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*COVER MICROPHOTOGRAPH: 20-day-old, late-umbo larva of Gould's shipworm (*Bankia gouldi *Bartsch) stained with oil-red O (see page 69). Larval dimensions: length, 220 μm; height, 240 μm. Light micrograph: Ektachrome 200; No. 80A filter. (Micrograph by Scott Gallager, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, 1981.)*

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GROWTH AND MORTALITY OF TWO TYPES OF SEED OYSTERS FROM THE WANDO RIVER, SOUTH CAROLINA[1]

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ABSTRACT Two age groups of seed oysters, one less than a year old, and the other several years old, were transplanted from the Wando River, South Carolina, to four sites in coastal South Carolina. Transplanting took place in March and in July 1974. Growth and mortality were determined every 2 months for 1 year.

The young seed grew much faster than did the old seed, and survival was twice that of the old seed. Initial mortalities were greater in seed transplanted in July than in March. Initial stunting of old seed from the Wando was not reflected in subsequent growth. Factors influencing growth and survival in the Wando River are discussed.

INTRODUCTION

Historically, the South Carolina oyster industry has been based on intertidal oysters. In recent years, however, interest has developed in the culturing of subtidal oysters as an alternative to lower-value intertidal oysters. A basic requirement for a subtidal oyster fishery is a source of high-quality seed. Naturally occurring, well-shaped, small single oysters grow in dense subtidal beds in the Wando River, South Carolina, a moderately polluted estuary closed to direct commercial shellfish harvesting. These oysters seldom grow to more than 6.25 cm (2.5 in.) in total length and, therefore, offer the greatest potential as seed for transplanting to commercial or recreational growing areas.

The South Carolina Marine Resources Research Institute has investigated growth and mortality of Wando seed oysters transplanted to several subtidal areas in the state. This paper compares growth and survival characteristics between the two types of transplanted Wando seed: naturally occurring stunted seed of unknown age, and young seed caught on planted cultch.

MATERIALS AND METHODS

Two types of seed oysters were dredged from the Wando River in March and in July 1974; naturally occurring old seed attached to bits of phosphate rock, and new seed from a bed which was established in July 1973 by planting oyster shell. The age of naturally occurring seed was not known. Age, however, was estimated to be at least several years since the seed was heavily shelled and relatively uniform in size. There was no indication of mortalities among larger oysters in the river which would be evidence of die-off upon reaching a certain age. New seed oysters caught on planted cultch were approximately 8 and 11 months old when transplanted. Seed oysters of each type (old and new) were placed in 1-cm^2 mesh hardware cloth trays measuring 1.2 x 0.61 x 0.14 m. These trays were reinforced with 1.25 cm (dia.) iron rods, and were supported on legs that raised the trays approximately 20 cm above the bottom. Old seed oysters were considerably larger than young seed and were stocked at 100 per tray (160/m^2). New seed oysters were stocked at 200 per tray or 320/m^2.

Two trays containing old seed and two trays containing new seed were placed in subtidal locations at Cape Romain and at Dale, South Carolina. One tray of each (old and new seed) was placed at Murrell's Inlet and in the Wando River, South Carolina (Table 1, Figure 1). All trays were positioned in March 1974; however, those in the Wando River and at Murrell's Inlet had to be replaced in July due to vandalism. Cape Romain and Murrell's Inlet are important commercial oyster growing aeas. Oysters at Dale were placed in a coastal impoundment, and those in the Wando were planted in close proximity to where the old seed had been obtained initially.

All oysters in each tray were examined every 2 months to determine survival. A subsample of 50 (all, when less than 50 remained alive) oysters from each tray was measured using Vernier calipers every 2 months during 1974, and in January and March of 1975. Measurements to the nearest millimeter were recorded from the umbo across the shell over the posterior adductor muscle to the distal edge of the shell. The experiment at Dale was terminated in September 1974, when the impoundment was drained. Water samples for salinity and temperature determinations were taken one-half meter above the bottom with a Kemmerer Bottle at each sampling date. Determinations were made by refractometer and by stem thermometer, respectively.

A sample of 25 oysters growing in natural beds adjacent to the trays in the Wando River and At Cape Romain was examined each month (except June through September at Cape Romain) for *Perkinsus marinus* (Dermo). The incidence of infection was determined using the method of Ray (1952) as modified by Quick (1972). Degree of infection was estimated using criteria established by Quick and Mackin (1971) with the exception that their very light and light categories were combined into a single class, designated as light; their light medium and medium into medium; and their medium heavy and heavy into heavy.

[1] South Carolina Marine Resources Center Contribution No. 131.

TABLE 1.

Growth and mortality study sites of seed oysters from Wando River, South Carolina.

Location	Area Description
Murrell's Inlet	A coastal estuary in northern South Carolina with little freshwater input. Trays were placed in one of many tidal creeks which drain extensive salt marshes. Tray depth at low tide, 1 meter.
Cape Romain	A large high-salinity estuary in Charleston County, South Carolina, protected on the seaward side by barrier islands and circumscribed by vast salt marshes. Depth at study site, 1 meter at low tide.
Dale Pond	A 18.2-hectare pond on Chisolm Island in southern South Carolina fed by South Wimbee Creek. Water exchange is restricted and occurs only during the last half of flood tide and first half of ebb. It is surrounded by maritime forest and salt marsh. Tray depth at low tide, 1 meter.
Wando River	An estuary of Charleston (South Carolina) Harbor draining approximately 134 km^2. It is bound on either side by extensive salt marshes. Water depth at the tray site was 1.5 meters at low tide.

RESULTS AND DISCUSSION

Old seed grew most rapidly at Dale Pond and at Murrell's Inlet during the first sampling period (Figures 2 through 5). Growth continued throughout the warm season at all stations except at Dale Pond where growth ceased after May. In spite of this, total length of oysters at the Dale Pond location equaled that of other locations for the entire warm season. The slow summer growth rate of old seed at the Dale location may have resulted from inadequate food, high temperature, or other factors associated with poor water circulation in the impoundment. With the onset of winter, growth rates decreased at Cape Romain and at Murrell's Inlet, and continued at a reduced rate until spring.

New seed grew at a rate twice that of old seed at all locations. At the Dale location the growth rate of new seed did not cease after May as it had in old seed, but continued until the final observation in September. New-seed controls at the Wando River location grew at a slow, but continuous rate throughout the warm season and stopped during winter. This was the same pattern observed by McGraw (1979) in Mississippi. In a subsequent study (Manzi et al. 1977), new seed from the same source were transplanted at age two in October 1975 into other trays in the Wando River. The seed averaged 45 mm at transplanting, and grew just 5 mm in 6 months in trays (October to April). These observations support the postulation that the majority of naturally occurring Wando River oysters (old seed) were several years of age, and that growth ceased at some period before the oysters reached market size (> 75 mm). Cole and Waugh (1959) found that early stunting in *Ostrea edulis* in many instances adversely affected growth when the oysters were

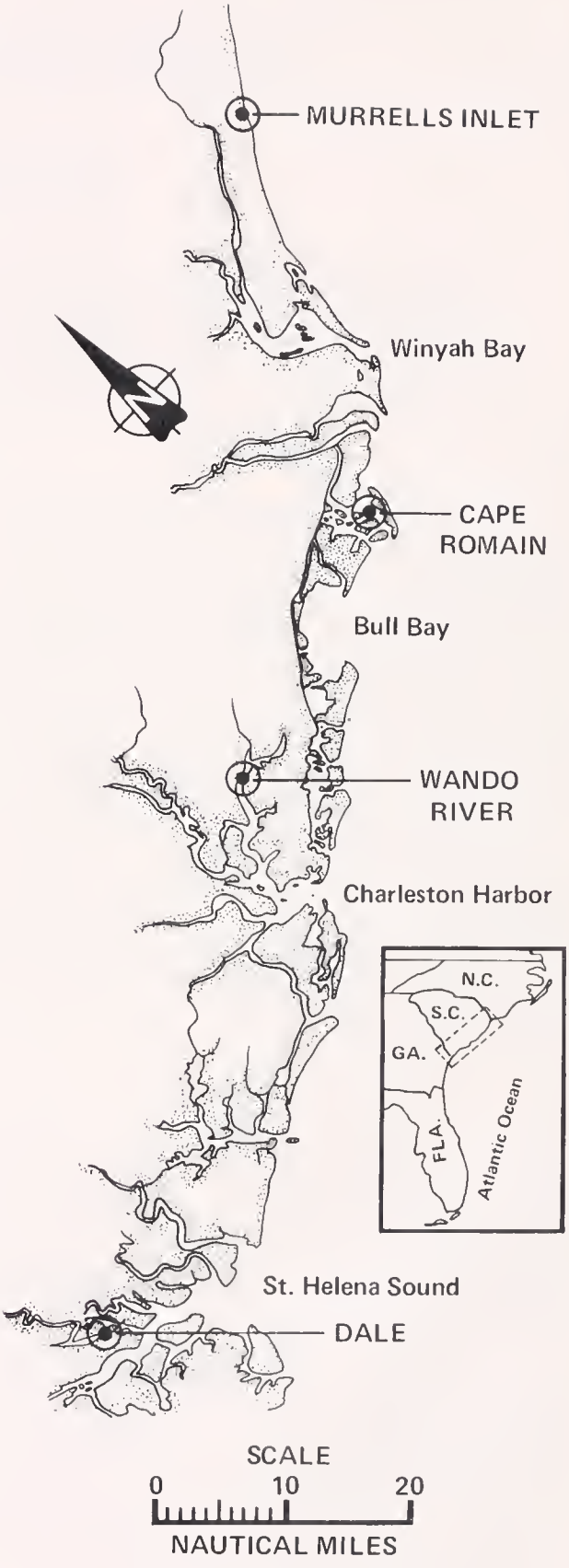

Figure 1. Locations of oyster trays.

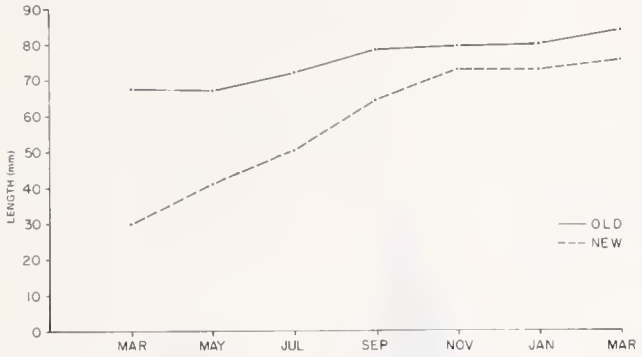

Figure 2. Growth of old and new seed oysters transplanted to Cape Romain, South Carolina.

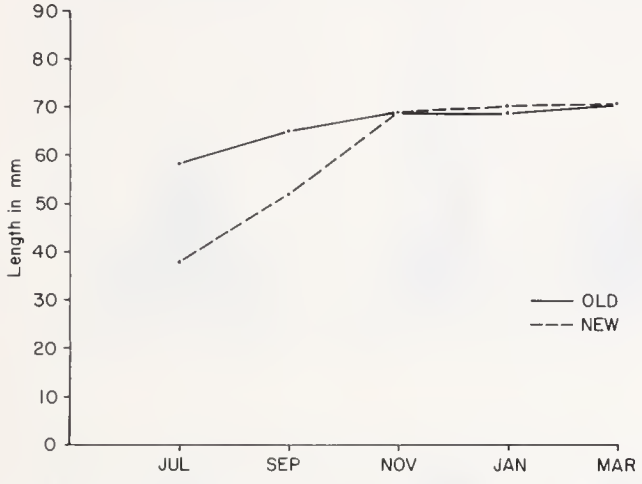

Figure 3. Growth of old and new seed oysters transplanted to Murrell's Inlet, South Carolina.

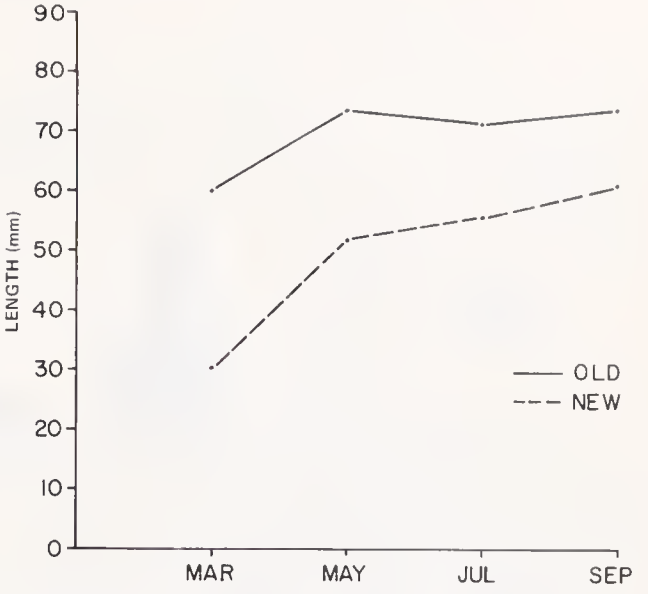

Figure 4. Growth of old and new seed oysters transplanted to an impoundment at Dale, South Carolina.

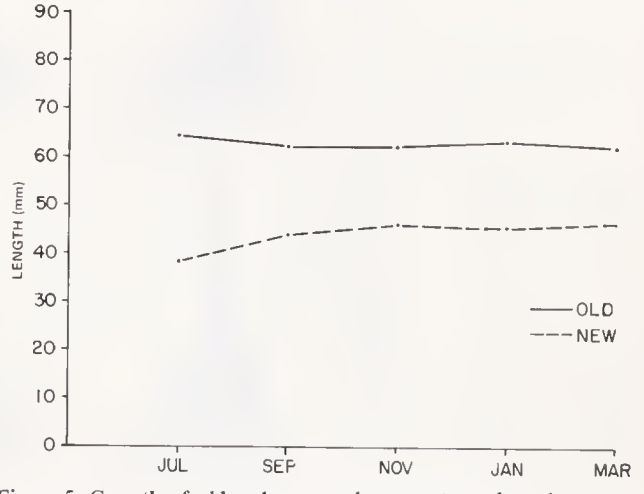

Figure 5. Growth of old and new seed oysters transplanted to trays in the Wando River, South Carolina.

transplanted to suitable growing grounds. This does not appear to be the case in transplanted Wando oysters. Young seed did grow faster than old, but the old seed when moved from the Wando grew at a rate expected of oysters above 3 or 4 years old. Size frequency distributions were determined for seed derived from the Wando bed. These approximated a normal distribution both at the beginning and at the termination of the experiment. This, if oysters were of one stock, would indicate that greater mortalities were not occurring in any particular size group. Growth rates appeared similar in all areas except for controls replanted in trays in the Wando River location (Figure 6).

Growth data were tested for normality with a chi-square goodness of fit test. Data were normalized with a log [log (x + 1)] transformation and tested for homoscedasticity with an F-max test. A two-way analysis of variance indicated significant differences between old and new seed, and between growth rates at the four locations. Inspection of the growth data indicated that only the Wando River controls (both old and new seed) did not conform to the relatively uniform growth rates expressed at the other locations (Figures 2 through 6).

It was not an objective of this study to determine why growth was poor in the Wando River location, other than to determine if genetic influence might be a possible cause. Several factors may enter into this phenomenon: water circulation, food availability, temperature, salinity, turbidity, disease, pollution, and shell pests. Salinity and temperature may be discounted because neither approached established extremes of oyster tolerance (Figures 7 and 8) (Galtsoff 1964); temperature never fell below that at which the oyster ceased to pump. Shell pests such as *Polydora* or *Cliona* were not present on Wando beds to the extent that they persisted at the other tray sites. Food supply may have been a factor, while density on the Wando beds was much less than Haven et al. (1978) reported on leased grounds in Virginia, the amount of food available in the Wando may have been more limited. Circulation in regard to current flow was adequate as evidenced by a 2-m semi-diurnal tide. Silt load carried by the tidal current may be

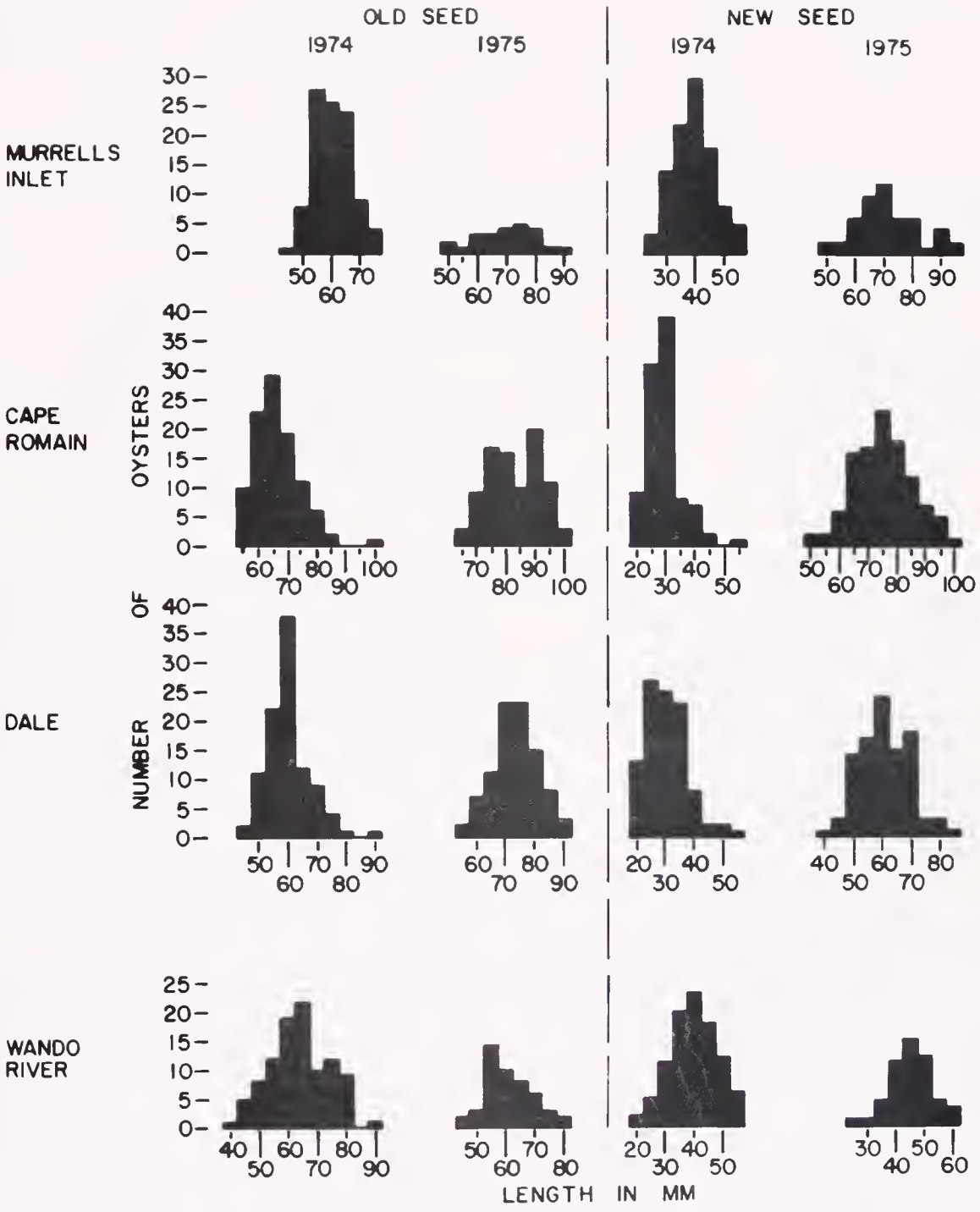

Figure 6. Growth in mm of transplanted seed oysters.

Figure 7. Salinity at tray locations during study period.

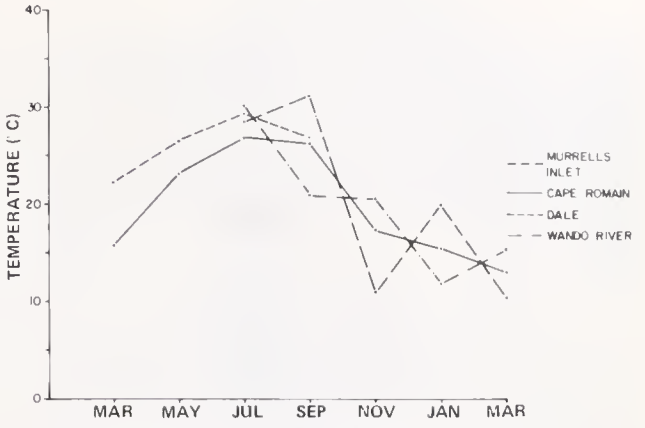

Figure 8. Temperature at tray locations during study period.

implicated if it was such that it reduced feeding time and shell-generating activities of the mantle (Cole and Waugh 1959). There was also a possibility that factors such as heavy metals may play some role in reducing growth. In a study of several metals, only copper concentrations in Wando oysters were unusually high when compared with concentrations in other growing areas. The Wando River copper concentration had an average of 108 μg/g as compared to an average of 19 μg/g at ten other South Carolina locations (Mathews and Boyne 1979). Shuster and Pringle (1969), however, found that copper apparently enhanced growth in oysters, so a direct affect here did not appear likely.

Survival data were normalized with an arcsine transformation and tested for homogeneity of variance with an F-max test. A two-way analysis of variance indicated a significant difference in survival between old and new seed, but no difference in survival rates between the four locations.

Mortality exceeded 50% of old seed at all locations except for the Wando River controls. Highest mortalities were recorded in the July transplant at the Wando River and Murrell's Inlet sites (Table 2). This could be a result of high air temperatures and concomitant dessication during transplanting. Highest mortalities were recorded in summer and fall, characteristics of those associated with *Perkinsus marinus* (Andrews and Hewatt 1957). Incidence of infection in Wando River and Cape Romain oysters was similar to that reported by Quick and Mackin (1971) in Sarasota Bay, showing a spring minimum and fall-winter maximum. After initial mortality, possibly associated with replanting, few additional old oysters died in the Wando River controls. Salinity may have been low enough for a sufficient time to control *Perkinsus marinus* in the Wando River controls as postulated by Quick and Mackin (1971); however, a similar decrease in infection was observed at Cape Romain where salinity remained high (Figures 9 and 10). Incidence and intensity of infection were remarkably similar at the two locations, making it difficult to attribute high mortalities in Cape Romain to *Perkinsus marinus* when they were not observed in the Wando River controls. As expected, mortality was low in winter at Cape Romain (Tray 1) and at the Wando River sites; however, at Cape Romain (Tray 3) and at Murrell's Inlet, high mortality was recorded on two cold weather sampling dates. These deaths could not be explained.

TABLE 2.

Percent mortality of new and old seed oysters during study period. Cumulative mortality is shown in first column, and relative mortality in parenthesis.

	Tray 1 Old		Tray 2 New		Tray 3 Old		Tray 4 New	
Cape Romain								
March 1974	--		--		--		--	
May	2	(2)	1	(2)	1	(1)	8	(8)
July	12	(10)	3	(2)	6	(5)	11	(3)
September	36	(27)	6	(3)	27	(22)	14	(3)
November	52	(25)	12	(6)	34	(10)	19	(5)
January 1975	54	(<1)	14	(2)	52	(27)	19	(0)
March	56	(<1)	21	(8)	55	(6)	20	(2)
Dale Pond								
March 1974	--		--		--		--	
May	16	(16)	9	(9)	4	(4)	3	(3)
July	37	(25)	11	(3)	26	(23)	3	(6)
September	58	(33)	23	(13)	47	(28)	22	(10)
Murrell's Inlet								
July 1974	--		--					
September	53	(53)	16	(16)				
November	58	(11)	21	(7)				
January 1975	58	(0)	22	(<1)				
March	73	(36)	22	(<1)				
Wando River								
July 1974	--		--					
September	21	(21)	9	(9)				
November	24	(4)	13	(4)				
January 1975	25	(1)	16	(3)				
March	27	(3)	20	(5)				

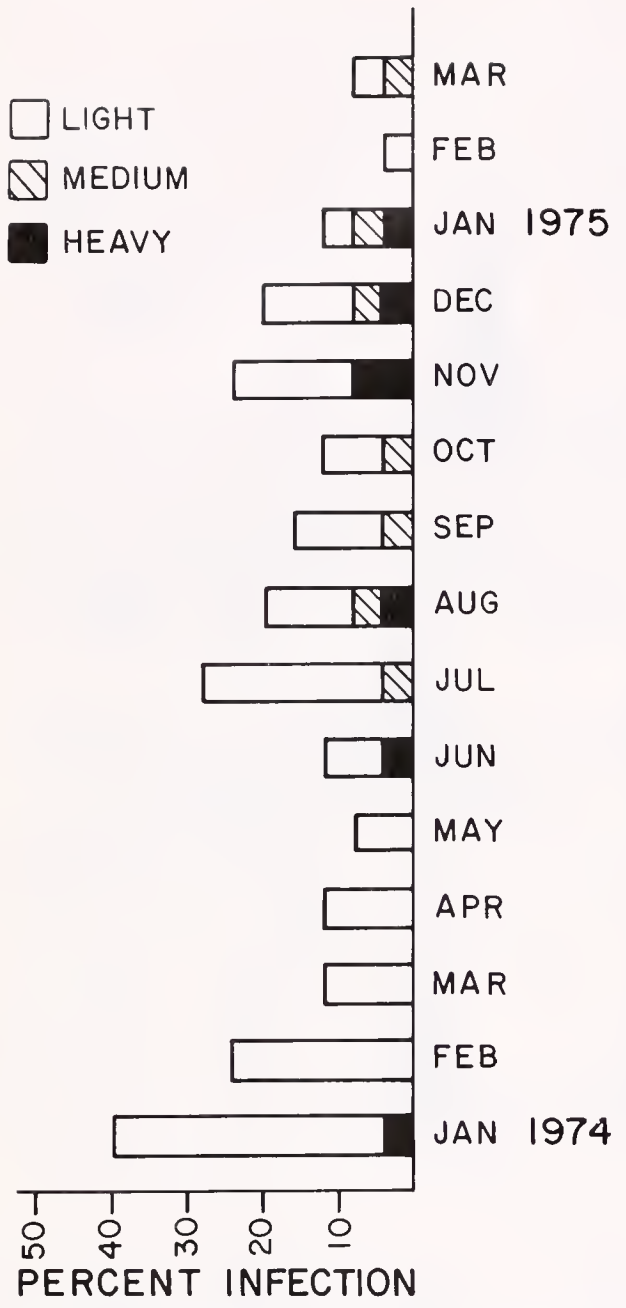

Figure 9. Percent and intensity of *Perkinsus marinus* infection in oysters from Wando River, South Carolina, January 1975 – March 1975.

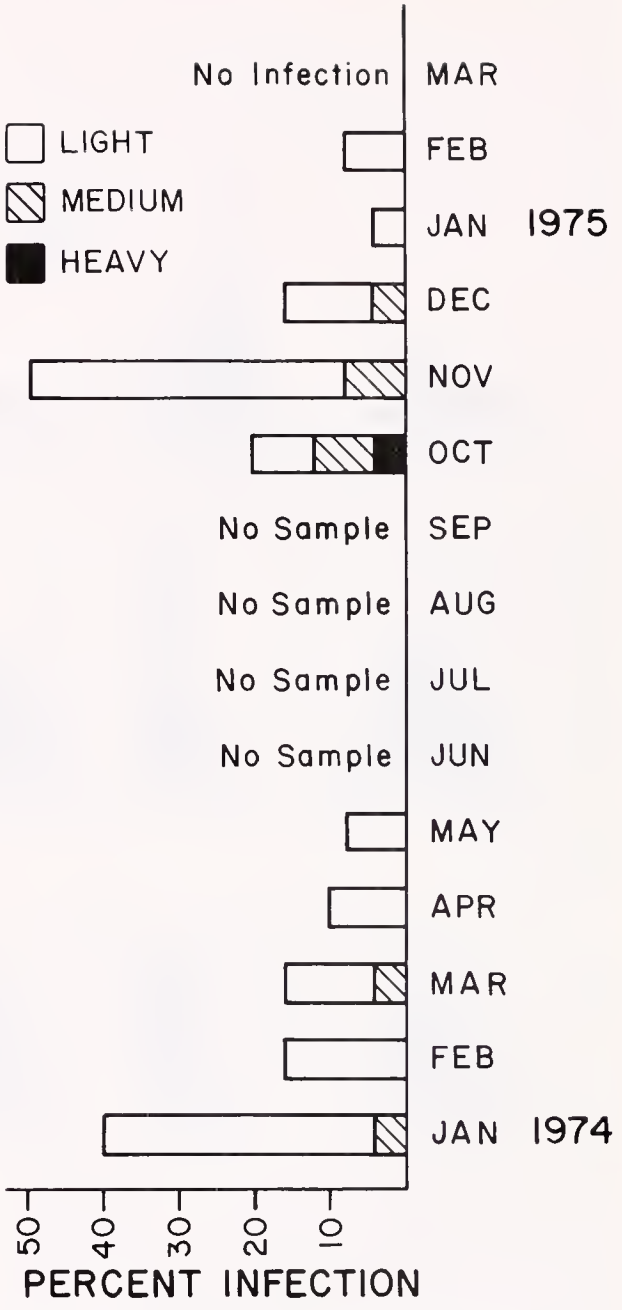

Figure 10. Percent and intensity of *Perkinsus marinus* infection in oysters from Cape Romain, South Carolina, January 1974 – March 1975.

Total mortality in young seed ranged from 20 to 22%, or less than half that for older seed. This again followed the *Perkinsus marinus* pattern described by Andrews and Hewatt (1957) which showed young oysters to be less susceptible to infection by this pathogen than older oysters. Mortality of oysters following transplanting was greater in July than in March, and was more pronounced among old than new seed.

CONCLUSIONS

Young seed oysters grew faster than older seed oysters when transplanted from the Wando River to other South Carolina growing areas. Early stunting in the older seed oysters did not appear to be reflected in subsequent growth rates. Mortalities, however, were much higher in older seed than in younger seed, and were greater when transplanting was carried out in summer than in winter.

Causes of mortality need to be investigated, and the impact of *Perkinsus marinus* in South Carolina waters needs clarification. Further studies are needed to assess growing potential of young seed on various oyster grounds. In addition, planting on natural bottoms in large enough quantities to project economic feasibility is necessary.

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SOME RELATIONSHIPS BETWEEN GAMETOGENIC CYCLE AND SUMMER MORTALITY PHENOMENON IN THE PACIFIC OYSTER (*CRASSOSTREA GIGAS*) IN WASHINGTON STATE[1,2]

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ABSTRACT During the summer of 1979, both commercial and experimental (F_2) oysters experienced summer mortalities in three commercial production areas. Mortalities among the experimental families were variable, ranging from 11% to 94.6%. Carbohydrate content and gonadal development were compared between those families that exhibited low and high mortalities. In all groups, carbohydrate levels dropped sharply from 25 to 30% in May to values as low as 3% in some families by late summer. The decline in carbohydrate content was negatively correlated with increased gonadal development. Absolute levels of carbohydrate could not be directly correlated to either high or low mortality; however, timing of mortality consistently occurred during the storage phase of the carbohydrate cycle, just following spawning and/or reabsorption. There was evidence that mortality was selective for females.

INTRODUCTION

Significant summer mortalities of Pacific oysters, *Crassostrea gigas*, have occurred in commercial growing areas of Washington State since the 1960's. The pattern of mortality was similar to that observed among Pacific oysters in Japan. In both Japan and the United States, growers had to resort to such methods as overplanting, transplanting, and early harvesting to "farm around" this summer mortality (Ogasawara et al. 1962, Scholz 1975). During the early to mid-1970's, the incidence of summer mortality was almost completely absent in Washington State, but beginning in 1976, increasing numbers of oyster-growing areas in southern Puget Sound experienced significant mortalities. In 1979, at least five bays in southern Puget Sound suffered significant mortalities among commercially harvestable oysters, with one growing area experiencing a 60% mortality of marketable oysters.

Research efforts in both the United States and Japan during the 1960's established the now, well-known characteristics of summer mortality (Glude 1975, Koganezawa 1975).

In both Japan and the United States, mortalities invariably occurred: (1) among two-year-old or older stocks, (2) in areas of high nutrient levels and high productivity, (3) during the late summer months when water temperatures approached 20°C and above, and (4) among oysters with relatively high condition indices.

Although the characteristics of summer mortality are well known, no direct cause has been clearly established. Japanese research indicated that summer mortalities were associated with abnormal gonadal maturation of oysters cultured in eutrophic bays, which resulted in physiological stress (Mori 1979). Lipovsky and Chew (1972) showed that mortalities of *C. gigas* could be induced in the laboratory under conditions of elevated water temperatures (greater than 18°C) and high nutrients. Large numbers of bacteria (*Vibrio* spp.) were found in moribund oysters; it was believed they played a significant role in the laboratory mortality. However, recent histological studies of moribund oysters from field mortalities have shown no evidence of bacterial infection (Dr. Marsha Landolt, personal communication).

In an effort to control summer mortality, the University of Washington established a selective breeding program to develop strains of Pacific oyster resistant to summer mortality (Beattie et al. 1978). Initially, survivors from thermal challenges in the laboratory were utilized, but with the reoccurrence of mortality, survivors of field challenges now are being used as broodstock for subsequent generations. Results of field studies in 1978 and 1979 appear promising, because a majority of experimental families have exhibited better survival than unselected control stocks (Beattie et al. 1978).

In addition to the selective breeding work, research at the University of Washington has been focused on the etiology of summer mortality; the reproductive cycles of experimental families exhibiting both high and low mortalities during field challenges have been compared. A baseline study was conducted during the summer of 1979 that compared the reproductive cycles of experimental groups of oysters during the observed mortality.

MATERIALS AND METHODS

Sampling Program

Oysters from 23 experimental families (F_2) selectively bred for survival, and control oysters were monitored for mortality in three bays in southern Puget Sound, that previously had exhibited high mortalities: Rocky Bay, Oakland Bay, and Mud Bay (Figure 1). Samples of all families were planted initially in all three bays. However, early spat mortality (due to siltation and predation)

[1] Supported by the Washington Sea Grant Program under the National Oceanic and Atmospheric Administration, U.S. Department of Commerce.
[2] Contribution No. 562, College of Fisheries, University of Washington.

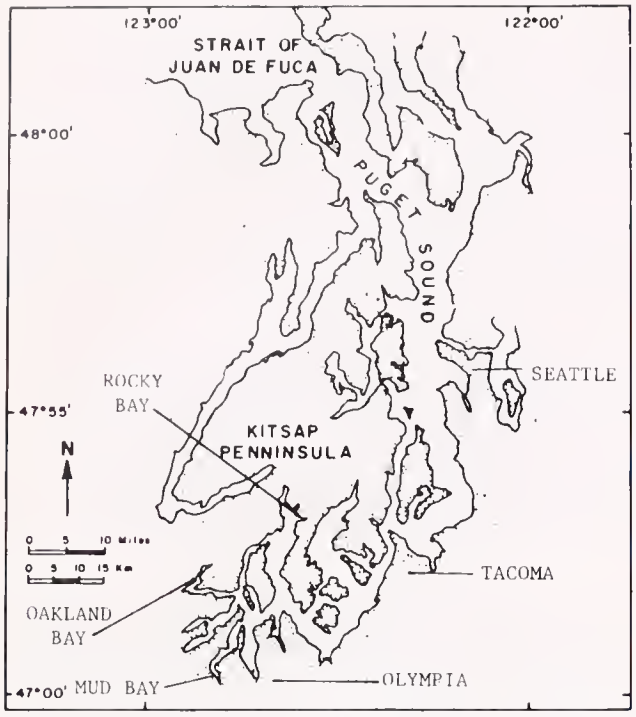

Figure 1. Locations of the three sampling areas in southern Puget Sound.

completely eliminated some families and diminished the numbers in other families below a level adequate for a complete sampling regime. Only families with adequate numbers of individuals were selected for analysis of gametogenesis and carbohydrate content (Table 1). A group of unselected, commercially caught seed from Dabob Bay, Washington (hereafter termed "Dabob control"), also was monitored in each bay. This group served as the control in evaluating the survival performance of the selected experimental families. Fifteen oysters from the preselected experimental families were sampled bimonthly from May through August, and monthly from September through December. Ten oysters from each sample were fixed in 10% formalin and sectioned for determination of gonadal development. The remaining five animals were used for determination of carbohydrate content.

Histology

Cross sections from oysters were cut through the mid-visceral mass behind the labial palps. Following imbedding in paraffin, 6 μm sections were stained in Myers hematoxylin and counterstained in picroeosin. Sections were then enlarged 13 times and gonadal development assessed using the quantitative morphological analysis of Chalkley (1943) as modified for oysters by Mori (1979). Percent development was determined by comparing the gonadal area with the total morphologic area in the cross section. Area was determined using either a point-counting system or a polar planimeter. In addition to gonad, digestive tubule areas also were determined in each animal.

Carbohydrate

Carbohydrate was determined on freeze-dried homogenized tissue from the five pooled animals of each group. Determinations were made by extracting 5 to 15 mg of freeze-dried tissue in trichloroacetic acid as described by Mann (1978). Carbohydrate was assayed using the methods of Strickland and Parsons (1972). Calibration was against oyster glycogen (Sigma Chemical Co., Type II).

RESULTS

Significant mortalities occurred among the experimental families and the control group in all three bays, with individual families exhibiting a wide range of cumulative mortalities (Table 1). Experimental families preselected for analysis of reproductive parameters represented both high and low mortality groups in Mud and Oakland bays. In Rocky Bay, however, the preselected groups exhibited similar cumulative mortalities. Timing of the mortality differed between bays (Figure 2). Mortalities among experimental animals in Mud, Oakland, and Rocky bays peaked in early August, early September, and early October, respectively.

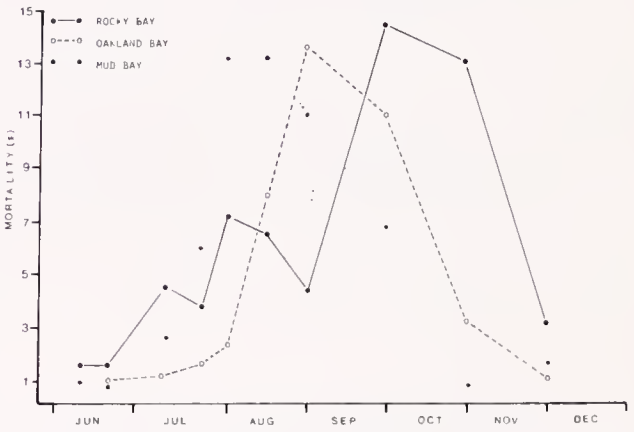

Figure 2. Percent mortality of all experimental oysters in Rocky, Oakland, and Mud bays in 1979.

Carbohydrate levels among oysters in the selected experimental families and in the Dabob control in all three bays exhibited a distinct sequence of change, with three discernible phases (Figures 3 through 5) during the sampling period May through December 1979. The first phase occurred from May through July, and was marked by an abrupt decline in percent carbohydrate from levels of 20 to 30% in late May to levels as low as 3 to 5% in July. During the second phase, percent carbohydrate remained at relatively low levels with few families exhibiting large fluctuations. The third phase was marked by a transition to increased carbohydrate levels again, which, by December, reached 70 to 80% of the May levels. Both timing and degree of change of this third phase varied between bays. In all three bays, however, the timing of the transition to

TABLE I.

Cumulative mortalities (%) of experimental families and the control (Dabob) in each of the three study areas as of December 1979.

Mud Bay			Oakland Bay			Rocky Bay		
Family	Number	Cumulative Mortality (%)	Family	Number	Cumulative Mortality (%)	Family	Number	Cumulative Mortality (%)
6–28AX	102	23.6	*1–16AX	520	11.3	6– 3AX	157	21.0
6– 3AY	69	26.1	7–29BX	170	15.3	8–15AX	120	23.4
*8– 5BY	366	31.0	8–23BX	120	17.5	7– 1AY	148	23.7
6–27AZ	99	34.3	8– 2BX	260	20.0	*–15BY	96	25.0
7–20BX	264	34.9	6–27BX	70	22.9	*6–28BX	190	30.0
6–27AY	77	36.4	7– 1AY	189	23.3	8– 2BX	118	33.0
*8–23AX	354	37.4	5– 3BY	276	26.1	*Dabob	264	35.2
7– 1AY	141	44.7	6–28BX	81	26.8	8–23BX	154	38.4
8– 2BX	190	45.3	*6–27AY	516	27.4	*6–27AY	446	38.9
8– 5AY	28	46.5	8– 3AY	358	32.8	8– 5AY	94	46.8
5– 3BY	137	48.2	*1–16BX	243	33.6	6– 3BY	71	49.3
6– 3BY	31	51.6	7–25AX	77	33.8	8–23AX	229	54.1
8–23BY	187	56.1	6– 3AX	219	35.1	7–25AY	114	54.4
*Dabob	249	56.1	8– 5AX	46	39.2	7–25AX	113	54.9
*8– 3AY	501	64.2	8–15BY	95	40.0	8– 5BY	170	57.0
7–25AX	68	66.2	6–22AY	50	42.0	8–15H	94	59.6
7–25AY	89	85.4	8– 5BY	167	43.2	8– 3AY	126	60.3
			7–25AY	42	47.7	7–20BX	197	84.2
			6–27AZ	83	50.6	6–27AZ	85	84.8
			7–25BY	11	54.6			
			*Dabob	549	56.6			
			8– 5AY	19	57.9			
			8–23AX	21	76.2			
			7–20BX	333	90.4			
			8–15H	55	94.6			

*Analyzed for physiological parameters.

NOTE: Family codes refer to date of spawning, and female and male used. For example, 6–28AX refers to a family resulting from a spawning of female "A" and male "X" on June 28. All spawnings occurred in 1977, and in January 1978. Family 8–15H was a functional hermaphrodite.

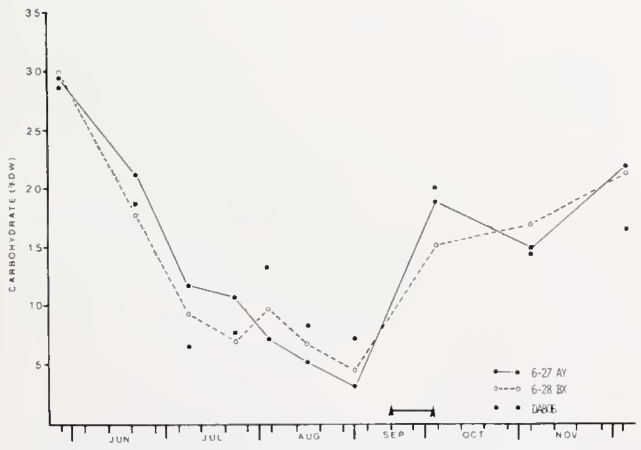

Figure 3. Percent (dry weight) carbohydrate of two experimental families and the control in Rocky Bay, Washington. Arrows indicate period of peak mortality.

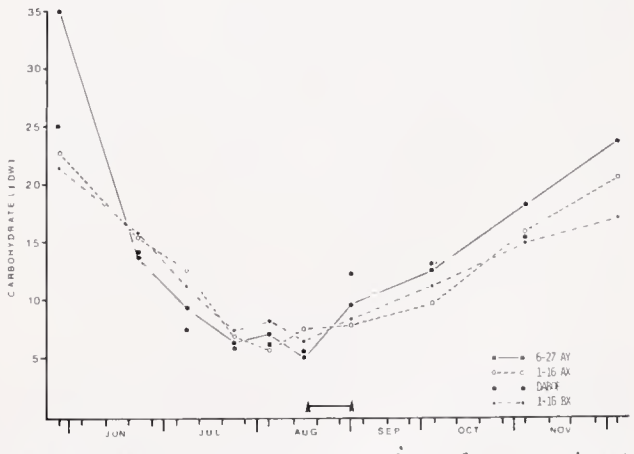

Figure 4. Percent (dry weight) carbohydrate of two experimental families and the control in Oakland Bay, Washington. Arrows indicate period of peak mortality.

increase carbohydrate levels (third phase) was associated with the timing of peak mortality (Figures 3 through 5).

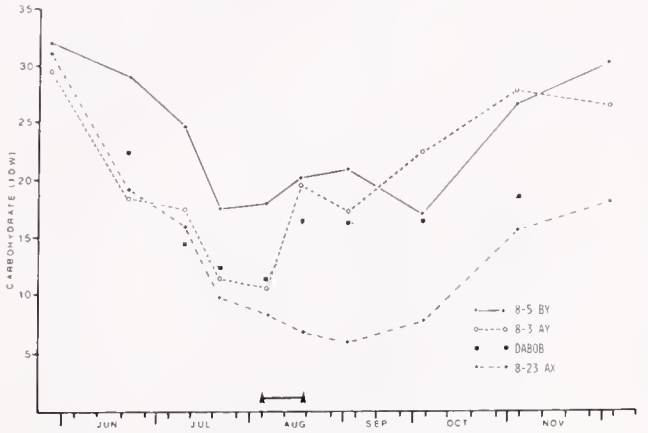

Figure 5. Percent (dry weight) carbohydrate of three experimental families and the control in Mud Bay, Washington. Arrows indicate period of peak mortality.

In both Rocky and Oakland bays, carbohydrate levels were similar among the experimental families sampled (Figures 3 and 4). In contrast, experimental families in Mud Bay exhibited variability in both carbohydrate levels and the timing of the late summer increase in percent carbohydrate (Figure 5). Experimental family 8–5BY exhibited carbohydrate values at least 50% greater than any other group sampled in Mud Bay from June through mid-August. In fact, percent carbohydrate in this family never went below 17.0% during the sampling period, which was higher than any group monitored from any bay. Experimental family 8–3AY and the Dabob control group in this bay exhibited abrupt increases in percent carbohydrate characteristic of the third phase described earlier. Both of these groups exhibited high cumulative mortalities (Table 1). Experimental family 8–23AX in Mud Bay exhibited prolonged low levels of percent carbohydrate, taking 3 months to attain levels of 15% or greater (Figure 5).

A comparison of a high mortality group (Dabob) and a low mortality group (1–16AX) in Oakland Bay revealed a similar relationship (Figure 4). During the mortality period in this bay, an abrupt increase in percent carbohydrate was noted in the high mortality group (Dabob), although the increase was not as dramatic as was observed in the high-mortality group in Mud Bay. Experimental family 1–16AX, on the other hand, exhibited a more gradual increase in carbohydrate levels during the mortality period.

Results of gonadal development of sampled experimental families are presented in Figures 6 through 8 for Rocky, Oakland, and Mud bays, respectively. Only groups that exhibited either high or low mortality are presented for comparison. Generally, gonadal size increased quickly during June and early July in all bays. Gonadal development peaked from late July to early August with gonadal tissue occupying 65 to 75% of the total cross-sectional area. Gonadal development then declined to lower levels. In some groups, the decline in late summer was dramatic,

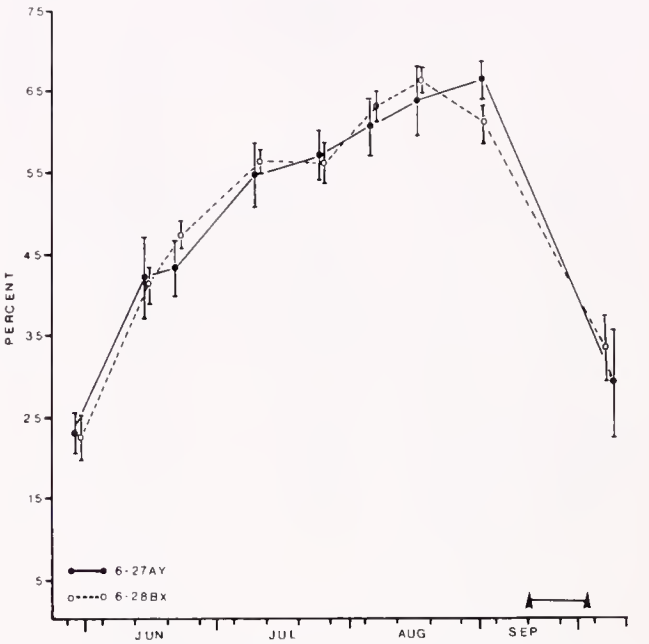

Figure 6. Gonadal development based on cross section percentage of two experimental families in Rocky Bay, Washington, in 1979. Standard error represented by brackets. Arrows indicate period of peak mortality.

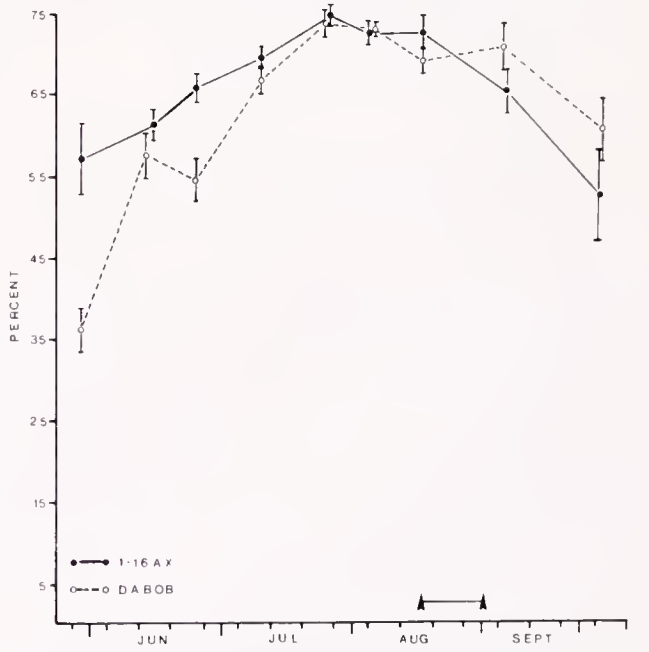

Figure 7. Gonadal development based on cross section percentage of two experimental families in Oakland Bay, Washington, in 1979. Standard error represented by brackets. Arrows indicate period of peak mortality.

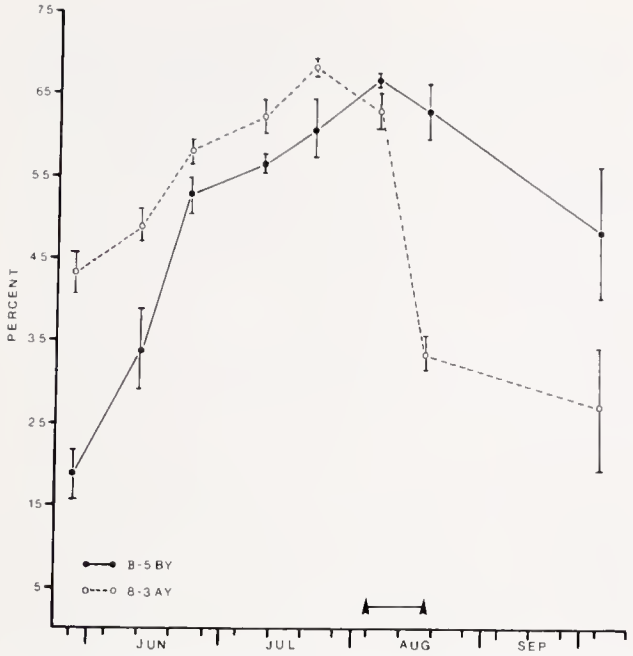

Figure 8. Gonadal development based on cross section percentage of two experimental families in Mud Bay, Washington, in 1979. Standard error represented by brackets. Arrows indicate period of peak mortality.

going from levels greater than 60% to levels approaching 30% in less than one month. Examination of these sections indicated evidence of spawning. Experimental families that exhibited a more gradual decline in gonad size showed extensive infiltration by leucocytes with little or no spawning occurring. In all three bays, the timing of mortality coincided with the decrease in gonad size. All groups examined showed an inverse relationship between gonadal development and carbohydrate content.

In addition to the gonad, digestive tubule area fluctuated during the summer in all groups observed. Examples are presented in Figures 9 and 10 for two families in Mud Bay. As the gonad developed in each family, less area was occupied by the digestive tubules. By midsummer when gonadal development had peaked, digestive tubules occupied approximately one half the area they did in May. As spawning and/or reabsorption progressed and gonad size declined, digestive tubule area increased. Gonadal area and digestive tubule area were negatively correlated. For example, the correlation between gonad and digestive tubule areas for the two families in Figures 9 and 10 was $r = -0.9904$ for family 8–5BY, and $r = -0.9165$ for family 8–3AY. Similarly, high negative correlations were noted for the other experimental families and controls observed.

Sex ratio of each experimental group was compared between the period prior to peak mortality and the period after peak mortality. Experimental groups that exhibited either high or low mortality in Mud Bay and in Oakland Bay are compared in Figures 11 and 12 (Mud Bay), and in Figures 13 and 14 (Oakland Bay). In both cases, the percentage of females declined significantly in experimental groups exhibiting high mortality, while the percentage of females remained the same in experimental groups exhibiting low mortality, indicating that mortality was selective for females.

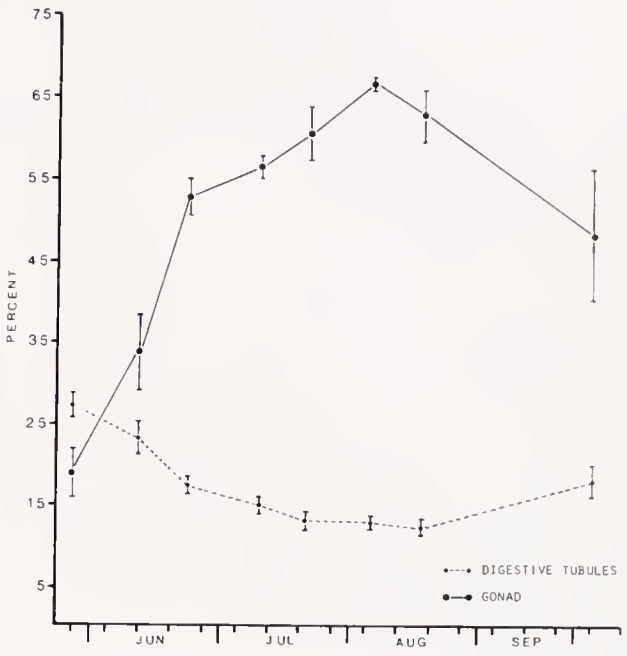

Figure 9. Changes in gonad and digestive tubule areas based on cross section percentage in experimental family 8–5BY in Mud Bay, Washington. Standard error represented by brackets.

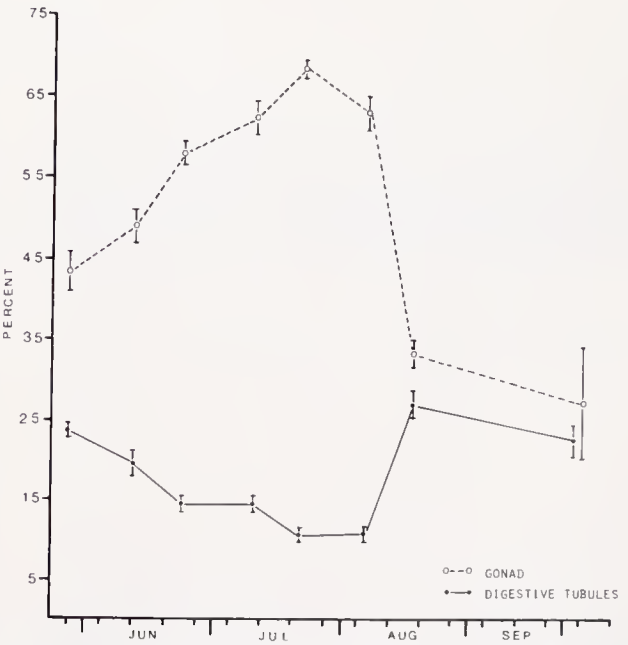

Figure 10. Changes in gonad and digestive tubule areas based on cross section percentage in experimental family 8 -3AY in Mud Bay Washington. Standard error represented by brackets.

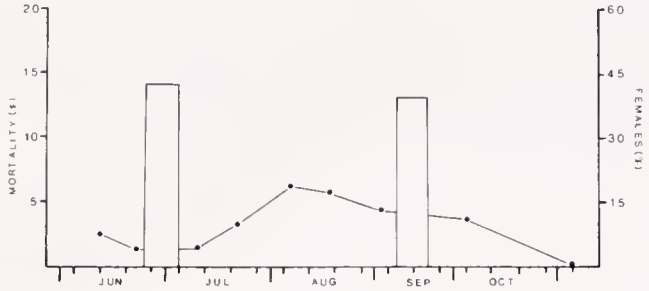

Figure 11. Percentage comparison of females in experimental family 8–5BY in Mud Bay, Washington, before occurrence of mortality (samples prior to July 24; N = 44), and after occurrence of mortality (samples after July 24, inclusive; N = 49).

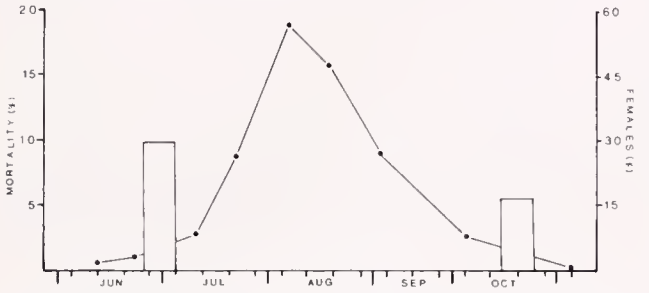

Figure 12. Percentage comparison of females in experimental family 8–3AY in Mud Bay, Washington, before occurrence of mortality (samples prior to July 24; N = 41), and after occurrence of mortality (samples after July 24, inclusive; N = 51).

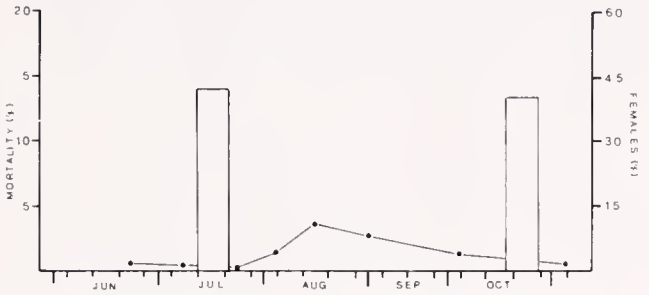

Figure 13. Percentage comparison of females in experimental family 1–16AX in Oakland Bay, Washington, before occurrence of mortality (samples prior to August 21; N = 59), and after occurrence of mortality (samples after August 21, inclusive; N = 40).

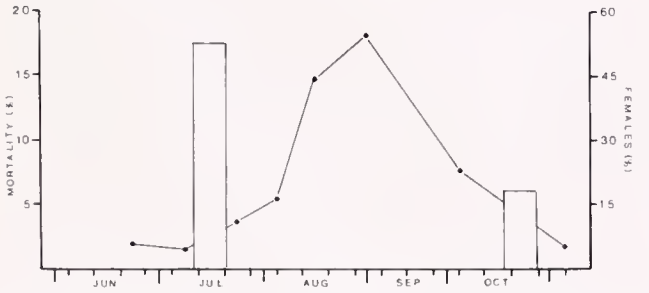

Figure 14. Percentage comparison of females in control (Dabob) group in Oakland Bay, Washington, before occurrence of mortality (samples prior to August 21; N = 58), and after occurrence of mortality (samples after August 21, inclusive; N = 36).

DISCUSSION

The wide range of cumulative mortalities observed among experimental families in each bay during this study is similar to results obtained during the field mortality observed among experimental groups in 1978, when mortalities ranged from 5 to 86% among 13 families (Beattie et al. 1980). The occurrence of experimental families exhibiting both high and low mortalities provides not only a valuable source of broodstock for selective breeding, but also an opportunity to better understand the etiology of summer mortality.

Results from this baseline study confirm the close relationship observed between summer mortality and the gametogenic cycle of *C. gigas*, first noted by Japanese researchers in the 1960's. They pointed out that oysters in areas of low mortality exhibited relatively high levels of glycogen and less extensive gonadal development, while oysters from high mortality areas exhibited extremely low glycogen levels and more extensive gonadal development (Mori et al. 1965). Results from this study indicate that there is no relationship between the absolute levels of carbohydrate and either high or low mortality exhibited in the experimental groups. There is evidence, however, that the timing of mortality coincides with a change in carbohydrate metabolism to a storage phase. It is possible that these increased levels of carbohydrate are partially due to a post-mortality selection of animals with higher levels of carbohydrate, although familes such as 8–23AX (Figure 5) and 1–16BX (Figure 4) would suggest that this is not the case.

The timing of mortality also coincides with the period when the gonad is most extensively developed and has begun to decrease, abruptly in groups that have spawned and more gradually in groups that have not spawned. The relationship between spawning and observed mortalities must be studied in more detail before any conclusions can be made.

The decline in digestive tubule area to levels approaching 40 to 50% of the May levels indicates that changes in tissues other than connective tissue occur during gametogenesis. Part of this decrease is due to an increase in tubule density. The high inverse correlation noted between digestive tubule area and gonadal area in *C. gigas* suggests that the process of gonadal maturation may occur at the expense of digestive tubules, similar to that found in *Mytilus edulis* (Thompson et al. 1974). Tamate et al. (1965) noted that digestive tubules of Pacific oysters in high mortality areas exhibited cellular destruction compared to those oysters in low mortality areas. In this study, digestive tubule area declined equally between high mortality groups and low mortality groups, and was dependent entirely on changes associated with the gonad. Morton (1977) indicated that the digestive diverticula of *C. gigas* undergoes a synchronized pattern of cytological changes in a sequence related to tidal as well as seasonal cycles. In summer, he found that the digestive tubules exhibited a short phase of absorption and a longer

phase in which interior cellular components (fragmentation spherules) broke down and were removed as fecal matter through the gut. Whether that process resulted in stress on the animal is unclear, but absorptive efficiency could conceivably decline as a result.

Sex ratio data indicated that mortality was selective against females, although male oysters were observed to die. This contradicts results obtained during the 1960's in Washington state where no difference in mortality was noted between males and females (Glude 1975). Although carbohydrate was not analyzed in females and males separately, there is evidence that, in the Pacific oyster, females deplete carbohydrate reserves faster and to a greater extent relative to males (Matsumoto et al. 1934, Mori et al. 1965).

Crassostrea gigas, like many other bivalves, undergoes a marked seasonal cycle of gametogenic activity, which has been linked with storage and utilization of reserve materials in the body (Mori et al. 1965). Carbohydrate levels in the Pacific oyster have been shown to vary inversely with gonadal development (Matsumoto et al. 1934, Mann 1978). The fate of carbohydrate reserves in bivalve molluscs during gametogenesis is probably as a respiratory substrate and as the precursor of lipid reserves of the developing eggs (Gabbott 1975, Holland and Hannant 1974). Data from this study underscore the relationship between gonadal maturation and carbohydrate depletion.

Control of carbohydrate metabolism in bivalves has been studied extensively (Bourcart and Lubet 1965, Gabbott 1975, Sastry and Blake 1971). Generally it is assumed that the reproductive cycle is controlled internally by neurohormones, and that external factors such as temperature and food act as synchronizers. The variability in the carbohydrate cycle and gonadal development of experimental groups in Mud Bay indicates that the response to environmental cues may have a strong genetic component. This suggests a potential for selective breeding for there are obvious market advantages for an oyster that maintains relatively high levels of carbohydrate and, consequently, delays gonadal development into the summer months as exhibited by experimental family 8–5BY in Mud Bay (Figure 5).

Results from this study confirm the relationship noted by Japanese researchers between summer mortality and aspects of the reproductive physiology of *C. gigas*. Environmental characteristics, such as long periods of exposure, warm temperatures, and dinoflagellate blooms, could conceivably "trigger" the mortality among animals already in a stressed state. Environmental studies are now underway that will coincide with continued studies of the reproductive physiology of experimental families (F_3). The combined studies will contribute further input into the etiology of summer mortality.

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SPAWNING OF THE CALICO SCALLOP *ARGOPECTEN GIBBUS* IN RELATION TO SEASON AND TEMPERATURE[1]

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ABSTRACT Analysis of previous research demonstrated that most spawning of the calico scallop *Argopecten gibbus* off Cape Canaveral, Florida, occurred between November and June. In 1970 and 1971, spawning intensity was highest from January to May when bottom water temperatures were below 22.5°C, and lowest from June to October when temperatures were usually above 22.5°C. Major spawning occurred when bottom water temperatures ranged from about 15.0° to 22.5°C at depths from 18 to 55 m (the zone of calico scallop concentrations).

Off Cape Canaveral, bottom water temperatures in the calico scallop zone are strongly influenced by seasonal atmospheric temperatures and by intrusions onto the Florida-Hatteras Shelf of deep, cold water. Movement of cold water from inshore or offshore into the scallop zone apparently initiates spawning.

Calico scallops are most abundant near Cape Canaveral and Cape San Blas, Florida, and Cape Lookout, North Carolina. Cold water intrusions near these capes produce environmental conditions that may be favorable or unfavorable to scallop abundance.

INTRODUCTION

The calico scallop *Argopecten gibbus* is harvested commercially off the south Atlantic coast of the United States, and in the northeastern Gulf of Mexico (Allen and Costello 1972). This species is subject to large yearly fluctuations in stock availability which are related to spawning success. Spawning is influenced by water temperature changes. In this paper we determine the spawning season of the calico scallop on the Florida-Hatteras Shelf off Cape Canaveral, Florida, and relate spawning to bottom water temperatures recorded in that area.

A brief summary of calico scallop biology follows. The calico scallop occurs in depths from less than 2 m to 370 m (Allen and Costello 1972). The species is hermaphroditic, extruding sperm and eggs for external fertilization; planktonic larvae set in about 16 days (Costello et al. 1973). Young scallops are strongly attached by byssal threads until about 1½ months after being spawned; older individuals may be weakly attached (Allen 1979). Growth is rapid, and scallops reach 55.0 mm shell height in about 9 months (Miller and Hudson, in preparation). (Shell height is a straight line measurement of the greatest distance between the umbo and ventral margin.)

Calico scallops are most abundant near coastal prominences such as Cape Canaveral and Cape San Blas, Florida, and Cape Lookout, North Carolina (Allen and Costello 1972). These concentrations indicate that environmental conditions near capes contribute to spawning success. Bullis and Cummins (1961) suggested that "the interruption and eddying caused by the Cape Canaveral projection probably permits repetitive settling of scallop larvae." Allen (1979) suggested that current reversals and convergence in the Cape Canaveral areas as reported by Bumpus (1973), could "retain scallop larvae on the grounds until settling occurs." From measurements of bottom current, Leming (1979) determined that the water flow was cyclic and capable of maintaining larval calico scallops on the Cape Canaveral grounds during their 16-day planktonic existence. Furthermore, upwelling near Cape Canaveral, Cape San Blas, and Cape Lookout may increase the abundance of plankton, which serves as food for the calico scallop (Allen and Costello 1972).

METHODS

Bottom water temperatures off Cape Canaveral were obtained from continuous recording thermographs operated concurrently with biological studies on the calico scallop conducted by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service), Miami, Florida. Temperatures were recorded at Buoy 1, located 9 km from land, depth 18 m (latitude 28°48.5′N, longitude 80°38.6′W), and at Buoy 2, located 22 km from land, depth 22 m (latitude 28°49.1′N, longitude 80°29.0′W) (Figure 1). Except when a thermograph was lost or malfunctioned, the daily bottom water mean temperatures at either Buoy 1 or Buoy 2 are available for most of the period from March 28, 1970 to August 24, 1971 (Figure 2).

DETERMINATION OF SCALLOP SPAWNING SEASON

Spawning periods of the calico scallop were determined from biological studies of ovarian developmental stages, spat abundance, length-frequency distributions, and fish predation on juvenile scallops. These studies are cited below.

[1] Contribution Number 80-57M, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

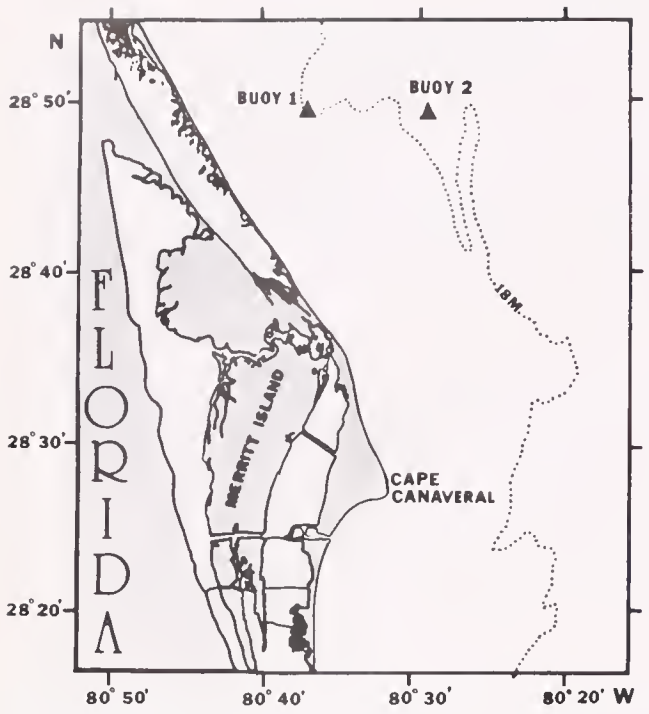

Figure 1. Locations of Buoys 1 and 2 off Cape Canaveral, Florida.

Ovarian Developmental Stages

Roe et al. (1971) used ovarian color to determine the degree of calico scallop maturation. Based on studies in 1967 and 1968, they concluded that the spawning period of the calico scallop on the Cape Canaveral grounds "begins in late February or March and continues to June" but "protracted spawning" occurs in some areas.

The developmental stages of calico scallop ovaries from the Cape Canaveral grounds were distinguished, primarily by color, from May 1970 to October 1971 by Miller et al. (1980). The spawning period was indicated by the occurrence of ripe and partially spawned scallop ovaries. According to Miller et al. (1980), "spawning intensity was apparently highest from January to May, decreased in June and July and was nonexistent in August and perhaps in September. In October, a high proportion of scallops was close to spawning condition. By November, spawning had apparently begun . . . and probably increased in December."

Spat Abundance

Calico scallop spat were monitored off Cape Canaveral by means of spat traps (Allen 1979). Based on seasonal abundance of spat from July 1970 to October 1971, Allen determined that "spawning apparently occurred during all seasons of the year, but intensity was greatest in the spring. Following low spawning intensity in July, and lower intensity from August into December, spawning increased in late December or January and peaked in March. High spawning intensity continued through April and May, followed by an abrupt decrease in June and low spawning intensity into September."

Length-Frequency Distributions

Length frequencies of calico scallops were obtained off Cape Canaveral from a bed at Buoy 2 from March 1970 to October 1971 (Miller and Hudson, in preparation). These length frequences (supported by data from marked scallops) showed major recruitment of age class 0 scallops occurred between December and June, indicating that major spawning occurred from about December to May.

Predation on Juvenile Scallops

Spawning season of the calico scallop also can be estimated from food habits of predators. A study of food

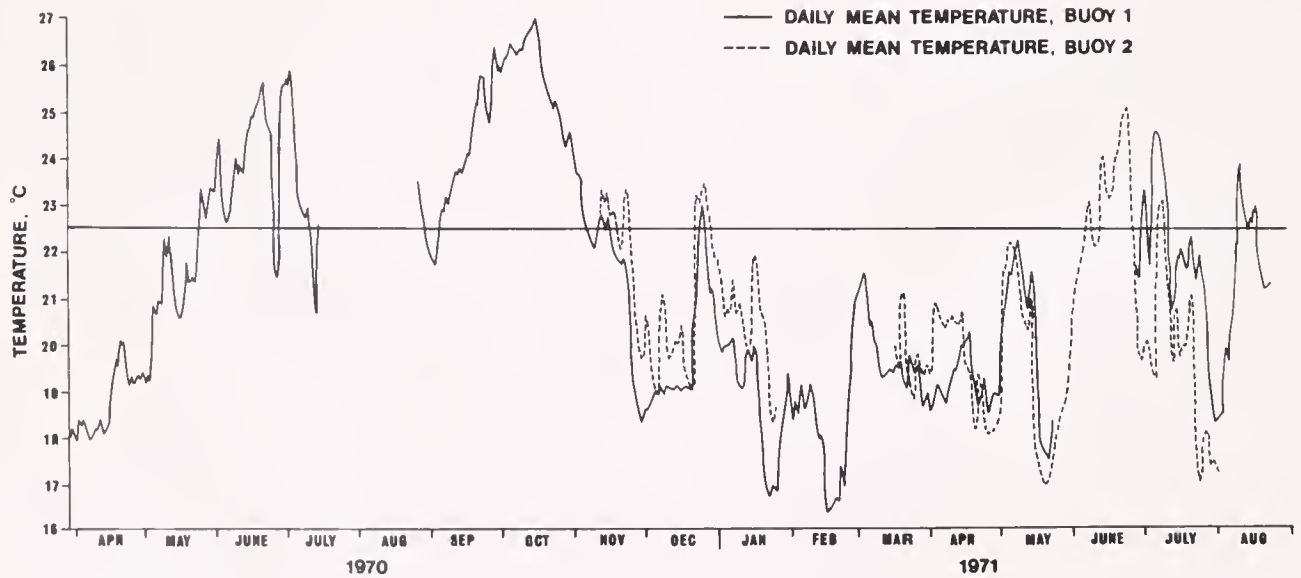

Figure 2. Bottom water temperatures at Buoys 1 and 2 off Cape Canaveral, Florida, 1970–71 (from data presented by Leming 1979).

habits of a batfish, *Ogcocephalus* sp., was conducted on specimens obtained off Cape Canaveral in 1974 (Winans 1976). The batfish consumed mostly scallops from December through June, and mostly gastropods from July through November. Although Winans (1976) did not identify the scallops as to species, the calico scallop is the predominant species off Cape Canaveral, constituting more than 99% of the identifiable spat caught in traps (Allen 1979). The batfish has a very small mouth, and we speculate that the maximum size of scallops consumed would not exceed 15 mm shell height. Calico scallops of 15 mm shell height are estimated to be about 54 days after spawning (Allen 1979). Based on these scallop ages, and the season of maximum predation (December through June), indications are that most calico scallop spawning occurred between November and May.

SCALLOP SPAWNING IN RELATION TO BOTTOM WATER TEMPERATURE REGIME

Range and fluctuations of bottom water temperatures are critical to the spawning of the bay scallop *Argopecten irradians,* and the closely related calico scallop. The bay scallop spawns naturally in mid-summer in Massachusetts when water temperatures rise above 16.4°C (Belding 1910). However, bay scallops spawn during declining temperatures of late summer and fall in North Carolina (Gutsell 1931) and in Florida (Sastry 1963). In the laboratory, bay scallops spawned only after the temperature was increased and then decreased (Gutsell 1931, Sastry 1963, Castagna 1975). Calico scallops were induced to spawn in the laboratory by raising the water temperature from 20° to 25°C (Costello et al. 1973). These temperatures, however, represent only part of the range within which calico scallops will spawn.

An understanding of calico scallop spawning off Cape Canaveral as affected by temperature first requires knowledge of scallop distribution as related to depth and temperature. Concentrations of calico scallops off Cape Canaveral are between depths of 18 and 55 m and, therefore, are within an environmental zone designated as the "Open-Shelf Habitat" by Struhsaker (1969). Bottom water temperatures in this zone range from about 11° to 27°C, and are warmer in the winter and cooler in the summer than those temperatures in the coastal zone, which extends out from shore to about 18 m (Struhsaker 1969). Mathews and Pashuk (1977), and Leming (1979) further indicate that waters deeper than about 55 m are cooler year-round than waters in the 18- to 55-m depths. Based on bottom water temperatures associated with the calico scallop, this species is classified as subtropical tolerant (Miller and Richards 1980). For this reason, temperatures colder than 15°C and warmer than 27°C may be lethal to the major portion of the calico scallop population, and may establish the minimum and maximum depth distributions of scallops on the shelf. Therefore, the calico scallop, with its distribution controlled by temperature requirements, is restricted to a well-defined depth range off Cape Canaveral, with the largest numbers of heavy concentrations in 33 to 42 m (Miller and Richards 1980).

Based on biological observations reported here for several different years, 1967 to 1968, 1970 to 1971, and 1974, most spawning of calico scallops off Cape Canaveral generally occurs between November and June, but not necessarily during all of those months each year. We believe that seasonal variations in the annual spawning pattern can be attributed to variations in the annual bottom water temperature cycle. In 1970 and 1971, spawning intensity determined from ovarian developmental stages, scallop spat abundance, and scallop length-frequency distributions, apparently was highest from January to May and lowest from June to October.

Spawning intensity in 1970 and 1971 can be correlated with bottom water temperatures recorded at Buoys 1 and 2 (Figure 2). Low spawning intensity occurred from June to October, when temperatures usually were above 22.5°C. High spawning intensity occurred from January to May when temperatures were below 22.5°C. From November through May, there were more than five rapid major fluctuations (4°C or more) in bottom water temperature. During this period, calico scallops apparently spawned intermittently as indicated by the repeated high percentage of ripe scallop ovaries (Miller et al. 1980), and the continued recruitment of age class 0 scallops (Miller and Hudson, in preparation).

In determining the temperature range for spawning of the calico scallop, we recognized that the heaviest concentrations of scallops off Cape Canaveral occurred in depths of 33 to 42 m. Therefore, most of the scallop concentrations were deeper than the 18 and 22 m depths where bottom water temperatures were recorded at Buoys 1 and 2. Some scallops in depths of 22 m at Buoy 2 were ripe in November 1970 (Miller et al. 1980). Based on the annual cycle of bottom water temperatures, these scallops were subjected to declining temperatures below 22.5°C beginning in late November 1970 (Figure 2). These declining water temperatures, a direct result of seasonal atmospheric cooling, apparently initiated limited spawning at Buoy 2 in late fall and early winter.

Records of bottom water temperatures deeper than 22 m off Cape Canaveral were inadequate for refined analysis, since they were only available from expendable bathythermograph records taken at intervals of about 1½ months from January to December 1971 (Leming 1979). However, temperatures associated with the heaviest concentrations of scallops (at 33 to 42 m) probably did not decline below 22.5°C until January 1971. The records (Figure 2; Leming 1979) suggest that during the major spawning season, January to May, bottom water temperatures at depths from 18 to 55 m ranged from about 15.0° to 22.5°C. As shown by Leming (1979), in January the 18°C isotherm intersected the bottom shoreward of the 55-m depth contour. Beginning in March, cold (18°C) bottom water, cooled by

intrusions, moved onshore from the outer shelf. As this water progressed onshore, it "passed over the concentrations of scallops expected to be mostly ripe during March, April, and May and perhaps triggered successive spawning" (Allen 1979). By June, the 18°C isotherm had extended shoreward to the 18-m depth curve, and the 15°C isotherm to the 55-m curve (Leming 1979). Intrusions occurring in August did not cause spawning because scallop ovaries either were spent, immature or developing (Miller et al. 1980).

In summary, major spawning of calico scallops on the Cape Canaveral grounds in 1970 and 1971 occurred from January to May when bottom water temperatures were between 15.0° and 22.5°C.

COLD WATER INTRUSIONS

Along the southern Atlantic and northeastern Gulf of Mexico coasts of the United States, cold water intrusions that create temperature anomalies in nearshore waters have been documented near Cape Canaveral (Taylor and Stewart 1959), and Cape Lookout (Wells and Gray 1960). Intrusions are not restricted to shelf areas near coastal prominences, but they may not commonly move across the entire shelf to shore in all areas. Near Cape San Blas and Cape Lookout, intrusions apparently contribute to the formation of bottom water temperature patterns similar to those off Cape Canaveral.

Factors controlling the annual bottom water temperature regime off Cape Canaveral were reviewed by Leming (1979). Seasonal warm or cold atmospheric temperatures have strong influences on bottom water temperatures, affecting initially those on the western or inshore border of the calico scallop zone. However, intrusions of deep, cold water onto the Florida-Hatteras Shelf influence initially the eastern or offshore border of the calico scallop zone. According to Atkinson et al. (1978), intrusions "can be forced by wind, eddies, meanders, or density motions."

Cold water intrusions had the following effects off Cape Canaveral. The offshore bottom water, repeatedly cooled by intrusions in late winter, spring, and summer, caused the 18°C isotherm to progress shoreward on the shelf (Leming 1979). In late June and July 1971, the mean bottom temperatures increased shoreward from 16.6°C at Leming's temporary offshore station, CM2, depth 60 m, to 22.3°C at the inshore station, Buoy 1, depth 18 m (Table 1). The range in temperature was the largest at CM2, 9.4°C, decreasing shoreward to Buoy 1, 3.8°C. Rapid decreases in temperatures occurred: at CM2 temperatures decreased 5.3°C in 4 days; while at Buoy 1 temperatures decreased 3.4°C in 3 days. Leming (1979) showed there was an 8- to 9-day lag in temperature between CM2 and Buoy 1 due to intrusions. It is assumed that the subtropical tolerant calico scallop could not survive at CM2 as the bottom temperature was below 15°C for three consecutive days, reaching a low of 12°C for 2 days at this location.

Intrusions of cold water on the shelf may be favorable or unfavorable to the calico scallop. Intrusions may be favorable when they (1) initiate scallop spawning by lowering the water temperature below 22.5°C; (2) transport nutrient-rich water shoreward (Atkinson et al. 1978), producing phytoplankton blooms as food for scallops; and (3) lower the bottom water temperature to a range within which the calico scallop can survive, about 15.0° to 27.0°C. Intrusions may be unfavorable when they lower the bottom water temperatures below the minimum tolerance level of the calico scallop, 15°C, causing mortalities of larvae, spat, juveniles, and adults. Thus, the distance these cold intrusions extend shoreward controls the outer limits of the calico scallop grounds and affects the magnitude of the stock.

Measurements of bottom water temperatures, monitored by thermograph arrays in depths from 18 to 110 m, may be useful in prediction of spawning success and survival of the calico scallop and, therefore, estimation of the size of the annual crop.

TABLE 1.

Daily mean bottom water temperatures off Cape Canaveral, Florida, June 26 to July 23, 1971 (from Leming 1979).

Date		Station and Water Depth: CM2 60 m	Buoy 2 22 m	Buoy 1 18 m
		Temperature °C		
June	26	15.8	21.7	–
	27	16.0	19.8	21.5
	28	17.1	19.5	21.1
	29	18.7	19.5	22.4
	30	18.0	19.8	23.1
July	1	16.1	19.9	23.1
	2	15.5	19.9	22.5
	3	14.4	19.3	21.5
	4	15.5	19.0	23.8
	5	16.4	20.6	24.3
	6	15.7	22.5	24.3
	7	16.6	22.8	24.3
	8	18.0	22.9	24.1
	9	17.7	22.3	23.9
	10	18.1	21.1	23.2
	11	21.1	20.5	21.6
	12	21.4	19.4	20.5
	13	19.6	20.5	20.8
	14	18.3	20.6	21.7
	15	16.1	19.5	21.7
	16	15.4	19.8	21.9
	17	14.5	19.8	21.7
	18	15.1	19.8	21.4
	19	15.6	20.2	21.5
	20	12.6	20.9	22.5
	21	12.0	19.7	21.6
	22	14.5	17.4	21.1
	23	18.2	16.8	21.7
Minimum and maximum °C		12.0–21.4	16.8–22.9	20.5–24.3
Mean temperature		16.6	20.2	22.3
Range		9.4	6.1	3.8

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REPRODUCTIVE CYCLES OF THE ATLANTIC SURF CLAM *SPISULA SOLIDISSIMA*, AND THE OCEAN QUAHOG *ARCTICA ISLANDICA* OFF NEW JERSEY

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ABSTRACT Annual reproductive cycles of two commercially important bivalves, the Atlantic surf clam *Spisula solidissima* and the ocean quahog *Arctica islandica*, were investigated using specimens collected off the New Jersey coast. Specimens of both species were recovered from commercial port landings during two consecutive years, April 1977 through March 1979. Gonadal tissues were prepared by standard histological techniques for a microscopic examination of seasonal gametogenesis, and for determination of time and duration of spawning.

Gametogenesis in inshore surf clams proceeded slowly over the winter months, but by late May or June, the gonads were characterized by an abundance of morphologically ripe eggs or sperm. Partially spawned individuals were first encountered in June or July; their abundance rose sharply in late summer-fall when spawning was heaviest. All were spent by November or December.

A similar pattern of gametogenic development was observed in the ocean quahog. All gonads contained morphologically ripe eggs or sperm by August. However, spawning activity in this species was highest in the fall and often persisted into the winter months, particularly in 1978–1979.

Temporal differences between reproductive cycles of consecutive years may be related to differences in environmental factors. Comparison of results obtained here with previously published studies revealed important similarities and differences.

INTRODUCTION

The Atlantic surf clam *Spisula solidissima* (Dillwyn) and the ocean quahog *Arctica* (= *Cyprina*) *islandica* Linné are two of the largest and most abundant bivalve species inhabiting marine waters of northeastern United States. *Spisula solidissima* lives in a zone from the shallowest subtidal out to depths of about 60 m. It is found from the Gulf of St. Lawrence, Canada, south to Cape Hatteras, North Carolina (Merrill and Ropes 1969, Ropes 1980). *Arctica islandica* overlaps the latitudinal range of the surf clam but has a more extensive distribution from Cape Hatteras northward to the southern coast of Newfoundland, around Iceland, and along the coast of Europe (Nicol 1951, Ropes 1979). Ocean quahogs most commonly occur farther offshore than surf clams, though overlapping of both species occurs and is most pronounced between depths of 18 to 55 m (Ropes 1979).

Both species are of great commercial importance. Surf clams have been heavily fished since the late 1940's; landings reached a peak of 96 million pounds in 1974 (Serchuk et al. 1979). Overfishing led to severe reductions in landings which dropped to 49 million pounds in 1976 (Serchuk et al. 1979). The decline in surf clam densities in the overfished beds prompted the shellfish industry to begin intensive harvesting of the ocean quahog in 1975–1976 (Ropes 1979). A management plan for both species, which included research on their biology and ecology, was initiated in 1977 by the Mid-Atlantic Regional Fisheries Council (Ropes 1979). Since both of these species are of economic significance, it is important to know as much about their life histories, including reproduction, as possible.

A unique opportunity to examine the reproductive cycles of surf clams and ocean quahogs from New Jersey for a continuous 2-year period arose in 1977. Specimens of each species were collected at regular intervals to study the annual cycle of shell formation (Jones 1980). At the same time, gonadal tissues of each clam were recovered. Analysis of this gonadal material provided comparative data on seasonal gametogenesis, and on times and duration of spawning for the two species.

Early attempts to document the reproductive cycle of surf clams using gonad distension (Westman and Bidwell 1946), and excision of gametes (Allen 1951, 1953; Schecter 1941) were followed by Ropes (1968), whose histological examination of gonads of New Jersey surf clams over a 3½-year period represents the most comprehensive study to date. Ropes (1968) used offshore surf clams, collected at depths of 18 to 32 m, living below the thermocline. Specimens used in the present study came from shallower, more inshore habitats, and they probably lived above the thermocline (based on hydrographic summaries by Bigelow [1933] and Bowman [1977]).

Loosanoff (1953) gave a detailed account of the reproductive cycle in ocean quahogs using specimens from Point Judith, Rhode Island. He examined 162 individuals during two thirds of one year (from March 22 to November 1). Other studies of the reproductive cycle of *A. islandica* in the Baltic Sea by Jaeckel (1952) and by von Oertzen (1972) are more qualitative and fragmentary. The present study, using twice as many specimens as Loosanoff (1953), reports the reproductive cycle of ocean quahogs in New Jersey waters during a 2-year period, thus representing the most complete study to date.

MATERIALS AND METHODS

All clams were collected from commercial port landings

between April 11, 1977 and March 15, 1979. Ten specimens of each species were taken at biweekly intervals in the spring, summer, and fall, and at monthly intervals during the winter. In all cases the clams were shucked and prepared within 2 hours after being obtained.

Ocean quahogs came predominantly from an offshore Asbury Park, New Jersey, location (40°15′N, 73°40′W; 25 to 32 m water depth), though some samples (April 1977, June 1978, February and March 1978) were collected from offshore Cape May, New Jersey (38°55′N, 74°25′W; 25 to 27 m water depth). A total of 320 ocean quahogs with shell lengths ranging from 58 to 125 mm were analyzed.

Most surf clams were harvested from inshore beds along Island Beach, between Pt. Pleasant, New Jersey, and Barnegat Inlet. Specimens lived within 1.5 km from shore at depths of 6 to 10 m. Samples for January, February, and March 1979, came from similar depths off Wildwood Beach. Shell lengths of the 350 surf clams analyzed ranged from 75 to 164 mm.

The entire visceral mass of each clam was held for 48 hours in Davidson's fixative. Tissues were then transferred to 70% ETOH. In preparing slides for microscopic examination, tissues containing gonad ventral to the heart were cut from each specimen, dehydrated, and infiltrated with paraffin. Sections, 5 μm thick, were cut and stained with Harris hematoxylin and eosin Y (Preece 1972). Serial sectioning of several individuals revealed some sequential gonadal development. Therefore, to minimize variability between samples, sections were cut from the central portion of the gonad ventral to the heart, which seemed to be most representative of the bulk of the gonad.

