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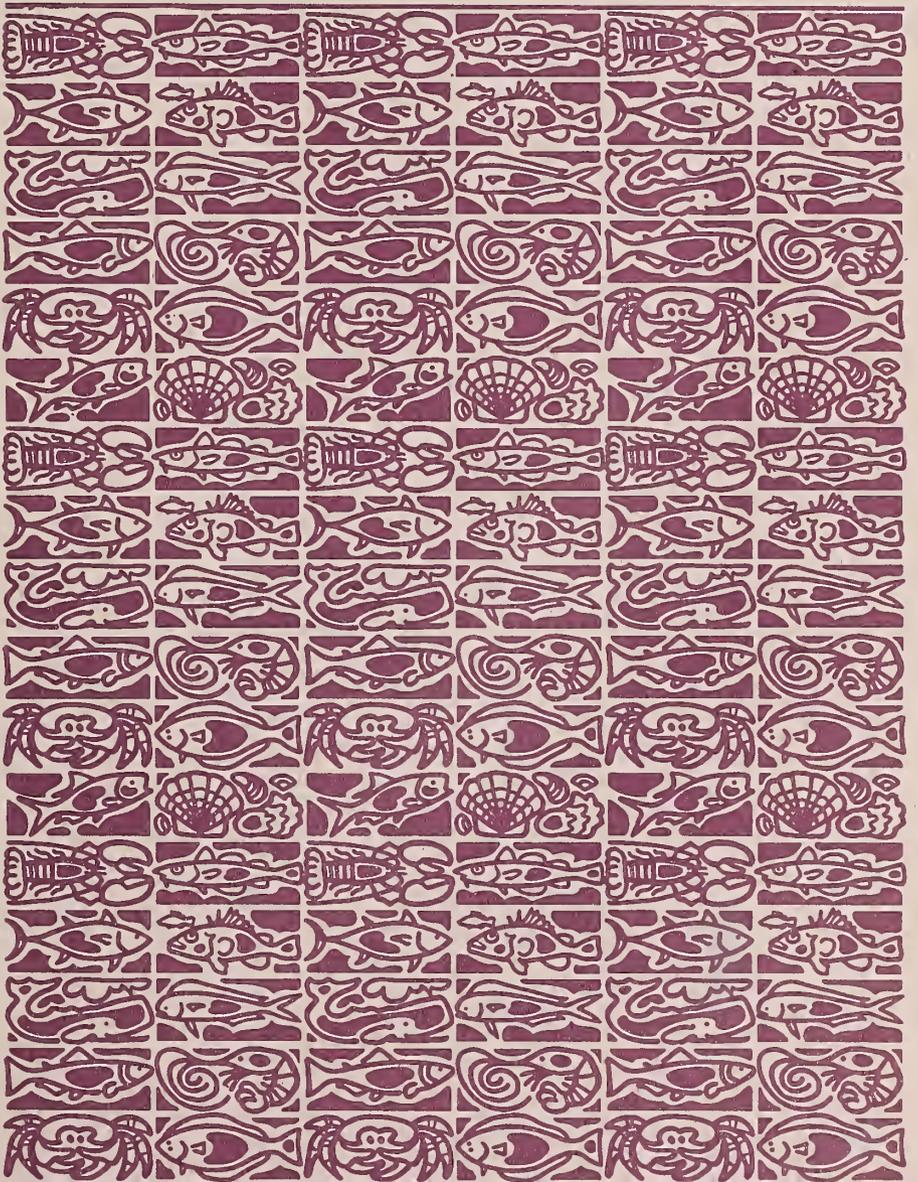


U.S. Department  
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January 1997

# Fishery Bulletin

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Volume 95  
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# Fishery Bulletin

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**Abstract.**—We studied phenotypic variation in larval and juvenile growth and development, using laboratory-reared winter flounder, *Pleuronectes americanus*. Larvae were reared individually to metamorphosis and beyond and were measured at weekly intervals. Growth in length was rapid until 30 d but slowed thereafter until metamorphosis. Standard length peaked and often declined as metamorphosis approached, and notochord length decreased during flexion. Length at 30 d (an index of larval growth rate) was inversely related to age at metamorphosis, confirming previous assertions that larvae that grow rapidly also develop most rapidly. The relation between growth rate and larval-period duration, however, was not straightforward. The time from the day of peak larval length until metamorphosis (7–35 d) appeared to be inversely related to larval growth rate. Juvenile growth rates during the first 3 weeks following metamorphosis were unrelated to length at 30 d. Additional juveniles, reared in groups as larvae and tracked as individuals following metamorphosis, showed no change in growth rates during the first 4 weeks of the juvenile period in relation to increasing age at metamorphosis or larval growth rates. These results are consistent with earlier findings that size at age does not diverge continually throughout the larval and juvenile periods. Compensatory juvenile growth among fish that grew slowly as larvae was observed but not to the same extent as previously reported. We emphasize the utility of the individual-based approach for identifying patterns of phenotypic variability in growth and development during the early life stages in fishes.

## Individual variation in growth and development during the early life stages of winter flounder, *Pleuronectes americanus*

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Mechanisms controlling survival and recruitment of fishes operate at the level of the individual (Crowder et al., 1992). Further, small initial differences among individual larvae and juveniles within fish populations may have disproportionate effects on the probability of their survival (Crowder et al., 1992; Rice et al., 1993). Consequently, research programs in fisheries have begun to focus on phenotypic variability within cohorts in an effort to identify particular traits that may be unique to the small minority of survivors (Fritz et al., 1990; Taggart and Frank, 1990). If survivors are not random subsets of the original cohort, interpretations of recruitment processes based upon analyses of population averages are likely to be misleading (Pepin and Miller, 1993). Consequently, individual-based approaches are increasingly favored (Crowder et al., 1992). However, there have been few quantitative measurements of either individual variation in early life history traits of fishes or in their survival consequences (but see Rosenberg and Haugen, 1982; Rice et al., 1987; Chambers et al., 1989; Chambers and Leggett, 1992; D'Amours, 1992; Bertram and Leggett, 1994; Lochmann et al., 1995; Miller et al., 1995). In theory, longitudinal data can be obtained from sequential

measurements of individuals or from back calculations of size at age from otolith microstructure.

Variation in larval growth rates is widely believed to be a central feature in year-class formation in fishes (Leggett and Deblois, 1994). Traditionally, growth parameters are estimated from a restricted number of samples of the population. Each sample includes a range of fish lengths and ages. Importantly, each fish provides only a single estimate of length at age. Such data are termed cross-sectioned. The calculated growth parameters represent composite pictures and cannot reveal variability among the growth patterns of individuals simply because they aggregate data at a level higher than the individual. Chambers and Miller (1995) have discussed the effects of the level of aggregation of data on the inferences that can be made. In addition, composite growth curves

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are subject to several potential biases (Chambers and Miller, 1995). For example, composite curves are not accurate in cases where mortality of individual age classes are biased towards small or large individuals (Litvak and Leggett, 1992; Pepin et al., 1992). Hence, if the survival consequences of variability in growth rates are to be evaluated adequately, individual phenotypic variability in growth must be quantified (Lynch and Arnold, 1988; Chambers, 1993). This requires that longitudinal data based upon repeated measures of individuals be collected. These problems are illustrated in the following example. Consider a cohort of 220 larvae with an average size of 5.5 mm and a uniform size distribution of 20 larvae in each of ten 0.1-mm size classes from 5 to 6 mm. In a hypothetical 7-d interval, no larval growth occurs, but a gape-limited predator consumes all larvae less than 5.5 mm, leaving 120 larvae with an average size of 5.75 mm. If only cross-sectional data were available, the larval growth rate was estimated as 0.11 mm/d for the 7-d interval. However, if longitudinal data were available (i.e. measurements of survivors at the beginning and end of the week), it would be clear that no growth had occurred.

Bertram et al. (1993) have argued that the dynamics of larval and juvenile growth rates should be examined in unison, rather than separately. Using laboratory-reared winter flounder, *Pleuronectes americanus*, they have shown that size-at-age trajectories do not diverge continually during the larval and juvenile periods. In fact, juvenile size-at-age trajectories converge because fish that grew slowly as larvae compensated for their slow growth by growing rapidly as juveniles. However, Bertram et al. (1993) assumed that larval growth was linear; therefore juvenile fish used in their experiments were pooled into groups. This approach precluded the study of individual phenotypic variability. The objectives of the present study were 1) to provide estimates of the individual variability in growth rate in fish during early life stages because it is upon this individual variability that phenotypic selection acts and 2) to evaluate the validity of previous estimates of larval growth rate. Also, we explore how individual variation in larval growth affects growth during the subsequent juvenile period.

## Methods

### Rearing protocol

The research in this study was conducted at the Huntsman Marine Science Centre, St. Andrews, New Brunswick, during summer 1991. In May, adult win-

ter flounder were collected from Passamaquoddy Bay with a bottom trawl and held at ambient seawater temperature (7–8°C). When ripe, eggs from individual females were combined with sperm pooled from three males to create half-sibling families. Families were maintained separately throughout the study. Fertilized eggs were placed in a slurry of diatomaceous earth for 12 h following fertilization to prevent clumping. Incubation temperature was 7 ( $\pm 0.5$ )°C (mean  $\pm$  SD). At approximately 24-h after fertilization, the eggs were immersed in solutions of penicillin (0.0158 g/L) and streptomycin (0.02 g/L) for 24 h. Filtered, UV-sterilized seawater was replaced every 2–3 d until hatching commenced at approximately 14 d after fertilization.

Upon hatching, 118 larvae from two families (families 1 and 2) were individually stocked into black cylindrical 0.4-L containers (15 cm diameter  $\times$  6.5 cm high) with clear plexiglass bottoms. Water temperature was maintained at 10 ( $\pm 0.5$ )°C in a temperature controlled room with a 16:8 day:night photoperiod. At weekly intervals, 75% of the water was removed from each container and replaced with UV-sterilized filtered seawater. Additional "reserve" larvae from the same families were reared in groups under identical conditions in 18-L cylindrical, black plastic containers. Individual larvae that died within the first 3 weeks were replaced with siblings from the appropriate reserve group.

Larvae were also reared in groups in 38-L aquaria covered externally with black plastic. Five aquaria were each stocked with four-hundred 1-d-old larvae drawn from another half-sibling family (family 3). Temperatures in the aquaria were maintained at 10 ( $\pm 0.5$ )°C. At weekly intervals, 3 liters of water were removed from each aquarium and replaced with UV-sterilized filtered seawater. Dead larvae were siphoned regularly from the tank.

