting in a methanol:chloroform:ether solution (1:1:1). Body fat content is expressed as a function of dry body weight.

RESULTS

Preparatory Season

The effects of pinealectomy on body lipid reserves were first examined during the gonadal preparatory period (January). The results of this experiment are summarized in Table 1.

Body lipid reserves were significantly depleted in both male and female sham operated fish maintained at 25°C (whether on a long or short photoperiod) compared to the initial January controls.

TABLE 1.–The effects of pinealectomy on body lipid reserves in *Notemigonus* maintained on various photoperiod-temperature regimes during the gonadal preparatory season (30-day treatment).

Treatment	*n*	Sex	Dry lipid index[1] $\bar{X} \pm$ SE	Gonosomatic index[2] $\bar{X} \pm$ SE
Initial controls	5	M	248 ± 11	1.48 ± 0.09
(January)	9	F	207 ± 10	3.03 ± 0.25
15.5L/8.5D photoperiod:				
25°C:				
Sham operated	6	M	136 ± 7	2.82 ± 0.07
	8	F	164 ± 11	4.67 ± 0.42
Pinealectomized	5	M	119 ± 5*	0.34 ± 0.18
	10	F	139 ± 8*	2.88 ± 0.37
12°C:				
Sham operated	6	M	235 ± 10	1.95 ± 0.16
	8	F	211 ± 7	3.42 ± 0.08
Pinealectomized	6	M	246 ± 9	1.20 ± 0.04
	10	F	237 ± 5*	3.47 ± 0.13
9L/15D photoperiod:				
25°C:				
Sham operated	5	M	118 ± 8	0.94 ± 0.09
	8	F	96 ± 6	1.78 ± 0.22
Pinealectomized	6	M	106 ± 5	0.89 ± 0.16
	9	F	109 ± 11	1.64 ± 0.21
12°C:				
Sham operated	6	M	263 ± 12	1.28 ± 0.11
	10	F	244 ± 9	3.40 ± 0.21
Pinealectomized	5	M	250 ± 15	1.19 ± 0.18
	8	F	221 ± 6*	4.12 ± 0.35

[1]Dry lipid index = mg lipid, less gonadal lipids/g dry body wt.
[2]Gonosomatic index = wt of gonads (g)/g body wt x 100.
*Significantly ($P < 0.05$) different than sham operated controls maintained under same photoperiod-temperature regime.

In both sexes of sham operated fish exposed to the long photoperiod-low temperature regime body lipid stores were maintained at the initial levels. Short photoperiod-low temperature treatment, however, caused a significant increase in fat stores in sham operated females, but not in sham operated males.

In sham operated control fish maintained on a long photoperiod, body lipid levels were significantly higher in the group at 12°C than in the group at 25°C. Fat levels were also significantly greater in sham operated *Notemigonus* maintained at 12°C than at 25°C on a short photoperiod. These data suggest that low temperatures, regardless of daylength, either maintain or favor body lipid deposition in this species.

At 12°C, a short photoperiod was more effective in maintaining or stimulating lipid deposition than a long photoperiod. Specificially, body fatness (in both sexes) was significantly greater in sham operated fish exposed to the short photoperiod-low temperature regime than in animals maintained on the long photoperiod-low temperature regime. Thus, short daylengths seem to compliment the effects of low temperatures on fat deposition. Body lipid levels were significantly lower in sham operated animals maintained on the short photoperiod-warm temperature regime than in fish exposed to the long photoperiod-warm temperature regime. Body fat depletion in *Notemigonus* at warm temperatures is therefore accentuated by short daylengths.

In animals maintained on the 15.5L/8.5D-25°C regime, body lipid levels were significantly lower in the pinealectomized group than in sham operated group. Pinealectomy also retarded fat deposition in female fish exposed to the 9L/15D-12°C regime. In contrast, body fat levels were significantly greater in the female pinealectomized fish than in the sham operated females maintained on the long photoperiod-low temperature regime. Body lipid levels in pinealectomized fish did not differ significantly from lipid levels in control sham operated animals under any of the other experimental conditions. These data suggest that the effects of pinealectomy on lipid metabolism depend on photoperiod and temperature conditions.

The effects of pinealectomy on reproductive function are discussed elsewhere (de Vlaming 1975). One should note, however, that pinealectomy retarded the stimulatory effects of the 15.5L/8.5D-25°C regime on gonadal maturation;

under these same conditions body lipid levels were also significantly lower in pinealectomized than in sham operated fish. Ovarian GSI was significantly higher in the pinealectomized than in sham operated group exposed to the 9L/15D-12°C regime; however, body fat levels were significantly lower in pinealectomized than in sham operated fish under these conditions. These data imply that the effects of pinealectomy on lipid deposition do not necessarily depend on the effects of this organ on reproductive activity.

Prespawning Season

The effects of pinealectomy on body fat reserves were examined again during the prespawning season (Table 2).

Regardless of photoperiod, low temperature treatment of both sexes of sham operated *Notemigonus* resulted in a significant increase in body fatness, compared to the initial March controls. Warm temperature treatment, however, caused a depletion of body lipids in sham operated fish compared to the initial controls; this fat depletion was observed in both photoperiod groups.

Body fatness (in females) was significantly greater in sham operated control fish exposed to the 9L/15D-12°C regime than in animals maintained on the 15.5L/8.5D-12°C regime. These data further confirm the suggestion that short daylengths compliment the effects of low temperatures on fattening. Body lipid levels (both sexes) were significantly lower in sham operated animals maintained on the short photoperiod-warm temperature regime than in sham operated fish exposed to the long photoperiod-warm temperature regime. The lipid depletion which occurs at warm temperatures is thus accentuated by short daylengths.

Body fat levels (both sexes) were significantly lower in the pinealectomized group than in the sham operated group maintained on the 15.5L/8.5D-25°C regime. In animals maintained on a long photoperiod-low temperature regime, body lipid levels were significantly greater in the pinealectomized fish than in the shams. Pinealectomized females contained significantly more fat than sham operated females exposed to the short photoperiod-warm temperature regime. In contrast, body lipid levels (both sexes) were significantly lower in pinealectomized than in sham operated fish maintained on the 9L/15D-12°C regime. At a low temperature, pinealectomy interferes with the complimentary effects of short photoperiods on lipid deposition. At a warm temperature, however, pinealectomy reverses the accentuating effects of short photoperiods on body lipid depletion.

Interestingly, body lipid levels in pinealectomized females maintained on the 9L/15D-12°C regime did not differ significantly from fat levels in sham operated females exposed to the 15.5L/8.5D-12°C regime. Fat levels were not significantly different in pinealectomized females on the 15.5L/8.5D-12°C regime and sham operated females on the 9L/15D-12°C regime. Similarly, body fat levels in pinealectomized fish (both sexes) exposed to the 9L/15D-25°C regime did not differ significantly from lipid levels in shams maintained on the 15.5L/8.5D-25°C regime. These data indicate that pinealectomy reverses the effects that photoperiod has on lipid levels at a given temperature.

Pinealectomy reverses the stimulatory effects of a long photoperiod-warm temperature regime, causing gonadal regression (de Vlaming 1975); under these conditions body lipid levels in pinealectomized animals are lower than in shams. Short photoperiods in combination with warm

TABLE 2.—The effects of pinealectomy on body lipid reserves in *Notemigonus* maintained on various photoperiod-temperature regimes during the prespawning season (21-day treatment).

Treatment	*n*	Sex	Dry lipid index[1] $\bar{X} \pm$ SE	Gonosomatic index[2] $\bar{X} \pm$ SE
Initial controls	5	M	209 ± 10	1.96 ± 0.17
(March)	9	F	184 ± 12	3.42 ± 0.09
15.5L/8.5D photoperiod:				
25°C:				
Sham operated	6	M	140 ± 11	1.35 ± 0.07
	8	F	131 ± 5	2.41 ± 0.15
Pinealectomized	6	M	112 ± 10*	0.80 ± 0.09
	7	F	107 ± 8*	1.58 ± 0.22
12°C:				
Sham operated	6	M	232 ± 8	2.00 ± 0.10
	7	F	244 ± 7	3.41 ± 0.26
Pinealectomized	6	M	251 ± 6*	1.79 ± 0.14
	7	F	264 ± 7*	3.18 ± 0.33
9L/15D photoperiod:				
25°C:				
Sham operated	8	M	129 ± 5	2.02 ± 0.15
	6	F	114 ± 6	1.74 ± 0.11
Pinealectomized	6	M	143 ± 9	1.62 ± 0.04
	7	F	132 ± 8*	2.03 ± 0.13
12°C:				
Sham operated	5	M	243 ± 5	1.31 ± 0.05
	5	F	267 ± 8	3.79 ± 0.28
Pinealectomized	6	M	187 ± 11*	1.20 ± 0.07
	4	F	240 ± 6*	3.43 ± 0.27

[1]Dry lipid index = mg lipid, less gonadal lipids/g dry body wt.
[2]Gonosomatic index = wt of gonads (g)/g body wt x 100.
*Significantly ($P < 0.05$) different than sham operated controls maintained under same photoperiod-temperature regime.

temperatures induce gonadal involution in *Notemigonus*. Pinealectomy under these conditions prevents gonadal regression, stimulating gonadal development and spawning. Body lipid reserves were significantly greater in pinealectomized fish than in shams maintained on the 9L/15D-25°C regime. Under the other photoperiod-temperature regimes, pinealectomy resulted in changes in body fat reserves without appreciably altering reproductive activity. Possibly then, changes in lipid metabolism due to pinealectomy may influence reproductive activity, but apparently the effects of pinealectomy on fat deposition are not totally dependent on changes in sexual activity.

Spawning Season

The effects of pinealectomy on body fat stores were again examined during the early spawning season (late April, Table 3).

In sham operated fish maintained at 25°C (both photoperiod groups), the lipid index was significantly lower than that of the initial controls. Body lipid reserves were also significantly depleted in sham operated female fish exposed to the 9L/15D-25°C regime, but not in sham operated females maintained on the 15.5L/8.5D-25°C regime compared to the initial controls. Low temperature treatment during the spawning season caused a significant increase in body lipid content of sham operated female fish regardless of photoperiod. The short photoperiod-low temperature regime stimulated fat deposition in sham operated males; however, body lipid levels did not differ significantly in the initial controls and sham operated males maintained on the long photoperiod-low temperature regime.

At 25°C, body lipid stores were slightly higher in sham operated female fish maintained on a long photoperiod than in females exposed to a short photoperiod; the reverse was true for males. At 15°C, sham operated fish maintained on a short photoperiod were significantly fatter than sham operated fish on the long photoperiod regime.

Lipid reserves were significantly lower in female pinealectomized than in sham operated female fish exposed to the 15.5L/8.5D-25°C regime. In fish (both sexes) maintained on the long photoperiod-low temperature regime, body lipid stores were significantly greater in pinealectomized than in sham operated control fish. Body fat content was significantly greater in both sexes of pinealectomized fish than in shams exposed to the 9L/15D-25°C regime. In contrast, lipid content in pinealectomized fish was significantly lower than in sham operated animals on the 9L/15D-15°C regime.

Body lipid reserves were not significantly different in pinealectomized female fish maintained on the 9L/15D-15°C regime compared to the females exposed to the 15.5L/8.5D-15°C regime. Fat composition of pinealectomized females exposed to the long photoperiod-low temperature regime did not differ significantly from fat composition in sham operated females which experienced the short photoperiod-low temperature regime. No significant difference was observed in body fatness in pinealectomized females on the 9L/15D-25°C regime and sham operated females on the 15.5L/8.5D-25°C regime. Similarly, body lipid stores were approximately the same in pinealectomized females maintained on the long photoperiod-warm temperature regime and in sham operated females exposed to the short photoperiod-warm temperature regime.

Many of the fish maintained on the 15.5L/8.D-25°C regime spawned; under these conditions pinealectomy resulted in the initiation of gonadal regression. Compared to sham operated animals

TABLE 3.–The effects of pinealectomy on body lipid reserves in *Notemigonus* maintained on various photoperiod-temperature regimes during the early spawning season (21-day treatment).

Treatment	*n*	Sex	Dry lipid index[1] $\bar{X} \pm$ SE	Gonosomatic index[2] $\bar{X} \pm$ SE
Initial controls	6	M	91 ± 2	3.10 ± 0.22
(Late April)	6	F	88 ± 3	6.53 ± 0.97
15.5L/8.5D photoperiod:				
25°C:				
Sham operated	7	M	56 ± 4	2.79 ± 0.25
	7	F	87 ± 6	5.13 ± 1.04
Pinealectomized	5	M	45 ± 5	2.10 ± 0.09
	8	F	62 ± 4*	4.08 ± 0.73
15°C:				
Sham operated	5	M	91 ± 5	2.16 ± 0.09
	6	F	114 ± 6	5.88 ± 0.89
Pinealectomized	5	M	132 ± 8*	2.38 ± 0.14
	6	F	129 ± 6*	7.81 ± 1.22
9L/15D photoperiod:				
25°C:				
Sham operated	5	M	68 ± 5	1.16 ± 0.15
	9	F	74 ± 6	2.87 ± 0.52
Pinealectomized	6	M	110 ± 6*	2.67 ± 0.16
	5	F	101 ± 7*	3.50 ± 0.88
15°C:				
Sham operated	6	M	155 ± 10	3.12 ± 0.17
	5	F	138 ± 8	6.43 ± 0.66
Pinealectomized	5	M	124 ± 9*	3.01 ± 0.15
	7	F	117 ± 5*	5.89 ± 0.57

[1]Dry lipid index = mg lipid, less gonadal lipids/g dry body wt.
[2]Gonosomatic index = wt of gonads (g)/g body wt x 100.
*Significantly ($P < 0.05$) different than sham operated controls maintained under same photoperiod-temperature regime.

exposed to the long photoperiod, body lipid levels in pinealectomized fish were significantly lower. Gonadal regression was also initiated in sham operated fish maintained on the 9L/15D-25°C regime; spawning was observed in pinealectomized animals on this regime. Body lipid levels were significantly greater in pinealectomized fish than in sham operated fish maintained on the short photoperiod-warm temperature regime. In animals maintained at a low temperature (both photoperiods), GSIs did not differ significantly in the pinealectomized and sham operated groups. Sham operated fish, however, were significantly fatter than the pinealectomized animals experiencing the 9L/15D-15°C regime. Furthermore, under the 15.5L/8.5D-15°C regime, pinealectomized fish contained significantly more fat than the sham operated controls.

DISCUSSION

Both temperature and photoperiod have a distinct effect on body lipid reserves in *N. crysoleucas*. During the prespawning and spawning seasons, low temperature treatment (12°-15°C) favors increases in body fat stores in both sexes of *Notemigonus*, regardless of photoperiod conditions. Low temperature treatment of *Notemigonus* during the gonadal preparatory season did not result in lipid deposition, but did maintain body fat composition at a level equivalent to that in the initial controls (sacrificed at the onset of the experiment). Animals collected during the preparatory period (January) were very fat. In fact, body fat stores in this species reach a peak in late December, January, and early February. The failure of laboratory low temperature treatment to stimulate lipid deposition during the preparatory season could be due to the presence of sufficient fat reserves in the initial controls. Regardless of season or photoperiod, high temperature (25°C) acclimation favors body lipid depletion in males. During the preparatory and prespawning seasons, body fat depletion is also observed in females exposed to warm temperatures. Compared to initial controls (animals sacrificed at the beginning of the experiment), lipid levels in *Notemigonus* maintained at warm temperatures during the early spawning season were not appreciably altered. The failure of warm temperature treatment to deplete lipid reserves in females during the early spawning season may be due to the relatively low levels of fat in the initial controls. Fish maintained at warm temperatures were fed twice daily whereas fish exposed to low temperatures were fed only once a day; warm temperature animals consumed four to five times more food than the low temperature fish. Since the fish in all experiments were fed ad libitum, the differences in body lipid levels should not be due entirely to higher metabolic rates at elevated temperatures. Lipid synthesis and deposition is also promoted at low temperatures in several other teleost species (Blazka 1958; Brown 1960; Dean and Goodnight 1964; Knipprath and Mead 1968; de Vlaming and Pardo 1975). The means by which temperature acts to control lipid metabolism is not fully understood, but Kinne (1960) reported that the efficiency of food conversion in *Cyprinodon macularis* is maximal at lower temperatures. Furthermore, enzyme systems (Hochachka 1969) and hormones (de Vlaming and Pardo 1975; Pardo and de Vlaming in press) involved in lipid metabolism in fishes appear to be temperature sensitive.

At low temperatures, short photoperiods are more effective than long photoperiods at stimulating lipid deposition in *Notemigonus*. In all of the experiments reported here, body lipid reserves were higher in female fish exposed to the short photoperiod-low temperature regimes than in females maintained on long photoperiod-low temperature regimes. With the exception of the experiment conducted during the prespawning season, similar results were obtained with males. Short photoperiods also compliment the lipid depleting effects of warm temperatures. In two of the three experiments summarized here, body fat reserves were significantly lower in fish (both sexes) exposed to the short photoperiod-warm temperature regime than in animals maintained on the long photoperiod-warm temperature regime. Thus, in *Notemigonus*, the effects of photoperiod on lipid metabolism are temperature dependent. Specifically, in combination with a low temperature, short photoperiods favor body fat deposition, but at a high temperature, short photoperiods accelerate depletion of lipid reserves. The fact that short photoperiods have opposing effects on lipid metabolism depending on temperature is, at the present time, an enigma. Apparently, however, changing environmental temperatures can differentially sensitize *Notemigonus* to daylength. Roberts (1964) showed that photoperiod changes can alter metabolic pat-

terns in sunfish. In *F. similis*, short photoperiods promote fattening whereas long photoperiods result in lipid depletion (de Vlaming, Sage, Charlton, and Tiegs; de Vlaming et al. in press). Other than these studies, little is known concerning the potential role of daylength in controlling fattening cycles in teleosts.

The results presented here on temperature and photoperiod effects on fat storage are consistent with environmental data. Lipid levels are lowest in *Notemigonus* collected during July, August and early September; environmental temperatures are high during this time and daylength is decreasing. From mid-September through December daylength and temperature continue to decrease. Fat stores increase progressively during this time. Beginning in mid or late February, lipid reserves are progressively depleted until late June or July. During this time, daylength and temperature are increasing.

A progressive decrease in body fat reserves was observed in *Notemigonus* collected during the preparatory, prespawning and spawning seasons respectively. These data indicate that there may be a relationship between lipid stores and reproduction. Other investigators presented evidence of body fat depletion associated with increasing gonadal activity (Lovern 1934; Lühmann 1953; Idler and Bitners 1960; Woodhead 1960; Wilkins 1967; Lasker 1970). A long photoperiod, in combination with warm temperatures, is required for final gonadal maturation and spawning in *Notemigonus* (de Vlaming 1975). These conditions result in depletion of fat stores in this species. The fat depleted from body storage sites could possibly be utilized for the energy demands of reproduction; in females, some of the body lipids may also be converted to yolk precursors and transported to the developing oocytes. So gonadal activation by long photoperiod-warm temperatures regimes may result in mobilization of body lipid reserves. Possibly, however, gonadal maturation may depend on the prior activation of lipid mobilization enzyme systems by long photoperiod-warm temperature regimes. The former hypothesis gains some support from observations of several investigators (e.g., Kobayashi 1953; Egami 1955; Oguro 1956) which indicate that sex steroids stimulate lipid synthesis in fishes. In vitro studies with *Notemigonus* liver preparations imply that estradiol-17β stimulates synthesis and transport of lipid by this tissue (Shing and de Vlaming unpubl. data). My intention is not to imply that only sex steroids are involved in regulation of lipid metabolism. Indeed, other hormones such as insulin (de Vlaming and Pardo 1975) and prolactin (see below) have distinct effects on fat metabolism in *Notemigonus*.

Low temperatures, regardless of photoperiod, maintain vitellogenesis and spermatocyte proliferation in *Notemigonus*, but will not stimulate final ovarian or testicular maturation (de Vlaming 1975). Low temperatures also maintain or increase body lipid reserves in this species. These observations lend further support to the suggestion that fat stores are in some way related to reproductive activity.

Short photoperiod-warm temperature regimes cause gonadal regression in *Notemigonus* (de Vlaming 1975). Body fat depletion also occurs under these conditions. Obviously this fat depletion is not associated with increased gametogenic activity. Body lipid reserves also decreased in fish maintained on long photoperiod-warm temperature regimes. Therefore, depletion of body fats may be primarily associated with increased energy requirements at high temperatures. In *Notemigonus*, however, there is some indication that sex steroid secretion is stimulated or remains high in fish maintained on a short photoperiod-warm temperature regime. Specifically, fish exposed to these conditions either develop or maintain nuptial coloration. If such is the case, sex steroids may be involved in mobilization and/or utilization of lipid reserves.

In a majority of the experiments reported here, pinealectomy had a pronounced effect on body fat reserves in *Notemigonus*. The effects of pinealectomy on fat metabolism depend on the photoperiod-temperature regime to which the experimental animals are exposed. In all three experiments, body lipid levels were significantly lower in pinealectomized than in sham operated females exposed to the long photoperiod-warm temperature regime; similar results were obtained with males in one experiment. Body lipid content was significantly greater in pinealectomized than in sham operated females in two of the three experiments where fish were exposed to a short photoperiod-warm temperature regime; similar results were obtained in only one experiment with males. These data indicate that, in fish maintained at warm temperatures, the effects of pinealectomy depend on photoperiod conditions. During the prespawning and spawning seasons, pinealectomy reversed the effects of photoperiod on fish

exposed to a warm temperature. For example, lipid levels were not significantly different in pinealectomized fish exposed to the short photoperiod-warm temperature regime and sham operated animals maintained on the long photoperiod-warm temperature regime; nor was fat content significantly different in sham operated animals exposed to the short photoperiod-warm temperature condition and pinealectomized fish maintained on the long photoperiod-warm temperature regime (Tables 2, 3).

In all three of the experiments summarized here, body fat reserves were significantly greater in pinealectomized than in sham operated females maintained on the long photoperiod-low temperature regime; similar results were recorded in two of the experiments with males. Body fat composition was significantly lower in pinealectomized than in sham operated females exposed to a short photoperiod-low temperature regime; similar differences were noted with males in two of the experiments. These data further confirm the suggestion that the effects of pinealectomy on lipid metabolism in *Notemigonus* depend on photoperiod. In two of the experiments, fat content did not differ significantly in pinealectomized fish maintained on the long photoperiod-low temperature regime and sham operated animals exposed to the short photoperiod-low temperature regime; nor were significant differences noted in fat levels when the reverse comparison was made (Tables 2, 3).

The data obtained at both high and low temperatures indicate that the pineal in *Notemigonus* may have some role in receiving and/or integrating light information. Such a suggestion seems likely since the pineal may either facilitate or retard lipid deposition in this species. Several morphological and electrophysiological studies suggest that the pineal in some teleosts functions as a photoreceptor (cf. de Vlaming 1974). Light microscope studies on the pineal of *Notemigonus* also indicate a sensory function (Vodicnik and de Vlaming unpubl. data). If the pineal in *Notemigonus* is a photoreceptor involved by some means in measuring daylength, then removal of this organ from fish maintained under different photoregimes might be expected to have variable effects on lipid metabolism. Urasaki (1972a, b) has also shown that the effects of pinealectomy on reproductive function in *Oryzias latipes* vary with photoperiod conditions.

The effects of the pineal on lipid metabolism in *Notemigonus*, however, do not depend entirely on light information. For example, in fish maintained on a long photoperiod during the prespawning and spawning seasons, pinealectomy accentuated lipid deposition at low temperatures and lipid depletion at a high temperature. Temperature may not, however, act on the pineal directly. High temperatures cause lipid catabolism and low temperatures favor lipid deposition. Temperature may act directly on lipid metabolism enzyme systems or indirectly to stimulate hormone secretion from various endocrine glands. In *Notemigonus*, light information serves only to modify the effects of temperature on lipid metabolism. Thus, the pineal could function at all temperatures as a light receptor and/or integrator. Light information may be differentially interpreted (at different temperatures or at different times of the year) at some other level such as the hypothalamus and/or pituitary.

Whether the pineal in *Notemigonus* exerts its effects on lipid metabolism via neural or hormonal pathways is not presently known. Most morphological studies on the teleost pineal have stressed the dual sensory and secretory appearance of this organ (cf. de Vlaming 1974). A dual sensory-secretory function is also indicated by light microscope studies on the pineal of *Notemigonus*. Histochemical and biochemical data show that the teleost pineal has an active indolamine metabolism (Quay 1965; Hafeez and Quay 1969; Fenwick 1970; Owman and Rüdeberg 1970). Melatonin has inhibitory effects on reproductive function in various teleosts (Fenwick 1970; Urasaki 1972c; de Vlaming, Sage, and Charlton 1974). Melatonin treatment decreases lipid reserves in *F. similis* maintained on a long photoperiod-low temperature regime (de Vlaming, Sage, Charlton, and Tiegs 1974); if melatonin acts as the mediator of pineal action in *Notemigonus*, one might then expect pinealectomy to increase fat levels in fish exposed to a long photoperiod-low temperature regime. Pinealectomy did indeed have these results under this regime. During July, melatonin therapy of *F. similis* exposed to a short photoperiod-low temperature regime stimulated lipid deposition (de Vlaming, Sage, Charlton, and Tiegs 1974). If the mediator of pineal activity in *Notemigonus* is melatonin, one might predict that pinealectomy would decrease body lipid stores in animals exposed to a short photoperiod-low temperature regime. Such results were observed in the experiments reported here. Interestingly,

lighting conditions were reported to alter the secretory activity in the glandular appearing pineals of *Gambusia affinis* and *Symphodus melops* (Chèze and Lahaye 1969; Chèze 1970). Possibly then, the pineal in some teleost species may function as a neuroendocrine transducer of photoperiod information. If the pineal is a neuroendocrine organ, melatonin could conceivably be one of the hormones produced by this organ. Although the pineal of *Notemigonus* does seem to be involved in photoreception, available evidence does not allow one to conclusively state that this organ is neuroendocrine in nature or that pineal-produced melatonin functions as a chemical messenger.

The pineal may modify fat stores in *Notemigonus* by influencing hypothalamic and/or pituitary function. Indeed, de Vlaming and Vodicnik (in press) showed that pinealectomy alters hypothalamic gonadotropin releasing activity and pituitary gonadotropin levels. Several investigators reported that prolactin has a pronounced affect on lipid metabolism in teleost fishes (Lee and Meier 1967; Meier 1969; Mehrle and Fleming 1970; Joseph and Meier 1971; Meier et al. 1971; de Vlaming and Sage 1972; Sage and de Vlaming 1973; de Vlaming et al. in press; Pardo and de Vlaming in press). Furthermore, melatonin treatment significantly reduces pituitary prolactin activity in *F. similis* (de Vlaming, Sage, Charlton, and Tiegs 1974). These authors suggested that the effects of melatonin on lipid metabolism in this species may be due in part to the effects of this indolamine on pituitary prolactin release. Whether pinealectomy alters pituitary prolactin secretion is not presently known. Investigations are presently in progress to examine this possibility. Prolactin does stimulate lipid depletion from in vitro liver preparations of *Notemigonus* incubated at high temperatures and promotes fat synthesis in liver preparations incubated at low temperatures (Pardo and de Vlaming in press).

The effects of pinealectomy on lipid reserves in *Notemigonus* may result from changes in reproductive activity. This suggestion seems rather unlikely since pinealectomy frequently resulted in significant changes in body fat levels without appreciably altering gonadal activity.

The data presented here favor the view that the pineal is a photoreceptor or integrates light information and plays an important role in regulating physiological processes in teleost fishes.

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RELATIONSHIPS BETWEEN ZOOPLANKTON DISPLACEMENT VOLUME, WET WEIGHT, DRY WEIGHT, AND CARBON[1]

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ABSTRACT

Interconversion of various measures of zooplankton biomass have great utility in studies requiring nondestructive techniques, or for interpretation of past data. In establishing predictive relationships between such measures, the appropriate regression to use is the geometric mean estimate, which provides a regression line in which the regressions of X on Y and Y on X are identical. We have employed this type of analysis in determinations on samples from diverse sea areas in different seasons and have determined that statistically significant relationships exist between carbon, wet weight, displacement volume, and dry weight when a constant technique is used. The slope of the regression line for log transformed values for carbon vs. dry weight and wet weight vs. displacement volume was sufficiently close to unity to assume a straight percentage conversion between these values. Carbon was 31-33% of dry weight and wet weight was 72-73% of displacement volume, according to our techniques. Comparability of different techniques for a biomass measurement may be poor, especially in the case of displacement volume and wet weight measurements due to variations in the interstitial water content. Moreover, interstitial water content varies inversely with total biomass density, which accounts for the absence of a simple percentage relationship between wet weight or displacement volume and other measures of zooplankton biomass.

Biomass is a classic and useful measure of the zooplankton standing crop. A number of techniques exist to measure it. Four commonly used techniques involve measurement of displacement volume (Yentsch and Hebard 1957; Frolander 1957; Sutcliffe 1957; Tranter 1960; Ahlstrom and Thrailkill 1963), wet weight (Nakai and Honjo 1962), dry weight (Lovegrove 1966), and carbon (Curl 1962; Platt et al. 1969). For most studies, especially those determining energy flow through food chains, carbon is the most fundamental of these gross measures. Many zooplankton collections frequently serve several purposes and the destructive techniques required to determine carbon or dry weight frequently cannot be employed. An alternative is to measure displacement volume or wet weight, and convert the data into either dry weight or carbon. These latter techniques, if done properly, are nondestructive since the organisms can still be identified when re-suspended in liquid. There is an obvious need for conversion factors that reliably define the relationship between the various biomass measures. This need also arises when data based on different techniques are compared. Although conversion factors exist in the literature, they often are based on data from restricted sea areas. Further, in some cases, biomass determinations were made by techniques which are no longer recommended (see Lovegrove 1966). The objective of this paper is to more satisfactorily define the relationships between the biomass measures mentioned above. Using both data derived from samples collected from diverse oceanic areas over the past 6 yr and data selected from the literature, we have empirically determined linear regression equations relating pairs of biomass measures.

THEORETICAL CONSIDERATIONS

Ideally, any two biomass measures, X and Y should be related by a constant of proportionality, a, such that

$$Y = a X^{\beta}, \tag{1}$$

where $\beta = 1.0$. A measurement error or bias which occurs as a constant fraction of the biomass results only in a change in the value of a. When natural variability or an error factor(s) in X or Y is disproportionate or inversely proportional to the amount of biomass, β cannot be assumed to equal

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1.0 and Y is not a simple percentage of X. If β is a constant, then the $\log_{10}$ of the two measures will be linearly related:

$$\text{Log}_{10}(Y) = \text{Log}_{10}(a) + \beta \text{Log}_{10}(X). \quad (2)$$

In the sections which follow, we will show that in most cases $\beta \neq 1.0$ and equation (2) is adequate for describing the linear relationship between log transformed measures of biomass.

METHODS

The station locations where samples were collected are shown in Figure 1 (symbol key given in Table 1). At many of these stations, more than one sample was collected. A single symbol may represent a number of collections as indicated in Table 1. Not shown are the stations of *Gosnold* 140, a cruise to the coastal upwelling region off Peru.

Collections were made with 70-cm or 100-cm diameter ring nets, 70-cm diameter Bongo nets (McGowan and Brown 1966), or the 50×50 cm net (Bé et al. 1971), all equipped with a flowmeter (Table 1). In shallow regions, Buzzards Bay, *Atlantis II* 52 (continental Atlantic shelf), *Gosnold* 140 (Peru Current), *Gosnold* 166 (New York Bight), tows were made to near the bottom. In deeper waters, oblique tows were generally made to below 300 m.

Ring net collections were generally split with a plankton splitter (McEwen et al. 1954). One-half was preserved in 10% buffered Formalin[4] for displacement volume analysis and the other half was frozen in a chest freezer for wet weight, dry weight, and carbon analyses (re Bermuda Table 1: Menzel and Ryther (1961) do not state how this half was stored prior to analysis). A similar procedure was carried out for Bongo net collections; one of the paired samples was preserved in Formalin while the other was frozen.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

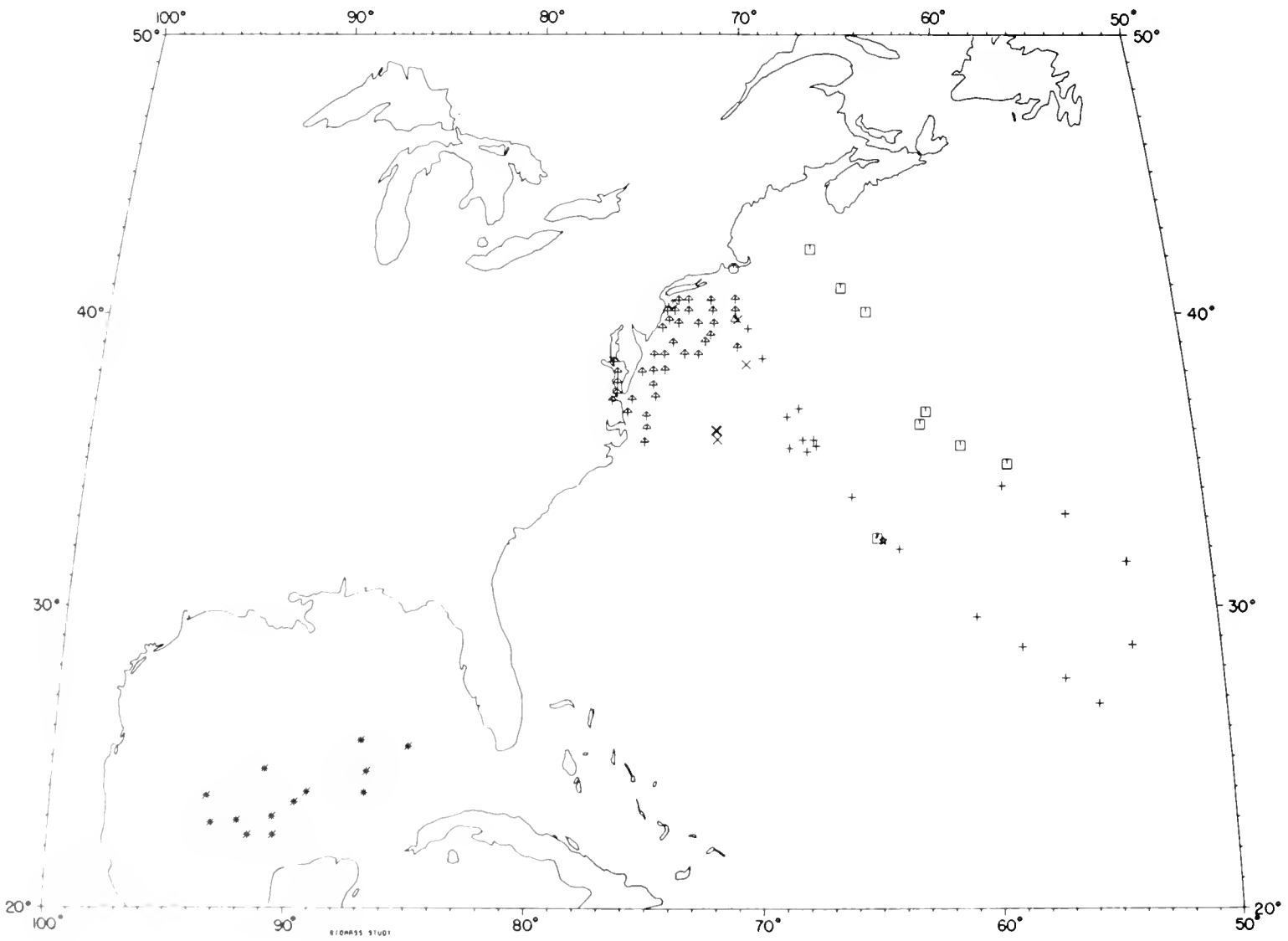

FIGURE 1.—Location of zooplankton collection sites. For symbols, see Table 1.

TABLE 1.—Number of observations and symbol designation for each cruise or area from which zooplankton samples were collected. The symbols are used in Figures 1 and 3-5.

Cruise or area	Symbol	Date(s)	Number of observations: Displacement volume	Wet weight	Dry weight	Carbon	Type of net (mesh)
Buzzards Bay	○	Jan.-June 1972	15	16	16	16	70 cm (240 μm) diam.
Slope	△	June-Aug. 1972	14	12	14	14	100 cm (333 μm) diam.
Bermuda[1]	☆	1957-59	52	0	52	0	100 cm (366 μm) diam.
Gosnold 140	□	May 1969	[2]0	0	33	33	70 cm (240 μm) diam.
Gosnold 166	◇	June 1970	32	0	33	33	70 cm (240 μm) diam.
Atlantis II 48	✦	Nov. 1968	0	0	20	20	70 cm (240 μm) diam.
Atlantis II 52	✢	Sept. 1969	0	0	37	37	70-cm (240 μm) diam. Bongos
Atlantis II 71	+	Sept. 1972	27	43	43	42	100 cm (333 μm) diam.
Chain 111	⊡	Feb. 1973	13	13	13	0	100 cm (333 μm) 70-cm Bongos
Knorr 35 II	×	Nov. 1973	10	11	11	0	100 cm (333 μm) 70-cm Bongos
Bé North Atlantic	◇	—[3]	229	229	229	0	50 × 50 cm (202 μm)
Bé South Atlantic	+	—[4]	176	192	193	0	50 × 50 cm (202 μm)

[1]Data from Menzel and Ryther (1961).
[2]Omitted, bad data.
[3]See Bé et al (1971) for geographical and seasonal coverage.
[4]Data from Bé (footnote 5).

Displacement volumes were measured by one of two techniques. The Mercury Immersion method of Yentsch and Hebard (1957) was used to determine the values given by Menzel and Ryther (1961-Bermuda), by Bé et al. (1971-North Atlantic) and Bé (1973-unpubl. data for the South Atlantic).[5] A modified version of the Mercury Immersion technique was used to measure displacement volumes on *Gosnold* 140, but further work has shown that the method has significant variable errors and is unreliable (Grice and Wiebe unpubl. data). We have not, therefore, used the *Gosnold* 140 displacement volume data. All other displacement volumes were measured by the method described by Ahlstrom and Thrailkill (1963) after removal of all organisms larger than 5 cc. For split samples, organisms larger than 5 cc were removed prior to the split. On *Gosnold* 166, displacement volumes were run prior to sample preservation (see Vaccaro et al. 1972 for data) and again 2 yr after preservation. Contrary to the findings of Ahlstrom and Thrailkill (1963), shrinkage did not occur (Figure 2). These samples were, however, heavily dominated by copepods (Wiebe et al. 1973) which are least likely to undergo shrinking.

Wet weight was measured by straining the plankton through a 333-μm plankton gauze, rinsing with freshwater, and blotting the remaining mass on absorbant paper towels until water was no longer absorbed onto the towel. The biomass was then transferred to a pre-weighed glass jar with a stainless steel spatula. The jar was weighed on a Mettler balance to ± 2.5 mg and the wet weight of plankton determined by subtracting the jar weight from the total. Each jar was then dried to constant weight in an oven at 60°C. This

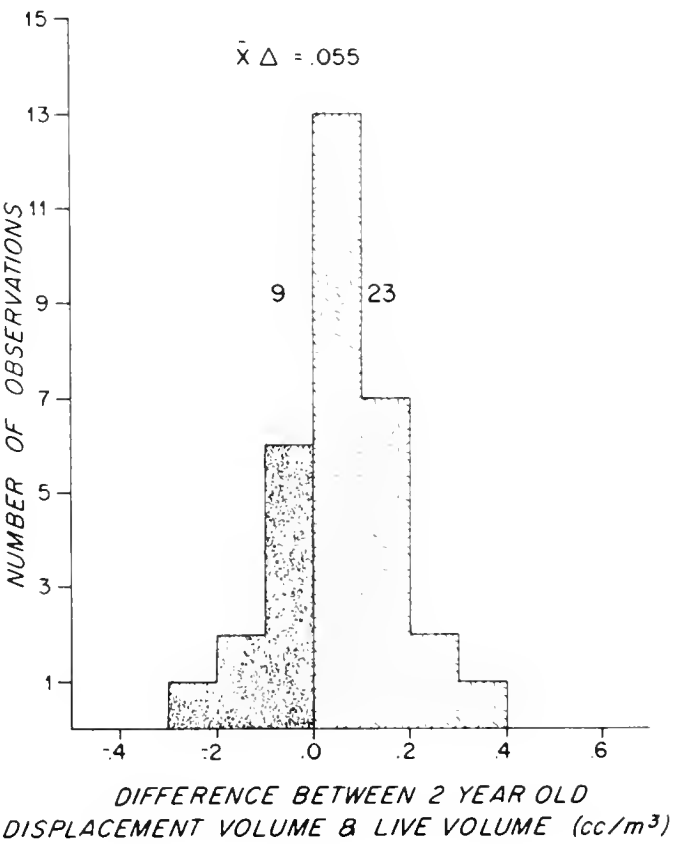

FIGURE 2.—Distribution of differences between displacement volumes measured 2 yr after preservation and the live displacement volume. The live displacement volumes ranged from 30 to 321 cc (0.57 to 2.53 cc/m³) and the 2-yr values ranged from 38 to 340 cc (0.58-2.40 cc/m³).

[5]Bé, A. W. H. 1973. Studies of zooplankton standing stock in the South Atlantic. Unpubl. final tech. rep. to Natl. Sci. Found., 14 p.

frequently took 2 wk or longer owing to the large volumes of plankton collected. Dried samples were pulverized and an aliquot(s) of the powder used to determined carbon in either a Perkin-Elmer No. 240 or a Hewlett Packard No. 185 B carbon, hydrogen, nitrogen analyzer. A number of exceptions to this procedure are evident in Table 1. In some cases, wet weight was not measured; in others, carbon was not determined.

All data presented below were standardized to biomass per cubic meter and then logarithmically transformed (base 10) before use in the regression analyses.

RESULTS

Several regression lines can be used to express the relationship between pairs of variables (Ricker 1973). The appropriate one is determined by the frequency distribution of the parent population as well as the nature of the error sources in the measurements (natural or measurement error). Since the biomass measures are all subject to natural variability and measurement error and since the observations presented cannot be assumed to be a random sample from a bivariate normal population, the "geometric mean (GM) estimate of the functional regression of Y on X" (Ricker 1973:412) is appropriate. As Ricker points out, this regression line minimizes the sum of the products of the vertical and horizontal distance of each point from the line. Thus, the GM regression lines of Y on X and X on Y are identical. Given the GM regression equation:

$$Y' = u + vX', \tag{3}$$

where Y' = log (Y) and X' = log (X), one can determine both an X given Y or Y given X. Although Ricker's (1973) paper should be consulted for an in depth discussion of the assumptions and computations, we note that the slope, v, is given by:

$$v = \pm \frac{b}{r} = \pm \sqrt{\frac{\Sigma(y_i' - \overline{Y}')^2}{\Sigma(x_i' - \overline{X}')^2}}, \tag{4}$$

where b is the slope of the predictive regression of Y' on X' and r is the correlation coefficient. The Y'-axis intercept, u, is easily determined by:

$$u = \overline{Y}' - v\overline{X}'. \tag{5}$$

Plots of the values used in the GM regressions are given in Figures 3-5. The equations are listed in Table 2. All equations have slopes significantly different from zero ($P<0.001$). As indicated above, in the case where β of Equation (1) (v of Equation (3)) is equal to 1.0, one biomass measure is a straight percentage of another. The only regressions with a v approaching 1.0 compare dry weight to carbon and displacement volume to wet weight. In these cases, predicted carbon varies from 31 to 33% of zooplankton dry weight and predicted wet weight varies from 72 to 73% of displacement volume. In all other regressions, a variable bias is present which causes v to deviate from 1.0. We believe that a large portion of the bias is caused by the interstitial water present in displacement volumes and wet weights. This bias is inversely proportional to the sample size; i.e., a small sample

TABLE 2.–Functional (geometric mean) regression equations for pairs of biomass measures. Carbon: C; dry weight: DW; wet weight: WW; displacement volume: DV; Bé et al. (1971) and Bé (footnote 5) wet weight: BWW; Bé et al. (1971) and Bé (footnote 5) displacement volume: BDV; Bé et al. (1971) and Bé (footnote 5) dry weight: BDW; Platt et al. (1969) dry weight: PDW; Platt et al. (1969) carbon: PC. Logarithms to the base 10.

Equation	Regression equation	N	Variance of slope	r^2
1	Log (DV) = −1.429 + 0.808 Log(C)	87	0.0003187	0.96
2	Log(WW) = −1.537 + 0.822 Log(C)	70	0.0008303	0.92
3	Log(DW) = 0.508 + 0.977 Log(C)	193	0.0001438	0.97
4	Log(DV) = −1.828 + 0.848 Log(DW)	161	0.0001814	0.96
5	Log(WW) = −1.983 + 0.922 Log(DW)	93	0.0005800	0.94
6	Log(DV) = 0.670 + 0.950 Log(WW)	77	0.0013729	0.90
7	Log(BWW) = −1.897 + 0.835 Log(BDW)	420	0.0009725	0.63
8	Log(BDV) = −1.826 + 0.754 Log(BDW)	404	0.0011106	0.56
9	Log(BDV) = −0.219 + 0.848 Log(BWW)	403	0.0006079	0.75
10	Log(PDW) = 0.558 + 1.024 Log(PC)	45	0.0148049	0.39
11	Log(DV)[1] = 1.048 + 0.821 Log(DW)	110	0.0010510	0.83
12	Log(WW)[1] = 0.975 + 0.946 Log(DW)	94	0.0010173	0.90
13	Log(DV)[1] = 0.078 + 1.026 Log(WW)	75	0.0022271	0.85

[1]Note that biomass data used to determine equations 1-10 were standardized to per cubic meter while the data used to determine equations 11-13 were not standardized.

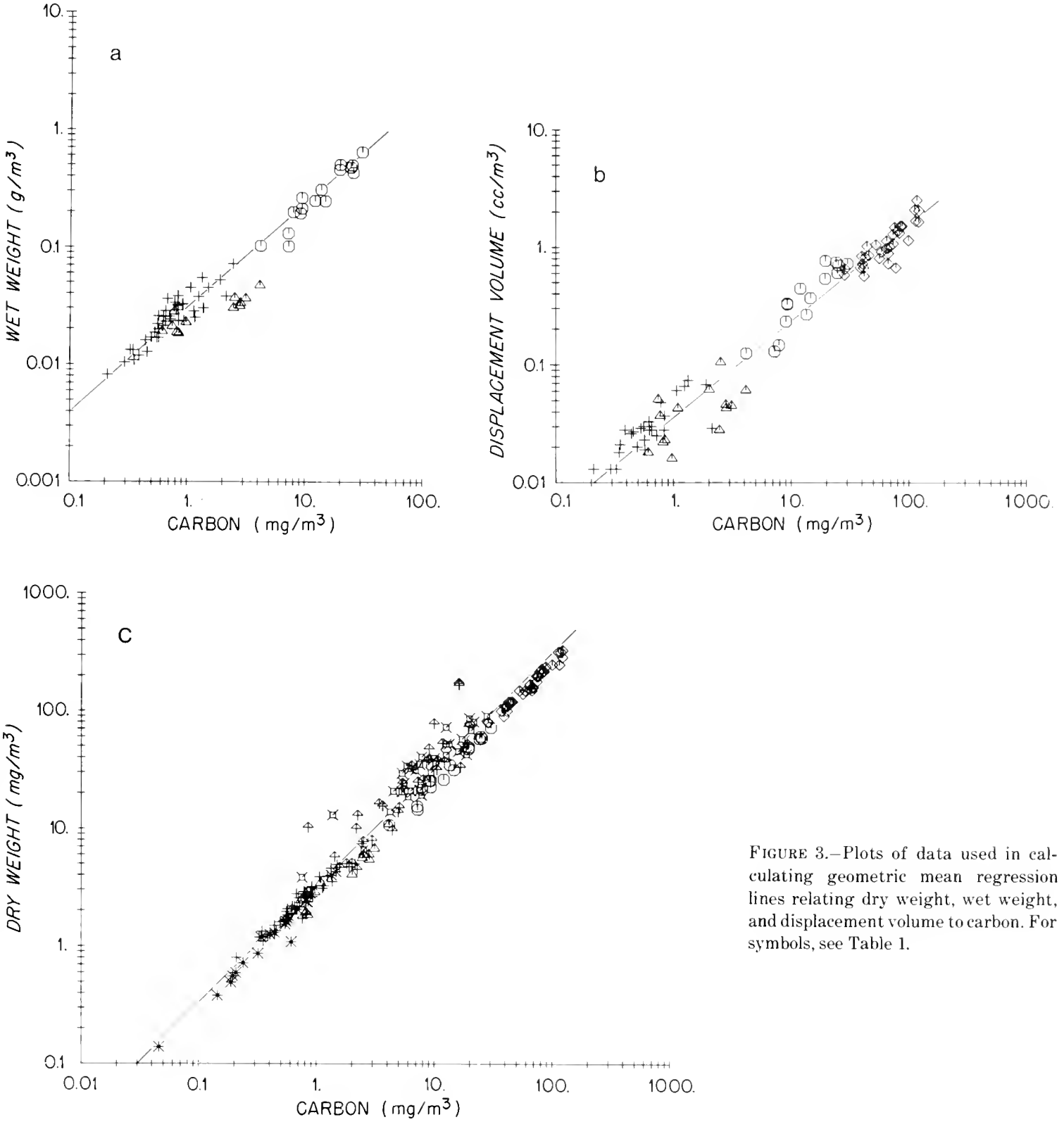

FIGURE 3.—Plots of data used in calculating geometric mean regression lines relating dry weight, wet weight, and displacement volume to carbon. For symbols, see Table 1.

appears to have a larger percentage of interstitial water than a large sample. It is evident in our log transformed raw data as well as the data standardized to biomass per cubic meter and then log transformed (see Table 4). The reason why the bias is not significantly influenced by the standardization to biomass per cubic meter results from the fact that the volume of water filtered in collecting most samples was quite similar, between 100 and 1,000 m^3, while the biomass per cubic meter varied by as much as four orders of magnitude. As a result of the variable bias, it is not valid to assume a simple percentage relationship between the other pairs of biomass estimators. For example, dry weight is approximately 5% of displacement volume for low biomass per cubic meter and approximately 13% for high biomass per cubic meter.

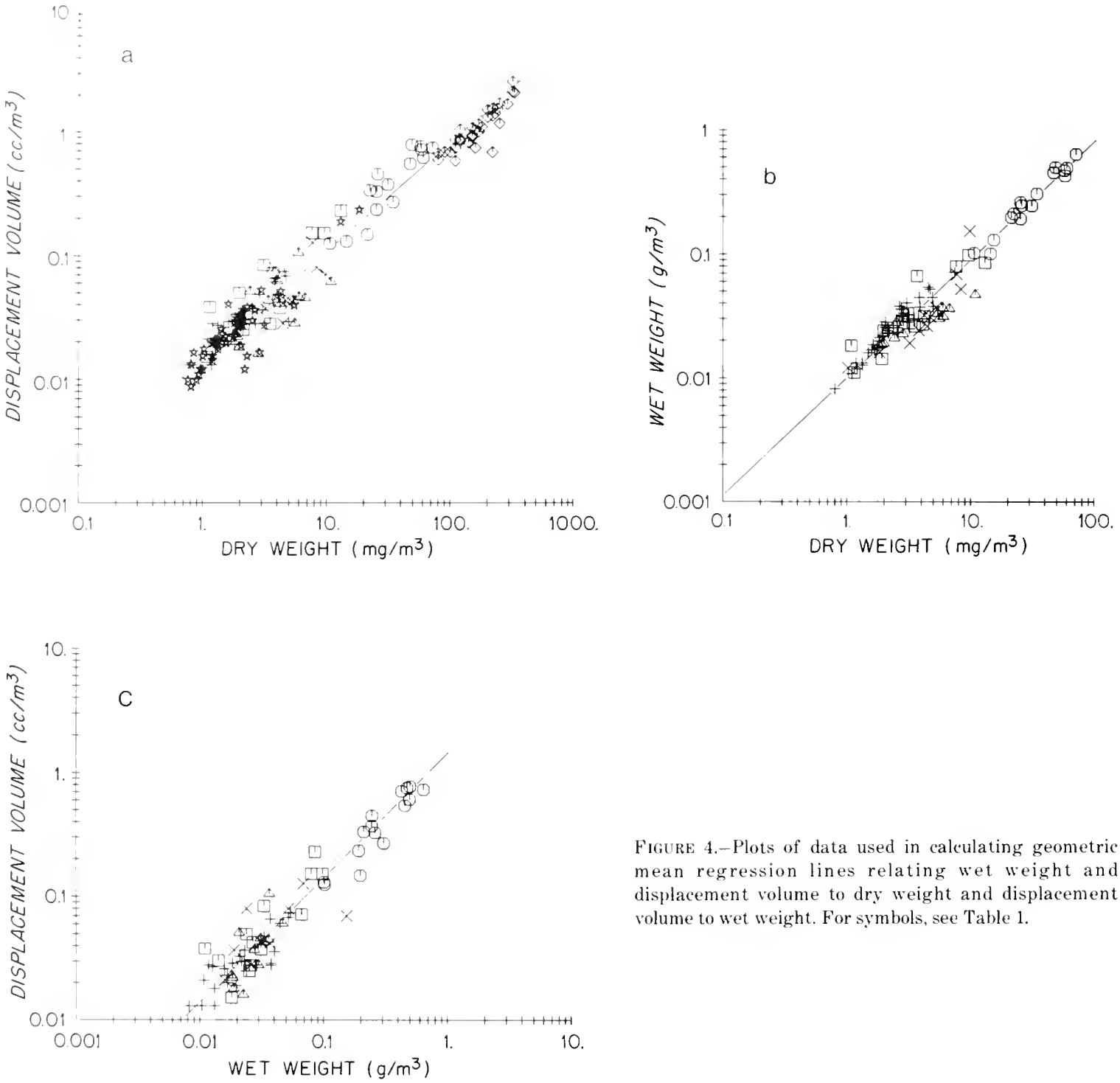

FIGURE 4.—Plots of data used in calculating geometric mean regression lines relating wet weight and displacement volume to dry weight and displacement volume to wet weight. For symbols, see Table 1.

Confidence limits can be calculated for predicted values of X or Y. Following Ricker (1973:411), the general form of the variance estimate for a single estimate of Y' given X' is:

$$S_{y'x'}^2\left(1+\frac{1}{N}+\frac{(P_{x'}-\overline{X}')^2}{SSX'}\right), \qquad (6)$$

where $S_{y'x'}^2$ is the variance of observations from the regression line in the vertical direction, N is the number of observation pairs in the regression, and $P_{x'}$ is the value of X' used to estimate Y'. In the reverse case where X' is being predicted, $S_{x'y'}^2$, SSY', $P_{y'}$, and $\overline{Y}'$ are substituted for $S_{y'x'}^2$, SSX', $P_{x'}$, and $\overline{X}'$. Because we have used GM regression equations rather than predictive regression equations, the use of Expression (6) is not strictly legitimate. However, Ricker (1973:413) finds the error involved is small and concludes that ". . . it is possible to recommend using ordinary symmetrical confidence limits for the GM regression. They are a reasonable approximation to the true limits and will rarely lead to incorrect conclusions."

The values required to use Expression (6) to calculate confidence limits for predicted X's or Y's are given in Table 3. This variance and the t_{95} value are used to construct confidence limits for the logarithms:

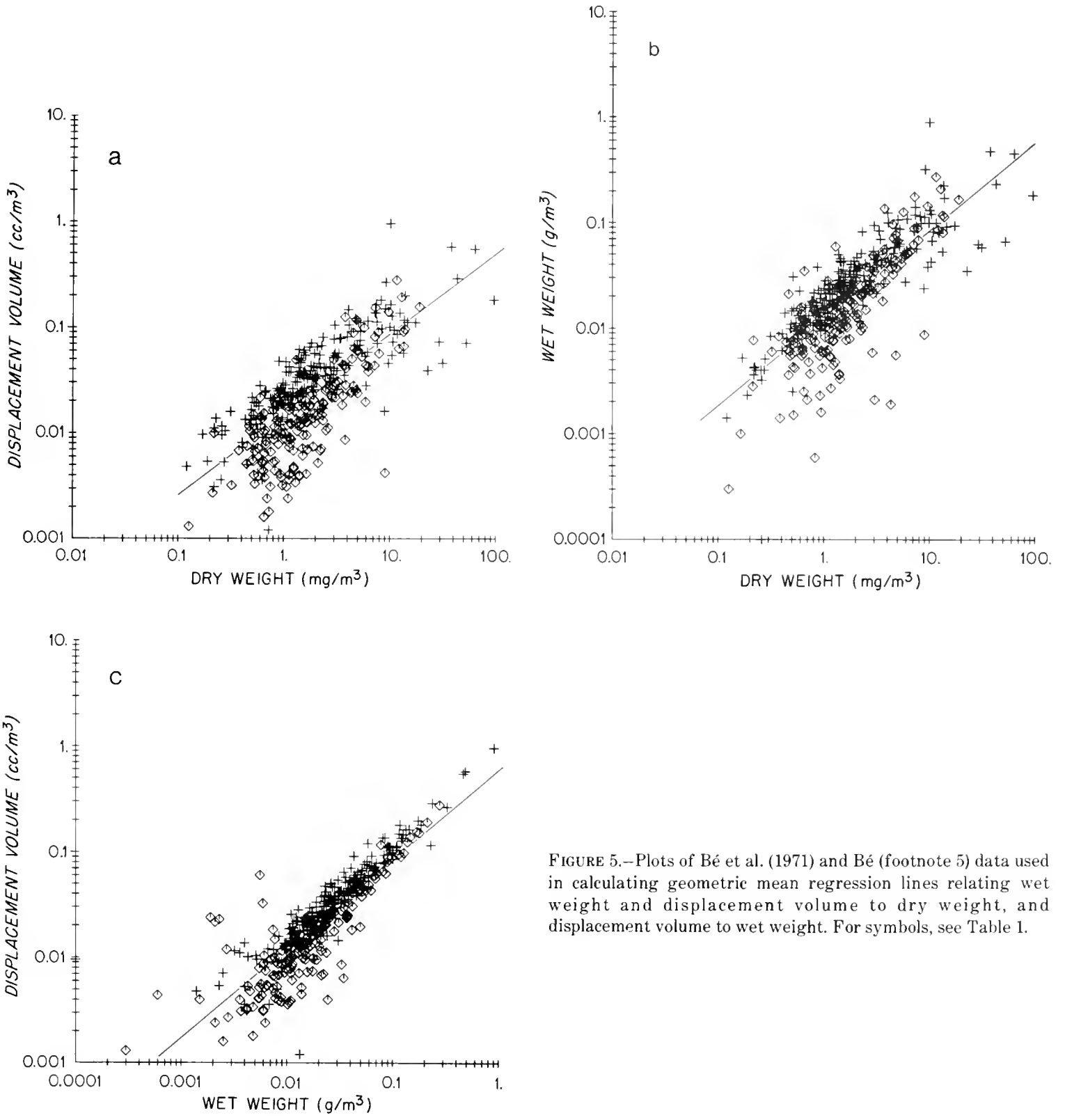

FIGURE 5.—Plots of Bé et al. (1971) and Bé (footnote 5) data used in calculating geometric mean regression lines relating wet weight and displacement volume to dry weight, and displacement volume to wet weight. For symbols, see Table 1.

$$Y' \pm t_{95}\sqrt{\hat{\mathrm{V}}\mathrm{ar}\, Y'} \text{ or } X' \pm t_{95}\sqrt{\hat{\mathrm{V}}\mathrm{ar}\, X'}.$$

Antilogging provides multiplicative limits for the untransformed data. For example, suppose an estimate of carbon is desired having measured a displacement volume (Y) of 0.1 cc/m^3. Using Equation 1 in Table 2 and Expression (6) the following values result:

Log (Y)	*Log* (X)	X(*mg*/m^3)	*Log (upper limit)*	*Upper limit*	*Log (lower limit)*	*Lower limit*
-1.0	0.557	3.61	0.916	8.25	0.198	1.58

Thus, the antilogged estimate of carbon is 3.6% of the displacement volume with upper and lower 95% limits of 8.3% and 1.6%.

Comparison of the regressions based upon the data of Bé et al. (1971) and Bé (footnote 5) with the

TABLE 3.—Values required to calculate 95% limits for values of X or Y predicted from regression equations in Table 2. The t_{95} value is based on the number of observations for each regression. For comparison abbreviations see Table 2 caption.

Comparison	t_{95}	Prediction of Y			Prediction of X		
		$\bar{X}$	SSX	S^2_{yx}	$\bar{Y}$	SSY	S^2_{xy}
DV vs. C	1.98	0.8310	69.3796	0.022095	−0.7573	47.1915	0.032483
WW vs. C	2.00	0.2076	22.0394	0.018282	−1.3663	16.1224	0.024992
DW vs. C	1.96	0.6456	117.7726	0.016987	1.1383	115.5700	0.017311
DV vs. DW	1.96	0.8369	106.4068	0.019299	−1.1181	79.6486	0.025782
WW vs. DW	1.98	0.6473	19.9736	0.011558	−1.3868	18.0252	0.012808
DV vs. WW	1.99	−1.3706	17.3509	0.023822	−1.2347	17.4390	0.023701
BDV vs. BDW	1.96	0.2408	85.9032	0.093843	−1.6446	63.8768	0.092518
BWW vs. BDW	1.96	0.2343	87.7505	0.085121	−1.7010	73.2612	0.077210
BDV vs. BWW	1.96	−1.6813	89.1699	0.054240	−1.6439	85.8228	0.056355
PDW vs. PC	2.02	0.6992	1.9394	0.028706	1.5742	2.0334	0.027378
DV vs. DW[1]	1.99	0.3918	25.6916	0.026995	1.3693	17.3094	0.040067
WW vs. DW[1]	1.99	0.1432	10.9063	0.011083	1.1101	9.7621	0.012383
WW vs. DV[1]	1.99	1.0998	7.1279	0.015876	1.2063	7.5091	0.015070

[1]Cafculated values based on biomass data which was not standardized to per cubic meter.

regressions based solely on our data reveals two notable features. First, the slopes of the regressions based on the same biomass estimators; i.e., displacement volume versus dry weight, wet weight versus dry weight, and displacement volume versus wet weight, are significantly different ($P<0.05$). This was tested by calculating approximately 95% limits for the difference in slopes using standard normal distribution theory: $(r_{w'} - r_{Bé}) \pm 1.96\sqrt{\hat{\mathrm{V}}\mathrm{ar}\, r_{w'} + \hat{\mathrm{V}}\mathrm{ar}\, r_{Bé}}$. As was true in our cases, if $\Delta r \pm 95\%$ limit does not cross 0, the slopes are significantly different. In all cases, slopes of the regressions derived from our data are closer to 1.0.

The second feature is that there is a significant difference ($P<0.005$) in the variance of observations from the regression lines. The Bé et al. (1971) and Bé (footnote 5) variance for displacement volume versus dry weight is 4.9 times larger than that calculated for our data; for wet weight versus dry weight, it is 7.4 times larger; for displacement volume versus wet weight it is 2.3 times larger.

These differences are probably due in large part to the differences in methods used to determine displacement volume and wet weight. The mercury immersion method Bé et al. (1971) and Bé (footnote 5) used to measure displacement volume provides estimates substantially more variable than the technique used by us (Grice and Wiebe unpubl. data). The increased variability of their wet weights may have resulted from their use of a vacuum to remove some of the interstitial water.

One implication of the lower slopes for the Bé et al. (1971) and Bé (footnote 5) data is that it appears the percentage of interstitial water in their samples may change more radically with increasing biomass than in our samples. This inference is drawn from the calculated values relating dry weight to wet weight and displacement volume in percent (Table 4). The alternate explanation is that as biomass per cubic meter increases, the percentage of wet weight or displacement volume that constitutes dry weight increases as a result of a decrease in intracellular water. It seems unlikely that this accounts for the differences between the two sets of data. Seasonal effects have been minimized by collection of samples at various times of the year and geographical effects should be similar since both studies covered wide geographical ranges.

TABLE 4.—Regression equation prediction of the percentage of displacement volume (DV) or wet weight (WW) that is dry weight (DW) for selected dry weight concentrations.

DW (mg/m^3)	Bé et al. (1971) and Bé (footnote 5)		This study		DW[1] (g)	This study	
	% DV	% WW	% DV	% WW		% DV	% WW
0.1	3.80	5.39	5.10	8.95	0.1	5.9	9.4
1.0	6.70	7.89	6.95	10.95	1.0	9.0	10.6
10.0	11.80	11.53	9.48	11.27	10.0	13.5	12.0
100.0	20.80	16.87	12.94	12.65	100.0	20.5	13.6

[1]Calculated values based on biomass data which were not standardized to per cubic meter.

DISCUSSION

Platt et al. (1969), in a comparison of the seasonal changes in dry weight, carbon, and caloric values of zooplankton collected from St. Margaret's Bay, Nova Scotia, found a fivefold variation in caloric content per unit dry weight. As a result they concluded ". . . that there is no single conversion factor that will serve to convert biomass of zooplankton, expressed as dry weight, to its energy equivalent." A similar conclusion was inferred for the conversion of dry weight to carbon. They found, however, that the carbon content of zooplankton could be used to predict the energy equivalent. These results appear to contradict our finding that a statistically significant relationship does exist between pairs of the different measures of biomass including dry weight and carbon. The explanation for this discrepancy lies in the fact that the data of Platt et al. represents a small segment of the extensive range of biomass per cubic meter which occurs in marine waters. This fact, coupled with high variation of the dry weight to carbon ratios, appeared to them to provide a nonsignificant relationship. We have used their data (as tabulated by Platt and Irwin 1968, table 4) to examine the fit of their data to our regression line. After transformation to logarithms (base 10), a linear GM regression line was calculated for their 45 pairs of dry weight and carbon values. While the slope of this line was significantly different from zero ($P<0.001$), it was nonsignificantly different ($P>0.05$) from ours (Table 2). However, the intercept was substantially different. This is a reflection of the fact that their carbon values average 14% of dry weight, whereas in our data the average is 32%. The wet-combustion method (described by Strickland and Parsons 1965) which they used to determine carbon apparently provides lower estimates (an average here of 58% lower) than the high temperature combustion technique we used. Sharp (1973) found that persulfate oxidation yields an average 22% lower values than high temperature combustion when these methods are used to measure total organic carbon in seawater.

In terms of variability, the observations of Platt et al. (1969) have a variance from the regression line significantly ($P<0.01$) larger than ours by a factor of 1.6.

It is clear from the comparisons of biomass measures we have carried out, and from other unpublished work performed at this laboratory, that the techniques used by various investigators in determining a particular biomass measure (such as displacement volume) provide substantially different answers which are not readily comparable. This is particularly true of displacement volume and wet weight and to a lessor degree, carbon. A similar conclusion was reached by Nakai and Honjo (1962). Only the procedure for measuring dry weight described by Lovegrove (1966) seems to have been widely adopted and values presented by various investigators using this technique seem to be intercomparable. With displacement volume and wet weight, the problem stems largely from the differing amounts of interstitial water adhering to the zooplankton at the time of measurement. We have found. as did Nakai and Honjo (1962), that for a given technique, the amount of interstitial water varies inversely with the amount of biomass being measured. The amount, however, varies from technique to technique. Efforts to significantly reduce the amount of interstitial water present appear to create additional error. Rather than simply concentrating on the reduction of interstitial water, it is more important to establish a reproduceable procedure that generates values which can be directly related to a more absolute standard such as carbon as we have tried to do. The data on which Equations 1 to 6 and 11 to 13 in Table 2 are based were developed using methods which appeared to us to involve the least amount of technique-derived error and which required little complex instrumentation.

The zooplankton biomass values used in this study encompass a significant part of the range of values an investigator is likely to encounter working in either coastal waters or the open ocean. Thus, the equations we have presented should be useful in a wide variety of situations providing the same techniques to measure biomass are employed. It is important to bear in mind, however, that situations do occur in which these equations may not apply. One example is where marine populations are dominated by salps, doliolids, jellyfish, or chaetognaths. The very high percentage of intracellular water in these organisms may cause the relationships between displacement volume or wet weight and dry weight or carbon to deviate strongly from our predicted relationships. In such cases, which in our experience occur infrequently, we recommend that dry weight or carbon be measured directly.

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EFFECTS OF VARIOUS CONCENTRATIONS OF DISSOLVED ATMOSPHERIC GAS ON JUVENILE CHINOOK SALMON AND STEELHEAD TROUT

EARL M. DAWLEY AND WESLEY J. EBEL[1]

ABSTRACT

Bioassays in shallow tanks (25 cm deep) with dissolved nitrogen and argon gas concentrations ranging from 100 to 125% of saturation in water at 15°C were conducted to determine lethal and sublethal effects on juvenile chinook salmon, *Oncorhynchus tshawytscha*, and steelhead trout, *Salmo gairdneri*. Significant mortality of both species commenced at 115% saturation of nitrogen and argon (111% saturation of total dissolved atmospheric gas pressure). Over 50% mortality of both steelhead and chinook occurred in less than 1.5 days in water at 120 and 125% of saturation. Significant differences in swimming performance, growth, and blood chemistry were measured in groups of fish tested at sublethal exposures in various concentrations of dissolved gases. Sublethal stress for 35 days at 110% dissolved nitrogen (106% total atmospheric gas) decreased normal swimming ability of chinook. Growth of both steelhead and chinook was affected by sublethal exposures in water saturated with atmospheric nitrogen and argon at 105, 110, and 115%. Blood chemistry was affected at sublethal exposures in water at 115% saturation.

Supersaturation of atmospheric gas (mainly nitrogen) in waters of the Columbia and Snake rivers—caused by spillway discharges from dams—has been well documented as a serious problem to valuable stocks of Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*. Gas bubble disease resulting from this supersaturation causes both direct and indirect mortalities. Direct mortality results from air emboli in the heart and gill filaments, destruction of vital organs, or characteristic red blood cell hemolysis (Marsh and Gorham 1905; Pauley and Nakatani 1967; Bouck et al. 1970[2]). Indirect mortality is a consequence of later invasion by disease organisms (Coutant and Genoway 1968[3]) or of increased predation due to reduced performance capabilities of the fish as the result of sublethal exposure to supersaturation.

The lowest level of nitrogen supersaturation at which juvenile salmon or steelhead trout can be exposed continually with no detrimental effects is not known. Several investigators have recorded the lowest level observed during various experiments where mortalities occurred from gas bubble disease; however, very little attention has been given to determining the effect of sublethal exposure on physiological and behavioral performance. Harvey and Cooper (1962) indicated 108-110% saturation produced gas bubble disease and subsequent mortalities in sockeye salmon alevins, *O. nerka*; Rucker and Tuttle (1948) indicated a level somewhere between 110 and 115% as being the critical range for trout. Shirahata (1966) conducted the most comprehensive study to date on the effects of various levels of nitrogen gas on rainbow trout (rainbow trout is the nonanadromous form of *S. gairdneri*, whereas the steelhead trout is the anadromous) from hatching to the swim-up stage, but such detail is lacking for other species of salmonids. In many experiments on gas bubble disease, either the water temperatures, nitrogen gas concentrations, or life stages of the test fish were omitted from record, thus making the results incomplete for critical applications.

Costs involved in alleviating the supersaturation problem in the Columbia and Snake rivers will be considerable. The extent of these costs will depend on the degree of protection required to afford a safe environment for the aquatic biota. It is imperative, therefore, that regulatory measures established to govern the level of saturation be

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[2]Bouck, G. R., G. A. Chapman, P. W. Schneider, Jr., and D. G. Stevens. 1970. Observations on gas bubble disease in adult Columbia River sockeye salmon (*Oncorhynchus nerka*). Pac. Northwest Water Lab. [Fed. Water Qual. Adm., Corvallis, Oreg.], June 30, 1970. Unpubl. manuscr., 19 p.

[3]Coutant, C. C., and R. G. Genoway. 1968. Final report on an exploratory study of interaction of increased temperature and nitrogen supersaturation on mortality of adult salmonids to U.S. Bur. of Commercial Fisheries, Seattle, Washington. Battelle Mem. Inst. Pac. Northwest Lab. Richland, Wash., November 28, 1968, 28 p.

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based upon a thorough understanding of the effects of dissolved gases on aquatic organisms.

This paper describes the results of dissolved gas bioassays with juvenile steelhead trout and spring chinook salmon, *O. tshawytscha*, conducted by the National Marine Fisheries Service during the spring of 1972. These experiments were designed to assess lethal and sublethal effects of supersaturation of atmospheric gases on test fish at levels found in the Columbia and Snake rivers during the spring freshet. Atmospheric nitrogen concentrations[1] were of major concern and test levels ranged from 100 to 125% of saturation. Special note is made of testing procedures and ramifications of the effects of these on the outcome of our tests.

METHODS

Bioassays were carried out in the laboratory in shallow tanks (25-cm water depth) to negate the effects of hydrostatic pressure compensation. These facilities were similar to those described by Ebel et al. (1971). Water flow into each test tank was maintained at 3 liters/min at a temperature of 15° ± 0.5°C. Test tanks were partitioned with perforated fiberglass plates to form four sections –in-flow area, test area A, test area B, and outflow section (Figure 1).

Supersaturated water was produced by metering 0.7 liter/min air into the suction side of a centrifugal pump which recirculated water through a 197-liter (52-gallon) closed receiver at a rate of about 190 liters/min (50 gal/min). Water pressure throughout the system was at 1.4 kg/cm^2 (20 psi) except in a short section of pipe on the discharge side of the pump where it was increased to 3.2 kg/cm^2 (45 psi) by use of a valve for additional back pressure necessary to achieve the required supersaturation. Water remained in the recirculatory system for about 10 min before passing to the test tanks. This arrangement supersaturated the water to about 145% of air saturation. Water was then piped to the test tanks where it passed over a series of perforated fiberglass plates into an inlet box with air bubbling through a bottom plate of porous polyethylene. The number of fiberglass plates and volume of air were adjusted to yield the various levels of saturation. An increase of air to water interface directly decreased the excess dissolved gas content.

Water samples for dissolved gas analyses were collected throughout the tests near the center of each test tank directly in front of the partition between A and B testing areas and in some tests at the center of each section of the tank. Frequency of analysis varied from once an hour to once a day depending on duration of test. Procedure for analysis of dissolved nitrogen was from Van Slyke and Neill (1924) using manometric blood gas apparatus; dissolved oxygen was analyzed using modified Winkler procedures

[1]Atmospheric nitrogen–nitrogen gas (98.8% by vol) plus argon gas (1.2% by vol) hereafter referred to as nitrogen or N_2 + Ar.

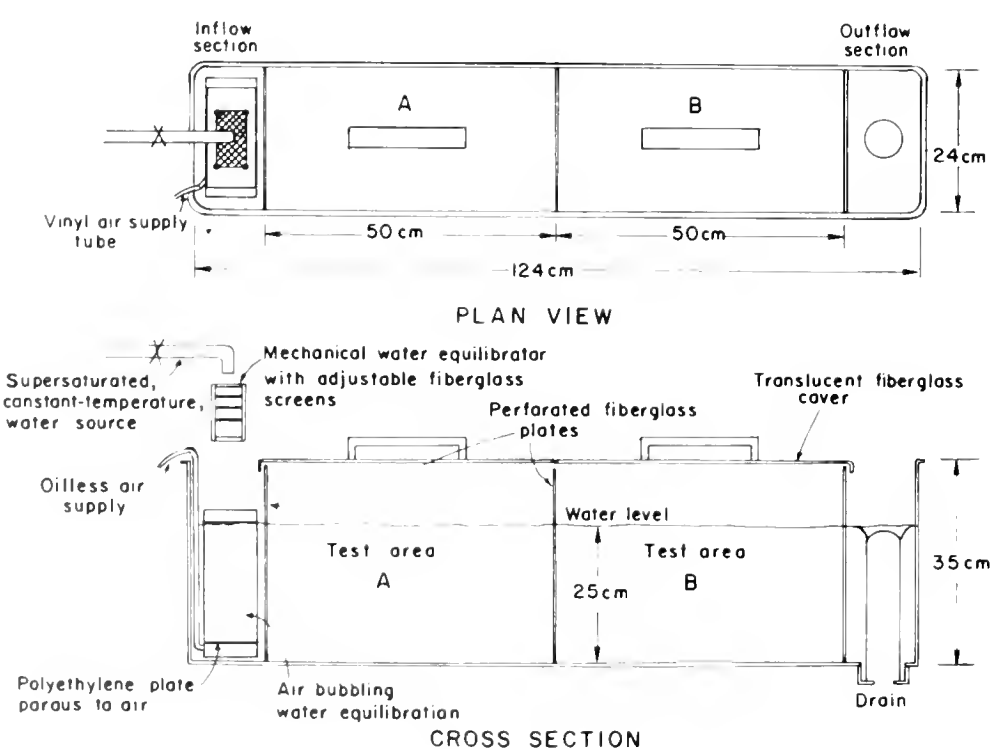

FIGURE 1.–Plan and cross-sectional views of test tank used for bioassay of dissolved gas.

(American Public Health Association et al. 1971). Gas concentrations at saturation (100%) were taken from Weiss (1970).

To obtain the dissolved gas levels for the various tests, we adjusted the water equilibrators of each tank (screens plus air bubbling boxes) until the nitrogen concentration remained within ±2% of the desired value. The oxygen concentration was then measured and we found that the saturation value was 5 to 10% lower than that of N_2+Ar for each tank. This did not differ appreciably from prevailing oxygen saturations in the Columbia and Snake rivers which are usually 5 to 10% lower than dissolved nitrogen values (Beiningen and Ebel 1971; Ebel 1971). After introducing fish, however, we noted that the oxygen concentration dropped further (presumably because it was consumed), resulting in values from 8 to 28% of saturation below that of N_2 + Ar, particularly in test area B and the outlet area of the tank. Due to large numbers of fish required for experiments on the survivors of these bioassays, and the complexity of changing the dissolved gas ratios of the water source, we did not alter the O_2 concentrations in the tests but carefully documented the mid-tank gas concentrations. Data affected by this drop in oxygen partial pressure are discussed later in this report.

One-year-old spring chinook salmon from Leavenworth National Fish Hatchery, Leavenworth, Wash., and steelhead trout from the Washington Department of Game Hatchery at Aberdeen, Wash., were used in the tests. Test populations were acclimated to laboratory water at 15°C with normal dissolved gas concentrations for at least 2 wk before testing. Groups of 30 or 60 fish were placed simultaneously in control (100% atmospheric nitrogen saturation) and test tanks set at 105, 110, 115, 120, and 125% of N_2 + Ar saturation and one to four replicates of each test were made, depending on test level. When 60 fish were being tested, 30 were in each of the two test sections A and B. Fish were randomized before introduction into individual test tanks. Mean sizes of the fish at completion of the tests are indicated in Table 1. Measurement of size at the beginning of the tests was omitted to avoid placing additional stress on the test animals. Feeding of fish during the test period began 48 h after introduction to test tanks; thereafter they were fed to satiation once each weekday.

Lethal exposure times to 10 and 50% mortality (LE_{10} and LE_{50}) were averaged for lots of test fish held in tank sections A and B during the same time period, and the mid-tank gas concentrations were used for analysis with the exception of the steelhead groups stressed at 115% nitrogen; in these tests, exposure times and gas concentrations were measured separately for A and B sections of the tanks. In addition, lethal exposure times to 100% mortality (LE_{100}) for chinook and steelhead at all levels of supersaturation were taken only from groups held in the A section of the tanks.

Observations of behavior, progression of external signs of gas bubble disease, and mortality were recorded continuously for the first 6 h then every ½ h for 24 h and every 3, 6, or 12 h thereafter—depending on test concentration—until termination of the bioassay at 35 days. Observations of change in degree of external disease signs among test fish after a recovery period in normally saturated (100%) water also were made from selected groups.

Sublethal effects of supersaturation were as-

TABLE 1.—Comparison of mean weights and lengths of surviving test and control fish held in 15°C water with N_2 + Ar levels at 100 to 125% of saturation, February-April 1972.

Test level (% of saturation of N_2 + Ar)	Testing period[1] (mo/day)	Duration (individual tests)	Test fish		Control fish (100% N_2 + Ar)	
			Weight (g)	Length (mm)	Weight (g)	Length (mm)
		Spring chinook salmon				
105	2/8-3/14	35 days	13.6	115	15.5	119
110	3/7-4/11	35 days	17.5	125	17.9	126
115	2/8-3/14	35 days	13.6	115	15.5	119
120	2/8-3/3	≤55 h	16.2	120	18.0	122
125	2/8-3/1	≤38 h	16.8	117	16.8	118
		Steelhead trout				
105	4/3-5/8	35 days	18.8	130	22.8	135
110	4/10-5/15	35 days	20.0	130	22.0	132
115	4/13-5/13	≤35 days	19.8	130	20.9	132
120	4/3-4/18	≤53 h	20.6	124	—	—

[1]Replicates of tests at 115-125% levels were made at various time intervals throughout the indicated test period; others lasted the full indicated period.

sessed by using measurements of maximal swimming performance, blood chemistry, and photic response. Measurements were made on groups of survivors from lethal exposure tests immediately after the LE_{10} and LE_{50} points were reached or following a 2-wk recovery period in 100% saturated water. Swimming performance was measured by distance gained and time of swimming against a constant water current of 1.25 m/s within a U-shaped inclined trough (14 m long and 8 cm wide). Blood samples were analyzed on a Technicon Sequential Multiple Analyzer (SMA 12/60).[5] Pooled serum samples were analyzed for Ca, Na, PO_4, K, Cl, albumin, total protein, cholesterol, alkaline phosphatase, glucose, urea, uric acid, total bilirubin, lactic dehydrogenase and serum glutamic oxaloacetic-acid transaminase. Photic response was evaluated by electrophysiological monitoring of the optic tectum during retina stimulation with flickering light. A more detailed description of the methods used in the swimming performance and blood chemistry measurements appear in reports by Schiewe (1974) and by Newcomb (1974),[6] respectively.

RESULTS

Relationships Among Mortality, Exposure Time, and Gas Concentration

Mean exposure times at which 10, 50, and 100% mortality occurred at 120 and 125% N_2 + Ar saturation indicate no substantial difference between susceptibility of juvenile chinook and steelhead trout (Table 2). However, at 115% N_2 + Ar saturation, steelhead appeared to be more susceptible than chinook; i.e., steelhead reached the 50% mortality level within 35 days, whereas LE_{50} was never reached in test groups of chinook.

Mortalities of control fish for all tests (105-125%) ranged from 0 to 3.3% throughout the 35-day test periods. Because of the comparatively minor losses of controls, data from test groups are given as observed (not compensated for loss of controls). Mortalities observed in tests at 105 and 110% of nitrogen saturation were 5% or less for both species, and gas bubble disease was not the apparent cause of death.

The onset of mortality attributable to gas supersaturation occurred at about 115% dissolved nitrogen among both steelhead and chinook.

At about 120% nitrogen saturation the means of lethal exposure times to 50% mortality (LE_{50}) were 26.9 and 33.3 h for chinook and steelhead, respectively. LE_{50}'s for chinook and steelhead at 125% nitrogen saturation were 13.6 and 14.2 h, respectively, which are similar to those (11.3 and 14.0 h) observed in earlier tests by Ebel et al. (1971) at test concentrations of 125 to 130% N_2+Ar. Test fish stocks used previously were from different hatcheries and earlier brood years and were slightly larger (spring chinook–23 g and 135 mm, steelhead–54 g and 179 mm).

TABLE 2.–Mean values of lethal exposure time for juvenile steelhead and chinook acclimated to 15°C and then subjected to various levels of gas saturation[1] from 100 to 125% in shallow tanks (25-cm depth).

Percent saturation (N_2 + Ar)	Percent mortality	Exposure time (h)	
		Steelhead	Chinook
125	10	10.3	10.6
	50	14.2	13.6
	100	[2]23.0	[2]32.1
120	10	26.0	19.3
	50	33.3	26.9
	100	[2]40.0	[2]55.0
115	10	[2]258.0	(7% mortality in 792 h)
	50	[2]486.0	Not reached
	100	Not reached	Not reached
110 105 100	Mortality of 5% or less recorded for either steelhead or chinook after 35 days at these concentrations. Gas bubble disease was not apparent cause of deaths.		

[1]Percentage saturation of nitrogen and argon was set as indicated in the table (± 2%). Oxygen concentrations ranged between 87 and 98% saturation in tanks set at 100-110% nitrogen plus argon saturation; in tanks set a 115-125% nitrogen saturation, O_2 levels ranged between 98 and 115%.

[2]Exposure times indicated for test replicates of section A only. Mortality in section B had not reached indicated level at termination of test.