Microscopic examinations of each section permitted assigning each specimen to a category of gonad development following those described by Ropes (1968): early active (EA), late active (LA), ripe (R), partially spawned (PS), and spent (S). These are divisions of convenience in a continuum; boundaries between phases are not sharp. Detailed descriptions of the histological characteristics of male and female surf clams in each of these phases can be found in Ropes (1968). Gametogenesis in ocean quahogs, described in detail by Loosanoff (1953), is similar to that of surf clams, so the same categories were applicable and detailed descriptions need not be repeated. Proportions of clams in each category were recorded and grouped by months to analyze the temporal progression of the reproductive cycles. Specimens, borderline between two successive phases, were counted as 50% in each phase. Photomicrographs of typical successive phases in male and female gonadal tissues of both species are shown in Figures 1 through 4.

Monthly sea surface temperatures for the collection dates and the localities of inshore surf clams living above the thermocline were assembled from the National Weather Records Center in Asheville, North Carolina, and from *Gulfstream*, published by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration. Bottom temperatures, for the localities where ocean quahogs were collected, were estimated from the summaries of Walford and Wickland (1968), Colton and Stoddard (1973), and Bowman (1977).

RESULTS

Spisula solidissima (Figure 5)

In April 1977, 5% of the surf clam population were in the early active phase of development, 85% were late active, and 10% were ripe. Ripening continued throughout May and June; by the end of June some clams had begun to spawn. A small percentage of partially spawned individuals was encountered throughout the summer months; September through November, all of the specimens were either partially spawned or spent. In December, only 10% of the surf clams appeared partially spawned, while 90% were spent. Lumina of the gonadal alveoli in spent clams were devoid of ripe spermatocytes or oocytes, but the already thickening alveolar walls contained gonia in the early stages of gametogenesis. By January, 80% of the gonads were in the early active phase and, by February, all clams were early active. About 20% reached the late active stage by March.

The pattern of the reproductive cycle in the following year was not greatly different. By April 1978, 70% of the surf clams had developed to the late active phase and, by May, 85% were late active. Though coming one month later than in 1977, ripening proceeded rapidly; by June, 75% of the surf clams sampled were ripe. Some partially spawned clams appeared in the following months, and the percentage of ripe individuals declined. Partially spawned clams dominated the September and October samples, accounting for 90% of the population by the end of October. The spawning cycle was completed in November when every specimen was categorized as spent. Similar gametogenic developments completed the cycle during the month of December in the previous year. In succeeding months, the number of individuals in the early active phase rose dramatically. By March 1979, 55% were in the early active stage, whereas 45% had already achieved the late active condition.

Of the 350 surf clams examined, 176 (50.3%) were males and 174 (49.7%) were females. The sex ratio was thus determined to be 1:1. The sexes were clearly separate; no hermaphrodites were encountered.

Arctica islandica (Figure 6)

The reproductive cycle of *Arctica islandica* also varied between the two years in which it was examined. The months of April through August were similar with gonadal ripening proceeding evenly; by August of 1977 and 1978, 90 to 100% of the clams were ripe. Thereafter, there were larger discrepancies between the two years. Partially spawned (65%) and spent (20%) clams comprised the bulk of the sample population in September 1977, whereas in September 1978, 100% of the population were still in the ripe phase.

Spawning activity continued vigorously through October 1977 and into November when, by the end of the month, 95% of the clams were spent. In contrast, partially spawned clams were not detected in 1978 until October, and a significant number of ripe specimens persisted until January. The principal months of spawning during the second year of investigation were November, December, and January, when both partially spawned and spent individuals predominated.

As indicated in Figure 6, the gametogenic portion of the reproductive cycle began earlier in the first year when all clams were in the early active phase by December 1978. Thereafter, more clams developed to the late active phase. No early active quahogs were detected during the second year until January 1979, and it was not until February that 90% were in the early active phase. This was about 2 months later than the preceeding year. As with the surf clam, it should be pointed out that the ocean quahog exhibited no "indifferent period" when the gonadal alveoli were totally free of germinal cells. Even in spent individuals, the early germinal cells of gametogenesis were evident in the thickened alveolar walls.

Of the 320 ocean quahog gonads examined in this study, 186 (58%) were males and 134 (42%) were females. To check the hypothesis that the sex ratio was 1:1 as in the surf clam, I used a two-sided test based on the normal approximation to the binomial distribution. The observed proportion was significantly different from the hypothesized value of 50% ($P = 0.008$). Sex ratio for ocean quahogs was not reported by previous workers (i.e., Loosanoff 1953, von Oertzen 1972, Landers 1976, Thompson et al. 1980). As with the surf clam, sexes were clearly separate; no hermaphrodites were encountered.

DISCUSSION

Spisula solidissima

Ropes (1968) observed a biannual reproductive cycle in gonads of surf clams during 3 of the 4 years in which he sampled from below the thermocline in offshore New Jersey. He found the biannual cycle was characterized by a major mid-year spawning, and by a minor late-year spawning, but allowed that the second cycle may not be an annual event.

Results reported in this investigation (Figure 5) of inshore surf clams living just above the summer thermocline are very similar to those of Ropes (1968) for the half year, January to June. Each year, this period was characterized by 90 to 100% of the surf clams in the early active phase in January, maturing to the ripe phase by June. During the remaining months (July though December), the two investigations report very different frequencies of individuals in each phase. In the years 1962, 1963, and 1964, Ropes (1968) reported two spawnings—a major mid-year event during July/August, and a second minor spawning during October/November. However, in 1965, when temperatures were considerably lower than in previous years, Ropes found only one spawning event, delayed and longer lasting than in the previous years.

As indicated in Figure 5, the results of this investigation suggest only one spawning period for inshore surf clams. While partially spawned individuals were encountered occasionally in June, they did not appear in high percentages until late summer. The bulk of spawning activity was concentrated in August through October and often into early November. By late November or December, all gonads appeared spent and the spawning phase was completed. Renewed gametogenic activities were already evident in the alveolar walls of the flaccid gonads.

Without adequate environmental data collected concurrently with the surf clams, hypotheses concerning the influence of environmental factors (e.g., temperature) upon the temporal progression of the reproductive cycle seem unwarranted. Also, with only 2 years of data it was impossible to ascertain which year was more typical. Certain generalizations can, however, be made: (1) inshore surf clams did not appear to undergo two spawning events as Ropes (1968) described for offshore clams from New Jersey; (2) spawning occurred most heavily in late summer and fall when water temperatures were highest; and (3) the rate of gametogenic development, gonadal ripening, and initiation and duration of spawning varied somewhat from year to year, probably in response to environmental factors.

Arctica islandica

All previous investigators reported roughly the same sequence of gametogenic events in the ocean quahog: (1) unripe oocytes and spermatocytes were present throughout the winter, (2) followed by gradual ripening of the gonads during spring and summer, and (3) spawning in summer or early fall. However, the timing of these events varied considerably, apparently depending on geography and oceanography. Loosanoff's (1953) observations on samples from Rhode Island were similar to some of those obtained here, particularly in the first year (1977–1978) of the study. Results of the second year of my investigation, however, indicated that spawning may be delayed well into the fall or winter months. In contrast, von Oertzen (1972) concluded the spawning period in samples from the Bay of Mecklenburg (Baltic Sea) extended from May to September. This was earlier (by 2 to 3 months) than was observed in the western North Atlantic, but the spawning duration (4 to 5 months) was approximately the same. It is interesting to note that Jaeckel (1952), working in the Bay of Lubeck, also in the Baltic Sea, reported the spawning period of *Arctica* commenced in July and proceeded for some undetermined months thereafter, a result more consistent with those from North America.

As with the surf clam, concurrent environmental data were not collected with the ocean quahogs because the specimens were obtained from commercial clammers.

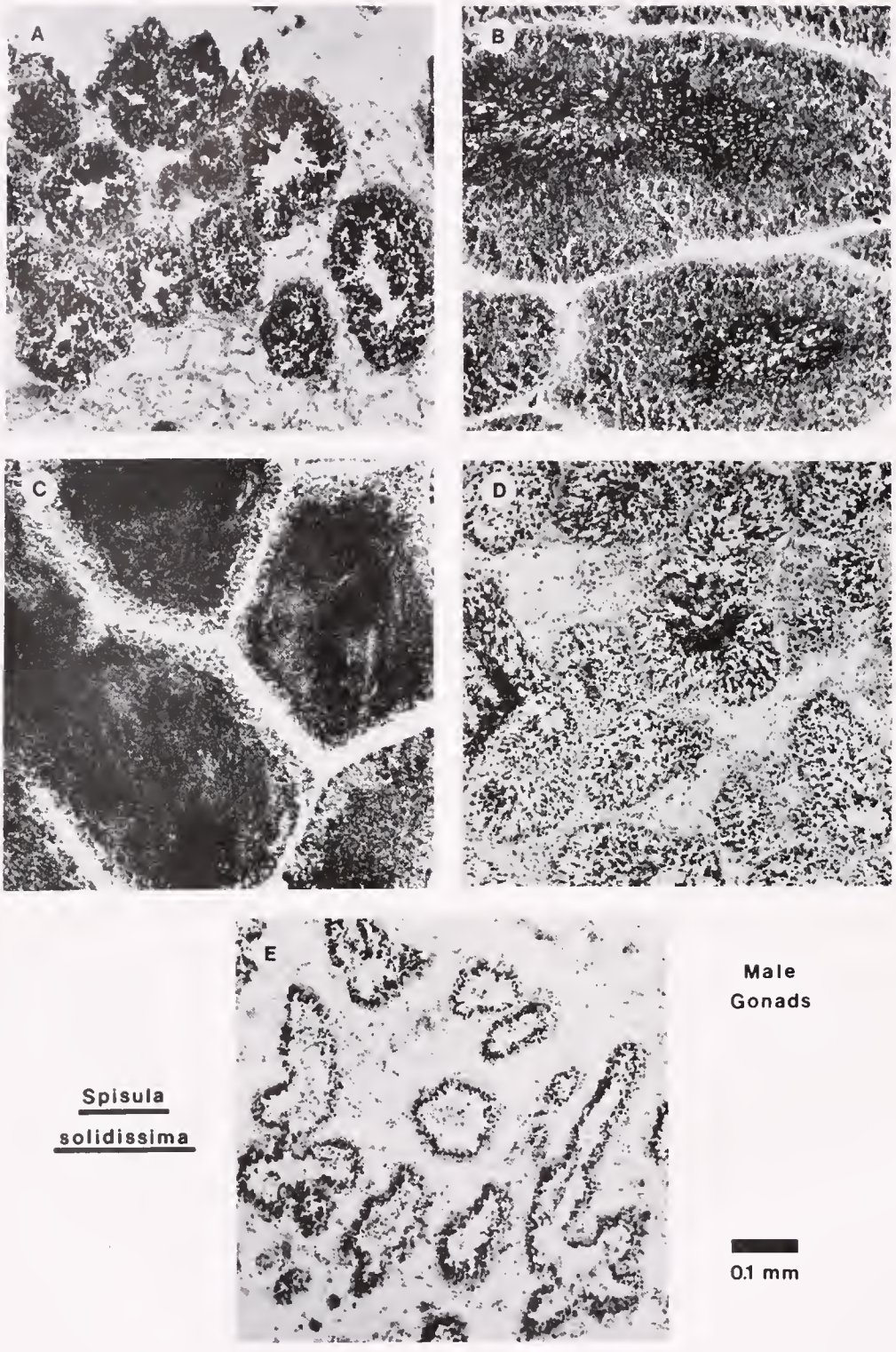

Figure 1. Sections of gonadal tissue from male surf clams *Spisula solidissima* in each phase of the reproductive cycle. A. Early active phase (EA)–thickened alveolar walls with spermatogonia, primary spermatocytes proliferating into lumen. B. Late active phase (LA)–secondary spermatocytes abundant, spermatids massing in lumen. C. Ripe phase (R)–mature sperm form dense, swirling masses in alveoli. D. Partially spawned phase (PS)–ripe sperm less dense than in previous phase, spermatogonia developing in alveolar walls. E. Spent phase (S)–lumina devoid of sperm, primary spermatogonia developing in thickening alveolar walls.

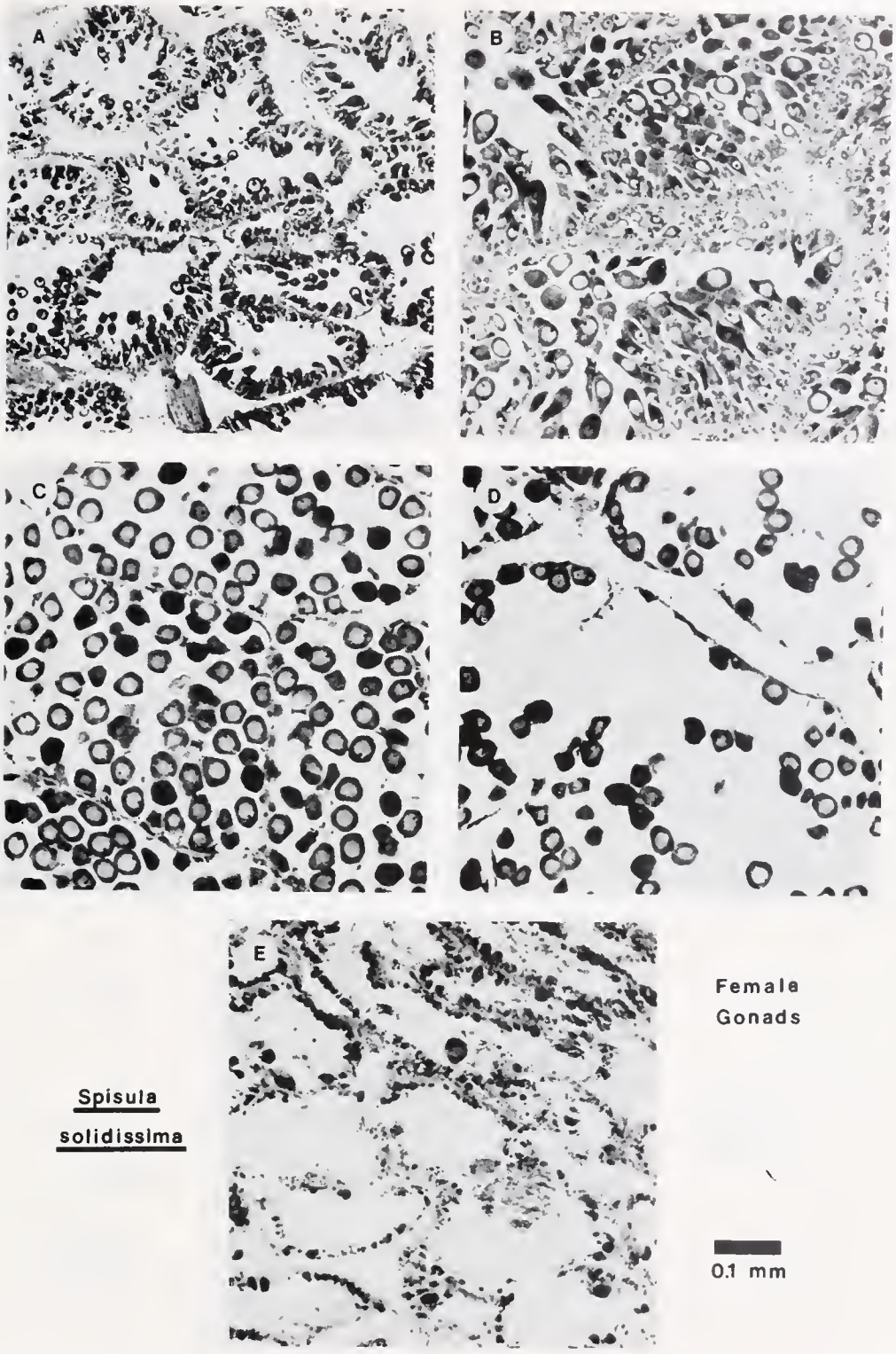

Figure 2. Sections of gonadal tissue from female surf clams *Spisula solidissima* in each phase of the reproductive cycle. A. Early active phase (EA)—oogonia embedded in alveolar walls while early oocytes remain attached to basement membrane. B. Late active phase (LA)—enlarging oocytes fill lumina, some are unattached while others remain attached. C. Ripe phase (R)—large, rounded, ripe oocytes are free in the lumina. D. Partially spawned phase (PS)—significantly less ripe oocytes in lumina than in previous phase, some lumina barren, gonad appears flaccid. E. Spent phase (S)—lumina of alveoli devoid of ripe oocytes, thickening walls contain developing oogonia.

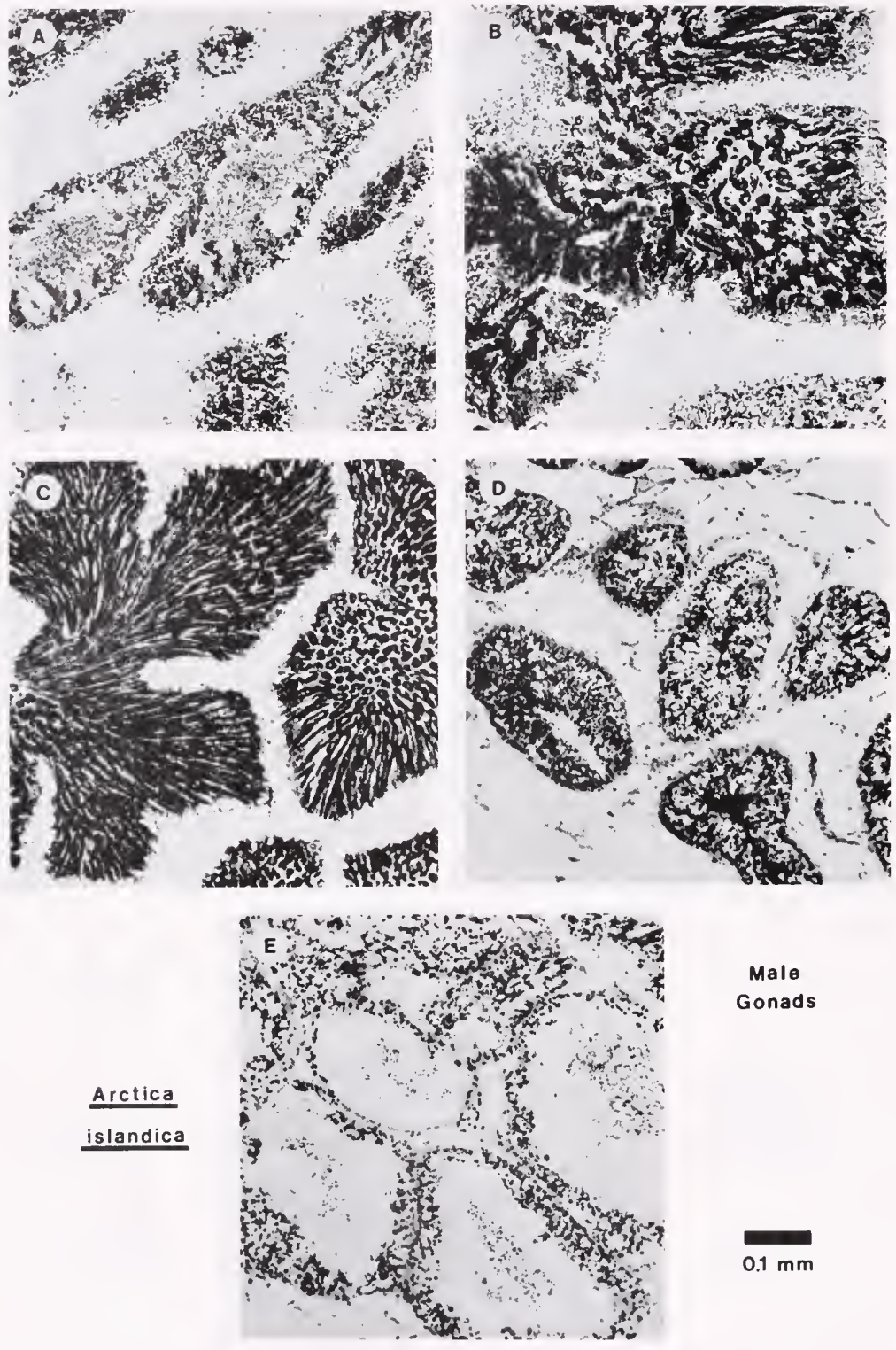

Figure 3. Sections of gonadal tissue from male ocean quahogs *Arctica islandica* in each phase of the reproductive cycle. A. Early active phase (EA)—spermatogonia developing from thickened alveolar walls. B. Late active phase (LA)—spermatogonia developing at periphery while ordered packing of spermatozoa has begun in the lumina. C. Ripe phase (R)—swirling masses of mature sperm fill gonadal alveoli. D. Partially spawned phase (PS)—ripe sperm much less dense than in previous phase, alveoli no longer distended. E. Spent phase (S)—lumina devoid of ripe sperm, spermatogonia developing along basal membrane.

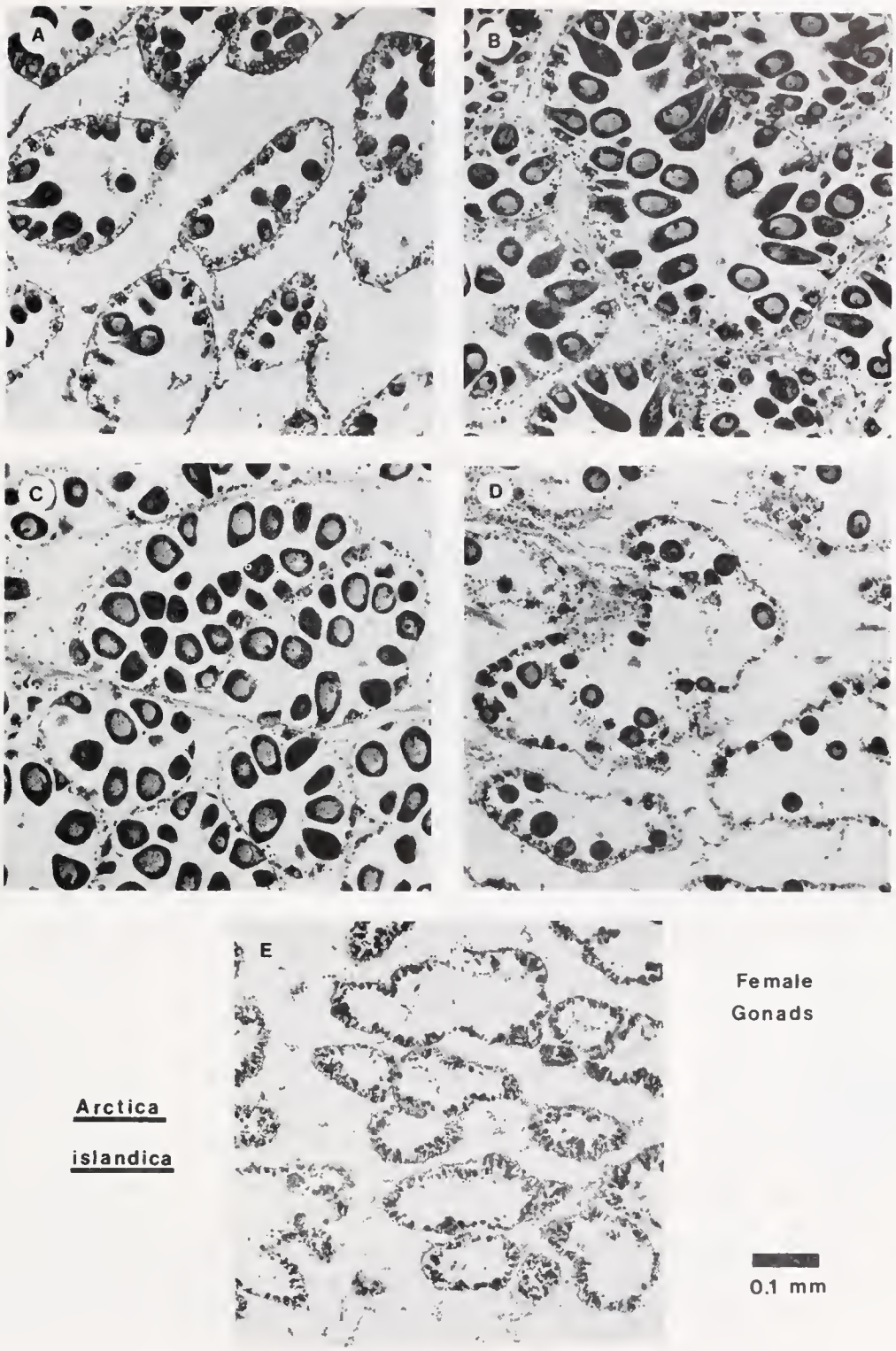

Figure 4. Sections of gonadal tissue from female ocean quahogs *Arctica islandica* in each phase of the reproductive cycle. A. Early active phase (EA)—oogonia maturing along periphery of alveoli. B. Late active phase (LA)—enlarging oocytes filling lumina, most still attached by stalk to basement membrane. C. Ripe phase (R)—ripe oocytes free in lumina, alveolar walls thin and gonad distended. D. Partially spawned phase (PS)—few ripe oocytes remain in alveoli, gonad is flaccid. E. Spent phase (S)—lumina devoid of ripe oocytes, alveolar walls thickening, oogonia developing at periphery.

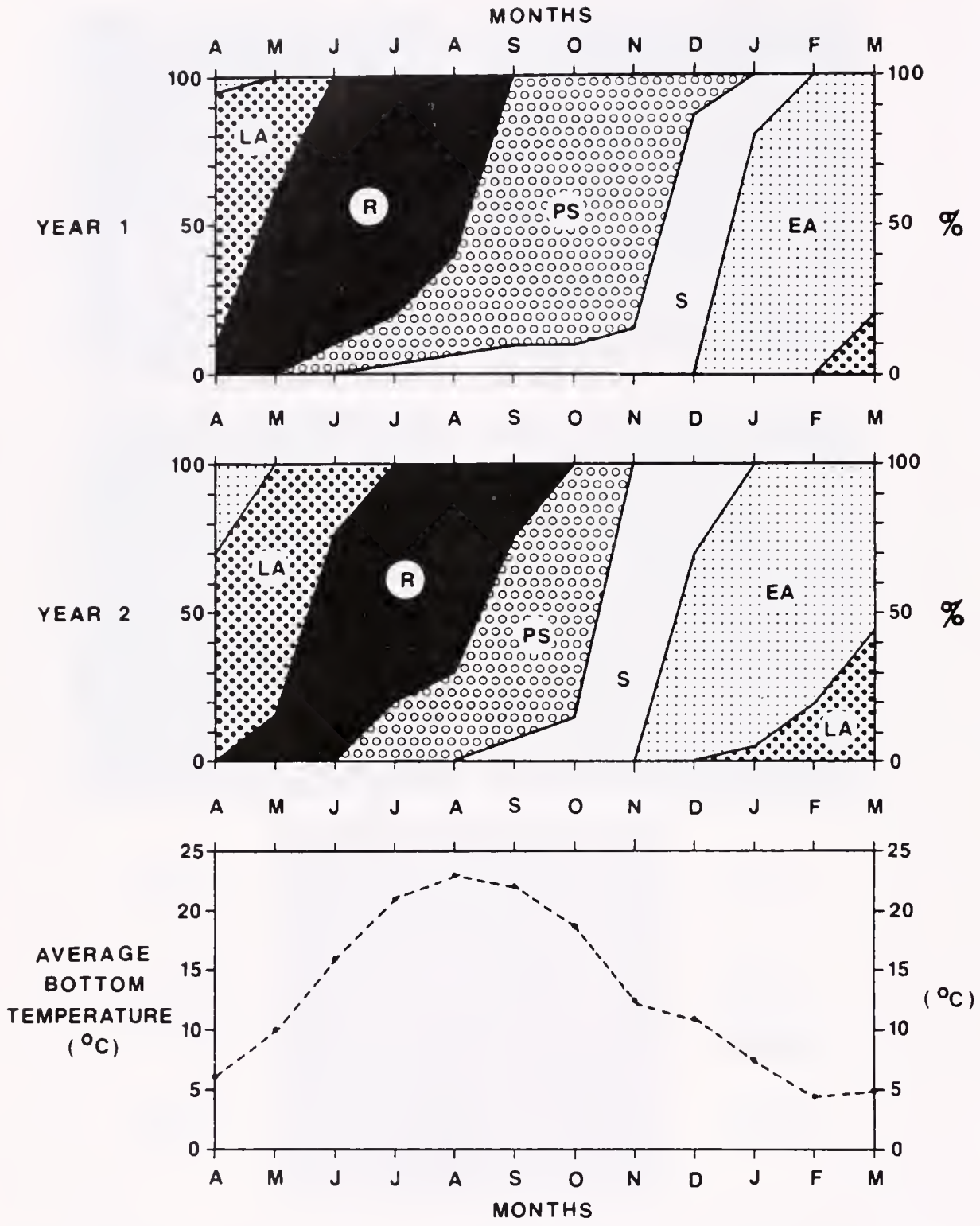

Figure 5. Percentages of inshore surf clams (*Spisula solidissima*) in each phase of the reproductive cycle during each month of this 2-year study are shown in the top two diagrams. YEAR 1 = April 1977 through March 1978; YEAR 2 = April 1978 through March 1979. Abbreviations for phases of reproductive cycle are explained in Figures 1 through 4. For comparison, a record of average monthly mean sea surface temperatures for the same time interval in the region where the surf clams were collected is included (bottom diagram).

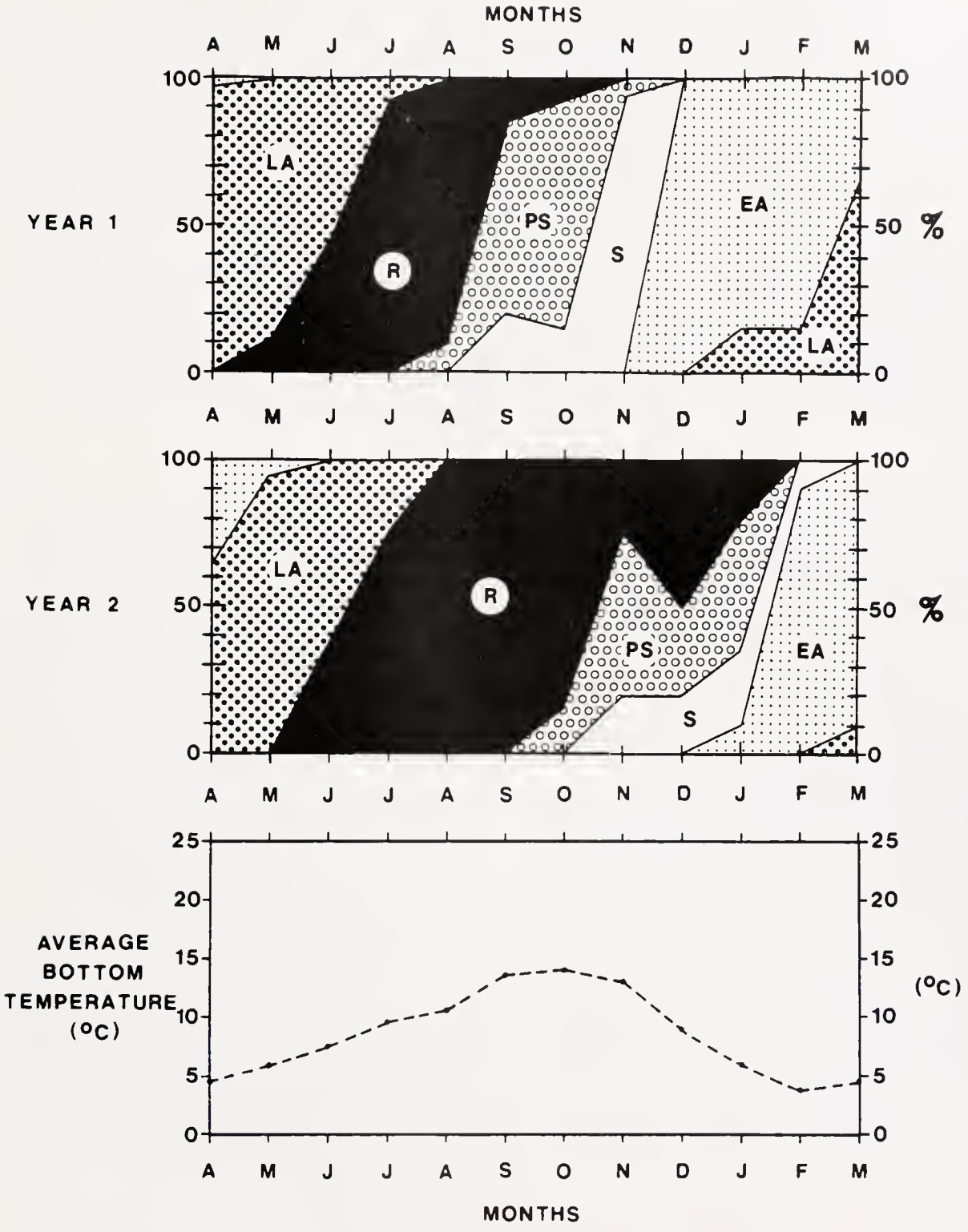

Figure 6. Percentages of ocean quahogs (*Arctica islandica*) in each phase of the reproductive cycle during each month of this 2-year study are shown in the top two diagrams. YEAR 1 = April 1977 through March 1978; YEAR 2 = April 1978 through March 1979. Abbreviations for phases of reproductive cycle are explained in Figures 1 through 4. For comparison, a record of average monthly mean sea surface temperatures for the same time interval in the region where the ocean quahogs were collected is included (bottom diagram).

Therefore, it was not possible to interpret accurately the events of the reproductive cycle in terms of environmental influences. Some useful observations may nevertheless be gleaned from the data: (1) in consecutive years, rate of gonadal ripening, and the initiation and duration of spawning may vary, probably in response to environmental factors; (2) spawning off New Jersey appeared to be an autumnal to early winter event rather than summer/early autumn as previous studies suggested; and (3) comparison of gonadal observations with average bottom temperatures for the area of collection (Figure 6) suggested that initiation of spawning was coincident with highest bottom water temperatures. Loosanoff (1953) concluded that spawning began when water temperatures reached ~ 13.5°C. This was consistent with the present study. It should be emphasized, however, that monitoring of bottom temperatures was not a part of either study. In both cases, temperatures were estimated from published summaries.

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DISTRIBUTION AND RELATIVE ABUNDANCE OF THE OCEAN QUAHOG *ARCTICA ISLANDICA* IN RHODE ISLAND SOUND AND OFF MARTHA'S VINEYARD, MASSACHUSETTS

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ABSTRACT Estimates of minimum biomass (total wet weight and meat weight) were derived for *Arctica islandica* in parts of southern New England. Total harvestable biomass for the survey area was estimated at 1.004×10^6 metric tons (mt) total wet weight, and 1.33×10^5 mt meat weight. Stepwise linear discriminant analysis was used to isolate sediment components which contribute to separation of regions of high- and low-ocean quahog densities (arbitrarily assigned values of $\geqslant 0.75$ kg/m^2 and $\leqslant 0.10$ kg/m^2 total wet weight, respectively). The percentage of four sediment fractions: gravel, coarse sand, medium sand, silt/clay, and the percentage of shell in the sample were sufficient to significantly ($P < 0.01$) discriminate between the two levels of ocean quahog densities. Size composition data and shell length-meat weight regressions for three depth intervals within the survey area are presented.

INTRODUCTION

The ocean quahog *Arctica islandica* supports a small but valuable commercial fishery in Rhode Island coastal waters. Initial exploitation of this resource in the United States was centered in Rhode Island (Arcisz and Neville 1945); until 1976, the entire United States fishery was based in New England. Declining yields in the highly exploited surf clam *Spisula solidissima* fishery (Serchuk et al. 1979, Ropes 1979) resulted in a marked increase in exploitation of *Arctica* along the Atlantic coast. The shift in directed effort from the surf clam to ocean quahog, particularly in the Mid-Atlantic Bight, resulted in a substantial increase in reported landings. Total catch in the Fishery Conservation Zone (FCZ) increased nearly five fold from 1976 to 1978 (*Fisheries of the U.S., 1976–1978*). The Rhode Island catch in the same period increased 86% from 1,446 mt to 2,684 mt (Rhode Island Landings 1976–1978).

Distribution of *Arctica* along the northeastern coast of the United States was examined in research surveys conducted by the National Marine Fisheries Service (NMFS) and its predecessor, the Bureau of Commercial Fisheries (Merrill and Ropes 1969, 1970; Parker and McRae 1970; Ropes 1979). Murawksi and Serchuk (1979a) summarized and integrated the results of these surveys to provide minimum biomass estimates for the Middle Atlantic (Cape Cod to Cape Hatteras) region.

The present study was undertaken to determine the distribution of *Arctica* in Rhode Island Sound and off Martha's Vineyard, Massachusetts, in relation to depth and sediment type. A quantitative assessment of some of the factors governing ocean quahog density was deemed important for predictive purposes in identifying potentially exploitable quahog concentrations. Bearse (1976) reviewed the known ecological determinants of ocean quahog distribution. This paper presents information on distribution, minimum biomass, substrate affinities, size composition, and length-weight relationships for *Arctica* within the survey area.

MATERIALS AND METHODS

Ocean quahog samples were obtained aboard a chartered commercial fishing vessel equipped with an hydraulic dredge with a 1.52-m blade, and a 3.8-cm spacing between the bars of the retaining cage. Standard sampling tows were of 4-minute duration at a speed of approximately 2.8 km/hr. Distance covered by the dredge was determined from LORAN C coordinates recorded to the nearest 0.1 μsec at the start and end of each tow. The mean distance covered was 190.2 m (± standard error [SE] = 5.13), resulting in an average areal coverage of 289.1 m^2 per standard tow.

A simple random sampling design was employed with stations selected from a grid interval of 1.8 x 1.8 km throughout the survey area in water depths ranging from 18.2 m to 45.7 m (Figure 1). Stations falling on an untowable bottom were randomly reassigned to an adjacent site. A total of 191 stations were occupied between June 15, 1978 and August 3, 1978, and an additional 21 stations were sampled on March 22, 1979. For comparative purposes, the survey area was divided into three arbitrary depth intervals (18.3–27.4, 27.5–36.5, and $>$ 36.6 m).

Survey catch data were analyzed according to Aitchison (1955) and Pennington (NMFS, Woods Hole Laboratory, personal communication), a method in which the data are partitioned into zero and nonzero catch values. The conditional distribution of the nonzero class is assumed to be lognormal (the Δ-distribution, Aitchison and Brown 1957).

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Figure 1. Location of sample sites for *Arctica* in Rhode Island Sound and south of Martha's Vineyard, Massachusetts.

An unbiased estimator of the sample mean (Aitchison 1955) is:

$$C = \frac{m}{n} \exp(\bar{y})\, \Psi_m(s^2/2)$$

and the variance of the sample mean (Pennington, personal communication) is given by:

$$\mathrm{Var}(c) = \frac{m}{n} \exp(2\bar{y}) \left[\frac{m}{n} \Psi_m^2(s^2/2) - \frac{m-1}{n-1} \Psi_m\left(\frac{m-2}{m-1} s^2\right)\right]$$

where m is the number of nonzero observations, n is the total number of observations, $\bar{y}$ and s^2 are the mean and variance of the log-transformed nonzero observations, respectively, and

$$\Psi_m(t) = 1 + \frac{n-1}{n} t + \sum_{j=2}^{\infty} \frac{(n+1)^{2j-1}}{n^j (n+1)(n+3)\ldots(n+2j-3)} \cdot \frac{t^j}{j!}$$

At each station the ocean quahog catch was weighed to the nearest 0.5 kg. In instances where the catch-per-tow was high (> 250 kg), two level 35-liter (1 U.S. bushel) containers of ocean quahogs were weighed to the nearest 0.5 kg, and the remaining catch recorded in number of 35-liter containers. Estimates of the total sample weight were then obtained by expanding the mean of the two weighed samples to the total number of containers.

A random sample of 100 ocean quahogs was retained for size frequency analysis at each station where *Arctica* were obtained. In instances where the total catch was less than 100 individuals, the entire catch was measured. A random subsample of 20 quahogs was selected from the length-frequency sample for length-weight analysis and taken to the laboratory for processing. Shell dimensions were recorded to the nearest millimeter and meat weights recorded to the nearest 0.5 gram. Regression equations relating drained meat weight and shell length were fit by nonlinear least squares using a modified Gauss-Newton algorithm (Ralston and Jennrich 1978). Comparisons between regression equations derived for the three depth intervals were made using Rao's homogeneity X^2 test (Rao 1973, pp. 389–391).

Sediment samples were collected at each station using a Mann sampler (Krumbein and Pettijohn 1938) with a 10.2-cm opening. The Mann sampler was attached to the hydraulic dredge and collected the sediment sample simultaneously with the biological sample. Stations at which residual sediment in the dredge differed from than in the Mann sampler, or where substantial quantities of rock and stone were retained, were not further analyzed. An attempt was also made to limit analyses to samples from unexploited sites based on prior knowledge of the fishery. Detailed grain-size analyses were completed for a total of 127 sediment samples. The substrate samples were washed, oven dried, disaggregated, and dry sieved. The sieves conformed to the standard Wentworth mesh dimensions (2.0, 1.0, 0.5, 0.25, 0.125, 0.062, and < 0.062 mm). No attempt was made to further separate the silt/clay (< 0.062 mm) fraction. Shell particles in each fraction were weighed separately.

Linear discriminant analysis (Fisher 1936) was used to differentiate between regions of high- and low-ocean quahog densities (arbitrarily assigned values of ≥ 0.75 kg/m^2 and ≤ 0.10 kg/m^2, respectively) on the basis of sediment composition and water depth. Sediment data were expressed in the linear Krumbein scale

$$\phi = -\log_2(d)$$

where d is the Wentworth particle size diameter in millimeters (Krumbein and Pettijohn 1938). Percentage values were treated with an arcsine transform prior to analysis (Cassie and Michael 1968).

RESULTS AND DISCUSSION

Minimum Biomass

Minimum biomass estimates (total wet weight and meat weight) were derived for the entire survey area and at each depth interval. These estimates must be considered minimum since the dredge is not completely efficient, and the selection characteristics of the dredge cage prevented the complete retention of quahogs < 70 mm shell length (Fogarty 1979).

Ocean quahogs were obtained at 139 (66%) of the stations sampled. The conditional distribution of the nonzero densities was approximately lognormal (Figure 2); therefore, estimation of the sample mean and its variance using Δ-distribution theory was considered appropriate. The estimated mean density (total wet weight) of *Arctica* for the entire survey area was 0.377 kg/m^2 (Table 1). No significant differences ($P < 0.05$) in quahog density between

depth intervals were discerned (Kruskal-Wallis test; $\chi^2_2 = 3.61$, ns [not significant]). A similar estimate of 0.401 kg/m^2 can be calculated from Bearse (1976) based on grab and SCUBA samples collected off Rhode Island.

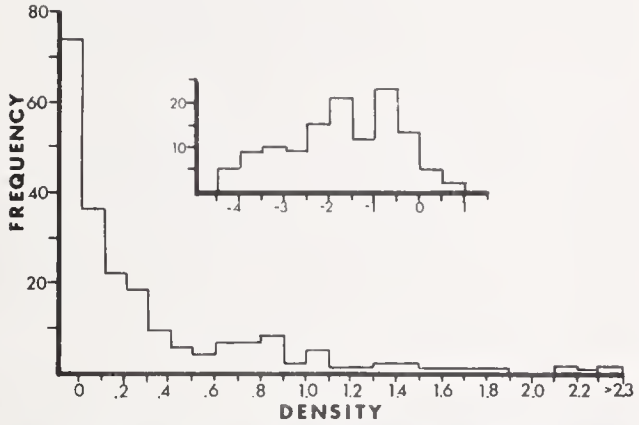

Figure 2. Frequency distribution of untransformed ocean quahog density (kg/m^2 total weight) and log-transformed nonzero density values (insert).

Estimates of total wet weight were converted to meat weight assuming a meat weight:total weight ratio of 0.133 for *Arctica* collected in Rhode Island Sound (Arcisz and Sandholzer 1947). Converted density of 0.051 kg/m^2 meat weight derived for the entire survey area, and estimates of 0.087 kg/m^2 for Rhode Island Sound (Bearse 1976) and 0.011 kg/m^2 for the offshore waters of southern New England (Murawski and Serchuk 1979b) were of the same order of magnitude.

TABLE 1.

Total area, sample size, estimated density (total wet weight [kg/m^2]), and estimated biomass (total weight and meat weight [mt]) for individual depth intervals and for the entire survey area.

	Depth Intervals (m)			
	18.3 – 27.4	27.5 – 36.5	36.6 – 45.7	Total
No. of samples	26	101	85	212
Stratum area (km^2)	6.0833×10^2	1.1197×10^3	9.3758×10^2	2.6656×10^3
Density (kg/m^2)	0.3746	0.3428	0.4176	0.3767
Variance	0.0199	0.0077	0.0082	
Total weight (mt)	2.279×10^5	3.838×10^5	3.915×10^5	1.004×10^6
Meat weight (mt)	3.03×10^4	5.10×10^4	5.21×10^4	1.33×10^5

Minimum biomass for the entire survey area was estimated at 1.004×10^6 mt total weight with a corresponding estimate of 1.33×10^5 meat weight (Table 1). Murawski and Serchuk (1979a) estimated the minimum biomass (meat weight) of *Arctica* for the southern New England region to be 1.59×10^5 mt.

Effect of Substrate Type

Stepwise linear discriminant analysis was used to differentiate between regions of high ($\geq$ 0.75 kg/m^2) and low ($\leq$ 0.10 kg/m^2) ocean quahog density on the basis of sediment grain-size characteristics and water depth (Table 2). Preliminary analyses indicated that the density of *Arctica* was highest in medium-to-fine grain sand, and density declined as mean particle size decreased (Figure 3). Estimated density also was low in very coarse sand environments. Ocean quahogs were not present in substrates comprised primarily of gravel and stone, nor in those with high levels of silt/clay.

TABLE 2.

Variables used in linear discriminant analysis differentiating regions of high ($\geq$0.75 kg/m^2) and low ($\leq$0.10 kg/m^2) ocean quahog densities.

Variable Code	Description
-1ϕ	% gravel (>2 mm)
0ϕ	% very coarse sand (1.0–1.99 mm)
$+1\phi$	% coarse sand (0.50–0.99 mm)
$+2\phi$	% medium sand (0.25–0.49 mm)
$+3\phi$	% fine sand (0.125–0.249 mm)
$+4\phi$	% very fine sand (0.062–0.1249 mm)
$+5\phi$	% silt/clay (<0.062 mm)
Shell	% shell fragments
Depth	water depth (m)
Mean	mean grain size (ϕ)
SC	sorting coefficient (standard deviation)

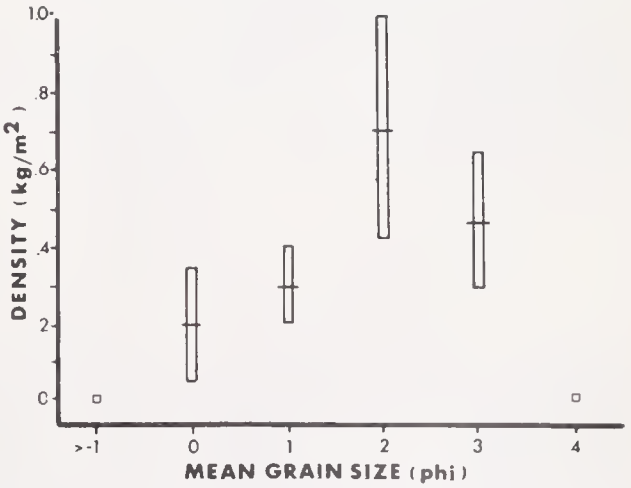

Figure 3. Ocean quahog density (kg/m^2 total weight) as a function of mean grain size (ϕ units). Data given as mean (horizontal line) ± 2 standard errors (enclosed rectangle).

Grain-size analyses were available for a total of 47 stations assigned to the low-density classification and for 26 stations designated as high-density sites. The stepwise discriminant analysis was based on the pooled covariance matrix, and the maximum F-ratio was used as the selection criterion.

Five variables were found to provide maximum group separation ($F_{5,67} = 14.67, P < 0.01$; Table 3). The relative magnitude of the standardized discriminant coefficients indicates the contribution of each variable to the discriminating power of the function; the sign of the coefficients denotes the direction of this contribution. The percentage of three grain-size fractions (gravel, coarse sand, and silt/clay) contributed negatively to the discriminant function while the percentage of medium-grade sand and shell contributed positively, confirming the results of preliminary analyses (Figure 3). The remaining grain-size fractions did not significantly enhance the discriminating power of the function. Water depth did not significantly contribute to the discriminant function, supporting inferences made earlier; however, the depth ranges sampled were restricted. The classification matrix indicating the actual and predicted group membership based on the five discriminating variables was:

	Predicted	
Actual	High Density	Low Density
High density	22 (84.6%)	4 (15.4%)
Low density	4 (8.5%)	43 (91.5%)

demonstrating the predictive power of the derived function (89% correct classification).

TABLE 3.

Standardized stepwise discriminant coefficients for five variables providing maximum separation of regions of high (≥ 0.75 kg/m^2) and low (≤ 0.10 kg/m^2) ocean quahog density.

Variable	Coefficient
-1ϕ	−0.60647
$+1\phi$	−1.23598
$+2\phi$	+0.48943
$+5\phi$	−0.95893
Shell	+0.23318

DeWolf and Loosanoff (1945) described the preferred substrate of *Arctica* as a mixture of sand and mud in Rhode Island Sound. Parker and MacRae (1970) indicated that the highest ocean quahog catches were made on sand and sandy mud in exploratory surveys in the western North Atlantic. Maurer et al. (1974) reported that *Arctica* was collected most frequently on medium grade and coarse sand/shell substrates in Delaware Bay.

Bearse (1976) utilized multivariate analyses to examine the effect of sediment characteristics on the abundance of *Arctica* at two locations in Rhode Island Sound. Stepwise linear discriminant functions derived for one of these locations and for combined data, isolated different discriminating variables. Patchy distribution of sediments in the areas studied was cited as a possible factor in conflicting results between these analyses.

Bearse (1976) isolated organic carbon as one factor of importance in determining ocean quahog distribution. Phelps (1959) and Saila et al. (1967) demonstrated the importance of organic carbon on hard clam (*Mercenaria mercenaria*) distribution in Narragansett Bay. Although carbon levels were not measured in the present study, it was recognized that this variable may play an important role in determining ocean quahog distribution patterns.

The observed relationship between ocean quahog density and sediment characteristics cannot be taken to imply substrate preference or selection. Particle-size distribution may simply be the visible manifestation of other factors (e.g., current velocity, food availability), critical to ocean quahog distribution (Bearse 1976). Further, dredge efficiency may have varied with substrate composition and compaction, resulting in biases in density estimates. These results retain a practical significance, however, since the data may be used to assess the probability of locating commercially exploitable ocean quahog beds based on a knowledge of substrate characteristics.

Size Composition

Shell length (standard length [SL], longest linear dimension) measurements were obtained for a total of 11,925 ocean quahogs. Little variation in size frequency distribution was noted between depth intervals (Figure 4), and no significant differences ($P < 0.05$) in mean shell length were detected when depth zones were compared using a one-way analysis of variance.

Bearse (1976) reported a mean shell length of 90.5 mm for samples collected by SCUBA and grab sample at two sites off Rhode Island. Mean shell length noted in the present survey was 88.5 mm; the similarity of these estimates may indicate that the dredge provided relatively unbiased estimates of size composition. DeWolf and Loosanoff (1945) reported a mean shell length of 83.8 mm for samples collected by mechanical dredge in Rhode Island Sound.

The maximum shell length noted in the present survey was 114 mm. Murawski and Serchuk (1979a) reported that ocean quahogs larger than 119 mm SL were seldom collected off southern New England during survey cruises in offshore waters, while samples collected off New Jersey frequently contained individuals $\geq$ 120 mm SL.

An attempt was made to separate the length-frequency distribution into component size classes by the method of Cassie (1954); however, it proved impossible to identify

probability modes with reasonable accuracy, a result consistent with the slow growth rates demonstrated for this species (Murawski et al., in press).

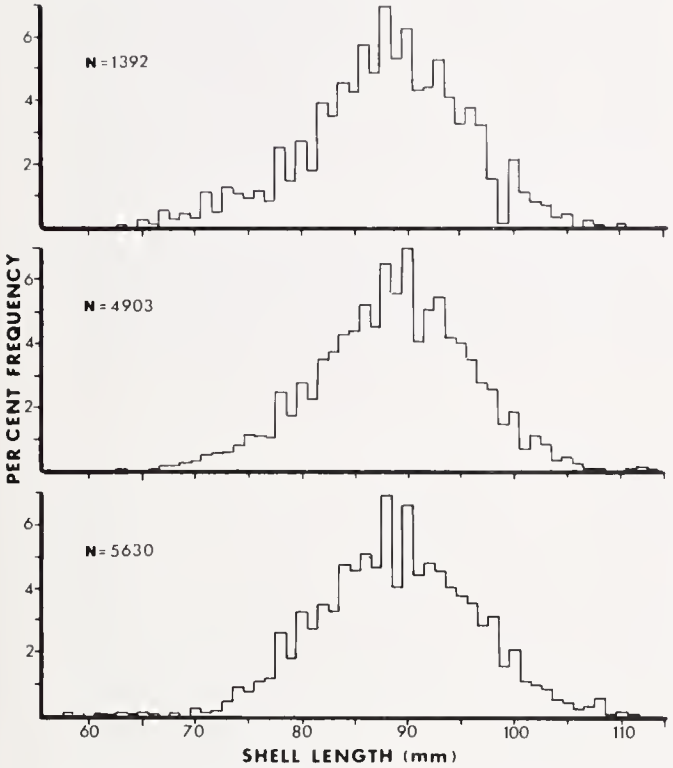

Figure 4. Shell length frequency distributions of ocean quahogs from arbitrary depth intervals of 18.3–27.4 m (upper), 27.5–36.5 m (middle), and 36.6–45.7 m (lower).

Regression equations relating meat weight and shell length were derived for ocean quahogs assigned to three arbitrary depth intervals and for combined data (Table 4). Bearse (1976) derived a similar length-weight relationship for *Arctica* in Rhode Island Sound:

$$W = 0.0009114\ L^{2.355} \qquad (n = 129).$$

Murawski and Serchuk (1979c) reported the length-meat weight relationship for ocean quahogs collected during winter in the southern New England-Long Island region as

$$W = 0.0001090\ L^{2.775} \qquad (n = 1{,}351).$$

Direct comparisons between this equation and regression equations developed in the present study were not possible because of differences in the size range of sampled individuals and in the time frame of sampling.

The higher meat yields predicted by the equations derived in the present study and by Bearse (1976) may be due to higher productivity in inshore waters, or by condition factors related to reproductive activity. Loosanoff (1953) noted that the spawning period for *Arctica* extended from June through October, with peak reproductive activity in August and September off Rhode Island. More recent work (Mann 1979) has indicated, however, that *Arctica* is capable of spawning throughout the year and that spawning activity may be intermittant.

Comparisons between parameter estimates for each depth zone using Rao's homogeneity χ^2 test (Rao 1973) indicated no significant differences between depth strata for the parameters a ($\chi^2_2 = 0.378$; ns) or b ($\chi^2_2 = 1.261$; ns). Further comparisons for all possible pairwise combinations for each parameter also indicated no significant differences between depth zones. Parameter estimates for the shallow depth strata exhibited relatively high variability (Table 4), possibly due to the low sample size. Murawski and Serchuk (1979c) did not detect any consistently significant differences in meat weight-shell length regression equations by depth for *Arctica* collected from the Middle Atlantic.

CONCLUSIONS

The estimated minimum biomass for the survey area, 1.36×10^5 mt meat weight, is high relative to recent landings in Rhode Island (1,228 mt in 1979), indicating that exploitation has not been severe. However, the slow growth rate of this species (Murawski et al., in press) and the presumably low natural mortality rate indicate that productivity of the resource may be very low. The fishery could conceivably be operating on accumulated biomass without comparable recruitment. Although density estimates derived from dredge data are necessarily minimum

TABLE 4.

Parameter estimates and asymptotically valid standard errors for allometric equation ($W = aL^b$) relating drained meat weight (g) and shell length (mm) for ocean quahogs off Rhode Island and Massachusetts.

Depth Interval	N	Parameter a	Asymptotic Standard Error	Parameter b	Asymptotic Standard Error
18.3 – 27.4	189	0.0013901	0.0012035	2.257166	0.183371
27.5 – 36.5	934	0.0006412	0.0002779	2.470849	0.095965
36.6 – 45.7	710	0.0006282	0.0002656	2.482145	0.093499
Combined	1,833	0.0006585	0.0001732	2.463526	0.077496

estimates, the results may be reliable indicators of total harvestable biomass. These survey results are similar to estimates derived using SCUBA and grab samples (Bearse 1976), indicating that the hydraulic dredge may provide reasonable density estimates. Medcof and Caddy (1971) reported an efficiency of over 90% for a commercial hydraulic dredge; there is considerable precedent for the use of dredge-type sampling devices in assessment surveys of commercially important marine bivalves (Saila et al. 1965; Russell 1972; Loesch 1974; Loesch and Ropes 1977; Murawski and Serchuk 1979a, 1979b).

Stratification of sample data into two classes, one of which contained only zero catch values, allowed measurement of the sample mean with relatively low variance. Aitchison (1955) noted that estimates of the sample mean derived in this manner can be best unbiased estimators, i.e., have minimum attainable variance. This approach also allows recognition of the fact that, in large scale surveys of marine organisms, areas of unsuitable habitat will necessarily contribute to a potentially high proportion of zero catches (Pennington, personal communication), resulting in highly skewed sample distributions.

Observations on the effect of sediment type on ocean quahog distribution indicate that density is highest in sediments containing high proportions of medium (0.25–0.49 mm) sand and shell fragments, and lowest in sediments containing a high silt/clay fraction or coarse sand-gravel. Stratification by sediment type may further increase the precision of population estimates for this species in areas where detailed substrate data are available.

Size-composition data for each depth interval generally were similar; no significant differences in mean shell length were detected. Estimated mean shell length for this survey was similar to that determined by Bearse (1976), off Rhode Island, based on *in situ* collections using SCUBA and grab samples, possibly indicating that small individuals were not a significant component of the population and that the potential bias of the selection characteristics of the dredge were minimized.

Shell length-meat weight regressions were similar to those derived for Rhode Island (Bearse 1976), and indicated higher meat yields than those predicted for the offshore waters of southern New England (Murawski and Serchuk 1979c).

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RESPONSE OF SOFT-SHELL CLAM (*MYA ARENARIA*) GROWTH TO ONSET AND ABATEMENT OF POLLUTION

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ABSTRACT Length-frequency analysis was used to generate age-length curves for six populations of the soft-shell clam *Mya arenaria* exposed to a sudden pollution event. Five populations were each subjected to a single oil spill. A sixth population was subjected to the onset and subsequent abatement of the effluent from a heavy metals mine. With one exception, the onset of pollution was accompanied by a noticeable break in the age-length curve representing a decrease in growth rate following the event. At the site where abatement occurred, the age-length curve showed a second break indicating resumption of near-normal growth. An attempt is made to relate severity and persistence of the pollution effect on growth to the degree of deflection in the age-length curve. A method that estimates prepollution growth is presented and applied to two populations.

INTRODUCTION

The need for more information on the effects of pollution in marine ecosystems has long been recognized. However, only recently has significant progress been made. Early investigators studied only acute lethal effects, and variability in the number and reliability of the methods involved led to much confusion (Hyland and Schneider 1976). With improving methodology there has been increased interest in chronic and sublethal effects (Anderson 1977). Coupled with this has been the realization that such research should concern itself with population processes rather than with individuals (Vanderhorst et al. 1978). Notable studies involving long-term monitoring of populations following a pollution event are those of the West Falmouth oil spill (Sanders et al. 1980), the Chedabucto Bay oil spill (Thomas 1978), and studies of pulp mill effects in Sweden (Rosenberg 1976). One major problem in studying the effects of a sudden environmental change is the availability of reliable control data from either measurements made prior to the change or from a suitable control area.

Recently, the status of soft-shell clam (*Mya arenaria*) populations and their relationship to various forms of pollution have been investigated (Brown et al. 1979). In this investigation samples were collected from several sites characterized by a sudden change in environmental quality due to onset or abatement of pollution. Growth was one of the parameters studied; the effect of each pollution event on growth obviously was of particular interest.

The primary purpose of this paper is to present age-length curves of soft-shell clam populations from sample sites where a pollution event occurred. Based on a few assumptions, these curves can be used to represent growth. This paper also shows that a sudden change in environmental quality resulting from the onset or abatement of pollution is reflected by a shift in the age-length curve. In addition, a method is presented whereby growth prior to a pollution event may be estimated.

METHODS

Clam growth was studied at six sites where a discrete pollution incident (either onset or abatement) occurred. Five of the sites were affected by spills of various types of oil. The sixth site was exposed to the effluent from an intertidal heavy metals mine. Table 1 lists the sampling sites, briefly characterizes each area, and provides estimates for the extent of polltuion.

Each site was sampled once with the exception of Searsport which was sampled quarterly in 1977 and 1978. Clams were dug with a standard clam hoe. All excavated clams were measured for length to the nearest millimeter using vernier calipers. For Searsport, length data for clams setting after the spill were obtained from Dow (1978, Table 2, p. 47), who used growth-ring measurements on live clams from the 1971 year-class.

Clams were aged using length-frequency analysis to obtain growth rates. The single exception was Goose Cove where shell-ring counts were used exclusively to age the clams. Length-frequency analysis was based on the assumption that modes in the length-frequency distribution represented different cohorts and that size was distributed normally within a cohort (Cassie 1954, Tanaka 1962, Tesch 1971). This assumption of normality was seldom exact because of stacking effects as growth decreased in larger individuals (van Sickle 1977), and because of size-dependent mortality, generally affecting the smaller members of each cohort. The degree of skewness introduced by these processes was assumed to be small. Because the interest was on relative shifts in the age-length curve rather than on the exact description of that curve, the consequences of skewness were rendered negligible.

Length-frequencies for each population were plotted at 1-mm intervals; modes on the resulting graph were broken down into a series of normal curves by the Peterson method using a Dupont 310 curve resolver, an analog computer which allowed the investigator to break down a complex

TABLE 1.

Description of sampling sites and estimate of magnitude of pollution at each site.

Area	Pollution Event	Date of Sampling	Hydrocarbon Concentration*	Sediment Characteristics	Pollution History
Basset's Island Red Brook Harbor Bourne, MA	No. 2 fuel oil spill from Brouchard No. 65, September 1974	5/12/76	11.4	Predominantly clean sand	Site initially covered by oil. Changing wind and current patterns eventually washed most oil out of area. Hampson and Moul (1977) reported some oil was still present in certain marsh areas, but little evidence of oil was found at sampling.
Wild Harbor North Falmouth, MA	West Falmouth oil spill No. 2 fuel oil and detergents from Florida, September 1969	5/ 3/77	47	Clean coarse sand	A sediment concentration of 590 μg/g (dry weight) was reported at Site II of Woods Hole Oceanographic Institute studies. Woods Hole site located up a tidal creek (Wild Harbor River) just below present sampling location. Later concentrations steadily declined reaching one third of initial value after 2 years (Sanders 1977).
Long Cove Searsport, ME	No. 2 fuel oil and JP-4† jet fuel spill, March 1971	4/15/77	58	Consolidated sand with silt and some gravel and	Located near innermost of three main culverts where oil entered the cove; equivalent to station 12 of Mayo et al. (1975) who found an initial concentration of 58 μg/g (dry weight). At adjacent stations 11 and 13 (Mayo et al. 1975) sampled the following year, the concentration had increased by an order of magnitude. Further contamination due to oil leaching from saturated sediments upslope.
Gleason Cove Perry, ME	Crude oil and detergents spill from Irving Oil Refinery, June 1974	8/15/78	11	Consolidated coarse sand and mud with rocks in a	Crude oil and detergents initially covered flat. Little evidence of contamination found at sampling.
Janvrin Lagoon Madame Island Chedabucto Bay, Nova Scotia, Canada	Chedabucto Bay oil spill, Bunker C oil from the Arrow, February 1970	7/18/78	38	Muddy sand with some rocks	Lagoon initially covered by 30 cm of oil. Much oil remained and periodically remobilizes. Measurements taken 6 years later by Thomas (1978) and by Gilfillan and Vandermeulen (1978) showed average concentrations at thousands of μg/g (dry weight). However, these measurements tended to vary by four orders of magnitude. At sampling, oil was still abundant and a slick would form on any depression made on the flat.
Goose Cove Harborside, ME	Effluent from a settling pond of a heavy metals mine, 1969–1972	7/20/76	--	Coarse sand to very consolidated sand with rock and shell in a patchy distribution	During mine operations, record levels of eight metals (Mn 341, Cd 1.7, Cr 29.5, Ni 4.1, Zn 195, Pb 55, Fe 2471, Co 1.5 ppm), and extremely high Cu levels were found in soft-shell clams near outflow. Levels typically ranged one to two orders of magnitude above those found in control clams (Dow and Hurst 1972).

*All hydrocarbon concentrations were for sediment (μg/g dry weight by gas chromophotography). Samples were taken at the time of clam collection. (Source: C. Brown, University of Rhode Island, Kingston, RI, personal communication).

†Originally reported as JP-5 (Gilfillan et al. 1977).

envelope into its basic components (in this case normal curves) in a graphical fashion. It utilized 10-function generator channels each capable of generating a normal curve on a cathode-ray tube. The images of those curves could then be projected onto a length-frequency histogram. The histogram was broken down from left-to-right (young-to-old) in the following manner.

One channel was switched on and the projected curve was positioned such that its location, width, and height corresponded to the left edge of the histogram. The remainder of the histogram was then resolved by successively turning on the channels and positioning them such that the envelope projected (formed by the summation of the outputs of all the "on" channels) matched the outline of the histogram. The optical output gave the observer immediate feedback, and repeated trials could be made quickly by varying size, shape, position, and number of curves until a reasonable "fit" to the data had been obtained. At that point, the output of each channel could be turned on and displayed independently, and its projection traced on the histogram. The result of this process is exemplified in Figure 1.

From the resulting graphs, mean and standard deviations of each distribution were obtained (Macdonald and Pitcher 1979). The mean occurred at the peak; the standard deviation was the half width at 61% of the height (Figure 1, curve 4). The curve resolver was equipped with an integrator enabling the investigator to obtain the percentage of the whole sample under each component curve.

Ages were assigned to each cohort (Brothers 1979) by inspecting the histograms and subsequent age-length curves, and taking into consideration local recruitment processes and sampling efficiency. These results were corroborated by comparing them to previously published age-length data for the same or nearby areas (e.g., Belding 1930, Dow 1978, Appeldoorn 1980). Additional corroboration was sought for the Searsport sample by using annual shell-ring counts on a subsample of clams to develop a rough age-length key.

The ages assigned were relative rather than absolute where the time beyond the least yearly increment represented the percent of expected yearly growth already obtained. Hypothetically, if a clam first set in the beginning of April and was collected in November, 3 years later, its relative age would be 4 rather than 3.6 because it no longer would be

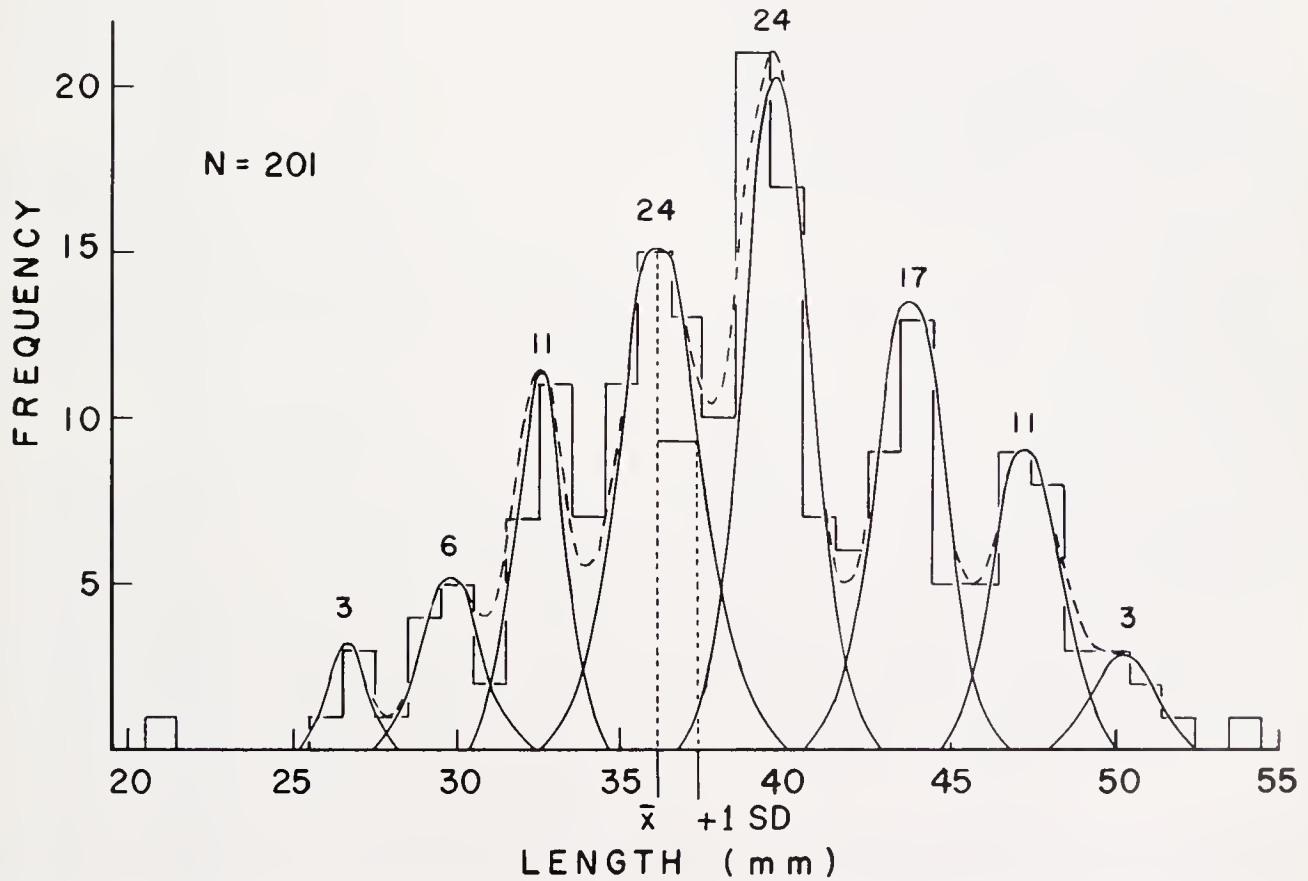

Figure 1. Length-frequency histogram for Janvrin Lagoon with superimposed distributions for each age group as determined with the curve resolver. Solid curves represent age groups. Dashed curves represent the total fitted envelope. The mean plus one standard deviation (SD) are shown for the fourth curve. Numbers above the curve represent the percentage of the sample under each curve, respectively.

expected to grow significantly during the rest of its third year. The size obtained by November would equal roughly its size at age 4. This process resulted in a smoother growth curve since it avoided the problems of seasonal variations in the growth rate which would otherwise necessitate the use of a more complex growth model (Cloern and Nichols 1978).

For three sites, West Falmouth, Searsport, and Janvrin Lagoon, sufficient numbers of year classes were represented to allow a von Bertalanffy growth curve to be fitted to the data (von Bertalanffy 1938). Only postspill age classes were used to fit the curve which reduced the number of points available for analysis. The growth curve was fitted by nonlinear regression according to Gallucci and Quinn (1979) using the NLIN procedure of SAS 76 (Barr et al. 1976). This procedure yielded estimates of the parameters for the von Bertalanffy growth equation:

$$L = L_\infty \left\{ 1 - \exp\left[-K\,(t - t_0)\right] \right\}$$

where t = time, L = length at time t, L_∞ = maximum asymptotic length, K = growth constant, and t_0 = time when L = 0.

Using the calculated von Bertalanffy curve, the growth rate prior to pollution was estimated. This analysis was based on the assumption that growth followed a fixed schedule or pattern. Growth prior to pollution may be different (i.e., have its own growth schedule) from growth after pollution. It was assumed that the postpollution growth schedule was adequately modeled by the calculated von Bertalanffy curve. The prepollution growth schedule was then approximated in the following manner.

The length (L_1) was found of the last year-class to set prior to pollution. Then the age was determined corresponding to that length on the von Bertalanffy curve. One year was subtracted from that age and its corresponding length (L_2) was determined on the growth curve. Next the length (L_3) was found corresponding to an age equal to age at $L_1 - 1$. The difference between L_2 and L_3 represented the extra growth experienced by clams having one year of growth on the prepollution growth schedule. That difference was then added to the expected length at year one on the postpollution curve (von Bertalanffy curve) to obtain the expected length at year one on the prepollution curve. The second point on the prepollution schedule was found by applying the above procedure to the year class that had set 2 years prior to pollution. That process was repeated for all available prepollution year classes.

RESULTS

Mean length and standard deviation are shown in Table 2 for each age group per site as obtained from the length-frequency analysis. These data are plotted in Figures 2 through 7. The calculated von Bertalanffy curves for West Falmouth, Searsport, and Janvrin Lagoon, are also plotted; parameters for those curves are given in Table 3. Prepollution growth approximations for Searsport and Janvrin Lagoon also are plotted. For the remaining three areas, approximate curves have been drawn "by eye" to smooth out the age-length relationship and to accentuate its change following a pollution event.

These figures demonstrate that changes in the incidence of pollution were reflected by changes in the growth rate. Only West Falmouth failed to show a significant change. Breaks in the curves clearly indicate that pollution has had an adverse effect on growth, and they also reflect the degree to which growth had been reduced. Growth was severely affected at Searsport, Janvrin Lagoon, and at Goose Cove. At Goose Cove growth improved following pollution abatement. At West Falmouth the lengths of the year classes existing prior to the spill failed to differ significantly from the lengths expected on the basis of postspill growth. It appears that the spill had no drastic effect on growth of clams from the collection site.

For comparison purposes, the age-length determinations for Potato Island (Appeldoorn 1980) are plotted in Figure 2. That area was used as a control site by Thomas (1978), and by Gilfillan and Vandermeulen (1978) in their studies of Chedabucto Bay. In the latter study, it was reported that soft-shell clam growth at Janvrin Lagoon and Potato Island were similar prior to the spill. The estimate of prespill growth calculated in this study agrees remarkably well with the age-length determinations for Potato Island.

The parameters of the von Bertalanffy curve for Searsport appear anomolous in comparison to the other values shown in Table 4. That probably resulted from sampling errors (note the standard deviations in Table 3) associated with a small sample size (N = 15), and from successive improvements in postspill growing conditions. The latter would tend to increase the initial slope of the age-length curve, thereby increasing K.

DISCUSSION

The problems inherently associated with the estimation of population age structure and growth through length-frequency analysis were reviewed by Brothers (1979), Macdonald and Pitcher 1979), and others. A reiteration of those problems is not necessary here. It should be pointed out, however, that the growth measured herein is for a cohort of the population and not for individuals (see Ricker 1975, pp. 217–218). The difference between the two arises because the older modes in the length-frequency histogram usually are composed of slower growing individuals. Gerking (1957) has shown for fish that rapidly growing individuals tend to mature, become senile, and die, earlier than slower growing individuals. In general, for *Mya arenaria*, an inverse relationship has been found between longevity and the rate of growth (Newcombe 1936), i.e., older clams are slow growers. A good example has been shown by Dow (1978) for clams growing at Searsport. As clams grow their burrow

TABLE 2.

Mean length and standard deviation as determined by length-frequency analysis for sample population at six sites.

Age (yr)	Length (mm)	Standard Deviation	Sample (%)
	Basset's Island, Bourne, MA (N = 187)		
1.15	22.7	2.2	8
2.15	30.6	2.4	5
3.15	40.8	2.4	14
4.15	48.2	2.3	27
5.15	54.4	1.3	10
6.15	58.9	1.5	9
7.15	64.3	2.1	12
8.15	70.5	1.3	8
9.15	75.7	2.0	3
	West Falmouth, MA (N = 183)		
1.15	28.6	2.6	9
2.15	38.8	2.6	3
3.15	45.2	1.5	2
4.15	53.3	2.9	27
5.15	61.6	1.5	8
6.15	68.2	1.9	20
7.15	73.4	1.7	7
8.15	78.8	1.4	5
9.15	84.5	2.6	1
	Goose Cove, Harborside, ME (N = 101)[1]		
3	24.1	1.9	7
4	34.3	3.8	12
5	36.4	4.1	25
6	39.6	3.2	23
7	46.6	9.8	5
8	47.7	17.2	17
9	55.2	6.9	6
10	61.5	2.1	2
11	59.5	5.8	4
	Janvrin Lagoon, Nova Scotia, Canada (N = 201)		
3.5	21.0		0.5
4.5	26.7	0.7	3
5.5	29.9	0.9	6
6.5	32.6	0.8	11
7.5	36.2	1.3	24
8.5	39.7	1.0	24
9.5	43.8	1.0	17
10.5	47.4	1.0	11
11.5	50.3	1.0	3
12.5	54.0		0.5
	Long Cove, Searsport, ME (N = 152)[2]		
1	10.0	3.0	
2	18.3	3.7	
3	24.9	3.7	
4	31.1	4.2	
5	34.4	4.5	
6.2	38.0	0.6	2
7.2	41.5	1.4	3
8.2	44.9	1.0	6
9.2	47.2	0.6	5
10.2	49.9	1.0	14
11.2	53.0	1.2	15
12.2	55.3	0.7	11
13.2	57.0	0.8	10
14.2	59.0	0.9	18
	Gleason Cove, Perry, ME (N = 180)		
3.67	36.4	1.5	3
4.67	41.1	1.5	11
5.67	47.1	1.8	29
6.67	55.2	2.3	46
7.67	62.3	0.8	5
8.67	66.9	0.8	3
9.67	70.9	1.9	3

[1] Ages determined by counting shell rings.
[2] First five year-classes from Dow (1978).

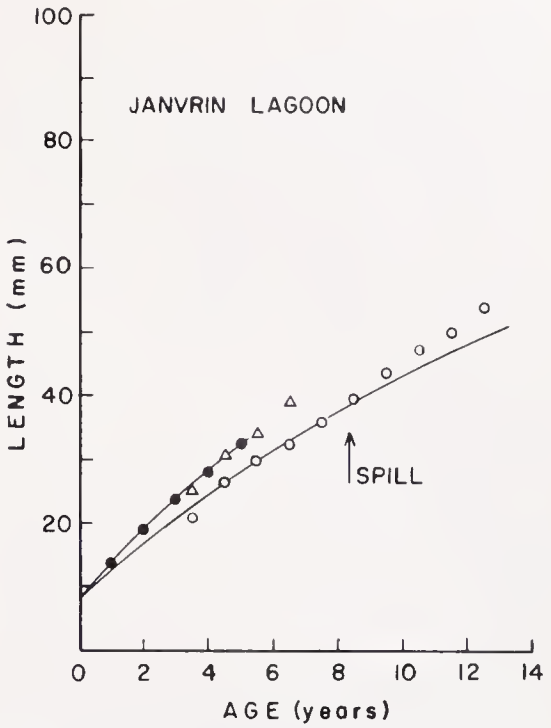

Figure 2. Age-length curve for Janvrin Lagoon, Nova Scotia, Canada. Open circles: mean length at age for each age-class. Closed circles: calculated estimates for mean length at age prior to spill. Triangles: mean length at age for Potato Island, a control site. Lower line: postspill growth predicted by the von Bertalanffy equation. Upper line: prespill growth and was drawn by eye.

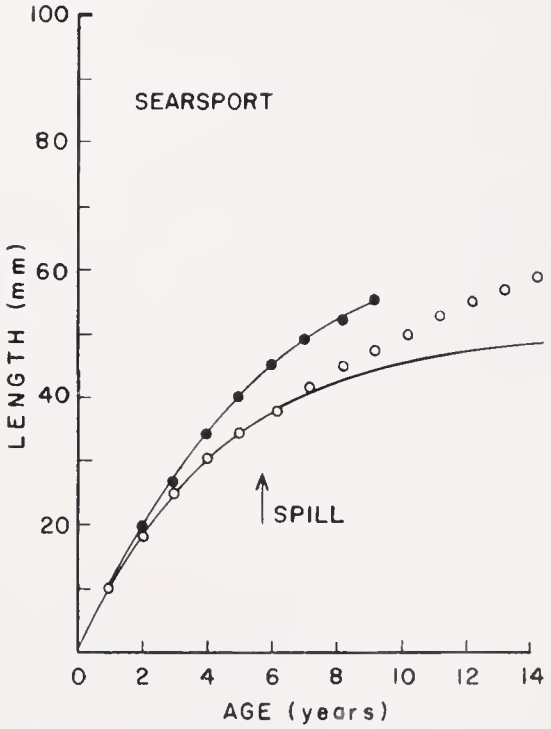

Figure 3. Age-length curve for Long Cove, Searsport, ME. (All symbols as in Figure 2.)

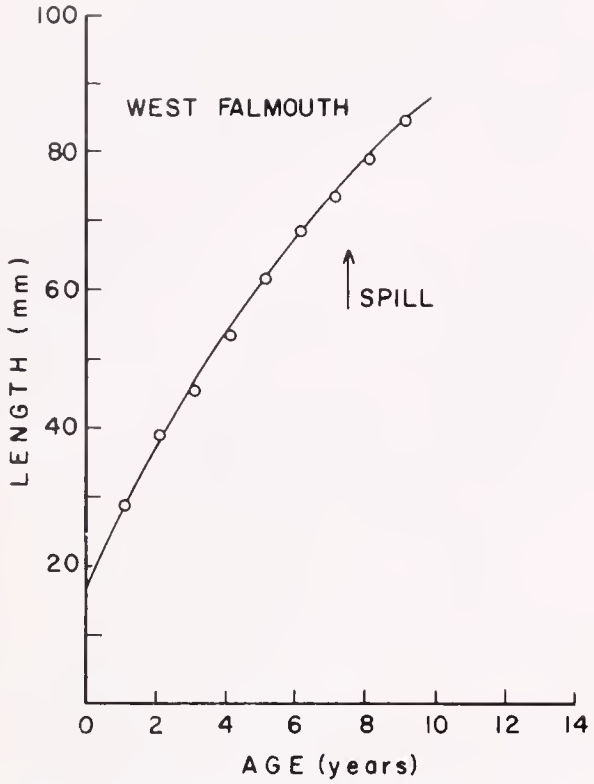

Figure 4. Age-length curve for West Falmouth, MA. (All symbols as in Figure 2.)

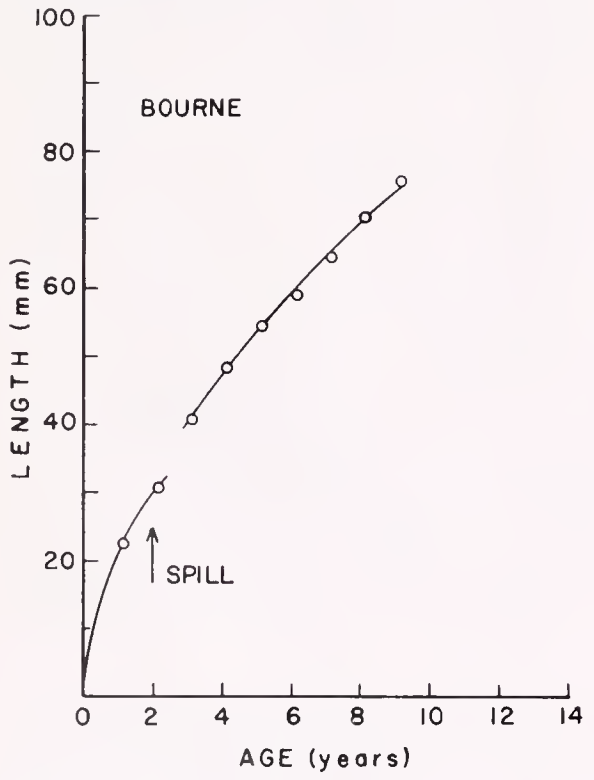

Figure 5. Age-length curve for Basset's Island, Bourne, MA. Circles: as in Figure 2. Solid line: age-length relationship (drawn by eye).

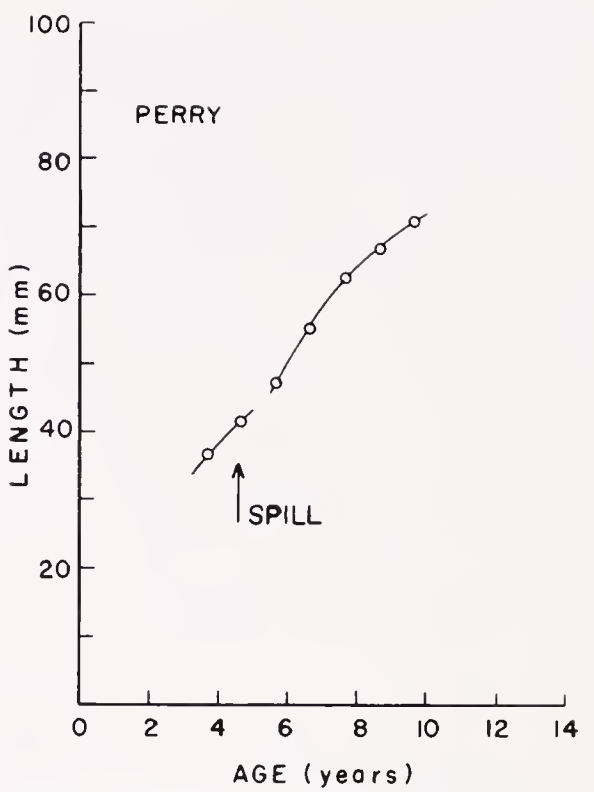

Figure 6. Age-length curve for Gleason Cove, Perry, ME. Circles: as in Figure 2. Solid line: age-length relationship (drawn by eye).

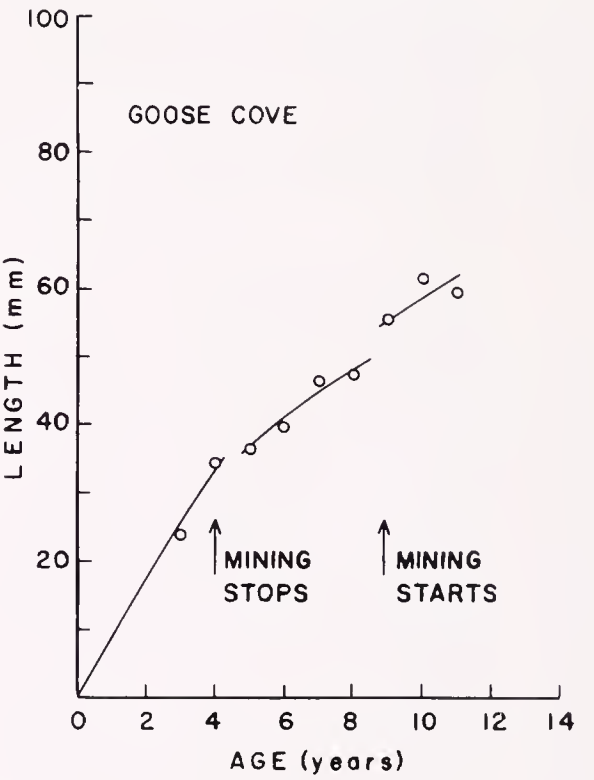

Figure 7. Age-length curve for Goose Cove, ME. Circles: as in Figure 2. Solid line: age-length relationship (drawn by eye).

TABLE 4.

Parameters for von Bertalanffy growth equation fitted to postspill age classes of soft-shell clams from three areas.

Area	K	L_∞	t_o
West Falmouth, MA	0.0917	136.73	−1.357
Janvrin Lagoon, Nova Scotia, Can.	0.0575	88.74	−1.622
Searsport, ME	0.2358	50.48	0.074

depth increases. Faster growing clams were penetrating the buried stratum of oil-polluted sediment at an earlier age whereup mortality occurred. Hence, only the slower growing individuals survived; they now constitute the bulk of the older age groups in the population.

The assumption that clams grow according to a fixed schedule (especially after a pollution incident) probably is not valid. For example, Dow (1978) has shown successive improvements in growth of *M. arenaria* for each year-class following the Searsport oil spill. This was due to both the further weathering of the oil, and the further deposition of clean sediment over the oil-contaminated sediment. However, at Searsport and at Janvrin Lagoon postspill recovery has been slow enough to allow the use of the von Bertalanffy curve to generate prespill growth estimates. Since only approximate growth estimates have been obtained, no effort was made to apply rigorous statistical analysis to the data.

The results show that there was a response in the growth rate to environmental changes caused by pollution. That response was characterized by a noticeable break in the age-length curve. In each case the onset of pollution was coupled with a reduction in growth. The exact mechanisms for the observed growth reductions at each site are unknown. The volume of literature on the effects of pollution on marine organisms in general, and on bivalves in particular, is vast but it is still difficult to relate specific effects in the laboratory to responses observed in the field.

Other field studies of *M. arenaria* have shown that the onset of oil pollution generally was followed by a reduction in growth and an increase in mortality. Dow (1975) found a 65% reduction in annual growth rate of clams transplanted to a site polluted with Iranian crude oil. At Searsport, Dow (1978) reported a reduction in growth of soft-shell clams following the spill. Mortality at Searsport greatly increased when clams burrowed into oiled sediment indicating either a direct toxic effect or smothering (Dow and Hurst 1975, Dow 1978). Smothering was considered the main cause of the large soft-shell clam mortality following the spill of Bunker C oil at Chedabucto Bay (Thomas 1973). Gilfillan and Vandermeulen (1978) found a reduced carbon flux in soft-shell clams from Janvrin Lagoon as compared to Potato Island. This was coupled with a calculated reduction in the rate of shell growth in Janvrin Lagoon clams following the spill. In an earlier study, Gilfillan et al. (1976) found a 50% reduction in the carbon flux of soft-shell clams polluted by No. 6 fuel oil. They concluded that for bivalves a reduction in the assimilation ratio was a general response to environmental stress which could be triggered by a number of factors including pollution.