All larvae were fed *Brachionus* sp. at 2/(mL·d) until the end of week 7. Rotifers were cultured by using *Isochrysis* sp. and *Chaetoceros* sp. Twenty-four hours prior to being fed to larvae, rotifers were provided with Microfeast artificial plankton (Provista Corporation) to enhance their nutritional quality. From the end of week 5 onwards, larvae were also offered *Artemia* nauplii (0.25/(mL·d)). Nauplii were enriched with Microfeast 24 h prior to use.

At metamorphosis, larvae from family 3, which had been reared in groups, were individually stocked into 0.4-L rearing containers (see above) to examine juvenile growth. To standardize the developmental stage of individuals used in this study, we used only fish whose left eye had just crossed the midline on its migration to the right side of the body (stage H of Seikai et al., 1986). All fish that metamorphosed on

the same day were treated as a discrete cohort. The creation of these cohorts was repeated at intervals of 3–8 d until all fish had metamorphosed. Table 1 summarizes the rearing conditions for the 3 families used in the study.

At weekly intervals, length data on individual larvae were recorded by using a dissecting microscope linked to a video system at 6× magnification. Larvae were filmed without being removed from their rearing containers. Fish were not anesthetized at any time. Larval movement was restricted by confining larvae within a 6-cm diameter plexiglass ring placed within the rearing container. Length data were collected only when fish were in the horizontal plane. To account for variation in the position of the larvae in the vertical plane, we constructed a small set of “stairs” with a plastic ruler segment attached at each level. After filming each larva, we immediately calibrated the image against the ruler segment that was in focus. For fish that were close to, or past, metamorphosis, the process of filming was simplified because these fish generally remained motionless on the bottom of the container. Following metamorphosis, individual juveniles were filmed weekly for up to 4 weeks, when rearing was terminated. Standard lengths of all fish were obtained by using an image analysis system (Optimus vers. 3.11, Bioscan Corporation, Seattle, WA). We used the image analysis system to “capture” two images for each fish for estimating standard length at age and used the largest value in all analyses.

## Analysis

We constructed individual growth trajectories for larvae that survived until metamorphosis, using spline functions fitted to repeated measures of size at age. Individual larval growth trajectories were based on between 3 and 9 weekly observations per larva. Individual growth trajectories were examined quantitatively by using four indexes: 1) larval size at  $30 \pm 1$  d (roughly midway through the development period, an index of larval growth rate [e.g. Travis, 1981]); 2) average larval growth rates, defined as the difference between the length at metamorphosis and the mean length at hatching for the family divided by the time elapsed between the two events; 3) latency period, defined as the time between the age at which maximum larval length was attained and the time of metamorphosis; and 4) larval-period duration, defined as the age at metamorphosis. Correlation analyses (Pearson’s correlation coefficient) were used to examine the relationships among pairs of the above variables for individual larvae. Variables were

**Table 1**

Summary of rearing conditions and filming schedules for the 3 families used in the study.

	Family 1	Family 2	Family 3
Larval container size (L)	0.4	0.4	38
Number of larvae/container	1	1	400
Weekly measures of larvae	Yes	Yes	No
Juvenile container size (L)	0.4	0.4	0.4
Number of juveniles/container	1	1	1
Weekly measures of juveniles	Yes	Yes	Yes

tested for normality with normal probability plots (Wilkinson, 1990). When heteroscedasticity was detected with techniques outlined in Zar (1984), variables were log-transformed. For comparison with the individual growth trajectories, we also constructed a composite size-at-age plot by using data for all larvae used in the study.

We checked for size-dependent mortality during the first part of the larval period by comparing the length of those fish that lived until their next weekly measurement with those that died during that time, using *t*-tests for independent samples. Size-dependent analyses were conducted for larvae after hatching (1–2 d); week 1 (8–9 d); week 2 (15–16 d); and week 3 (22–23 d). Group-reared larvae that were used as replacements for fish that died during the first 3 weeks were not included in the analysis.

Individual juvenile growth rates were estimated from the slope of a least squares fitted to weekly measures of individual size at age from metamorphosis to week 3 of the juvenile period. Thus, growth estimates were based upon up to 4 size-at-age measurements. Growth parameters were not calculated when less than 3 size-at-age measurements were available. We examined the correlations between juvenile growth rates and both age at metamorphosis and length at 30 d. Juvenile growth rates were also examined in relation to Bertram et al.’s (1993) measure of average larval growth rate estimated as the difference between the mean length at metamorphosis for fish that metamorphosed on the same day and the mean size at hatching for the family, divided by the number of days between the 2 events.

For comparison with the work of Bertram et al. (1993), we restricted the analysis of juvenile growth to weeks 1 through 4 for fish that had been reared together as larvae. The relation between juvenile growth rates and age at metamorphosis was examined by using regression and correlation analyses. Similar analyses were performed to examine the re-

relationship between juvenile growth rates and average larval growth rate. For fish that had metamorphosed early, measurements of size at age were available until week 7 of the juvenile period. For these individuals we compared growth rates during weeks 1–4 with those during weeks 5–7, using a paired *t*-test.

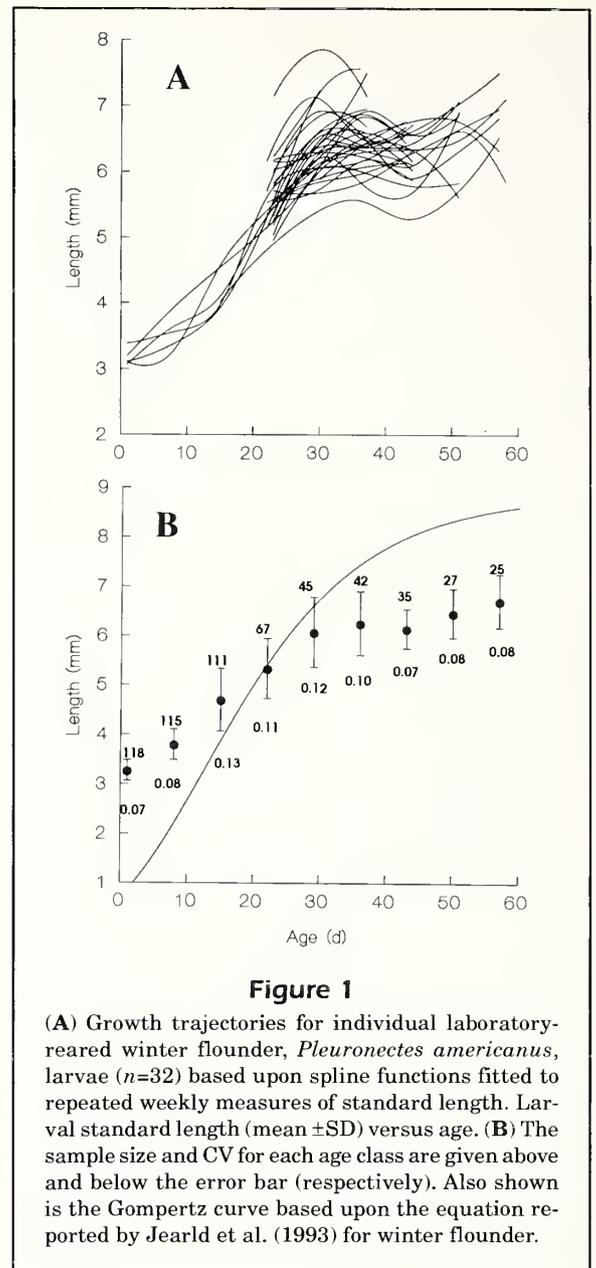
## Results

### Individually reared larvae

Thirty-two individually reared fish, 31 of which were from a single family (family 1), survived until metamorphosis. For 5 of these fish, weekly measures were available from hatching to metamorphosis. For the remaining 27 larvae weekly measures began at day 22. We could not detect size-dependent mortality in the weeks following: hatching ( $t=1.83$ ,  $df=116$ ), week 1 ( $t=0.18$ ,  $df=87$ ), week 2 ( $t=1.4$ ,  $df=32$ ), or week 3 ( $t=0.21$ ,  $df=11$ ). Data from the 32 fish provided estimates of individual larval growth trajectories (Fig. 1A). The trajectories exhibited considerable phenotypic variation in size at age, maximum larval size, size at metamorphosis, latency period, and the duration of the larval period (Fig. 1A). To demonstrate the loss of information introduced by basing growth parameters on cross-sectional data, we treated the original individual-level longitudinal data as cross-sectional. When individual larval sizes were depicted in this composite fashion (Fig. 1B), mean larval length at age increased rapidly from day 1 until day 30 and then leveled off. Important information, however, can be obtained only from cross-sectional data. For example, coefficients of variation (CV) for length at age increased from 0.07 on day 1 to 0.12 on day 30 but declined subsequently and leveled off at approximately 0.08.

The largest larvae at 30 d were also largest at 22 d ( $r=0.66$ ,  $n=18$ ,  $P=0.03$ ) and at 36 d ( $r=0.5$ ,  $n=18$ ,  $P=0.034$ ), indicating positive covariance in size at age for individually reared larvae that were alive at each of those ages. There was a significant positive relationship between larval length at 30 d and maximum larval size ( $r=0.6$ ,  $n=27$ ,  $P=0.001$ ). However, larval length at 30 d and age at metamorphosis were negatively correlated ( $n=27$ ,  $r=-0.589$ ,  $P=0.001$ ; Fig. 2A). The negative correlation coefficient between size at 30 d and age at metamorphosis was larger than correlation coefficients calculated for all other age classes. Average larval growth rate and length at 30 d were positively correlated ( $n=25$ ,  $r=0.49$ ,  $P=0.01$ ; Fig. 2B).