Effect of Oxygen Concentrations on Time to Death Measurements

The role of atmospheric gases other than nitrogen (particularly oxygen) in causing gas bubble disease has been questioned by several investigators. Arguments for and against the assumption that dissolved atmospheric nitrogen is the exclusive cause of gas bubble disease are prevalent throughout the literature (Marsh and Gorham 1905; Doudoroff 1957; Egusa 1959, 1969; Shirahata

[5]Trade names referred to in this publication do not imply endorsement of commercial products by the National Marine Fisheries Service, NOAA.

[6]Newcomb, T. W. 1974. Changes in juvenile steelhead (*Salmo gairdneri*) blood chemistry following sublethal exposure to various levels of nitrogen supersaturation. Northwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash. Unpubl. manuscr.

1966; Bouck 1972[7]; Rucker 1972). Most of the comprehensive studies, however, have been analyzed in terms of nitrogen concentration, assuming it to be the controlling influence upon the effects of gas bubble disease (even greater than indicated by the 80/20 ratio of the partial pressures N_2 /O_2). This assumption was based upon supposed biochemical decrease of the effective oxygen partial pressure within the fish.

In comparing data from this experiment with that from past research we should acknowledge that our primary criterion during planning and set-up stages was dissolved nitrogen + argon concentration. At the outset of these experiments, oxygen levels were monitored primarily for documentation of overall water quality rather than for use in analysis of their effect upon the test organisms. However, upon examination of initial results derived from each of the tests carried out to lethal exposures, we found that the times for LE_{10} and LE_{50} were consistently less in test section A than in Section B. Analyses of individual gas pressures in each of the two sections of the tanks were made to determine whether variations occurred among the component gases. We found that nitrogen concentrations were constant in both areas, but oxygen concentrations remained consistently lower (5-10%) in section B than in section A. The lower oxygen concentrations–thus lower (1-2%) total dissolved gas (TDG) saturations–appeared directly correlated with the lower mortality rates in section B of the test tanks. For example, when we examined mortality rates of individual groups of steelhead from A and B test sections at 115% N_2 + Ar, we found: N_2 + Ar saturation (in section B) of 116.0% and 88.2% of O_2 saturation (TDG at 110.0% of saturation) caused no mortality in 35 days for one replicate of 30 fish, whereas N_2 + Ar saturation (in section A) of 116.0% and 98.8% O_2 (TDG at 112.1%) caused 50% mortality in an average of 20 days for two replicates.

Effect of Supersaturation Stress on Growth

Exposure to sublethal concentrations (concentrations at which no substantial mortality occurred within 35 days) of N_2+Ar appeared to affect growth of both juvenile chinook and steelhead. Mean weights and lengths of test fishes after 35 days in dissolved nitrogen concentrations of 105, 110, and 115% of saturation (Figure 2) were in each instance less than those of controls.

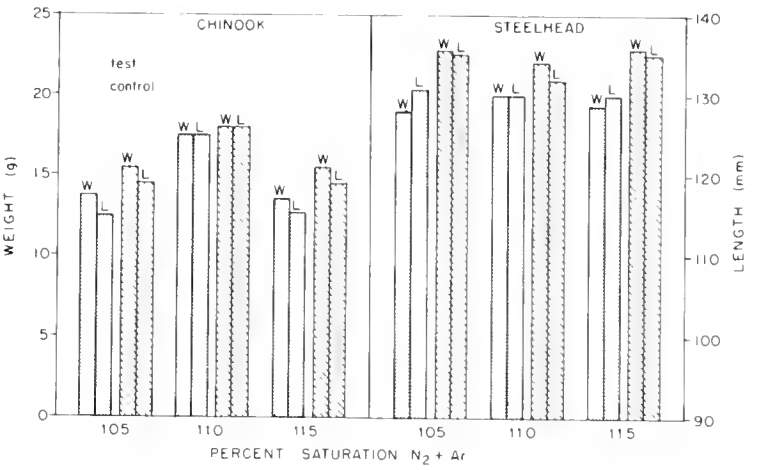

FIGURE 2.–Comparison of mean weights (W) and lengths (L) for test and control groups of juvenile chinook salmon and steelhead trout after 35 days at saturation levels of 100% (control), 105%, 110%, and 115%.

A statistical test of the hypothesis–that the slopes of the regression of mean weight of control fish groups and mean weight of test fish groups were equal–yielded a value of $t = 4.938$ ($P<0.02$ at 4 df). The same statistical test of mean lengths of control vs. test groups yielded $t = 1.36$ ($P<0.25$ at 4 df). The lower t value calculated from length data is attributable to the duration of the test not being long enough to significantly overcome the variation in lengths between individuals within groups. We attribute the difference between size of test and control lots to the effect of supersaturation on the normal growth of the test fish.

After 30 days of testing at the 115% level, feeding response of the chinook fingerlings became lethargic. Many of the test fish had spinal flexures, exophthalmia, and large buccal cavity gas blisters and were unable or unwilling to move and accept food when made available. By contrast, control fish exhibited aggressive feeding behavior throughout the tests. Gross gas bubble disease signs and behavioral changes were less evident at 110% N_2 +Ar and nonexistant at 105%.

Testing for changes in the condition factor of juvenile fall chinook and steelhead during long-term (2-4 mo) holding in water saturated 100 to 127% N_2+Ar is currently underway. Results of these tests may provide further information on effects of gas supersaturation on growth rate.

[7]Bouck, G. R. 1972. Effects of gas supersaturation on salmon in the Columbia River. West. Fish. Toxicol. Stn., Environ. Prot. Agency, Corvallis, Oreg. Paper presented at Ecol. Soc. Am. Symp. Aug. 1972, 29 p.

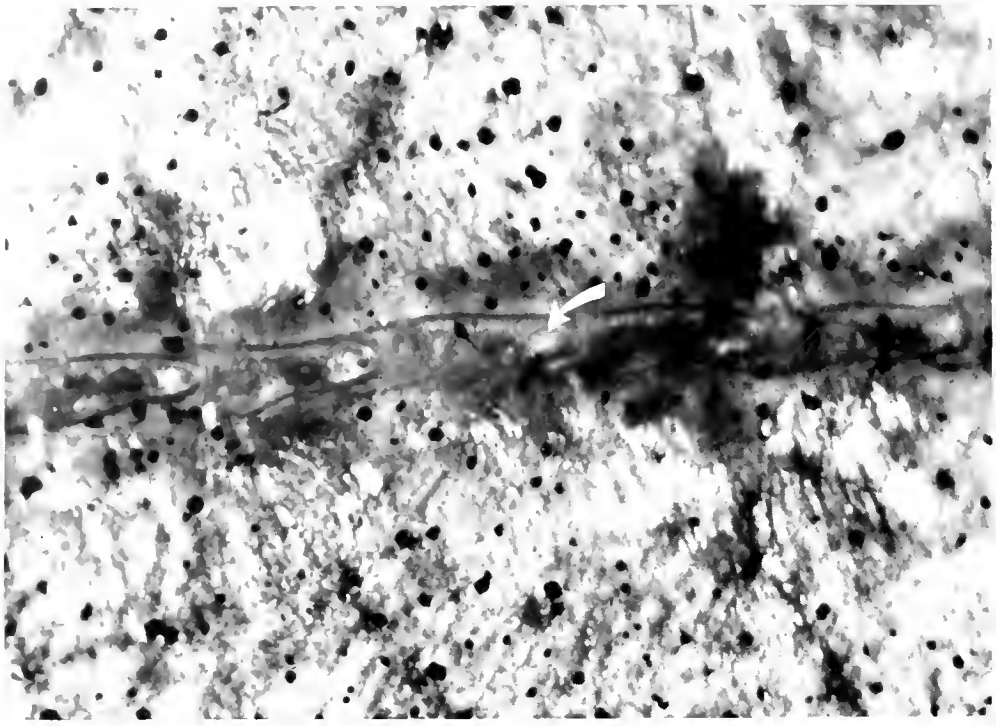

FIGURE 3.–Gas bubbles (arrow) in lateral line of juvenile chinook salmon.

Progression of Gas Bubble Disease

Observations on the progression of external signs of gas bubble disease in spring chinook exposed to various levels of supersaturation revealed that the first developments such as bubble formation in the lateral line (Figure 3) appear within 2 h of exposure at 125%. Subcutaneous gas blisters between fin rays of at least one fin were present on each of the test animals before 11.5 h at 125%, and before 55 h at the 120% level. Several days' exposure were required before these signs occurred on fish tested at 115%. After 35 days, 56% of the fish at 110% had lateral line bubbles but only 4% had fin bubbles. Exophthalmia or "popeye," hyphema, cutaneous blisters of the head and buccal cavity, and spinal flexures were absent among fish tested at 120 and 125% but began appearing after 6 days on fish held at 115% and after 11 days on those held at 110% of nitrogen saturation. Apparently at the higher saturation levels, the fish died from cardiac occlusion or branchial artery occlusion (Figure 4) before development of these signs. By the end of 35 days, fish held at 115%

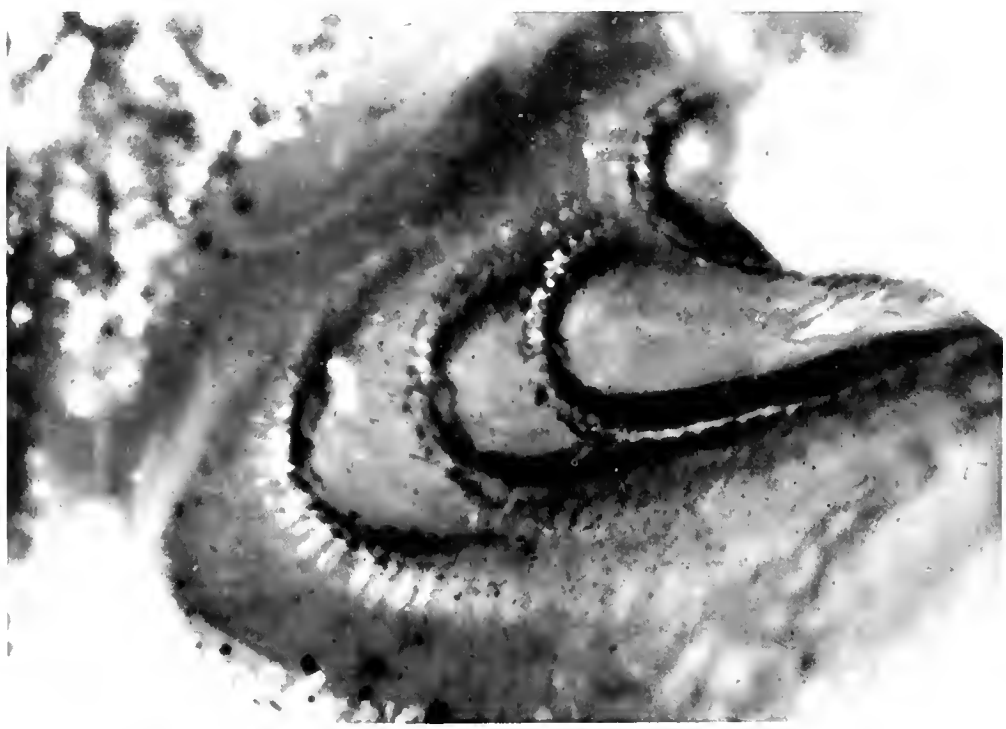

FIGURE 4.–Gas emboli occluding gill filaments and branchial artery of chinook salmon held in 125% nitrogen saturation for 20 h.

exhibited more than a 75% incidence of exophthalmia, 20% of the fish had spinal flexures, and 25% of the fish in section A became more or less immobile. After 35 days of exposure at 110% N_2 +Ar, only 12% of the test fish exhibited signs other than the lateral line bubbles. No apparent signs of gas bubble disease were observed in fish tested at 105% nitrogen.

Development of gas bubble disease signs in steelhead was similar to that of chinook—the signs occurred in the same sequence but the exposure time required to produce the signs was slightly less.

Recovery From Gas Bubble Disease

Observations on disappearance of gas bubble disease signs and delayed mortality following tests were made on groups of survivors of fish stressed to the LE_{50} level at 120, 125, and 130% of saturation. These survivors were placed in water at 100% gas saturation for up to 15 days. No delayed mortality could be attributed to prior exposure to supersaturation in either the chinook or the steelhead. The only significant mortality in any recovery group was a 10% loss of one replicate of steelhead subjected to 125% N_2+ Ar until LE_{50}, followed by a burst swimming performance test. Some mortality occurred after 102 h of recovery time, but the only observable disease sign was the presence of lateral line bubbles on one fish. Other mortalities during recovery were less than 3% of the fish held; no gas bubble disease signs were found. All external symptoms that were readily visible at the time the fish were removed from the recovery tanks had disappeared after 15 days in both species.

Steelhead that had undergone 16, 24, and 35 days' exposure at 115% nitrogen saturation still showed gas bubbles after being held 3 days in normally (100%) saturated water. After 1.5 days' recovery, 64% exhibited lateral line bubbles or fin ray gas blisters and one fish (7%) retained unilateral exophthalmia; after 2 days' recovery, 88% of another group retained signs of lateral line bubbles and fin gas blisters; at 3 days, 54% of the third group retained like signs of gas bubble disease. After 15 days' recovery, no gas bubble disease signs were observed on groups of test fish examined.

Effect of Supersaturation Stress on Survivors

Burst swimming performance and blood chemistry were examined as potential indices of stress from sublethal exposures to supersaturated water.

Swimming performance (Schiewe 1974) of chinook that survived from tests at 110-125% was significantly lower than that of control fish. Visual observations of behavior during swimming performance tests indicated genuine debilitation (inability to swim in some cases) which in turn resulted in lower swimming performance (i.e. less distance gained and less swimming time against a constant water current stimulus). No difference was apparent between performance of chinook salmon tested at 105% saturation and the control fish.

Swimming performance of steelhead trout that survived tests at 105-125% was not significantly different from the performance of control fish. Performance of test and control lots of steelhead trout was highly variable. Fish stressed by exposure to supersaturation often responded in an irritated or stimulated fashion, which often resulted in a high measure of performance. Further tests with steelhead are needed to determine whether swimming performance is a useful index of stress from supersaturation and, if so, whether test results in the laboratory apply to survival of fish in the river.

Blood serum from groups of chinook and steelhead surviving supersaturation tests to LE_{10} and LE_{50} were analyzed (Newcomb see footnote 6) using a SMA 12/60. A 5% decrease in serum calcium was noted in chinook exposed to 115% nitrogen plus argon when compared to those exposed to lower levels of supersaturation. Steelhead exposed to 115% nitrogen showed a 10 to 17% decrease in serum calcium and a decrease in serum albumin, total protein, serum chloride, cholesterol, and in alkaline phosphatase activity when compared to controls and those exposed to lower saturations. No significant changes in blood serum components were observed in samples taken from test groups exposed to levels of 105 and 110% of saturation when these were compared with controls.

Measurements of photic response of salmonids failed to provide any consistent evidence of stress-related phenomena due to supersaturation so these tests were discontinued.

DISCUSSION

Data from these tests indicate that the critical level of supersaturation of nitrogen where juvenile spring chinook and steelhead began to show mortality was about 115% N_2+Ar when O_2 saturations were about 95% (111% TDG). These data agree closely with the findings of Shirahata (1966), who indicated that the critical level for 2-mo-old rainbow trout was about 111.3%, N_2+Ar and 99.7% O_2 (109% TDG).

Although mortality from supersaturation did not occur until fish were exposed beyond 110% (± 2%) N_2 + Ar, swimming performance measurements with juvenile chinook showed some effect from stress caused by exposure to supersaturation at levels as low as 110% N_2 + Ar (106% TDG). We believe that one can infer from the results of these tests, that something less than normal survival will result when juvenile chinook and steelhead are exposed for 35 days or longer at or above 110% N_2+Ar (106% TDG).

Results of our testing program indicate that oxygen as well as nitrogen is responsible for causing gas bubble disease, even when O_2 concentrations are below saturation. The immediate conclusion drawn from this observation would be that total dissolved gas is the cause rather than any one or combination of component atmospheric gases. However, fish tolerance research by Egusa (1969) and by Rucker (1975) with various ratios of dissolved gas indicate that mortality from gas bubble disease is not necessarily in linear correlation with TDG. Egusa showed that oxygen saturation values of 400 to 500% were required to produce initial mortality of goldfish, *Carassius auratus*, and an eel *Anguilla japonica* when nitrogen concentrations were near 100% (TDG 160-180%). In earlier work with the same two species, however, Egusa (1959) recorded high mortality of goldfish with N_2+Ar at 132% and O_2 at 75% of saturation (TDG 123%), and of eel with N_2+Ar at 124%, O_2 at 66% (TDG 112). Rucker found that mortality rate of juvenile salmon declines considerably if the ratio of oxygen to nitrogen is increased even though the same TDG pressure is maintained.

It is apparent from our tests and those of Egusa and Rucker that the ratio of O_2 and N_2 must be considered as well as TDG when assessing possible effects from supersaturation.

Additional information is needed to quantify the effects of various gas ratios (nitrogen to oxygen) on tolerance limits of fish in general. It is probable that most fish could tolerate higher total gas pressure if the major portion of the excess gas were oxygen.

Dissolved gas measurements and resulting percentage saturations for the Columbia and Snake rivers (Ebel 1969, 1971; Beiningen and Ebel 1971) have been based on surface or atmospheric pressure plus vapor pressure. Corrections for the hydrostatic pressure (or depth) at which a sample was taken were not made. Thus, the calculations of percentage saturation were made as though the samples were collected at the surface. This is convenient when limnologists or oceanographers wish to compare values taken at various depths, but leads to confusion when attempting to assess how a given saturation measurement will affect a fish at depth.

The depth that populations of fish travel must be considered when one attempts to determine the effects of an exposure to supersaturated levels of dissolved gases. Bubble formation in the circulatory system or tissues of fish is directly dependent on the external hydrostatic pressure. For example, a fish traveling at a depth of only 1 m will be provided with enough hydrostatic pressure to compensate for a gas pressure in excess of 10% (110% saturation at surface pressures). A fish traveling at 3 m can compensate for 30%, or 130% saturation at surface pressures; a fish traveling at 10 m can compensate for an excess of 100% of saturation and so on. These tests were conducted in shallow tanks at essentially zero hydrostatic pressure with only a few centimeters depth compensation possible. The lethal exposure times we measured could only be applied directly to fish populations that could not compensate by sounding. Much more information is needed to determine how a given gas level in a river affects the population inhabiting the river. Information regarding the behavior of fish is obviously essential. We believe, however, that data from our tests support the 110% maximum allowable limit established by the Environmental Protection Agency primarily because significant mortalities did not occur until concentrations exceeded 110% TDG.

Gas bubble disease signs either singly or in combination with one another did not correlate well with mortality. Those generated from stress conditions of 120% saturation and higher seemed to be nearly the same at LE_{10} as at LE_{100} (gas blisters in the fins and lateral lines of most live and

dead fishes). Signs that developed at lower levels (110-115%) were obviously different from those appearing at the higher saturations; i.e., gas blisters in and around the eye, exophthalmia, cutaneous gas blisters on the head and in the mouth, and spinal flexures. Neither set of signs (low-level or high-level types) correlate by percent of incidence or severity, with accumulative mortality. But they showed that one could determine with reasonable accuracy, whether fish observed in the river had been exposed to supersaturation for a long or short duration. Populations with signs of chronic exposure (exophthalmia, spinal flexures, etc.) could have been either 1.5 to 2.0 m deep in highly supersaturated water (130-135%) or near the water surface at near 115% saturation.

SUMMARY AND CONCLUSIONS

Bioassays in shallow tanks (25 cm) with dissolved nitrogen and argon gas concentrations ranging from 100 to 125% of saturation were conducted to determine lethal and sublethal effects on juvenile chinook salmon and steelhead trout.

Juvenile steelhead (130 mm fork length) reached the LE_{50} level within 35 days when exposed to 115% of nitrogen and argon saturation (112% TDG), whereas mortality of juvenile chinook (115 mm) did not exceed 7%. There appeared to be no substantial difference between susceptability of chinook and steelhead at 120 or 125% saturation N_2 +Ar. No mortality related to supersaturation occurred in either juvenile chinook or steelhead trout exposed to 110 or 105% saturation N_2 +Ar. Signs of gas bubble disease (such as bubbles in lateral line and exophthalmia) were evident on both species, however, after 35 days exposure to 110%.

Time to death decreased in test tanks with higher oxygen concentrations (thus higher TDG) even though nitrogen and argon concentrations were identical, indicating that oxygen as well as nitrogen and argon concentrations must be considered when time to death values are compared.

The first notable sign of gas bubble disease was appearance of bubbles in the lateral line which appeared in some degree at all gas concentrations tested. Exophthalmia, dermal gas blisters of the buccal cavity and cephalic regions, and spinal flexures did not occur with short-term exposure (6 days) or at the higher levels (120 and 125%) but was prevalent after long exposure at both 115 and 110% saturation N_2 + Ar. External gas bubble disease signs disappeared within 15 days when fish were placed in normally saturated water (100%).

Fish stressed with supersaturation at sublethal levels for 35 days grew less than controls and the swimming performance of juvenile chinook exposed for sublethal periods to 110-125% nitrogen saturation was significantly lower than controls. Blood chemistry measurements indicated that significant differences occurred between blood samples taken from test and control chinook and steelhead after they were exposed to levels of 115% saturation. Serum calcium, for example, was 10-17% lower in samples taken from test groups of steelhead.

We concluded from these experiments that:

1. Significant mortality of both juvenile chinook and steelhead trout commences at about 115% saturation of nitrogen and argon (111% TDG).
2. Sublethal exposures to various concentrations of dissolved gas significantly affects swimming performance, growth and blood chemistry of chinook, and growth and blood chemistry of steelhead trout.
3. The first externally evident sign of gas bubble disease on juvenile chinook and steelhead trout exposed to supersaturation occurs as bubbles in pores of the lateral line.
4. Fish returned to normally (100%) saturated water appear to recover within 15 days from exposure to supersaturated water.

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BIOLOGY AND TAXONOMY OF THE GENUS *NEMATOSCELIS* (CRUSTACEA, EUPHAUSIACEA)

K. GOPALAKRISHNAN[1]

ABSTRACT

The seven species of *Nematoscelis*, *N. difficilis*, *N. megalops*, *N. gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*, are described in a comparative manner, and keys for their identifications are provided. The key to the larvae is based on structural differences in the carapace and rostrum of furcilia stages, whereas the key to adults is mostly based on diagnostic features of the first thoracic leg (maxilliped) and a male secondary sexual structure, the petasma. *Nematoscelis gracilis* is represented by two distinct forms; they are considered ecophenotypes, since their patterns of geographical distribution appear correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column. Diagnostic features of these forms are pointed out. The antennule and carapace are sexually dimorphic in adults of all *Nematoscelis*. Abdominal photophores in the males show species-specific patterns of enlargement.

The genus *Nematoscelis* consists of seven species. It was described by G. O. Sars (1883, 1885) as consisting of *N. megalops*, *N. tenella*, *N. microps*, and *N. rostrata*. Hansen synonymized *N. rostrata* with *N. microps* and added four species: *N. gracilis* and *N. atlantica* in 1910, *N. difficilis* in 1911, and *N. lobata* in 1916. *Nematoscelis lobata* was not found by subsequent workers but the other species were discussed by Ruud (1936), Boden (1954), Boden et al. (1955) and Mauchline and Fisher (1969). Taxonomically *Nematoscelis* has been a difficult genus.

Like other species of euphausiids, *Nematoscelis* species have been identified mainly on the basis of differences in the male copulatory organ, the petasma. Since the petasma is an adult character, it has been difficult to identify immature specimens and mature females. Characters such as the shape of the eyes and structure of the second thoracic leg have been used to discriminate species. Einarsson (1942) showed structural differences in spermathecae (thelyca) of females, but such differences appear slight and are difficult to examine. Mauchline and Fisher (1969) pointed out difficulties encountered in the identification of species of this genus. In the present study an attempt is made to point out the diagnostic value of the first thoracic leg (maxilliped) in discriminating all species of *Nematoscelis*. This appendage usually remains attached to the animal caught by nets (as compared with the elongate second leg which is usually lost). It can be used as a diagnostic character in both sexes. The structural differences among the petasmae are also reexamined. The morphology of individual species will not be given separately, but species differences will be pointed out in a comparative manner. Since all species of this genus are sexually dimorphic, it is necessary to describe both sexes.

Another aspect to which little attention has been paid is the significance of developmental features in determining phylogenetic associations. Larvae of *Nematoscelis* are often difficult to separate as to species. The taxonomy of the larvae is yet to be worked out because the recognized adult characteristics are of no use in the larval identification. Gopalakrishnan (1973) summarized the available information on the sequential morphological development of an individual species. As Gordon (1955) and others have pointed out, larval characteristics may be more useful than those of adults in recognizing phylogenetic interrelationships of species. Adults show a greater degree of differentiation than the larvae, and their characters are more useful in the identification of the species than determining phylogeny. Moreover, part of the morphological variability observed in adults is sometimes ascribed to nongenetic modification that probably has no phylogenetic significance. Usually phylogenetic interrelationships are summarized in a classification. In this connection, larval characters are used

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extensively in classifying insect groups, such as Diptera and Hymenoptera. It is the intention of this taxonomic study to provide as much information as possible so that one can examine the systematic value of both larval and adult characters of *Nematoscelis*.

MATERIAL AND METHODS

The material used in this study consisted of 286 Isaacs-Kidd Mid-water Trawl (10 feet) collections and 1,950 plankton samples, including those collected during the International Indian Ocean Expedition (1960-65). These materials came from different geographical regions of the Atlantic, Indian, and Pacific oceans, mostly between lat. 40°N and 40°S. They are deposited at the Scripps Institution of Oceanography, La Jolla, Calif. All the trawl collections were not quantitative for estimating species abundance. A paper on the distribution and abundance of *Nematoscelis* based on plankton samples was already published (Gopalakrishnan 1974). Measurements were taken on 55 adult morphological characters for examining relative degree of differences. Ten males and ten females of each species were selected for these measurements. Statistical significance was determined on the basis of nonoverlapping confidence levels (95%) of the means. For making drawings, 10-20 individuals of each species were treated in heated 10% aqueous KOH to remove nonchitinous tissues. They were then stained in 1% aqueous Chlorazol Black E. Materials treated in KOH solution could be kept in 60-80% glycerol without shrinkage. Drawings were made with the aid of a camera lucida fitted to monocular and binocular microscopes.

The larval key was prepared on the basis of furcilia characters only. However, a few comments are made on characters of calyptopis and juvenile stages thought to have some diagnostic value. The adult key was prepared based on features of the first thoracic leg (maxilliped), eyes, antenna, and the carapace. Diagnostic features of the petasma are also included in the present key. Many characters are, therefore, used in the present key to facilitate its use on juveniles and adults of both sexes. Most of the commonly used adult characters are illustrated in Figure 1a. The terminology used here is the same that has been followed by most other workers. Larval terminology is defined and described in Gopalakrishnan (1973).

RESULTS

Larval Development

Between hatching and sexual maturity all species of *Nematoscelis* pass through four developmental phases: metanauplius, calyptopis, furcilia, and juvenile. A modified version of the nomenclature of larval development of euphausiids is given in Gopalakrishnan (1973). The metanauplius phase consists of one developmental stage, calyptopis of three (C_1, C_2, and C_3) and furcilia of three (F_1, F_2, and F_3). The strong differentiation of mouth parts and other thoracic legs shows similarities among larvae of all species of this genus. The development of larvae follows either of two pathways: *N. difficilis* and *N. megalops* follow one pathway and the other five species follow the other. During the third furcilia stage the second thoracic leg develops spines on both dactylus and propodus in *N. difficilis* and *N. megalops*, whereas in the rest of the species spines develop only on the dactylus. In all species of *Nematoscelis* this leg becomes the longest of all thoracic appendages.

Other developmental differences between the two species groups are as follows: during the juvenile phase, the maxillules of *N. difficilis* and *N. megalops* develop pseudexopods from the posterior face of the coxa as the four-setose larval exopods disappear; but in the remaining species, at about the same stage, the larval exopod disappears without the development of a pseudexopod. The lacina externa (lobes of basis) of the maxilla is trilobed in larvae of all species, but becomes bilobed in adults of *N. difficilis* and *N. megalops* and single lobed in adults of the remaining species.

The differences in the sequential development of pleopods and telson spines (terminal) are summarized in Figure 2. These features are consistent and appear to be characteristic of each subgroup. The terminal spines of the telson in species of both subgroups show differences not only in their sequential reduction but also in their external morphology (Figure 3A). This structural difference can be seen even during calyptopis stages of all species of this genus. This is a diagnostic feature and may have significance in understanding the evolution of the larvae. The dorsal keel and rostrum of the carapace also appear to be of important diagnostic value for furcilia (Figure 3B)

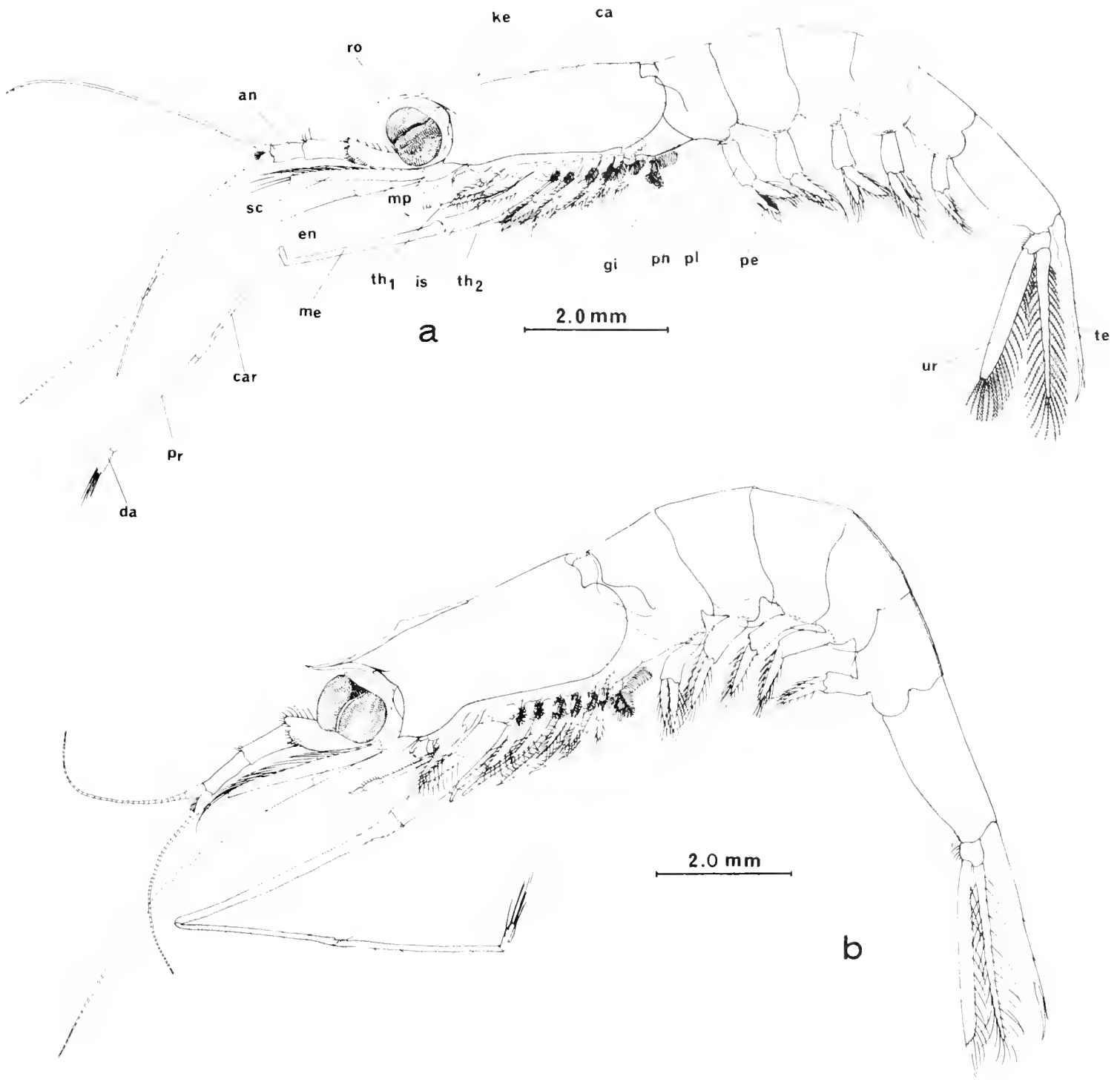


FIGURE 1.—*a. Nematoscelis atlantica*, male (length = 13.2 mm; Indian Ocean, position: lat. 28°08′S, long. 66°09′E); *b. N. microps*, female (length = 16.3 mm; Indian Ocean, position: lat. 10°06′S, long. 41°51′E). *an*, antennule; *ca*, carapace; *car*, carpus of second leg; *da*, dactylus of second leg; *en*, endopod of antenna; *gi*, gill; *is*, ischium of second leg; *me*, merus of second leg; *mp*, mandibular palp; *pe*, petasma; *ph*, photophore; *pl*, pleopod; *pr*, propodus of second leg; *ro*, rostrum; *sc*, scale of antenna; *te*, telson; th_1, first thoracic leg; th_2, second thoracic leg; *ur*, uropod.

The furcilia phase of *Nematoscelis* was defined in Gopalakrishnan (1973) as follows: compound eyes no longer under carapace, but project outside; antenna retains larval natatory function; pleopod becomes functional, each appears first as non-setose rudiment which develops setae at following moult; furcilia, therefore, with different states of development of pleopods. The following key for identifying furcilia larvae to species is based mostly on diagnostic features of the carapace. There are three developmental stages in the furcilia phase.

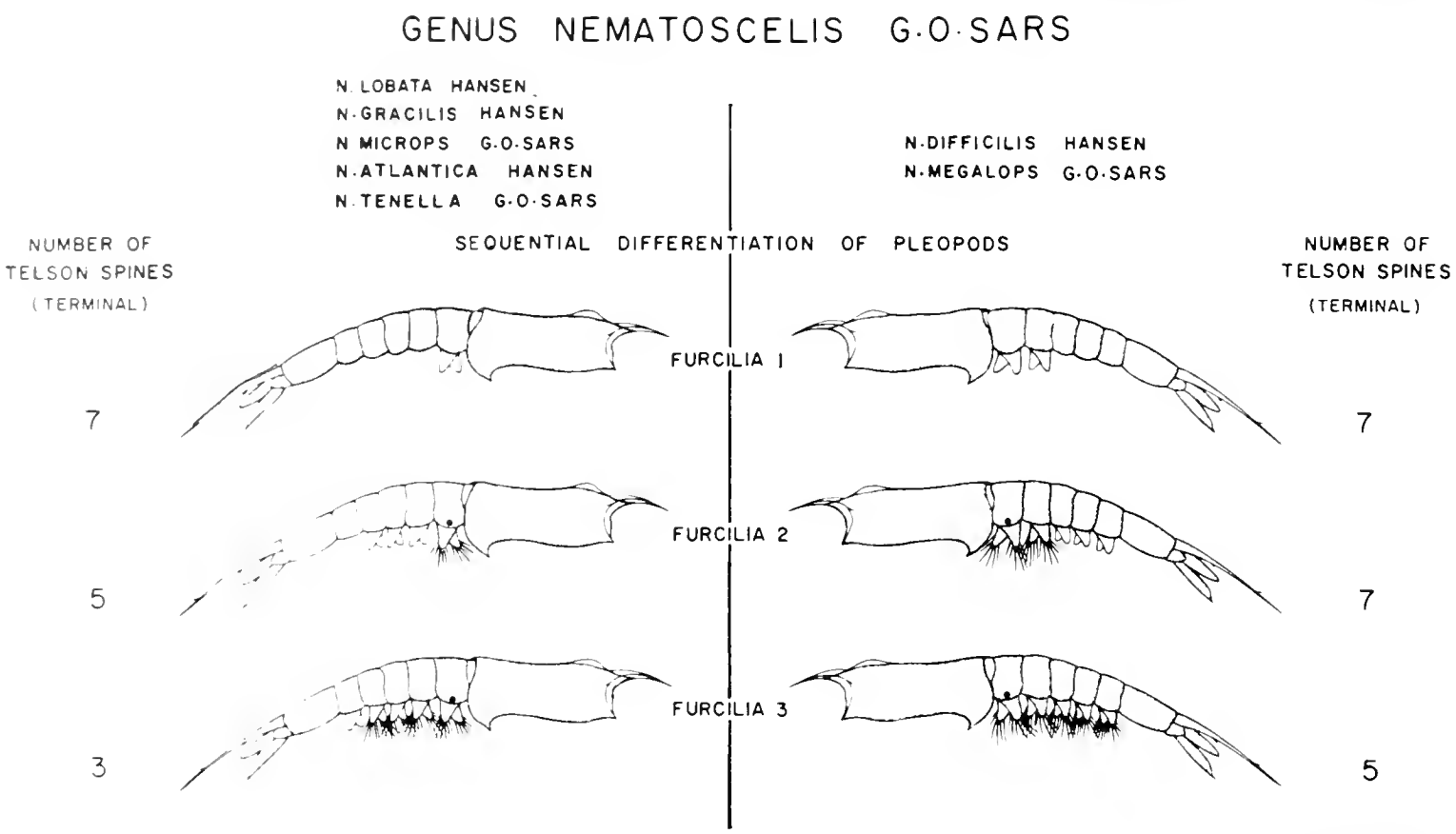


FIGURE 2.–Developmental sequence of differentiation of pleopods and terminal spines of the telson in species of *Nematoscelis* (adapted from Gopalakrishnan 1973).

Key for Identifying Furcilia Larvae of *Nematoscelis*

1a. Each terminal spine of telson with a pair of conspicuous lateral subspines (Figure 3A,a); setules present only above these subspines. F_1 stage with seven terminal spines and one pair of non-setose pleopods; F_2 with five terminal spines, one pair of setose pleopods and three pairs of non-setose pleopods; F_3 with three terminal spines, four pairs of setose pleopods and one pair of non-setose pleopods (Figure 2) 2

1b. Each terminal spine of telson without subspines, but with lateral setules along three-fourths of its length (Figure 3A,b). F_1 stage with seven terminal spines and two pairs of non-setose pleopods; F_2 stage also with seven terminal spines but two pairs of setose pleopods and three pairs of non-setose pleopods; F_3 stage with five terminal spines and five pairs of setose pleopods (Figure 2) 5

2a. Rostrum rectangular with truncated anterior end (Figure 3B,b,c) 3

2b. Rostrum triangular with pointed anterior end (Figure 3B,a,d) 4

3a. Carapace keel very large and hump shaped; rostrum usually curved downwards (Figure 3B,b); length of sixth abdominal segment relatively short and its ventral margin largely convex ..... *N. tenella*

3b. Carapace keel small, usually triangular shaped (Figure 3B,c); ventral margin of sixth abdominal segment not convex ..... *N. gracilis*

4a. Rostrum broad and stough, keel large and platelike; carapace compressed anteroposteriorly (Figure 3B,a) ..... *N. microps*

4b. Rostrum elongate and slender; keel less conspicuous (Figure 3B,d) ..... *N. atlantica*

5a. Rostrum broad, thick and triangular (Figure 3B,e) ..... *N. megalops*

5b. Rostrum slender and narrow (Figure 3B,f) ..... *N. difficilis*

Furcilia larvae of *N. atlantica* and *N. lobata* are difficult to separate. More samples are necessary to complete the larval description of *N. lobata*. This species is known to occur only in the semi-isolated

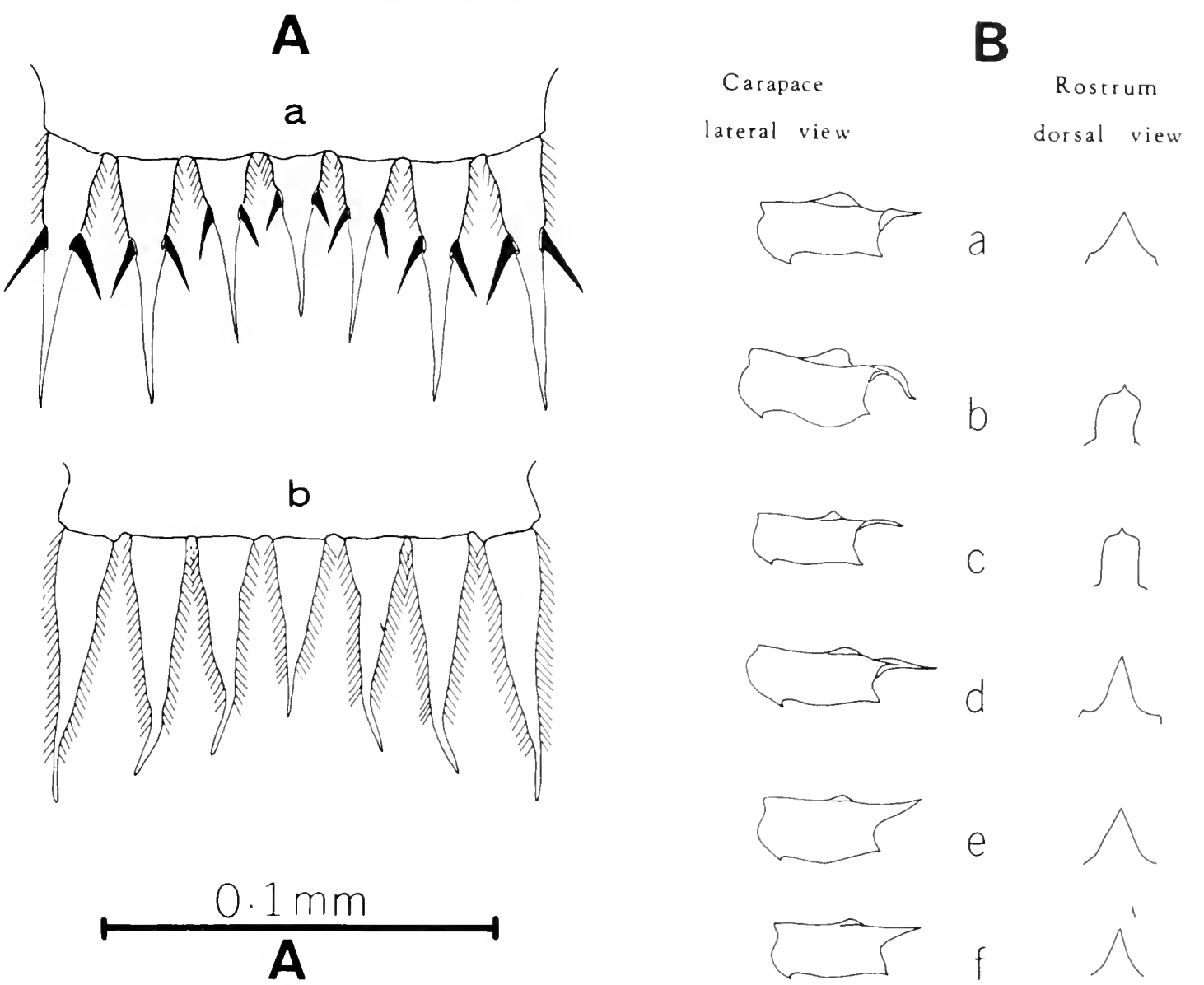


FIGURE 3.—*A*, terminal spines on larval telson: *a*, *Nematoscelis gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*; *b*, *N. difficilis* and *N. megalops*. *B*, carapace and rostrum of furcilia larvae of *Nematoscelis*: *a*, *N. microps*; *b*, *N. tenella*; *c*, *N. gracilis*; *d*, *N. atlantica*; *e*, *N. megalops*; *f*, *N. difficilis*.

Sulu and Celebes seas in the region of the Indo-Australian Archipelago (Gopalakrishnan 1974). The distribution of *N. atlantica* appears not to extend into this area. Within each species, the body sizes of metanauplii ranged from 0.8 to 1.0 mm. However, body size differences among all species became apparent from the first calyptopis stage onwards (Table 1). It is at this stage that the larvae start feeding (Gopalakrishnan 1973). Evidently *N. tenella* larvae are the smallest, and *N. megalops* the largest. Length measurements of furcilia larvae also show size differences among

TABLE 1.—Body lengths (mm) of calyptopis stages of *Nematoscelis*. (Medians were based on 10 to 36 individuals of each species for each stage.)

Species	Stage 1		Stage 2		Stage 3	
	Median	Range	Median	Range	Median	Range
N. gracilis	1.4	1.3-1.4	2.1	2.0-2.2	2.6	2.5-2.7
N. microps	1.4	1.3-1.4	2.0	2.0-2.1	2.7	2.6-2.8
N. atlantica	1.5	1.4-1.5	2.2	2.1-2.3	2.8	2.6-2.9
N. tenella	1.2	1.2-1.3	1.8	1.7-1.9	2.5	2.4-2.7
N. megalops	1.6	1.5-1.7	2.4	2.1-2.5	3.2	2.9-3.3
N. difficilis[1]	1.4	1.3-1.5	2.0	1.9-2.1	2.8	2.2-2.8

[1]Data taken from Gopalakrishnan (1973).

TABLE 2.–Body lengths (mm) of furcilia stages of six species of *Nematoscelis*. (Medians were based on 6 to 20 individuals of each species for each stage.)

Species	Stage 1		Stage 2		Stage 3	
	Median	Range	Median	Range	Median	Range
N. gracilis	2.8	2.6-3.0	3.0	2.9-3.4	3.3	3.2-3.5
N. microps	2.9	2.6-3.1	3.2	3.0-3.3	3.5	3.3-3.5
N. atlantica	3.4	3.2-3.5	3.9	3.9-4.1	4.3	4.2-4.5
N. tenella	2.7	2.6-2.9	3.2	3.1-3.3	3.5	3.5-3.6
N. megalops	3.7	3.6-4.0	4.3	4.2-4.3	4.8	4.7-5.0
N. difficilis[1]	3.1	2.7-3.2	3.5	3.4-3.7	3.9	3.6-4.2

[1]Data taken from Gopalakrishnan (1973).

species (Table 2). Between the species pair *N. megalops* and *N. difficilis*, there is a significant size difference during both the calyptopis and furcilia stages.

Juveniles of all species of *Nematoscelis* are identified on the basis of their morphological similarities to adults, especially in such characters as the carapace, the rostrum, and the eye. During the juvenile stages of *N. tenella*, the carapace becomes elongate and narrow as in adults; the dorsal keel on the carapace elongates anteriorly and posteriorly; the broad and curved larval rostrum becomes short and pointed; and the larval eye develops narrow upper and lower lobes (in the adult eye only the lower lobe remains narrow). These diagnostic features help to distinguish juveniles of *N. tenella* from similar stages of other species.

The propodus of the first thoracic leg (maxilliped) is a useful character to identify juveniles, as it is in adults. Although the number of setae on the propodus of this leg is fewer in juveniles than in adults, it is possible to examine the differences in the "style" of setation among juveniles of *Nematoscelis*. For example, in adults of *N. gracilis* there are two rows of setae on the propodus of the maxilliped (Figure 6c); in the juvenile stage this segment develops at least one seta from each position of these two rows. In *N. atlantica* the same segment has only one row (marginal) of setae in adults, and in juveniles at least one seta is present at the position of this marginal row. This difference in the style of setation can be used to distinguish *N. gracilis* and *N. atlantica* juveniles. The propodus of the maxilliped of *N. microps* also has one row of marginal setae, but its inner margin is convex; the carpus of this appendage is shorter than its propodus. The prominent dorsal keel on the carapace is a good diagnostic feature of *N. microps* juveniles.

Nematoscelis G. O. Sars—Generic Characters

The shape of the rostrum variable in males and females; eyes large and bilobed; the peduncle of the first antenna slender in females and thicker in males. Dactylus of the first thoracic leg (maxilliped) triangular, flattened and furnished with comblike setae on its inner lateral margin. The second pair of legs greatly produced and with spines on the distal segment or on both the penultimate and the distal segments. The endopod of the seventh leg biarticulate in the female, lacking in the male. Eighth leg a simple setose plate. All the four processes–proximal, terminal, lateral, and spine-shaped process–present in the petasma; the spine-shaped process always straight and the lateral without any hooks.

Key for Identifying Adult Species of *Nematoscelis*

The following key is adopted from Hansen (1910, 1912), Boden (1954), Boden et al. (1955), and Mauchline and Fisher (1969). It is modified to include additional information:

1a. Second pair of thoracic legs with long spines from both terminal segment (dactylus) and distal end of propodus. Third to sixth thoracic legs with three segments beyond knee. Maxillule with well-developed pseudexopod. Basis of maxilla bilobed. Ventrolateral spine on coxa of antenna greatly produced (Figure 4A,e,f). Carapace with conspicuous cephalic ridge (Figure 5f,g). Eyes large (Figure 4B,e,f). Propodus of first thoracic leg with setae

arranged in three rows (Figure 6e,f). Proximal process of petasma with serrations in two rows (Figure 7a,b) 2

1b. Second pair of thoracic legs with long spines from terminal segment (dactylus) only. Third to fourth thoracic legs with only two segments beyond knee, and fifth and sixth with only one. Maxillule without a pseudexopod. Basis of maxilla with one lobe only. Ventrolateral spine on coxa of antenna small or greatly reduced (Figure 4A,a-d). Cephalic ridge on carapace absent or inconspicuous (Figure 5a-e). Eyes relatively small (Figure 4B,a-d). Propodus of first leg with setae arranged in one or two rows (Figure 6a-d). Proximal process of petasma without serrations, or when present in one row only (Figures 7c and 8) 3

2a. Proximal process of petasma reaching almost middle of serrated margin of terminal process (Figure 7a). Serrated part of terminal process slightly curved towards median lobe. Propodus of first leg usually with six setae in outer (dorsal) row and five in middle row ..... *N. megalops*

2b. Proximal process reaching much beyond middle of distal part of terminal process (Figure 7b). Distal end of terminal process greatly curved towards median lobe, reaching slightly over distal end of proximal process. Propodus of first leg usually with five setae in dorsal row and four in middle row ..... *N. difficilus*

3a. Propodus of first thoracic leg with setae arranged in two separate rows (Figure 6c,d). Lateral process of petasma much longer than both terminal and spine-shaped processes (Figures 7c and 8a). Distal end of lateral process serrated. 4

3b. Propodus of first thoracic leg dorsoventrally flattened and furnished with setae in one row only (Figure 6a,b). Lateral process of petasma much smaller than both terminal and spine-shaped processes (Figure 8b-d). No serrations on lateral process or any other processes of petasma 5

4a. Ventrolateral spine on coxa of antenna highly reduced to a hump (Figure 4A,d). Lower part of eye much smaller than upper part (Figure 4B,d). A long seta projecting from dorsal surface of dactylus of first thoracic leg (Figure 6d). Distal end of lateral process always reaching beyond distal end of proximal process (Figure 8a)..... *N. tenella*

4b. Ventrolateral spine on coxa of antenna not reduced to a hump (Figure 4A,a). Lower part of eye larger than or nearly equal to upper part (Figure 4B,a). No seta on dorsal surface of dactylus of first thoracic leg (Figure 6c). Distal end of lateral process not reaching beyond distal end of proximal process (exception: "old forms" from the Pacific Ocean to be discussed in a later section) (Figure 7c)..... *N. gracilis*

5a. Upper part of eye slightly narrower than lower part (Figures 4B,b and 9c). Propodus of first thoracic leg with less convex inner margin (Figure 6b and 9d). Keel on carapace less prominent and without conspicuous hump. Abdominal segments without any elevated dorsal keels. Shapes and relative lengths of processes of petasma as shown in Figure 8c,d. Lengths of propodus and carpus of first leg nearly equal 6

5b. Upper lobe of eye slightly wider than lower lobe; lateral evagination much deeper in upper than in lower lobe (Figure 4B,c). Propodus of first thoracic leg with highly convex inner margin (Figure 6a). Keel on carapace quite prominent and with conspicuous hump (Figures 5c and 1b). Fourth and fifth abdominal segment characterized by less elevated dorsal keels. Carpus of first leg shorter than propodus. Shapes and relative lengths of processes of petasma as shown in Figure 8b..... *N. microps*

6a. Proximal process thick; terminal process much shorter than both proximal and spine-shaped processes. Lateral process small. Median lobe greatly flattened and broad; its outer and inner margins broadly convex, inner margin forming an acute distal angle with outer margin (Figure 8c). Adult female without lateral denticle on carapace..... *N. lobata*

6b. Proximal process thin, a little shorter than terminal process; lateral process slightly curved toward median lobe, its distal end reaching to or almost to distal end of proximal process (Figure 8d). Adult female with lateral denticle on carapace..... *N. atlantica*

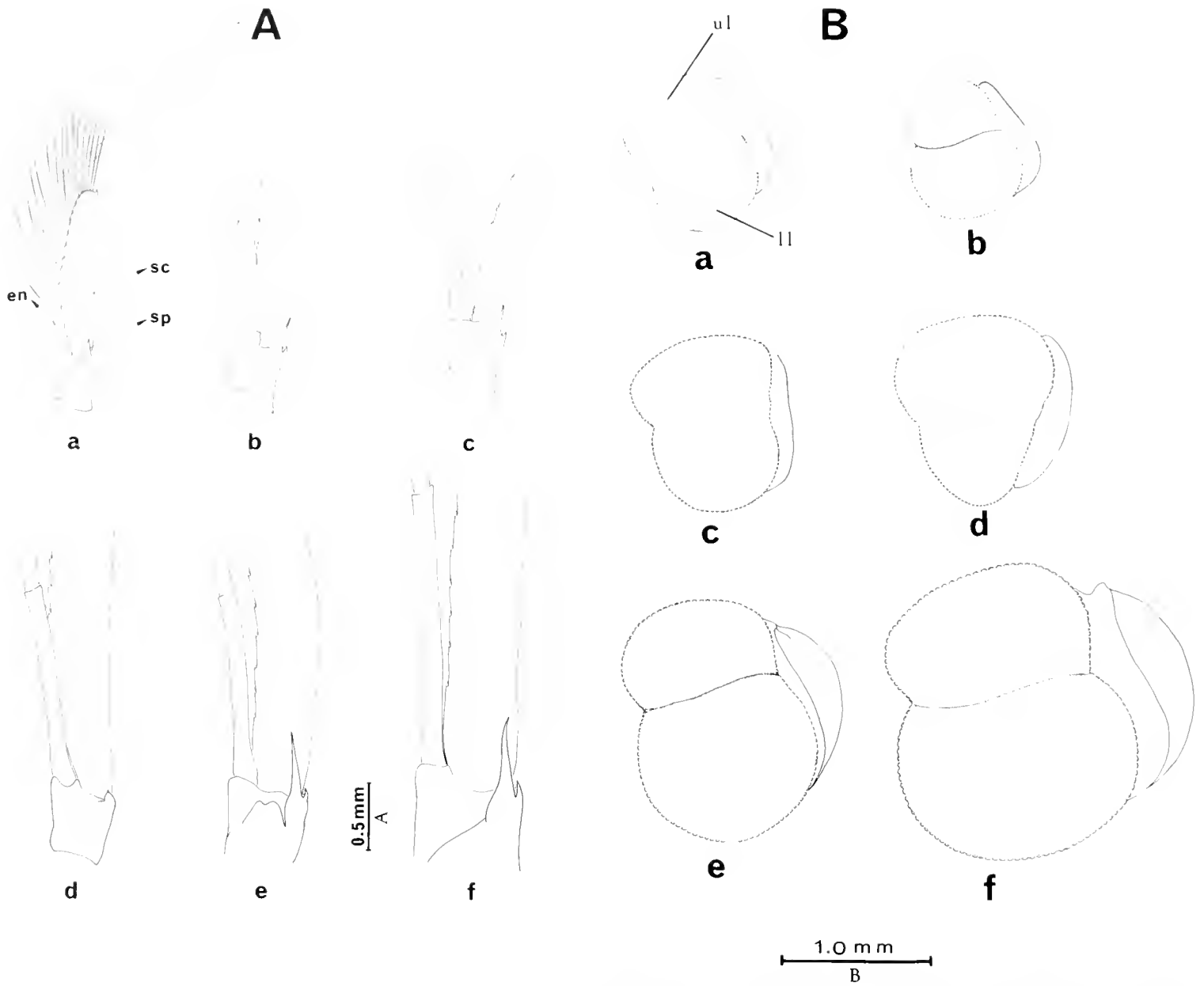


FIGURE 4.—*A*, antenna (ventral view) and *B*, eye (lateral view) of *Nematoscelis*: *a*, *N. gracilis*; *b*, *N. atlantica*; *c*, *N. microps*; *d*, *N. tenella*; *e*, *N. difficilis*; *f*, *N. megalops*. *en*, endopod; *sc*, scale; *sp*, spine on proximal segment of protopod; *ul*, upper lobe; *ll*, lower lobe.

The present study shows that there are two distinct forms in *Nematoscelis gracilis*. They are distinguished as ecophenotypes and are referred to here as the "old form" and the "new form." The old form is identical in morphological characters with the typical form described by Hansen (1910) from the waters of the Indo-Australian Archipelago, and the new form is distinguished from the typical form on the basis of morphological differences on the proximal process of the petasma. There is also an apparent size difference between the two forms: Body length of the old form is significantly larger than that of the new form (cf. Figure 5a,b). The upper lobe of eye in the new form is slightly narrower than that in the old form. Both forms are distinguishable only as adults. The old form occurs mostly in the northern section of the tropical Indo-Pacific subregion and has maximum abundance in the oxygen-poor waters of the Arabian Sea, Bay of Bengal, and eastern tropical Pacific Ocean. The new form occurs in the region of the South Equatorial Current. Along the equatorial zone, where the two forms overlap, an "intermediate" of the two forms, with regard to the length of the proximal process of petasma, is also encountered. Geographical distributions of these forms are described in Gopalakrishnan (1974). There are apparent morphological differences between the old forms of the Indian and Pacific oceans. The following key is prepared for identifying the forms of *N. gracilis*:

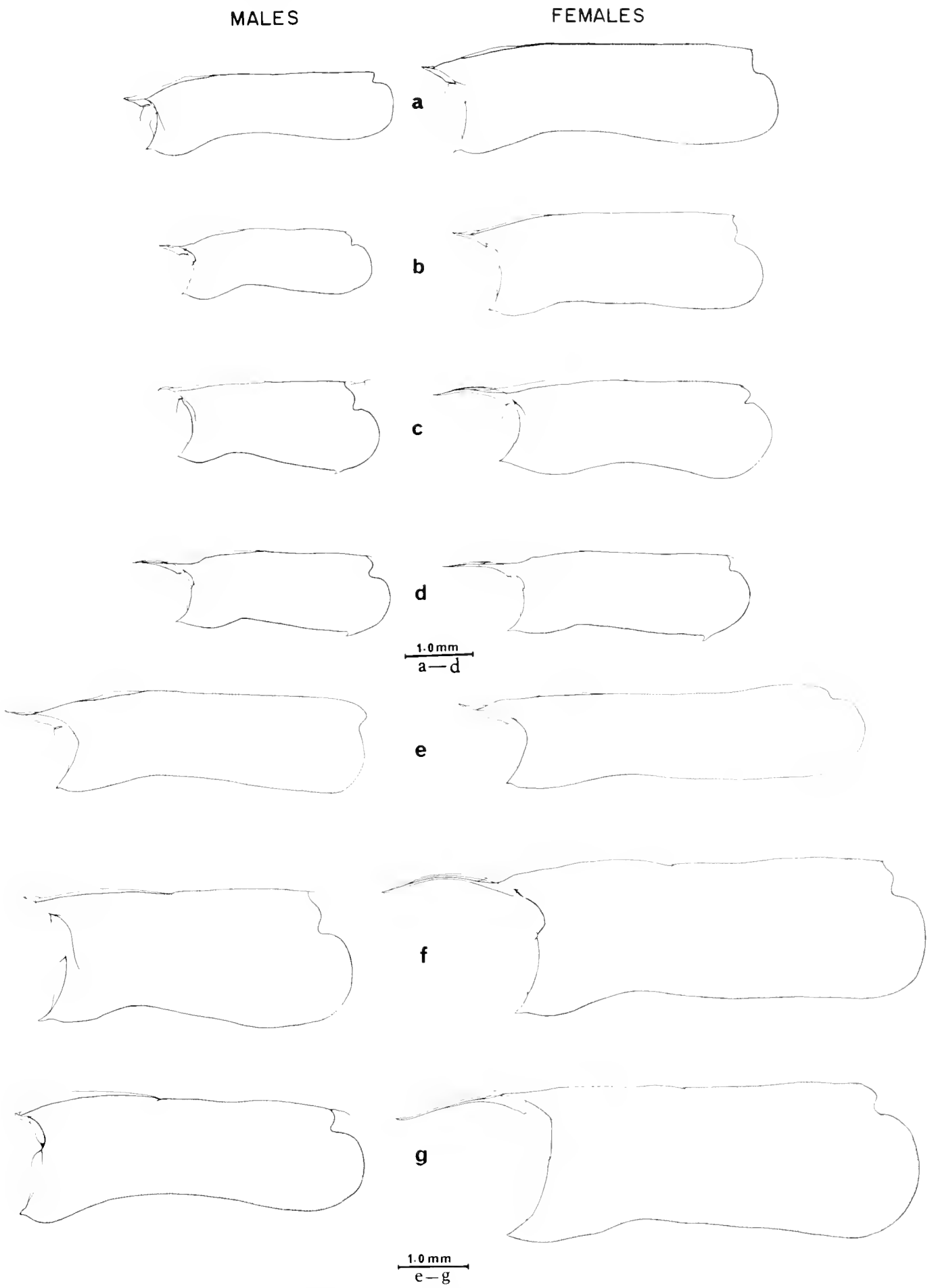


FIGURE 5.—Carapace of *Nematoscelis*: *a*, *N. gracilis* "old form" (length: male = 15.1 mm, female = 16.9 mm); *b*, *N. gracilis* "new form" (length: male = 11.7 mm, female = 15.0 mm); *c*, *N. microps* (length: male = 15.3 mm, female = 17.0 mm); *d*, *N. atlantica* (length: male = 12.9 mm, female = 13.7 mm); *e*, *N. tenella* (length: male = 18.0 mm, female = 19.1 mm); *f*, *N. difficilis* (length: male = 19.0 mm, female = 23.4 mm); *g*, *N. megalops* (length: male = 21.7 mm, female = 25.2 mm).

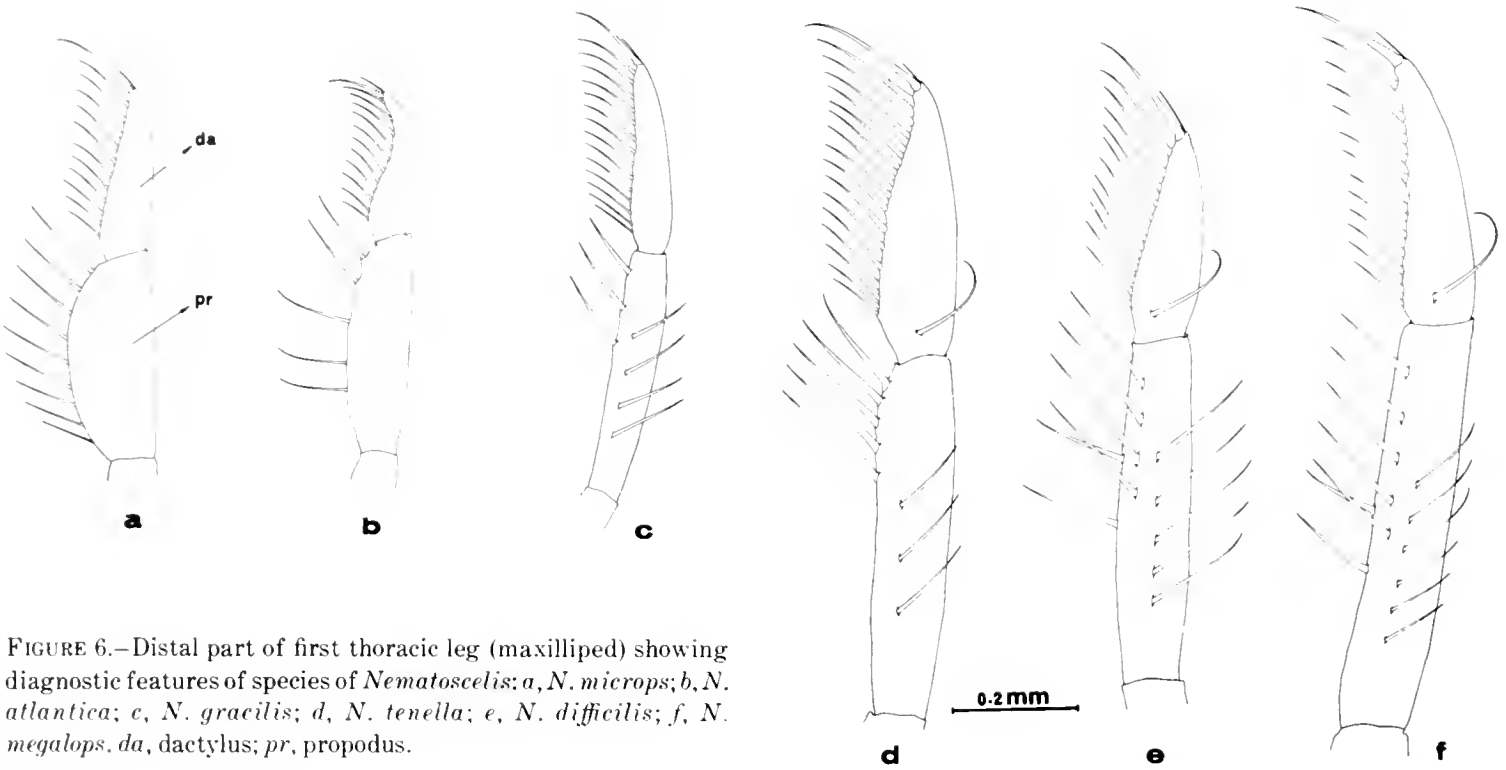


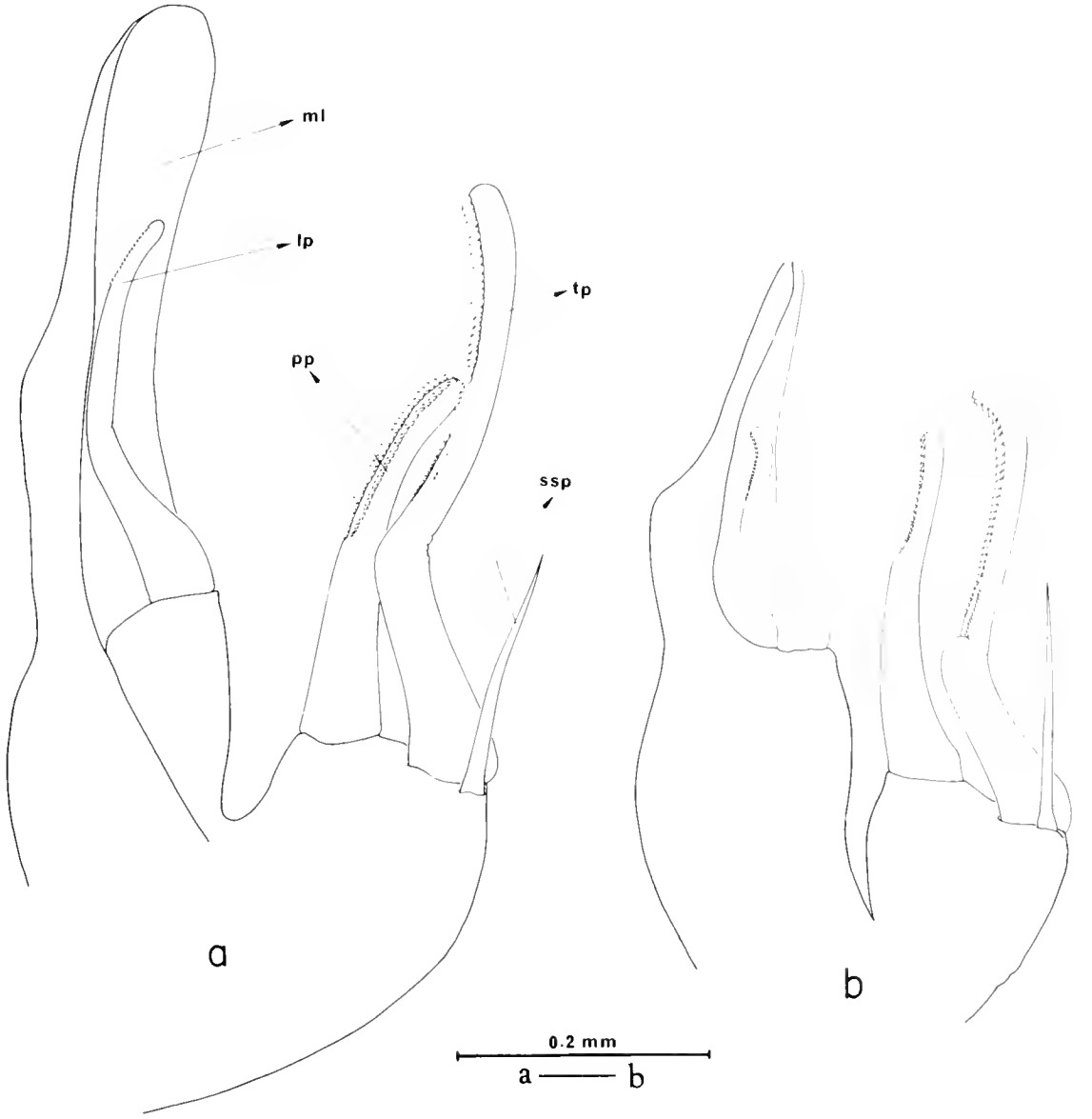
FIGURE 6.—Distal part of first thoracic leg (maxilliped) showing diagnostic features of species of *Nematoscelis*: *a*, *N. microps*; *b*, *N. atlantica*; *c*, *N. gracilis*; *d*, *N. tenella*; *e*, *N. difficilis*; *f*, *N. megalops*. *da*, dactylus; *pr*, propodus.

i. Distal end of lateral process always reaching far beyond distal end of proximal process; proximal process strongly serrated (average number of teeth 10) (Figure 7c) .... Pacific old form
ii. Distal end of proximal process always reaching beyond distal end of lateral process, but not reaching distal end of median lobe; proximal process moderately serrated (average number of teeth 6) (Figure 7c) ..... Indian old form
iii. Proximal process extremely long, reaching far beyond distal end of median lobe. Proximal process without any serrations (Figure 7c)..... new form
iv. Proximal process much longer than lateral process, its distal end reaching as far as distal end of median lobe. Proximal process slightly serrated (average number of teeth 3) (Figure 7c) ..... intermediate of old and new forms

The two forms of *N. gracilis* can also be separated with certainty by plotting the ratio of the proximal process to the median lobe of petasma against carapace length (Figure 10). The intermediate forms represent the presumed intergradation of new and old forms, although they appear to be much closer to the old form than to the new form with respect to this character. The difference in body lengths between old forms of the Indian and Pacific oceans is also apparent from this figure. Table 3 shows results of an analysis of covariance on proximal process of the petasma and carapace length of *N. gracilis* old and new forms. Length of the proximal process of petasma of the old form is significantly different statistically from that of the new form. Body lengths of the old forms in the Pacific and Indian oceans are significantly different statistically. Both intermediate and new forms are smaller than the old forms. Lengths of both the median lobe and lateral process are also different in these forms.

Of the 55 morphological characters measured, many showed statistically significant differences between species pairs. For example, the following characters of *N. gracilis* were different from those of *N. microps*: basal length of keel; length of carpus of first thoracic leg; lateral length of carapace; length of carapace between apex of keel and its posterolateral margin; length of carapace between apex of keel and point above photophore on seventh thoracic segment; distance between photophore on coxa of second thoracic leg and photophore on coxa of seventh thoracic leg; lengths of

FIGURE 7.—Petasmae of *Nematoscelis*: *a*, *N. megalops*; *b*, *N. difficilis*; *c*, *N. gracilis* forms. *lp*, lateral process; *ml*, median lobe; *pp*, proximal process; *ssp*, spine-shaped process; *tp*, terminal process.


ml
lp
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pp
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a
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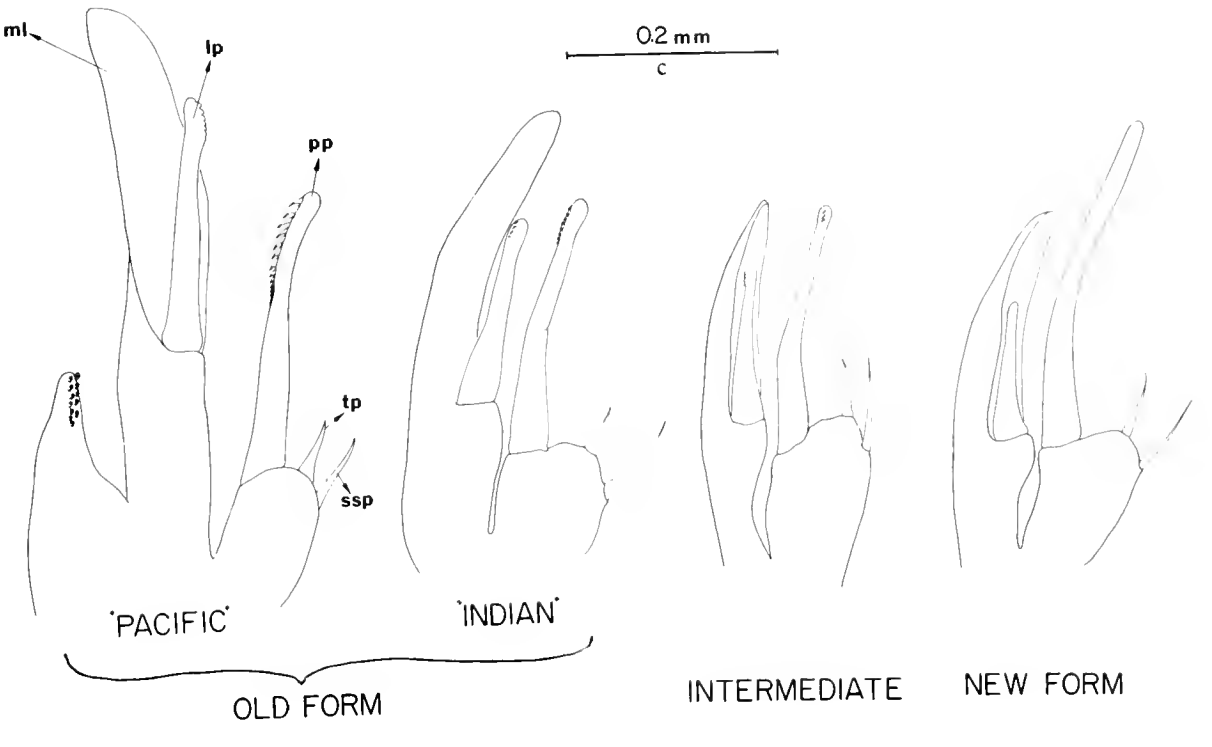
ml
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OLD FORM
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NEW FORM
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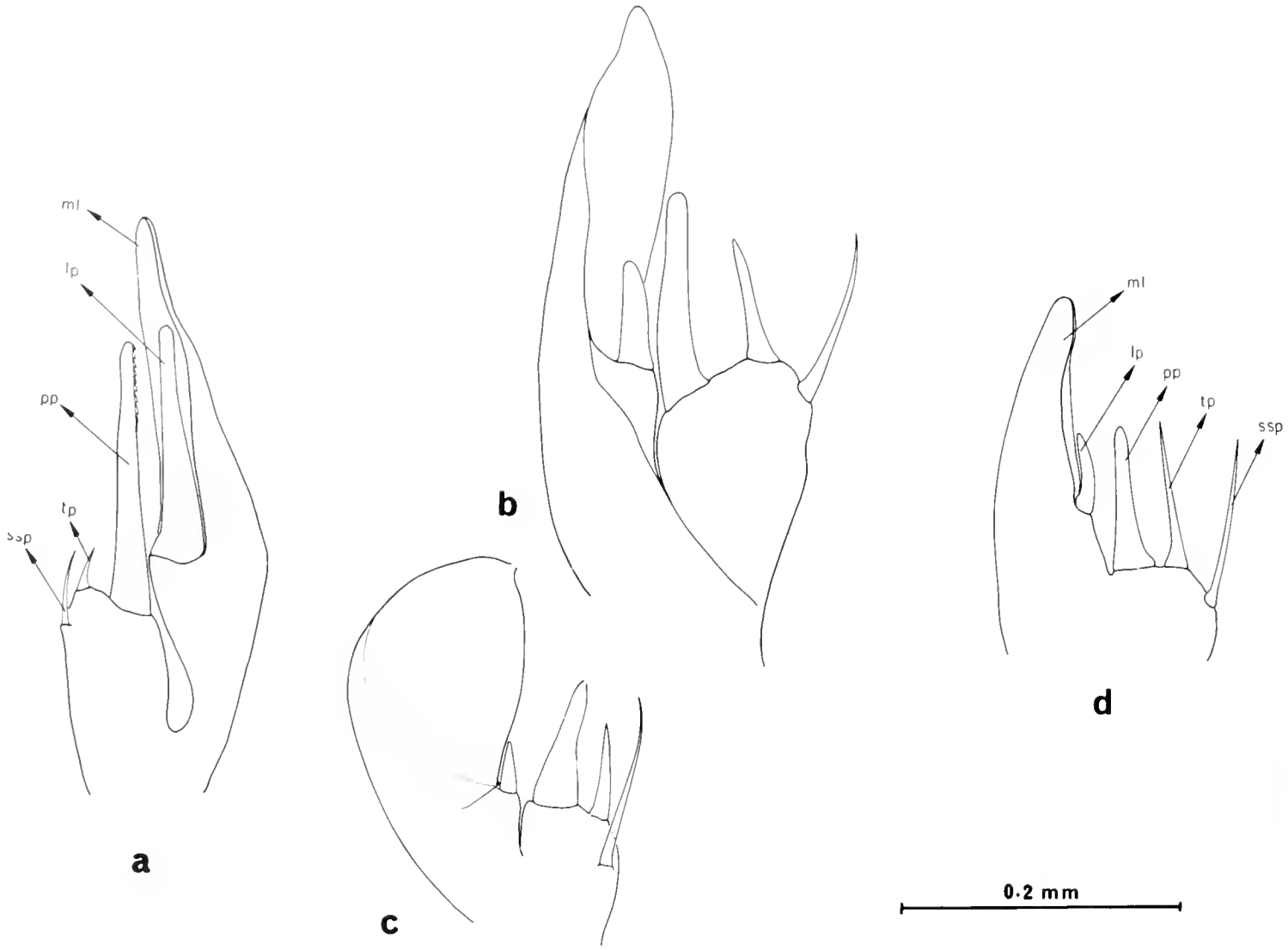


FIGURE 8.–Petasmae of *Nematoscelis*: *a*, *N. tenella*; *b*, *N. microps*; *c*, *N. lobata*; *d*, *N. atlantica*. *lp*, lateral process; *ml*, median lobe; *pp*, proximal process; *ssp*, spine-shaped process; *tp*, terminal process.

TABLE 3.–Analysis of covariance on proximal process of the petasma and carapace length of *Nematoscelis gracilis* "old form" (Indian Ocean) and the "new form."

Source	Sum of squares	Degrees of freedom	Mean square	*F* ratio	Probability
Proximal process alone:					
Between means	26.934	1	26.934	$F_{1,58} = 328.463$	<0.0001
Within groups	4.786	58	0.082		
Total	31.720	59			
After accounted for differences in carapace lengths:					
Between means	21.136	1	21.136	$F_{1,57} = 289.534$	<0.0001
Within groups[1]	4.186	57	0.073		
Regression (overall)	6.398	1			
Total	31.720	59			

[1]0.600 is *within SS* (regression) removed.

spine-shaped process, terminal process, proximal process, and lateral process of petasma; basal width of lateral process of petasma; number of marginal setae on exopod of maxilla; number of setae on second segment of mandibular palp. Similarly, *N. atlantica* and *N. microps* differ as follows: in dorsal length of first abdominal segment; length of keel on carapace; lateral length of sixth abdominal segment; length of carpus of first thoracic leg; width of upper lobe of eye; lateral length of carapace; length of carapace between apex of keel and its posterolateral margin; length

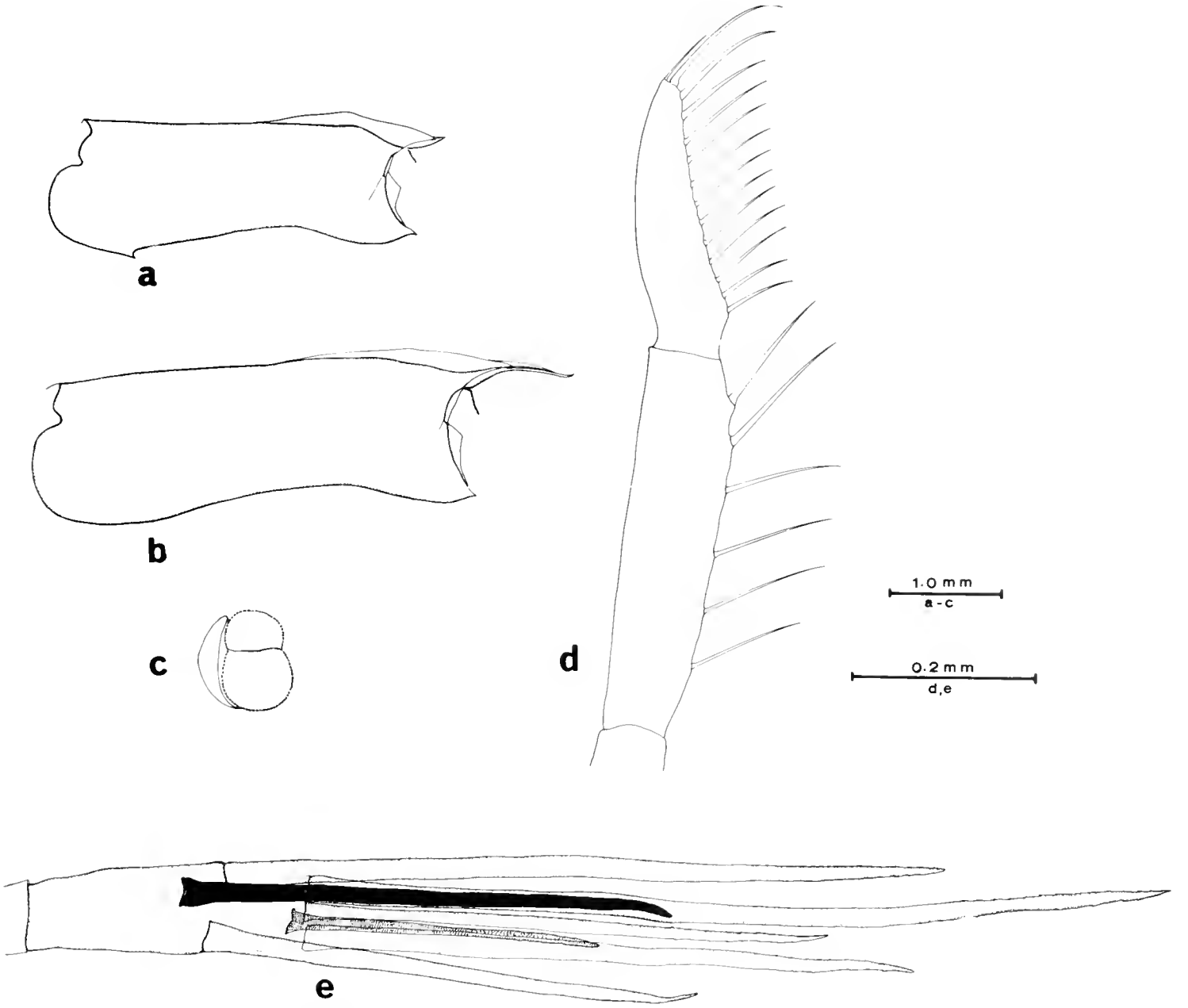


FIGURE 9.—*Nematoscelis lobata*: *a*, male carapace (body length = 12.1 mm); *b*, female carapace (body length = 13.5 mm); *c*, eye; *d*, distal part (propodus and dactylus) of first thoracic leg (maxilliped); *e*, dactylus of second thoracic leg showing arrangement of apical spines.

of carapace between apex of keel and the point above photophore on seventh thoracic segment; distance between photophore on coxa of second thoracic leg and photophore on coxa of seventh thoracic leg; length of proximal process of petasma; basal widths of lateral and proximal processes of petasma.

Nematoscelis tenella differs from other species in length of carpus of second thoracic leg, width of lower lobe of eye, lengths of merus and propodus of second thoracic leg, length of lateral spine of protopod of antenna, lengths of spine-shaped process and terminal process of petasma and basal widths of spine-shaped process and terminal process of petasma.