The age-length curve for West Falmouth failed to show a break at the time of the spill. There are two possible explanations for this. First, because sampling took place 8 years after the spill, it could be possible that the sample age masked any true effect. Only 6% of the sample consisted of clams that had set prior to the spill. Such a small sample size could have led to underestimation of the mean lengths for each age class.

Second, the curve could accurately reflect the true effect of the spill on growth. While this may be true, studies made after the spill indicated initially severe effects. Blumer et al. (1970) reported numerous mortalities among the benthos, including shellfish, immediately following the spill. Site II particularly was devastated (Sanders 1978); high concentrations of hydrocarbons were found in shellfish from the tidal creek (Blumer et al. 1970) one month after the spill. It seems unlikely, then, that clam growth would have remained unaffected. With improving conditions, however, any effect might become unnoticeable. Sediment oil concentrations at Site II decreased steadily over time reaching 140 μg/g after 2 years, only twice the level reported for indigenous sedimentary hydrocarbons within the area (Blumer and Sass 1972). The degree of this decrease may be attributable to sediment characteristics at the sampling site. Loose, coarse, shifting sand should facilitate rapid depuration or burial of the oil; therefore, growth may have been affected only during the first few years. Significantly improving conditions invalidate the assumption of a fixed postspill growth schedule. Hence, the von Bertalanffy curve cannot be expected to approximate the growth of an affected population. With the sampling problems mentioned above, and the 8-year time lag between sampling and the spill, any initial effect on growth now would be undetectable by the methods used. The West Falmouth situation differed from both the Bourne and the Perry sites, where little oil was found when sampled shortly after the spill, and the Searsport and Janvrin Lagoon sites, which were sampled several years after contamination but still contained enough oil to affect growth adversely.

Mining operations at Goose Cove could have led to a reduction in growth via three mechanisms: siltation, food destruction, and direct heavy metal toxicity. Dow and Hurst (1972) suggested that much of the damage caused by the mining operations resulted from heavy siltation and smothering. These would definitely interfere with feeding by clogging the gills of the clams. They also reported that the mine effluent was highly toxic to phytoplankton, the main food source for soft-shell clams, and that alone could contribute to malnutrition and starvation. Eisler (1977) reported that *M. arenaria* was susceptable to heavy metal

contamination. Many of the metal concentrations reported by Dow and Hurst (1972) were higher than the lethally toxic concentrations found in bioassay studies dealing with pure (Eisler and Hennekey 1977) and mixed (Eisler 1977) metal solutions. Conditions in the field and laboratory differed significantly, thus, the observations were not directly comparable, but it was evident that the levels found at Goose Cove were relatively high.

Concentrations of metals in soft-shell clams at Goose Cove were still high at the time of sampling, 4 years after mining operations had ceased (L. Fink, University of Maine, Walpole, personal communication). It can be seen from the graph in Figure 7 that growth improved following pollution abatement, although it did not return to its original rate. If starvation and smothering were major factors contributing to reduced growth, then growth should have improved dramatically upon cessation of mining activities. This could have been the case; however, the exact degree of recovery was difficult to assess because of variability of the data. These observations showed that smothering and starvation were major factors working in conjunction with direct toxicity to reduce growth during the period of mining operations. In addition, to some extent, it appeared that growth was still being affected adversely at the time of sampling perhaps because of direct toxic effects.

The pronounced growth reduction at Goose Cove can be attributed to (1) the variety of ways in which the mining effluent affected the clams, and (2) the constant output of effluent during mining operations. Once mining operations ceased, recovery was fairly rapid. This was in contrast to growth recovery at oil-polluted sites, and reflected the persistence of oil remaining in the sediment, and the different mechanisms by which oil and mining effluents affect clams. Major contributing factors to reduced growth at Goose Cove, such as siltation and food reduction, were removed after mining operations ceased. On the other hand, oil itself is a major factor in growth reduction. Oil can be taken in through the siphons (Fong 1976), and oil leaching from saturated sediments following a spill can result in a contaminated water supply for an extended period of time (Mayo et al. 1975). Because oil can be detrimental upon contact (Dow 1978), the effects of a spill can persist after burial of the oiled sediment. In addition, Vandermeulen (1977), and Vandermeulen and Penrose (1978) found that significant quantities (40%) of oil remained in polluted soft-shell clams following a 3-month exposure to clean water. All of those factors contributed to the persistance of a growth reduction effect following initial hydrocarbon contamination.

Some areas sampled, though, did show signs of recovery. No break in the age-length curve was observed at West Falmouth as discussed earlier. Bourne seems to be a similar case. Little evidence of oil was found at the time of sampling, and the break in the curve (Figure 5) appears like a short depression in an otherwise normal growth curve. This would indicate that growth was disrupted only for a short period of time, on the order of a few years.

The techniques used here are considered valuable in assessing pollution effects. Primarily they are useful in detecting gross responses in growth due to changes in environmental quality and they allow estimation of prepollution growth. This is helpful because measurements taken prior to a pollution event are rare and usually fortuitous. A number of studies have used shell-growth bands to monitor, in detail, subtle environmental changes (e.g., Kennish and Olsson 1975). However, these techniques are limited in their application and the methods are involved and costly. The techniques used here sacrifice detail but have more general applicability. For example, by using these techniques, studies are possible of *M arenaria* populations south of Cape Cod where annual ring formation is unreliable (Mead and Barnes 1904, Shuster 1951). The responses observed only directly reflect the effects on growth. They do not directly reflect changes in mortality, settlement, or population age structure. As was observed at Searsport, however, continued size-dependent mortality may indirectly affect the resulting growth curve.

ACKNOWLEDGMENTS

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RECENT ADVANCES IN HARD CLAM MARICULTURE[1]

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ABSTRACT Failure to develop a satisfactory method of hard clam aquaculture, despite about 70 years of research, may be based on faulty premises. There is no problem raising hard clams to market size under artificial conditions provided adequate attention is given to care and to cleanliness. The only impediment is cost, which under present methods is too high for economic gain. The flaw may be reliance on small numbers of clams, thinking millions are sufficient when billions may be required to smother predation.

Another flaw may be lack of adequate law enforcement. Grounds must be patrolled constantly to keep out violators. That means adequate coverage 24 hours a day, 7 days a week, and 365 days a year. It also means adequate support in the courts so that the penalty for being caught is not worth the risk.

Experimental management of the grounds might be a better method. An area could be divided into three parts, keeping one open and two closed—rotating the closed areas each year. If enforced adequately that would give sufficient protection to seed clams, and the management plan could be adjusted accordingly as knowledge accumulates of local conditions.

INTRODUCTION

Interest in the possibility of growing hard clams (*Mercenaria mercenaria*) artificially has been evident in this country for at least 70 years. Shortly after the turn of the century, Belding (1909) advocated mariculture as a means of halting overfishing and increasing the supply of clams. Kellogg (1910) also believed that mariculture was the answer. Beginning in the late 1930s, Loosanoff and Davis (1949, 1963), and their associates believed that mariculture was feasible, and they developed many of the techniques on which present-day artificial propagation is based. Carson (1945) said that the fishery could be greatly developed by extensive farming. Since that time many people have toyed with the idea that artificial production of clams is feasible; but to date I am not aware of any enterprise operating on a consistently profitable basis. If it was, one would think that such procedures would be routine by now, and that substantial quantities of the hard-clam catch would be produced by artificial means. But they are not.

What is the problem? Were the early enthusiasts too optimistic in their views? Were there unexpected difficulties not anticipated at first? Has development proceeded too haphazardly, failing to capitalize upon earlier breakthroughs or failures? Which of those or other circumstances have interfered with success? What are the prospects for the future?

STATUS OF KNOWLEDGE

It is not necessary to go into great detail to show that there is no insuperable handicap to rearing hard clams under artificial conditions from fertilization of the egg to metamorphosis, or to market size. Environmental conditions are known; food requirements are understood; disease can be controlled; and growth and survival are more than adequate. The chief problem is the cost of doing all those things. Production under artificial conditions to market size is simply not financially feasible, even though growth under ideal conditions can be several times faster than natural, and survival is much greater.

Large quantities of eggs can be raised to metamorphosis at acceptable cost, and some growth of young also is possible. But at some stage, well before commercial size is reached, juveniles must be transferred to the natural environment if costs are to be held down. At the juvenile stage, clams are highly vulnerable to predators, of which there are many, and not enough survive to make the operation cost effective.

Mike Castagna, of Chincoteague Bay, has come closest to solving that problem. He plants early juveniles in beds covered with an appropriate layer of crushed stone aggregate or other suitable material, provides baffles to cut down the disturbing action of waves, and also fences to keep out larger predators. He has been able to produce market-size clams at a cost of about 2.2 cents each (in 1976 dollars [Castagna and Kraeuter 1976]). That appears to be well within the economic feasibility of clam growing, especially since young clams are the most valuable and can be brought to market size in about two years. Yet, despite this apparent advantage there is no evidence that people in the industry are rushing to try the method. In fact, it has been tried in other places but with only limited success.

More recently, MacKenzie (1979) proposed that predation could be controlled easily by removing predators mechanically and at a reasonable cost. His method seems so simple that it is difficult to believe it is not already standard procedure. MacKenzie pointed out that the method must be demonstrated, must clearly be beneficial, that political support must be stimulated, and that clam-production specialists must guide the program until it is working properly. In addition, MacKenzie suggested that other

[1] The studies on which this paper is based were supported by grants from the New York Sea Grant Institute and the National Oceanic and Atmospheric Administration, United States Department of Commerce.

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regulations including adequate protection of undersize clams must be continued, which could be the least workable portion of his method.

ENFORCEMENT

Enforcement of laws (or rather the lack of enforcement) could be one reason for failure of all clam-management plans. We cannot be sure of the reasons in other states, but in New York there certainly is reason to doubt that laws are being observed or enforced. It is most important that the minimum size law, especially, be rigidly observed because the basis of a clam-management plan is to assure an adequate nucleus of spawners to provide recruitment of new stocks. The present minimum size limit of one inch across the valves probably is satisfactory. A sizable take of clams less than one inch could have serious effects because the numbers of eggs produced would drop rapidly. In 1976, when the catch was only about 63% or less of the maximum, the lack of adequate law enforcement at the present time could seriously reduce the available brood stock.

In Great South Bay, where most of New York's clam production is made, very few clams survive beyond littleneck stage because harvesting is so intense (Greene 1978). When production declines as it has in Great South Bay, and when prices are high, there is considerable incentive to ignore the cull law especially if law enforcement is inadequate. There is no doubt regarding the laxity of present enforcement (Mirchel 1980). Even if the laws are being applied well at the harbormaster level, judges are notably easy on violators, and may often reduce charges to lesser levels. It is not much of a deterrent to a violator if he pays $25 for the privilege of taking $100 or $200 or more worth of clams when there is a reasonably good chance he may get away with it altogether.

DIFFERENCES BETWEEN MAJOR CLAM SPECIES

The decline in clam landings of the major species has not been significantly different. Hard-clam landings have dropped from almost 20 million pounds in 1947, to about 7.2 million in 1979, a decline of about 63.9% (Figure 1). Soft-clam landings have dropped from about 17.4 million in 1939, to about 8.3 million in 1979, a drop of about 52.4% (Figure 2). Surf-clam landings have dropped from about 96.1 million pounds in 1974, to 33.7 million pounds in 1979, a drop of about 65% (Figure 3).

The main difference is the time it took to decline by those amounts. Surf-clam landings took only five years to show a decline. Surf-clam fishery history is shorter than the other clam fisheries, not beginning as a major fishery until after World War II. The hard- and soft-clam fisheries are much older. Despite their apparently greater vulnerability, they have taken much longer to decline from their peaks—hard clam: 32 years, and soft clam: 40 years. Intuition would suggest that just the opposite should have taken place. Easily accessible in nearshore shallow waters, hard and soft clams are taken with relatively inexpensive gear and boats, are considerably more vulnerable to pollution, and are subject to violation of laws, all of which would tend to indicate that they would also decline more quickly. That obviously was not so, and the question arises, why? An answer to that question might help to correct some management problems; but the answer is not clear. It is possible that restrictions on inshore clamming, which some biologists and others have criticized as being unnecessary, have actually helped. For example, hard- and soft-clams cannot be taken with mechanical devices in most places. They must be harvested with tongs, rakes, or by hand. Nonmechanical harvesting is relatively easy on the bottom and usually does not break large numbers of clams. Heavy dredges, however, used on surf clams may break large numbers of clams, especially young clams. Dredges may also bury large numbers of young, thus effectively destroying much of the recruitment that otherwise could be available.

That difference is largely one of degree, however. Although they have declined more slowly, hard and soft clams also

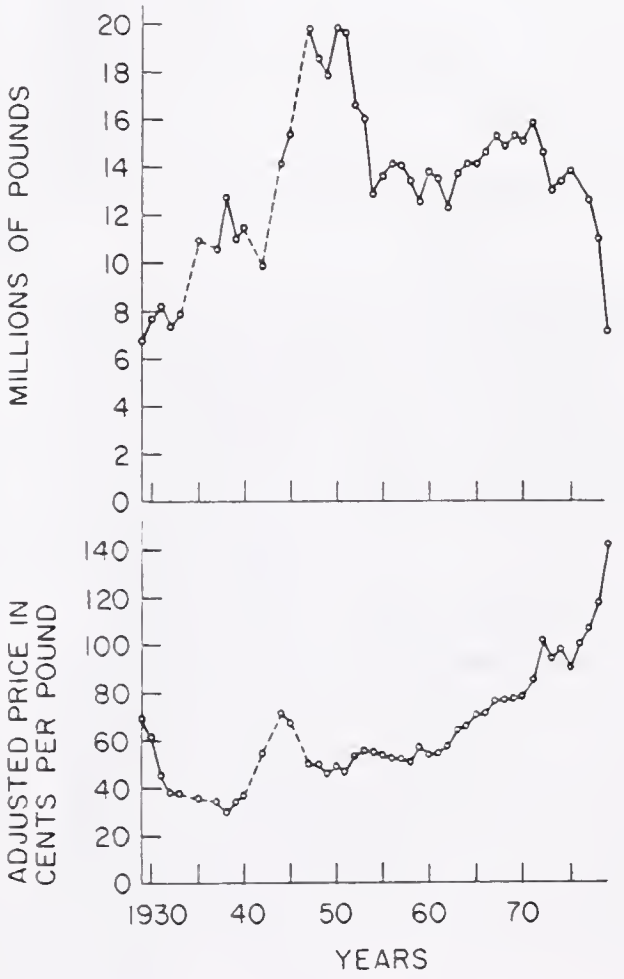

Figure 1 Commercial catch of hard clam *Mercenaria mercenaria* along the Atlantic coast from 1929 to 1979, and the total value to fishermen (adjusted by the consumer price index for all products).

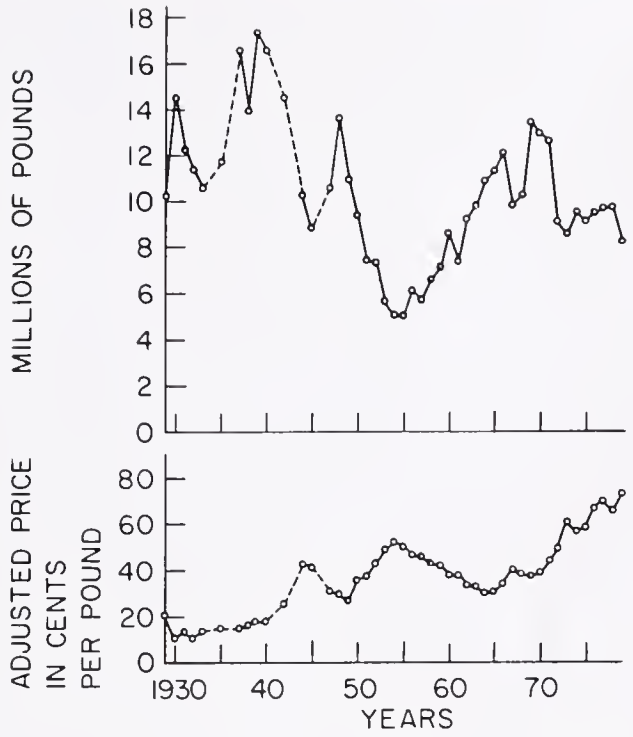

Figure 2. Commercial catch of soft clam *Mya arenaria* along the Atlantic coast from 1929 to 1979, and the total value to fishermen (adjusted by the consumer price index for all products).

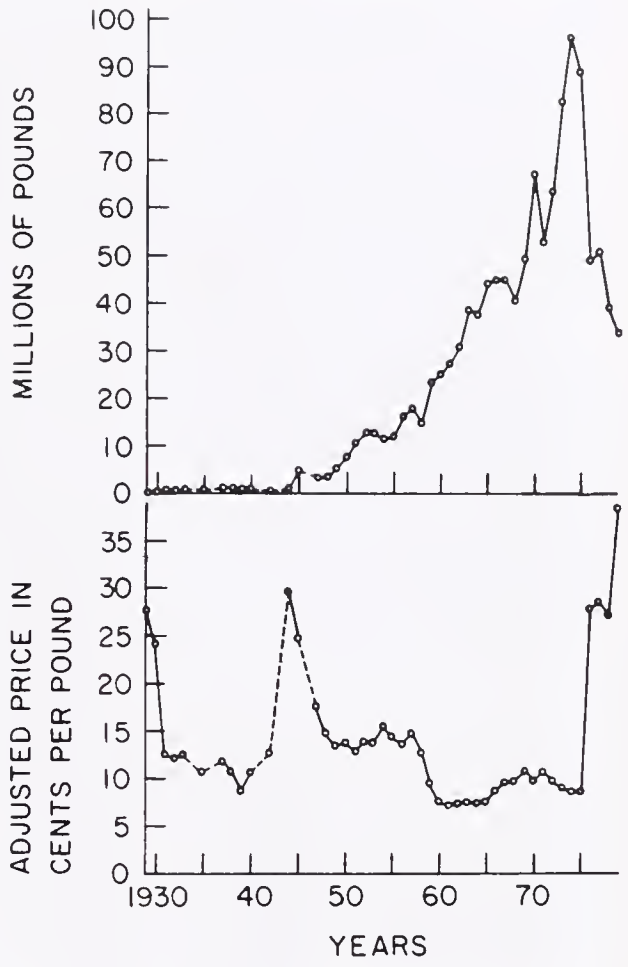

Figure 3. Commercial catch of surf clam *Spisula solidissima* along the Atlantic coast from 1929 to 1979, and the total value to fishermen (adjusted by the consumer price index for all products).

have declined to less than half their peak levels. Hard clam is seriously reduced in Great South Bay where it is more abundant than anywhere else. There is no sign that the situation will improve. Although the adjusted total value of the hard-clam catch reached a peak in 1945, it did not rise as high again until 1966. It reached an all-time peak in 1972, and since that time has dropped to below the 1945 level. The adjusted total value of the soft-clam catch rose to a peak in 1944, and did not rise as high again until 1969. The catch reached an all-time high in 1977, and since has dropped slightly to about 93% of the 1977 level. It is still considerably higher than in 1944. The adjusted total value of the surf-clam catch reached a peak in 1977, and has since dropped to about 60% of that level. What is the best strategy for improving hard-clam production?

HARD-CLAM MARICULTURE

Apparently the bottleneck in growing hard clams under artificial conditions lies somewhere between metamorphosis and market size. Perhaps 4 or 5 mm is the lower limit, and somewhere between 15 mm and 25 mm (about one inch) is the upper limit. Within those size limits, costs are too great to continue rearing clams in captivity, but clams that size also are highly vulnerable to predation. It is not clear if Castagna's method of growing juvenile clams under aggregate with louvers and fences would be practical on a large scale or applicable in different environments. People have tried various methods in many places, but none have perfected a reliable, replicable method. In fact, most experiments have resulted in total failure. The reason for these failures may be very simple and may represent a fatal flaw in thinking. It simply may be that the numbers of clams used are so small that the odds of having survivors are minimal. Let us examine that possibility.

The largest number of seed clams produced in hatcheries at the present is between 250 and 500 million. As far as I have been able to determine, the greatest number of clams planted in one place in the natural environment was about 20 million. That sounds like a large number of clams, but is it really? Considering the number of eggs produced per clam, it is not. The largest figure, 500 million, could be produced by about 167 littlenecks or by about 83 cherrystone clams according to figures carefully worked out by Bricelj (1979). Those are not impressively large numbers. Allowing a 20% mortality rate in the period from fertilization to metamorphosis, that would only increase those numbers five times.

Another way of looking at it would be to consider a small section from the bottom of Great South Bay; for

example, the Town of Islip's portion has about 20,000 acres. Density of clams on the bottom varies greatly, but 4,750 clams per square meter appears to be about maximum for small clams, and 160 clams per square meter for adults. Over a large area containing various types of bottom, the number of clams per square meter could be much less; perhaps averaging one clam per square foot. For 20,000 acres, that would be about 870 million clams or an average of about 54 bushels per acre, which is probably not far from the true figure. If 20 million, 5-mm clams were planted, it could be expected that predators would destroy at least 99 out of 100 the first year, leaving 200,000 clams. At a conservative estimate, 50% of the first-year clams would be destroyed during the second year, leaving 100,000. Only under ideal conditions would those clams be large enough to harvest at the end of the second year. That is only $(1 \times 10^5)/(870 \times 10^6)$ or 1 in 8,710 clams, again hardly a large amount. If predators were present at the time of planting and began eating immediately, they easily could eat large numbers before the clams could dig in, thus reducing the final yield further. If the clams must remain on the bottom longer to grow to market size, the yield would be less again. It appears that very large quantities of small clams would have to be planted to assure an adequate supply for harvesting. At present no hatchery is raising the numbers of clams necessary to exceed the capacity of predators to eat them all, except perhaps in special areas where predators are low in abundance or absent. The very fact of supplying additional small clams, which are placed on the bottom unprotected and must dig in, probably increases the likelihood that predators will be there the next time.

Another way of looking at it is to consider the standing crops of clams in a polluted area of similar characteristics, say the New York portion of the Raritan Bay complex. Campbell (1967) calculated that the standing crop in that area was 291,200 bushels of littlenecks and 3,153,000 bushels of large clams, or 1.05 clams per square foot. On the 20,000 acres of bottom in Great South Bay, Town of Islip, that would equal 915 million clams. At 6 million eggs per clam, that would total roughly 5.5×10^{15} eggs. The logistics of producing enough clams to add significantly to that enormous basic production appears obvious. Our sights must be raised considerably if we are to surpass natural production.

The same can be said of the prevalent practice of bringing in spawners from colder areas to extend the spawning season and, thereby, to increase the odds that significant numbers of eggs will survive. The impact of 1- or 2,000 bushels of spawners is likely to be insignificant as compared with the spawning potential of the clams already there. The cost of bringing in enough spawners in good condition to have an impact appears to be prohibitive, and the only benefit of the present practice is to satisfy certain believers, thus buying time for other more promising activities.

CAN OPTIMUM YIELDS BE PRESERVED?

If yields cannot be improved economically by aquaculture, what, if anything, can be done to at least preserve present yields, and to possibly improve them to some extent? The situation does not appear to be entirely hopeless, even though on the average yields have been dropping for a long time. The most effective way might be to experiment with managing clam populations to find out what level of density on the bottom would sustain the best harvest and, perhaps, also what sizes of clams. One way to do that would be to establish an arbitrary limit below which a ground should not be allowed to deteriorate. Just for the sake of argument, the limit might be set at 30 bushels per acre. When a ground drops to that level, it should be closed and thereafter be monitored to see how quickly the stock rebuilds. That obviously would be too complicated to manage if large numbers of small sections of ground were handled in that manner. It would be better to close fairly large strips at a time, even if part of a strip yielded more than the minimum 30 bushels. The simplest means, although not the only one, would be to divide an area (for example, the bottom area of Great South Bay, Town of Islip) into three parts; two of which would always be closed and the third one open. Those areas would then be rotated each year, so that one part would be open every third year. That would be fairly easy to patrol and to enforce, and the time sequence would be about right for clams to become littlenecks in the natural environment in most places. It would be well worth a try if there were sufficient law enforcement personnel to be effective; that is, a patrol boat in a closed area 24 hours a day, 7 days a week. The potential of the clam harvest would warrant that kind of surveillance.

CONCLUSIONS

It appears that the failure to develop a satisfactory method of clam aquaculture, despite about 70 years of research, may be based on faulty thinking. There is no problem in raising clams to market size under artificial conditions provided adequate attention is given to care and to cleanliness. The only impediment is the cost, which under present methods, is too high for economic viability. What may be the flaw in thinking is the reliance on small numbers of clams, thinking millions are sufficient when billions may be required to exceed the capacity of predators to eat them.

Another fatal flaw may be the lack of adequate law enforcement. Grounds must be patrolled constantly to keep out violators, and that means adequate coverage 24 hours a day, 7 days a week, 365 days a year. It also means adequate support in the courts, so that the penalty for being caught is not worth the risk.

An alternative method might be to try experimental management. One possibility would be to divide an area into three parts, keeping one open and two closed, then rotating the closed areas each year. If the closed areas

were adequately patrolled by law enforcement personnel, then the seed clams would be protected, and the plan could be adjusted to provide optimum yields as knowledge accumulated.

All three methods probably should be tried, and adjusted as necessary to provide the best yields. That would be far better than the present system, which is haphazard and not notably successful.

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OYSTER MARICULTURE IN SUBBOREAL (MAINE, UNITED STATES OF AMERICA) WATERS: CULTCHLESS SETTING AND NURSERY CULTURE OF EUROPEAN AND AMERICAN OYSTERS[1]

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ABSTRACT This paper describes the development of cultchless setting and nursery culture techniques for European and American oysters [*Ostrea edulis* L. and *Crassostrea virginica* (Gmelin), respectively] as adapted for the subboreal Maine, United States of America, environment. For several years the University of Maine has functioned as a supplementary commercial seed source and has evolved commercially workable techniques by a combined experimental and iterative approach.

Ideally, the Maine oyster culturist should receive a 10- to 20-mm seed oyster at the end of May to most efficiently take advantage of the delayed but long-growing season. This may be achieved by starting the hatchery operation in late winter with a complete dependence on cultured algae. The alternative is a seed-hatchery operation during the optimal summer season necessitating development of overwintering techniques for very small cultchless oysters.

Initially in developing cultchless setting techniques, it was found that polished marble was highly stimulatory as a setting surface. Unavoidable shell damage upon removal of the set and subsequent invasion of the protozoan *Uronema marinum*, however, compelled the development of small particle substrate to procure the cultchless seed oysters, in the interest of immediate production.

Several kinds of calcium carbonate particles were found that stimulated setting including tropical beach sand, foraminiferal sand, marble chips, and mollusk shell chips. All larval setting techniques involved placing the particles in screened boxes housed in recirculating water baths. Larvae were stimulated to set by increased water temperatures and by the addition of adult oyster metabolites or extrapallial fluid.

Nursery culture of cultchless oysters to commercial seed (10 to 20 mm) proceeded in two phases. Early nursery culture (to 2-mm size) was accomplished best in floating screened trays housed in recirculating water baths with cultured algae fed commensurate with clearing rates. Late nursery to market size seed was reared best either in field rafts housing nested screened boxes, or indoor stacked screened modules which could be operated either as open or closed systems. Culture gear including some overwintering apparatus is described and illustrated.

INTRODUCTION

This is the first in a series of papers describing the development of hatchery and growout techniques for European and American oysters, *Ostrea edulis* L. and *Crassostrea virginica* (Gmelin), respectively, on the subboreal Maine, United States of America, coast. In 8 years of hatchery-related research at the University of Maine, a purely experimental approach has evolved into a production role for a predictable supply of seed to commercial oyster culturists. Resultant advances in techniques and gear innovations reported herein should be useful to commercial hatcheries in similar environments around the world.

In 1970 and 1971, it was found that hatchery-reared cultchless oysters of both species performed exceptionally well in many of the diverse estuarine environments of Maine (Packie et al. 1976). Commercial use of hatchery-produced cultchless seed was attractive because Maine lacks a consistent natural-seed supply for either American or European oysters. Availability of cultchless oysters, by air freight from the west coast of the United States, further enhanced the feasibility of a new Maine oyster industry at that time. Through a modest extension program, Maine citizens were encouraged to experiment with commercial culture using a three-dimensional technique. By the mid-1970's, over 100 persons were in various stages of experimentation with several beginning commercial and pilot-commercial culture operations. In 1976 and 1977, the west coast seed supplies became unreliable compelling the University of Maine to begin a commercial seed-production role to ensure that the new Maine growout industry would survive and grow.

This subsidiary commercial role required that hatchery research be viewed from an entirely different perspective, i.e., from the view of a commercial operation trying to develop a financially viable business. Because yearly demand for seed oysters had increased to between 5 and 10 million cultchless seed oysters, it was necessary to construct culture gear and to innovate new techniques without benefit of an adequate reserach base. Techniques that sufficed on an experimental scale often were quite useless on a production scale. Because equipment had to be built before the season got underway, it was very difficult to change course in mid-season if the gear or technique proved inadequate. Occasionally crisis experiments were necessary to improve gear and techniques for the following season. This situation, we surmised, was very similar to that encountered by a new commercial hatchery. If some production was to be maintained, time did not permit the luxury of more basic but relevant research. Faculty and students, however, developed research centered around the problems encountered (Hidu et al. 1975, Packie et al. 1976, Hidu et al. 1978, Plunket and Hidu 1978). This research, plus improvements in gear and technique through a process of

[1] Ira C. Darling Center Contribution No. 154.

iteration, led to significant advances in culture technology particularly with European oysters.

Recently the seed-production mission was transferred to three private entrepreneurs* in Maine. The real value of this unusual University seed-production role is that significant advances in culture techniques can be reported; similar development accomplished privately would remain proprietary. Presented here are integrated descriptions of cultchless setting and nursery techniques that either incorporate original research, employ significant gear innovations, or are improvements on known hatchery techniques.

HATCHERY LOCATION

The University of Maine aquaculture facility is located at Wentworth Point, midway on the Damariscotta River estuary, in south-central Maine. The estuary is a narrow drowned river mouth, properly a ria, approximately 24 km in length. The selection of this site was dictated in part by nonhatchery-related considerations, although the location proved to be, for the most part, very favorable for a hatchery operation.

Hydrography of the basin has been described by McAlice (1977). At the Wentworth Point site, which has a 0.75 km width and a 12-m depth, the estuary approaches a well-mixed condition. Seawater from the Gulf of Maine moving upstream at depth dominates the circulation. A mean tidal height at Wentworth Point of 2.8 m produces currents up to 1 m/sec, assuring excellent water circulation in field nursery trays adjacent to the hatchery. Annual salinities range between 27 and 33 ppt with only slight influence from the freshwater Damariscotta Lake discharging 12 km landward. Temperatures range from below 0.0°C (−1.8° during January and February) to midsummer maxima of 17 to 18°C during July, August, and many times, into September. The location is free of domestic, farm, or industrial pollution and is relatively productive (Packie et al. 1976); as much as 1.1 mg Carbon/L was fixed per 24 hr during the spring and late summer plankton blooms. These blooms have been dominated by chain-forming diatoms from the Gulf of Maine, most notably *Skeletonema costatum*, *Asterionella japonica*, and *Chaetoceros* spp. These algal species, however, were not useful as a supplement for larval and early juvenile feeding; therefore, reliance on cultured algae in hatchery operation has been necessary.

HATCHERY STRATEGY

Most Maine oyster growers prefer 10- to 20- mm seed in late May or early June to allow best utilization of the growing season which, in most areas, lasts from June to November. There have been difficulties associated with smaller seed (< 10 mm), most importantly the need for increased equipment and handling. If oysters have been received late in the summer, the grower cannot take advantage of the full growing season and the chances for overwinter loss of small oysters increased. Growers should strive to have the bulk of their seed reach a size of at least 25 mm during the first season.

To produce seed oysters of a suitable size and at the right time, the hatchery operator is faced with two alternatives, each with its advantages and disadvantages. The first option is for an early season operation. It is possible to produce 10- to 20-mm oysters in May by starting conditioning of broodstock in late winter, i.e., February or March. The advantage of this alternative is the short inventory period from hatchery to sale, eliminating the need of risky overwintering procedures. Disadvantages include the cost of maintaining a seawater system during a difficult period, costly heating of seawater, and, most importantly, the absolute dependency on cultured algae for all phases of hatchery and nursery operations. The other alternative is a summer hatchery operation followed by a fall and winter nursery period to produced seed oysters of the proper size for the following spring. In Maine, conditions are optimal for a hatchery operating during the summer; hatchery systems are maintained easily; there is a minimal need to heat seawater; natural broodstock conditioning is advanced or retarded easily; and finally, natural algal populations are abundant for feeding the spat in the late nursery phase. The drawback is that the seed stock must be overwintered before sale, and overwintering of small European oysters is unreliable. If this element can be made secure, we would opt for a strong summer hatchery program.

HATCHERY TECHNIQUE

Setting

Early experiments investigated the feasibility of using a variety of substrates including glass, various plastics, and polished granite, none of which was stimulatory to the setting of American and European oysters. Similarly, the use of "Mylar" sheets (Dupuy and Rivkin 1972) did not appear feasible because European oysters were not stimulated to set, and the space and labor involved in incubation of sheets to finally obtain cultchless oysters appeared prohibitive in cost in a commercial application (Lipschultz and Krantz 1978). Polished marble, which is largely calcium carbonate, was found to be highly stimulatory to setting larvae of both species (Hidu et al. 1975). However, very large losses in the juvenile phase, described later, forced abandonment of these techniques in favor of small calcium carbonate particles in setting.

Other experiments investigated factors that might stimulate setting in mature European oyster larvae. Earlier work with American oysters indicated that a waterborne phermone from adult oysters stimulated setting of their larvae

*Marine Bioservices Inc., South Bristol, ME; Cozy Harbor Sea Farms, Southport Island, Boothbay Harbor, ME; and Intertide, Inc., Harpswell, ME.

(Hidu 1969, Veitch and Hidu 1971). A concentrated source of pheromone was found in extrapallial fluid (EPF); EPF was utilized routinely in the setting process with American oysters. With European oysters, however, British workers strongly contented that the "gregarious setting response" was mediated by contact with specific compounds on the setting surface (Crisp 1965, 1974; Bayne 1969). No material stimulated metamorphosis in European oysters when added in solution or suspension by the British. However, we felt the surface chemistry versus waterborne pheromone mechanisms needed further study since the outcome could have considerable bearing on our setting procedures.

Contrary to British findings, all our experiments indicated stimulatory action of a waterborne pheromone in setting of European oysters (Hidu et al. 1978). Initially, extensive trials indicated that the addition of EPF in suspension was stimulatory immediately to setting in European oysters. A waterborne factor was demonstrated further by exposing mature European oyster larvae to EPF prior to exposure to cultch surface. The "pretreated" larvae then set at significantly higher rates than untreated controls but significantly lower than larvae in cultures that contained EPF and cultch shell together. Thus evidence was obtained that European oyster larvae would respond to metabolites in suspension similar to American oysters. Ultimately, all of this information was utilized in our hatchery setting procedures.

WORKABLE SETTING TECHNIQUES

By using 300-μm calcium carbonate particles and changing nursery techniques, survival rates of mature larvae to 2-mm spat quickly rose from less than 10% to over 50%. Small particle techniques are still being refined, but for the present, the following has been the most workable method.

The objective has been to obtain a batch of uniform mature larvae, the majority of which would set on the small particles in a relatively short time. This has been accomplished by grading larvae with stainless steel screens. Mature larvae have been removed selectively using a sieve series of 70, 80, and 90 meshes per inch. The larvae retained on the 70-mesh screen should have the ability to set when stimulated to do so. Metamorphosis should be delayed as long as possible before putting the larvae into setting baths to ensure the best response to the particles. This has been accomplished by retaining graded mature larvae in 400-liter polyethylene vessels before introduction into the setting baths. Polyethylene surfaces have not (in most cases) been stimulatory to setting, especially to European oysters. An early workable system utilized a 60-liter polyethylene vessel into which a PVC-lined screened box was placed. Setting particles were added to cover the screen to a depth of about 5 mm and cultured algal foods were added in excess. The water was then recirculated gently through the box with an air-lift system. More recently, the screened boxes with larvae and chips were merely inserted into the recirculating baths which also were used for initial rearing of early juveniles (Figure 1).

In the setting baths conditions were manipulated to obtain a massive set in as short a time as possible. Water quality in the setting baths was maintained and the conversion of larvae to spat maximized. Since it has been demonstrated that adult waterborne oyster metabolites and increased temperatures may stimulate setting in oysters (Lutz et al. 1969), the water temperature was raised to 24 to 26°C; several liters of 1 μm filtered seawater from the adult oyster conditioning baths were added. With a vigorous brood of larvae which have delayed setting, these conditions produced a heavy set on the small particles within several hours up to a day. The setting bath was then maintained for several days with daily water changes until the spat achieved a sufficient size to be screened away from the 300-μm particles. Spat reaching a diameter of 500 μm were separated from the particles using a 50-mesh/inch screen.

Behavioral differences between American and European oysters in setting have been noted; therefore, apparatus and procedures had to be modified accordingly. For example, European oysters were delayed easily in their metamorphosis in polyethylene larval culture vessels, but American oysters would set, *en masse*, on the sides of the vessel almost instantly. American oysters have a high tendency to set on the sides of the PVC-lined box inserts, whereas European oysters "seek out" the particles on the screens. Therefore, it appeared necessary to have very shallow inserts for American oysters or to construct the inserts of material that was not conducive to setting. Adding a thin layer of petroleum jelly to the sides of the inserts prevented setting on the vessel sides and apparently was not detrimental to the oysters. The two species have different preferences for calcium carbonate particles. European oysters would set well on a variety of particles including shell chips, marble chips, tropical beach sand, and foraminiferal sand from marine deposits. The American oyster was more selective, with beach sand giving poor results. Overall, the European oyster at setting was a more cooperative animal in the hatchery than its American cousin.

NURSERY CULTURE

Cultchless oysters must be carefully nurtured to a size that would allow a commercial grower to efficiently handle the product. Originally, the culturists purchased a 3- to 6-mm "window screen" size oyster; commercial growers, however, experienced variable performance and handling difficulties with the very small seed oysters. The optimal size salable seed oyster was 10 to 20 mm. To achieve that size, the hatchery-nursery system had to be divided into two or three components: (1) an early nursery, entailing an indoor controlled system to grow seed oysters from metamorphosis to 2- to 3-mm size; (2) a late nursery, a controlled indoor or outdoor system to produce 10- to 20-mm seed, and/or (3) an overwintering procedure if small oysters were produced late in the growing season.

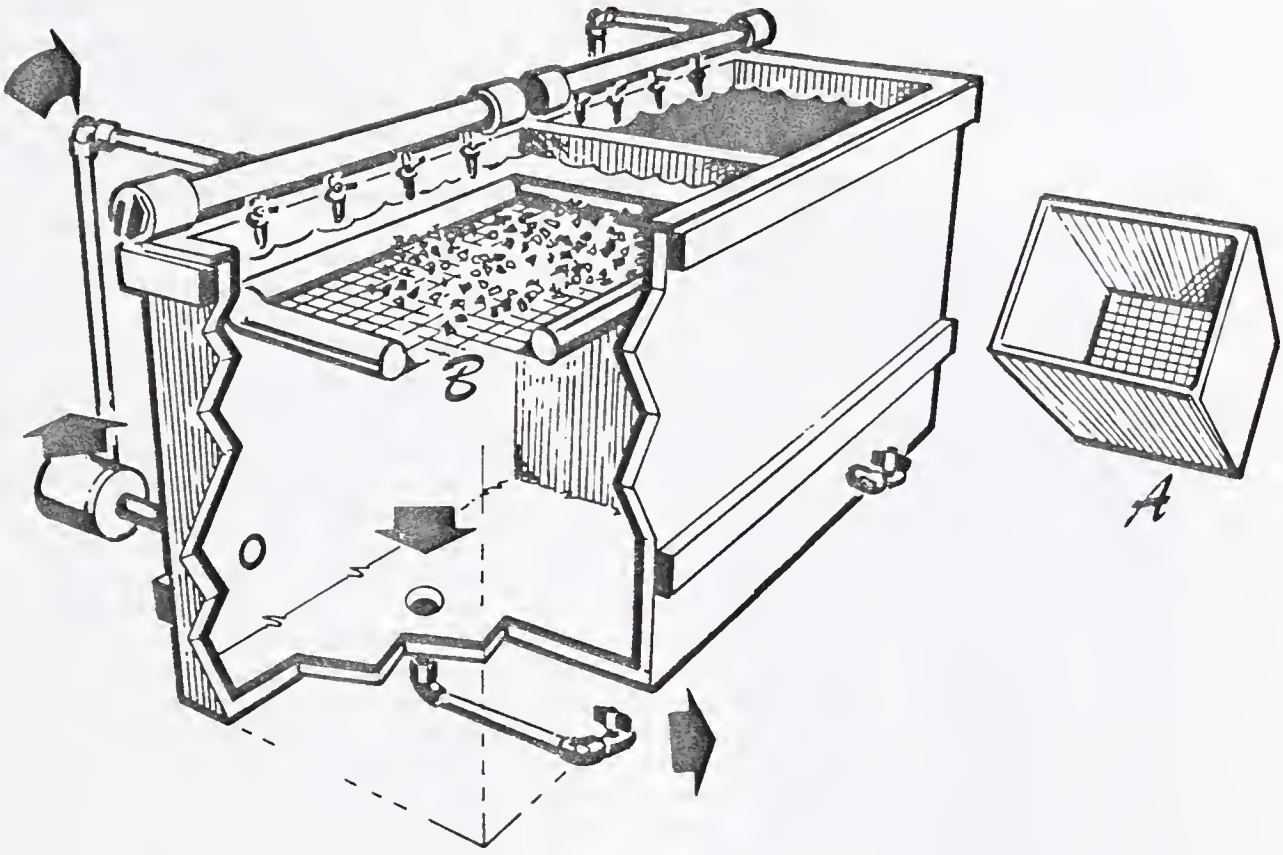

Figure 1. Setting and early nursery dual tanks each with a 270-liter capacity.

Construction materials: 1.9 cm exterior plywood, 5.08 cm x 10.16 cm planks, 0.25 cm PVC sheet stock, PVC Sch 80 pipe, PVC ball values, and plastic magntic drive pumps.

Construction: laminate the PVC sheets to the plywood sheets before cutting plywood for the tank, eliminating cumbersome procedure of fitting PVC sheets to tank interior. Weld all PVC seams to ensure a watertight seal. Mount pump for each side behind tank in a wooden enclosure for protection from salt spray.

Overall inside tank dimensions: 0.6 x 0.6 x 1.8 m with entire system resting on a 0.6 x 2.4 m plywood base.

Cost: approximately $250 per tank plus 25 hours labor for construction using purchased materials for five dual units (1978 dollar value).

In use, the tank is filled just below the PVC ball valves. Tank water is drawn into the pump from a port location one-third the distance from the bottom of the tank and is pumped to a manifold at the top rear of the tank. Each tank is drained centrally. The recirculating system, including pumps and piping, should be drained and rinsed periodically with fresh water. On a regular schedule the entire tank should be filled with freshwater detergent or Clorox mixture and recirculated for several hours to remove protozoan, bacterial and algal film buildup.

Tank inserts include (a) early design wooden PVC impregnated setting boxes, and (b) floating PVC frames with mesh. Wooden boxes were constructed of 1.27 cm exterior plywood painted with heavy duty PVC cement. Bottoms were covered with 180 Nytex mesh with a surface area of 2,173 cm^2 and can accommodate 250,000 setting larvae. The newer floating frames were constructed of 3.8-cm PVC-DWV pipe, mitered and welded at the corners. These were fitted with 180 Nytex mesh when used as setting trays, or fiberglass window screen when used for spat growth. The Nytex mesh must be glued to the frames; the fiberglass window screen may be welded on. A bead of clear silicone sealer was laid between the inside mesh edge and the PVC frame to prevent larvae or spat entrapment. Frames were built 2.5-cm smaller than inside dimension of the tanks to facilitate handling. The PVC frames have a mesh surface area of 3,825 cm^2 and easily accommodate 350,000 setting larvae. These frames also may be used in conjunction with the spat growing module described in Figure 3.

Early Nursery Culture–Evolution of Technique

Cultchless oysters have to be nurtured up to the 2- to 3-mm size under closely controlled hatchery conditions. New cultchless oysters were very fastidious in their food requirements. The fine screens necessary for holding them were very resistant to water flow due to a surface-tension effect. Thus, an early outdoor placement was impractical, whatever the season.

Nursery operations in the first 3 years suffered catastrophic losses of cultchless spat, preventing any significant hatchery production. Losses, in most cases, followed a similar pattern. Spat (removed from polished marble and placed under a variety of closed systems) were observed to repair damaged shell edges readily and to grow rapidly until an 0.8- to 1.0-mm size was attained. Then the spat became very transparent, ceased significant growth, and eventually were lost in a mass mortality. A free-swimming ciliated protozoan, *Uronema marinum*, and attached cilhates *Vorticella* sp. and *Zoothamnium* sp. became epizootic prior to and during the mortalities.

At the time, several probable causes for the losses seemed apparent and, no doubt, the causes were interrelated. It was apparent that uncoated fiberglass in a closed system with a 2-day period between water changes was marginally toxic to spat. Further, severe damage to some spat removed from the marble may have allowed buildup of ciliated protozoan *U. marinum* populations (Plunket and Hidu 1978). Although studies have indicated that *U. marinum* is entirely a bacterial feeder, the protozoan readily entered healthy appearing oysters and, in large numbers, probably contributed to the oyster mortalities.

Cessation of oyster growth at intermediate sizes, in the presence of sufficient food, suggested that food quality was not a problem but that some other element (either depleting or excessive) became limiting with the larger oyster biomass in the tanks. Ammonia buildup or calcium depletion also appeared possible, either of which would affect oyster growth. The slowed growth rates contributed to the eventual mass invasion of commensal protozoans; thus, the protozoans became food competitors and, in severe cases, appeared to prevent the oysters from feeding.

Because of these continued losses, and the urgent need to produce large numbers of seed oysters as quickly as possible, a change in approach became necessary. The following simultaneous steps were taken in the nursery system:

1. Change of cultchless setting procedure eliminating the polished marble technique and utilizing small particle technology.

2. Elimination of fiberglass and metal from all water-contact surfaces in rearing modules.

3. Change of maintenance protocol to more frequent changes with more coarsely filtered seawater, and the use of redundant culture modules that had been purged with a water-Clorox mixture during downtime.

With these new techniques, oyster survivals increased dramatically to over 50%. At once, *U. marinum* became rare in the cultures, and the epifaunal protozoa, although always present in low numbers, never built up to epidemic proportions.

Workable Early Nursery Techniques

Cultchless spat of either species at 0.5 mm size were separated by screening from vacant 300-μm particles in the setting containers and placed on floating screens in a 270-liter closed system (Figure 1). Initially, a 0.5 x 0.5 m screen carried 250,000 new spat with the numbers reduced to 50,000 spat at 2 mm.

Baths were drained daily, and new seawater added was coarsely bag-filtered to 10 μm and held at 25 ± 1°C for both species. Spat were sprayed daily on the screens with cold fresh water to reposition the oysters and to remove as much particulate waste material as possible. On alternate days the oysters were removed to a clean screen and placed in a culture module purged with a water-Clorox mixture during the previous 48 hours. Cultured algae *Isochrysis galbana*, *Monochrysis lutheri*, and *Cyclotella nana* were added daily at an initial rate of 8×10^{10} cells per 250,000 spat. As the seed oysters grew, food demands increased to several times the original amount. In all cases, the feeding rate was varied commensurate with clearing rates of the spat. A reduction in clearing rates from the previous day was an indication of adverse conditions or loss of vigor of the spat. The early nursery phase normally ended when the spat reached 2 mm; about the same time we were no longer able to meet the demand for cultured food. Larger culturing facilities may find it advantageous to extend the early nursery phase.

Late Nursery Culture

The late nursery stage began when daily food requirements of growing seed exceeded the ability to provide them with cultured algae, and extended to the time optimal salable size had been attained. If conditions were adequate in the outdoor nursery area, the cultchless spat were placed directly outside in floating invertible boxes (Hidu and Richmond 1974, Gillmor 1978, Walker 1979), or in a rafted tray culture module similar to that pictured in Figures 2a and 2b. In either case, testing with small batches of seed prior to a large placement was essential.

More research is needed to determine acceptable outdoor conditions for early cultchless spat. An adequate algal standing crop of the proper species with adequate salinity, temperature, and current velocity are obvious necessities. To illustrate the uncertainty of outdoor placement, in 1974, a batch of 2-mm European oysters was placed in invertible floating trays. Temperatures were 9°C in mid-May with a very apparent bloom of natural phytoplankton. The seed oysters responded immediately, doubling and redoubling their size in a short period time. In the following year,

The field module (Figure 2A) is constructed in two separate parts—the flotation collar-workdeck and the inner submersed tray stacking frame. Workdeck is constructed of 2 x 4" and 4 x 4" spruce, 0.62 x 10.16-cm steel plate, and styrofoam flotation (2,475 kg). Overall dimensions are 2.14 x 0.46 x 6.71 m. The inner stacking frame is constructed of 2 x 4", 4 x 4" and 2 x 8" spruce, 0.63 cm steel plate, 1.27-cm steel rods, and 0.64 x 3.81-cm steel angle iron. Overall dimensions are 1.83 x 0.076 x 5.2 m. The inner framework is divided into six bays constructed 1.27-cm larger than the 0.61 x 0.61-m wooden trays it accepts. It is crossbraced and stiffened with 1.27-cm steel rods running from corner to corner, and others running between the bays. There are four angle-iron brackets which hang from the inner framework and act as self-locking stiffeners for the workdeck when the frame is bolted up into the floating workdeck.

The inner unit is removable to allow placement of spat on bottom during Maine winter-ice conditions. Each bay in the submerged frame will accept 14 stacked trays. The top tray is a spacer to keep the stack properly submerged; the bottom tray is fitted with stryofoam to provide a constant positive flotation when the wooden trays are water sodden. With flotation on the bottom, the stacked trays behave much like trays in a cafeteria tray dispenser. When the top tray is removed, the next tray will float and the remainder continue to surface as the top trays are removed. Trays are constructed of 3.48-cm spruce, 3.48-cm galvanized epoxy-dipped lobster trap staples, and appropriate mesh sizes on two ends and on the bottom of the tray. The upper and lower edges of the trays are rabbeted to provide positive locking of the stacked trays and to help prevent small spat from being washed out by wave action. Nylon line (0.64 cm diameter) looped about the tray stack and tied taut on the top easily secures the trays within the stack preventing spat loss. This facilitates raising the stacks when the submerged tray framework is heavily fouled.

In the field, the complete module is positioned perpendicular (Figure 2B) to the prevailing current to provide maximum water exchange in the trays. This unit is a highly stable work platform, and provides ample work space with all the trays removed and stacked on deck for periodic air drying. Total cost of the finished unit plus 200 trays was approximately $2,100 (1978 dollars). The unit requires 125 to 140 manhours of labor to assemble.

The field nursery unit has been in use for 5 years and shows only minor wear and rusting on the flotation collar-workdeck. Underwater inspection of the submerged framework has revealed no appreciable erosion or deterioration of the wood, and no noticeable corrosion of the steel rods. This unit is expected to provide continuous service for at least 7 to 10 years.

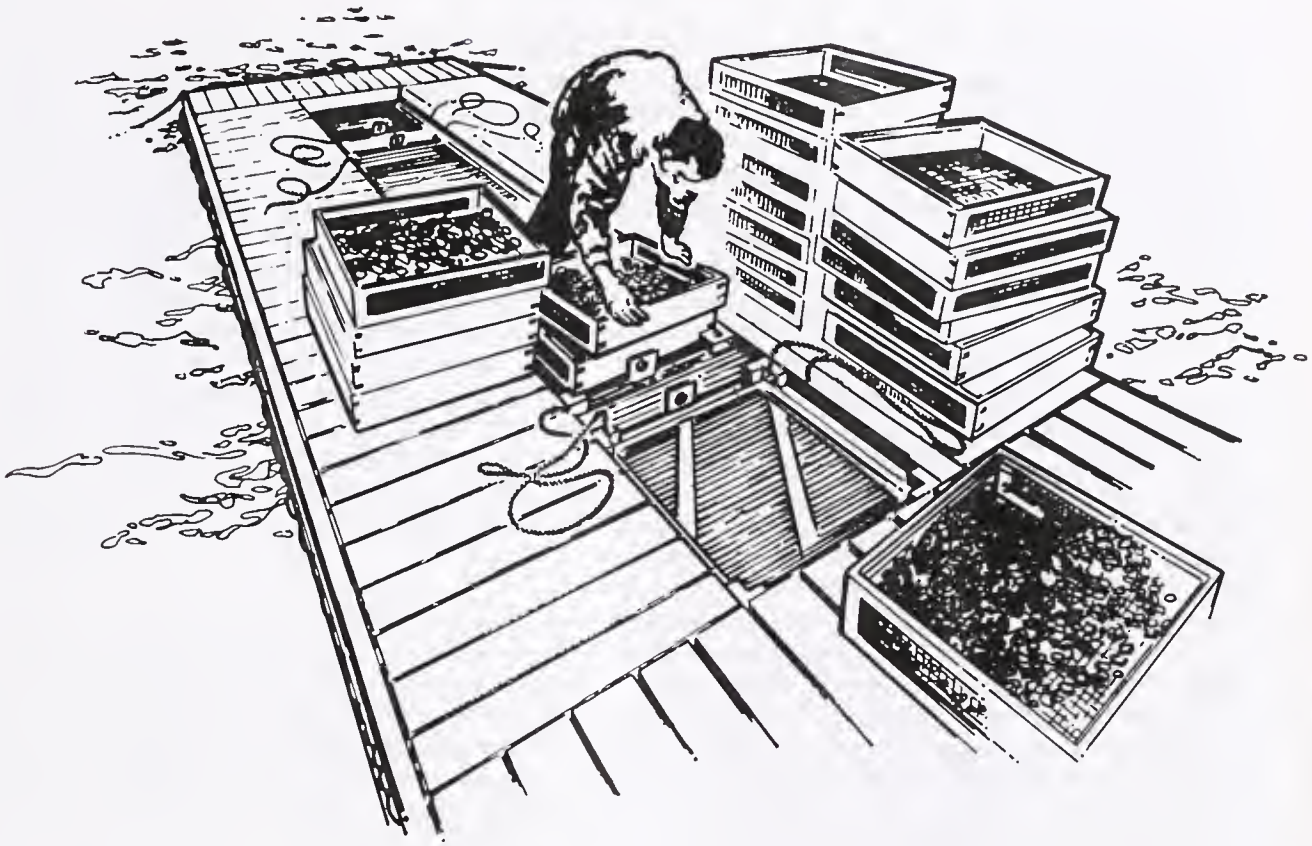

Figure 2A. Field module designed to accept stacked wooden trays to grow cultchless spat in an outdoor nursery environment.

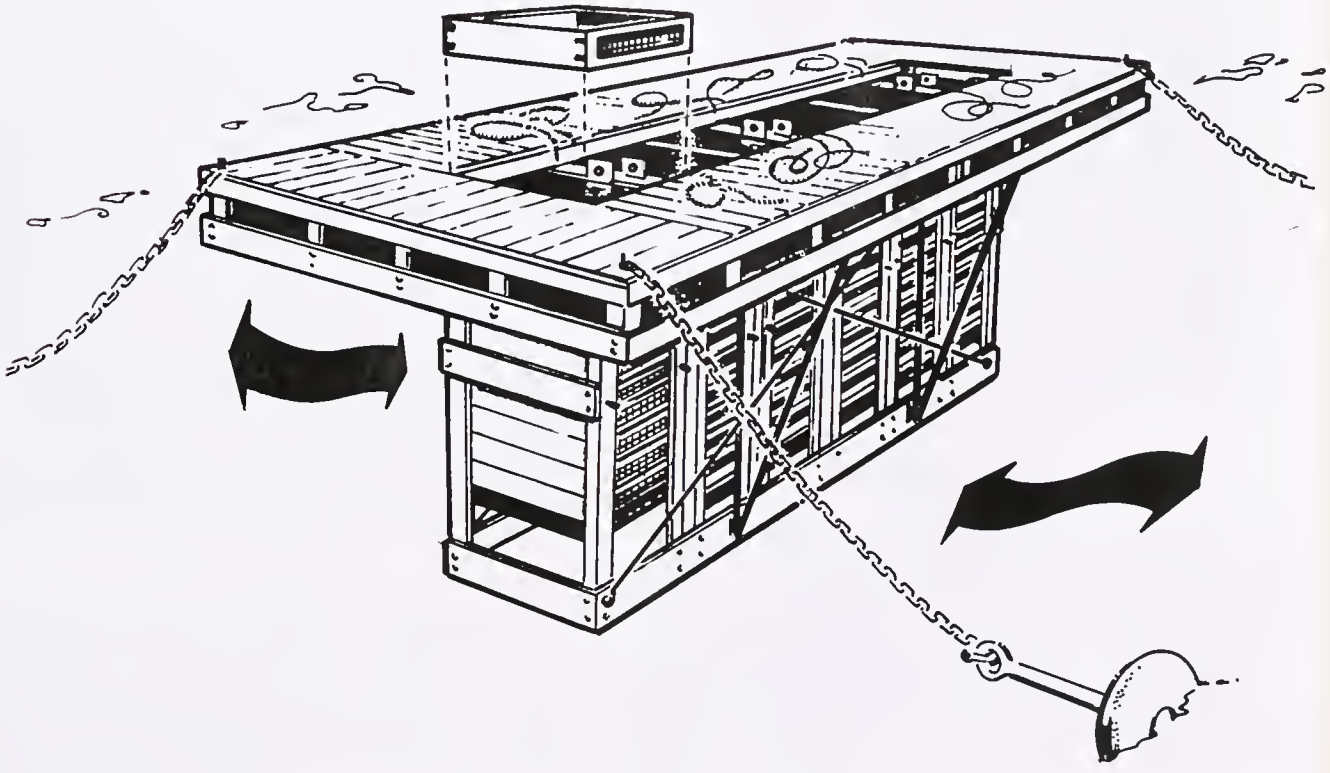

Figure 2B. Field module positioned perpendicular to prevailing current.

however, with temperatures at 11°C and an apparent similar bloom, a test group of Europeanseed oysters did not grow and eventually were lost. Therefore, the qualitative nature of the phytoplankton bloom, i.e., presence of usable small forms, may be crucial to the early field success of seed oysters. Commercial growers also have noted this effect, reemphasizing the need for hatchery production of larger seed oysters.

A major problem with outdoor nursery culture in any area is marine fouling of the tray mesh resulting in reduced water flow and food transport. Provisions must be made for redundant trays so that oysters can be transferred to clean trays, thus allowing several days of air drying and cleaning of the fouled trays before reuse. A system of floating invertible trays (Hidu and Richmond 1974, Gillmor 1978, Walker 1979) which allows periodic air drying also is an effective method for reducing fouling of the small tray mesh.

Overwintering

Successful overwintering of small seed oysters would allow hatchery operations to be continued to the summer season when the operations are most efficient. Studies, now in progress, are defining an optimal overwintering procedure; several helpful suggestions for optimal overwintering can be offered. Initially, there appeared to be strong species differences in winter hardiness. Overwintering small (down to 5 mm) American oyster seed presented no problem regardless of condition. Small European oysters, however, did present a problem. European oysters, whatever their size, did not withstand prolonged periods of water temperature below 0.0°C. Overwintering, either in a tempered laboratory or in a more stenothermal oceanic situation, appeared mandatory. Size of seed oysters was a factor. While overwintering large experimental batches of European oysters in the Great Bay estuary, New Hampshire, Kevin Tacey (personal communication) experienced high losses of seed oysters below a 35-mm size; his larger size oysters suffered little mortality. Late handling (December) also may be detrimental because shell margins may be chipped when the spat can no longer repair themselves.

Equipment for overwintering small European seed oysters is under development (Figures 3 and 4). It may be possible to hold large numbers of small seed oysters with slightly tempered water temperatures and periodic, low-level feeding. Preliminary results are encouraging but no definite recommendations can be made at this time.

CONCLUSIONS

The development of cultchless setting techniques raises important questions concerning the legal or proprietary nature of the process. It is difficult to work with any aspect without apparently infringing on patents which often are broadly stated. If this situation is not resolved, then the cultchless oyster may not achieve its potential in marine food production.

The origin of the concept of cultchless setting, and the legal right to patent the concept appear questionable. The French appear to have originated the concept before the turn of the century with naturally produced seed oysters. Lime-coated tiles were placed in a spat-collecting area throughout the summer and fall, and "cultchless oysters" were procured during the winter months by stripping the tiles. The French procured about 1 billion cultchless seed oysters (*O. edulis*) in this manner annually for use in their on-bottom growout beds (Bardach et al. 1972). The concept of procuring cultchless oysters in the hatchery is attributed generally to William Budge of Pacific Mariculture, Inc., of California, U.S.A. (Budge 1970). The Budge Patent No. 3,526,209 was filed on November 30, 1967, and patented, September 1, 1970. A second patent, however, by Long Island Oyster Farms, Inc. (LIOF 1970) was filed later on April 12, 1968, but patented earlier, February 17, 1970. If both patents are valid, then one must conclude that the concept of cultchless setting is not patentable but specific approaches to the process are.

Although the processes and apparatus reported herein were derived in a completely independent fashion, several aspects of our methods appear to infringe on rather broadly stated patents. For example, it is difficult, if not impossible, to rear early cultchless oysters without housing the spat on a screen and passing food-laden water through the screen. Our nursery apparatus (Figures 1 and 3) depends on this and yet the patents of Budge and LIOF both claim the method. Similarly, our field-rearing module (Figures 2A and 2B) depends on stacked screened cages secured in a floating raft to allow algae-laden seawater to pass through. But such an apparatus is specifically prohibited by Fordham (1972), Patent No. 3,650,244. The floating invertible tray, although we picture it (Hidu and Richmond 1974), and mention it (Gillmor 1978) herein, has been patented by Walker (1979). These interactions border on the ludicrous and the ridiculous; however, the overall effect may be to stifle all progress in cultchless oyster culture. It is literally impossible to rear a cultchless seed oyster without infringing on someone's broadly stated patent. Unfortunately, the remaining problems with rearing cultchless oysters appear not to be biological, but legal.

ACKNOWLEDGMENTS

The authors acknowledge the support of NOAA, Office of Sea Grant, University of Maine at Orono, Project No. R/A–1, and the financial support of the University of Maine at Orono through Dr. Frederick E. Hutchinson, Vice President for Research and Public Service. Mr. William Bowers of Wiscasset, Maine, drafted the figures; Mr. Samuel Chapman, the second author, originated many of the concepts and constructed all of the culture gear pictured herein. Dr. Malvern Gilmartin and Mr. Ronald Dearborn added encouragement throughout the study.

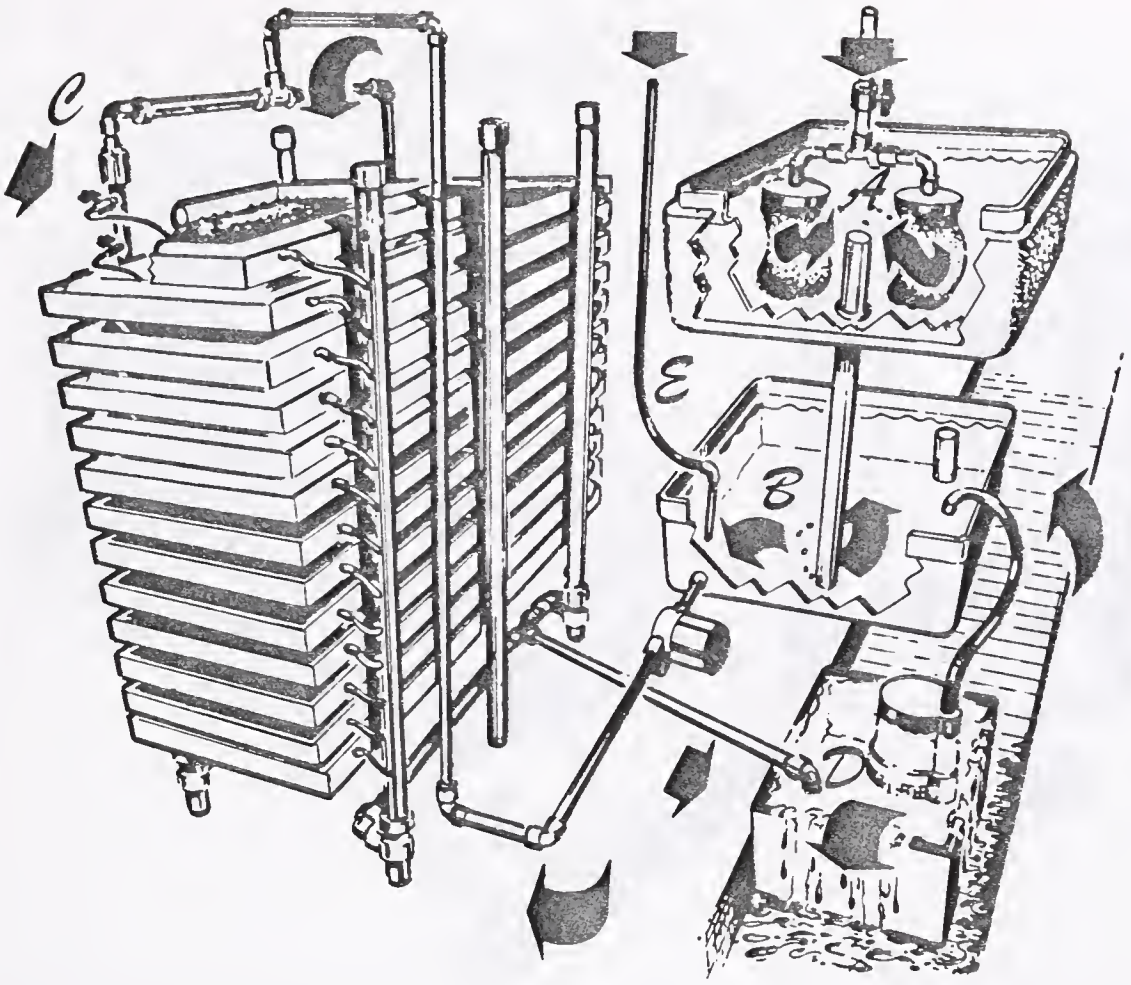

Figure 3. Experimental module for overwintering small cultchless oyster spat.

Essential components of this unit consist of a series of stacked trays housing floating PVC frames, dual holding tanks for particulate settlement, degassing and algal food reservoir, and an apparatus to operate the unit either as an open or as a closed system.

The stacked tray unit is constructed of 5.08-cm Sch 80 PVC pipe, 0.64-cm exterior plywood painted with floor enamel, various Sch 80 PVC fittings, and floating PVC framed screens as described in Figure 1. The structural frame for the trays consists of six 5.08-cm Sch 80 support legs, and fourteen 1.91-cm Sch 80 pipe sections welded onto 0.61 x 1.5 m rectangular frames and spaced 10.16 cm apart for sliding the plywood trays. The 5.08-cm PVC legs also serve as the water distribution and drainage mechanism. Threaded tees 5.08-cm fitted with threaded plugs attach to the bottom of the legs and allow for watertight drainage plus the ability to level the entire unit by adjusting the threaded plugs.

The painted plywood trays accept the PVC floating trays and provide a water depth of 3.81 cm. The wooden trays are fabricated from 0.64-cm exterior AB plywood, with pine sides nailed and glued with a water-resistant glue, and painted with three coats of floor enamel. Inside dimensions of the trays are 4.45 x 52.68 x 85.09 cm. The PVC welds between the 1.91-cm pipe and the 5.08-cm legs are strong enough to preclude the necessity of cross bracing. This unit is capable of handling 7 million oyster spat in the 1- to 2-mm range, and 3 to 5 million spat in the 5- to 10-mm range.

During a flow-through operation, seawater at the proper temperature enters tank A through 10 μm nylon filter bags. Tank A overflows through a standpipe into tank B. Residence time for both tanks is 12 minutes which is adequate for degassing when the ΔT is no greater than 8°C above ambient. From tank B the water is pumped through PVC piping into the leg manifold (C) of the stacked module. Here water flow is adjusted to between 1 and 2 liters per minute into each tray by 0.64-cm PVC ball valves. The stream of water flows in diagonally, and drains from a portal opposite the entry point. The drains are 1.27-cm 90° male insert adapters that have had their openings enlarged with a 1.27-cm drill. The 90° adapter is connected to the drain leg by vinyl tubing which is secured to the drain leg with a bored stopper. The drain support legs are connected to and empty into a sump well (D).

During the feeding operation, the unit is operated as a closed-recirculating system. The mixed temperature water is shut off at tank A. Algae is added to tank B through fill-line E. The water and algae mixture follows path B–C–D–B. During this feeding phase, the sump pump in well D pumps algae-laden water back into tank B. By controlling the algal flow from E to B, specific feeding regimes for specific times may be achieved with minimal algal wastage.

Cost of the PVC framework is about $280 plus approximately 40 hours of assembly time. The wooden trays cost about $7 each including materials and labor; the floating frames cost $12 each. It is recommended a minimum clearance of 10 cm be allowed between wooden trays. This provides enough space to visually monitor the spat without disturbance. Wooden trays are removed easily if a bottom drain plug is included for draining prior to sliding trays from the module.

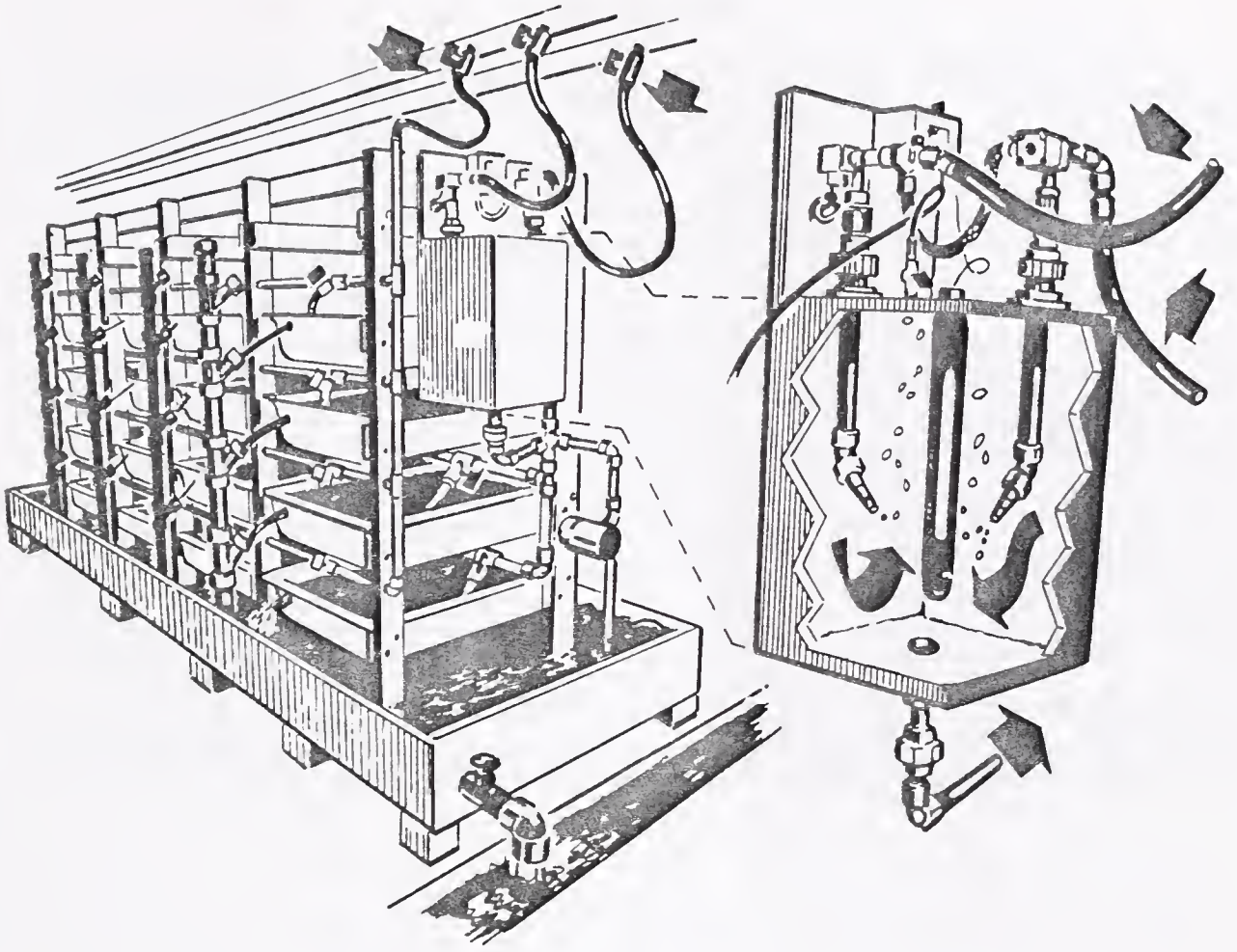

Figure 4. Universal laboratory module which allows advancement or retardation of conditioning broodstock or holds cultchless seed oysters under ambient or a modified temperature regime.

This unit may be operated as a closed system in artificial feeding. In that case, the catch basin acts an an algal reservoir and the trays are supplied by activating the recirculation pump.

The ambient seawater to this sytem is coarsely filtered through a 1-mm mesh to take advantage of natural phytoplankton production. Water is piped to this unit through a 2.54-cm PVC drop-down. Manifolds of 1.91-cm PVC then branch out horizontally across the tray levels and deliver water through 0.64-cm PVC ball valves. The ball valve openings have been drilled to 0.64 cm, and will deliver 4 liters per minute when water pressure is 4.5 to 5 psi. All of the piping in this unit can be disassembled for periodic cleaning which is mandatory under constant usage. This is accomplished by using PVC unions which may be expensive initially but quickly pay for themselves in time saved when cleaning the system.

The water temperature control may be attached to the end of the module. A water-filled glass tube houses the copper temperature probe near the bottom of the unit. The mixing tank holds 42 liters of water and measures 0.3 x 0.3 x 0.45 m. The back is constructed of 1.27-cm PVC stock, while the front and other sides are 0.64 cm PVC sheeting. The corners of the tank are welded to form a sturdy, watertight compartment. The 0.64-cm thickness will withstand drilling and tapping for additional connections and drains. Temperature mixing is accomplished by the thermostat switching on and off solenoids. One solenoid is always open and, at a water pressure of 4.5 to 5 psi, provides a constant flow of 81 liters per minute at $\pm$ 3°C. In the 26.5-liter trays, a lesser flow (1 liter per minute) allows the temperature to be controlled within $\pm$ 0.25°C. Solenoids are the dry type, no seawater touches the metal plunger which valves the water. The body is nylon, the plunger diaphragm is neoprene, and the valving is "normally closed." Normally closed solenoids stop water flow when deenergized. This assures that, in the case of a power failure, experiments or animals fed by the mixing tank will not be killed by high temperatures. All electrical connections are made with watertight fittings to make the unit as safe as possible. However, there is a measurable electrical leakage from the metal solenoid core to the seawater ground.

Required maintenance of the mixing tank includes cleaning the interior with hot fresh water whenever fouling is noticeable, keeping the glass sensing bulb full with fresh water, and occasional replacement of a solenoid coil or diaphragm. A 0.64-cm PVC ball valve is threaded into the top of the mixing tank and serves as an escape vent for gases evolved in heating water. One of these units has been continuously used for 5 years with only occasional replacement of component parts. Total cost of materials for this mixing box was $140 in 1974, and at least 8 hours of assembly time was required.

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USE OF LIPID-SPECIFIC STAINING TECHNIQUES FOR ASSAYING CONDITION IN CULTURED BIVALVE LARVAE[1]

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ABSTRACT A simple, inexpensive, rapid technique for qualitatively assaying the nutritional status of bivalve larvae in large-scale cultures is described and evaluated. Lipid has been identified as being the major energy reserve of developing and metamorphosing larvae. Adverse culture conditions affect normal patterns of lipid accumulation and utilization. A lipid-specific staining technique, using either Sudan Black B or Oil Red O, was used to monitor metabolic dysfunction and larval health as related to culture conditions, and subsequently evaluated as a diagnostic tool for culture assessment.

In a series of matrix design experiments with larvae of the bivalve *Teredo navalis* Linné [three temperatures: 10°, 20°, and 30°C; and two food species, *Isochrysis galbana* (Parke) and *Phaeodactylum tricornutum* (Bohlin), plus relevant starvation controls], both temperature and food species were demonstrated to have profound affects on growth, on size of the stained lipid reserve area of the digestive gland, and on the extent of lipid mobilization as indicated by the presence of diffuse coloration in the tissues following staining. The high lipid content of healthy larvae and subsequent depletion during imposed starvation periods were visualized with the staining technique and substantiated by comparative gross biochemical analysis of actively growing and starved larvae.

The study concluded that the lipid staining technique could be used as a diagnostic tool for rapidly assessing condition of cultured larvae.

INTRODUCTION

With the development of refined techniques for large-scale culture of bivalve larvae by Walne (1956), and by Loosanoff and Davis (1963), hatchery rearing of bivalve seed offered a realistic option for restocking the depleted natural supply of bivalve shellfish. Since that time hatchery techniques have been modified and improved so that excellent production usually can be expected (Dupuy et al. 1978). However, the inability to adequately control certain parameters, such as state of broodstock or periodic changes in water quality, and to predict the effects of such variability on larval growth has led most hatchery operators to adopt an array of larval-condition monitoring techniques. These include shell growth rate, larval mortality rate, microscopic examination of behavior, morphology, and disease signs (Elston and Leibovitz 1980). More involved assay procedures, such as histological examination for tissue necrosis and respiration rate measurements as an indicator of metabolic activity, generally have been confined to research laboratories.

Lipid plays an essential energetic role in the normal pattern of growth and metamorphosis in bivalve larvae (see Holland 1978, for review). Helm et al. (1973) described a direct relationship between total lipid content of newly released larvae of the oyster *Ostrea edulis* L. and subsequent viability and larval growth rate. These studies suggested that continuous monitoring of total lipid content of larvae in intensive culture systems could provide valuable information concerning their general condition and relative metabolic state (e.g., stressed, starved, or healthy). Techniques necessary to effect such analyses are labor- and time-intensive, and require expensive equipment not found in average hatchery operations. A simple and inexpensive technique has been developed to qualitatively monitor both accumulation of larval lipid reserves during normal growth and changes in lipid distribution associated with adverse culture conditions or environmental stress. The technique involves staining subsamples of culture populations with a lipid-specific stain and microscopic examination of whole larvae.

METHODS AND MATERIALS

A series of matrix experiments were designed to determine the effects of two environmental variables, temperature and food species, on growth and lipid accumulation in larvae of the bivalve *Teredo navalis* L. Two species of unicellular algae, *Isochrysis galbana* (Parke) and *Phaeodactylum tricornutum* (Bohlin), were grown in semicontinuous culture using the methods of Walne (1965) and Ukeles (1973) on f/2 medium (Guillard and Ryther 1962) at 20°C.

Nine groups of *T. navalis* larvae were grown in four L-glass jars at an initial density of 1 larva/ml; seawater (0.22 μm filtered) and food were changed at 2-day intervals. Three of the nine groups were maintained at 10°C, three at 20°C, and three at 30°C. One group from each temperature regime was fed *I. galbana* at a density of 5×10^4 cells/ml, one was fed *P. tricornutum* at the same density, and the third was maintained in the 0.22 μm filtered seawater with no food additions (hereafter termed starved).

At each change of seawater and food, subsamples of approximately 100 larvae were removed from each of the nine groups. These were, in turn, narcotized by a modification of the method of Turner and Boyle (1974), and stained specifically for lipid with either Sudan Black B

[1]Contribution No. 4772 from Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

(C.I. 26150) or Oil Red O (C.I. 26125) by the procedure outlined below. After staining, the shell length and height, and the diameter of the stained digestive gland area were recorded for 30 individuals from each group. Larvae representing the mean of both parameters were photographed at a magnification of 250X with high contrast black and white film (Kodak Technical Pan 2415) to accentuate the stained material.

Procedure for Narcotizing and Staining Bivalve Larvae

I. Narcotizing and Fixing
   A. Pipet larvae (10 to 1000) into 6 ml vial or small petri dish with ~ 2 ml seawater.
   B. Add 2 drops 7.5 $MgCl_2$ solution, wait 5 minutes; add 1 ml $MgCl_2$, wait 5 minutes; add 2 ml $MgCl_2$, wait 5 minutes.
   C. Remove fluid leaving larvae on bottom—replace with $MgCl_2$.
   D. Test state of larvae by pipetting a few into 10% buffered formalin, when ready (i.e., larvae do not contract), add ~ 5 drops formalin.

II. Preparation of Stain
   A. Dissolve 0.75 g Sudan Black B (C.I. 26150) or Oil Red O (C.I. 26125) in 100 ml ethylene glycol heating to ~ 60°C.
   B. Filter hot through Whatman no. 2 paper and refrigerate, filter again when cool.

III. Staining for Lipid
   A. Allow larvae to settle from step ID, remove all fluid leaving larvae on bottom.
   B. Add ~ 1 ml Sudan Black B or Oil Red O solution and stain for a minimum of 1 hour.
   C. Pipet off stain solution and add pure ethylene glycol (~ 1 ml) to clear excess stain.
   D. Let stand for a minimum of 30 minutes for Oil Red O or for 4 hours for Sudan Black B (large larvae in Sudan Black B may require up to 24 hours to clear).
   E. Pipet off discolored ethylene glycol and replace with pure ethylene glycol; clearing is completed when excess stain ceases to color the medium.
   F. Observe and photograph/mount in viscous medium (e.g., glycerol jelly).

The narcotization procedure is not absolutely necessary to achieve desired results but does increase the potential for localizing lipid droplets in the velum. If necessary, larvae may be left in 10% buffered formalin (step ID) for a few days prior to staining. There is no maximum time for the staining procedure (step IIIB) since ethylene glycol should not alter gross lipid distribution (Humason 1962). Further information for obtaining permanent whole mounts of larvae may be found in Humason (1962).

Tissues surrounding the digestive gland remained stained after a prolonged clearing period of up to 48 hours for some groups. This diffuse coloration of the tissues did not photograph well with black and white film making it necessary to note the coloration present while observing through the microscope.

Quantitative data for total lipid levels of *T. navalis* larvae grown at 20°C and fed *I. galbana* with subsequent 3-day starvation periods were determined colorimetrically on groups of 1,000 to 2,000 freeze-dried larvae after chloroform-methanol extraction using the method of Marsh and Weinstein (1966).

RESULTS

Prior to feeding, the straight hinge stage larvae contained many small lipid droplets spread throughout the tissues with a major concentration at the base of the velum (Figure 1). Upon starvation, these disappeared gradually over a period

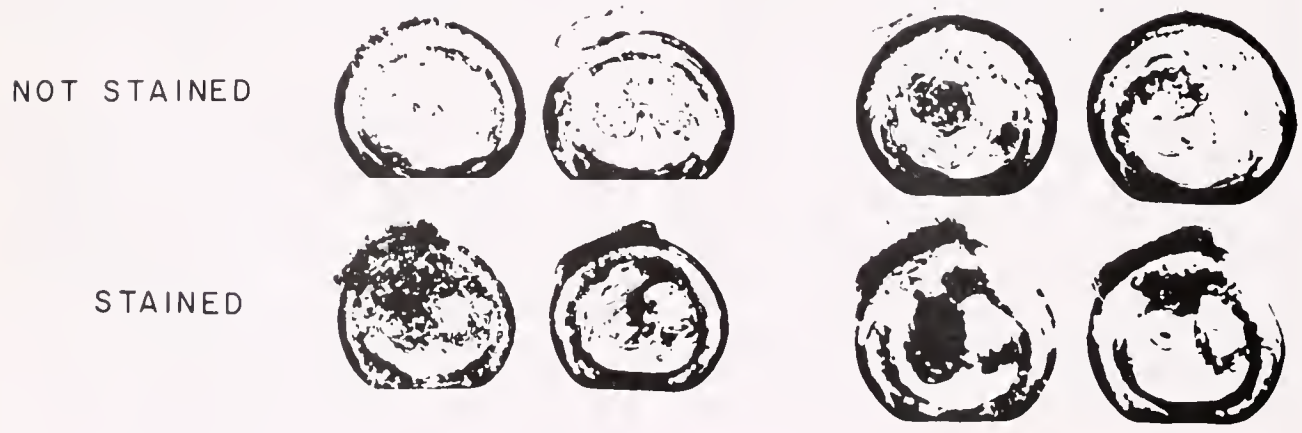

Figure 1. Newly spawned larvae of *Teredo navalis* (0 days), starved for 3 days (starved), and either preserved in formalin (not stained) or stained with Sudan Black B (stained). Larvae after 4 days of feeding (4 days) and a subsequent 3-day starvation period (starved).

of a few days, while the area surrounding the digestive gland became more heavily stained as growth continued.

Sudan Black B worked especially well for young larvae and was retained in the tissues for a longer period of time than Oil Red O. However, if microscopic examination of the larvae was possible within a few days of staining and color photographs were to be taken, then the visually striking bright-red coloration of the lipid droplets produced by Oil Red O was far superior to the coloration obtained with Sudan Black B.

Shell growth was poor at 10°C regardless of the food species, and greatest at 30°C when *I. galbana* was the food source (Figure 2). The diameter of the darkly stained area representing the digestive diverticula increased with growth of the larvae at both 10° and 20°C (Figures 2 and 3). Larvae fed either *I. galbana* or *P. tricornutum* at 10°C accumulated large lipid reserves relative to their shell size. There was no major accumulation of lipid at 30° with either food species. Dispersed tissue coloration was present in all starved larvae at 20°C and 30°C, in larvae fed *P. tricornutum* at 20° and 30°C, and in larvae fed *I. galbana* at 30°C.

Quantitative analysis of total lipid levels of *T. navalis* larvae grown at 20°C on *I. galbana* revealed a steady increase in lipid level throughout development, reaching a maximum of 0.12 μg lipid/larva at the pediveliger stage (Figure 4). Obvious decreases in total lipid level occurred at each developmental stage when 3-day starvation intervals were imposed.

DISCUSSION

The variable culture conditions and subsequent larval growth encountered in any bivalve hatchery system necessitates the use of condition indicies throughout larval development. Since all of these indicies (e.g., growth rate, mortality, disease signs, etc.) are essentially *post facto* in nature, the culturist has little real-time control over problems that may arise during development. It is possible that the normal pattern of storage and utilization of biochemical components concerned with energy metabolism would be influenced by adverse culture conditions. If the progression of this dysfunction could be monitored on a routine basis with a simple assay then such a technique could be used as a diagnostic tool for early reparative measures.

The biochemical component utilized during times of energetic imbalance in invertebrate larvae has been identified as lipid rather than protein or carbohydrate because it is the most abundant and easily mobilized storage material (Holland 1978). Helm et al. (1973) concluded that healthy adult oysters (*Ostrea edulis*), fed a food supply supplemented with phytoplankton during conditioning, produced more viable larvae, with higher lipid levels, upon release at the straight hinge stage than those oysters whose diets had not been supplemented. Millar and Scott (1967) also have shown that larval lipid levels were dramatically reduced within a few days when newly liberated *O. edulis* larvae were starved. These results were visually reproduced in this study with shipworm larvae indicating that the present lipid staining technique could be used to make viability judgments on newly spawned larvae as well as throughout larval development.

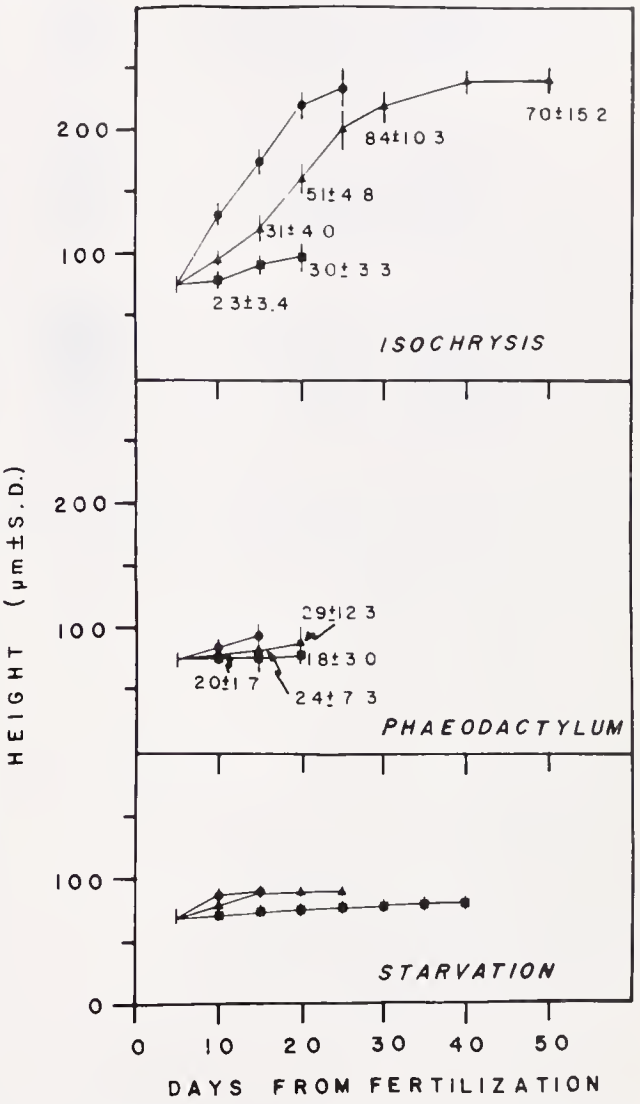

Figure 2. Shell growth of *Teredo navalis* larvae at three temperatures: 10°C (■), 20°C (▲), and 30°C (●) on two food species and a starvation control. Bars represent 1 standard deviation (SD). Numerical values are the mean ± SD of the diameter of the darkly stained area of the digestive diverticula at various stages of development (N = 30 for each value).