The age of maximum larval size (log-transformed) was negatively correlated to length at 30 d ( $r=-0.71$ ,  $n=27$ ,  $P<0.001$ ; Fig. 3A). The latency period (range:7–

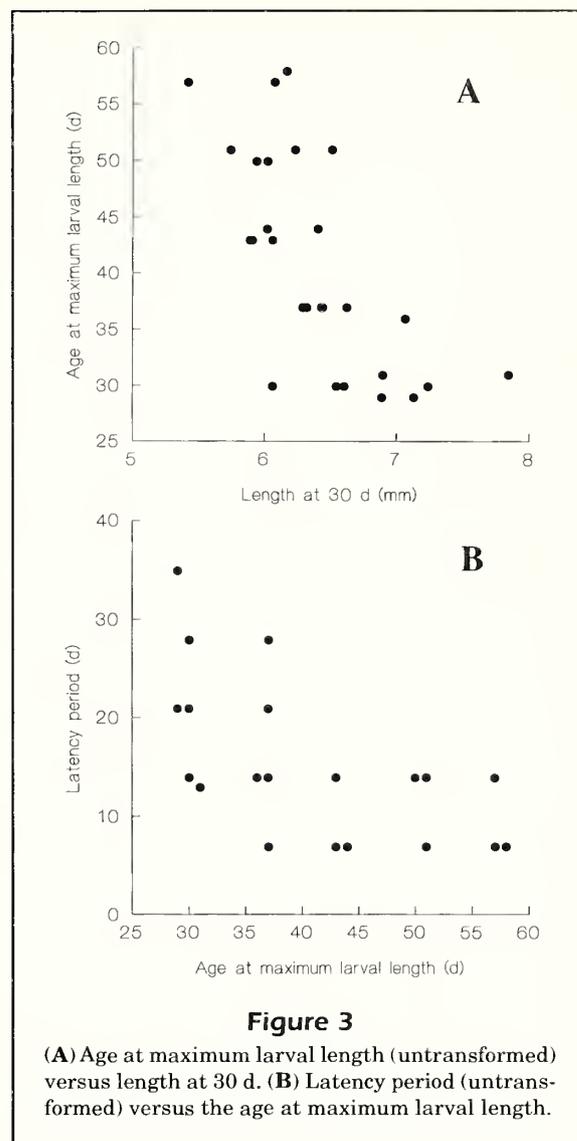
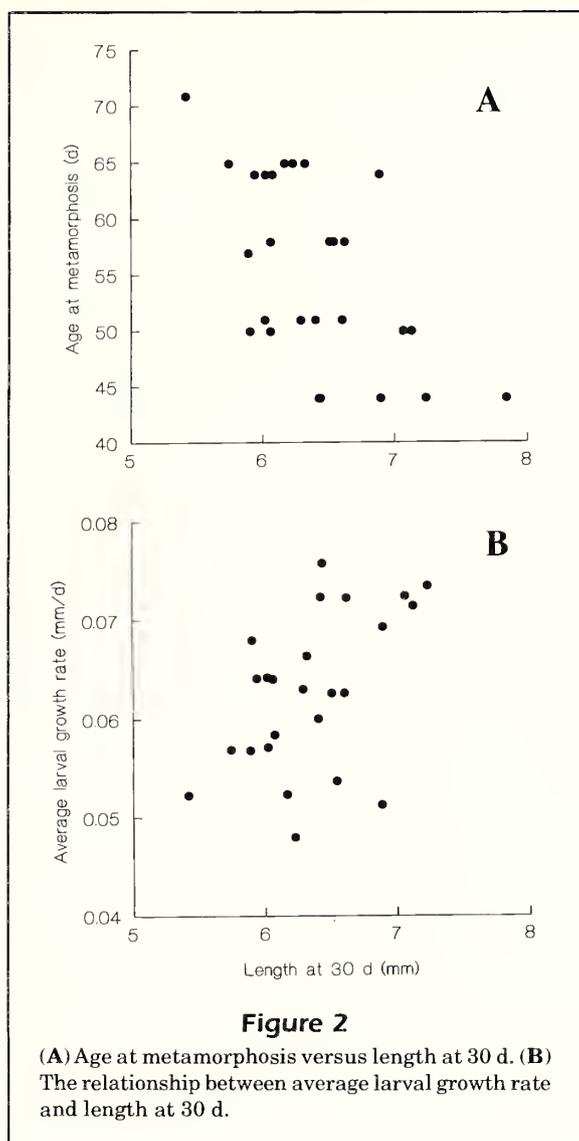


**Figure 1**

(A) Growth trajectories for individual laboratory-reared winter flounder, *Pleuronectes americanus*, larvae ( $n=32$ ) based upon spline functions fitted to repeated weekly measures of standard length. Larval standard length (mean  $\pm$  SD) versus age. (B) The sample size and CV for each age class are given above and below the error bar (respectively). Also shown is the Gompertz curve based upon the equation reported by Jearld et al. (1993) for winter flounder.

35 d;  $14.4 \pm 7.5$  d,  $n=31$ ) (log-transformed) was inversely related to age of maximum larval size ( $r=-0.58$ ,  $n=31$ ,  $P=0.001$ ; Fig. 3B). In contrast, the latency period showed a positive trend with increasing length at 30 d, but the relationship was not significant ( $r=0.2$ ,  $n=26$ ,  $P=0.38$ ). Age at metamorphosis ranged from 44 d to 71 d ( $55.2 \pm 7.9$  d). Length at metamorphosis ranged from 6.1 mm to 7.5 mm ( $6.6 \pm 0.3$  mm). Length and age at metamorphosis were positively correlated for individually reared larvae ( $r=0.46$ ,  $n=29$ ,  $P=0.012$ ).

Among individually reared larvae, subsequent juvenile growth rate during the first 3 weeks of the juvenile stage bore no relation to age at metamor-



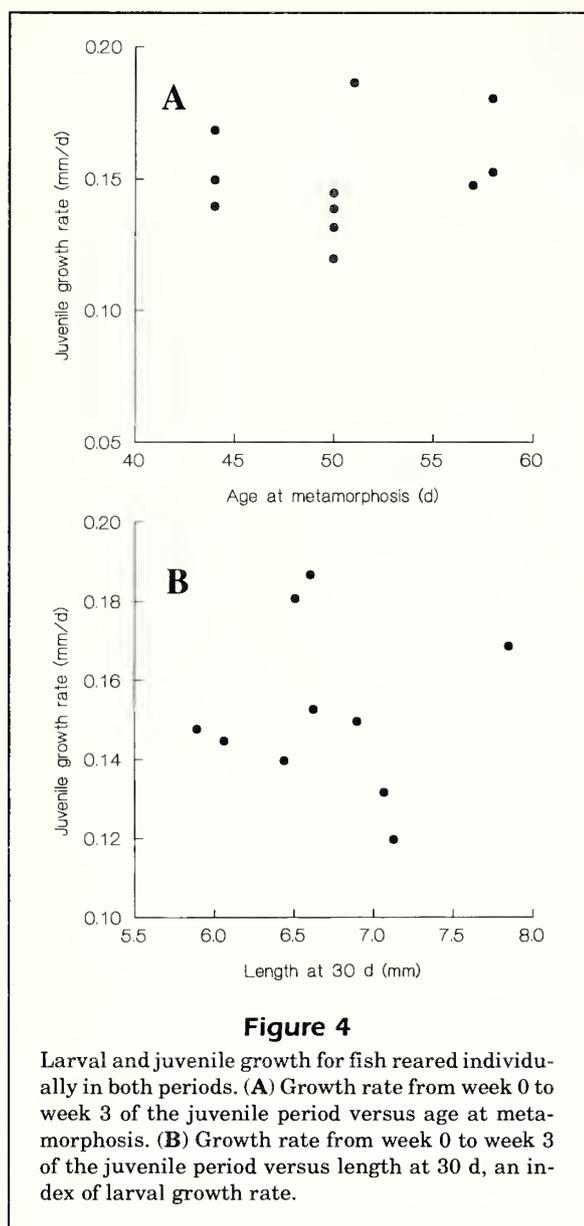
phosis ( $r=0.22$ ,  $n=11$ ,  $P=0.52$ ; Fig. 4A). Similarly, juvenile growth rate showed no relationship to length at 30 d ( $r=-0.001$ ,  $n=10$ ,  $P=0.99$ , Fig. 4B). For comparative purposes, juvenile growth rate was also regressed against the measure of larval growth rate used by Bertram et al. (1993). The slope of the relationship,  $-0.18$  mm/d, although not significantly different from 0, was identical to that reported by Bertram et al. (1993).

### Group-reared larvae

Length at metamorphosis was independent of age at metamorphosis among members of family 3 ( $r=-0.09$ ,  $n=205$ ,  $P=0.23$ ) reared in groups as larvae and individually as juveniles. (Note that 175 of these larvae came from a single rearing aquarium and that the

remainder were also from a single tank.) Length at metamorphosis ranged from 5.6 mm to 7.36 mm ( $6.6 \pm 0.3$  mm). Age at metamorphosis ranged from 32 d to 59 d ( $42.6$  [ $\pm 6.7$ ] d). Individual growth rates during weeks 1–4 of the juvenile period were unrelated to age at metamorphosis ( $r=0.055$ ,  $n=52$ ,  $P=0.71$ ; Fig. 5A). Juvenile growth rates were unrelated to larval growth rates ( $r=0.14$ ,  $n=52$ ,  $P=0.322$ ; Fig. 5B). Because juvenile growth rates were equivalent, we pooled cohorts that metamorphosed at different times on the basis of the number of days after metamorphosis. Coefficients of variation for size-at-d postmetamorphosis were unrelated to postmetamorphic age (weeks 1–4) and never exceeded 0.08.

Individual juveniles exhibited significantly faster growth rates during weeks 1–4 than during weeks 5–7 ( $t=9.45$ ,  $df=17$ ,  $P<0.0001$ ).



## Discussion

Our data on growth dynamics of larval fishes show that size at age is highly variable during the larval period. Patterns in CV's for size at age demonstrate that most of the variation upon which selection can act is found during the early to mid phase of the larval period. Chambers et al. (1988), who analyzed average growth rates of larvae reared in groups, also found that CV's for size at age increased from hatching to a peak of 0.135 at 28 d and subsequently declined as metamorphosis approached. In this study, most larval growth occurred during the first 30 d. Individual larvae that grew most rapidly and reached

the largest size at about day 30, midway through the larval period, metamorphosed at the youngest ages. Travis (1981), who reared anuran larvae individually, also reported that age at metamorphosis was inversely related to size midway through the larval period. Despite the nonlinear growth observed, the length at 30 d and the average larval growth rate were positively correlated. Thus, the general conclusion (derived from those studies where average larval growth was used and larval growth was assumed to be linear) that rapid growth reduces the duration of the larval period is supported (Chambers and Leggett, 1987; Chambers et al., 1988; Bertram et al., 1993).

The relationship between larval growth rate and larval-period duration, however, may not be straightforward. Although larval growth rate is the primary factor influencing larval-period duration, its effects appear to be modified by the duration of the latency period. Larvae that grow rapidly tend to reach maximum larval length at an early age. However, individuals that reach maximum larval length at an early age have a longer latency period than those larvae that reach maximum length late in the larval period. This finding suggests that rapid growth is associated with a long latency period. Slower-growing larvae, in comparison, may reach metamorphosis at a later age but have a considerably shorter latency period. Moreover, this suggests that metamorphosis may require a minimum duration, independent of size. These findings are consistent with Ricklefs' (1973, 1979) hypothesized tradeoff between growth rate and the acquisition of mature tissue function in birds. In this connection, it is noteworthy that a tradeoff between growth rate and the rate of protein turnover has been documented for the mussel *Mytilus edulis* (Hawkins et al., 1986). Our findings are also consistent with Balon's (1990) suggestion that through epigenetic interactions, individuals within a clutch may form distinct developmental groups—some being more altricial and others more precocial.