The lengths of the spine-shaped process and proximal process of the petasma and number of marginal setae on the pseudexopod of the maxillule of *N. difficilis* are different from *N. megalops*. The species pair *N. difficilis-N. megalops* differs from other species in the following characters: basal length of keel; length of scale of antenna; lengths of carpus, dactylus, and longest spine on distal end of second leg; lengths of ischium and merus of first thoracic leg; vertical length and width of lower lobe of eye; dorsal length of first abdominal segment; length and basal width of terminal process of petasma; number of marginal setae on exopod of maxilla, endopod and pseudexopod of maxillule, and on

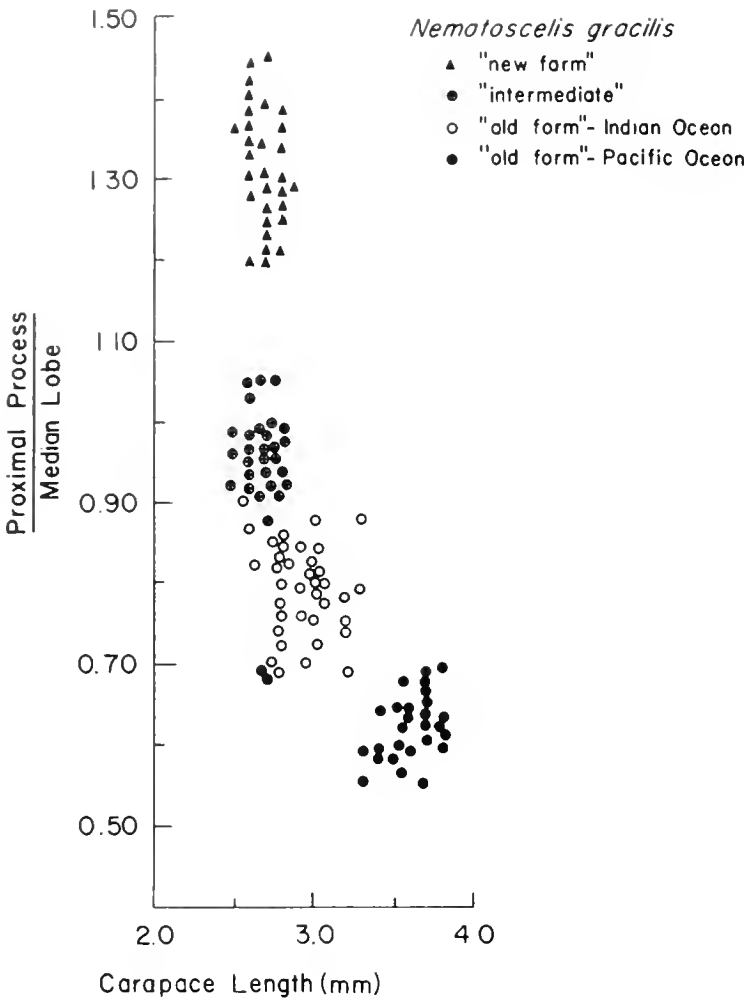


FIGURE 10.—*Nematoscelis gracilis* forms: ratio of proximal process to median lobe of petasma plotted against carapace.

propodus of first thoracic leg; number of marginal spine on lacina externa of maxillule; number of setae on second segment of mandibular palp.

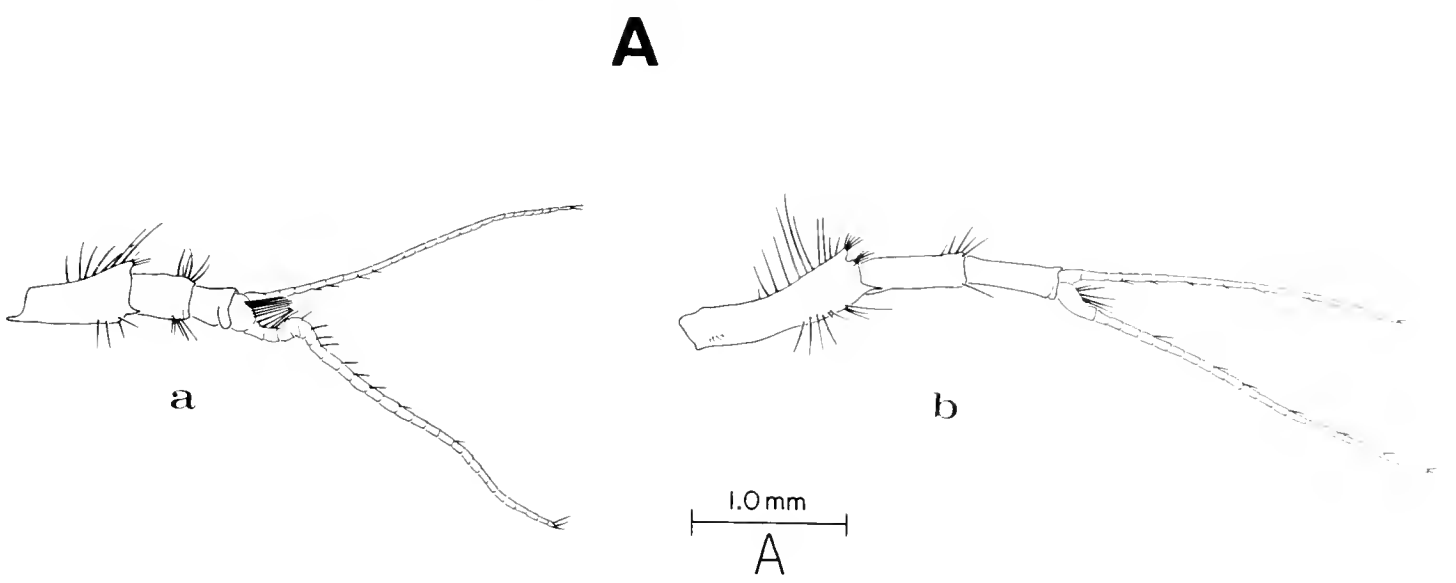
Sexual Dimorphism in *Nematoscelis*

Sexual dimorphism in euphausiids was best documented by Hansen (1910, 1912). Einarsson (1942) and Nemoto (1966) provided further details. The most sexually dimorphic characters are: the lateral denticle, keel, and rostrum of carapace; antennule; eyes; sixth and seventh thoracic legs; first and second abdominal pleopods; preanal spine.

The states of the lateral denticle, keel, and rostrum in both sexes of *Nematoscelis* are illustrated in Figure 5. The carapace and rostrum are shorter in males than in females. The rostrum in the male is rarely variable; in the female it is always long and slender, except in *N. gracilis* and *N. tenella*. The lateral denticle is absent in all species except in males of *N. microps* and both sexes of *N. atlantica*. McLaughlin (1965) reported the occurrence of this denticle in both subadult and adult stages of *N. difficilis* caught from the northeastern Pacific Ocean. In the present study, the lateral denticle on the carapace was found only in immature specimens of this species, but not in adults. These individuals were collected from the North Pacific Drift and California Current areas. No sexual dimorphism was observed in the shape of eyes in *Nematoscelis*. The antennular peduncle in males has the two distal segments much thicker than in females; the second segment somewhat shorter and the third segment much shorter than in females (Figure 11A,a,b). The lower flagellum of the antennule has the basal segment much thickened in males and furnished with tufts of sensory setae. In *N. gracilis* males, the proximal part of this flagellum bends downward so as to accommodate the enlarged basal segment (Figure 11A,a).

Sexual dimorphism in abdominal photophores is characteristic of *Nematoscelis*. Einarsson (1942) pointed out a few examples of enlargements of abdominal photophores in this genus. James (1973) reported the existence of this feature in the North Atlantic species of *N. tenella*, *N. atlantica*, and *N. microps*. In the course of examining the material from all oceans, certain interspecific differences of photophore enlargement have become evident. In females of all species of *Nematoscelis*, the photophores on each of the first four abdominal segments are more or less alike in size and shape (Figure 1b). However, in males, one or more of these photophores often show considerable enlargement. The patterns of this enlargement appear to be consistent, species specific, and therefore of diagnostic value.

Associated with photophore enlargement is the occurrence of paired chitinous saddle-shaped plates on the dorsal side of the abdominal segment anterior to that in which the photophore is enlarged (Figure 11B). Types of photophore enlargement in species of *Nematoscelis* are shown in this figure. In the Indian Ocean, *N. gracilis* males have the first abdominal photophore enlarged and lack chitinous plates on the dorsal side of the abdomen. *Nematoscelis microps* males have the second photophore enlarged and either with a dorsal hump (Figure 11B,b) or paired chitinous plates on the dorsal side of the first abdominal segment. Taniguchi (1966) reported occurrence of this hump on *N. microps* collected from the northeastern Indian Ocean. Humped males of this species are frequently found in the tropical



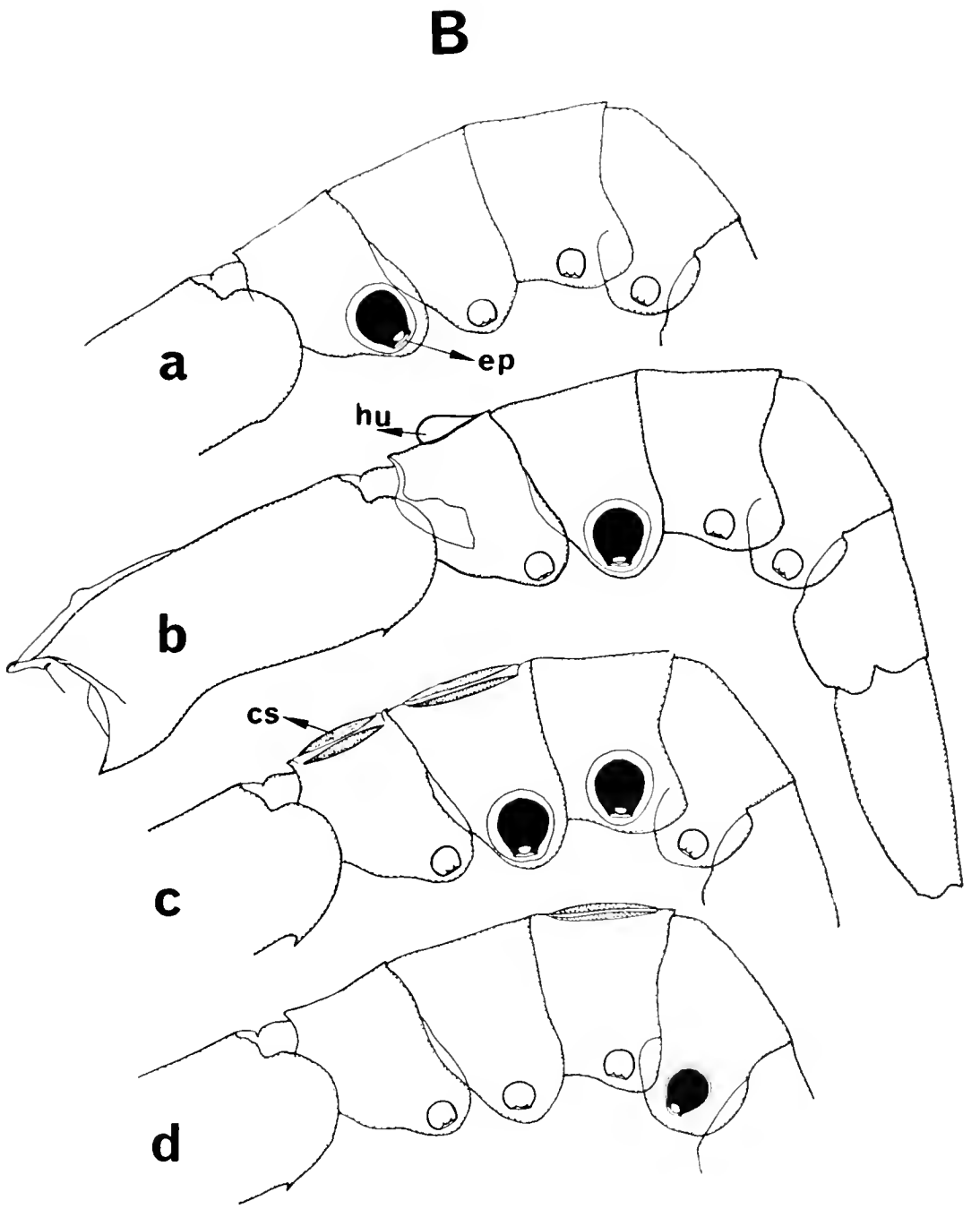


FIGURE 11.—*A*, dimorphic antennule of *Nematoscelis gracilis*: *a*, male; *b*, female. *B*, enlarged photophores of *Nematoscelis* males: *a*, *N. gracilis* forms; *b*, *N. microps*; *c*, first form of *N. tenella* and *N. atlantica*; *d*, second form of *N. tenella* and *N. atlantica*. *ep*, enlarged photophore; *hu*, dorsal hump; *cs*, chitinous "saddle."

Indo-West Pacific subregion. *Nematoscelis microps* males with paired chitinous plates on the first abdominal segment occur mostly in the tropical regions of the Pacific, Atlantic, and Indian oceans. James (1973) found this form of *N. microps* occurring in the northeast Atlantic south of lat. 20°N. Adult males of *N. microps* without any photophore enlargement were also found in all oceans, but they occur mostly in the subtropical regions.

Nematoscelis tenella and *N. atlantica* males have two forms of photophore enlargement (Figure 11B,c and 11B,d): one form has the second and third photophores enlarged along with the presence of saddle-shaped paired plates on the dorsal side of both the first and second abdominal segments; the other form shows photophore enlargement on the fourth abdominal segment along with paired plates on the third abdominal segment. These two species occur together in the northern and southern subtropical provinces of all oceans. They also occur together in the tropical regions of the Atlantic Ocean. When the two species occur in the same geographical area, the males of both species do not show the same pattern of photophore enlargement. In such cases the pattern of photophore enlargement is as follows:

Species	*Subtropics*	*Tropics*
Nematoscelis tenella	First form*	Second form**
Nematoscelis atlantica	Second form**	First form*

*Saddle-shaped plates on first and second abdominal segments and photophore enlargements on second and third.
**Saddle-shaped plates on third abdominal segment and photophore enlargement on fourth.

Nematoscelis atlantica does not occur in the tropical regions of the Pacific and Indian oceans; *N. tenella* males in this region have the second form of photophore enlargement. There is no clear evidence of photophore enlargement in *N. difficilis* and *N. megalops*.

Even though a pattern of photophore enlargement appears to be characteristic of each species, not all mature males show this feature. When present, about 60-80% of the males in each sample had specific patterns of photophore enlargement as described above. Structure of the petasma of these forms did not differ from the typical forms. One is tempted to speculate on the evolutionary significance of this feature. The occurrence of the dorsal chitinous plate and the enlargement of the photophore in adult males may have some joint functional importance, probably related to sexual behavior. Evidently, these abnormal conditions are not random phenomena; patterns are of specific nature and have clear association with sexual maturity. The fact that *N. tenella* and *N. atlantica* do not have the same form of photophore enlargement when they occur together in a geographical area suggests the possible role of these specific patterns in enhancing species recognition for mating.

DISCUSSION

Among the morphological characters of a species, feeding and reproductive structures afford specific features that have diagnostic value. The specificity of the feeding appendages reflects presumed niche specializations. The structural uniqueness in the reproductive system ensures reproductive isolation of the species upon which the biological species concept is founded (Mayr 1942). Therefore, a key based on these characters should be the best in distinguishing individual species. The selection of the maxillliped as a diagnostic character has the advantage that the same key may be used for both sexes. However, it did not prove possible to make such a key for the larva.

The species of *Nematoscelis* can be grouped into two subgroups, one with *N. difficilis* and *N. megalops* and the other with the rest of the five species. The present study has brought out both ecological and systematic evidences to support such a grouping. The sequential development of larval characteristics also suggests phylogenetic differences between the two subgroups. Hansen (1912), using the structure of adult maxillule, proposed a division of *Nematoscelis* into these two groups. A similar division was also made by Mauchline (1967) on the basis of structural differences in the adult maxilla.

When closely related species are partially sympatric, behavioral mechanisms might operate to insure reproductive isolation of the species (Mayr 1966). Usually the presence or absence of intergradation between sympatric populations serve as indicators of interbreeding or reproductive isolation. Presumably, the absence of intergradation between species of *Nematoscelis* occupying the same geographical area suggests reproductive isolation. However, the absence of reproductive isolation between the two forms of *N. gracilis* is probably shown by the occurrence of sexually mature intermediate forms in the

overlapping regions of their distribution. The fact that the observed diagnostic feature lies on the reproductive structure would suggest probable genetic separation. Nonetheless, until more is known about the ecology and behavior of these forms, I do not wish to formally describe them as species or subspecies and will consider them ecophenotypes. The pattern of geographical distribution of these forms appears to be correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column (Gopalakrishnan 1974).

Allopatric populations are inferred to have undergone reproductive isolation if they are morphologically distinct and do not show any overlap in their diagnostic features. *Nematoscelis difficilis* and *N. megalops* are allopatric, occupying the northern and southern transitional zones of the Pacific respectively. *Nematoscelis megalops* also occurs in the Atlantic and Indian oceans. On the basis of similarities in the structure of the petasma of *N. difficilis* and *N. megalops*, Karedin (1971) questioned the validity of *N. difficilis*. Brinton (1962) considered them a sibling species pair evolved as a result of complete geographical separation. Although closely related, there are certain morphological features that distinguish one species from the other. Both quantitative and qualitative features of the reproductive system, the petasma in this case, indicate significant differences. The petasmae of *N. megalops* in the South Pacific, South and North Atlantic, and South Indian oceans show no apparent structural difference. These populations are probably in continuum facilitating gene exchange. (Communication between North and South Atlantic populations of *N. megalops* appears possible from the fact that only in this ocean does the characteristically subtropical species *N. atlantica* occur also in the tropics. This suggests that in the Atlantic the low-latitude boundaries of distribution of subtropical species approach the equator, permitting at least occasional north-south communication). The validity of *N. difficilis* can be supported by the fact that this species and *N. megalops* do not overlap geographically in the Pacific Ocean. Both species live in comparable environments (narrow mid-latitude zones) and therefore are probably exposed to similar selection pressures. In such a situation, even though geographical isolation would be complete, morphological differentiation might be slow. In the absence of gene exchange, the populations would be expected to have diverged genetically. The relative lengths and shapes of the median lobe, proximal, terminal, and lateral spines of petasmae of the two species differ, supporting the validity of *N. difficilis*. In Hansen's words (1916) these differences are "certainly so sharp, so important, and so constant that they are sufficient for separating *N. difficilis* from *N. megalops*."

The *N. atlantica* population in the North Pacific is spatially separated from its counterpart in the South Pacific Ocean. No morphological distinctness was evident in this population, although it may prove to be genetically separate from others. *Nematoscelis lobata* is endemic to the Sulu and Celebes seas in the Indo-Australian Archipelago (Gopalakrishnan 1974). According to Hansen's (1916) description, this species is very similar to *N. microps*. The present study indicates that in many morphological characters *N. lobata* is more related to *N. atlantica* than to *N. microps*. *Nematoscelis lobata* and *N. atlantica* are allopatrically distributed and have probably acquired characters which promote or guarantee their reproductive isolation.

The observed differences in the structure of the first thoracic leg (maxilliped) of species of *Nematoscelis* indicate presumed specialization in feeding habits. All species of this genus are recognized to be omnivores. From a comparison of the first thoracic legs, it appears that species would be expected to show different types of feeding. *Nematoscelis microps*, *N. atlantica*, and *N. lobata*, having marginal setae (one row) on their propodus of the first thoracic legs, may be better fitted for filtering a large proportion of phytoplankton in their food, whereas *N. difficilis* and *N. megalops*, having three rows of setae on the propodus of the first leg, may select more animal food. In this respect *N. gracilis* and *N. tenella* are intermediate. Existing information on the gut contents of species of *Nematoscelis*, e.g., Nemoto (1967) and Weigmann (1970), is inadequate to substantiate this.

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FOOD, ACTIVITY, AND HABITAT OF THREE "PICKER-TYPE" MICROCARNIVOROUS FISHES IN THE KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Diets, daily activity, and habitat preference were compared between the kelp perch, *Brachyistius frenatus*; the señorita, *Oxyjulis californica*; and the white seaperch, *Phanerodon furcatus*, all of which co-occur in areas of reef and kelp off Santa Barbara, Calif. The kelp perch and señorita often clean ectoparasites off larger host fishes, whereas the white seaperch is a more generalized picker-type microcarnivore.

The kelp perch and señorita, which co-occur in the kelp canopy, showed the least amount of total overlap in resource use, expressed as a combination of individual overlaps in food, activity, and habitat. The señorita had the narrowest breadth of diet but the widest breadth of habitat (within the kelp-bed areas). Señoritas and white seaperch ate mostly bryozoans encrusted on plants, whereas kelp perch ate mostly plankton and other tiny motile prey. As species, neither the kelp perch nor the señorita derives substantial amounts of food from cleaning, although some individual señoritas may. Unlike the two "cleaners," the white seaperch also ate substantial numbers of bottom prey. None of the species forage at night, when all are relatively inactive, and when the señorita actually buries itself in patches of rubble and sand on the reef. The two perches showed the greatest overlap in daytime activity, as measured both by bi-hourly counts of feeding bites in the field and of swimming movements in a laboratory tank.

Fishes that exploit the same class of environmental resources in similar ways may be thought of as forming a "guild" of species having similar ecological roles regardless of their taxonomic affinities (Root 1967). In and about the forests of giant kelp off southern California, fishes that can select relatively small prey from mid-water and from kelp or other surfaces form a foraging guild of "pickers" (cf. Hobson 1971). Hubbs and Hubbs (1954) stressed the fact that two common and taxonomically unrelated pickers have remarkably similar mouth structures and dentitions: the kelp perch, *Brachyistius frenatus*, which is in the primarily temperate family of surfperches Embiotocidae, has evolved the same general type of pointed snout, tiny jaws, and protruding canines that characterize the señorita, *Oxyjulis californica*, and most other members of the primarily tropical family of wrasses Labridae.

Hobson (1971) noted that the habit of cleaning ectoparasites off larger fishes is widespread among the picker-type fishes. Señoritas, kelp perch, and young of another embiotocid, the sharpnose seaperch, *Phanerodon atripes*, are the most consistent "cleaner fishes" of the kelp beds (Limbaugh 1961; Hobson 1971). Compared to some small tropical wrasses (Randall 1958), however, these species are less specialized as cleaners: their cleaning activities are sporadic and/or confined to certain individuals, and so their principal forage must be elsewhere (Hobson 1971).

With this in mind, we compared the diets, daily activity patterns, and habitat preferences of the señorita and kelp perch, which are the principal cleaner fishes in the Santa Barbara area, with those of a more generalized picker, the white seaperch, *P. furcatus*. These three species have been studied off San Diego (Limbaugh 1955; Quast 1968a, b; Hobson 1971). Yet little has been published on their habits and distribution off Santa Barbara. Here the Channel Islands and the east-west oriented coastline protect kelp beds from swells, enabling giant kelp to anchor on low-relief and soft bottoms as well as to high-relief reefs. Also, species with centers of distribution located far to the north are more frequently encountered (Quast 1968a; Ebeling et al. 1971).

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METHODS

Kelp perch, white seaperch, and señoritas were observed in the field and laboratory. Over a 2-yr period, scuba divers spent more than a total of 125 h watching and collecting fish both day and night at depths ranging from 1 to 20 m. Study localities included areas of reef and kelp in the Santa Barbara Channel—off the Santa Barbara mainland and off Santa Cruz Island located across the Channel some 42 km to the south.

Food

During 27 scuba dives made between February, 1971 and March, 1973, we collected a total of 115 kelp perch (measuring 43-142 mm, averaging 103 mm standard length), 111 white seaperch (74-203, 139 mm), and 65 señoritas (110-227, 169 mm). Gut contents were found in and identified from 50 kelp perch, 55 white seaperch, and 53 señoritas. All fish were taken with a small, 15-prong pole spear. Later they were slit ventrally, fixed in 10% Formalin,[2] washed, and preserved in 45% isopropanol. During the analysis, fish were identified by numbered tag only so as to minimize any bias that might result from forehand knowledge of time of collection, etc.

For all three species, the simple, tubular gut, which is "stomachless" in the sense of Chao (1973), was excised, measured, and divided from front to back into three sections of equal length, here arbitrarily called the "fore-," "mid-," and "hindgut," respectively. Fullness of each section was scored subjectively from 1 (empty) to 5 (full and distended). Scores were plotted against time of day. Because fish were sampled throughout the year, their times of collection were seasonally adjusted relative to times of sunrise and sunset as listed in solar tables for the particular dates. Adjusted time of collection, rounded to the nearest 2-h interval, was measured on the relative scale with sunrise arbitrarily set at 0600 h and sunset at 1800 h.

Displayed under a dissecting scope, the contents of the foregut were sorted into broad taxonomic categories of food items, which were segregated in a small, partitioned tray. Then the percent volume of each item in the array was estimated by eye. Estimates were made quickly to the nearest percent, and their total over the array often exceeded 100% per fish. Yet at the outset, independent estimates of the same item did not vary substantially among successive trials, and series tended to regress toward a mean value (an observer's overestimation of volume on one trial was often countered by his underestimation of the same volume on the next). Item volumes were later standardized to 100%. In computing species means, fish with empty guts were not counted and all others were weighted equally, regardless of fish size or gut fullness (cf. Zaret and Rand 1971).

The frequency of occurrence of a dietary item was expressed as the percent of fish with non-empty foreguts that contained the item. The rank order of item frequencies was highly correlated with that of volumes. Kendall's tau correlation coefficients for the kelp perch, white seaperch, and señorita were 0.51, 0.85, and 0.70, respectively ($P<0.01$).

Activity

In the field, feeding bites made by individuals of each species were counted in six, 2-h intervals between dawn and dusk. Standardized as bites per minute, these counts were necessarily limited to solitary individuals that could be followed by a scuba diver for periods of about 3 to 5 min. It was impossible, for example, to discern the very rapid movements of señoritas feeding in large aggregates, which often formed during the early morning hours. The species value for each 2-h interval is the mean of 13-37 observations, each of a different fish. All counts were made during the first week of October, 1974.

To supplement field observations, swimming movements of individuals were observed in an outdoor tank. Fish were caught live either by hook and line during the day or by hand net underwater at night and transported in aerated containers to a 1-m-deep, 500-gallon, circular concrete tank at the University of California Santa Barbara Marine Laboratory. The tank was located outdoors under a lath roof and so was exposed to a natural, but subdued, 24-h cycle of light and dark. To eliminate visual disturbance, a black opaque plastic shroud perforated with several small peep holes was erected around the sides of the tank. Two, 10-W incandescent red lights, placed 1.5 m above the waterline, provided continuous dim light, especially useful for nocturnal observations. The temperature of the continuously running, filtered seawater, which varied no more than 3°C during

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

any 24-h experimental trial, probably approximated that encountered naturally by the species in nearby shallow inshore waters.

A grid of 10-cm squares was painted on the tank bottom, so that the activity of a fish could be measured as the number of grid lines it crossed during 5-min sample periods, one for each of twelve 2-h intervals (cf. Bortone 1971). On the bottom of the tank were arranged small patches of concrete blocks, rubble, freshly cut kelp, and sand to simulate a natural reef area as much as possible. After each fish had acclimated for a day, it was observed from a platform directly overhead or through the peep holes in the plastic shroud.

Habitat

Habitat occurrences of the three species were determined from previous observations of 414, 2.5-min Super-8 mm underwater movie strips in color (cinetransects) filmed by scuba divers. Cinetransects were made between 1000 and 1500 h during all seasons of 1969-70 and during the fall of 1971 and 1972 in a variety of kelp-bed habitats off the Santa Barbara mainland and Santa Cruz Island (Ebeling, Larson, and Alevizon in prep.). Each cinetransect recorded most fish in a 5-m wide path through or over a particular habitat type and so was classified into scored categories of bottom relief, kelp density, density of low algae on the bottom, and position in the water column ("canopy" or near the bottom). ("Kelp" herein refers to the giant kelp *Macrocystis*; "algae" refers to smaller plants other than giant kelp; and "canopy" refers to the zone of the upper spreading layer of the kelp bed—in our study, within 3 m of the surface.) Fish were tabulated by species as the film was projected in slow motion, reverse, and stop action. Later the frequency of occurrence of each species among all cinetransects was recorded for every habitat parameter.

Concordance, Breadth, and Overlap

For each species, dietary arrays were compared among four "seasons" that correspond roughly to different hydrographic periods off Santa Barbara (cf. Brown 1974): December-February, March-May, June-August, and September-November. Kendall's W coefficient of concordance (Tate and Clelland 1957) was used to measure differences in rank orders of volumes of food items pooled by season. To estimate dietary variability among individuals, concordance was also calculated for each of five or six samples of four to nine fish that were speared at the same general time and place. Thus we assumed that food items must have been about equally available to all the fish in a particular sample.

Breadth and overlap of resource use were computed from values of p_i, the proportion of item i in the sample (fish), or pooled sample of fish (species). For food breadth, p_i is the proportionate volume of any of the species total (S) of different food items; for activity breadth, it is for any of six 2-h daytime intervals, either the proportionate number of bites per minutes by fish in the field or the proportionate number of grid-line crossing per 5-min period by fish in a tank; and for habitat breadth, it is the proportionate occurrence of a species in any of 12 scored categories of habitat: 5 each of kelp density and bottom relief and 2 of depth. Sample values derive only from those resources or activities for which an entire array of items are observable for individual fish, i.e., from food and swimming activity only. Only the habitat parameters that seemed to be mutually independent were included in the analysis. "Density of low algae on the bottom," which was highly correlated with "bottom relief," was excluded. Yet "kelp density" was included. In the study area off Santa Barbara, kelp density is more or less independent of bottom relief because here kelp can anchor to flat as well as high relief bottoms. Because cinetransects were not evenly distributed among habitat categories—most films were taken in relatively dense kelp and high reef—the proportionate frequencies were standardized by total films taken per category.

The sum of p_i^2 over S items in the array equals the probability that any two units selected at random will be of the same item (see Simpson 1949). Thus, the reciprocal, $B = 1/\sum_{i=1}^{S} p_i^2$, measures breadth or diversity (Levins 1968; MacArthur 1972). Or, B is the theoretical number of equally used resources. For example, if all items are in equal proportions, B equals the total items in the array, S. It follows that the value of S determines the maximum value of B. B was computed for fish (individuals within a species) and for pooled sets of fish (individuals pooled by species) as unscaled values and as scaled values. The unscaled values incorporate two contributions to breadth: that of richness (S), and that of evenness of the distribu-

tion of amounts among the S items or classes. Values are scaled as B/S between zero, the most uneven distribution possible among S items, and unity, the most even possible.

Proportionate overlap of resource use may be thought of as a measure of mutual use by two species of the same items. The coefficient used here measures overlap between species j and k (Horn 1966):

$$C_\lambda = \frac{2\left(\sum_{i=1}^{S} P_{ij}P_{ik}\right)}{\sum_{i=1}^{S} P_{ij}^2 + \sum_{i=1}^{S} P_{ik}^2}$$

Among the three possible species pairs, activity overlap calculated from field observations of feeding rate varied in the same manner as activity overlap calculated from laboratory observations of swimming rate. For the subsequent calculation of total overlap in food, activity, and habitat, therefore, we used the arithmetic mean of these two independent estimates to express a single activity component.

Two estimates were made of total overlap. If, e.g., food and habitat are mutually independent, i.e., the same foods are available in the same proportions in different habitats, overlap between any species pair is the product of the separate measures for food and habitat. But if food is completely dependent on habitat, i.e., different habitats contain totally different foods, then overlap is the arithmetic mean of the two measures (Pianka 1974). (In the latter case, food and habitat measure the same resource axis, and the separate measures can be thought of as independent estimates of the same overlap.) In general, the actual relation between resource distributions is somewhere between complete independence and dependence. Thus, total overlap as expressed by the mean of the separate overlaps in food, activity, and habitat is a maximum value, and true overlap is somewhere between this and the product estimate (see Pianka 1974).

Kolmogorov-Smirnov tests of goodness-of-fit showed that the distributions of the variates of food breadth (s, b, b/s) differed significantly from normal (were skewed) for the white seaperch and señorita (P = 0.05-0.01), though not for the kelp perch (P>0.05). Therefore, we computed medians, ranges, and the Kruskal-Wallis measure H of differences in location of the ranked variates to test for differences among the three species (see Sokal and Rohlf 1969).

RESULTS

Food

Seasonal Effect

Food arrays were generally correlated among seasons. The rank concordance of diets was significant for all species (Table 1). The same items, which often made up more than 70% of the total food volume, usually occupied one or another of the first three ranks from one season to the next; seldom did the first three positions for any one season contain items not among the first three for the others. Consequently, all samples were pooled by species, regardless of season, for the remaining analyses.

Individual Variability

Food items were generally uncorrelated among fish of the same species collected at the same time and place. Rank concordance was significant for but one of five collections of kelp perch (W = 0.55, P<0.01), and for no collection of white seaperch or señoritas. This might indicate that members of the same species that co-occur were choosing different items from the same forage base. But such a conclusion may be misleading for white seaperch and señoritas. A single item (plant-encrusting bryozoans) usually dominated their foregut contents, and although the second and third ranked items varied considerably among fish, they made up but a minor part of the total.

Kelp Perch

Tiny plankters, mainly copepods, made up more than half of the food consumed by the kelp perch (Table 2). Of 18 categories of items eaten by kelp perch, small calanoid and cyclopoid copepods led in both abundance and frequency; foreguts of six fish contained copepods only, and one was packed with more than 300 individuals. The distinctive genus *Corycaeus* occasionally dominated the contents. Large calanoids longer than 4 mm, which were found in fish collected during late winter only, were relatively rare. Tiny ostracods were frequently consumed, but only in small numbers.

TABLE 1.—Among-season comparison of diets of the three fishes. The first three ranking food items with their percent volume are listed in order for each period. Sample size is the number of diets (fish) pooled per period; W is Kendall's coefficient of rank correlation.

Species	December-February		March-May		June-August		September-November		
	Item	%	Item	%	Item	%	Item	%	W
Kelp perch	Sample size = 19		Sample size = 0		Sample size = 12		Sample size = 19		
18 total items	Small copepods	50			Gammarid ampnipods	67	Small copepods	42	0.51*
	Plant-encrusting bryozoans	12			Small copepods	14	Gammarid amphipods	26	
	Large copepods	10			Caprellid amphipods	13	Plant-encrusting bryozoans	6	
White seaperch	Sample size = 4		Sample size = 24		Sample size = 9		Sample size = 18		
13 total items	Plant-encrusting bryozoans	92	Plant-encrusting bryozoans	42	Plant-encrusting bryozoans	45	Plant-encrusting bryozoans	51	0.48*
	Bare plants	5	Bare plants	18	Polychaete worms	25	Crushed shells	28	
	Gammarid amphipods	1.5	Gammarid amphipods	11	Gammarid amphipods	6	Gammarid amphipods	12	
Señorita	Sample size = 0		Sample size = 17		Sample size = 17		Sample size = 19		
19 total items			Plant-encrusting bryozoans	35	Plant-encrusting bryozoans	65	Plant-encrusting bryozoans	86	
			Gammarid amphipods	11	Serpulid worms	10	Hydroids	5	0.39*
			Hydroids	9	Parasitic copepods	7	Parasitic copepods	3.5	

*Significant at $P < 0.01$

TABLE 2.—Mean proportionate volume and percent frequency of occurrence of 25 food items in foreguts of 50 kelp perch, 55 white seaperch, and 53 señoritas. Food items are listed by their presumed major source.

Food item	Kelp perch		White seaperch		Señorita	
	% vol	% freq.	% vol	% freq.	% vol	% freq.
Primarily planktonic	51.6	—	—	—	7.0	—
Cladocerans	0.5	18.8	—	—	—	—
Ostracods	1.1	20.8	—	—	1.1	13.7
Small copepods (<4 mm)	42.0	81.2	—	—	1.5	15.7
Large copepods (>4 mm)	3.3	18.8	—	—	2.7	11.8
Nauplius larvae	0.2	2.1	—	—	—	—
Zoea larvae	4.3	18.8	—	—	1.7	11.8
Fish eggs	0.2	2.1	—	—	—	—
From process of "cleaning"	2.9	—	—	—	5.4	—
Parasitic copepods	1.4	22.9	—	—	3.5	11.8
Gnathiid isopod larvae	1.4	2.1	—	—	0.2	3.9
Fish scales	0.1	6.2	—	—	1.7	7.8
Primarily substrate oriented: kelp, other algae, and bottom	45.0	—	81.8	—	87.1	—
Free moving	36.2	—	18.1	—	9.7	—
Mysids (kelp)	4.1	18.8	—	—	0.4	7.8
Isopods	0.7	10.4	1.9	9.8	1.3	7.8
Gammarid amphipods	25.7	62.5	8.4	49.0	4.2	27.4
Caprellid amphipods	4.7	12.5	3.3	23.5	2.2	5.9
Decapod shrimps	1.0	8.3	3.2	5.8	0.4	5.9
Unident. crustaceans	—	—	—	—	1.2	5.9
Pycnogonids	—	—	1.3	5.8	—	—
Attached	9.0	—	63.7	—	77.4	—
Bare kelp and other algae	1.5	12.5	0.3	1.9	5.6	15.7
Plant-encrusting bryozoans	7.3	10.4	63.4	63.4	65.5	80.4
Hydroids	0.2	2.1	—	—	5.2	17.6
Serpulid worms	—	—	—	—	1.1	2.0
Primarily substrate oriented: bottom only	—	—	17.7	—	0.2	—
Crushed shells and debris	—	—	12.6	27.4	—	—
Polychaete worms	—	—	3.7	5.8	0.2	2.0
Cumaceans	—	—	0.5	3.9	—	—
Brittle stars	—	—	0.9	1.9	—	—

Small crustaceans that normally move freely on and about the kelp surfaces were almost equal to plankton in dietary importance. Gammarid amphipods, which may cluster just as abundantly about the kelp as in and about the tufted mat of plants and animals on the bottom, ranked second in overall abundance and frequency. Surprisingly unimportant were the so-called "kelp mysids," which are very abundant in the canopy and are commonly eaten by other fishes (Clarke 1971).

Forage on attached organisms was less important. Cheilostomate bryozoans, principally *Membranipora* ("plant-encrusting bryozoans"), ranked a distant third in overall volume. *Membranipora* is the dominant bryozoan encrusting kelp, where it often covers large areas of the plant (Woollacott and North 1971), and most of the bryozoans in the gut contents were associated with bits of kelp blades. Kelp perch apparently ate no benthic prey.

Cleaning activity was but a minor food source. Parasitic copepods, gnathiid isopod larvae, and fish scales were the only items likely to have been ingested in the process. The combined items never contributed more than 5% to the foregut food volume in a single fish.

White Seaperch

Virtually all prey of the white seaperch were substrate oriented, probably picked from off the kelp or bottom (Table 2). Plant-encrusting bryozoans predominated, and when present, averaged 85% of the foregut contents of individual fish. Moving prey, primarily amphipods and shrimps, were much less important. Many of the gammarid amphipods were quite small (<2 mm long); in one fish, e.g., all of 70 individuals did not fill the foregut.

Only the white seaperch ingested appreciable amounts of bottom items. Crushed shells and sand particles, which often were cemented into tubes, ranked second in overall abundance and third in frequency. The remains of polychaete worms were found in but 3 of 14 sand-containing guts, which did, however, include substantial numbers of the gammarids that commonly inhabit such burrows in the tufted mat on the bottom. Relatively large amounts of loose sand in the mid- and hindguts indicated that these fish generally do not winnow non-food items in their mouth.

Señorita

Most of its prey was substrate oriented, probably picked from off the kelp (Table 2). Like white seaperch, señoritas contained a predominance of plant-encrusting bryozoans, but unlike perch, had almost no bottom prey in the foregut. A third of all fish examined contained only the bryozoan *Membranipora* encrusted on pieces of kelp, and bits of bare plant material were found frequently among the encrusted pieces; of a total of 18 categories of food items found in señorita guts, no other so dominated the contents of even a single fish. Hydroids, another item attached to plants and other substrates, ranked third in overall importance. Moving prey, primarily amphipods, were less important.

Unlike kelp perch, señoritas did not exploit plankton as a major source of food. Although some items occurred frequently, they contributed but little to the overall volume.

Cleaning activity did not produce substantial forage, although it contributed relatively more to the diet of señoritas than to that of kelp perch. Of 10 adult señoritas, 142-184 mm long, that contained items likely to have been ingested during cleaning (parasitic copepods, gnathiid isopod larvae, and/or fish scales), the diets of seven were dominated by other food items. Ectoparasites and scales in guts of most señoritas were mixed with other food items, suggesting that the fish had both cleaned and foraged during the same day. However, guts of two of the remaining three fish contained nothing but parasitic copepods and scales. One specimen, collected at 1400 h, contained 465 fish scales, about 90% of the total contents, and 45 parasitic copepods. Both items were distributed more or less evenly throughout the length of the gut, indicating that this fish had cleaned during most of the day.

Diel Forage

All three species fed mostly, if not exclusively, during the day. Foreguts of kelp perch apparently were beginning to fill soon after dawn, were generally full by midmorning, and contained variable amounts of food through dusk (Figure 1). Of 54 day and 38 late-night (midnight-dawn) foreguts examined, 89% and 13%, respectively, contained food. Guts of white seaperch seemed to reach maximum fullness during midmorning and late afternoon. Of 64 day and 22 late-night foreguts examined, 88% and 4%, respectively, contained food. Fullness of mid- and hindguts of both species generally substantiated this daily cycle of feeding (Figure 2). Most foreguts were empty by midnight, when midguts still averaged at least half full and hindguts usually more. Then, by dawn most hindguts were empty, while foreguts were beginning to fill, a general pattern shown by fish whether collected during moonlit or dark nights. Señoritas seemed to feed actively through early afternoon, showing maximum gut fullness about

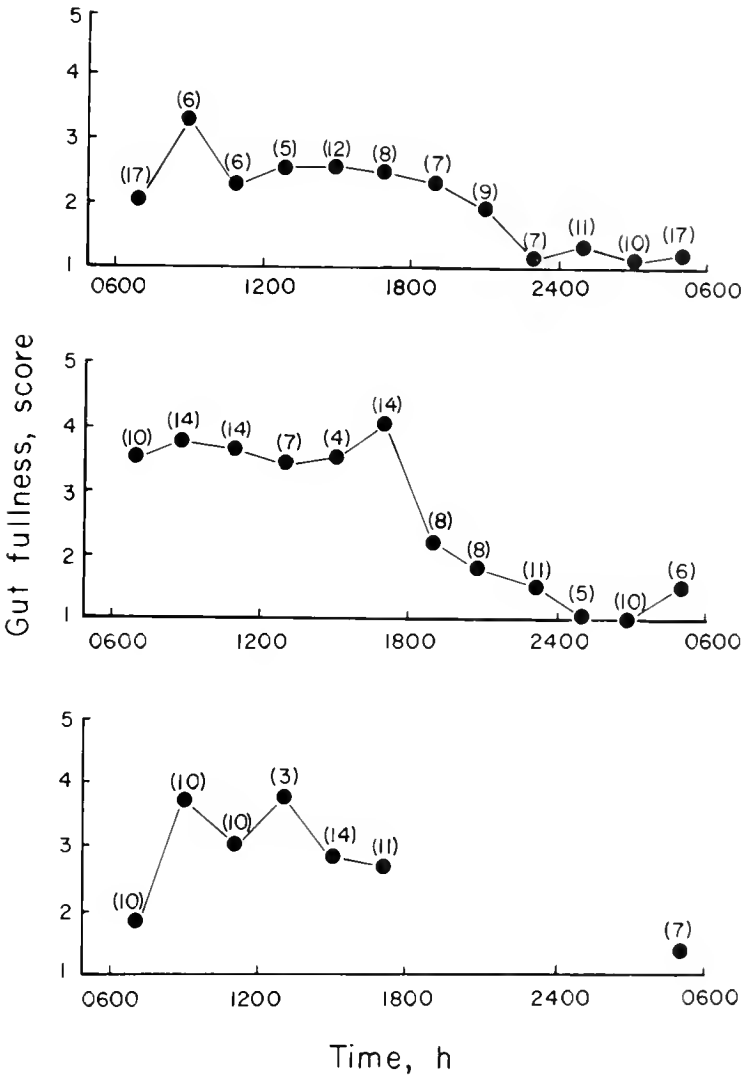

FIGURE 1.–Scored fullness (1, empty - 5, full) of foreguts of: top, kelp perch; middle, white seaperch; and bottom, señorita (which buries itself at night). Each point represents the mean value for (n) individuals collected over a 2-h interval. Time is measured relative to sunrise (0600 h) and sunset (1800 h–see text).

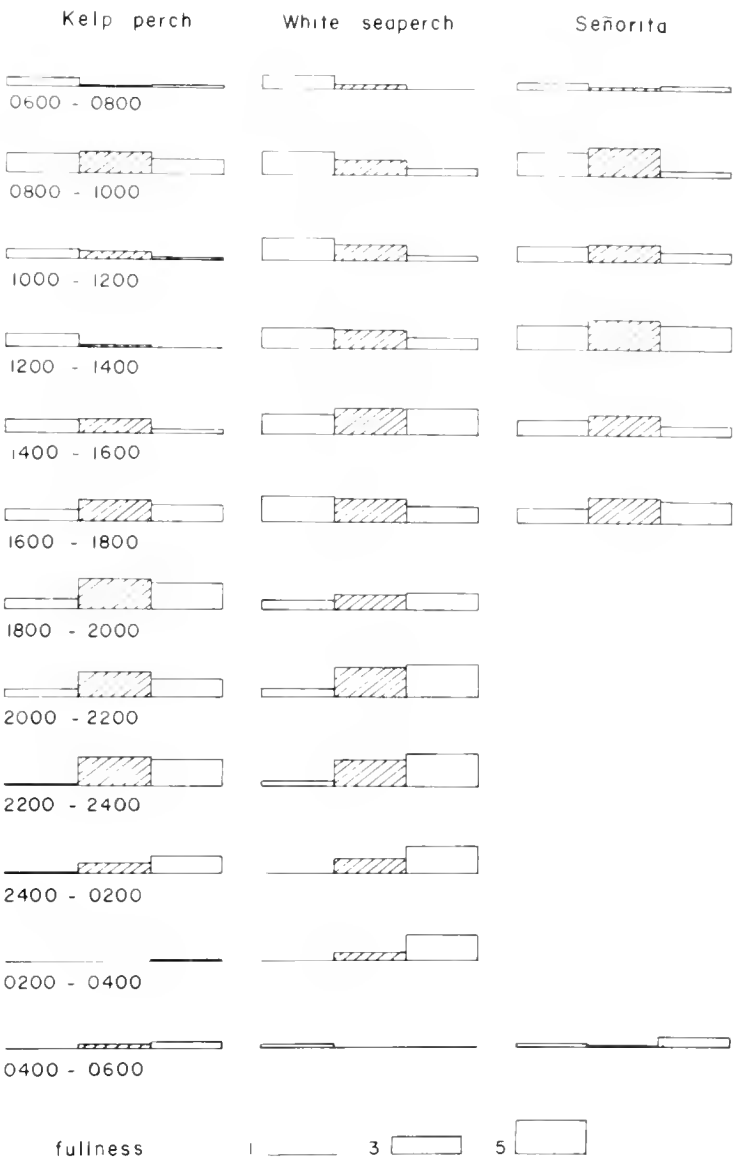

FIGURE 2.–Scored fullness of: foreguts (left open bars), midguts (middle hatched bars), and hindguts (right open bars) for the three fishes over 2-h intervals, beginning at dawn. Heights of the bars, scaled at the bottom of the figure, represent mean scores for the numbers of individuals indicated in Figure 1.

midday. Of 65 diurnal foreguts examined, 78% contained food. At night the fish bury themselves in soft areas of bottom (see next section). However, six of seven guts of fish collected at dawn were completely empty.

The duration of passage of food through the guts of the two perches was estimated from their diel feeding cycles. Assuming that feeding stops at dusk when almost half the foreguts were full or nearly so, and that almost all hindguts have emptied by dawn when almost all were, the retention time is probably no more than 10-12 h.

Activity

Feeding Rate

Field observations of feeding bites indicated that kelp perch fed frequently, at a maximum average rate of 20 bites/min around midday, decreasing to zero toward sunset (Figure 3). White seaperch and solitary señoritas fed much more slowly, at maximum rates of only 3.0 and 1.0 bites/min, respectively. Whereas both perches were seen feeding actively throughout the day, señoritas seemed to feed much less intensely after midafternoon. None of the particular individuals followed during the last two daytime intervals were seen to bite. During this time, however, a few other fish were observed picking away at bits of kelp. But this does not modify our general impression that, during the late afternoon hours, most señoritas feed much less actively than earlier in the day.

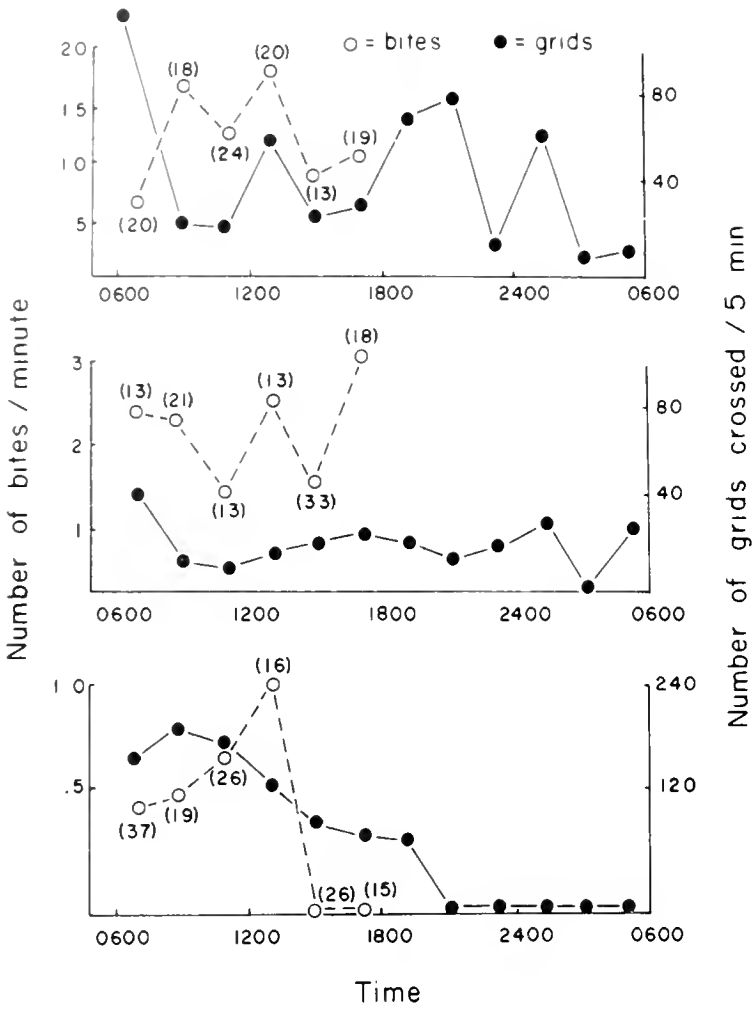

FIGURE 3.—Feeding and swimming activity of: top, kelp perch; middle, white seaperch; and bottom, señorita. Open circles are feeding rates observed in the field and standardized as bites per minute (fish do not feed at night); solid circles are swimming rates observed in a laboratory tank and measured as grid-line crossings per 5-min period. Each point represents the mean value for (n) individuals (feeding rates) or five or six individuals (swimming rates) observed for a 2-h interval.

Swimming Rate

Showing little if any spatial or temporal pattern, the two perches swam sporadically throughout the experimental tank during the day and night (Figure 3). Kelp perch swam in spurts and were slightly more active during the day than at night; white seaperch were most active at dawn; and neither species showed any marked change at dusk. The apparent increase in kelp-perch activity at dawn reflected intense swimming by one individual, whose exclusion from the sum would lower the mean species rate to 38 grid-line crossings per 5-min period, about the same as for white seaperch.

In the field during the day, white seaperch swam more continuously in mid-water and near the bottom than did kelp perch, which tended to hover camouflaged among the kelp canopy and only occasionally darted in and out. At night, white seaperch were occasionally seen drifting slowly in mid-water or over the bottom, while kelp perch tended to hang motionlessly among the kelp stipes or even in open water. Kelp perch, especially, were quiescent at night and easily caught with a small hand net then.

Señoritas swam most actively during the morning, then progressively slower throughout the day before finally burying themselves in the sand for the night (Figure 3). Beginning 20 min before sunset during one 24-h trial, a fish that was observed continuously first swam actively throughout the tank, then more restrictively over the sandy area. Finally after swimming in smaller circles about 4-6 cm off the bottom, it turned on its side and, with a few flicks of its caudal fin, proceeded head first into the sand. This entire episode lasted about 10 min, after which the area became dark. Observations by flashlight showed that the fish had buried itself completely, as had three others that accompanied the fish during the trial. Beginning 5 min after sunrise, the four fish emerged within 12 min. Two first stuck their heads above the sand to expose their pectoral fins, then after a short pause, swam out and milled about in small circles. The second pair emerged in a single movement to join the others in a small school, which soon moved throughout the tank. Of the total of seven fish observed in two trials, all buried themselves but one, which lay motionlessly against some bricks and assumed a mottled color pattern.

In the field, three fish observed on separate occasions over a reef about 10 m deep showed settling and burying behavior like that of the experimental animals, although they did not leave to seek a surrounding area of sand flat. Instead, they left a loose aggregation of fish before dusk to remain near the rocky substrate. They gradually restricted their spheres of activity to a small circular area above depressions filled with coarse sand and rubble. Just before sunset when visibility had decreased to about 3 m, the fish became hypersensitive to a diver's light and would dart away quickly when illuminated. About 15 min after sunset, the fish buried themselves in the depressions, first rolling on their sides and then swimming headfirst into the loose substrate. Gentle excavations caused the fish, which were probably buried within the upper 8 cm, to flee quickly. In more than 150 h of scuba diving at

night, we have never seen an exposed señorita either over the reef or the surrounding sand flats.

Habitat

Kelp perch were mostly restricted to the canopy, whereas señoritas were more evenly distributed in the water column (Table 3). The kelp perch, whose frequency of occurrence was highly correlated with kelp density, seemed to require the close presence of kelp and was most abundant in the thick of the canopy far above relatively flat bottom areas. Although most frequently filmed in or near the canopy, señoritas ranged throughout the kelp beds and over relatively naked areas of reef. They were recorded from 48% of all cinetransects, as compared to but 26% for kelp perch.

White seaperch were more bottom-oriented than the others, even though they were occasionally seen schooling in mid-water and singly in the canopy. The occurred most frequently in cinetransects taken over areas of sparse kelp and flat bottom at the margins of reefs and kelp beds, but large numbers have also been seen sporadically in areas of highest reef and densest kelp. The cinetransects were limited to areas of reef and kelp and the immediate environs and did not cover the white seaperch's relatively broad range of habitats. Although the kelp perch and señorita are more or less restricted to the habitats covered by the cinetransects, the white seaperch ranges far afield throughout the marginal sandy areas to bays and submerged artifacts, such as piers and docks. Its frequency of occurrence among cinetransects, 10%, was by far the lowest of the three species.

Resource Breadth

Food

Both as a species and as individuals, the kelp perch had the greatest food breadth (Table 4, *B*,*b*). The kelp perch ate more items (*S*) than the white seaperch, though amounts were about equally even in distribution (*B*/*S*). The señorita actually ate the most items, but in variable and often small amounts. Although the median number of items in individual foreguts (*s*) was the same for all three species, division between one- and multi-item

TABLE 3.—Distributions of the three fishes among scored categories of four habitat parameters. Parameters of kelp density and density of bottom algae are scored from 1 (absent) to 5 (very dense); bottom relief from 1 (flat) to 5 (high relief rock); and position in water column as C, the canopy within about 2-3 m of the surface, or B, the bottom and immediately overlying waters. Frequency is given as the actual percent (given as whole percent) of total cinetransects scored in the particular category, and as the percent standardized (given as 0.1%) by the total films in each category (see text).

		Kelp density					Bottom relief					Density of bottom algae					Position in water column	
Species	Frequency	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	C	B
Kelp perch	Actual	0	10	15	36	42	52	20	32	4	17	44	27	18	13	14	61	6
	Standardized	0	10.4	14.9	34.3	40.3	40.7	16.2	25.7	3.4	13.4	37.7	23.4	15.4	11.4	12.0	90.8	9.2
White seaperch	Actual	18	9	8	5	11	34	11	7	2	3	22	12	6	1	5	16	1
	Standardized	34.8	17.4	15.9	10.1	21.7	57.0	20.2	12.7	5.1	5.1	45.8	26.4	13.9	2.8	11.1	32.5	67.5
Señorita	Actual	37	48	50	52	34	40	40	53	55	35	33	48	49	32	45	54	45
	Standardized	17.0	21.6	22.6	23.3	15.5	18.2	17.9	23.6	24.3	15.9	15.8	23.2	23.5	15.8	21.9	54.4	45.6
No. of cinetransects per category		16	120	127	125	26	44	59	88	69	131	27	127	148	73	35	154	259

TABLE 4.—Food breadths of the three fishes. The text defines the measure *B* of resource breadth. *S* is the number of food items; *B*/*S* measures the evenness of distribution of proportionate amounts among the *S* items; medians and ranges (in parentheses) describe the individual (fish) variates; and the Kruskal-Wallis *H* statistic, distributed as chi-square with 2 df, tests for differences among species in the sample variates.

		Species (pooled) values			Individual (fish) values		
Species	Sample size	*S*	*B*	*B*/*S*	*s*	*b*	*b*/*s*
Kelp perch	50	18	4.57	0.25	2.0(1-6)	1.70(1.00-3.14)	0.74(0.34-1.00)
White seaperch	55	13	3.39	0.26	2.0(1-5)	1.00(1.00-2.41)	1.00(0.31-1.00)
Señorita	53	19	2.47	0.13	2.0(1-6)	1.22(1.00-4.84)	1.00(0.41-1.00)
				H	12.82*	13.65*	11.61*

*Significant at $P<0.005$

diets was most even in kelp perch. Distributions of all measures (s, b, b/s) did not differ significantly from normal for the kelp perch, but were strongly skewed for the others. In fact, median dietary evenness (b/s) equalled the maximum possible (1.0) for the others, because most foreguts contained either a single item or, occasionally, two items in equal amounts: 55% of the white seaperch and 47% of the señoritas had but a single item, as compared with only 24% of the kelp perch. Moreover, one-item diets of white seaperch and señoritas were more predictable in composition: 73% (of 30 foreguts) and 88% (of 25), respectively, contained the same item, plant-encrusting bryozoans. Other one-item foreguts of seaperch contained either plants (4 foreguts), shrimps (2), or polychaete worms (2). Other one-item foreguts of señoritas had either small copepods (1), gnathiid isopod larvae presumably from cleaning (1), or serpulid worms (1). The 12 one-item kelp-perch foreguts contained either small copepods (6), gammarid amphipods (4), bryozoans (1), or caprellid amphipods (1).

Activity

Activity breadths measured by feeding rates in the field (Table 5, B) correspond to breadths measured by swimming rates observed experimentally (Table 6, B), even though these two independent measures vary inversely among species. The señorita had the smallest feeding-rate breadth, because bites were observed over the fewest 2-h intervals (Table 5, S). From mid-afternoon on, the particular individuals followed during the test were not seen to bite, even though they swam actively about in the kelp canopy and below. (Recall that a few other individuals were feeding, but the general impression was of curtailment of feeding activity then.) Yet the señorita had the largest swimming-rate breadth because it swam actively and continuously during all six daytime intervals (Table 6, S). Thus both scaled measures (B/S) were relatively large for the señorita: the distribution of counts, whether of bites per minute or swimming movements per 5-min period, was relatively even among all intervals in which the action occurred (S). But it may be misleading to conclude that señoritas were then most consistent in their daytime feeding activity. During the first four daytime intervals when bites were observed for all species, 40-96% of the kelp perch and 46-69% of the white seaperch were recorded as biting. However, only 13-26% of the señoritas were so recorded. Therefore, señoritas show more variability in feeding activity; i.e., individuals may bite very rapidly for a few minutes then stop for extended periods. On the other hand, individual señoritas were the most consistent in their swimming activity. Señoritas led the others in breadth (b) and evenness (b/s), although the inter-species difference in b values was not significant (Table 6).

TABLE 5.—Activity breadths of the three fishes, as measured by their feeding bites per minute in the field. Sample size is the total fish observed in each species; S is the number of 2-h intervals (maximum of 6) in which fish were observed to make the biting motions. See Table 4 for further explanation (note that the nature of feeding-bite breadth precludes samples estimates).

Species	Sample size	S	B	B/S
Kelp perch	114	6	5.29	0.88
White seaperch	111	6	5.60	0.93
Señorita	139	4	3.62	0.91

Habitat

By all measures, the señorita had the greatest breadth of habitat within the area of reef and kelp where all three species co-occur (Table 7). The kelp perch, which was more or less restricted to the canopy, was most specialized in distribution.

Overlap

The white seaperch and señorita overlapped

TABLE 6.—Activity breadths of the three fishes, as measured by their daytime swimming movements in a large outdoor tank. S is the number of 2-h intervals (maximum of 6) in which fish swam across one or more grid lines during a 5-min observation period. See Table 4 for further explanation.

Species	Sample size	Species (pooled) values			Individual (fish) values		
		S	B	B/S	s	b	b/s
Kelp perch	6	6	4.19	0.70	6.0(2-6)	2.47(1.16-4.63)	0.52(0.29-0.77)
White seaperch	5	6	4.59	0.76	6.0	3.47(2.09-4.85)	0.59(0.35-0.81)
Señorita	6	6	5.53	0.92	5.0(2-6)	4.41(1.95-5.82)	0.96(0.87-1.00)
				H	3.52(NS)	2.39(NS)	11.23*

*Significant at $P<0.005$

TABLE 7.–Habitat breadths of the three fishes, measured relative to kelp-density, bottom-relief, and position-in-water-column classifications of the cinetransects (see text and Table 2). Sample size is the number of cinetransects from which the species was recorded; *S* is the number of habitat categories (maximum of 12) in which fish were photographed. See Table 4 for further explanation (note that the nature of habitat breadth precludes sample estimates).

Species	Sample size	*S*	*B*	*B/S*
Kelp perch	109	11	6.32	0.57
White seaperch	42	12	7.61	0.63
Señorita	201	12	9.84	0.82

most in total resource use, with food the main contributor (Table 8). Yet their large food overlap was caused not by any overall similarity in dietary arrays, but by their sharing one predominating item, the plant-encrusting bryozoans. In fact, rank orders of their food items were not significantly correlated (tau = 0.20, $P = 0.16$).

The kelp perch had the least amount of total overlap with others. Sharing the kelp-canopy area to a great extent, the kelp perch and señorita overlapped most in habitat even though the señorita had the broader overall spatial distribution within the kelp bed. Also, the two species' small food overlap and different activity patterns tended to minimize their total overlap. Actually, rank orders of their food items were significantly correlated (tau = 0.50, $P<0.001$), because the two species shared similar proportions of a number of minor items. Yet overlap was small because they did not share the same predominating item. A low amount of overlap in total resource use was shown by the two perches. Although their activity patterns were similar, their diets and habitat preferences differed markedly. In diet, they shared neither a predominating food item nor an array of minor items, and rank orders of their items were uncorrelated (tau = 0.06).

DISCUSSION

The kelp perch and señorita–the two species most often involved in cleaning activity–co-occur to a great extent in the sunlit upper waters and eat few if any benthic prey. Kelp perch typically feed in loose aggregations of a few to over 30 individuals. Constantly changing direction and depth, feeding individuals flit about to pick particles from mid-water or, occasionally, from the surfaces of kelp and from other fishes. In calm, clear water, these aggregations often extend to the more open areas between kelp plants. In strong currents, however, the fishes gather in back of kelp columns where the water is quieter and where food swept off the surfaces of kelp may be consumed. Solitary señoritas occasionally nip at various substrates and large drifting particles, but they feed most intensely when in large schools. These schools move in and about kelp stands, momentarily dispersing for individuals to pick and tear at kelp fronds and encrustations, then re-assembling and moving on to another stand of kelp.

The habit of kelp perch and señoritas of cleaning other mid-water fishes probably is incidental to the co-occurrence of the two species in the kelp canopy. Cleaning is not the principal occupation of either species (Limbaugh 1961, Hobson 1971). Their presence in the canopy better relates to their ability to pick small prey from off and from about the kelp blades. Seldom straying far from the heavy foliage where prey may become densely concentrated (Wing and Clendenning 1971), kelp perch also select plankton from incoming currents. Like other diurnal planktivores (Hobson 1974), the kelp perch has a relatively slender body, deeply forked caudal fin, and a slightly upturned mouth (Hobson 1971). Señoritas, which range more widely in the water column from canopy to near bottom, eat much less plankton. They favor attached food, primarily plant-encrusting bryozoans, either from the drift or torn from living plants.

White seaperch, which usually range nearer the bottom and only clean occasionally (Hobson 1971),

TABLE 8.–Overlap in resource use between members of all pairs of the three fishes. Activity overlap is the mean of two independent estimates: from feeding bites observed in the field, and from swimming movements observed in the laboratory. Habitat overlap is measured relative to kelp-density, bottom-relief, and depth classifications of the cinetransects (see Table 3). Total overlap is somewhere between the minimum and maximum estimates.

		Activity				Total overlap	
Overlap between:	Food *F*	Feeding bites *T*	Swimming movements *M*	Activity *A=(T+M)/2*	Habitat *H*	Minimum *FAH*	Maximum *(F+A+H)/3*
Kelp perch and white seaperch	0.25	0.92	0.95	0.94	0.63	0.15	0.16
Kelp perch and señorita	0.21	0.85	0.79	0.82	0.79	0.14	0.61
White seaperch and señorita	0.92	0.72	0.78	0.74	0.74	0.50	0.80

show more generalized behavior and are less specialized for picking than either kelp perch or señoritas. Like señoritas, white seaperch ate mostly plant-encrusting bryozoans, but their foraging behavior is quite different. White seaperch typically feed alone or in very small and loose aggregations. Feeding individuals often hover head down within 1 m of the substrate and, judging from their eye movements, search carefully for food. Even so, the substantial amounts of sand and other debris mingled with the more select items in white seaperch guts indicate that once the fish find their sedentary bottom prey, they engulf it in relatively large and indiscriminate mouthfuls.

Underwater disturbances attract white seaperch and señoritas. For example, the two fishes commonly aggregate and feed where bat ray, *Myliobatis californica*, are stirring up the bottom with their wings. They are also quick to follow and assemble about actively working scuba divers. This seems to be an adaptation to forage opportunistically in the wake and disturbance left by others, a strategy which is commonly used by tropical wrasses (Hobson 1974). In contrast, the kelp perch appears to be much less aware of such disturbances and often seems oblivious of an observer at close range.

Indirect evidence suggests that the plant material ingested with the bryozoans is not a primarily source of food for the fish. Only 10% of the ingested material was bare of bryozoans, indicating that white seaperch and señoritas select the heavily encrusted bits. Also, their relative gut lengths are less than expected for herbivores and many omnivores. Odum (1970) noted that the ratio of gut to fish length is usually less than unity in carnivores, one to three in omnivores, and greater than three in herbivores. Mean ratios from 74 white seaperch and 65 señoritas are only 0.82 + 0.028 (95% confidence interval) and 0.75 ± 0.036, respectively. They do not differ significantly from the mean ratio of 0.76 ± 0.024 from 95 kelp perch, which ingest comparatively little plant material. Likewise, Chao (1973) found no evidence that the cunner, *Tautogolabrus adspersus*, a temperate labrid from off the Atlantic Coast, assimilates the algae it ingests. Small undigested amounts from the intestine of the cunner are usually associated with digested epiphytic animals, including bryozoans. Primarily a shellfish eater, the cunner also has a gut ratio that is less than unity.

Individual diets of kelp perch and señoritas vary considerably from fish to fish, but this is not likely attributable to facultative cleaning. Diets of white seaperch, which do not commonly clean, were no more concordant than those of the other two species. Instead, opportunistic feeding in general may account for most of the variability. Kelp perch may switch from one patch of plankton to another, or feed on the kelp surface as the opportunity arises. Individuals were seen to dart back and forth between open areas and the kelp surface, selecting prey from either source. Although most señoritas eat large amounts of bryozoans, many select small crustaceans, especially amphipods. Hobson (1971) noted that señoritas not only eat mid-water plankton, but are occasionally seen picking about on the bottom. We observed that they are usually among the first to arrive at underwater chumming stations where sea urchins are broken open.

Yet cleaning contributes to the food breadth of kelp perch and señoritas by adding items that can be taken only by that process. And this points out a major problem in measuring food breadth by the "richness" or number-of-items measure, S. The categories of food items cannot be defined objectively, from the fish's point of view at least. For example, the total number of items recorded for the white seaperch would obviously increase if we further diversified the benthic categories (which are not exploited by the cleaners) by—say—distinguishing gastropods from bivalves within the category of "crushed shells." Even though cleaning increases S, its total nutritional importance to the cleaner species may be negligible.

Likewise, it is difficult to conclude whether or not cleaners have specialized diets. The total items eaten by either cleaner exceeded that eaten by the supposedly more generalized white seaperch, and the unscaled food breadth of the kelp perch was greatest of all three species. But the kelp perch and, to a lesser extent, the señorita are in fact limited to smaller items because they have smaller mouths. The 25 subjectively determined food categories included some 15 "small items" (usually <3 mm in diameter) but only 10 "large" (usually >3 mm). Therefore, the diet of the kelp perch appeared to be relatively broad because it includes all of the small items, several of which are exclusively planktonic. On the other hand, the diet of the white seaperch, which rarely visits the canopy, appeared to be more narrow because it includes relatively few of these small prey. Yet having a

larger mouth, the white seaperch may eat not only small items, but also an array of items too large to be ingested by the other two.

Other studies indicate that white seaperch forage opportunistically in a relatively broad range of kelp-bed and adjacent habitats. Although plant-encrusting bryozoans were by far their major food in the Santa Barbara areas of kelp and reef, they were of minor importance in fish collected off San Diego. Quast (1968b) reported that 18 fish from a kelp bed contained mostly small crustaceans, worms, and bivalves, while Hobson (1971) noted that 5 fish from shallow areas of surf grass contained small crustaceans, especially caprellid amphipods. DeMartini (1969) concluded that the white seaperch is almost "cosmopolitan" among habitats, including bays and artifacts far from the kelp beds. He observed that, unlike the kelp perch, it has uniformly broad and densely set pharyngeal teeth and commonly eats large, hard-shelled items like barnacles and clams.

Although the kelp perch and señorita have superficially similar feeding mechanisms, they do not overlap broadly in their diets. Off Santa Barbara, in fact, food overlap is least between señorita and kelp perch and greatest between señorita and white seaperch, whose mouth structure and dentition are more generalized. These relations prevail because the kelp perch does not eat substantial amounts of the plant-encrusting bryozoans, the overwhelmingly predominate food item of the other two. Disregarding bryozoans, the remaining (minor) food array of the señorita actually resembles more closely that of the kelp perch than that of the white seaperch. Likewise, off San Diego, kelp perch favor copepods and gammarid amphipods (Quast 1968b), and señoritas favor bryozoans (Quast 1968b; Hobson 1971) but may eat a variety of small crustaceans associated with giant kelp as well (Limbaugh 1955).

Because food overlap between the two cleaners is effectively small, they may co-occur with minimal mutual interference, even though their habitat overlap in the upper kelp bed is relatively broad. Also, their daytime activity patterns differ noticeably. Whereas kelp perch dart sporadically among the kelp blades and seem to feed almost continuously, señoritas move continuously about in open water as well as in dense kelp and seem to feed more sporadically. Also, solitary kelp perch continue their rapid picking about well past mid-afternoon after señoritas were observed to curtail their feeding activity.

It would seem that the señorita and white seaperch are greater potential competitors because they overlap almost completely in both food and habitat within the kelp-bed area. But even so, it is doubtful that availability of their principal food, bryozoans, is a limiting factor in the Santa Barbara area, where encrustations are widespread over the kelp and other substrates. Furthermore, the frequency of occurrence of white seaperch within the kelp bed is quite low compared to that of the señorita. Even though fairly large aggregations are seen occasionally over the reef, the center of abundance of white seaperch may be in more peripheral areas where alternative prey are readily available.

The señorita, which belongs to the large tropical family of wrasses, is more specialized in diel behavior than are the kelp perch and white seaperch. Whereas at night the perches simply slow down and become less responsive, the señorita buries itself in pockets of sand or gravel on the reef. Wrasses in general are strickly diurnal: they seek cover and become quiescent at night, as has been observed for tropical species (Hobson 1965, 1968, 1972, 1974; Stark and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972) and for other temperate species (Chao 1973; Olla et al. 1975). Various species hide in holes, bury themselves, and/or protect themselves with mucus envelopes (Hobson 1965, etc.). In the tropics, they are among the first fishes to take cover at dusk and the last to emerge at dawn, a practice that may minimize their vulnerability during the crepuscular hours when predation is most intense (Hobson 1968, 1972; Collette and Talbot 1972). In the kelp beds of the temperate zone, there may be relatively few nocturnal piscivores as compared with the tropics. Thus, the señorita may retain the burying habit of its family (which implies a complex genetic basis) simply because there are no pressures actively selecting against this trait (cf. Hobson 1972).

Many tropical "pickers" have elongated snouts and small mouths with projecting teeth for selecting and removing tiny prey from otherwise inaccessible places (Alexander 1967; Hobson 1968, 1974). These are also adaptations for picking ectoparasites from larger fishes, and indeed many of the small and sharp-nosed tropical-reef fishes are part-time or "facultative" cleaners (Hobson 1971, 1974; Losey 1972). Likewise, the tendency of kelp perch and señoritas to clean may vary among situations or individuals (Hobson 1971) and may

provide most fish with only a minor dietary supplement.

CONCLUSIONS

In and about kelp beds off Santa Barbara, the kelp perch, the señorita, and to a lesser extent the white seaperch, belong to a foraging guild of picker-type microcarnivorous fishes. Throughout the year, the kelp perch and señorita, which commonly pick ectoparasites from larger fish, spend most of the day in the sun-lit upper waters in and about the kelp canopy. Here they can discern and pick small prey from various surfaces and from the open water. A more generalized picker, the white seaperch, occurs a bit deeper in the water column and, unlike the two cleaner fishes, eats substantial amounts of benthic prey.

Even though the two co-occurring cleaner fishes have superficially similar feeding mechanisms, they seem to minimize mutual interference in resource use by foraging in somewhat different ways. Thus their total overlap in resource use is relatively small because the kelp perch feeds actively all day and does not eat substantial amounts of plant-encrusting bryozoans, the predominate staple of the señorita and white seaperch.

Within the kelp-bed area, the señorita has the widest habitat breadth. It broadly overlaps the white seaperch's range below the canopy and near the bottom. Their sharing of food and habitat would seem to make these species the greater potential competitors. But even so, they may seldom actually interfere with one another because the white seaperch is not limited to the kelp bed and occurs there less frequently than the señorita.

None of the three species forages at night, when all are relatively inactive and the señorita buries itself in soft substrates on the reef.

Neither the kelp perch nor the señorita obtains substantial amounts of food from cleaning, although some individual señoritas may. Of the two species, the señorita is more specialized in its diel behavior and may be somewhat more nutritionally dependent on cleaning.

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FISHERY REGULATION VIA OPTIMAL CONTROL THEORY[1]

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ABSTRACT

This paper attempts to show how control theory can be used to formulate a regulatory scheme for fisheries. The regulatory mechanism considered is a limit imposed on fishing effort. It is shown that static optimization methods, such as maximum equilibrium yield analysis, need to be supplemented with dynamic methods, such as optimal control theory, which take into account the variable nature of a fishery. The dynamic analysis is used to show that the size of a limit on effort should be a feedback function of the variables in the state of the fishery. The concept of the Linear-Quadratic Optimal Control Problem is introduced as a method for devising such a feedback scheme for fishery regulation.

A single-variable logistic model is used to introduce the basic concepts. A model with three variables is then analyzed to show how the techniques are easily extended to the general multivariable case. Details of the general method are given in an Appendix.

The need for fishery regulation is apparent and will become even more important with the establishment of resource management zones off our coasts. Regulatory mechanisms include catch quotas and limits on fishing effort (number of boats permitted entry into the fishery, number of hooks used, etc.). A mathematical model of the fishery, which includes biological and perhaps economic factors, is useful for determining the best regulatory scheme. Some of the more familiar examples of these models are given by Schaefer (1954, 1968), Beverton and Holt (1957), Ricker (1958), Larkin (1963, 1966), Pella and Tomlinson (1969) and Fox (1970). The above models are said to be dynamic because they utilize differential equations to describe how the fishery changes with time. The inclusion of economic factors, multiple species, and other biological variables, such as size and age, results in multivariable models which are quite complex.

Much of the analysis of fisheries is based on the concept of an equilibrium. Perhaps the best known is the maximum equilibrium yield analysis. However, equilibrium is an idealization and is never actually encountered in reality because continually changing environmental influences act as disturbances which displace the system from its equilibrium condition. For unstable systems this is disastrous because equilibrium is never regained, and for stable systems with large time constants, the return to equilibrium might take so long as to negate the assumptions and usefulness of the equilibrium-based analysis. Thus "static" or equilibrium-based analysis should be supplemented with dynamic methods which take into account the variable nature of the fishery. A purpose of this paper is to show that the above considerations indicate that any regulatory scheme should contain "feedback"; that is, the size of any quota or limit should be a function of the state of the fishery. Also, the concept of the Linear-Quadratic Optimal Control Problem will be introduced as one way of devising such a feedback scheme for fishery regulation.

The Linear-Quadratic Optimal Control Problem, which has been widely applied in engineering, is one method within the larger framework of optimal control theory. Other optimal control methods have recently been applied to problems in fishery management which are unlike the problem treated here. Goh (1969, 1973) applied the so-called "singular" control method to the problem of maximizing yield with a single-species model. Saila (in press) describes Goh's results in more detail. Clark et al. (1973) analyze the problem of optimal reduction of effort in an overexploited fishery. They calculate the fishing mortality function which maximizes the total present value of all profits and utilize a Beverton-Holt model for the fishery. Clark (1973) has presented a similar analysis for a logistic fishery model. The above three analyses lead to control functions which have been loosely described as a "bang-bang" control

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because the optimal values of the control variable lie at its boundaries. Thus the control variable switches between a lower value (usually zero) and an upper value which might be difficult to specify.

There are advantages as well as limitations with the linear-quadratic approach as compared with the bang-bang control approach. With the linear-quadratic approach, quantities such as yield and present value of profits are not directly maximized to obtain the feedback control function, as is done with the bang-bang approach. Rather, the maximization is first done with static methods, and then a feedback control function is constructed to keep the system near the resulting equilibrium condition. To do this, the system equations are linearized about the equilibrium. If disturbances carry the system far from equilibrium, the linearization breaks down. However, this is generally not a serious limitation, since the feedback control function is designed to counteract disturbances and to keep the system near equilibrium. The method is not restricted to equilibrium analysis, and frequently the two approaches are combined by using bang-bang control methods, instead of static methods, to compute an optimal "open-loop" control function. Linearization of the model around the resulting trajectory enables the linear-quadratic method to be used to synthesize a closed-loop (feedback) control function to keep the system on the optimal trajectory (Ho and Bryson 1969).

A significant advantage of the linear-quadratic approach is that it allows the use of linear control theory, whose techniques are more highly developed and easier to apply than the nonlinear techniques required for bang-bang control analysis. Powerful methods of compensating for incomplete information, uncertainties in measurements, model parameters, and model structure are available for the linear-quadratic approach but are scarce for the bang-bang control approach. Also, solutions to bang-bang control problems are extremely difficult to obtain if the model contains more than two variables.

First a single-variable model is used to illustrate the basic concepts. A model with three variables is then analyzed to show how the techniques are easily extended to the general multivariable case. The details of the general method are in the Appendix. There it is also shown in more detail why static optimization methods, such as linear programming, and dynamic optimization methods, such as optimal control theory, should not be treated as competing methods but rather should be used together as part of the total approach to the problem because they are mutually complementary methods. This is mentioned because there is a tendency among economics-oriented analysts to use static methods, whereas analysts with control-theory backgrounds tend toward dynamic methods.

It is assumed that the reader is familiar with the fundamentals of differential equations and matrix operations. A matrix will be denoted by brackets [ ]; a matrix transpose by $[\ ]^T$; and a column vector by a bar underneath, as $\underline{x}$.

SINGLE-VARIABLE MODEL

The following model is the Schaefer or logistic model:

$$\frac{dN}{dt} = aN - bN^2 - qfN, \tag{1}$$

where N is the biomass or number of catchable fish in the fishery, t is time, q is the catchability coefficient, and f is the fishing effort. The constant a is the intrinsic rate of natural increase of the population, and the constant b is related to the carrying capacity of the environment c by the relation: $b = a/c$. The system's equilibrium (N_{eq}, f_{eq}) is found by setting the derivative in Equation (1) equal to zero:

$$0 = aN_{eq} - bN^2_{eq} - qf_{eq}N_{eq}.$$

The equilibrium yield Y_{eq} is:

$$Y_{eq} = qf_{eq}N_{eq} = (a - bN_{eq})\,N_{eq}.$$

To find the maximum equilibrium yield, we differentiate Y_{eq} with respect to N_{eq}, and set this result equal to zero.

$$\frac{dY_{eq}}{dN_{eq}} = a - 2bN_{eq} = 0.$$

Solving this for the population size and fishing effort corresponding to maximum equilibrium yield, we obtain:

$$N_{eq} = a/2b,$$

$$f_{eq} = \frac{(a - bN_{eq})\,N_{eq}}{q\,N_{eq}} = \frac{a}{2q}.$$

Note that a static optimization method, calculus, has been used to find an optimal equilibrium. To analyze the model's behavior in the vicinity of the equilibrium point, Equation (1) is linearized by expanding the right-hand side in a two-variable Taylor series about the point (N_{eq}, f_{eq}), and keeping only the first-order terms (see Appendix). This gives:

$$\frac{dx}{dt} = \left(\frac{\delta g}{\delta N}\right)_{eq} x + \left(\frac{\delta g}{\delta f}\right)_{eq} u$$

where: $g = aN - bN^2 - qfN$

$$x = N - N_{eq} \quad (2)$$

$$u = f - f_{eq}. \quad (3)$$

The new variables x and u are the deviations in population density and fishing effort from their equilibrium values. After evaluating the derivatives of g at the equilibrium point, we obtain:

$$\frac{dx}{dt} = -\frac{a}{2} x - \frac{aq}{2b} u. \quad (4)$$

If the fishing effort is kept constant at its equilibrium value, then $u = 0$ and

$$\frac{dx}{dt} = -\frac{a}{2} x.$$

This system is stable for all positive values of a, which means that if disturbed from equilibrium, the population will eventually return to it. The solution is:

$$x(t) = x(t_o)\, e^{-\frac{a}{2}(t - t_o)},$$

where $x(t_o)$ is the deviation at time t_o. Since the time constant for this system is $2/a$, it will take that amount of time for the deviation to decay by 63% and for four time constants to decay by 98%. If the constant a is small, this time can be very large. Also, by keeping the fishing effort constant, we cannot take advantage of higher yields obtainable when $x(t_o)>0$, and risk overexploiting when $x(t_o)<0$. We will show that by making the fishing effort a function of population level, we can change the system's time constant and also avoid the above difficulties.

For example, the results of Schaefer (1954) give the following values for the Pacific halibut:

$$a = 0.67$$
$$b = 3.05 \times 10^{-9}$$
$$q = 3.95 \times 10^{-5}$$

where N is in pounds, t in years, and f in number of skates. A standard skate of halibut gear consists of eight lines of 300 feet each in length, with shorter lines with hooks attached at 10-foot intervals (Carrothers 1941). The time constant is 3 yr, and thus 12 yr are required for a deviation in population to disappear, assuming no other disturbances act during that time.

If we now specify, by means of a "performance index," that we wish to keep N near N_{eq} while minimizing the variation in f required to do so, we can design a regulatory procedure which will keep the fishery near the maximum equilibrium yield condition. The performance index J which specifies this desire is the so-called quadratic index:

$$J = \int_0^\infty (Qx^2 + Ru^2)\, dt.$$

The squared terms indicate that we make no distinction between positive and negative deviations from equilibrium. The positive constants Q and R are the weighting factors which indicate the relative importance placed on keeping N near N_{eq} (x near 0) versus keeping f near f_{eq} (u near 0). The infinite upper limit indicates that we are interested in long-term as well as short-term effects of our fishing effort regulation.