Bayne (1965) observed that large numbers of oil droplets began to appear at the onset of metamorphosis in *Mytilus edulis* larvae. When metamorphosis was delayed, these droplets gradually disappeared. A similar pattern occurred during periods of starvation. The author suggested that this could represent an important food supply during times of stress and metamorphosis. Culliney (1975) observed clusters

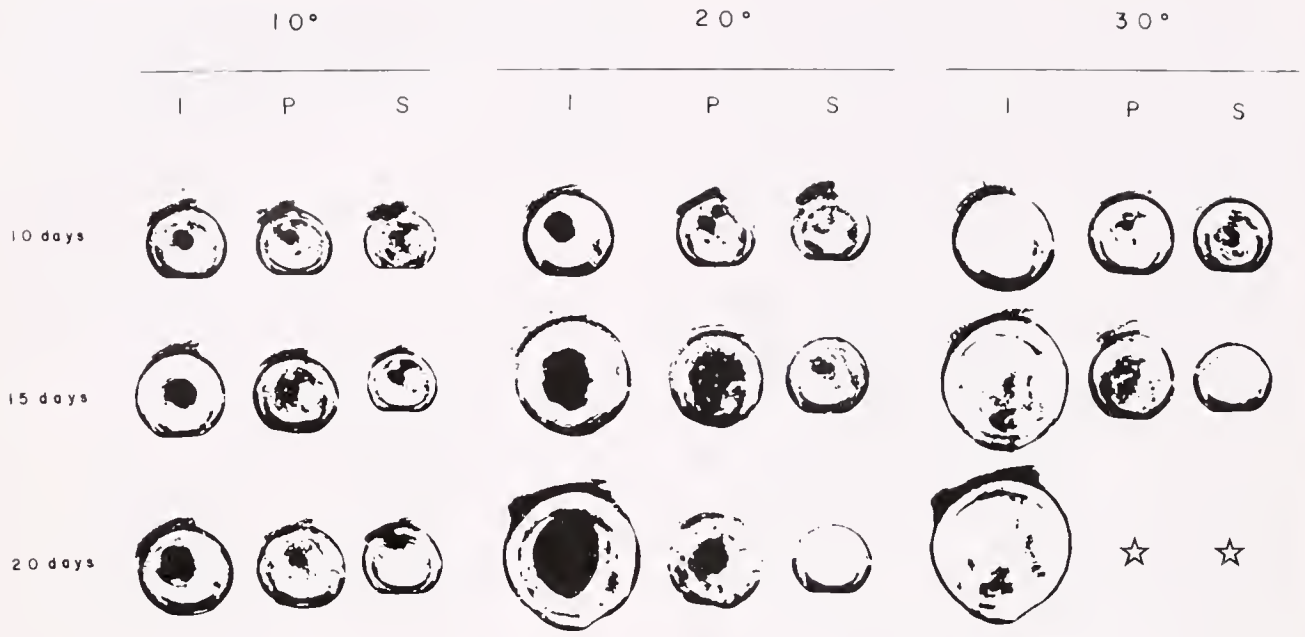

Figure 3. Three stages of *Teredo navalis* larvae fed *Isochrysis galbana* (I), *Phaeodactylum tricornutum* (P), and starved (S) grown at three temperatures. All larvae were stained with Sudan Black B (☆, died; bar = 200 μm).

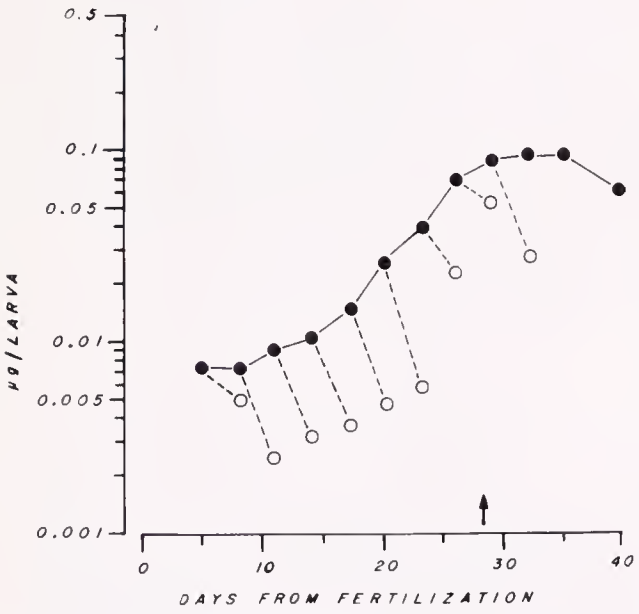

Figure 4. Total lipid levels of *Teredo navalis* larvae fed *Isochrysis galbana* at 20°C before (●) and after (○) a 3-day starvation period. Arrow indicates 50% of population attained functional pediveliger.

of "transparent globules" in umbo stages of *Teredo navalis* surrounding the digestive gland. The 10 to 20 μm globules, thought to be important food reserves, were equivalent in size to the lipid droplets described in this study. Other molluscan larvae have similar patterns of reserve accumulation. Fretter and Montgomery (1968) noted the increase in size and darkening in color of the digestive gland of prosobranch veligers throughout growth and development. They suggested that this could be used as an index of feeding because varying color regimes were produced in the gland with different diatoms in the diet.

The diffuse tissue coloration and relatively small digestive gland area observed upon staining larvae grown at high temperatures, fed *P. tricornutum* or starved, could represent a shift in the pattern of lipid storage. These forms of stress may necessitate mobilization of stored energy reserves into the tissues surrounding the digestive gland to meet imposed metabolic demands. Conversely, larvae grown at low temperatures retained relatively greater quantities of lipid in the digestive gland area, presumably due to decreased energetic costs. Elston et al. (1981) have shown that the normal pattern of lipid accumulation and utilization was disrupted in the larval disease "vibriosis". Staining subsamples of large cultures specifically for lipid could be used to test for early signs of this disease; staining will show an abnormal distribution of lipid droplets in the digestive diverticula (R. L. Elston, Cornell University, personal communication).

The present staining technique illustrates gross lipid accumulation and depletion in relation to environmental variables. These results have been substantiated by total lipid analysis. It may be possible to employ this method as a diagnostic tool for determining food quality, larval condition, and potential for rapid growth in large-scale bivalve cultures.

ACKNOWLEDGMENTS

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NITROGEN BALANCE OF JUVENILE SOUTHERN QUAHOGS (*MERCENARIA CAMPECHIENSIS*) AT DIFFERENT FEED LEVELS[1,2]

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ABSTRACT A Tahitian strain of *Isochrysis* sp. was grown in outdoor continuous culture and fed at four different cell densities to juveniles of the southern quahog clam *Mercenaria campechiensis* (Gmelin). Those cell densities were: 1×10^4, 5×10^4, 1×10^5, and 5×10^5 cells/ml. Controls consisted of trays without animals receiving an inflow cell density of 5×10^4 cells/ml, and trays with animals, but receiving only filtered seawater. Duplicate populations of 100 animals received each treatment; each population had a whole wet weight of 10 g. The total flow rate to each population was 120 ml/min.

Incoming filtered seawater, incoming algal culture, and effluent from each shellfish population were collected daily and analyzed for nitrite, nitrate, ammonia, urea, dissolved free amino acids (DFAA), soluble protein, total dissolved nitrogen, and particulate protein nitrogen (PPN).

A nitrogen balance for juveniles of *M. campechiensis* in a continuous flow system was calculated; 85 to 95% of all total incoming nitrogen was accounted for in the different treatments.

Change in concentration of the various nitrogen-containing compounds as a result of passage through the shellfish culture containers is described. Only those populations receiving an inflow algal protein concentration of 5.75 μgat PPN/l showed a significant excretion of ammonia. Any excretion of DFAA or urea was absorbed by microorganisms present in the shellfish culture containers. Both nitrite and nitrate were absorbed by algae present in the copious biodeposits of shellfish populations receiving an inflow algal protein concentration of 56.01 μgat PPN/l, and a significant uptake of soluble protein by shellfish populations receiving $\geqslant 5.75$ μgat PPN/l was noted.

INTRODUCTION

The successful cultivation of bivalves requires control of the reproductive cycle of the organism and knowledge of its environmental and nutritional requirements. This latter criterion requires investigating the best type(s) and amounts of food. Criteria for determining the best type and/or amount of food include growth, feeding rate, food chain efficiency, ecological efficiency, protein conversion efficiency, and condition index.

These criteria help to determine the best feeding regime for the organism, but may not indicate the best feeding regime insofar as the total culture system is concerned. No organism can be cultured without regard to its role in the culture system. If a particular food type is difficult and/or expensive to grow, it may not be the best food organism to use in the culture system, even though it may be very nutritional for the bivalve. A particular food density that is optimal for growth of the bivalve may result in the excretion of toxic ammonia.

For these reasons, a complete study of the nutritional requirements of a bivalve being considered for intensive aquaculture must take into account the role of the animal in the managed food chain. One must determine how a culture system affects the bivalve and how the bivalve affects the system.

An excellent way to gauge those affects is by constructing a nitrogen balance of the entire managed food chain. A nitrogen balance should be constructed because: (1) nitrogen often is the limiting nutrient of the growth of the primary trophic level (Ryther and Dunstan 1971), (2) nitrogenous waste products of the bivalve can be toxic to the animals themselves or to other organisms downstream, (3) these nitrogenous waste products may be used for the growth of macrophytes, and (4) the production of animal protein is often the primary goal of such managed food chains.

An important byproduct of studying nitrogen dynamics of bivalves in a continuous-flow, managed food chain is understanding the role of bivalves in the nitrogen cycle of their natural environment. The results of such a study may not be as realistic as a field study, but is more controllable and subject to more intensive investigation, i.e., studying the effect of varying different elements of the biotic and abiotic environments of the animal. Those studies in which a small number of clams were unfed for 24 hours prior to the experiment, placed into a small bowl of static, synthetic seawater, and the change in concentration of different nitrogen compounds measured in the medium, may be even more controlled and precise than studies involving a continuous-flow, managed food chain. However, they are so far removed from "real" life as to render the results interesting but almost irrelevant.

A continuous-flow, managed food chain perhaps is the best method to use to study the physiological responses of an organism to biotic and abiotic factors of its environment.

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Field studies can raise questions and validate the results of studies in managed food chains.

A nitrogen balance was constructed for juveniles of *Mercenaria campechiensis* (Gmelin) that were fed *Isochrysis* sp. at different densities. Juveniles were used because little is known of the bioenergetics and nitrogen cycling of juvenile shellfish, and the greater growth rate of juveniles resulted in more measurable growth in a shorter period of time. The increased metabolism of juveniles resulted in more measurable changes in various physiological responses, such as ammonia excretion, in a shorter period of time. *Mercenaria campechiensis* was used because little information is available in the literature on its growth and physiology, although the clam is abundant along the Gulf coast. Its growth is usually faster than that of the northern quahog *Mercenaria mercenaria* (Linné), or their reciprocal hybrids; it is more tolerant to high temperatures than *M. mercenaria.*

MATERIALS AND METHODS

Algae

The alga used in this study is a Tahitian strain of *Isochrysis* (T. *Iso.*) obtained from Dr. K. C. Haines of the St. Croix, U.S. Virgin Islands, Artificial Upwelling Project.

The algae were grown in outdoor continuous culture at the Port Aransas Marine Laboratory on the Texas Gulf coast during October through November 1978, at a daily turnover of 0.4. Guillards' F medium was used to enrich the incoming 1 μ-filtered seawater to a level of 150 μgat $NO_3 - N/L$.

Shellfish

Brood stocks were collected in an intertidal area of Redfish Bay, an estuarine area between the mainland and the barrier islands of the Texas Gulf coast near Corpus Christi, in late February 1978. The clams were kept in the laboratory for acclimation and gonad ripening, and were fed T. *Iso.*, exclusively. Spawning was induced by thermal shock and the addition of stripped gonad suspensions. The experimental animals were the progeny of one female and two males. The larvae were fed a variety of phytoplankton species including T. *Iso.*, *Chaetoceros* sp., and others. There was no mortality after spat settlement indicating that water quality was good and that T. *Iso.* (fed exclusively after spat settlement) was a good food for juveniles of *M. campechiensis.*

Prior to the experiment, 1,100 clams with shell lengths of 7.62 ± 0.4 mm were divided into 11 groups of 100 each. The average whole wet weight of each of those groups was 10.2 g ± 0.01. Group 11 was used to determine the shell length, whole wet weight, and protein content of the other experimental groups.

Each experimental group was kept in round plastic bowls with tapered sides. Top and bottom diameters were 14 cm and 10 cm, respectively. A plastic standpipe in the center of each bowl maintained the water level at a depth of 4 cm for a total volume of 250 ml. The inflow of cultured algae and/or filtered seawater created a vortex in the containers ensuring thorough mixing. The clams were spaced evenly on the bottom of each bowl. Each group received a continuous flow of 1 μ-filtered seawater and/or cultured algae as indicated in Table 1.

TABLE 1.

Flow rates and cell densities of experimental treatments.

Treatment	Algal Culture Flow (ml/min)	Filtered Seawater Flow (ml/min)	Cell Density (cells/ml)	Corresponding Inflow Algal Protein–N Concentration (μgat/l)
1	120	0	5×10^5	56.0
2	24	96	1×10^5	11.3
3	12	108	5×10^5	5.7
4	2.4	117.6	1×10^4	1.3
5	0	120	0	0

Two replicate populations were utilized for each treatment. Treatment 5, the control, received filtered seawater only. Another control, which consisted of an identical experimental setup but no clams, received 5×10^4 cells/ml (Figure 1).

Experimental clams were kept in the dark throughout the experimental period. Water temperatures ranged from 23° to 28°C, and salinities from 25 to 29 ppt during the 4-week experiment.

At the end of each week, the clams were removed from their containers, blotted dry, and each group weighed after the effluents from each clam group had been taken and flow rates checked. The groups were then culled back to their starting whole wet weights, and the remaining clams returned to the experimental culture containers. The culled clams were frozen for later analysis.

Biodeposits or tank deposits from the experimental containers were removed and stored for later analysis prior to returning the clams.

ANALYTICAL METHODS

Cell Densities

Cell densities were measured with a Speirs-Levy eosinophil counter.

Particulate Protein Nitrogen (PPN)

The method of Dorsey et al. (1977) was modified for use with the Auto Analyzer II. The auto analyzer (AAII) dispensed 1N phenol reagent and absorbance was read on the AAII colorimeter.

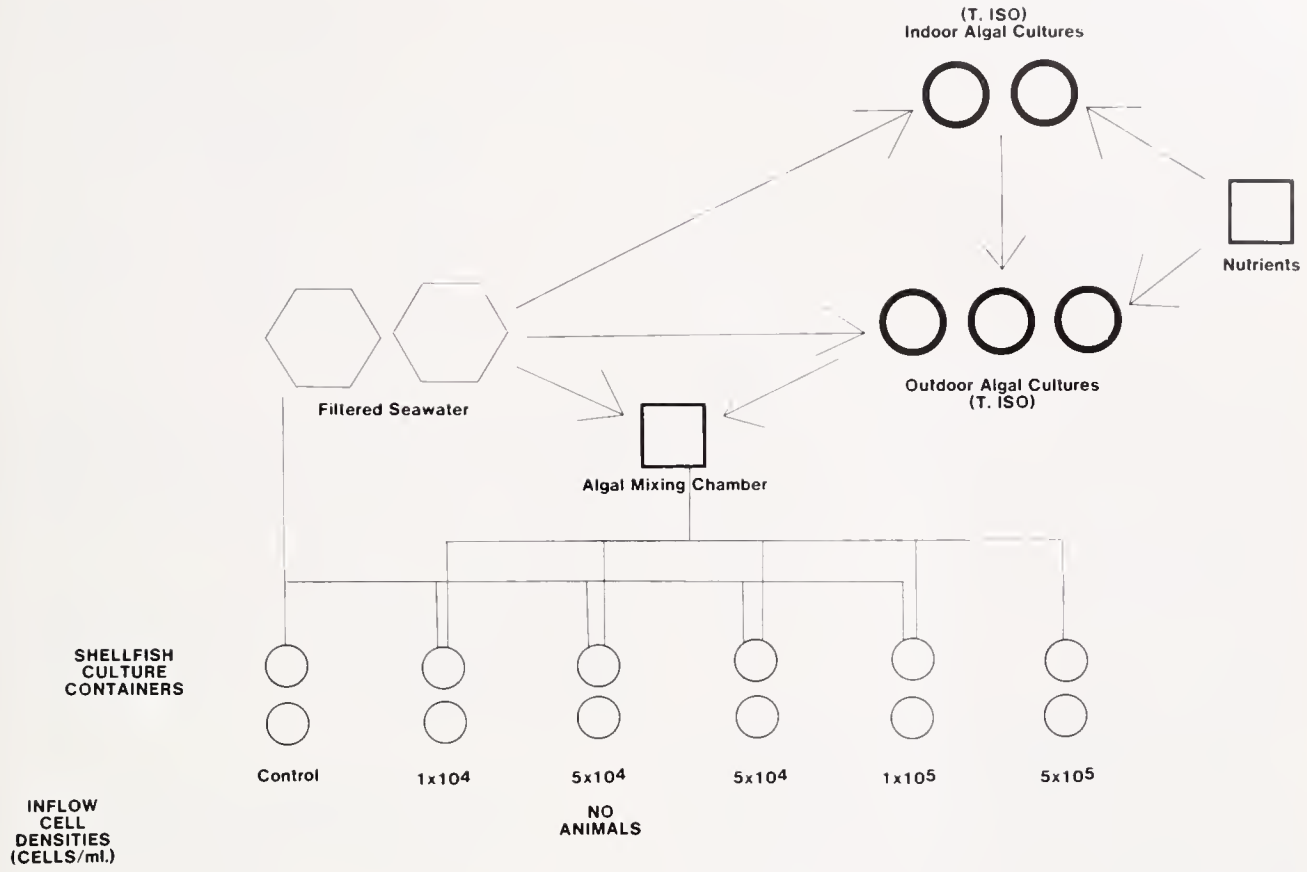

Figure 1. Experimental design.

Soluble Protein Nitrogen (SPN)

For this method, developed by the authors, the sample was filtered through a 47-mm Gelman glass fiber filter, 0.45-μ pore size, and the filtrate was retained. Dissolved protein was precipitated by the addition of 5.0 ml of concentrated perchloric acid per 100 ml of sample. The sample was carefully mixed by swirling and cooled in a circulating water bath for 2 hours at 5°C. It was then filtered through double 25-mm Gelman glass fiber filters (0.45-μ pore size). The sample container, filter holder, and filters were washed with glass-distilled water. Precipitated protein remaining on the filters was then determined by the PPN method of Dorsey et al. (1977).

The lower limit of sensitivity of the method was determined by the reagent blank. At least 0.10 μgat protein nitrogen must be present on the filters. Thus, a 100-ml sample with a concentration as low as 1.0 μgat protein nitrogen per liter was sufficient for an assay.

This method was linear over the range of 1.0 to 80 μgat protein nitrogen per liter.

Other Nitrogen-Containing Compounds

Standard methodologies were used to analyze nitrate plus nitrite (Technico Corp. 1978), ammonia (Berg and Abdullah 1977), urea (DeManche et al. 1973), DFAA (Coughanower and Curl 1975), and total dissolved nitrogen (TDN) (D'Elia et al. 1977).

Shellfish Wet Weight, Dry Weight, and Protein Content

Clams were blotted dry with a paper towel and weighed on a Mettler analytical balance H54AR (precision: ± 0.01 mg). They were then frozen for later analysis. This gave the whole wet weight value.

When needed for further analyses, the frozen clams were placed in pretared aluminum weighing dishes and kept at room temperature for at least 2 hours to ensure that all clams were gaping. They were then dried in an oven at 70°C for 24 hours. This gave the whole dry weight value.

No more than 5.0 g whole dry weight of clams were put into 100 ml of 1N NaOH in a 125-ml glass Erlenmeyer flask. The flask was covered and boiled at 100°C for 100 minutes along with two flasks containing a standard of Bovine Serum Albumin and a 1N NaOH blank. The flasks were swirled and allowed to cool to room temperature.

Duplicate 0.5-ml aliquots were taken from each flask and placed into acid-washed test tubes that were rinsed in glass-distilled water.

The supernatant from the flasks was decanted, and the remaining shells were rinsed repeatedly with glass-distilled water to remove all traces of NaOH. They were then dried

to constant weight at 70°C for 24 hours in a pretared aluminum weighing dish to obtain dry shell weight. Dry meat weight was taken as the difference between whole dry weight and dry shell weight.

Tank Deposits

Tank deposits that accumulated over 1 week in each clam container were collected at the end of the week in a 1-ℓ polyethylene screw-cap bottle and the volume brought to 1 ℓ with filtered seawater.

Contents of the bottle were filtered through 47-mm Gelman glass fiber filters (0.45-μ pore size). Different numbers of filters were necessary for different samples depending on the amount of particulates present. The filters were stored frozen for later analysis of protein content. When needed, the filters were put into a pretared aluminum weighing dish and dried in an oven to constant weight at 70°C for 24 hours.

Filters were digested as described for clams, and protein content was determined using the method of Dorsey et al. (1977).

Statistical Tests

Statistical tests used included Edwards' (1972) factorial analysis of variance (ANOVA) for both independent groups and repeated measures, Scheffé's test for pairwise differences, and the one-sample t-test described by Edwards (1972). A 95% confidence level was the minimum acceptable level.

RESULTS

Nitrogen Balance

Overall Nitrogen Balance. A nitrogen balance is an accounting of all nitrogen-containing compounds entering and leaving a system. In the present study, the concentration of a number of nitrogenous compounds flowing into and out of experimental groups of clams was determined. The total amount of nitrogen "going" to each group of clams was determined by summing the inflow amounts (in mg nitrogen) of particulate protein, nitrite ion, nitrate ion, ammonium ion/ammonia, dissolved free amino acids, urea, and soluble protein. The total amount of nitrogen "leaving" each group of clams was determined in a similar manner except that the protein of the biodeposits (tank deposits) and the protein gain of the shellfish themselves were added to this total.

The fraction of total inflow nitrogen (TIN) accounted for was determined by the calculation:

$$TIN_{in} = 100 - (N_{in} - N_{out})/N_{in} \times 100.$$

A summary of those calculations for each of the experimental treatments is shown in Table 2.

TABLE 2.

Nitrogen balance of juveniles of *Mercenaria campechiensis.*

Treatment	ΣN_{in} (mg/week)	ΣN_{out} (mg/week)	% Accounted For
1	1761.41	1502.31	85.29
2	485.39	425.06	87.57
3	325.88	298.18	91.49
4	198.28	180.63	91.10
5	166.39	159.59	95.91

Total dissolved nitrogen was determined in all influents and effluents. That analysis measured all dissolved nitrogen regardless of its form. Strong oxidizing agents, and high temperatures and pressures (via autoclaving) oxidized all N-containing compounds to a nitrite ion which was then assayed directly.

Thus, a different nitrogen balance can be constructed using PPN and TDN only. The percent of inflow nitrogen accounted for when using PPN and TDN only was fairly constant (see Table 3).

TABLE 3.

Nitrogen balance using PPN and TDN only.

Treatment	Mean Weekly Nitrogen In (mg)	Mean Weekly Nitrogen Out (mg)	% Accounted For
1	2202.002	1983.078	90.06
2	755.488	680.079	90.02
3	574.676	521.757	90.79
4	430.024	382.847	89.26
5	393.864	351.261	89.18

Particulate protein nitrogen of the outflow included the PPN of tank deposits (biodeposits) and the gain in protein by the clams.

Individual Nitrogen-Containing Compounds

Ammonia. The ammonia-N excretion increased with increasing inflow algal protein concentration (APC). Maximum excretion of ammonia-N was noted for those clams receiving an inflow APC of 5.75 μgat PPN/l. Further increases in inflow APC decreased ammonia excretion (Table 4).

A t-test (Edwards 1972) was used to determine if the change in concentration (difference between inflow and outflow concentrations) of ammonia-N was significant at the 95% confidence level. Only the change in ammonia-N concentrations of treatment 3 was significant at the 95%

confidence level. That treatment resulted in the fastest growing animals (see Table 5).

TABLE 4.

Percent of total nitrogen accounted for by individual nitrogen compounds.

Nitrogen Compound	In	Out
Treatment 1		
PPN	49.9	38.9
NO_2^-	1.6	1.8
NO_3^-	40.1	42.2
$NH_4^- + NH_3$	1.1	1.1
DFAA	1.8	2.2
Urea	1.7	1.4
SP	3.8	2.6
Treatment 2		
PPN	36.6	30.3
NO_2^-	1.8	2.0
NO_3^-	46.4	50.6
$NH_4^- + NH_3$	2.4	4.3
DFAA	3.1	4.0
Urea	5.0	5.0
SP	4.7	3.9
Treatment 3		
PPN	27.7	21.1
NO_2^-	1.9	2.1
NO_3^-	50.6	51.3
$NH_4^- + NH_3$	3.3	7.6
DFAA	4.1	6.0
Urea	7.2	7.3
SP	5.2	4.6
Treatment 4		
PPN	10.2	7.9
NO_2^-	2.2	3.1
NO_3^-	58.8	58.3
$NH_4^- + NH_3$	5.1	7.4
DFAA	5.9	8.3
Urea	11.5	8.6
SP	6.4	6.5
Treatment 5		
PPN	1.6	1.9
NO_2^-	2.3	2.5
NO_3^-	62.9	63.8
$NH_4^- + NH_3$	5.9	6.5
DFAA	6.8	7.7
Urea	13.7	9.9
SP	6.9	7.6

All treatments had the same size, weight, and number of animals at the start of the experiment. Thus, any difference in ammonia excretion rates during the first week must be due primarily to differences in feeding regime. The rate of excretion of ammonia-N per gram of dry meat weight for the first week was maximum for those clams receiving an inflow APC of 5.57 μgat PPN/l. Those clams receiving more or less APC had lower excretion rates (Figure 2).

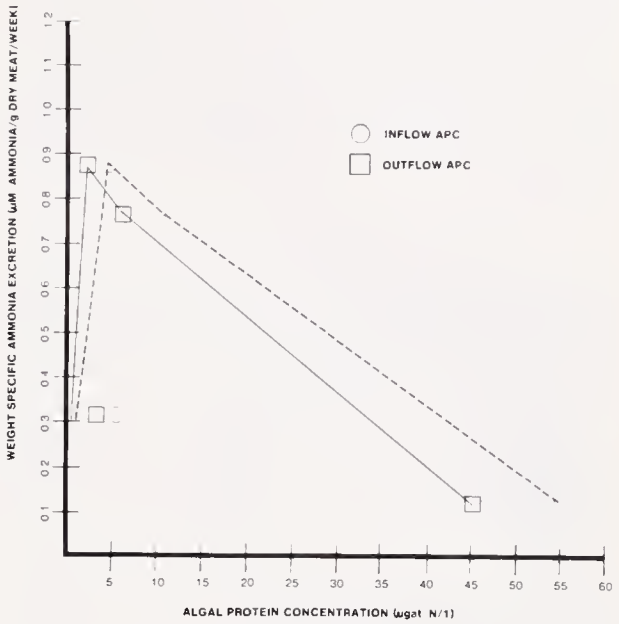

Figure 2. Weight specific ammonia excretion rates as a function of inflow and outflow algal protein concentration.

Urea. An ANOVA was performed on urea-N concentrations of the outflows, and on the dfference between inflow and outflow concentrations. No significant differences existed between treatments for either outflows or net concentrations. Mean weekly inflow concentrations for each treatment were nearly identical (Table 5).

A t-test showed that changes in urea-N concentrations were not significant at the 95% confidence level for any treatment.

Dissolved Free Amino Acid. The DFAA excretion rate increased with increasing inflow APC until a maximum "excretion" rate was recorded by those clams receiving an intermediate inflow APC of 5.75 μgat PPN/l. Further increases in inflow APC resulted in a decreased excretion rate (Table 5).

A t-test did not detect a significant difference between the average weekly mean value of DFAA-N of inflow and the effluent concentrations. There was no significant uptake or excretion of DFAA in any of the experimental treatments at the 95% confidence level.

Soluble Protein. An ANOVA showed a significant difference (at the 95% confidence level) among treatments between inflow and effluent soluble protein concentrations. The net uptake of soluble protein was greatest at the densest food treatment, and decreased with decreases in the inflow APC until a net excretion of soluble protein was noted for those clams receiving only filtered seawater. However, a t-test showed that the difference between

average weekly inflow and effluent concentrations of soluble protein for the two lowest food densities was not significant at the 95% confidence level. There was a net uptake of soluble protein by those clam populations receiving an inflow APC greater than or equal to 5.75 μgat PPN/l.

A multiple regression analysis of the difference between inflow and effluent concentrations of soluble protein on ingested protein showed a strong (R^2 = 0.87), positive, nonlinear relationship that was significant at the 95% confidence level.

TABLE 5.

Mean weekly inflow and effluent concentrations (μgat N/l).

Nitrogen Compound	In	Out
Treatment 1		
PPN	56.01	45.40
NO_2^-	1.77	1.67
NO_3^-	45.76	41.06
$NH_4^- + NH_3$	1.28	1.05
DFAA	2.05	2.06
Urea	1.88	1.34
SP	4.49	2.62
TDN	85.31	80.73
Treatment 2		
PPN	11.33	7.03
NO_2^-	0.55	0.53
NO_3^-	14.49	13.81
$NH_4^- + NH_3$	0.76	1.17
DFAA	0.97	1.10
Urea	1.54	1.36
SP	1.51	1.06
TDN	37.15	35.40
Treatment 3		
PPN	5.75	2.93
NO_2^-	0.39	0.39
NO_3^-	10.58	9.84
$NH_4^- + NH_3$	0.69	1.44
DFAA	0.84	1.14
Urea	1.50	1.42
SP	1.14	0.90
TDN	31.14	29.45
Treatment 4		
PPN	1.28	0.69
NO_2^-	0.27	0.36
NO_3^-	7.45	6.71
$NH_4^- + NH_3$	0.64	0.85
DFAA	0.73	0.95
Urea	1.47	0.98
SP	0.84	0.76
TDN	26.32	23.54
Treatment 5		
PPN	0.16	0.16
NO_2^-	0.24	0.26
NO_3^-	6.67	6.49
$NH_4^- + NH_3$	0.63	0.66
DFAA	0.70	0.78
Urea	1.46	1.01
SP	0.76	0.80
TDN	25.12	22.27

Nitrate. Most of the nitrate flowing to the clams came from the mass algal cultures as excess nitrate supplied to the algae. This was shown by the decrease in nitrate concentration of the inflows as the algal cultures were diluted more and more with filtered seawater to make up the different food densities. The incoming filtered seawater had a mean concentration of 6.7 μgat NO_3^-— N/l.

An ANOVA indicated significance at the 95% confidence level among treatments in the difference between nitrate concentrations of inflow and effluent. However, a Scheffé test for pairwise differences indicated that only the densest treatment showed a net change in concentration of NO_3^- which was significantly different from the other treatments at the 95% confidence level. The net uptake of nitrate in this treatment was probably by living algae in the copious biodeposits produced by the clams (Table 5).

Nitrite. A pattern of inflow nitrite concentrations indicated that most of the nitrite came from the algal cultures. The mean weekly nitrite concentration of the filtered seawater was 0.24 μgat N/l.

An ANOVA indicated a significant difference at the 95% confidence level among treatments in changes in nitrite concentration between inflow and effluent. However, a Scheffé test for pairwise differences indicated that only the treatment with the greatest inflow APC was significantly different (at the 95% confidence level) from the other treatments. The net uptake of nitrite in this treatment was probably caused by living algae in the biodeposits produced by the clams (Table 5).

Clam growth, expressed as the mean weekly production of wet meat, was optimum with the treatments providing an inflow APC of 11.3 and 5.7 μgat protein-N/l (treatments 2 and 3) (Figure 3).

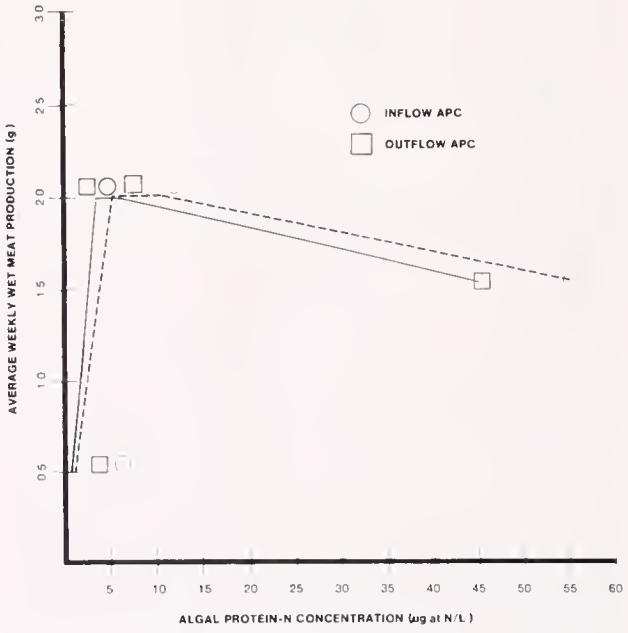

Figure 3. Growth as a function of inflow and outflow algal protein nitrogen concentration.

Clam growth was significantly higher than that shown with the higher or lower food densities. It should be stressed that the food concentration experienced by the clams was somewhat lower than the inflow concentrations (7.0 and 2.9 μgat protein-N/l, respectively) (i.e., effluent PPN concentrations).

DISCUSSION

An overall determination of the fate of incoming nitrogen was accomplished by summing the individual concentrations or amounts of the different compounds. The difference between total nitrogen of the inflow, and of the effluent divided by the total nitrogen of the inflow, was the fraction of total nitrogen not accounted for. In this study, the percent of inflow nitrogen accounted for varied between treatments from 85 to 95%.

The missing nitrogen may, in part, be attributed to loss of free ammonia from the system and from the sample bottles during analyses. Additionally, only PPN was assayed in the algal cells and in the clams. The nitrogen present as nucleic acids, amino sugars, or other forms was not determined and, thus, was not accounted for. Also, some organic nitrogen compounds may have been formed as the result of chemical transformation and not detected in the effluents from the clams by the analytical techniques used in this study. Finally, some of the missing nitrogen may be actually the accumulation of sampling, measurement, and calculation errors.

Only rarely does a single nitrogen-containing compound, other than PPN or nitrate, account for more than 10% of the total nitrogen. Thus, quantitatively, PPN and nitrate are the most important components of the nitrogen balance, but some of the other nitrogen-containing compounds have a qualitative importance. However, in many instances, the weekly mean change in concentration between inflow and effluent of a particular compound(s) was not statistically significant at the 95% confidence level.

The small changes in concentration of nitrogen-containing compounds between influent and effluent that were noted in this study may have resulted from attempts to measure concentrations in a continuous-flow system in which the volume of seawater flowing past the animals was very great compared to the biomass of the animals. Thus, very large amounts of a compound have to be taken up or generated by the clams to cause a significant change in concentration between influent and effluent.

Measuring concentration changes of nitrogen-containing compounds in such a system gives more realistic results than other types of determinations. Studies in which the clams were not fed for 24 hours prior to an experiment and then placed in a bowl of standing synthetic seawater for 24 hours resulted in larger changes in concentration of a particular compound. However, the results cannot be used to describe the normal metabolic activity of the animals. The method described herein approximates more closely the normal metabolic activity of a feeding clam.

An improvement of this method may result from increasing the biomass to volume ratio, leading to greater concentration changes of a nitrogen-containing compound as it passes through shellfish-culture containers in a continuous-flow system. That may result in better resolution of concentration changes associated with static methods of excretion measurements, but will maintain the realism of a continuous flow system.

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A STUDY OF TWO SHELLFISH–PATHOGENIC *VIBRIO* STRAINS ISOLATED FROM A LONG ISLAND HATCHERY DURING A RECENT OUTBREAK OF DISEASE

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ABSTRACT Two bacterial strains belonging to the genus *Vibrio* were implicated in a recent outbreak of disease in larvae of *Crassostrea virginica* at a Long Island shellfish hatchery. Bacteriological observations made during the disease period suggested that the two bacterial pathogens represented an extremely small proportion of the total bacterial population in the seawater system of the hatchery. This was further supported by the appearance of spontaneous disease only after the tenth day of larval development. Although the two strains were morphologically distinct, their biochemical and physiological characteristics suggested that they were closely related to *Vibrio anguillarum*. The disease could be initiated in the laboratory when small numbers of the two pathogenic strains were added (2 cells/ml) after each change of larval culture water. The two strains could be recovered from larval cultures 3 days after a single inoculum of less than 10 cells/ml of larval culture water, even though the water in the cultures was changed daily. This carry-over of bacterial cells shows that extremely small numbers of pathogenic cells present in a seawater system can eventually lead to a disease situation. Ultraviolet radiation was found to be an effective method of eliminating one of the two pathogens. The other partially recovered from exposure within 24 hours.

INTRODUCTION

In 1956, Walne suggested that too little attention was being given to the effect of bacteria on shellfish larvae. His experiments showed that bacterial populations in larval cultures might be 100 times greater than those in the sea. Three years later the first laboratory experiments proving the pathogenicity of specific bacteria were reported by Guillard (1959). Since that time, many studies have been conducted to find effective methods of eliminating or, at least, substantially reducing the occurrence of bacterial diseases.

The need for routine sanitary procedures has been recognized as good preventative medicine (Tubiash 1975). Leibovitz (1978) reported that, since individual hatcheries are different, it is also important to monitor the qualitative physical, chemical, and bacterial changes in larval culture media to determine optimal conditions for each hatchery. Certain antibiotics, i.e., neomycin and chloramphenicol, are recognized as being effective against some bacteria pathogenic for shellfish (Tubiash et al. 1965, Le Pennec et al. 1973); their routine use is not recommended, however, because it can lead to drug resistance. Blogoslawski et al. (1978) reported that ozone can be an effective disinfectant when used with adequate precautions.

A combination of filtration and ultraviolet (UV) light irradiation of seawater also has been found to reduce substantially the occurrence of larval diseases (Brown and Russo 1979). Although these and other disinfection methods have been reported, shellfish hatcheries generally do not use them and, therefore, continue to be plagued by intermittent occurrences of bacterially related diseases which commonly destroy larval cultures around the sixth day of development. One such outbreak occurred during the summer of 1979 at a Long Island (New York) hatchery. The present paper discusses the findings of an ensuing investigation.

MATERIALS AND METHODS

Isolation and Identification of Bacteria

During a visit to the hatchery, samples were taken of the bay water, moribund 10-day-old oyster larvae, and seemingly healthy 5-day-old oyster larvae. Portions of the samples were immediately streaked on seawater agar plates consisting of 0.1% trypticase (BBL)*, 0.1% yeast extract (Difco), 1.0% agar (Difco) in 80% aged, membrane-filtered seawater, and 20% distilled water. Remaining portions of the samples were held overnight in screw-capped test tubes at room temperature and then streaked on seawater agar plates. All plates were incubated for 2 weeks at 26°C; dominant, morphologically distinct colonies were selected from plates inoculated with moribund larvae and grown in seawater broth (same constituents as agar plates minus the agar). Broth cultures were incubated at 26°C overnight and streaked on agar plates for verification of purity. Procedures described by Evelyn (1971) were used to determine the physiological and biochemical characteristics of the suspect pathogens.

Tests for Pathogenicity

The ability of suspect shellfish-pathogenic bacteria to cause mortality was tested by adding from 10^3 to 10^8 bacterial cells from 24-hour broth cultures of the microorganisms to 1 liter of oyster embryonic culture water

*Trade names referred to in this publication do not imply endorsement of commercial products by the National Marine Fisheries Service.

just prior to addition of fertilized oyster eggs, and daily after each change of culture water. In all cases, including untreated controls, the fertilized oyster eggs were reared in 1.3-liter polypropylene beakers at a density of about 15,000 fertilized eggs/liter of 10-μm-filtered, UV-treated seawater (Brown and Russo 1979). Cultures were maintained in a constant-temperature water bath at 26°C. Larval culture water was changed on a daily basis; larvae were fed a mixture of laboratory-grown phytoplanktonic cultures of *Isochrysis galbana, Monochrysis lutheri,* and *Dicrateria inornata.* Larval cultures were sampled and counted on the second and sixth or seventh day of development using the procedure described by Brown (1973). Larvae sampled on the second day were classified into two groups: normal larvae, those which had developed the standard "D"-shaped larval shell; and abnormal larvae, those which had shells that deviated from the standard "D" shape. These two groups were further subdivided according to whether they were living or dead prior to fixation. Larvae sampled on the sixth or seventh day were classified only as alive or dead prior to fixation, and 50 or 100 live larvae were measured to the nearest 5 μm. In preliminary experiments to determine which isolate(s) was pathogenic, culture water was seeded with an isolate only once, prior to the addition of fertilized oyster eggs. These embryonic cultures were neither changed nor fed; on the second day, they were sampled and discarded. The Student's *t* test was used to determine significant differences between controls and experimentals at $P < 0.05$. Koch's postulates were satisfied by reisolating the experimental bacterial strains from moribund larvae and infecting healthy larvae with the isolates.

Bacterial Control

A modification of procedures described by Brown and Russo (1979) was used to test the killing efficiency of UV radiation on the two pathogenic bacterial strains. A black fiberglass tank having a capacity of 135 liters was filled with 10-μm-filtered, UV-irradiated seawater and seeded with a cell suspension of one of the pathogenic isolates, bringing the number of pathogenic cells to 10^4 to 10^5/ml of seawater. Sterile 1.5-liter glass beakers were filled to the 1.0 liter mark with water taken either directly from the seeded tank or after UV irradiation, using a flow rate of 3 liters/minute through an Aquafine Aluminum SL-1 Sterilizer. Samples were taken from the beakers for total plate counts at zero time and 24 hours after the beakers had been filled. Plates were incubated for 1 week at 26°C and counted.

RESULTS AND DISCUSSION

It is not uncommon for a shellfish larval culture to begin to show overt signs of microbial disease after the tenth day of development. This is consistent with the possibility that the responsible microbe(s) is present in the seawater system at very low numbers but, with time, can reach lethal proportions in larval culture containers. Last summer such an outbreak of disease occurred at a Long Island hatchery. Oyster larval cultures routinely were kept for 5 to 6 days in a small room and then moved to a larger one; within 5 days of the move, they would succumb to disease. The larvae showed no signs of bacterial swarming at this time. Globules, however, were found in the umbo of otherwise healthy looking animals. The nature of these globules is unknown, but some investigators at the Milford Laboratory have associated their appearance with disease.

Two bacterial isolates were found capable of producing mass mortality in laboratory experiments. Preliminary experiments showed that 3×10^8 cells of Strain 1, or 1×10^8 cells of Strain 2, added to 1 liter cultures of fertilized oyster eggs resulted in mass mortality within 24 hours. If the number of bacterial cells added was reduced to 10^5/liter, 48 hours were required to produce mass mortality.

Examination of the original plates revealed that the two bacterial isolates grew on plates inoculated with moribund larvae, and on all plates inoculated with samples that had been held overnight before culturing: moribund larvae, bay water, and seemingly healthy larvae. Apparently, the pathogens were present in the seawater in very low numbers, but increased with time to a lethal population size since they did not grow on plates inoculated at the hatchery.

The two bacterial isolates, although they form colonies that are morphologically distinct from each other and have some biochemical differences, may be strains of *Vibrio anguillarum.* Strain 1 forms colonies that are translucent and have diffusing edges, while Strain 2 forms white, nondiffusing colonies. Although Strain 1 is morphologically identical to the *Vibrio* sp. described by Brown and Losee (1978), some biochemical and physiological differences do exist between the two isolates. Table 1 shows common characteristics of the two isolates from the present study, and the strain reported by Brown and Losee (1978) with the emerging archetype of *V. anguillarum* described by Evelyn (1971). They were Gram-negative, nonpigmented motile rods capable of fermenting glucose without gas production. The strains were oxidase positive and could attack arginine but not lysine. They were sensitive to Vibriostat. Growth was inhibited when sodium chloride was either absent or present in a high concentration (10%). Differences among the isolates are presented in Table 2. Although vibrios normally are resistant to penicillin (Shewan 1963), Strain 2 was sensitive to 10 units of penicillin. Strain 2 was able to produce acid in salicin but not in trehalose. It did not produce nitrate from nitrite, but it did produce hydrogen sulfide and deaminate phenylalanine. Unlike the vibrios described by Evelyn (1971) and by Brown and Losee (1978), neither Strain 1 nor Strain 2 grew at 5°C. Strain 1 did not produce acid in fructose, mannose, or trehalose. Whether the differences among the bacterial isolates are enough to warrant placing them in separate species is not yet known. The answer must await determination of the DNA base ratios, moles percent guanine plus cytosine.

TABLE 1.

Common characteristics of three shellfish-pathogenic vibrios and the emerging archetype of *Vibrio anguillarum**.

Characteristics	Reaction	Characteristics	Reaction
Gram stain	−	Citrate as sole	
Pigmented	−	C-source for	
Motility	+	growth	+
Fermentative (glucose)	+	Methyl red	
Gas from glucose	−	reaction	+
Oxidase (Kovacs)	+	Acetoin	
Acid from:		produced	−
Adonitol	−	Gluconate	
Dulcitol	−	utilized	−
Inositol	−	Lysine	
Inulin	−	decarboxylated	−
Lactose	−	Arginine	
Maltose	+	attacked	+
Raffinose	−	Urease	
Rhamnose	−	produced	−
Sorbose	−	Ammonium	
Sucrose	+	produced	+
Xylose	−	Growth in:	
Sensitive to 0/129	+	0% NaCl	−
Catalase produced	+	3% Nacl	+
Starch hydrolyzed	+	7% NaCl	+
Gelatin hydrolyzed	+	10% NaCl	−

*Characteristics of the emerging archetype of *V. anguillarum* as reported by Evelyn (1971).

Table 3 shows that the addition of 10^3 cells of either one of the two strains, or a combination of the two, will cause mortality in a liter larval culture within 48 hours. Live-normal development was significantly less ($P < 0.05$) in cultures exposed to Strain 1 (6×10^1 cells/ml) or Strain 2 (4×10^1 cells/ml) than in untreated controls. Live-normal development of fertilized oyster eggs was only 41% in the presence of Strain 1, and 43% when exposed to Strain 2, compared to 75% in controls. Exposure to a combination of the two isolates (5×10^1 cells/ml) resulted in 47% live-normal development. Table 4 shows that survival and growth were significantly less ($P < 0.05$) in the presence of Strain 2 than in untreated controls. Survival and size averaged 34% and 99 μm, respectively, during exposures to Strain 2, while controls averaged 79% and 116 μm, respectively. Strain 1 appeared to affect survival (40%) but not growth; mean size was 115 μm. Only survival was significantly affected ($P < 0.05$) during exposure to a combination of the two strains. Data indicate that Strain 2 was more virulent than Strain 1. Thirty-three percent fewer cells of Strain 2 were added to cultures than Strain 1 cells, yet the effect was more severe in the presence of the former. The fact that a combination of the two strains did not substantially reduce larval growth suggests that 4×10^1 Strain 2 cells/ml of culture water is very close to the minimal number of cells required for larval growth inhibition.

TABLE 2.

Characteristic differences between three shellfish-pathogenic vibrios and *Vibrio anguillarum*.

Characteristics	Strain 1 (3)*	Strain 2 (2)	Brown and Losee (1978) *Vibrio* sp.	Evelyn (1971) *Anguillarum*
Sensitive to penicillin (10 units)	−	+	−	−
Acid in:				
Arabinose	−	−	−	+? V†
Cellobiose	−	+	+	+
Fructose	−	+	+	+
Galactose	−	−	−	+ V
Glycerol	−	−	+	+
Mannitol	+	+	−	+
Mannose	−	+	+	+
Salicin	−	+	+	−
Sorbitol	−	−	−	+ V
Trehalose	−	−	+	+
Nitrate produced	±	−	+	+
Indole produced	−	±	+	+ V
Hydrogen sulfide produced	−	+	−	−
Phenylalanine deaminated	−	+	−	−
Growth at:				
5°C	−	−	+	+
37°C	−	−	+	−

*Number within parenthesis indicates number of isolates tested.
†V signifies that 20% or more of the strains compared by Evelyn (1971) gave reactions different from that indicated for the emerging archetype.

TABLE 3.

Percentage development of fertilized oyster eggs after two days of exposure to 10^4 bacterial cells.

	Strain 1	Strain 2	Both	Control
Number of replicates	12	12	12	12
Live-normal ($\bar{x} \pm$ SE*)	41 ± 7†	43 ± 3†	47 ± 5†	74 ± 11
Dead-normal ($\bar{x} \pm$ SE)	30 ± 6†	22 ± 5†	27 ± 4†	1 ± 1
Live-abnormal ($\bar{x} \pm$ SE)	1 ± 1	1 ± 0	0 ± 0†	1 ± 0
Dead-abnormal ($\bar{x} \pm$ SE)	1 ± 0†	1 ± 0	1 ± 0†	0 ± 0
No. bacterial cells added/ml	6×10^1	4×10^1	5×10^1	None

*Standard error at 95% confidence interval.
†Significantly different ($P < 0.05$).

TABLE 4.

Percentage survival and average size (μm) of oyster larvae after six days of exposure to 10^4 bacterial cells added daily at each change of culture water.

	Strain 1	Strain 2	Both	Control
Number of replicates	10	10	10	10
Survival ($\bar{x} \pm$ SE*)	40 ± 5†	34 ± 7†	35 ± 3†	79 ± 9
Size ($\bar{x} \pm$ SE)	115 ± 4	99 ± 5†	110 ± 3	116 ± 7
No bacterial cells added/ml	6×10^1	4×10^1	5×10^1	None

*Standard error at 95% confidence interval.
†Significantly different ($P < 0.05$).

Figure 1 shows that one small inoculum of bacteria could remain in larval cultures for many days, even when the cultures were changed daily. Both Strain 1 and Strain 2 were recoverable from the culture water three days after a single inoculum of 1 x 10^1 cells/ml and 3 x 10^1 cells/ml, respectively, was added. The counts increased the first two days, 1 x 10^5/ml for Strain 2 and 6 x 10^4/ml for Strain 1, and then started to decline. This carry over of bacterial cells illustrates that extremely small numbers of pathogenic cells present in a seawater system can eventually lead to a disease situation. The decline may have been due to invasion into larvae.

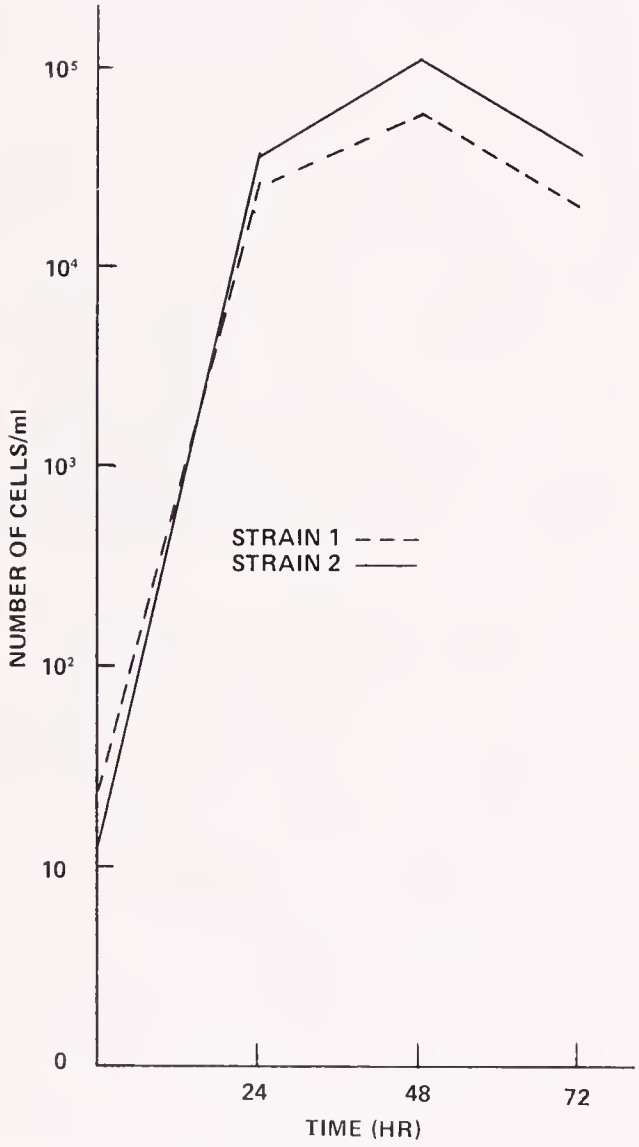

Figure 1. Growth of two pathogenic bacterial strains in oyster larval cultures over a three-day period.

When the number of bacterial cells was further reduced, live-normal development was significantly greater in the presence of Strain 1 (1 cell/ml) than in untreated controls after two days (Table 5). Development was only 77% in controls, compared to 84% in exposures to Strain 1. Although live-normal development was greater in the presence of Strain 2 (2 cells/ml) than in controls, the difference was not considered significant; live-normal development for cultures exposed to Strain 2 was 81%. Contrary to what was found in the presence of 10^1 cells/ml, Table 6 shows that the addition of very small numbers of two bacterial strains together had a greater effect than either of the two used singly. Survival in the presence of Strain 1 (3 cells/ml) was 75%, and 70% in the presence of Strain 2 (1 cell/ml). Survival and growth of larvae were significantly less ($P < 0.05$) in cultures exposed to both strains (2 cells/ml) than in control cultures. Survival averaged 63%, while size was 116 μm in the presence of both strains. Survival and growth, on the other hand, averaged 71% and 121 μm, respectively, in the controls.

TABLE 5.

Percentage development of fertilized oyster eggs after two days of exposure to 10^3 bacterial cells added daily at each change of culture water.

	Strain 1	Strain 2	Control
Number of replicates	10	10	10
Live-normal ($\bar{x} \pm$ SE*)	84 ± 6†	81 ± 6	77 ± 6
Dead-normal ($\bar{x} \pm$ SE)	5 ± 2	4 ± 2	5 ± 3
Live-abnormal ($\bar{x} \pm$ SE)	2 ± 1	3 ± 1†	2 ± 1
Dead-abnormal ($\bar{x} \pm$ SE)	2 ± 1†	1 ± 1	1 ± 1
No. bacterial cells added/ml	1 x 10^0	2 x 10^0	None

*Standard error at 95% confidence interval.
†Significantly different ($P < 0.05$).

TABLE 6.

Percentage survival and average size (μm) of oyster larvae after six days of exposure to 10^3 bacterial cells added daily at each change of culture water.

	Strain 1	Strain 2	Both	Control
Number of replicates	15	15	15	15
Survival ($\bar{x} \pm$ SE*)	73 ± 5	70 ± 8	63 ± 8†	71 ± 7
Size ($\bar{x} \pm$ SE)	120 ± 4	118 ± 3	116 ± 3†	121 ± 4
No. bacterial cells added/ml	3 x 10^0	1 x 10^0	2 x 10^0	None

*Standard error at 95% confidence interval.
†Significantly different ($P < 0.05$).

Data indicate that at 10^1 cells/ml the two strains, singly and together, have an adverse effect after only 2 days. If less than 10 cells/ml are employed, a beneficial effect is seen at the straight-hinge stage. This effect, however, slowly declines with time. The decline is probably due to an increase in bacterial numbers caused by the carry over of bacteria during changes in the culture water. One possible

explanation of the data is that the microbes produce a metabolite which is beneficial in minute quantities, but becomes detrimental in larger amounts. If this is so, then it is conceivable that development to the straight-hinge stage was enhanced during the spontaneous outbreak of this disease in the commercial hatchery; the number of pathogenic cells was very small in the bay water.

Table 7 illustrates that the dosage of UV radiation used in this study was effective in killing cells of Strain 2 but not of Strain 1. Strain 1 suffered growth inhibition immediately after the radiation dosage; some cells, however, were able to recover within 24 hours. It must be kept in mind, however, that very high numbers of bacteria were used in this study; whereas, very low numbers were present in the bay water used by the hatchery. Hence, there is reason to believe that UV treatment could be effective; Tables 5 and 6 show that at very low numbers both pathogenic strains were required for the disease process. Killing Strain 2 then would prevent an outbreak of the disease, at least until Strain 1 could reach a lethal level. Since it took 10 days for mortality to occur without treatment, with treatment the animals should be able to metamorphose before this level is reached. The animals then would be more resistant to infection because larval resistance increases with age (Brown 1973). Juvenile clams held at the hatchery were affected during the outbreak of disease that occurred during the summer of 1979.

TABLE 7.

Effect of ultraviolet (UV) radiation on survival of two pathogenic *Vibrio* strains.

	0 Hours		24 Hours	
	UV*	No UV	UV	No UV
Strain 1	0	4×10^4	4×10^1	3×10^5
	0	2×10^4	3×10^2	1×10^5
	0	7×10^4	6×10^2	2×10^5
Strain 2	0	5×10^4	0	5×10^5
	0	3×10^4	0	3×10^5
	0	3×10^5	0	9×10^5

*Number of pathogenic bacterial cells/ml of seawater.

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DIET OF GREEN CRAB *CARCINUS MAENAS* (L.) FROM PORT HEBERT, SOUTHWESTERN NOVA SCOTIA

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ABSTRACT Stomach contents of 762 green crabs *Carcinus maenas* collected from the intertidal zone at Port Hebert, southwestern Nova Scotia, during May and August 1978, were examined. Present in the 608 stomachs that contained food were 20 different, identifiable food items. Bivalves, such as *Mya arenaria* and *Mytilus edulis*, were the most important food items in terms of both estimated volume and frequency of occurrence. Algae, gastropods, and crustaceans appeared of lesser importance. *Cancer* crab remains were identified in some stomachs, but there was no evidence of green crab predation on lobsters. Significant differences were apparent between the green crab diet in May and in August, although the order of importance of the various food items remained relatively constant. Green crab diet appears to overlap that of sympatric crab and lobster species. High abundances of 69 and 99 green crabs per-man-hour-searched were found on both sampling dates, respectively. There were significant differences in crab mean carapace width and male:female sex ratio between the two samples.

INTRODUCTION

The green crab *Carcinus maenas*, introduced accidentally from the eastern Atlantic, is found along the eastern coast of Canada and the United States from southern Nova Scotia to Virginia (Holthuis and Gottlieb 1958). Green crab population size appears closely associated with long-term temperature trends, reaching maximum abundance during periods of increasing temperature (Welch 1968). Green crabs were first observed in Nova Scotia in the early 1950's, in phase with such a period of increasing temperature (Glude 1955, MacPhail et al. 1955).

Green crabs are commonly found from the high tide level down to 3 fathoms (5.5 m) (Crothers 1969), although some have been reported as deep as 10 fathoms (18.3 m) (Perkins and Penfound 1971). They occur on all shore types, but attain maximum abundance in the most sheltered habitats where they outcompete all other crab species (Crothers 1970). Adult green crabs migrate up and down the shore with the tide, but are regularly stranded, under cover, between tide marks at low tide (Naylor 1958). In contrast, juveniles appear to remain fairly stationary on the shore and show no rhythmical migration patterns (Atkinson and Parsons 1973).

American lobsters *Homarus americanus* can be found intertidally in southwestern Nova Scotia, and are trapped commercially in depths as shallow as 3 m (MacKay 1926, Stasko and Campbell 1980). Sheltered inshore areas are possibly important 'nurseries' for juvenile lobsters (Mann 1977). Similarly, rock crabs *Cancer irroratus*, and jonah crabs *Cancer borealis*, occur in intertidal and sublittoral zones. Therefore, since green crabs, *Cancer* crabs, and lobsters can coexist in the same habitat in southwestern Nova Scotia, these species may compete for common resources.

The only previously published analyses of North American green crab stomachs were performed on specimens from Massachusetts and New Hampshire (Ropes 1968), and suggest that prey eaten largely reflects the species available in the immediate habitat. The present study investigates the diet of green crabs from the northerly limit of their North American range to determine how that diet corresponds with the diet of lobsters and *Cancer* crabs from the same general region; and whether small lobsters and *Cancer* crabs are part of the diet of green crabs.

METHODS

Male and female green crabs were collected by hand from a sheltered, rocky bay close to Port Hebert, Queens County, Nova Scotia, at low tide on the afternoons of May 18 and August 17, 1978. Collections were timed in terms of crabs found per-man-hour-searched so that approximate abundance estimates could be made for both dates. All crabs collected were in a hard-shell condition. They were sexed and measured across the widest part of the carapace, from tip to tip of the most distal marginal teeth to enable assessment of size frequency.

Within an hour of capture, the top of each crab's carapace was pulled away to reveal the stomach sac which was then removed and preserved in 10% formalin. Contents of each stomach were identified with the aid of a dissecting microscope. The importance of each food category was evaluated by a points method, which considers abundance and volume, and by frequency of occurrence.

The points method (Swynnerton and Worthington 1940) is especially useful when the food consists of many small organisms. Points were allotted according to the amount of food each stomach contained. For example, a full stomach was allotted 100 points, and a one-third full one was allotted 33 points. The relative amount of each food category present was then estimated visually and allocated points, e.g., the mass of bivalve shells making up three quarters of the bulk of a half-full stomach (worth 50 points) is worth

38 points, while the remaining quarter of the bulk, comprised of algae, is then worth 12 points. Although the personal element influences the visual assessment of the relative amounts of the different organisms, the method was felt to indicate adequately the composition of the bulk of the animals' diet. However, differences in digestion rate and feeding behavior probably enhance the actual importance of some food items over others.

Frequency of occurrence of each food category was recorded on a presence or absence basis. Data from both points and frequency of occurrence methods were expressed in percentage terms based on the number of stomachs that contained food, not on the total number of stomachs examined. Data from both sexes were combined; Ropes (1968) and Elner (1977) failed to demonstrate sexual differences in green crab diet.

RESULTS

Diet of Green Crabs

From the green crab collection in May, 364 stomachs were analyzed, and from the August collection, 398. From those crabs collected in May and in August, 71 (20%) stomachs and 83 (21%) stomachs, respectively, were empty. Skeletal structures were largely used to identify prey in the remaining stomachs. Because of the form and fragmented nature of the remains, assigning a food item to a definite species was not always possible, but the food usually could be identified to a more general taxonomic group. Therefore, the total percentage of stomachs or points for a general taxonomic group is not necessarily the sum of the percentages from all categories within that group. Figures 1 and 2 show percentage frequencies of occurrence of each major prey category for the two collection dates. Quantitative results based on percentage points for each collection date are given in Figures 3 and 4. Chi-square (X^2) tests indicate significant changes in the relative proportions of the food categories in the diets of crabs between May and August, both in terms of frequency of occurrence ($X^2 = 72.3$; df = 13; $P < 0.001$) and points ($X^2 = 18.27$; df = 10; $P < 0.005$). However, the order of dietary importance of each food category, in terms of frequency of occurrence and points, is similar in both samples.

Molluscs appeared to be the most important food items in terms of frequency of occurrence and points, and were further separated into four categories. Bivalves, such as *Mytilus edulis* and *Mya arenaria*, could be recognized by their shell shape, color, and hinge structure. Although present, other bivalves, such as *Ensis directus* and *Macoma baltica*, were not plentiful enough to be placed into separate categories. The gastropods *Hydrobia totteni* and *Littorina* spp. were identified from shell fragments and operculae. These snails, although encountered frequently, were of low importance in terms of the points method.

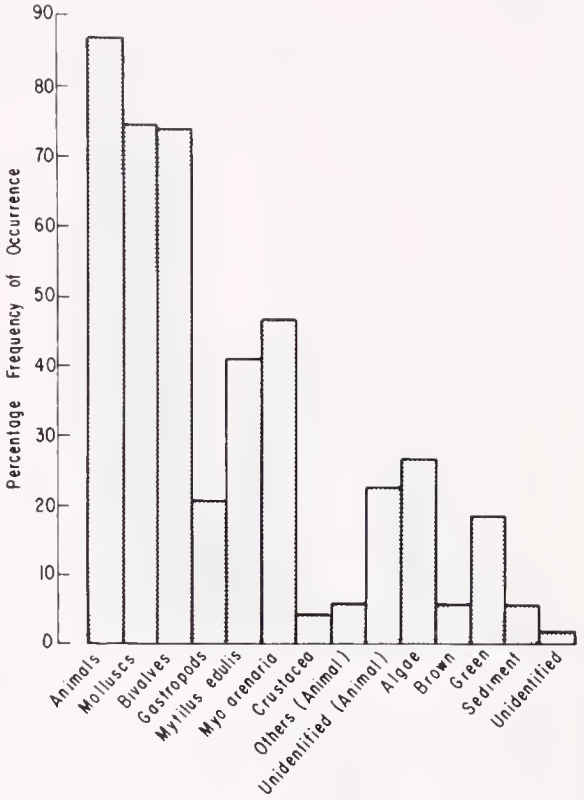

Figure 1. The relative importance of food types (analyzed by their percentage frequency of occurrence) in the stomachs of green crabs from Port Hebert, May 1978 (n = 293).

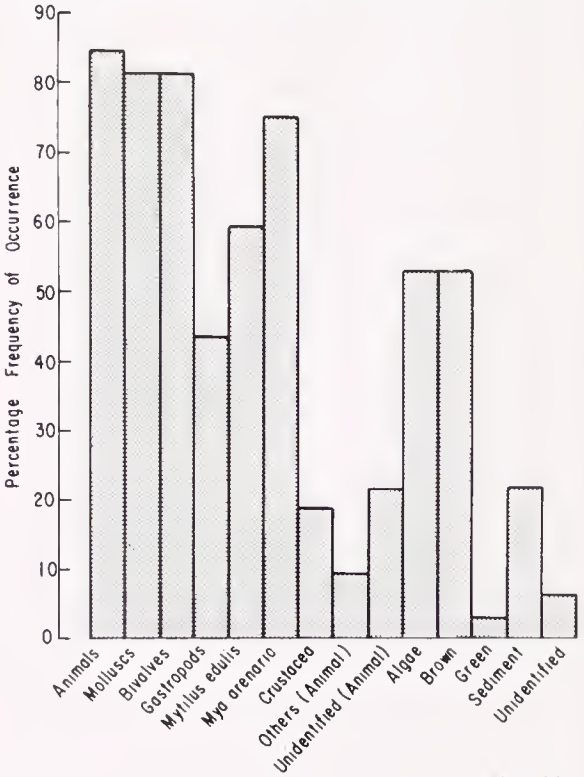

Figure 2. The relative importance of food types (analyzed by their percentage frequency of occurrence) in the stomachs of green crabs from Port Hebert, August 1978 (n = 315).

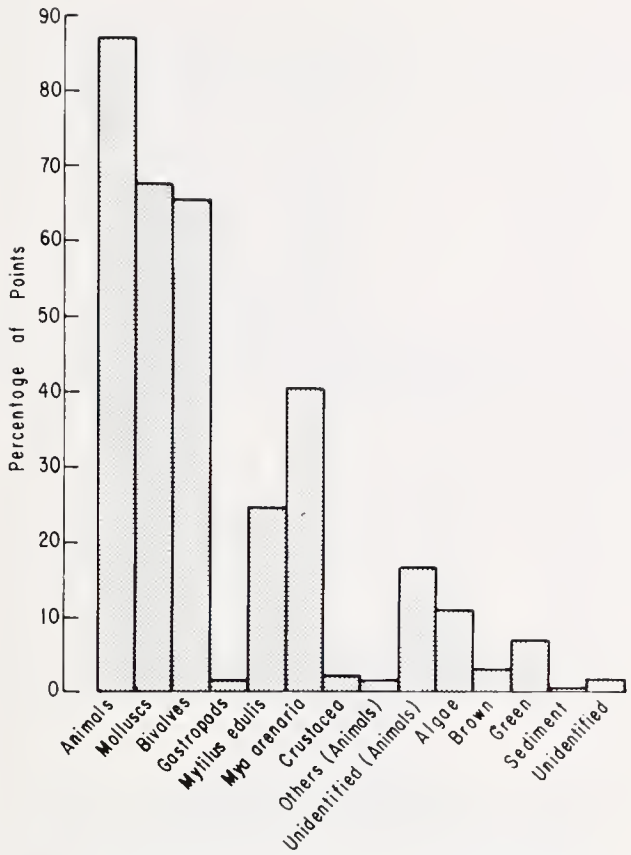

Figure 3. The relative importance of food types (analyzed by the percentage points method) in the stomachs of green crabs from Port Hebert, May 1978 (n = 293).

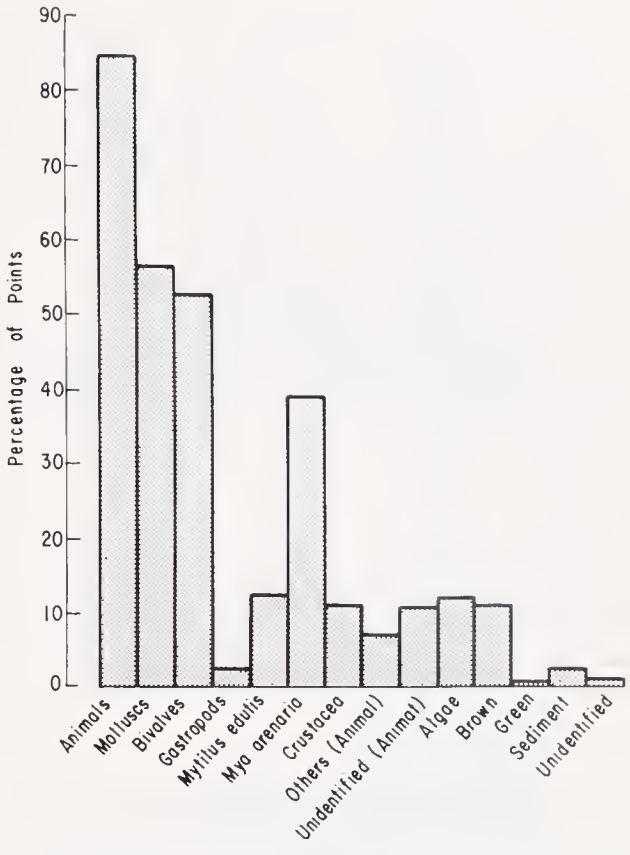

Figure 4. The relative importance of food types (analyzed by the percentage points method) in the stomachs of green crabs from Port Hebert, August 1978 (n = 315).

Crustacea were not common enough to warrant subdivision into separate food categories. Green crabs and rock crabs were identified from their chelae, limbs, color, and exoskeleton. Barnacles, *Balanus* spp., were identified from their thick white shells and cirripedia; and amphipods from their light brown, flattened exoskeletal plates. Other crustaceans such as Isopoda and hermit crabs (*Pagurus* spp.) occurred more rarely. No lobster remains were identified in the stomachs examined.

Prey items, such as colonial hydroids, bryozoans, various unidentified eggs, polychaetes (*Nereis* spp.), and echinoderms (*Strongylocentrotus droebachiensis, Asterias vulgaris*), were identified infrequently and were placed in a universal group, 'Others (animals)'. Crescent-shaped pieces of algae were encountered frequently but in relatively small quantities, and were separated into brown and green categories when possible. Material that was unidentifiable by visual techniques was classed as either 'Unidentified' or 'Unidentified (animals)'. Frequently contained in stomachs examined were inorganic materials (such as mud or sand particles) which were classed as 'Sediment'. More exotic nondigestible materials, such as plastic and paint flakes, were also included in this latter group.

It should be noted that certain epifauna, such as barnacles or hydroids, could have been ingested accidentally when the crab ate mollusc or alga prey to which epifauna were attached.

Size Frequency and Littoral Abundances of Green Crabs

In the May and August surveys, 69 and 99 green crabs, respectively, were found per-man-hour-searched. Size and sex composition for samples on both dates are shown in Figures 5 and 6. The male:female sex ratio changed from 1:0.85 in May to 1:1.26 in August. In the May survey, the mean carapace width (± standard error) for male green crabs, 36.4 ± 1.2 mm, was significantly larger than that for females, 28.0 ± 0.9 mm ($t = 2.33$, $df = 362$, $P < 0.02$). Similarly, there was a significant difference between the mean carapace widths for male (41.7 ± 0.9 mm) and female (36.5 ± 0.7 mm) crabs in the August survey ($t = 4.59$, $df = 396$, $P < 0.001$). Mean carapace width for both male and female green crabs increased significantly between May and August (males: $t = 3.58$, $df = 371$, $P < 0.001$; females: $t = 7.28$, $df = 387$, $P < 0.001$).

DISCUSSION

Stomach analysis strongly suggests that green crabs from Port Hebert rely on mostly bivalves and, to a lesser extent, on algae and crustaceans as prey. This trend was confirmed by both points and frequency of occurrence methods. Dietary importance of bivalves substantiates the reputation of green crabs as a major pest of bivalve fisheries (Dare and

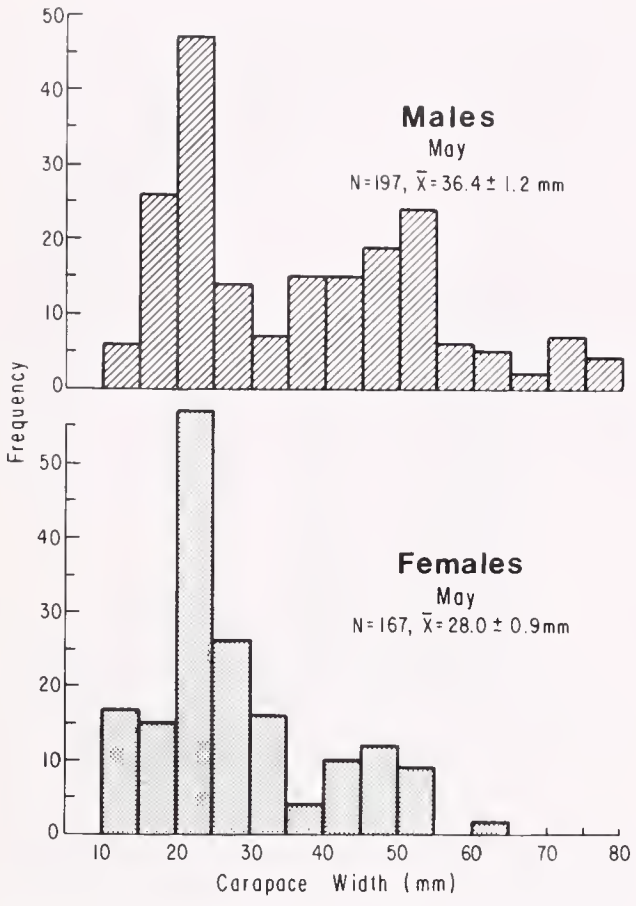

Figure 5. Size frequency of male and female green crabs sampled at Port Hebert, May 1978.

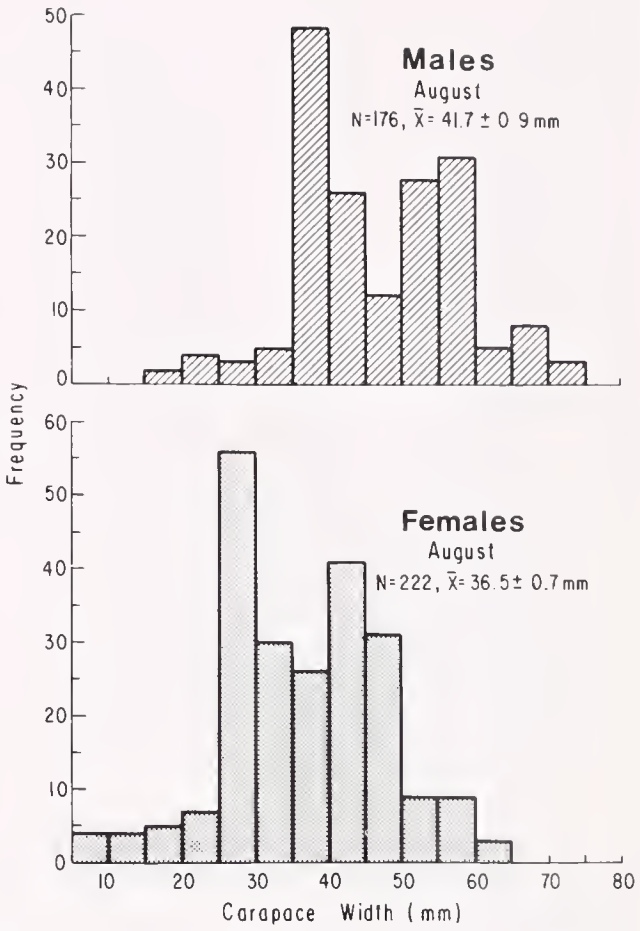

Figure 6. Size frequency of male and female green crabs sampled at Port Hebert, August 1978.

Edwards 1976, Welch 1968). Furthermore, presence of infaunal bivalves, such as *Mya arenaria* and *Ensis directus* in the stomachs examined, suggests that the green crab is an efficient burrower.

Significant differences between green crab diets in May and in August, in terms of points and frequency of occurrence, possibly reflected seasonal variations in the abundance of certain prey.

The only other North American survey on green crab diet (Ropes 1968) revealed a more diverse diet than the Port Hebert study but a similar dependence on bivalves. Elner (1977) analyzed green crab stomach contents from the Menai Straits, North Wales, and found the diet to consist mainly of crustaceans and algae. Polychaetes, which were almost entirely absent from the Port Hebert survey, were only slightly less important by frequency of occurrence than molluscs in the North Wales samples. Differences in diet among the three locations probably reflect the availability of food types in each particular habitat, and the crab's opportunistic foraging behavior.

Differences in mean carapace width and sex ratio of the green crabs sampled between the May and August surveys could have been caused by seasonal migration as observed by Naylor (1958). Increases in mean carapace width also may have been due to molting and growth between sampling dates.

In the laboratory, adult green crabs are able to capture and feed on juvenile lobsters, and adult lobsters and rock crabs prey on adult green crabs (R. W. Elner, unpublished data). Although no lobster remains were identified in the stomachs examined, there was evidence of cannibalism and predation on *Cancer irroratus*. Klein-Breteler (1975) suggests that predation by larger green crabs on smaller ones is an effective density-dependent mortality factor. Laboratory observations (R. W. Elner, unpublished data) have shown that all sizes of green crabs are vulnerable to cannibalism after ecdysis.

In surveys of lobster diets from Newfoundland (Ennis 1973, Squires 1970), and from the Northumberland Strait (Miller et al. 1971), bivalves, gastropods, crabs, polychaetes, and echinoderms were the most frequently occurring food items. However, each survey produced different proportions and positions of importance for each food category. This variability is probably explained by the different habitats, and subsequent differences in prey availability in which the sampling took place. Scarratt and Lowe (1972) determined

the diet of the rock crab in the Northumberland Strait to be composed principally of polychaetes, mussels, and sea urchins. In a study off Shelburne, southwestern Nova Scotia (R. W. Elner, unpublished data), crabs, bivalves, and brittle stars were the major food items in lobster stomachs based on the points method; bivalves, crabs, and amphipods were dominant in rock crab stomachs. There are no published data on jonah crab diet, although it can be expected to be similar to that of the rock crab. The many similarities in diet among green crabs, rock crabs, and lobsters indicate that in food-limiting situations these species probably compete for food types such as bivalves, gastropods, polychaetes, and crustaceans. Elner and Hughes (1978), Elner and Jamieson (1979), and Elner and Raffaelli (1980) have shown that green crabs, rock crabs, and lobsters are versatile molluscan predators able to open the shells of a wide size range of prey; therefore, competition is unlikely to be lessened substantially by any partitioning of food resources on the basis of prey size.

Miller et al. (1971) determined that American lobsters endure intense interspecific competition for food within kelp communities. Scarratt (1968) for American lobsters, and Chittleborough (1970, 1975) and Chittleborough and Phillips (1975) for western rock lobsters (*Panulirus longipes*), found evidence of intense spatial competition on lobster grounds. Competitive interactions can depress the carrying capacity of a habitat for the species concerned, and displace members into marginal habitats where they may be inadequately nourished and subject to increased predation. High abundances of green crabs, as observed in these surveys, may be capable of sufficiently depressing the carrying capacity of an inshore habitat, in terms of space and food, resulting in a decreased abundance of lobsters and *Cancer* crabs. Therefore, the green crab should be viewed not only as a proven direct pest of commercial molluscs but also as a possible indirect and direct competitor of lobsters and other crab species.

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VARIATIONS IN SOME REPRODUCTIVE ASPECTS OF FEMALE SNOW CRABS *CHIONOECETES OPILIO*[1,2]

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ABSTRACT Knowledge of the reproductive biology of female snow crabs (*Chionoecetes opilio*) from northern Alaska waters is important because of the potential impact on this dominant species from increased petroleum-related activities there. Size at 50% maturity for female snow crabs from the southeastern Chukchi Sea is 50 mm carapace width. Fecundity of three North American populations of *Chionoecetes opilio* decreases progressively at a given body size with increasing latitudes. Crabs from the southeastern Chukchi Sea have a smaller body-size range and larger eggs than those from the southeastern Bering Sea and from the Gulf of St. Lawrence. Also, a small percentage (3.3%) of female Chukchi Sea crabs of egg-bearing size are ovigerous.

INTRODUCTION

Snow (tanner) crabs *Chionoecetes opilio* (O. Fabricius) are present on both sides of the North Pacific Ocean—to the west in the Sea of Japan, and to the east in the Bering Sea—where they extend northward to Chukchi Sea and Arctic Ocean (Wolotira et al. 1977; Yoshida 1941; K. Frost, Alaska Department of Fish and Game, personal communication). In the Atlantic Ocean, they range from the Gulf of Maine northward through the Gulf of St. Lawrence (Garth 1958).

Various reproductive aspects (i.e., maturity, mating, egg deposition, fecundity, and egg size) of female *C. opilio* have been reported from many geographic localities (Brunel 1960, 1961, 1962; Ito 1963, 1967; Powles 1968; Watson 1969, 1970; and Haynes et al. 1976). This paper compares some reproductive aspects of *C. opilio* toward the northern limit of its range, the southeastern Chukchi Sea (68°18.0′N), with data from the southeastern Bering Sea (56°15.0′N), from the Gulf of St. Lawrence (48°43.5′N and 48°21.0′N) (Haynes et al. 1976), and, to a limited extent, from the Sea of Japan (approximately 35° 50.0′N) (Ito 1963).

Additionally, baseline knowledge of various reproductive aspects of female snow crabs from northern Alaska waters is important because of the potential increase in petroleum-related activities in that area. Baseline data can be compared with data from future impacts, if any, on this dominant crab species.

METHODS

In the Chukchi Sea near Point Hope, Alaska, 193 new-shell females (130 immature and 63 mature individuals) were collected during a northeastern Bering Sea-southeastern Chukchi Sea benthic trawl survey in September–October 1976 (Wolotira et al. 1977, Feder and Jewett 1978). Specimens were selected to encompass the size range of ovigerous individuals and to determine size at maturity.

Carapace width, the widest portion of the carapace excluding spines, was measured to the nearest 0.1 mm.

Eggs were dried to a constant weight at 60°C (see Lovegrove [1966] for drying technique) and weighed to the nearest 0.001 g.

After drying, the eggs were rubbed gently to free them from connective tissue. Two estimates of egg number were obtained for each crab by comparing the weight of a 200-egg subsample to the weight of the entire egg mass (Lagler 1957). The mean of the two estimates was used in all calculations.

The number of eggs from crabs of the same size have been reported to decrease approximately 50% from the time of egg extrusion to the time of hatching (Brunel 1962, Kon 1976); presumably this egg loss was due to predation, unfertilization, and/or abnormalities. Therefore, to make adequate latitudinal comparisons in snow crab fecundity, crabs with eggs in the early stages of development were collected for comparison with eggs of similar stages of development from the southeastern Bering Sea and from the Gulf of St. Lawrence. Fecundity may be a function of spawning history, i.e., differences in clutch size may exist between primiparous and multiparous spawners. This aspect was not examined.

To determine egg diameter, a sample of 10 eggs from each of five crabs was removed from the blotted egg mass, and the diameter measured to 0.01 mm with an ocular micrometer.

RESULTS AND DISCUSSION

The geometric mean (GM) regression (Ricker 1973) was used as the measure to express the functional regression of number of eggs (Y) on carapace width (X). The GM regression method also was used by Haynes et al. (1976) for *C. opilio* fecundity data from the southeastern Bering Sea

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[2]Contribution No. 437, Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99701.

and from the Gulf of St. Lawrence. It is presented here for comparison. The relationship between log fecundity and log carapace width is expressed as:

$$\log_e Y = \log_e \mu + \nu \log_e X.$$

The correlation coefficient for Chukchi Sea crabs was 0.767, indicating a reasonably good relationship between number of eggs and carapace width (Table 1). Similar correlation coefficients were obtained for crabs from the southeastern Bering Sea and from the Gulf of St. Lawrence, i.e., 0.808 and 0.733, respectively.

Ninety-five percent confidence intervals of the regression coefficients (ν) were used to test the null hypothesis that the slope equaled 3 for *C. opilio* in the Chukchi Sea; a similar test was made on crabs from the southeastern Bering Sea and from the Gulf of St. Lawrence (Haynes et al. 1976). Regression coefficients for crabs from the Chukchi Sea, as well as those from the southeastern Bering Sea, were not significantly greater than 3, indicating that egg number and carapace width increased at similar rates. The number of eggs of *C. opilio* from the Gulf of St. Lawrence increased at a rate greater than the width of the crab (Haynes et al. 1976).

TABLE 1.

Relationship of $\log_e$ number of eggs to $\log_e$ carapace width for *Chionoecetes opilio* from three geographic localities.

Parameters	Southeastern Chukchi Sea	Southeastern Bering Sea[1]	Gulf of St. Lawrence[1]
Latitude	68°18.0′	56°15.0′	48°43.5′ 48°21.0′
Number of crabs	63	23	99
Regression coefficient			
ν	3.4822	2.7206	4.2000
95% confidence limits	± 0.5720	± 0.7265	± 0.5686
Intercept $\log_e$ (μ)	- 3.6905	- 0.7125	- 6.7472
Correlation coefficient (ν)	0.7670	0.8086	0.7329

[1]Source: Haynes et al. 1976.

Size at Maturity

The smallest mature and largest immature female crabs were 40.3 mm and 54.0 mm, respectively, indicating an approximate 14 mm size difference between the smallest and largest immature female ready to molt to maturity. Size at 50% maturity was the same as that for females from the Gulf of St. Lawrence (Watson 1970), i.e., about 50 mm. Female *C. opilio elongatus* from Korean waters mature at 63 mm (Yoshida 1941), whereas 50 to 55 mm was the size at maturity of the same species from the Sea of Japan (Kato et al. 1956, Ito 1967). Female *C. bairdi* from the Gulf of Alaska reached 50% maturity at approximately 80 mm (Hilsinger 1976).

Carapace Width–Fecundity

Observed mean number of eggs for a given carapace width group (5 mm) was smaller for *C. opilio* from the Chukchi Sea than for *C. opilio* from the southeastern Bering Sea and Gulf of St. Lawrence (Table 2; Figure 1). The smallest ovigerous female size class from Chukchi Sea was approximately 10 mm smaller than the smallest ovigerous female size class from the southeastern Bering Sea and the Gulf of St. Lawrence. The largest Chukchi Sea female size class was approximately 15 mm smaller than the largest Bering Sea crab size class and nearly 25 mm smaller than the largest Gulf of St. Lawrence crab size class (Table 2). Maximum difference between the lowest and highest number of eggs in a 5-mm size group in Chukchi Sea crabs was 24,773 eggs (50 to 54 mm); the mean difference was 10,647 eggs. Maximum and mean differences in the southeastern Bering Sea crabs were 30,452 eggs (55 to 59 mm) and 17,857 eggs, respectively; in the Gulf of St. Lawrence the differences were 64,787 eggs (70 to 74 mm) and 52,088 eggs, respectively.

TABLE 2.

Observed mean fecundity (x 10^3 eggs) of *Chionoecetes opilio* (number of crabs in parentheses) from three localities.

Carapace width (mm)	Gulf of St. Lawrence[1]	Southeastern Bering Sea[1]	Southeastern Chukchi Sea
40–44			12.9 (8)
45–49			19.2 (19)
50–54	31.8 (1)	28.2 (2)	25.5 (22)
55–59	39.6 (8)	33.3 (5)	28.0 (11)
60–64	44.1 (21)	37.4 (5)	37.1 (3)
65–69	65.5 (28)	44.6 (5)	
70–74	70.9 (23)	49.8 (5)	
75–79	97.9 (12)	74.8 (1)	
80–84	117.5 (3)		
85–89	114.9 (3)		

[1]Source: Evan Haynes, National Marine Fisheries Service, Auke Bay, Alaska.