Growth rate estimates will be biased if mortality is size dependent. Biased growth-rate estimates will, in turn, reduce estimates of variation in growth rate. However, the extent of variability in larval growth rates reported here are not due to size-dependent mortality. Our analysis could not detect size-dependent mortality, and there was no reduced variability in growth until the end of week 4. Survival to metamorphosis was relatively high (26 out of 53 [49%] from family 1) for individuals replaced on day 22. High survival from day 1 to metamorphosis (175 out of 400 [44%]) was also observed for group-reared larvae in one of the rearing aquaria for family 3. Importantly, the CV for size and age at metamorphosis was similar for the individual and group-reared larvae. The CV for age at metamorphosis was 0.14 and 0.17 for individually reared and group reared larvae ( $n=175$ ), respectively. The CV for size at metamorphosis was 0.045 and 0.046 for individually reared and group-reared larvae ( $n=175$ ), respectively. (Note that the CV's for age and size at metamorphosis for the full data set of group reared larvae [ $n=205$ ] were indistinguishable from those reported above for the reduced data set [ $n=175$ ]). The similarity of CV's for age and size at metamorphosis implies similar scope for variation in growth rate despite differences in the rearing protocol.

We used a small number of female broodstock. This small number of fish, however, did not preclude in-

sight into the potential for variation in larval growth and development at the population and species level. Previous research on early life history traits in winter flounder has shown that most of the total variation in metamorphic traits (age and size at metamorphosis) occurred within rather than among maternal families (Chambers and Leggett, 1992). Differences between families in the relationship between size and age at metamorphosis (Chambers and Leggett, 1987; see below) and length at metamorphosis (Chambers and Leggett, 1992, Bertram et al., 1993), although detectable, appear small in comparison with the similarities between families for variation in age at metamorphosis. Indeed, Chambers and Leggett (1992) reported that most variation in age at metamorphosis resided within each rearing aquarium. The CV's for age and size at metamorphosis reported here are similar to those reported by Chambers and Leggett (1987) despite differences in rearing temperatures and origins of broodstock employed in the two studies. Chambers and Leggett (1992) developed several qualitative expectations for parental influences on larval flatfishes. They suggested that parentage is likely to influence larval traits but that its contribution to the total phenotypic variation in larvae is expected to diminish during the larval period. In addition, the degree of parental influence is likely to be trait-specific. The absence of parental effects on important traits such as larval-period duration (age at metamorphosis) supports the potential generality of our results on early life history traits based on few parents. Moreover, in the absence of field data, laboratory-based research such as this represents the only basis for characterizing and predicting the dynamics of patterns of individual larval growth and development.

The survival consequences of individual variation in larval growth and development reported here are presently unknown. We do not know whether individuals that grow rapidly and metamorphose at an early age have a survival advantage over those that grow more slowly and metamorphose at an older age. Despite the limited supporting evidence, there has been widespread acceptance of the hypothesis that rapid larval growth conveys a survival advantage because those individuals are large at age and often have a reduced larval-period duration (Bertram, 1993; Leggett and Deblois, 1994). D'Amours (1992) tested directly the hypothesis that rapid larval growth increases survival by using wild 0-group (17–47 d) Atlantic mackerel, *Scomber scombrus*. Comparing the otolith microstructure of larvae from one cohort captured at two different intervals in time, he found no evidence of higher survivorship among faster-growing larvae. In addition, two studies have

found that larvae that are small at age may, under certain circumstances, be less vulnerable to predation than are large members of a cohort (Litvak and Leggett, 1992; Pepin et al., 1992; Bertram, 1996). In flatfishes and in other fishes that switch habitats at metamorphosis, the time of transition is likely to be associated with high mortality. In recent laboratory experiments, Whiting and Able (1995) demonstrated that mortality from shrimp (*Crangon septemspinosa*) predation on settled winter flounder (10.1–14.5 mm) was twice that of presettled individuals ( $\leq 11$  mm). Bertram and Leggett (1994), however, could detect no difference in shrimp-induced mortality for winter flounder that differed in either length or age at metamorphosis. In the present study, there was a positive relation between length and age at metamorphosis for individually reared winter flounder, but this trend was not evident from the larger sample of group-reared fish (see also Bertram et al., 1993). However, the results may not be strictly comparable because different families were used for the individual and group rearing. Chambers and Leggett (1987) reported a positive relation between length and age at metamorphosis for 8 of 18 families of laboratory-reared winter flounder from Newfoundland. The appropriate experiments have not been conducted to determine whether both large size and old age at metamorphosis reduce mortality due to predation. Therefore, to date, there is no firm basis for interpreting the survival consequences of the individual variation in larval growth and development patterns reported here.

The results of this study are consistent with Bertram et al.'s (1993) finding that size at age does not diverge continuously during the larval and juvenile periods. Overall, the results show that juvenile growth rates are parallel, despite differences in larval growth rates and age at metamorphosis. The parallel nature of juvenile growth rates shows that slow-growing larvae partially compensated for their small size at age by increasing their juvenile growth rates to a greater degree than did fish that grew rapidly as larvae. However, the compensatory growth among slow-growing larvae was not sufficient to cause convergence in juvenile size at age. If these growth rates are maintained, differences in size at age of juveniles that metamorphosed early and late would remain.

Previous work has shown that growth rates of group-reared fish were maintained from weeks 1–7 of the juvenile period (Bertram et al., 1993). In the present study, however, the growth rate of individually reared juveniles was slower in weeks 5–7 than during weeks 1–4. There is reason to believe that food availability was a factor in this difference. Ju-

veniles reared in groups in 7-L containers were exposed to concentrations of 292 prey/d per fish. Juveniles reared individually in 0.4-L containers received 100 prey/d because rations were 0.25 *Artemia* nauplii/(mL·d) for both container sizes. Consequently, food availability may have limited the growth rate of individually-reared juveniles during weeks 5–7 when fish were relatively large and food requirements were maximal.

An important conclusion from this study is that the insight into the dynamics of larval growth and development was gained only because the data were presented as individual-based observations. Although the CV's of size at age would have been available if the weekly length measures of individuals had been pooled, the underlying growth dynamics and individual variability would have been concealed. Moreover, a single "growth" curve fit to such size-at-age data would not accurately reflect the growth patterns of individual larvae. In this connection, we point out that a recent description of winter flounder larval "growth," based upon reconstructions of size at age from otolith microstructure (Jearld et al., 1993), bears little resemblance to the individual growth trajectories shown here.

Darwin (1859) wrote: "No one supposes that all individuals of the same species are cast in the very same mould"; but it is only recently that fishery scientists have begun to investigate the potential population consequences of phenotypic variability in early life history stages. Because mechanisms controlling survival and recruitment of fishes operate at the level of the individual (Crowder et al., 1992), baseline estimates on phenotypic variability are required. This study clearly shows that rearing marine fish larvae individually in the laboratory can provide such estimates. We have shown that there is considerable variability in the dynamics of individual larval growth and development. Studies that examine the survival consequences of such variability represent a logical next step in research programs designed to provide a mechanistic understanding of the factors that affect survival during fish early life history.

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**Abstract.**—This study presents archeological evidence for the presence of adult bluefin tuna, *Thunnus thynnus*, in waters off the west coast of British Columbia and northern Washington State for the past 5,000 years. Skeletal remains of large bluefin tuna have been recovered from 13 archeological sites between the southern Queen Charlotte Islands, British Columbia, and Cape Flattery, Washington, the majority found on the west coast of Vancouver Island.

Vertebrae from at least 45 fish from 8 sites were analyzed. Regression analysis (based on the measurement and analysis of modern skeletal specimens) was used to estimate fork lengths of the fish when alive; corresponding weight and age estimates were derived from published sources. Results indicate that bluefin tuna between at least 120 and 240 cm total length (TL) (45–290 kg) were successfully harvested by aboriginal hunters: 83% of these were 160 cm TL or longer. Archeological evidence is augmented by the oral accounts of native aboriginal elders who have described strategies used until the late 19th century for hunting bluefin tuna.

Despite this information, there are no 20th-century records of adult bluefin tuna in the northeastern Pacific. Archeological evidence suggests that either perturbations in the distribution of Pacific bluefin have occurred relatively recently or the specific environmental conditions favoring the movement of large tuna into northeastern Pacific waters have not occurred in this century.

## Archeological evidence of large northern bluefin tuna, *Thunnus thynnus*, in coastal waters of British Columbia and northern Washington

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Evidence is presented here for the occurrence of adult bluefin tuna, *Thunnus thynnus*, in waters of the northeastern Pacific, off the coast of British Columbia and northern Washington, for the past 5,000 years. The physical evidence consists of archeological remains of large bluefin tuna harvested by aboriginal hunters. Aboriginal North Americans of this area (part of the so-called "Northwest Coast" culture region) were accomplished seamen and skilled hunters of marine mammals (Mitchell and Donald, 1988). Coastal archeological sites throughout this region often contain abundant skeletal remains of the many fish and marine mammal species that sustained human populations over thousands of years (Calvert, 1980; Huelsbeck, 1983; Mitchell, 1988).

Skeletal remains of large bluefin tuna have been recovered from 13 archeological sites. The archeological deposits containing tuna date from at least 5,000 years ago until the early 20th century. The existence of bluefin tuna remains from this region have been previously reported (McMillan, 1979), but none were systematically analyzed until now.

For this study, 78 intact vertebrae from 8 archeological sites were measured and the data compared with those from vertebrae of modern specimens (specimens from the re-

maining 5 sites could not be examined, owing largely to difficulties in retrieving archived specimens but, in one case, because all skeletal material had been discarded by museum staff). Tentative estimates of the size of the archeological specimens were made by comparing the size of vertebrae from modern specimens of known length with the size of vertebrae collected from archeological deposits. The resulting length estimates were then used to calculate weight and age estimates by using length-weight algorithms derived from recent data. Data are presented in a manner that should facilitate the analysis of any additional archeological specimens recovered.

In addition to the results of the analysis of the archeological material, anecdotal evidence is presented from ethnographic accounts of tuna-fishing methods related by native elders of the Mowachaht tribe who live on the west coast of Vancouver Island. These recent oral accounts substantiate and augment the physical evidence: they describe bluefin tuna ethology, pinpoint the time of year that bluefin tuna were present and confirm that large bluefin tuna were being harvested in the northeastern Pacific until the late 19th century. The historic evidence for bluefin tuna occurrence in this area, although sparse, is also presented.

The archeological evidence and ethnohistoric accounts are significant because of the absence of modern records for adult bluefin tuna in the northeastern Pacific. Consequently, the distribution of northern bluefin tuna of all age classes in the Pacific and all modern records for adults in the eastern Pacific are reviewed. The addition of historical information presented here to our present state of knowledge of modern bluefin tuna distributions has important implications for our understanding of changing environmental conditions over time and perhaps also for determining the impact of 20th-century fisheries on Pacific bluefin tuna populations.