The problem of determining the function u, which minimizes the performance index, is solved by the application of optimal control theory. Since the system, Equation (4), is linear, and the index is quadratic, the problem formulated above is referred to as the Linear-Quadratic Optimal Control Problem.

The solution for the control function is (see Appendix):

$$u = -Kx \quad (5)$$

$$K = -\frac{1}{R}\frac{aq}{2b} P$$

where P is the positive steady-state solution of the so-called Riccati equation:

$$\frac{dP}{dt} = -aP - \frac{1}{R}\left(\frac{aq}{2b}\right)^2 P^2 + Q$$

with initial condition $P(0) = 0$. The solution for P is:

$$P = \frac{-aR + a\sqrt{R^2 + q^2a^2RQ/b^2}}{q^2a^2/2b^2}$$

Thus P and K are functions of the weighting factors R and Q, which must be specified.

Note that this method yields three results: 1) that the optimal control function for u is a linear function of x (a linear feedback law); 2) the means to calculate the feedback gain K, once R and Q are specified; and 3) that K is negative in this example (we assume that a, b, and q are positive). The third result indicates that the control law, Equation (5), opportunely calls for an increase in fishing effort when the population increases ($x > 0$), and conservatively calls for a decrease in effort when the population decreases ($x < 0$).

In this simple single-variable case we can utilize the first result and avoid specifying R and Q by substituting u from Equation (5) into Equation (4). The result is:

$$\frac{dx}{dt} = \left(\frac{qa}{2b}K - \frac{a}{2}\right)x.$$

The time constant for this system is:

$$\tau = \frac{1}{\frac{a}{2} - \frac{qa}{2b}K}. \qquad (6)$$

Using this approach it is possible to choose K so as to give a desired value of the time constant.

Alternately, K may be chosen by specifying the magnitude of the deviation in fishing effort we will allow in order to counteract an expected deviation in population level. Written in terms of magnitudes, Equation (5) becomes:

$$K = -\frac{u_m}{x_m}$$

where: x_m = maximum magnitude expected for x
u_m = maximum magnitude specified for u.

Once K has been determined, f as a function of N can be found by substituting x and u from Equations (2) and (3) into Equation (5) to obtain:

$$f = f_{eq} - K(N - N_{eq}). \qquad (7)$$

To evaluate the effects of the above regulation scheme under various conditions, the above expression is substituted into Equation (1), which can then be solved by computer for N and f as functions of time.

As an example with the previously mentioned results of Schaefer (1954) for the Pacific halibut, a maximum deviation in N of 5% from N_{eq} was postulated, and a maximum deviation in f of 5% from f_{eq} was specified. Thus:

$$N_{eq} = a/2b = 1.098 \times 10^8$$
$$f_{eq} = a/2q = 8.48 \times 10^3$$
$$x_m = 0.05N_{eq}$$
$$u_m = 0.05f_{eq}.$$

Using the second method for computing K, we obtain:

$$K = -\frac{0.05f_{eq}}{0.05N_{eq}} = -0.772 \times 10^{-4}.$$

From Equation (6) the new time constant is found to be 1.5 yr, which is one-half the value for the case without feedback control. The fishing effort found from Equation (7) is:

$$f = \frac{a}{2q} + \frac{b}{q}\left(N - \frac{a}{2b}\right) = \frac{b}{q}N = 0.772 \times 10^{-4}N. \qquad (8)$$

In view of the impossibility of continuously and instantly measuring population size and varying fishing effort, f as given by Equation (8) was interpreted as follows. It was assumed that a limit is imposed on fishing effort at the beginning of each year and held constant during that year, and its value f is calculated from Equation (8), with N being the average population over a yearly interval terminating three-tenths of a year before the imposition of the new limit. That is, three-tenths of a year is allowed for collecting and analyzing the population data used to calculate the next year's limit. With this discretized version of f, computer simulation results show that the system time constant is 1.8 yr, which is reasonably close to the 1.5 yr predicted by the continuous model. Thus it is possible to use the analysis based on the continuous model in the realistic situation involving data-collection limitations and limit-imposition constraints.

THREE-VARIABLE EXAMPLE

An advantage of the optimal control method is

its ability to accommodate multivariable system models such as multispecies models; models describing economic as well as biological phenomena; and detailed population models incorporating size, age, temperature, food supply, etc. Once a three-variable example is presented, generalization of the technique to models with more than three variables is straightforward. The following model of a single species population was developed by Timin and Collier (1971) and contains three state variables: N, the population density; W, the mean biomass per organism; and E, the food density. The model is given in dimensionless form, and thus the values of the model variables are relative to reference values. The system's dynamics are described by the following equations:

$$\frac{dN}{dt} = (b\text{-}d)N - f \tag{9}$$

$$\frac{dE}{dt} = \sigma - qN - \theta E \tag{10}$$

$$\frac{dW}{dt} = gq - (W+c)b - \mu W - \frac{(W_h - W)f}{N} \tag{11}$$

where: t = time measured in a dimensionless unit equal to the time required for the organism to metabolize an amount of food equal to its own dry weight (usually between two and four weeks for commercial fish species)

b, d = birth and death rates per individual

f = fishing rate

g = the ratio of the quantity (energy ingested minus energy not assimilated, minus energy expended to catch, ingest and assimilate the ingested food) to the amount of energy ingested

q = food ingestion rate per individual

c = coefficient of energy loss associated with births

μ = metabolic heat loss coefficient

σ = rate of food supply

θ = proportionality constant for the rate of food leaving the system through decay or flushing

W_h = mean organism biomass of harvested individuals.

Functional forms and parameters given as typical by Timin and Collier are:

$$b = 3.8W^2 - 3.8W + 0.95 \qquad \theta = 0.1$$
$$d = 0.19/(2W\text{-}1) \qquad g = 0.2$$
$$\sigma = 3 \qquad c = 0.05$$
$$q = \frac{W^{2/3}E}{1 + 0.1E} \qquad \mu = W^{-1/3}.$$

Static optimization can be used to determine the maximum equilibrium yield condition. For $f_{eq} = 0.005$, the equilibrium values are: $N_{eq} = 0.16$, $E_{eq} = 20.3$, $W_{eq} = W_{h_{eq}} = 0.8$. Following the procedures outlined in the Appendix (Equations (A-2) through (A-4)), Equations (9), (10), and (11) were linearized around this equilibrium to obtain:

$$\begin{bmatrix} \frac{dx_1}{dt} \\ \frac{dx_2}{dt} \\ \frac{dx_3}{dt} \end{bmatrix} = \begin{bmatrix} 0.03 & 0 & -0.56 \\ -5.73 & -0.12 & -0.81 \\ 0.14 & 0.02 & -2.02 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix} + \begin{bmatrix} -1 \\ 0 \\ 0 \end{bmatrix} u \tag{12}$$

where: $x_1 = N - N_{eq}$

$x_2 = E - E_{eq}$

$x_3 = W - W_{eq}$

$u = f - f_{eq}$.

The following performance index J describes our desire to keep the system near the desired equilibrium (Appendix, Equation (A-6)):

$$J = \int_0^\infty (Q_{11}x_1^2 + Q_{22}x_2^2 + Q_{33}x_3^2 + Ru^2)\,dt. \tag{13}$$

Here the weighting matrix $[Q]$ becomes:

$$[Q] = \begin{bmatrix} Q_{11} & 0 & 0 \\ 0 & Q_{22} & 0 \\ 0 & 0 & Q_{33} \end{bmatrix}$$

and the matrix $[R]$ becomes a scalar R. A substantial difference between the single-variable and multivariable cases is that in the latter case we can no longer easily determine the feedback gains by specifying the desired values of the time constants. Instead, the gains are calculated by

specifying the components of the weighting matrices. A common procedure for doing this is to choose the components by the rule:

$$Q_{11} = \frac{1}{x_{1m}^2} \qquad R = \frac{1}{u_m^2}$$

where x_{1m} is the maximum desired magnitude of the deviation x_1 of the population N, and u_m is the maximum desired magnitude of the deviation u of the fishing rate f. The components Q_{22} and Q_{33} are chosen in a similar manner. Here we assume the maxima are specified to be:

$$\begin{aligned} x_{1m} &= 5\% \text{ deviation from } N_{eq} = 0.008 \\ x_{3m} &= 1\% \text{ deviation from } W_{eq} = 0.008 \\ u_m &= 50\% \text{ deviation from } f_{eq} = 0.0025. \end{aligned}$$

Thus:

$$\frac{1}{x_{1m}^2} = \frac{1}{x_{3m}^2} = 1.6 \times 10^4 = 0.1 \frac{1}{u_m^2}.$$

Assuming that the variation x_2 in the food density is not of direct interest, we set $Q_{22} = 0$. Since J from Equation (13) depends only on the relative magnitudes of the weighting factors, we can choose these factors to be:

$$\begin{aligned} R &= 1 \\ Q_{11} &= Q_{33} = 0.1 \\ Q_{22} &= 0. \end{aligned}$$

For this three-variable model, the symmetric Riccati matrix $[P]$ has nine elements, three of which are redundant. Computer solution of the six coupled differential equations resulting from Equation (A-9) and use of Equations (A-7) and (A-8) yield the following feedback control function:

$$u = -[K]\underline{x} = 0.149x_1 + 0.00027x_2 + 0.026x_3. \quad (14)$$

Use of Equation (14) and the definitions of x_1, x_2, x_3, and u gives the optimal fishing effort as a feedback function of the system variables:

$$f = f_{eq} + 0.149\,(N - N_{eq}) + 0.00027\,(E - E_{eq}) + 0.026(W - W_{eq}).$$

Substitution of the equilibrium values gives:

$$f = -0.045 + 0.149N + 0.00027E + 0.026W. \quad (15)$$

Substitution of u from Equation (14) into Equation (12) gives the set of linearized equations describing the behavior of the model under feedback control. The matrix $[A]$ to be used in Equation (A-5) becomes

$$[A] = \begin{bmatrix} -0.119 & -0.00027 & 0.534 \\ -5.73 & -0.12 & -0.81 \\ 0.14 & 0.02 & -2.02 \end{bmatrix}$$

The roots of Equation (A-5) are: $s = -2.09, -0.096 \pm 0.17j$, where $j = \sqrt{-1}$. The dominant time constant is the negative reciprocal of the least negative real part, and here is equal to $1/0.096 = 10.4$ time units. In a similar way the dominant time constant for the system without feedback is 45.5 time units. Thus the feedback control given by Equation (15) reduces the effects of disturbances in one-fourth the time. These linearized results have been verified by simulation of the original nonlinear model. Other simulations are discussed by Palm (1975).

Before concluding this example, we note from Equation (15) that f is a function of all three variables. This is due to the coupling between the three equations. Also, although the choice of the weighting factors is somewhat arbitrary, this should not obscure the fact that the Linear-Quadratic Optimal Control Problem provides a systematic method for determining the feedback gain matrix $[K]$. A systematic approach is needed because the number of components of $[K]$ becomes so large for multivariable problems that a trial-and-error approach is prohibitive. As long as $[Q]$ and $[R]$ are chosen to be positive-definite, the resulting $[K]$ will stabilize the system. Various choices of $[Q]$ and $[R]$ merely affect the time constants and form of response (oscillatory vs. nonoscillatory return to equilibrium). This is the main advantage of this technique.

With this model the effects of mesh size regulation can be studied by using W_h as an additional control variable. Also, the food supply rate σ is another possible control variable if the model is used to analyze fish farming. The linear-quadratic control technique could be used in both cases.

CONCLUSION

In this introductory paper we have presented only the deterministic case of the Linear-Quadrat-

ic Optimal Control Problem. In order to set limits on fishing effort which are functions of system variables such as population density or mean organism weight, it is necessary to measure these variables. Any measurement process is stochastic or noisy, and it is necessary to compensate for this in the design of a feedback regulation scheme. In many engineering applications this has been successfully accomplished by the use of the Kalman-Bucy filter (Athans 1971). In addition, it may be impossible even to measure some variables. This problem of incomplete information has been frequently solved by the use of the Observer Theory (Kwakernaak and Sivan 1972).

Also there will be uncertainties in the determination of the model constants. In fact the "constants" may not be constants at all, but merely the representation of several effects lumped together. Thus there is also error in the model structure, since the model constants are actually variables dependent upon a variety of effects. For the Schaefer model these effects would be interspecies interactions, age structure, availability and vulnerability of the age groups, and physical environment influences on the biological processes. Such difficulties are amenable to solution by adding a "noise" term to the model equations and by modifying the linear-quadratic techniques to accommodate these stochastic effects (Athans 1971). It should also be pointed out that compensation for modeling errors is one of the purposes of feedback control.

The change in model parameters with time can be compensated for by regularly recomputing the feedback gains as more data becomes available. Finally, while no pretense is made of being able to predict exact time paths, the methods described in this paper should prove useful in providing management guidelines. The effects of stochastic processes and uncertainties can be handled in a manageable way by computer simulation, and prediction of the future course of the managed fishery, in an average sense, can be made with appropriate error bands placed on the predictions.

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APPENDIX

The Linear-Quadratic Optimal Control Problem and its solution are now outlined. For a thorough discussion, see Ho and Bryson (1969) or Kwakernaak and Sivan (1972). By use of state variable notation, any set of time-invariant ordinary differential equations can be put into the following form:

$$\frac{d\underline{y}}{dt} = \underline{g}\,(\underline{y}, \underline{f}) \tag{A-1}$$

where $\underline{g}$ is a general n-dimensional vector function, $\underline{y}$ is the n-dimensional state vector for the model, and $\underline{f}$ is the m-dimensional input or forcing function vector. If this system has an equilibrium ($\underline{y}_{eq}, \underline{f}_{eq}$, the following set of algebrais equations must be satisfied:

$$\underline{0} = \underline{g}\,(\underline{y}_{eq}, \underline{f}_{eq}).$$

The values of $\underline{y}_{eq}$ and $\underline{f}_{eq}$ depend on the system's parameters, and static optimazation methods such as calculus or linear programming can be applied to find the optimal $\underline{y}_{eq}, \underline{f}_{eq}$ and system parameters according to some criterion. This was done in the first example to determine the condition of maximum equilibrium yield. Since any real system is subjected to varying conditions and disturbances, it will be continually displaced from equilibrium. Thus for unstable systems or stable systems with large time constants, a static method of analysis is not sufficient. In such a case the next step is to apply a dynamic optimization method, such as the method presented here, to devise a control scheme which ensures that the system will return to equilibrium with a satisfactory time constant. Thus static and dynamic methods should not be viewed as alternative approaches to optimization, but rather as mutually complementary methods.

After the equilibrium is determined, Equation (A-1) is linearized by expanding the function $\underline{g}$ in a Taylor series in $\underline{y}$ and $\underline{f}$, and keeping only the first-order terms. This gives the linearized model:

$$\frac{d\underline{x}}{dt} = [A]\,\underline{x} + [B]\,\underline{u} \tag{A-2}$$

where: $\underline{x} = \underline{y} - \underline{y}_{eq}$

$\underline{u} = \underline{f} - \underline{f}_{eq}$

$$[A] = \left[\left(\frac{\delta \underline{g}}{\delta \underline{y}}\right)_{eq}\right] \tag{A-3}$$

$$[B] = \left[\left(\frac{\delta \underline{g}}{\delta \underline{f}}\right)_{eq}\right] \tag{A-4}$$

in which the subscript eq indicates that the partial derivatives of $\underline{g}$ are evaluated at the equilibrium. The stability of the equilibrium can be determined from the roots of the determinant equation:

$$\left|s\,[I] - [A]\right| = 0 \tag{A-5}$$

where $[I]$ is the $(n \times n)$ identity matrix. The equilibrium is stable if and only if all of the roots s have negative real parts.

By finding the function $\underline{u}$ which minimizes the following quadratic performance index, $\underline{x}$ and $\underline{u}$ are kept near zero and thus the system is kept near equilibrium.

$$J = \int_0^\infty (\underline{x}^T\,[Q]\,\underline{x} + \underline{u}^T[R]\,\underline{u})\,dt. \tag{A-6}$$

The feedback control function which minimizes J has been shown to be:

$$\underline{u} = -[K]\,\underline{x}. \tag{A-7}$$

The feedback "gain" matrix $[K]$ is calculated from:

$$[K] = [R]^{-1}[B]^T[P] \tag{A-8}$$

where the Riccati matrix $[P]$, an $(n \times n)$ symmetric matrix, is the steady-state solution of the Riccati matrix differential equation:

$$\frac{d[P]}{dt} = [Q] + [A]^T[P] + [P][A] - [P][B][R]^{-1}[B]^T[P] \tag{A-9}$$

with the initial condition:

$$[P(0)] = [0].$$

The matrix $[P]$ is usually found by numerically solving the Riccati equation until all the components of the solution $[P]$ become constant. This will always occur.

DIFFERENTIATION OF FRESHWATER CHARACTERISTICS OF FATTY ACIDS IN MARINE SPECIMENS OF THE ATLANTIC STURGEON, *ACIPENSER OXYRHYNCHUS*

R. G. ACKMAN, C. A. EATON, AND B. A. LINKE[1]

ABSTRACT

Lipids and fatty acids of two marine-caught specimens of the Atlantic sturgeon, *Acipenser oxyrhynchus*, which spawns and also feeds in freshwater, were examined. Specific fat contents, respectively 47.2 and 25.0% in orange-colored dorsal tissue and 8.5% in both livers, were high but not unexpected for sturgeons generally. In each fish a very consistent basic fatty acid composition of depot fats showed that this fat in various parts of the body had a common function. Depot fat from the fatter fish had high iodine values (ca. 190) while in the leaner fish values were lower (ca. 135) and more typical of sturgeons generally. The fatty acid details of depot fats showed some characteristics of marine fats, such as the presence of the unusual $\omega 1$ and $\omega 4$ polyunsaturated fatty acids, the low figure for linoleic acid and relatively high proportions of long chain polyunsaturated fatty acids, but were more typical of freshwater fats in the virtual absence of eicosenoic and docosenoic acids. Broadly speaking, the fatty acids of the Atlantic sturgeon seem to place it in a special class of fish with fats generally resembling freshwater fish fats in composition, despite its marine origin.

The Atlantic sturgeon, *Acipenser oxyrhynchus* Mitchill, is widely distributed along the Atlantic coast of North America and is to be distinguished from *A. sturio*, the common sea sturgeon of Europe (Scott and Crossman 1973). The Atlantic sturgeon is an anadromous fish, spawning in freshwater,[2] whereas some other sturgeon species, such as the lake sturgeon, *A. fulvescens*, are restricted to freshwater. The most recent and detailed study of sturgeon lipids and fatty acids has been based on an *A. sturio* specimen, apparently of freshwater origin, as it showed a fatty acid pattern which is characteristic of lipids in freshwater fish (Reichwald and Meizies 1973).

The standard reference book on fatty acids states that sturgeon fats are "of the freshwater type" (Hilditch and Williams 1964) although this view was based on a single analysis of a specimen of *A. sturio* caught in the North Sea (Lovern 1932). We wish to report that a study of two saltwater *A. oxyrhynchus* shows that, during its marine period, the Atlantic sturgeon deposits fat with some composition details corresponding to marine fatty acid characteristics. However the fat definitely lacks other details characteristic of fats of higher marine organisms and thus reinforces the published viewpoint based on the common sea sturgeon of the Northeast Atlantic.

MATERIALS AND METHODS

Samples

Two *A. oxyrhynchus* were acquired from fish traps located in an area of the entrance to Halifax Harbour known as Eastern Passage. Both were male, that taken on 12 October 1968 (A) being 150 cm in length and that taken 30 August 1973 (B) being 155 cm. Fish A was frozen whole at -40°C until dissected in March 1969. Fish B was held overnight in an aquarium and dissected immediately after sacrifice. In both cases sections were cut transversely through the middle of the fish. In fish A this was done while frozen and the cut section included liver which was recovered for study, while in fish B the liver was removed separately from the fish. Both fish showed a soft fatty orange layer between the dorsal skin and muscle, of one or more centimeters in thickness, but thinning down the flanks. Parts of this layer penetrated the muscle, especially between myotomes, and streaks of similar colored material appeared in the muscle. A section through fish B was observed to have a

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[2]Sturgeon were once so common that those blocked by the falls in the Hudson river were taken in large quantities and marketed in New York City as "Albany veal." They appear to be returning to their former habitat in large numbers (R. Severo, New York Times, 9 July 1975).

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white layer 2-3 mm in thickness between the epidermis and the soft orange layer.

Lipid from the orange tissue of fish A was extracted by blending with n-hexane in a Waring Blendor.[3] All other lipids were extracted by the method of Bligh and Dyer (1959). For fish A the samples examined, and lipid recoveries, were liver, 8.5%, orange tissue, 47.2%; muscle freed of all visible orange tissue and fat, 2.0%; and whole steak section, 7.2%. Lipid recoveries from fish B samples were liver, 8.5%; orange tissue, 25.0%; muscle freed of all visible orange tissue and fat, 1.2%; and subdermal white layer, 1.3%. Total lipids from the fish A samples were saponified and non-saponifiable materials removed. The recovered fatty acids were converted to methyl esters with boron trifluoride in methanol. White layer and orange tissue samples from fish B were treated similarly, but the muscle and liver lipids were fractionated on a column of divinylbenzene copolymer beads and eluted with benzene. The purity of the various fractions was monitored by thin-layer chromatography on silicic acid. The major fractions, the triglycerides and the polar lipids with the mobility of phospholipids, were transesterified with BF_3-MeOH. Analyses of recovered methyl esters of fatty acids are given in Tables 1 and 2. Further details of these methods, including gas-liquid chromatography of methyl esters on open-tubular polyester columns, will be found elsewhere (Sipos and Ackman 1968; Ackman, Hooper, and Frair 1971; Ackman and Hooper 1973).

RESULTS AND DISCUSSION

The triglycerides in the two marine *A. oxyrhynchus* were distributed throughout the body in the dorsal fatty layer, in the form of muscle infiltration by this fatty layer, and also in the liver. This is most clearly made evident by comparing the iodine values of the different fats isolated from sturgeon B (Table 2). The white subdermal layer, the orange tissue fat, estimated from thin-layer chromatograms to be >95% triglycerides, and the triglycerides isolated from muscle and liver lipids, all have calculated iodine values in the range 132-139. The two phospholipid fractions have much higher iodine values, as expected for this class of lipids (Ackman 1966). In fish A, the orange tissue fat (a clear oil, estimated to be >95% triglycerides from thin-layer chromatograms) had a calculated iodine value of 186 (Table 1). The liver lipid, also estimated to be mostly

TABLE 1.–Fatty acid composition, in weight percent,[1] for lipids recovered from four tissues of Atlantic sturgeon A.

Fatty Acid[2]	Orange tissue	Muscle (no visible fat)	Whole steak section	Liver
14:0	5.13	2.80	3.61	2.82
Iso 15:0	0.35	0.21	0.27	0.21
Anteiso 15:0	0.16	0.11	0.14	0.10
15:0	0.78	0.53	0.90	0.78
Iso 16:0	0.23	0.12	0.19	0.14
16:0	16.21	17.05	16.34	17.38
Iso 17:0	0.29	0.21	0.31	0.26
Anteiso 17:0	0.15	0.10	0.12	0.09
17:0	0.48	0.39	0.40	0.33
3,7,11,15-TMHD	0.37	0.44	0.46	0.09
Iso 18:0	0.11	0.08	0.14	0.12
18:0	1.65	2.91	1.83	2.58
Total saturates	25.3	25.2	25.0	25.1
16:1ω9	0.42	0.59	0.44	0.39
16:1ω7	7.45	5.61	6.25	6.45
16:1ω5	0.29	0.26	0.17	0.26
17:1ω8	0.42	0.30	0.38	0.45
18:1ω11+9	15.69	15.22	15.11	18.27
18:1ω7	4.04	4.35	3.93	5.49
18:1ω5	0.47	0.45	0.31	0.38
19:1ω9	0.33	0.39	0.32	0.56
20:1ω11	0.35	0.20	0.41	0.16
20:1ω9	1.23	0.96	1.34	1.19
20:1ω7	0.86	0.84	1.25	0.81
22:1ω13+11	0.15	0.05	0.13	0.08
Total monoenes	31.9	29.4	30.2	34.7
16:2ω6	0.26	0.12	0.26	0.04
16:2ω4	1.42	1.03	1.17	0.78
18:2ω6	0.85	0.77	0.85	0.84
18:2ω4	0.28	0.31	0.29	0.57
20:2ω6	0.24	0.15	0.35	0.26
16:3ω4	1.61	0.93	1.47	0.43
18:3ω6	0.08	0.13	0.10	0.13
18:3ω4	0.40	0.20	0.32	0.30
18:3ω3	0.28	0.26	0.30	0.33
20:3ω6	0.18	0.16	0.28	0.21
20:3ω3	0.10	0.10	0.12	0.12
16:4ω3	0.17	0.19	0.15	0.03
16:4ω1	1.40	0.90	1.25	0.15
18:4ω3	2.78	1.62	2.25	1.28
18:4ω1	0.83	0.54	0.64	0.67
20:4ω6	1.37	1.63	1.53	1.72
20:4ω3	1.64	1.41	1.64	1.97
22:4ω6	0.13	0.19	0.20	0.26
20:5ω3	18.37	19.15	19.40	14.33
21:5ω3 or 2	0.99	0.84	0.92	0.94
22:5ω6	0.38	0.74	0.54	0.42
22:5ω3	2.21	3.10	2.82	3.40
22:6ω3	6.85	10.88	7.91	10.94
Total polyenes	42.8	45.4	44.8	40.2
Calc. iodine value	186	199	194	182

[1]NSA = no significant amount. Average percentages for some minor components were: iso 14:0, 0.07%; 4,8,12-TMTD, 0.03%; 2,6,10,14-TMPD, 0.03%; 19:0, 0.09%; 20:0, 0.04%; 14:1ϖ7, 0.02%; 15:1ω8, 0.3%; 19:1ω10, 0.07%; 19:1ω8, 0.06%; 20:1ω5, 0.01%; 22:1ω9, 0.04%; 22:1ω7, NSA; 22:1ω9, NSA; 16:2ω7, 0.02%; 18:2ω9, NSA; 20:2ω9, NSA; 16:3ω3, NSA.

[2]3,7,11,15-TMHD (phytanate) = 3,7,11,15-tetramethylhexadecanoic acid. 4,8,12-TMTD = 4,8,12-trimethyltridecanoic acid. 2,6,10,14-TMPD (pristanate) = 2,6,10,14-tetramethylpentadecanoic acid.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Fatty acid composition, in weight percent,[1] for lipids recovered from four tissues of Atlantic sturgeon B.

Fatty acid[2]	White subdermal layer	Orange tissue	Muscle (no visible fat)		Liver	
			Triglyceride	Polar lipid	Triglyceride	Polar lipid
14:0	3.75	3.81	3.50	0.75	2.42	1.53
Iso 15:0	0.37	0.35	0.31	0.21	0.20	0.14
Anteiso 15:0	0.20	0.26	0.22	0.11	0.09	0.04
15:0	0.71	0.66	0.52	0.43	0.62	0.72
Iso 16:0	0.18	0.20	0.14	ND[3]	0.16	0.11
16:0	15.46	15.24	14.75	22.42	18.32	25.72
7-MHD	0.33	0.25	0.22	0.11	0.19	0.20
2,6,10,14-TMPD	0.22	0.28	0.18	ND	0.16	NSA
Iso 17:0	0.35	0.29	0.28	0.10	0.33	0.24
Anteiso 17:0	0.19	0.25	0.18	0.07	0.20	0.16
17:0	0.27	0.31	0.27	0.27	0.32	0.74
3,7,11,15-TMHD	1.08	1.38	0.55	0.14	0.05	0.27
Iso 18:0 ?	0.14	0.20	0.20	0.08	0.23	0.35
18:0	2.17	1.98	3.14	8.71	2.67	11.77
19:0	0.15	0.13	0.12	0.33	0.07	0.43
20:0	0.18	0.19	0.14	0.09	0.08	0.31
Total saturates	25.9	26.1	25.1	33.9	26.3	43.0
16:1ω9	0.20	0.25	0.21	0.03	0.20	0.61
16:1ω7	6.22	6.08	5.47	1.01	4.50	1.13
17:1ω8	0.75	0.70	0.63	0.31	0.52	0.09
18:1ω9	25.94	25.67	25.75	11.81	31.16	9.03
18:1ω7	4.00	3.91	5.94	3.94	4.46	4.44
18:1ω5	0.43	0.49	0.71	0.21	0.56	0.21
19:1ω10+8	0.54	0.32	0.61	0.10	0.43	0.14
19:1ω6	0.20	0.22	0.48	0.05	0.21	0.07
20:1ω11	1.27	1.29	1.05	0.13	0.31	0.80
20:1ω9	2.76	2.70	2.40	0.55	2.44	2.00
20:1ω7	2.41	2.40	1.72	0.27	1.41	0.89
20:1ω5	0.22	0.23	0.17	0.02	0.13	0.10
22:1ω13+11	0.51	0.46	0.18	0.10	0.14	0.62
22:1ω9	0.26	0.36	0.16	0.01	0.19	0.13
22:1ω7	0.15	0.16	0.05	ND	0.10	0.09
Total monoenes	46.0	45.5	45.7	18.7	46.9	20.8
16:2ω6	0.15	0.21	0.16	ND	0.04	0.16
16:2ω4	0.95	0.85	0.84	0.12	0.52	0.24
18:2ω6	0.84	0.84	0.77	0.22	0.68	0.52
18:2ω4 ?	0.21	0.20	0.26	0.10	0.51	ND
20:2ω9	0.12	0.07	0.15	Trace	0.19	0.03
20:2ω6	0.52	0.56	0.48	0.19	0.35	0.27
20:2ω4	0.25	0.18	0.18	Trace	0.12	ND
NMID [20:2]	0.44	0.48	0.24	0.03	0.10	0.03
NMID [22:2]	0.50	0.52	0.18	0.01	0.20	0.05
16:3ω4	0.65	0.64	0.70	Trace	0.32	ND
18:3ω6	0.26	0.29	0.19	Trace	0.07	Trace
18:3ω4	0.74	0.68	0.52	ND	0.48	ND
18:3ω3	0.48	0.41	0.38	0.11	0.24	0.18
20:3ω6	0.26	0.19	0.12	0.05	0.14	0.06
20:3ω4	0.16	0.30	0.15	ND	0.35	ND
20:3ω3	0.18	0.27	0.13	0.05	0.31	0.08
16:4ω1	0.61	0.60	0.52	0.02	0.08	0.01
18:4ω3	1.29	1.18	1.12	0.07	0.51	0.09
18:4ω1 ?	0.38	0.37	0.47	0.03	0.33	0.01
20:4ω6	1.40	1.28	1.37	4.78	0.84	6.90
20:4ω3	1.42	1.41	1.18	0.26	1.24	0.37
22:4ω6	0.17	0.51	0.20	0.20	0.29	0.32
20:5ω3	0.62	10.21	10.19	18.61	6.95	7.35
21:5ω2 or 3	0.64	0.66	0.67	0.06	0.62	0.05
22:5ω6	0.56	0.44	0.44	0.26	0.56	0.64
22:5ω3	2.44	2.52	2.57	2.02	4.87	2.86
22:6ω3	3.85	3.32	4.40	18.77	5.10	16.46
Total polyenes	28.1	28.4	29.2	47.4	26.8	36.2
Calc. iodine value	139	136	136	201	132	161

[1]NSA = no signficant amount. Average percentages for some minor components from subdermal layer, orange tissue, and triglycerides were: 12:0, 0.04%; 13:0, 0.01%; iso 14:0, 0.04%; 4,8,12-TMTD, 0.05%; anteiso 16:0, 0.02%; anteiso 18:0, 0.02%; iso 19:0, 0.05%; anteiso 19:0, 0.02%; 22:0, 0.01%; 14:1ω7, 0.02%; 14:1ω5, 0.01%; 16:1ω11, NSA; 16:1ω5, 0.08%; 17:1ω6, 0.03%; 18:1ω13, NSA; 18:1ω11, trace; 20:1ω15(?), 0.06%; 22:1ω5, NSA; 18:2ω9, 0.05%; 22:2ω6, 0.11%; 16:3ω3, trace in TG; 20:3ω9, 0.03%; 16:4ω3, 0.01%; 22:4ω3, 0.06%.

[2]7-MHD = 7-methylhexadecanoic acid from 7-methylhexadecenoic acid (Hooper et al. 1973), measured in hydrogenated esters. 2,6,10,14-TMPD (pristanate) = 2,6,10,14-tetramethylpentadecanoic acid. 3,7,11,15-TMHD (phytanate) = 3,7,11,15-tetramethylhexadecanoic acid. NMID=non-methylene-interrupted dienoic acids. 4,8,12-TMTD = 4,8,12-trimethyltridecanoic acid.

[3]ND = not determined.

triglyceride by thin-layer chromatography, had a similar iodine value, as did the lipid from the steak section of high fat content. This high fat content appears to be normal as Fraser et al. (1961) reported 6.2% fat in a steak from this species. Evidently, the fatty acid compositions of triglycerides for fish A would give high iodine values similar to those for phospholipids, for example in the lean muscle extract which would include about half of each type of lipid. The actual iodine value of the triglyceride of sturgeon A is unusually high for marine fish triglycerides (Ackman 1966) but a considerable range of iodine values appears possible for sturgeon depot fats. The "peritoneal cavity" depot fat of the *A. sturio* examined by Lovern (1932) had an iodine value of 126.5, and that of the corresponding liver lipids was 125. A Pacific coast sturgeon (species unknown) had body and liver oils with respective iodine values of 90 and 95 (Bailey et al. 1952), and the iodine values of fats of three types of flesh from the freshwater *A. sturio* of Reichwald and Meizies (1973) were also low. Two *A. baeri* kept in captivity for several years in the Freshwater Fisheries Research Laboratory in Tokyo were slightly different from each other in fatty acid compositions (Table 3) but the fats in each body sample, dorsal flesh and ventral flesh, were respectively quite similar in each fish although they differed in some details from the liver fatty acids (Shimma and Shimma 1968). These authors specifically note the absence of mesentary fat (cf. Lovern 1932), although they found the testes to be unexpectedly high in fat. Oil from American sturgeon of unspecified origin had an iodine value of 125.3 (Bull 1899) and the liver oil from *A. mikadoi* an iodine value of 157.7 (Tsujimoto 1926). Russian data shows Caspian and Atlantic sturgeon fats as having respective iodine values of 122 and 125 (Zaitsev et al. 1969).

In comparative detail, the fatty acid analyses from sturgeon A show little differences between the fat from steak section, orange tissue, lean muscle, and liver (Table 1). However, the high proportions of 22:6ω3 in the lean muscle and in the liver may reflect inclusion of phospholipids which contained relatively high proportions of 22:6ω3 (compare fish B, polar lipids, Table 2). The analysis of particular lipids from fish B is more appropriate for detailed discussion. The fatty acid composition shows that fat from the subdermal white layer, the orange tissue fat, and the muscle triglycerides are all essentially the same fat. Hake skin fats (*Merluccius capensis* and *M. paradoxus*) resemble adjacent dark muscle fat in fatty acid composition (Wessels and Spark 1973). The fatty acid composition of triglycerides in the liver of sturgeon B is also basically similar but has a few fatty acid characteristics shared with the liver phospholipids. Thus the level of 14:0 is lower and the proportion of 16:0 is higher. However 18:0 is not affected in the liver triglyceride, relative to the other triglycerides, so there is no effect on the total of saturated acids. The total for monoethylenic acids in the liver triglycerides is also nearly the same as in the other triglycerides. Although in detail the 16:1 acids are less in parallel to the phospholipid composition, the 18:1 acids are unexpectedly higher, a characteristic confirmed by fish A liver (Table 1). This intermediate status of the liver triglycerides is also apparent in many details and subtotals among the polyunsaturated acids. A singular exception lies in the low proportion of 20:4ω6, which does not seem to extend to any other "ω6" acid. On the other hand, the observation that 20:5ω3 in the liver triglyceride is not intermediate between the other triglycerides and the liver phospholipid is offset by the higher level of the homologous 22:5ω3. In fish A it is possible that 20:4ω6 is also low in liver lipid (of which a large proportion would be triglyceride) but the lower level of 20:5ω3 is less marked in the fatty acid

TABLE 3.–Some fatty acid details, in weight percent, for fats from tissues of three sturgeon examined in Japan (from Shimma and Shimma 1968).

Sample		Fat (%)	Percentages of some important fatty acids in fat								Calc. iodine value
			4:0	16:0	16:1	18:1	18:2	20:1	20:5	22:6	
A. baeri (A)	dorsal	7	2.5	18.5	7.5	29.8	1.4	3.3	8.0	16.9	171
	ventral	71	2.3	16.6	9.0	31.0	1.4	4.0	6.9	13.8	160
	liver	38	2.6	15.5	7.6	44.1	1.6	3.5	3.8	9.9	130
A. baeri (B)	dorsal	14	3.7	21.6	10.5	33.1	1.3	2.8	6.5	11.4	140
	ventral	76	3.7	19.7	9.7	29.5	1.7	3.5	6.6	13.6	154
	liver	51	1.6	23.7	6.7	54.4	—	1.9	2.7	5.3	95
A. shrenki	liver	41	1.1	18.5	9.8	45.1	7.9	2.2	2.5	1.8	99

composition of the total lipids of the liver. The significance of these observations is obscure but it is probable that the liver is active in de novo biosynthesis of 16:0 and 18:0 acids. If 18:0 is desaturated to 18:1ω9, it could explain the higher level of the latter in the liver triglyceride in terms of a temporary storage function before distribution elsewhere. The same role could result in the liver triglyceride accumulating 22:5ω3 at an intermediate stage between 20:5ω3 and 22:6ω3 for either conversion or catabolism. The two Atlantic sturgeon do not appear to have as much fat in the liver as observed in other species or perhaps in animals from other habitats. Zaitsev et al. (1969) show 8-16% oil in livers of other than Danube sturgeon, and 8-20% in the latter. The liver of an *A. mikadoi* taken at sea near Hokkaido yielded 52% oil by boiling (Tsujimoto 1926) and Shimma and Shimma (1968) report 38 and 51% lipid in livers of two *A. baeri*.

Among the unusual fatty acids observed in the fat of fish B, special mention should be made of the NMID (nonmethylene-interrupted dienes) [20:2] and [22:2] (Ackman and Hooper 1973; Paradis and Ackman 1975). In vertebrate lipids these unusual fatty acids are apparently deposited in parallel with 20:1 and 22:1. The generally lower levels of the latter in the lipids of fish A resulted in the NMID [20:2] and [22:2] being barely detectable (≤0.01%) and they are not included in Table 1. The food of sturgeons on the Nova Scotian shelf is probably basically bottom invertebrates (Scott and Crossman 1973). Many of these organisms are potential sources of these unusual acids (Ackman and Hooper 1973; Watanabe and Ackman 1974; Ackman et al. in press). These acids do not appear to occur significantly in the oils from pelagic fish and it can be assumed that their occurrence in the sturgeon is a food web effect rather than a peculiarity of the species. The absence of 16:1ω11 and 18:1ω13 suggests that indigenous biosynthesis is unlikely.

The levels of isoprenoid acids in triglycerides of fish B, especially 3,7,11,15-tetramethylhexadecanoic acid (phytanic), are unusually high for marine fish oils (Ackman and Hooper 1968), but the exclusion of these acids from the biospecific phospholipids of animals higher than molluscs has been observed previously (Ackman et al. 1970; Ackman and Eaton 1971; Ackman and Hooper 1973; Hooper et al. 1973). The properties of phytanic acid resemble those of 18:0 and a possible unusual low turnover rate for C_{18} acids (see below) could explain the accumulation of phytanic acid. On the other hand, the relatively lower levels of 4,8,12-trimethyltridecanoic acid and 2,6,10,14-tetramethylpentadecanoic acid (pristanic) are not easily reconciled with this explanation. Some gas-liquid chromatographic evidence based on calculation of retention times indicated the presence of the chain extension product of phytanic acid, 5,9,13,17-tetramethyloctadecanoic, and of 6,10,14-trimethylpentadecanoic acid derived from 4,8,12-trimethyltridecanoic acid (Maxwell et al. 1973). However, these components were only present in trace amounts ≥0.01% and identifications are speculative.

The importance of marine algae (the primary source of phytol from which phytanic acid is derived) in the diet of sturgeons is not known (Scott and Crossman 1973). In freshwater, Atlantic sturgeon do eat algae (Leim and Scott 1966). The unusually high levels of 16:2ω4, 16:3ω4, and 16:4ω1, all of which are primarily algal in origin (Ackman et al. 1968), indicate that plants provide a significant proportion of dietary lipids. The tentatively identified higher homologues 18:2ω4, 18:3ω4, and 18:4ω1 behaved as appropriate polyunsaturated fatty acids on nitromethane enrichment (Jangaard 1965) and on thin-layer chromatography on silver nitrate impregnated silicic acid (Morris 1966), and were eliminated (probably converted to 18:0) on hydrogenation. The retention times in gas-liquid chromatography were appropriate to the proposed structure (Ackman et al. 1974). All of these acids may be found in trace amounts in many marine oils, but in both of the sturgeon oils were of much greater importance than usual. As far as we are aware, these acids originate in marine and not freshwater plant lipids. Their exclusion from the polar lipids indicates that they are biochemically functional. It is known that 16:4ω1 does not chain extend to 18:4ω1 in the rat (Klenk 1963) and the reason for the apparent facile chain extensions in sturgeon could be due to a steady intake of the unusual C_{16} acids or their C_{18} homologues from primary plant lipids, or from the fats of marine invertebrates feeding on macrophytes or unicellular algae, or to a general tendency of sturgeons to chain extend C_{16} acids to a stable accumulation of C_{18} acids. The latter possibility, suggested to explain the accumulation of phytanic acid, is part of the larger question of turnover rates for fatty acids in the marine sturgeon and is linked in turn to the freshwater aspects of their lipid biochemistry. It is probable that

marine sturgeon, migrating into freshwater to spawn, live off fat reserves (Scott and Crossman 1973).

The subject of freshwater versus marine fatty acid composition for fish oils and fats has been discussed by various authors (Ackman 1967; Farkas 1971; Ikekawa et al. 1972; Reichwald and Meizies 1973), but not always from the same viewpoint. There is, however, clear agreement that in the depot fats of the sturgeon, from either the freshwater or marine milieu, 18:2ω6 (linoleic acid) is a minor (≤1-2%) component and 20:4ω6 (arachidonic acid) is also of limited significance. The low level of 18:2ω6 is probably a "marine" fat characteristic as most freshwater fish have fats with 5% or more of this acid (Ackman 1967; Farkas and Herodek 1967; Mangold 1973; Reichwald and Meizies 1973). In some other animals such as the turtles, freshwater species freely deposit 18:2ω6 and marine forms do not (Ackman, Hooper, and Frair 1971). Unfortunately, many reports on the composition of freshwater fish fats are confused by fatty acid depositions from rearing on artificial diets exceptionally rich in 18:2ω6 and the normal species pattern may be masked by this factor (Albrecht and Breitsprecher 1969). The higher polyunsaturated acids in depot fats of all sturgeons studied to date are dominated by the C_{20} and C_{22} polyunsaturated fatty acids of the "ω3" (linolenic) family, in all analyses. The figures for total C_{20} and C_{22} polyunsaturated acids in Atlantic sturgeon A correspond fairly closely to those for the marine *A. sturio* examined by Lovern (1932). The tissues sampled by various authors are not always clearly comparable. The "pink calf-like" tissue (3.3% fat) of the sturgeon examined by Reichwald and Meizies (1973) occurs dorsally above the abdominal cavity and is also the main caudal tissue, with the "white lard-like" tissue (52.9% fat) interposed in an arrowhead fashion when viewed in longitudinal section (I. Reichwald, pers. commun.). The location of a transverse section could show quite different relative locations for either tissue. From the fat contents, it appears that our "orange" layer corresponds to the "white" layer of an European sturgeon (Reichwald and Meizies 1973) and possibly to the ventral layer of a Japanese sturgeon (Shimma and Shimma 1968), and our "muscle" corresponds to the "pink" tissue of the former. Among differences in fatty acids of interest listed for different animals may be mentioned 20:5ω3 = ½ 22:6ω3 for two animals kept in captivity on a marine fish diet (Shimma and Shimma 1968, see Table 3) and the virtual absence of 20:5ω3 in the fat of the "white" tissue described by Reichwald and Meizies (1973), although in the "pink" tissue 20:5ω3 > 22:6ω3 agrees with our data, as also reported in less comprehensive studies of European sturgeon (Mangold 1973; Meizies and Reichwald 1973). The depot fats of the marine sturgeon we have investigated had 22:6ω3 at about half the level of 20:5ω3, and we interpret the analysis of the marine *A. sturio* by Lovern (1932) to agree with our data. It appears that at some point in the animals' spawning migration the proportions of these two fatty acids could reverse. Interestingly enough, only one out of four freshwater fish oils (from maria or *Lota lota*) examined earlier contained larger proportions of 22:6ω3 than of 20:5ω3 (Ackman 1967).

The spawning period for Canadian Atlantic sturgeon is presumably in early summer. The two male fish examined showed no gonad development and, therefore, if mature presumably they had spawned and returned to the ocean. Oleic acid (Σ18:1) at 44-49% and palmitic acid (16:0) at 21-23% are indicated by Reichwald and Meizies (1973) and other studies (see above) to be the major components of freshwater sturgeon fats. The depot fats of the two marine Atlantic sturgeon we have investigated differ in that both 18:1 totals are 20-30% (magnitude inversely related to iodine value) and 16:0 is about 15%. The original marine *A. sturio* had about 36% 18:1 and 16-19% 16:0, or in other words, the fats examined by Lovern (1932) displayed a composition for these two fatty acids intermediate to two more recent studies.

The very different iodine values for sturgeon A and B are accounted for mainly by the differences in percentages of 20:5ω3, 22:5ω3, and 22:6ω3 in lieu of 18:1 and other monoethylenic acids, as total saturated acids are in the same proportion of fat in both fish and the proportions of most minor unsaturated acids are not important enough to matter. The monoethylenic fatty acids of fish B (total about 45%) probably are more normal as judged by the various low iodine values in the literature for sturgeon fat. The resolving power of open-tubular gas-liquid chromatograph for methyl esters of monoethylenic fatty acids extends our knowledge of the fatty acid biochemistry of the two Atlantic sturgeon in this study. Virtually no 18:1ω11, which could only come from 20:1ω11, was observed. This indicates that the fish were depositing fat and not catabolizing it. On the other hand, the percentage of 20:1ω7 was about the same as that of 20:1ω9 in

the body fats of both sturgeon A and B. Therefore, the pathway 16:1ω7→18:1ω7→20:1ω7 appears to be important, suggesting a period of fatty acid biosynthesis rather than of deposition of exogenous fatty acids. Both fish had about the same percentages of 16:1. Fish A had higher proportions of fat in the muscle than Fish B, and 18:1ω7 was about a quarter of 18:1ω9 in this fat. In the leaner fish B, 18:1ω7 was only about one-fifth of 18:1ω9, suggesting less activity in de novo biosynthesis. It is possible that the diet of fish A was rich in the polyunsaturated fatty acids, the deposition of which was disturbing the typical species-fat composition. Accordingly, fish A may have been more actively engaged in synthesizing monoethylenic fatty acids, via 16:0→16:1ω7→18:1ω7, to achieve this composition. Seals, whose depot fat has a higher iodine value than that of most whales, may show the same monoethylenic fatty acid activity (Ackman, Epstein, and Eaton 1971).

Earlier work on oils from four freshwater fish showed 1-3% 20:1 and about 0.3-0.4% 22:1 (Ackman 1967). Marine fish oils, in our experience, usually show 10% or more of 20:1 and 5% or more of 22:1. The absence of large proportions of 20:1 and 22:1 acids in the marine sturgeon depot fat, even in fish B with the less unsaturated fat, is the key reason for our placing the fat of the marine Atlantic sturgeon in a rather special class of marine fat, or more broadly, in the generally freshwater class of fish fats, as recorded by Hilditch and Williams (1964).

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ZOOPLANKTON ABUNDANCE AND FEEDING HABITS OF FRY OF PINK SALMON, *ONCORHYNCHUS GORBUSCHA*, AND CHUM SALMON, *ONCORHYNCHUS KETA*, IN TRAITORS COVE, ALASKA, WITH SPECULATIONS ON THE CARRYING CAPACITY OF THE AREA

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ABSTRACT

Juvenile pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, 28 to 56 mm long (fork length) from Traitors River in southeastern Alaska, fed little in freshwater but fed heavily in the estuary, mainly on pelagic zooplankters. Fry did not feed on cloudy moonless nights. The rate of evacuation of pink salmon stomachs ranged from 6 h at 12.8°C to 16 h at 8.5°C. The abundance of zooplankton ranged from 9 to 154 organisms per liter and quantitatively did not change noticeably while fry were in the estuary. In 1964, 1965, and 1966, the estimated numbers of fry in Traitors Cove was 7, 1, and 4 million, respectively. An attempt was made to estimate the carrying capacity of Traitors Cove, using food consumption and evacuation rates in conjunction with estimates of standing crop of zooplankton. It was concluded that 50 to 100 million additional fry from hatcheries would probably exceed the carrying capacity of the estuary.

With the rapidly growing demand for animal protein and the emergence of new hatchery techniques for pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta* (Bams 1972; Bailey and Heard 1973; Bailey and Taylor 1974), we believe that it is timely to speculate on the capacity of estuaries to support more fry. The Japanese, Russians, and Canadians have a number of major pink and chum salmon hatcheries and spawning channels in operation. Japanese hatcheries released over 800 million pink and chum salmon fry in 1973 (source: Japan Fishery Agency). Individual Russian hatcheries are capable of releasing up to 120 million fry annually (Kanid'yev et al. 1970). The Qualicum River in British Columbia, Canada, now produces about 50 million chum salmon fry annually through a combination of flow control in the natural spawning areas and the operation of a spawning channel (Fraser 1972). The problem of evaluating the carrying capacity of estuaries for artificially produced fry is most pertinent. What, for example, would be the impact of 100 million fry on the available food in Traitors Cove?

Recent technological advances in rearing salmon in hatcheries and spawning channels now make it possible to release tens of millions of pink and chum salmon fry into individual estuaries, but lack of knowledge of the food requirements of these two species in nature makes even the immediate results of such releases uncertain. It is conceivable that a spawning channel or hatchery operation could produce such large numbers of fry that their migratory behavior might be altered, or growth and survival might be reduced because of severe competition for a limited food supply. Ivankov and Shershnev (1968) reported that young pink and chum salmon (50 to 80 mm) had fuller stomachs in years of "scarcity" of salmon than in years of "abundance" in the coastal zone of the southern Kuril Islands.

The survival of fry to a large extent depends on their rate of growth and on their ability to escape from predators. Rapid growth requires suitable temperature, an abundance of food, and a rapid transition from endogenous nutrition, based on yolk reserve, to exogenous feeding on small aquatic organisms. In a study of size-selective predation, Parker (1971) demonstrated that predation decreases with increase in size of the prey species.

The study reported in this paper was undertaken in a southeastern Alaska estuary, Traitors Cove (Figure 1), in 1964-66 to gain further insight into the food requirements and feeding habits of pink and chum salmon fry. Questions asked were: How soon in life does feeding begin? How does the diet of the fry compare with the available food organisms? What are the food consumption rates

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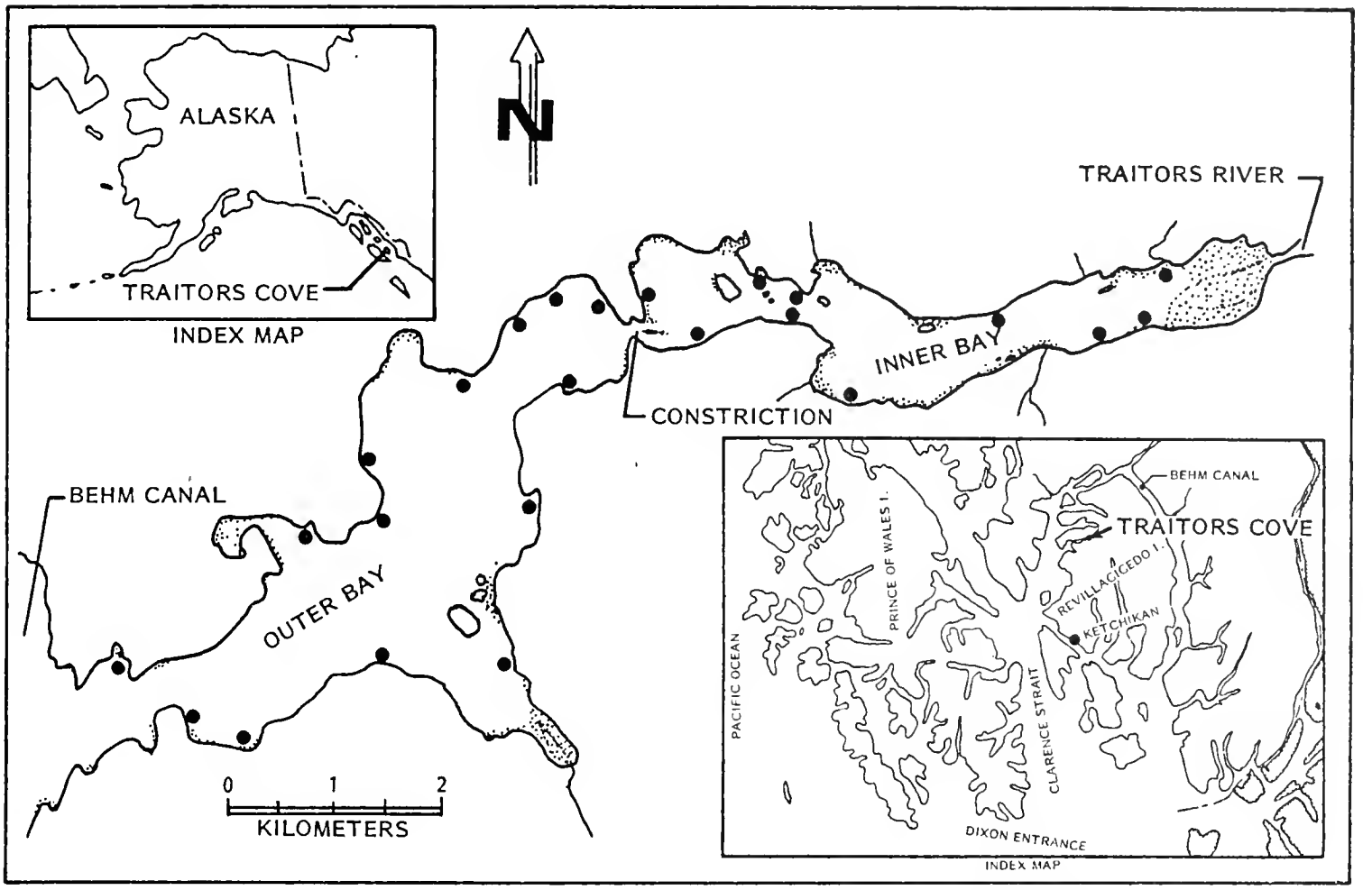

FIGURE 1.—Traitors Cove estuary, Revillagigedo Island, Alaska, 1963-65 (from McLain 1968), showing locations of plankton sampling stations.

for fry in relation to water temperature? How many fry can the estuary support based on estimates of abundance of food organisms and grazing rates?

Traitors Cove is about 50 km north of Ketchikan, Alaska. Several tributaries used by pink and chum salmon enter Traitors Cove, the major one being Traitors River, which has about 55,000 m^2 of spawning grounds. The dominant feature of the estuary is a narrow constriction with a sill, 1 or 2 m below mean low water, which divides the estuary into two basins. The inner bay is about 5.9 km long and 0.7 km wide and has a maximum depth of 46 m. The outer bay is about 6.5 km long and 1.3 km wide and has a maximum depth of 130 m. The tidal range of about 7 m and the constricted flow at the sill create exceptionally strong currents and a reversing tidal falls throughout the year. The turbulence and surface currents affect distribution and movement of fry for at least 0.5 km on both sides of the constriction. We measured surface temperatures of 5° to 13°C in the estuary when fry were present. Some aspects of the oceanography of Traitors Cove have been described by McLain (1968).

Pink and chum salmon fry from the tributary streams enter the estuary from mid-April to late June. Schools with thousands of fry are typically present until late June.

METHODS

To determine if juvenile salmon feed while still in Traitors River, we compared the contents of the entire digestive tracts of individuals excavated from redds with those trapped in nets while migrating downstream at night. All specimens were preserved whole in 10% Formalin solution.[2] The contents of the digestive tract were later removed in the laboratory and examined under a stereoscopic microscope. To determine the kinds and numbers of food organisms eaten in the estuary, we compared stomach contents of fry samples collected in the estuary in 1964, 1965, and

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1966. Individual food items were measured to the nearest 0.01 mm of body length and diameter with an ocular micrometer to determine volume. Fry in the estuary were collected with a dip net from a skiff and by floating traps anchored near the shoreline. The dip nets and traps were effective in collecting fry less than 60 mm long, which are the subject of this report, but were not effective in collecting larger salmon. The larger fish were able to evade capture by sounding. Most of the fry examined for stomach contents were collected from the estuary during daylight (1100 to 1500). On three occasions, however, fry were collected during nights (0230) when the sky was overcast or moonless and incident light intensity was 0.0 footcandle near the water surface. No stomachs were collected during bright moonlight nights, which were rare.

To estimate the volume of water grazed per day by fry, we measured velocities of water currents close to shore-oriented fry while observing their behavior in relation to the current and food items. Current velocities close to shore-oriented schools of fry were measured by two methods. One method was to record the time it took suspended particles in the water to drift 1 to 5 m along a floating anchored line graduated to 0.1 m. The second method was to measure the velocity by holding a current meter near a school of fish; the meter was attached to the end of a rod about 4 m long. The current meter dial was calibrated to read to the nearest 3 cm/s. Both methods required the observer to operate either from an anchored skiff or from shore. Polaroid glasses were used to reduce glare from the water surface and improve visibility.

Feeding at night by fry was tested in two experiments in an aquarium with known densities of zooplankton. The aquarium consisted of a 7-mil plastic bag suspended in the estuary from a float and containing 76 liters of seawater. The fry were captured in the outer bay and held in a 1-m no. 10 mesh (158-μm openings) plankton net for 20 h to deny them food and to ensure that their stomachs were empty. The starved pink and chum salmon fry together with a known quantity of zooplankton were then placed in the aquarium and held under various light intensities. After timed intervals in the aquarium, fry were removed, killed, and their stomach contents removed.

In the first experiment, fry (length, 32 to 41 mm) in groups of five were placed in an aquarium that contained 240 zooplankters per liter of seawater. A cursory examination of the zooplankters revealed that they were predominantly copepods and barnacle nauplii. Each group of fish was allowed to feed 13 to 28 min before being removed and preserved in 10% Formalin solution. The experiment was started in the evening before sunset and continued until the light meter read 0.0 footcandle. In the second experiment, 14 fry were placed in an aquarium containing about 260 zooplankters per liter; they were kept there for 4 h and 20 min at night before they were removed and preserved in Formalin. The light meter read 0.0 footcandle throughout the experiment.

The time required for fry to evacuate their stomach contents was determined experimentally at 8.5°, 10.0°, and 12.8°C. The procedure was to capture 200 to 300 salmon fry in the estuary and place them in strained seawater in a floating cage of no. 10 mesh plankton net, which prevented entry of prey from the surrounding water. At the start of each test, 10 pink and 5 chum salmon were killed and preserved; at hourly intervals thereafter 5 fish of each species were killed and their stomach contents examined until all 10 fish of two successive samples contained no food in their stomachs. The pink salmon fry examined in these tests ranged from 32 to 57 mm in length and the chum salmon from 34 to 54 mm. Water temperatures were recorded by a thermograph to the nearest 1°C. The sensing probe of the thermograph was located 1 m below the water surface.

The zooplankton in Traitors Cove was sampled only in 1965 and 1966 while fry were in the bay. A 5-inch Clarke-Bumpus sampler with a no. 10 mesh net was towed at a depth of about 0.5 m until about 50 liters of water (2 to 10 s) had been strained. Seventy-nine samples were collected—in 1965, 7 stations in the outer bay were each sampled in 1 day; and in 1966, 10 stations in the inner bay and 14 in the outer bay were each sampled on 3 different days (Figure 1). Only one sample was taken at each station. The zooplankton catch was preserved in 5% buffered Formalin solution. The plankton samples were subsampled by two methods for analysis. In the first method, each of the 79 samples was analyzed from 1-ml subsamples (approximately 1/100 of the sample) placed in a Sedgewick-Rafter chamber. The kinds, numbers, and size of the various plankters were determined. Volumes of the different plankters were computed from lengths and average diameters, assuming a cylindrical shape for each plankter. In the second method, all 7 of the 1965

samples and 66 of the 1966 samples were examined to determine numbers of plankters from larger subsamples ($^1/_{64}$ to $^1/_4$ of the sample) taken with a Cushing subsampler (Cushing 1961). A comparison of the results of the two analyses indicated that the data from 1-ml subsamples overestimated the number of organisms by an average of 20% (range 15 to 30%). Therefore, estimates of zooplankton densities using the first method were reduced by 20%. Plankton samples contained protozoans (mostly tintinnids) and phytoplankton, but these were not included in the estimate of standing stock of plankton because salmon fry consumed only the larger zooplankters. Rotifers and copepod nauplii were the smallest plankters included in the counts.

FEEDING IN TRAITORS RIVER

Although most of the pink and chum salmon excavated from redds in Traitors River contained items such as sand or detritus in their digestive tracts, only a few individuals contained food organisms. Chironomids (dipterans) were the most frequently observed food item. Seventy juvenile pink salmon (fork length, 33 to 41 mm) were collected from spawning gravels for analysis of contents; only three contained food—a chironomid pupa and some unidentifiable insect remains (Table 1). Seventy juvenile chum salmon (fork length, 33 to 41 mm) were collected from spawning gravels; nine contained food. Chum salmon had eaten only chironomid larvae and pupae, plecopteran nymphs, ephemeropteran nymphs, and an arachnid (spider). One chum salmon (41 mm) contained the remains of 24 chironomid pupae, 2 chironomid larvae, 3 ephemeropteran nymphs, and 3 plecopteran nymphs. The other eight chum salmon that contained food were 37 to 38 mm long and had eaten only one to three items each.

Table 1.—Frequency of occurrence of items in digestive tracts of 70 pink and 70 chum salmon juveniles excavated from redds in Traitors River in 1964-65.

Item	Pink salmon		Chum salmon	
	Number	Percent	Number	Percent
Arachnids	0	0	2	3
Ephemeropterans	0	0	2	3
Plecopterans	0	0	2	3
Dipterans	1	1	4	6
Insect remains	2	3	3	4
Plant detritus	15	21	16	23
Fine sand	33	47	44	63
Empty	22	31	12	17

Table 2.—Frequency of occurrence of items in digestive tracts of 40 pink salmon fry and 40 chum salmon fry trapped in nets while migrating down Traitors River, May 1964.

Item	Pink salmon		Chum salmon	
	Number	Percent	Number	Percent
Plecopterans	0	0	2	5
Dipterans	0	0	9	22
Insect remains	0	0	2	5
Detritus	1	2	1	2
Fine sand	8	20	22	55
Empty	31	78	19	48

Although none of the 40 downstream-migrating pink salmon fry (length, 32 to 37 mm) contained food, 9 of the 40 chum salmon (length, 35 to 42 mm) contained substantial numbers of chironomid pupae and plecopteran nymphs (Table 2). The average for those that contained food was 6.7 food items (range 1 to 27 items).

Fine sand (diameter, 0.05 to 0.90 mm) and plant detritus were common items in the digestive tracts of both the gravel-resident and the migrating pink and chum salmon (Tables 1, 2). The sand and detritus were more common in fish taken from the redds than in those captured in the downstream traps.

FEEDING IN THE ESTUARY

We studied four aspects of the feeding of pink and chum salmon fry in the estuary: 1) stomach contents, 2) feeding behavior in relation to water currents, 3) effect of daylight on feeding, and 4) time required for evacuation of stomach contents.

Stomach Contents of Pink Salmon Fry

In the springs of 1964, 1965, and 1966, a total of 140 pink salmon (length, 28 to 56 mm) were collected from the estuary during daylight, and 30 (length, 31 to 58 mm) were collected at night (Table 3). All of the stomachs from the fry collected in daylight contained food. Copepods (calanoids and cyclopoids) occurred in 94% of the stomachs and constituted 77% of the total volume of stomach contents. Barnacle nauplii (cirripedes) and cladocerans (*Podon* sp. and *Evadne* sp.) each occurred in 56% of the stomachs and constituted 6% of the total volume. The remaining 11% of the food volume consisted of various other planktonic forms and occasional epibenthic organisms. Most of the food items were between 0.3 and 3.0 mm long. The smallest item in pink salmon stomachs was a disc-shaped diatom and the largest were fish

TABLE 3.—Zooplankters and other organisms from stomachs of 140 pink salmon fry (length, 28 to 56 mm) collected in daylight and 30 (length, 31 to 58 mm) collected at night in Traitors Cove, 1964-66, and percentage relative importance by volume.

Item	Collected in daylight				Collected at night			
	Percentage stomachs containing item	Mean items per stomach		Percentage relative importance by volume[1]	Percentage stomachs containing item	Mean items per stomach		Percentage relative importance by volume[1]
		Number	Percent			Number	Percent	
Diatoms	32	3.3	3	+	26	0.4	2	+
Rotifers	15	4.0	3	+	0	0.0	0	0
Bryozoans (cyphonautes)	2	0.0	0	+	0	0.0	0	0
Gastropods (veligers)	12	0.5	0	+	3	0.1	1	+
Pelecypods (veligers)	26	0.9	1	+	6	0.1	1	+
Polychaetes (larvae)	31	1.1	1	1	9	0.3	2	1
Arachnids	2	0.0	0	+	3	0.0	0	+
Cladocerans	56	10.3	8	6	9	0.7	4	3
Copepods	94	70.7	52	77	76	10.7	67	85
Cirripedes (nauplii)	56	18.6	14	6	53	2.1	13	5
Cirripedes (cyprids)	25	1.9	1	2	9	0.4	2	3
Cirripedes (casts)	2	0.1	0	+	9	0.1	1	+
Mysids	4	0.1	0	+	0	0.0	0	0
Cumaceans	3	0.1	0	+	0	0.0	0	0
Isopods	1	0.0	0	+	0	0.0	0	0
Amphipods	4	0.0	0	+	0	0.0	0	0
Euphausiids (larvae)	2	0.1	0	1	0	0.0	0	0
Decapods (zoeae)	9	0.3	0	1	0	0.0	0	0
Unidentified crustaceans (nauplii)	23	1.4	1	+	9	0.1	1	+
Dipterans (larvae)	3	0.0	0	+	3	0.0	0	+
Dipterans (pupae)	6	0.1	0	+	3	0.0	0	+
Larvaceans	26	1.8	1	3	9	0.2	1	2
Eggs (invertebrates)	49	20.8	15	3	23	0.8	5	1
Fish	4	0.0	0	+	0	0.0	0	0

[1]+ indicates less than 0.5%

larvae (up to 8 mm long). Unidentifiable material occurred in only 11% of the stomachs and constituted an insignificant fraction of the volume.

The 30 pink salmon fry collected from the estuary at night all had food in their stomachs, but they probably had not feed recently. Many more food items were found in the stomachs of pink salmon fry collected in daytime than in those collected at night—an average of 136 items versus 16. Also, digestion had not progressed as far in the daytime fry—only 11% of their stomachs contained unidentifiable items, whereas 80% of the stomachs from nighttime fry contained unidentifiable items. On three moonlight nights, fry were seen dimpling the water surface while apparently feeding. Incident light intensity at the water surface at such times was 0.016 to 1.0 footcandle.

Stomach Contents of Chum Salmon Fry

In the springs of 1964, 1965, and 1966, a total of 124 chum salmon (length, 32 to 51 mm) were collected from the estuary during daylight and 20 (length, 35 to 43 mm) were collected at night (Table 4). All of the fry taken during daylight contained food. Copepods occurred in 73% of the stomachs and constituted 30% of the total food volume. Larvaceans occurred in 54% of the stomachs and constituted 34% of the total food volume. Dipteran (chironomid) pupae occurred in 51% of the stomachs and constituted 11% of the volume. The remaining 25% of the food volume was primarily other planktonic forms (including cladocerans and eggs) but also a few epibenthic animals. Unidentifiable material occurred in 20% of the chum salmon stomachs but constituted an insignificant fraction of the volume and was not included in the final comparisons. Food items eaten by chum salmon fry were similar in size to those eaten by pink salmon, mostly from 0.3 to 3.0 mm long. The largest item was a larval fish 20 mm long. Chum salmon fry, however, tended to feed on larger (Table 5) and harder shelled items than pink salmon, as evidenced by the greater incidence of harpacticoid copepods, collembolans (intertidal springtails), cumaceans, and chironomids in the chum salmon (Tables 3, 4). The chum salmon fry could have picked up some of the so-called epibenthic or intertidal organisms in the form of neuston, or drift material.

Many more food items were found in the stomachs of the chum salmon collected in daytime than in those collected at night—an average of 124 items versus 4. Only 20%of the stomachs collected in daytime contained unidentifiable items versus 70% at night.

TABLE 4.—Zooplankters and other organisms from stomachs of 124 chum salmon fry (length, 32 to 51 mm) collected in daylight and 20 (length, 35 to 43 mm) collected at night in Traitors Cove, 1964-66, and percentage relative importance by volume.

Item	Collected in daylight				Collected at night			
	Percentage stomachs containing item	Mean items per stomach		Percentage relative importance by volume[1]	Percentage stomachs containing item	Mean items per stomach		Percentage relative importance by volume[1]
		Number	Percent			Number	Percent	
Diatoms	15	0.4	1	+	4	0.2	5	+
Rotifers	7	0.5	1	+	0	0.0	0	0
Gastropods (veligers)	3	0.2	0	+	0	0.0	0	0
Pelecypods (veligers)	14	0.4	1	+	0	0.0	0	0
Polychaetes (larvae)	21	1.3	2	2	4	0.3	7	6
Arachnids	9	0.1	0	2	0	0.0	0	0
Cladocerans	58	12.9	18	8	0	0.0	0	0
Ostracods	1	0.0	0	+	0	0.0	0	0
Copepods	73	16.3	22	30	39	1.7	41	37
Cirripedes (nauplii)	34	2.3	3	1	29	0.5	12	4
Cirrepedes (cyprids)	20	0.6	1	1	14	0.1	2	1
Cirripedes (casts)	1	0.0	0	+	0	0.0	0	0
Cumaceans	6	0.1	0	1	0	0.0	0	0
Isopods	2	0.0	0	+	0	0.0	0	0
Amphipods	3	0.0	0	+	0	0.0	0	0
Euphausiids	1	0.0	0	+	0	0.0	0	0
Decapods (zoeae)	21	0.4	1	2	0	0.0	0	0
Unidentified crustaceans (nauplii)	10	0.8	1	+	4	0.0	0	+
Collembolans	18	0.4	1	1	0	0.0	0	0
Dipterans (larvae)	10	0.2	0	+	9	0.1	2	2
Dipterans (pupae)	51	3.4	5	11	59	1.3	31	50
Dipterans (adults)	4	0.1	0	+	0	0.0	0	0
Unidentified insect remains	6	0.1	0	+	0	0.0	0	0
Larvaceans	54	18.2	25	34	0	0.0	0	0
Eggs (invertebrates)	19	14.0	9	4	4	0.0	0	+
Fish	6	0.1	0	3	0	0.0	0	0

[1] + indicates less than 0.5%

Feeding Behavior in Relation to Water Currents

Our visual observations of individual chum and pink salmon fry in shore-oriented schools indicated that their feeding varied with the speed of the water currents. At velocities of 0 to 10.7 cm/s, a fry would typically swim a darting course as much as three times its body length to capture a food item. At higher velocities, 10.8 to 19.8 cm/s, schools of fry sometimes held position relative to the shore or bottom while facing the current, and an individual would typically deviate up, down, or to the sides no more than one-third of its body length to capture oncoming food. At still higher velocities, 19.9 to 24.4 cm/s, fry in schools often held a constant position relative to shore or bottom but did not feed. Fry that appeared to be in visual contact with the shore or bottom avoided currents above 24.4 cm/s unless frightened.

Effect of Daylight on Feeding

The cessation of feeding at night by pink salmon fry was confirmed by the two feeding experiments we conducted in the aquarium. In the first experiment, feeding rate was directly related to light intensity. During a 78-min period when light intensity ranged from 65 to 170 footcandles (three tests), the average consumption was 2.2 to 3.1 zooplankters per minute per fry (Figure 2). At light intensities of 2 footcandles or less, the average feeding rate was only 0.5 zooplankter per minute per fry (three tests). In the second experiment, performed entirely in darkness, little feeding took place. One fry had eaten 48 plankters (less than 0.2 plankter per minute), and the remaining 13 had eaten 13 plankters (0 to 0.001 plankter per minute). These observations agree with laboratory experiments of Hoar (1942) in which young salmon fed little during darkness.

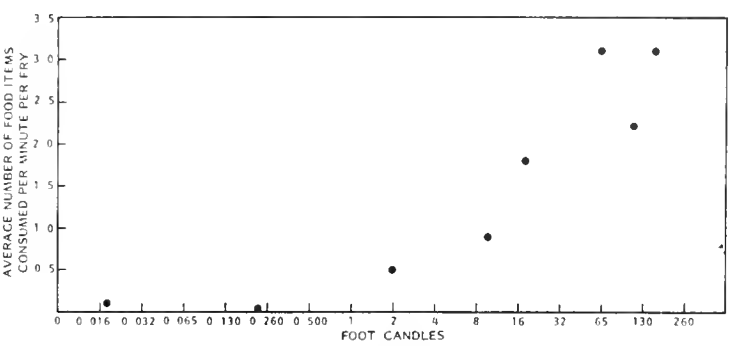

FIGURE 2.—Effect of darkness on feeding rate of pink salmon fry confined in an aquarium. Each dot represents a single test of feeding rate.

TABLE 5.—Average size of zooplankters and other organisms collected by Clarke-Bumpus sampler and present in the stomachs of pink and chum salmon fry at Traitors Cove, 1965-66.

Item and place collected	Number measured	Length (mm)		Diameter (mm)		Average volume (mm^3)
		Average	Range	Average	Range	
Diatoms:						
Clarke-Bumpus sampler	24	0.09	0.06- 0.11	0.18	0.12-0.23	0.0023
Pink salmon	9	0.10	—	0.28	0.21-0.31	0.0062
Chum salmon	4	0.10	—	0.31	0.30-0.33	0.0075
Tintinnids:						
Clarke-Bumpus sampler	1	0.25	—	0.14	—	0.0038
Pink salmon	—	—	—	—	—	—
Chum salmon	—	—	—	—	—	—
Hydromedusans:						
Clarke-Bumpus sampler	2	0.18	—	0.31	—	0.0136
Pink salmon	—	—	—	—	—	—
Chum salmon	—	—	—	—	—	—
Rotifers:						
Clarke-Bumpus sampler	9	0.24	0.18- 0.31	0.16	0.11-0.20	0.0048
Pink salmon	9	0.32	0.30- 0.36	0.19	0.16-0.23	0.0091
Chum salmon	2	0.32	0.31- 0.33	—	—	0.0091
Gastropods (veligers):						
Clarke-Bumpus sampler	1	0.20	—	0.14	—	—
Pink salmon	9	0.58	0.30- 0.75	0.38	0.20-0.49	0.0658
Chum salmon	1	0.68	—	0.44	—	0.1034
Pelecypods (veligers):						
Clarke-Bumpus sampler	4	0.28	0.19- 0.40	0.18	0.15-0.21	0.0071
Pink salmon	12	0.34	0.22- 0.42	0.31	0.22-0.38	0.0257
Chum salmon	6	0.35	0.28- 0.38	0.32	—	0.0281
Polychaetes (larvae):						
Clarke-Bumpus sampler	2	0.46	0.38- 0.55	0.17	0.13-0.21	0.0104
Pink salmon	11	0.94	0.61- 1.60	0.24	0.19-0.30	0.0425
Chum salmon	10	2.04	1.01- 4.00	0.29	0.29-0.47	0.1347
Arachnids:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	1.20	—	1.20	—	1.3572
Chum salmon	9	1.38	0.30- 1.80	1.38	0.18-3.50	2.0641
Crustaceans (nauplii):						
Clarke-Bumpus sampler	11	0.30	0.23- 0.43	0.14	0.10-0.19	0.0046
Pink salmon	7	0.37	0.28- 0.45	0.17	—	0.0084
Chum salmon	7	0.45	0.30- 0.50	0.21	—	0.0156
Cladocerans:						
Clarke-Bumpus sampler	11	0.50	0.31- 0.71	0.28	0.20-0.39	0.0308
Pink salmon	33	0.62	0.32- 0.91	0.33	0.17-0.49	0.0530
Chum salmon	31	0.60	0.20- 1.10	0.32	—	0.0482
Copepods:						
Clarke-Bumpus sampler	13	0.62	0.40- 1.23	0.19	0.12-0.32	0.0176
Pink salmon	98	1.00	0.26- 3.20	0.37	0.10-1.12	0.1075
Chum salmon	62	1.12	0.30- 3.20	0.41	0.11-1.19	0.1479
Cirripedes (nauplii):						
Clarke-Bumpus sampler	24	0.39	0.39- 0.61	0.22	0.16-0.42	0.0148
Pink salmon	28	0.47	0.28- 0.82	0.29	0.17-0.50	0.0310
Chum salmon	10	0.55	0.30- 1.20	0.34	0.18-0.56	0.0499
Cirripedes (cyprids):						
Clarke-Bumpus sampler	1	0.53	—	0.28	—	0.0326
Pink salmon	18	0.85	0.60- 1.00	0.37	0.26-0.46	0.0914
Chum salmon	14	0.84	0.62- 1.00	0.37	0.27-0.46	0.0903
Mysids:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	2.10	—	0.25	—	0.1031
Chum salmon	—	—	—	—	—	—
Cumaceans:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	2	1.80	1.50- 2.10	0.46	—	0.2991
Chum salmon	3	2.11	1.52- 2.50	0.54	—	0.4832
Isopods:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	0.76	—	0.50	—	0.1492
Chum salmon	3	0.62	0.52- 0.80	0.31	0.26-0.40	0.0468
Amphipods:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	1.48	—	0.59	—	0.4046
Chum salmon	3	1.05	0.90- 1.25	0.42	—	0.1455
Euphausiids:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	3	2.67	2.50- 2.70	0.48	—	0.4832
Chum salmon	1	2.70	—	0.49	—	0.5092

TABLE 5.—Continued.

Item and place collected	Number measured	Length (mm) Average	Length (mm) Range	Diameter (mm) Average	Diameter (mm) Range	Average volume (mm^3)
Decapods (zoeae):						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	10	1.79	0.54- 5.80	0.39	0.12-1.27	0.2138
Chum salmon	10	2.05	1.28- 3.04	0.45	0.28-0.67	0.3260
Collembolans:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	—	—	—	—	—	—
Chum salmon	14	1.57	0.67- 1.94	0.41	0.20-0.50	0.2073
Dipterans (larvae):						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	3	1.43	1.20- 1.60	0.13	0.11-0.14	0.0190
Chum salmon	8	2.96	1.40- 4.00	0.27	0.13-0.37	0.1695
Dipterans (pupae):						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	2.00	—	0.39	—	0.2389
Chum salmon	21	1.80	1.20- 2.90	0.43	0.27-0.70	0.2614
Dipterans (adults):						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	—	—	—	—	—	—
Chum salmon	4	2.58	1.60- 3.50	0.39	0.24-0.52	0.3082
Unidentified insect remains:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	—	—	—	—	—	—
Chum salmon	—	0.52	—	—	—	0.0616
Larvaceans:						
Clarke-Bumpus sampler	1	0.20	—	0.14	—	0.0031
Pink salmon	9	0.69	0.50- 1.05	0.39	0.28-0.60	0.1498
Chum salmon	30	0.69	0.41- 1.30	0.39	0.23-0.74	0.1498
Polyzoans:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	1	0.60	—	0.19	—	0.0032
Chum salmon	—	—	—	—	—	—
Eggs (invertebrate):						
Clarke-Bumpus sampler	7	—	—	0.32	0.20-0.40	0.0172
Pink salmon	11	—	—	0.31	0.11-0.40	0.0156
Chum salmon	14	—	—	0.34	0.10-0.42	0.0206
Eggs (vertebrate):						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	5	—	—	0.88	0.80-0.98	0.3568
Chum salmon	1	—	—	0.85	—	0.3216
Fish:						
Clarke-Bumpus sampler	—	—	—	—	—	—
Pink salmon	3	5.67	4.00- 8.00	0.14	—	0.0873
Chum salmon	3	16.70	15.00-20.00	0.42	—	2.3137

Stomach Evacuation

The time required for satiated fry in the aquarium to evacuate food in their stomachs was inversely related to temperature. In tests at 12.8°C, the stomachs of two of five pink salmon were empty after 2 h without food. However, 6 h elapsed before successive samples of five fish contained no food, and 6 h was therefore accepted as the time required for pink salmon to evacuate their stomachs at a temperature of 12.8°C (Table 6). For chum salmon, the first empty stomach was observed after 1 h without food at 12.8°C. Only after 10 h did successive samples of five chum salmon have empty stomachs. This longer evacuation time for chum salmon probably resulted from the larger and different kinds of organisms eaten. Using the same criterion for time of evacuation as described above for 12.8°C, pink salmon fry confined without food had empty stomachs after 9 h at 10°C and after 16 h at 8.5°C. We did not test chum salmon at the lower temperatures.

TABLE 6.—Time required for pink and chum salmon fry to evacuate food from their stomachs at various temperatures.

Temperature (°C)	Pink salmon (hours)	Chum salmon (hours)
8.5	16	—
10.0	9	—
12.8	6	10

ZOOPLANKTON ABUNDANCE AND DISTRIBUTION

The abundance of zooplankton in the near-surface waters was determined from the samples we collected in the inner and outer bays of Traitors

Cove in June 1965 and in April, May, and June 1966 when salmon fry were present. The lowest abundance in the inner bay, an average of 9 organisms per liter, occurred in April 1966, when the abundance was comparatively high in the outer bay, 51 per liter (Table 7). During the rest of the 1966 season, mean numbers ranged from 27 to 28 organisms per liter in the inner bay and 24 to 40 in the outer bay. The highest numbers were observed in the outer bay in June 1965 after most of the fry had passed through the estuary. Zooplankters tended to be more abundant at the mouth of the bay, near the constriction, and at the head of the bay than at intervening points along the shoreline.

Fifty-two categories of zooplankters were identified from the Clarke-Bumpus samples, and seasonal qualitative and quantitative changes were evident in the composition of the zooplankton (Table 8). The peak abundance for polychaete larvae and cirrepede (barnacle) nauplii occurred in April, whereas the peak for other invertebrate larvae occurred in May. Rotifers, copepods (including nauplii), and barnacle nauplii were also very abundant in May. Cladocerans did not become abundant until June. Variation between years is indicated by the high abundance of rotifers in June 1965 (~120,000/m^3) and the much lower abundance of rotifers (~3,000/m^3) and possibly higher abundance of other forms in June 1966.

The predominant zooplankters during the period of fry outmigration were larvae of barnacles, polychaetes, and molluscs and nauplii and early copepodites of the copepods *Acartia clausii*, *A. longiremis*, and *Oithona helgolandica*. Over 98% of the zooplankters in the outer bay on 16 April 1966 were larvae, and as late as 7 June 1966 larvae constituted more than 65% of the zooplankton. In the inner bay on 18 April 1966 and 7 June 1966, the proportions of larvae in the zooplankton were 72 and 58%, respectively. Late copepodites and adults of calanoid and cyclopoid copepods were the next most abundant groups of zooplankters and contributed relatively more to the zooplankton as the season progressed. An abundance of larval forms was also characteristic of another southeastern Alaska estuary, Auke Bay (Wing and Reid 1972). Rotifers, although of minor importance in the diet of salmon fry, were often the most abundant zooplankters in the samples. Cladocerans and larvaceans were rare in April and May but by June constituted a significant portion of the zooplankton. Adults and juveniles of benthic invertebrates were rare in the plankton samples. Species composition of zooplankters differed between the inner and outer bays of Traitors Cove (Table 8).

TABLE 7.—Abundance of zooplankters determined from Clarke-Bumpus sampler with no. 10 mesh net (158μm) at Traitors Cove.