Ito (1963) examined the fecundity of *C. opilio* from the southeastern part of the Sea of Japan and determined that most crabs carried 30,000 to 80,000 eggs per individual (range = 5,500 to 150,000); the mode was approximately 50,000 to 60,000 eggs. Corresponding crab sizes were not presented.

Egg Size

The range (0.64 to 0.88 mm) and mean size (0.71 mm) of eggs from Chukchi Sea crabs were greater than those for eggs from the southeastern Bering Sea (range: 0.56 to 0.74 mm; mean: 0.66 mm), and from the Gulf of St. Lawrence (range: 0.56 to 0.75 mm; mean: 0.65 mm). Coefficients of variation of egg size among Chukchi Sea crabs ranged from 2.4 to 5.5%, indicating uniform egg size.

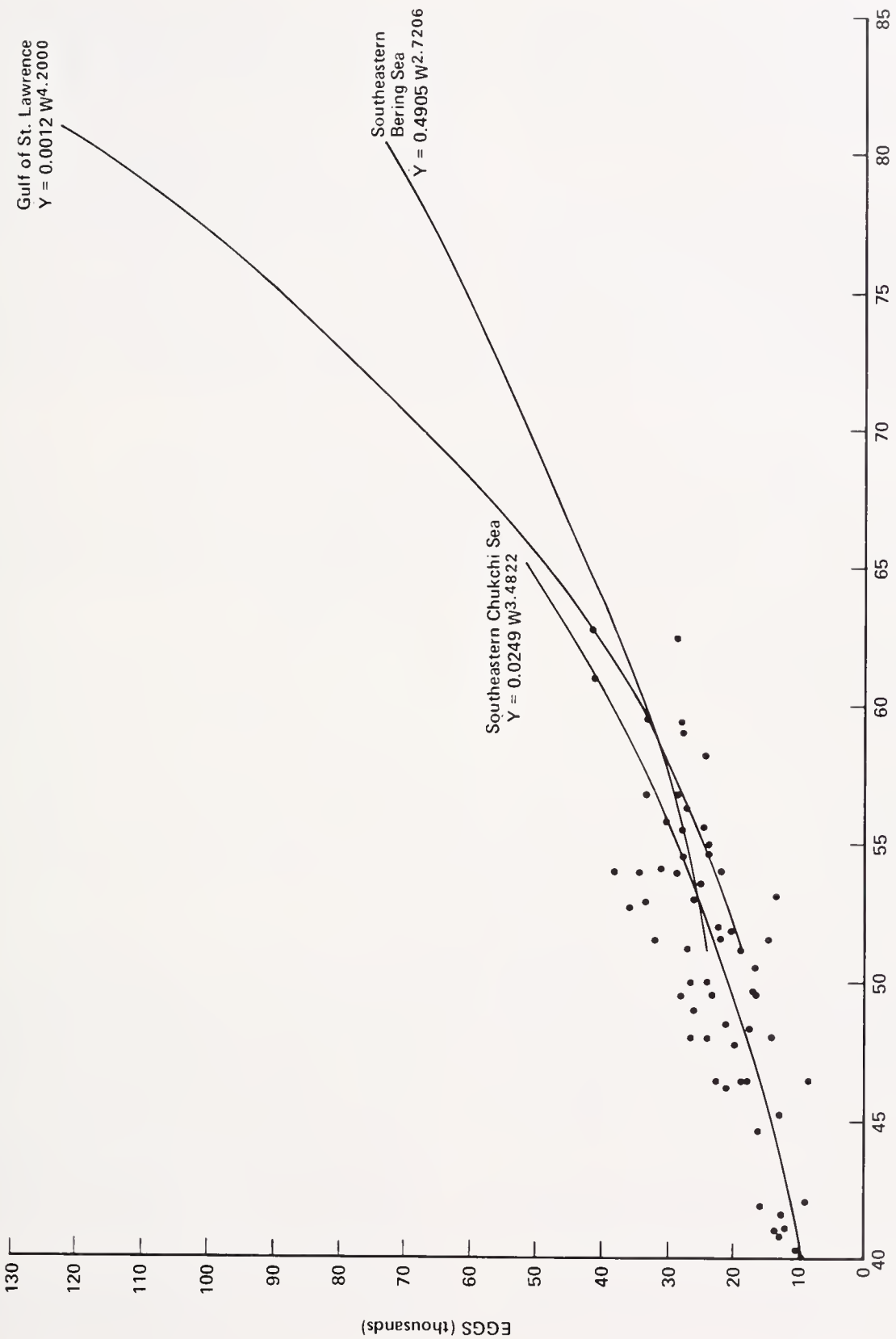

Figure 1. Estimates of number of eggs of 63 *Chionoecetes opilio* collected in the southeastern Chukchi Sea in 1976, and computed linear regressions of number of eggs on carapace widths for crabs from Chukchi Sea, southeastern Bering Sea, and Gulf of St. Lawrence.

Similar uniformity in egg size of crabs existed for crabs from the southeastern Bering Sea and the Gulf of St. Lawrence. No significant correlation was found between mean egg size and crab size for crabs of the Chukchi Sea region ($r = -0.530$); this lack of relation between sizes of crab and egg was consistent with data from the other two areas.

Gravid Females

Changes in percentages of egg-bearing females may indicate that stocks were over-exploited or under environmental stress (Hilsinger 1976). Only a small proportion of female *Chionoecetes opilio* of the northeastern Bering Sea and the southeastern Chukchi Sea were gravid. Among 5,200 females exceeding 40 mm in carapace width (size of the smallest ovigerous female), only 169 (3.3%) were bearing eggs (Wolotira et al. 1977). Additionally, examination of the ovaries of 130 immature and 63 mature females revealed that 48 and 97%, respectively, had developing internal orange ova (Table 3). This high proportion of females with advanced ovarian development and low proportion of egg-bearing females seems paradoxical. The seminal receptacles of mature females were not examined to determine the presence or absence of sperm. Snow crabs are not commercially exploited in the northeastern Bering Sea or in the southeastern Chukchi Sea; therefore, the reduction of egg-bearing females may be environmentally related, but no information is available to substantiate this.

ACKNOWLEDGMENTS

Special thanks go to Mr. Evan Haynes for his assistance and critical review of this manuscript, and to Mr. Robert Sutherland for his statistical assistance.

TABLE 3.

Maturity of 130 immature and 63 mature *Chionoecetes opilio* from southeastern Chukchi Sea.

Maturity[1]	Carapace Width (mm)											
	15–19	20–24	25–29	30–34	35–39	40–44	45–49	50–54	55–69	60–64	Totals	Percent
	Number of Crabs											
Immature												
ovary absent	8	3	3	3	3	3	0	0	0	0	23	18
ovary present, empty and white	7	4	5	12	3	12	1	1	0	0	45	34
ovary orange	0	0	0	1	1	3	34	23	0	0	62	48
											130	100
Mature												
ovary orange	0	0	0	0	0	8	18	22	10	3	61	97
ovary empty and white	0	0	0	0	0	0	1	0	1	0	2	3
											63	100

[1] Source: Hilsinger (1976).

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ABSTRACTS OF TECHNICAL PAPERS

Presented at 1980 Annual Meeting

NATIONAL SHELLFISHERIES ASSOCIATION

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ROLE OF CHEMORECEPTION IN PREDATION BY THE OYSTER DRILL *UROSALPINX CINEREA*. I. FEEDING BEHAVIOR[1]

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Research has been initiated to investigate the chemical ecology of feeding behavior in oyster drills, *Urosalpinx cinerea* and *Ocenebra inornata*, as a basis for drill control. To date, this work has focused on (1) quantifying the influence which feeding attractants, produced by the oyster *Crassostrea virginica*, have on the behavior of *U. cinerea*, and (2) isolating additional variables which may significantly modify feeding behavior.

A Y-maze choice chamber has been designed which tests quantitatively the response of drills to a variety of stimuli (such as feeding attractants) presented to them. Observations on the influence of oyster feeding attractants show that *U. cinerea:* (1) preys on oysters reared in the laboratory on a unialgal diet of the diatom *Thalassiosira pseudonana;* (2) migrates perferentially toward a high biomass of these oysters; (3) migrates preferentially toward well fed, as opposed to starved, oysters; (4) has a low frequency (less than 40%) of response to oysters in the winter under non-hibernating conditions (20 to 25°C); (5) searches for its prey most actively at night; (6) is slow in its response to oyster prey; and (7) feeds sporadically rather than continuously. Results from these experiments will assist in development of a rapid screening bioassay to elucidate in more detail the chemical nature of feeding attractants produced by oysters.

[1]Originally presented at NSA Annual Meeting, Vancouver, B.C., August 1979.

NONRADIOLOGICAL STUDIES OF TRAY-HELD OYSTERS, *CRASSOSTREA VIRGINICA*, IN THE VICINITY OF THE CALVERT CLIFFS NUCLEAR POWER PLANT IN CHESAPEAKE BAY, 1970–1979[1]

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Growth and mortality of three age classes of tray-held oysters, *Crassostrea virginica* Gmelin, were monitored from 1970 to 1979 at several stations in Chesapeake Bay in the area of the Baltimore Gas and Electric Company's Calvert Cliffs Nuclear Power Plant. Additional oysters were monitored for uptake of copper and nickel.

During the preoperational years (1970–1975), one continuous study was conducted, but during the operational period (1975–1979), several separate studies were initiated because of heavy losses of oysters and research platforms due to ice.

Station differences in growth and mortality were minimal during preoperational years, but accelerated growth during operational years was evident in thermally affected areas. Overall growth rates during operational years, however, were not as high as those of 1970–1972. No differences in mortality rates occurred between the two periods.

Nickel concentrations in oysters showed seasonal effects, but did not appear to be influenced by the plant. Mean wet-weight copper concentrations at the plant during the pre-operational period (59.6 mg/kg), and operational period (50.6 mg/kg) were both about twice those which occurred at a control station (29.8 and 19.6 mg/kg) during the same periods. Thus, the higher concentrations of copper in oysters at the plant appear to be unrelated to plant operation.

[1]This study was supported by the Baltimore Gas and Electric Company.

THE SHORT-FINNED SQUID *ILLEX ILLECEBROSUS* FISHERY IN EASTERN CANADA

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The squid *Illex illecebrosus* traditionally had been important to Canada only as a small inshore fishery in Newfoundland. Fluctuations in inshore squid landings, common prior to 1975, probably were related to the availability of squid. Since 1975, the inshore and offshore fisheries have shown tremendous increases in landings, and that has resulted in an upsurge in the economy and effort in the fishery.

Historic trends related to the inshore fishery are discussed. Recent statistics on the inshore fishery provide information on catch, season, area, and gear. Offshore statistics, prior to 1975, were not completely separated by species. Statistics compiled on the international and Canadian offshore fisheries from the FLASH computer information system provide a monitor of all activities since 1977.

The historic and present state of the fisheries are presented in relation to the management of the resource.

A STUDY OF THE GROWTH AND FEEDING PARAMETERS OF THE SHORT-FINNED SQUID *ILLEX ILLECEBROSUS* IN RELATION TO A FISHERY MODEL

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Growth curves were determined for *Illex illecebrosus* from data collected between 1977 to 1979 from commercial fishing vessels and research cruises on the Scotian Shelf. The estimated asymptotic lengths ranged from 232 to 278 mm and 294 to 347 mm for males and females, respectively, while estimated time of birth was between December and February. The onset of sexual maturation of males was recorded at a mean length of 228 mm in late November; in females, the onset was between late November and early December. Diurnal feeding patterns showed "recently fed" *I. illecebrosus* descend from the upper region of the water column shortly after sunrise. Gut contents are given and three major prey types, Crustacea, fish, and squid, are identified. A progression from an exclusively crustacean diet at squid sizes less than 145 mm to predominantly squid and fish diets at squid sizes greater than 225 mm was attributed to size-related preference and availability. Cannibalism was an important phenomenon, while predation on fish was relatively unimportant. Estimates of feeding, food conversion, and growth are discussed in relation to a fishery model.

FACTORS AFFECTING THE DEVELOPMENT OF MOLLUSCAN NEOPLASIA IN THE SOFT-SHELL CLAM *MYA ARENARIA*: INDICATIONS FROM LABORATORY AND FIELD OBSERVATIONS

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An intensive multidisciplinary investigation of molluscan neoplasia as it occurs in the soft-shell clam *Mya arenaria* has been in progress for the past 4 years. The soft-shell clam has been found to be particularly susceptible to this disease and it is an ideal organism to study the factors affecting the development of neoplasia. The investigation, consisting in part of a field survey, seasonal sampling, field experiments, and laboratory transmission experiments, has indicated a viral etiology of neoplasia. Consistant patterns in the development and progression of neoplasia have been observed throughout the various surveys and experiments. A review of these patterns can elucidate some of the factors which affect neoplasia development. Four specific factors: temperature, size, dosage, and stress, have been indicated. Both cold and warm temperatures seem to suppress the development and progression of neoplasia. High temperature may be detrimental to the infecting virus. The mechanism whereby cold temperature reduces neoplasia remains enigmatic, possibly acting on the clam, virus, or both. Temperature affects are evidenced by an annual biphasic cycle of neoplasia incidence, and by the scarcity of neoplasia at the extremities of the geographical distribution of the soft-shell clam. Neoplasia was not found in newly settled individuals indicating an age-related or exposure-related affect. Young clams (< 40 mm) had a significantly lower incidence of neoplasia compared to adults. Neoplasia has been successfully transmitted by exposing healthy clams to the effluent of diseased clams. In replicate experiments, it was found that the incidence and severity of the developing neoplasia were dependent upon the effluent concentration. Evidence for that effect in the field has been observed in transplant experiments. Transmission studies using healthy clams held under varying sediment conditions have resulted in consistant differences between the treatments regarding neoplasia incidence and severity. The constancy of those effects suggests that they are nonrandom and predictable. The factors responsible for the observed differences are as yet unknown but it is postulated that stress resulting from certain environmental conditions increases the susceptibility of clams to neoplasia. More prevalent and severe cases were found in clams kept without sediment, and in very compacted, moderately oiled sediment. In a field experiment, the incidence and severity of neoplasia developing within different clam populations were found to be related to the initial conditions (an index of stress) of each population. Healthier populations (more weight per size) experienced reduced neoplasia development. These observations indicate directions where further research would be useful. Using direct viral inoculation techniques, controlled laboratory experiments could resolve some of the mechanisms underlying these observations.

ISOLATION, CHARACTERIZATION, AND CONTROL OF A *VIBRIO* SP. PATHOGENIC TO *CRASSOSTREA VIRGINICA* AND *OSTREA EDULIS* LARVAE

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During a disease outbreak at a west coast shellfish hatchery, ground-up samples of infected *Ostrea edulis* larvae and their culture water were placed on marine agar. Of the predominant isolates taken, one was shown consistently to cause greater than 90% mortality to both developing *O. edulis* larvae and *Crassostrea virginica* embryos in challenge tests. Exponential growth of the suspect bacterium occurred immediately upon exposure to eggs; embryonic mortality increased steadily throughout 48-hour challenges. This bacterium was identified as a member of the genus *Vibrio* through a series of over 60 morphological and biochemical tests. Sensitivity to various antibiotics also was determined. Chlorine, ultraviolet, and ozone were evaluated as disinfectants for this pathogenic *Vibrio* which is presently controlled by ultraviolet treatment of shellfish hatchery seawater.

ASPECTS OF REPRODUCTION OF HARD CLAMS, *MERCENARIA MERCENARIA*, IN GREAT SOUTH BAY, NEW YORK

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A spectrophotometric method was developed for rapid quantification of hard clam (*Mercenaria mercenaria*) sperm and egg concentrations. An optimum gamete ratio of approximately 1.8×10^5 sperm per 100 eggs was determined. Hard clams repeatedly were induced to spawn in the laboratory. Unfertilized spawned ova ranged in size from 50 to 97 μm, and were characterized by a bimodal size-frequency distribution. In spite of the high variability in egg production among individuals, correlation between size (length) and egg production of clams from Great South Bay, New York, was signficant; 15 to 25% of the variation in fecundity was attributable to the difference in size of clams. Maximum egg production recorded for a single female over the spawning season was 16.8 million eggs. No significant differences in fecundity, size of eggs, or larval survival were detected between clams from two diverse Bay habitats. Quantitative comparison between gonads of clams from the Bay, and those spawned for this study suggested that laboratory spawning tends to underestimate natural fecundities. The proportion of sexes was approximately equal. The smallest clam to spawn was a sublegal female 33.1 mm in length. Seed clams were capable of producing viable spawn but had extremely low fecundities. The significance of the results was examined in the context of local management practices.

POPULATION MAINTENANCE, MANAGEABILITY, AND UTILIZATION OF INTRODUCED SPECIES: PATHWAYS, PATTERNS, AND CASE HISTORIES

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The intentional or accidental introduction of exotic species into an ecosystem can be viewed in terms of species success along sequential pathways that consider (1) the presence of, or likelihood of establishment of, reproducing populations; (2) energy inputs required; (3) maintenance and manageability of the exotic species; (4) economic or ecological disadvantages, and (5) final management practices (in terms of continued maintenance or utilization). Modeling of these pathways permits rapid comparisons of most case histories of nonnative species introduced into marine and estuarine waters, and further permits the rapid identification of both "ideal" pathways (leading to economic success of a fishery based on an exotic species requiring no energy inputs), "detrimental" pathways (leading to the establishment of exotic species harmful to the ecosystem), and many intermediate stages. Ideal pathways that lead to economic success thus can be readily framed in terms of both aquaculture and fishery enhancement; (1) for a species that does not establish reproducing populations, this pathway consists of maintenance by seeding (that is not economically prohibitive), through either protected cultivation (aquaculture) or by seeding the environment (fishery enhancement); while (2) for a species that does establish reproducing populaions, this pathway consists of a species that does not require management (no energy input or manipulation by man to maintain the population), is not

detrimental to the ecosystem, and can be utilized in a fishery. The detrimental status of an exotic species can upon occasion be dually scored: it may produce conspicuous changes in the native ecosystem (biologically detrimental) but it may enhance a local fishery (economically nondetrimental). Comparisons of case histories of exotic species in freshwater, terrestrial, and marine environments lead to the conclusion that nondetrimental and detrimental introductions in the sea both almost always lead off on an identical pathway: once established, an exotic species in the sea is unmanageable in a biological sense (the halting of reproduction and dispersal cannot be controlled by man), and this is also the case in some, but not all, land and freshwater environments. This phenomenon paradoxically emphasizes both the far greater potential benefit and danger of introductions in the ocean than in many land or freshwater ecosystems.

NEW INFORMATION ON THE FUNCTIONAL ULTRASTRUCTURE OF THE VALVES OF THE OYSTER *CRASSOSTREA VIRGINICA*

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The oyster forms most of its shell from three basic mineralized microstructures (simple calcitic prisms, regularly and irregularly foliated calcitic laths, and irregular aragonitic myostracal prisms), their transitional microstructures, and conchiolinal materials. The periostracum is very thin and nonmineralized. Prismatic structure is present on both right and left valves; that of the left valve has been overlooked in previous studies. Prisms increase in size away from the margin of the valves. Multilayering of prismatic strata occurs primarily in the right valve. All shell structure contains organic matrix, but that of prisms is most prominent. The bulk of both valves consists of regularly foliated and chalky structure. Laths in the region of valves between the adductor muscle and ventral edge generally point ventrally; those between the adductor muscle and hinge are variably oriented. Motility of mantle on the ventral side may partly explain this orientation. Chalky shell, composed of blades and leaflets, bounds a system of pores. The surface of the adductor muscle scar is extremely smooth. The ventral edge of the myostracum is a narrow transitional zone laid down in advance of muscle attachment as the muscle migrates with growth of the animal. Conchiolin patches commence as a thin granular layer on laths. A band of ligostracal prisms is deposited in advance of deposition of ligamental resilium and tensilia as the shell grows. A rugose, pitted, foliated structure follows this and probably anchors the mantle isthmus to the shell. The resilium is reinforced by aragonitic fibers; tensilia lack these. Transitional zones of granular crystallites join juxtaposed prismatic, foliated, chalky, and myostracal layers. In young dissoconchs umbonal plicae strengthen attachment of the left valve to the substratum. Microscopic shell annuli are present in the outer prismatic layer, resilium, chondrophoral and nymphal ligostraca, and adductor myostraca. The study provides new insights on shell structure, and suggests profitable avenues for future research on shell formation.

GROWTH RATES AND FOULING IN SEDIMENT-FREE RAFT CULTURING OF JUVENILE HARD CLAMS, *MERCENARIA MERCENARIA* (L.)

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Juvenile clams, collected from natural *Mercenaria* intertidal beds, were transferred to all plastic (PVC) trays which were suspended from plastic flotation collars in the intake canal of a nuclear power plant. The clams ranged in size from 2 to 15 mm in length, and were maintained according to a size-frequency distribution similar to a natural population under study. Mortality over a 5-month period was less than 10%, in contrast to a mortality rate of nearly 90% for juveniles in natural beds. The maximum growth rate in sediment-free trays was 0.4 mm per week which occurred during September 1979. The influence on the growth rate of 10-mm clams of fouling organisms attaching to the trays was examined for screens composed of galvanized hardware cloth and two commercially available plastic meshes. Mortality was 5% or less in trays which held sediments in the range of 0.5 to 1.0 mm grain size, and which were covered by galvanized-wire mesh.

DIAGNOSIS AND PROGNOSIS OF AN HEMATOPOIETIC NEOPLASM IN THE SOFT-SHELL CLAM *MYA ARENARIA* L.

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The severity of a disease can be determined by considering the number of organ systems involved and/or the degree of organ damage. The degree of tissue damage generally is correlated with the health of the animals, the course of the disease, and the final outcome. Three histopathologic methods were employed to diagnose neoplasia in 991 soft-shell clams, *Mya arenaria:* (1) bright-field microscopy of hematoxylin- and eosin-stained tissue sections, (2) phase-contrast microscopy of fresh hemolymph, (3) bright-field microscopy of methanol-Glemsa fixed hemolymph. The accuracy of the blood cytologic techniques when compared to the histologic tissue diagnosis was 94%. The number of circulating neoplastic cells (as determined from hemolymph samples) correlated with the extent of organ system damage. Five degrees of malignancy (with 5 as the most severe) are proposed for grading the disease. The higher the malignancy level the greater the probability of death. Clams diagnosed at a 4 or 5 malignancy level had 100% mortality and a life expectancy of less than 6 and 3 months, respectively. An hematopoietic neoplasm followed one of three courses: (1) the disease progressed to a higher severity and resulted in death (this occurred at all degrees of malignancy), (2) the disease remained at a stable level for up to 10 months (this occurred at 1, 2, and 3 degrees of malignancy), and (3) the disease diminished in extent or disappeared entirely (this occurred at 1, 2, and 3 degrees of malignancy).

In summary, an hematopoietic neoplasm of *M. mercenaria* can be accurately diagnosed and the severity determined from hemolymph samples.

THE GEODUCK CLAM FISHERY IN BRITISH COLUMBIA, CANADA

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Harvesting of subtidal stocks of the geoduck clam *Panope generosa* (Gould) in British Columbia began in the fall of 1976. Less than 43.4 metric tons were landed that year from areas in the Gulf of Georgia. By 1979, landings increased to 2,405 metric tons, and main fishing effort was focussed on the western coast of Vancouver Island in Clayoquot and Barclay sounds. Indications for 1980 are that the fishery will continue to expand into northern coastal regions with landing approaching 3,000 metric tons. A quota of 3,630 metric tons has been set for the fishery. Surveys to date indicate standing stocks in excess of 80,000 metric tons. Many coastal areas remain to be surveyed.

The fishery is restricted to diver-harvesters who dig each clam individually using a high-pressure water jet. Present harvesting occurs between the 10- to 60-foot level. Average weight of adult geoducks in British Columbia is 1.1 kilos, and under good conditions a single diver can harvest 350 kilos per day.

DEVELOPMENT OF THE NEWFOUNDLAND *ILLEX ILLECEBROSUS* FISHERY AND MANAGEMENT OF THE RESOURCE

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The Newfoundland squid fishery has experienced unprecedented success in recent years. Nominal catch has increased continuously since 1974 and reached a record high in 1979. The greatest proportion of the catch has come from the Newfoundland inshore jigger fishery, although in recent years a small proportion has been taken offshore.

Improved market conditions have contributed greatly to the recent success of this fishery. Traditionally, squid (*Illex illecebrosus*) had been sold as bait in the line fishery for cod in the Northwest Atlantic. Recently, however, a foreign market for squid as food for human consumption has developed. Fishermen received higher prices for squid and more effort was invested in the inshore fishery. Improved fishing technology and an abundance of squid led to the high catches in the late 1970's.

The general biology of *Illex illecebrosus* is outlined, and factors which affect its distribution and availability are considered. Annual catches throughout the development of the fishery are presented. Fluctuations in nominal catch are related to changes in fishing technology, squid abundance, and market demand. The forum for management of this resource also is described and changes in management initiatives with the recent success of the fishery are discussed.

The success of the Newfoundland squid fishery in recent years has relied heavily on demand by the Oriental market, especially Japan, for squid as food. Future success in

marketing Newfoundland squid will depend on the quality of the product, on the status of *Illex illecebrosus* as a preferred species among squids, and on the success of other squid fisheries. Implications are considered in managing a fishery which may be limited more by market potential than availability.

FORECASTING INSHORE ABUNDANCE OF SQUID *ILLEX ILLECEBROSUS* FROM A PRESEASON BIOMASS SURVEY

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The advance prediction of available biomass is fundamental to the management of most fisheries. Conventional methods are based on calculating the contribution to the fishery for the next year by the various year classes which were represented in the catch of the previous year. Such methods are not applicable to the advance prediction of biomass of short-finned squid because of its short life cycle. The life span of *Illex illecebrosus* is approximately 1 year, rendering the fishery dependent entirely on new recruits. This is based on direct estimation of the strength of the new year-class from a preseason survey.

In 1957, it was suggested that catch rates from otter-trawl surveys on the Grand Bank in May-June could be used to forecast inshore abundance of squid at Newfoundland. Since 1947, information is available on the relationship between otter-trawl catch rates and inshore abundance from incidental captures of *Illex illecebrosus* in spring groundfish surveys. Using that relationship, prediction of inshore abundance generally has been successful, especially in recent years. However, predictability is not certain and forecasts have been wrong in some years.

Details of the annual preseason survey are presented here and criteria for short-term forecasting of inshore abundance are described. Possible causes of fluctuations in otter-trawl catch rates and inshore abundance are considered and the reliability of this relationship is assessed as a means of prediction. Also, factors are discussed which complicate the interpretation of forecast information. Prospects are considered for more reliable predictions with respect to improvements in survey design and better estimation of inshore abundance. The possibility also is discussed of establishing a base for an earlier forecast.

PROGRESS TOWARD VALIDATING THE AGING OF SHORT-FINNED SQUID USING STATOLITHS

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Management of the fishery for the short-finned squid (*Illex illecebrosus*) has been hampered by an incomplete understanding of the biology of the species. Paramount in this respect is the lack of a valid aging technique, without which such population parameters as natural mortality, growth, and recruitment cannot be estimated accurately.

Recently, attention has been focused on the study of statoliths as a possible means of aging short-finned squid. The statolith is similar to the teleost otolith in structure, function, and chemical composition. Growth rings have been observed in statoliths of *Illex illecebrosus*, and the possibility has been investigated of chronological interpretation. Back calculation has shown that ring formation most closely approximates a daily cycle but poor correlation exists between days elapsed and number of rings counted. This could be due to inadequacies in preparation technique, interpretation of rings, or method of validation. Further, ring formation may be irregular.

The procedure used to prepare statoliths for study, and the criteria for identification of growth rings are described. Other possible methods are discussed which have been used to prepare otoliths for aging studies. Data acquired from two studies are presented and analyzed with respect to problems in detecting and interpreting growth rings. Validation is discussed with respect to its limitations as attempted in those studies, and the relative merits are assessed of other possible means of validation.

GROWTH OF SIBLING HARD CLAMS, *MERCENARIA MERCENARIA*, IN A CONTROLLED ENVIRONMENT

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Sibling populations of clams were raised in a controlled environment with excess algal food. Within each population wide variations among individuals were observed in shell length and volume. Given populations were divided at an early stage into five successively larger size classes. It was found that clams in the larger size classes always grew at a much more rapid rate than smaller clams at both 18°C and 25°C.

Sibling populations in the laboratory exhibit an obvious nonnormal distribution in shell length within a few days of spawning. Setting time may be used to further subdivide the population within each size class. Early-setting clams grow at a more rapid rate than late-setting clams and comprise only a small fraction of the population.

Size-frequency distribution of a sibling clam population maintained in the laboratory is strongly skewed toward the larger sizes. Such a size-frequency distribution pattern is observed in hatchery-raised populations for at least a year after setting, indicating that the late-setting clams never match the growth rate of the early-setting clams and, consequently, remain small relative to their larger siblings.

Clam growth in the laboratory during the first 2 months after setting is composed of three distinct periods, each with a characteristic growth rate. During the first 4 weeks, growth of spat continues at the larval rate. This rate of increase then decreases (growth pause) for the next 2 weeks. Following the growth pause, rapid growth resumes, although at a reduced rate typical of juvenile clams. The growth pause may be associated with growth of the siphons.

With proper selection of early-setting larvae, fast-growing commercial strains, as well as uniform groups of clams, may be produced for studies in such fields as toxicology and nutrition. In hatchery operations, where initial larvae numbers are large, experience indicates that fast-growing larvae comprise fewer than 5% of the population.

DIAGNOSIS OF VIBRIOSIS IN A COMMERCIAL OYSTER HATCHERY EPIZOOTIC, A CASE HISTORY*

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A case of epizootic vibriosis of American oyster larvae, *Crassostrea virginica,* in a commercial oyster hatchery is described from both hatchery records and observations, and by using laboratory diagnostic tools. Hatchery production of oyster larvae for the 1979 season was only half that of the 1978 season. This resulted primarily from a severe 6-week depression in hatchery output in the spring of 1979. Larvae from 2 of the 6 weekly spawns during that period were examined in the laboratory using interference microscopy, the trypan blue dye exclusion test, histological methods, and the fluorescent antibody test. The dye exclusion test was useful in demonstrating early signs of the disease such as detached mantle and velar cells. Histological examination demonstrated attachment of bacteria to the larval shell and its growth through the mantle into the visceral cavity. Extensive vacuolation of digestive system organs, apparently related to lipid retention, also was a consistent feature of the disease. The *Vibrio*-specific fluorescent antibody test provided rapid identification of the etiologic agent.

The possible relationship of a nutritional imbalance, signaled by the vacuolation of the digestive tract organs, to a too rapid growth rate and low production is discussed. The trypan blue dye exclusion test proved to be a useful hatchery management tool for assessment of larval health. The fluorescent antibody test, while rapid and highly specific, is suited for laboratory use only. The pathogenesis of vibriosis in this commercial hatchery epizootic was identical to that previously described in experimental vibriosis.

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REPRODUCTIVE RESPONSE TO INCREASED DENSITY: SOME OBSERVATIONS FROM MOLLUSCS

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Increased population density is known to influence growth and fecundity in molluscs. Few reports exist for bivalves, and most of those neglect the reproductive response accompanying reduced growth with increased density. Recent studies have demonstrated a significant density-dependent reduction in growth of hard clams (*Mercenaria mercenaria*); however, histological evidence has provided no indication that gametogenesis has been affected by increased density. In the present study, the amount of gonadal tissue in clams grown at three population densities were compared. Clams at the lowest density were larger, weighed more, and had more gonadal tissue than clams from higher densities. Gonadal-somatic indices indicated that the density-dependent reduction of growth did not fully account for the reductions in the amount of gonadal

tissue. These results are discussed in relation to existing literature on density-dependent changes in the reproductive biology of molluscs with emphasis on ecological advantages and consequences of some changes.

AN INVESTIGATION OF SEA SCALLOPS (*PLACEOPECTEN MAGELLANICUS*) OF THE MID-ATLANTIC FROM COMMERCIAL SAMPLES IN 1979

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Bushel samples of sea scallops (*Placopecten magellanicus*) for height-frequency analysis were obtained aboard the commercial scalloper VIRGINIA SURF from the mid-Atlantic region on two trips during the summer of 1979. Fishing effort was concentrated in three areas of the shelf: (1) 60 miles east of the Virginia-North Carolina border, (2) 70 miles east of the coast from Cape Henlopen, Delaware, to Atlantic City, New Jersey, and (3) 45 miles south of Long Island from Moriches Bay to Bridge Hampton. Individuals (214), ranging in size from 60 to 149 mm shell height, were retained for age analysis from the catches of the two northern areas.

The mean size of scallops caught in the southern region of the mid-Atlantic was smaller than those caught in the northern region. Ninety percent of the southern scallops measured were between 75 to 119 mm shell height with a peak occurring between 95 to 99 mm. A peak in height frequency for the two northern samples occurred at 110 to 114 mm, and 90% of the scallops measured ranged between 95 to 134 mm. Most of the scallops represented by the peak in the southern sample were of the 1975 year-class, while the northern sample peak was composed of the 1972–1974 year classes. Smaller, younger scallops appeared more frequently in the southern area, possibly indicating more successful recruitment since 1975 than in the northern areas samples.

Catch-per-unit of effort (pounds per paired 15-foot dredge tow) was higher in the southern (41.3) area than in either of the two northern areas (20 and 30.8, respectively).

AN APPARATUS FOR THE MEASUREMENT OF GRAZING ACTIVITY OF FILTER FEEDERS AT CONSTANT FOOD CONCENTRATIONS*

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An apparatus is described which measures the grazing activity of filter feeding invertebrate larvae and adults in an environment in which the phytoplankton food concentration can be maintained at a constant level. The "sensing" portion of the apparatus consists of a Model III Turner fluorometer equipped with a modified flow-through door. Sensitivities of ± 1 % of a selected phytoplankton concentration were achieved in experiments in which the flagellate *Isochrysis galbana* was fed to larvae of the bivalves, *Teredo navalis* and *Mytilus edulis,* the gastropod, *Aplysia californica,* and adults of the copepod, *Acartia tonsa.* The apparatus can be used effectively with as few as 100 mollusc larvae.

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INTERTIDAL GROWTH IN *MYTILUS EDULIS* L.[1]

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Although a number of commercially important bivalve species occur intertidally and, in some instances, are actively cultured on the shore, no study has investigated systematically the growth responses of bivalves to intertidal exposure. This paper reports some results of an initial attempt at such an investigation, and focuses in particular on the blue mussel *Mytilus edulis.*

Several hypothetical curves are considered relating instantaneous growth rate to shore level (expressed as percent aerial exposure). Energy-conserving adaptations, decreasing energy losses which are a consequence of intertidal exposure, will produce growth curves having greater x-intercept values, i.e., higher shore levels where growth goes to zero. The presence of energy-supplementing adaptations that compensate, to some extent, for the tidally restricted time available for feeding, will be apparent in nonlinear growth curves, convex upward.

The integral of a growth curve over the range of exposures for which growth is positive, a value referred to as the

intertidal scope for growth, reflects the energetic contributions made by both types of adaptation and may be used in comparative work among intertidal suspension feeders. The intertidal scope for growth will be minimal when growth is not possible at any level on the shore, and maximal when intertidal growth equals subtidal growth at all shore levels.

Instantaneous growth curves for *M. edulis* juveniles subjected to known levels of aerial exposure were derived from data on changes in dry meat weight, dry shell weight, length, and width. Experiments were run in the laboratory as well as on a natural shore. Both sets of curves showed a bilinear, convex-upward form, indicating compensation may have occurred. Growth in the laboratory decreased slowly with increasing exposure up to the 40% exposure level, and more rapidly thereafter, falling to zero at 90% exposure (for dry meat weight). On the shore, growth declined more rapidly at exposure levels greater than 20%, going to zero at about 80% exposure.

The lower x-intercept value for the shore-grown mussels indicated higher intertidal energy losses in that group compared with the laboratory group. Despite these higher losses, both groups had similar intertidal scopes for growth, about one half of the theoretical maximum. This implies that energy supplementation in *Mytilus* just balances intertidal energy losses so that, overall, growth performance simply reflects the limitations placed on feeding time. This result is contrasted with that obtained for *Ostrea edulis*, a low-shore species in which no compensating ability is apparent and a doubling of energy losses in going from laboratory to shore conditions reduces the intertidal scope for growth from one-third to one-fourth the theoretical maximum, a drop of 25%.

Also noted was the higher meat-to-shell ratio of intertidal mussels, and their thicker and more globose shells, as compared to subtidal specimens.

[1] Winner of the Thurlow C. Nelson Award for the outstanding paper by a student or junior scientist.

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PRELIMINARY CHEMICAL CHARACTERIZATION OF MANTLE CAVITY FLUID OF THE OYSTER *CRASSOSTREA VIRGINICA*

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Previous investigations have shown that *Crassostrea virginica* releases chemical stimuli that attract its larvae as well as predators and scavengers such as *Ilyanassa obsoleta*, *Asterias forbesi*, and *A. vulgaris*. Many behavioral investigations have inferred that such stimuli also attract oyster drills, *Urosalpinx cinerea* and *Ocenebra inornata* (=*japonica*). The purpose of the present investigation was to identify and characterize chemical substances present in seawater filtered by *C. virginica* (mantle cavity fluid) that may be primary chemical attractants to oyster drills such as *U. cinerea* and *O. inornata*.

Mantle cavity fluid was sampled directly from the suprabranchial cavity with a hypodermic needle placed between the valves of an actively pumping oyster dorsal to the rectum, or indirectly by collection of aquarium water in which oysters had been feeding actively for 24 to 36 hours. Samples were then concentrated by pressure dialysis, and characterized by means of gel filtration, thin layer chromatography, and gel electrophoresis.

Results of gel filtration show two peaks of ultraviolet (UV) absorbing material, representing fractions with molecular weights greater than 67 K daltons and less than 1 K daltons, respectively. Thin layer chromatographic results show that one substance occurring in mantle cavity fluid is hydrophilic and behaves as a protein or peptide, while a second substance appears neutral or hydrophobic. Results from gel electrophoresis revealed low concentrations of 3 to 4 peptides (20,000 to 46,000 daltons), and high concentration of a PAS positive and Coomassie Blue negative substance believed to be mucopolysaccharide. The PAS positive material occurs in two major bands, 400 K and 200 K daltons, that degrade into 60 K and 30 to 40 K subunits. Carbohydrate analysis reveals 0.3 to 4.7 μg carbohydrate per ml mantle cavity fluid measured as galactose equivalents, 0.5 to 1.4 μg/ml hexose amine, 0.1 to 0.7 μg/ml hexuronic acid, and 0.2 to 7.0 μg/ml hexamine. Only trace quantities of protein were present (0.03 to 0.06 μg/ml). Additional studies are needed to investigate the carbohydrate constituent of mantle cavity fluid in more detail as well as examine its efficacy in attracting the oyster drill *Urosalpinx cinerea*.

MYA ARENARIA–NONOBLIGATE INFAUNA

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Natural adult soft-shell clams that are removed from their burrows to trays will regress and eventually die. Hatchery-reared clams, however, confined exclusively in a nonsediment environment, exhibit considerable change in shell allometry and outperform sibling infaunal groups. After 2 years the trayed clams showed similar mean lengths as the infaunal groups; however, they exhibited a significant increase in degree of shell inflation, shell weight, and dried meat weight. These findings are discussed in the general context of life habitat of bivalve molluscs, and for the importance they may hold as a research tool and in commercial mariculture.

A COMPARISON OF FEEDING AND GROWTH IN NATURAL AND CAPTIVE SQUID (*ILLEX ILLECEBROSUS*)

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With the rapid development of the international fishery directed toward the short-finned squid, the biology of the species has received increased attention. Investigations of the physiology of feeding and growth of these squid were conducted in the 15-m circular pool in the Aquatron Laboratory of Dalhousie University in 1978 and 1979.

Squid, captured locally in a net trap, ranged in size from 70 to 250 g (16 to 25 cm mantle length), and fed *ad libitum*. For whole schools daily feeding rate to supply maintenance requirements was 1 to 2% of body weight (BW). Daily feeding rates of 3.6 to 7.8% BW yielded daily growth rates of 1.0 to 2.2% BW, and varied with size and temperature. Conversion (growth) efficiency ranged from 35 to 60%, after allowing for maintenance. These ranges of values held for both fish and crustacean diets.

Observations on individual squid suggest that they grow most efficiently at daily feeding rates of about 10% of body weight. A simple nonlinear model fitted to data conforms to this estimate, and indicates decreased growth efficiency at higher feeding rates.

Lower growth rates in the natural population suggest that food supply becomes increasingly limited as the season progresses. Most of the natural population biomass results from feeding before July when crustaceans are the principal prey; feeding rates are lower in late summer. Captive squid begin to cannibalize smaller or less healthy individuals after 3 to 5 days of starvation, and cannibalism could be an important nutrient reserve when other food is lacking, particularly during spawning migrations.

GROWTH, FECUNDITY AND ESTIMATED LIFE SPAN OF THREE LOLIGINID SQUID SPECIES IN THE NORTHWESTERN GULF OF MEXICO

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Growth of *Lolliguncula brevis*, *Loligo plei*, and *Loligo pealei* was estimated from (1) length-frequency analyses of seasonal trawl samples, (2) laboratory-rearing studies, and (3) maximal size and proposed age estimates. Using these estimates, growth rates of *Lolliguncula brevis* ranged between 0.0 and 21.4 mm per month, *L. plei* from −7.0 to 59.0 mm per month, and *L. pealei* from 6.5 to 60.0 mm per month. In general, maximal growth rates observed in the laboratory were double those derived from trawl data. Fecundity was estimated from laboratory observations of spawning females. Two *L. pealei* produced four separate broods of eggs totaling 21,000 and 53,000 eggs, respectively, and one *Lolliguncula brevis* spawned 2,000 eggs in a single brood. The life span of all three species in the northwestern Gulf of Mexico was estimated to be approximately 1 year, with a few individuals surviving up to 18 months.

PRELIMINARY NOTES ON A PILOT PLANT FOR THE FEEDING OF ADULT AMERICAN OYSTERS

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Based on previous work showing the efficacy of using finely ground cornmeal as a food to increase the quality of oysters, a plant was constructed to adapt the methods, previously developed on a laboratory scale, to more nearly commercial levels. Results of initial experiments in the facility corresponded to those previously carried out in the laboratory. Experiments were of 2 to 3 weeks duration. Percent glycogen of dried oyster meats increased dramatically but, in general, increases were less impressive as feeding continued. The cornmeal slurry was delivered to the oysters

in a semi-recirculating system showed a build up of bacteria which was reflected at times by somewhat less pronounced high counts in tank water. However, oyster bacterial counts were high whether feed was added or not. Yield increase appeared to vary inversely as salinity, independent of the glycogen content. Yield increases due to osmotic effects could be expected to be transient while those resulting from glycogen increases could be considered more stable. At present, the details of the nutritional mechanisms are not understood. Oysters have been thought to accept only small-size particles, perhaps less than 60 μ. Examination of cornmeal used in feeding was found to consist of components 87% of which would not pass through a 70-μ screen.

REPRODUCTIVE CYCLES OF THE OCEAN QUAHOG *ARCTICA ISLANDICA* AND THE ATLANTIC SURF CLAM *SPISULA SOLIDISSIMA* OFF NEW JERSEY

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The annual reproductive cycles of the two commercially important bivalves *Spisula solidissima*, the Atlantic surf clam, and *Arctica islandica*, the ocean quahog, were investigated using specimens collected from the New Jersey coast. For two consecutive years, April 1977 through March 1979, specimens of both species were recovered from commercial port landings at biweekly or monthly (during winter) intervals. Gonads of the 324 surf clams and 320 ocean quahogs were examined histologically.

By late May or June, the gonads of *Spisula solidissima* were characterized by morphologically ripe eggs or sperm. The percentage of individuals with partially spawned gonads rose sharply in the late summer and, by November or December, 100% appeared spent. Gametogenesis then proceeded slowly over the winter months, speeding up in the spring. The sex ratio of the surf clams analyzed was exactly 1:1.

A somewhat similar pattern was exhibited by *Arctica islandica*. The percentage of individuals with ripe eggs or sperm rose steadily from May ($< 10\%$) to August ($\sim 100\%$). During the first year partially spawned clams predominated in September and October before spawning out by late November. In the second year, partially spawned or spent individuals persisted into early February. Gametogenesis progressed slowly in the winter and more rapidly in the spring. Of the 320 ocean quahogs analyzed, 58% were males.

Temporal differences between the reproductive cycles of consecutive years may be related to differences in marine temperatures. Comparison of the results achieved here with previously published studies indicates important similarities and differences, and the need for further work.

SHELLFISH PROPAGATION ON MARTHA'S VINEYARD

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The Martha's Vineyard Shellfish Group, a consortium of the shellfish departments of five island towns, has initiated a program to improve and expand the traditional shellfisheries in the waters of the member towns under funding from the Economic Development Administration. For 4 years, our program of community resource development has concentrated on nursery-raft culture methods for hatchery-reared seed quahogs, *Mercenaria mercenaria*. Of various raft designs tested, economical, sand-filled wooden trays suspended from floats gave the best growth and survival. We observed over 80% survival of 480,000 seed quahogs raft-cultured in 1979. Seed quahogs as small as 2 mm have been successfully cultured in the nursery rafts. The survival of raft-cultured quahogs (12 to 25 mm) seeded in natural beds also is under investigation.

The bay scallop *Argopecten irradians* supports an important island fishery providing employment in the off-season when tourist dollars are scarce. Preliminary work suggests that maintaining an adult spawning population in backwater areas can help stabilize harvest in ponds where strong circulation patterns frequently flush larvae from the ponds before they set.

Seed quahogs and scallops have been produced in the Group's small pilot hatchery. During the summer of 1979, we spawned and cultured scallops through larval and post-set stages in the hatchery, and at 2 mm moved them to experimental floats in the pond. Over 230,000 of the lab-spawned and cultured scallops (12 mm and greater) were seeded in natural and experimental beds in the five-town waters.

As part of our hatchery work, we crossed orange-shelled scallops in the hope of developing a genetically tagged scallop to be used as a research tool in studying larval movements in the field. About 80% of the F_1 generation of orange parents exhibited orange-shell color.

WATER CIRCULATION AND OYSTER SPAT SETTLEMENT IN TWO ADJACENT TRIBUTARIES OF THE CHOPTANK RIVER, MARYLAND

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Studies of water circulation in Chesapeake Bay tributaries, which have had consistently good oyster spat settlement success, have indicated that hydrographic (advective and dispersive) conditions may act to retain larvae in the system. There has been no study of an area with poor settlement success. Broad Creek and Tred Avon River are adjacent tributaries with good and poor oyster spat settlement success, respectively. Many physical factors (temperature, salinity, tidal range, dissolved oxygen) and biological factors (adult sex ratios and gametogenic patterns) generally are similar in both tributaries. An intensive study employing current measurements and dye diffusion experiments was performed in early July 1979, while oyster larvae were in the water column and setting in both tributaries. The results of that study revealed circulation differences between both tributaries and suggested that flow variability may be as important as mean motion in affecting larval distribution.

HISTORY AND PRESENT CONDITIONS OF SQUID, *LOLIGO PEALEI* AND *ILLEX ILLECEBROSUS*, FISHERIES OFF THE NORTHEASTERN COAST OF THE UNITED STATES

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The fishery for squids, *Loligo pealei* and *Illex illecebrosus*, in the Northwest Atlantic, off the northeastern United States, has undergone significant changes over the past decade. Annual catches by the domestic fleet (primarily incidental to other directed fisheries) averaged between 1,000 and 2,000 metric tons during the period from 1887 to 1967. However, in 1967, a directed fishery for those species was developed by distant water fleets, and catches increased to an average of 45,000 metric tons a year (1969–1978).

Management of these fisheries began in 1974, under ICNAF, with establishment of a preemptive quota for the entire squid catch. Subsequently, separate quotas have been established for each species. Since 1977, under the Fisheries Conservation and Management Act, the United States has had management jurisdiction over those stocks. Since 1977, total catches of both species have declined sharply.

YIELD-PER-RECRUIT ANALYSIS FOR SQUID, *LOLIGO PEALEI* AND *ILLEX ILLECEBROSUS*, FROM THE NORTHWEST ATLANTIC

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Yield-per-recruit analyses of squid, *Loligo pealei* and *Illex illecebrosus*, were conducted based on representations of their life history and the fisheries for them. Each species has an extended (about 6 months) spawning season, resulting in significant differences in growth and mortality to different segments of a year-class. Two cohorts were, therefore, assumed for each year-class, one hatched early in the season, and the second hatched later, to account for such differences.

A modified Ricker yield-per-recuit model was used to analyse the differences in varying levels of fishing and natural mortality rates on these stocks. Instantaneous growth, and relative fishing and spawning mortalities were varied on a monthly basis to represent their effects on each proposed cohort, for several sets of natural and total mortalities. Several assumptions of year-class cohort structure were made (percent of cohort spawned early in the season) to determine the significance of time of spawning on potential yields. Effects of increasing size of entry to the fishery by increasing mesh size also were examined.

Yield-per-recruit for both *L. pealei* and *I. illecebrosus* was found to increase for all assumptions of fishing and natural mortality rates, and for time of spawning when mesh sizes were increased to 60 mm (from 15 mm). Further increases in yield were calculated when the mesh size was raised to 90 mm.

REPRODUCTION IN *ARCTICA ISLANDICA* AND ITS RELATIONSHIP TO THE OCEANOGRAPHY OF THE MIDDLE ATLANTIC BIGHT

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A review is made of the present knowledge of the biology of *Arctica islandica* with special reference to the reproductive cycle. *Arctica islandica* extends throughout a range in the Middle Atlantic Bight which is noted for seasonal thermal stratification of the water column. It is hypothesized that the intense summer thermocline forms an effective barrier to larval dispersion during the summer months, and that the functional reproductive period of this species occurs during the late fall and winter months and not in the late summer. The implications of this hypothesis on the range of larval dispersion in *A. islandica* are discussed. A continuing program of research to test this hypothesis is described.

COMPARATIVE GAMETOGENESIS IN SUBTIDAL AND INTERTIDAL OYSTERS (*CRASSOSTREA VIRGINICA*) FROM BULLS BAY, SOUTH CAROLINA

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Subtidal and intertidal oysters were collected monthly from December 1977 to January 1979 at two tidal marsh creeks in the Bulls Bay area of the South Carolina coast. Whole shucked oysters were fixed in FAA, gonadal tissue was excised, dehydrated in alcohol, cleared in toluene, and infiltrated in 57°C paraplast. Longitudinal and serial cross sections were made of each gonad at 7-μ on a rotary microtome, stained with Gill's hematoxylin, counterstained with eosin, and examined at 100× and 400× with a light microscope.

Initial observations indicated the inadequacies of established gametogenic indices for mollusca, and necessitated the formulation of an index suitable for the prolonged spawning periods and reduced inactive period characterized by the southern oyster. The application of this index, incorporating even stages of gametogenesis (one inactive, two primary, two secondary, and two tertiary) indicated little difference between gametogenic progression in intertidal and subtidal oysters. Both populations exhibited the same temporal patterns in development and appeared to spawn during the same periods.

A proposed index for gametogenesis in southern oysters is described, and gametogenic progression in subtidal and intertidal populations is discussed.

PHAGOCYTOSIS AND DEGRADATION OF A UNICELLULAR ALGAE BY HEMOCYTES OF THE HARD CLAM *MERCENARIA MERCENARIA*

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Hemocytes of the hard clam *Mercenaria mercenaria* were observed to phagocytize *Isochrysis galbana* and several other species of unicellular algae, as well as congo red-stained yeast. The "blunt" cytoplasmic granules were shown to receive degraded materials from the phagosomes containing the algae but not those enclosing a yeast cell. Transfer of the degradation product(s) was traced by observing visually the fluorescence emission of the phagocytized material, and by spectral analysis with a microspectrofluorimeter. Blunt granules were further observed to participate in the intracellular processing of the hemocyte of vital dyes and endotoxin. Observations at the light microscopy level have been correlated with ultrastructural data. It is suggested that the blunt granules represent a mechanism whereby the hemocytes can contain and/or further degrade foreign material.

A PROBLEM OF GIANT SEED: A PRELIMINARY STUDY OF THE BAY SCALLOP *ARGOPECTEN IRRADIANS* IN PLEASANT BAY, CAPE COD

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In the winter of 1979, the population of bay scallops *Argopecten irradians* in Pleasant Bay, Massachusetts, was dominated by large individuals without a well-defined raised annulus or growth line. According to the legal definition, these animals were considered large seed scallops and, thus, were protected from being harvested. Atypically, relatively few scallops were present which possessed a well

defined annulus of any kind. Those that did have an annulus could be classified into one of two groups: those with an annulus close to the hinge line and those with an annulus approximately 1-1/5-inch to 1-3/5-inch from the hinge line. Scallops from all three groups were approximately the same size. Large seed scallops generally had a glossy black covering over the gonads. The other two groups showed variable coloration. Histological analysis of gonadal material from January 1980 samples indicated that gametogenesis had begun in all three groups of scallops. Periodic sampling of scallops, and monitoring of the gametogenic cycle are currently being conducted to assess the value of these large seed scallops in the overall scallop population of Pleasant Bay.

POPULATION BIOLOGY OF THE OCEAN QUAHOG IN THE MIDDLE ATLANTIC BIGHT

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The ocean quahog *Arctica islandica* has become increasingly important to the clam industry of the United States. Landings of shucked meat increased thirty-fold between 1975 and 1979; from 570 metric tons to 15,610 metric tons. Data on the distribution, relative abundance, and size compositions of Middle Atlantic stocks have been gathered during a series of dredge surveys since 1965. Additional information on age and growth is available from recent field and laboratory studies. A review of important biological features, and a current assessment of Middle Atlantic populations are presented.

DO FAST GROWING OYSTER LARVAE PRODUCE FAST GROWING ADULT OYSTERS?

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In several lines of European oysters, *Ostrea edulis*, the correlation between larval growth rate and juvenile size (mean length = 22 mm) is positive but small. As the oysters continue to grow, the effect of larval growth rate diminishes; it is virtually zero by the time the oysters are 43 mm, average size. In one line, the correlation remained nonzero for 2 years, but was so small that very little of the variation in size could be attributed to variation in larval growth rate. Consequently, it appears there is little to be gained in improving juvenile and adult growth rates by selecting faster growing larvae. Selecting faster growing larvae may improve hatchery performance, but to improve growout, selection must be done at a later stage.

STUDIES ON VARIOUS SUBSTRATES IN RELATION TO SETTING OF OYSTER LARVAE WITH COMMENTS ON COMMERCIAL APPLICATIONS

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Setting oysters in a hatchery along the Gulf of Mexico must be inexpensive and adaptive to bottom planting to be competitive with natural setting. Preference of oyster larvae for setting on clam shell was compared to three other substrates in the laboratory; however, many larvae (57%) were "lost" to the tanks and containers. Setting on oyster valves was comparable whether the shells were held in boxes or bags. Freshly shucked "green" shells, aged shells, and washed oyster valves caught spat equally well when planted in the bay. However, in the hatchery, washed shells caught three times as many spat as did aged shells and sixteen times as many spat as "green" shells. A system for handling the required volumes of clam shell for setting hatchery-reared larvae is proposed for a pilot seed operation.

EVIDENCE FOR A VIRUS CAUSING NEOPLASIA IN THE SOFT-SHELL CLAM (*MYA ARENARIA*)

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Hematopoietic neoplasia is a terminal cancer of the hemocytes of soft-shell clams (*Mya arenaria*), and is endemic to the northeastern United States. No association has been made between bacteria, mycoplasmas, or protozoan parasites and the disease, nor has there been any correlation with environmental pollution.

We have isolated a virus from neoplastic soft-shell clams with physical and chemical properties similar to RNA tumor viruses. Further, neoplasia has been induced upon injection of the purified virus into nonneoplastic clams. RNA tumor viruses have long been associated with neoplasms in mice,

cats, and fowl. Virus has not been isolated from any non-neoplastic samples, and because the virus does cause neoplasia, it seems likely that the virus isolated is the etiological agent of molluscan hematopoietic neoplasia.

SQUID CATCHES ALONG THE UNITED STATES CONTINENTAL SLOPE

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During October–November 1979, the Federal Republic of Germany research vessel ANTON DOHRN conducted a trawl survey along the continental slope between Georges Bank and Cape Canaveral (Florida). Primary depth coverage ranged from 400 to 1,000 meters using commercial-size otter trawls. Some limited coverage was accomplished on the continental shelf.

Illex squid represented the largest volume of any one species sampled during the cruise. These squid were extremely cosmopolitan in their distribution with large catches at both the most northerly and southerly locations fished. The results experienced provide new information on the ubiquitous distribution of *Illex* in the slope area during the fall season. Hydrographic information was recorded at each trawl station, and other biological observations were made on the size and maturity of the squids.

GROWTH OF MUSSELS AT DEEP-SEA HYDROTHERMAL VENTS ALONG THE GALAPAGOS RIFT

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The deep-diving submersible ALVIN marked the posterior shell margins of mussels with a file on February 12, 1979. ALVIN returned to recover the marked mussels on December 3, 1979, after a period of 294 days.

New shell growth beyond the file mark was linearly related to premark shell length ($r > 0.95$). The smallest marked mussel (3.5 cm) added 17 mm of new shell in 294 days ($\bar{x}$ = 0.06 mm day^{-1}); specimens 12 cm long at the time of marking added 6.5 to 10 mm of new growth in 294 days ($\bar{x}$ = 0.02 to 0.03 mm day^{-1}); and the largest marked specimen (16.5 cm) added 2 mm of shell in 294 days ($\bar{x}$ = 0.01 mm day^{-1}).

Small mussels (N = 25; 8 to 27 mm long) also were recovered from a slide box and bottle rack (N = 9) placed at the rift vents for microbiological sampling. The slide box and bottle rack were deployed for 294 days. If we assume that the largest of these mussels represents an early primary settlement of spat on the box and bottle, juvenile growth rates are on the order of 0.09 mm day^{-1}.

The growth data for file-marked mussels and juvenile growth rates allow one to construct an ontogenetic growth curve which predicts absolute age from shell length. Our growth model indicates that the largest specimen collected (16.7 cm) was 14 to 16 years old. Half of this maximum length was obtained by the mussels in 3 to 4 years. The modal age of the file-marked mussels ranged from 6 to 11 years.

The growth rates deduced for the Galapagos mussels were among the highest growth rates documented for deep-sea invertebrates. The ontogenetic growth curve for Galapagos mussels is comparable to growth curves of shallow-water mytilids.

STATISTICAL ANALYSIS OF DIGESTIVE GLAND TUBULE VARIABILITY IN *MERCENARIA MERCENARIA* (L.), *OSTREA EDULIS* L., AND *MYTILUS EDULIS* L.

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Recent investigations indicate that marine bivalves apparently demonstrate rhythms of intracellular digestion, often correlated with the tidal cycle. Evidence is based primarily, and often solely, on the diverse histological appearances of the digestive gland tubules from different individuals over a period of time. In general, four main tubule types, signifying various stages of intracellular digestion, can be recognized: I, holding; II, absorptive; III, fragmenting; and IV, reconstituting. Digestive tubules and similar tubule types are not distributed randomly within the digestive gland, but are grouped together around common secondary ducts. This necessitates the use of a cluster sampling technique for proper statistical analysis. In *Mercenaria mercenaria*, *Ostrea edulis*, and *Mytilus edulis*, variability of tubule types is high within individual digestive glands as well as between individuals sampled at the same time. Based on calculations to minimize total variance, it

is better to sample a small area from numerous individuals rather than a large area from a few animals. Intra-animal variability is similar in all three species. Similarly, inter-animal variability is the same in the subtidal quahog and mid-intertidal mussel, but much less in the low intertidal oyster. The problems imposed by variability and tubule clustering have not been considered adequately in previous investigations of bivalve digestion.

THE ECONOMICS OF ARTIFICIAL UPWELLING MARICULTURE[1]

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To determine the economics of artificial upwelling mariculture, the clam *Tapes japonica* was grown over a 12-month period in the St. Croix system, operated in pilot-plant fashion.

Seawater from a depth of 870 m was pumped continuously into ponds (100 m^2, 1 m deep) onshore. The ponds were inoculated with the diatom *Chaetoceros curvisetus* (STX 167) which was grown in continuous culture and pumped to a *Tapes japonica* production line. The system produced 81 kg of phytoplankton protein, and 423 kg (whole wet weight) of clams in 12 months, corresponding to a yield of 8.1 tons plant protein, and 42.3 tons of clams per hectare per year.

An aquaculture budget generator was developed to predict costs of artificial upwelling mariculture systems of different sizes. Thus, for a plant producing 21,900 tons of clams per year, the cost would be $0.77/kg of clams produced. The deep seawater costs represent $0.10 of that total, the phytoplankton production $0.32, the shellfish area costs $0.25, and supervisory costs represent $0.10.

The deep seawater system and the phytoplankton production system are subject to considerable economies of scale. The costs in the shellfish area do not vary much with the capacity of the plant.

The economics of clam production obviously are most sensitive to the phytoplankton cost.

[1]This work was supported by Sea Grant, National Oceanic and Atmospheric Administration, and U. S. Department of Commerce.

SIZE AND AGE AT SEXUAL MATURITY OF OCEAN QUAHOGS *ARCTICA ISLANDICA* LINNÉ, FROM A DEEP OCEANIC SITE

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Gonadal tissues and the corresponding shells of ocean quahogs *Arctica islandica* were collected during late July to early August 1978, from off Long Island, New York, for an examination of sexual development and growth line formation. The collection dates were before the known time of spawning for the species and when gonadal development was expected to be in a ripe stage. Most of the clams were of small size ($\bar{x}$ = 39.2 mm; standard deviation (SD) ± 8.13), ranging from 18.7 to 60.4 mm in shell length. A 5-year-old (41.0 mm) and three 6-year-old (36.4 to 41.0 mm) clams were the youngest containing well developed gonads and numerous sex cells, but a 10-year-old (47.9 mm) clam only had moderately developed gonads containing few sex cells. Gametogenesis indicative of the female sex was in older (5-year-old) clams than in males (3-year-old), suggesting a later attainment of sexual maturity of female clams. Gonadal tubule development, gametogenesis, and attainment of sexual maturity were variable with respect to size and age.

SURVIVAL OF RECENT LARGE SOFT-SHELL CLAM SETS IN HAMPTON-SEABROOK ESTUARY AND PROGRESS TO HARVESTABLE SIZE

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Soft-shell clam population dynamics have been monitored in Hampton-Seabrook Estuary for more than 9 consecutive years. By far the largest clam set was recorded in 1976, when an average of approximately 7 spat per ft^2 settled on five flats, totaling 165 acres.

Initially growth rate and survivorship were low, probably because of crowding and predation. Sufficient numbers survived, however, to restore badly depleted harvestable stocks to near historic levels. Rates of recruitment to harvestable size were determined by following year-to-year changes in size-frequency distributions. Recruitment rates, in turn, were used to predict future standing-stock levels given various management alternatives. Among the interesting observations arising during the study were: (1) indications

that survivorship and growth rate improved with succeeding year classes (1977 and 1978), and (2) coincidence of a six-fold increase in abundance of sexually mature clams with an eight-fold increase in midsummer abundance of soft-shell clam larvae.

The present policy of restricting digging to 2 days per week, September through May, appears to have helped the stocks recover. However, the two largest and most productive flats probably could be opened to summer digging for up to 2 years to the advantage of clam diggers and without long-term adverse effects on the resource.

OYSTER SETTING–PAST, PRESENT, AND FUTURE

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Natural oyster sets are still essential if a viable oyster industry is to continue in the United States. Although a number of oyster hatcheries have been established, at best, they can only supplement natural sets.

Many speculations have been made regarding the recent causes of low setting rates, especially in the Chesapeake Bay. Yet, no single cause can be found.

There is no question that the loss of brood stock from MSX in the high-salinity waters of Virginia seriously affected setting in the James River. Yet, setting has declined in other Virginia rivers, the cause of which cannot be totally related to brood stock losses from MSX.

In Maryland, MSX losses of any significance occurred only in the southern part of the state. Major seed areas were not in those areas. Still, especially during the past decade, setting has been of low intensity.

Scientists in Japan have just completed extensive studies related to oyster setting in Matsushima Bay. Number of parent oysters, quantity of larvae produced, number of seed collected, and efficiency of seed collecting were determined. Based on those studies, new setting areas were found and utilized. Those studies are described, and recommendations are made that similar studies should be considered in the Chesapeake Bay.

POLYPLOIDY INDUCED IN THE EARLY EMBRYO OF THE AMERICAN OYSTER WITH CYTOCHALASIN B*

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An attempt was made to induce polyploidy in the American oyster by treating the zygote with cytochalasin B. This antibiotic caused significant delay in the first cleavage division, presumably without interfering with chromosome replication. As a result, a significant number of larvae were polyploid; 13 of 22 treated with 0.1 mg/l cytochalasin, and 3 of 4 treated with 1.0 mg/l. Survival at 24 hours was about 33% that of the controls for the larvae from the 0.1 mg/l treatment, and 15% for larvae receiving 1.0 mg/l cytochalasin. Survival was greater for oysters treated for 15 minutes beginning immediately after fertilization than if treatment began later at 15 or 40 minutes. Oysters from the treated zygotes set normally and subsequent survival was indistinguishable from those of controls. At 8 months, control and treated oysters were 13 mm in length.

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USE OF AN OYSTER RACK FOR OFFBOTTOM CONTAINERIZED-RELAYING OF POLLUTED OYSTERS IN MISSISSIPPI SOUND

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An experimental oyster rack was used to relay 48 sacks of naturally contaminated oysters into approved shellfish growing waters south of Deer Island, MS, during two separate trials. The 3.6 × 1.8 × 1.2 m rack (patent E. R. Gollott), constructed primarily of welded angle iron, was designed to hold 48, 86 × 56 × 10 cm, plastic chicken-coop bottoms (polyethylene structural foam) in a sliding tray arrangement. The trays were positioned in a 6-tray × 2-row × 4-level arrangement, with a space of 5 cm between the four levels. During the first experiment, oysters eliminated fecal coliforms from an initial median value of 1,400 MPN/100 gm to a median of 45 MPN/100 gm after 7 days. A second attempt produced a median value of 20 MPN/100 gm after 10 days, following an initial median value of 23,000 MPN/100 gm. No attempt was made to acclimate oysters to the higher salinities of the relaying waters. Mean condition

indices increased by 2.5 gm/ml over the relaying period. The mean oyster mortality was 1.3%. The rack eliminates the problems associated with onbottom relaying while guaranteeing complete second harvests.

AN OVERVIEW OF THE SNOW CRAB (*CHIONOECETES OPILIO*) FISHERY IN NEWFOUNDLAND

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The fishery for snow crabs (*Chionoecetes opilio*) in Newfoundland is comparatively new. Fishing began in 1969 with landings for that year of 90.7×10^3 kg. Landings have risen dramatically in recent years peaking in 1979 at approximately 10.9×10^6 kg. A summary of annual landings for Newfoundland since the fishery started is presented. Also presented is a breakdown of annual catch-per-unit of effort and total effort in management areas for which data are available. Management policy and research projects along with their objectives are discussed.

PRELIMINARY INVESTIGATIONS OF LOCAL POPULATIONS OF THE BAY SCALLOP *ARGOPECTEN IRRADIANS* LAMARCK IN FALMOUTH, MASSACHUSETTS

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In May 1979, a preliminary investigation of local populations of *Argopecten irradians* in Waquoit Bay, Falmouth, Massachusetts, was begun. The specific problems investigated in this preliminary program were: (1) migrations of adult populations; (2) gonad development and time of maturation and spawning of local populations; and (3) growth of newly set juveniles during the harvesting season.

Movements of scallops were monitored at three stations in the bay, and these movements appeared to be random throughout the summer. Gonads of bay scallops were ripe in May, and in a partially spawned condition during June and July. Juveniles exhibited high growth rates throughout the summer and fall; 90% of the individuals examined reached a length of > 50 mm by the end of the year (December 1979).

The findings of this preliminary study form a basis to assess the appropriateness of the current harvesting season, and the potential success of local seed transplant programs.

METHODOLOGY FOR SPECIFIC DIAGNOSIS OF CEPHALOPOD REMAINS IN STOMACH CONTENTS OF PREDATORS WITH REFERENCE TO THE BROADBILL SWORDFISH *XIPHIAS GLADIUS*

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The stomach contents from 65 broadbill swordfish, *Xiphias gladius*, from the Straits of Florida were examined. Previous studies have demonstrated the importance of cephalopods in the diet of this predatory vertebrate, but have omitted critical analyses of these remains. The majority of the stomach contents encountered in the present study were in extremely poor condition because of mechanical and chemical breakdown incurred during ingestion and digestion. Identification of remains became increasingly difficult as the traditional sequence of character assessment was interrupted by the deterioration and/or loss of morphological and meristic characters.

Identifications were by necessity based on a synthesis of less frequently utilized characters, inherently more resistant to gastric breakdown. These included mantle musculature, buccal membrane connectives, light organs, gladii, beaks, spermatophores, and radulae. In addition, an examination of viscera, when present, provided taxonomic information as well as data concerning sex, state of maturity, and fecundity.

Earlier studies based on sample sizes an order of magnitude greater than the present indicated a low diversity of cephalopod species in the prey composition of *X. gladius*. The utility of the approach outlined here is demonstrated by the fact that 15 species representing 11 families in two orders were encountered. The significance of this type of analysis is further emphasized considering 11 of these taxa have not been reported previously in the diet of swordfish. In addition, one was a first record of occurrence in the Atlantic, another was the largest known representative of its family, and still another was the smallest recorded mature male from the family Architeuthidae, the giant squids.

PROTEIN DIGESTIBILITY IN THE LOBSTER *HOMARUS AMERICANUS*

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The digestibility of five different proteins (casein, whole egg protein, soybean protein, shrimp protein concentrate, cod fish protein concentrate) was determined in canner lobsters (65 to 85 mm carapace length) using the chromic oxide indicator method. No significant differences were obtained in average total digestibility of the diets (60%), but there were differences in protein digestibility. The average percent apparent digestibility of the casein, whole egg, and shrimp proteins was > 96%; soybean protein, 93%; and cod fish protein, 85.5%. Factors contributing to differences in protein digestibilities, and problems encountered doing digestibility studies with aquatic animals are discussed.

SEASONAL REPRODUCTIVE CYCLE AND SHOW FACTOR VARIATION OF THE GEODUCK CLAM *PANOPE GENEROSA* (GOULD) IN BRITISH COLUMBIA

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Geoduck clams, *Panope generosa* (Gould), were collected on a monthly basis from Cherry Point, Saanich Inlet, 35 km north of Victoria, and gonads analyzed for reproductive phase. Samples were harvested from May 1977 to August 1978, at a depth of 9 m. The reproductive cycle was divided into five phases: early active, late active, ripe, partially spent, and spent.

Four 100-m^2 plots were simultaneously observed to determine what percentage of the population were visible (siphons extended) at various times of the year, indicating seasonal activity patterns. Plot populations were established.

Gametogenesis was observed first in September samples and by early January, 98% of the clams were in the early active phase. Six percent were ripe already. Most ripe specimens occurred during April (54%) and May (91%). Spawning began in May, and by June, 77% of the samples were partially spent. All samples were in the spent phase by August.

A total of 624 geoducks was collected during 1977 and 1978, from 52 locations; reproductive phases of these clams were compared to those of the Cherry Point samples. No significant variations were observed from the Cherry Point cycle.

Siphon-show factor increased rapidly from February to April and remained at a high, but reduced level during the summer months. Shows decreased in the fall, and in January monitoring, no animals were observed in any of the four plots. A total of 1,175 animals were monitored.

ASPECTS OF *LOLIGO PEALEI* EARLY LIFE HISTORY

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In the Middle Atlantic Bight off New Jersey and Virginia, *Loligo pealei* was the most common squid species collected in 2 years of zooplankton sampling. Planktonic *L. pealei* were found in that area in spring, summer, and fall, and there were no indications of multiple stocks. This species was captured in waters with a salinity range of 31.5 to 34.0 ppt, and was confined to coastal waters except during conditions when the Gulf Stream eddy resulted in strong offshore surface transport. While highest abundances were found in night surface samples, night subsurface collections took larger specimens, indicating ontogenetic descent. Tentacle length was correlated closely with dorsal mantle length in preserved specimens of less than 7.5 mm dorsal mantle length, indicating that tentacles are noncontractile in newly hatched specimens.

LIMITATIONS AND POTENTIALS OF BAY SCALLOP (*ARGOPECTEN IRRADIANS*) CULTURE IN NEW ENGLAND

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The Wampanoag Fisheries Project has completed a 3-year aquacultural feasibility study to improve and stablize the bay scallop population in Menemsha Pond, Gay Head, Massachusetts. The potential of bay scallop culture in New England was demonstrated by growth of hatchery-reared seed during the summer and fall of 1978 in Menemsha Pond.

Two groups of hatchery seed averaging 3 to 4 mm in length were planted in May–June, and reached a harvestable size of 50 to 60 mm by November 1978. Seed that set naturally in the pond in August averaged less than 10 mm in length by November.

More important from an aquacultural point of view was that the early seeding of Menemsha Pond resulted in scallops exhibiting excellent growth characteristics (420 to 720 μ/day), and no spawning activity during the summer months. Water temperatures were declining by the time the scallops were big enough to develop gonads. Declining water temperatures apparently favored a rapid increase in the weight of the adductor muscle. This was evidenced by a 161% increase in the weight of the muscle of the 1977 year-class during the period August–October 1978. Similar gains were identified qualitatively in the 1978 year-class hatchery seed.

A vertically integrated aquaculture business consisting of a 10,000 square-foot hatchery, a seafood processing facility, and a shellfish brokerage firm, coupled with a fishermen's cooperative, was envisioned initially as a possible means of stabilizing the unpredictable scallop harvest, and of providing employment for the Wampanoag Tribe. However, a careful evaluation of this entire proposal during the third year of the program indicated that implementation of this scallop aquacultural plant was not feasible at the present time.

Problems facing scallop aquaculture in New England fall into three major areas: (1) hatchery design and operational time table, (2) field grow out of hatchery-produced seed, and (3) harvest, sale and/or processing of the scallop crop. Problems in hatchery design and operation include translating the current laboratory-scale culture of scallops into a commercial production concept, and the development of techniques for mass culturing of selected species of algae. Problems in field grow out of hatchery-reared seed include the logistical, legal, political, and economical ramifications of using nursery techniques such as rafts, fenced-in areas, or pumped raceways. Problems in the harvesting, selling, and/or processing of the adult scallop include destruction of scallop seed during harvesting of adults, difficulties in establishing a single-product brokerage, and the high cost of developing new seafood products that might utilize the visceral portion of the scallop which presently is discarded.

SEASONAL VARIATIONS IN BODY COMPONENT INDICES AND ENERGY STORES IN THE SEA SCALLOP *PLACOPECTEN MAGELLANICUS* (GMELIN)[1]

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Index values were determined on gonadal mass, digestive gland, and the quick-and-catch components of the adductor muscle in adult specimens of the sea scallop *Placopecten magellanicus* collected at 6- to 8-week intervals over a 12-month period. All tissue indices were found to vary significantly over the year. Somatic tissues displayed a biphasic annual pattern with highest values in late spring and fall, and lowest values in midusmmer and midwinter. The gonadal mass displayed a single annual peak in the summer just prior to spawning. No significant sex-specific differences were noted.

Energy stores were estimated by measuring total lipid and glucose plus glycogen concentrations in the indexed tissues. Concentrations of both storage types exhibited seasonal patterns similar to those of the tissue indices.

The reciprocal nature of the gonadal mass and tissue indices, and energy store concentrations in late spring and summer suggests movement of energy stores from somatic tissues to the gonad.

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ABSTRACTS OF TECHNICAL PAPERS

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WEST COAST SECTION

NATIONAL SHELLFISHERIES ASSOCIATION

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INTERTIDAL CULTURE OF THE MANILA CLAM *TAPES JAPONICA* USING HATCHERY-REARED SEED CLAMS AND PROTECTIVE NET ENCLOSURES

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Commercial feasibility of intertidally culturing the Manila clam *Tapes japonica* was investigated at Filucy and Wescott bays in Puget Sound, Washington. Hatchery-produced seed clams were marked and planted at densities of 1,000 clams/m^2 in areas protected by two layers of 12.5-mm mesh lightweight plastic netting. Unprotected areas were seeded at densities of 900 clams/m^2. Recovery and growth of the marked clams were studied after 3, 6, and 12 months.

Recovery in protected areas (30 to 60%) was higher than in unprotected areas (2 to 12%); this was attributed to greater predation and washout in the unprotected areas. Because of that, growth could be evaluated only for the protected areas, in which mean shell lengths were similar in both bays after 12 months. Clams were larger at lower tidal heights; the growth rate appeared to decrease with increasing tidal height.

At Filucy Bay, the average population density of large ($\geqslant$ 8 mm), wild Manila clams in the protected area increased tenfold to 191 clams/m^2; the density of those wild clams in the unprotected area decreased twofold to 16 clams/m^2. This suggests that the netting may act to concentrate juvenile clams from the wild population as they are moved about by wave activity. It is further speculated that the density of larval settlement may be higher in the protected area.

Net value of the potential harvestable biomass/m^2 suggests that this type of commercial culture operation is both practical and economically feasible.

THE JAPANESE OYSTER DRILL (*OCENEBRA INORNATA*)

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The Japanese oyster drill *Ocenebra inornata*, introduced on imported seed oysters, continues to be a problem in certain areas on the western coast of the United States. In the past, control has been attempted unsuccessfully by a variety of methods such as the handpicking of aggregations, tilling or discing infested grounds, draining pools to increase dessication stress, chemical treatments, and physical and chemical barriers. Pheromone-baited traps were suggested as a potential control technique during the spring and fall periods of snail aggregations. A study started in June 1980, is attempting to prove the existence of aggregation pheromones, determine the sites of pheromone production, and extract and concentrate chemicals acting as attractants for the Japanese oyster drills. Future studies should include isolation, identification and synthesis of pheromones, and development of pheromone-baited traps.

HATCHERY REARING OF THE OLYMPIA OYSTER *OSTREA LURIDA*

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The Olympia oyster industry was once a thriving industry on the western coast of North America and especially in the state of Washington. It began simply as a fishery on existing natural stocks and, eventually, developed into an intensive culture operation. Depleted populations, lack of recruitment, the Japanese oyster drill, and the flatworm have had a role in the decline of the now decimated populations. Hatchery-grown seed is the only apparent method to restore beds to production levels.

Hatchery techniques are described for rearing this species from the brooding larval phase through to setting size. Three groups of brood stock in different quantities were maintained in a closed system at different times of the year to determine the desirable number of adults needed for hatchery production. About 1 million larvae were obtained from a brood-stock size of 50 oysters from June 12 through August 9; 104 million larvae were obtained from 5,000 oysters kept in the hatchery from December 6 through February 8; and 23 million were liberated from a group of 1,000 oysters from March 12 through April 22.

Larval-rearing techniques are described which resulted in growth periods of 15 to 23 days from liberation to setting. Setting was successful; however, a high mortality occurred in the first 2 weeks after setting for all groups.

INVESTIGATION OF SHELL DISEASE IN ALASKA KING AND TANNER CRABS

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The commercial crab industry in Alaska has experienced problems due to the poor condition of both the king crab *Paralithodes camtschatica*, and the tanner crab *Chionoecetes bairdi*. These problems include low meat yield, low vigor, soft shell, inability to molt, and the presence of dark lesions which pit the exoskeleton. Bacterial and histological studies were initiated to find solutions to these problems. Preliminary studies indicated no difference in numbers of types of bacteria present in normal or diseased crabs. Pseudomonads, aeromonads, and myxobacteria were isolated most commonly. Chitinoclastic bacteria seldom were isolated although the exoskeletons were pitted by lesions. No one organism was associated with the lesions. Through these, bacteria were able to gain entrance to the interior of the crab. Blood or lymph could become infected easily through the lesions.

Rapid death of tanner crabs ensued following injection of either of two common isolates. The isolates were a *Moraxella* sp. and a *Pseudomonas* sp., most closely related to *Pseudomonas stutzeri*. Infection of healthy crabs and repeated recovery from diseased ones indicated pathogenicity although some crabs survived infection and some were able to eliminate the bacteria. The susceptibility of a particular crab probably related to its overall health. Additional studies may reveal mechanisms of transmission, distribution of pathogenic bacteria in host tissue, and management strategies to minimize future loss.

CELLULAR RESPONSE TO CARMINE IN THE BROWN SHRIMP *PENAEUS AZTECUS* WITH OBSERVATIONS ON VIRUS-LIKE PARTICLES IN THE HEART

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Crustaceans generally combat infection by recognizing and clearing the hemolymph of 'nonself.' Although humoral factors act synergistically with cellular defense mechanisms, the latter are the principle means of internal defense and include coagulation, phagocytosis, and encapsulation. In penaeid shrimp, circulating hemocytes play an important role in such reactions, but noncirculating cells in the heart, gills, and hepatopancreas also participate in the surveillance and clearance of foreign substances. The purpose of the present study was to examine by transmission electron microscopy the clearance of carmine particles in the gills and heart of the brown shrimp *Penaeus aztecus* to demonstrate the phagocytic capabilities, functional relationships, and ultrastructural characteristics of circulating and noncirculating phagocytic cells. During this study, virus-like particles were observed within cardiac cells and their significance is discussed.

A 1.4% carmine-saline solution was injected into the sternal sinus, and the shrimp were sacrificed for light and electron microscopy at intervals up to 8 days postinjection. Within 1 hour carmine particles were clumped in the hemolymph and phagocytized or encapsulated by hemocytes. Hyalinocytes and semi-granulated hemocytes were more phagocytic than mature granulocytes. No carmine was observed in the gill podocytes, but their large dense vacuoles appeared to increase in size and number. Podocytes share structural characteristics with cells of the vertebrate renal glomerulus and probably aid in clearing the hemolymph of fine particulate material. Fixed phagocytes in the heart were attached loosely to the basal lamina surrounding myocardial cells and were weakly phagocytic for carmine particles, which accumulated in a large cytoplasmic vacuole containing cellular debris and dense flocculent material.

Viral inclusions were observed in the characteristic vacuole of fixed phagocytes in the heart. Inclusions measured ca. 1 μm in diameter, and often were surrounded partially by a membrane. Each consisted of a tightly packed aggregate of small, nonenveloped, osmiophilic particles ca. 23 nm in diameter. Some of the particles appeared to be square-shaped, and many were organized in linear arrays. If the particles are an eucaryotic virus, they may belong to either the parvovirus or the picornavirus group. However, the virions may be phages infecting a phagocytized prokaryote whose cell wall and/or membrane were partially digested.

BLUE MUSSEL (*MYTILUS EDULIS*) CULTURE IN SOUTH COASTAL BRITISH COLUMBIA

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A project to investigate the commercial feasibility of blue mussel (*Mytilus edulis*) culture in British Columbia was

begun in 1979 at eight locations. Biological parameters investigated were growth, mortalities, fouling, predation, and recruitment.

Surveys of wild mussel beds showed that stocks of seed mussels suitable for culture in Netlon socks were plentiful only at a few locations in the Strait of Georgia but were common on the western coast of Vancouver Island. Wild mussels from the intertidal zone that were placed in Netlon socks and suspended from rafts grew to approximately 50 mm shell length in 12 months after suspension. Severe unexplained mortalities were experienced at all sites.

Fouling by barnacles (*Balanus glandulus*) was heavy at most sites; fouling by hydroids, bryozoans, algae, and anemones was common.

Heavy predation by ducks, Barrow's goldeneye (*Bucephala islandica*), and by surf scooters (*Melanitta perspicillata*) was experienced at all sites during the winter months. Starfish (*Pisaster ochraceus*) destroyed mussel seed at one site, and pile perch (*Rhacochilus vacca*) were observed feeding on small mussels at another.

Suspended ropes successfully collected commercial quantities of seed at seven sites in both 1979 and 1980. Seed collected in the summer of 1979 grew to market size (50 mm shell length) in 10 to 12 months at some locations but again heavy unexplained mortalities were experienced in 1980.

The problems of heavy mortalities and predation must be overcome if commercial mussel culture is to become feasible in British Columbia. Some mechanization also is required for processing mussels in areas of heavy fouling.

At present there are six mussel culture pilot projects (including the one described here) underway in British Columbia, and seven lease applications for mussel culture are pending.

PARALYTIC SHELLFISH POISONING IN WASHINGTON STATE, 1978–1980

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During the past 10 years (1970–1980), there has been a dramatic increase in the paralytic shellfish poisoning sampling program in Washington State. Samples processed for PSP toxin have increased from 100 in 1970 to 1,200 in 1980. Factors contributing to the increased sampling include: (1) movement of the causative agent to previously unaffected areas, (2) increased public awareness and interest in the problem, and (3) paralytic shellfish poisoning research projects. Sampling locations have been expanded to cover nearly all shellfish growing areas in Puget Sound. An extensive dinoflagellate bloom occurred in late summer of 1978, and it affected a large area in central Puget Sound, primarily sport shellfish beaches. Sport shellfish samples have increased from 16% of total samples in 1970, to 60% of total samples in 1980. Butter clams from areas that have been affected for a number of years remain toxic year around, but butter clams from newly affected areas lose their toxicity during the winter months. Further information on uptake and release of toxin by various shellfish species is being examined.

NEW CANDIDATES WITH AQUACULTURE POTENTIAL IN WASHINGTON STATE: PINTO ABALONE (*HALIOTIS KAMTSCHATKANA*), WEATHERVANE SCALLOP (*PECTEN CAURINUS*), AND PURPLE-HINGE ROCK SCALLOP (*HINNITES MULTIRUGOSUS*)

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Three under-utilized native species are being investigated for their commercial aquaculture and enhancement potential. These aquaculture candidates include the pinto abalone (*Haliotis kamtschatkana*), and two scallop species: the weathervane (*Pecten caurinus*) and the purple-hinge rock scallop (*Hinnites multirugosus*).

An experimental minihatchery facility has been established at the Point Whitney Shellfish Laboratory, Brinnon, WA, and progress has been made in culturing the larvae of all three species. The pinto abalone have spawned consistently when exposed to 10^{-6} m concentration of hydrogen peroxide buffered with tris (hydroxymethyl) aminomethane to pH = 9. Adult abalone have been conditioned for over a year in the laboratory, and spawnings have occurred successfully each month from March through November. Metamorphosis was stimulated with gamma aminobuteric acid on day 9 after spawning. Juvenile abalone were grown to 25 mm in 14 months in unfiltered seawater at ambient temperatures (8.5 to 14.0°C).

Spontaneous spawnings in May for the weathervane scallops, and in May and September for the purple-hinge rock scallop provided viable larvae for study, although all attempts to stimulate spawnings have been unsuccessful. Larvae of each species were cultured to metamorphosis in 34 to 40 days at which time high mortality occurred. Larval scallops were grown in seawater filtered to 10 μm at temperatures of 9 to 16°C in static culture, and fed a mixture of *Monochrysis* sp., *Isochrysis* sp., and *Psuedo-isochrysis* sp. at concentrations of 10,000 to 50,000 cells/ml.

Further investigations of scallop spawning techniques and methods, as well as larval culture and grow-out methods, will be conducted in future studies.

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SPECIAL SQUID SYMPOSIUM

Presented at

ANNUAL MEETING OF THE NATIONAL SHELLFISHERIES ASSOCIATION

Hyannis, Massachusetts

June 8–12, 1980

INTRODUCTION

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Cephalopods represent a major fishery resource widely distributed throughout the oceans of the world. Of the several hundred species harvested, squids of the families Loliginidae (*Loligo opalescens, L. pealei, L. plei*), and Ommastrephidae (*Illex illecebrosus*) are important to North American fisheries.

Expansion of world squid fisheries in recent years has led to a rapid increase in the exploitation of North American stocks. Japan, as the world's foremost harvester and consumer of squid, has led in this expansion, although the Soviet Union and a number of other countries have also directed considerable effort toward increased harvest of the resource.

The fishery for short-finned squid, *I. illecebrosus*, on the Atlantic coast of Canada illustrates this expansion, showing a rapid increase from an annual average catch of about 4,500 metric tons (MT) during the 1970–74 period to roughly 153,000 MT in 1979. This huge increase in landings, by both foreign and domestic fishermen, has quickly brought the biological and management problems into focus, and has stimuated a number of new research initiatives on the part of both governmental and nongovernmental research institutions.

The current interest in squid as a major fishery resource has provided what must be one of the most exciting and biologically challenging areas for fisheries research and management. The scope of problems involved are again illustrated by *Illex*, with its short life span (generally estimated at 12 to 18 months); its unknown spawning distribution; poorly known distribution of larval, juvenile, and adult stages; unknown migration patterns; and unknown stock relationships. Unlike most finfish, where a number of year-classes may be monitored for several years prior to recruitment to the fishery, and where predictive population assessments can be used to establish harvest levels, an *Illex* year-class is first seen in the same year as the fishery; there is no possibility of applying currently available assessment and predictive models to determine optimal harvest levels.

It was in consideration of the commercial importance and the challenging biological problems presented by our North American squid resources that the National Shellfisheries Association asked that I organize a *Special Session on Squid* for its 1980 Annual Meeting in Hyannis, Massachusetts.