## Distribution of Pacific bluefin tuna

The distribution of northern bluefin tuna in the Pacific is somewhat enigmatic, especially that of the adult portion of the population (Foreman and Ishizuka, 1990; Bayliff, 1994; Smith et al., 1994). Sexual maturity in Pacific northern bluefin is reached at about 5 years, and most spawning is reported between April and July in waters off Japan and the Philippine Islands, and in August in the Sea of Japan (Bayliff, 1994). Northern bluefin tuna are transoceanic migrators in both the Atlantic and Pacific; the movements of these fish are largely deduced by tagging experiments and catches of various age classes at specific times and locations (Nakamura, 1969; Rivas, 1978; Bayliff, 1994).

Some of the population of Pacific bluefin tuna migrate from the western to the eastern Pacific Ocean during their first or second year. The proportion of the population that undertakes this migration appears to vary from year to year (Bayliff et al., 1991). These migrating fish spend a period of one to six years in the eastern Pacific, a sojourn which may or may not be interrupted by visits to the central or western Pacific before the survivors return to spawn in the west (Bayliff, 1994). Adult fish in the Pacific appear to follow a general pattern of being distributed farther to the west during the spring (when spawning occurs) and farther to the east in the fall (Bayliff, 1993).

It is not known if all fish return to spawn every year after sexual maturity is reached. Tagging experiments indicate that although the journey from west to east may take 7 months or less, the journey from east to west takes nearly 2 years; therefore there does not appear to be enough time for mature adult fish migrating from the eastern Pacific to spawn in the west every year. In addition, because a few adult fish have been captured in the eastern Pacific either just before or after the spawning season, some adults

probably do not return to the western Pacific every year but rather spend variable lengths of time in the eastern Pacific (Bayliff, 1994).

Most harvested adult bluefin tuna are caught in the western Pacific, where they are known to range as far north as the Sea of Okhotsk at about 50°N (Bayliff, 1980). Catch records of large bluefin tuna are noted at feeding areas off northeastern Honshu, Japan (ca. 40°N), off eastern Taiwan (about 25°N), and in the central Pacific near the Emperor Seamount (40°N, 175°E) (Nakamura, 1969).

Adult bluefin tuna are considered rare everywhere in the eastern Pacific; sporadic records have come from southern California and northern Mexico only. Although small bluefin tuna (less than 120 cm total length [TL] and 5–45 kg) are caught regularly off California and Mexico and somewhat larger fish (120–160 cm TL and 45–80 kg) occasionally, adults over 160 cm TL (80 kg) are seldom encountered (Foreman and Ishizuka, 1990; Bayliff, 1994).

In the northern portion of the eastern Pacific, few modern records exist for bluefin tuna. Neave (1959) mentioned three occurrences in British Columbia waters during August 1957 and 1958, but no sizes or numbers were given. These reports came from an area approximately 200–400 miles off the west coast of Vancouver Island (49°N, 134°24'W; 48°N, 131°06'W; 51°N, 130°W). A 7.5-kg bluefin tuna was caught in a salmon seine in July 1958, near Kodiak, Alaska, and on 1 October 1957, bluefin tuna were sighted 80–100 miles off Cape Flattery, Washington (Radovich, 1961). Sea-surface temperatures off the British Columbia coast were reported as being warmer than usual during both years.

I presume (because no sizes are mentioned in the reports) that these recent northern records are for relatively small fish of 5–45 kg because this size range is the most common in the eastern Pacific. Bluefin tuna larger than 45 kg in the eastern Pacific are rare enough that they are noteworthy when encountered. Although the earliest modern record of a very large bluefin tuna in southern California appears to be that of 1899 (Holder, 1913), sporadic occurrences of bluefin tuna over 50 kg have been reported since then (Dotson and Graves, 1984; Foreman and Ishizuka, 1990).

The largest reported catch of giant bluefin tuna in the eastern Pacific was made in 1988 (Foreman and Ishizuka, 1990). Seiners caught an estimated 987 adult bluefin tuna between November and early January off southern California, including many over 100 kg and some more than 250 kg, including one that broke California records at 458 kg and 271.2 cm TL. Seiner operators involved in this fishery reported that large bluefin tuna travelled in small

schools of less than 10 similar-size individuals, often less than 5 for very large fish.

Analysis of stomach contents of some of these fish indicated that they had been feeding at the surface on chub mackerel, *Scomber japonicus*, and the opalescent inshore squid, *Loligo opalescens*, a strongly phototactic species (Recksiek and Frey, 1978). Bluefin tuna are also reported to be phototactic (Bayliff, 1980). When water temperatures were recorded for these 1988 catches, they indicated lower than average sea-surface temperatures (mean 14.1°C) for southern California waters in the eastern Pacific. Bluefin tuna are generally found associated with water temperatures of 17–23°C (Bell, 1963).

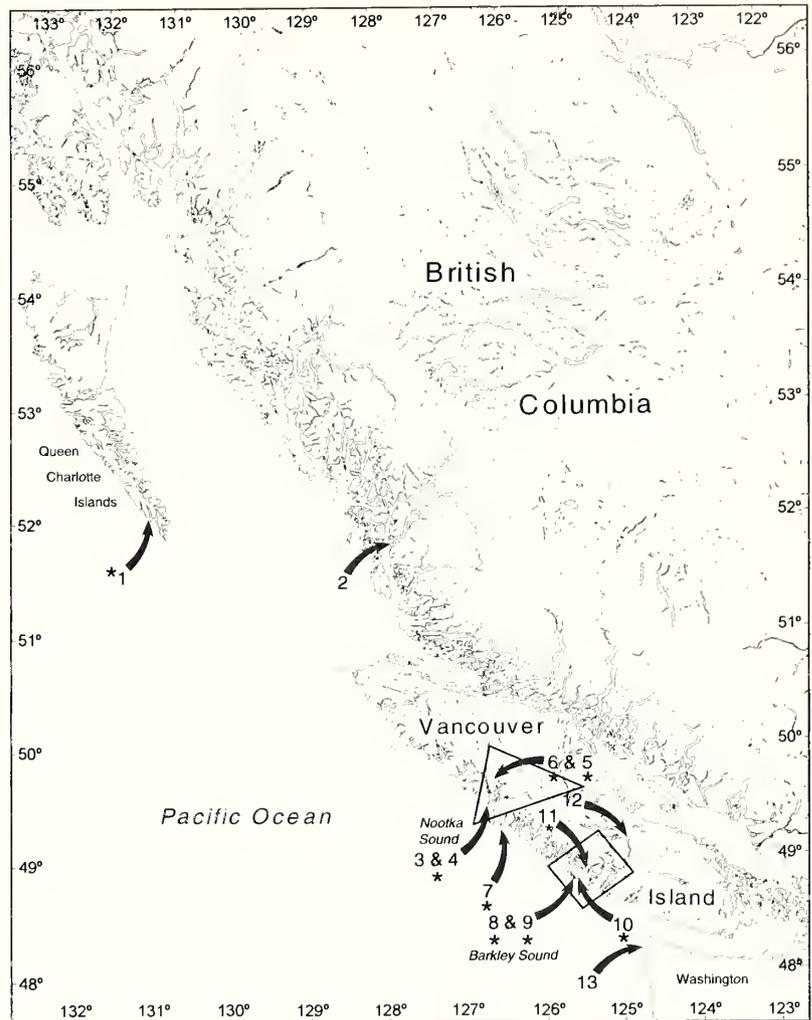
The commercial catch of such high numbers of large fish in 1988 has raised the possibility that adult bluefin tuna may occur regularly off California but are only occasionally recognized or observed. Foreman and Ishizuka (1990) have suggested that small schools of adult bluefin tuna may go unrecognized if mistaken for pods of marine mammals or go undetected if travelling or feeding at depth. If so, it may be that the conditions that govern their infrequent movement into inshore feeding areas are very specific and thus rarely occur.

## Analyses and results

### The archeological sample

Vertebrae were examined from 8 of the 13 sites from which remains of bluefin tuna were found. As is typical for faunal remains recovered from archeological sites, chronological dates for tuna specimens are estimated in relation to the <sup>14</sup>C-dated strata from which they were recovered: none of the bluefin tuna remains have yet been dated directly.

The northernmost archeological evidence for the occurrence of bluefin tuna is from the southern Queen Charlotte Islands (Fig. 1), whereas Namu on the central British Columbia mainland is the oldest known deposit yielding bluefin tuna remains (dated at 4050–3050 BC). Bluefin tuna have also been recovered from sites at Hesquiatic Harbour and Shoemaker Bay on the west coast of Vancouver Island and from the



**Figure 1**

Map of the Pacific northwest coast of North America, showing the location of archeological sites from which bluefin tuna, *Thunnus thynnus*, remains have been recovered. \* indicates samples examined in this study. \*1 = FaTt 9 Louscoone Point; 2 = ElSx 1 Namu; 3 = DjSp 1 Yuquot village; \*4 = DjSp 3 Yuquot midden; \*5 = DkSp 1 Kupti; \*6 = DkSp 3 Tahsis midden; \*7 = DiSo 1 Hesquiatic; 8 = DfSi 4 Macoah; \*9 = DfSi 5 Ch'uumat'a; \*10 = DfSj 23A T'ukw'aa village; \*11 = DfSj 23B T'ukw'aa defensive site; 12 = DhSe 2 Shoemaker Bay; 13 = 45CA24 Ozette village.

Ozette site near Cape Flattery, Washington (see Table 1 for more details). Vertebrae are the only traces of bluefin tuna recovered from the above sites, and only specimens from the Hesquiatic Harbour and Queen Charlotte Islands were available for analysis.

Archeological excavations at four sites each in both Nootka and Barkley Sounds on the west coast of Vancouver Island also yielded bluefin tuna remains and, in contrast to other area sites, both vertebral and nonvertebral skeletal remains are represented. Neither scales nor otoliths, however, were found. Tuna were reported from all strata of the 1966 excavation at the village of Yuquot on Nootka Sound

Table 1

Archeological sites from which bluefin tuna, *Thunnus thynnus*, remains have been recovered, with excavation information, dates, references and numbers of remains reported that could not be analyzed in this study.