	Inner bay			Outer bay		
	Number of	Organisms per liter		Number of	Organisms per liter	
Date	samples	Mean	Range	samples	Mean	Range
16 June 1965	—	—	—	7	154	8-563
16-18 Apr. 1966	10	9	1-28	14	51	6-180
16 May 1966	10	28	2-76	14	24	10-44
7 June 1966	10	27	2-62	14	40	4-95

The plankton samples contained zooplankton of the kinds and sizes eaten in great numbers by pink and chum salmon fry as well as smaller plankters, which were not important in the diet of fry. As a result, the average size of plankters in the net was slightly smaller than the average size of items eaten (Table 5).

DISCUSSION

Initiation of Feeding

Neither pink nor chum juvenile salmon ate very much before leaving Traitors River, although chum salmon fed more than pink salmon. Some fry may have fed before they emerged from the redds. The size (41 mm) of the largest fry collected in the river suggests that at least a few individuals actually grew as a result of exogenous feeding before they finally left the river. Mason (1974) collected chum salmon fry up to 70 mm long from Lymn Creek on Vancouver Island, British Columbia, where they moved into and out of high-salinity water and apparently fed in both media over a period of 1 to 4 wk or more.

Immature stages of chironomids were most commonly eaten, but other bottom-dwelling aquatic organisms also occurred in stomachs of pink and chum salmon from Traitors River. Two workers (Disler 1953; Sparrow 1968) reported that zooplankton and bottom-dwelling aquatic organisms occurred in the diet of chum salmon in freshwater. Although pink salmon apparently eat little or nothing while migrating seaward in short streams (Kazarnovskii 1962; Kobayashi 1968), as at Traitors River, they are more likely to feed while migrating long distances from large rivers (Levanidov and Levanidova 1957; McDonald 1960).

Once they had left the stream, pink and chum salmon fry in Traitors Cove fed extensively on such zooplankters as calanoid copepods, lar-

TABLE 8.—Average species composition of zooplankton samples during salmon fry outmigration at Traitors Cove, June 1965[1] and April to June 1966. (See Table 4 for number of samples. Numbers of zooplankters per cubic meter rounded to nearest whole number. Percentages rounded to 0.1%; + indicates less than 0.5%.)

	Inner bay						Outer bay							
	18 Apr. 1966		16 May 1966		7 June 1966[2]		16 June 1965		16 Apr. 1966		16 May 1966		7 June 1966[2]	
Item	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Hydromedusans:														
Bougainvillia sp.	—	—	1	+	—	—	—	—	—	—	2	+	—	—
Obelia sp.	4	+	26	+	—	—	17	+	—	—	5	+	—	—
Phialidium sp.	—	—	2	+	—	—	—	—	—	—	1	+	—	—
Sarsia tubulosa (M. Sars)	—	—	1	+	—	—	—	—	—	—	1	+	45	+
Unidentified	2	+	—	—	—	—	15	+	—	—	—	—	—	—
Ctenophores:														
Pleurobrachia pileus (Müller)	—	—	1	+	—	—	—	—	—	—	—	—	—	—
Nemertines (pilidium)	—	—	—	—	—	—	—	—	—	—	3	+	—	—
Rotifers	930	10.0	1,523	5.4	229	0.8	124,670	80.8	10	+	1,514	6.4	2,802	6.8
Bryozoans (cyphonautes)	10	+	30	+	—	—	—	—	—	—	108	+	89	+
Molluscs:														
Littorina scutulata Gould (egg cases)	—	—	41	+	107	+	35	+	8	+	280	1.2	46	+
Gastropoda (veligers)	221	2.4	345	1.2	84	+	53	+	102	+	127	0.5	—	—
Pelecypoda (veligers)	716	7.7	1,008	3.6	228	0.8	322	+	22	+	694	2.9	1,929	4.7
Polychaetes (larvae)	1,370	14.8	685	2.4	—	—	62	+	891	1.7	547	2.3	205	0.5
Tardigrades	2	+	—	—	—	—	—	—	—	—	—	—	—	—
Cladocerans:														
Evadne nordmanni Loven	2	+	4	+	—	—	419	+	4	+	8	+	—	—
Podon leuckarti Sars	—	—	3	+	—	—	670	+	—	—	3	+	—	—
Unidentified	—	—	—	—	1,096	3.8	—	—	—	—	—	—	2,104	5.1
Ostracods	—	—	1	+	—	—	—	—	—	—	—	—	—	—
Copepods (late copepodites and adults):														
Acartia clausii Giesbrecht	8	+	783	2.8	—	—	3,087	2.0	2	+	47	+	—	—
A. longiremis (Lilljeborg)	17	+	723	2.6	—	—	336	+	110	+	148	0.6	—	—
Acartia spp.	79	0.9	4,571	16.2	—	—	4,498	2.9	45	+	2,852	12.1	—	—
Calanus linmarchicus (Gunnerus)	—	—	399	1.4	—	—	—	—	—	—	159	0.7	—	—
Centropages abdominalis Sato	—	—	--	—	—	—	—	—	—	—	9	+	—	—
Metridia sp.	2	+	155	0.0	—	—	—	—	2	+	111	+	—	—
Pseudocalanus minutus (Krøyer)	84	0.9	1,621	5.8	—	—	95	+	143	+	862	3.6	—	—
Tortanus discaudatus (Thompson and Scott)	1	+	16	+	—	—	—	—	—	—	4	+	—	—
Calanoids spp.	14	+	—	—	—	—	81	+	—	—	1	+	—	—
Oithona helgolandica Claus	486	5.2	687	2.4	—	—	981	0.6	469	0.9	514	2.2	—	—
Cyclopoids spp.	58	0.6	158	0.6	—	—	—	—	7	+	134	0.6	—	—
Harpacticoids spp.	58	0.6	14	+	—	—	34	+	2	+	21	+	—	—
Unidentified	—	—	—	—	10,422	36.5	—	—	—	—	—	—	9,201	22.4
Copepods (nauplii)	1,980	21.4	10,237	36.3	—	—	9,972	6.5	909	1.8	4,264	18.0	—	—
Cirripedes (nauplii)	2,334	25.2	4,041	14.3	10,261	35.9	6,994	4.5	48,067	93.9	9,714	41.1	13,706	33.4
Cirripedes (cyprids)	—	—	236	0.8	131	+	70	+	—	—	893	3.8	92	+
Cumaceans:														
Cummella vulgaris Hart	1	+	—	—	—	—	—	—	—	—	—	—	—	—
Amphipods:														
Corophiidae	—	—	1	+	50	+	—	—	—	—	—	—	—	—
Euphausiids (calyptopis)	—	—	—	—	—	—	—	—	—	—	10	+	—	—
Euphausiids (nauplii)	99	1.1	429	1.5	—	—	—	—	206	+	168	0.7	—	—
Carids (zoeae)	—	—	—	—	—	—	—	—	2	+	1	+	—	—
Brachyurans (zoeae)	—	—	16	+	—	—	—	—	—	—	7	+	—	—
Pagurians (zoeae)	—	—	—	—	—	—	—	—	2	+	—	—	—	—
Crustaceans (nauplii):														
Unidentified	—	—	—	—	5,955	20.8	—	—	6	+	1	+	10,418	25.4
Chaetognaths:														
Sagitta elegans Verrill	4	+	2	+	—	—	—	—	9	+	—	—	—	—
Echinoderms:														
Echinopleutei	4	+	32	+	—	—	—	—	1	+	19	+	—	—
Bipinnaria	—	—	—	—	—	—	—	—	—	—	3	+	—	—
Tunicates:														
Fritillaria borealis Lohmann	5	+	12	+	—	—	—	—	8	+	—	—	—	—
Oikopleura sp.	—	—	—	—	—	—	—	—	11	+	—	—	92	+
Tunicata (larvae)	—	—	—	—	—	—	107	+	2	+	—	—	—	—
Tunicata (eggs)	—	—	20	+	—	—	12	+	33	+	—	—	—	—
Unidentified invertebrate larvae	17	+	39	+	—	—	51	+	9	+	15	+	—	—
Unidentified invertebrate eggs	764	8.2	309	1.1	—	—	1,765	1.1	86	+	379	1.6	—	—
Fish larvae	—	—	—	—	—	—	—	—	1	+	1	+	—	—
Fish eggs	—	—	5	+	—	—	—	—	—	—	—	—	362	0.9
Total	9,272	—	28,177	—	28,563	—	154,346	—	51,169	—	23,630	—	41,091	—

[1]No sampling was done in the inner bay in 1965.
[2]June 1966 samples were not available for taxonomic breakdown.

vaceans, barnacle nauplii, cladocerans, and other small crustaceans. Chum salmon fry tended to eat more larger hard-shelled organisms and epibenthic organisms than did pink salmon fry. The food of pink and chum salmon fry at Traitors Cove in general was similar to that reported at Uala and Anapka bays on the east side of the Kamchatka Peninsula (Andrievskaya 1968), the San Juan area of northern Washington (Annan 1958), the Strait of Georgia in southern British Columbia (Barraclough 1967; Robinson et al. 1968), Chatham Sound off the northern coast of British Columbia (Manzer 1969), and Moser Bay of southeastern Alaska (Chamberlain 1906). In contrast, in Puget Sound epibenthic organisms (especially harpacticoid copepods) were more important than pelagic zooplankters to pink and chum salmon fry (Gerke and Kaczynski 1972).

Food Selection

Salmon fry in Traitors Cove did not eat the same kinds and sizes of zooplankters in the same relative numbers as they appeared in the samples of zooplankton, i.e., the fry fed selectively. Selective feeding in relation to sizes of prey and juvenile chum salmon has been reported by LeBrasseur (1969). The average size of the zooplankton eaten by the fish was greater than the zooplankton collected by the Clarke-Bumpus sampler (Table 5). A coarser net such as a no. 6 mesh (233 μm) would probably have collected the zooplankters that were usually eaten by salmon fry and would not have collected so many of the small forms that are seldom eaten such as tintinnids, rotifers, and others.

Selective feeding by pink and chum salmon fry was also demonstrated by the occurrence of certain food items relatively more often in the stomachs of fry (Tables 3, 4) than in the plankton samples (Table 8). Relatively more cladocerans, decapod zoeae, and larvaceans were eaten by salmon than appeared in the plankton samples. Another example of the marked disparity is the barnacle nauplii which were very abundant in most of the plankton samples (4 to 94% of the number of plankters) but constituted only 14% of the animals actually eaten by pink salmon and only 3% of the number of food items eaten by chum salmon.

The high incidence of larvaceans in the stomach samples, especially in the chum salmon, may be the result of selective feeding on a scarce but very visible plankter. Larvaceans, in particular *Oikopleura* spp., form mucous feeding nets which may increase the visibility of the larvacean to the salmon fry. Once learning to capture *Oikopleura*, the fry may prefer that food item.

Benthic and intertidal forms of mysids, cumaceans, isopods, amphipods, and insects were rare in the plankton samples and their presence in some of the stomachs shows that pink and chum salmon fry did on occasion feed in these ecological niches. This type of feeding behavior could not predominate at Traitors Cove because most of the shoreline is rocky and precipitous and offers little opportunity for benthic feeding.

Grazing Rate

The average number of zooplankters comsumed daily by a pink salmon fry in Traitors Cove was calculated from estimates of average stomach contents and evacuation rates. Stomachs of pink salmon collected from Traitors Cove estuary during daylight contained an average of 136 zooplankters. Stomach evacuation required 6 and 16 h at temperatures of 12.8°C and 8.5°C, respectively, although Brett and Higgs (1970) observed slower stomach evacuation rates at comparable temperatures in sockeye salmon fingerlings that had been fed a commercial pelleted food. The fry did not feed during darkness, which extended from about one-half hour after sunset to one-half hour before sunrise on cloudy or moonless nights. The duration of feeding at Traitors Cove when fry are present typically is about 16.5 h (range 15 to 18 h); the water temperature at 1 m ranges from 5° to 13°C.

Thus, it appears that fry would consume a volume of food required to fill their stomachs once a day at cooler temperatures (8.5°C) and four times a day at warmer temperatures (12.8°C). The number of zooplankters consumed daily would, therefore, range between 136 and 544 per pink salmon fry for temperatures that are normal during the time fry are in Traitors Cove. By the same line of reasoning, chum salmon would consume about 120 to 480 food items per fry per day in Traitors Cove.

Some insight into the availability of food for salmon fry at Traitors Cove was obtained by considering the abundance of plankton in relation to the feeding habits of the fry. For example, fry 39 mm long that were holding a position relative to the shore while feeding in a current of 11 cm/s were in effect grazing a cylindrical mass of water

at the rate of about 3.5 liter/min. Even at the lowest observed abundance of 1 zooplankter per liter (Table 5), each fry would theoretically encounter about 3.5 zooplankters per minute, which is slightly greater than the estimated feeding rate of 3 zooplankters per minute in floating aquaria at 10°C. At this rate of feeding, a single fry could fill its stomach in about 39 to 155 min and could therefore easily ingest zooplankters faster than they could be evacuated.

Abundance of zooplankton in the outer bay of Traitors Cove ranged from 4 to 563 organisms per liter (Table 7), and this was theoretically enough to satiate feeding fry as shown above. Furthermore, the abundance of zooplankton as estimated from Clarke-Bumpus samples did not decrease during the time that salmon fry were in the estuary. Therefore, we conclude that there was an abundant food supply in Traitors Cove for salmon fry. LeBrasseur et al. (1969), who conducted feeding experiments with wild juvenile pink and chum salmon in the Fraser River estuary in 1967 (an off-cycle year of pink salmon in the Fraser system), arrived at a similar conclusion for that area.

Carrying Capacity of Traitors Cove

Fry of pink and chum salmon emerged from the gravel of Traitors River at night, and most of them migrated to the estuary before dawn. Some of the fry, as evidenced by their size and the contents of their digestive tracts, lingered a few days in the stream where they fed on freshwater organisms. The tendency to linger and feed in freshwater, most pronounced for chum salmon, has been described by Mason (1974). After the fry left Traitors River, they gathered in schools close to shore and began feeding and migrating oceanward. The time spent in the estuary is unknown but was probably from a few days to a few weeks.

We estimated the abundance of pink and chum salmon fry in Traitors Cove by making counts each day along the shore from a moving skiff or by a mark-and-recapture technique. In 1965, the greatest number estimated from counts on any day was 7 million fry, but in 1966 the greatest estimate was under 1 million fry. The number of salmon fry in Traitors Cove in 1968 was estimated by mark and recapture to be 4 million ($\pm$1.3 million, 95% confidence limits). The mark-and-recapture estimate was made on a different annual fry migration than those covered by this study of feeding habits, but it strengthened our confidence in the visual estimates of fry abundance in 1965 and 1966.

It did not appear that the Traitors Cove estuary was overgrazed by wild fry at the time of this study. In 1966, zooplankton abundance was always greater than 1.0 zooplankter per liter, which would allow maximum feeding rates by fry. During May and June 1966, when 1 million fry were present, the average abundance was about 29 zooplankters per liter. In June 1965, abundance was 154 zooplankters per liter after 7 million fry passed through the estuary.

The number of fry that migrate through Traitors Cove each year is probably limited to less than 20 million by the productivity of the spawning grounds in Traitors River and Margaret Creek, the major salmon streams in the cove. We used stream survey data from Martin (1959) and applied a correction factor of 0.5 to correct for pools and stream bottoms of mud, sand, and bedrock to calculate 66,000 m^2 of spawning grounds—55,000 m^2 in Traitors River and 11,000 m^2 in Margaret Creek. These spawning grounds would yield about 7 million fry if they produced 100 fry per square meter or about 20 million fry if they produced 300 fry per square meter. Fry densities of 0.1 to 589 per square meter (average 250 fry per square meter) have been observed in Traitors River,[3,4] but these densities were in sections of the stream consistently favored by spawning salmon. Less favored areas were not sampled.

The installation of a hatchery or spawning channel in a drainage system such as Traitors River could potentially result in a production of 100 million fry annually, or 5 to 100 times the estimated production of wild fry. Available data are inadequate to determine the carrying capacity of Traitors Cove with certainty, but it is possible to make very speculative estimates based on the standing crop of zooplankton.

Before presenting the estimates of carrying capacity, we wish to cite 10 necessary assumptions (required because we lack knowledge of the ecology of estuarine nursery areas) and some of the factors which may invalidate the estimates.

1. Zooplankton abundance was the same in Behm Canal as in Traitors Cove. Plankton samples

[3]Mattson, C. R., and J. E. Bailey. 1966. Chum and pink salmon studies at Traitors Cove, September 1963 to September 1964. On file, Auke Bay Laboratory.

[4]Mattson, C. R., and R. G. Rowland. 1963. Chum salmon studies at Traitors Cove Field Station June 1960 to March 1963. On file, Auke Bay Laboratory.

were not collected outside Traitors Cove in Behm Canal. Several years later extensive plankton collections were made in open channels and several small adjacent bays of northern southeastern Alaska as a part of the 1972 MARMAP[5] investigation. Within the May 1972 samples, average zooplankton abundance was nearly twice as great at 14 outside stations as at 4 stations within bays. Therefore, our estimates of carrying capacity based on influx of zooplankton from Behm Canal would be conservative.

2. Salmon fry were the only predators on zooplankton. We ignored the requirements of all other planktivorous animals of the area. The requirement of local planktivores other than salmon are only qualitatively and poorly known. Herring were not seen in large numbers during the years of this food study. A school of herring entered the inner bay in 1967 while being fed on by a whale. We do not know how long these herring remained in Traitors Cove, but they were not conspicuous 2 wk after their entry.

3. Zooplankton concentrations were constant. We ignored the strong seasonality of reproduction and growth in the holoplankton and the fact that meroplankton may be present for only a limited time. We ignored the probability that some larval forms reach a life history stage where their behavior would make them unavailable to the salmon fry. We ignored natural mortality of larval forms other than from predation by salmon fry. Some of these factors would increase zooplankton concentrations while others would decrease them. In the absence of information on reproduction, growth, mortality, and life histories, we assumed these factors would balance so that the zooplankton concentration would be constant.

4. Distribution of the zooplankton was uniform. Physical and biological factors controlling the patchiness of zooplankton in estuaries and nearshore environments are poorly understood and not easily modeled.

5. All zooplankton were equally available, equally desirable, and of equal quality as feed for salmon fry. We ignored the size selectivity and preference for calanoid copepods shown in our own data. It is highly probable that the species of zooplankton vary in quality as food.

6. Salmon fry had a constant feeding requirement of 544 zooplankters per day. This is the highest of our estimates of pink salmon feeding rates and ignores variations in food requirements that would accompany variations in physical environment and physiological state.

7. No behavioral changes in either the salmon fry or zooplankton were induced by changes in densities, physical environment, or biological states.

8. The number of salmon fry was constant.

9. All the zooplankton would be utilized as food. If this actually occurred, no survivors would be left to produce new zooplankton crops or to replenish stocks of other resources that have planktonic larval stages such as herring, crabs, and shrimp.

10. Models of circulation in the estuary would be of the simplest type. We do not know the flushing rates in Traitors Cove or the potential of transport of zooplankton food to and from the bay by estuarine circulation.

Some additional assumptions peculiar to each estimate are described with each estimate. Only the outer bay is considered because fry in Traitors Cove appeared to move quickly through the inner bay and then spend a longer time in the outer bay.

Our first estimate of carrying capacity is based on standing stock of zooplankton in the top meter of water of the outer bay. Fry were in the outer bay in relatively high densities for about 30 days each year. The surface area of the outer bay is about 7.6×10^6 m^2, and the average density of zooplankters was estimated to be 24,000 per cubic meter or higher. The product of area and plankton density divided by 544 (the estimated maximal number of organisms consumed per day by pink salmon fry) results in a plankton stock equivalent to 335×10^6 fry feeding days. This estimate divided by 30 days expresses the food supply in fry months—11 million fry could feed for 1 mo on the standing stock of food in the surface meter of outer bay. This establishes a lower limit for the carrying capacity of Traitors Cove because it ignores saltwater entrainment by outflowing freshwater and the consequent addition of plankton from deeper water.

For our second estimate, we calculated the quantity of zooplankton that would be brought into the outer bay from Behm Canal each day by a combination of two factors: circulation due to freshwater runoff from Traitors River and circulation due to tidal action. Records of the U.S. Geological Survey indicate that discharge from Traitors River generally averages about 8 m^3/s in

[5]Marine Resources Monitoring, Assessment, and Prediction—program sponsored by National Marine Fisheries Service on a nationwide scale.

the spring when fry are migrating. Assuming an equal flow of seawater with plankton density of 24,000 organisms per cubic meter into Traitors Cove from Behm Canal and surface entrainment near the constriction, we calculated that 16.5×10^9 organisms would be brought daily into Traitors Cove by freshwater-driven circulation. Dividing the number of organisms by 544 (the high estimate of organisms eaten by one fry daily) yields a conservative estimate of 30 million fry that could be fed by an amount of food added daily by circulation. Although it is naive to assume that all of the plankton brought into Traitors Cove as a result of circulation would become available to the fry, the upwelling and thorough mixing that occur at the constriction between the two bays result in a continual resupplying of zooplankton to the upper meter of depth where grazing apparently takes place. Field observations did indicate that the largest concentrations of fry were consistently found in eddies near the constriction, lending some credence to the theory that upwelling of deep water created a favorable supply of food in this area.

The effects of tidal circulation and freshwater-runoff-driven circulation are often additive. Therefore, we calculated the influx of food organisms by tidal exchange. We assumed that the surface waters were flushed completely by the outgoing tide; that complete mixing of incoming water with water present occurred on each tide; and that all zooplankton in the upper meter had been consumed before the waters were mixed. The influx of new food can then be estimated from the tidal prism as

$$F = [T/V] \times P$$

where F is the net influx of new food organisms as zooplankters per cubic meter per tide; T is the volume of the tidal prism; V is the volume of the outer bay; and P is the density of zooplankton outside the bay. (We used $P = 24 \times 10^3/\text{m}^3$ because we assumed that abundance was the same outside the bay as it was inside.)

The resulting calculation assuming a mean tidal range of 4.11 m (McLain 1968) and a mean depth of 90 m gives for the net influx of organisms per tide:

$$F = \frac{4.11\ \text{m/tide}}{90\ \text{m}} \times 24 \times 10^3/\text{m}^3 = 1.09 \times 10^3$$

zooplankters per cubic meter per tide.

Only those in the upper meter are available, and since there are two tides per day, the calculated quantity of new food available to salmon fry per day is:

$$Q = 2 \times F \times [\text{area of bay}] \times 1\ \text{m} = 2\ \text{tides/day} (1.09 \times 10^3\ \text{zooplankton per cubic meter per tide}) \times (7.6 \times 10^6\ \text{m}^2 \times 1\text{m}) = 16.6 \times 10^9\ \text{zooplankters per day.}$$

This number will feed 30×10^6 fry per day (16.6×10^9 zooplankters ÷ 544 zooplankters per day per fry). The estimate is high because mixing is not complete, as implied by the calculations. By adding fry that could be fed from the effects of freshwater runoff to fry that could be fed by tidal action, we get an upper estimate of carrying capacity of 60 million fry.

The numbers of fry that could theoretically be fed by the two sources of zooplankton, i.e., standing crop in the surface water and plankton in the net circulation, are not strictly additive. Although some plankton in deep seawater would be continuously entrained upward to flow seaward on the surface, some would never reach the surface of the bay and a portion of the surface stock would be removed from the bay by outflow. Therefore, it would seem prudent to consider that populations numbering more than 30 million pink and chum salmon fry might cause reduced growth of fry (because of the competition for food). Also, such large populations might stimulate a more rapid migration of fry through the estuary to areas where food organisms were more abundant.

On the basis of available spawning grounds, it seems unlikely that Traitors Cove has ever had to support more than 20 million pink and chum salmon fry, although it is possible that 11 to 60 million fry could be supported in years when food abundance equaled or exceeded that observed in 1966. The release of 50 to 100 million additional hatchery fry into this estuary would probably exceed the carrying capacity of the area. Competition for food, especially if zooplankton production were lower than average, and increased potential infection by disease, parasitism, and predation could theoretically result in increased mortality, slower growth, or accelerated movement of fry out of the estuary. Further, a great increase in numbers of salmon fry in Traitors Cove could deplete planktonic food and planktonic larvae required to support other fisheries. We have used Traitors Cove to discuss carrying capacity of estuaries only because

observations on fry and food were available. We know of no plans for the operation of a hatchery in Traitors Cove. The discussion is merely intended to focus attention on an important factor to be considered in choosing sites and operating salmon fry hatcheries.

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EFFECTS OF TRAP SELECTIVITY AND SOME POPULATION PARAMETERS ON SIZE COMPOSITION OF THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, CATCH ALONG THE MAINE COAST[1]

JAY S. KROUSE AND JAMES C. THOMAS[2]

ABSTRACT

Information collected aboard commercial lobster boats along the Maine coast (1971-73) revealed, among other things, high numbers of sublegal lobsters (<81 mm carapace length) being handled by fishermen while sorting their catches. Throw-back ratios of illegal to legal lobsters (1.8 to 12.4:1) varied in association with lath spacing. Traps with spacings of 1⅝ to 1¾ inches accounted for markedly fewer sublegals than those traps with 1¼- to 1½-inch spacings.

Selectivity curves calculated for research traps with escape ports of 1½, 1⅝, and 1¾ inches and a trap escapement study demonstrate that a spacing of 1¾ inches is large enough to allow escapement of most sublegals yet small enough to retain legal lobsters. A regression of carapace length on carapace width shows that only an insignificant percentage of legal lobsters could physically squeeze through a 1¾-inch opening. Thus, results of this study led us to recommend that with a minimum legal length of 81 mm, traps should have 1¾-inch escape vents.

While riding aboard commercial lobster boats along the Maine coast (1971-73) to collect detailed catch and effort information, we frequently observed lobster fishermen sort and throw back from their traps excessive numbers of sublegal lobsters (<81 mm carapace length). When one considers that Maine lobstermen presently haul their traps more than 20 million times each year, the magnitude of this sorting becomes apprent. Lobstermen not only lessen the efficiency of their fishing operations by needlessly handling sublegal lobsters but they also inadvertently increase the lobsters chances of becoming a cull (missing claw[s]) or a victim to predatory fish while descending to the ocean floor (D. G. Wilder, pers. commun.), which in either case represents an economic loss to the industry.

A solution to this detrimental fishing practice became apparent to us after a cursory analysis of data from our earlier boat trips revealed an inverse relationship between lath spacing and numbers of sublegal lobsters. Templeman (1939) and Wilder (1945, 1948, 1954) also reported the same relationship based on size composition of catches from traps of various lath spacings. Although these Canadian scientists have long advocated the use of wider latch spacings to allow sublegals to escape, presently only Newfoundland has a lath spacing regulation of 1¾ inches.

Because of the management implications of this association between lath spacing and size composition of the catch, we undertook this investigation to quantitatively assess this situation with several independent approaches, namely: 1) selectivity curves; 2) trap escapement study; and 3) certain morphological dimensions of lobsters. Certain facets of this study were also valuable in corroborating some previously estimated population parameters such as natural mortality rates, sex ratios, and spawning stock structure and size.

These analyses have become increasingly important because we have recommended raising the legal minimum size from the present 81 mm ($3^3/_{16}$ inches) to 89 mm (3½ inches) carapace length. Then this study not only has application for the present situation, but also provides pertinent information for management of lobsters in the future.

METHODS

Samples from Commercial Gear

From 1971 through 1973, we spent 21 days riding aboard nine different commercial lobster boats (three boats were sampled more than once) from

[1]This study was conducted in cooperation with the Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-153-R.

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four coastal areas. These boats were selected on a nonrandom basis because not all vessel-captains could or would accommodate us, nor could we reallocate committed time from our ongoing surveys of the natural lobster population and the commercial catch. While aboard these vessels we recorded the following: 1) numbers of sublegal and legal lobsters for each trap haul; 2) carapace length and sex of lobsters from a systematic sample of the catch, along with the corresponding measurements of lath spacings in these traps; 3) time expended in actual fishing as well as fishing time for each trap (number of set-over-days); 4) whether the fisherman was hauling one trap at a time (singles) or two attached traps with one buoy (pairs), or three or more attached traps (trawls) with two buoys, one at each end of the string; and 5) amount and kind of bait used.

Carapace lengths were measured in millimeters from the posterodorsal edge of the eye socket to the posterior margin of the carapace. In most cases, we attempted to measure all the lobsters in every *n*th trap (depended on whether traps were set as singles, pairs, or trawls); however, sometimes with two samplers, we were able to measure and record all the lobsters in each of the total number of traps hauled for the day.

Length compositions of the catches for each boat trip were used to calculate what we refer to as retention curves. These curves are simply an accumulative percentage of the number of lobsters by 1-mm carapace increments that were retained in the systematic sample of the traps hauled, along with measurements of the lath spacings of these traps. Because lath spacings were not uniform for each of the traps hauled per boat, the term "modal spacing" was used to imply that at least a majority of the traps per boat had a spacing more frequently measured by us than any other.

Samples from Research Gear

Since 1968 we have recorded the carapace length, weight, sex, condition (hard or soft shell, lost appendages) of individual lobsters caught in our research traps. Our research gear consisted of: 1) modified wooden traps, with plastic escape vents of 1½, 1⅝, and 1¾ inches (Figure 1), and 2) 1×1 inch wire meshed traps especially designed to catch sublegal lobsters. The modified commercial gear was fished from July 1972 through 1973, while the wire traps were used since 1968.

We also conducted a trap escapement study

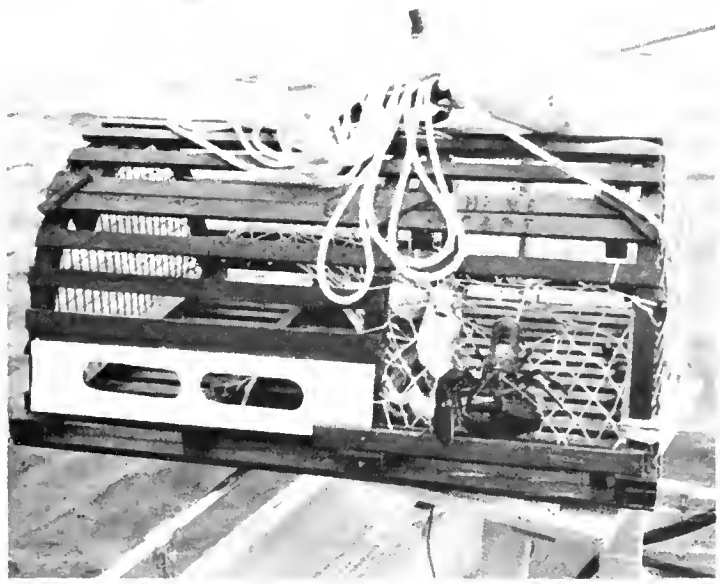

FIGURE 1.—Modified commercial lobster trap equipped with a plastic escape vent.

whereby lobsters of known sizes were placed in wooden traps with vents of 1¼, 1½, 1¾, and 2 inches. Because the heads or entrances were sealed, any escapement should have been accomplished between the laths. Through a 2-wk period traps were usually checked daily for escapement.

Comparison of Samples from Commercial and Research Gear

Following the methodologies of Beverton and Holt (1957), Pope (1966), and Gulland (1969), we calculated selectivity curves which were based upon carapace lengths of lobsters retained in the commercial gear with modal lath spacings of 1¼, 1⅝, and 1¾ inches. These data were proportioned with the same range of lengths retained in the 1×1 inch wire meshed research traps. Both sets of data, commercial and research, were weighted by trap-haul-set-over-days (THSOD). These comparisons were from the same general area, but not with the same groups of traps nor necessarily during the exact same period of time.

In addition, we used the cited methods to make selectivity determinations from the modified commercial traps that had specific lath spacings of 1½, 1⅝, and 1¾ inches. These spacings were proportioned with the data from the wire research traps (1×1 inch mesh). In this case, the modified commercial and wire research traps were fished

simultaneously with the same spatial and temporal arrangements.

Body Proportions of Lobsters

To circumvent the spatial and temporal problems between commercial (boat trips) and research gear to a certain extent, we took body measurements of 217 lobsters, specifically carapace length, width, and height for sizes between 70 and 90 mm carapace length. These measurements should enable us to reach a more objective determination concerning the retention and escapement potential of various sized lobsters through different lath spacings.

RESULTS AND DISCUSSION

Samples from Commercial Gear

For the 21 boat trips with commercial fishermen, we counted their entire catch of 12,071 lobsters of which there were 2,311 legal lobsters (Table 1). This catch resulted from 4,026 trap hauls for a catch of 0.57 legal lobsters per trap haul or 0.22 legal lobsters per THSOD.

There are omissions in some of the data categories per boat trip because the sampling procedure evolved from successive trips aboard vessels; thus samplers learned by experience and observation what could or could not be accomplished under different physical conditions in each vessel. Nevertheless, subtotals can be gleaned from the boat trips with the more complete information. For example, there were 156 berried and/or "V"-notched females from 18 of the 21 boat trips. Even though this is a subtotal, it is an alarmingly low number. Of course, such things as season of year, area fished, and availability of berried females could affect this number. Still, we continue to be concerned about the possibility of a precarious limit of an adequate spawning stock (Thomas 1973; Krouse 1973).

The percent females is another estimate related to the reproduction potential of the exploited population of lobsters. For those lobsters that we measured and determined sex, 52.9% were females (sublegal and legal). This estimate is close to the 49.0 to 53.8% females that we estimated by year (1966-73) from the survey of the commercial (legal lobsters) and natural (mostly sublegal) population of lobsters.

These estimates are in conflict with the expectation that there should be more males than females in the commercial catch because berried and/or V-notched females must be returned to the ocean by law. Again, this situation points to a low number of sexually mature females.

To reach definite conclusions concerning the stock-progeny-recruitment relationships, we should follow the procedures of Beverton and Holt (1957) and Ricker (1958). This will be possible with continued support of this program and continued surveys on the commercial and natural populations of lobsters.

Length Frequencies

We measured the carapace length of 3,595 lobsters; the sex ratio (male:female) was 1:1.2. A histogram of these length frequencies (Figure 2) portrays the same situation that we have demonstrated from the commercial and natural surveys. That is, there are relatively large numbers of lobsters (2,937 or 81.7%) under the legal minimum size, while there are considerably fewer lobsters (658 or 18.3%) at and above the legal minimum size of 81 mm ($3^3/_{16}$ inches) carapace length. In fact, 94.0% of the legal catch is constrained within a ½-inch size range immediately above the legal minimum size. These conditions confirm the high exploitation rate of 0.86 that can be calculated from Thomas (1973).

Considering the modal lath spacings of traps used in each boat trip, there is a marked difference in the number of sublegal- and legal-sized lobsters.

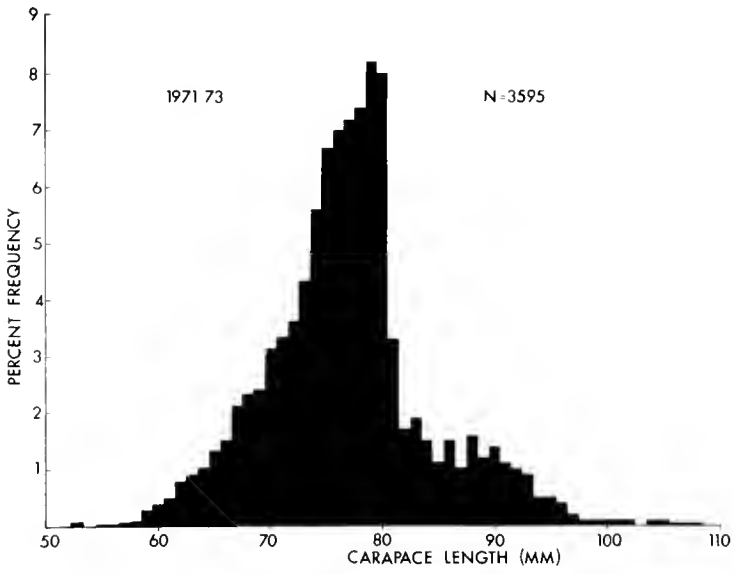

FIGURE 2.—Length-frequency distributions of lobsters caught in traps several lath spacings) used by commercial fishermen (1971-73).

TABLE 1.–Catch and effort statistics of 21 daily lobster catches for nine commercial fishing boats, September 1971 through September 1973.

Area / Boat trip (Date of trip)[1]	Catch, counted: Total no.	Illegals: legal	Females: Berried non V notch	Females: Berried V notch	Females: Non-berried V notch	Females: Sub-total	Catch, measured: Total no.	Catch, measured: Females (%)	Catch-effort: Legals per trap haul	Catch-effort: Sub-legals per trap haul	Catch-effort: No. of trap hauls	Catch-effort: No. of set-over-days	Catch-effort: Boat hours	Trap specifications: No. of par-lors	Trap specifications: Modal vent spacing (inches)	Bait: Amount (bu)	Bait: Type
Boothbay:																	
1. (Sept. 71)A	434	10.4:1	0	3	1	4	—	—	0.29	2.97	132	3	7.5	1	1.25	2	redfish
2. (Oct. 71)A	298	8.3:1	0	2	4	6	55	61.8	0.27	2.22	117	5	6.0	1	1.25	2	redfish
3. (Aug. 72)B	642	2.4:1	0	2	2	4	144	46.5	0.56	1.37	329	2	6.5	1	1.62	—	—
4. (Aug. 72)C	109	8.1:1	0	0	1	1	109	39.4	0.41	3.31	29	3	3.0	1	1.25	1	flatfish
5. (Aug. 72)B	696	2.6:1	0	3	3	6	134	57.5	0.62	1.61	310	—	6.5	1	1.62	5	redfish
6. (Sept. 72)A	428	12.4:1	0	3	0	3	204	52.0	0.13	1.58	248	3	7.3	1	1.25	2	redfish
7. (July 73)B	624	1.8:1	0	5	7	12	136	56.6	0.74	1.28	303	4	7.0	1	1.62	6	redfish and menhaden
8. (Aug. 73)B	637	2.9:1	0	2	25	27	128	50.8	0.65	1.79	250	2-4	8.0	1	1.62	4	redfish
9. (Sept. 73)A	340	8.7:1	0	0	6	6	245	57.6	0.27	2.32	129	5	7.0	1	1.25	2	redfish
Medomak:																	
10. (Sept. 71)D	1,247	5.6:1	0	3	12	15	—	—	0.76	4.18	249	3-4	12.5	1-2	—	6	redfish
11. (Nov. 71)D	1,606	3.5:1	4	3	9	16	347	[2]	1.34	4.62	267	6	11.0	1-2	—	6	redfish
12. (Sept. 72)D	1,234	4.5:1	3	6	8	17	260	57.7	0.96	4.22	235	4	12.0	1-2	1.25-1.50	6	redfish
13. (Sept. 73)D	926	3.6:1	0	4	12	16	56 / 145	[2] / 59.3	1.32	4.70	151	3	7.3	1-2	1.25-1.50	3	redfish
Jonesport:																	
14. (July 72)E	277	7.2:1	—	—	—	—	57	54.0	0.17	1.23	198	—	8.0	—	—	—	—
15. (Aug. 72)F	244	5.8:1	—	—	—	—	43	44.2	0.24	1.40	149	—	7.0	—	—	—	—
16. (Sept. 72)G	291	3.3:1	—	—	—	—	72	44.4	0.45	1.49	150	—	—	—	1.25	—	—
Newagen:																	
17. (Aug. 72)H	441	11.6:1	1	1	5	7	441	51.5	0.27	3.04	131	1-2	—	1	1.13-1.25	2	herring
18. (June 73)H	186	8.3:1	0	0	4	4	180	54.1	0.18	1.45	112	2-5	5.0	1	1.13-1.62	2	pollock
19. (July 73)H	329	4.9:1	0	5	1	6	327	51.7	0.43	2.05	130	1	5.0	1	1.13-1.62	1	herring
Cundy's:																	
20. (Sept. 72)I	554	9.7:1	0	0	4	4	232	54.7	0.30	2.91	171	2-3	7.3	1-2	1.75	4	redfish
21. (Sept. 73)I	528	3.2:1	0	2	0	2	280	51.4	0.53	1.69	236	2-3	7.3	1-2	1.75	4	redfish
Total	12,071	4.2:1	[3]8	[3]44	[3]104	[3]156	[3]3,595	[3]52.9	0.57	2.39	4,026	[3]1-6	[3]141.2	[3]1-2	[3]1.13-1.75	[3]58	

[1]Letters (A, B, etc.) represent boat trips with the same or different fishermen.
[2]Sex not determined.
[3]Data omissions.

For example, the catches of boat trips numbered 3, 5, 7, 8, 20, and 21 (modal lath spacings of $1^{5}/_{8}$ or $1^{3}/_{4}$ inches) consisted of a low number of sublegal lobsters compared to the high number of sublegals in catches of boat trips numbered 2, 4, 6, 9, 17, 18, and 19 (modal lath spacings of $1^{1}/_{4}$ to $1^{1}/_{2}$ inches) (Table 2).

Effects of Throw Backs on the Fishery

The throw-back ratios of illegal (sublegal plus berried and/or V-notched females) to legal lobsters which ranged from 1.8 to 12.4:1, confirmed our earlier observations that a considerable number of lobsters are being handled needlessly (Table 1). It is not difficult to envision sublegal, V-notched, or berried female lobsters spending a portion of their lives airborne. One of the important considerations in this situation is whether these lobsters suffer a higher natural mortality than those lobsters less than 51 mm (2 inches) carapace length which are seldom caught because of their possible secretive behavioral patterns and the selectivity of lobster traps. However, we might reach some tentative conclusions from the lengths of lobsters collected in the present study along

TABLE 2.—Length-frequencies by 1-mm increments for lobsters collected in 21 commercial boat trips, September 1971 through September 1973 (successive boat-trip numbers are identical to those in Table 1).

Carapace length (mm)	Successive boat trips																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Totals
≤59	[1]	—	—	2	—	—	—	—	1	[1]	—	—	—	—	—	—	9	4	11	—	1	28
60		—	—	—	—	—	—	—	—		—	1	—	—	—	—	5	1	5	1	1	14
61		—	1	—	—	2	1	—	2		2	—	1	—	—	—	4	1	4	—	—	18
62		1	—	2	—	1	—	—	3		—	1	—	—	—	2	10	7	2	1	—	30
63		2	—	1	—	1	—	—	1		—	1	1	3	—	2	9	3	6	3	—	33
64		—	—	1	1	2	—	1	2		2	1	1	2	3	—	8	2	10	1	—	37
65		—	—	1	—	4	—	—	3		2	3	1	—	3	2	10	6	9	1	—	45
66		1	—	2	—	6	—	1	10		2	—	2	1	1	1	10	3	12	3	—	55
67		—	—	4	—	4	1	—	5		3	3	4	1	1	1	23	6	18	1	—	75
68		1	1	4	—	5	—	1	2		7	5	2	3	4	2	15	10	16	5	—	83
69		6	1	3	—	3	2	1	12		2	3	6	3	2	3	14	9	10	6	—	86
70		1	—	7	—	4	1	—	8		11	13	9	1	4	2	22	7	14	5	3	112
71		2	2	2	1	8	1	2	8		13	8	10	—	2	—	21	8	13	8	8	117
72		5	1	6	1	9	1	2	12		10	7	3	1	1	3	20	11	15	11	9	128
73		—	2	7	3	7	4	4	21		16	6	6	2	5	8	20	6	14	15	10	156
74		7	2	2	7	18	10	6	9		11	21	10	1	1	1	33	9	18	20	16	202
75		3	7	8	11	20	9	6	14		29	14	14	1	1	6	29	12	22	23	11	240
76		5	11	7	11	14	10	7	14		29	18	15	3	3	5	34	13	10	20	22	251
77		2	13	8	13	11	14	8	23		23	15	13	2	2	—	35	10	14	21	31	258
78		2	15	6	12	23	10	12	18		31	20	15	2	2	7	11	14	15	23	29	267
79		6	13	11	14	16	19	18	13		31	31	20	1	1	1	27	11	14	17	29	293
80		2	17	5	14	19	7	14	19		33	32	15	3	1	3	30	7	10	18	40	289
81		1	12	7	5	8	9	3	10		12	7	11	—	—	4	3	2	8	3	15	120
82		2	4	2	3	1	5	4	2		5	3	6	1	—	1	4	1	5	3	8	60
83		1	10	1	8	1	3	5	7		3	2	2	2	—	1	6	2	9	2	5	70
84		—	3	2	3	1	5	5	4		7	2	4	4	1	—	5	2	5	—	1	54
85		—	5	2	2	2	3	4	—		1	5	4	1	—	—	—	1	2	2	6	40
86		2	2	—	4	5	2	4	2		4	4	6	3	—	4	2	—	2	2	7	55
87		—	4	—	1	1	5	1	1		2	4	1	1	—	—	4	1	4	1	6	37
88		—	3	—	4	2	4	5	5		8	4	4	—	—	1	2	2	5	3	5	57
89		—	3	1	2	1	3	3	2		9	1	4	3	—	1	1	1	3	3	2	43
90		1	1	2	2	2	2	2	3		11	3	2	3	—	3	4	—	4	2	5	52
91		1	2	1	3	1	2	4	—		5	5	—	—	1	—	1	1	5	2	4	38
92		—	2	—	1	—	1	2	1		5	3	2	—	—	2	2	2	5	2	4	34
93		—	2	—	3	2	2	2	—		3	2	1	1	2	—	5	1	3	3	1	33
94		—	2	—	—	—	—	—	2		6	2	2	1	—	—	—	—	1	—	—	16
95		—	2	—	1	—	—	—	1		3	2	3	1	—	—	1	1	1	—	1	17
96		—	—	—	1	—	—	—	1		2	2	—	5	—	1	—	—	1	—	—	13
97		—	—	—	1	—	—	—	1		—	1	—	1	2	—	1	—	—	—	—	7
98		—	—	—	—	—	—	—	—		—	1	—	—	—	1	—	1	1	—	—	4
99		—	1	—	—	—	—	—	—		—	—	—	—	—	1	—	2	—	—	—	4
100		—	—	—	—	—	—	—	1		1	1	1	—	—	—	—	—	1	—	—	5
101		—	—	—	—	—	—	1	—		—	—	—	—	—	2	—	—	—	—	—	3
102		—	—	—	—	—	—	—	—		—	1	—	—	—	—	—	—	—	1	—	2
104		—	—	—	—	—	—	—	—		—	1	—	—	—	1	—	—	—	—	—	2
105		—	—	1	—	—	—	—	1		1	—	—	—	—	—	—	—	—	—	—	3
106		—	—	—	—	—	—	—	—		1	—	—	—	—	—	—	—	—	—	—	1
107		1	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	1
108		—	—	—	—	—	—	—	—		—	1	—	—	—	—	—	—	—	—	—	1
≥110		—	—	1	2	—	—	—	1		1	—	—	—	—	—	1	—	—	—	—	6
Totals		55	144	109	134	204	136	128	245		347	260	201	57	43	72	441	180	327	232	280	3.595

[1]No lengths taken.

with those from the commercial and natural surveys (Thomas 1973; Krouse 1973). The commercial survey shows that about 6% of the yearly catch are culls (one or both claws missing). Because most of the legal catch is recently recruited, this may indicate that frequent removal from traps of sublegal lobsters is, in part, responsible for this percentage of culls in the commercial catch. This could occur because the claws of those sublegals might grasp laths, knitted heads and parlor entrances, hands of fishermen, and the like. When such lobsters are pulled from the traps by fishermen, the claws are occasionally broken off. Another contributing factor might be that sublegal and legal lobsters sometimes extrude their claws through the lath spacings as the trap is hauled aboard the vessel. In this way, claws could be broken off. The design of the proposed "vented" trap, discussed later, takes this situation into consideration.

In order to evaluate more fully the possibility of a higher natural mortality due to handling, we used three independent approaches as follows:

1. Our observations aboard vessels show that the percentage of culls of sublegals is between 5 and 10%. This might indicate that natural mortality has not increased due to handling because of the similarity of the percentage of culls in the sublegal and legal size range of lobsters. Autotomy of the lobster could also confound the percentage of culls; however, we theorize that this particular percentage should not be different from the sublegal to legal sizes that we are studying.
2. Another insight on the effect of natural mortality would be the length frequencies of the sublegal lobsters caught by research gear in the sampling of the natural population (Figure 3), as well as the length frequencies from sampling aboard commercial vessels (Figure 2), although gear selectivity is a factor in this case. We should expect a higher mortality due to handling to show a significant decline in the number of sublegal lobsters as the size range increases by 1-mm increments from 70 (fully vulnerable size) to 81 mm (legal minimum size). Then the number of lobsters at, say, 80 mm should be less than those at 70 mm, not only due to the higher incidence of handling this larger size, but also because of the natural mortality that would occur without handling. These numbers at the specific sizes do not show this decline that could be attributed to a higher mortality due to increased handling (Figure 3).
3. As a supplement to the incidence of handling lobsters and the resultant natural mortality, we feel that our observations on the storage of lobsters in "pounds" (this procedure is described in Thomas 1973) might give information on the amount of natural mortality in the natural population and that mortality due to handling. The pound owners, stocking at the rate of one to two lobsters per square foot, tell us that a reduction of around 5% in numbers is normal for legal lobsters stocked to those reclaimed 3 to 5 mo later. Under these adverse conditions of crowding and handling in the pound as opposed to the situation in the natural environment, we infer that the annual natural mortality is low in the ocean (5 to 15%) and that handling has a minimal effect.

   The loss in lobster pounds is sometimes much higher than 5%, but in most of these situations the higher loss can be attributed to disease, adverse environmental conditions, and escapement.

Despite these speculative premises concerning the negligible effects of handling on natural mortality, the fishermen should still eliminate this needless sorting of large numbers of sublegal lobsters to reduce: 1) the time spend sorting sublegal from legal lobsters in traps, and 2) the eventual number of culls in the legal catch. Culls not only lessen the total poundage of the commercial catch but possibly the growth rate of culls may be slower than that of nonculls; Stewart and Squires (1968) suggest that molting of unduly stressed lobsters may be inhibited. The section on selectivity will

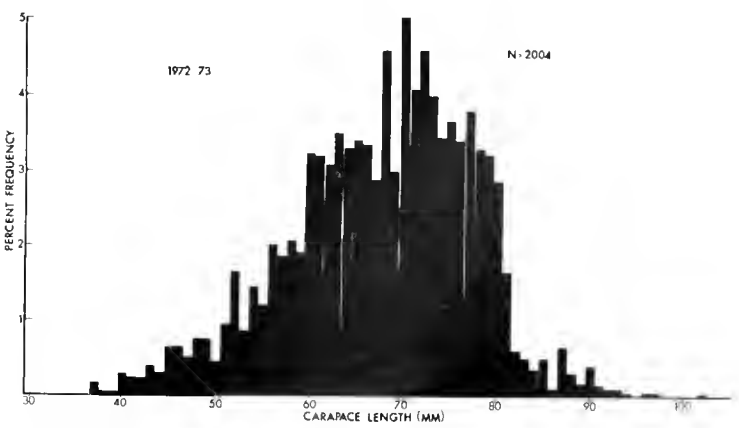

FIGURE 3.—Length-frequency distributions of lobsters collected with wire traps (1×1 inch mesh) at Boothbay Harbor (1972-73).

demonstrate the potential benefit of proper lath spacing.

Retention Curves

The accumulative length frequencies by 1-mm increments from two selected boat trips reflect a characteristic sigmoid curve (Figure 4). Snedecor (1956) and others caution that although these curves are characteristic of normal distributions, other types of distributions could result in a sigmoid curve. For our purposes, we assume that these data represent normal distributions.

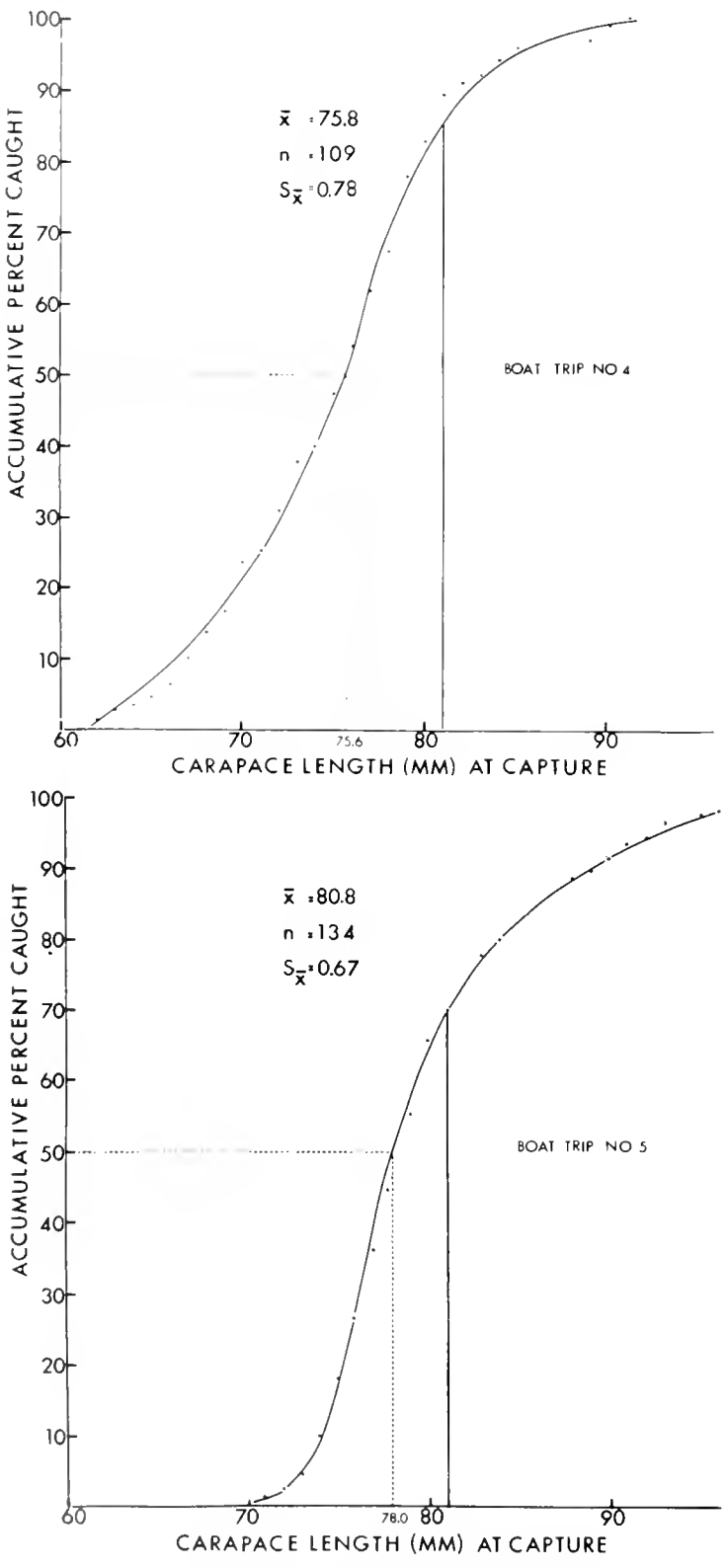

FIGURE 4.—Retention curves for two commercial boat trips (refer to boat trips 4 and 5 in Tables 1 and 2) in Boothbay Harbor (1972). Boat trips 4 and 5 had modal vent spacings of 1¼ and 1⅝ inches, respectively.

These curves are interesting in themselves because the 50% accumulative point demonstrates the influence of different lath spacings on the size, composition of the catch. For instance, boat trips 4 (1¼-inch vent) and 5 (1⅝-inch vent) had 50% accumulative points of 75.6 and 78.0 mm, respectively; thus demonstrating that traps with 1¼-inch vents are more selective for smaller lobsters (85% of catch ≤81 mm) than traps with 1⅝-inch vents (70% of catch ≤81 mm); while we are not advocating using these curves in place of selectivity curves, however we do suggest that these "retention curves" could be used as a quick, preliminary approximation of the influence of different lath spacings (gear selectivity) on the size composition of the catch in a trap fishery.

Selectivity Curves

Based upon the length composition of our catches with modified commercial traps equipped with escape ports (plastic vents) of 1½, 1⅝, and 1¾ inches and the 1×1 inch wire meshed traps, we calculated selectivity curves in accordance with the methodology of Beverton and Holt (1957). These catch data by 1-mm increments were weighted by THSOD and then the resultant values for each of the three vents (lath spaces) were proportioned with those of the wire traps over the same range of carapace lengths.

Traps with the same lath spacings had similar selectivity curves for the 1972 and 1973 catches while conspicuous differences are evident between the various size vents (Figure 5). In both years the 1½-inch vent was selective for the smaller sizes (50% retention ranged from 68.2 to 68.6 mm carapace length), the 1⅝-inch vent for the intermediate sizes (50% retention ranged from 71.4 to 73.5 mm carapace length), and the 1¾-inch vent for larger sizes (50% retention ranged from 75.4 to 78.8 mm carapace length). Contrary to most selectivity studies the important consideration in this study is not the mean selection length (50% point at which half the lobsters escape and half are retained); but rather, the proximity of the curve to the minimum legal size (81 mm carapace length) and whether or not the 100% retention point occurs below or above the minimum legal size. According

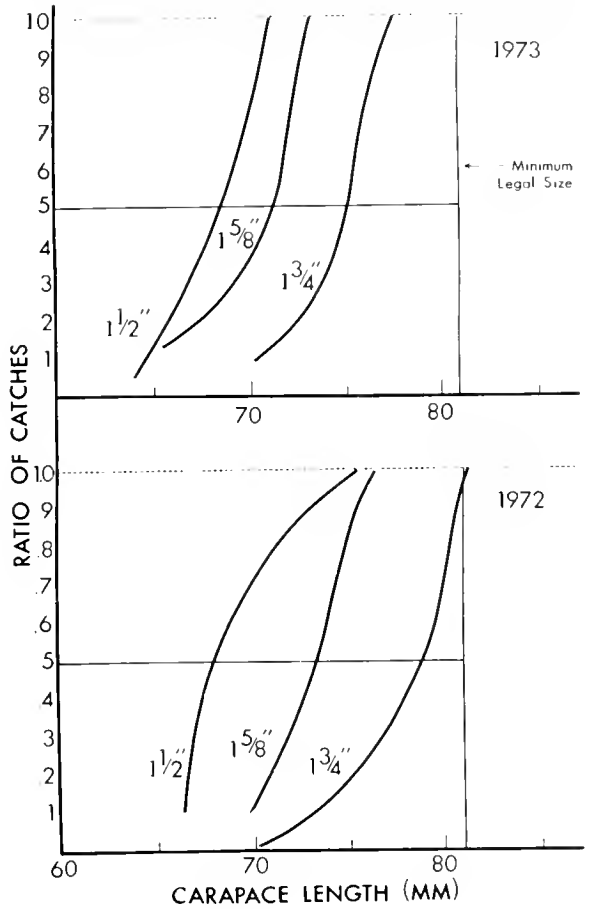

FIGURE 5.—Selectivity curves for each of the three vent sizes (1½, 1⅝, and 1¾ inches) of the modified commercial traps compared to wire (1×1 inch mesh) traps for 1972 and 1973.

to the selectivity curves, all three vents would prohibit the escapement of legal-sized lobsters. However, the 1¾-inch curve falls closer to the 81-mm line, thus demonstrating that this size vent allows a greater percentage of sublegal lobsters to escape than the 1⅝- or 1¼-inch vents.

Effects of Vent Size on Trap Efficiency

Catches with modified commercial traps reveal an inverse relationship between vent size and the ratios of sublegal to legal lobsters (Table 3). Overall catches with traps having a 1¾-inch vent always consist of more legal than sublegal lobsters while this size composition is reversed in the catches from traps with smaller vents. This further substantiates our contention that excessive handling of short lobsters in the lobster fishery can be minimized with the addition of a 1¾-inch vent to all lobster traps.

Throughout this study, traps with 1⅝- and 1¾-inch vents not only retained fewer sublegal lobsters but seemed to capture proportionally more legal-sized lobsters than did those traps with 1½-inch vents. To assess this situation, we calculated separate catch-effort values (numbers of lobsters per THSOD) for legal-sized and all-sized lobsters combined for each of the three vent sizes (Figure 6). Indeed, our data indicate that traps with larger vents (1⅝ and 1¾ inches) are more successful in retaining greater numbers of legal lobsters than traps with smaller vents. However, because of our limited field sampling, we cannot validly conclude that this disparity in efficiency between vents is conclusive evidence, but rather that our data strongly suggest this possibility.

TABLE 3.—Ratios of sublegal to legal lobsters captured with wire (1×1 inch mesh) and modified commercial (1½-, 1⅝-, and 1¾-inch vents) lobster traps, 1972 through 1973. Actual numbers of sublegal and legal lobsters appear in parentheses.

	Vent size (inches)			
Year	1 × 1 (wire)	1½	1⅝	1¾
1972	11.73:1 (962:82)	3.94:1 (71:18)	2.60:1 (78:30)	0.75:1 (21:28)
1973	28.09:1 (927:33)	5.86:1 (164:28)	1.44:1 (133:92)	0.76:1 (104:136)

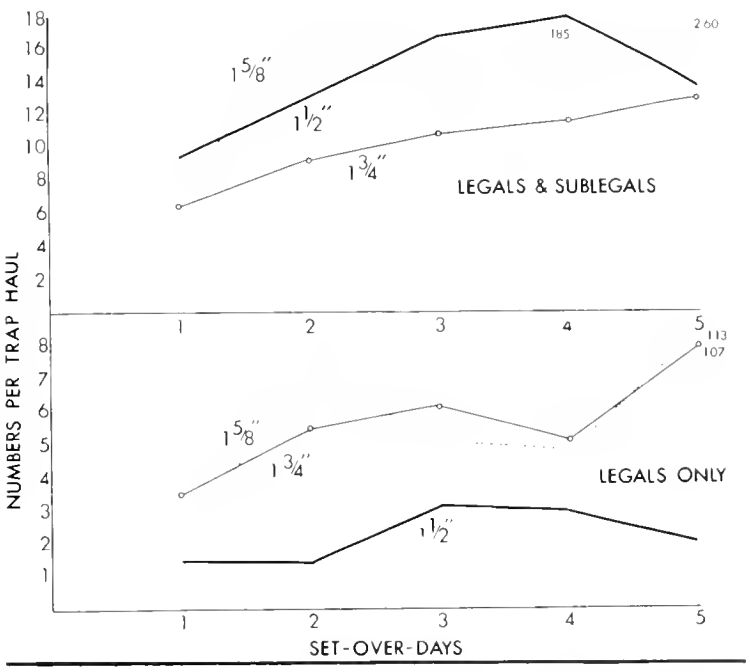

FIGURE 6.—Comparisons of the number of lobsters (legals, sublegals, and legals combined) per trap-haul-set-over-day for modified commercial traps with vents of 1½, 1⅝, and 1¾ inches (1972-73).

Body Proportions of Lobsters

The escapement of lobsters of given sizes from traps with varying lath spacings depends upon certain morphological dimensions such as carapace length, width, and height. We contend that the width of the carapace is more important than the height because we observed in the laboratory that

lobsters, attempting to escape through different lath spacings, would twist on their sides when encountering a tight fit between laths. This, coupled with the fact that the width is always smaller than the height for any carapace length, led us to the opinion that the relationship between carapace length and width in association with lath spacing is the important consideration for gear selectivity studies. We calculated the regression of carapace length (X) on width (Y) for 217 lobsters (114 females and 103 males) by the method of least squares. The calculated equation was $Y = -4.367 + 0.649X$ (Figure 7). Data for sexes were combined because analysis of covariance on the regression coefficients (Steel and Torrie 1960) showed that carapace length-width ratios of males and females did not differ significantly.

According to this relationship, lobsters at the minimum legal size of 81 mm carapace length would be expected to have a mean carapace width of 48.2 mm + 0.18 with individual widths within the 95% prediction interval ranging from 45.6 to 50.9 mm. The magnitude of these measurements relative to a 1¾-inch (44.5-mm) lath spacing suggests that only a very small percentage of legal-sized lobsters might escape through that size vent.

We should mention that some compression of the shell, particularly if the lobster is newly molted, is possible as a lobster struggles to get through the lath spacing of a trap. However, based upon our laboratory observations, we would not expect this compression to exceed 2 to 3 mm for soft-shelled lobsters (1 to 2 wk since ecdysis) and 1 mm for a hard-shelled lobster. Because this soft-shelled condition is of rather brief duration and the frequency of trap hauls is greatest during the shedding season (a shorter period of time for escapement), these situations should minimize escapement.

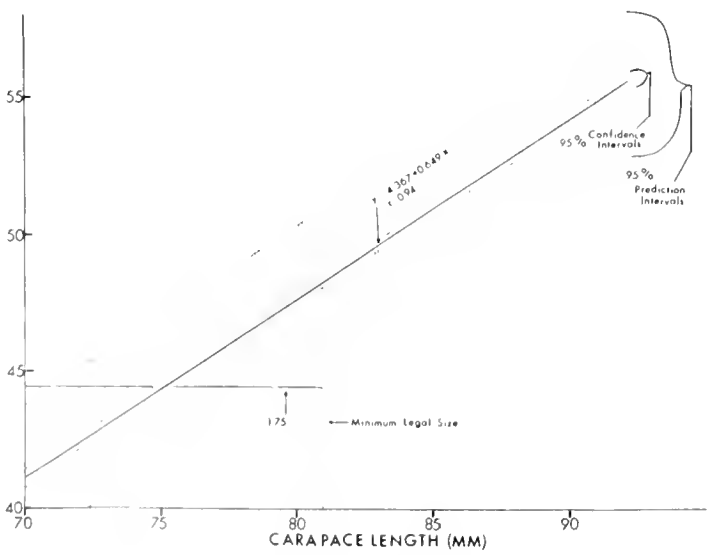

FIGURE 7.—Carapace length-width relationship for lobsters with 95% confidence and prediction intervals.

Trap Escapement Study

Retention curves, based on the escapement of lobsters of known lengths from traps with lath spacings ranging from 1¼ to 2 inches, graphically display the pronounced effect escape vent size has on lobster escapement (Figure 8). Retention of sublegal lobsters was high for the 1¼- and 1½-inch traps while most sublegals were able to escape from traps with the 1¾- and 2-inch vents. With the present minimum size of 81 mm (3 3/16 inches), a 2-inch vent would be unsatisfactory as many legal lobsters could escape, whereas escapement of legals through a 1¾-inch vent would be extremely minimal. Although the curve for the 1¾-inch vent did show some escapement, we believe this escapement is exaggerated by the methodology (plotting midpoints) employed in the derivation of this curve. This contention is further substantiated by the fact that only one of seven lobsters with a carapace length of 82 mm escaped and there was no escapement for lobsters larger than 82 mm.

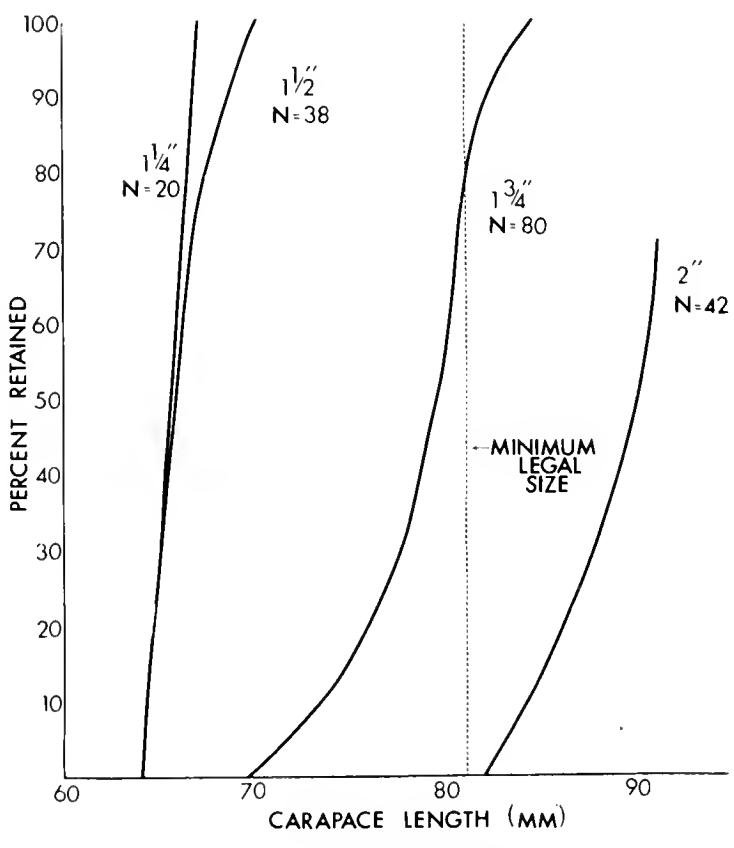

FIGURE 8.—Retention curves for lobsters placed in modified commercial traps with 1¼-, 1½-, and 1¾-, and 2-inch vent dimensions.

RECOMMENDATIONS

Based on the foregoing analysis of the effects different lath spacings have on the size composition of lobster catches, we recommend that all lobster traps fished along the Maine coast have an escape vent of 1¾ inches. Of course, if the minimum legal size (81 mm) is increased then the vent size should be altered accordingly.

We emphasize that it is not necessary for the entire trap to consist of the desired lath spacing; but rather, only one lath spacing either on the side or end (preferably near the bottom) of the parlor section of the trap. The remaining laths could be spaced at the fisherman's discretion.

We believe an escape port (vent) fabricated from some type of durable material and manufactured to our specifications could be incorporated into any conventional lobster trap (Figure 1). Merits of this vent would be: 1) easy installation in both new and old traps without requiring drastic modification; 2) modest cost to the fishermen; and 3) retention of its original dimensions over time (unlike wooden laths which eventually wear, causing a larger opening, thus permitting escapement of legal lobsters).

If this recommendation of venting traps is adopted as a conservation measure, we would expect reductions in: 1) the number of culls (which in turn would increase the weight of the total landings) and, if of consequence, the natural mortality; 2) time expended by lobstermen in sorting their catches; 3) perhaps the illicit trade of sublegal lobsters (shorts) which is considered by some dealers and fishermen to be of an alarming magnitude; and 4) if a real problem, the number of lobsters imprisoned in lost traps.

ACKNOWLEDGMENTS

We thank the fishermen who allowed us, often at inconvenience to themselves, to accompany them on their fishing trips. Cecil Pierce, a fisherman from Southport, Maine, designed the plastic vent. Gary Robinson, Louis Kazimer, Curt Crosby, Andrew Dolloff, and William Sheldon of the Maine Extension Service made many of these trips. Their comments and experience aided greatly in collecting meaningful data. We express gratitude to Gareth Coffin, formerly with the Northeast Fisheries Center, National Marine Fisheries Service, West Boothbay Harbor, Maine, for his photographic work.

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EXPERIMENTAL EXPLOITATION OF COMPETING FISH POPULATIONS

RALPH P. SILLIMAN[1]

ABSTRACT

Populations of the guppy, *Poecilia reticulata*, and the swordtail, *Xiphophorus maculatus* × *X. helleri*, were grown both independently and in competition under controlled conditions. Independent populations were permitted to grow for about a year and then successively exploited at two different rates for each species. In the control (unfished) pair of competing populations, both species grew for about 30 weeks, followed by decline and extinction of the swordtail and fluctuations in the guppy. Similar initial growth in the test pair was followed by exploitation of both species at various combinations of rates.

Measures of recruitment were available as weights of juveniles returned to adult tanks from separate nursery tanks. Data from fitted curves showed that guppy recruitment exceeded that of the swordtail under both independent and competing conditions. Depression of recruitment by competition was greater in the swordtail than in the guppy.

A mathematical model for competing populations consisted of a pair of differential equations including elements of the Volterra competition formulae and the Fox exponential surplus-yield model. By using the exploitation rates applied in the experiments, and constants from the independent populations, the model was applied to biomass data from the control pair of competing populations. Successive trials resulted in a reasonably good fit, and competition coefficients from this were used to fit data from the exploited test pair. Yield isopleths calculated from the fitted model showed that maximal yields were obtained when exploitation for the swordtail was lower than for the guppy, suggesting lower productivity in the swordtail. The maximum sustainable yield represented about 20% of food placed in tanks, and indicated at least as great efficiency from competing populations as from independent ones.

Results from the experiments clearly suggest that exploiting both members of a competing pair is preferable to exploiting either alone, provided fishing rates are adjusted in relation to the productivity of each species.

Classical studies of fishery dynamics, such as those discussed in the works of Beverton and Holt (1957) and Ricker (1958), deal mostly with single populations treated as if they existed independently. Fishery biologists have come to recognize, however, that in many situations the fish stock cannot be so treated (Larkin 1963; Murphy 1973). The exploited population of interest is interdependent with others (which may be either exploited or unexploited) through competitive or predator-prey relations. Any effect of exploitation on one stock may produce a reaction in another, resulting in readjustments in both populations, and invalidating the expected response to exploitation based on single-species dynamics.

A familiar example of an apparent competitive situation is contained in the population histories of the Pacific sardine, *Sardinops sagax*, and the northern anchovy, *Engraulis mordax*, off the coast of California. The sardine suffered a catastrophic decline in the mid-1940's, followed by an increase in the anchovy. An analog computer model of Silliman (1969a, b) demonstrated that at least part of the change in the anchovy population size could be simulated with data on the sardine population size and the differential equations of Volterra (1928). Murphy (1973) provided recent verification of the sardine-anchovy relation and suggested that similar relations may prevail in the Japanese and South African sardines.

Laboratory experiments on the exploitation of self-sustaining fish populations have been reported fairly extensively (Silliman and Gutsell 1958; Silliman 1968; Nagoshi et al. 1972). Experiments with competing populations have included such diverse organisms as yeast cells (Gause 1932); Protozoa (Gause 1934); *Daphnia* (Frank 1957); beetles (Park 1962); and warblers (MacArthur 1958). To the best of my knowledge, however, exploitation of competing laboratory fish populations has not previously been reported.

The purpose of the experiments reported below was to ascertain experimentally the reaction of two competing fish populations to exploitation.

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Within this general objective, it was desired to determine which combination of exploitation rates applied on the two species would provide the maximum sustainable yield. To approach this problem, test and control pairs of populations were established in aquariums and allowed to grow several months under controlled conditions. Various combinations of exploitation rates were then applied to the test pair to determine population interactions and total yields. A "base line" for evaluating the results was obtained by growing and exploiting each of the competing species independently.

APPARATUS AND PROCEDURES

Experimental Animals

A lengthy fund of experience (Silliman 1948, 1968; Silliman and Gutsell 1958) built up with the guppy, *Poecilia reticulata*, dictated this as one of the experimental fishes. For the other, it was desired to have a species that was similar to the guppy in size, reproduction, and feeding habit but readily distinguishable from it in a mixed population.

A fish that met these requirements fairly well was the red swordtail hybrid, *Xiphophorus maculatus* × *X. helleri*, which will be referred to simply as "swordtail." It is somewhat larger than the guppy, but lived in the same sized aquarium. It is a live-bearer, like the guppy, and will readily eat the foods commonly fed guppies. Its brilliant red color permits easy distinction in the adults, and even the newborn young are pink or orange and may be distinguished from newborn guppies. In both species, adult males can be distinguished from adult females by external inspection. Distinguishing male characters are the modified anal fin (gonopodium) and fin and body color in the guppy and the elongated lower caudal fin ("sword") in the swordtail.

Aquarium Tanks

Fish were grown in four conventional glass-walled aquariums, each with a water surface of 44 cm by 24 cm, a water depth of 19 cm, and a volume of 20 liters. Inside each tank was an air-stone and a fiber-charcoal filter. Tanks were placed in a row with their longer axes parallel, and lettered A, B, C, D from left to right.

Tanks A and C were for juvenile and adult fish together. They each had a refuge in the left front corner for the escape and subsequent removal of recently born fish, or "fry." This refuge was formed with a fence consisting of 21 cm by 3 mm glass rods placed 1.5 mm apart, enclosing a right isosceles triangular space of 15 cm hypotenuse.

Although guppies could survive and achieve population growth in the above-described tanks, preliminary experiments showed this not to be true for the swordtails. Tanks B and D were therefore provided as "nurseries" for the temporary relocation of newborn young from tanks A and C, respectively. The juveniles were placed back in tanks A and C when they had grown to such size that they would no longer pass through a sieve consisting of 3-mm plastic rods placed 2 mm apart, thus making them recruits to the fishable stock.

Food and Feeding

A diet previously developed for guppies (Silliman 1968) was fed to all fish (Table 1). The food *Artemia* nauplii, however, requires special mention. The original intention was to feed the fish in the nursery tanks one-half the amount fed those in the adult tanks. The weight of nauplii produced was mistakenly believed to be directly proportional to amount of *Artemia* eggs placed in the culture beakers and, therefore, one-half the amount of eggs placed in the beakers for the adult tanks was placed in those for the nursery tanks. Production tests (Table 2) based on duplicate hatchings produced under standard conditions, however, showed production not to be proportional to the amount of eggs. Amounts of eggs inserted were kept the same, nevertheless, on the chance that unhatched eggs were eaten (observed on one occasion).

Artemia nauplii provided so small a proportion (1/100%) of the total diet that the lack of proportion noted above would have no significant effect on total food intake. The small amount of living food provided by the nauplii was regarded in the same sense as vitamins in human nutrition: as something required in small amounts for good health, but not furnishing a significant proportion of total food intake by weight. It is pertinent to note that the smallest number of nauplii (1,500) indicated by any of the tests (Table 2) would provide over four nauplii per fish for the largest

TABLE 1.—Food placed in tanks, grams.

Dates included	3-wk periods	Day of week	Adult tanks				Nursery tanks			
			Dry[1]	Frozen *Artemia*	*Artemia* nauplii	Total	Dry[1]	Frozen *Artemia*	*Artemia* nauplii	Total
25 Oct. 1965	0-71	Sun.	0.1	—	—	0.1	0.05	—	—	0.05
to		Mon.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
6 Dec. 1969		Tues.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Wed.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Thurs.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Fri.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Sat.	0.1	—	([2])	0.1	0.05	—	([2])	0.05
		Total	0.7	5.0	—	5.7	0.35	2.5	—	2.85
7 Dec. 1969	71-124	Sun.	0.1	—	—	0.1	0.05	—	—	0.05
to		Mon.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
1 Jan. 1973		Tues.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Wed.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Thurs.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Fri. A.M.	0.1	1.0	([2])	1.1	0.05	0.5	([2])	0.55
		Fri. P.M.[3]	0.1	—	([2])	0.1	0.05	—	([2])	0.05
		Total	0.7	5.0	—	5.7	0.35	2.5	—	2.85

[1]Tropical fish food.
[2]Hatch from 0.4 g (adult) or 0.2 g (nursery) of eggs (Table 2). Silliman and Gutsell (1958) found that the hatch from 0.4 g of eggs weighed 0.125 mg. Test hatches of nauplii were not proportional in weight to the amount of eggs used (Table 2), and since the total weight would be only 1/100% of the diet, no weight is indicated in the table.
[3]This was combined with the Friday A.M. feeding in 35 out of 161 wk and with the Sunday feeding once.

TABLE 2.—*Artemia* production tests. All 48-h hatches at 24°C in 800 ml 3% salt water. Counts from 20 samples for each test. Samples were 0.3 ml, withdrawn by pipette from vigorously stirred cultures killed in 0.75% formaldehyde, and replaced.

Test dates	Source of eggs[1]	Wt of eggs (g)	Mean no. in samples		Est. 1,000s in culture[2]	
			Nauplii	Eggs[3]	Nauplii	Eggs[3]
1970:						
1/28-30	A	0.2	2.10	7.50	5.6	20.0
1/28-30	A	0.4	1.45	18.05	3.9	48.1
3/23-25	A	0.2	1.85	6.95	4.9	18.5
3/23-25	A	0.4	2.05	16.30	5.5	43.5
4/13-15	B	0.2	1.75	10.35	4.7	27.6
1971:						
5/ 3- 5	B	0.4	0.55	32.95	1.5	87.9
5/17-19	B	0.2	0.85	23.30	2.3	62.1
5/24-26	C	0.2	3.50	30.70	9.3	81.9
10/ 4- 6	C	0.2	3.65	33.40	9.7	89.1
11/29-12/1	C	0.2	2.75	34.30	7.3	91.5
1972:						
5/15-17	C	0.2	6.85	27.80	18.3	74.1
11/13-15	C	0.2	2.75	36.10	7.3	96.3

[1]All were commercial suppliers.
[2]Sample numbers times 800/0.3.
[3]Includes shells (from hatched eggs) and unhatched eggs.

number of fish recorded in any tank (343 guppies in tank C during the last week of 3-wk period 65).

Dry food was placed on the surface of the water and sank slowly if not eaten immediately (as occurred with large populations). Frozen food sank and was eaten as it thawed. *Artemia* nauplii were hatched in 800-ml glass beakers (Table 2). The entire water mass, including shells and unhatched eggs, was poured through a cloth filter which was rinsed with freshwater and then rinsed into the fish tanks.

Cleaning and Treatment

Detritus including uneaten food (none in large populations) was siphoned daily from the tanks onto a cloth filter and the siphoned water returned to the tanks. Once a week all the water was removed from the tanks and one-half the volume was replaced with tap water aged for 1 wk. At this time the tanks and their equipment were thoroughly cleaned, and the filter fiber and charcoal were replaced. Also, fish in the adult tanks were treated for 15 min in a 1:200 solution of a commercial aquarium disinfectant "Fungistop."[2]

Water Characteristics

Water temperature in tanks A and D (Tables 3, 4; Figure 1) was recorded daily (Saturday excluded during 3-wk periods 71-124). These end tanks were chosen to reveal any temperature gradient that might exist. Although there was a slight tendency for tank D to vary from tank A (Figure 1), the differences were mostly less than 1°C and are not believed to have significantly affected population growth. It will be shown in the section on oscillatory fluctuation that deviations of population size from the theoretical were not correlated with tank temperature.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3.–Mean temperatures, °C, 3-wk periods, competing populations. Daily readings (21) to period 70, Sunday to Friday (18) from period[1] 72 on.

Period	Tank A	Tank D	Period	Tank A	Tank D
0	[2]24.2	[2]24.6	38	23.6	23.9
1	24.5	24.6	39	23.8	24.2
2	24.9	24.7	40	23.9	24.4
3	24.6	24.5	41	23.5	23.8
4	24.7	24.5	42	23.3	23.5
5	24.6	24.6	43	24.1	24.4
6	24.5	24.6	44	24.5	24.7
7	24.7	24.8	45	24.1	24.7
8	24.5	24.8	46	24.9	25.2
9	24.4	24.6	47	24.9	25.1
10	24.4	24.7	48	24.3	23.5
11	24.6	24.8	49	24.8	24.9
12	25.6	25.6	50	24.1	24.3
13	25.9	25.9	51	24.1	24.4
14	26.4	26.0	52	23.7	23.9
15	25.6	25.7	53	23.7	23.8
16	25.5	25.4	54	23.5	23.6
17	25.0	25.1	55	23.4	23.9
18	25.0	24.8	56	23.7	23.9
19	25.6	25.1	57	23.9	23.8
20	26.4	25.1	58	23.6	23.6
21	26.2	24.9	59	23.5	23.7
22	26.0	25.5	60	23.2	23.5
23	25.9	24.8	61	24.3	24.5
24	25.2	24.5	62	24.5	24.5
25	25.6	24.6	63	24.9	24.9
26	26.0	25.0	64	24.7	24.9
27	25.7	25.2	65	23.8	23.8
28	26.4	25.8	66	23.9	23.8
29	26.2	25.9	67	24.4	24.3
30	26.3	25.8	68	21.5	21.4
31	25.9	26.0	69	24.0	24.0
32	24.5	25.1	70	24.0	23.8
33	23.8	24.5	71	[1]23.9	[1]23.8
34	23.1	23.8	72	23.7	23.4
35	23.7	23.6	73	23.8	23.5
36	23.4	23.8	74	23.9	23.5
37	23.7	23.8	75	23.9	23.5

[1]One Friday and two Saturday readings missing, period 71.
[2]Based on 1 wk only.

TABLE 4.–Mean temperatures, °C, 3-wk periods, independent populations. Sunday to Friday readings (18).

Period	Tank A	Tank D	Period	Tank A	Tank D
79	24.6	24.1	102	24.5	24.3
80	23.5	23.2	103	24.7	24.2
81	25.0	24.5	104	24.5	23.6
82	24.7	24.3	105	24.4	23.6
83	24.4	24.2	106	24.3	23.5
84	24.5	24.5	107	24.1	23.8
85	24.3	24.3	108	24.2	23.8
86	23.9	23.7	109	24.3	23.9
87	24.2	23.8	110	24.4	23.9
88	24.2	23.6	111	24.3	23.8
89	24.6	23.9	112	24.5	23.9
90	24.6	23.9	113	24.6	23.9
91	24.6	24.2	114	24.6	23.9
92	24.5	23.8	115	24.1	23.5
93	24.5	23.9	116	25.8	25.2
94	24.6	23.7	117	25.6	24.9
95	24.2	24.0	118	25.4	24.7
96	24.3	23.9	119	24.9	24.1
97	24.2	23.6	120	24.5	23.6
98	24.4	24.2	121	24.7	23.6
99	25.6	25.4	122	24.1	22.9
100	25.7	25.4	123	24.5	23.3
101	24.7	24.5	124	[1]24.7	[1]24.2

[1]Last three readings missing.