For that Special Session, contributed papers were requested to focus on one of three topic areas: (1) on the historical overview and description of the fisheries; (2) on biological and ecological studies important to understanding the resource and its management; and (3) on population biology, modeling, and prediction as applicable to squids. A total of twelve papers were presented at the Special Session; nine are being published in this dedicated issue. Abstracts of all the papers appeared in Volume 1, Number 1 of the *Journal of Shellfish Research*. These papers provide new information on adult and larval distribution, growth and feeding and geographically related growth variances, and recognition of cephalopod species and species groups in predator stomach contents. Information is also provided on the current status of the squid fisheries of eastern North America, yield-per-recruit analysis for the two most important east coast species, *L. pealei* and *I. illecebrosus*, and on abundance forecasting and aging of *I. illecebrosus*.

Journal of Shellfish Research, Vol. 1, No. 2, 137–142, 1981.

DEVELOPMENT OF THE NEWFOUNDLAND SQUID (*ILLEX ILLECEBROSUS*) FISHERY AND MANAGEMENT OF THE RESOURCE

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ABSTRACT The Newfoundland short-finned squid fishery has traditionally been prosecuted inshore using small boats and jigging devices. Catches from that fishery have historically been small because of limited markets. Recently, with the development of new markets, that fishery has experienced unprecedented success and catch level has increased dramatically since 1974.

The life history of *Illex illecebrosus* is outlined herein, and the development and management of the Newfoundland squid fishery are reviewed. Prospects for further expansion of that fishery are considered to be closely related to market conditions. Development of new markets and increasing access to existing markets will depend on the success of other worldwide squid fisheries and the quality of Canadian squid exports.

INTRODUCTION

The short-finned squid has long supported a small inshore fishery at Newfoundland (Squires 1957, Mercer 1973a, Hurley 1980a). A seasonal migrant to the Newfoundland fishing area (Northwest Atlantic Fisheries Organization [NAFO] Subarea 3), *Illex illecebrosus* is fished between July and November using small open boats and jigging devices (Quigley 1964, Mercer 1970, Voss 1973, Rathjen et al. 1979, Hurley 1980a). Until recently yearly catch levels have usually been less than 11,000 metric tons (MT) (Mercer 1973a), primarily because of the unavailability of substantial markets for squid resources in general.

New markets, however, have developed for squid as food for human consumption. In response to increasing foreign demand for seafoods and dwindling traditional resources, attention has focused on exploitation of previously underutilized species (Rathjen 1977). Further, a worldwide trend in recent years toward claiming national jurisdiction over coastal fishing zones has led to attrition of far-seas fisheries traditionally prosecuted by some major squid-consuming nations (Hurley 1980a). Coincidentally with evolution of foreign markets for cephalopod resources, yearly catch levels in the Newfoundland squid fishery have risen (Beck et al. 1980, Hurley 1980a). With the rise in level of exploitation comes the need for sound management strategies regarding conservation and determining levels of optimum exploitation.

The basic life history of *I. illecebrosus* is outlined herein and the Newfoundland squid fishery is described. Historic and recent trends in catch and inshore abundance are discussed, and current management strategies are described. Also, the present status of this fishery is assessed in relation to perspectives for its further development.

BASIC LIFE HISTORY

The life history of *Illex illecebrosus* is not completely understood, because concentrations of spawning adults and egg masses have not been encountered. Spawning is believed to take place during January-February within the influence of the Gulf Stream. Larvae and juveniles of less than 5.0 cm in mantle length have been found during February and March research cruises in 1979 (Fedulov and Froerman 1980) and in 1981 (Dawe et al. 1981). Occurrence of those early stages is temperature related. Fedulov and Froerman (1980) found the major center of early-stage distribution during March-April 1979 to be within the slope water mix, near the northern boundary of the Gulf Stream. Greatest catches occurred when temperature at fishing depth ranged from 14.3 to 16.3°C (Fedulov and Froerman 1980).

In May-June, squid have historically been found on the Grand Bank where their occurrence was also temperature related. Greatest catches usually occurred where bottom temperatures exceeded 5.0°C (Mercer and Paulmier 1974, Hurley 1980b). Squid generally range from 9.0 to 18.0 cm in mantle length at that time (Squires 1957, Mercer and Paulmier 1974). Since 1974, incidental catches of squid on the Grand Bank during May-June groundfish surveys have provided an indication of later inshore abundance (Squires 1957, 1959; Hodder 1964; Mercer 1973b; Hurley 1980b).

During the summer short-finned squid are distributed between Hamilton Inlet and Cape Hatteras (Squires 1957, Templeman 1966). However, fishable concentrations usually occur between northern Newfoundland and Cape Cod. Squid are fished by bottom trawl off the coast of the United States and on the Nova Scotian Shelf. In Newfoundland, they usually move inshore in July, although timing of

inshore migration varies yearly, and between July and November they support a fishery on the northeastern and southern coasts of Newfoundland. They usually move offshore again in November when most fall within the 20- to 28-cm range in mantle length (Squires 1957, Mercer 1975, Collins and Ennis 1978, Hurley et al. 1979, Beck et al. 1980). Females leave the inshore area later than males and show little sign of sexual maturation by the time they migrate. Males are smaller than females and many have reached advanced stages of maturity at migration (Squires 1957, Mercer 1973c, Collins and Ennis 1978, Hurley et al. 1979, Beck et al. 1980).

The fate of post-spawning adults is still largely a matter of conjecture, because a reliable method of aging this squid is not yet available (Hurley and Beck 1979a). However, from laboratory research (Durward et al. 1980) and examination of length-frequency distributions, it is believed they live approximately 1 year and die after spawning. Thus, each year the fishery would be entirely dependent on the recruiting year-class.

THE NEWFOUNDLAND SQUID FISHERY

Trends in Catch and Inshore Abundance

Historical trends in inshore nominal catch of short-finned squid at Newfoundland and corresponding qualitative estimates of annual inshore abundance are presented in Figure 1. A general feature of squid abundance is that it is subject to severe year-to-year fluctuations with no regular or predictable cyclic nature. However, years of very high squid abundance are more common than scare or very scare years. Fluctuations in year-to-year inshore abundance may reflect fluctuations in actual population abundance or yearly variations in that portion of the population which becomes available to the inshore fishery. Hydrographic and feeding conditions on the Grand Bank have been cited as possible factors affecting yearly variations in the extent of inshore migration (Ennis 1978). Irregular year-to-year fluctuations in abundance are to be expected in such a short-lived species, since recruitment would be highly dependent on environmental perturbations.

Until recently, trends in annual catch have been similar to yearly fluctuations in abundance (Figure 1). However, the increasing magnitude of those catches reflect developmental stages of the fishery. Until about 1950, catches were small because the only major market for *Illex illecebrosus* was dried squid for foreign markets, mainly China. In the early 1950's, catches increased as a market developed to supply bait to European interests fishing in the northwestern Atlantic. Fishing technology improved considerably in 1965 with the introduction of the Japanese mechanized jigger (Quigley 1964). Using that device fishermen experienced much greater catch rates than they had previously using a single lead jigger.

In the mid-1970's, a market for squid as food for human consumption developed, mainly in Japan and in European

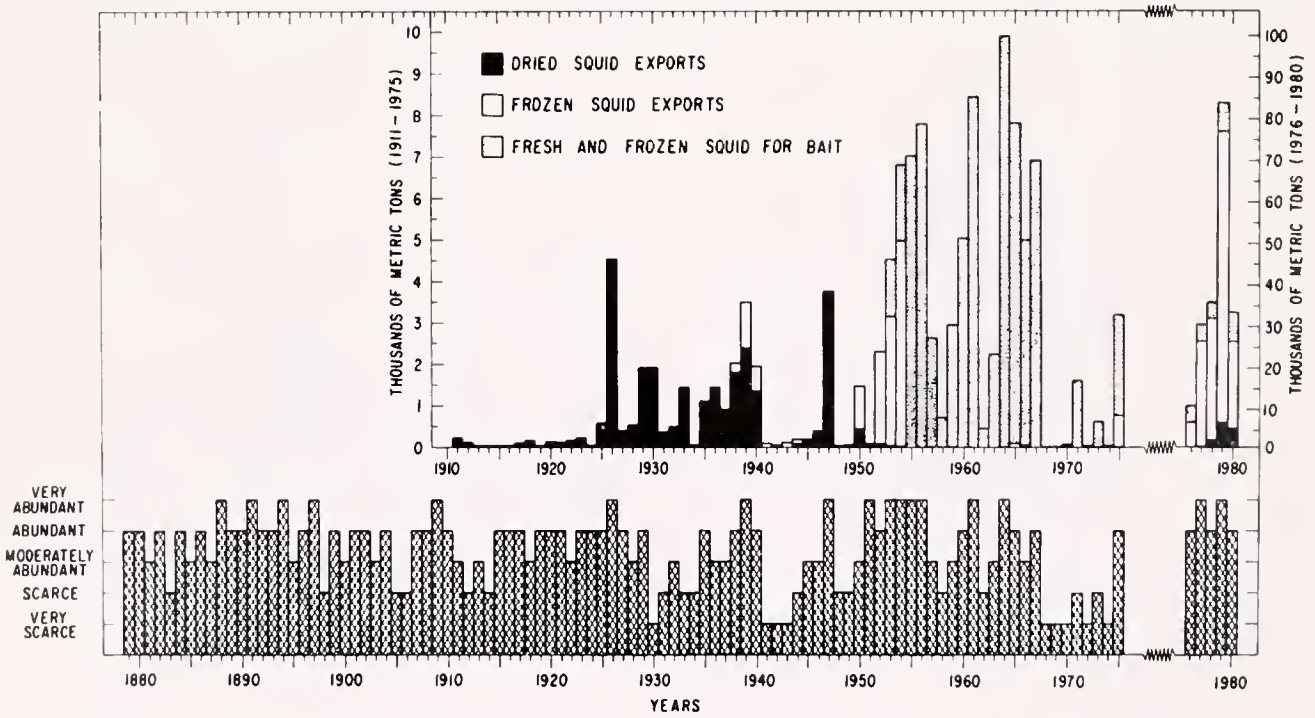

Figure 1. Qualitative estimates of inshore abundance of squid at Newfoundland, 1879–1980, and breakdown of inshore catch, 1911–1980, into processing categories. Data sources include Templeman (1966), ICNAF (1978), NAFO (1980), and unpublished data provided by the Economics and Intelligence Branch, Department of Fisheries and Oceans. (Note change in scale of the ordinate in describing catch for the period 1976–1980.)

countries. As a result, and with consistently high levels of inshore abundance, Newfoundland inshore nominal catch increased steadily to a record high of 83,000 MT in 1979 (Figure 1). Other factors which contributed to such high catch levels included the rejuvenation of the squid-drying industry in 1978, and the development of a large international fishery in Canadian waters. The offshore squid fishery is prosecuted mainly on the Nova Scotian Shelf; however, since 1970, small offshore catches have occurred in NAFO Subarea 3 as well (Figure 2). Offshore Subarea 3 catch remained less than 40 MT until 1975. Yearly catch increased steadily until 1978 when approximately 5,700 MT, representing 14% of the Subarea 3 total catch, were taken by the international fleet. Since that time the offshore catch in Subarea 3 has declined with less than 1 MT caught in 1980 (Figure 2). An increase in inshore processing facilities has further contributed to recent expansion of the Newfoundland fishery (Hurley 1980a).

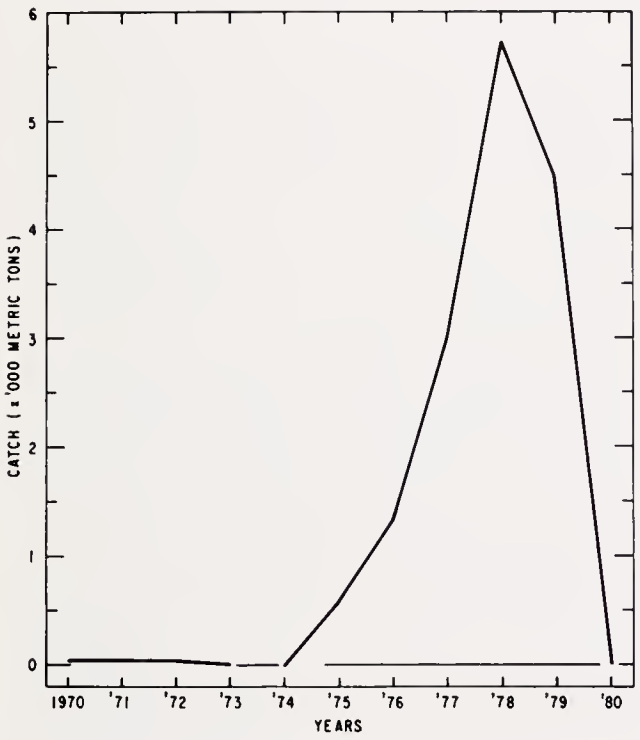

Figure 2. Trends in offshore Subarea 3 catch of short-finned squid, 1970–1980. Data sources include the FLASH information system, *ICNAF Redbook* (1978), *NAFO Scientific Council Report* (1979–1980), and unpublished data provided by the Economics and Intelligence Branch, Department of Fisheries and Oceans.

Despite continued abundance of squid in 1980, the Newfoundland inshore catch (32,000 MT) dropped considerably below the level of the previous year (Figure 1). That was primarily because of poor market conditions for *I. illecebrosus* which resulted in low prices offered to fishermen and a reduction of effort in the inshore fishery. A dispute between fishermen and processors during the summer of 1980 resulted in a further reduction in fishing effort. Production of dried squid decreased also because of declining prices and availability of the resource, as well as poor weather conditions during the summer.

Management of the Resource

The short-finned squid fishery in Canadian Atlantic waters is managed internationally by the NAFO, formerly the International Commission for Northwest Atlantic Fisheries (ICNAF). Prior to 1975, regulation of the fishery was not restrictive because exploitation was light. Usually yearly catch levels did not exceed 11,000 MT, the only major fishery being prosecuted inshore at Newfoundland. With increasing foreign catches on the Nova Scotian Shelf in the 1970's, catch regulation was first implemented in 1975. Because of the unpredictable nature of fluctuations in abundance or availability of the resource, a conservative approach was taken in allocating catch quotas. Between 1975 and 1977, an open-ended yearly total allowable catch (TAC) of 25,000 MT was determined with 15,000 MT allocated to the USSR and 10,000 MT reserved for the Canadian domestic fishery. In addition, all other participating countries without specific allocations were allowed 3,000 MT each (NAFO 1980).

International involvement in the offshore trawl fishery increased dramatically over the 1975–1977 period. With continued abundance of squid and no specific restrictions in the Newfoundland inshore fishery, total catch for Subareas 3 and 4 reached a high of 80,000 MT in 1977 (ICNAF 1979). In 1978, it was felt that during those years of high squid abundance the existing level of TAC was restrictive and resulted in losses of potential yield (ICNAF 1978). Thus, in 1978, a TAC of 100,000 MT was set, assuming the 1978 squid abundance would be similar to that of the previous year. As a means of avoiding over-exploitation, should abundance be lower in 1978, effort regulation was also introduced (ICNAF 1978). Catch rates from the 1977 international fishery were applied to the 1978 TAC to ensure that the exploitation rate would remain constant even if squid abundance decreased.

In recent years, abundance has remained high and post-season estimates of population size (Hurley and Beck 1979b, Dawe and Beck 1980) have consistently indicated that the exploitation rate and the TAC could be increased the following year without serious risk of over-exploitation (NAFO 1980). Thus, the level of the TAC for Subareas 2, 3, and 4 has risen to 120,000 MT in 1979, and to 150,000 MT in 1980 (NAFO 1980). Effort regulation in the international offshore fishery has been maintained, based on 1978 catch rates, as a safeguard against over-exploitation in years of low squid abundance.

Other management initiatives included the introduction of a June 15 opening date for the offshore fishery in 1978 (ICNAF 1978). That restriction was based on the fact that by-catch of other species in the offshore fishery was high early in the season and market value of squid was low

because of their small size. In 1979, the commencement date of the fishery was advanced to July 1 (ICNAF 1979).

Specific regulations have not been applied to the Newfoundland inshore squid fishery because it was felt that high catches from that fishery were not likely to cause overexploitation of the resource. The inshore fishery focuses on only a portion of the stock, the offshore component being regulated by catch-and-effort restrictions. Thus, restrictions in the offshore fishery provide for sufficient spawning escapement should the inshore portion be heavily exploited. Moreover, over-exploitation is less likely inshore because the fishery is passive and does not seek out concentrations of squid in years of low abundance, as is possible in the offshore fishery (NAFO 1980). In years of low abundance the inshore fishery would likely fail and fishing mortality would remain fairly constant because squid would not be available to jigging devices.

CONSIDERATIONS IN MARKETING SHORT-FINNED SQUID

Newfoundland inshore squid production has increased dramatically in recent years in response to the development of new markets. However, international competition for market access is intensive. In 1977, world cuttlefish and squid production reached almost 1 x 10^6 MT with *Todarodes pacificus* and *Illex illecebrosus*, respectively, being the most important species (Ramalingam 1978). However, world cephalopod resources are still underexploited and annual potential production could be 90 to 600 x 10^6 MT (Ampola 1974, Rathjen et al 1977, Voss 1973). With recent developments in technology for harvesting squids (Kato 1970; Rathjen 1973, 1977; Voss 1973) and availability of squid resources to many countries (Ramalingam 1978), world production is limited primarily by market demand.

The most extensive markets for squid exist in Japan and southern Europe. Japan is by far the greatest squid consuming and importing nation. In the 1970's, the Japanese market developed largely as a result of increased Japanese demand for seafood, loss of foreign squid fisheries, and recent decline in the domestic Japanese fishery for *T. pacificus*. During the 1960's, Japanese domestic catch averaged approximately 600,000 MT yearly (Voss 1973). However, yearly catch levels declined during the 1970's, with total landings of squid and cuttlefish being 480,000 MT in 1979. As a result of decreased domestic production, squid and cephalopod imports into Japan have increased during the 1970's, from an estimated 37,000 MT in 1973 (Ramalingam 1978) to 156,000 MT in 1979. The regulation of cuttlefish and squid imports into Japan is through import quotas set twice yearly for unprocessed products.

Gaining access to that market is difficult because more than 30 exporting nations compete for a share of the inport quotas. Problems in marketing *I. illecebrosus* include the belief that *T. pacificus* and *Loligo* spp. are preferred as raw material. Short-finned squid is further processed in Japan and that species is not well suited to the Japanese processing system (Court 1980). Markets other than Japan exist mainly in southern Europe. The most important of those smaller squid-importing countries include Spain, Portugal, Italy, France, and Greece. Outside Japan, markets for dried squid exist in Hong Kong and Taiwan. Although each of those markets is small compared to Japan, their combined potential for absorbing squid and squid products is considerable.

The importance of Canadian short-finned squid (*I. illecebrosus*) as a Japanese import has increased considerably during recent years to the point where, in 1979, Canada supplied 15,483 MT which represented 10% of total imports by Japan. Although Japan imported only 83,991 MT of cuttlefish and squid in 1980, Canada supplied 18,409 MT (22%), mostly 1979 production, and was the largest supplier of squid to Japan.

That increased market access for Canadian squid (*I. illecebrosus*) may reflect Japan's recognition of Canada as a stable source of future squid imports. Also, through developmental charters with Canada, Japan landed high quantities of short-finned squid in 1978 and 1979. That and a considerable increase in direct allocations to Japan in 1980 were considered to be important steps toward increasing Canadian access to the Japanese market. Despite relative success in marketing Canadian short-finned squid in 1980, markets were poor, which was reflected in a decline in catch below that of the previous year. The sharp decline in the inshore Newfoundland catch (Figure 1) was due to a reduction of fishing effort which partly resulted from a reduction in the price paid to fishermen. The domestic Japanese inshore fishery for *T. pacificus* experienced unprecedented success in 1980, resulting in a total Japanese catch of squid and cuttlefish of approximately 600,000 MT. Consequently, there were no Japanese import requirements and Canadian processors were offered low prices for squid. That price was ultimately reflected in the price offered to fishermen, approximately half that of the previous year. Also, because of the self-sufficiency of the Japanese market, no import quota was announced until November, and Canadian processors were reluctant to purchase squid with no firm purchase commitments from Japanese interests.

At least in the short term, the success of the Newfoundland inshore fishery and the Canadian fishery, in general, will depend on resource abundance and market demand. Canadian catches will probably fluctuate yearly depending on success of other squid fisheries, especially by Japan, and on the extent of import requirements by squid-consuming nations.

To increase access to existing and future markets, the status of *I. illecebrosus* as a desired import must be maintained. Measures should be taken to maintain and improve the quality of the product. Grading of both dried and frozen squid would render those products more attractive to Japanese interests for further processing. Reliable facilities

for both short-term and long-term storage are essential because spoilage occurs rapidly if the squid are not handled properly (Learson and Ampola 1977, Botta et al. 1979). Futher expansion of processing has several advantages in that processed products may be better able to compete with innovative products in foreign markets. Marketing such products may be facilitated further because they are not restricted by Japanese import quotas. However, marketing such products is complicated by the fact that Japan presently prefers to purchase unprocessed squid to support its extensive processing industry. Education in quality requirements has already been initiated. In 1978 and 1979, Japanese technicians were present in Canadian plants to supervise production.

Jigging of squid will probably be encouraged in the future because squid caught in that manner are in better physical condition than trawl-caught squid. Presently, the best quality squid probably come from the Newfoundland inshore fishery because those squid are caught by jigging and landed within hours of capture. Also the offshore jigging of squid will probably be encouraged for reasons of quality. That method is commonly used in the Japanese domestic fishery, resulting in as much as 90% of their total catch of *Todarodes pacificus* in some years (Rathjen 1973). In Japan, jigged squid are sometimes sold at a higher price than trawl-caught squid (Court 1980).

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THE SHORT-FINNED SQUID (*ILLEX ILLECEBROSUS*) FISHERY IN EASTERN CANADA

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ABSTRACT The short-finned squid *Illex illecebrosus* had traditionally been important to Canada only as a small inshore fishery in Newfoundland. Fluctuations in inshore landings, common prior to 1975, were probably related to the availability of squid. Since 1975, the inshore and offshore fisheries have shown tremendous increases in landings.

Historic trends of the fishery are discussed. Recent statistics on the fishery provide information on catch, season, area, and gear. Offshore statistics prior to 1975 are not complete. Statistics compiled on the international and Canadian offshore fisheries from the FLASH computer information system has provided a monitor of all activities since 1977.

The historic and present status of the fisheries are presented in relation to the management of the resource.

INTRODUCTION

For many years the short-finned squid *Illex illecebrosus* has been important to Canada only as a small inshore bait fishery which was concentrated in Newfoundland. In recent years, however, this species has become commercially important with the development of international markets. Since 1975, there has been a dramatic increase in landings from the inshore fishery in Newfoundland as well as parts of the Maritimes; a large offshore fishery has also developed on the Scotian Shelf. Those increases have been related to increased abundance and increased fishing effort. In this report, recent international squid catch statistics in eastern Canada are reviewed, and the historic and present status of the fisheries are presented in relation to the management of the resource.

DISTRIBUTION AND FISHERY

Illex illecebrosus is widely distributed in the northwestern regions of the Atlantic Ocean. Data compiled from various sources (Clarke 1966, Roper et al. 1969, Lu 1973, Roper and Lu 1979) show distribution from Labrador and Newfoundland to central Florida (Figure 1). In a recent survey, larvae and juveniles of *I. illecebrosus* were recorded in large numbers for the first time in the Scotian Shelf slope water and Gulf Stream water mix (Amaratunga et al. 1980).

Each year *I. illecebrosus* is recruited to the fishery when a new year-class migrates onto the continental shelf and inshore areas for the summer and fall. Its distribution in Nova Scotia (Amaratunga et al. 1978) and Newfoundland (Squires 1957) waters is usually limited to the warmest period of the year, from spring (April to May) to late fall (as late as December). During that period, active fisheries operate in the Northwest Atlantic Fisheries Organization Subarea 4 (NAFO SA4) off Nova Scotia and in Subarea 3 (SA3) off Newfoundland (Figure 1).

Until the early 1970's, Canadian squid were utilized as bait for other fisheries. Fishing methods during that time were mainly limited to inshore jigging operations. Jigging operations were usually conducted using hand-line jiggers from small boats. During the early 1970's, Canadian squid stocks became attractive in the international markets as a commodity for human consumption. That, in turn, induced international offshore trawlers to start fishing for squid on the continental shelves in SA3 and SA4, primarily in SA4. Offshore trawlers are usually large factory ships fishing with bottom, off-bottom, or pelagic trawls, as in the finfish fishery. Concurrently, inshore techniques improved with the use of semi- or totally automated jigger lines.

HISTORIC TRENDS

Nominal catch statistics since 1963 for the entire *Illex illecebrosus* distribution are shown in Table 1 and Figure 2 (from Roberge and Amaratunga 1980). Statistics for SA5–6 are included to show relative differences from those of SA2–4. Catches fluctuated in SA2–4 until 1974. Mercer (1973) reported similar fluctuations in inshore landings from Nova Scotia between 1920 and 1968. Those fluctuations probably reflect availability of squid, especially in SA3, and not any change in effort. On the other hand, relatively large catches in SA4 between 1970 and 1973 probably related to the introduction of offshore trawlers into the fishery. In SA5–6, a considerable international offshore squid fishery has been in operation since the late 1960's, accounting for the difference in pattern.

Prior to 1973, the offshore fishery in SA2–4 was considered relatively unimportant. Therefore, although upward trends in landings began in the early 1970's, catch statistics were incomplete. Often landings alone were reported with no details on effort and other fisheries statistics. Also, squid catches were not reported by species and it is likely that some catches of *Loligo pealei* were included in the SA4 statistics (distribution of *L. pealei* does not extend into SA3).

After 1973, a concerted effort was made by the International Commission for the Northwest Atlantic Fisheries

Figure 1. Known distribution (shaded area) of *Illex illecebrosus* in the northwest Atlantic region.

Figure 2. Annual total catches of *Illex* in the Northwest Atlantic from 1963–1979, for ICNAF Subareas 3 and 4, and Subarea 5 and Statistical Area 6.

TABLE 1.

Nominal catches (metric tons) of *Illex illecebrosus* by Subareas, 1963–1979 (from Roberge and Amaratunga 1980).

Year	Subareas 2	3	4	Total SA2–4	Total SA5–6
1963		2,199	103	2,222	1,210[1]
1964		10,408	369	10,777	193[1]
1965		7,831	433	8,264	563[1]
1966		5,017	201	5,218	1,562[1]
1967		6,907	126	7,033	2,662[1]
1968		9	47	56	4,948[1]
1969		21	65	86	2,802[1]
1970		111	1,274	1,385	2,453[1]
1971		1,067	7,299	8,906	4,036[2]
1972		26	1,842	1,868	14,713[2]
1973	2	620	9,255	9,877	15,178[2]
1974	31	17	389	437	16,653[2]
1975		3,764	13,993	17,757	13,790[2]
1976		11,254	30,510	41,764	27,717[2]
1977	6	32,748[3]	47,199[3]	79,953[3]	24,792[3]
1978		45,472[3]	53,118[3]	98,590[3]	17,695[3]
1979		81,820[3]	71,279[3]	153,099[3]	

[1]Combined *I. illecebrosus* and *L. pealei*, USSR catches included.
[2]Excludes USSR catches which did not report *I. illecebrosus* and *L. pealei* separately.
[3]Preliminary data.

(ICNAF) to obtain complete statistics for individual species (ICNAF *Redbook* 1973). Offshore catch statistics were then obtained at the end of the season from each vessel operating in the ICNAF area. In 1977, the Foreign Licensing and Surveillance Hierarchy (FLASH) computer information system was introduced by Canada to monitor all offshore fishing activities in SA3 and SA4. As input into the system, all actively fishing vessels were required to provide information weekly on the area fished, catch by species, and effort. These data were stored in the computer to permit immediate access to fisheries information. Statistics on the inshore fishery were obtained from sales slips which contained information on catch weight, date, areas, and gear used.

The weekly catch for the international offshore fishery in SA3–4 from 1977 to 1979 is summarized from FLASH data in Table 2. Because FLASH reports Canadian domestic catches separately, those are excluded from Table 2. Figure 3 depicts cumulative catch in SA3–4 for 1977, 1978, and 1979. In 1977, with no opening date for the fishery, the catch began to increase the week of 20 May; fishing was concentrated between the weeks of 10 June and 9 September. In 1978, with an opening date of 15 June, fishing was concentrated between the week commencing 23 July and the week of 1 October. The 1979 fishery opened on 1 July and fishing was concentrated between the week commencing 8 July and 4 November. It must be noted that in all three years participating countries fished within quota allocations.

In 1978, FLASH reported a total of 29,570 metric tons (MT) of squid caught offshore by the international fishing fleet; 2,922.3 MT and 26,647.7 MT were caught in ICNAF SA3 and SA4, respectively. Sixty-four percent (SA3) and 95.8% (SA4) of the total squid catch was a result of directed fishing. Directed and nondirected squid catches fluctuated throughout the year in SA3 without apparent pattern. However, in SA4, directed fishing was concentrated between the weeks of 23 July and 6 August (Figure 4), while three smaller peak periods occurred in the weeks commencing 27 August, 17 September, and 29 October.

Effort (reported in days fished) was high during the months of July and August. Catch rates, however, fluctuated over the year with highs of 20.32 and 22.68 MT occurring during the weeks of 30 July and 5 November, respectively.

In 1979, FLASH reported a total catch by the international fishing fleet of 44,510 MT in SA3–4; 2,144.8 and 42,365.2 MT were caught in SA 3 and SA4, respectively. Ninety-six percent (SA3) and 82% (SA4) of the total squid catch resulted from directed squid fishing. In SA3, directed and nondirected squid catches once again fluctuated throughout the year without apparent pattern, while, in SA4, fishing was concentrated over a 17-week period from 15 July to 4 November. Intensive directed fishing occurred between the weeks of 15 July and 2 September (Figure 5). Effort showed a similar pattern. The highest catch rates occurred in the months of July and September, 22.44–23.79 and 20.77–21.85 MT, respectively.

Fish catch statistics are usually reported in units of weight such as metric tons. In the squid fishery, statistics given in weight are deceptive because the numbers of squid landed per-unit-weight change rapidly throughout the fishing season due to their rapid growth (Amaratunga 1980). This is demonstrated in Table 3 where the 1978 and 1979 international offshore directed catches in SA4 are translated into number of individuals removed. The number of squid being landed has been a major consideration in the resource management of *I. illecebrosus* (Amaratunga et al. 1978).

HISTORY OF FISHERY MANAGEMENT

The International Commission of the Northwest Atlantic Fisheries was instated in 1949 (renamed Northwest Atlantic Fisheries Organization [NAFO] in 1979), to provide fisheries management advice to the coastal countries of the Northwest Atlantic. However, until 1974, the squid fishery of the ICNAF area was considered to have no commercial importance and, hence, no advice was provided. The history of subsequent advice provided by ICNAF and NAFO is summaried below. Because the most important management regime has been the Total Allowable Catch (TAC), this is listed separately; other regimes, such as opening dates for the fishery, are listed under the remarks column. It should be noted here that the United States withdrew from ICNAF in 1976, and TAC for SA5 and SA6 are shown only for those years in which they were recommended by ICNAF.

TABLE 2.

FLASH catch statistics for the international squid (*Illex illecebrosus*) fishery summarized by week and year for Subareas 3 and 4.

		Total Squid Catch (MT)					Total Squid Catch (MT)		
Week	Year	Subarea 3	Subarea 4	Subareas 3 and 4	Week	Year	Subarea 3	Subarea 4	Subareas 3 and 4
16	1977	--	0.3	0.3	34	1977	--	975.2	975.2
	1978					1978	255.1	666.3	921.4
	1979					1979	61.0	3,234.5	3,295.6
17	1977	--	1.0	1.0	35	1977	--	1,726.3	1,726.3
	1978					1978	557.3	1,715.7	2,273.0
	1979					1979	362.3	2,351.1	2,713.4
18	1977	--	8.7	8.7	36	1977	0.4	1,344.3	1,344.7
	1978					1978	368.4	1,413.3	1,781.7
	1979					1979	137.5	3,588.6	3,726.1
19	1977	--	18.0	18.0	37	1977	0.1	1,551.3	1,551.4
	1978		7.2	7.2		1978	255.8	829.4	1,085.2
	1979					1979	294.8	2,024.4	2,319.2
20	1977	--	10.2	10.2	38	1977	--	441.8	441.8
	1978	--	31.3	31.3		1978	128.7	1,279.1	1,407.8
	1979	--	0.3	0.3		1979	189.3	2,026.2	2,215.5
21	1977	--	171.8	171.8	39	1977	0.2	598.4	598.6
	1978	--	21.5	21.5		1978	93.9	1,389.2	1,483.1
	1979	--	4.2	4.2		1979	67.9	1,580.0	1,617.8
22	1977	19.4	480.6	500.0	40	1977	0.1	854.7	854.8
	1978	0.4	19.7	20.1		1978	97.0	1,249.2	1,346.2
	1979	--	3.5	3.5		1979	292.8	1,434.6	1,727.4
23	1977	1.0	955.2	956.2	41	1977	--	853.9	853.9
	1978	8.2	35.1	43.3		1978	10.0	585.4	595.4
	1979	--	23.5	23.5		1979	121.3	1,154.0	1,275.1
24	1977	--	1,706.5	1,706.5	42	1977	--	592.9	592.9
	1978	4.0	38.9	42.9		1978	10.0	420.4	430.4
	1979	2.6	61.6	64.2		1979	1.5	1,171.8	1,173.3
25	1977	--	2,295.4	2,295.4	43	1977	--	71.0	71.0
	1978	--	28.5	28.5		1978	47.4	722.2	769.6
	1979	--	196.6	196.6		1979	--	1,415.5	1,415.5
26	1977	2.0	3,942.9	3,944.9	44	1977	--	28.5	28.5
	1978	215.2	74.6	289.8		1978	--	967.5	967.5
	1979	9.8	393.7	403.5		1979	137.3	1,190.3	1,327.6
27	1977	23.3	3,476.4	3,499.7	45	1977	--	106.9	106.9
	1978	67.9	201.4	269.3		1978	--	778.3	778.3
	1979	5.0	392.5	397.5		1979	--	1,074.3	1,074.3
28	1977	--	2,828.8	2,828.8	46	1977	85.8	75.2	161.0
	1978	210.1	213.6	423.7		1978	--	388.3	388.3
	1979	14.2	1,493.4	1,507.6		1979	0.02	732.6	732.6
29	1977	35.0	3,849.9	3,884.9	47	1977	--	164.3	164.3
	1978	196.6	358.8	555.4		1978	--	98.0	98.0
	1979	108.5	1,965.7	2,074.2		1979	53.3	227.0	280.3
30	1977	16.4	3,753.1	3,769.5	48	1977	--	128.8	128.8
	1978	47.7	3,286.3	3,334.0		1978	--	8.0	8.0
	1979	98.1	2,926.4	3,024.5		1979	--	--	--
31	1977	21.0	3,967.9	3,988.9	49	1977	13.0	37.7	50.7
	1978	70.9	6,848.1	6,919.0		1978	--	--	--
	1979	144.2	4,591.8	4,736.0		1979	--	--	--
32	1977	3.0	2,054.2	2,057.2	50	1977	--	6.3	6.3
	1978	136.1	2,001.1	2,137.2		1978	--	--	--
	1979	32.8	3,862.8	3,895.6		1979	--	--	--
33	1977	--	1,636.6	1,636.6	Total	1977	220.7	40,715.0	40,935.7
	1978	141.6	971.3	1,112.9		1978	2,922.3	26,647.7	29,570.0
	1979	10.6	3,244.3	3,254.9		1979	2,144.8	42,365.2	44,510.0

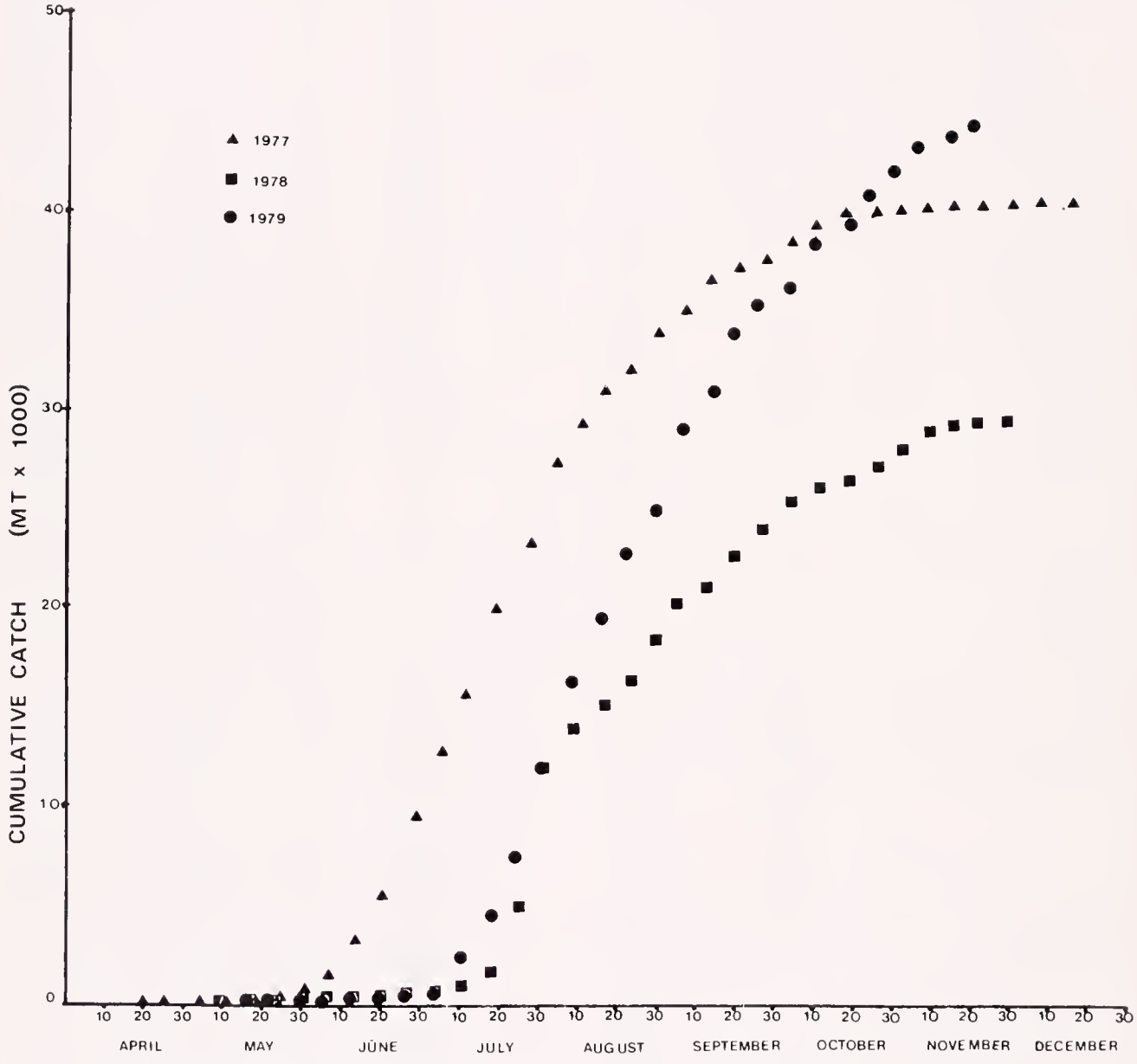

Figure 3. Cumulative catch (MT) of *Illex* in ICNAF Subareas 3 and 4 in 1977, 1978, and 1979 as reported to FLASH.

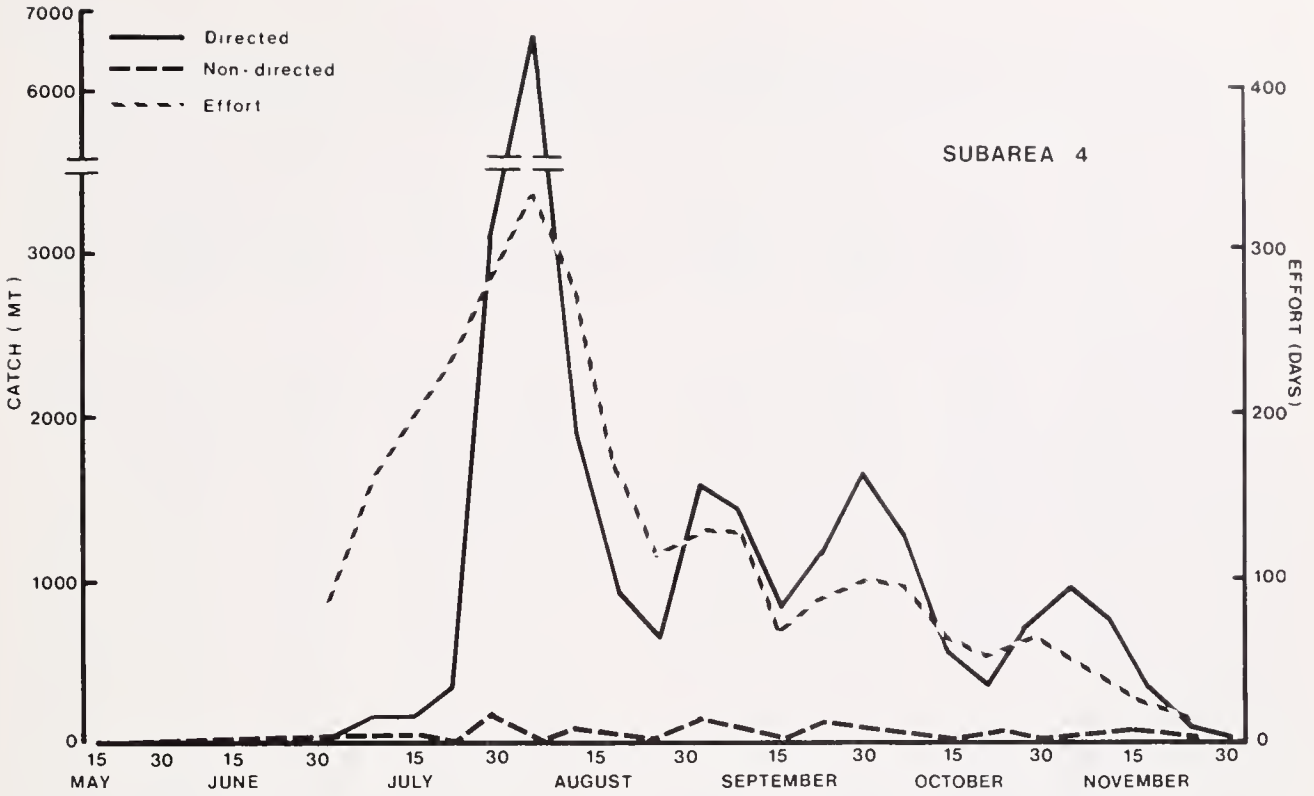

Figure 4. Directed and nondirected squid catch and effort as reported to FLASH for 1978.

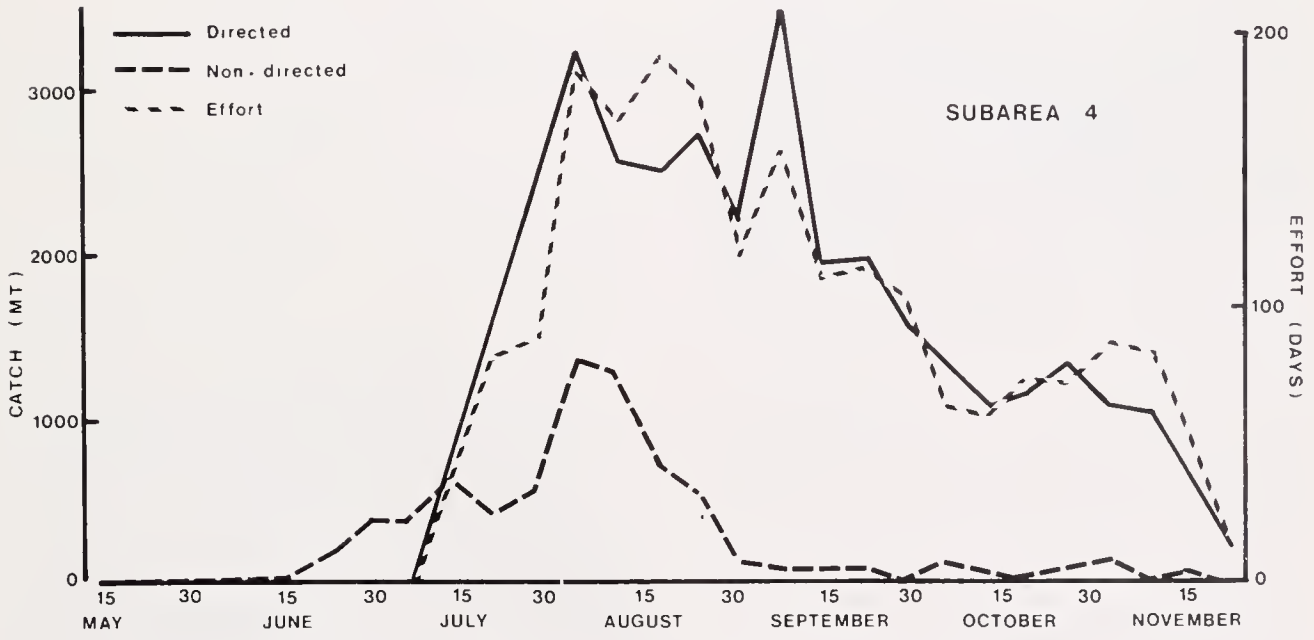

Figure 5. Directed and nondirected squid catch and effort as reported to FLASH for 1979.

TABLE 3.

Estimated number of *Illex illecebrosus* removed by the international-directed squid fishery in Subarea 4, 1978 and 1979.

1978						1979					
Date	Week	Directed Squid Catch (MT)	Estimated Mean Weight (gm)	Estimated Number of Squid	Cumulative Estimated Number	Date	Week	Directed Squid Catch (MT)	Estimated Mean Weight (gm)	Estimated Number of Squid	Cumulative Estimated Number
Jun 25	26	36.5									
Jul 2	27	161.4	137.9	1.17×10^6	1.17×10^6	Jul 1	27	5.0	137.12	3.65×10^4	3.65×10^4
9	28	164.5	134.8	1.22×10^6	2.39×10^6	8	28	852.6	133.95	6.37×10^6	6.41×10^6
16	29	357.2	138.4	2.58×10^6	4.97×10^6	15	29	1,559.8	138.08	1.13×10^7	1.77×10^7
23	30	3,905.1	189.6	2.06×10^7	2.56×10^7	22	30	2,354.8	149.90	1.57×10^7	3.34×10^7
30	31	6,828.8	159.9	4.27×10^7	6.83×10^7	29	31	3,209.1	159.78	2.01×10^7	5.35×10^7
Aug 6	32	1,899.5	171.1	1.11×10^7	7.94×10^7	Aug 5	32	2,587.0	169.66	1.52×10^7	6.87×10^7
13	33	924.3	179.8	5.14×10^6	8.45×10^7	12	33	2,517.0	179.54	1.40×10^7	8.27×10^7
20	34	650.9	189.8	3.43×10^6	8.80×10^7	19	34	2,719.0	189.42	1.44×10^7	9.71×10^7
27	35	1,572.7	199.3	7.89×10^6	9.59×10^7	26	35	2,198.1	199.30	1.10×10^7	1.08×10^8
Sep 3	36	1,413.3	209.4	6.75×10^6	1.03×10^8	Sep 2	36	3,496.1	209.18	1.67×10^7	1.25×10^8
10	37	818.1	219.3	3.73×10^6	1.06×10^8	9	37	1,952.5	219.06	8.91×10^6	1.34×10^8
17	38	1,157.5	229.2	5.05×10^6	1.11×10^8	16	38	1,965.8	228.94	8.59×10^6	1.42×10^8
24	39	1,389.2	239.1	5.81×10^6	1.17×10^8	23	39	1,555.9	238.83	6.51×10^6	1.49×10^8
						30	40	1,329.2	248.71	5.34×10^6	1.54×10^8
Oct 1	40	1,249.2	248.8	5.02×10^6	1.22×10^8	Oct 7	41	1,079.2	258.59	4.17×10^6	1.58×10^8
8	41	582.1	258.7	2.25×10^6	1.24×10^8	14	42	1,158.1	268.47	4.31×10^6	1.63×10^8
15	42	378.8	268.7	1.41×10^6	1.26×10^8	21	43	1,340.6	308.18	4.35×10^6	1.67×10^8
22	43	716.9	309.0	2.32×10^6	1.28×10^8	28	44	1,085.4	311.49	3.48×10^6	1.70×10^8
29	44	955.6	312.3	3.06×10^6	1.31×10^8						
Nov 5	45	748.6	314.5	2.38×10^6	1.34×10^8	Nov 4	45	1,024.8	313.75	3.27×10^6	1.74×10^8
12	46	327.4	277.5	1.18×10^6	1.35×10^8	11	46	671.6	275.54	2.44×10^6	1.76×10^8
19	47	97.3	292.2	3.33×10^6	1.35×10^8	18	47	220.1	291.82	7.54×10^5	1.77×10^8
26	48	8.0	--	--	--						

History of *Illex illecebrosus* Resource Management

Year	Total Allowable Catch (TAC) (x 10^3 MT)	Catch (x 10^3 MT)	Remarks (Catch x 10^3 MT)
1974	No TAC	SA2–4 = 0.4 SA5 and SA6 = 16.7	1973 catch: 9.9 in SA2–4; 15.2 in SA5 and SA6. Catch constitutes both *Illex* and *Loligo*. Commercial catches incidental and not taken in a directed fishery. Pilot whale-consumption study suggests potential catch could be substantially greater.
1975	No TAC	SA2–4 = 17.8 SA5 and SA6 = 13.8	1974 catches considered commercially unimportant. Catches suggest *Illex* forms a stock complex from SA2–6, with a spring migration northward from SA5 and SA6 to SA2–4. Research survey biomass assessments for 1974 were 90 to 100,000 MT. TAC for SA2–4 should be separate from SA5 and SA6 so that fishing effort cannot be directed entirely to one component of the stock.

1976	Preemptive: SA2–4 = 15.0 SA5 and SA6 = 30.0	 SA2–4 = 41.8 SA5 and SA6 = 27.7	Substantial catches in 1975 warranted TAC. Stock complex from SA2–6. Catches not separated by species (*Illex*, *Loligo*), but SA2–4 catch considered to be *Illex* because of its distribution patterns.
1977	Preemptive: SA2–4 = 25.0 SA5 and SA6 = 30.0	 SA2–4 = 80.0 SA5 and SA6 = 24.8	Recognized SA2–4 catches in 1976 considerably higher than TAC. Recognized effort regulation should be considered. Requested catch and effort statistics from each country. NOTE: Special meeting for squid called before 1978 fishery to provide scientific advice to management.
1978	SA3 and SA4 = 100.0 (i.e.,) SA3 = 45.0 SA4 = 55.0	 SA3 = 45.5 SA4 = 53.1	Considered 1977 catches and biomass estimations. TAC subject to stock remaining as high as 1977 and target exploitation rate of 0.40. Necessary to take conservative approach and spread effort: TAC partitioned; effort regulations used to control exploitation rate. Partition between SA3 and SA4 based on relative magnitude of biomass estimations. NOTE: Implementation of TAC conditional upon control of fishing effort, based on 1977 catch rates, with **no** increase in number of days fished in 1978, if catch rates in 1978 were lower than those of 1977. Directed *Illex* fishery opened on 15 June. Some measures taken to limit by-catch of *Illex* in other fisheries before 15 June.
1979	SA3 and SA4 = 120.0 (i.e.,) SA3 = 50.0 SA4 = 70.0	 SA3 = 81.8 SA4 = 71.3	Partitioning based on 1978 biomass estimations. Recognized effort very difficult to regulate. Should abundance be reduced, then fishing mortality (F) in SA3 will self-regulate in the inshore activities, but in SA4, F should be limited by effort regulation based on 1978 catch rates. NOTE: Because migration patterns vary from year to year (squid arrived late in 1979), opening date of fishery was set for 1 July.
1980	SA2–4 = 150.0	—	Using 10-year series of biomass estimates, relative abundance indices developed from research vessel data. Catch associated with target exploitation rate of 0.40 could be in the range of 100,000 to 200,000 MT. 1980 TAC would not be associated with serious risk of over-exploitation. If biomass is high, inshore allowance could be exceeded without excessive exploitation.

The present management regime is based upon a TAC set within the range considered unlikely to pose serious risk of over-exploitation. The estimations used to establish this range are, however, tenuous because we lack sufficient understanding of stock recruitment and distribution patterns, and also our estimations of levels of stock abundance of previous years vary widely. The main constraint faced by researchers is that this species has a short life span and each year a new year-class is recruited, replacing the stock of the previous year (Amaratunga 1980). As a result, standard fishery models do not adequately describe this fishery. Further research in the areas of stock recruitment, distribution, and biology is required for the management of the *I. illecebrosus* fishery.

ACKNOWLEDGMENTS

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EXPLORATORY SQUID CATCHES ALONG THE CONTINENTAL SLOPE OF THE EASTERN UNITED STATES

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ABSTRACT During October–November 1979, the Federal Republic of Germany Research Vessel ANTON DOHRN conducted an otter trawl survey along the continental slope between Georges Bank and Cape Canaveral, Florida. Sampled depths ranged from 62 to 1,075 m at 58 trawl stations. Some limited coverage was accomplished on the continental shelf.

The short-finned squid *Illex illecebrosus* represented the largest volume of any squid group sampled during the cruise. Those squid were widely distributed with large catches made at both the most northern and most southern stations fished. The results provide new information on the broad distribution of *I. illecebrosus* in the slope area during the fall. Data on the abundance of that species are of interest in assessing its resource potential and its possible relationship to more northerly stocks.

Data were also provided on the distribution and abundance of the long-finned squid *Loligo pealei*, and on several other species of cephalopods.

INTRODUCTION

In recent years there has been a growing world interest in harvestable stocks of cephalopods. In the northwestern Atlantic rapid commercial developments have occurred (particularly off North America), and in the southwestern Atlantic off Argentina similar exploitation has taken place. In the Indo-Pacific area, additional commercial developments have been evident in the vicinity of the Phillipines, Thailand, Austrialia, and New Zealand. Increased harvest of squids have caused concern among some about the role of squid as prey of other marine animals. Present assessment information on squid is meager, and even small contributions from limited surveys add to the knowledge base. This paper presents a report on squid catches from such a survey along the continental slope of the eastern United States.

Until the early 1970's, squid received little attention as a fishery resource along the eastern coast of the United States. Fishing activity began to increase (Rathjen 1973, Kolator and Long 1979) with a modest beginning in the late 1960's.

South of Cape Hatteras only limited and fragmented information existed on potentially commercial squid. Voss (1971) indicated the presence of squid of the genus *Illex* from sightings made from the research submersible ALUMINANT off Miami. Roper et al. (1969) discussed the ranges of three species of *Illex* found in the northwestern Atlantic and indicated the complex relationships of their respective distributions. During recent years, investigations were undertaken as a result of increasing commercial and biological interests.

Mercer (1969a, b, c) reported on a series of squid surveys by the Canadian research vessel A. T. CAMERON (Cruises 130, 150, and 157). Cruise No. 157 took place in February 1969, and included otter trawl stations from Cape May, New Jersey (39°N), southward to Fort Pierce, Florida (28°N). Trawling was limited to depths between 38 and 415 m. Mercer noted only small catches of squid south of Cape Hatteras with decreasing abundance off Georgia and Florida. During December 1977, the Soviet trawler ARGUS searched for squid off Jacksonville, FL (Massey and LaCroix 1978). *Loligo pealei* was taken at depths from 105 to 215 m but only in small quantities. Small catches of *Illex* sp. were taken at 210 and 300 m.

From 1973 to 1977, resource assessment cruises were conducted to the edge of the United States continental shelf under the Marine Resource Monitoring Assessment and Predictions Program (MARMAP) and squid data were summarized by Whitaker (1980). He found *Loligo* widely distributed throughout the year over the continental shelf south of Cape Hatteras. He also observed that *I. illecebrosus* was well represented along the outer continental shelf. (*Illex* occurred in 50% of trawl hauls between 184 and 367 m.) Although most of the squid catch rates were low, one 30-minute winter tow east of the Florida–Georgia border yielded 713 kg at 223 m. That study also reported squid catches of the Spanish exploratory vessel PESCAPUERTA SEGUNDO during the spring of 1978. Although depth coverage was oriented toward squid, catches south of Cape Hatteras were not impressive between the depths of 99 and 375 m.

During the present review, Billy Burbank (Fernandina, FL, personal communication, June 1980) who is familiar with the commercial "royal-red" shrimp fishery in deep water off the eastern coast of Florida was consulted. He indicated that squid were regularly taken as a by-catch. Burbank also stated that in the fall of 1979, a large catch of "red squid" (probably *Illex*) which completely "plugged up the trawl" was taken during experimental use of a "mongoose" trawl off Cape Canaveral. Hess and Toll (1981)

reported a high incidence of *Illex* in the stomach contents of swordfish (*Xiphias gladius*) from the Straits of Florida.

The information available for the area from Cape Hatteras to Cape Canaveral indicates general occurrence of several commercially attractive squids with varying degrees of real abundance and potential.

MATERIALS AND METHODS

The Federal Republic of Germany Institute for High Seas Fisheries invited North American fisheries scientists to participate in an exploratory fishing cruise along the continental slope off eastern North America during the fall of 1979. Cruise No. 213 (leg 3) on the R/V ANTON DOHRN (see McRae 1967) occurred from 21 October to 16 November 1979, between Georges Bank (40°N) and Cape Canaveral (29°N). The primary objective of the cruise was to assess the availability of traditional or alternate fish and invertebrate stocks that might be commercially exploited.

Sampling occurred in relatively deep water (400 to 1,000 m), utilizing a large, 43-m otter trawl (31.2-m headrope; 19-m footrope; 4-m vertical opening; mesh size: 120 to 145 mm; cod end included a fine liner).

The trawl was deployed with 41-m ground cables and 53-cm rollers on the footrope. The trawl was a standard, 2-seam groundfish trawl commonly used in the northeastern Atlantic; it was not designed for the capture of squids. Thirty-minute tows were made along the 400-, 600-, 800-, and 1,000-m depth contours. The tow routes were flexible and dependent on slope and availability of trawlable bottom. In addition to trawl coverage, hydrographic parameters were routinely recorded. Most trawling was done during daylight; the vessel steamed to new positions and searched for suitable bottoms during the night.

Routine procedures at each trawl station included dumping trawl contents through a deck hatch to a work area below the weather deck. The scientific staff sorted, weighed, and made other appropriate observations. Questionable material was preserved for taxonomic examination ashore to determine the species composition of the squid catches.

Starting and terminating at Woods Hole, MA, the cruise track covered 8,121 km. During the cruise, 58 trawl hauls were successfully accomplished. Considering the area involved, coverage was generally representative of the upper slope between 40°N and 29°N lattitude. Because of a number of factors including precipitous slopes, deep canyons, rocky outcrops, and the occasional presence of lobster traps, some planned stations were impossible to complete. Generally, coverage southeast of Georges Bank was quite limited because of steep slope conditions, while west of 70°W longitude favorable bottom prevailed. A large amount of lobster gear, particularly south of the Hudson Canyon, limited operations in that area. In the immediate vicinity of Cape Hatteras, precipitous slopes were a primary deterrent to trawl operations. South of Cape Hatteras, the bottom was more favorable; however, the Gulf Stream system complicated effective trawling in some instances. Figure 1 indicates the general area covered and the approximate locations of each station; more precise positions are included in Table 1.

Questions were raised during the cruise concerning the effectiveness of the trawls and whether sufficient power was available aboard the R/V ANTON DOHRN (3,000 shaft hp). The formal cruise report (Inst. Fischwirtschaft 1980) stated that the trawl was probably not optimal for the conditions experienced.

RESULTS

Good squid catches were made throughout the area sampled, and squids were the predominant animals captured by the trawl. The short-finned squid *Illex illecebrosus*, the dominant species caught, was taken at 46 of the 58 trawl stations occupied. When catches were examined for depths between 300 and 900 m, *I. illecebrosus* occurred at 30 of 31 (97%) stations.

Catch rates of short-finned squid for areas north and south of Cape Hatteras (35°N lattitude) were generally comparable (Figure 2). Trawl catches from the apparent preferred range of *I. illecebrosus* (300 to 900 m) averaged 132 kg of squid per 30-minute tow. It should be noted that at many stations as much as one half of the squid catch was taken from the wings and foreparts of the trawl, suggesting that they were actively attempting to evade capture. That observation reinforces previous discussions with captains of foreign squid vessels working off the northeastern United States who cited similar experiences when fishing commercially for *I. illecebrosus*.

The average bottom water temperature, where most short-finned squid were caught, ranged from 5.4 to 8.0°C (Figure 3). Length frequencies of 1,508 specimens of *I. illecebrosus* indicated that mantle lengths ranged from approximately 15.0 to 34.0 cm (Figure 4). The mean lengths of squid taken at depths greater or less than 500 m north and south of Cape Hatteras ranged from 22.0 cm (shallower than 500 m south of Cape Hatteras) to 25.8 cm (deeper than 500 m north of Cape Hatteras).

Because of the possible occurrence of other species of *Illex* in the survey area (Roper et al. 1969), the squid were examined carefully onboard ship. Representative and/or taxonomically marginal specimens were preserved and sent to C. Roper (Division of Mollusks, Smithsonian Institute, Washington, D.C.) for identification. According to Roper (personal communication, 1980), all of the specimens examined were *Illex illecebrosus*.

Of the 70 specimens examined by Roper, 36 were females (mantle length, 9 to 32 cm) and varied from immature (2) to fully mature (1). Thirty-four specimens were males (mantle length, 16 to 23 cm) and varied from immature (5) to fully mature (21). (Length-frequency data from those 70 specimens were not utilized in the preparation of Figure 4.)

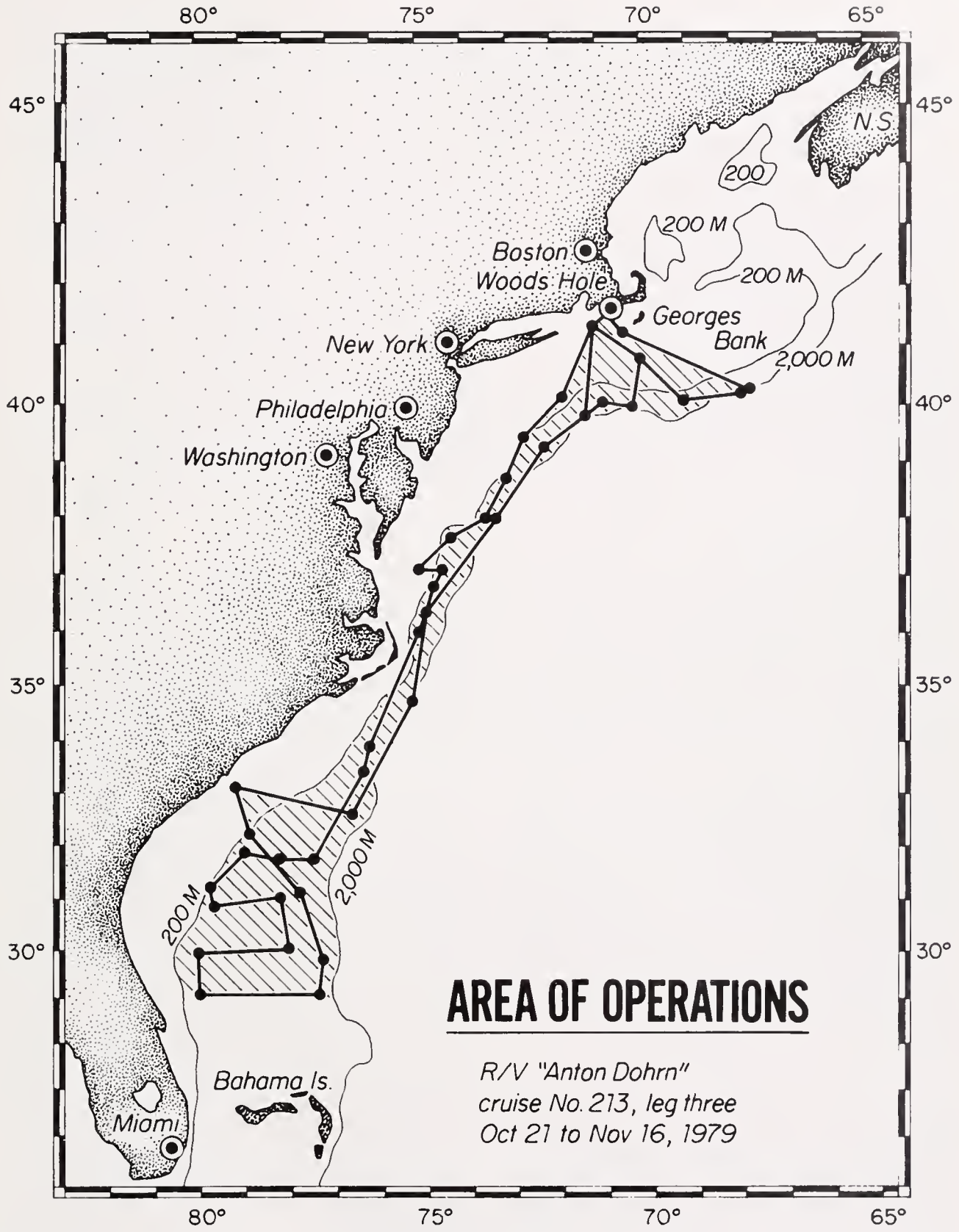

Figure 1. Area and cruise track of the R/V ANTON DOHRN during the October–November 1979 trawl survey along the continental slope off the eastern United States.

TABLE 1.

Trawl stations and locations covered by R/V ANTON DOHRN during cruise of October–November 1979, using a 43-m otter trawl.

Sta. No.	Date	Lat. N	Long. W	Time	Depth (m)	Bottom Temp. (°C)	*Illex* Catch (kg)	Sta. No.	Date	Lat. N	Long. W	Time	Depth (m)	Bottom Temp. (°C)	*Illex* Catch (kg)
6334	24 Oct	40°21′	67°35′	1215	400– 500	7.0	300	6387	4 Nov	29°05′	78°57′	0705	806– 808	9.4	1
6344	26 Oct	39°50′	70°55′	0710	1025–1035	4.3	5	6389	4 Nov	29°00′	79°47′	1415	608	7.1	5
6346	26 Oct	39°52′	70°55′	1020	805– 855	4.8	23	6391	4 Nov	29°07′	79°59′	1705	376– 392	7.4	325
6347	26 Oct	39°54′	70°54′	1245	645– 675	5.1	116	6392	6 Nov	30°49′	79°49′	0645	384– 392	7.8	656
6348	26 Oct	39°51′	70°56′	1500	417– 430	7.7	315	6394	6 Nov	30°50′	79°58′	0930	196– 200	11.7	251
6350	27 Oct	39°12′	72°13′	0720	1000–1075	4.3	2	6396	6 Nov	30°58′	79°57′	1105	150– 154	17.6	4
6352	27 Oct	39°12′	72°17′	1040	820– 920	4.7	9	6398	6 Nov	30°58′	80°00′	1250	98– 100	25.3	–
6353	27 Oct	39°20′	72°16′	1300	580– 650	5.3	335	6400	6 Nov	31°00′	80°03′	1425	80	24.8	–
6354	27 Oct	39°15′	72°19′	1450	415– 460	8.9	128	6402	6 Nov	31°12′	79°50′	1655	120– 124	18.4	–
6356	28 Oct	36°22′	74°42′	1110	1020–1030	4.4	6	6404	7 Nov	31°50′	79°17′	0650	400– 408	7.9	74
6358	28 Oct	36°25′	74°44′	1430	820– 800	4.7	150	6406	7 Nov	31°47′	79°23′	1325	625	8.7	–
6359	28 Oct	36°24′	74°44′	1735	610– 760	5.9	52	6408	8 Nov	33°28′	76°07′	0735	990–1010	4.2	75
6361	29 Oct	34°42′	75°30′	0823	608– 600	4.7	147	6410	8 Nov	33°38′	76°04′	1015	796– 800	4.6	153
6362	29 Oct	34°41′	75°33′	1043	410– 400	5.6	25	6412	8 Nov	33°46′	76°06′	1300	604– 608	5.5	243
6364	29 Oct	34°41′	75°30′	1330	800– 832	4.6	10	6414	8 Nov	33°54′	76°11′	1555	416	8.9	82
6365	29 Oct	34°37′	75°32′	1600	980–1000	4.2	–	6416	9 Nov	36°23′	74°43′	1500	800– 812	4.8	170
6367	30 Oct	33°12′	76°15′	0725	1016–1006	4.8	5	6418	10 Nov	36°52′	74°40′	0705	120– 140	12.7	4
6369	30 Oct	33°19′	76°16′	1135	800– 820	5.8	28	6420	10 Nov	36°46′	74°40′	0910	140	12.9	3
6370	30 Oct	33°25′	76°21′	1425	600	6.5	5	6422	10 Nov	36°43′	74°40′	1115	124– 140	14.3	2
6371	30 Oct	33°34′	76°31′	1720	410	8.3	37	6424	10 Nov	36°39′	74°45′	1335	140	13.8	3
6373	31 Oct	32°36′	76°38′	0715	970– 985	4.9	2	6426	10 Nov	36°43′	74°48′	1525	100	14.1	–
6375	31 Oct	32°46′	76°38′	1018	796– 820	5.5	2	6427	10 Nov	36°40′	74°47′	1710	62	13.8	–
6376	31 Oct	32°58′	76°51′	1315	550– 570	7.4	4	6428	12 Nov	39°24′	72°41′	0640	69– 100	12.6	2
6377	31 Oct	33°03′	77°00′	1600	392– 404	9.8	22	6430	12 Nov	39°55′	72°18′	1210	80	12.1	2
6379	1 Nov	32°20′	78°54′	1550	128	–	–	6432	12 Nov	40°05′	72°08′	1425	78	–	–
6380	1 Nov	32°17′	78°56′	1640	148– 156	15.2	7	6442	14 Nov	39°46′	71°28′	0705	1000–1016	4.4	12
6381	2 Nov	31°03′	77°49′	0710	1007–1016	4.5	–	6444	14 Nov	39°46′	71°33′	0950	824– 844	4.7	8
6383	2 Nov	29°52′	77°09′	2340	1004	8.7	–	6446	14 Nov	39°49′	71°34′	1230	600– 650	5.2	122
6385	3 Nov	29°11′	77°07′	0920	1000–1008	6.1	–	6448	14 Nov	39°51′	71°32′	1455	440	6.0	443

Although trawl coverage was heavily biased to sampling of locations beyond 400 m, some incidental coverage at lesser depths on the continental shelf was conducted between the Florida–Georgia border and Georges Bank. Long-finned squid (*Loligo pealei*) were captured at 14 locations at depths from 62 to 408 m. Those catches ranged from 1.9 to 60 kg per trawl. Bottom temperatures at those locations ranged from 7.9 to 24.8°C (Table 2).

A variety of other cephalopds were collected (Table 3). In terms of catchability via trawl gear and potential commercial exploitation, virtually all of those species could be considered inconsequential at the present time.

DISCUSSION

During the October–November 1979 cruise of the Federal Republic of Germany Institute R/V ANTON DOHRN, trawl coverage along the continental slope between 40°N and 29°N latitudes indicated the presence of a sizable squid resource. Of the six species recorded, the short-finned squid *Illex illecebrosus* was most abundant and widely distributed. Limited catches of long-finned squid (*Loligo pealei*) were taken during intermittent sampling along the outer continental shelf north and south of Cape Hatteras.

Catch patterns for short-finned squid revealed unexpected heavy concentrations of that species south of Cape Hatteras, particularly in the slope area between Cape Canaveral, FL, and Georgia. Previous trawl survey data from the South Atlantic Bight area (Whitaker 1980) and incidental catches by commercial fishermen suggested that this resource south of Cape Hatteras was greater than previously expected. Toll and Hess (1981) indicated that *I. illecebrosus* was a major component of the stomach contents of swordfish examined from the Straits of Florida (south of Cape Canaveral). A large catch of *I. illecebrosus* was taken in the Gulf of Mexico (Bennie Rohr, National Marine Fisheries Service, Pascagoula, MS, personal communication, May 1980) by the National Marine Fisheries Service research vessel OREGON II, in June 1971. On that occasion about 1,000 kg of *I. illecebrosus* were taken with a 40-m "whiting trawl" in approximately 366 m near the head of DeSoto Canyon, south of the Florida panhandle.

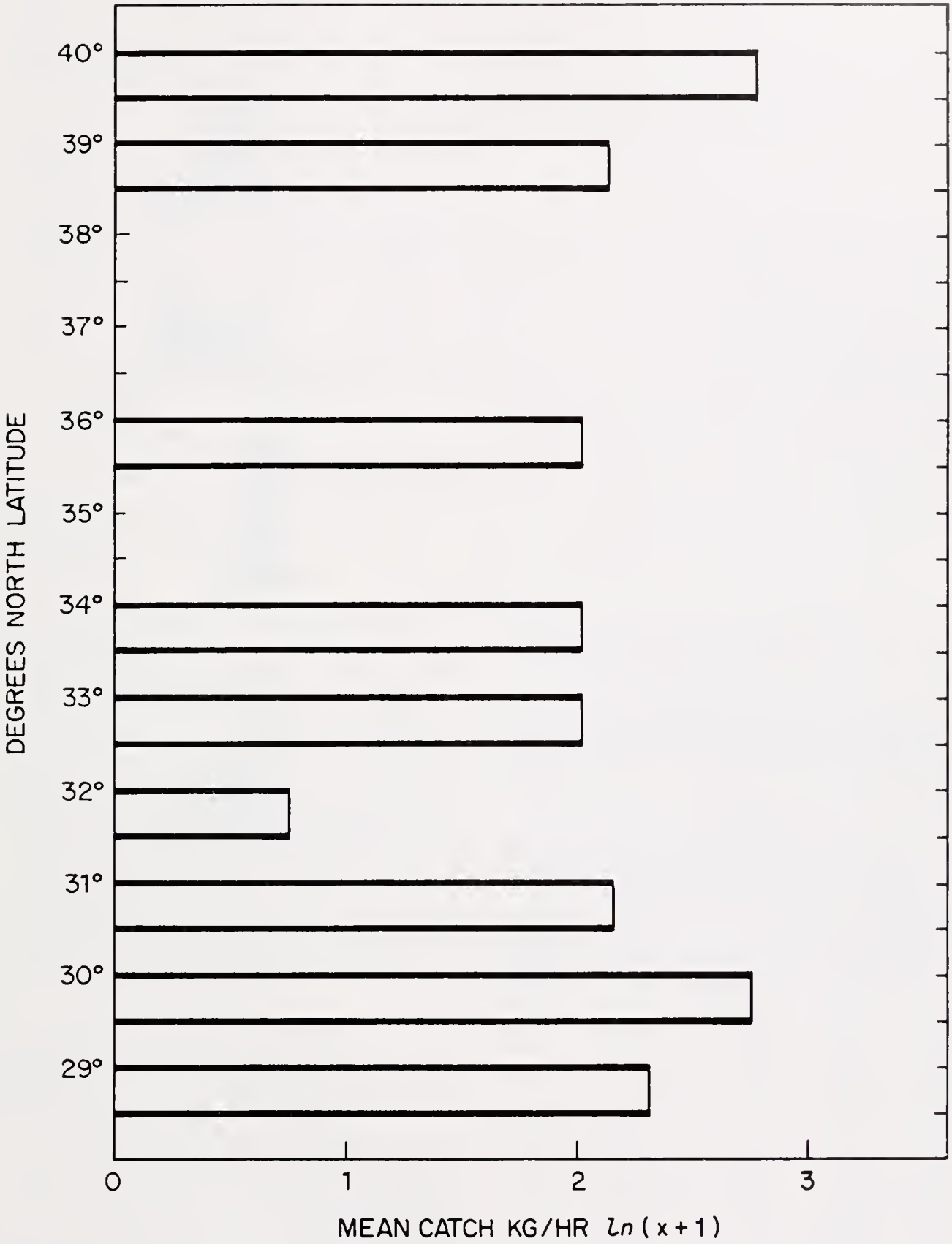

Figure 2. Comparison of catch rates of short-finned squid expressed as a natural logarithm of the mean catch and plotted by latitude north.

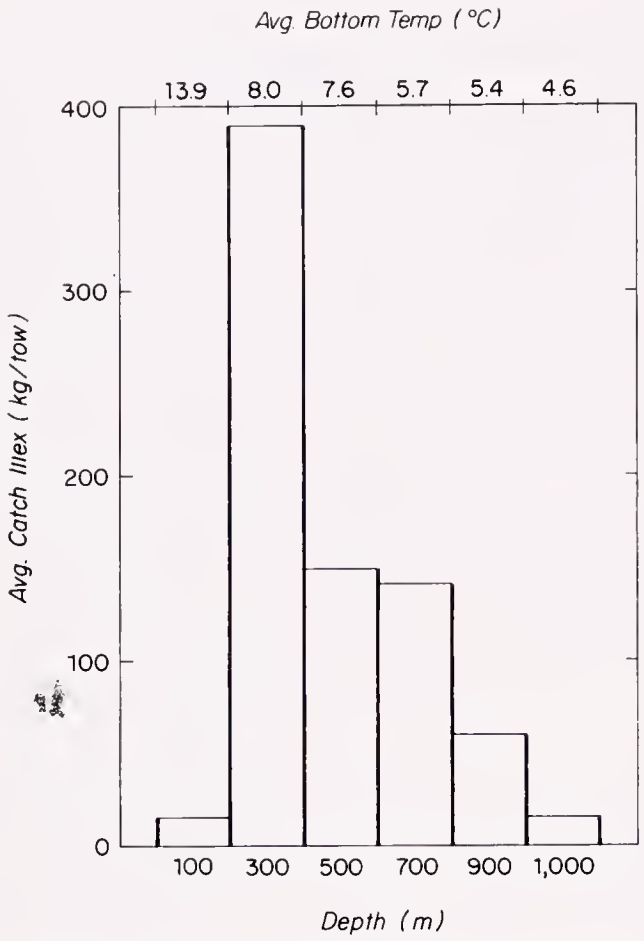

Figure 3. Mean catch of *Illex illecebrosus* per trawl tow as a function of depth. Greatest catch rates (390 kg/tow) were taken at locations where the bottom water temperature averaged 8.0°C.

TABLE 2.

Loligo catches taken during cruise of R/V ANTON DOHRN, October–November 1979.

Station No.	Latitude N	Weight (kg)	Size Range (cm)	Depth (m)	Bottom Temperature (°C)
6379	32°20′	1.9	3–14	128	–
6380	32°17′	12.5	8–18	150	15.2
6394	30°50′	8.0	9–13	200	11.7
6396	30°58′	10.0	8–19	154	17.6
6400	31°00′	5.0	5–20	80	24.8
6404	31°50′	4.0	9–13	408	7.9
6420	36°46′	40.0	11–25	140	12.9
6422	36°43′	3.5	6–26	140	14.3
6424	36°39′	60.0	10–21	140	13.8
6426	36°43′	54.0	9–23	100	14.1
6427	36°40′	58.0	3–26	62	13.8
6428	39°24′	53.0	5–21	100	12.6
6430	39°55′	47.0	6–22	80	12.1
6432	40°05′	30.0	6–21	78	–

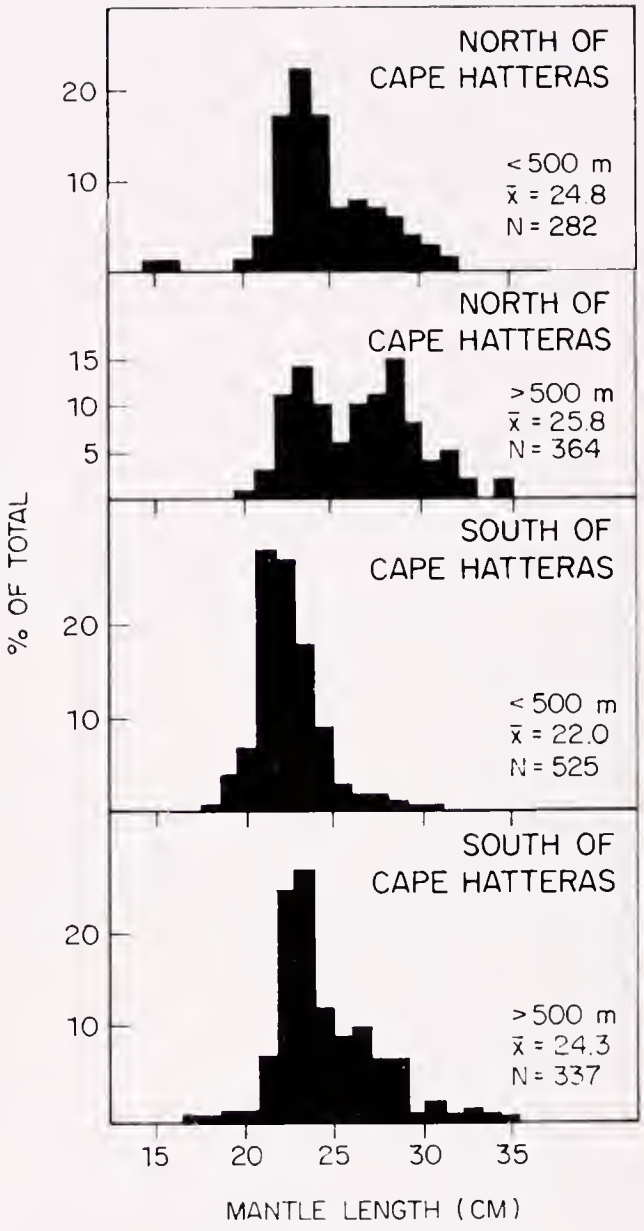

Figure 4. Length frequency of *Illex illecebrosus* at depths greater or less than 500 m north and south of Cape Hatteras, North Carolina.

From discussions with foreign captains fishing commercially off northeastern United States, it is known that short-finned squid are active swimmers and are frequently taken in the foreparts of the trawl while apparently trying to avoid capture. It is very likely that successful capture by trawl gear necessitates large, high-opening nets with greater dimensions than those traditionally used in deep-water exploratory surveys in that area.

The implications of those catches may affect future considerations of stock size and management plans, since a substantial squid resource appears to exist along the

TABLE 3.

Station occurrence of cephalopods other than *Illex* and *Loligo* taken during cruise of R/V ANTON DOHRN, October–November 1979.

Species	Station Number
Decapods:	
Rossia sp.	6410, 6346, 6371[1] 6369[2]
Pholidoteuthis sp.	6369, 6410, 6347, 6375, 6346[1] 6446, 6373, 6383, 6408, 6344[3]
Octopoteuthis sp.	6442[1]
Histioteuthis sp.	6381[1] 6359[2]
Octopods:	
Alloposus mollis	6347, 6346, 6356[1] 6375, 6387[2] 6446, 6385[3]
Bathypolypus arcticus	6371, 6334, 6416, 6358[1] 6356, 6354[2]

[1]Identified by Clyde Roper and Michael Sweeny of the Smithsonian Institution (U.S. National Museum).
[2]Identified by Michael Vecchione, Virginia Institute of Marine Science (VIMS).
[3]Field identification by W. F. Rathjen.

continental slope south of Cape Hatteras, at least during part of the year.

In that connection, it will be interesting for future workers to consider the relationship between the stocks north and south of Cape Hatteras and the possible recruitment of northern stocks from southern populations.

ACKNOWLEDGMENTS

I express my grateful appreciation to Matthias Stehmann and Frau Shultze of the Institute fur Seefischerei in Hamburg for the privilege of participating in Cruise No. 312 (III) of the R/V ANTON DOHRN; to Captain Grimm of the R/V ANTON DOHRN for his services; to Clyde Roper and Michael Sweeny of the Smithsonian Institution for their prompt assistance in identifying questionable specimens; to Michael Vecchione of the Virginia Institute of Marine Science for assistance in identifying incidental cephalopods; to Fred Lux, Ron Toll, Clyde Roper, Gilbert Voss, Ray Hixon, Terry Rowell, and Bob Temple for reviewing this manuscript and making helpful suggestions; to John Lamont of the Northeast Fisheries Center for assistance with the illustrations; and finally, to my wife Helga, for translations and overall encouragement and liason during the preparation of this manuscript.

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METHODOLOGY FOR SPECIFIC DIAGNOSIS OF CEPHALOPOD REMAINS IN STOMACH CONTENTS OF PREDATORS WITH REFERENCE TO THE BROADBILL SWORDFISH, *XIPHIAS GLADIUS*

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ABSTRACT Cephalopods were found to be a major component of the stomach contents of 65 broadbill swordfish examined from the Straits of Florida. Previous studies have failed to provide critical taxonomic analyses due in part to the poor condition of stomach remains. Alternative methodologies to identify remains are presented. Use of these techniques resulted in the identification of 15 species representing 11 families in two orders; 11 of these species had not been reported previously in the diet of the swordfish.

INTRODUCTION

Previous studies of the feeding ecology of the broadbill swordfish *Xiphias gladius* Linnaeus, 1758 have shown the importance of cephalopods in the diet of this predator, but, in general, have omitted specific analysis of remains (Bigelow and Schroeder 1953, Yabe et al. 1959, Cavaliere 1963, Scott and Tibbo 1968, Maksimov 1969). In this study, the stomach contents of 65 swordfish, ranging in size from 11 to 203 kg taken from the Straits of Florida, were examined (also see Toll and Hess 1981b). The majority of remains were in poor condition because of mechanical and chemical breakdown incurred during ingestion and digestion. Identification of remains became increasingly difficult as the traditional sequence of character assessment was prevented by deterioration and loss of morphological and meristic features.

Identifications were based on a synthesis of less frequently used characters inherently more resistant to gastric breakdown. These included mantle musculature, light organs, gladii, beaks, spermatophores, and radulae. In addition, examination of viscera, when present, provided taxonomic information, as well as data concerning sex, state of maturity, and fecundity. The purpose of this paper is to discuss the taxonomic methodologies employed.

The utility of the approach outlined herein is demonstrated by the high species diversity encountered in comparison to previous studies. The significance of these techniques is further emphasized in that 73% of these species had not been reported previously in the diet of the swordfish. In addition, one cephalopod specimen was the largest known representative of its family (Ctenopterygidae) and another was the smallest recorded mature male from the family Architeuthidae, the giant squids.

We hope the methodologies described here will be useful in feeding studies of swordfish from other oceanic areas, as well as of other cephalopod predators.

MATERIALS AND METHODS

Stomach contents were removed at dockside and immediately placed in 10% formalin for approximately 1 week. They were then rinsed in fresh water and placed in 70% ethyl alcohol for storage. Examination of each lot began with the sorting of material into cephalopod, fish, and crustacean components. Soft-tissue remains of cephalopods were weighed and measured and, when possible, information on condition, sex, and state of maturity was recorded.

Specific-level diagnoses of cephalopods normally depend on the use of external soft-tissue characters including cornea, buccal membrane connectives, arm and tentacular suckers, and, in one family (Ommastrephidae), funnel-groove pockets. It is just these parts, however, that are first subject to digestion and quickly lost. Therefore, traditional keys (e.g., Roper et al. 1969a) are of only limited value. As a result, identifications were based on a composite of several less frequently used morphological features which are more resistant to chemical breakdown by digestive enzymes. These characters include the gladius, spermatophores, internal anatomy, dermal cartilage, mantle musculature, photophore number and position, beaks, and radulae. The use of these characters necessitated a departure from traditional sequences of identification proceeding strictly from higher to lower taxonomic levels.

Abbreviations used in the text are: ML, mantle length; GL, gladius length; FL, fin length as defined in Voss (1963).

RESULTS

Members of the Ommastrephidae predominated both in total weight and number. In order of decreasing frequency were ommastrephids, histioteuthids, onychoteuthids, thysanoteuthids, cranchiids, lepidoteuthids, enoploteuthids, ctenopterygids, architeuthids, bolitaenids, and argonautids. The last six families were represented by a single specimen each. In total, 15 species representing 11 families in two

orders were identified. Of these 15 species, 11 were new records of swordfish prey.

DISCUSSION

The points considered in the process of identifying stomach remains are: (1) basic comments on subfamilial taxonomy, (2) existing systematic problems, (3) remarks on specimens with reference to the characters used for identification, and (4) distributional patterns.

Class Cephalopoda Cuvier, 1798
Subclass Coleoidea Bather, 1888
Order Teuthoidea Naef, 1916
Suborder Oegopsida d'Orbigny, 1845

Family Enoploteuthidae Pfeffer, 1900
Subfamily Ancistrocheirinae Pfeffer, 1912

Genus *Ancistrocheirus* Gray, 1849
Species *A. lesueuri* (d'Orbigny, 1839)

Figure 1

This species and *Thelidioteuthis alessandrinii* (Verany) traditionally comprise the subfamily Ancistrocheirinae, but there is evidence that the two species may be synonymous (Okutani 1976). If that is the case, *A. lesueuri* takes precedence and becomes the sole member of the subfamily.

Stomach remains of that animal are distinguished most easily by the large fins which occupy almost the entire length of the mantle except for an acute, projecting tail, and a distinct pattern of 21 photophores on the ventral surface of the mantle. There are also photophores present on the ventral surface of the head and a single row along the tentacular stalks.