Area and site no.	Description of site and excavated remains
<b>Queen Charlotte Islands and the North Coast, British Columbia</b>	
1 (FaTt 9)	Louscoone Point village, Kughit Haida territory; 52°08'N, 131°14'W; small test excavation 1985 (Wigen <sup>1</sup> ; Acheson <sup>2</sup> ); from deposits dated ca. AD 800–ca.1800.
2 (ElSx 1)	Namu village, Bella Bella territory; 51°52'N, 127°52'W; major excavation 1969–71; from deposits dated 4050–3050 BC (Cannon, 1991); 1 vertebra reported.
<b>Vancouver Island, British Columbia</b>	
Nootka Sound area sites, Mowachat territory; ca. 49°40'N, 126°37'W	
3 (DjSp 1)	Yuquot village; major 1966 excavation; from all deposits 2300 BC–AD 1880 (McMillan, 1979); 87 vertebral and nonvertebral specimens reported.
4 (DjSp 3)	Yuquot fishing station; from surface collection 1968; no dates (Marshall <sup>3</sup> ).
5 (DkSp 1)	Kupti village; small 1968 excavation; from deposits ca. AD 1260–1460 (Marshall <sup>3</sup> ).
6 (DkSp 3)	Tahsis Inlet midden; from 1990 shovel test; no dates (Marshall <sup>3</sup> ).
7 (DiSo 1)	Hesquiat village, Hesquiat territory; 49°24'N, 126°28'W; major 1973–75 excavation; from deposits dated AD 1230–1430 (Calvert, 1980).
Barkley Sound area sites, Toquat territory; ca. 49°N, 125°20'W; 1991–93 excavations (McMillan and St. Claire <sup>4</sup> )	
8 (DfSi 4)	Macoah village; bluefin from upper levels of deposits dated 2460 BC–ca. AD 1880.
9 (DfSi 5)	Ch'uumat'a village; bluefin from deposits dated ca. AD 1370.
10 (DfSj 23A)	T'ukw'aa village; bluefin tuna from deposits dated AD 760–1310.
11 (DfSj 23B)	T'ukw'aa defensive site; bluefin tuna from deposits dated AD 1175–1880.
12 (DhSe 2)	Shoemaker Bay, Tseshah territory; 49°15'N, 124°49'W; major 1973/74 excavation; from deposits dated AD 500–820 (Calvert and Crockford, 1982); 17 vertebrae reported.
<b>Olympic Peninsula, Washington State</b>	
13 (45CA24)	Ozette village, Cape Alava; Makah (Nuu-chah-nulth subdivision) territory; 48°10'N; 124°44'W; major 1971–80 excavation; from house floor deposits dated AD 1510 (Huelsbeck, 1983); 2 vertebrae reported (one modified).

<sup>1</sup> Wigen, R. J. 1990. Identification and analysis of vertebrae fauna from eighteen archaeological sites on the southern Queen Charlotte Islands. British Columbia Heritage Trust, 800 Johnson St. Victoria, British Columbia, Canada V8W 1N3. Unpubl. rep., 79 p.

<sup>2</sup> Acheson, S. 1992. Archaeology Branch, British Columbia Ministry of Small Business, Tourism, and Culture, 800 Johnson St., Victoria, British Columbia, Canada V8W 1N3. Personal commun.

<sup>3</sup> Marshall, Y. M. 1990. The Mowachat archaeology project, phase 1, 1989. Archaeology Branch, British Columbia Ministry of Small Business, Tourism, and Culture, 800 Johnson St., Victoria, B.C., Canada V8W 1N3.

<sup>4</sup> See Footnote 3 in the main text of this paper.

(dated from about 2300 BC to ca. AD 1880), making this the longest continuous record of *Thunnus* occurrence in the region (McMillan, 1979; Marshall, 1993). Unfortunately, these specimens are archived in Ottawa and could not be retrieved easily for analysis: three other small excavations undertaken during 1968 and 1990 at sites along Nootka Sound, however, recovered remains of bluefin tuna and these specimens were available for inclusion in this analysis.

It is pertinent to mention that all fish remains from the 1966 excavation of the village at Yuquot were identified to genus level only (McMillan, 1979), perhaps giving the impression that the tuna remains might be albacore (*T. alalunga*), a species that oc-

curs regularly in the eastern Pacific (Hart, 1973). However, crew working on the excavation of Yuquot reported that remains of some very large fish were recovered (Dewhirst<sup>1</sup>). According to the literature (and in my own twenty years experience analyzing faunal remains from this area), albacore have never been reported from any archeological site in British Columbia. Moreover, albacore rarely, if ever, exceed 50 kg; it therefore seems unlikely that *Thunnus* remains from Yuquot are albacore rather than bluefin tuna.

<sup>1</sup> Dewhirst, J. 1992. Archeo Tech Associates, 1114 Langley St., Victoria, British Columbia, Canada V8W 1W1. Personal commun.

**Table 2**

Calculated fork lengths (cm) and estimated weights (kg) of comparative specimens—USNM catalog numbers 269001, 269004, 268964, 269002 (Nankai collection numbers 1, 2, 3, 6) National Museum of Natural History (NMNH), Smithsonian Institution.

	Nankai 1 269001	Nankai 2 269004	Nankai 3 268964	Nankai 6 269002
Skull length (cm)	26.2	25.3	23.5	28.5
Total of vertebral lengths (1–39 cm) <sup>1</sup>	148.1	124.1	121.2	146.9
Total skeletal length (SL) (cm)	174.3	149.4	144.7	175.4
Estimate of intervertebral cartilage—40 spaces	20.0	20.0	20.0	20.0
Estimate of snout and tail flesh (cm)	10.0	10.0	10.0	10.0
Estimated fork length (cm)	204.3	179.4	174.7	205.4
Estimated weight (kg) <sup>2</sup>	184	130	121	187

<sup>1</sup> All measurements available from the author or NMNH, Smithsonian Institution.

<sup>2</sup> Foreman and Ishizuka, 1990; 184.

Recent excavations at four locations along Toquart Bay in Barkley Sound on the west coast of Vancouver Island have recovered relatively large numbers of both vertebral and nonvertebral bluefin tuna skeletal remains. Full analysis of this material is still in progress: only a few of the nonvertebral remains have been examined thus far. All vertebrae, however, are included in this study.

### Modern skeletal samples

In order to estimate the size of fish represented by isolated vertebrae from archeological samples, it was necessary to determine the size relationship between individual vertebrae and the corresponding fork length in modern samples of the fish. Measurements taken from the vertebrae of modern skeletal specimens of known-size fish of comparable size were used for this purpose (Casteel, 1976; Wheeler and Jones, 1989).

Recent skeletal specimens of large (160 cm TL and over) Pacific bluefin tuna were found to be extremely rare, and the only known specimens had, unfortunately, no corresponding size data (length or weight); therefore fork lengths (snout to fork of the tail) had to be estimated for these specimens as well. Fortunately, these four recent specimens of bluefin tuna (loaned by B. Collette, Museum of Natural History, Smithsonian Institution, Washington, D.C.) have skulls that are still articulated, and it was possible to determine a “skeletal length” for these specimens (Table 2). The skeletal length is defined as the basal length of the skull plus the combined lengths of all 39 vertebrae. The vertebral column of the comparative specimens had been sawed into sections during skeletal preparation, sometimes by cutting through

a centrum. Vertebra no. 30, either by itself or with portions of no. 29 and no. 31 attached, was apparently removed from the specimens at some point and not returned. Estimates of the length measurements of all three of these vertebrae were used in the regression equations. These four fish appear to be the only disarticulated skeletal specimens of large Pacific bluefin tuna available for analysis (however, several museums have reconstructed skeletal specimens of large individuals on display). All raw data for these specimens are available on request from the author and are also on file at the National Museum of Natural History, Smithsonian Institution.

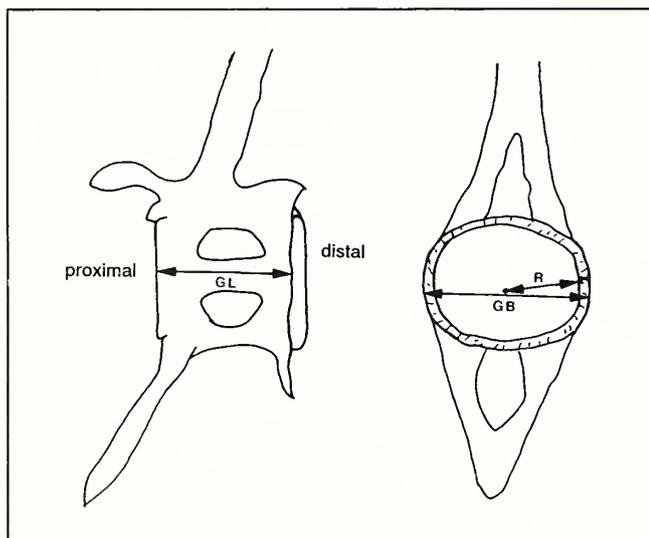
In order to estimate a fork length from the skeletal length for these comparative specimens, I assigned a value of 0.5 cm to the intervertebral cartilage (40 spaces, 20 cm total) and an additional 5 cm each for flesh on the snout and the tail. These values consistently added 30 cm to the measured skeletal length and yielded an estimated fork length. This method was chosen so that if a more accurate determination of the “soft tissue” component of the fork length of bluefin tuna is subsequently developed, the estimates given in this report can be easily adjusted.

The vertebral centrum length and breadth measurements from the four comparative specimens (Fig. 2) were used in single (least-squares) regression equations for each of the 39 vertebrae in the spinal column by using logarithmic transformations of vertebral and skeletal length measurements to determine their linear relationship. Because the size and shape of vertebrae change (sometimes quite dramatically) over the length of the fish, it was necessary to calculate a separate algorithm for each vertebra in the spinal column.

Table 3 presents the resulting values for the relationship between the greatest centrum length, GL, and greatest proximal centrum breadth, GB(p), to the skeletal length, SL, for the recent specimens as calculated by regression analysis. In this table, some values are missing or are based on only 3 specimens owing to the original preparation of the comparative skeletons. Standard deviations and confidence limits are not given but are available on request.

### Size determination of archeological specimens

The standard formula used to estimate the size of fish represented by the archeological specimens is given by Casteel (1976, p. 96) as:  $\log(\text{fork length}) = a + b \times \log(\text{GL or GB})$ . The constant ( $a$ ) and the slope—or  $x$  coefficient—( $b$ ) are taken from Table 3 (i.e. the values derived from the comparative specimens), and the logarithm of the greatest length, GL, or proximal breadth, GB(p), from each archeological specimen (Table 4).



**Figure 2**

Definitions of vertebral measurements taken from both comparative and archeological specimens of bluefin tuna. Greatest length (GL): maximum length of the centrum, taken at the lateral midpoint with digital calipers and measured to the nearest mm. Greatest breadth (GB) = maximum breadth of the centrum, taken at the lateral midpoint of the proximal face, GB(p), and distal face, GB(d), taken with digital calipers and measured to the nearest mm. Radius (R) = the maximum distance from the center of the cone to the edge, of the proximal face, R(p), and distal face, R(d), taken at the lateral midpoint. This measurement was taken with a plastic ruler cut diagonally to fit into the cone of the centrum; in this way the amount of growth from the center of the cone to the sharp raised ridge at the lip of the centrum was measured to the nearest 0.5 mm.