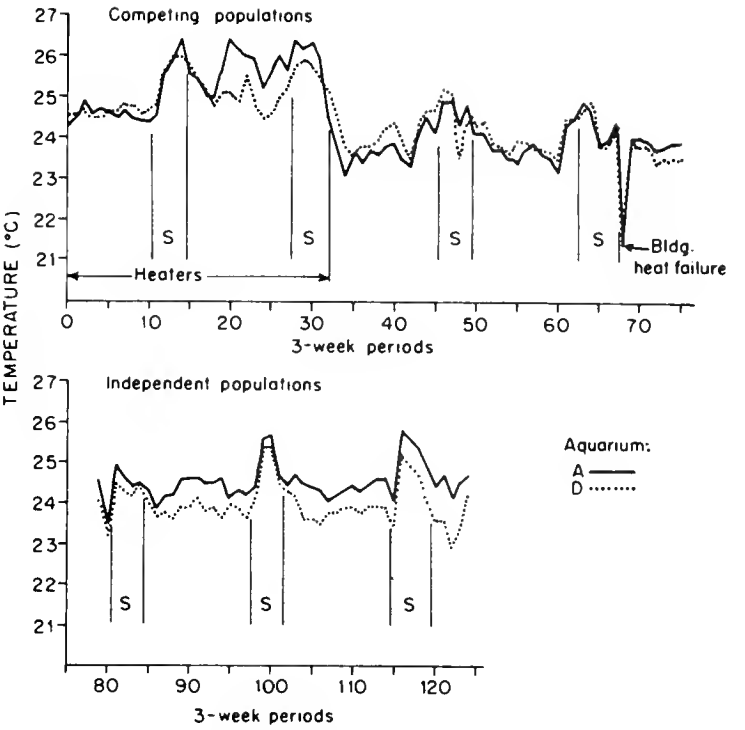

FIGURE 1.–Water temperatures (3-wk means). "S" indicates summer periods (approximately 20 June to 20 September).

Heaters were placed in tanks during periods 1-32 (Figure 1) but caused excessive temperature fluctuation and one instance of mortality from a nonfunctioning thermostat. During periods 33-174 the tank water was at room temperature. This was thermostatically controlled except that no cooling was available in the summer. Summer temperatures were thus somewhat higher than during the balance of the year (Figure 1), but the change was the same for all tanks.

Measurements of dissolved oxygen and carbon dioxide concentrations and pH were made at irregular intervals during the course of the experiment (Table 5). All O_2 readings were within or above the 3-5 ppm range considered satisfactory for warmwater fishes by Lewis (1963), and the CO_2 and pH readings were within the range he considered safe (CO_2<30 ppm., pH 5.0-9.0).

Light was provided from overhead fluorescent fixtures with standard tubes to period 11. After period 11, pink tinted tubes were used.

Handling, Enumeration, Exploitation, and Weighing

Areas behind the refuge fences described under "Aquarium Tanks" were inspected daily. If any newborn fish were found there or in other corners of the tanks, they were removed by netting or siphoning, counted, and placed in the nursery

TABLE 5.–Water condition on selected dates.

Dates	3-wk period	O_2, ppm. Tank A	O_2, ppm. Tank D	CO_2, ppm. Tank A	CO_2, ppm. Tank D	pH Tank A	pH Tank D
1968:							
Aug. 9	48	7.0	7.0	—	—	—	—
16	48	6.0	—	—	—	—	—
29	49	6.6	6.4	10	10	6.9	6.9
Sept. 6	49	6.2	6.8	—	—	—	—
13	49	6.2	6.4	—	—	—	—
20	50	6.4	6.4	10	10	—	—
27	50	6.4	6.4	—	—	—	—
Oct. 4	50	6.4	6.4	—	—	—	—
11	51	6.0	6.4	—	—	—	—
18	51	6.4	6.8	—	—	—	—
25	51	6.2	6.4	—	—	—	—
Nov. 8	52	6.0	6.6	—	—	—	—
15	52	6.4	7.2	—	—	—	—
28	53	6.4	7.0	—	—	—	—
Dec. 6	53	6.4	6.8	—	—	—	—
13	54	6.4	6.6	—	—	—	—
26	54	6.4	6.8	—	—	—	—
1969:							
Jan. 2	55	6.4	7.0	—	—	—	—
Sept. 17	67	6.6	6.6	10	10	8.0	8.0
Oct. 2	68	7.8	7.8	—	—	—	—
9	68	7.4	8.2	—	—	—	—
23	69	6.6	7.6	—	—	—	—
30	69	6.2	7.6	—	—	—	—
Dec. 4	71	6.8	7.4	10	10	8.0	8.7
1971:							
Feb. 25-26	92	6.6	8.2	10	10	8.0	8.0
1972:							
Mar. 23	111	5.0	7.2	10	10	8.5	8.0

tanks. At the time of weekly cleaning, the water in the nursery tanks was poured through the sieve also described under Aquarium Tanks. Any fish remaining on the sieve were placed back in the adult tanks.

Fish were counted and weighed weekly during periods 0-71. During periods 71-124, this was done only at the approximate brood intervals of the fish, which were 3 wk for the guppy and 4 wk for the swordtail. Fish were counted simply by netting them from one container to another. Counts were categorized into "immature" (those whose sex could not be determined from external inspection), male, and female. Fry and juveniles were counted when moved between adult and nursery tanks. Dead fish found in tanks were recorded as mortalities.

Exploitation was done at the time of counting. To apply an exploitation rate of $1/n$, each nth fish was removed (n was always an integer). This was applied equally to juveniles and adults, but not at all to fish in the nursery tanks.

Population and catch weights were also determined at the time of counting. Fish were drained and placed in a previously weighed container of water. Total weight was measured and fish weight obtained by subtracting the tare.

COURSE OF POPULATIONS

Independent Populations

Although chronologically the competing populations preceded the independent populations, the more logical order of presentation is to deal with the independent populations first. This arrangement will be followed in the remainder of the report.

Separate populations of guppies and swordtails were started on 19 May 1970 (3-wk period No. 79). Each of these was permitted to grow for an initial period of about 1 yr (Figures 2, 3) before exploitation was begun. Even though complete equilibrium had not been reached, exploitation was started at 25% per brood interval (3 wk) for the guppy and 10% per interval (4 wk) for the swordtail. The lower rate for the swordtail was based on previous experience showing lower productivity for that species. Initial rates were maintained during weeks 289-334 for the guppy and 290-334 for the swordtail. Final rates were 33.3% for the guppy (weeks 337-373) and 16.7% for the swordtail (weeks 338-374). Responses were in accord with expectations for the guppy (Figure 2) and the early swordtail history, but there was an increase in both number and weight in the swordtail in the last five brood intervals (Figure 3). This anomaly will be discussed under "Oscillatory Fluctuation."

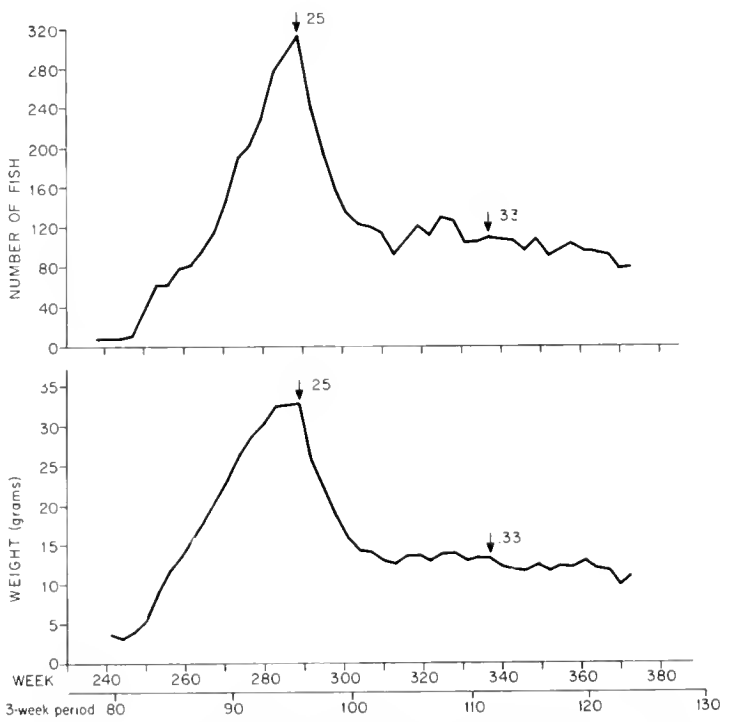

FIGURE 2.–Course of independent guppy population. Numbers indicate target exploitation rates.

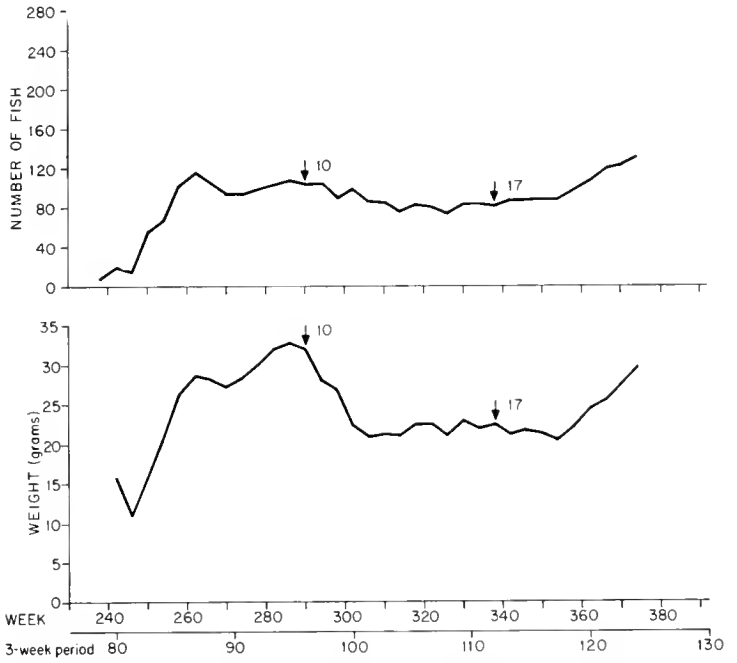

FIGURE 3.—Course of independent swordtail population. Numbers indicate target exploitation rates.

Competing Populations

The two mixed populations, each composed of both guppies and swordtails, were started 24 October 1965 (week 0). Three-week period 0 started with week 1, since weights were not recorded in week 0.

In the control (unexploited) pair of populations (Figure 4), both species grew for an initial period of about 30 wk. The swordtail population then began to decline and disappeared at week 129. This will be discussed in the section on competitive exclusion. Extinction of the swordtail was followed by a large oscillatory fluctuation in the guppy (about -39% to +26% of the asymptotic level), which will be discussed in the section on such fluctuations.

Initial growth in the test (exploited) pair was similar to that in the control pair (Figures 4, 5). Exploitation was started first on the swordtail

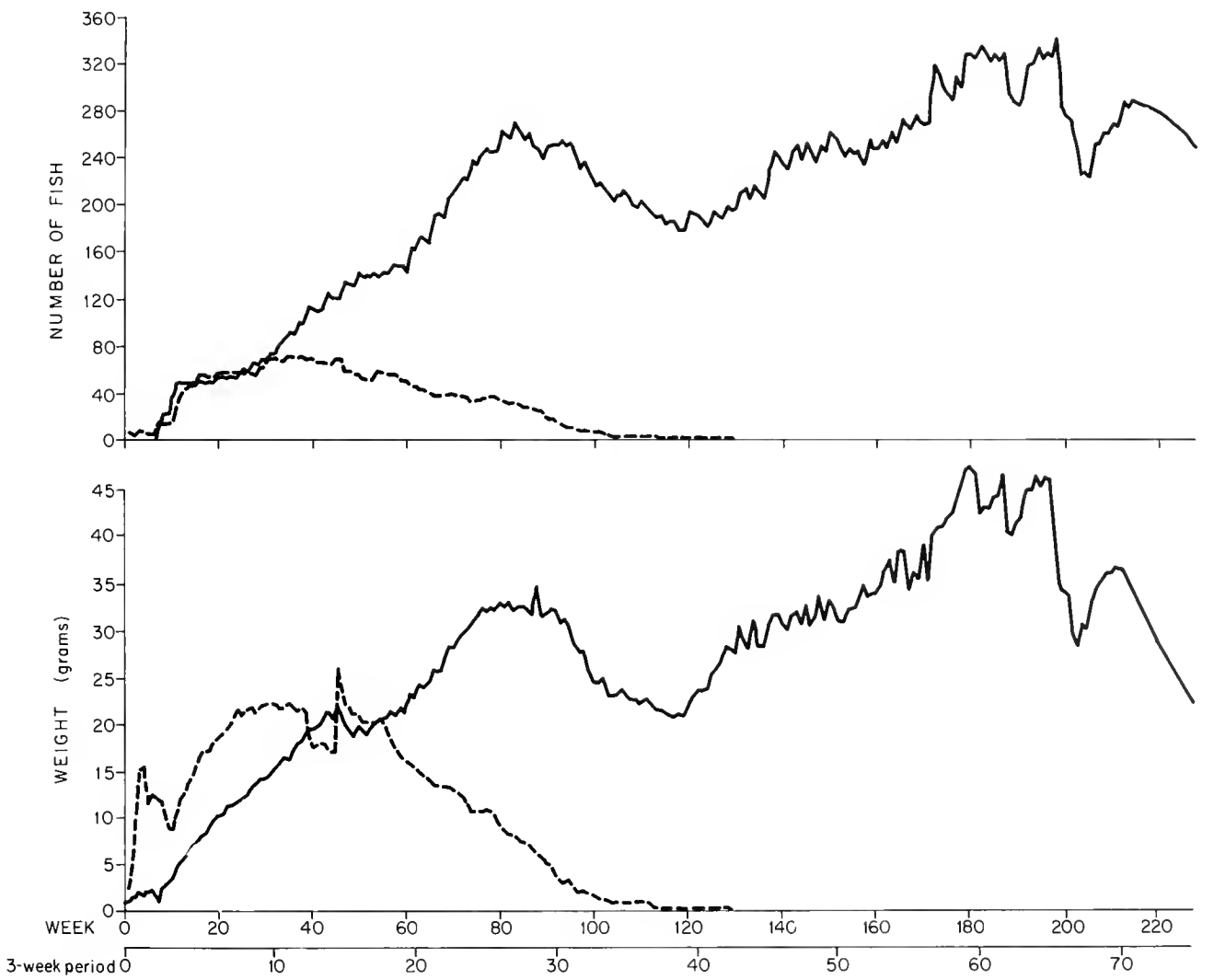

FIGURE 4.—Course of competing populations, control pair. Solid line, guppy; broken line, swordtail.

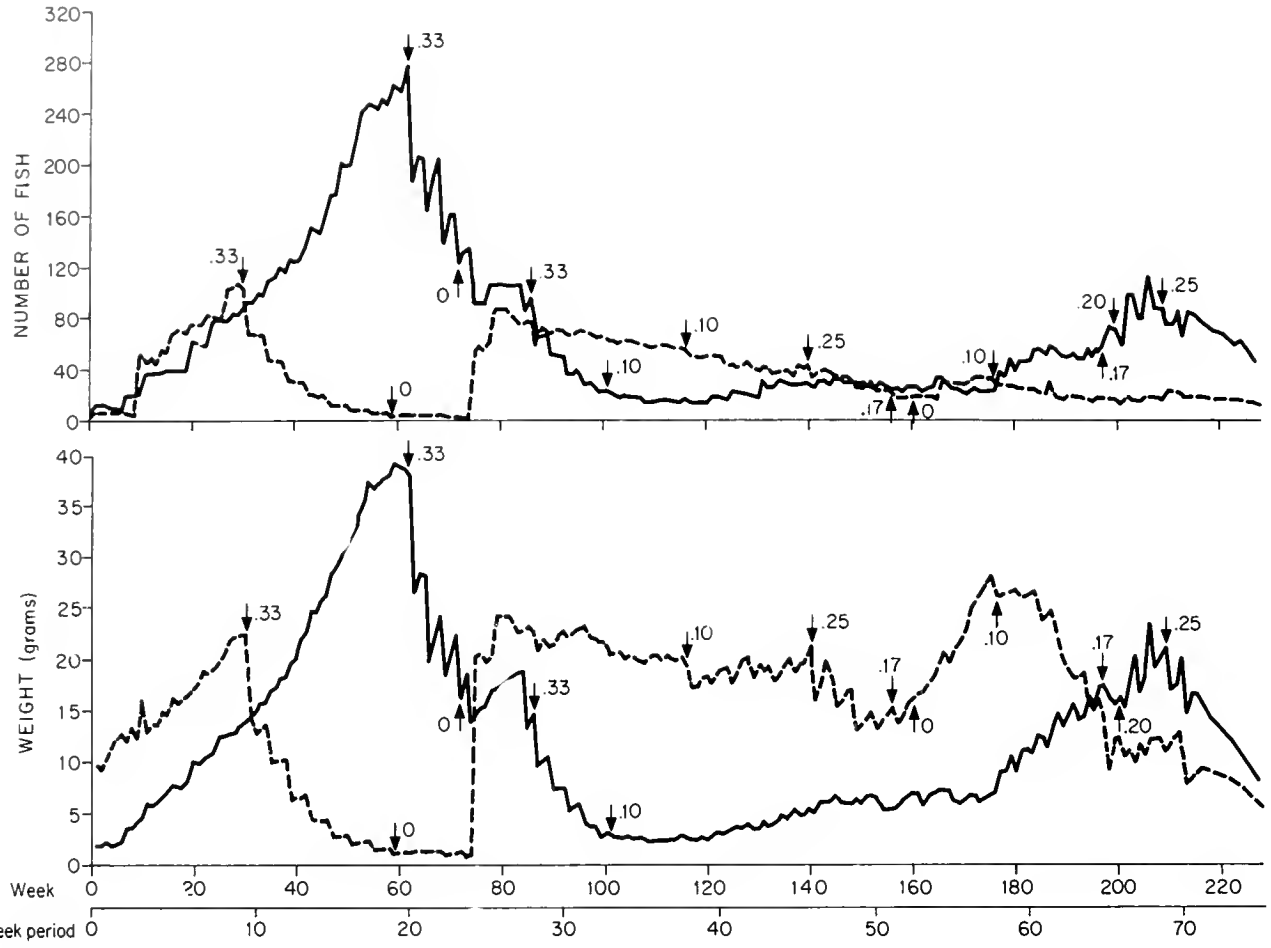

FIGURE 5.—Course of competing populations, test pair. Solid line, guppy; broken line, swordtail. Numbers indicate target exploitation rates.

(week 30), under the mistaken impression that the greater biomass then achieved by the swordtail indicated a greater productive capability. Exploitation produced a rapid decline in the swordtail to a low population level (Figure 5). Cessation of swordtail exploitation at week 59 and initiation of guppy exploitation at week 62 did not lead to recovery of the swordtail, in spite of a drastic decline in guppy abundance (Figure 5).

By week 74, it became apparent that the swordtail would require a lengthy period for recovery, even if guppy abundance were further reduced. To accelerate the study of exploitation, the populations were reconstructed during weeks 74-85, using fish from exploited populations that had been placed in a reserve tank. After reconstruction, the populations approximated fairly closely their number and weight at the time exploitation was started (compare week 85 with week 30 in Figure 5). Exploitation rates after week 85 were adjusted to keep both the guppy and swordtail at productive levels while trying as wide a range of pairs of exploitation rates as possible.

RECRUITMENT RELATIONS

Juvenile fish were counted both when removed from and returned to the adult tanks; it was thus possible to obtain a measure of recruitment. Numbers were converted to weights by use of factors (mean weights per fish) based on weighings of the juveniles: guppy, 0.0656 g based on 1,417 fish in 126 weighings spread over 199 wk; swordtail 0.0678 g, 337, 61, 196, respectively. At the beginning of the experiments, when few fish were in the nursery tanks, it was possible to distinguish individual groups of recruits by size, count them, and thereby estimate the "reproductive lag" from birth to recruitment. The lag was found to be approximately one brood interval (guppy, 3 wk; swordtail, 4 wk) for each species. In constructing the stock-recruitment relations, the recruitment for each brood interval was compared with the mean stock in the adult tanks during the preceding brood interval. During periods of exploitation, the catch was subtracted from the stock at the beginning of the interval.

Because of the great variability in the recruitment data, group means were used for both species. The basis of the grouping was an interval of 5 g (0.0-4.9, 5.0-9.9, etc.) in the adult tank stock weight. Data used in calculating recruitment curves were pairs consisting of the mean adult stock weight and mean recruit weight for each group.

The stock-recruitment data for the guppy (Figure 6) could be fitted by a Ricker (1958) curve of the type:

$$R_{N+1} = a\bar{S}_N \exp(-b\bar{S}_N),$$

where R_{N+1} is recruitment during brood interval $N+1$ and $\bar{S}_N$ is mean adult stock during brood interval N, both in grams. Fitting of the curves shown (Figure 6) was by least squares to the rectilinear logarithmic form of the relation:

$$\log_e R_{N+1}/\bar{S}_N = \log_e a - b\bar{S}_N.$$

Values of the constants are given in Table 6.

Data for the swordtail (Figure 7) did not conform well to the Ricker relation, as shown by the parabolic nature of the points for the competing stock, and were fitted better by a simple parabola:

$$R_{N+1} = a\bar{S}_N - b\bar{S}_N^2,$$

symbols as above. Curves shown (Figure 7) were fitted directly to the grouped data by least squares. Values of the constants are in Table 6.

Comparison of results for the two species (Figures 6, 7; Table 6) reveals both similarities and differences. Despite the different types of recruitment curves, there is the suggestion in both species that maximum recruitment occurs at intermediate rather than very high or very low adult stock levels, as has been observed for other species (Ricker 1958; Silliman 1969b). Also, recruitment for both species was depressed by competition. However, the depression was greater for the swordtail, as shown in the comparison of standardized recruitment (last column, Table 6). This is in keeping with the finding to be reported below that the guppy is more productive than the swordtail. This finding is also supported by the fact that guppy recruitment was greater than swordtail recruitment in both independent and competing situations (last column, Table 6).

Some additional information on recruitment was obtained from a study of count discrepancies. Because all additions to and removals from the adult tanks were recorded, it was possible to calculate an "expected" count (the previous count

TABLE 6.—Stock-recruitment data comparing populations of the two species with data from the relations: guppy, $R_{N+1} = a\bar{S}_N \exp(-b\bar{S}_N)$; swordtail, $R_{N+1} = a\bar{S}_N - b\bar{S}_N^2$.

Species and situation	No. of pairs of observations[1]	Constants, per brood interval		Recruitment at value of $\bar{S}_N$ for R_{max}, independent situation (g)	
		a	b	Per brood interval[2]	Per week
Guppy:					
Independent	76	0.343	0.061	2.07	0.69
Competing	117	0.092	0.028	0.95	0.32
Swordtail:					
Independent	32	0.229	0.007	1.90	0.48
Competing	86	0.068	0.003	0.42	0.10
Total	311				

[1]In fitting curves, data were grouped by 5-g intervals of $\bar{S}_N$.
[2]Guppy, 3 wk; swordtail, 4 wk.

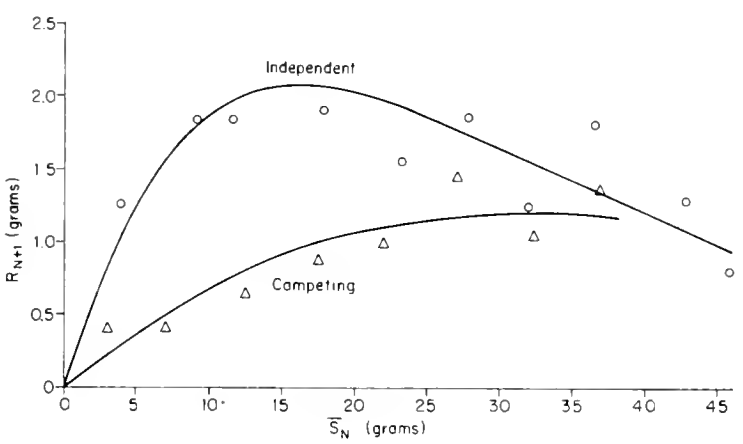

FIGURE 6.—Stock-recruitment relation for the guppy. Data grouped by 5-g intervals of $\bar{S}_N$. N is the number of the 3-wk brood interval.

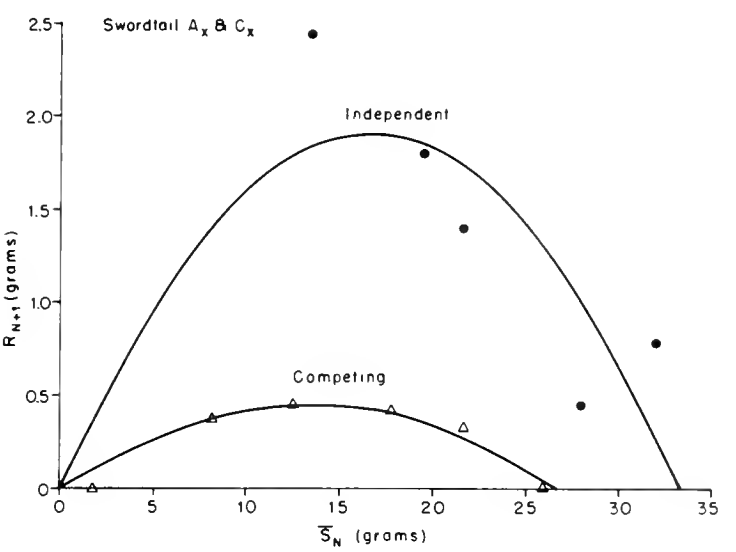

FIGURE 7.—Stock-recruitment relation for the swordtail. Data grouped by 5-g intervals of $\bar{S}_N$. N is the number of the 4-wk brood interval.

plus recruits and minus catch and deaths) to be compared with the actual counts made. Some of the observed discrepancies were no doubt due to unobserved deaths (dead fish eaten by others before seen) or to errors in counting. That some errors occurred is not surprising. Each expected-actual comparison involved as many as 17 separate counts. During each main count while exploiting the stocks the counter had to keep in mind the total number, the number caught, the state of maturity of each fish, and the sex of each mature fish.

The distribution of discrepancies for selected (to provide representative data) periods (Table 7)

TABLE 7.–Count discrepancies for selected periods: swordtail, April 1970 to June 1972; guppy, March 1970 to June 1972. Values represent "expected" number subtracted from the actual count.

Discrepancy	Swordtail	Guppy
−20	—	1
−12	—	1
−11	—	—
−10	3	1
−9	—	2
−8	2	1
−7	2	1
−6	1	1
−5	3	—
−4	3	2
−3	3	1
−2	1	3
−1	2	3
0	1	2
+1	1	3
+2	—	1
+4	—	1
+5	—	1
+6	—	3
+7	—	1
+8	—	2
+9	1	—
Total	23	31

shows that negative discrepancies (actual less than expected) exceed the positive for both swordtails and guppies. This no doubt arose from the unrecorded natural mortalities mentioned above. The two positive discrepancies for the swordtail probably represent counting errors. For the guppy, however, the fairly large proportion of positives exceeding three fish suggests that unrecorded recruitment occurred. Apparently some of the guppy "fry" escaped detection, even though a thorough search of the tanks was made. This phenomenon is in keeping with the observed greater hardiness of the guppy, and suggests that the superiority in recruitment for the guppy was even greater than indicated in the stock-recruitment relations reported above.

SIMULATION MODEL

Mathematical Derivation

Data of population weight reflect growth of individual fish as well as recruitment and mortality, and all of the analyses below will be in terms of weight. Development of the formulae requires a fairly extensive list of symbols, which are defined below.

P = Total population weight in grams.
t = Time from start, in 3-wk periods.
X = Fishing effort in arbitrary units.
q = Catchability coefficient.
F = Instantaneous rate of fishing mortality ($=qX$).
m = Three-week rate of fishing mortality.
G = Constant of the Gompertz growth curve.
k = Constant of the Gompertz growth curve and of the Fox (1970) population model.
c, h, j = Empirical constants.

Adding a term for the effect of fishing to the formulae of Volterra (1928) gives a pair of differential equations:

$$dP_1/dt = f(P_1) - f(P_2) - f(X_1), \quad (1)$$
$$dP_2/dt = f(P_2) - f(P_1) - f(X_2). \quad (2)$$

In these equations, the first term of the right hand side is for population growth; the second, for competition; and the third, for the effect of fishing. The development is exactly parallel for the two equations, and only that for Equation (1) will be outlined below.

For the growth term Volterra (1928) used $f(P_1) = j_1P_1 - h_1P_1^2$. This is the logistic growth curve, which requires symmetrical population growth. Growth for the guppy under fishing (equilibrium yield) was shown by Silliman and Gutsell (1958) and Silliman (1968) to be distinctly asymmetrical. The Gompertz (1825) curve, introduced as a population yield model by Fox (1970), is suitable for asymmetrical growth and will be shown in the section on determination of constants to be suitable for initial population growth in both the guppy and the swordtail. This is expressed:

$$P_t = P_0 \exp[G - G\exp(-kt)]. \quad (3)$$

It can be shown by mathematical analysis of

Equation (3) that the limit $P_\infty = P_0 \exp(G)$, and by substituting this in Equation (3), differentiating and taking logs a growth term may be derived for Equation (1):

$$f(P_1) = P_1 k_1 (\log_e P_{1\infty} - \log_e P_1). \quad (4)$$

For the competition term, Volterra (1928) used $f(P_2) = c_1 P_1 P_2$. Preliminary experimentation showed that this term was unsatisfactory for the guppy-swordtail experiments, since it was impossible to obtain even a reasonably good fit using it. I also experimented with $f(P_2) = c_1 (P_1 + P_2)$ on the theory that the sum of the populations, rather than their product, might be controlling, but it was equally unsatisfactory. The most suitable term proved to be simply:

$$f(P_2) = c_1 P_2. \quad (5)$$

This term agrees with the reasonable idea that the competitive effect on one population is proportional to the size of the other.

For the fishing term I adopted from Fox (1970):

$$f(X_1) = q_1 X_1 P_1 = F_1 P_1. \quad (6)$$

Substitution of Equations (4), (5), and (6) in Equation (1) provides the model for the first population:

$$dP_1/dt = P_1 k_1 (\log_e P_{1\infty} - \log_e P_1) - c_1 P_2 - F_1 P_1. \quad (7)$$

By exactly parallel derivation the model for the second population is:

$$dP_2/dt = P_2 k_2 (\log_e P_{2\infty} - \log_e P_2) - c_2 P_1 - F_2 P_2. \quad (8)$$

Thus the model for the competing populations represents a modification of the Fox (1970) expoential surplus-yield model, with the addition of a term for competition.

Determination of Constants

Growth data were obtained from the independent populations. Gompertz (1825) curves were fitted to the initial growth period for both species (Figures 8, 9), using the analog computer method of Silliman (1967). Asymptotic levels were 38.7 g for the guppy and 33.7 g for the swordtail. These values were used for the zero exploitation levels in fitting the Fox (1970) model. The zero points plus two other exploitation rates (relatively stable periods considered to be equilibrium points: guppy, weeks 316-334 and 355-373, Figure 2; swordtail, 322-334 and 342-354, Figure 3) gave three fitting points for each species (Figures 10,

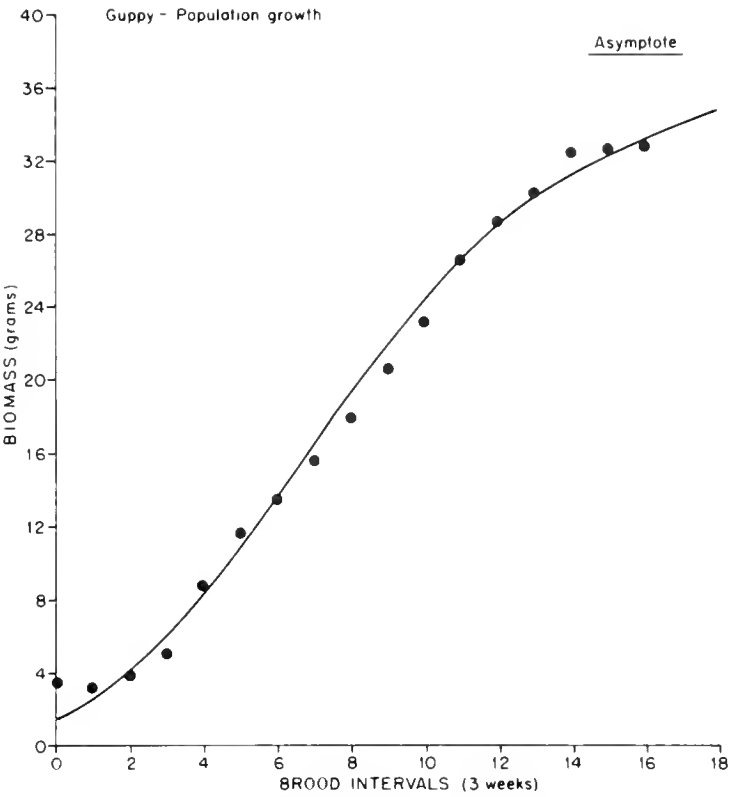

FIGURE 8.—Initial growth for the independent population of the guppy, with fitted Gompertz curve.

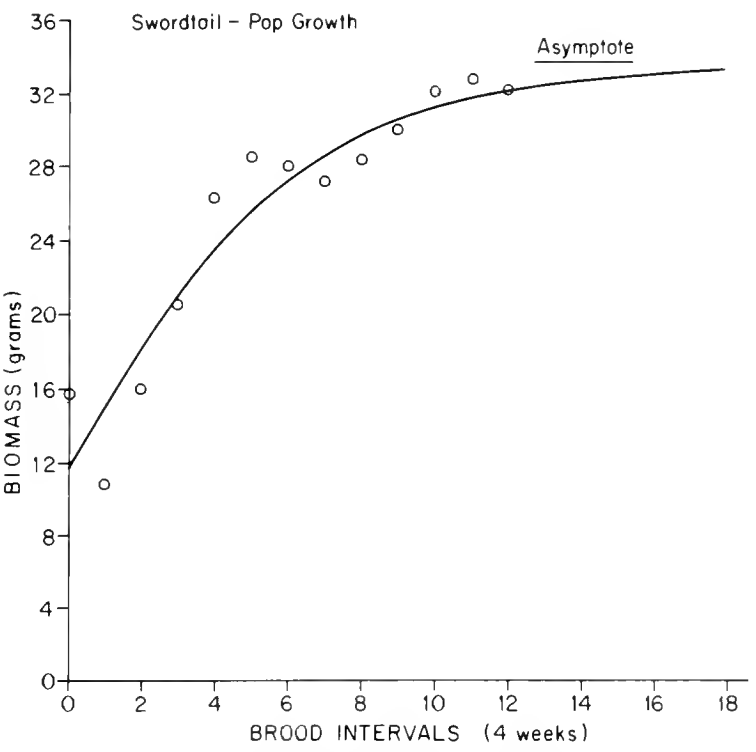

FIGURE 9.—Initial growth for the independent population of the swordtail, with fitted Gompertz curve.

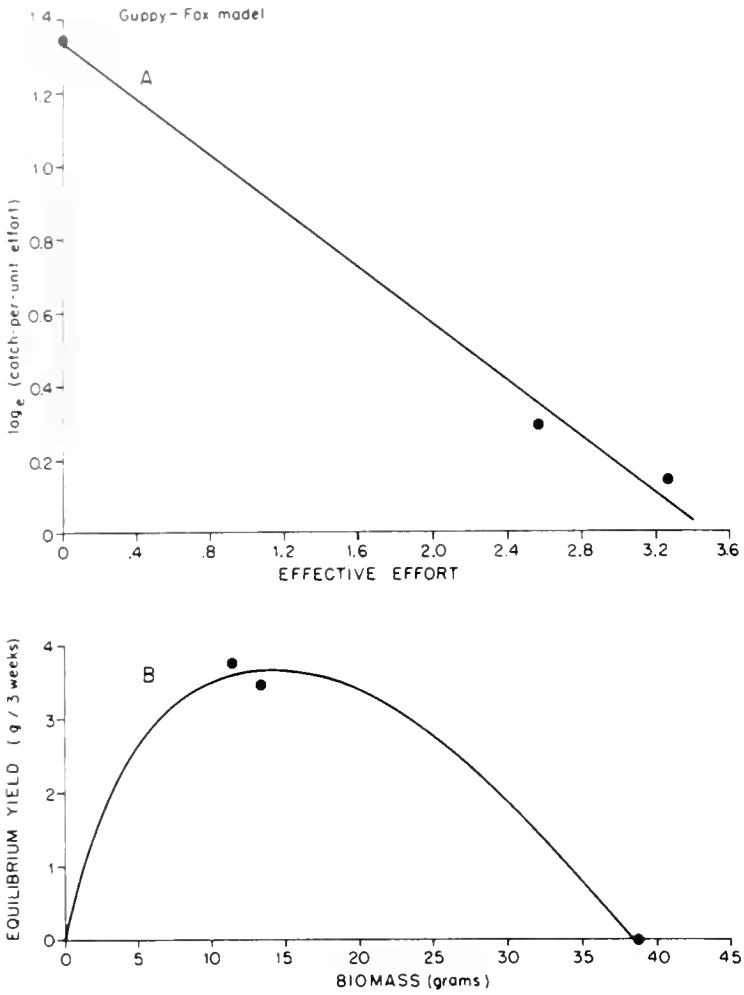

FIGURE 10.—Fox (1970) model fitted to yield data for the guppy. Exploitation rates are 0.000, 0.257, and 0.326 per 3-wk period (left-to-right in upper panel, reversed in lower panel).

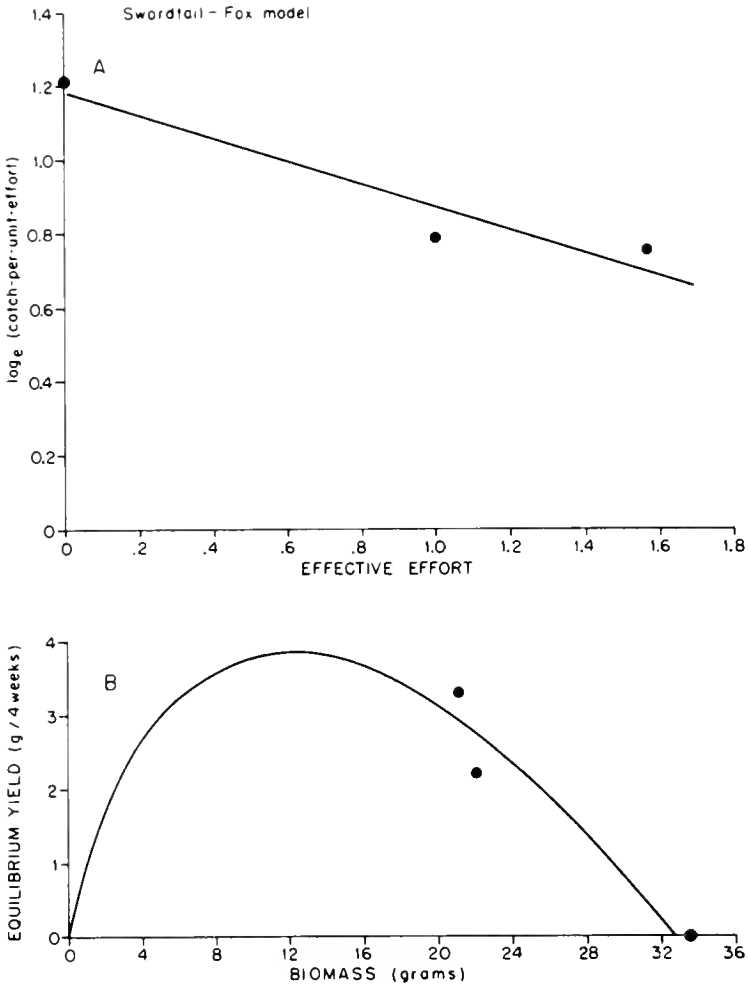

FIGURE 11.—Fox (1970) model fitted to yield data for the swordtail. Exploitation rates are 0.000, 0.100, and 0.157 per 4-wk period (left-to-right in upper panel, reversed in lower panel).

11). Effective exploitation rates shown varied slightly from the "target" rates because of lack of infinite divisibility of the populations and because of errors. The fitted Fox models yielded values of k of 0.260 per 3 wk and 0.321 per 4 wk for the guppy and swordtail, respectively. Comparable values for the Gompertz curves were 0.193 and 0.260. It was considered more appropriate to use the values from the Fox model because the analyses were based on that model. To place the swordtail on the same time scale as the guppy, the value of k was multiplied by ¾, or ¾(0.321) = 0.241.

Data of catch and biomass for the competing populations (Table 8) were used to calculate exploitation rates. Again the effective rates varied from the target rates as explained in the preceding paragraph. Also, it was again necessary to adjust the effective rates for the swordtail to the same time scale as the guppy. This was done by the formula $m = 1 - (1 - m')^{3/4}$, where m' is the unadjusted rate. Finally, for use in the differential equations, the 3-wk rates must be converted to instantaneous rates. The formula is: $F = -\log_e(1 - m)$, from Ricker (1958).

The use of instantaneous exploitation rates as employed herein assumes that P declines continuously, whereas the experimental technique was to remove all the fish at the beginning of the brood interval. It can readily be shown, however, that the reduction in population resulting from the application of m at the beginning of a period is exactly the same as the application of the equivalent F throughout the period, even if both are superimposed on a constant natural mortality.

A summary of all the constants used in applying Formulae (7) and (8) to biomass data from the competing populations is given in Table 9. Where both unadjusted and adjusted data are shown, the latter were the ones used.

Application of the Model

Using standard analog computer techniques (Ashley 1963) values of guppy and swordtail

TABLE 8.—Exploitation of competing populations. Rates are per brood interval: guppy, 3 wk; swordtail, 4 wk.

Week	Target rate	Effective rate	Biomass (g)	Catch (g)
		Guppy		
62	0.333	0.335	38.0	12.1
65			28.3	11.1
68			24.2	7.7
71			22.5	7.0
86	0.333	0.344	14.8	5.2
89			10.4	3.7
92			7.4	2.4
95			5.9	2.0
98			3.9	1.3
101	0.100	0.113	3.0	0.4
104			2.8	0.4
107			2.7	0.5
110			2.3	0.1
113			2.5	0.1
116			2.6	0.2
119			2.6	0.1
122			3.2	0.3
125			3.5	0.1
128			4.0	0.7
131			4.2	0.5
134			4.6	0.4
137			5.3	0.4
140			5.4	0.3
143			6.2	0.6
146			6.2	0.4
149			6.3	0.7
152			6.8	0.7
155			5.4	0.4
158			6.2	0.4
161			6.8	0.8
164			6.8	0.5
167			7.1	0.8
170			6.2	0.6
173			6.1	0.7
[1]175			6.7	2.0
179			10.3	1.2
182			11.0	1.0
185			12.2	1.1
188			14.5	1.5
191			15.5	3.4
194			16.2	1.8
197	0.200	0.223	17.5	6.4
200			16.3	2.5
203			20.2	3.6
206			23.1	4.7
209	0.250	0.259	21.0	5.3
212			19.9	5.1
215			16.6	4.5
218			14.1	3.6
221			12.4	3.5
224			10.6	2.8
227			8.3	1.9
		Swordtail		
30	0.333	0.346	22.3	8.0
34			13.5	3.9
38			10.2	4.0
42			6.7	2.6
46			4.3	1.5
50			2.8	0.8
54			2.2	0.8
58			1.5	0.4
116	0.100	0.112	19.0	2.6
120			18.2	2.4
124			19.1	1.3
128			20.2	2.5
132			19.2	2.3
136			20.1	1.9
140	0.250	0.254	21.2	5.9
144			18.8	4.9
148			16.9	4.5
152			15.0	3.0
156	0.100	0.112	15.2	1.7
176	0.100	0.088	26.2	1.2
180			26.6	1.2
184			26.5	1.5
188			22.0	2.2
192			18.0	4.0
[2]197			14.4	0.2
200			12.1	1.0
204			11.5	1.3
208			12.1	1.6
212			12.8	1.7
216			9.3	1.0
220			8.6	0.8
224			7.5	0.6
228			5.6	0.5

[1]Should have been 176.
[2]Should have been 196.

biomass were simultaneously generated using Formulae (7) and (8). A number of trials were made on data from the control populations (Table 10) to find the most suitable values of the competition coefficients c_1 and c_2. Values of $c_1 = 0.071$ (guppy) and $c_2 = 0.120$ (swordtail) produced curves (Figure 12) which fitted reasonably well except for the oscillatory variations to be discussed below.

TABLE 9.—Constants used in fitting simulation model to biomass data for competing populations.

Guppy k_1 = 0.260 (3-wk), $P_{1\infty}$ = 38.2 g				Swordtail k_2 = 0.321 (4-wk), k_2 = 0.241 (3-wk), $P_{2\infty}$ = 32.7 g				
3-wk period	m_1 Target	m_1 Effective	F_1	3-wk period	m_2 Target	m_2 Effective	m_2 Adjusted	Adjusted F_2
20-23	0.333	0.335	0.408	9-19	0.333	0.346	0.273	0.319
28-32	0.333	0.344	0.422	38-45	0.100	0.112	0.085	0.088
33-64	0.100	0.113	0.120	46-50	0.250	0.254	0.197	0.219
65-68	0.200	0.223	0.252	51 only	0.100	0.112	0.085	0.088
69-75	0.250	0.259	0.300	58-75	0.100	0.088	0.067	0.069

TABLE 10.—Biomass levels, 3-wk means, control populations.

Period	Weight (g)		Period	Weight (g)	
	Guppy	Swordtail		Guppy	Swordtail
0	1.6	8.2	38	21.0	0.3
1	2.1	13.2	39	21.4	0.3
2	2.4	10.6	40	23.4	0.3
3	4.5	10.5	41	25.0	0.3
4	6.6	14.0	42	27.8	0.3
5	8.2	17.0	43	29.0	0.0
6	10.1	18.5	44	29.1	0.0
7	11.5	20.4	45	30.2	0.0
8	12.6	21.4	46	30.8	0.0
9	14.0	21.7	47	31.4	0.0
10	15.2	22.1	48	31.6	0.0
11	16.6	22.0	49	32.7	0.0
12	18.6	19.4	50	31.4	0.0
13	19.8	17.8	51	32.5	0.0
14	21.0	17.3	52	34.1	0.0
15	20.4	23.5	53	35.2	0.0
16	19.3	20.9	54	37.0	0.0
17	19.7	20.3	55	36.4	0.0
18	20.9	19.5	56	36.5	0.0
19	21.4	16.9	57	40.7	0.0
20	23.4	15.4	58	42.6	0.0
21	25.1	14.2	59	[1]47.3	0.0
22	27.3	13.4	60	44.1	0.0
23	29.1	12.8	61	43.9	0.0
24	30.8	11.1	62	42.4	0.0
25	32.3	10.8	63	42.7	0.0
26	32.6	9.4	64	45.5	0.0
27	32.7	8.0	65	44.4	0.0
28	32.2	7.2	66	34.4	0.0
29	32.7	5.7	67	29.7	0.0
30	32.0	4.0	68	32.5	0.0
31	30.1	3.0	69	35.8	0.0
32	27.1	2.0	70	36.7	0.0
33	24.8	1.5	71	[2]34.1	0.0
34	23.1	1.0	72	[2]30.9	0.0
35	23.3	0.9	73	[2]28.0	0.0
36	22.5	1.0	74	[2]25.5	0.0
37	21.9	0.6	75	[1,2]22.8	0.0

[1]Based on two observations.
[2]Based partly on interpolation.

TABLE 11.—Biomass levels, 3-wk means, test populations.

Period	Weight (g)		Period	Weight (g)	
	Guppy	Swordtail		Guppy	Swordtail
0	2.0	9.6	38	2.6	18.7
1	2.0	[1]12.6	39	2.5	17.9
2	3.8	13.0	40	3.1	18.4
3	5.6	14.2	41	3.4	18.5
4	6.8	14.3	42	3.7	19.5
5	7.6	16.0	43	3.8	19.2
6	9.4	17.2	44	4.4	18.5
7	10.6	18.9	45	4.9	19.5
8	12.6	20.5	46	5.2	18.9
9	13.4	22.3	47	6.2	18.6
10	15.1	13.4	48	6.3	15.9
11	16.6	11.1	49	6.1	14.5
12	18.7	8.9	50	6.6	14.0
13	21.5	6.6	51	5.4	14.5
14	25.0	4.3	52	6.1	14.7
15	27.9	3.1	53	6.5	16.5
16	30.8	2.5	54	6.8	18.3
17	35.4	2.1	55	6.8	20.6
18	37.1	1.5	56	6.2	22.7
19	38.5	1.2	57	6.4	[1]26.0
20	34.3	1.1	58	7.5	26.8
21	25.6	1.2	59	9.5	26.4
22	21.6	1.2	60	10.9	26.2
23	19.7	1.1	61	12.0	24.8
24	([2])	([2])	62	13.7	22.2
25	([2])	([2])	63	14.6	18.3
26	([2])	([2])	64	15.3	16.3
27	([2])	([2])	65	16.9	13.1
28	12.7	22.0	66	15.6	11.6
29	9.2	21.4	67	18.5	10.9
30	6.7	22.4	68	20.1	11.6
31	5.2	22.9	69	19.3	11.7
32	3.5	22.0	70	17.3	11.0
33	2.9	20.9	71	[3]16.3	[3]8.8
34	2.7	20.3	72	[3]14.2	[3]9.0
35	2.6	19.9	73	[3]12.4	[3]8.3
36	2.3	20.1	74	[3]10.5	[3]7.4
37	2.5	20.1	75	[3]8.7	[3]6.1

[1]Based on two observations.
[2]Reconstruction interval.
[3]Based partly on interpolation.

These values were used in applying Equations (7) and (8) to data from the exploited test populations (Table 11). Curves for the test populations (Figure 13) followed the general trend of the biomass levels, even though oscillatory deviations were great.

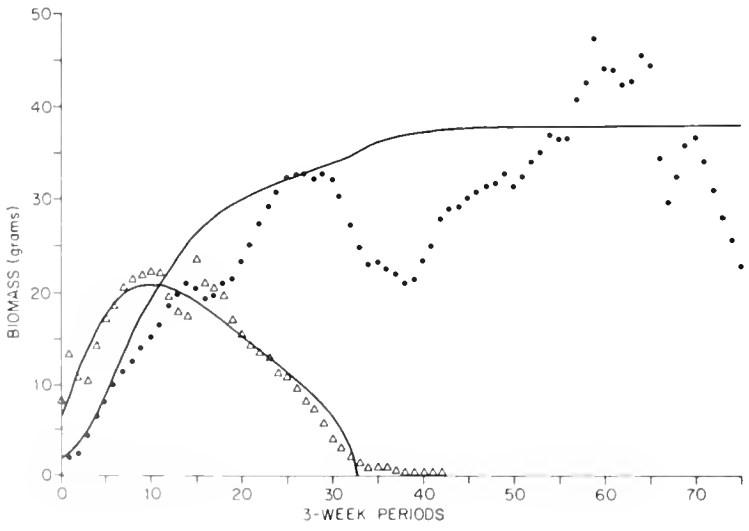

FIGURE 12.—Fitting of simulation model to control populations. Dots are for guppy, triangles for swordtail. Solid lines are fitted curves.

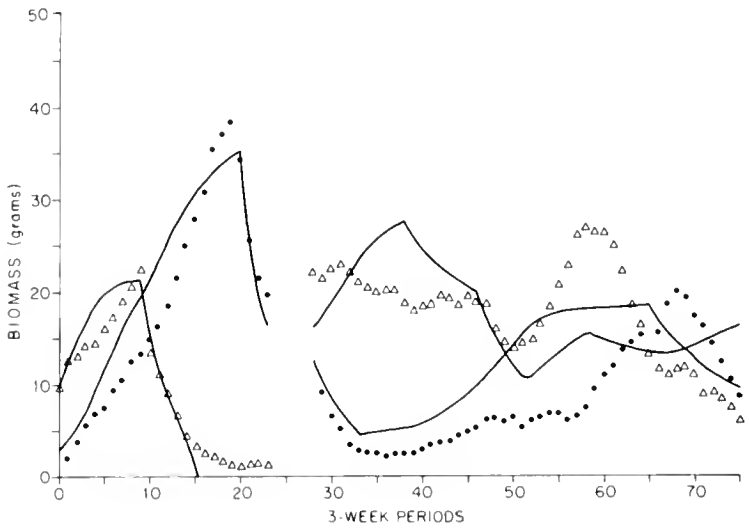

FIGURE 13.—Fitting of simulation model for test populations. Dots are for guppy, triangles for swordtail. Solid lines are fitted curves.

Oscillatory Fluctuations

The substantial oscillatory deviations evident in comparisons of observed and simulated biomass levels (Figures 12, 13) suggest the need for special study. Deviations can be evaluated more readily if they are plotted along a straight baseline (Tables 12, 13; Figure 14). Viewed in this manner, deviations appear at least roughly regular with respect to time. Also, they tend to be similar for control and test populations of the guppy for comparable periods. They did not, therefore, result solely from perturbations due to exploitation, although in the test populations deviations were somewhat greater post-exploitation than pre-exploitation.

Oscillations of the type described above seem to be basic to many populations. Walter (1973) points out that such a fluctuation occurred in Lake Michigan alewives. He developed delay-differential equations which are compatible with "an oscillatory sort of behavior centered about the equilibrium level." Although it would be of interest to apply such models to the guppy-swordtail data, it is unlikely that they would provide substantially different results insofar as the basic relations between exploitation and yield are concerned. It is with such relations that I am primarily concerned in this paper.

Since there were some fluctuations in water temperature (Figure 1) during the course of the experiments, it seemed possible that these might have caused all or part of the oscillatory population changes. To test this, a regression was erected for periods 33-75, when temperature fluctuations were fairly regular. The independent variable was water temperature, and the dependent variable was deviation of the control guppy population biomass from that predicted by the simulation model (Table 12, Figure 14). Results showed no significant correlation between biomass deviations and temperature ($r = 0.087$, $P > 0.1$).

It is worthwhile in this discussion of oscillatory

TABLE 12.—Deviations of actual biomass from theoretical, on basis of fitted model, guppy.

Period	Deviation (g) Control	Test	Period	Deviation (g) Control	Test
0	−0.4	−1.0	38	−15.7	−2.7
1	−0.4	−1.8	39	−15.5	−2.9
2	−1.1	−1.5	40	−13.7	−2.6
3	−0.4	−1.5	41	−12.2	−2.8
4	−0.1	−2.3	42	−9.6	−3.0
5	−0.5	−3.7	43	−8.4	−3.5
6	−0.7	−4.1	44	−8.4	−3.6
7	−1.5	−5.2	45	−7.3	−3.9
8	−2.7	−5.1	46	−6.8	−4.5
9	−3.2	−6.0	47	−6.2	−4.6
10	−3.8	−6.2	48	−6.0	−5.5
11	−4.0	−6.6	49	−5.0	−6.9
12	−3.5	−6.5	50	−6.3	−7.6
13	−3.7	−5.7	51	−5.2	−9.9
14	−3.8	−3.9	52	−3.6	−10.1
15	−5.6	−2.6	53	−2.5	−10.4
16	−7.7	−1.0	54	−0.7	−10.6
17	−8.2	2.4	55	−1.3	−10.9
18	−7.7	3.1	56	−1.2	−11.7
19	−7.9	3.8	57	3.0	−11.6
20	−6.4	−1.0	58	4.9	−10.5
21	−5.2	0.0	59	9.6	−8.6
22	−3.5	1.6	60	6.4	−7.3
23	−2.1	3.4	61	6.2	−6.3
24	−0.9	(1)	62	4.7	−4.7
25	0.3	(1)	63	5.0	−3.9
26	0.3	(1)	64	7.8	−3.2
27	0.0	(1)	65	6.7	−1.7
28	−0.8	0.2	66	−3.4	−0.9
29	−0.7	−1.2	67	−8.1	3.2
30	−1.7	−1.9	68	−5.3	5.6
31	−4.1	−1.9	69	−2.0	5.6
32	−7.4	−2.3	70	−1.1	4.6
33	−10.2	−1.8	71	−3.7	4.6
34	−12.4	−2.0	72	−6.9	3.2
35	−12.6	−2.2	73	−9.8	2.0
36	−13.7	−2.7	74	−12.3	0.6
37	−14.6	−2.7	75	−15.0	−0.7

[1]Reconstruction interval.

TABLE 13.—Deviations of actual biomass from theoretical, on basis of fitted model, swordtail.

Period	Deviation (g) Control	Test	Period	Deviation (g) Control	Test
0	2.2	0.1	38	0.3	−8.8
1	4.5	0.3	39	0.3	−8.0
2	−0.8	−1.8	40	0.3	−6.2
3	−3.3	−2.6	41	0.3	−5.0
4	−1.9	−4.1	42	0.3	−3.1
5	−0.6	−3.7	43	0.0	−2.6
6	−0.4	−3.3	44	0.0	−2.7
7	0.5	−2.1	45	0.0	−1.0
8	0.9	−0.8	46	0.0	−0.9
9	0.9	1.0	47	0.0	1.3
10	1.3	−2.4	48	0.0	0.7
11	1.2	−0.8	49	0.0	1.1
12	−1.2	0.1	50	0.0	2.0
13	−2.4	0.2	51	0.0	3.8
14	−2.4	0.3	52	0.0	4.0
15	4.5	2.1	53	0.0	4.7
16	2.6	2.5	54	0.0	5.6
17	2.6	2.1	55	0.0	7.1
18	2.7	1.5	56	0.0	8.5
19	0.7	1.2	57	0.0	11.2
20	0.1	1.1	58	0.0	11.4
21	−0.4	1.2	59	0.0	11.2
22	−0.4	1.2	60	0.0	11.4
23	−0.2	1.1	61	0.0	10.3
24	−1.1	(1)	62	0.0	8.0
25	−0.6	(1)	63	0.0	4.5
26	−1.2	(1)	64	0.0	2.7
27	−1.7	(1)	65	0.0	−0.2
28	−1.6	5.8	66	0.0	−1.7
29	−2.0	4.1	67	0.0	−2.4
30	−2.5	3.6	68	0.0	−1.8
31	−2.0	2.4	69	0.0	−2.0
32	−1.1	0.2	70	0.0	−3.1
33	1.5	−2.3	71	0.0	−5.7
34	1.0	−4.2	72	0.0	−6.0
35	0.9	−5.6	73	0.0	−7.1
36	1.0	−6.3	74	0.0	−3.5
37	0.6	−6.9	75	0.0	−5.2

[1]Reconstruction interval.

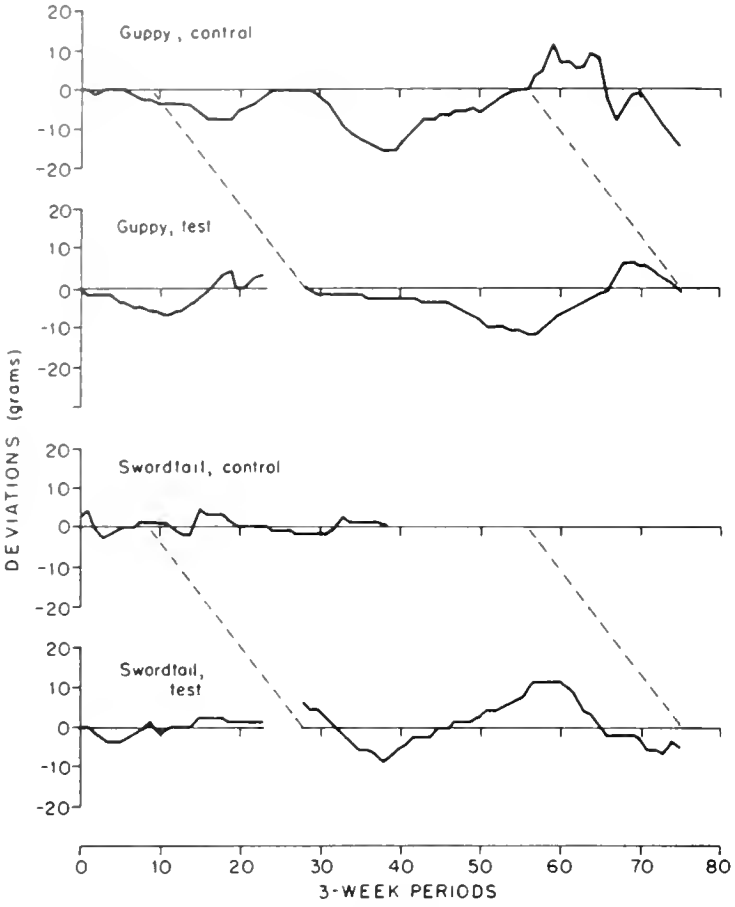

FIGURE 14.—Deviations from simulation model. Broken lines show lags for comparable portions of test and control populations.

fluctuations to consider the models fitted under independent and competing conditions. The former were based on equilibrium population conditions, whereas the latter recognized non-equilibrium conditions and used nonlinear differential equations capable of expressing continuous variation in population and yield under stable-limit cyclic variation. Conclusions for management may be different under the second type of formulation, nevertheless I feel that the conclusions drawn below are of value.

Finally, it is pertinent to discuss what seems likely to have been the start of an oscillatory fluctuation in the independent population of the swordtail. As mentioned under "Course of Populations," number and biomass increased during the final five brood intervals, contrary to what might be expected as a result of the 16.7% exploitation rate applied. The incipient oscillation may have been triggered by the low level of biomass reached just before it began, through overcompensation of the population. This level was lower than any that had been in effect since the initial growth of the population, and it may have moved the population toward the high recruitment rates shown in Figure 7.

CONCLUSIONS

Extinction of the swordtail population in the control pair (Figures 4, 12) as mentioned under "Course of Populations," is compatible with the theory of competitive exclusion first advanced by Gause (1934). He stated that where two populations are fully competing, one will have a slight advantage in growth or aggression and eventually displace the other. This occurrence illustrates one of the values of conducting population experiments over a sufficient period for natural phenomena to develop. The extinction of the swordtail could hardly have been anticipated during the first few months of the experiment, when growth of the swordtail actually outstripped that of the guppy. Gause's phenomenon of "mutual depression" (Gause and Witt 1935) also was exemplified in the experiments. Quantitative measures of this were provided by the coefficients of competition, c_1 and c_2, determined (by successive trials) for Formulae (7) and (8). These were 0.071 and 0.120 for the guppy and swordtail, respectively. These values show greater depression for the swordtail than for the guppy and, therefore, the superior competitive ability of the guppy. Growth advantage for the guppy was indicated by the values of k and P_∞ (Table 9), both of which were greater for the guppy.

My greatest interest in these experiments was to discover what combination of exploitation rates would produce the greatest sustainable yield for the two populations. This problem can be approached by calculating equilibrium yields for pairs of population sizes P_1 and P_2. At equilibrium, the left hand sizes of Equations (7) and (8) are equal to zero; with the constants already determined, F_1 and F_2 can be calculated for any pair of values P_1 and P_2. To obtain 3-wk yields, F_1 and F_2 were converted back to m_1 and m_2 by the formula $m = 1 - \exp(-F)$. Then total 3-wk yields, comparable to the yields actually obtained in the experiments (Table 8), represent the sum of m_1P_1 (guppy) and m_2P_2 (swordtail). Yields are directly comparable for the guppy, but values in Table 8 must be multiplied by three fourths for the swordtail.

I expressed the total yields ($m_1P_1 + m_2P_2$) in the form of yield isopleths (Figure 15). Inspection of

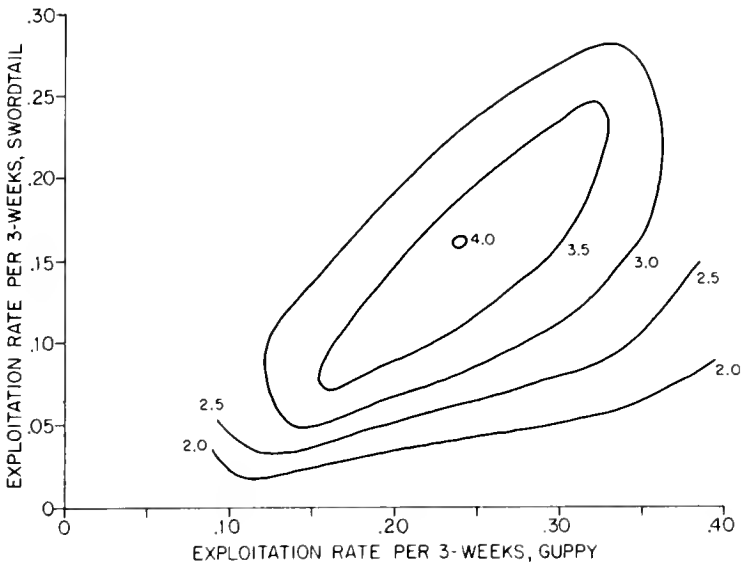

FIGURE 15.—Yield isopleths from data supplied by the simulation model. Numbers by isopleths indicate guppy yield plus swordtail yield per 3-wk period, in grams.

these isopleths reveals a ridge of high yields running roughly from $m_1 = 0.16$, $m_2 = 0.08$ to $m_1 = 0.33$, $m_2 = 0.24$. Thus, the optimal exploitation rate for the swordtail was always lower than that for the guppy, in agreement with the previously mentioned lower productive capacity of the swordtail. Also, moving from the high yield ridge toward either of the axes is moving toward lower yields. To the extent that they can be generalized, these two findings suggest that where two populations are competing, fishing both will produce greater sustainable catches than fishing either alone, provided that fishing rates are adjusted to the relative productivity of each species. The conclusion provides some support for the idea that excessive fishing of the sardine alone led to the catastrophic decline in catches in the California sardine-anchovy situation mentioned in the introduction. It is recognized that in many real fisheries, species are fished jointly by the same gear. In this case it is not possible to adjust the fishing rates separately, and results will be different (yields for a joint F will be less than for separate F's).

The maximum sustainable two-species yield, as indicated in Figure 15, is 4 g per 3-wk period, with $m_1 = 0.24$, $m_2 = 0.16$. It is of interest to see how efficiently food was used at these exploitation rates. Since juvenile fish were returned to the adult tanks from the nursery tanks, food placed in the latter must be included. During exploitation, all of the food in the adult tanks was eaten but not in the nurseries. Therefore the food consumed was between 1.0 and 1.5 times the adult amount, since food amounts for the nurseries were one-half those for the adult tanks. Three times the weekly totals of Table 1 gives 17.10 g for adult tanks only and 25.65 g for adult plus nursery tanks (weights of *Artemia* nauplii were negligible in data to two decimal places). The 4 g per 3-wk yield therefore represents food conversion efficiencies of between 0.16 and 0.23

The above efficiencies may be compared with those from the independent populations. The Fox (1970) models fitted as described under "Determination of Constants" provided estimated maximum 3-wk sustainable yields of 3.7 g for the guppy and 2.9 g for the swordtail (the latter converted from 4-wk to 3-wk basis). Food amounts were the same as for the competing populations and the comparable conversion efficiencies were 0.14 to 0.22 for the guppy and 0.11 to 0.17 for the swordtail. The range for the guppy is in reasonable agreement with the 0.20 reported by Silliman and Gutsell (1958) and 0.23 by Silliman (1968). That the guppy range is higher than the swordtail range is in keeping with other findings of superior guppy productivity reported above. Both ranges are below that for the competing populations. If significant, this difference suggests a slight gain in efficiency of the competing populations over either species growing alone.

Because the above conclusions have been derived from a mathematical model developed from the Volterra (1928) and Fox (1970) models, it is of value to refer to the work of Larkin (1963). He too used the Volterra equations as a point of departure. He applied his analyses only to hypothetical data, but his conclusions are nevertheless in general agreement with those given above. It is of interest to note his statement: "It is concluded that this formulation of interspecific competition together with variations should be applied to laboratory or natural situations to test its usefulness as a basis for prediction."

ACKNOWLEDGMENTS

George F. Slusser contributed part of the initial stocks of guppies and maintained the experimental populations during the first 20 mo of the experiment. Subsequent maintenance was performed successively by Christopher E. Mathews, Martin G. Beam, Jimmy R. Chrnaoski, and Judy A. Trauth. All of these persons are present or past

members of the National Marine Fisheries Service (formerly Bureau of Commercial Fisheries).

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PHEROMONAL STIMULATION AND METABOLITE INHIBITION OF OVULATION IN THE ZEBRAFISH, *BRACHYDANIO RERIO*[1]

LO-CHAI CHEN AND ROBERT L. MARTINICH[2]

ABSTRACT

Female zebrafish, *Brachydanio rerio*, would not ovulate in the absence of males in waters previously inhabited by the fish. Chemical presence of males and fresh, dechlorinated tap water each induced ovulation in about half of the trials. Application of the two factors in combination gave 100% ovulation. These results suggest that in the zebrafish a pheromone released by the males stimulates ovulation and that metabolites produced by the fish repress ovulation. It is postulated that metabolites restrict spawning of the fish to the rainy season and that the pheromone functions in synchronizing reproductive readiness between sexes or in conserving courtship energy expenditure.

In a study concerning egg size, incubation period, and growth in the zebrafish, *Brachydanio rerio* (Hamilton-Buchanan), we encountered the problem of having to strip eggs from the females to synchronize the fertilization of the eggs artificially. We tried the method described by Hart and Messina (1972) without successes. We have regularly been able to induce natural spawning by introducing ripe individuals of both sexes from their holding tanks at 27°C together into a bowl of fresh, dechlorinated tap water at 21°C. Some of the changes associated with this introduction, such as the chemical presence of the males (pheromone), the physical presence of the males (visual, auditory, tactile, and lateral line), fresh tap water (absence of accumulated metabolites), and temperature shock (from 27° to 21°C), may be capable of inducing ovulation.

The roles of these factors in controlling reproduction in fishes have been well documented. Some of the examples are:

Pheromones–Aronson 1945; Tavolga 1956; Amouriq 1965; Gandolfi 1969; Rossi 1969; and Chien 1973.

Visual–Aronson 1945, 1965; Tavolga 1956; Rossi 1969; and Chien 1973.

Auditory–Tavolga 1956; Brawn 1961; Gray and Winn 1961; and Myrberg and Spires 1972.

Tactile–Egami and Nambu 1961.

Metabolites–Swingle 1956; and Greene 1966.

Temperature–Harrington 1959; Aronson 1965; and de Vlaming 1972a, b.

Much of the information in the literature, however, does not clearly distinguish between gonad development, ovulation, and spawning. The present study was undertaken to single out such ovulation-inducing factors.

MATERIALS AND METHODS

Female zebrafish were kept at 27.0 ± 1.0°C in 40- or 60-liter aerated aquaria subdivided into three or four compartments by perforated plastic dividers, one female per comparment to enable identification. Male zebrafish were isolated in aerated 20-liter aquaria at room temperature (21.0 ± 1.0°C). No visual contact was permitted between sexes. All individuals were subjected to 12 h of light per day and were generously fed "Tetramin"[3] in the morning and frozen brine shrimp in the evening. To ensure fertility, each fish was initially permitted to spawn naturally. This was done by introducing the fish into fresh, dechlorinated tap water at room temperature in a 20-cm finger bowl with another individual of the opposite sex. A total of 27 fertile females and 19 fertile males were used.

Eight experiments were designed to test the relative contribution of each factor individually, and in combination, on ovulation in the zebrafish (Table 1). In experiments 1 to 7, a female was transferred from the holding compartment into

[1]The data in this paper were extracted from the master's thesis of R. L. Martinich.

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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TABLE 1.—Design and results of experiments to test factors suspected of influencing ovulation in the zebrafish. Symbol "+" indicates presence of the factor and symbol "0" indicates absence of the factor. The chi-square values are for comparing results of any experiment with that of the control (experiment 8), and the 0.01 level critical limit is 6.63.

Item	Experiment								
	1	2	3	4	5	6a	6b	7	8
Factors:									
Pheromone	+	+	+	+	0	0	0	0	0
Temperature shock	0	+	+	+	+	+	+	0	0
Fresh tap water	+	+	+	0	+	+	+	+	0
Visual image of male	0	0	?	0	+	0	0	0	0
Auditory and/or lateral line stimulation	0	0	+	0	0	0	0	0	0
Number of females used	18	14	19	14	9	19	18	16	14
Results:									
Trials eggs obtained	20	15	21	8	5	17	10	7	0
Trials no eggs obtained	0	0	1	8	5	18	13	10	17
Chi-square	33.1	28.1	31.4	8.7	7.4	10.2	7.7	6.5	—
% positive responses	100	100	95	50	50	49	44	41	0

the experimental chamber for 12 to 18 h in nearly all the trials but for only 4 h in several instances in experiment 2, and then stripped by applying gentle pressure onto the abdomen. The release of ripe ova indicated that the fish had completed ovulation. Failure to give eggs, or the release of immature or ruptured eggs, was considered a negative response. Ripe ova are nearly translucent, round, and about 0.8 mm in diameter before taking on any water, and are not attached to each other. Immature ova are often opaque, may be undersized and irregularly shaped, and are often in clumps. In experiment 8, the female was stripped immediately upon removal from the holding compartment.

After successful stripping, the female was immediately permitted to spawn naturally with a male in order to assure release of all ovulated ova. After approximately 4 to 8 h, the male was removed, and the female was returned to her compartment the following day. Between experiments each female was allowed to rest for 8 to 12 days, and males 4 to 6 days.

After an unsuccessful attempt of stripping eggs, the female was presented with either male pheromone and/or fresh tap water, whatever was lacking originally in the experimental chamber, and then stripped again 4 to 18 h later. If the second stripping failed again, then the female was permitted to spawn naturally with a male. In cases where natural spawning failed, data pertaining to that female were rejected. This procedure assured that an unsuccessful attempt at stripping a female of eggs was due to the subjected treatment and not due to an unripe condition of the female.

Trials of different experiments were alternated randomly without any definite chronological sequence.

The experimental chambers in experiments 1, 2, 5, 6, and 7 were 5-liter all-glass aquaria. In experiment 3, 20-liter aquaria were used and were partitioned into two halves, one the experimental chamber and the other the male chamber. The partitionings were done with 1-mm thick opaque plastic divider perforated with holes 1.5 mm in diameter and 3 mm apart. In experiment 4, a 60-liter aquarium was used and was partitioned with nonperforated black plastic dividers into a 30-liter metabolite chamber, a 15-liter male chamber, and a 15-liter experimental chamber. Water was circulated from the metabolite chamber into the male chamber, and then to the experimental chamber and back to the metabolite chamber by means of pumping and siphoning.

The presence of the male pheromone in experiments 1 and 2 was established by air lifting into the experimental chambers water from a 5-liter aquarium into which a male was introduced simultaneously with the introduction of the female into the experimental chamber, the water then was siphoned back into the male aquarium. In experiments 3 and 4, male pheromone was provided by placing, during the experimental period, a male into the male chamber which was chemically continuous with the experimental chamber because of the perforations or water circulation.

The presence or absence of temperature shock was established by maintaining the experimental chamber respectively at room temperature (21.0± 1.0°C) or at the temperature of the holding compartments (27.0 ± 1.0°C).

The absence of metabolites in experiments 1, 2, 3, 5, 6, and 7 was attained by filling the experimental chamber and the male chamber with fresh, dechlorinated tap water. In experiment 4, metabolites were presented by conditioning the system for at least 2 wk with 75 mature zebrafish of both sexes in the metabolite chamber which is

chemically continuous with the experimental chamber because of the water circulation.

Visual stimuli from a male were provided in experiment 5 by allowing the test female to be in visual contact with a mature male in a separate, chemically discontinuous all-glass aquarium. In experiment 3, the perforations of the divider partitioning the male chamber and the experimental chamber provided questionable visual stimuli from the male. In all other experiments (1, 2, 4, 6, and 7), visual stimuli from males were screened by visually isolating the experimental chambers with cardboard or black plastic sheet.

Possible auditory and lateral line stimuli from male were allowed in experiment 3 through the perforated condition of the partition separating the experimental chamber from the male chamber.

In experiment 6a, the experimental chamber was a simple 5-liter all-glass aquarium, whereas in experiment 6b a current similar to that in experiments 1, 2, 4, and 7 was provided by air lifting and back-siphoning of water between the experimental chamber and a vacated 5-liter aquarium.

Prior to each experiment, the glass aquaria and hoses were scrubbed, soaked, and thoroughly rinsed with tap water. Experiments testing the pheromonal responses utilized a different set of hoses from those used in experiments lacking the male pheromones. Different nets were used for netting males and females as a precaution against contacting a test female with the slime of a male.

RESULTS

The number of positive responses (trials eggs obtained) and negative responses (trials no eggs obtained) are given for each of the eight experiments in Table 1. The results of each experiment were compared with those of experiment 8 and the chi-square value was calculated. The percent of trials resulting in a positive response is also given for each experiment.

It is apparent from the results that presence of pheromone and absence of metabolites are the two most influential factors stimulating ovulation in the zebrafish. Experiments 1, 2, and 3 in which pheromone was provided and metabolites were absent invariably gave nearly 100% ovulation. Experiments 4, 5, 6, and 7 in which either pheromone was provided or metabolites were absent gave 40-50% ovulation. However, in experiment 8 in which pheromone was absent and metabolites were present, no ovulations were observed. The roles of metabolites and male pheromone are further indicated by the fact that females which initially responded negatively in experiments lacking the male pheromone and/or fresh tap water (experiments 4, 5, 6, and 7) gave eggs in the second stripping in all cases upon being presented with the missing factor(s).

None of the other factors tested, including temperature shock and auditory and/or lateral line stimulations seem important in controlling ovulation, as in no cases did their presence or absence significantly alter the results. The influences of water movement between the experimental chamber and the male chamber were insignificant, as there is no difference between results of experiments 6a and 6b.

Successful stripping was recorded at all times over the morning, afternoon, and early evening. After the stripping, without exception, a pair would commence natural spawning immediately upon introduction regardless of the time of day.

DISCUSSION

In the absence of the male pheromone and the presence of the metabolites, females consistently failed to ovulate (experiment 8). Under similar condition, Eaton and Farley (1974) also failed to strip eggs from isolated females. Histological studies of zebrafish ovaries by Hisaoka and Firlit (1962) indicated that oocytes are not released from the ovarian stroma into the central lumen and oviducts (ovulation) until stimulated by males during the breeding process. Eaton and Farley (1974) were able to obtain ripe ova from isolated females in the morning only after a brief (7 h) introduction of a male into the female's tank on the previous day. They suggested that the vigorous chasing behavior exhibited by the male toward the female might have provided the stimulus, although no supporting data were provided.

The results of the present study clearly establish that a male pheromone stimulates ovulation of the female. Little is known about the nature of the male pheromone. It appears not to be species specific since circulation of water between aquarium containing male *Brachydanio albolineatus* and aquarium containing female *B. rerio* elicited ovulation in the female in four out of four trials. Intrageneric interspecific effec-

tiveness of sex pheromone has also been demonstrated by Rossi (1969) in *Colisa lalia* and *C. labiosa*. In this case a female pheromone can induce nest building in heterospecific males.

As to the chemical nature of piscine sex pheromones, Amouriq (1965) identified an estrogen as the pheromone inducing hyperactivity in male *Lebistes reticulata*, and Tavolga (1956) identified the internal fluid of the ovary as the source of the chemical stimulus eliciting courtship behavior of male in *Bathygobius soporator*. In the present study, of six trials consisting of placing test females into fresh tap water previously occupied for 24 h by a male, only four positive responses were recorded. Since the metabolites produced by a male in 24 h are far below the threshold level for inhibiting ovulation, as we have experienced and as Greene (1966) has reported, the two failures out of six trials in the above experiment suggest either that the male pheromone is short lived or that less male pheromone was released in the chemical absence of the female.

The selective advantage of an ovulating pheromone in the zebrafish is not clear. Although Hart and Messina (1972) claimed to be able to obtain sperm from male zebrafish at all times under laboratory conditions, we often encountered unsuccessful milking of males. If both sexes are not sexually ready at all times, it would be advantageous to synchronize sexual readiness between sexes. If release of the ovulating pheromone corresponds with male readiness, synchronization would be guaranteed. However, males appeared to release the pheromone quite regularly, even while in the presence of metabolites as suggested by the 50% ovulation in experiment 4. Yet, it is possible that while the metabolites may repress testicular development or spermiation and the release of the pheromone by the males, the test male introduced at the same time as the test female into the two small chambers of experiment 4 was often already sexually ready at that time and would thus release the pheromone regardless of the presence of metabolites.

Such a pheromone, if functioning in synchronization, would be advantageous for a species with a long spawning interperiod. Although female zebrafish can spawn every 1 or 2 days under laboratory conditions (Eaton and Farley 1974), the spawning interperiod in the native habitat is not known.

In some fishes, it is possible that the active chasing of the female by the male prior to spawning takes part in stimulating ovulation. An ovulating pheromone would conserve such chasing energy and therefore, be selectively advantageous.

The inhibitory effect of metabolic wastes on fish reproduction has been reported by Greene (1966) who found that an increase in metabolite concentration resulted in a decrease in the number of successful natural spawnings in the zebrafish. Lin (1935) observed that grass carp, *Ctenopharyngodon idellus*, would spawn only after a rise in the river water due to rain. Similar observations confirming the coincidence of heavy rain and spawning have been made by von Ihering and Wright (1935) and Lake (1967). Lake suggested that the stimulatory effect of rain on fish spawning was through addition of soil elements through runoffs. However, according to Swingle (1956), draining a pond crowded with goldfish or largemouth bass and refilling it subsequently with new water could induce spawning in the pond fish. One of us (Chen) had observed on numerous occasions that goldfish spawned during or after rain in outdoor concrete tanks. In these cases, spawning occurred without input of soil elements. Swingle (1956) suggested that the effect of rain was to dilute a spawning repressive factor. It is obvious from the present experiment that this repressive factor is metabolites.

Tang (1963) noted that the testes of silver carp, *Hypophthalmichthys molitrix*, would develop only after the volume of the reservoir had been increased by rain, thus suggesting that maturation of testes may be retarded by waste products from fish and that new water, or dilution of these wastes, is necessary for sexual development. It is possible that removal of the metabolites can also induce the release of the pheromone by the male zebrafish, indirectly stimulating ovulation in the females. In the present study, however, removal of the metabolites apparently had a direct effect on the females, as mere exposure of the females to fresh tap water resulted in ovulation in nearly half of the trials (experiment 7). Tang (1957) reported that female common carp inhibited from spawning by metabolic wastes would release eggs in the absence of males upon introduction of new water.

The chemical nature of the inhibiting metabolites is not known. Greene (1966) believed that they were ammonia. From the observation made by Swingle (1965) that crowding of bluegill inhibited spawning in the largemouth bass in the

same pond, the inhibiting metabolites cannot be species specific.

As discussed earlier, many of the freshwater fishes in the tropics spawn only in the rainy season. During this period, there is an addition of flooded lowland suitable for the deposition of eggs, an increase in the dissolved oxygen favorable for embryological development, and an increase of organic and inorganic nutrients which promote growth of food plankton. Rain would also dilute any metabolic wastes accumulated during the dry season. In this context, metabolites may serve as a controlling factor, repressing ovulation until the rainy season when environmental conditions are more favorable for both embryo development and larval growth.

The results of the present study clearly indicate the stimulatory effect of the male pheromone and the inhibitory effect of metabolites on ovulation in the zebrafish. As gonadotropin is known to be effective in inducing ovulation in fishes, either directly, or via stimulating the synthesis of corticosteroids and/or progesterone (Donaldson 1973; de Vlaming 1974), the action of the ovulating pheromone and the metabolites is probably to activate or to deactivate the hypothalamus-pituitary-gonad axis. A pheromonal facilitation of gonadotropin-induced ovulation has been reported in mouse (Zarrow et al. 1973). Further studies are needed to clarify the route of action of the pheromone and the metabolites.

Aronson (1965) cited numerous examples in fishes in which gonadal development and subsequent spawning were stimulated by either an increase or a decrease in temperature. An increase in temperature has been reported to affect the gonadal response to treatment with gonadotropin in *Lepomis cyanellus* by Kaya (1973) and in *Gillichthys mirabilis* by de Vlaming (1972c). In the present study, a sudden decrease in temperature alone does not seem important in stimulating ovulation in the zebrafish.

In the zebrafish, visual or auditory and lateral line stimuli between sexes do not seem important in enhancing ovulation, although some of these factors may be pertinent in eliciting the proper behavior during the actual spawning act.