The single specimen examined (FL = 44 mm) was missing the tail and several of the ventral light organs. The combination of fin shape and photophores was diagnostic. This species has been reported only rarely from the western North Atlantic. Additional records indicate a worldwide distribution in tropical and temperate waters.

Family Onychoteuthidae Gray, 1849

Genus *Onychoteuthis* Lichtenstein, 1818
Species *O. banksii* (Leach, 1817)

Figure 2

This family contains six genera presently distinguished on the basis of soft-tissue features such as the presence or absence of tentacles, neck folds, and visceral light organs, and tentacular club sucker arrangement. These characters, however, are often indistinguishable in material retrieved from predator stomachs.

In these cases, several other characters clearly distinguish remains of *O. banksii*. These include a prominent, longitudinal, mid-dorsal ridge along the mantle resulting from a keel on the gladius. The gladius is further characterized by narrow reduced vanes and a sturdy rachis which is V-shaped in cross section. *Onychoteuthis banksii* is the sole member of its genus in the Atlantic. This species is reported to have a worldwide distribution (Young 1972).

Family Lepidoteuthidae Naef, 1912

Genus *Tetronychoteuthis* Pfeffer, 1900
Species *T. massyae* Pfeffer, 1912

Figure 3

The major character of this family is the presence of scales on the mantle, hence the common name "scaled squid." Three genera are recognized; of those, *Lepidoteuthis* and *Pholidoteuthis* are additionally characterized by the absence or reduction of tentacles in the adults of the former, and unstalked, plate-like scales in the latter. The third genus, *Tetronychoteuthis*, is distinguished by terminal fins and stalked, star-shaped scales with a central pit. The single lepidoteuthid examined (ML = 75 mm) possessed remnants of fully developed tentacles and stalked, star-shaped scales, characters clearly indicating its identity.

Subgeneric systematics presently are confused, with larger specimens conforming to the characters of *T. dussumieri* and smaller specimens to those of *T. massyae*, suggesting conspecific growth stages. Until this problem is resolved, the present material must be attributed to *T. massyae*. This species is widely distributed in the Indian, Atlantic, and Pacific oceans.

Family Architeuthidae Pfeffer, 1900

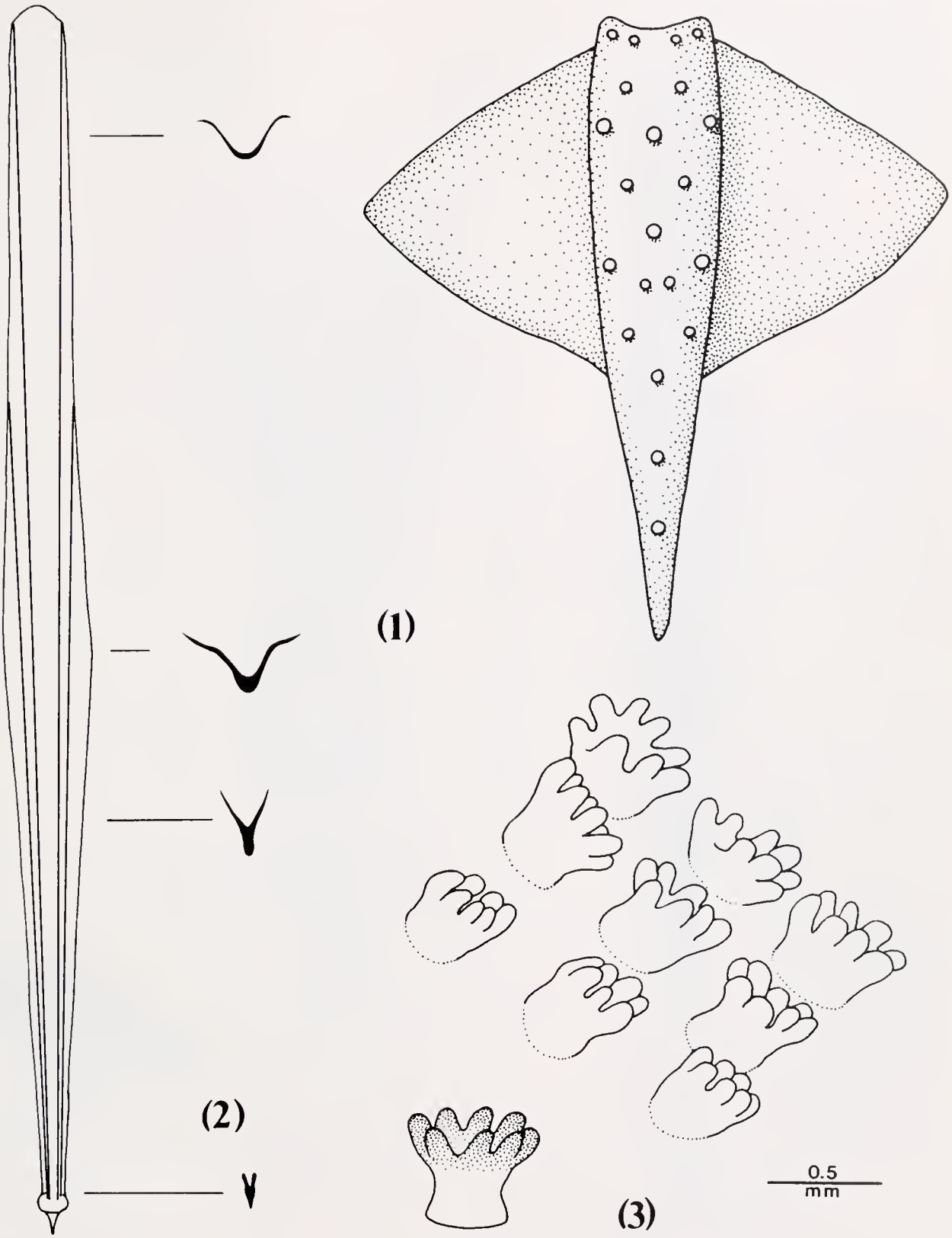
Genus *Architeuthis* Steenstrup, 1857
Species *Architeuthis* sp.

Figure 4

This family contains the so-called "giant squids." A single genus, *Architeuthis*, is recognized. Since its original description, the genus has become a catchall for new species, often based on fragmentary remains. The result is a thoroughly confused assemblage of about 20 poorly defined species. Revision of the family probably will reduce that number substantially.

The single specimen examined in this study (GL = 179 mm) was missing head, arms, and tentacles, but was identified based on a combination of fin shape and gladius morphology. The specimen is the smallest mature *Architeuthis* recorded; it possessed fully developed genitalia and two spermatophores (Toll and Hess 1981a).

This family occurs in all of the world's oceans from 75°N to 62°S latitude (Clarke 1966). Specific-level distributional patterns are not reliable because of taxonomic problems.



Figures 1–3. (1) *Ancistrocheirus lesueuri.* Ventral view of mantle; note fin morphology and distribution of photophores (redrawn from d'Orbigny [1835–1848]). (2) *Onychoteuthis banksii.* Dorsal view of gladius (redrawn from Rancurel [1970]) with cross sectional profiles. (3) *Tetronychoteuthis massyae.* Morphology and arrangement of dermal scales.

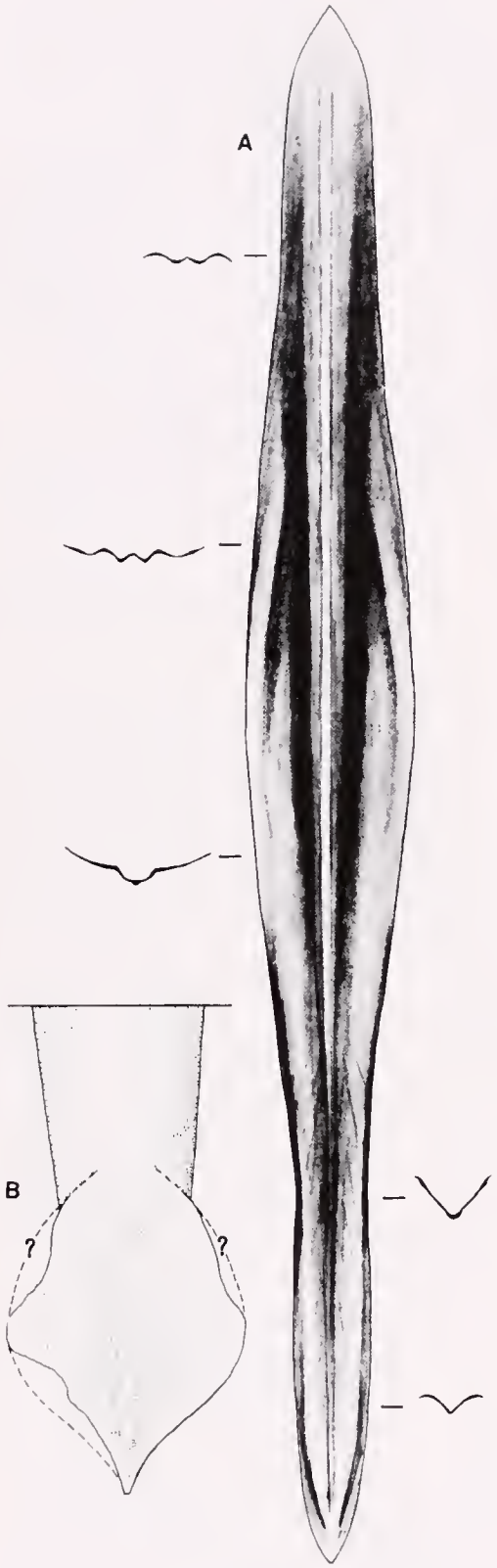


Figure 4. *Architeuthis* sp. (A) Ventral view of gladius with cross sectional profiles. (B) Dorsal view of mantle and fins.

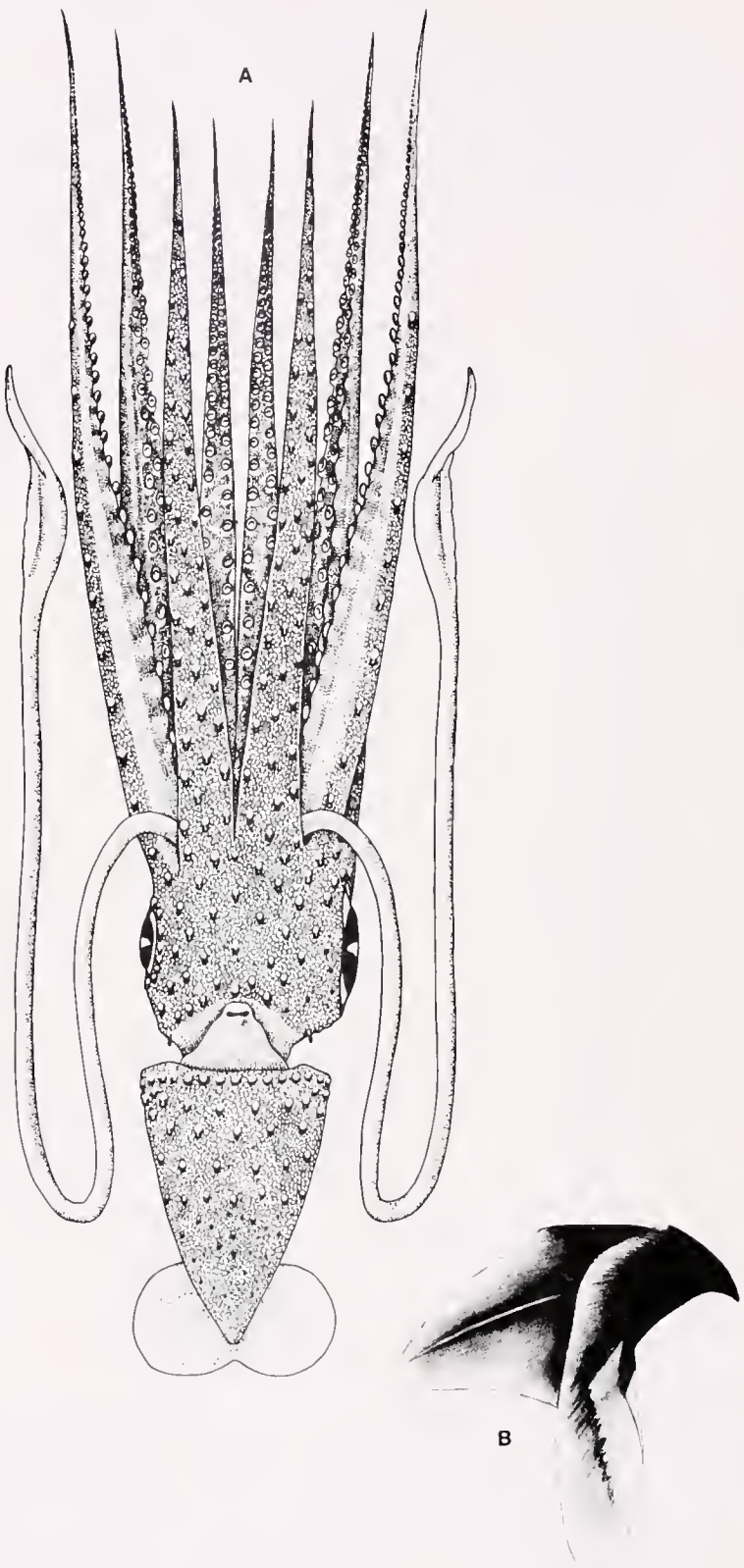


Figure 5. *Histioteuthis dofleini.* (A) Ventral view of mantle; note fin shape, distribution of light organs and asymmetry of eyes. (B) Lower beak; note median ridge (both from Voss [1969]).

Family Histioteuthidae Verrill, 1881

Genus *Histioteuthis* d'Orgibny, 1841
Species *H. dofleini* (Pfeffer, 1912)

Figure 5

A detailed monographic revision of this family has been published by Voss (1969).

This family contains a single genus, *Histioteuthis,* characterized by large, anteriorly directed photophores covering the mantle, head, and arms; an asymetrical head with the left eye larger than the right; a conical mantle of spongy consistency; and small, round, terminal fins.

Several specimens of *H. dofleini* were found including gravid females and mature males with spermatophores. Specimens were identified using circumocular photophore numbers (17 on right eye) and, in male specimens, the unique occurrence of paired genitalia, as well as spermatophore morphology. In addition, the lower beak of most histioteuthids bears a strong median ridge on the lateral walls that extends from the midanterior margin to the mid-posterior point. This character is particularly useful in making familial-level identifications when only heads and buccal masses are available.

Histioteuthis dofleini is recorded from the Atlantic, Indian, and Pacific oceans from 50°N to 40°S latitude.

Family Ctenopterygidae Grimpe, 1922

Genus *Ctenopteryx* Appellöf, 1899
Species *C. sicula* (Verany, 1851)

Figure 6

Specimens of this monotypic family are easily distinguished by fins supported with transverse trabeculae. Adults have fins extending the full length of the mantle. In juveniles, the fins occupy only the posterior portion of the mantle and lengthen anteriorly with growth. The fins are delicate and often torn, so that the separated fin supports appear comb-like.

While several species have been described, they commonly are combined with *C. sicula* (*fide* Voss). Rancurel (1970) described *C. sepioloides* from the Pacific Ocean.

Ctenopteryx sicula has been recorded from the North and South Atlantic, the Pacific, the Mediterranean Sea, and from the southwestern Indian Ocean (Cairns 1976). At present, Atlantic specimens are considered to be *C. sicula.* Our single specimen is the second record from the tropical western Atlantic and is the largest specimen (ML = 88 mm) of this species yet reported.

Family Ommastrephidae Steenstrup, 1857

Figure 7

Ommastrephids are recognized by a ⊥-shaped mantle locking apparatus. The three subfamilies, Ommastrephinae, Illicinae, and Todarodinae are characterized by combinations of membranous pockets (foveola) and side pockets in the funnel groove. Because of the delicate nature of these membranous skin folds, they are rarely found in specimens from stomach contents. Identification, therefore, must be made at the generic-and specific-level.

Subfamily Ommastrephinae Steenstrup, 1857

Five genera are recognized in this subfamily of which *Ommastrephes, Ornithoteuthis,* and *Hyaloteuthis,* occur in the North Atlantic.

Genus *Ommastrephes* d'Orbigny, 1835
Species *O. pteropus* Steenstrup, 1855

The presence of a large patch of photogenic vesicles near the anterior mantle margin in the dorsal midline clearly distinguishes this species. Based on the color of the light emitted by this tissue, the animal is commonly called the "orange-back" squid. When partially digested, this luminous patch appears as a dense aggregation of tough, conical nodules. Specimens of this species attain a large size. Our material ranged from 155 mm to greater than 350 mm ML.

Genus *Ornithoteuthis* Okada, 1927
Species *O. antillarum* (Adam, 1957)

The two species assigned to this genus, one of which occurs in the Atlantic, share a unique character, a strip

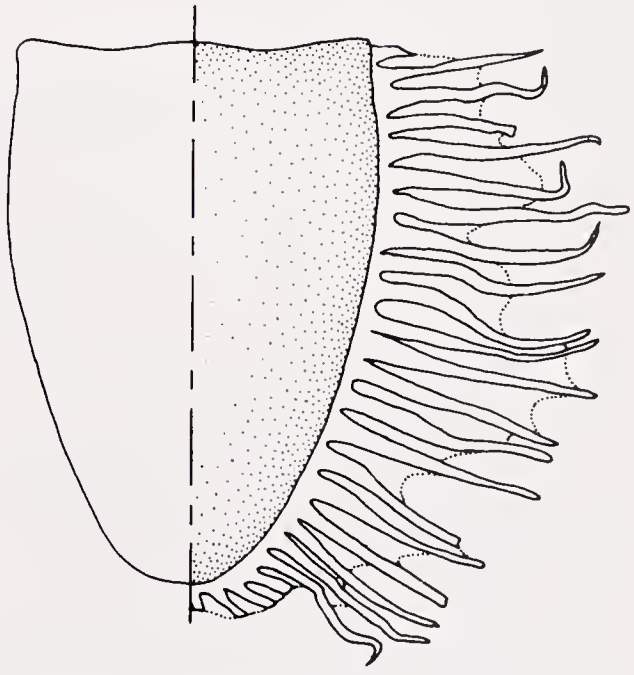


Figure 6. *Ctenopteryx sicula.* Ventral view of mantle; note fins with trabeculae.

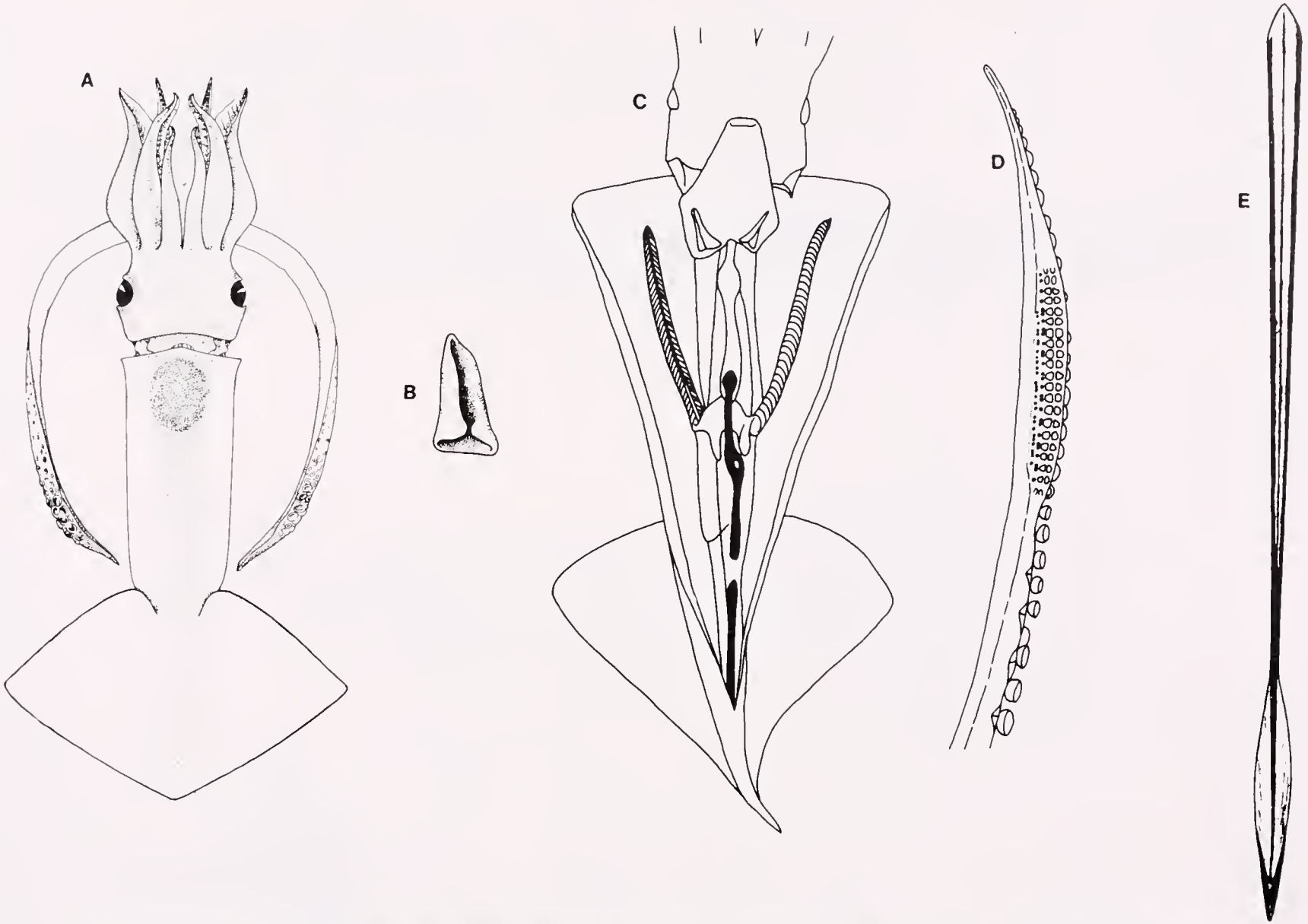


Figure 7. Ommastrephidae. (A) Dorsal view of *Ommastrephes pteropus* (from Roper [1978]). (B) Typical ommastrephid mantle locking apparatus (from Roper [1978]). (C) Visceral photogenic strip (redrawn from Rancurel [1970]). (D) Ventral view of hectocotylus of *Ornithoteuthis antillarum* (redrawn from Voss [1957]). (E) Typical ommastrephid gladius from *Illex* sp.

of pigmented luminous tissue along the ventral mid-line of the viscera. This light organ originates as a round patch on the antero-ventral surface of the liver and continues as a thin strip to the posterior tip of the mantle. There is a single, oval light organ on the ventral surface of each eye. Males of this species may be distinguished by a honeycomb-like structure on the ventral surface of the hectocotylized arm.

Subfamily Illicinae Posselt, 1890

Genus *Illex* Steenstrup, 1880
Species *I. illecebrosus* ? Lesueur, 1821
***I. coindetii* ? (Verany, 1837)**
***I. oxygonius* ? Roper, Lu and Mangold, 1969**

Five nominal species in two genera are assigned to this subfamily. One of these, *Todaropsis eblanae* (Ball), is restricted to the eastern Atlantic and the Mediterranean. The remaining four species are included in the poorly understood genus *Illex*. *Illex argentinus* (Castellanos) occurs along the Argentinian coast and is excluded from our discussion. Problems occur when considering the remaining species, *I. illecebrosus*, *I. coindetii* and *I. oxygonius*, all of which have been reported from the Straits of Florida (Roper et al. 1969b). Those authors attempted to stabilize the systematics of these species and reemphasized the systematic and distributional complexities of this polytypic genus, especially in waters included in the present study area. Numerous specimens examined in this study conformed to the specific characters assigned to each nominal species; therefore, all three species are included in the results presented. However, taxonomic difficulties were encountered in the form of intergrades, which were most evident in the *I. illecebrosus*–*I. coindetii* complex. For the purposes of this paper and for quantitative analyses, the authors thought it best to deal with the group at the generic level rather than possibly adding to the underlying systematic and zoogeographic confusion.

Family Thysanoteuthidae Keferstein, 1866

Genus *Thysanoteuthis* Troschel, 1857
Species *T. rhombus* Troschel, 1857

Figure 8

Two nominal genera comprise the family: *Thysanoteuthis* and *Cirrobrachium*. The latter is generally considered a synonym of the former and all nominal species assigned to *T. rhombus* (Sasaki 1929).

Four characters can be used to identify mantle remains alone: large, rhomboidal fins that extend the full length of the mantle; gladius with anteriorly projecting, quadrangular vane extensions; ⊣-shaped mantle locking apparatus; and strong, thick, mantle musculature.

Specimens examined included a mantle only (ML = 400 mm; weight, 487 grams). Members of this species are known to reach 800 mm ML and 19 kg in weight (Nishimura 1966). This species is cosmopolitan in tropical and temperate waters.

Family Cranchiidae Prosch, 1849
Subfamily Cranchiinae Prosch, 1849

Genus *Cranchia* Leach, 1817
Species *C. scabra* Leach, 1817

Figure 9

Cranchiids are extremely diverse, even in respect to basic morphological characters. A monographic revision by Voss is presently underway with a generic review already published (Voss 1980). All members of the family exhibit fusion of the dorsal portion of the mantle and head in the nuchal area and of the mantle to the postero-lateral corners of the funnel. All members of the subfamily Cranchiinae bear one or two cartilaginous strips extending posteriorly from the area of each funnel-mantle fusion on the ventral mantle surface. *Cranchia scabra* has two such rows, as well as cartilaginous tubercles that cover the saccular mantle and the small, terminal, circular fins, and 14 small photophores on each eye.

This species is common circumglobally in tropical and subtropical waters (Voss 1980).

Order Octopoda Leach, 1818
Suborder Incirrata Grimpe, 1916

Family Bolitaenidae Chun, 1911

Genus *Japetella* Hoyle, 1885
Species *J. diaphana* Hoyle, 1885

Figure 10

Thore (1949) revised the bolitaenids basing his specific diagnoses on characters including relative size of eye, optic nerve length, and sucker size and spacing. Thore also illustrated the radulae and beaks. Of the four genera, *Japetella*, *Bolitaena*, *Dorsopsis*, and *Eledonella*, the latter three are monotypic.

The single specimen encountered in this work consisted of fragmentary remains of an arm crown and buccal mass. Based primarily on Thore's radula illustration, the material was assigned to *J. diaphana*, a common component of the pelagic octopod fauna of the western Atlantic. *Japetella heathi* and an unnamed species are known from the Pacific (Young 1972).

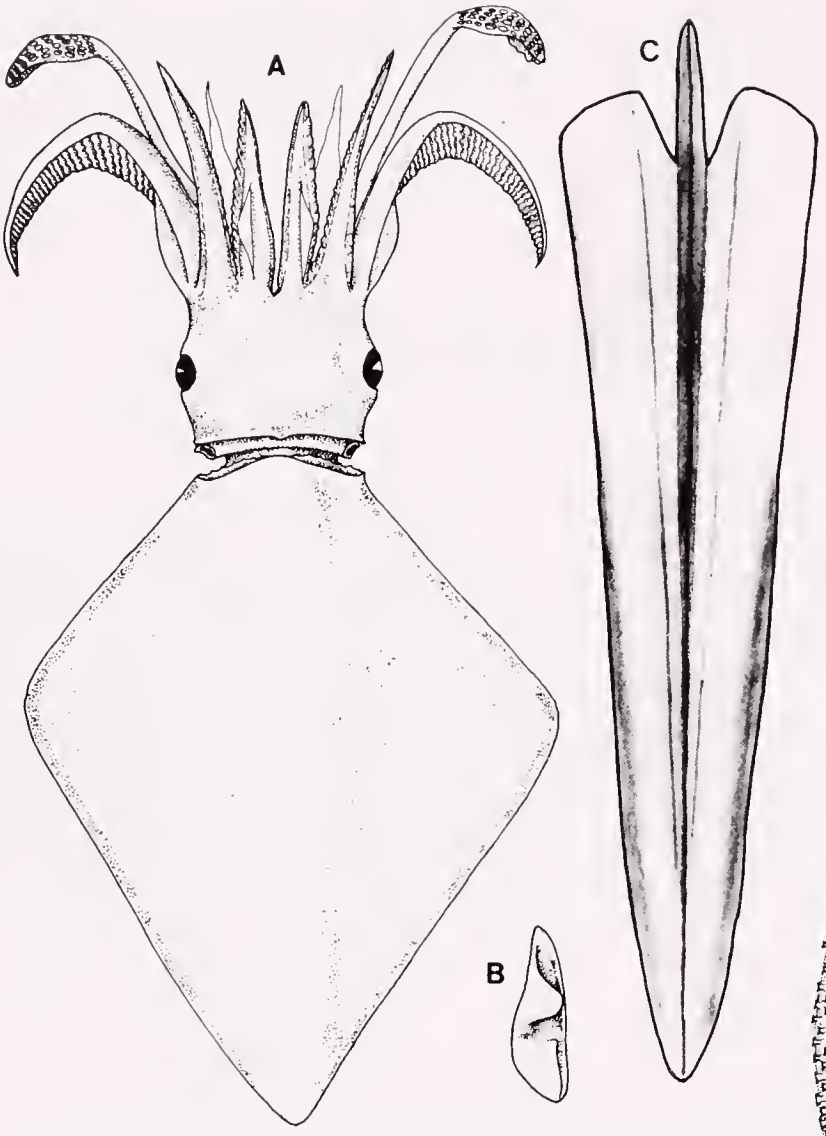


Figure 8. *Thysanoteuthis rhombus.* (A) Dorsal view; note rhomboidal fins. (B) Mantle locking apparatus (from Roper [1978]). (C) Gladius.

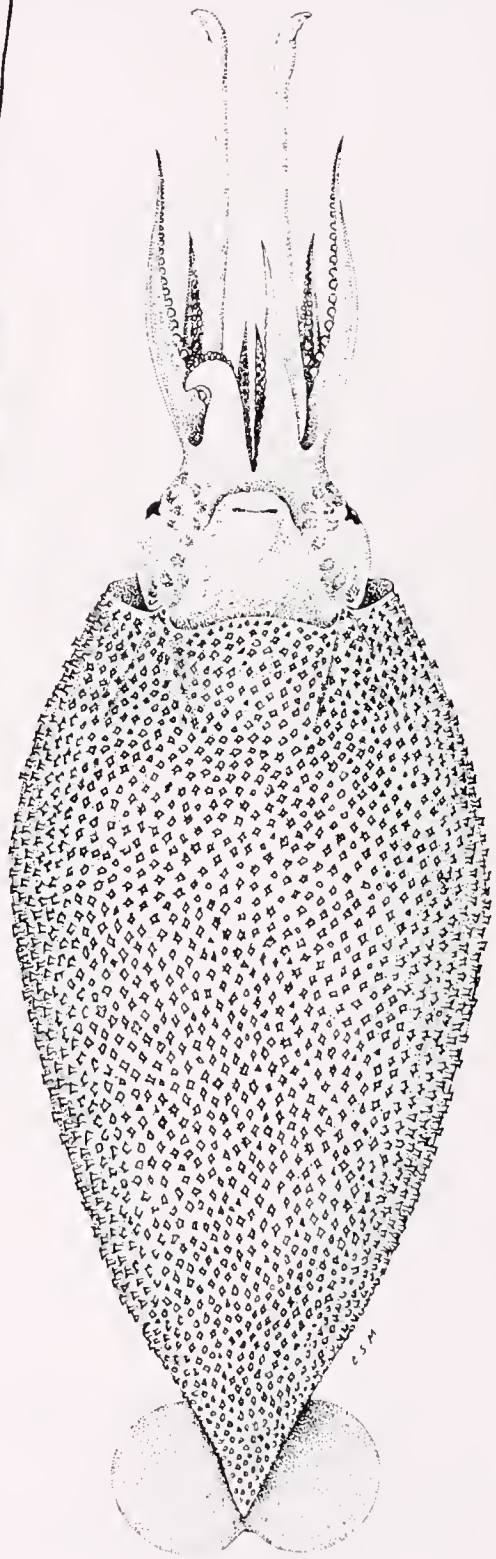


Figure 9 (right). *Cranchia scabra.* Ventral view; note fin shape and cartilaginous tubercles (from Voss [1980]).

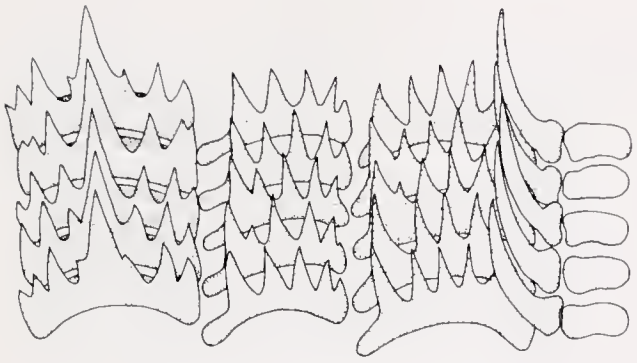


Figure 10. *Japetella diaphana.* Radula.

Family Argonautidae Naef, 1912

Genus *Argonauta* Linnaeus, 1758
Species *Argonauta* sp.

Figure 11

This family of pelagic octopods includes seven nominal species of the genus *Argonauta,* commonly referred to as "paper nautiluses." Two species occur in the Atlantic, *A. argo* and *A. hians.* The sole specimen examined consisted of the head and buccal mass with beaks and radula.

Upper and lower beaks of *Argonauta* show no clear demarcation between rostrum and shoulder, hence, no jaw angles are apparent. In addition, the beaks are poorly chitinized and are broad with flaring wings. Beaks from the present specimen conformed to the characters delineated by Clarke (1962), to which the reader is referred for a full consideration of beak morphology.

Specific-level identification was impossible because of the poor condition of the specimen.

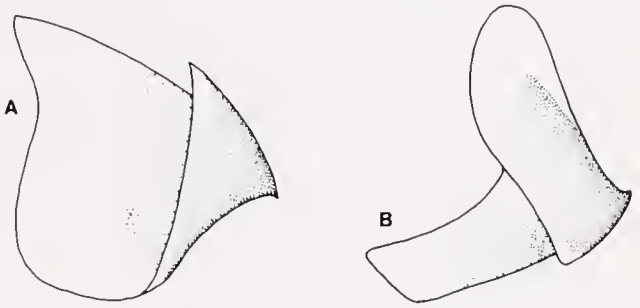


Figure 11. *Argonauta* sp. (A) Upper beak. (B) Lower beak (redrawn from Naef [1923]).

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This is a scientific contribution of the Rosenstiel School of Marine and Atmopsheric Science, University of Miami.

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ASPECTS OF THE EARLY LIFE HISTORY OF *LOLIGO PEALEI* (CEPHALOPODA; MYOPSIDA)[1]

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ABSTRACT The long-finned squid *Loligo pealei* was the most common squid collected in 2 years of zooplankton sampling over the Middle Atlantic Bight off New Jersey and Virginia. Planktonic specimens of *L. pealei* were found in that area during spring, summer, and fall; there were no indications of multiple stocks. This species was captured in waters with a salinity range of 31.5 to 34.0 ppt, and was confined to coastal waters except when current conditions, such as the passage of a Gulf Stream eddy, resulted in strong, offshore surface transport. While abundances were greater in night surface samples, larger specimens occurred in night subsurface samples indicating ontogenetic descent. Tentacle length was closely correlated with dorsal mantle length (DML) in preserved specimens of less than 4.5 mm DML, indicating that tentacles are noncontractile in newly hatched specimens. This may be part of a major discontinuity in the development of *L. pealei* which separates hatchlings from juveniles.

INTRODUCTION

The long-finned squid *Loligo pealei* Lesueur, 1921 is a commercially and scientifically important cephalopod species (Voss 1973). Although the biology of this squid has been studied for many years (Verrill 1882, Mesnil 1977) and is better known than the biology of most other cephalopods (Voss 1952), little is known of its early life history. Summers (1971) stated that two broods arise each year in the Middle Atlantic Bight, one an ubiquitous July brood, and the other a November brood which probably originates in the southern Middle Atlantic Bight. Mesnil (1977) suggested two, 20-month, alternating reproductive cycles occurred.

Although adults of *L. pealei* are demersal during the day and disperse vertically at night (Summers 1969), McMahon and Summers (1971) found that newly hatched specimens of *L. pealei* actively maintained position at the surface under all conditions of illumination. With impending petroleum resource development on the continental shelf of the Middle Atlantic Bight and the possible impacts of oil spills on surface biota, the research reported here was initiated to provide a descriptive summary of the distribution of planktonic juveniles of *L. pealei*. Specifically, I was looking for distributional discontinuities indicating the presence of multiple stocks in the Middle Atlantic Bight, and I wanted to determine the importance of the sea-surface layer in the early life history of *L. pealei*.

A standard set of measurements taken during this study showed surprisingly little variability of tentacle length in small specimens. I propose in this report an hypothesis to explain the apparent discontinuities in several parameters relating to the early life history of *L. pealei*.

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MATERIALS AND METHODS

Squid were collected during a 2-year baseline study of zooplankton in the Middle Atlantic Bight, which was begun in the fall of 1975 and included four quarterly cruises per year. During the first year, six 24-hour stations were occupied on a cross-shelf transect off Atlantic City, NH, extending from shallow inshore waters to the shelf break (Figure 1). At each of those stations surface collections were made every 3 hours using a neuston frame rigged with a standard 1 m, 505-μm mesh net that sampled to a depth of approximately 12 cm. Subsurface oblique tows were made at night with 60 cm opening-closing bongo systems rigged with both 202- and 505-μm mesh nets. The volume filtered during the subsurface collections was calculated from measurements made with General Oceanics flow meters; the volume filtered during the surface collections were determined likewise beginning with the third cruise (June 1976). Readings for each meter were compared in terms of revolutions per minute and outliers were discarded and replaced with the mean value for that meter.

During the second year, two stations to the north and a second transect of four statons off Wachapreague, VA, were added. Three of the original stations, D1, N3, and F2, were shortened with two subsurface tows and a single surface tow taken at night. Three additional replicates of the subsurface tows were collected at stations A2, B5, and E3. The filtered volumes were monitored similarly to the first year. Surface water temperatures and salinities were measured concurrently with all surface samples. All specimens were fixed and preserved in a 2 to 4% solution of formaldehyde in sea water buffered with borax.

Relative abundances in both surface and subsurface collections were calculated as numbers of specimens collected per 100 m^3 of filtered water. Distributional statistics were computed based on all samples collected at stations where *L. pealei* was captured. Several pairwise comparisons between the most similar collecting methodologies (night,

surface, 505-μm mesh versus night, subsurface, 505-μm mesh) are presented here. Because the t-test assumes equal variances, I used an F-test for equality of variances between the sets of observations to be compared. That test generally failed to demonstrate equality among the variances, so I chose to use the t′ approximation (Sokal and Rohlf 1969, p. 374) for comparisons of observation sets. The comparisons were one-tailed with alpha significance set at 0.05.

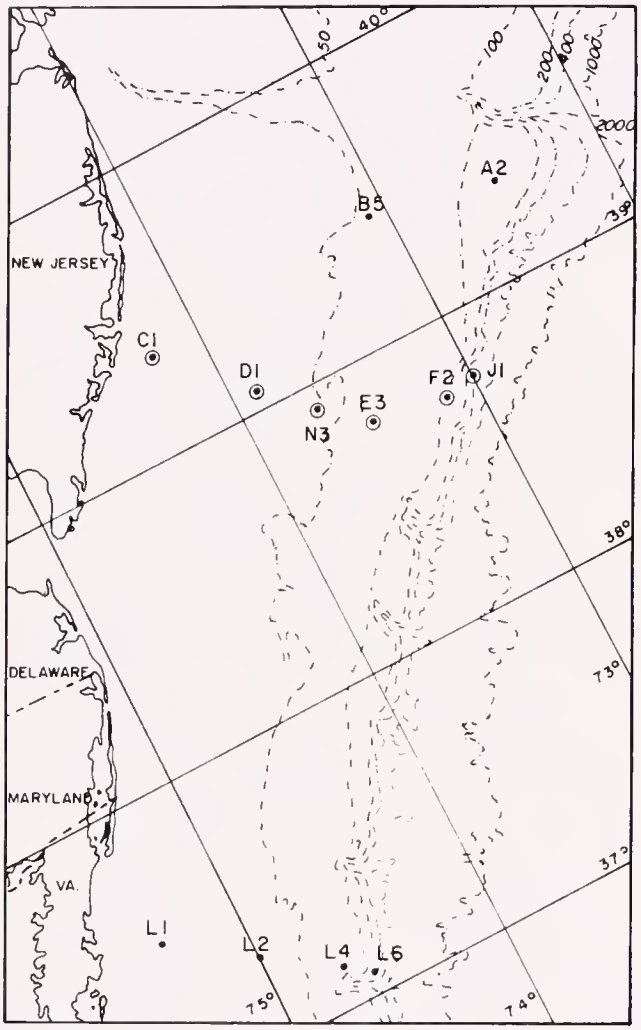

Figure 1. Stations sampled. Open circles: first year; solid dots: second year.

All measurements (Figure 2) were made to the nearest 0.05 mm using a dark-field dissecting microscope equipped with an ocular micrometer. Dorsal mantle length (DML) was measured on all specimens. Mantle width (MW), head length (HL), head width (HW), fin length(FL), width across fins (WAF), length of the third pair of arms (AL), and tentacle length (TL) were measured on 150 specimens for morphometric analysis. Although a few fairly large specimens were collected (up to 75 mm DML), a discontinuity in size distribution occurred at about 15 mm DML, so I have considered specimens ≤ 15 mm DML to be planktonic.

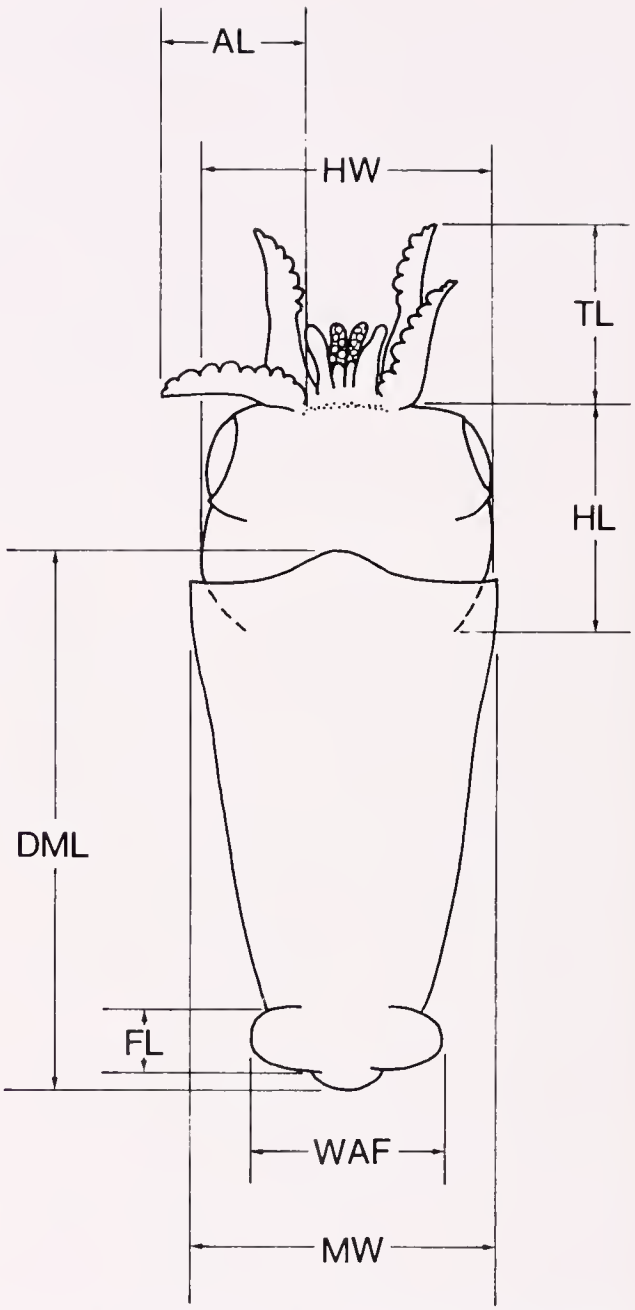

Figure 2. Morphometric characters used in this study: mantle width, MW; width across fins, WAF; fin length, FL; dorsal mantle length, DML; head length, HL; tentacle length, TL; head width, HW; and third arm length, AL.

RESULTS

The 635 loliginid specimens constituted the most numerous group of cephalopods collected during this study. Squids of the family Loliginidae that may occur in the study area include *Loligo pealei, Loligo plei,* and *Lolliguncula brevis* (Voss 1956, Cohen 1976). The last species was excluded from consideration because it is an estuarine spawner (Hall 1970). Of the *Loligo* species, *L. pealei* is by far the most

common in the Middle Atlantic Bight. *Loligo plei* reaches the northern limits of its geographic range in the study area (Cohen 1976), but is very rare north of Cape Hatteras (A. C. Cohen, National Museum of Natural History, Washington, D.C., personal communication, 1977). Circulation on the continental shelf of the Middle Atlantic Bight is a flow-through system from northeast to southwest (Beardsley et al. 1976, Bishop and Overland 1977) with only occasional short-term reversals of surface drift (Bumpus 1969). Thus, it is unlikely that many of the specimens drifted into the area from south of Cape Hatteras. McConathy et al. (1980) have described differences in chromatophore arrangements among species of hatchling loliginid squids and the smallest specimens collected in this study most closely matched their description of *L. pealei*. Therefore, I concluded that my loliginid specimens were *L. pealei*.

Planktonic specimens of *L. pealei* were collected during spring, summer, and fall cruises, but were absent from all winter collections (Figure 3). Peak abundances on both transects occurred in late summer. Although a few specimens were collected during the day, at those stations where *L. pealei* was most abundant, almost all were taken at night.

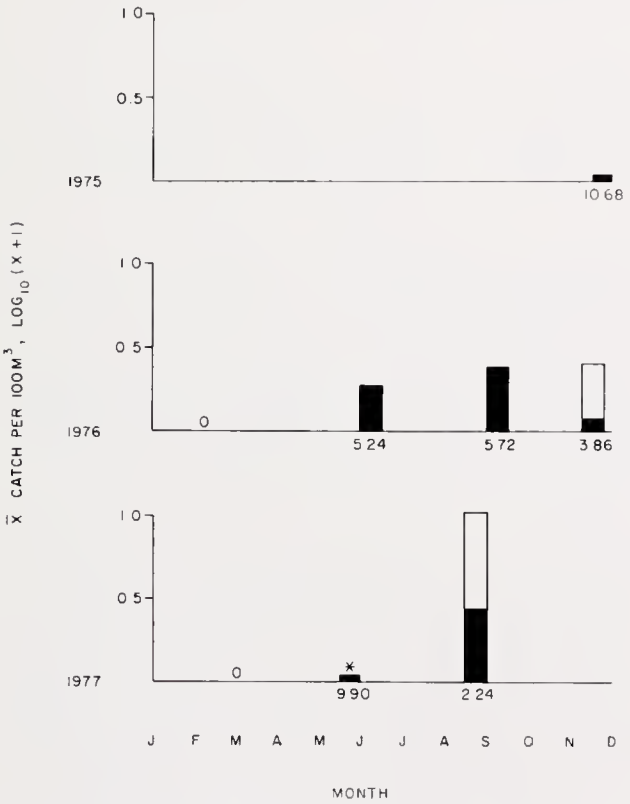

Figure 3. Seasonal distribution of planktonic *Loligo pealei*: solid bars, northern transect; open bars, northern and southern transects combined; *, southern transect value lower than that of northern transect; numbers below bars, mean dorsal mantle length (mm) for that cruise.

Abundance variability existed within the nighttime period but no pattern was apparent (Figure 4). The difference in mean DML between day and night surface collections was not significant.

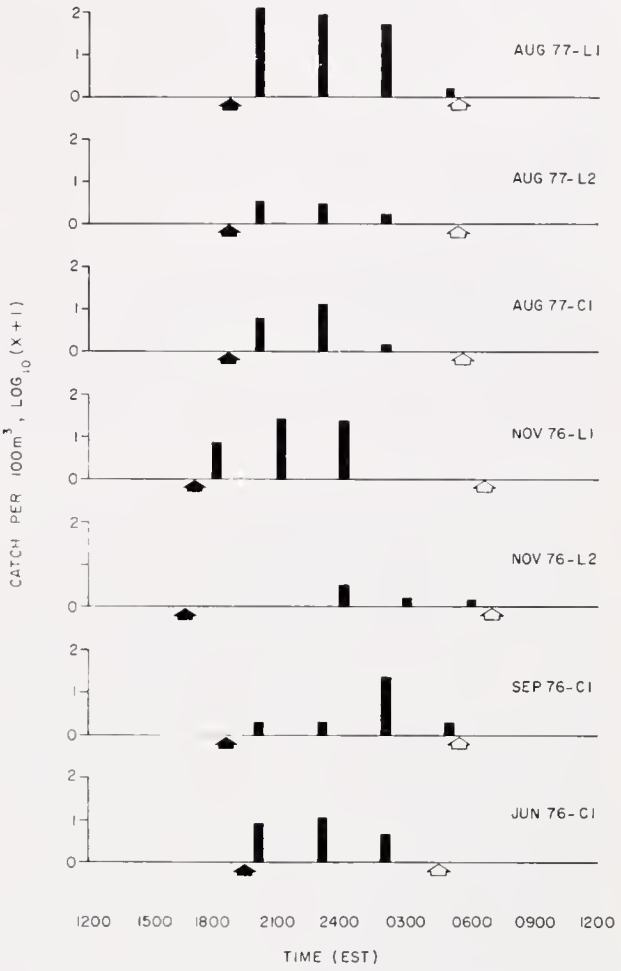

Figure 4. Diurnal variation in surface catch: ↑, sunset; ⇑ sunrise.

Relative abundance was significantly higher in surface samples taken at night than in night subsurface samples using the same mesh size (Table 1). Conversely, mean DML was significantly higher in subsurface (night, 505-μm mesh) than in surface (night, 505-μm mesh) samples (Table 2).

TABLE 1.

Comparison of surface and subsurface abundances[1].

	Surface	Subsurface
$\bar{X}_{ab}$	6.09	1.18
s_{ab}	18.77	3.75
N	58	20
t′	1.886	

[1] Based on night collections with 505-μm mesh nets. Abundances in N/100 m^3.

TABLE 2.

Comparison of dorsal mantle lengths in surface and subsurface collections[1].

	Surface	Subsurface
$\bar{X}_{DML}$	2.47	3.87
s_{DML}	1.32	1.79
N	432	87
t′	6.926	

[1] Based on night collections with 505-μm mesh nets. Dorsal mantle lengths in mm.

Loligo pealei was present only in trace numbers (defined here as $< 1/100$ m^3) during fall of the first year and was absent from winter collections. During spring, *L. pealei* was taken at the surface at coastal station C1 with trace numbers at midshelf stations N3 and E3. *Loligo pealei* was also present at the surface at C1 during summer, as well as in subsurface samples at inner-shelf station D1 (Table 3).

TABLE 3.

Calculated mean abundances (N/100 m^3) for first year, night 505-μm mesh collections.

		Station					
		C1	D1	N3	E3	F2	J1
Nov 75	Surface	0	0.07	0	0	0	0
	Subsurface	0	0	0	0	0	0
Feb 76	Surface	0	0	0	0	0	0
	Subsurface	0	0	0	0	0	0
Jun 76	Surface	4.95	0	0.48	0.25	0	0
	Subsurface	0	0	0	0	0	0
Sep 76	Surface	5.80	0.42	0	0	0	0
	Subsurface	0	1.06	0	0	0	0

During the fall of the second year, a few individuals of *L. pealei* existed at northern central-shelf stations B5, D1, and N3, but the greatest abundances were concentrated along the southern transect at the surface at coastal station L1 and in subsurface samples at central-shelf station L2. This species was absent from winter collections. During spring, trace numbers were collected at southern stations L1 and L2, but larger numbers were taken at the surface at outer-shelf station F2 on the northern transect. Peak abundance during summer was found in both surface and subsurface collections from southern coastal station L1, and in surface collections from southern central-shelf station L2 and northern coastal station C1 (Table 4).

This species was confined to coastal water (based on a classification by Welch and Ruzecki 1979), but was fragmented into five separate areas of the temperature-salinity (T–S) regime (Figure 5). That fragmentation is more

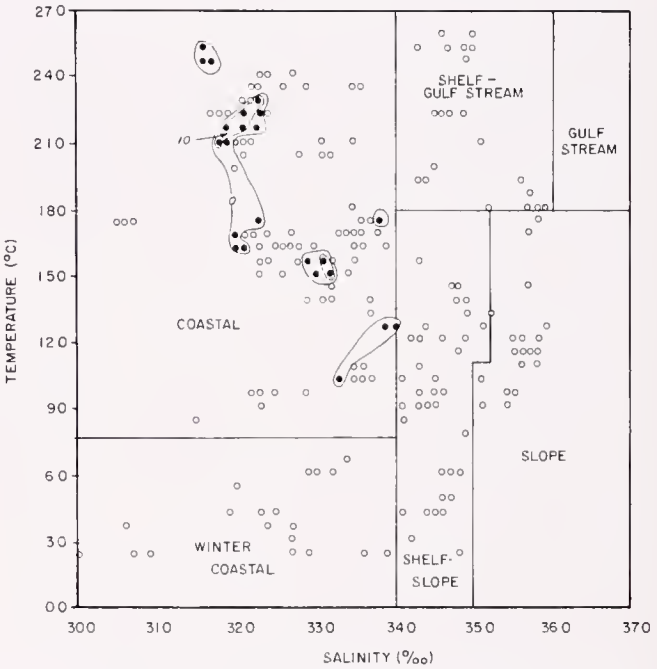

Figure 5. Night surface temperature-salinity distribution of *L. pealei*. Filled circles: samples with *L. pealei*; open circles: samples without. (Isopleths of abundance in numbers per 100 m^3.)

TABLE 4.

Calculated mean abundances (N/100 m^3) for second year, night 505-μm mesh collections.

		Station										
		A2	B5	C1	D1	N3	E3	F2	J1	L1	L2	L4	L6
Nov 76	Surface	0	0.09	0	0	0	0	0	0	11.70	0.77	0	0
	Subsurface	0	0.14	0	0.46	0.56	0	0	0	0	2.64	0	0
Mar 77	Surface	0	0	0	0	0	0	0	0	0	0	0	0
	Subsurface	0	0	0	0	0	0	0	0	0	0	0	0
May 77	Surface	0	0	0	0	0	0	0.91	0	0.14	0	0	0
	Subsurface	0	0	0	0	0	0	0	0.33	0	0.21	0	0
Aug 77	Surface	0	0	4.39	0	0	0	0	0	58.57	1.16	0	0
	Subsurface	0	0	0	0	0	0	0	0	16.90	0.80	0	0

understandable when compared with the distribution of *Limacina retroversa* (Figure 6), an abundant boreal pteropod that is seasonally advected down the central-shelf region from the northeast (Vecchione 1979a). *Loligo pealei* was absent from waters in which *L. retroversa* was most abundant.

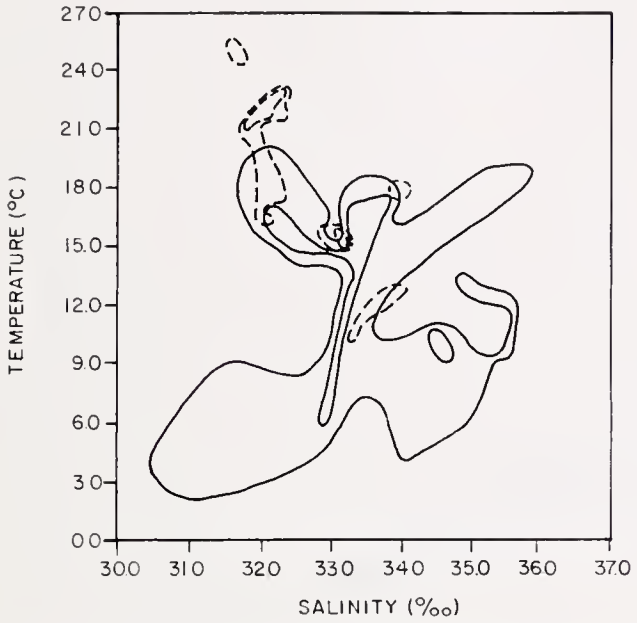

Figure 6. Comparison of night surface distributions in temperature-salinity regime. Solid lines: *Limacina retroversa;* dashed lines: *Loligo pealei.* Presence/absence and second highest abundance isopleths are shown for both species.

Based on limited size-frequency data from a series of samples taken 3 hours apart, mean growth rate at night was about 0.05 mm per hour (Figure 7). Although modal displacement indicated a similar overall rate of growth, the amount of modal increase was greater from 2400 to 0300 hours than from 2100 to 2400 hours.

Although all morphometric parameters that I measured were significantly correlated (Pearson's r) with DML, a discontinuity appeared to exist at about 4.5 mm DML. The amount of variability in tentacle length was much greater in specimens larger than 4.5 mm DML than in the smaller specimens (Figure 8). Tentacle length in specimens less than 4.5 mm DML ranged from 21.1 to 54.4% of DML, whereas the range was 24.0 to 98.8% of DML in larger specimens. A similar increase in variability was not apparent in arm-length data (Figure 8), but an inflection downward in relative growth rates at about 4.5 mm DML was obvious in several parameters, including head length, head width (Figure 9), and mantle width (Figure 10).

DISCUSSION

Data from the National Marine Fisheries Service (NMFS) bottom trawl survey show great variability in catch of

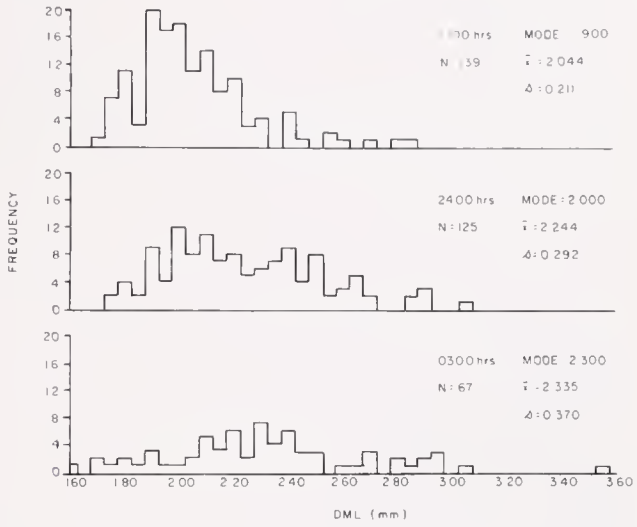

Figure 7. Size frequency histograms for collections made 3 hours apart.

Loligo pealei, both between geographical areas and within each area (Clark and Brown 1977). With increasing pressure on this species from foreign and domestic commercial fisheries (Lyles 1968, NMFS 1977), an urgent need exists to identify stocks, spawning areas, and seasons. The results presented here do not agree well with either Summers' (1971) finding of two separate broods or with Mesnil's (1977) alternating dual-cycle hypothesis. Based on data pooled from two years of collections, the only major distribution discontinuity noted was the absence of this species from winter samples. However, since the entire Middle Atlantic Bight was not sampled during this project, it is possible that separate stocks existed farther to the northeast. Within the New York and Chesapeake bights, though, it appears that hatching takes place onctinuously from early May through early November. Because embryonic development in this species takes from 257 to 642 hours, depending on temperature (McMahon and Summers 1971), it appears likely that spawning is also continuous in the area.

Most specimens of *L. pealei* were collected at night during this study. I believe that the paucity of specimens in day surface samples was a result of net avoidance rather than absence. Newly hatched specimens of *Loligo forbesi* have an escape speed of up to 25 cm sec^{-1} (Mileikovsky 1973), whereas the neuston sampler, which draws approximately 12 cm, was towed at about 75 cm sec^{-1}. If *L. pealei* has an escape speed similar to that of *L. forbesi,* newly hatched young that are capable of detecting the sampler about 40 cm away, should have enough time to avoid it. Visual acuity in cephalopods is well documented (Wells 1966), and increased avoidance would be expected during daylight hours. The fact that some specimens were collected during the day may reflect a common avoidance reaction characteristic of *Loligo opalescens* which consists of simple

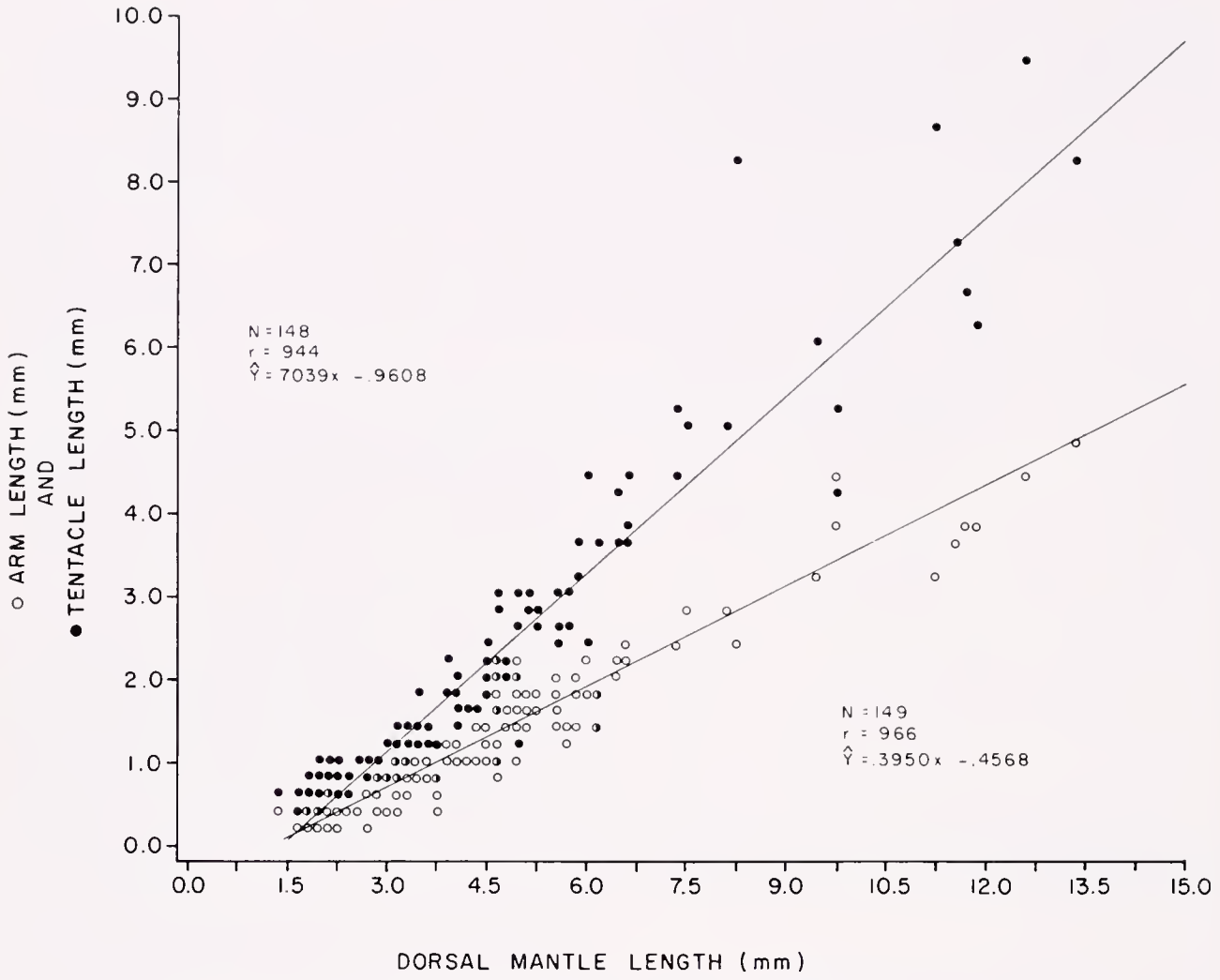

Figure 8. Linear regression of AL and TL with DML.

cessation of swimming so that the colorless animal sinks (Fields 1965). While such passive behavior could avoid visual predation, it would not prevent net-capture. Since hatchlings of *L. pealei* exhibit positive phototaxis in the laboratory (McMahon and Summers 1971), they are probably present at the surface during the day.

Loligo pealei was collected primarily at coastal and central-shelf stations, with greatest abundances consistently found at coastal stations. This nearshore distribution was reflected by the salinity range of the species, which was relatively narrow for the continental shelf of the Middle Atlantic Bight. Although a close relationship exists between the distribution of adult *L. pealei* and bottom water temperatures (Serchuk and Rathjen 1974), the planktonic stages were found across a moderately broad temperature range. At higher temperatures, *L. pealei* was collected at lower salinities and vice versa.

The mutual exclusion of *L. pealei* and *L. retroversa* on the temperature-salinity diagram (Figure 6) indicates separate origins of the two species even though the environmental conditions in which they were found were similar. Based on distributional relationships with other planktonic molluscs, Vecchione (1979a) suggested that *L. pealei* was part of a distinct coastal-zooplankton community, perhaps confined within a coastal boundary layer (Beardsley and Hart 1978, Grant 1979). Boundary layer conditions would be subject to runoff and wind conditions because strong southwest winds and reduced runoff reduce the strength of alongshore surface flow (Bumpus 1969).

There are two possible explanations for the capture of *L. pealei* at the surface at outer-shelf station F2 in May 1977. West and southwest winds, which were common at that time of year and were recorded for 11 of the 14 days prior to the 23 May collection date (NOAA 1977), result in surface transport offshore (Boicourt 1973). Also, a warm-core Gulf Stream eddy was present (Figure 11) offshore of the shelf-edge front (Wright 1976), and such eddies have been shown to entrain shelf water along their trailing edges (Saunders 1971). Either phenomenon would result in offshore transport of surface fauna.

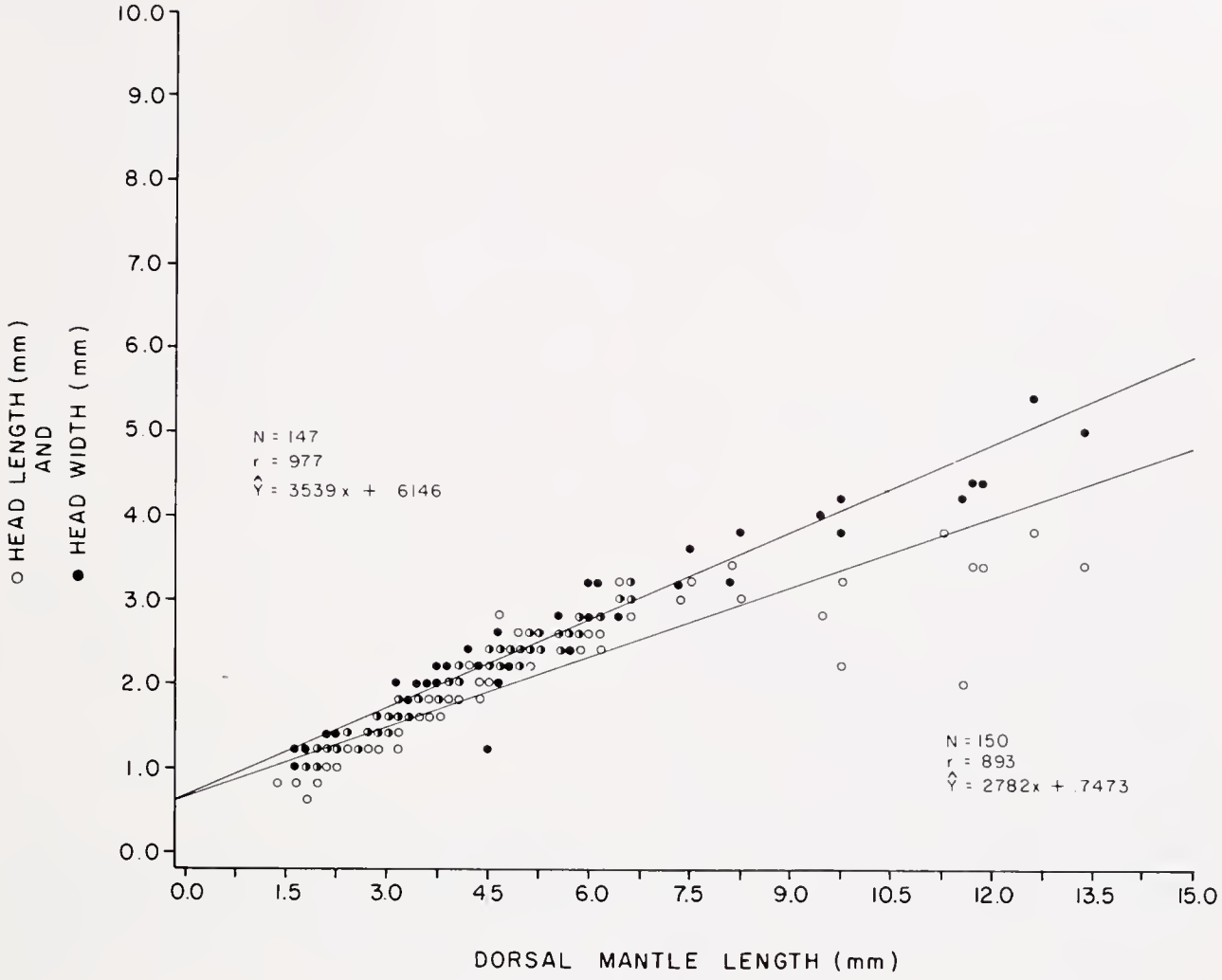

Figure 9. Linear regression of HL and HW with DML.

Ontogenetic descent through the water column is known for many species of oceanic cephalopods (Roper and Young 1975). The pattern of size distribution between surface and subsurface samples shows that a similar phenomenon occurs in this neritic species. The surface waters in continental shelf areas constitute an important biotope for feeding, particularly for the early stages of visual predators which require high-light intensities to find their food items (Hempel and Weikert 1972). The presence of comparatively large numbers of smaller specimens at the surface and small numbers of larger specimens in subsurface water indicates that hatchlings of *L. pealei* probably rise to the surface, feed for a short period, and then begin living deeper in the water column. They eventually assume the adult pattern of vertical distribution in which they are demersal during the day and dispersed at night (Summers 1969).

The overall growth rate of 0.3 mm in 6 hours presented here is consistent with Summers' (1968) estimate of 18 mm per month only if some modifying assumption is accepted. I propose two hypotheses, neither of which is strictly testable with this data set. Feeding and growth are probably not continuous throughout a 24-hour period. A visual predator such as *L. pealei* would not be consistently efficient in all light regimes. Periodicity in growth may follow feeding periodicity by an unknown time lag since digestion in adult *Loligo* is extracellular and rapid (Bidder 1966). The difference in increase in modal length between equal time periods shown in Figure 7 may be preliminary evidence of such noncontinuous growth.

An alternate hypothesis is that a change in overall growth rate occurs at some period of the early life history of *L. pealei.* A discontinuity existed in the morphometric growth of this species at about 4.5 mm DML. Particularly noteworthy is the close correlation between TL and DML in smaller specimens. This contrasts with the adult situation in which tentacles are highly contractile and, therefore, extremely variable in preserved specimens. I noted a similar lack of tentacle length variability in planktonic *Illex illecebrosus* (Vecchione 1979b), and Roper and Lu (1979) found this character sufficiently consistent to be of taxonomic use

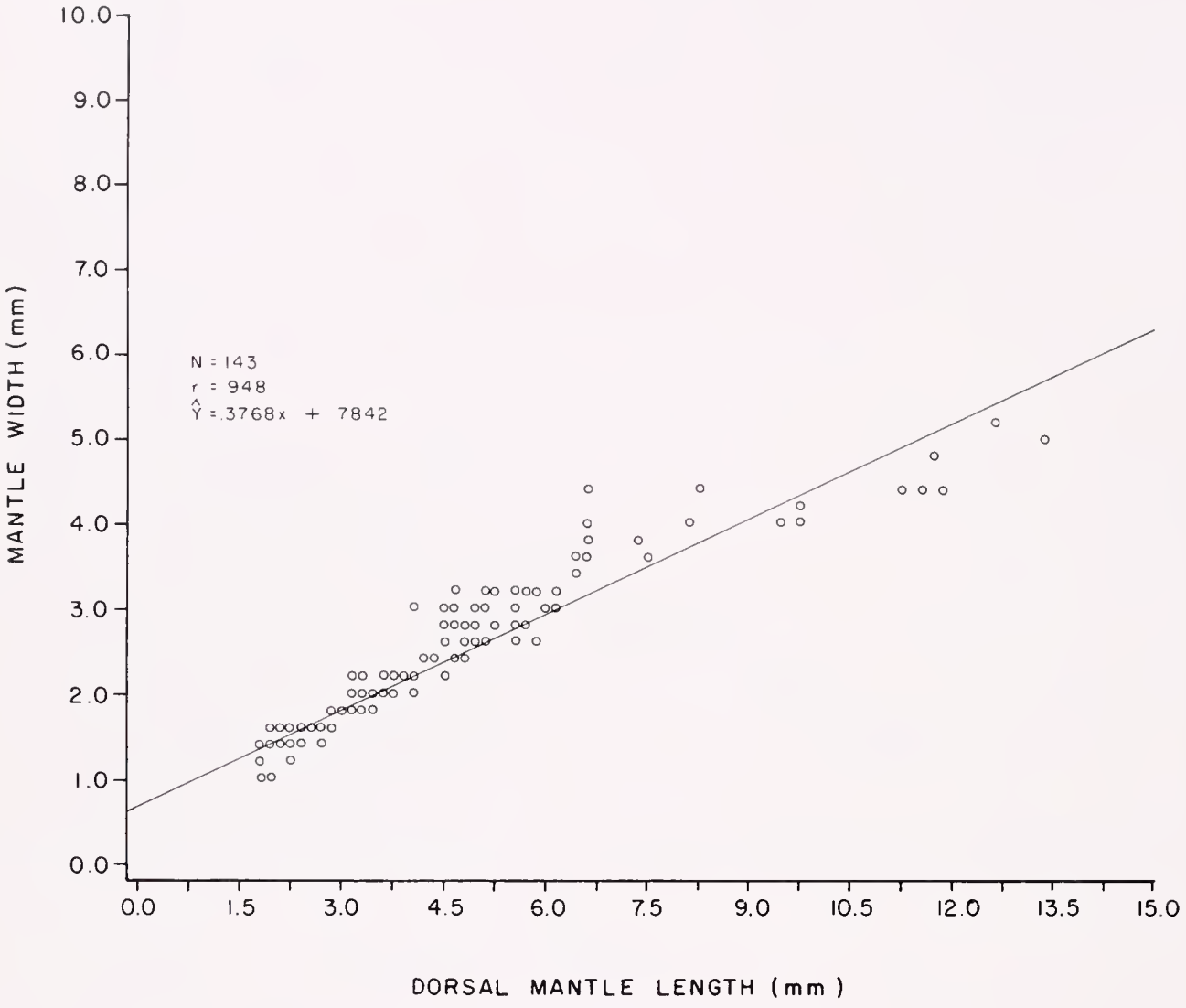

Figure 10. Linear regression of MW with DML.

in separating species of ommastrephid squid larvae. Although such lack of variability may result from uniform tentacle contraction in smaller specimens, the following statement by Boletzky (1974) indicates rather that the tentacles are not functionally contractile in hatchling squids:

> "The attacking distance is smaller in young squids than in Sepioidea because the tentacles cannot be ejected like the tentacles of cuttlefish . . .. Instead, the animal shoots forward when attacking."

The morphometric discontinuity occurred at about the same size at which *L. pealei* undergoes ontogenetic descent. That is also approximately the size at which the pigmentation pattern of the young squids begins changing from reverse (ventro-dorsal) countershading to dorso-ventral countershading, another phenomenon as yet unexplained in loliginid development (McConathy et al. 1980). The simultaneous occurrence of all of these phenomena indicates strongly that a major discontinuity is occurring in the life history of this species. A long-standing, although inconclusively proven, hypothesis on the early life history of fishes states that the first feeding after yolk absorption constitutes a critical stage in development (May 1974, Houde 1978). A similar critical stage may exist for hatchling squids which must feed at the surface until their tentacles become fully functional, at which time their behavior, distribution, appearance, and growth rate change.

CONCLUSIONS

1. No evidence was found of multiple stocks of *L. pealei* in the central and southern Middle Atlantic Bight. The species hatches continuously during the warm months throughout the study area.
2. Planktonic specimens of *L. pealei* are found within a relatively narrow salinity range reflecting their coastal distribution. That distribution is subject to perturbations by wind conditions or passage of Gulf Stream eddies

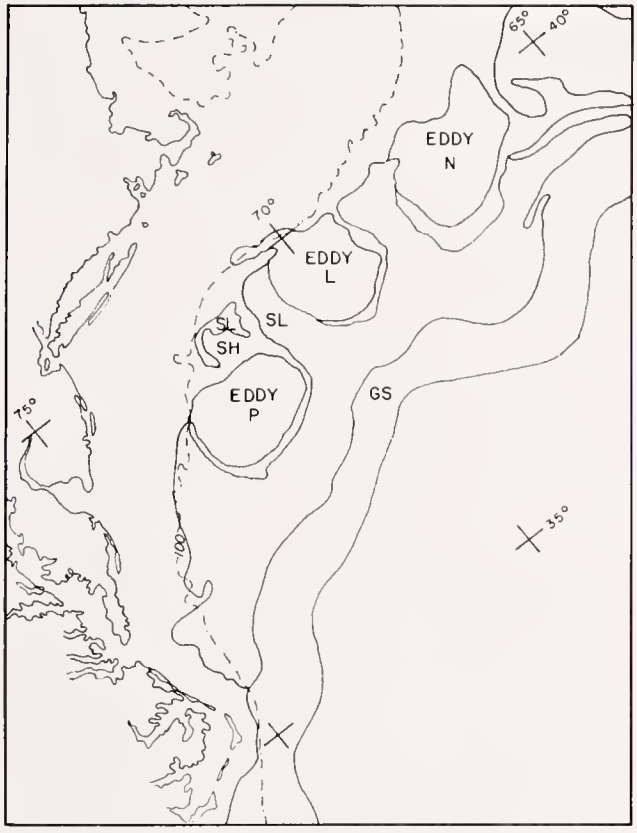

Figure 11. Locations of Gulf Stream and shelf-edge fronts on 1 June 1977, based on U.S. Naval Oceanographic Office Experimental Ocean Frontal Analysis (GS, Gulf Stream; SH, shelf water; SL, slope water).

which result in strong offshore transport of surface water.

3. The surface layer is extremely important to hatchlings of *L. pealei*; the hatchlings subsequently move deeper in the water column as they grow larger.

4. Tentacles of hatchlings may not be functionally contractile. This may be part of a major life history discontinuity which separates hatchlings (at the surface with reverse countershading and noncontractile tentacles) from juveniles (subsurface with dorso-ventral countershading and functional tentacles).

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GROWTH AND MAXIMAL SIZE OF THE LONG-FINNED SQUID *LOLIGO PEALEI* IN THE NORTHWESTERN GULF OF MEXICO

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ABSTRACT Growth of *Loligo pealei* in the northwestern Gulf of Mexico is estimated using length-frequency analyses of seasonal samples obtained via trawling and jigging or dipnetting of specimens attracted to lights at night. Maximal size and age are estimated. Growth of males of *L. pealei* ranged from 6.5 to 24.5 mm per month, while female growth ranged from 8.6 to 14.2 mm per month. Maximal sizes (mantle length) of males and females were 285 mm and 207 mm, respectively, suggesting a somewhat shorter life span than the 14 to 24 months found in more temperate-water populations.

INTRODUCTION

Many animals attain a larger maximal size, grow slower, and live longer in the cooler parts of their range (Thompson 1966, Ricker 1979). In the western Atlantic, the long-finned squid *Loligo pealei* Lesueur (family Loliginidae) is widely distributed from Nova Scotia to Colombia (Cohen 1976). It is primarily a temperate-water species with its largest population occurring between Cape Cod (Georges Bank), MA, and Cape Hatteras, NC. Recent studies have suggested that *L. pealei* may also be moderately abundant off the coast of Texas (Hanlon et al. 1978, Rathjen et al. 1979, Hixon et al. 1980). The purpose of this study was to compare estimates of the maximal size and growth rate of this species obtained from the temprate-water populations to estimates derived farther south in the northwestern Gulf of Mexico.

HISTORICAL REVIEW

The maximal size and growth rate of *L. pealei* have been estimated most often through studies conducted on the temperate-water population of this species. The largest specimens have been reported from New England coastal waters; the largest reported male measured 465 mm mantle length (ML), and the largest female, 303 mm ML (Summers 1968, Macy 1980). South of Cape Hatteras the largest reported male (262 mm ML) and female (187 mm ML) were much smaller (LaRoe 1967, Cohen 1976, Whitaker 1978). Table 1 presents a historical summary of maximal size and growth rate estimates for *L. pealei.*

Estimates of the growth rate of *L. pealei* (Table 1) have been derived almost entirely from analyses of length-frequency distributions based upon seasonal sampling data. The prominent spring and fall broods of this species can be followed by this method. However, the uncertainty of the life span, the lack of a reliable age marker, and the prolonged spawning season of this species have often resulted in a wide range of estimated growth rates.

The most consistent estimates of growth have been made during the first few months following the peak spring spawning in temperate-water populations. Generally, the growth rate is thought to be highest during the first few months after hatching. Measurements provided by Verrill (1881) from southern New England suggest that the growth rate during the first month after hatching is 28 to 46 mm/month, and that it drops to 2 to 10 mm/month by age 4.75 months (Table 1). Using Verrill's data, Summers (1968) calculated a mean monthly growth rate of 16 to 17 mm/month for the first 4.75 months. This estimate is close to the mean growth rate of 17.8 mm/month (range approximately 11 to 28 mm/month) up to age 4 months obtained by Summers (1968) for young-of-the-year specimens of *L. pealei* near Woods Hole, MA. Later work by Mesnil (1977) also supports an early mean growth rate of 17 to 20 mm/month for the first 4 months following the spring spawning. Most studies indicated that after 4 months, the average monthly growth rate declined with increasing age. During the first 12 months, the mean monthly growth rate of the spring brood has been estimated to be 13 to 16 mm/month (Verrill 1881), 13 to 15 mm/month (Summers 1971), and 14.5 mm/month (Lange 1980).

The growth rate of *L. pealei* is also dependent upon the sex, the season, and the date of hatching. Males grow faster than females. For example, Summers (1971) indicated that, following the first few months, the mean monthly growth rate of males averages 11 mm/month, and that of females, 9 mm/month. The seasonal effects are best exemplified by Mesnil's (1977) data. In his study the spring hatch grew 17 to 20 mm/month during the first summer, 10 to 15 mm/month during the fall, and only 4 to 6 mm/month during the winter. Similarly, late summer and fall-hatched broods grew more slowly, presumably because of lower temperatures. Fall broods have been estimated to grow 9 to 14 mm/month (7 months, Verrill 1881), and 10 mm/month (13 months, Mesnil 1977).

TABLE 1.

Historical summary of maximal size and growth rate estimates for *Loligo pealei*.

Maximal Size (mm ML)		Growth Rate	ML Increase		Time		Temp		
Males	Females	(mm/mo)	(mm)	Sex	(mo)	Period	(°C)	Location	Reference
425	239	28–46	2 to 30– 48	M & F	1.00	Jun–Jul	~15–19	Southern	Verrill (1881)
		20	30–48 to 50– 68	M & F	1.00	Jul–Aug	~15–19	New England	
		10–14	50–68 to 60– 82	M & F	1.00	Aug–Sep	~15–19		
		2–10	60–82 to 79– 85	M & F	1.75	Sep–Nov	~15–19		
		14–18	2 to 70– 90	M & F	5.00	Jun–Nov			
		9–14	2 to 62–100	M & F	7.00	Oct–May	~ 8–15		
		13–16	2 to 152–188	M & F	12.00	Jun–Jun	~ 8–19		
		7– 9	2 to 175–225	F	24.00	Jun–Jun	~ 8–19		
		8–11	2 to 200–275	M	24.00	Jun–Jun	~ 8–19		
		8–12	2 to 300–425	M & F	36.00	Jun–Jun	~ 8–19		
236	187							Jacksonville, FL to Colombia	LaRoe (1967)
465		11–28	2 to 45–110	M & F	4.00	Jul–Nov	~ ? –19	Woods Hole, MA	Summers (1968)
465	~230	11–18	2 to ~250	M	18.00	*	~ 8–19	Woods Hole, MA	Summers (1971)
		9–18	2 to ~210	F	18.00	*	~ 8–19		
~200	~128							"Warmer waters of range"	Cohen (1976)
		17–20	2 to 70– 90	M & F	4.00	Jun–Sep		Scotian Shelf,	Mesnil (1977)
		10–15	70–90 to 110	M & F	2.00	Sep–Nov		Georges Bank	
		4– 6	110 to 130–150	M & F	5.00	Dec–May			
		~ 10	2 to 130–140	M & F	13.00	Sep–Oct			
262		11.4	88 to 138	M & F	4.40	Spr–Sum	~10–22	Cape Hatteras to	Whitaker (1978)
		7.6	138 to 175	M & F	4.90	Sum–Win	~10–22	Cape Canaveral	
		10.9	88 to 138	M & F	4.60	Sum–Win	~10–22		
413	303	16–24	32 to 116–148	M	2.70	Jul–Dec	~12–22	Rhode Island	Macy (1980)
		15–23	32 to 110–136	F	4.30	Jul–Dec	~12–22		
		14	2 to 397	M & F	28.00	*		Northwest	Lange (1980)
		12	2 to 376	M & F	31.00	*		Atlantic	
		10–15		M & F				Northwest Atlantic	Lange and Sissenwine (1980)

*Actual time period differs between spring and fall broods.

MATERIALS AND METHODS

Data for this study were derived from trawl and night light stations occupied between 1976 and 1978, as part of a study of the cephalopods of the northwestern Gulf of Mexico along the Texas continental shelf. Twenty-five trawl stations on four inshore-to-offshore transects were sampled three times a year in 1976 and 1977 during the winter, spring-summer, and fall (Figure 1). Trawl samples taken aboard the R/V LONGHORN consisted of 15-minute bottom tows at approximately 2.7 km/h (2 kn) with a typical 10.7-m Gulf shrimp (otter) trawl of 45-mm stretch-mesh netting. Night lighting was routinely conducted from the R/V ERIN LEDDY JONES over the continental shelf south of Galveston with quartz iodide, mercury vapor, and incandescent lights. Squid attracted to the lights were collected with dipnets or squid jigs.

All squid were fixed in a 10% formalin-seawater solution and later transferred to 55% isopropanol-freshwater mixture. The dorsal mantle length was measured to the nearest mm. This preservation technique caused an approximate 5% shrinkage.

Growth was evaluated using trawl samples from the six seasonal collections made in 1976 and 1977. Separate male and female length-frequency distributions were obtained for each seasonal collection. The mean length of each mode was derived by the probability paper method described by Cassie (1950, 1954). Increases in the modal mean length between the actual cruise dates of successive seasonal collections were used to obtain growth rates.

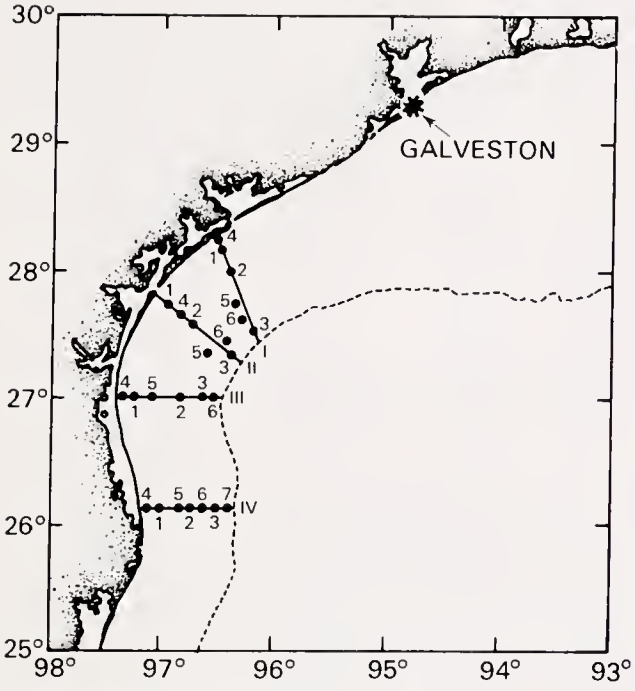

Figure 1. Geographical location of 25 trawling stations across the continental shelf along the Texas coast. Night lighting stations were conducted primarily south of Galveston. Dashed line indicates edge of the continental shelf (183-m isobath). Numbers designate locations of station 1 through 6 on transect I, II, and III, and location of station 1 through 7 on transect IV.

RESULTS

Maximal Size

A total of 5,490 specimens of *L. pealei* were examined in this study. The largest male and female from trawl samples measured 244 mm ML and 207 mm ML, respectively. Slightly larger males up to 285 mm ML were collected by dipnet at night light stations.

Growth

The length-frequency analysis was based upon 618 males and 733 females. Two or three modes were present in each season except winter 1976, when the sample size was too small for analysis (Figure 2). Seven estimates of growth rate were made between seasons for both males and females (Table 2). The growth rates of males varied from 6.5 mm/month in the fall 1976 and winter 1977 period, to 24.5 mm/month in the winter to spring-summer 1977 period. The mean growth rate of males was 15.6 mm/month (standard error of the mean, $S\bar{x}$ = 2.3 mm). The growth rates of females ranged from 8.6 mm/month in the period between spring-summer and fall 1976, to 14.2 mm/month between fall 1976 and winter 1977. The mean growth rate of females was 11.7 mm/month ($S\bar{x}$ = 0.8 mm). Although the maximal growth rate of males was higher than that of females, no statistically significant differences were detected in the distribution of growth rate (Wilcoxon two-sample test).