Casteel (1976) noted that although the regression method is the most accurate way to estimate fish length from bone size, these length estimates always vary somewhat between vertebrae from the same individual, even when the predictive value ( $r$ ) of the equation is high. When both length and breadth measurements were available for an archeological specimen, the measurement that produced the length estimate with the highest correlation coefficient ( $r$ ) value for that individual was used to represent that fish. Alternatively, an average of all available measurements could have been made, although this method allowed both comparative and archeological specimens to be treated similarly.

The method used in the present study required that vertebral specimens be identified to exact column position. This can be problematic for archeological specimens because several of the centra in the vertebral column are almost identical and because archeological specimens may often lack diagnostic neural or haemal arches and spines. However, an archeological specimen can almost always be defined to a small range within the column (e.g. vertebrae numbers 14–16). Vertebrae not identified to exact position were found to be so similar in size and proportion to adjacent vertebrae that they could be treated as interchangeable for the purpose of the estimations attempted here. Where the exact position of an archeological specimen was uncertain (which occurred for less than one third of the specimens examined), the number of the vertebra used to calculate the size estimates is given in parentheses, e.g. (15).

Table 4 presents all archeological vertebrae measured (by vertebra number) and the length estimates derived from them. Where eroded edges prevented accurate measurement, an estimate was taken if it was likely to be accurate to within 1 mm. A total of 78 vertebrae were measured, representing at least 45 individuals. Several vertebrae were found attached (occasionally in articulated position) or could potentially have belonged to the same individual by virtue of similar size and proximity within the archeological deposit (this is a standard assumption for determining the minimum number of individuals represented by skeletal remains recovered from archeological contexts). Radius measurements of these specimens were also taken (because this dimension is preferred by some researchers for ageing purposes) but are not reported or used in the calculations. All measurements are available on request from the author.

The fork-length estimates for the archeological sample listed in Table 4, as for the comparative skeletons, are derived by adding 30 cm to the estimated skeletal length to yield a fork length (to account for

Table 3

Regression analysis values: log of vertebral lengths, *GL*, and proximal breadth, *GB(p)*, vs. log of skeletal length, *SL*, of 4 modern bluefin specimens (USNM 269001, 269004, 268964, 269002). NA = not applicable. Number of observations=4 (\*=3); Degrees of freedom=2 (\*=1).

Vertebra no.	Constant <i>GL</i>	X Coefficient <i>GL</i>	<i>r</i> value <i>GL</i>	Constant <i>GB(p)</i>	X Coefficient <i>GB(p)</i>	<i>r</i> value <i>GB(p)</i>
1	4.8553	0.7814	0.903	NA	NA	NA
2	4.6692	0.8328	0.881	3.8396	0.9154	0.892
3	4.4210	0.9155	0.917	4.0180	0.8634	0.945
4	4.6286	0.8486	0.901	4.4710	0.7433	0.965
5	5.2932	0.6351	0.908	4.5377	0.7295	0.997
6	4.9966	0.7257	0.933	4.6478	0.7096	0.981
7	4.2052	0.9593	0.992	4.3649	0.8043	0.970
8	4.1994	0.9492	0.932	4.0022	0.9111	0.970
9	4.6598	0.8064	0.955	3.9509	0.9272	0.985
10	4.7950	0.7543	0.928	3.9373	0.9300	0.994
11	3.9914	0.9810	0.993	3.8234	0.9561	0.996
12	5.3210	0.5964	0.908	4.2293	0.8463	0.985
13	4.6473	0.7785	0.971	4.3599	0.8081	0.994
14	4.4486	0.8287	0.983	4.0404	0.8918	0.992
15	4.5968	0.7815	0.954	4.4404	0.7807	0.988
16	4.6118	0.7746	0.991	4.4515	0.7768	0.986
17	4.2226	0.8808	0.972	4.3918	0.7903	0.989
18	3.5879	1.0526	0.962	4.3059*	0.8088*	1.000
19	4.3551	0.8328	0.997	4.2695	0.8175	0.988
20	4.3449	0.8360	0.994	4.4124	0.7797	0.983
21	4.1621	0.8809	0.985	4.3422	0.7963	0.987
22	4.2308	0.8604	0.987	4.2783	0.8129	0.991
23	5.1630*	0.5922*	0.705	NA	NA	NA
24	4.3756	0.8189	0.987	4.4521	0.7663	0.989
25	4.2320	0.8561	0.989	4.1347	0.8494	0.988
26	4.0288	0.9085	0.997	4.2699	0.8127	0.975
27	3.8883	0.9387	0.995	4.4668	0.7626	0.984
28	3.8464	0.9475	0.996	3.9946	0.8854	0.993
29	3.4217	1.0551	0.976	4.1875	0.8305	0.979
30	4.0737	0.8741	0.937	4.1472	0.8386	0.999
31	3.6730	0.9715	0.886	NA	NA	NA
32	4.0061	0.8852	0.876	NA	NA	NA
33	4.5576	0.7398	0.859	3.7206	0.9430	0.995
34	5.1867	0.5850	0.598	3.9220	0.9076	0.998
35	5.6621	0.4777	0.595	4.3345	0.8317	0.976
36	5.3978	0.5952	0.942	5.8817*	0.4347*	0.713
37	5.7937	0.6068	0.921	3.5138	1.1630	0.990
38	6.2246	0.5138	0.862	3.1768	1.3458	0.988
39	3.7247	0.9270	0.901	4.5084	0.9313	1.000

intervertebral cartilage [20 cm] and flesh on the snout and tail [10 cm]). Weight estimates have been calculated from the formula derived by Foreman and Ishizuka (1990) for large Pacific bluefin and are presented in Table 5.

Age estimations included in Tables 5 and 6 are compiled from data presented by Bayliff (1994) that was based on fork-length estimates. However, Hales and Reitz (1992) cautioned that age data determined

from modern population samples may differ from prehistoric populations. They report a distinct change in growth rates over time for Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae), from Florida, a change determined from the analysis of otolith growth increments from prehistoric samples. Compared with modern populations, croakers from populations of several centuries ago grew more slowly and lived much longer.

Although the results of the croaker study suggest that modern data relating size to age may not accurately predict the age of prehistoric fish specimens, no data are currently available to address this phenomenon for any population of bluefin tuna. Should bluefin tuna be shown to exhibit the same pattern as croaker, the archeological specimens of bluefin tuna reported here would actually represent fish older than those predicted by this analysis. However, length measurements were converted to age and weight estimates in this study primarily so that comparisons could be made with modern tuna distribution data, which are often reported by age class or

weight. The critical point was to establish whether adult, rather than juvenile, tuna were more abundant in the archeological sample, because these age classes display distinctive behaviors and, more importantly, have different ecological requirements.

### Size of bluefin tuna represented by the archeological sample

Table 5 presents the final length, weight, and age estimates of bluefin tuna by geographic area. By far the majority of fish within the total sample (83%) were at least 6 years or older, ranging between 160

**Table 4**

Archaeological bluefin tuna vertebrae measurements and fork length estimates, by vertebrae number. All specimens. Measurements are defined in Figure 2.

Vertebra no.	Centrum GL (mm)	Centrum GB(p) (mm)	Estimated FL (cm)	Vertebra no.	Centrum GL (mm)	Centrum GB(p) (mm)	Estimated FL (cm)
01	27.0	44.4	198.7	21	38.3	45.1	189.6
02	26.3	48.2	191.5	22	39.2	44.8	189.6
04	22.5	39.6	164.7	22	39.2	46.5	188.6
04	31.6	65.1	224.9	24	39.4	47.5	193.5
05	27.1	58.7	212.4	24	45.1		195.3
06	30.8	58.9	218.2	25	40.8	48.3	209.8
09	25.6	34.4	168.2	26	40.1	47.6	194.8
(09)		48.7	220.8	(28)	30.2	35.9	190.7
(09)	22.3	30.5	153.6	29	33.7	36.3	159.3
(10)	33.4	45.0	206.7	29	45.3	49.5	155.3
11	24.4	34.6	165.5	29	50.3	58.2	201.1
(11)	31.0	37.8	177.5	30	28.1	32.0	221.1
(12)	35.0		200.5	30	36.7		138.5
(12)	36.7	46.5	206.9	30	38.3	44.0	167.1
(12)	34.9	41.9	192.0	30	46.7		172.3
14	33.5		187.0	30	47.3	50.0	199.2
(14)	33.9	40.9	185.4	30	47.5	51.2	201.1
(14)	34.1	42.0	189.3	31	48.6	52.8	201.7
(14)	32.5	42.1	189.7	31	52.7	53.8	201.3
(14)	27.7	32.8	157.8	32	41.7	45.6	215.3
15	35.4	42.5	188.4	32	43.7		179.3
(15)	31.4	42.5	188.4	32	49.7	54.4	185.6
16	35.9	45.6	191.2	33	26.6	27.0	204.4
16	36.1	42.9	191.9	33	43.8	44.8	122.4
(16)	31.3	35.4	175.0	33	44.5	47.2	178.9
(16)	33.8	40.9	183.9	33	44.7	45.6	186.5
(16)	40.2	47.2	206.0	33	47.9	53.9	181.4
(16)	41.2	51.8	209.4	33	52.2	53.7	207.3
17	36.0	42.8	187.3	33	53.7	55.2	206.7
17	37.5	47.3	200.2	34	48.1		211.3
(17)	37.0	43.9	190.4	34	48.2		202.4
(17)	38.2	44.2	191.3	35	41.2	42.0	202.6
18	37.2	46.5	195.4	36	30.5		200.8
(18)	26.8	32.4	153.5	38	11.9	28.2	198.9
19	39.4	47.2	196.0	38	16.5	31.8	210.3
(19)	27.2	32.7	151.9	39		23.0	243.2
20	35.5	44.5	182.4	39		19.5	198.3
(20)	38.0	45.0	191.3				
(20)	44.3	54.0	213.4				

**Table 5**

Archeological bluefin tuna length and age estimates, per individual represented, listed by geographic area. The length estimate associated with the highest correlation coefficient (*r*) for individuals represented by several elements is used here. See Figure 1 for locations.