The onset of light alone is not sufficient to stimulate ovulation, as demonstrated by the complete failure to strip eggs during the morning hours from females tested directly from their holding compartments (experiment 8). Furthermore, these females were stimulated to ovulate later that day, after exposure to the male pheromone and fresh tap water. Ovulation and natural spawning were induced regardless of time of day. One of us (Chen) has observed natural spawning of zebrafish to commence at midnight in darkness and continue for hours. These observations conflict with all previous accounts that the onset of light is important to trigger ovulation and spawning in the zebrafish (Legault 1958; Hisaoka and Firlit 1960; Eaton and Farley 1974).

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ACTIVITY, MOVEMENTS, AND FEEDING BEHAVIOR OF THE CUNNER, *TAUTOGOLABRUS ADSPERSUS*, AND COMPARISON OF FOOD HABITS WITH YOUNG TAUTOG, *TAUTOGA ONITIS*, OFF LONG ISLAND, NEW YORK[1]

BORI L. OLLA, ALLEN J. BEJDA, AND A. DALE MARTIN[2]

ABSTRACT

Field observations off Long Island, N.Y., using scuba and ultrasonic tracking, showed the cunner, *Tautogolabrus adspersus*, to be active during the day and inactively lying in shelter at night. Fish restricted their movements during the day, remaining within 2 m of the structure providing the nighttime shelter. The fish overwinter within their home territory in a torpid, nonfeeding state. Cunner fed primarily on invertebrates, foraging both benthically and in the water column. Competition between cunner and young tautog, *Tautoga onitis*, for *Mytilus edulis* was apparent during May-June when it is the major food item for both species. But beginning in July and extending through October, while tautog continued to feed primarily on mussels, cunner shifted to a diet consisting mainly of the isopod, *Idotea baltica*.

Almost any bottom relief, natural or man-made, including rock outcroppings, piers, pilings, and boat docks, provides the basic physical structure for temperate-water reef communities of fishes. While not as diverse in the number of residents as tropical and subtropical coral reefs, these communities represent an important component of the inshore marine resources of the Atlantic coast of North America. The cunner, *Tautogolabrus adspersus*, is a prominent member of temperate-water reef communities. This ubiquitous inshore species ranges from northern Newfoundland to the mouth of Chesapeake Bay (Leim and Scott 1966) and between Cape Cod and Delaware Bay is often found co-residing with the tautog, *Tautoga onitis*, the only other labrid inhabitant of the region. The close relationship of the cunner to inshore structures makes the species highly available to the angler while at the same time placing the fish in proximity to the potential effects of inshore pollution.

Our aim in this study was to describe daily and seasonal movements of the cunner as well as their feeding habits as compared with those of young tautog of similar size.

MATERIALS AND METHODS

Observations of activity and movements of the cunner were made indirectly by ultrasonic tracking of individual fish and directly with scuba. The detailed procedures used in capturing, handling, and tracking individual fish have been described by Olla et al. (1974). The ultrasonic transmitters, manufactured by Chipman Instruments,[3] (Henderson et al. 1966) measured 30×9 mm and emitted pulsed signals at frequencies of 58 to 70 kHz. These were attached externally to the fish by monofilament line passed through the dorsal musculature just below the midpoint of the dorsal fin. The transmitters were made neutrally buoyant by the addition of a styrofoam collar encased in silicone.

Eight fish were captured and tracked at one of three locations (Sites A, B, and C; Figure 1) in the west end of Great South Bay, Long Island, N.Y., during July and August 1973. Site A was the end of a small peninsula with 0.2- to 0.6-m diameter riprap covering the bottom from 1.2 m above the high water mark extending out 100 m. Water depth ranged from 2.0 to 10.0 m. Site B, the Fire Island Coast Guard basin, was a 110×52×47 m open pentagon, constructed of tongue-and-groove

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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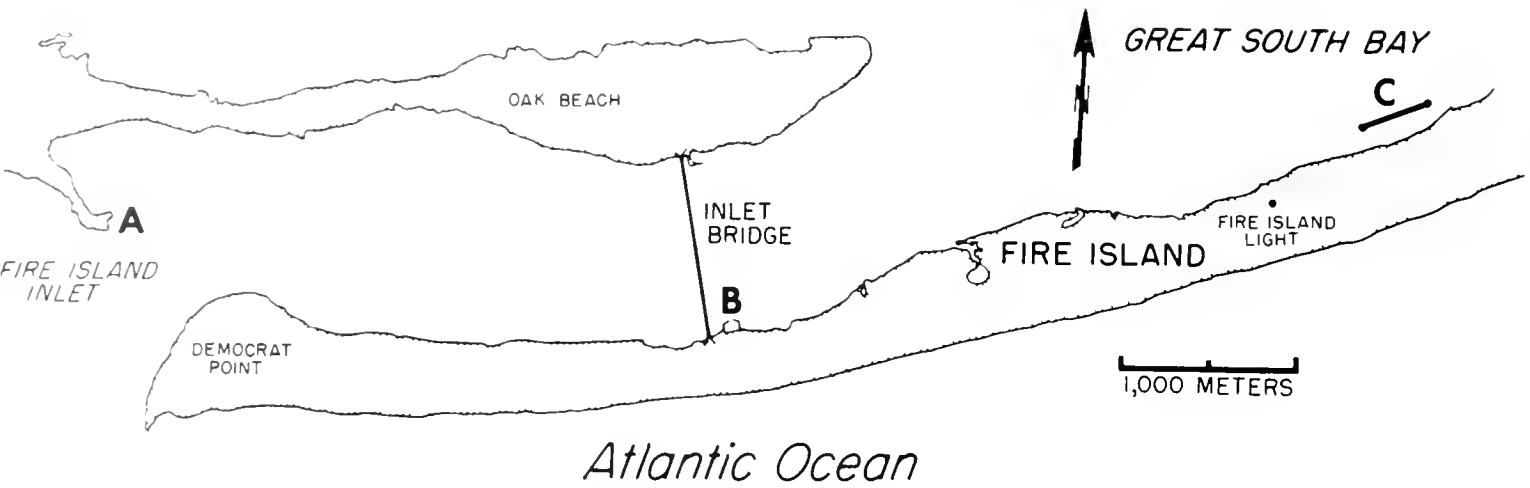

FIGURE 1.–Study area and Sites A, B, and C where cunner were tracked.

planks, steel sheeting, and piles. Water depth along the basin walls varied between 2.4 and 8.8 m with the bottom composed primarily of sand, gravel, and shell. Site C was an artificial reef, 457×46 m, consisting of submerged barges and tires on a sand and gravel bottom in 6 to 7 m of water (Briggs and Zawacki 1974).

Cunner were observed directly with scuba both day and night at weekly intervals from May through October in 1972 and 1973, and at monthly intervals from November 1972 to April 1973 for a total of 200 h (150 h daytime; 50 h nighttime).

Cunner and tautog were collected weekly, May through October at Site A for food habit analysis. The fish were either speared by scuba divers or trapped, and specimens were preserved in 10% Formalin. The contents of the entire digestive tract were examined, the food was identified, and its volume measured (Windell 1968).

RESULTS

Daily Activity and Movements

All fish tracked (Table 1) were active during the day and inactive at night. Tagged fish initiated daytime activity 16 to 41 min following the start of morning civil twilight; cessation of activity occurred 5 to 55 min before the end of evening civil twilight (Table 2). Direct scuba observations confirmed that the fish were active by day and inactive during the night. During the night, the fish were lying against, in, under, or between bottom or vertical structures. While the fish were quiescent at night, general responsiveness was low as indicated by divers being able to touch or capture fish with a hand-held net.

TABLE 1.–Release site, tracking duration, and the maximum distance traveled along the shelter site structure.

Cunner no.	TL (mm)	Release site[1]	Release date	Release time	Tracking duration (h)	Distance traveled (m)
1	190	B	7/10/73	1010	70.8	50
2	197	B	7/11/73	0920	46.7	50
3	172	B	7/16/73	1415	89.8	50
4	180	B	7/17/73	0935	34.9	5
5	215	B	7/23/73	1300	91.0	30
6	200	C	7/31/73	0937	70.8	75
7	220	C	8/ 6/73	1345	90.8	150
[2]8	220	A	7/24/73	0932	69.0	25

[1]Refers to Figure 1.
[2]Track intermittent.

TABLE 2.–The onset (minutes after morning civil twilight) and the end (minutes before evening civil twilight) of the daily activity of individual cunner as determined by ultrasonic tracking.

Cunner no.	Time	Day 1	Day 2	Day 3	Day 4	Day 5
1	Morning	—	36	34	20	—
	Evening	55	22	23	—	—
2	Morning	—	22	16	—	—
	Evening	37	39	—	—	—
3	Morning	—	22	24	34	18
	Evening	37	30	26	34	—
4	Morning	—	31	—	—	—
	Evening	44	41	—	—	—
5	Morning	—	28	—	29	25
	Evening	16	—	15	21	—
6	Morning	—	39	41	25	—
	Evening	42	35	43	—	—
7	Morning	—	26	31	27	24
	Evening	19	13	20	5	—

All of the fish tracked (Table 1) were highly localized in their daily movements, remaining within 2 m of the structures affording cover. The maximum distance traveled by any of the fish along structures ranged from 5 to 150 m.

Due to extreme ambient interference of the transmitter signal encountered during adverse water conditions, cunner no. 8 (Table 1) was

tracked intermittently. When tracking was possible, the fish exhibited the same movement pattern as the other seven fish. All observed movements were restricted to the area of riprap surrounding the release point and did not exceed 25 m from the release point.

While using scuba, we were able to sight three of the tagged fish directly (no. 1, 2, and 4; Table 1). They were feeding and appeared to be normally responsive. The attached transmitter had no apparent effect on orientation or swimming ability.

Seasonal Activity

In late fall, when water temperatures dropped to 5° to 6°C, cunner were observed to be inactive and torpid, lying in cracks and crevices both day and night, similar to what Green and Farwell (1971) described for cunner in Newfoundland and what we described for young tautog (Olla et al. 1974). Some of these fish were covered with a fine layer of silt. Examination of digestive tracts from 17 torpid fish indicated that they were not feeding. The fish remained torpid throughout the winter with water temperatures ranging from 2.5° to 5.0°C until the early spring when they became active as the water temperature rose above 6°C.

Feeding

Cunner generally occur in loosely formed aggregations and feed primarily as individuals rather than in any organized social grouping. One exception to this is the social interaction and facilitation which occur when one or more fish come upon a particularly abundant concentration of food. An increase in the intensity of feeding above that which constitutes the normal grazing, picking, and searching activity serves to attract cunner from the surrounding areas. As the number of fish attracted to the feeding area increases, so does the intensity of feeding, serving to attract more and more fish until the food has been consumed. On a number of occasions (30-40), after placing a clump of *Mytilus edulis* with crushed shells at a particular place on the bottom, we have observed the attraction of 50 or more cunner within 1 to 2 min after the first few fish had found the food and begun to feed.

Cunner feed both in the water column and benthically. When feeding in the water column with a current present, the fish face into the current while maintaining position and visually scanning for suspended food items. Water column foraging is typified by high frequency of eye and head movements as the fish search in all directions. When a food item is sighted, the fish swims to it, grasps the item, and then returns to the original search posture. Fish often search the water column while remaining in close proximity to objects affording cover from the full force of the current. Only after sighting a food item does the fish move into the current to ingest it and then return to its searching position. In this manner, the fish effectively conserves energy otherwise required to maintain its position in the current between ingestions. Discontinuities of the bottom, while providing cover from the current, also act to cause turbulence and upwellings, aiding in separating and spreading the food items. Fish may feed in this manner during the day for an entire tidal cycle, the duration and frequency depending both on food density and level of satiation. A typical food item which cunner may be ingesting during this type of feeding and which occurred in significant quantities in stomach samples was the isopod, *Idotea baltica* (Table 3). This species may occur free floating, attached to bits of flotsam, such as algae or eel grass, or on fixed substrates.

In situations where there is little or no current, cunner search the water column by actively moving. There is a general dispersal and lack of any particular directional orientation in the absence of a current which is similar to Stevenson's (1972) observations of reef inhabitants at Bimini.

When feeding on bottom or vertical substrates, the fish, exhibiting a high intensity of eye movements, visually search the forage area, their snouts touching or within several centimeters of

TABLE 3.—Contents of cunner and tautog digestive tracts.

	Percent of total contents[1]					
	Cunner			Tautog		
Item	May-June	July-Aug.	Sept.-Oct.	May-June	July-Aug.	Sept.-Oct.
Mytilus edulis	57.1	4.3	13.0	74.3	87.9	83.1
Idotea baltica	0.5	72.1	61.7	4.6	2.7	—
Microcrustaceans[2]	4.4	—	—	0.5	—	—
Cirripeds	0.2	1.6	1.9	15.3	2.7	7.4
Brachyurans	13.4	2.0	10.9	4.2	3.6	5.9
Fish remains	11.8	18.1	10.6	—	—	—
Debris	7.6	1.9	1.9	1.1	3.1	3.6
Fish eggs	0.4	—	—	—	—	—
Gastropods	1.2	—	—	—	—	—
Carideans	3.2	—	—	—	—	—
No. fish	31	21	12	14	12	13
TL (mm)	63-215	108-240	154-223	105-254	136-260	177-235

[1]Determined by volume (Windell 1968).
[2]Amphipods, copepods, and mysids.

the substrate surface. On a vertical substrate, they may swim up and down and from side to side, slowly searching an encrusted pile or bulkhead wall for food. When a food item is sighted, the fish grasps and ingests it as well as some of the encrustations, ejecting much of the excess. Foraging in this manner, the fish may cover an area of no more than 4 to 5 m^2 until satiated. Similar search patterns occur along the bottom or in close proximity to rocks, logs, and other structures.

When feeding on *M. edulis*, which comprise a significant part of their diet during part of the year (Table 3), the fish grasp and ingest with the anterior canine teeth, then crush the shell with their pharyngeal teeth in much the same manner as described for tautog (Olla et al. 1974).

Food Habits

Our analysis of digestive tract contents showed that cunner forage on a variety of organisms (Table 3), mainly invertebrates, as has been reported previously (Richards 1963; Chao 1973). While Richards found amphipods to be the most important food item for cunner in Long Island Sound and Chao reported mussels (both *Mytilus edulis* and *Modiolus modiolus*) to occur most frequenty in gut contents of fish collected at Nahant, Mass., our analysis for the sizes studied showed two major food items, *Mytilus edulis* and *Idotea baltica*, comprising 24.8% and 44.8%, respectively, of all food consumed. Our data showed a significant seasonal shift in the utilization of these two major forage species. During the May-June period, *M. edulis* predominated with 57.1% with only 0.5% *I. baltica* present. During July-August, the foraging pattern changed with *I. baltica* then being the major component of the diet at 72.1% and only 4.3% *M. edulis* present. This trend continued into the September-October period with 61.7% and 13.0% for *I. baltica* and *M. edulis*, respectively.

Examination of the digestive tract contents from young tautog (105-260 mm) showed that they were feeding predominantly on *M. edulis* throughout the feeding season (Table 3). Other items present occurred in varying and significantly lesser amounts. Olla et al. (1974) reported the same pattern in feeding for larger tautog.

DISCUSSION

Cunner and tautog, the only labrid inhabitants of north temperate waters of the western Atlantic, are often found co-residing on "reef" habitats south of Cape Cod. The geographical area in which these animals are found is beyond the northern limit for hermatypic corals. Hence, the "reef" habitat, as we define it, includes any natural or artificial structure or relief which provides a habitat for various species dependent, to some degree, on shelter sites (Smith and Tyler 1972), e.g., cracks and crevices, and also serves as a substrate for a variety of attached fauna and flora utilized as food items for resident fish.

Both cunner and tautog are active during the day and inactive at night. The inactive phase of nighttime is characterized by complete quiescence or sleep, a typical trait for labrid species in general (for examples see Hobson 1965, 1968, 1972; Starck and Davis 1966; Tauber and Weitzman 1969; Collette and Talbot 1972).

As was discussed in an earlier paper (Olla et al. 1974), the low level of responsiveness which is characteristic of the sleep phase of labrids and species of similar habit indicates that there is a reduction in the potential to avoid or escape environmental stress that may be imposed during the night.

Both of these species require shelter sites as resting places during the night sleep phase. Cunner of all sizes and tautog of less than 250 mm also appear to require a close association with objects affording shelter by day and during the winter, when they remain in a torpid condition. It is, therefore, obvious that the "reef" habitat, as a provider of shelter sites, would be a limiting factor in the population size of these two species. Any interspecific competition for shelter sites encountered by the cunner would probably be limited to tautog less than 250 mm, with both species requiring shelters of similar type and size. The amount of available shelter for coral reef species is an obvious limiting factor of population size (Sale 1972; Smith and Tyler 1972, 1973).

An attempt to attract or to increase populations of shelter-dependent species has been the development of man-made reefs using a variety of substances including automobile tires and bodies, construction rubble, sunken barges or ships, etc. (see Rickards 1973; Steimle and Stone 1973). The construction of man-made reefs would be most successful in areas in which sufficient food resources are available for the fish to be attracted or where the potentiality for food accretion would be increased by the addition of an appropriate

substrate. These structures would be most effective when placed where both forage species and fish species may be recruited naturally, the only element having prevented their presence previously being the absence of the structure.

The most obvious difference in the feeding habits of cunner and tautog is the greater diversity of organisms eaten by cunner (Table 3). While *Mytilus edulis* makes up the bulk of the diet during the feeding year of the tautog, it comprises a significant part of the cunner diet only during May and June. For the remainder of the feeding year, *Idotea baltica* predominates, with a variety of other invertebrates and fish being ingested by the cunner. The food habits of these fish not only show a change of season, as in this study, but also vary widely with geographic location. Comparing the results of this study with those of Richards (1963) in Long Island Sound and Chao (1973) at Nahant, the diversity in the cunner's feeding is even more apparent.

The more diverse diet of the cunner as compared with the rather restricted one of the tautog in this particular habitat may in part be related to morphological differences between the two species. The cunner, with its narrower, more streamlined body, pointed snout, and thinner lips, is well suited for feeding on the small motile crustaceans, e.g., *I. baltica*, occurring both benthically and in the water column. Davis and Birdsong (1973) in their review of water column foraging in coral reef fishes show morphological differences distinguish water-column foragers from benthic foragers within the same family.

The depletion of specific foods such as *M. edulis* (Olla et al. 1974) in this community, would appear to be far more detrimental to tautog than to cunner. Competition for the same food items would likely occur only during May and June.

Shifts in feeding habits may relate to other variables besides obvious differences in the abundance of the forage species. For example, *I. baltica*, occurring in waters of Denmark, shift their daily rhythm of activity on a seasonal basis while held in the laboratory (Hørlyck 1973). In the spring this species is primarily nocturnal; during late spring and early summer the species becomes more active by day. The cunner, which feeds by day, ingested significantly larger amounts of *I. baltica* during approximately the same time that this species had changed to a diurnal activity pattern. Of course this is, at best, conjecture, since it is not well understood how closely these laboratory observations relate to the field and whether this species would show the same seasonal shift in such widely separated geographic locations.

All of the cunner tracked and observed directly remained within several meters of some structure. This behavior agreed with earlier observations on young tautog (≤250 mm; Olla et al. 1974). Furthermore, we found that tautog of this size and cunner of all sizes studied (50-240 mm) remained inshore during the winter in a torpid state, agreeing with the observations of Green and Farwell (1971). Apparently, the home range for cunner of this size is restricted throughout all seasons to the length and breadth of the structure to which they were originally recruited.

Offshore reefs (primarily shipwrecks) appear to support a population of older and larger cunner than are found in inshore waters. During trawl vessel surveys conducted by the Northeast Fisheries Center (see Grosslein 1969 for a description of the survey program) cunner, 21 to 42 cm, have been collected at stations approximately 100 km southeast of Cape Cod, Mass. These larger fish do not represent any significant part of the cunner population as far as is known at this time, but it is of interest that they do exist. Whether they were originally recruited to these offshore areas and remained there, or were part of an inshore population that moved offshore when reaching a certain size (as is the habit of older tautog) and then remained there, can only be surmised.

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CORRELATION OF UPWELLING INDEX AND DUNGENESS CRAB CATCH

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ABSTRACT

The statistical relationship between upwelling intensity and the annual *Cancer magister* catch is examined using techniques of time series analysis. The statistical relationships between upwelling in different years and crab catch in different years are examined. The statistic used is the correlation coefficient for varying time lag. The results correlating upwelling and crab catch indicate that time lag is short enough to demonstrate that adults are affected, and that the time lag is shorter in California than in Oregon or Washington. The crab catches appear to be cyclic with a period of 9 yr in California and 12 yr in Washington and Oregon. Possible causal mechanisms for the statistical relationships are presented. Results suggest that variations in crab catches may be due primarily to biological rather than abiotic influences.

Large fluctuations in yearly catch in the Pacific Coast Dungeness crab fishery have been observed over the years for which records were kept. The catch in some years is as low as 20% of the catch in good years. Furthermore, the fluctuations seem to be of a cyclic nature: 3 or 4 yr of low catch are often followed by 3 or 4 yr of high catch after which the same pattern occurs. Based on the fact that the variation in catch was similar along the entire west coast, the Pacific Marine Fisheries Commission (1965:38) concluded that a large-scale abiotic influence was responsible.

Many other explanations of the fluctuation in crab catch have rested on Cleaver's (1949) contention that abundance of adult crabs fluctuates widely in accordance with conditions affecting the early stages, e.g., the Pacific Marine Fisheries Commission (1965:38) suggested that seasonal currents possibly sweep the larvae to unfavorable settling areas. However, although the larvae may be more sensitive than juveniles to environmental changes and the percentage of them surviving is certainly less, there has been no experimental proof that fluctuation in abundance depends primarily on larval survival.

Peterson (1973) was the first to examine the statistical relationship between the Dungeness crab fishery and upwelling. (His paper serves as a good introduction to our work; much valuable information is not repeated here.) He compared the upwelling index developed by Bakun (1973) to the crab catch records for the years 1949 to 1972. The comparison was made for three different locations: Washington (lat. 48°N, long. 125°W), Oregon (lat. 45°N, long. 125°W), and northern California (lat. 42°N, long. 125°W).

Peterson used graphical comparison and two statistical techniques—the corner test and the contingency table—to evaluate the relationship between upwelling index (summed over the summer months) and the annual crab catch for several different lag times at each location. The conclusion was that good crab catch followed a good upwelling summer by 1½ yr in California and Oregon and ½ yr in Washington. Two aspects of these results are unexpected: 1) the short lag times and 2) shorter lag time in Washington than in California and Oregon. The short lag times seem to preclude the effect of upwelling on larval or early stages being the dominant cause of the large catch. The shorter lag time in Washington is unexpected because of the shorter generation times of most species in the marine food chain at the higher temperatures of more southerly waters.

Peterson explained the lag differences by proposing that the final molt from sublegal to legal size was the determining factor. Dungeness crabs molt later in more northerly waters (late fall in Washington, late summer in Oregon, and early summer in California). It was hypothesized that the Washington animals were molting after the summer upwelling and benefited from the increased food supply, whereas animals in more southerly waters molted prior to the increased food supply and did not benefit until the following summer molt.

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In this paper we have used a different statistical technique than Peterson's and have reached a different result regarding lag differences. We have computed the correlation coefficient for varying lag times. This technique uses higher resolution in the data than the techniques used by Peterson and results in a graphical presentation of the magnitude of correlation at each lag. The results show that significant correlation extends for longer lag times than ½ or 1½ yr and reverse the order of the difference in lag times along the coast. Also, we have used the same technique to describe the relationship between catches in different years. These results show that the primary cause of the cyclic nature of the variations may not be upwelling.

MATERIALS AND METHODS

The data used were the same as those used by Peterson (1973). The catch data are based primarily on the annual reports of the Pacific Marine Fisheries Commission and the California Department of Fish and Game (see Peterson 1973 for detailed discussion of sources). The total catch for each year (Figure 1) is believed to represent almost all that year's legal-size male crabs (Pacific Marine Fisheries Commission 1965:38). The completeness of this yearly sample makes the Dungeness crab an attractive species for analysis of population dynamics.

The upwelling index developed by Bakun (1973) is based upon measurements of atmospheric pressure. Upwelling and downwelling are the result of Ekman transport which is, in turn, due to surface winds. Bakun developed a method of estimating the intensity and direction of Ekman transport by relating the wind speed and direction to atmospheric pressure measurements. Using this method, he computed monthly averages of the component of Ekman transport perpendicular to and away from the shoreline. This upwelling index is assumed to indicate the average monthly upwelling. Peterson (1973) summed the monthly Bakun upwelling index over the summer upwelling season to compute a seasonal upwelling index (Figure 2). The upwelling indices were summed over the time periods from May through September for California.

These data were analyzed using a technique commonly employed in analysis of random processes to determine the degree to which two processes (or separated points of one process) covary. The formula used was:

$$R_{xy}(i) = \frac{1}{(n-i)} \sum_{j=1}^{n-i} x(j)\, y(j+i)/S_x S_y$$

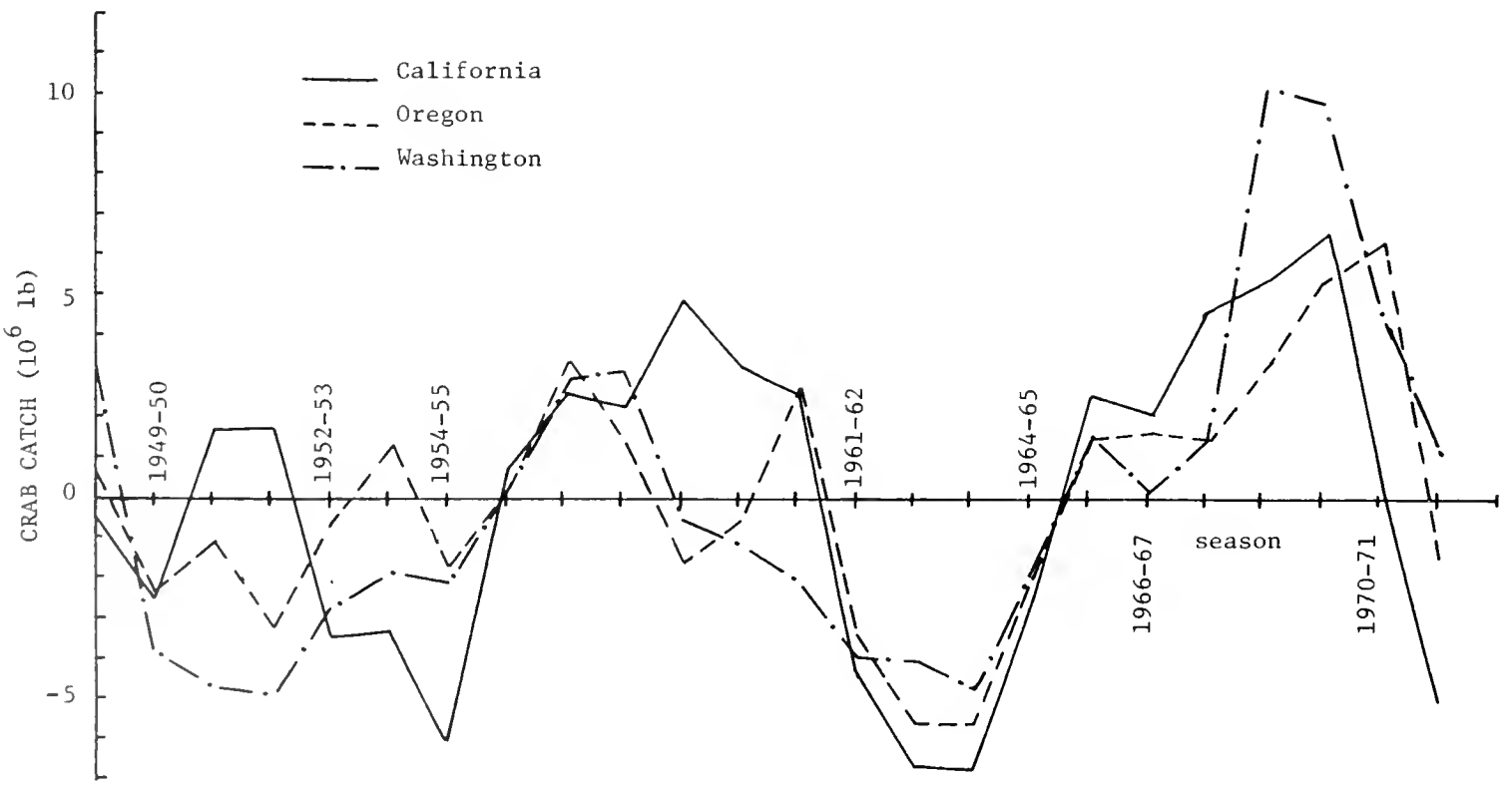

FIGURE 1.—Crab catch data for Washington, Oregon, and California (mean removed).

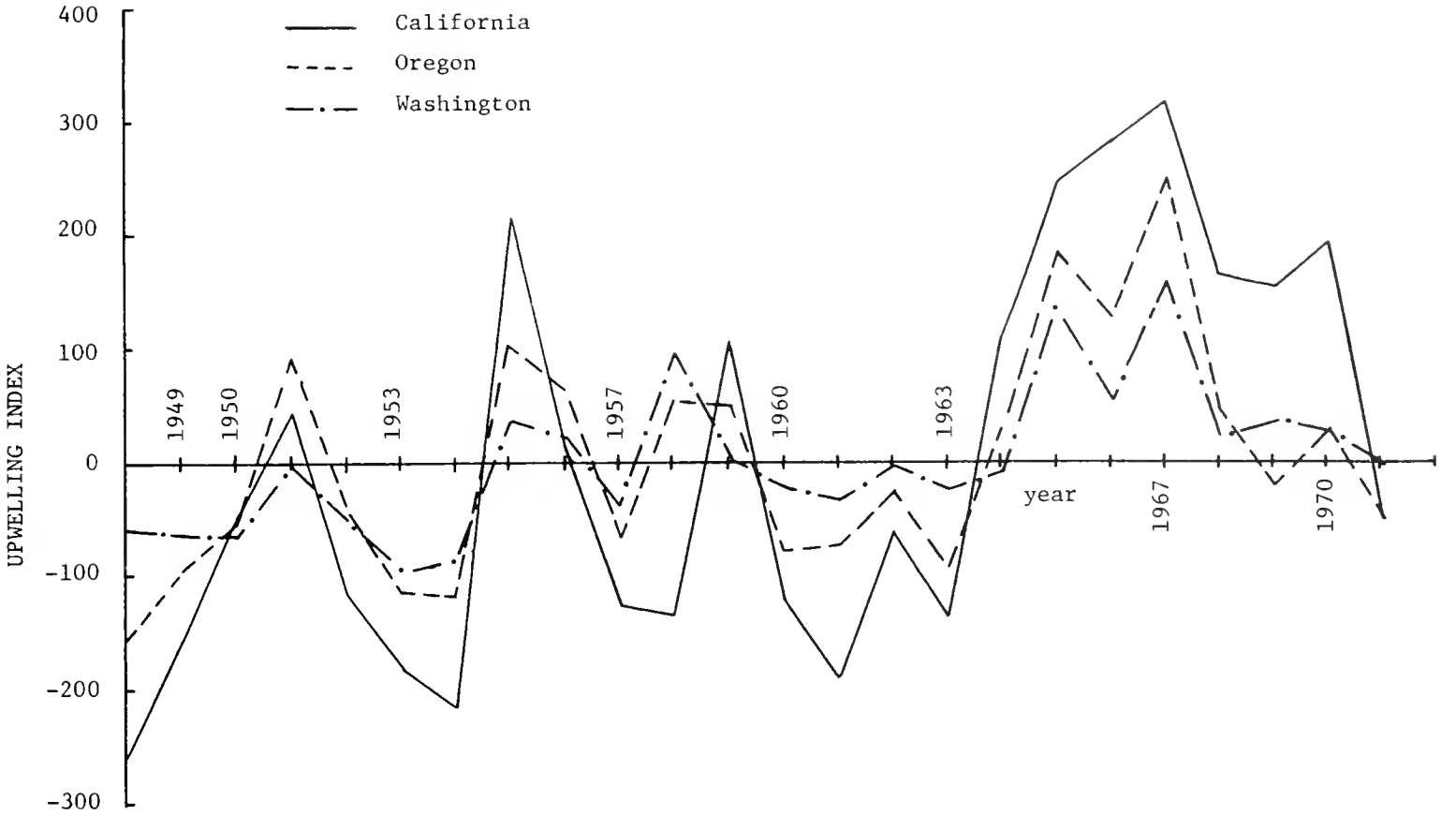

FIGURE 2.—Bakun's upwelling index for Washington, Oregon, and California (mean removed). Units are cubic meters of water upwelled per second per 100 m of coastline.

where $x(j)$ = the value of process x at time j (mean removed)
$y(j)$ = the value of process y at time j (mean removed)
S_x = the sample standard deviation of process x
S_y = the sample standard deviation of process y
n = the total number of samples.

The result of this formula is the product-moment correlation coefficient for each value of lag i. A graph of $R_{xy}(i)$ along the ordinate and i along the abscissa is termed the correlogram (Kendall and Stuart 1968). Assuming that the processes are stationary and ergodic, R_{xy} is an estimate of the expected value of the product of the two variables at each lag time. If x and y are different processes, it is termed the cross-correlation coefficient. If x and y are the same process, it is termed the auto-correlation coefficient.

Because R_{xy} is a sample statistic, the significance of its value must be considered. Although the technique is commonly used in time series analyses, the sampling theory of serial correlations has been developed only for restricted types of data (e.g., normally distributed data). Because the significance decreases as n increases, the serial correlation coefficient is usually only calculated for lags up to 30% of the total length of the data. The interpretation of our results depends only on lags of this length. However, the results are presented for lags beyond this length because they are of interest.

Another consideration in the computation of serial correlations is that of trend removal (Kendall and Stuart 1968; Ontes and Enochson 1972). Trends in the data (linear or higher order) which are not pertinent to the analysis are subtracted from the data before the correlation coefficients are computed. The trend is usually a deterministic artifact of known origin which is not present in the actual data of interest. Although upwelling, and to some extent catch data, seemed to increase over the 24 yr considered, this effect was not irrelevant to the purpose of the analysis. The results presented, therefore, include no trend removal. However, computation of the correlation coefficients was performed after trend removal and the results were similar.

RESULTS

The cross-correlation coefficients for upwelling and crab catch are plotted in Figure 3 as a function of lag time. The general shape of the function is similar for the three different locations. The coefficient for California at 0.5 yr lag is greater than for the other two. The value of the correlation coefficient for California decreases while the value increases for 1 yr at the other locations. This may indicate that high correlation exists at a shorter time lag in California than in ther other locations.

The auto-correlation coefficients for upwelling are plotted in Figure 4. Significant correlation

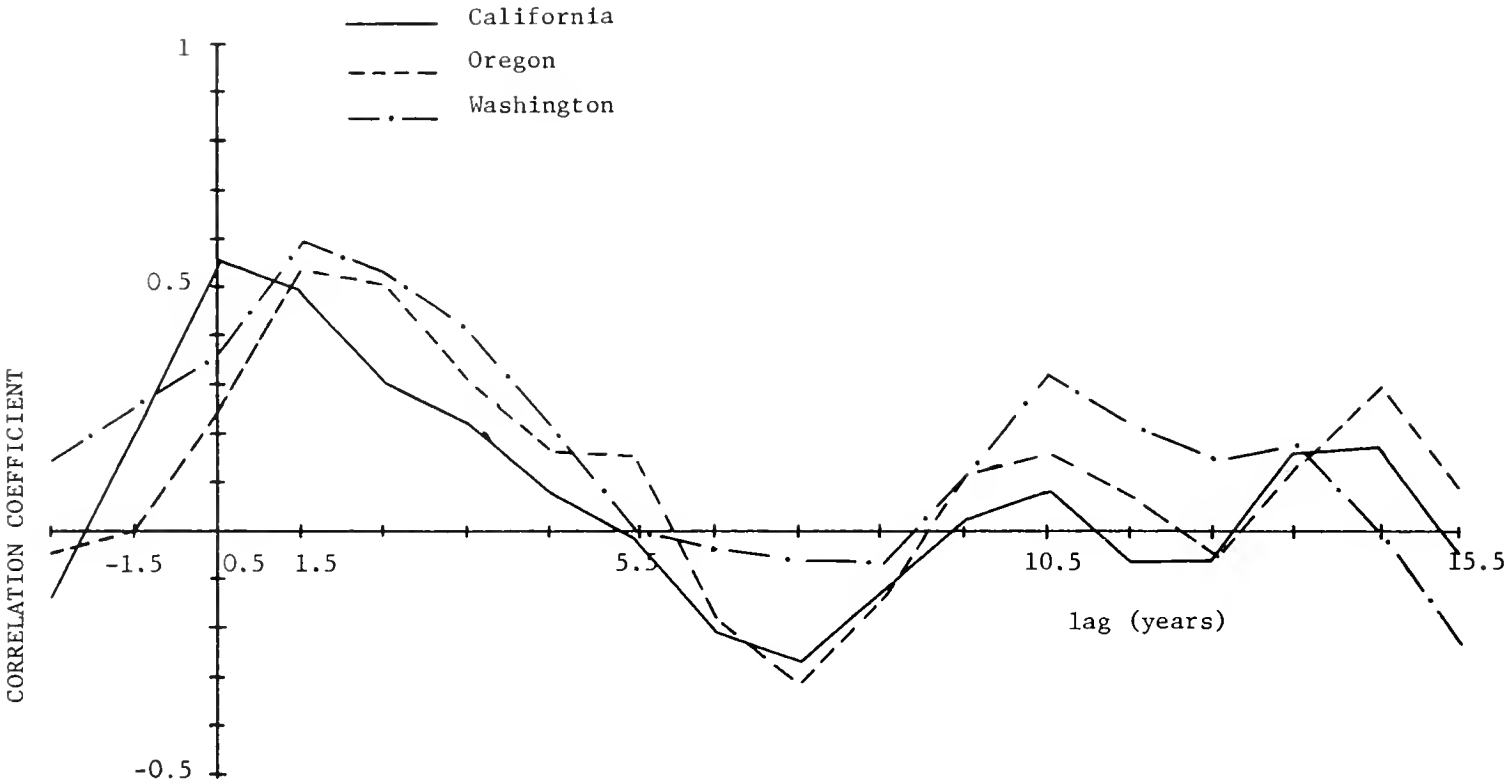

FIGURE 3.—Cross-correlation of upwelling and crab catch for Washington, Oregon, and California.

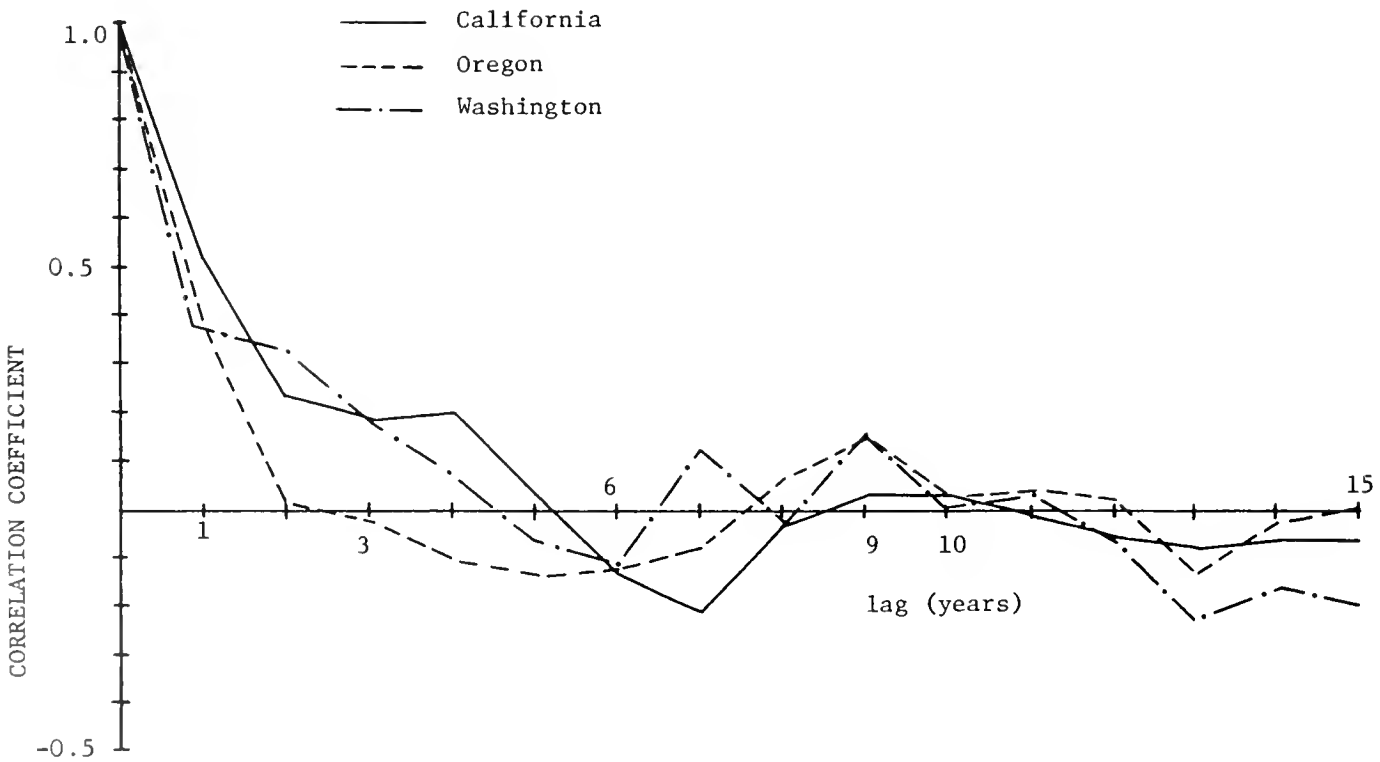

FIGURE 4.—Auto-correlation of upwelling for Washington, Oregon, and California.

exists for all three locations at a lag of 1 yr. For greater time lags no significant characteristics appear.

The auto-correlation of crab catch is plotted in Figure 5. The correlation function for each location decreases to a point of significant negative correlation. This is a characteristic of a cyclic process with a period of twice the lag value at that point. For California the period of the cycle would be 9 yr, and for Washington and Oregon it would be 12 to 13 yr. A subsequent increase to a positive correlation at a lag of twice that of the negative peak is further indication of a cyclic process. However a lag of that length is greater than 30% of the total length of the data.

DISCUSSION

These results must be interpreted in light of the general implications and limitations of statistical correlation. The correlation coefficient is used to measure the intensity of association between two variables and determine whether or not it is greater than that expected by chance alone. A high correlation coefficient serves only as an indication that a causal relationship may exist. The nature of the causal mechanism may take several forms. A high value of the correlation coefficient between two variables may be caused by one variable directly influencing the other. It may also be caused by a third variable influencing them both. Other possible alternative forms are more complicated combinations of these two. The causal mechanism may be very complex and indirect. Conclusions from the results obtained must, therefore, serve only as indications of areas of possibly fruitful investigation.

The results in Figure 3 indicate a possible relationship between upwelling and catch. The positive correlation at 0.5 yr lag which continues for several years could result from increased crab growth or survival due to increased food which may be due to nutrients provided by upwelling. The correlation at low lag time indicates agreement with Peterson's (1973) contention that adults are affected. The maximum correlation, however, appears at a shorter lag time in California than in Washington or Oregon. The fact that a significant correlation continues for an additional year may also be due to the same cause with the longer lag being the sum of the time required for the effect of nutrients to be felt at a point in the food chain in which the crab feeds plus the time required for that crab to reach a catchable size.

The cause of the apparent periodic nature of catch data indicated by Figure 5 is of primary

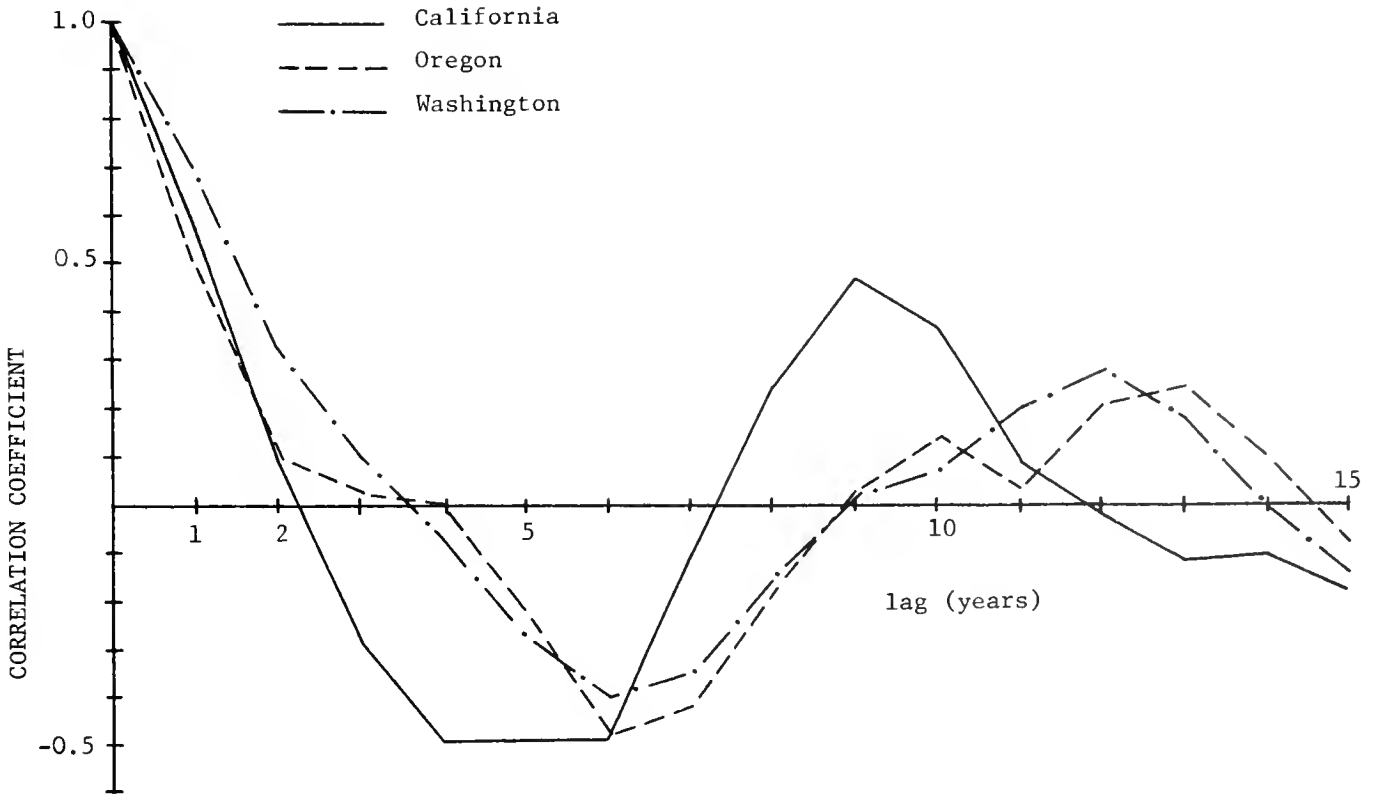

FIGURE 5.—Auto-correlation of crab catch for Washington, Oregon, and California.

concern to fisheries biologists. A possible explanation is that crab catch is merely following the cyclic upwelling. However, the auto-correlation of upwelling (Figure 4) does not indicate significant periodicity and the weak cycles suggested have different periods from those for the catches. This result may be due to the fact that the data used by Bakun (1973) were taken from four different sources covering the time periods January 1946-March 1955, April 1955-December 1959, January 1960-June 1962, and July 1962-December 1971. The data within each time period may differ by a multiplicative factor from the others but are consistent within the time period. This would affect the auto-correlation function more for longer than for shorter lags. The total effect of possible inconsistencies in the data upon the auto-correlation function is difficult to assess since the magnitudes of the multiplicative factors are not known.

A second possible explanation is that years of good catch indicate that a higher than normal percentage of the population is being caught thus depleting the adult reproductive stock. This explanation, however, is not commensurate with the widely held belief that almost all legal males are caught every year.

A third possible cause of the cyclic variations in abundance is predation. The observed cycles may be the result of interaction of crabs with a predator species. However, there is no a priori reason to expect that the period of the cycles would be slightly greater than twice the generation time. Also, the large number of predator species suggests that predation would maintain a fairly constant level unless all predator species were cycling in abundance.

A fourth possible explanation involves interactions between members of the population rather than external causes as dominant factors. Density-dependent factors which limit reproduction or growth and survival of the younger members of a population as the numbers of adults increase may cause cycles in abundance of adults. Ricker (1954) provides a discussion of density-dependent recruitment in fisheries and a simulation of time variation of abundance based on several different density-dependent recruitment relationships. One of the forms of compensatory mortality which could cause density dependent recruitment is cannibalism (Ricker 1954). Butler (1954) reported finding small Dungeness crabs (about 1 cm) among the stomach contents of older Dungeness crabs. For certain stock-reproduction curves the simulated populations oscillated in numbers. The requirements for permanent oscillation were a rapid decrease in reproduction (or survival of the young) beyond the peak of the stock-recruitment curve and mixing of generations in the breeding populations. The period of the oscillations was twice the mean length of time from parental to filial eggs.

Our results show a period of approximately 9 yr in California and 12 yr in Washington and Oregon. This would indicate a generation time of 4.5 yr in California and 6 yr in Washington and Oregon. Poole and Gotshall (1965) stated that mating occurs in California after 2.5 yr and males enter the fishery at 3.5 or 4.5 yr. Cleaver (1949) reported that in Washington maturity occurs at 3 yr and legal size occurs at the end of the fourth year. McKay and Weymouth (1935) reported that female crabs in southern British Columbia probably reach sexual maturity during the fourth or fifth year. The longer generation times in the northerly waters are commensurate with our results, although the period of the cycles indicated by our results is greater than would be expected based on Ricker's simulation and estimates of age at maturity. This disparity may be due to inaccuracies in the estimates or in our results. One possibility is an inaccurate estimate of when, in the life cycle, a major portion of reproduction occurs. If upwelling increases growth rate, the determination may have been made in good years, thereby yielding shorter time periods. A second possible explanation is inaccurate determination of the period of the cycle in our analysis. The length of the data (two or three cycles) is not adequate for accurate determination of the period of the cycle, especially when external influences appear to have caused large variations. Examination of the raw data reveals a reasonable explanation and also demonstrates correlations implied in this paper. In Figure 1, catch for northern California goes from a peak at 1950-51 or 1951-52 through a low point to a peak in 1958-59, a 7- or 8-yr cycle. It then passes through a low point and 7 yr later is again at a high point. However, instead of beginning to decrease, it rises even higher for the next several years before dropping. Figure 2 indicates that this is also the time when upwelling index is at a very high value. That the crab population reached a high density in 1965, but did not suffer the expected decline because the upwelling had provided enough food resources to sustain a larger population is a plausible explanation.

SUMMARY AND CONCLUSIONS

The correlation analysis at different lag times indicates a significant correlation of crab catch with upwelling for several years following upwelling. Auto-correlation of crab catch indicates that catch is of a cyclic nature. The same analysis of upwelling does not show a significant cyclic nature (although this may possibly be due to inconsistencies in Bakun's data). These analyses are not rigorous proofs of the indicated characteristics but rather provide impetus and direction for further research. They suggest that the cyclic variation of crab catch may be primarily due to density-dependent biotic factors rather than upwelling, although upwelling does influence catch. Further conclusions regarding the biological basis for the cyclic nature of catch data require research in the natural history and ecology of the Dungeness crab. A specific question to be answered is over what age groups are the niches similar enough for significant competition to occur. Further conclusions regarding the relationship between upwelling and catch require additional research in the nature of energy transfer from the pelagic to the benthic environment. Research in these directions may provide basis for a more dynamic fishery management policy. For instance, the importance of deciding whether the variations in crab catch are due primarily to density-dependent factors is illustrated by the implication that if competition is occurring between adults and juveniles, limited fishing of females (removing them as competitors) during years of great abundance may provide greater catches in the following years.

The statistical relationships presented also provide a basis for predicting crab catch. The values of upwelling index and crab catch over several years may be used to predict catch for the ensuing years (Rauch et al. 1975). Additional variables may be added to the basis for prediction such as temperature and results of plankton tows. This type of prediction is based on statistical relationships and does not necessarily require causal explanations of the various effects.

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NET FEEDING IN MESOPELAGIC FISHES

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ABSTRACT

In an investigation of net feeding, 11 species of fish (5 gonostomatids, 6 myctophids) captured in a double-net Tucker trawl were examined. Stomach contents of fish retained by a coarse mesh "fish-catcher" in one net were compared to contents of fish which had accumulated with plankton in the cod end of the adjacent net. Out of 19 species-collection pairs (700 fish), there were significant ($P<0.05$) differences in number of prey items in stomachs of only three species in five collections. Two pairs, fish from the cod end and in three pairs, those from the "fish-catcher," contained significantly more prey than fish from the adjacent trawl. There were little or no significant differences between trawls in number of fish scales, prey diversity, or prey size. These results suggest that literature data on diet of mesopelagic fishes is not heavily biased from net feeding and that existing collections can be used for feeding investigations.

Diet studies of mesopelagic fishes taken from plankton net cod ends of mid-water trawls could be seriously biased if fish feed extensively in the cod end. Indirect evidence for net feeding in pelagic shrimp has been presented by Judkins and Fleminger (1972) and in myctophid fish by Anderson (1967). DeWitt and Hopkins (in press) also suggest the possibility of net feeding in *Pleuragramma antarcticum*, a mid-water notothenioid fish. The problem of net feeding, though recognized by the above authors and others (e.g., Holton 1969; Collard 1970; Hopkins and Baird 1973), is largely unresolved; consequently the validity of published data on the diet of mesopelagic fishes is questionable. The present study was initiated to estimate the nature and degree of net feeding in the cod end of plankton net trawls by mid-water fishes to better judge the reliability of published information on diets of these fishes, and to determine if existing collections and present methods of collecting are adequate for trophic studies.

METHODS

Most of the material examined was collected from the eastern Gulf of Mexico with a double (side-by-side) closing Tucker trawl (Figure 1). One side of the trawl had an unmodified plankton net at the cod end. The mouth of the cod end plankton net of the adjacent trawl was fitted with a coarse mesh (1.1 cm stretched) conical "fish-catcher." In principal, the conventional trawl allowed the passage of fish into the cod end where plankton was concentrated; in the adjacent trawl fish were prevented from accumulating with plankton in the cod end by the fish-catcher. The body of the trawl was constructed of 1.1-cm stretched, knotless mesh. The cod ends for most collections were 333-μm mesh, 0.5-m diameter plankton nets. In collections subsequent to tow 152 (see Table 1), 1,050-μm mesh nets were substituted for the finer 333-μm mesh cod ends to improve the internal flow characteristics of the trawl. Other details of trawl design are in Hopkins et al. (1973). We have also included data from tow 98, a Caribbean sample, made with a single-net closing Tucker trawl (Hopkins et al. 1973). Fish gilled in the body of the trawl in this tow were compared with specimens from the cod end. Trawl hauls represented discrete depth samples which ranged from horizontal tows ($\pm$10 m) to stepped oblique tows which sampled over a specified segment of the water column.

Fish were preserved in 10% Formalin[2] and subsequently transferred to 40% isopropyl alcohol. Specimens selected for analysis (370 from cod end; 332 from fish-catcher) were measured to the nearest millimeter (standard length, SL) prior to stomach removal. Contents of the pigmented distensible region posterior to the esophagus and anterior to the intestine were identified to genus when possible, measured, and counted (see Hopkins and Baird 1973; Baird et al. 1975). Prey

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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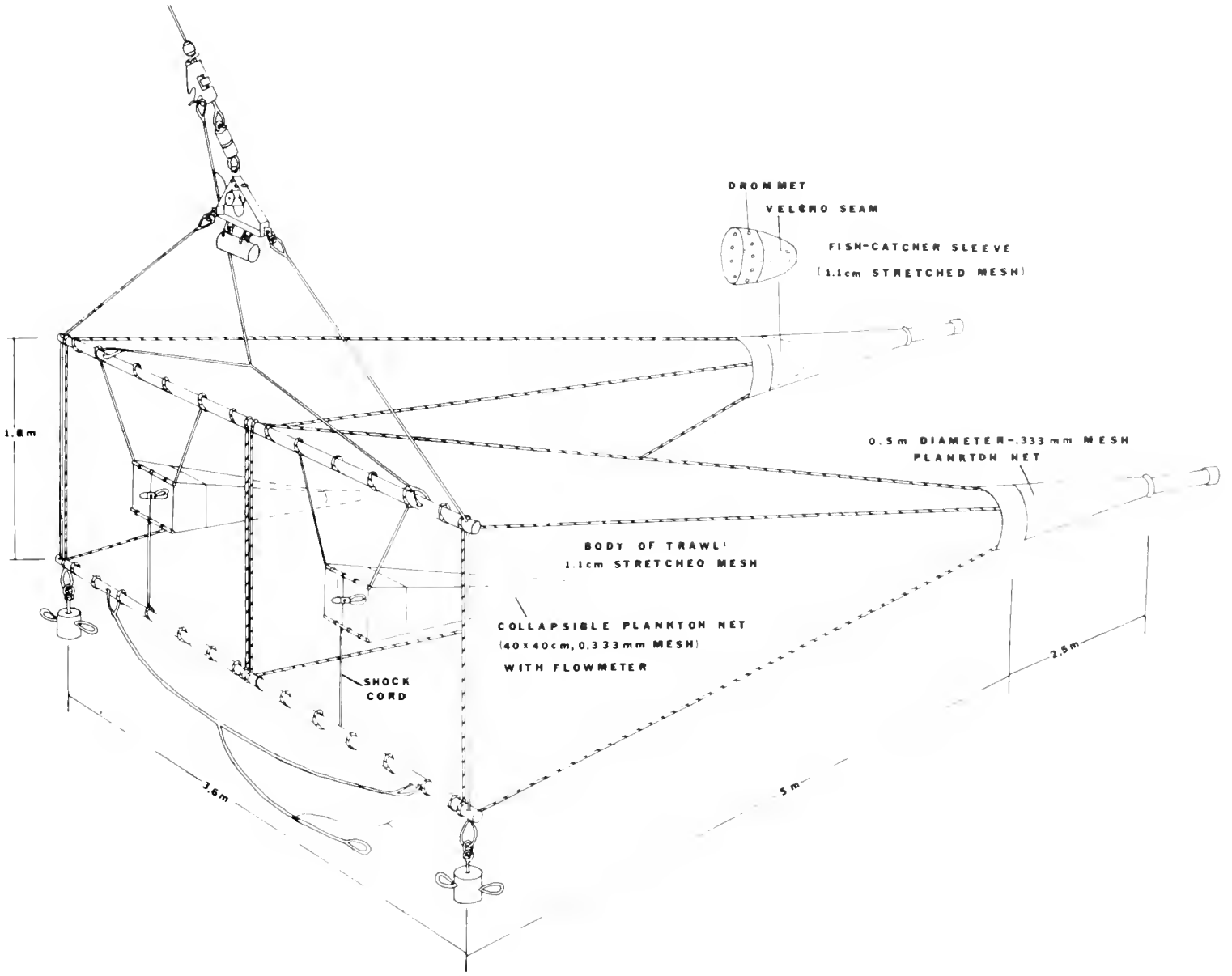

FIGURE 1.—Double-net closing Tucker trawl showing modified (fish-catcher sleeve) and conventional cod ends.

items contained in the mouth, pharyngeal region, esophagus, or intestine were not included in the analysis. Student's *t*-test was used for most statistical comparisons, the distributions being first tested for skewness and kurtosis (Sokal and Rohlf 1969). If the data to be tested were not normally distributed, then a log or square root transform was applied and the resulting distributions retested for skewness and kurtosis. *F*-tests were used to determine homogeneity of variances; the few exceptions to homogeneity will be discussed under the appropriate section. Standard chi-square tests were used to test the similarity of prey size distributions.

To compare prey availability in the trawl cod end with fish stomach contents, plankton was examined from tows 135, 137, and 141-144 (Table 2). Trawl mouth plankton net collections were used in preference to cod end catches because of possible losses of small plankton incurred in sorting larger fish and shrimp from the latter. Both cod end and trawl mouth nets for these particular tows had the same mouth area (0.2 m^2) and mesh size (333 μm) and were considered comparable in fishing characteristics, at least for the smaller plankton typically found in fish stomachs. Trawl mouth plankton collections for tow 137 were not available, consequently the catch from the cod end net of the fish-catcher side of the trawl was substituted. This particular cod end collection had not been "rough sorted" for larger organisms and was in excellent condition.

Zooplankton was identified, usually to genus, and counted in each of two subsamples. One plankton net collection (two subsamples) was analyzed for tows 135, 137, and 142 while two collections (four subsamples) were examined for the remaining tows. The mean number of

TABLE 1.—Comparison of diet characteristics of fish examined in net feeding investigation. F = "fish-catcher" side of double trawl; P = unmodified side of double trawl (see Figure 1); G = gilled in meshes of body of trawl; *t*-tests:* = $P<0.05$, ** = $P<0.025$, *** = $P<0.01$, **** = $P<0.005$.

Species	Trawl no.	Depth (m)	Time of collection	Trawl side	No. fish	Fish size (mm) $\bar{x}$ (range)	Prey items per stomach $\bar{x}$ (range)	Prey size (mm) $\bar{x}$	Prey diversity (taxa)	No. fish scales[2]
			Night (post-midnight)[1]							
Argyropelecus aculeatus	144	156-197	0220-0515	F	6	29 (24-36)	2.8 (0-8)	2.7	5	0
				P	8	31 (22-38)	6.4 (1-14)	3.7	15	2
Benthosema suborbitale	137	94	0227-0543	F	27	28 (23-31)	3.0 (0-7)	1.9	17	0
				P	25	28 (25-33)	3.5 (0-15)	2.0	20	6
Ceratoscopelus warmingi	137	94	0227-0543	F	25	33 (28-52)	8.5 (2-18)	1.8	42	0
				P	25	32 (28-48)	10.1 (1-28)	1.8	52	2
Gonostoma elongatum	144	156-197	0220-0515	F	23	96 (71-113)	2.7 (0-7)	6.2		
				P	29	97 (68-117)	2.0*(0-5)	5.4		
Lampanyctus alatus	141	128	0240-0350	F	32	39 (29-46)	5.8 (0-13)	2.9	26	1
				P	32	39 (28-45)	7.3***(1-17)	3.2	39	7
Lepidophanes guentheri	137	94	0227-0543	F	36	50 (38-58)	6.6 (0-19)	4.0	31	9
				P	35	50 (37-58)	7.2 (0-17)	3.0	35	3
Notolychnus valdivae	141	128	0240-0350	F	10	20 (17-22)	2.7 (0-6)	2.9		
				P	39	20 (16-23)	2.6 (0-9)	2.5		
Valenciennellus tripunctulatus	152	397-450	0140-0545	F	8	28 (25-31)	2.3 (0-5)	2.7	6	0
				P	6	28 (25-32)	2.8 (2-4)	2.9	5	0
			Night (pre-midnight)							
Ceratosropelus warmingi	161	90-130	2047-2321	F	20	38 (32-45)	5.5 (0-13)	2.3		
				P	13	34*(29-45)	3.5****(0-7)	2.3		
Diaphus dumerili	173	30-130	2108-2355	F	6	51 (37-66)	17.7 (7-29)	3.7	22	0
				P	6	48 (41-63)	11.3 (2-22)	4.1	17	0
Cyclothone pallida	147	781-844	2130-0100	F	23	44 (33-52)	0	0	0	0
				P	24	43 (28-52)	0.04 (0-1)	4.5	1	0
Lampanyctus alatus	167	60-130	2102-2350	F	30	41 (34-48)	3.2 (0-9)	3.9		
				P	24	38 (29-48)	4.8*(0-16)	4.2		
Lepidophanes guentheri	167	60-130	2102-2350	F	7	55 (48-59)	9.7 (3-19)	4.4	12	1
				P	7	33 (44-59)	11.7 (2-46)	5.2	12	0
Valenciennellus tripunctulatus	143	257-348	2117-2352	F	6	24 (23-27)	10.2 (3-16)	1.8		
				P	24	24 (21-29)	10.3 (0-23)	1.7		
			Day (morning)							
Argyropelecus hemigymnus	142	363-545	0920-1240	F	18	23 (17-29)	4.2 (0-11)	1.8		
				P	11	26 (19-33)	5.2 (0-11)	1.7		
Gonostoma elongatum	145	660-1,000	0830-1130	F	12	108 (93-120)	3.0 (1-5)	6.6	8	0
				P	10	110 (99-130)	1.3*(0-4)	4.2	6	0
Lepidophanes guentheri	98	570-705	0755-1112	F	15	46 (38-54)	9.1 (0-22)	4.1		
				G	19	49 (39-62)	9.3 (1-27)	3.7		
Valenciennellus tripunctulatus	142	363-545	0920-1240	F	19	27 (21-30)	3.7 (0-11)	2.1	12	0
				P	22	27 (24-31)	3.8 (9-10)	2.2	12	0
			Day (afternoon)							
Valenciennellus tripunctulatus	135	340-627	1435-1830	F	9	25 (21-29)	10.9 (0-16)	2.4	14	0
				P	11	24 (18-28)	11.5 (2-24)	2.0	13	0

[1]Time of tow initiation.
[2]Fish scales only; no other fish remains present.

plankters counted in each subsample was 775 (range: 453-1,079).

RESULTS

Fish Size Distribution

Because of possible relationships between number of items in stomachs (also other diet characteristics) and size of predator (e.g., Nesis 1965; Hopkins and Baird 1973), the mean length and size range of fish from each trawl were compared for each pair (Table 1). There were no significant differences in mean length (*t*-test, $P>0.05$) in 18 of 19 pairs. For the single exception, *Ceratoscopelus warmingi* from tow 161, the mean size of fish from the catcher size was larger ($P<0.05$; $\bar{x}$ (SL): 38 vs. 34 mm). However, since the distributions had considerable overlap, this set was included in the study.

Prey Abundance in Stomachs

It was necessary to apply a square root transform ($\sqrt{X+0.5}$) to the data on number of prey per stomach since the high frequency of empty

TABLE 2.–Relative abundance of principal (top 3) food items in fish stomachs and in plankton taken concurrently with fish, with 333-μm mesh nets mounted in the mouth of the double trawl (see Figure 1): F = "fish-catcher" set of fish; P = cod end plankton net set.

Species	Tow	Top 3 prey items in stomachs	Numerical abundance of prey in stomachs (%)			Numerical abundance in plankton nets (%)	Top 3 items in plankton nets	Numerical abundance in plankton nets (%)
			F	P	$\bar{x}$			
Argyropelecus hemigymnus	142	*Oncaea*	45	42	43.5	12	*Eucalanus*	41
		Conchoecinae	17	23	20.0	5	*Oncaea*	12
		Eucalanus	12	9	10.5	41	Scolecithricidae	10
Benthosema suborbitale	137	*Oncaea*	23	24	23.5	9	Conchoecinae	12
		Pleuromamma	21	17	19.0	9	*Pleuromamma*	9
		Conchoecinae	11	10	10.5	12	*Clausocalanus*	9
Ceratoscopelus warmingi	137	*Limacina*	13	17	15.0	3	Conchoecinae	12
		Conchoecinae	12	14	13.0	12	*Pleuromamma*	9
		Siphonophores	12	11	11.5	2	*Clausocalanus*	9
Gonostoma elongatum	144	*Stylocheiron*	16	21	18.5	2	*Sagitta*	19
		Pleuromamma	13	33	23.0	1	Conchoecinae	18
		Conchoecinae	13	9	11.0	21	*Oithona*	14
Lampanyctus alatus	141	*Pleuromamma*	23	25	24.0	4	*Oithona*	14
		Stylocheiron	16	13	14.5	4	*Sagitta*	8
		Conchoecinae	8	6	7.0	8	Conchoecinae	8
Lepidophanes guentheri	137	*Pleuromamma*	25	31	28.0	9	Conchoecinae	12
		Euphausia	14	6	10.0	<1	*Pleuromamma*	9
		Conchoecinae	11	9	10.0	12	*Clausocalanus*	9
Valenciennellus tripunctulatus	142	*Oncaea*	24	12	18.0	12	*Eucalanus*	41
		Pleuromamma	19	22	20.5	3	*Oncaea*	12
		Euchaeta	10	(6)	8.0	1	Scolecithricidae	10
		Eucalanus	(3)	15	9.0	41		
Valenciennellus tripunctulatus	143	*Oncaea*	40	38	39.0	9	*Pleuromamma*	15
		Pleuromamma	23	25	24.0	15	Conchoecinae	14
		Conchoecinae	6	8	7.0	14	*Oithona*	10
Valenciennellus tripunctulatus	135	*Eucalanus*	19	16	17.5	20	*Pleuromamma*	23
		Pleuromamma	16	14	15.0	24	*Eucalanus*	20
		Euchaeta	10	(9)	9.5	<1	*Euphausia*	7
		Oncaea	(3)	19	11.0	1		

stomachs resulted in significant skewness in the distributions of many untransformed data sets. In three set comparisons there were significant differences (F-tests, $0.05 > P > 0.025$) in variance (*Benthosema suborbitale*, tow 137; *C. warmingi*, tow 137; *Lampanyctus alatus*, tow 167). In these cases, tests comparing means of normal distributions when population variances are unequal were applied as described by Johnson and Leone (1964:226).

There were significant (t-tests, $P < 0.05$) differences in 5 of 19 comparisons of number of prey items per stomach. *Lampanyctus alatus* in two collections contained more prey items per individual in fish taken from the plankton net cod end (tow 141: $0.025 > P > 0.01$; tow 167: $0.05 > P > 0.025$). However, for *Gonostoma elongatum* in two sets (tows 144, 145: $0.05 > P > 0.025$), and *C. warmingi* in one set (tow 161: $P < 0.005$), individuals from the fish-catcher side averaged more prey per stomach. Because of possible diurnal feeding periodicity in mid-water fishes (Anderson 1967; Holton 1969; DeWitt and Cailliet 1972; Baird et al. 1975), fish entering the trawl at different periods in their feeding cycle may be satiated or have a different predisposition to feed in varying degrees. The five sets of fish showing significant differences in number of food items, however, are not conspicuously grouped in any single time period (see Table 1) and no general relationship is apparent in our results between time of capture and relative abundance of prey in fish from either side of the trawl.

Mean Prey Size

In 8 of 19 data sets, mean prey size was smaller in cod end fish. The major size modes were coincidental in all 19 set comparisons as judged from visual inspection. A t-test of the grand means (mean of 19 individual means for each cod end type), however, revealed no significant ($P > 0.05$) difference in mean size of food item for fishes in either side of the trawl (variance of means homogeneous). Though the sensitivity of this test is weakened to some degree by comparing different species of fish collected at different times, a strong bias in prey size resulting from net feeding is not apparent.

Prey size distributions for 14 paired sets were also compared using the contingency chi-square test. Significant ($P < 0.05$) differences were found

in only two pairs: *Lepidophanes guentheri*, tow 167 ($P<0.001$) and *Valenciennellus tripunctulatus*, tow 135 ($0.005>P>0.001$). In the former, those individuals from the cod end took more prey items in smaller size classes while in the latter the reverse occurred. We have no simple explanation for these results. It is difficult to attribute them, however, to net feeding since other diet characteristics tested showed no significant differences for these same sets. Additionally, paired samples of the same species from other collections revealed no significant differences.

Prey Diversity

In comparison to the coarse mesh fish-catcher, the unobstructed cod end net of the adjacent trawl contained a much greater variety of plankton and consequently a more diverse potential food source for net feeding. A comparison was made of diversity of food items in stomachs of fish from each side of the trawl using 12 (of 19) species-pair collections represented by sets of approximately equal numbers of individuals for each cod end type. Total diversity was scored for each set of fishes, yielding two diversity values for each species-pair collection. Diversity scores were then summed to give grand means for each cod end type.

On the basis of a t-test on $\log_{10}$ transformed data, no significant ($P>0.05$) difference was indicated for the two cod end types though total diversity was considerably greater in fishes from the plankton net cod end in some sets (e.g., *Argyropelecus aculeatus*, tow 144; *L. alatus*, tow 141).

Fish Scales

Anderson (1967), in his analysis of the diet of *Bathylagus stilbius*, frequently encountered fish scales in stomachs yet no other remains of fish of the size indicated by the scales. This, in addition to the absence of scales in intestines and the occurrence of scales and copepods in the mouths of fish, he considered as evidence of net feeding. In the present study, fish in half the sets of samples (6 of 12) for which data are presented contained no fish scales. In four of the remaining six pairs, more scales were found in fish from the cod end where scales would be expected to accumulate during the course of a tow, but none of the differences were significant (t-test on $\sqrt{X+0.5}$ transformed data; $P>0.05$).

The occurrence of fish scales in stomachs does not necessarily stem from predation on smaller fish or from eating scales abraded from fish within the trawl. Fish scales appear to be common in the water column and thus available as separate forage items. In a series of paired 30-liter bottle casts made between 0 and 1,000 m in August 1972, in the eastern Gulf of Mexico where most of the fish examined were taken, scales occurred in collections (60 liters/sample) from 7 of 15 depths sampled at densities of 17-83 per m^3. Scales ranged from 0.5 to 5 mm in diameter. No fish were taken in the sample bottles and the probability of contamination from other sources appears low.

Taxonomic Composition of Stomach Contents and Plankton

Table 2 presents the principal taxonomic components of prey found in nine sets of fish from both sides of the trawl. The principal diet item was the same in both sets of fish in six of nine collections, the same prey constituted the top three food items by number in seven of nine collections and the prey taxa were in the same rank order in five of nine collections. The principal three prey taxa in fish from either side of the trawl were within $\pm 3\%$ of the mean value for both sides from each tow in 25 of 29 food item comparisons and all values were within $\pm 10\%$ of the means. These results show that the taxonomic composition of at least the principal components of the diet was similar in fish from both sides of the trawl for all comparisons.

Comparison of food items in stomachs of fish from the cod end, where net feeding is assumed mostly likely to occur, with plankton catches reveals little similarity in the top three taxonomic components. In none of the nine collections was the principal taxon the same in either the plankton net catch or in the stomachs of fish from the cod end. Of particular importance are tows 137, 141, 144, 152, and 161 which sampled relatively narrow depth zones and consequently were potentially less influenced by vertical stratification of plankton. Also, three species of fish collected in the same haul (tow 137) each contained a different principal food item, none of which matched the most abundant taxon in the cod end plankton catch. The major diet components for *Benthosema suborbitale*, *C. warmingi*, and *L. guentheri* from tow 137 were *Oncaea*, *Limacina*, and *Pleuromamma*; the most abundant plankton in the cod end net were ostracods (Conchoecinae). This particular haul was

a horizontal tow in which a discrete depth was maintained throughout.

DISCUSSION

While studies of the behavior of mesopelagic fishes in small mid-water trawls used for research are nonexistent, there is considerable information available on fish behavior in larger commercial trawls of many kinds (e.g., Ben-Tuvia and Dickson 1968). Generally, fish move in front of or away from the walls of the trawl until they are exhausted and are collected in the cod end. Mesopelagic fishes from trawl cod ends often show signs of abrasion (Harrisson 1967); consequently, the likelihood of active and extensive net feeding would appear low. Several authors (e.g., Collard 1970; Hopkins and Baird 1973) have suggested that trauma induced by stress conditions in the trawl environment would operate against active feeding behavior. Reflexive gulping or "pseudo" feeding behavior, however, resulting in the ingestion of significant amounts of prey from the plankton rich cod end is a potential mechanism whereby stomach contents could be biased by net feeding. Several studies have revealed diel periodicity in feeding in mid-water fishes which indicates that at certain times, at least, net feeding cannot be extensive (Holton 1969; DeWitt and Cailliet 1972; Baird et al. 1975).

The possibility of fishes foraging in front of the cod end or fish-catcher can also be evaluated. At standard trawling speeds (3.7-4.6 km/h) the trawl moves at a rate of 1.0 to 1.3 m/s. For those epipelagic species which have been examined, foraging and cruising speeds range from about 1 to 4 body lengths per second and maximum burst speeds are on the order of 10 to 30 body lengths per second (e.g., Blaxter 1969; Baird et al. 1975). Assuming similar swimming capabilities for mid-water fishes and a fish size of 3 inches (76 mm), a conservative estimate of foraging speeds should be less than 0.3 m/s and burst rates of 0.8 to 2.3 m/s. All of the species examined here were less than 76 mm in length except *G. elongatum* which may have somewhat limited swimming capabilities (Marshall 1971). In view of the swimming speeds required, extensive foraging in front of the cod end appears remote. In addition, the data from *L. guentheri* (tow 98), where prey of individuals gilled in the net were compared with those from the cod end, failed to reveal indications of net feeding.

The present results support the contention that if net feeding does occur, it is not extensive in the relatively small fragile fishes typical of the oceanic mesopelagic enrivonment. Only the data on prey abundance in stomachs of *L. alatus* could be construed as statistical evidence of net feeding. In both of these collections, however, mean size of prey items and taxonomic composition of diet were very similar in both sets of fish, while the diet showed little agreement in terms of principal taxonomic components (Table 2) with plankton in the cod end, as might be expected from net feeding. In three collections (tows 144, 145, 167), *G. elongatum* (2 sets) and *C. warmingi* (1 set) from the "control" side contained more food items than fish from the cod end. Here again comparisons of mean prey size, taxonomic composition of diet, and major taxa in diet with that in cod end plankton samples failed to reveal evidence of net feeding. Furthermore, there were often substantial differences between principal taxonomic components of diet and plankton from cod end catches from the same haul. Mean prey size (with two exceptions) and composition of principal taxa of diets were nearly identical for all sets of comparison which further indicate the limited nature of net feeding in this study.

The use of fish scales as a criterion for net feeding poses a number of difficult problems. Our hydrocasts reveal, for instance, that fish scales occur naturally in the water column. Further, several studies of both marine and freshwater teleost fishes have shown that scales (probably also the covering mucous and epidermis) can serve as a major component of the diet, appear to be easily digested, and may possibly have considerable nutritive value (e.g., Roberts 1970, 1973; Carr and Adams 1972, 1973). Scales were relatively rare in stomachs examined here but did occur in fishes from both sides of the trawl. Since scales are present in the natural environment, may have nutritive value, and are possibly easily seen, captured, and eaten, they could serve as a natural food source or provide appropriate stimuli to elicit ingestion. Until more evidence is obtained concerning the role of scales in the natural diets of fishes and their abundance in oceanic environments, the presence of scales in the stomachs of mid-water fishes cannot be used with assurance as an indicator of net feeding.

Because of the difficulty of replicating trawl conditions and obtaining sufficient material for analysis, the variability in distributions of mid-

water fishes with respect to time and space, and possible variations in feeding cycles, the present collections are not ideal in all respects. The study did include representatives of most of the major groups of common mesopelagic fishes from a variety of depths and times, and the results may be expected to be broadly applicable to many midwater environments. Considering the simultaneous time-depth collections with the double trawl of both "control" fish and those with the opportunity to ingest food in the cod end, this study provides the first reasonably good test of net feeding in mesopelagic fishes. The relatively small differences in the mean number and taxonomic composition of prey items in most sets of stomachs are encouraging. The results presented here suggest that the published literature on the diets of mesopelagic fishes is not seriously biased by net feeding and that existing collections can be used for trophic investigations.

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NOTES

GAS-BUBBLE DISEASE: MORTALITIES OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN WATER WITH CONSTANT TOTAL GAS PRESSURE AND DIFFERENT OXYGEN-NITROGEN RATIOS[1]

A review of the literature regarding gas-bubble disease can be found in a recent publication by Rucker (1972); one by the National Academy of Science (Anonymous in press); and an unpublished report by Weitkamp and Katz (1973).[2] Most discussions on gas-bubble disease have dealt with the inert gas, nitrogen—oxygen was given a secondary role. It is important to know the relationship of nitrogen and oxygen when we are concerned with the total gas pressure in water. Where water becomes aerated at dams or falls, oxygen and nitrogen are usually about equally saturated, however, many of the samples analyzed from the Columbia River indicate that nitrogen is often about 7% higher than oxygen when expressed as a percentage. When oxygen is removed from water by metabolic and chemical action, or when oxygen is added to the water by photosynthesis, there is a definite change in the ratio of oxygen and the inert gases (mainly nitrogen with some argon, etc.). This present study shows the effect of varying the oxygen and nitrogen ratio in water on fingerling coho salmon, *Oncorhynchus kisutch*, while maintaining a constant total gas pressure.

The primary purpose of these experiments was to determine differences in lethality of various gas ratios of oxygen and nitrogen at a constant total gas pressure of 119%. I also wished to determine whether there was a difference in susceptibility between sizes and stocks of juvenile coho. Also to be examined was the effect of reducing the oxygen while holding the nitrogen constant.

Methods

Juvenile coho salmon averaging 6 cm in length, obtained from the Quilcene National Fish Hatchery, Quilcene, Wash., and the Northwest Fisheries Center of the National Marine Fisheries Service, NOAA (National Oceanic and Atmospheric Administration), Seattle, Wash., were used during all the tests concerning differences in lethality of O_2/N_2 ratios. During these tests water temperatures were 13.6° + 0.1°C. Gas concentrations usually varied slightly from the desired ratios. The tank facility consisted of six troughs, two of which were used to hold experimental fish at normal saturation (100%) and two pairs of troughs used to test fish at different gas ratios.

Control of gas concentrations and the test apparatus is described in a subsequent section. During initial testing of the gas control system, I determined that a ratio of 114% O_2 to 121% N_2 could be achieved by merely allowing air to be sucked into the intake side of the recirculation pump. Since this gas ratio did not require injection of either oxygen or nitrogen, the resultant concentration (114% O_2 and 121% N_2) was used as a quasi control for comparison with the other gas ratios. Several replicates were completed at this concentration. Water saturated at this ratio and concentration was also used to test for differences in size and stock and to provide base line data in determining effect of reduced oxygen concentrations while maintaining a constant nitrogen level.

In all the tests free carbon dioxide was near normal, or about 2 ppm. Oxygen is expressed as "O_2" and the inert gases as "N_2."

The number of days required to kill 25% of the fish at the different gas levels is expressed as the lethal exposure—LE_{25} and to kill 50%—LE_{50}.

Apparatus shown in Figure 1 was used to supply water with a definite oxygen and nitrogen content. The tank (1) was divided so that two experiments could be carried on simultaneously with similar equipment. Water was circulated by a centrifugal pump (2) with a valve (3) on the effluent side to cause a controlled back pressure as read on a gauge (4). This created a vacuum on the inflow side (5) so that air could be introduced into the water with either oxygen or nitrogen (6)

[1]Research performed under contract with the U.S. Army Corps of Engineers.

[2]D. E. Weitkamp and M. Katz. 1973. Resource and literature review of dissolved gas supersaturation in relation to the Columbia and Snake River fishery resources. Submitted to Northwest Utilities Cooperative, c/o Idaho Power Co., Boise, Idaho, Apr. 3, 1973, by Seattle Marine Laboratories, Div. of Xelco Corp., Seattle, Wash., 55 p. (Typewritten.)