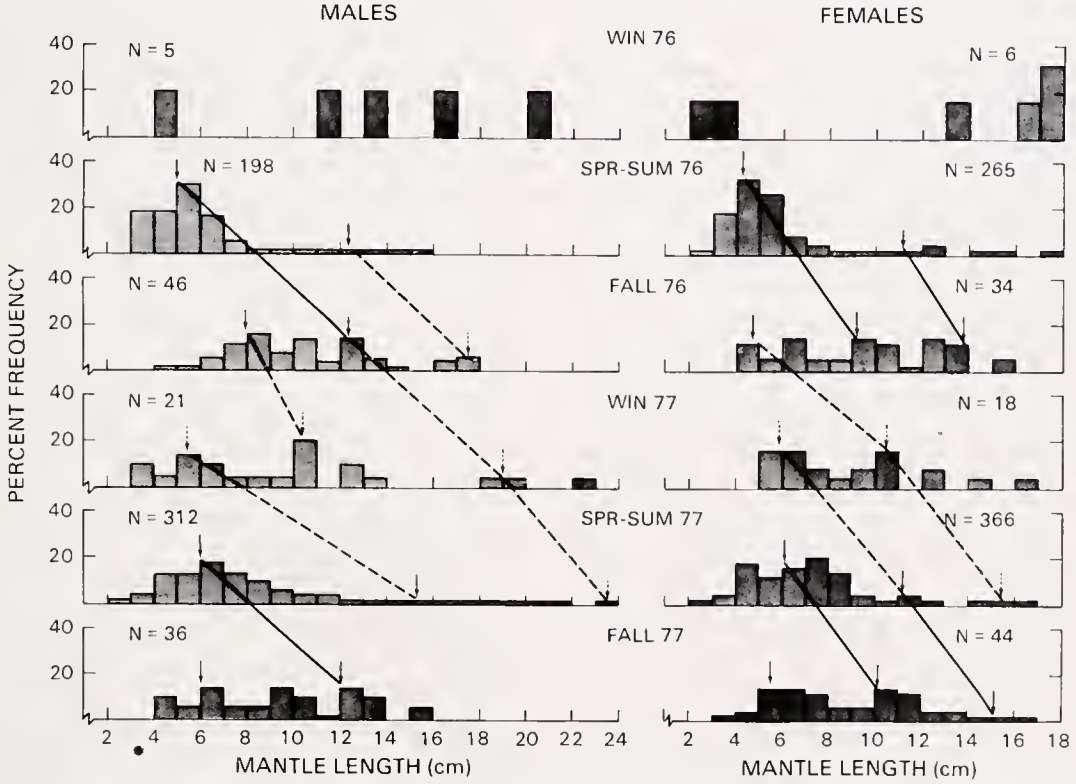

Figure 2. Size frequency distribution of males and females of *Loligo pealei* obtained from six seasonal collections in 1976 and 1977. Mean lengths of well defined modes designated by a solid arrow. Dashed arrows indicate less certain mean modal lengths estimated by the probability paper method. Lines drawn between modes depict increases in mantle length between successive seasons. Solid lines indicate growth between well defined modes; dashed lines designate growth based on less certain modes.

TABLE 2.

Summary of estimates of the growth rate of males and females of *Loligo pealei* derived from the length-frequency analysis of seasonal trawl collections.

Sex	Seasons	Year	Number of Months	Temperature (°C)	ML Increase (mm)	Growth Rate (mm/mo)	$S\bar{x}$*
♂	Spring-summer to fall	1976	3.5	18–22	50–124	21.1	
♂			3.5	18–22	124–174	14.3	
♂	Fall to winter	1976–77	4.0	17–22	79–105	6.5	
♂			4.0	17–22	124–190	16.5	
♂	Winter to spring-summer	1977	4.0	17–22	55–153	24.5	
♂			4.0	17–22	190–235	11.2	
♂	Spring-summer to fall	1977	4.0	18–22	60–121	15.2	
♂ Mean growth rate						15.6 ($\bar{x}$)	2.3
♀	Spring-summer to fall	1976	3.5	18–22	44– 93	14.0	
♀			3.5	18–22	112–142	8.6	
♀	Fall to winter	1976–77	4.0	17–22	48–105	14.2	
♀	Winter to spring-summer	1977	4.0	17–22	60–112	13.0	
♀			4.0	17–22	105–155	12.5	
♀	Spring-summer to fall	1977	4.0	18–22	61–101	10.0	
♀				18–22	112–151	9.7	
♀ Mean growth rate						11.7 ($\bar{x}$)	0.8

*Standard error of the mean.

DISCUSSION

Maximal size estimates obtained for *L. pealei* from the northwestern Gulf of Mexico suggest that squid from this area are intermediate in size to specimens of the same species occurring either farther north or farther south. None of the Gulf specimens captured by either trawling or night lighting were comparable to the very large specimens reported from New England by Verrill (1881), Summers (1968, 1971), or Macy (1980). In more southern areas both LaRoe (1967) and Cohen (1976) noted that the smallest mature specimens of *L. pealei* were observed off the Caribbean coast of Colombia. Unfortunately, neither author included data on the largest animals collected from that area. However, a comparison of the smallest size at maturity suggested that southern populations did not reach as large a maximal size as individuals from the northern Gulf of Mexico. Cohen (1976) recorded mature males as small as 61 mm ML and mature females of 73 mm ML from the Caribbean. In comparison the smallest mature male and female from the Gulf of Mexico were 104 mm ML and 111 mm ML, respectively.

It is evident from the known data that maximal size is dependent upon geographic locations, sex, and the size at which sexual maturation occurs. Differences in the maximal size of various populations of *L. pealei* also support the hypothesis that this species is made up of several morphometrically variable populations. Such populations were proposed by Cohen (1976) for this species based upon temperature differences throughout its range. She was able to demonstrate variation in gill length, the mean number of transverse sucker rows, and size at sexual maturation between northern and southern populations in the western Atlantic.

A comparison of the growth rates obtained from this study to previous estimates suggests that the growth rate of *L. pealei* in the northwestern Gulf of Mexico is similar to that from more northern areas. The range of male and female growth rates from the Gulf (Table 2) is almost the same as those given by Summers (1971) from Woods Hole, MA, and by Macy (1980) from Rhode Island (Table 1). Similarly, the mean male (15.6 mm/month) and female (11.7 mm/month) growth rates from the Gulf are very close to the average growth rate of 10 to 15 mm/month assumed by Lange and Sissenwine (1980) for populations in the northwest Atlantic.

It appears that observed differences in maximal size for various populations of *L. pealei* do not result entirely from differences in growth rate. Differences are also due to variance in size at onset of sexual maturation; southern populations generally mature and probably spawn at smaller sizes than northern populations. Because *L. pealei* probably dies after spawning, individuals in the northern Gulf probably live shorter lives than those from more temperate populations. This is consistent with Summers' (1971) hypothesized latitudinal differences in age structure.

He concluded the usual life span of *L. pealei* to be 14 to 24 months. The results of the present study suggest that the average life span of the species is somewhat shorter in the northwestern Gulf of Mexico.

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FEEDING, GROWTH, AND METABOLIC RATES IN CAPTIVE SHORT-FINNED SQUID, *ILLEX ILLECEBROSUS*, IN RELATION TO THE NATURAL POPULATION

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ABSTRACT Feeding and growth of individual squid of about 100 g at 7°C on *ad libitum* diets of fish and crustaceans were compared. Daily feeding rates (percentage of body weight) on crustaceans were lower than on the fish diet, but growth per unit ration was comparable. Mean daily feeding rate (5.2%) and daily growth rate (1.3%) were consistent with earlier experiments on populations of larger squid at higher temperatures, but daily feeding rates for individual squid ranged from 0 to 15% apparently because of behavioral interactions in the school. A nonlinear equation relating daily growth rate and daily feeding rate fitted to the data on individuals predicted a starvation weight loss of 1.3% and a daily feeding rate for maintenance of 1.8% as well as a decreased efficiency at daily feeding rates above 10%. The caloric value of maintenance rations was comparable to routine metabolic rates determined by respirometry at various activity levels. A physiological explanation for the high individual variability and intraschool cannibalism, which occurred on restricted rations, is suggested, and the treatment of schools as a growth unit proposed. This treatment avoids the complications of heterogeneity and cannibalism when measuring growth parameters of squid on reduced rations.

INTRODUCTION

Feeding and growth of schools of commercial size, short-finned squid *Illex illecebrosus* on a diet of fish (*Fundulus* spp.) have been reported previously (O'Dor et al. 1980a). Crustaceans are an equally important dietary component in natural populations (Amaratunga 1980). The experiments reported here were conducted to compare feeding and growth on these two diet types. Techniques were modified to give more information on the variation in the two parameters for individual squid.

Estimates of metabolic rates based on maintenance requirements and determined independently through oxygen consumption measurements, are compared and used in a simple nonlinear model of squid growth on a fish diet. This is a first step towards a description of the bioenergetics of the species which may help in assessing and possibly predicting the effects of changes in feeding and growth rates of squid on the squid population and its ecosystem.

MATERIAL AND METHODS

On 25 June 1979, 300 live squid taken from a local net trap were transferred to the 15-m diameter Aquatron Pool as described by O'Dor et al. (1977). They were held without food until 28 June, when 60 animals in good condition were selected, weighed, and tatooed on the fins to allow individual identification; unmarked squid were removed to other tanks. The initial mean and standard deviation in mantle length for the 60 squid was 16.9 ± 1.2 cm, and in weight, 84 ± 22 g; 55% were male and all were immature. A regime of 16 h light and 8 h dark was maintained throughout the study, with the light phase commencing at 0500 h. Water temperature was 7 ± 1°C.

The 12-day feeding experiment was subdivided into four 3-day periods. The two prey types, fish (*Fundulus* spp.) and crustacean (*Crangon* spp.), were offered in alternate periods as shown in Table 1. Both were local, intertidal species. Fish sizes were: length, 5 to 10 cm; weight, 1.5 to 18 g. Shrimp sizes were: length, 3 to 8 cm; weight: 0.3 to 8.0 g.

The squid were fed twice daily, at 0700 and 1900 h. Prey were weighed and presented individually; the prey weight and the identification code of the squid taking the prey were recorded. Feeding was stopped when several consecutive prey items were ignored. Uneaten prey were removed from the pool.

Squid were weighed every 3 days and rejected portions of prey (heads, tails, bony structure, etc.) were removed with a pool vacuum cleaner and weighed to assess the amount of ration not actually ingested. Fecal material passed through the filter used to recover rejected prey portions. The experimental schedule is shown in Table 1.

The crustacean ration ingested by each squid was calculated as follows:

$$R_1 = (1 - k)\, R_t \qquad (1)$$

where R_1 is rations ingested per 3 days, R_t is the total rations taken by a squid per 3 days, and k is the total waste divided by total rations taken by all squid per 3 days. The ratio of edible to total weight for fish increased with weight, and for 11 fish over the weight range used, the amount of inedible material was $0.59W^{\cdot 66}$ with $r = 0.84$. Thus, the ingested ration equals $W - 0.59W^{\cdot 66}$ where W is the weight of an individual fish. This calculation was carried out for each fish taken.

TABLE 1.

Overall schedule of feeding experiment. Weighing and tank cleaning took place midway between AM and PM feedings on days indicated. Diet changes started at PM feedings.

	Day 0		Day 1		Day 2		Day 3		Day 4		Day 5		Day 6		Day 7		Day 8		Day 9		Day 10		Day 11		Day 12		Day 13	
Feeding	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
	Not fed. . .		Fish						Crustacean						Fish						Crustacean							
Weighed			*						*						*						*						*	
Clean tank			*						*						*						*						*	

Rations ingested, growth, and metabolic expenditure are expressed as percent of mean weight of an individual or group for the appropriate 3-day feeding period. Daily growth rate (DGR) for individuals was calculated after Mangold and Boletzky (1973) as:

$$DGR = (w_f - w_i)/[(w_f + w_i)/2] \cdot (100/t) \qquad (2)$$

where w_i is the initial body weight, w_f is the final body weight, and t is the time interval in days.

Daily feeding rates (DFR) for individuals were calculated as in O'Dor et al. (1980a) as:

$$DFR = F/[(w_f + w_i)/2] \cdot (100/t) \qquad (3)$$

where F is the weight of food consumed by each individual (Figure 1).

Oxygen consumption, an indirect measure of metabolic rate, was determined at constant temperature in a closed recirculating respirometer with a total volume of 13 ℓ. A 15-cm square chamber of plexiglass, 45 cm long, housed the squid and perforated rubber sheets were fitted in each end to allow the squid to swim without damaging themselves as they bumped the ends. An *in situ*, polarographic oxygen probe (Beckman model 0260 oxygen analyzer) measured the decrease in concentration of dissolved oxygen over a period of 10 to 30 minutes as the squid respired. Activity levels were uncontrolled, but recorded.

RESULTS

Feeding and Growth

In general, greater numbers of shrimp were taken per meal than fish. The maximum numbers of fish and shrimp taken at a meal were 9 and 28, respectively. Even so, weight of ingested rations on the shrimp diet were consistently lower than on fish diet, as a comparison of Figures 2a and 2b indicates.

The largest single meal observed on the fish diet was 21.5 g of food ingested by a 169-g animal, 13% of the body weight (bw). The following meal was only 6.6 g (4% of bw), but the next meal showed an increase to 16.0 g (9% of bw). The animal skipped the meal following and maintained a meal size of $< 10\%$ subsequently. This trend is representative of the feeding patterns of the majority of healthy animals. The largest single meal, in terms of body weight percentage, was 21%, by a 79-g squid on fish diet. This animal ingested 13% of its body weight at the next meal, and subsequently ingested $< 10\%$ of its body weight on a consistent basis.

As indicated in Figure 1, population DGRs and DFRs were reasonably close to regressions for several population means plotted by O'Dor et al. (1980a) for squid on a fish diet. Both DFR and DGR were lower for shrimp diet than for fish diet. However, DGR for a given DFR was similar for both diets.

Figures 2a and 2b show DGR plotted against DFR for individual squid on crustacean and fish diets, respectively. Differences between the regressions appeared to result primarily from the higher proportion of feeding squid ($DFR > 0$) in the crustacean diet regression (Figure 2a). In general, data for individual squid reflect the similarity between the figures for DGR at a given DFR noted from Figure 1.

Metabolic Rates

The activity of squid in the respirometer chamber ranged from continuous swimming to continuous inactivity in the resting posture (Bradbury and Aldrich 1969). The mean time spent swimming was 28 ± 26% (mean + s) for 65 experiments. For one 135-g squid, activities ranging from 0 to 100% swimming were obtained in nine experiments. In a regression of oxygen consumption on percent activity for this animal, the intercept was 14 ml O_2/h at rest, and a slope of 0.73 gave 68 ml O_2/h at 100% activity ($r = 0.86$). These values were similar to the standard and maximum aerobic metabolic rates measured by tunnel respirometry in *Loligo opalescens* (O'Dor 1982). At 82% activity, the oxygen consumption would be 29 ml O_2/h.

The 65 sets of oxygen consumption data were fitted to the equation,

$$T = aW^{\gamma} \qquad (4)$$

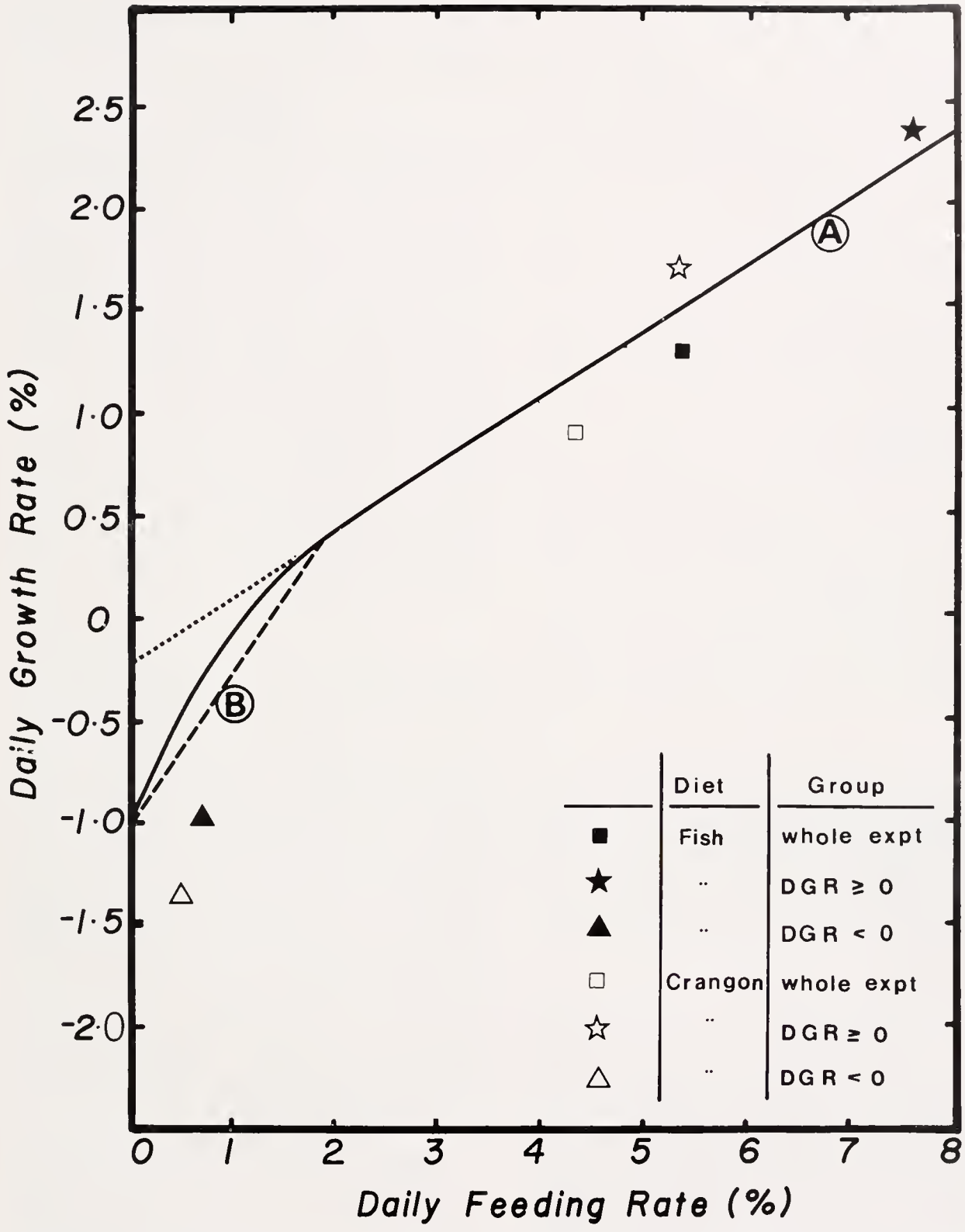

Figure 1. Mean relations between daily growth rate (DGR) and daily feeding rate (DFR) for experimental populations of squid on fish or crustacean diets. Regression lines are from a previous feeding experiment (O'Dor et al. 1980a), included for comparison. Regression A is for experiments showing no weight loss (DGR = 0.33 · DFR − 0.24; r = 0.94). Regression B is for experiments at 10°C showing no weight gain (DGR = 0.66 · DFR − 0.95; r = 0.80).

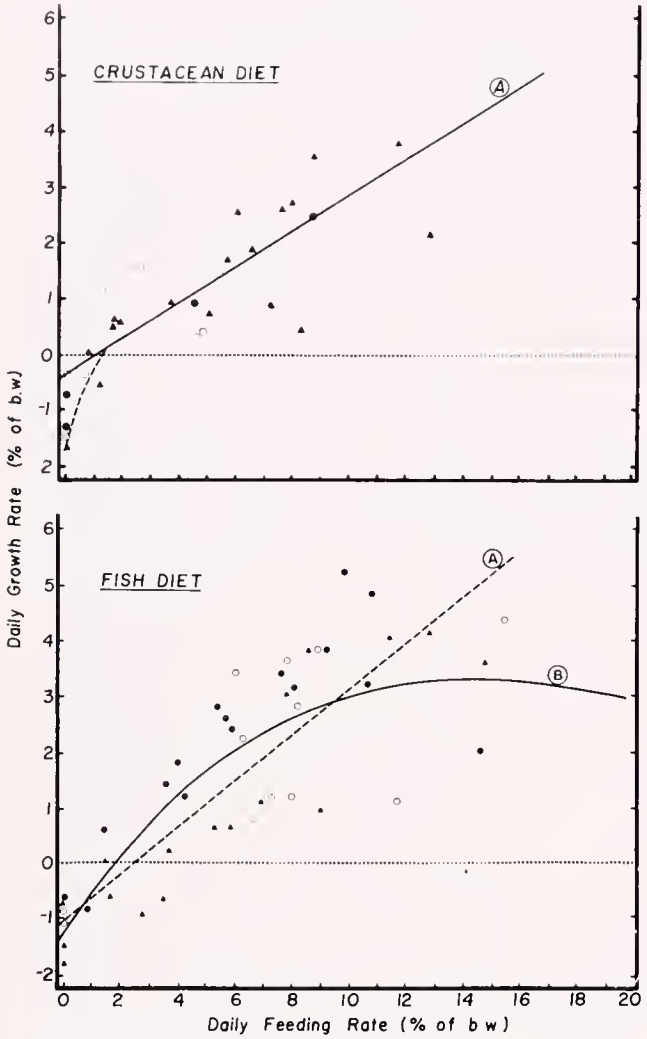

Figure 2. (a) Relation between daily growth rate and daily feeding rate for individual squid on crustacean diet. A: fitted regression (DGR = 0.32 · DFR − 0.37; r = 0.79, n = 40). (b) Relation between daily growth rate and daily feeding rate for individual squid on fish diet. A: linear regression for all observations (DGR = 0.39 · DFR − 0.99; r = 0.79, n = 60). B: DGR = 0.86 · DFR exp (−0.069 DFR) − 1.3 (r = 0.85, n = 60). Body weights of squid: ●, 75–89g; ○, 90–99g; ▲, >100g.

(Paloheimo and Dickie 1965) where a is a constant with dimensions of ml O_2/g per hour, γ is a dimensionless constant, T is oxygen consumption in ml O_2 per hour, and W is the weight of the squid. These data were fitted using the Marquardt nonlinear method, as implemented in any Statistical Program for Social Science (SPSS) Nonlinear Program (Anon. 1977). The values obtained for a and γ were 0.99 and 0.71, respectively. Because of the variation in activity, the r was low (0.62), but the residuals were uniform over the range and the equation should reasonably estimate the metabolic rate at the mean activity level for squid of various weights. The predicted value for the 135-g squid mentioned above was 32 ml O_2/h, while for the average 104-g squid in the feeding experiments, T was 27 ml O_2/h at 28% activity. This translated to a T at 0% activity (approximating the standard metabolic rate) of about 12 ml O_2/h, if the slope of 0.73 found above was applied.

DISCUSSION

A general discussion relating feeding and growth of *Illex illecebrosus* in the laboratory to similar experiments on other cephalopods and to natural populations of squid was given by O'Dor et al (1980a). The present study confirmed those earlier observations and extended the range of squid weights and temperatures studied; it indicated the similarity of feeding and growth parameters on the two principle food types, fish and crustaceans. The results emphasize, however, that many of the generalizations about growth and feeding, which can be applied to a school of squid as a whole, do not hold for individuals, which vary widely in their behavior and physiology.

Several approaches to estimate metabolic requirements of squid are possible with the two data sets presented; these approaches are generally supportive of each other. From Figure 2b an average daily metabolic rate (DMR) can be calculated from a linear regression of weight-specific metabolic rate (T/W) against ration level (R) where T is calculated from Winberg's (1956) energy balance equation:

$$T = E \cdot R - \Delta W \qquad (5)$$

using an assimilation efficiency (E) of 0.86 (Wallace et al. 1981). This gives a DMR at the intercept of 0.013 g wet weight of squid tissue per gram per day (1.3% bw/day) with r = 0.80. To compare this value to oxygen consumption figures requires an estimate of the oxycalorific equivalent of squid tissue which is not available. But if the approximation of 1 mg dry tissue equals 1 ml O_2 used for fish (Paloheimo and Dickie 1966) is applied with a water content of 75% (Giese 1969), the tissue equivalent of the 12 ml O_2/h is 1.1% of bw per day. Thus, the DMR calculated from the Winberg equation is, as expected, slightly higher than the approximation of standard metabolic rate estimated from oxygen consumption.

A simple linear regression (Figure 2b, line A) gives a value of 1.1% bw as the metabolic requirement during starvation, and 2.6% as the daily feeding rate required for weight maintenance (DFRM). A slightly better fit and a more realistic approximation are obtained using line B (Figure 2b) in which the equation

$$DGR = E \cdot DFR \cdot \exp(\beta \cdot DRF) - DMR) \qquad (6)$$

was fitted to the data using the same nonlinear regression technique mentioned previously. This equation incorporates the DMR estimate (1.3%) and assimilation efficiency (E = 0.86) used before, and gives $\beta = -0.069$. The exponential term is included to allow for the higher metabolic requirements of individuals taking larger rations. The predicted

DFRM is a more realistic 1.8% bw, and the curve predicts that DGR will approach a maximum as DFR rises above 10% bw. This is consistent with the data and although very large meals are possible, they are not common in regularly feeding animals. All of the meals in excess of 10% bw occurred on the first day when the animals had not been fed for 2 days. Maximum conversion efficiency (45%) occurs at a DFR of 10 to 11% bw.

Estimates of starvation weight loss and DFRM are needed if predictions of growth or feeding rates in natural populations are to be made since such populations are feeding well below *ad libitum* rates (O'Dor et al. 1980a). The need for extrapolation to obtain such estimates arises because cannibalism is common within schools and occurs whenever rations are experimentally restricted. Such cannibalism of the smallest individuals by the largest, and the large variation seen in feeding rates despite *ad libitum* feeding, show clearly that a school of squid is highly heterogeneous. Some large aggressive animals eat very well and prevent other smaller squid from eating. Yet, when whole schools are fed and growth averaged, results are repeatable as seen in Figure 1. The simplest way to avoid the complication of heterogeneity may be to treat a school or population as a single entity, measuring total school weight changes and food consumption on restricted diets, ignoring cannibalism as an "internal" phenomenon. Selective cannibalism of expendable individuals may be analogous to the selective utilization of metabolic reserves in an individual. Since cephalopods do not appear to lay down large reserves (Hochachka et al. 1975), but do make extensive migrations (Shevtsov 1974), which create a high energy demand, cannibalism may be a "sociologocial" compensation for this physiological deficiency. If such an approach proves appropriate, it will be important to examine population dynamics within the school; the smaller size of males of *I. illecebrosus* makes them the most likely targets which may result in unexpected relationships between food availability and fecundity (O'Dor et al. 1980b).

Two additional factors, important in any attempt to project from feeding and growth rates in captive animals to those in nature, are the effects of temperature and animal size. These were confusing variables in the present and earlier experiments (O'Dor et al. 1980a); both increased as the season progressed as they would in nature. Table 2 compares the present DFRs, DGRs, and conversion rates on the fish diet to similar data from previous experiments which used only fish. In poikilotherms, higher temperatures (up to some optimum) are usually associated with higher feeding rates. Higher body weights are usually associated with lower weight-specific feeding rates. Thus, although mean experimental temperatures ranged from 7.0 to 15.5°C and mean weights from 104 to 232 g, DFR and DGR varied relatively little with the combination of intermediate weight and temperature giving lower values than extremes of either. Gross conversion efficiency tended to increase with size, presumably because of decreased weight-specific maintenance requirements for larger squid. Additional growth experiments with controlled temperatures are needed to completely resolve these interactions.

TABLE 2.

Summary of squid growth parameters on a fish diet.

Date	Mean Weight (g)	Mean Temperature (°C)	DFR (%)	DGR (%)	Food Conversion Rate (%)
6/28/79 – 7/10/79	104	7.0	5.2	1.3	25
8/ 1/78 – 8/ 7/78*	159	9.7	3.6	1.0	29
8/11/78 – 8/24/78*	183	10.3	3.8	1.4	36
8/25/78 – 9/ 7/78*	232	15.5	6.7	1.9	35

*From earlier experiments (O'Dor et al. 1980a).

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OVERVIEW OF PRESENT PROGRESS TOWARDS AGING SHORT-FINNED SQUID *(ILLEX ILLECEBROSUS)* USING STATOLITHS

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ABSTRACT Recent advances in research on statoliths of *Illex illecebrosus* as a possible means of age determination are reviewed. Most studies on this and other species of squid have used a grinding technique to prepare statoliths for examination. Rings, viewed as dark and light alternating bands, are believed to be formed on a daily basis. However, problems exit in validating this method in that ring counts do not compare well with days elapsed between times of sampling. That may be due to technical problems in preparing statoliths for study, or to irregularities in daily ring formation caused by physiological stress.

Future research could involve other techniques for preparing statoliths, and laboratory experiments on factors affecting ring formation. Validation of the method may be facilitated by the use of known age specimens or antibiotics which label rings on statoliths of live animals.

INTRODUCTION

Management of the fishery for short-finned squid (*Illex illecebrosus*) has been hampered by an incomplete understanding of the biology of the species. Paramount in that respect is the lack of a valid aging technique, without which such population parameters as mortality rate, growth, and recruitment cannot be estimated accurately. To date only implied age of short-finned squid can be esimated, based on analysis of length-frequency distributions (Squires 1967, Summers 1971, Mesnil 1977).

Recently, however, attention has been focused on the study of statoliths as a possible means of age determination of this species. Growth rings have been found in statoliths and the possibility of chronological interpretation has been investigated (Hurley and Beck 1979, Hurley et al. 1979). Statoliths have been used successfully in age determination for market squid (*Loligo opalescens* [Spratt 1978]) and arctic squid (*Gonatus fabricii* [Kristensen 1980]).

This paper reviews recent progress towards validating the aging of the short-finned squid *I. illecebrosus* using statoliths. Methods used in extracting and preparing statoliths for study are presented and general features of prepared statoliths are described. Results of recent comprehensive studies (Hurley and Beck 1979, Hurley et al. 1979) are assessed in relation to problems encountered and avenues of future research.

PREPARATION OF STATOLITHS

Statoliths are paired calcareous structures located in the ventro-posterior region of the skull (Hurley and Beck 1979). They are similar in structure and function to the teleost otolith, being composed of aragonite (Dilly 1976, Clarke 1978, Hurley and Beck 1979). Specimens preserved for statolith studies should be preserved in ethanol, or by freezing. Formalin should not be used because statoliths dissolve even in weak acids (Hurley and Beck 1979, Kristensen 1980). Methods used to extract statoliths, either by dissection or by dissolving the skull in bleach, have been described by Clarke (1978), Spratt (1978), Hurley and Beck (1979), Hurley et al. (1979), and Lipinski (1980). Once extracted, statoliths can be stored indefinitely in gelatin (Spratt 1978).

Methods used to expose growth rings in cephalopod statoliths have been described by Lipinski (1978, 1980), Spratt (1978), Hurley and Beck (1979), Hurley et al. (1979), and Kristensen (1980). Most studies have employed a technique for grinding statoliths. That technique is successful in exposing rings in the statoliths of *I. illecebrosus* (Lipinski 1978, Hurley and Beck 1979, Hurley et al. 1979). Clearing agents have also been used and are believed to be as efficient in exposing growth rings as the polishing method (Lipinski 1978, 1980). Euparal has been used to clear otoliths of the butterflyfish *Chaetodon miliaris* for use in aging that species from daily growth rings (Ralston 1976).

Growth rings were first described from statoliths of *I. illecebrosus* by Lipinski (1978). The rings are seen under the light microscope as alternating dark and light bands, which probably result from differential deposition of $CaCO_3$ (Mina 1968, Degens et al. 1969, Panella 1971, Hurley and Beck 1979). Kristensen (1980) first detected organic material in cephalopod statoliths and showed that it was important in the formation of dark bands.

INTERPRETATION OF GROWTH RINGS

Rings formed with various temporal periodicities have been found in cephalopod statoliths. Daily and lunar monthly rings have been detected in ground statoliths of *Loligo opalescens* (Spratt 1978). Kristensen (1980) described daily, fortnightly, and monthly rings in ground statoliths of *Gonatus fabricii;* however, Dilly (1976)

could not detect growth rings in statoliths of various cephalopods, but that may have been due to formalin fixation of his specimens (Kristensen 1980).

Lipinski (1978) was the first to attempt chronological interpretation of growth rings in statoliths of *Illex illecebrosus.* He considered fine growth increments in the nuclear region to be daily rings. Outside of that 'juvenile statolith' region rings were believed to be monthly.

Hurley and Beck (1979) and Hurley et al. (1979) conducted the most comprehensive studies to date on age validation of short-finned squid using statoliths. In one study, statoliths were extracted from squid sampled offshore and throughout the inshore season in Newfoundland (Hurley and Beck 1979). Mean length of squid sampled corresponded to modal length from length-frequency distributions. In that way, it was hoped the statoliths would be extracted from a single cohort of squid as they progressed through the season (ICNAF 1978). Relationships were established between mantle length and both maximum statolith radius and number of rings. Using the relationship of mantle length and number of rings, and assuming rings were formed daily, back-calculated mantle lengths were obtained and compared to modal lengths from length-frequency distributions of samples. It was found that back calculation consistently underestimated mantle length, indicating that fewer rings were counted than there were days elapsed between samplings. That agrees with results of an earlier study (Hurley et al. 1979) where the number of rings underestimated the elapsed days. That was also found in a study of statoliths of *Loligo opalescens* (Spratt 1978).

Although age validation of *I. illecebrosus* was not achieved in those studies, more rings were counted than in an earlier study (Lipinski 1978), and it was found that the frequency of ring formation closely approximated a diurnal periodicity. Daily rings have been found in statoliths of other decapods (Spratt 1978, Kristensen 1980). Choe (1963) found daily stripes in the shell of cuttlefish, *Sepia esculenta,* and suggested that stripe formation may have been affected by a physiological periodicity. Daily growth rings have also been found in otoliths of many fish species (Panella 1971, 1974; Lim 1974; Brothers et al. 1976; Ralston 1976; Strusaker and Uchiyama 1976; Taubert and Coble 1977). Panella (1971) suggested that daily growth rings may be a universal feature of fish otoliths.

Shortcomings of recent attempts at age validation of *I. illecebrosus* using statoliths could be accounted for in several ways. Comparison of back-calculated mantle lengths to actual lengths from length-frequency distributions of samples may be confused by the presence of mixed age groups within a single year-class (Hurley and Beck 1979). Also, rings found inside the nuclear region may require a different interpretation than those found outside that region. It has been suggested for *Gonatus fabricii* that the nucleus may be present on hatching (Kristensen 1980). The use of known age specimens would greatly facilitate such problems of interpretation (Hurley and Beck 1979). With recent success in spawning and hatching of *I. illecebrosus* in captivity (Durward et al. 1980), use of known age specimens may soon be possible. The use of antibiotics, such as tetracycline, to put a 'time' mark on statoliths has also been suggested (Hurley and Beck 1979). Tetracycline has been used successfully to mark vertebrate bones, especially fish otoliths for aging studies (Harris 1960, Kobayashi et al. 1964, Jensen and Cumming 1967, Weber and Ridgway 1967, Holden and Vince 1973, Wild and Foreman 1980).

Failure to detect enough growth rings to correspond to the number of elasped days may also be due to the preparation technique used (Hurley and Beck 1979, Hurley et al. 1979). It is possible that grinding statoliths either failed to expose all the growth rings present or, alternatively, sloughed off rings, especially on the periphery. The use of a suitable clearing agent may eliminate the need for grinding in future studies. Lipinski (1980) found eukitt and euparal to be more successful in exposing growth rings than the polishing method. Other techniques, which have been used to prepare fish otoliths, include burning (Christensen 1964), and dyeing (Albrechtsen 1968).

A further possibility is that rings may be formed daily but ring formation may be interrupted by periods of physiological stress. Clarke (1965) noted that ring formation in beaks of the oegopsid squid *Moroteuthis ingens* was affected by temperature and food supply. Choe (1963) cited nutritive conditions and hydrographic factors, such as salinity, oxygen content, and temperature, as factors which affected daily stripe formation in the shell of the cuttlefish *Sepia esculenta.* Regular daily ring formation in statoliths of *Gonatus fabricii* is believed to be related to circadian rhythms in feeding (Kristensen, 1980). Disruption of regular daily ring formation in statoliths of *I. illecebrosus* may be due to opportunistic feeding of squid sampled inshore at Newfoundland (Hurley and Beck 1979). Thus laboratory experiments on short-finned squid would be useful in determining factors associated with regular periodicity of ring formation in statoliths.

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YIELD–PER–RECRUIT ANALYSES FOR SQUID, *LOLIGO PEALEI* AND *ILLEX ILLECEBROSUS*, FROM THE NORTHWEST ATLANTIC

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ABSTRACT Modified Ricker yield-per-recruit analyses for squid, *Loligo pealei* and *Illex illecebrosus*, were conducted based on hypothetical representations of their life histories and fisheries. Instantaneous growth, and relative fishing and spawning mortalities were varied on a monthly basis to represent their effects on each stock for several levels of natural and total mortalities. Several assumptions of cohort structure within a year-class were made to determine the significance of time of spawning on potential yields. Effects of increasing size of entry to the fishery by increasing mesh size were also examined.

Yields per recruit for both *L. pealei* and *I. illecebrosus* increased for all assumptions of fishing and natural mortality rates, and time of spawning when mesh sizes were increased from the present 45 mm to 60 mm. Further increases in yield were also realized when the mesh size was raised to 90 mm. Greater yields were also apparent when spawning occurred later in the spawning period considered for *L. pealei*, and earlier in the period considered for *I. illecebrosus*.

INTRODUCTION

Fisheries for squid, *Loligo pealei* (Lesueur) and *Illex illecebrosus* (Lesueur), off the United States developed rapidly during the early 1970's. Catch quota management under the auspices of the International Commission for the Northwest Atlantic Fisheries (ICNAF) was initiated in 1974, and has been continued to date under the auspices of the Fisheries Conservation and Management Act of 1976 (FCMA). In addition, mesh size, and the spatial and temporal distributions of fishing by non-United States vessels have also been regulated since 1977.

Part of the scientific bases of management has been an analysis of yield per recruit conducted by Sissenwine and Tibbetts (1977). Various parameters characterizing the fishery have changed since their analysis; therefore, the analysis presented in this paper was undertaken.

The yield-per-recruit model presented here was designed to simulate the effects of fishing on stocks of *L pealei* and *I. illecebrosus*, incorporating infomation about the life history of each species. This model accepts monthly values of the instantaneous growth rate, spawning, and fishing and natural mortality rates. It was applied for several hypothetical representations of the cohort structure of each squid stock to account for various assumptions about the system.

The effects of several choices of mesh size on yield per recruit were also simulated, based on estimates of mesh selectivity and monthly growth rates. Results from these simulations were used with estimates of average annual recruitment to estimate total yields. These were then compared with recent catches to test the appropriateness of the model.

METHODS

Representation of the Fishery

Development of the yield-per-recruit model was based on the following descriptions and assumptions regarding the life histories of and fisheries for *L. pealei* and *I. illecebrosus*.

A protracted spawning season for *L. pealei*, demonstrated by the presence of mature adults and egg capsules throughout the time of their inshore distribution (April–October), produces a single year-class varying in age by as much as 6 months. However, modal analysis of length-frequency distributions (Lange 1980) indicate that it may be appropriate to separate each year-class into at least two distinct cohorts in most years. Generally, these are late spring (April–June) and late summer (August–October) cohorts. These cohorts have shown different growth rates and, based on growth schemes and mean sizes at maturity described for these cohorts (Lange 1980), differences in age at spawning. Post-spawning mortality is assumed to be high for *L. pealei*, so differences in age at spawning are significant.

I assumed that some individuals from the spring cohort matured over their first winter and began spawning late in the summer of their second year (about 14 to 15 months at 18 to 22 cm), with the remainder of the cohort spawning during the following season (April through September, 22 to 23 months). Individuals of the late summer cohort were too small to mature during their first winter and did not begin to spawn until about April of their second year (18 months at 22 to 25 cm). Although some individuals may survive to spawn at 35 to 37 cm in the following spring, most will spawn and die by October (about 24 months).

Assuming that *Loligo pealei* has a mesh selection factor (1.92) similar to that found by Ikeda (I. Ikeda, Far Seas Fisheries Laboratory, Shimizu, Japan, personal communication, 1973) for *Loligo* sp. in the eastern central Atlantic, these cohorts are also subjected to different rates of fishing mortality. Fifty percent retention (at 8.6 cm with the 45-mm mesh currently used in the fishery) occurs in November for the spring-hatched cohort and during the following March for the summer cohort.

In most years it appears that the spring cohort is more significant than the late summer cohort and that it contributes more to the fishery, although the exact timing of hatching in any year may significantly alter that pattern.

Instantaneous monthly growth rates (g) were determined for each cohort (Lange 1980) from estimates of mean weight at age as:

$$g_t = \log_e (W_{t+1}/W_t); \quad (1)$$

where: g_t = instantaneous average monthly growth rate, W_t = weight in grams at time t, and W_0 was assumed to be 0.349 and 0.664 g for cohorts I and II, respectively.

Spawning rates (S) were chosen such that, for the unexploited fishery, the number spawning in the second season would be 60% of those spawning during the first season for cohort I (hatched April–June), and 10% for cohort II (hatched August–October). The choice of these percents is based on the ratio of percent frequencies (from a 1973–79 survey cruise length-frequency data) of spawning sized individuals for each cohort during their first and second spawning seasons (i.e., for cohort I–the percent of 29- to 33-cm individuals in spring: the percent of 18- to 24-cm individuals in autumn surveys). Spawning rates were set for each cohort within the first season such that the ratio of spawned-to-nonspawned individuals at the end of each month of the spawning season was nearly constant, because analyses indicated constant percents of mature individuals throughout the spawning season. All individuals were assumed to perish by the end of the second spawning season.

Several choices of monthly natural mortality rate (M), held constant over the lifespan of each cohort, were used in this analysis. These were based on a wide range of assumptions of life expectancy which produced effective monthly M's ranging from 0.01 to 0.15 ($\hat{M} = 1/T$, where T = life expectancy in months).

The seasonal nature of the *L. pealei* fishery is represented by estimates of relative monthly fishing mortality rates (F_r). Each monthly value is the ratio of the catch for that month (average from the 1977–79 fisheries) to the catch from the month with the greatest average catch (February). These relative F's are used in conjunction with a range of F-multipliers (Paulik and Bayliff 1967) held constant over the lifespan and representing several assumptions of instantaneous fishing mortality rates to reflect changes in fishing effort over the fishing year. The F-multipliers used ranged from 0.05 to 0.50. The relative F's were reduced in months prior to full recruitment, based on approximated selection curves, to reflect the effects of mesh selection on retention of different size *L. pealei*.

Monthly values of model parameters as described here are presented in Table 1 for each cohort of *L. pealei*.

Less is known of the maturation and spawning of *Illex illecebrosus* than of *L. pealei*, but it was assumed to spawn in deep waters off the edge of the shelf between December and June. This, as with *L. pealei*, produced a single year-class with as much as 6 months difference in age. Unlike

TABLE 1.

Monthly population parameters of fishing, natural and spawning mortality, and growth rates for two hypothetical cohorts of *Loligo pealei* under the present (1977–79) fishery.

	Cohort I				Cohort II			
Month	F_1	M_1	S_1	G_1	F_2	M_2	S_2	G_2
Jul	0.00	(a)	0.00	1.399				
Aug	0.00	(a)	0.00	0.919				
Sep	0.00	(a)	0.00	0.686				
Oct	0.00	(a)	0.00	0.547				
Nov	0.30	(a)	0.00	0.455	0.00	(a)	0.00	0.999
Dec	0.65	(a)	0.00	0.390	0.00	(a)	0.00	0.729
Jan	0.51	(a)	0.00	0.341	0.00	(a)	0.00	0.574
Feb	1.00	(a)	0.00	0.303	0.00	(a)	0.00	0.474
Mar	0.58	(a)	0.00	0.273	0.29	(a)	0.00	0.403
Apr	0.08	(a)	0.00	0.248	0.08	(a)	0.00	0.351
May	0.27	(a)	0.00	0.227	0.27	(a)	0.00	0.311
Jun	0.11	(a)	0.00	0.210	0.11	(a)	0.00	0.279
Jul	0.04	(a)	0.00	0.195	0.04	(a)	0.00	0.253
Aug	0.02	(a)	0.22	0.182	0.02	(a)	0.00	0.232
Sep	0.01	(a)	0.29	0.170	0.01	(a)	0.00	0.213
Oct	0.08	(a)	0.00	0.160	0.08	(a)	0.00	0.198
Nov	0.59	(a)	0.00	0.151	0.59	(a)	0.00	0.184
Dec	0.65	(a)	0.00	0.143	0.65	(a)	0.00	0.173
Jan	0.51	(a)	0.00	0.136	0.51	(a)	0.00	0.162
Feb	1.00	(a)	0.00	0.130	1.00	(a)	0.00	0.153
Mar	0.59	(a)	0.00	0.124	0.58	(a)	0.00	0.145
Apr	0.08	(a)	0.22	0.118	0.08	(a)	0.16	0.138
May	0.27	(a)	0.29	0.113	0.27	(a)	0.19	0.131
Jun	0.11	(a)	0.41	0.109	0.11	(a)	0.24	0.125
Jul	0.04	(a)	0.69	0.105	0.04	(a)	0.32	0.120
Aug	0.02	(a)	∞	0.101	0.02	(a)	0.47	0.115
Sep					0.01	(a)	0.92	0.110
Oct					0.08	(a)	0.00	0.106
Nov					0.59	(a)	0.00	0.102
Dec					0.65	(a)	0.00	0.098
Jan					0.51	(a)	0.00	0.095
Feb					1.00	(a)	0.00	0.091
Mar					0.58	(a)	0.00	0.088
Apr					0.08	(a)	0.69	0.084
May					0.27	(a)	∞	0.079

F_i – Fishing mortality relative to month with greatest catch applied to cohort$_i$.

M_i – Monthly natural mortality rate for cohort$_i$, constant through lifespan (0.01, 0.03, 0.80, 1.50).

S_i – Monthly spawning mortality rate for cohort$_i$.

G_i – Monthly growth rate for cohort$_i$ (see text for derivation).

Loligo pealei, the separation of year-classes into more than one cohort was not apparent every year, although remnants of more than one cohort were present in most months. Lange (1980) found individuals which had spawned early in the season (December–January) have growth rates similar to those spawned later (May–June). However, differences in size between these groups resulted in differences in time of subsequent spawning and differences on the effects of F throughout their lifespan. Therefore, separate cohorts were assumed for this species as well, even though spawning probably occurred over a continuum.

I assumed that each cohort will mature and spawn at about 22 to 24 months and 21 to 26 cm (Lange 1980). Differences in the effects of fishing on these hypothetical cohorts would result from individuals of each cohort reaching recruitment size during different phases of the seasonal fishery. The winter cohort was partially recruited to the offshore fishery in July of its first year (about 8 cm), and made up a significant portion of the less-important inshore fishery throughout the summer. This cohort was taken in the directed *L. pealei* fishery as it moved offshore in the autumn and winter, and made up the major portion of the catch in the directed *I. illecebrosus* fishery during the following summer. The spring cohort was first susceptible to fishing as incidental catch in the winter *L. pealei* fishery (7 to 10 cm), and was fully recruited to the directed *I. illecebrosus* fishery in the summer (13 to 14 months and 13 to 17 cm). As it moved offshore, this cohort was again taken in the *L. pealei* fishery until about April when it moved off the shelf to spawn. However, the winter cohort was presumed to comprise the major portion of each year-class and, in fact, the proposed second cohort may not be apparent in some years as the continuum of spawning was skewed towards the earlier months of the spawning season.

Instantaneous growth rates (g) for each hypothetical cohort were estimated as described for *L. pealei* with initial weights of (W_0) 0.283 and 0.269 g (Lange 1980). Spawning rates were chosen for each cohort such that an equal number of individuals in the unexploited fishery would spawn in each month of the spawning season of that cohort. These spawning rates were equivalent to spawning mortality rates because it was assumed that individuals die after spawning.

Estimates of monthly natural mortality (M) ranging from 0.01 to 0.10, assumed reasonable for the life expectancy of this species (as described for *L. pealei*), were used in this analysis. Natural mortality (M) was held constant throughout the life of the cohort.

Monthly values of relative fishing mortality (F_r) were calculated as for *L. pealei* and applied in the model to reflect the seasonality of the fishery. Multipliers of F, ranging from 0.05 to 1.50, were used to simulate a variety of possible monthly fishing mortality rates.

Table 2 presents monthly estimates of the model parameters described here for each *I. illecebrosus* cohort.

TABLE 2.

Monthly estimates of population parameters of fishing, natural and spawning mortality, and growth rates for two hypothetical cohorts of *Illex illecebrosus* under the present (1977–79) fishery.

	Cohort I				Cohort II			
Month	F_1	M_1	S_1	G_1	F_2	M_2	S_2	G_2
Jan	0.00	(a)	0.00	1.150				
Feb	0.00	(a)	0.00	0.806				
Mar	0.00	(a)	0.00	0.621				
Apr	0.00	(a)	0.00	0.505				
May	0.00	(a)	0.00	0.426				
Jun	0.00	(a)	0.00	0.368				
Jul	0.50	(a)	0.00	0.324	0.00	(a)	0.00	1.180
Aug	0.58	(a)	0.00	0.290	0.00	(a)	0.00	0.820
Sep	0.18	(a)	0.00	0.262	0.00	(a)	0.00	0.629
Oct	0.15	(a)	0.00	0.238	0.00	(a)	0.00	0.511
Nov	0.28	(a)	0.00	0.219	0.00	(a)	0.00	0.430
Dec	0.13	(a)	0.00	0.203	0.00	(a)	0.00	0.371
Jan	0.02	(a)	0.00	0.189	0.01	(a)	0.00	0.326
Feb	0.04	(a)	0.00	0.177	0.04	(a)	0.00	0.291
Mar	0.02	(a)	0.00	0.166	0.02	(a)	0.00	0.263
Apr	0.01	(a)	0.00	0.156	0.01	(a)	0.00	0.240
May	0.01	(a)	0.00	0.148	0.01	(a)	0.00	0.221
Jun	0.28	(a)	0.00	0.140	0.28	(a)	0.00	0.204
Jul	1.00	(a)	0.00	0.133	1.00	(a)	0.00	0.180
Aug	0.58	(a)	0.00	0.127	0.58	(a)	0.00	0.177
Sep	0.18	(a)	0.00	0.121	0.18	(a)	0.00	0.166
Oct	0.15	(a)	0.00	0.116	0.15	(a)	0.00	0.157
Nov	0.28	(a)	0.00	0.111	0.28	(a)	0.00	0.148
Dec	0.13	(a)	0.41	0.107	0.13	(a)	0.00	0.141
Jan	0.02	(a)	0.69	0.103	0.02	(a)	0.00	0.134
Feb	0.04	(a)	∞	0.101	0.04	(a)	0.00	0.127
Mar		(a)	0.00		0.02	(a)	0.00	0.122
Apr		(a)	0.00		0.01	(a)	0.41	0.117
May		(a)	0.00		0.01	(a)	0.69	0.112
Jun		(a)	0.00		0.28	(a)	∞	0.107

F_i – Fishing mortality relative to month with greatest catch applied to cohort$_i$.
M_i – Monthly natural mortality rate for cohort$_i$, constant through lifespan (0.01, 0.03, 0.80, 1.50).
S_i – Monthly spawning mortality rate for cohort$_i$.
G_i – Monthly growth rate for cohort$_i$ (see text for derivation).

The Model

A modified Ricker (1958) yield model incorporating information about the proposed cohorts was developed. Let NO be the number of squid from both cohorts in the initial population, and PN1 the proportion of the initial population from cohort 1 (therefore [1–PN1] is the proportion of cohort II). For each cohort during any time period (t), N is the number of squid in the cohort, W the average weight of an individual in that cohort, YN the catch in numbers, and Y the catch in weight from the cohort. Then

$$N_0 = NO \cdot PN1 \text{ for cohort I } (= NO(1-PN1) \text{ for cohort II}) \quad (2)$$

$$N_t = N_0 \exp -(F + M + S)t \quad (3)$$

$$W_t = W_0 \exp gt \quad (4)$$

$$YN = [FN_0/(F + M + S)]\ [1 - \exp -(F + M + S)t] \quad (5)$$

$$Y = [FN_0W_0/(F + M + S - g)]\ [1 - \exp -(F + M + S - g)t] \quad (6)$$

where F, M, S and g are instantaneous average monthly fishing mortality, natural mortality, spawning mortality, and growth rates, respectively, for the appropriate cohort during time t. N_0 and W_0 are initial conditions for the given time period for the cohort.

The sum of the number of individuals of both cohorts at the time, in months, when the first cohort is recruited, was assumed to be 1,000 for the virgin stock, although the portion of this number associated with the second cohort will not actually be present until the time of hatching (t + a delay time, in months). Equations 2 through 6 were then applied to each cohort on a monthly basis with F, M, S and g assumed constant within each month throughout the proposed lifespan of the year-class. Monthly results from the two cohorts were then summed to provide monthly values of stock size and yield in weight and number.

The total yield per 1,000 recruits summed over all months of the lifespan was calculated for combinations of M and F-multipliers as described for each species. The effects of annual differences in time of spawning were examined by varying the cohort structure represented by the proportion of the year-class which was assumed to be from each cohort.

RESULTS AND DISCUSSION

The simulated yield per recruit of *L. pealei* in weight (kg) per 1,000 individuals recruited to the fishery was plotted (Figure 1) against F-multipliers (FM) ranging from 0.05 to 0.50, for monthly M values of 0.01, 0.03, 0.08, and 0.15, by assuming three possible cohort compositions (PN1 = 0.60, 0.75, 0.80). These cohort ratios reflected the observation that in most years the spring cohort was more significant than the late summer cohort. The results were similar for all three assumptions of cohort structure (Table 3) at high levels of M (0.15), but for lower M values, higher yields per recruit were obtained when significant portions ($\geq 25\%$) of the year-class were assumed to be from the second cohort (PN1 = 0.60, 0.75). This seemed reasonable because if major spawning occurred later in the spawning season, as happens in some years, fewer individuals from a year-class were susceptible to the winter-directed fishery. By the time they attained recruitable size, the directed fishery was about over and significant increases in weight with low mortality from fishing occurred before the directed fishery of the following winter.

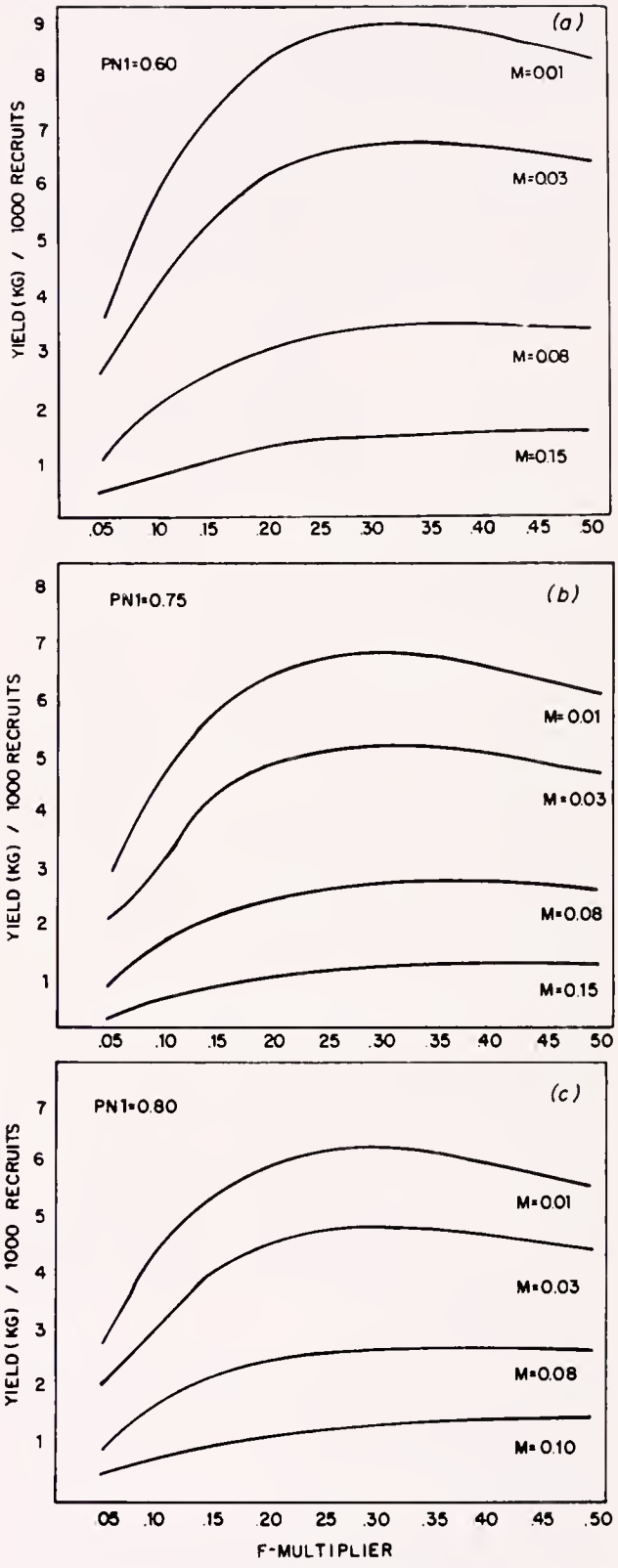

Figure 1. ***Loligo pealei*****: Yield (kg) per 1,000 recruits for M = 0.01, 0.03, 0.08, and 0.15. (a) When 60% of the year-class was assumed from the spring cohort. (b) When 75% of the year-class was assumed from the spring cohort. (c) When 80% of the year-class was assumed from the spring cohort.**

TABLE 3.

Loligo pealei yield (kg) per 1,000 recruits for four values of monthly natural mortality rate (M) for a range of F-multipliers, and three cases of cohort composition (PN1–proportion of year-class in spring cohort).

		Monthly Natural Mortality Rate			
PN1	F-multiplier	0.01	0.03	0.08	0.15
0.60	0.05	3.68	2.68	1.19	0.51
	0.10	6.04	4.08	2.15	0.88
	0.15	7.50	5.55	2.74	1.15
	0.20	8.36	6.22	3.12	1.34
	0.25	8.80	6.59	3.36	1.47
	0.20	8.97	6.77	3.50	1.56
	0.35	8.96	6.80	3.57	1.63
	0.40	8.83	6.74	3.58	1.67
	0.45	8.63	6.63	3.57	1.69
	0.50	8.39	6.47	3.53	1.70
0.75	0.05	3.00	2.20	1.00	0.40
	0.10	4.90	3.20	1.30	0.80
	0.15	6.00	4.50	2.30	1.03
	0.20	6.60	5.00	2.60	1.19
	0.25	6.90	5.20	2.80	1.30
	0.30	7.00	5.30	2.90	1.38
	0.35	6.90	5.30	2.90	1.43
	0.40	6.70	5.20	2.90	1.46
	0.45	6.50	5.00	2.90	1.47
	0.50	6.30	4.90	2.80	1.47
0.80	0.05	2.78	2.07	0.92	0.45
	0.10	4.50	3.00	1.72	0.77
	0.15	5.50	4.15	2.16	0.99
	0.20	6.03	4.58	2.43	1.14
	0.25	6.25	4.78	2.58	1.25
	0.30	6.28	4.84	2.66	1.32
	0.35	6.19	4.80	2.68	1.36
	0.40	6.03	4.70	2.67	1.39
	0.45	5.82	4.57	2.64	1.40
	0.50	5.60	4.42	2.59	1.40

Maximum yields per recruit generally occurred at FM = 0.30 for M = 0.01 and 0.03, and at higher FM's (0.35 to 0.50) when M was assumed to be higher.

The simulated yield in weight (kg) per 1,000 individuals of *I. illecebrosus* recruited to the fishery was plotted against FM (ranging from 0.05 to 1.50) for M values of 0.01, 0.04, and 0.10, by assuming two possibilities of cohort composition (PN1) of the year-class (Figure 2). The results were similar for each PN1, with no significant difference ($P < 0.01$) between the results of analyses assuming 80 or 90% of the year-class could be assigned to the first cohort. Maximum yield per recruit occurred at FM = 0.40 for M = 0.01 and 0.04, and at FM = 0.50 for M = 0.10 (Table. 4).

Yield-per-Recruit Analyses and Management

The results of the yield-per-recruit analyses discussed thus far were based on the effects of the 1977–79 squid fishery, which primarily employed 45-mm mesh nets.

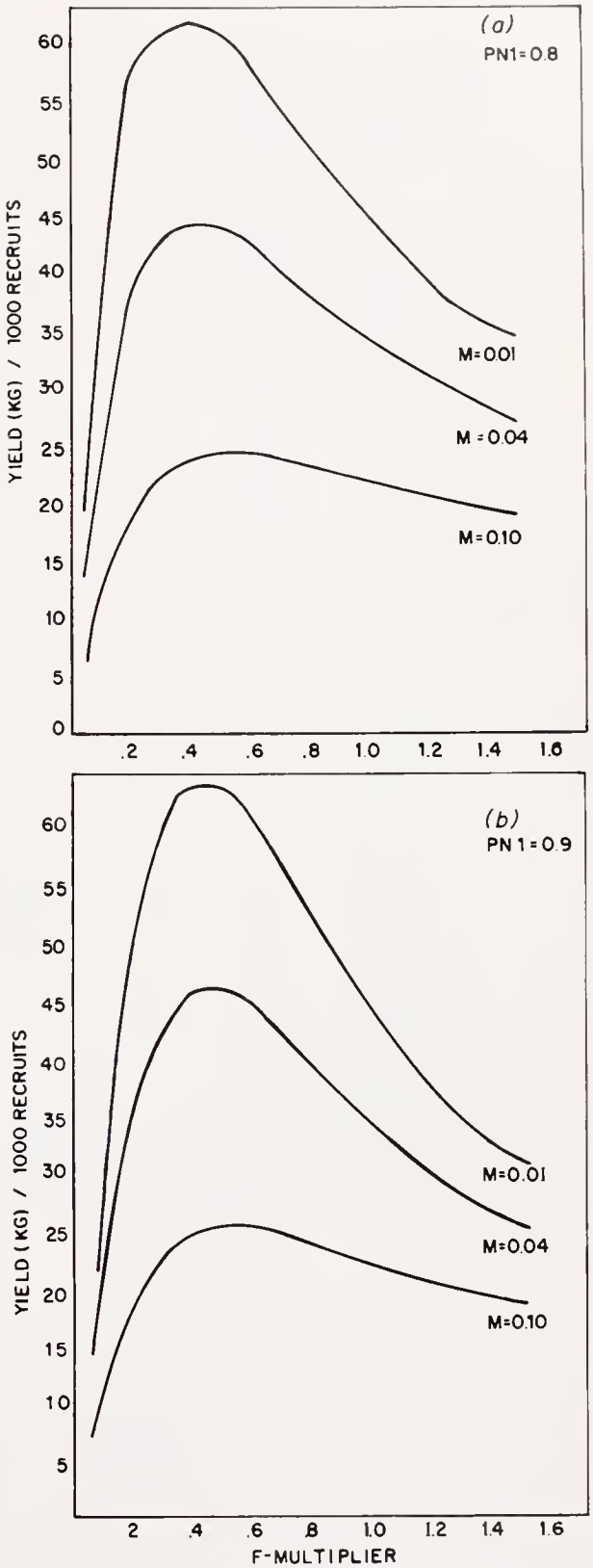

Figure 2. *Illex illecebrosus* yield (kg) per 1,000 recruits for M = 0.01, 0.04, and 0.10: (a) when 80% of the year-class was assumed from the winter cohort; and (b) when 90% of the year-class was assumed from the winter cohort.

TABLE 4.

Illex illecebrosus yield (kg) per 1,000 recruits for three values of monthly natural mortality rate (M) for a range of F-multipliers, and two cases of cohort composition (PN1–proportion of year-class in winter cohort).

		Monthly Natural Mortality Rate		
PN1	F-multiplier	0.01	0.04	0.10
0.90	0.05	21.49	14.78	7.35
	0.10	37.05	25.62	12.91
	0.20	55.50	38.83	20.14
	0.30	63.09	44.71	23.91
	0.40	64.56	46.36	35.59
	0.50	62.73	45.69	26.05
	0.60	59.30	43.82	25.82
	0.70	55.23	41.26	25.23
	0.80	51.08	38.91	24.46
	0.90	47.14	36.45	22.50
	1.00	43.54	34.16	22.83
	1.20	37.51	30.27	21.35
	1.30	35.05	28.66	20.71
	1.40	33.17	27.25	20.13
	1.50	31.10	26.03	19.62
0.80	0.05	20.20	13.90	6.80
	0.10	35.00	24.10	12.10
	0.20	52.90	36.90	18.90
	0.30	60.70	42.80	22.60
	0.40	62.70	44.80	24.30
	0.50	61.60	44.50	24.90
	0.60	58.80	43.10	24.80
	0.70	55.40	40.70	24.40
	0.80	51.80	38.90	23.70
	0.90	48.40	36.80	22.00
	1.00	45.20	34.80	22.40
	1.20	39.70	31.30	21.10
	1.30	37.50	29.80	20.50
	1.40	36.70	28.60	20.00
	1.50	33.90	27.40	19.50

However, increases in mesh size and, therefore, age at entry in the directed fisheries of both *L. pealei* and *I. illecebrosus* would effect yield per recruit. I, therefore, used the described model to compare the potential effects on yield per recruit in these fisheries when mesh regulations were changed to 60 mm. I also simulated the use of 90-mm mesh nets.

All population parameters were assumed to be as described for the present fisheries of *L. pealei* and *I. illecebrosus*. I then decreased the relative monthly fishing mortality rates (F_r) in the months when each cohort first entered the fishery based on mesh-selection information to reflect changes in age at entry from increases in mesh size.

A selection factor of 1.92 assumed for *L. pealei*, corresponds to a 50% retention length of 11.5-cm individuals for 60-mm mesh, and 17.3-cm individuals for a 90-mm mesh. The spring cohort would, therefore, not reach 50% selection size until about February (8 months) or June (12 months), while the late summer cohort would not be recruited until July (9 months) or December (14 months) for 60-mm and 90-mm mesh, respectively. Reductions in F attributed to partial recruitment were made in months prior to 50% selection according to selection curves for *Loligo* sp. (I. Ikeda, personal communication, 1973).

Preliminary mesh studies for *I. illecebrosus* (Clay 1979) indicated 50% retentions at approximately 14.4 cm for 60-mm and about 20 cm for 90-mm meshes. These correspond to entry dates to the fishery of December (12 months) and the following June (18 months) for the winter cohort, and July (12 months) and January (18 months) for the spring cohort for 60-mm and 90-mm mesh, respectively. Relative fishing mortalities were reduced in months when mean lengths were less than these retention sizes, and until cohorts were of fully recruitable size according to approximated selection curves (Lange 1980).

Table 5 presents the reduced values of relative fishing mortality compared to those in the present fishery by cohort and species.

Yield estimates, in weight per recruit, for *L. pealei* for both the 60-mm and 90-mm mesh nets were consistently greater than for the 45-mm mesh net for all choices of M and F-multipliers (Figure 3, Table 6), and for each assumption of proportions of the year-class attributed to cohort 1. However, the yield of *L. pealei* appeared to be more sensitive to changes in natural mortality than to mesh selection. Although size at entry (caused by mesh selectivity) was an important factor in potential yields at low levels of M, this factor became less important when M was large (0.15).

Time of spawning was also an important factor, as demonstrated by increased yield when the simulated proportion of the year-class attributed to the second cohort was increased for both the 60-mm and 90-mm mesh nets. That was also the case based on the 1977–79 fishery. Again, this seemed reasonable; where individuals hatched early in the season would still be recruited to the winter fishery in about February for the 60-mm mesh, and the late-hatched cohort would not be recruited until the period of reduced fishing in the inshore fisheries. Consequently, rapid growth in weight per individual would more than counteract weight declines due to M, even though yield in number was substantailly reduced in all cases.

Simulated yield per recruit for *I. illecebrosus* was well above that expected in the present fishery (45-mm mesh) for both the 60-mm and 90-mm meshes, and for both cases of strength of the first cohort (PN1 = 0.80 and 0.90) over the entire range of F-multipliers (Figure 4, Table 7). In all cases, estimated yield was greater for 90-mm than for 60-mm mesh as well. Small yet consistant differences were also demonstrated when different proportions of the year-class were attributed to the first cohort. For *I. illecebrosus*, greater yields were observed when PN1 was assumed at 0.90 than at 0.80, indicating that the greater delay for entry of the second cohort into the fishery resulted in a significant increase in the effect of natural mortality and

TABLE 5.

Relative monthly fishing mortality rates (F_t) associated with three mesh sizes in the *Loligo pealei* and *Illex illecebrosus* fisheries by cohort in months when recruit reductions are caused by increased mesh size.

	Loligo pealei						*Illex illecebrosus*					
Mesh (mm)	45		60		90		45		60		90	
Cohort	I	II	I	II	I	II	I	II	I	II	I	II
Month												
Jul							0.50					
Aug							0.58					
Sep							0.18					
Oct							0.15					
Nov	0.30						0.28		0.07			
Dec	0.65		0.21				0.13		0.13			
Jan	0.51		0.25				0.02	0.01	0.02			
Feb	1.00		1.00				0.04	0.04	0.04			
Mar	0.58	0.29	0.58		0.10		0.02	0.02	0.02			
Apr	0.08	0.08	0.08		0.02		0.01	0.01	0.01			
May	0.27	0.27	0.27	0.09	0.13		0.01	0.01	0.01			
Jun	0.11	0.11	0.11	0.05	0.11		0.28	0.28	0.28	0.07	0.28	
Jul	0.04	0.04	0.04	0.04	0.04		1.00	1.00	1.00	1.00	1.00	
Aug	0.02	0.02	0.02	0.02	0.02		0.58	0.58	0.58	0.58	0.58	
Sep	0.01	0.01	0.01	0.01	0.01		0.18	0.18	0.18	0.18	0.18	
Oct	0.08	0.08	0.08	0.08	0.08	0.02	0.15	0.15	0.15	0.15	0.15	
Nov	0.59	0.59	0.59	0.59	0.59	0.27	0.28	0.28	0.28	0.28	0.28	0.07
Dec	0.65	0.65	0.65	0.65	0.65	0.65	0.13	0.13	0.13	0.13	0.13	0.06
Jan	0.51	0.51	0.51	0.51	0.51	0.51	0.02	0.02	0.02	0.02	0.02	0.02
							0.04	0.04	0.04	0.04	0.04	0.04

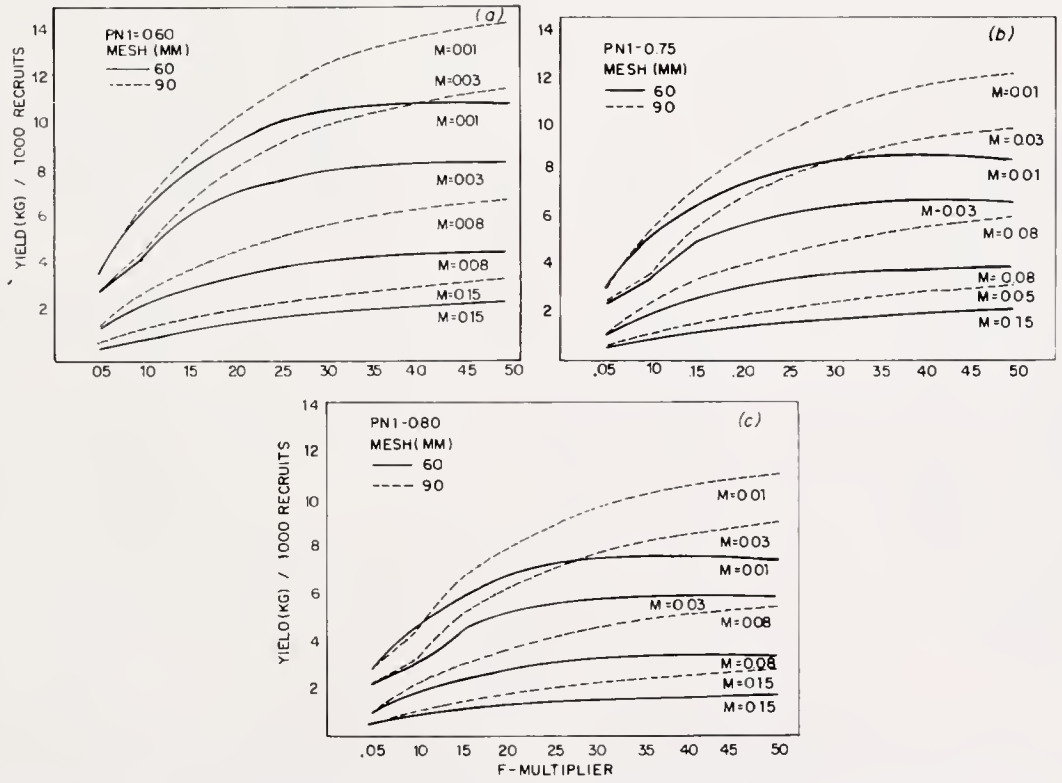

Figure 3. *Loligo pealei* yield (kg) per 1,000 recruits for M = 0.01, 0.04, 0.08 and 0.15, and for mesh sizes of 60 mm and 90 mm: (a) when 60% of the year-class was assumed from the spring cohort; (b) when 75% of the year-class was assumed from the spring cohort; and (c) when 80% of the year-class was assumed from the spring cohort.

TABLE 6.

Loligo pealei yield (kg) per 1,000 recruits for four values of monthly natural mortality rate (M) for a range of F-multipliers where PN1* = 0.60, 0.75, and 0.80, and mesh sizes of 60 mm and 90 mm.

		Mesh Size = 60 mm				Mesh Size = 90 mm			
		Monthly Natural Mortality Rate (M)				Monthly Natural Mortality Rate (M)			
PN1	F-multiplier	0.01	0.03	0.08	0.15	0.01	0.03	0.08	0.15
0.60	0.05	3.78	2.79	1.27		3.76	2.91	1.44	0.71
	0.10	6.40	4.36	2.38		6.63	4.63	2.84	1.30
	0.15	8.19	6.14	3.11		8.81	6.90	3.84	1.78
	0.20	9.40	7.08	3.64		10.48	8.24	4.64	2.18
	0.25	10.18	7.72	4.02		11.74	9.29	5.29	2.52
	0.30	10.67	8.14	4.29		12.70	10.09	5.80	2.79
	0.35	10.94	8.39	4.48		13.41	10.70	6.21	3.02
	0.40	11.07	8.53	4.60		13.94	11.17	6.53	3.21
	0.45	11.09	8.58	4.68		14.32	11.51	6.79	3.37
	0.50	11.04	8.58	4.73		14.59	11.77	7.00	3.51
0.75	0.05	3.09	2.32	1.05	0.51	3.08	2.41	1.16	0.62
	0.10	5.19	3.46	2.02	0.90	5.45	3.68	2.41	1.13
	0.15	6.59	5.00	2.62	1.19	7.26	5.73	3.36	1.56
	0.20	7.49	5.72	3.05	1.41	8.64	6.86	3.94	1.90
	0.25	8.05	6.18	3.34	1.58	9.69	7.73	4.48	2.19
	0.30	8.36	6.46	3.54	1.70	10.49	8.39	4.92	2.43
	0.35	8.51	6.61	3.67	1.79	11.08	8.90	5.26	2.63
	0.40	8.54	6.67	3.75	1.86	11.51	9.29	5.53	2.80
	0.45	8.49	6.66	3.79	1.92	11.82	9.57	5.75	2.93
	0.50	8.39	6.61	3.81	1.95	12.04	9.78	5.91	3.05
0.80	0.05	2.86	2.16	0.98	0.49	2.86	2.24	1.07	0.59
	0.10	4.79	3.17	1.91	0.87	5.06	3.37	2.26	1.08
	0.15	6.05	4.62	2.46	1.14	6.74	5.35	3.07	1.48
	0.20	6.86	5.27	2.85	1.35	8.03	6.40	3.71	1.81
	0.25	7.34	5.67	3.11	1.51	9.01	7.21	4.21	2.08
	0.30	7.60	5.90	3.29	1.63	9.75	7.83	4.62	2.31
	0.35	7.70	6.02	3.40	1.71	10.30	8.30	4.94	2.50
	0.40	7.70	6.05	3.46	1.78	10.70	8.66	5.20	2.66
	0.45	7.63	7.02	3.49	1.82	10.99	8.92	5.40	2.79
	0.50	7.51	5.96	3.50	1.86	11.19	9.11	5.55	2.90

*PN1—proportion of year-class from the spring (April–June) cohort.

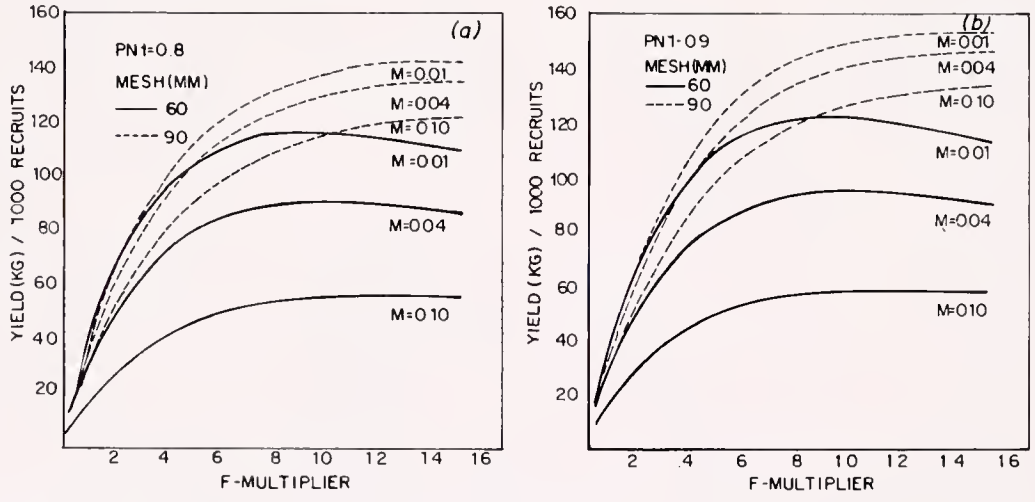

Figure 4. *Illex illecebrosus* yield (kg) per 1,000 recruits for M = 0.01, 0.04 and 0.10, and for mesh sizes of 60 mm and 90 mm: (a) when 80% of the year-class was assumed from the winter cohort; and (b) when 90% of the year-class was assumed from the winter cohort.

TABLE 7.

Illex illecebrosus yield (kg) per 1,000 recruits for three values of monthly natural mortality rate (M) for a range of F-multipliers where PN1* = 0.80 and 0.90, and mesh sizes of 60 mm and 90 mm.

		Mesh Size = 60 mm			Mesh Size = 90 mm		
		Monthly Natural Mortality Rate (M)			Monthly Natural Mortality Rate (M)		
PN1	F-multiplier	0.01	0.04	0.10	0.01	0.04	0.10
0.80	0.05	20.80	15.60	8.90	10.00	18.30	15.60
	0.10	38.40	28.90	16.60	37.40	34.30	29.20
	0.20	65.80	49.70	28.80	65.50	60.30	51.70
	0.30	84.90	64.50	37.80	86.50	80.00	69.00
	0.40	98.20	74.90	44.40	102.30	94.80	82.30
	0.50	107.10	82.10	49.20	114.00	106.10	92.50
	0.60	112.80	86.90	52.60	122.70	114.50	100.40
	0.70	116.20	89.50	55.00	129.20	120.80	106.50
	0.80	118.00	91.80	56.70	133.90	125.50	111.20
	0.90	118.60	92.70	57.80	137.30	129.10	114.90
	1.00	118.40	93.00	58.50	140.00	131.70	117.70
	1.20	116.50	92.30	59.10	142.90	135.10	121.60
	1.30	115.10	91.60	59.10	143.80	136.10	122.90
	1.40	113.60	90.70	59.00	144.40	136.90	124.00
	1.50	112.00	89.70	59.00	144.80	137.50	124.80
0.90	0.05	22.20	16.70	9.50	22.30	20.40	17.40
	0.10	40.90	30.80	17.70	41.60	38.20	32.60
	0.20	69.90	52.90	30.80	72.70	67.10	57.70
	0.30	90.20	68.60	40.40	96.00	88.90	76.90
	0.40	104.10	79.60	47.40	113.30	105.30	91.60
	0.50	113.40	87.20	52.40	126.10	117.60	103.00
	0.60	119.40	92.20	56.0	135.50	126.70	111.70
	0.70	122.90	95.20	58.60	172.30	133.50	118.30
	0.80	124.70	97.30	60.30	147.30	138.50	123.40
	0.90	125.30	98.20	61.50	150.10	142.20	127.30
	1.00	125.00	98.40	62.20	153.20	144.90	130.30
	1.20	122.80	97.50	62.70	156.00	148.10	134.30
	1.30	121.20	96.70	62.70	156.60	149.00	135.60
	1.40	119.50	95.70	62.60	157.00	149.60	136.60
	1.50	117.70	94.60	62.70	157.20	150.0	137.40

*PN1—proportion of year-class from the winter (January–February) cohort.

subsequent declines in yield. Also, for 90-mm mesh, the spring cohort reached recruitable size at a time of reduced fishing and, therefore, produced lower yields.

Increased mean weights of *I. illecebrosus* with increased mesh size are illustrated in Table 8.

Based on the analyses presented here, significant increases in yield in weight per recruit of both *L. pealei* and *I. illecebrosus* may result from increases in size at entry to the fishery, as would occur with an increase in mesh size. This increase was evident in all combinations of natural mortality, F-multipliers, and for each case of year-class structure that was tested for each species. However, it should be noted that increased yields for either *L. pealei* or *I. illecebrosus* would not be realized immediately. The effects of the smaller mesh nets on the present year-class would result in reduced catches until the new year-classes entered the fishery using the larger mesh.

Total Yield Estimates

Total yields from an average year-class, based on results of yield-per-recruit analyses, stock size, and prerecruit estimates, were calculated assuming constant annual recruitment. The average annual ratio of the number of prerecruit sized individuals to total individuals was applied to the average (1968–78) abundance for each species (Lange 1980) to estimate the average number of recruits to the fishery. However, minimum abundance estimates from bottom-trawl surveys for *I. illecebrosus* probably do not adequately represent the entire population of this species off the northeastern United States. The average population size for *I. illecebrosus* was, therefore, calculated from minimum biomass estimates determined by the USSR (1971–1976) (Georges Bank, Nova Scotia, Konstantinov and Noskov 1977) divided by the approximate mean weight of individuals during the time when those estimates were made (88 g).

Expected yield values for various combinations of M, F-multipliers, time of spawning, and mesh size for *L. pealei* and *I. illecebrosus* were then calculated as follows:

$$\hat{Y} = YP \cdot NR/1000; \quad (7)$$

where $\hat{Y}$ is total expected yield in metric tons (MT), YP is the yield (kg) per 1,000 recruits, and NR is the mean annual number of recruits to the fishery.

Annual recruitment was estimated at 2.624×10^9 individuals for *L. pealei* (88.5% prerecruits from an average abundance of $2.964\ [\pm 2.035] \times 10^9$) and 386.6×10^6 individuals for *I. illecebrosus* ($1.741\ [\pm 1.033] \times 10^9$ with 22.2% as prerecruits).

Total average yield estimates for *L. pealei* (calculated from values given in Table 3) ranged from 1,049 MT (PN1 = 0.75, M = 0.15, FM = 0.05) to 23,533 MT (PN1 = 0.80, M - 0.01, FM = 0.30) for the present fishery (45-mm mesh); while expected yields (calculated from Table 6) increased to a range of 1,286 MT (PN1 = 0.80, M = 0.15, FM = 0.05) to 29,095 MT (PN1 = 0.60, M = 0.01, FM = 0.45) from 60-mm mesh, and from 1,548 MT (PN1 = 0.80, M = 0.15, FM = 0.05) to 38,277 MT (PN1 = 0.60, M = 0.01, FM = 0.50) for 90-mm meshes (Table 6). These values were somewhat lower than those presented by Sissenwine and Tibbetts (1977). This may have been due, in part, to differences in assumptions of year-class structure and related growth and mortality estimates.

Estimates of total average yield of *I. illecebrosus* (calculated from values in Table 4) for the present fishery (45-mm mesh) ranged from 2,629 MT (PN1 = 0.80, M = 0.10, FM = 0.40) to 24,959 MT (PN1 = 0.80, M = 0.10, FM = 0.40). Increases in mesh size resulted in increases in expected yields

TABLE 8.

Mean weight (g) of *Illex illecebrosus* taken under different assumptions of F-multiplier, monthly natural mortality rate, and PN1*, for mesh sizes of 60 mm and 90 mm.

		Mesh Size = 60 mm			Mesh Size = 90 mm		
		Monthly Natural Mortality Rate (M)			Monthly Natural Mortality Rate (M)		
PN1	F-multiplier	0.01	0.04	0.10	0.01	0.04	0.10
0.80	0.05	173.60	169.40	159.60	206.20	206.00	201.90
	0.10	171.60	167.10	157.20	205.30	208.00	199.90
	0.20	167.00	162.50	152.50	202.00	200.40	197.20
	0.30	162.50	158.00	147.90	199.40	197.50	194.20
	0.40	158.10	153.70	143.60	196.30	195.80	191.80
	0.50	154.00	149.50	139.40	193.90	192.10	189.20
	0.60	150.00	145.40	135.40	191.20	189.80	187.00
	0.70	146.10	140.80	131.70	188.80	187.60	185.30
	0.80	142.50	137.90	128.10	186.70	185.40	183.30
	0.90	138.90	134.40	124.70	184.60	183.30	181.20
	1.00	135.50	131.10	121.50	182.80	181.60	179.70
	1.20	129.40	125.00	115.70	179.30	178.40	177.00
	1.30	126.50	122.20	113.00	178.00	177.00	175.60
	1.40	123.80	119.60	110.50	176.60	175.70	174.40
	1.50	121.30	112.30	108.10	175.40	174.50	173.10
0.90	0.05	182.50	177.20	167.40	208.20	204.40	202.00
	0.10	180.10	178.00	164.30	205.80	203.40	200.00
	0.20	175.40	170.10	158.80	202.60	201.00	197.40
	0.30	170.70	165.40	154.20	199.60	198.00	194.60
	0.40	166.20	160.90	149.50	197.10	195.00	191.70
	0.50	161.80	156.50	144.80	194.30	192.40	189.60
	0.60	157.50	152.20	140.80	191.60	190.30	187.30
	0.70	153.50	147.80	136.80	189.30	187.80	185.40
	0.80	149.60	144.30	132.80	187.10	185.70	183.40
	0.90	145.80	140.60	129.40	185.00	183.70	181.60
	1.00	142.30	137.00	125.90	183.00	182.00	179.90
	1.20	135.70	130.70	119.50	179.50	178.60	176.90
	1.30	132.60	127.50	116.70	178.00	177.20	175.70
	1.40	129.80	124.70	114.00	176.60	175.80	174.50
	1.50	127.00	121.90	111.40	175.90	174.60	173.50

*PN1–proportion of year-class from the winter (January–February) cohort.

(from yield-per-recruit values, Table 7) ranging from 3,441 MT (PN1 = 0.80, M = 0.10, FM = 0.05) to 48,441 MT (PN1 = 0.90, M = 0.01, FM 0.90) for 60-mm mesh, to between 6,030 MT (PN1 = 0.80, M = 0.10, FM = 0.05) and 66,611 MT (PN1 = 0.90, M = 0.01, FM = 0.70) for 90-mm mesh.

Although the lower ranges of these estimates are below the actual catches of *L. pealei* and *I. illecebrosus* observed since the onset of directed fisheries for these species, annual catches have fallen within the range (± standard deviation) of the average estimates based on the present fishery. This indicates that, if the estimated mortalities used here were reasonable for the present squid fisheries, increases in yield may result from increased mesh size.

As better estimates of growth, mortality, and spawning rates, and annual recruitment become available, this model could provide more accurate estimates of expected yield. However, because results were similar for all combinations of growth, mortality, and spawning rates which were simulated for the mesh size tested, better parameter estimates probably will not change the general results regarding increases in yield with increased mesh size. However, improved estimates of mesh selectivity for either species will probably produce changes in these results.

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COVER MICROPHOTOGRAPH: A 2-day old larva of the short-finned squid, *Illex illecebrosus* (Lesueur), spawned in captivity in the Aquatron Laboratory of Dalhousie University. The 1.2-mm (mantle length) larva is viewed head-on to accent the ring of suckers on the proboscis, a key taxonomic feature of the species. The larva was fixed in alcoholic Bouin's solution and dehydrated in acetone. After critical-point drying, the larva was affixed to an aluminum stub with silver paint, sputter-coated with gold, and photographed with a Cambridge Steroscan 180 scanning electron microscope at 10 kv. [Photomicrograph by R. D. Durwood and A. K. Ball, Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4H8.]