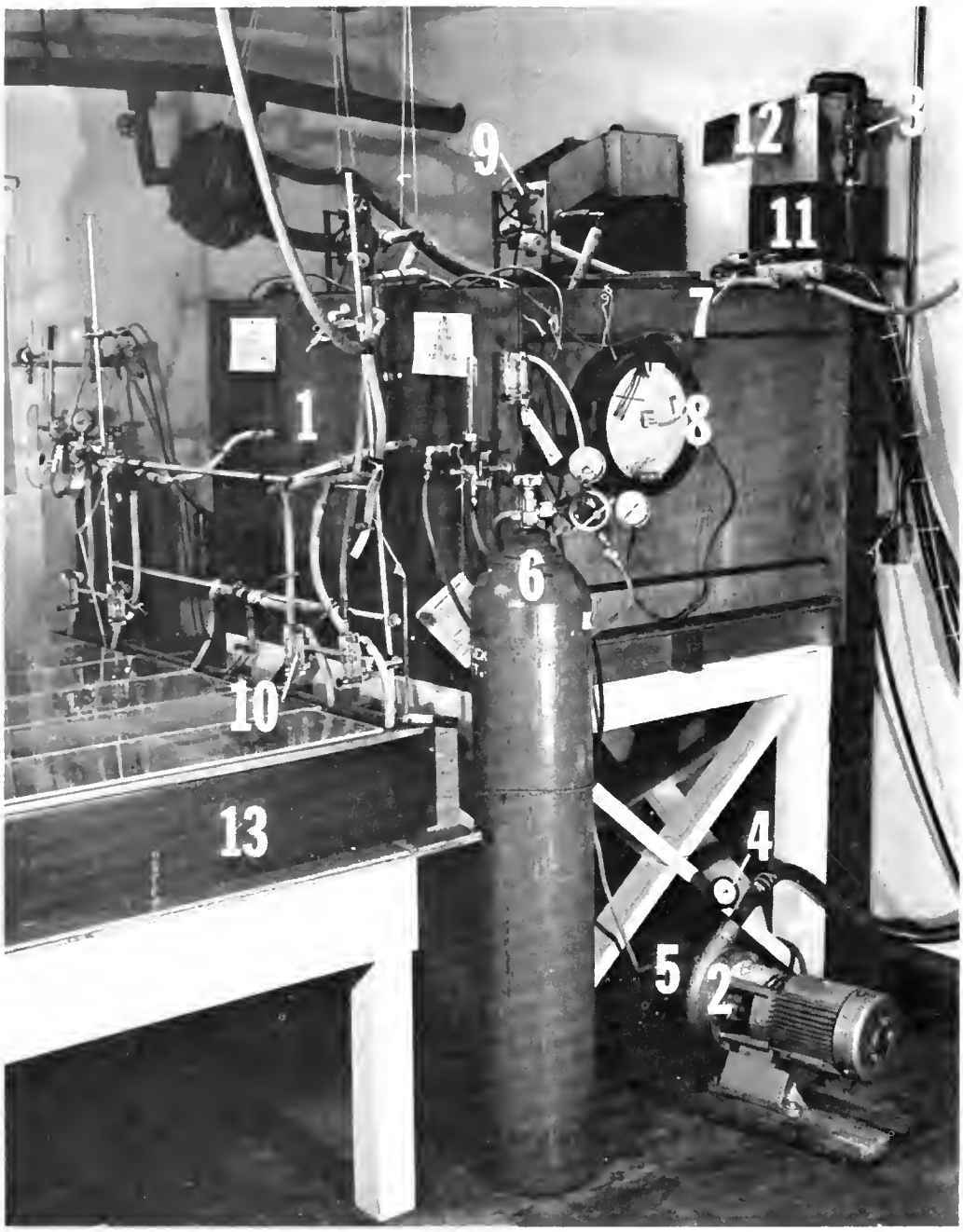

FIGURE 1.—Apparatus for subjecting fish to constant-temperature, flowing water with a definite oxygen and nitrogen content.

through a "Y" tube. Circulation of the water caused an increase in temperature which was maintained at approximately 13.6°C by means of a refrigeration system (7) and recorded on a thermograph (8). Water level in the tank was maintained by float valves (9). Each trough was supplied with 1 liter per minute of water regulated with flow meters (10). The water used was from the municipal supply, was soft, and was passed through activated charcoal to remove the chlorine. A greater depth of water was needed for absorption of the gases than was afforded by the tank (1), so two towers (11) were added to the system. The spout (12) at the top of the towers was to direct possible overflow water back into the system.

Inside dimensions of troughs in the fish holding area (13) were 104.5 × 23.5 × 20 cm high. Water depth was maintained at 14 cm. Each trough could be separated into three compartments with screens—"A" was at the inflow end of the trough, "B" middle, and "C" outflow end. In a few cases a compartment was divided longitudinally so that two groups of fish could be subjected to almost identical conditions.

Results

Effect of Variation in O_2/N_2 Ratios on Mortality

Times to death (LE_{25} and LE_{50}) of juvenile coho salmon at various concentrations of O_2 and N_2 during constant total gas saturation of 119% appear in Table 1 are shown graphically in Figure 2. All tests were run in duplicate with 50 fish per test, except one at 22.9% O_2 and 90% N_2 which involve 50 fish but one test. With one exception (19.2% O_2 and

TABLE 1.–Time to death of groups of juvenile coho salmon (about 6 cm long) in 13.6°C water with total gas pressure of 119% of saturation and different ratios of O_2 and N_2.

Gas concentration (% saturation)		Time to death (days)			
		25% of all fish		30% of all fish	
O_2	N_2	Range	Average	Range	Average
50	138	1.8- 1.9	1.9	3.2-4.0	3.7
75	131	1.8- 2.7	2.3	3.5-4.3	3.9
114	121	3.2- 4.1	3.8	6.3-7.3	6.9
159	109	3.2- 5.3	4.5	6.5-9.1	8.2
173	105	33.5-35.3	34.4	—	(1)
192	100	—	[2]32.0	—	(3)
229	90	—	(4)	—	(4)

[1]Not reached, 28% mortality in 39 days.
[2]One replicate reached 24% mortality in 30 days; the other, 25% in 32 days.
[3]Not reached, test concluded at 33 days.
[4]Not reached, 20% mortality in 35 days.

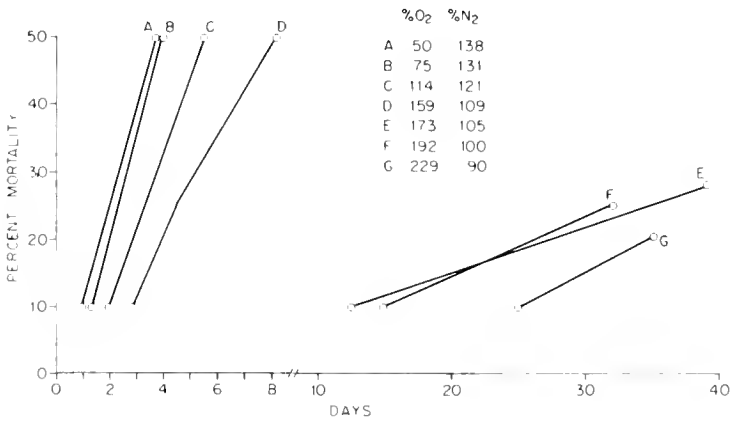

FIGURE 2.–Mortality pattern of 6-cm coho salmon reared at different O_2/N_2 levels at 13.6°C with a 119% total gas pressure.

100% N_2), all increases in ratio of O_2 to N_2 resulted in increased tolerance to the total gas saturation. A marked increase in tolerance to total gas pressure occurred between concentrations of 159%/109% and 173%/105% saturation of O_2 and N_2 (Figure 3).

Effect of Size and Stock of Fish on Mortality

A number of tests were carried out in the water containing 114% O_2 and 121% N_2 to determine effect of size and stock of fish on susceptibility to gas supersaturation (Table 2). Two groups of 3.8-cm coho from the Northwest Fisheries Center which had just started feeding were initially tested. One group of 96 fish reached LE_{25} in 22.9 days and LE_{30} after 30 days. The other group of 50 fish reached LE_{25} in 10.9 days. No further losses occurred until the 27th day. Loss at 30 days was 34%. Averages of the two groups placed LE_{25} at 16.9 days. Average loss at 30 days was 32%.

Two groups of 50, 4.6-cm fish from the Quilcene National Fish Hatchery were also tested. These tests produced LE_{25} of 15.1 and 18.3 days. LE_{50} was

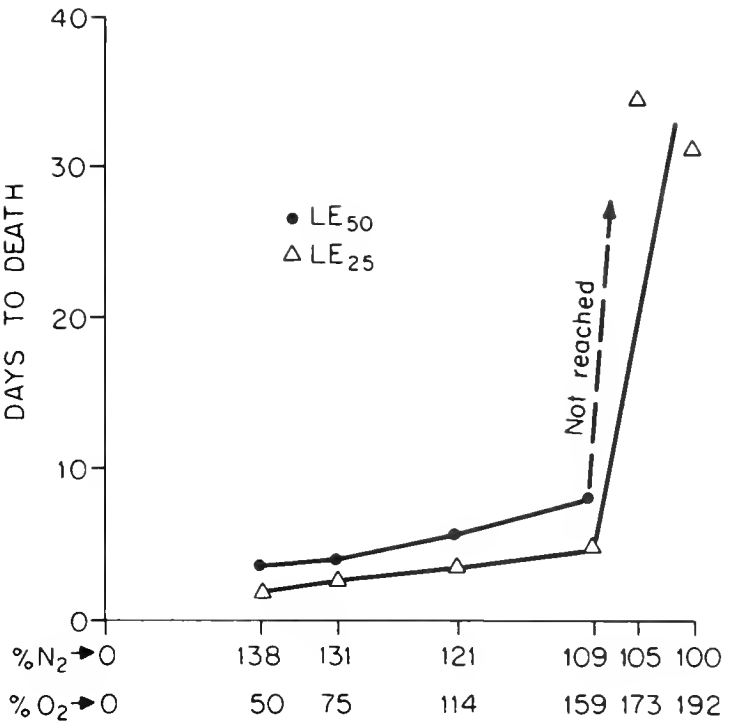

FIGURE 3.–Relationship between O_2/N_2 levels and time to death of 6-cm coho salmon fingerlings at 13.6°C and total gas concentration of 119%.

TABLE 2.–Time to death of groups of juvenile coho salmon of different body length and stock composition in 13.6° ± 0.1°C water with gas concentrations of 114% O_2 and 121% N_2.

Average body length and (in parentheses) stock of fish	Time to death (days)	
	25% of all fish	50% of all fish
3.8 cm (Seattle)	16.9	Not reached in 30 days
4.6 cm (Quilcene)	16.7	27.4
10 cm (Seattle)	2.1	2.6
10 cm (Quilcene)	2.9	4.2

reached in 24.7 and 30 days. Averages of the above placed LE_{25} at 16.7 and LE_{50} at 27.4 days.

Five groups of fish (8, 12, 16, 16, and 16 in number), and approximately 10 cm long, from the Northwest Fisheries Center were then tested. The average for all groups gave an LE_{25} of 2.1 days and an LE_{50} of 2.6 days.

Three groups of 12 fish each approximately 10 cm long from the Quilcene National Fish Hatchery were similarly tested. Averages were 2.9 days for LE_{25} and 4.2 days for LE_{50}.

These results indicate that the larger fingerlings approximately the same age are definitely more subject to harm from excess air in the water than the smaller fish. These data agree with those of Meekin and Turner (1974) and Dawley et al.[3]

[3]E. Dawley, B. Monk, M. Schiewe, and F. Ossiander. 1974. Salmonid bioassay of supersaturation of dissolved gas in water. Northwest Fish Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., unpubl. manuscr.

Although the data are limited, there appears to be little difference between susceptibility of the Montlake and Quilcene stocks.

Effect of Reduced O_2 Concentration on Mortality

Fish held in compartments in a trough utilize oxygen so that the water in compartment C (outflow end) would have less oxygen than in compartment A (inflow end). Compartment B in the central part of the trough would have O_2 levels somewhere between those in A and C. Nitrogen levels in these compartments, however, were the same. To demonstrate the effect of reduced oxygen in relation to gas-bubble disease, 48 coho of 8.5 cm fork length were randomly distributed into compartments A, B, and C. Two additional replicates of the C compartment tests were run using 32 coho (8.5 cm) in each trial. These are listed as C_1 and C_2 in Table 3.

TABLE 3.–Time to death of groups of juvenile coho salmon (about 8.5 cm long) in 13.6°C water with 121% N_2 and different concentrations of O_2.

Trough compartment	Gas concentration (% saturation)		Time to death (days)	
	O_2	Total pressure	25% of all fish	50% of all fish
A	113	119	2.5	3.3
B	110	118	3.6	5.3
C	105	117	3.8	5.3
C_1	105	117	4.2	6.6
C_2	105	117	5.4	6.6

Inspection of these data indicates that when 121% N_2 is maintained, oxygen plays a more significant role above 110% than below 110%.

Some of the data obtained when the oxygen-nitrogen ratio tests were done also illustrated the effect of reduced oxygen on the mortality rate. This was apparent in the experiment using 173% O_2 and 105% N_2. At 173% O_2 there were losses of 26 and 30% in 39 days, whereas slightly larger fish at the lower end of the troughs subjected to 169% O_2 had losses of only 7% in 39 days.

Pathology

Generally the fish died suddenly in the higher nitrogen concentrations. Never was tissue damage or any progressive pathology demonstrated. The fish always seemed to die from gas embolism, restricting the flow of blood through the gills. When the nitrogen was near normal and the oxygen high, the fish were moribund for many days before succumbing. These fish had blebs in the mouth which interfered with feeding and caused emaciation.

Summary

Coho salmon fingerlings were subjected to a total gas pressure of 119% at 13.6°C with the O_2/N_2 varying from 50%/138% to 229%/90%. The small fish (3.8 to 6 cm) were the most resistant and the larger fish (8 to 10 cm) the least resistant to gas-bubble disease at the gas concentrations used. A drastic decrease in lethal effect of individual ratios of O_2 to N_2 occurred between 159% O_2/109% N_2 and 173% O_2/105% N_2 at the same total gas pressure (119%).

Acknowledgments

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The information in the section on pathology was furnished by William T. Yasutake, pathologist, Western Fish Disease Laboratory.

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AGE-LENGTH-WEIGHT AND DISTRIBUTION OF ALASKA PLAICE, ROCK SOLE, AND YELLOWFIN SOLE COLLECTED FROM THE SOUTHEASTERN BERING SEA IN 1961

Japanese fishing companies explored the trawl fish resources of the eastern Bering Sea in 1929 and 1931. They began commercial fish meal production in 1933 and continued until 1937; a frozen fish operation was initiated in 1940 but was interrupted by World War II (Bourgois 1951).[1] In 1954, Japan resumed trawling in the eastern Bering Sea, again producing fish meal and frozen fish. The Soviet Union began sending bottom trawl fleets to the eastern Bering Sea in 1959, and combined annual catches of flatfishes (excluding Pacific halibut, *Hippoglossus stenolepsis*) by Japan-USSR rose to a peak in 1961 when it exceeded 600,000 metric tons (Fadeev 1965). In the years following 1961, eastern Bering Sea flatfish catches by Japan decreased and in the period 1963-1970 have averaged less than 20% of the 456,890 metric tons caught in 1961 (International North Pacific Fisheries Commission 1973). Comparable Soviet data are not available.

Prior to intensive exploitation of eastern Bering Sea resources, there were two groups of surveys in which samples of flatfish were taken to assess the age-length structure of the population. One such series was conducted by the U.S. Fish and Wildlife Service in 1947-49 (King 1949; Ellson et al. 1950; Wigutoff and Carlson 1950). The other surveys were made 10 yr later by the Soviet Union (summarized by Moiseev 1965). Age-length determinations from flatfish samples collected in 1949 were reported by Mosher (1954); the Soviet collections of 1957-60 were studied by Fadeev (1963), Mineva (1964), and Shubnikov and Lisovenko (1964).

In July-August 1961, personnel of the Bureau of Commercial Fisheries (now National Marine Fisheries Service) conducted a trawl survey of the southeastern Bering Sea. This survey, although conducted principally to estimate the abundance of Alaska king crab, *Paralithodes* spp., provided an opportunity to sample several flatfish species. The purpose of the present report is to present biological information on the distribution, age, length, and weight by sex for three commercially important species of Bering Sea flatfish: yellowfin sole, *Limanda aspera* (Pallas); rock sole, *Lepidopsetta bilineata* (Ayres); and Alaska plaice, *Pleuronectes quadrituberculatus* Pallas.

[1]Bourgois reported that Alaska pollock was the principal species taken by these Japanese fisheries. However, Alverson et al. (1964) pointed out that the areas of the eastern Bering Sea fished by Japanese trawlers from 1933 to 1941 were the same locations as post-World War II flounder fisheries, so there is reason to doubt the complete accuracy of Bourgois' information as to species.

Methods and Materials

Sample Collection

Otter trawl hauls of 1-h duration were made at 51 predesignated stations 20 nautical miles (37 km) apart (Figure 1). The trawling speed of the vessel was about 2.5 knots (4.6 km/h). The trawl was a 400-mesh, Eastern type, as described by Greenwood (1958). A 1.5-inch (3.8 cm) mesh liner was laced into the cod end to retain small specimens which might otherwise pass through the 3-inch (7.6 cm) meshes in that part of the trawl. At the completion of each haul, the catch was examined, and the weight of each major component was estimated. At five of the stations where one or more of the target species was abundant, samples of yellowfin sole, rock sole, and Alaska plaice was selected for length-weight-age determination. Specimens were measured to the nearest centimeter to obtain a representation of individuals throughout the available length range. Each fish to be retained was then frozen individually in a plastic bag which was sealed to prevent shrinkage and weight loss through dehydration.

At the laboratory, 3 mo after collection, the specimens were thawed, the total length (snout to longest rays of the tail fin) was measured, the weight recorded to the nearest gram, and sex determined from an examination of the gonads.

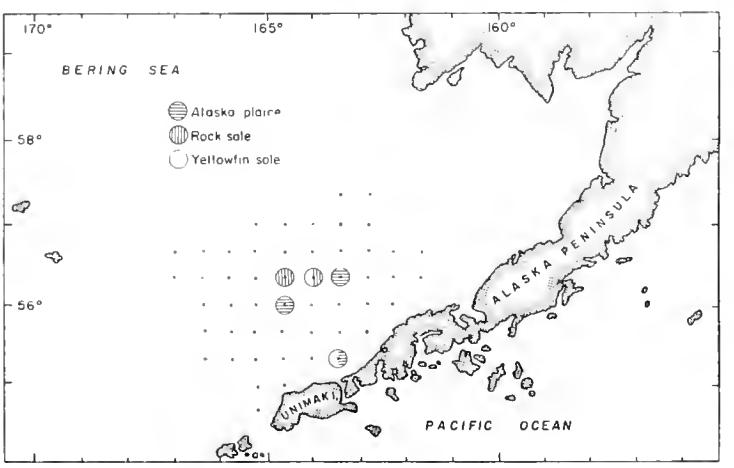

FIGURE 1.–Sampling station pattern and location of sample collections for 7 July-4 August 1961 survey.

Both otoliths were removed and placed in 95% ethyl alcohol.[2]

Age Determination Procedure

Studies by Hatanaka (1968) of yellowfin sole from the southeastern Bering Sea indicate that the translucent zone of an otolith is formed once a year during the winter months. In our readings on otoliths from all species, each translucent zone was considered an annular mark. The outermost edge of each otolith was also translucent except in the younger fish where there was evidence of some beginnings of opaque summer growth. Thus, the ages recorded are the number of translucent rings starting with the smallest observable and including the outermost. For example, a fish captured in July 1961 with 10 rings on its otolith was considered to have been spawned and hatched in 1951. Fadeev (1965), through gonad examination, stated that Bering Sea yellowfin sole spawn in June-August, Alaska plaice in April-June, and rock sole in February-May. Shubnikov and Lisovenko (1964), who reported that rock sole in Bristol Bay spawn in March-June, are in general agreement with Fadeev.

For reading, the otoliths were immersed in water in a petri dish with a black mat background and examined at 10× under reflected light with a dissecting microscope. Both otoliths were considered in age determination, but when a discrepancy occurred between the two otoliths, a decision was based on the eyed-side (right) otolith. In situations where the annular rings were not clear, the otoliths were ground on fine, water soaked, carborundum paper. In most samples grinding improved interpretation of annular rings, but the grinding of rock sole otoliths often exposed additional opaque and translucent zones to further confuse the readers.

Consistency of Age Determinations

Without reference to fish size, otoliths were interpreted by each author. A third, independent interpretation was made by an experienced otolith reader at the Northwest Fisheries Center. The observed ages, as agreed upon between the two authors, were compared with ages determined by the experienced reader. Initial agreement between authors and reader was 76% for yellowfin sole, 72% for Alaska plaice, and 85% for rock sole. Disagreements were not confined to a particular age class; only 3% differed by more than 1 yr, and these differences were equally negative and positive. The similarity of results by authors and reader suggests that the method used produced consistent age-growth data. Otolith interpretations not in agreement between the authors and the reader were reread and a joint decision was made on the most probable age of the fish.

Results and Discussion

Distribution

Yellowfin sole is the most abundant flatfish taken in the eastern Bering Sea. Alaska plaice (33% by weight of yellowfin sole caught) was usually encountered together with yellowfin sole and share a similar distribution within the sampling area (Figure 2). Fadeev (1970) and Maeda et al. (1967) note that yellowfin sole concentrate in the colder waters of Bristol Bay during the spring and summer months. In July of 1961, a tongue of cold water extended into the sampling area and the greatest concentrations of yellowfin sole and Alaska plaice were taken at bottom temperatures of 3°C or less.

The distribution of rock sole within the sampling area (28% by weight of yellowfin sole catch) was spotty with the denser concentrations occurring toward the eastern edge of the area inhabited by yellowfin sole and Alaska plaice. The 1961 observations are compatible with the contention of Shubnikov and Lisovenko (1964) that rock sole disperse during the summer into shallower water than they occupy in winter and spring.

Age-Length Observations

The age-length-weight composition for the three southeastern Bering Sea flatfish species sampled in 1961 are given in Tables 1-3.[3] It is difficult to compare the 1961 data with any earlier reports except in a generalized manner since in only one instance (Pruter and Alverson 1962) is there a determination of age by sex. The data presented in Tables 1-3, and also in studies of eas-

[2]All otoliths from the 1961 collection are in permanent storage at the Northwest Fisheries Center, Seattle, Wash.

[3]Individual age determinations and related lengths and weights, by sex, are available upon request from the Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash.

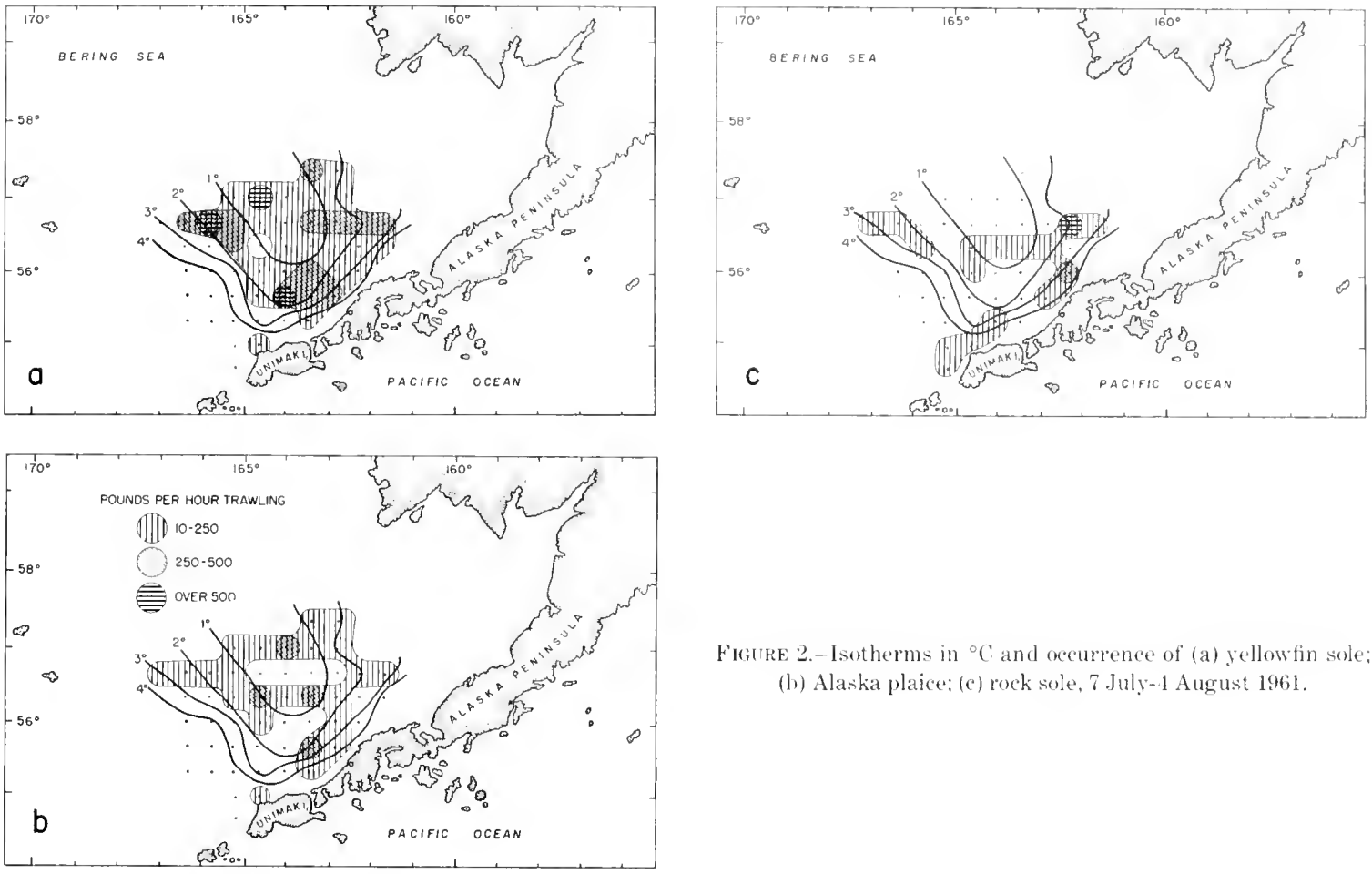

FIGURE 2.–Isotherms in °C and occurrence of (a) yellowfin sole; (b) Alaska plaice; (c) rock sole, 7 July-4 August 1961.

TABLE 1.–Observed age and length distribution of male (M) and female (F) yellowfin sole taken in the southeastern Bering Sea in 1961.

Length (cm)	4		5		6		7		8		9		10		11		12		13		Total		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
17.5	1	1																			1	1	2
18.5				1			1														1	1	2
19.5			2	1	1		1			1	1										5	2	7
20.5					2		1	1	3	2	1										7	3	10
21.5				2	1		2	4	6	4	4										13	10	23
22.5			1	2	2	1	4	2	7	4	3										17	9	26
23.5							4	1	3	2											7	3	10
24.5					1		1		5	3			1	1							8	4	12
25.5						1	1		6	2	2	2				1					9	6	15
26.5									1	4	2		1								4	4	8
27.5								1	1	2	2	1	2	2			1				6	6	12
28.5								1	1		2	2	1	1	1						5	4	9
29.5										1		1		1		1		1				5	5
30.5												1					1				1	1	2
31.5																		2	1		1	2	3
32.5														2								2	2
33.5																1		1				2	2
34.5																				1		1	1
Total	1	1	3	6	7	2	15	10	33	25	17	7	5	7	1	3	2	4	1	1	85	66	151
Average length[1] (M)	18.0		20.6		21.8		22.5		23.6		24.3		27.2		28.5		28.9		32.0				
(F)	17.3		21.2		23.9		23.3		24.2		28.0		29.1		30.0		31.6		34.8				
Average weight (g) (M)	57		94		130		128		145		150		226		280		269		409				
(F)	54		108		145		147		163		262		310		350		364		538				

[1]Calculated from ungrouped data.

tern Bering Sea yellowfin and rock sole by Hatanaka (1968), Maeda (1969), and Levings (1967), indicate that growth is different for each sex.

The ages of 12 yellowfin sole (10 female, 2 male) taken 50 miles south of Nunivak Island in the eastern Bering Sea in August 1959 (Pruter and Alverson 1962) fall within the range of our observations with some suggestion that the younger fish in their samples are slightly smaller. Maeda (1969) and Hatanaka (1968) derived age-length curves

TABLE 2.–Observed age and length distribution of male (M) and female (F) Alaska plaice taken in the southeastern Bering Sea in 1961.

Length (cm)	4		6		7		8		9		10		11		12		14		16		Total		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
21.5		1																				1	1
22.5	1																				1		1
23.5																							
24.5																							
25.5	1																				1		1
26.5																							
27.5			1																		1		1
28.5			1																		1		1
29.5			1																		1		1
30.5			4	1					1												5	1	6
31.5									1				1	1							2	1	3
32.5			1	1	4	1			2		1	1	1								9	3	12
33.5			2	1		2	2			1			1								5	4	9
34.5			1		1	1	2	1	1		1		1	1							7	3	10
35.5						1	1	1	1			1	3			1					5	4	9
36.5								1	2		1	2									3	3	6
37.5				1				1					1	1		1					1	4	5
38.5										1		1	1		1						2	2	4
39.5										1		1						1		1		4	4
40.5												1		1								2	2
41.5										1						1						2	2
42.5										1				1								2	2
43.5										1												1	1
44.5																1						1	1
Total	2	1	11	4	5	5	5	4	8	6	3	7	9	5	1	4		1		1	44	38	[1]82
Average length[2] (M)	23.7		31.0		33.1		34.4		34.0		34.5		35.0		39.0								
Average length[2] (F)		21.5		33.7		33.9		36.4		40.0		37.2		37.3		40.1	40.0		39.5				
Average weight (g) (M)	168		384		438		484		503		531		538		690								
Average weight (g) (F)		108		545		530		651		925		687		738		860	715		862				

[1]One additional male, age 18 yr, length 47.6 cm, 1,380 g.
[2]Calculated from ungrouped data.

TABLE 3.–Observed age and length distribution of male (M) and female (F) rock sole taken in the southeastern Bering Sea in 1961.

Length (cm)	4		6		7		8		9		10		11		Total		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
18.5	1														1		1
19.5																	
20.5																	
21.5																	
22.5																	
23.5							1								1		1
24.5							1				1				2		2
25.5			2				2		2	1		1			6	2	8
26.5					3			2	6		5				14	2	16
27.5					1		1	2			2	1			4	3	7
28.5							1	2	2	2	1	4		1	4	9	13
29.5							1			2		3			1	5	6
30.5										2		3		1		6	6
31.5										1						1	1
32.5										1				2		3	3
33.5												1		1		2	2
34.5												1				1	1
Total	1		2		4		7	6	10	9	9	14		5	33	34	67
Average length[1] (M)	18.1		25.7		27.1		26.6		26.8		26.8						
Average length[1] (F)								27.6		29.8		29.9	31.6				
Average weight (g) (M)	55		198		217		216		212		219						
Average weight (g) (F)								223		330		320	404				

[1]Calculated from ungrouped data.

from large samples of eastern Bering Sea yellowfin sole collected in 1963 and 1965-66, respectively. There is no appreciable difference between the two above age-length curves and our 1961 data (Figure 3).

With rock sole, the only comparative age-length data by sex is presented by Levings (1967) for samples collected in the northeastern Bering Sea in 1963. Levings' age-length observations on male rock sole are similar to our collections, but a considerable difference exists in female lengths-at-age. The females taken in 1963 are older and at a

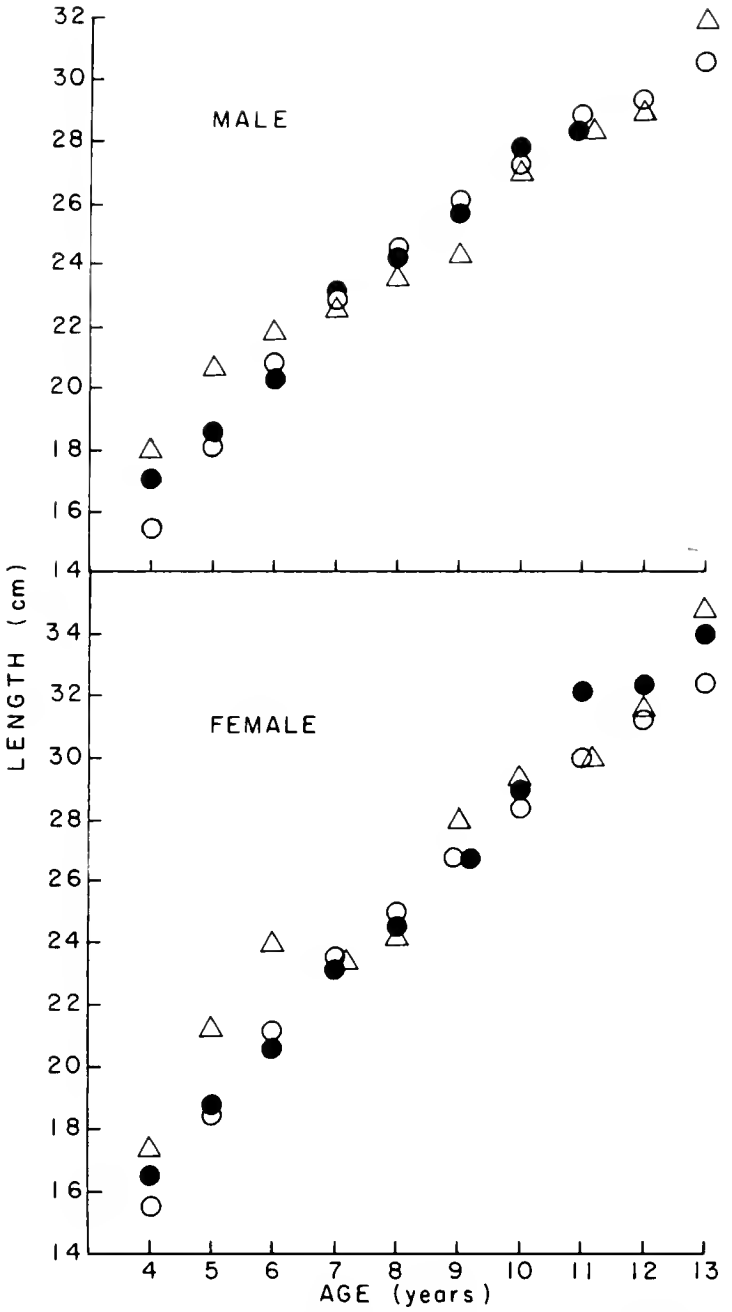

FIGURE 3.—Age-length comparison for yellowfin sole taken in the eastern Bering Sea in 1961 (open triangles); 1963 (closed circles, Maeda 1969); and 1965-66 (open circles, Hatanaka 1968).

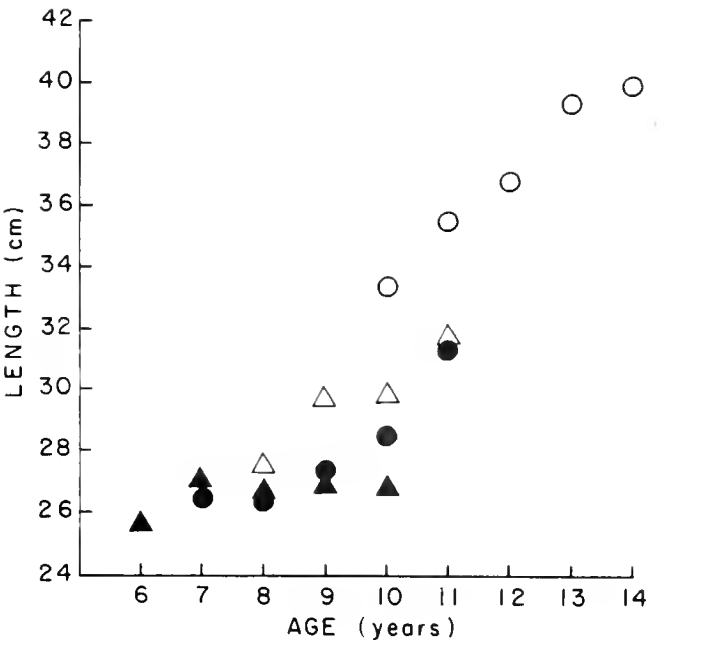

FIGURE 4.—Age-length comparison for rock sole taken in the eastern Bering Sea in 1961 (open triangles, female; closed triangles, male), and in 1963 (open circles, female; closed circles, male; from Levings 1967).

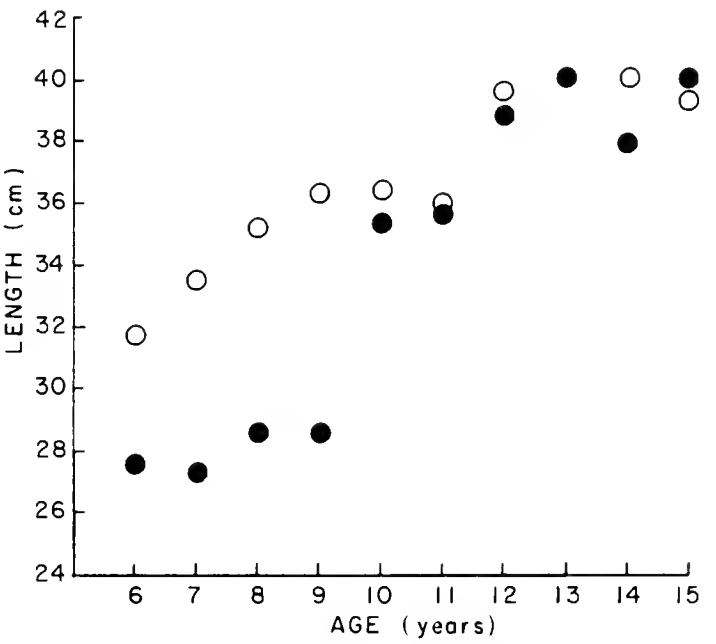

FIGURE 5.—Age-length composition (average length of combined sexes) for Alaska plaice taken in the eastern Bering Sea in 1949 (closed circles, from Mosher 1954) and 1961 (open circles).

comparable age average 10% greater in length (Figure 4).

No age-length information has been reported for Alaska plaice except that by Mosher (1954). The otolith observations by Mosher in 1949, though not separated by sex, indicate a markedly slower growth rate for younger fishes than that observed in our 1961 samples (Figure 5). Mosher (1954) comments that in his sample of Alaska plaice the first three to seven annular rings on each otolith were compressed and that beyond this zone, the annuli were farther apart. We noticed this same growth pattern in some of the otoliths from our collection, but it was not consistent.

In reflecting on the significance of similarities or differences between our results and those obtained by other authors, we feel that a number of points should be considered. First, we recognize that our samples were collected from the southern part of the distribution of these species in the eastern Bering Sea, and some of the specimens with which we make comparisons were taken in another part of the range and may represent another population. It was determined by Fadeev (1970) that the yellowfin sole of the southeastern

Bering Sea do constitute a single population, but no such determinations have been made for rock sole and Alaska plaice. Second, there is no evidence of validity for the ages we obtained from otoliths; that is to say that we do not know how well the otolith ages represent the true age of the fish. Additionally, we must assume that otoliths were interpreted and recorded in essentially the same manner by all investigators.

Acknowledgments

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FURTHER STUDIES REGARDING EFFECTS OF TRANSPORTATION ON SURVIVAL AND HOMING OF SNAKE RIVER CHINOOK SALMON AND STEELHEAD TROUT

Losses to juvenile and adult Pacific salmon, *Oncorhynchus* spp., and steelhead trout, *Salmo gairdneri*, populations migrating in the Columbia and Snake rivers have increased dramatically in recent years. The principal migratory route over which most salmonids must pass has been artifically altered by construction of a series of dams. The dams, with their associated reservoirs, are a major source of mortality to migrating salmonids. Ebel et al. (1973) summarized the primary causes of mortality which include gas bubble disease, turbines at dams, and predation.

There is evidence that certain stocks of salmonids are in grave danger unless ways are found to increase their populations. For example, 1973 returns of summer-run chinook salmon, *O. tshawytscha*, to the Columbia and Snake rivers reached all-time low proportions.[1] Other wild stocks of steelhead trout and chinook salmon also continue to decline.

The National Marine Fisheries Service conducted transportation experiments at Ice Harbor Dam during 1968-70 to find ways of increasing survival of Snake River salmonids.

In these experiments, juvenile salmon (spring- and summer-run chinook) and steelhead were collected at Ice Harbor Dam and transported to two locations downstream. Evaluation of these tests depended upon adults returning to Ice Harbor Dam and, subsequently, to their native streams. Data on adults returning from releases of juvenile chinook in 1968 and of juvenile steelhead in 1969 were analyzed and reported by Ebel et al. (1973). Analyses of adult returns from releases of juvenile chinook in 1969-70 and of juvenile steelhead in 1970 are covered in this addendum report.

Methods

General Procedures

Migrating juvenile chinook salmon (spring- and summer-run populations) and steelhead trout were collected at Ice Harbor Dam by dipnet from gatewells (Bentley and Raymond 1969) in 1969 and from a bypass collection area (Park and Farr 1972) at Ice Harbor Dam in 1970. Collection from the bypass area differed from dipnetting in that fish were accumulated in a holding area over a 24-h period. After accumulation, the fingerlings were raised by a fish pump about 15 m to an aerated tank truck for hauling to the fish marking facility. In both years populations were mixed and randomized before marking. The adipose fin was excised, a thermal brand (Mighell 1969) placed on the side of the fish, and a magnetic wire tag (Jefferts et al. 1963) injected into the snout of each fish. The control or nontransported group was released about 15 km above Ice Harbor Dam. The transported groups were released 5 km downstream from John Day Dam on the Oregon side of the Columbia River and 1 km downstream from Bonneville Dam on the Washington side of the river (Figure 1). Distinguishing brands and color-coded wire were assigned to each experimental group.

Numbers of juvenile chinook salmon and steelhead trout marked and released at various locations are shown in Table 1. In both 1969 and 1970, collection of juveniles fell below expectations. For example, we were able to mark only 28,956 chinook salmon in 1970. Therefore, numbers of marked returning adults were reduced accordingly.

Evaluation of Returning Adults

The effect of transportation of juveniles on their survival and homing as adult fish was evaluated by comparing recoveries of transported and nontransported adults at various sites in the river system as they returned on their spawning

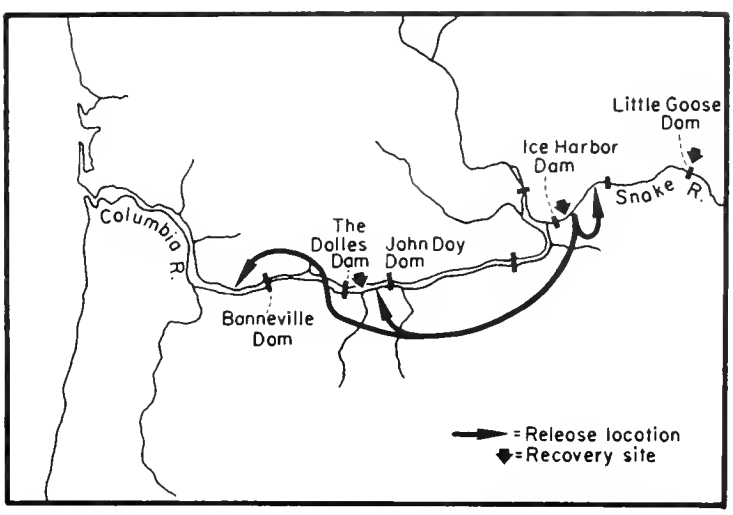

FIGURE 1.—Columbia and Snake rivers, showing release and recovery sites of migrating chinook salmon and steelhead trout.

[1] Annual fish passage report Columbia River projects, 1973. North Pacific Division, U.S. Army Corps of Engineers, P.O. Box 2946, Portland, OR 97208.

TABLE 1.–Number of transported and nontransported (control) juvenile chinook salmon and steelhead trout that were marked and released, 1969-70 (figures adjusted for tag loss)[1].

Release site (experimental group of fish)	1969		1970	
	Chinook	Steelhead	Chinook	Steelhead
Ice Harbor Dam (control)	24,217	25,313	8,624	18,347
John Day Dam (transported)	14,782	20,430	10,159	20,935
Bonneville Dam (transported)	13,529	—	10,173	31,282
Total	52,528	45,743	28,956	70,564

[1]Initial tag loss was determined for the control releases by examination of juveniles after recovery at Ice Harbor Dam, 1969-70; tag loss for the test groups were determined by fish held at release sites after transport.

migration. These included returns to the sport, commercial, and Indian fisheries in the Lower Columbia River; to Ice Harbor and Little Goose dams on the Lower Snake River; to Rapid River and Dworshak hatcheries in Idaho; and to the spawning grounds.

Most of the tagged adults were captured at Ice Harbor Dam or Little Goose Dam. At Ice Harbor Dam about 80% of the run of adult fish ascend the south ladder enroute to the spawning grounds. At Little Goose Dam all fish must ascend the single ladder installed there. Adults were recovered at Ice Harbor Dam by a detector-separator device that intercepted tagged salmon and trout (Durkin et al. 1969). At Little Goose Dam, recoveries were made by an improved but similar detector apparatus. A major modification of the system included a Denil-type fishway instead of the pool-and-overfall ladder used at Ice Harbor Dam.[2] Improvements incorporated in the facility at Little Goose Dam increased detection efficiency markedly in 1970.

Results

Returns of Adult Spring and Summer Chinook to Ice Harbor and Little Goose Dams

Numbers of returning adult salmon successfully detected, separated, and identified at the adult separator are listed in Table 2. It should be stressed that the observed return of adults represents only a fraction of the total return of marked fish to Ice Harbor and Little Goose dams. The observed tally is low for the following reasons: 1) approximately 20% of the adult run at Ice Harbor Dam passed up the right bank (north) fishway which did not have a tag detection device; 2) at Little Goose Dam, the barrier gates at the entrance to the automatic separator were open at night (2100-0500) allowing some adults to pass undetected; 3) some tag loss had occurred between tagging and recovery as adults; 4) the tag detection system was less than 100% efficient; 5)

[2]Slatick E. 1974. Laboratory evaluation of a Denil-type steeppass fishway with various entrance and exit conditions for passage of adult salmonids and American shad. Unpubl. manuscr. Natl. Mar. Fish. Serv., NOAA, Pasco, Wash.

TABLE 2.–Percentage of transported and nontransported (control) juvenile chinook salmon (released in 1969 and 1970) that were recaptured as adults at Ice Harbor and Little Goose dams, 1 April through 18 August 1971-73.

Release site and (in parentheses) experimental group of fish	Number of juveniles released[1]	Number recaptured as adults	Percentage return as adults	
			Observed	Estimated[2]
1969:				
Ice Harbor Dam (control)	24,217	47	0.194	0.497
John Day Dam (transported)	14,782	19	0.129	0.356
Bonneville Dam (transported)	13,529	33	0.244	0.581
1970:				
Ice Harbor Dam (control)	8,624	17	0.197	0.323
John Day Dam (transported)	10,159	7	0.069	0.113
Bonneville Dam (transported)	10,173	29	0.286	0.467

[1]Adjusted for initial tag loss.
[2]Based on a comparison of the known recovery of fish with magnetized wire tags at Ice Harbor and Little Goose dams and the subsequent recovery of these and other marked fish at a hatchery upstream. Returning fish identified at the dam were marked with dart tags and released to continue their migration upstream. Numbers of dart-tagged fish arriving at Rapid River Hatchery were compared with the recovery of other wire-tagged fish not previously detected and identified at Ice Harbor and Little Goose dams.

presumably some adults could have passed upstream through the navigation locks at Ice Harbor and Little Goose dams.

Throughout this section of the report, percentage figures are given which indicate either an increase or decrease in survival of groups of juveniles transported downstream in comparison to control groups not transported but released near the collection point. Some of the increases are statistically significant, some are not; generally those that are significant are indicated. We present the data even though some of it is not statistically significant because it parallels earlier data reported by Ebel et al. (1973).

The combined adult returns—of spring- and summer-run chinook salmon from juveniles transported from Ice Harbor Dam and, subsequently, released at Bonneville Dam—were greater than adult returns from control releases made at Ice Harbor Dam. The combined transportation benefit (Table 2) for spring- and summer-run chinook salmon released in 1969 was 27%; in 1970, 47%.

An analysis of comparative survival to adults for spring- and summer-run chinook salmon by year of transport are presented in Table 3. The transportation benefit indicated for juveniles released in 1969 was 27% for spring-run chinook salmon and 29% for summer-run chinook salmon. Benefits from the 1970 release were 40% for spring-run chinook salmon and 57% for summer-run chinook salmon.

Combined spring and summer adult returns from the John Day release were 34% less in 1969 and 65% less in 1970 than returns from the controls. Although the lower adult returns from juvenile releases at John Day are unexplained at this time, it is possible that the cumulative stress from collection, handling, and hauling combined with the stress from having to pass two dams (The Dalles Dam and Bonneville Dam) may have been detrimental for fish released at this site.

Returns of Adult Steelhead Trout to Ice Harbor and Little Goose Dams

Table 4 lists the returns of adult steelhead trout (released as juveniles in 1969-70) that were successfully detected, separated, and identified at the automatic separator at Ice Harbor and Little Goose dams. We identified 148 adult steelhead trout from those released in 1969. Of these, 46 were from the control release and 102 from the John Day transport release, which give a transportation benefit of 174%—a significant ($\chi^2 = 34.370$; df = 1) increase.

Adult steelhead trout returns from the 1970 juvenile releases totaled 324 fish. Of these, 71 were from the control release, 75 from the John Day transport release, and 178 from the Bonneville transport release. The transportation benefit from the Bonneville release was 47% ($\chi^2 = 7.315$; df = 1); however, no benefit was derived from transport of juveniles to the John Day release site (adult re-

TABLE 3.—Comparison between transported (released at Bonneville and John Day dams in 1969-70) and nontransported (control) groups of chinook salmon based on numbers of transported and nontransported juvenile fish recaptured as adults at Ice Harbor and Little Goose dams, 1971-73.

Release site (of juveniles) and seasonal race of salmon[1]	No. of salmon recaptured as adults at Ice Harbor and Little Goose dams[2]		Transportation benefit or deficit (−) (Percent)
	Transported	Nontransported	
1969			
Below Bonneville Dam:			
Spring chinook salmon	38	30	27
Summer chinook salmon	22	17	29
Below John Day Dam:			
Spring chinook salmon	23	30	-23
Summer chinook salmon	8	17	-53
1970			
Below Bonneville Dam:			
Spring chinook salmon	14	10	40
Summer chinook salmon	11	7	57
Below John Day Dam:			
Spring chinook salmon	4	10	-60
Summer chinook salmon	2	7	-71

[1]Seasonal races of chinook salmon in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn.
[2]Numbers recaptured adjusted in relation to numbers released (Table 1).

TABLE 4.–Percentage return and benefit or deficit (-) of transported to nontransported (control) juvenile steelhead trout (released in 1969-70) that were recaptured as adults at Ice Harbor and Little Goose dams, 1970-73.

Release site and (in parentheses) experimental group of fish	Number of juveniles released[1]	Number recaptured as adults				Percentage return as adults		Percentage transported to control benefit or deficit (−)
		One ocean	Two ocean	Three ocean	Total	Observed	Estimated[2]	
1969:								
Ice Harbor Dam (control)	25,313	43	3	0	46	0.182	0.792	—
John Day Dam (transported)	20,430	76	25	1	102	0.499	1.600	174
1970:								
Ice Harbor Dam (control)	18,347	12	58	1	71	0.387	0.729	—
John Day Dam (transported)	20,935	8	66	1	75	0.358	0.610	−7
Bonneville Dam (transported)	31,282	14	162	2	178	0.569	0.924	47

[1]Adjusted for initial tag loss.
[2]Based on comparison of the known recovery of fish with magnetized wire tags at Little Goose Dam and the subsequent recovery of these and other marked fish at a hatchery upstream from Little Goose Dam. Returning fish identified at the dam were marked with dart and jaw tags and released to continue their migration upstream. Numbers of externally-tagged fish arriving at Dworshak Hatchery were compared with the recovery of other wire-tagged fish not previously detected and identified at Little Goose Dam.

turns from this release were 7% less than returns from controls).

Recovery of Marked Chinook Salmon in Commercial and Sport Fisheries

Although only 43 adult chinook salmon (Table 5) were recovered in the commercial and sport fisheries from juvenile releases in 1969, returns indicate a definite benefit from transportation. The benefit of transported fish (John Day-Bonneville releases combined) was 19%.

It was not possible to distinguish between returns of adults to the fishery from juvenile releases at Bonneville and John Day because of the loss of the identifying brands. Brands which would have enabled identification by release site were obliterated by gillnet abrasion. Transported and control groups of juveniles could be distinguished as adults by magnetic tags, but only two codes were used–one for the controls and one for the transported fish (Bonneville and John Day combined). However, if the percentage of adult returns obtained at Ice Harbor and Little Goose dams–where brands of fish returning from releases at Bonneville and John Day were visible–is applied to the total returns of adults as obtained in the commercial fishery, the benefit from transporting juveniles becomes 59% for chinook salmon transported to Bonneville Dam.

Adult recoveries in the lower river commercial and sport fisheries from juvenile chinook salmon released in 1970 were insufficient (seven transported and eight control fish) for analysis of transport to control return ratios.

TABLE 5.–Comparison between transported and nontransported groups of chinook salmon based on numbers of transported and nontransported juvenile fish (released in 1969) that were captured as adults by commercial and sport fisheries in the lower Columbia River, February through August 1971 and 1972.

Location of fisheries	No. of salmon recaptured as adults	
	Transported	Nontransported
Upstream from Bonneville Dam (Indian fishery)	8	4
Downstream from Bonneville Dam	17	14
Total	25	18

Returns of Adult Chinook Salmon to Spawning Grounds

Spawning ground surveys (Figure 2) and examination of tagged adult chinook salmon at Rapid River Hatchery near Riggins, Idaho, provided further information concerning benefits at their "home" destination from transport of juvenile spring- and summer-run chinook salmon.

In 1971, 12 tagged adult fish (from the 1969 juvenile release) were recovered from the Rapid River Hatchery; an additional 15 were from sport fishermen and spawning ground surveys. Of the total, 15 adults were from the transported groups and 12 from the control group. By adjusting from the ratio of John Day to Bonneville adult returns, we estimated that 12 of the 15 transported fish

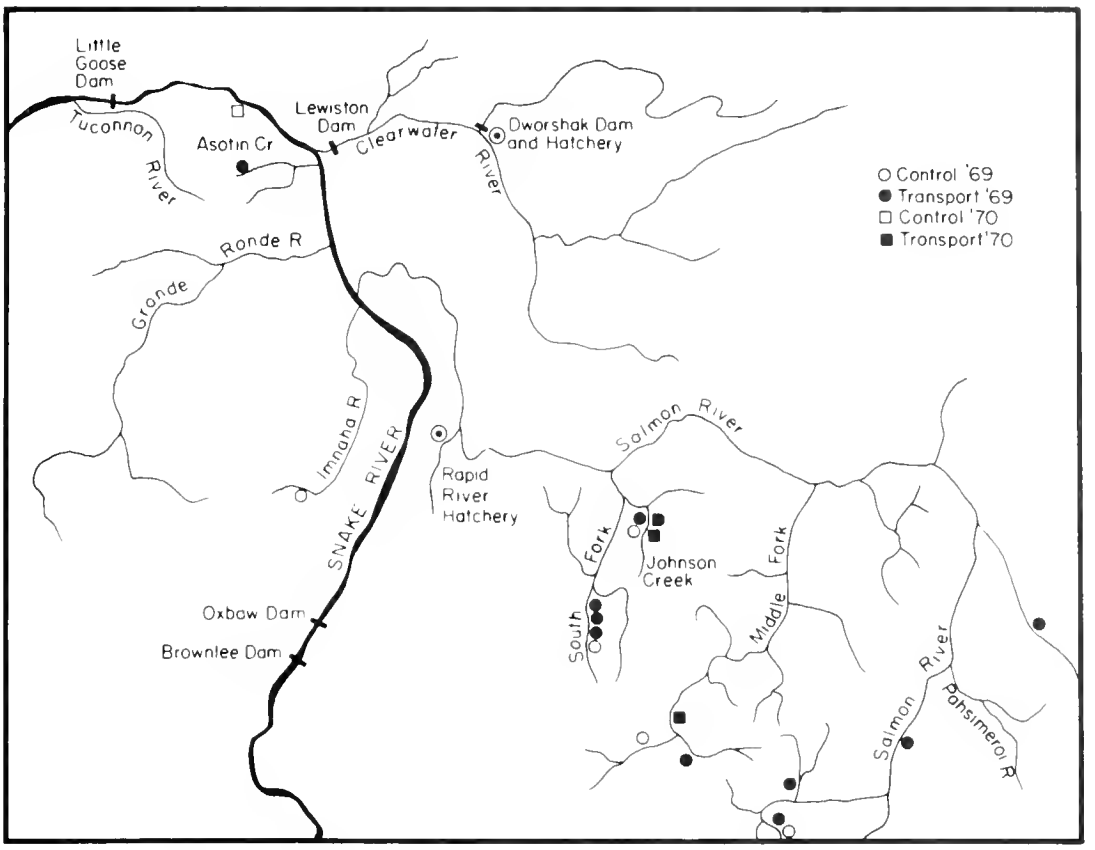

FIGURE 2.–Location of recoveries of tagged adult chinook salmon returning to spawning grounds from 1969-70 experiments.

were from the group released at Bonneville Dam. The transport benefit for the groups of juveniles released at Bonneville becomes 78% when computed on the basis of the number of juveniles released per group.

Too few tagged adult chinook (five Bonneville transports and one control) from the 1970 juvenile releases were collected in 1972 from all sources to make conclusions regarding the effect of transportation.

Discussion

Results from this study, which was a continuation of a study begun by Ebel et al. (1973), corroborated earlier findings, i.e., homing of adults after transportation downstream as juveniles was not seriously affected and survival was increased. Throughout this study, we found no evidence of straying among adults returning from the experimental releases. All comparisons between the adult returns from transported and control groups of juvenile chinook salmon and steelhead trout indicated that survival was definitely increased by transporting juvenile fish to a release site downstream from Bonneville Dam.

We have been particularly concerned with how the percentage return from these experiments might compare with that of unhandled or undisturbed juvenile migrants. Some insight into this matter is shown by a comparison between estimated adult returns from juveniles marked and released as controls and returns of unhandled adult fish to Rapid River Hatchery in Idaho (Table 2); the data indicate that survival of chinook salmon released in our 1968 experiment was greater than that indicated for salmon returning to the Rapid River Hatchery. Adult returns from controls released in 1969 were comparable to hatchery returns, but returns from those released in 1970 were lower than returns to the hatchery.

It is assumed that some stress was placed on juveniles in the collection, handling, marking, and transport processes. These cumulative stresses were not outwardly apparent in the physical condition of the juvenile smolts at the time of handling, but differences in survival of returning adults indicated that condition of the fish at the time of marking must have varied among years.

Our collection methods were changed in 1970 by addition of a fish pump; this added a pumping stress to our fish handling process. Although Park and Farr (1972) indicate no immediate mortality or observed stresses due to pumping from the

facility, it is possible there could have been significant delayed effects. The effect of pumping on juvenile chinook salmon and steelhead trout—when added to other cumulative stresses associated with handling in our transport process—is indicated by the lower percentage of adult returns from control releases of juveniles in 1970.

Although smaller numbers of juvenile chinook were released in 1969-70 than in 1968 and a correspondingly small number of adults returned, we believe that the lower percentage of returning adults does indicate that stress factors due to handling were higher in 1970 than in 1969. The addition of two dams—Lower Monumental and Little Goose—placed in operation in 1969 and 1970, upstream from Ice Harbor Dam, must also be considered. Fish had to pass through Lower Monumental Reservoir and Dam in 1969 before being collected at Ice Harbor Dam. In 1970, they had to pass through both reservoirs and dams before being collected. Supersaturation of dissolved nitrogen also became a problem between Little Goose and Ice Harbor dams at this time. Turbines from both Lower Monumental and Little Goose dams were not scheduled for installation until after the spring freshet and as a result large volumes of water had to be passed over the spillways, causing dissolved gas concentrations to be high; a large percentage of the fish arriving at Ice Harbor Dam exhibited obvious signs of gas bubble disease.

If we use the percentage adult returns in relation to juveniles released at the Rapid River Hatchery in Idaho as an indicator of the rate of return of naturally migrating chinook salmon and we compare our percentage return figures, we find our estimate of return of controls was 4.3% in 1968—much higher than the 0.48% adult return recorded for Rapid River Hatchery.[1] The estimated control return of 0.497% for the 1969 outmigration is comparable to the 0.493% return to Rapid River Hatchery, but estimated returns from controls released in 1970 dropped to 0.323% whereas the return to the Rapid River Hatchery was 0.477%. Thus, the stresses placed on juvenile fish prior to collection, in addition to those involved in the handling process, conceivably were instrumental in causing the lower return of adults from the 1969-70 experiments.

When we examine adult returns from juvenile control releases of steelhead trout, we find that the percentage return from control releases of steelhead trout in 1969-70 were much greater than for comparable juvenile releases of chinook salmon. This indicates that the ability of steelhead trout to withstand the cumulative effects of stress is greater than that of chinook salmon.

Using the adult return percentage of steelhead trout to the Dworshak Hatchery from juvenile migrants released at that site in 1970 as a base indicator of the adult return of naturally migrating steelhead trout to Idaho streams, we find that our estimated adult returns from control releases to Ice Harbor and Little Goose dams of 0.792 and 0.729% (in 1969 and 1970, respectively) were somewhat greater than the 0.682%[1] return to Dworshak Hatchery. When our adult control returns are adjusted for the upriver sport catch on steelhead trout, our revised return (0.713% from the juvenile control releases in 1969) was comparable to the 0.682% return to Dworshak Hatchery. The return from the 1970 (control) release of 0.598% was, however, less than the hatchery return of 0.682%.

Based on the foregoing rationale, we believe that our control releases of juvenile chinook salmon and steelhead trout in 1969 returned as adults at rates comparable to those of natural migrating salmonids and that benefits on survival to adults indicated for our transported salmon and steelhead trout represent real increases.

Studies to further define stress problems associated with diversion, collection, and handling of naturally migrating juveniles are currently underway. To maximize the effectiveness of a collection and transportation system, stresses from all sources must be minimized.

Conclusion

The homing of adult fish, captured during their seaward migration as juveniles and transported downstream (from Ice Harbor Dam to Bonneville Dam), was not reduced by the transport operation. Although numbers of returning adults were small, comparisons of returns of transported fish versus control fish to Ice Harbor Dam, the spawning grounds, and hatcheries in Idaho indicated that they "homed" satisfactorily. No evidence of straying of transported fish was observed in our surveys.

[1]Pers. commun. Evan Parrish, Hatchery Manager, Rapid River Hatchery, Riggins, Idaho.

[1]Pers. commun. Einer Wold, Hatchery Pathologist, Dworshak Hatchery, Ahsahka, Idaho.

Adult returns indicate a definite benefit is achieved from transporting juvenile chinook salmon and steelhead trout from a collector dam (Ice Harbor) to a release site below Bonneville Dam. Transport benefits were lower than reported from releases made in 1968, but a benefit of 27-47% was still indicated. No steelhead trout were released at Bonneville Dam in 1969, but a 47% benefit was realized from transportation of juveniles to that site in 1970.

Data from returning adults indicate that in general the John Day release site was a poor one. In 1969, however, returns from juvenile steelhead trout releases there were 174% greater than controls. The reduced transport benefit for our John Day release can probably be best explained by the fact that juveniles must still pass over The Dalles and Bonneville dams before entering the ocean. These further stresses probably nullify any initial transport benefit.

The rate of adult return from those juvenile fish transported in 1969 was better than the adult returns from those transported in 1970. Data suggest that stresses to juveniles encountered prior to collection at Ice Harbor and the changed handling procedures in 1970 were a factor.

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COMPARATIVE VULNERABILITY OF FRY OF PACIFIC SALMON AND STEELHEAD TROUT TO PREDATION BY TORRENT SCULPIN IN STREAM AQUARIA

Predation on fry of salmon and trout by sculpin, *Cottus* spp., is intense in certain situations (Hunter 1959; Sheridan and Meehan 1962; Patten 1962, 1971a, 1972) or of little consequence in others (Ricker 1941; Patten 1971a, 1972). Variation in intensity may be related to such important causes as the environment or to specific differences of the predators or prey.

In this paper I report the comparative ability of steelhead trout, *Salmo gairdneri*, and of five species of Pacific salmon, *Oncorhynchus* spp., to avoid predation by torrent sculpin, *C. rhotheus*, in a fixed environment—stream aquaria. The vulnerability of a species of salmon or steelhead trout, as determined from this study, is related to known information on the duration of residency and behavior of a species in streams. These results help in the assessment of natural causes of mortality that affect the productivity of salmon and steelhead trout. The study was conducted in stream aquaria adjacent to Cedar River near Ravensdale, Wash., in 1966.

Facilities and Procedures

The facilities consisted of two stream aquaria and eight holding aquaria that received water from the Cedar River (more fully described by Patten 1971b). Two stream aquaria used for tests of predation were 2.4 m long and 0.6 m wide and high; water depth ranged from 2 to 18 cm depending on bottom contour. The eight holding aquaria used in the study (to incubate the eggs and maintain the young fish before tests) were 34 cm wide by 41 cm long by 36 cm high; water depth was 18 cm.

Water from the Cedar River was taken at a low dam and supplied by gravity flow to the head box and then to the stream aquaria. Each aquarium had a continuous flow. The water was usually clear, and temperatures recorded at 0800 ranged from 5° to 10°C during the course of the study.

The experimental procedure exposed salmon or trout fry to predation by torrent sculpin under pseudo-natural but controlled conditions. Torrent sculpin were collected by electrofishing in Soos Creek, Wash.; the salmon and steelhead trout fry were reared from eggs to insure that they had no previous experience with predators.

Eggs from pink salmon, *O. gorbuscha*, chum salmon, *O. keta*, sockeye salmon, *O. nerka*, fall chinook salmon, *O. tshawytscha*, coho salmon, *O. kisutch*, and from steelhead trout of Puget Sound stocks were placed in holding aquaria and covered with coarse gravel.

The salmonid fry were subjected to predation tests as soon as the yolk sacs were absorbed. Since the time of emergence from the gravel by the fry of these six species varies, the tests extended from March to June, during which period water temperatures (Table 1) and day lengths differed. The salmon and trout fry were not fed but could be seen mouthing particles entering the holding aquaria. I assume growth of fry negligible and size differences to be fixed by the species and race used. Observations of viability and vigor of fry in the holding aquaria were made before, during, and after testing as a standard of comparison for test fish. Samples of the salmon and trout fry were measured in millimeters from snout to fork of tail (Table 1); their volumes were determined by displacement in a graduated tube. Sculpins were measured in millimeters from snout to end of tail (Table 1).

Twenty sculpins were placed in holding aquaria without food the first day of the experiment. On the second day 10 fry of one species were placed in each stream aquarium and on the third day, 10 sculpins were quietly introduced at the downstream end of each stream aquarium. On the fifth day the fry surviving after 48 h were counted; then both predators and prey were removed. These subjects were not used again. Two to seven replicate tests were made for each species of salmon or trout (Table 1).

Comparative Survival of Salmon and Trout Against Predation

The positions and activities of the salmon, trout, and sculpins in the stream aquaria are first described because these varied between species, affecting predator-prey interrelations. The following sections report on the viability and vigor of fry and on the survival rates of the species of salmon and trout.

The positions and activities of a species of salmon or trout during daylight tests varied. Fish in the stream aquaria maintained positions and apparently fed; chinook and coho salmon displayed intraspecific aggression, indicating accommodation to the enclosure. All species were observed in the deepest areas of the stream aquaria where they distributed themselves vertically 1 cm from the bottom to the water surface. Most of the steelhead trout fry and some pink and chum salmon fry hid under rocks, but this behavior was seldom exhibited by the other salmon species except for short periods when they were frightened.

Torrent sculpin typically spaced themselves through the deeper parts of the stream aquaria. They were distributed through its length with the greatest number at the upstream end. They were inactive and curled around large rocks or partially buried themselves in areas with soft bottoms. The concealment of the sculpins was so complete that I often had to search for as long as 20 min to remove all of them after an experiment.

After the sculpins were placed in the stream aquaria, the salmon and trout fry, on recovering from the disturbance, modified their vertical distribution. Salmon fry reacted to an active sculpin by moving away laterally and upward. In the presence of sculpins all salmon fry increased their distance from the bottom to about 5 cm. Steelhead trout fry, that usually hid under rocks when undisturbed, moved off the bottom and maintained positions near the water surface when sculpins were present. Behavior of the steelhead trout fry was apparently more disturbed by sculpins than was that of the salmon fry.

Sculpins rarely stalked the fry in bright daylight but waited immobile for them to come

TABLE 1.—Survival of salmon and trout fry subjected to predation in 1966 by torrent sculpin, *Cottus rhotheus*.

Species	Date of testing	Water temp[1] (°C)	Test (prey) fish		Mean length of predator (mm)	Number of tests	Number of survivors		Percentage survival
			Number	Length range (mm)			Total	Range/test	
Chinook salmon	3-25 to 4-15	6.2	60	38-42	92.0	6	31	1-8	51.7
Chum salmon	5-16 to 5-23	8.7	60	35-38	88.7	6	3	1-2	5.0
Coho salmon	3-25 to 4-15	6.2	70	36-39	91.7	7	53	6-9	75.7
Pink salmon	3- 2 to 3-11	6.2	60	35-37	92.5	6	1	0-1	1.7
Sockeye salmon	4-15 to 4-19	6.1	20	41-43	97.5	2	4	1-3	20.0
Steelhead trout	5- 4 to 5-13	8.9	60	29-31	91.4	6	14	0-7	23.3

[1]Average temperature (°C) at 0800 for 2 days of test.

near. Then they made short, quick lunges at the prey. Little predation occurred during the day and I never observed a sculpin catching a salmon.

Stocks of fry used for testing appeared normal, healthy, and vigorous. A reserve of fry of a species was maintained in holding aquaria during and after testing without mortality—in fact dead or inferior fry were never observed over 2 yr. Pretest salmonids held in stream aquaria often maintained positions in the faster moving water. Individuals that may have been inferior as indicated by use of slow water shallows, by swimming at the downstream end, or by impingement on the outlet screen were never observed.

Results showed variation between rates of predation on a prey species, size of prey species, and on temperature and length of daylight during testing. Predation by torrent sculpin was least on coho and chinook salmon, intermediate on sockeye salmon and steelhead trout, while practically complete on pink and chum salmon (Table 1). Chi-square analysis showed significant differences between all species except for 2 of the 10 combinations tested: sockeye salmon-steelhead trout and pink-chum salmon. The number of survivors per test varied considerably for the chinook salmon and steelhead trout. Steelhead trout were relatively deep bodied but shorter than salmon fry and among the salmon, chum and pink were thin bodied (Table 1 shows lengths; body volume determinations indicated chinook, coho, and sockeye salmon had as much as twice the displacement of the other species). Testing of chum salmon and of steelhead trout was a month or two later in the spring when temperatures were higher (Table 1) and duration of daylight was longer than for other species.

Innate Predator Avoidance of Species

Differences in rates of predation on the study species are not well explained by observed differences in behavior, size of prey, ambient conditions, or predator related effects but may be due to innate behavior after emergence of fry from the gravel. The only species with greatly divergent behavior in the stream aquaria was the steelhead trout. Remaining near the water surface during day effectively removes them from the influence of sculpin predators; however, they may settle to the substrate at night, a time when sculpins are more effective predators (Patten 1971b).

The larger prey species, those having the longest body lengths and being relatively deep bodied, were not always those with the higher survival. Chinook, coho, and sockeye salmon were the largest. Chinook and coho had the highest survival but the sockeye salmon, the largest prey, had survival similar to the steelhead trout, the smallest prey. Chum and pink salmon were slim and as long as coho and longer than steelhead trout, but their survival was lowest of the species studied. If size of prey or satiation of predators from greater food volumes influenced rates of predation, these factors were apparently less important than other effects on a species level.

Length of day or temperature had no apparent effect on rate of predation. Sculpins are most predaceous on salmon at times of marginal light intensity (Patten 1971b), which might suggest they are more serious predators at times of shorter day lengths. Trends between intensity of sculpin predation on fry and temperatures observed during this and other studies have never been observed.

The data show strong interspecific variations of the study species in vulnerability to predation by the torrent sculpin. I suspect a difference in innate behavior exists; some species are better able to evade predation. Furthermore, the early life history and behavior of the study species may be linked to their predator avoidance abilities. Chum, pink, and sockeye salmon quickly migrate from a stream environment to the sea or a lake where they form schools (Mason 1974, has observed chum salmon forming loose aggregations in estuaries). Schooling may aid these species in avoiding predation (Shelbourn 1966). Chinook and coho salmon and steelhead trout on the average form loose aggregations in streams during a period of growth before migrating to the sea. Forming loose aggregations would increase feeding opportunities in streams. Density of predators may be high in this situation (Patten 1971a) and survival is attained by a well-developed avoidance response for chinook and coho salmon.

Steelhead trout fry had a comparatively high mortality among stream resident species that may have been related in part to their behavior during tests, to their small size or an inferior predator avoidance response. Their survival, at least during the early fry stage, may be increased by unavailability through selection of a protective habitat. Hartman (1965) described the microhabitat of recently emerged steelhead trout and coho salmon in the Chilliwack River, British Columbia,

as shallows at stream edges or in close proximity to physical objects. Recently emerged steelhead trout fry, observed adjacent to my study area in the Cedar River in 1965-66, were rarely found along sandy shore areas but were commonly seen among rocks at depths of 1 to 5 cm—when disturbed they hid under the rocks. The use of extreme shallows by steelhead trout fry may in part be an innate response to predators since this type of habitat in streams is relatively barren of other fish.

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HERITABLE RESISTANCE TO GAS BUBBLE DISEASE IN FALL CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*[1]

Construction of a series of dams on the Columbia River has resulted in air-supersaturation of the river during spring and early summer. Air-supersaturation is caused by the entrainment of air in water at depths as great as about 15 m in the plunge basins of the spillways below each dam. The level of air-supersaturation varies according to the amount of water-flow over the spillways (Ebel 1969). Supersaturation levels which are known to be fatal to salmonid fishes (Rucker and Hodgeboom 1953; Westgard 1964; Ebel 1969; and Blahm et al. 1975) are often sustained in the Columbia River from April through July, the period when many juvenile salmonids emigrate to the ocean.

Salmonids vary greatly in their tolerance for supersaturation (Ebel 1969). If a portion of this variability is related to additive genetic factors, an increase in the average tolerance of salmon populations to air-supersaturation can be expected as a result of selection. The purpose of this study was to estimate the influence of genetic factors on resistance to gas bubble disease for fall chinook salmon, *Oncorhynchus tshawytscha*. Specifically, the objectives were: 1) To determine the heritability of resistance to death from gas bubble disease for a stock of Columbia River fall chinook salmon, and 2) to determine the inherent level of resistance to gas bubble disease for several fall chinook salmon stocks.

Methods

Estimation of Heritability

Juvenile fall chinook salmon representing 80 families were reared at the Abernathy Salmon Cultural Development Center, near Longview, Wash. The families were produced by mating 20 males to 80 females, 4 females per male, in a nested breeding experiment. One hundred fish from each family were marked by cold-branding (Everest and Edmundson 1967) when they were 4 mo old and their weights averaged 2 g. Each group of 100 fish received a unique mark.

[1]This work was carried out in cooperation with the U.S. Fish and Wildlife Service, Oregon Fish Commission, Oregon Wildlife Commission, and Oregon State University.

Thirty marked fish from each family were put into each of three tanks (1.8 m in diameter and 0.3 m deep) at the Abernathy Center. These groups of 30 fish will be referred to as tank-families. The remaining 10 fish from each family were put into a similar tank as a control. The test tanks were supplied with 18.9 liter/min of water which was air-supersaturated to 130 ± 1.5%.

Two variables, time to death for each fish after exposure to air-supersaturated water and the percentage survival for each family after 36 h of exposure, were examined.

Water to be air-supersaturated was directed into a pump to create a line pressure of 1.4 kg/cm^2. A controlled amount of air was injected into the line through an air stone inserted at a joint in the line. Aeration occurred under pressure in a 1.5-m vertical section of line. The test water then entered a pressurized tank where excess air was vented. Air-supersaturated water from the pressure tank was then jetted below the surface into the test tanks.

Stock Comparisons

Since differences between stocks of fish in their resistance to gas-bubble disease arise from both genetic and environmental factors, the fish used in the present experiments were reared in one location under controlled conditions to minimize differences related to environment. Differences in the groups of fish tested then were assumed to have a genetic basis.

Locations on or near the Columbia River that are discussed in this report are the following approximate distances (kilometers) upstream from the Pacific Ocean: Abernathy Salmon Cultural Development Center, 72; Kalama Hatchery, 105; Bonneville Dam, 234; Little White Salmon Hatchery, 265; Little Goose Dam, 635.

Experiment I.—In the fall of 1972, eggs were taken from mature fall chinook at Little Goose Dam on the Snake River, and at Trask River Salmon Hatchery. Smolts migrating downstream from Little Goose Dam must pass over seven dams and swim through water which may be air-supersaturated up to 130% (Beiningen and Ebel 1971). The Trask River enters the Pacific Ocean about 80 km south of the Columbia River and has never been known to contain lethal levels of air-supersaturated water. Eggs obtained at the Trask River Salmon Hatchery were taken from a large number of crosses, and eggs obtained at Little Goose Dam were from crosses between two males and two females.

Fertilized eggs from each source were transported to Oregon State University where they were incubated at 9.5°C. The fry were fed for 2 mo before being exposed to 127% air-supersaturated water. At the time of testing, the fish weighed between 1.3 and 1.5 g.

Air-supersaturated water was produced by aerating water under a hydrostatic head of 3 m in a vertical column of 15.2-cm pipe. A regulated amount of air was injected into the lower portion of the column through four air stones. Water drawn from the bottom of the column was 123% air-supersaturated. This water was then heated to 13.5°C to attain the test level of 127 ± 2% supersaturation.

Experiment II.—In 1973, fall chinook eggs were obtained from Abernathy Salmon Cultural Development Center, Little White Salmon Hatchery, and Kalama Hatchery—all on the Columbia River—and from the coastal Trask River Salmon Hatchery. Eggs from fish at Columbia River hatcheries were taken on 2 October, and those from fish at Trask River Hatchery on 28 November. All eggs were taken to Oregon State University for incubation, rearing, and testing.

Because of differences in ages, the experimental groups had to be tested at different times. We held the test fish in a constant environment at equal densities during the rearing period. The fingerlings were reared at 13.5°C in a 5.2 m × 0.3 m × 0.3 m Plexiglas[2] tank which was divided into 16 sections. The sections were divided into four blocks of four tanks each. Fifty fish from each of the four stocks were put into one section in each of the four blocks establishing a randomized block design. Fish were reared for 50 days, at the end of which time they weighed from 1.0 to 1.7 g. Seven days before testing, each group of fish was marked with a group-specific cold brand.

The fish were exposed to 127 ± 2% air-supersaturated water at 11°C in a 16.5-liter tank. Time to 50% mortality, proportion dead in 96 h, and proportion dead in 150 h were determined. An apparatus similar to that described above for tests at the Abernathy Center was used in this experiment. In all tests, we measured the total

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

uncompensated hyperbaric dissolved gas pressure with a Weiss saturometer.

Results

Estimation of Heritability

Initial mortalities occurred 3 h after the test fish were placed in 130% air-supersaturated water. All fish were dead after 132 h. The grand means of time to death (hours) in the three tanks were 22.62, 24.66, and 25.04. Two fish died in the control tank.

Because of counting errors at time of marking, individuals per tank-family ranged from 5 to 54. Few tank-families varied greatly from the expected number per family (28.4) as was indicated by the harmonic mean (26.8). Because of the unequal numbers of individuals per tank-family and the large number of observations, an unweighted means analysis of variance was used (Kempthorne 1957). First, the unweighted means of each family in each tank were subjected to an analysis of variance (Table 1). Second, all observations were used in a one-way analysis of variance to compute the within tank-families (error) sum of squares. Because the distribution of time to death for fish in each tank followed a poisson distribution, a square root transformation of time to death was applied before the analysis of variance was carried out. The square root transformation is the most appropriate for poisson data (Bartlett 1936).

Variance components were estimated as:

$$\sigma^2_M = (MS_M - MS_F)/tf = 0.027$$

$$\sigma^2_F = (MS_F - MS_{MFT})/t = 0.041$$

$$\sigma^2_{MFT} = (MS_{MFT} - (1/\bar{n}_h)MS_W) = 0.024$$

$$\sigma^2_W = MS_W = 2.800.$$

The additive genetic variance, V_A, was estimated as $4\sigma^2_M$, and the total phenotypic variance, V_P, as $\sigma^2_M + \sigma^2_F + \sigma^2_{MFT} + \sigma^2_W$. Heritability, h^2, or V_A/V_P, was 4(0.027)/2.892 = 0.037. The standard error was 0.022 (Dickerson 1959).

Survival for each tank-family after 36 h of exposure to the test conditions ranged from 53.8 to 0%. The angular transformation was applied to these data before the analysis of variance described above was performed. The theoretical binomial variance, 821, was then used as an estimate of error variance. Heritability of resistance to gas bubble disease estimated in this analysis was: $V_A/V_P = 30.68/840.87 = 0.036$.

Stock Comparisons

Resistance to gas bubble disease by offspring of fall chinook salmon from Little Goose Dam and Trask River Salmon Hatchery exposed to 127% supersaturation in Experiment I differed markedly. Time to 50% mortality, averaged from two replicates, was 73.5 h for Trask River fish and 154 h for fish from Little Goose Dam; the difference of 80.5 (SE = 3.39) was highly significant.

The difference in time to 50% mortality in Experiment II (Table 2) between Columbia River and Trask River stocks (22.25 h; SE = 6.37) was

TABLE 1.—Analysis of variance of the square root of time to death for juvenile fall chinook salmon exposed to air-supersaturated water.

Source of variation	Degrees of freedom	Mean squares	Expectation of mean square
Tanks (*T*)	(*t*-1) = 2		
Males (*M*)	(*m*-1) = 19	0.575	$\sigma^2_{MFT} + \frac{1}{\bar{n}_h}\sigma^2_W + f\sigma^2_F + tf\sigma^2_M$
Females within males (*F*)	*m*(*f*-1) = 60	0.250	$\sigma^2_{MFT} + \frac{1}{\bar{n}_h}\sigma^2_W + t\sigma^2_F$
Male-females by tanks (*MFT*)	(*mf*-1) (*t*-1) = 158	0.128	$\sigma^2_{MFT} + \frac{1}{\bar{n}_h}\sigma^2_W$
Error (*E*)[1]	*N* . . . -*mft* = 6,566	2.800	σ^2_W

where: *m* = number of males
f = number of females per male
t = number of tanks (replicates)
N . . . = total number of individuals
$\bar{n}_h$ = harmonic mean number of individuals per tank family = 26.82

[1]Error mean square obtained in separate analysis (see Kempthorne 1957:459).

TABLE 2.—Hours to 50% mortality (ET_{50}), and percentages dead in 96 h (P96) and 150 h (P150) for juvenile chinook salmon exposed to air-supersaturated water in Experiment II. Each value represents an average of four replicates; ranges are shown in parentheses.

Stock	ET_{50}	P96	P150
Abernathy	92.5 (70-116)	53 (43-64)	68.5 (63-80)
Little White Salmon	86.5 (82-94)	61 (57-67)	77.0 (75-80)
Kalama	73.8 (64-79)	64 (60-70)	86.0 (73-95)
Trask	62.0 (48-75)	70 (64-82)	86.8 (75-96)

TABLE 3.—Analysis of variance in time to 50% mortality for Trask and Columbia River chinook salmon (Experiment II).

Source of variation	Degrees of freedom	Mean squares	F
Total	15		
Blocks	3	367.7	3.02
Between stocks	3	739.5	6.07*
Columbia vs. Trask	1	1,485.2	12.19**
Within Columbia	2	366.6	3.01
Error	9	121.8	

*, **, statistical significance at the 0.05 and 0.01 levels, respectively.

significant (Table 3). Variation between the three Columbia River stocks was not significant.

Similar comparisons were made from data summarized after 96 and 150 h of exposure (Table 2). On the average, differences between Columbia and Trask stocks remained significant, but variation between Columbia River stocks became significant only after 150 h of exposure ($F = 5.01$). This difference was between the Kalama stock and other lower Columbia River stocks, suggesting that a difference in resistance to gas bubble disease exists even between stocks separated by relatively short distances. The reason for the similarity of resistances between lower Columbia River stocks probably was their common origin: Abernathy brood stock were originally taken from Spring Creek and Willard hatcheries, both of which are located upstream from Bonneville Dam.

The much greater difference in time to 50% mortality between fish taken from Little Goose Dam and fish from the Trask River (80.5 $\pm$ 3.39 h) than between combined lower Columbia stocks and the Trask stock (22.25 $\pm$ 6.37 h) indicates that fall chinook salmon migrating as far as Little Goose Dam are more resistant to gas bubble disease than are lower Columbia River stocks. This conclusion could be made only by comparing results from Experiments I and II, and by assuming that the results were not biased by the small number of crosses made at Little Goose Dam.

Discussion

Differences between stocks indicated that selection for phenotypes with greatest resistances to gas bubble disease has occurred in the Columbia River. This conclusion was supported by the observation that stocks with the longest histories of exposure to air-supersaturated water were most resistant to gas bubble disease.

Because additive genetic variance contributing to the observed differences probably has been reduced, and reduced at an unknown rate, it is impossible to estimate accurately the selection intensities that must have occurred in the past to produce the differences in resistance observed between Trask and Columbia River stocks. The low heritability for resistance to gas bubble disease in fall chinook salmon indicates that no great increases in resistance can be expected even at relatively high selection intensities.

The results further indicate that stocks transferred from coastal streams to hatcheries within the Columbia River drainage may experience high levels of mortality from gas bubble disease. On the other hand, Columbia River stocks may provide a source of brood fish that are resistant to gas bubble disease for stocking in other waterways.

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