Specimen no.	Site no.	Vertebra no.	Estimated fork length <sup>1</sup> (cm)	Estimated weight <sup>2</sup> (kg)	Estimated age class <sup>3</sup> (yr)
<b>Barkley Sound, Vancouver Island, n = 36</b>					
52	DfSi5	33	122.4	47	4
84	DfSj23a	30	138.5	65	5
51	DfSi5	(19)	151.9	83	5-6
54	DfSj23a	(18)	153.5	86	5-6
59	DfSj23a	29	155.3	88	5-6
30	DfSj23a	(14)	157.8	92	5-6
58	DfSj23a	11	165.5	105	6
25	DfSi5	30	167.1	107	6
55	DfSj23a	09	168.2	109	6
85	DfSj23a	30	172.3	117	6-7
83	DfSj23a	(16)	175.0	122	6-7
49	DfSi4	33	178.9	129	6-7
56	DfSj23a	33	181.4	134	7
48	DfSj23a	(16)	183.9	139	7
61	DfSj23a	33	186.5	144	7
39E	DfSi4	17	187.3	146	7
36C	DfSi4	22	188.6	149	7
47	DfSi4	(14)	189.3	150	7
60	DfSj23a	(14)	189.7	151	7
69F	DfSj23b	26	190.7	153	7
86	DfSi4	(20)	191.3	154	7
87	DfSj23a	02	191.5	155	7
57	DfSi5	01	198.7	171	7-8
26	DfSj23b	(12)	200.5	175	7-8
32	DfSi4	30	201.1	176	7-8
24	DfSj23a	(16)	206.0	188	8
44	DfSj23a	33	206.7	190	8
31	DfSj23a	(12)	206.9	190	8
68	DfSj23a	(16)	209.4	197	8
45A	DfSi4	24	209.8	198	8
64	DfSj23a	05	212.4	204	8
67	DfSj23b	31	215.3	212	8
63	DfSi4	06	218.2	219	8
72	DfSi4	(09)	220.8	226	8-9
66	DfSi4	29	221.1	227	8-9
80	DfSj23a	38	243.2	293	9-10
<b>Hesquiat Harbour, Vancouver Island, n = 2</b>					
21	DiSo1	32	186.0	143	7
20	DiSo1	(20)	213.4	207	8
<b>Nootka Sound, Vancouver Island, n = 6</b>					
NA	DkSp1	(28)	159.0	94	5-6
NA	DkSp1	(11)	177.0	125	6-7
1	DjSp3	39	198.3	170	7-8
3E	DkSp1	36	198.9	171	7-8
4	DkSp1	(10)	206.7	190	8
2	DkSp1	38	210.3	199	8
<b>Queen Charlotte Islands, n = 1</b>					
15E	FaTt9	19	196.0	165	7-8

<sup>1</sup> All raw data and calculations available from the author.

<sup>2</sup> Log (weight, kg) = (-9.02408) + 2.6767 × log (length, cm) (Foreman and Ishizuka, 1990).

<sup>3</sup> After Bayliff 1994a: 246.

**Table 6**

Distribution of estimated age and size classes of bluefin tuna harvested within the Barkley Sound area only, based on archeological remains from Barkley Sound area sites.

Estimated fork length (cm)	Number of individuals	Estimated age class (yr) <sup>1</sup>
120-129	1	4
130-159	5	5-6
160-179	8	6-7
180-199	11	7-8
200-219	8	8
220-239	2	8-9
240-260	1	9-10
Total = 36		

<sup>1</sup> After Bayliff, 1994a: 246 (data for vertebrae only).

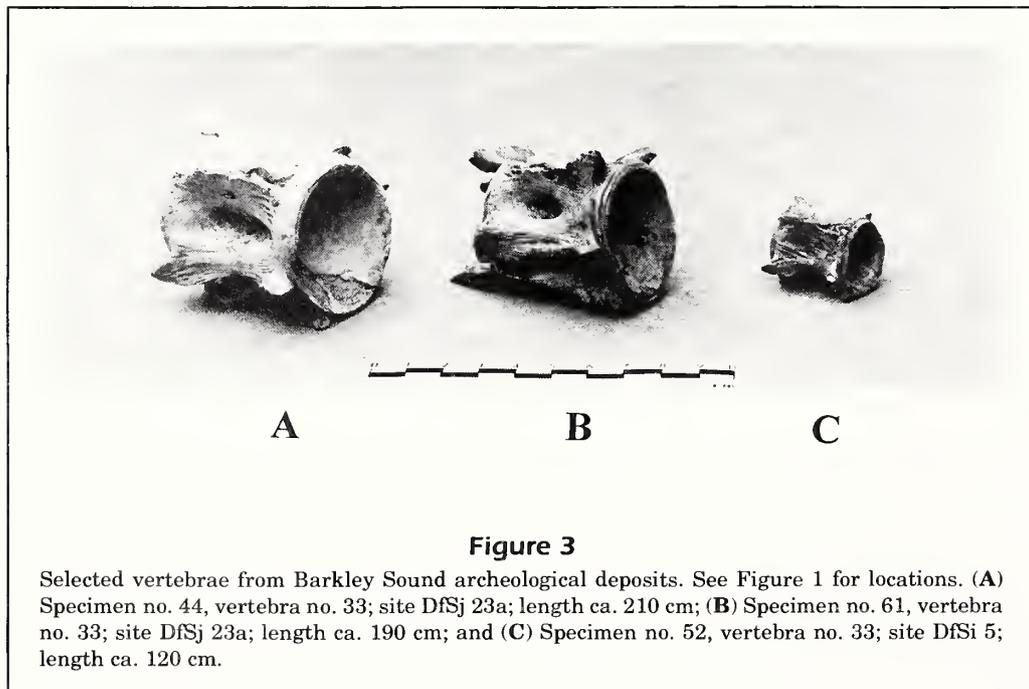
and 240 cm TL and between approximately 96 to 293 kg in weight. The youngest fish was estimated at 4 years (120 cm TL) and the oldest between 9 and 10 years (240 cm TL). Of the total sample of 45 individuals, 36 were recovered from the Barkley Sound area on the southwest coast of Vancouver Island, and the range of sizes from that area is summarized in Table 6. The relative size range of the bluefin tuna vertebrae harvested from Barkley Sound is shown pictorially in Figure 3.

## Ethnographic and historic information

Information from ethnographic sources substantiates and augments archeological evidence indicating that large bluefin tuna were present and harvested by Nuu-chah-nulth people of Vancouver Island well into the 19th century. Elders of the Mowachaht group from Nootka Sound on Vancouver Island have contributed invaluable details about tuna hunting strategies employed by their elders, some through interviews with Richard Inglis of the Royal British Columbia Museum, Victoria, British Columbia during 1991 and 1992 (Inglis<sup>2</sup>). These accounts represent the only ethnographic description of aboriginal tuna hunting on the northwest coast (McMillan, 1979). Pertinent details that substantiate the occurrence of adult bluefin tuna during the historic period are presented here.

The month of August is said to have been the time when tuna could be found feeding at the surface in inshore waters (sea-surface temperatures during August usually average about 14°C [Sharp, 1978]). The occurrences of large tuna were apparently preceded and accompanied by recognizable changes in water and weather conditions and by a unique set of associated fauna. Tuna traveled well inside Nootka Sound into protected inlets and were harpooned at night as

<sup>2</sup> Inglis, R. 1993. British Columbia Ministry of Aboriginal Affairs, #100-1810 Blanchard St., Victoria, British Columbia, Canada V8V 1X4. Personal commun.

**Figure 3**

Selected vertebrae from Barkley Sound archeological deposits. See Figure 1 for locations. (A) Specimen no. 44, vertebra no. 33; site DfSj 23a; length ca. 210 cm; (B) Specimen no. 61, vertebra no. 33; site DfSj 23a; length ca. 190 cm; and (C) Specimen no. 52, vertebra no. 33; site DfSi 5; length ca. 120 cm.

they fed at the surface in shallow inshore waters (located by spotters positioned on nearby cliffs). Bioluminescent plankton present in the water made the big fish especially visible at night, even from a distance.

A fire was sometimes built in the bow of the hunter's canoe to attract the fish to within spearing distance, a strategy called "pit-lamping." Another method was to paddle the canoe quickly away from an area where tuna were spotted: the canoe created a path of light as it moved through the bioluminescence. The tuna would follow the light, right up to and under the canoe, and were harpooned as they emerged at the bow. The word for tuna ("silthkwa") means "like the bow wave made by a boat," and undoubtedly reflects their surface-feeding behavior. These tuna were always referred to as "big fish, 6 to 8 feet (ca. 180–244 cm TL) long."

George Louis of the Ahousat Band was about 80 years old when interviewed in 1992. He said that his father told a story about the tuna hunting he observed as a small boy (perhaps when about 10 years old) sometime between 1880 and 1890. No official records or unofficial accounts have been found which indicate that large tuna have been observed in British Columbia waters since that time. Large bluefin tuna were captured, however, by sport anglers during the 1890's in southern California (Holder, 1913).

The only written reference to tuna found to date in the historic record is a footnote in the account of a meeting between George Vancouver and Bodega y Quadra at Nootka Sound in 1792. Mention is made of a porpoise and tuna stew ("large Tunny and a Porpus") being served during a feast given in their honor by Nuu-chah-nulth chief Maquinna on 4 September 1792 (Lamb, 1984, p. 304). There is, of course, no way of knowing if the "tuna" was bluefin tuna, some other tuna species, or some other taxon altogether. The capture of porpoise, however, would have required similar hunting skills and equipment as those described above for bluefin, and both could have been caught during a single hunting expedition. "Porpoise" remains are reported from a number of coastal shell middens (Mitchell, 1988) and are most likely to be either harbour porpoise, *Phocoena phocoena*, white-sided dolphin, *Lagenorhynchus obliquidens*, or Dall's porpoise, *Phocoenoides dalli* (Leatherwood et al., 1988). Moreover, bluefin tuna (even very large ones) would have been quite familiar to the Europeans exploring the coastal waters of British Columbia because the similar Atlantic subspecies occurs in European coastal waters. In marked contrast to the many unknown species regularly encountered by explorers in the north Pacific, large bluefin tuna might have been so familiar that they did not warrant special comment.

## Discussion

### Archeological evidence and potential sampling bias

The archeological remains described above represent a size class of bluefin tuna previously unknown in the northern portion of the eastern Pacific and constitute a small but valuable biological sample of the ancient population. However, some of the cultural and taphonomic (postdepositional) influences that affected the sample must be considered before ecological or zoogeographic interpretations can be made.

The archeological shell middens from which the bluefin tuna specimens have been recovered are essentially garbage dumps created over many centuries by the disposal of food and other household waste. The calcium carbonate leaching from abundant shellfish remains in these midden deposits effectively neutralizes acids in the soils that would otherwise rapidly destroy bone. Preservation of vertebrate skeletal remains is often excellent under these conditions, even after several thousand years.

The bones of animals recovered during archeological excavation of a shell midden represent a very small portion of the animals harvested by aboriginal people. Many processes operate on the carcass of a harvested animal to reduce the number of bones that might eventually be discarded into a midden (Davis, 1987; Lyman, 1994). These include butchering methods, distribution of edible parts (sharing), cooking procedures, and consumption of the edible portions. Some bones may have been set aside for tool or ornament manufacture (only one piece of altered bluefin tuna has been recovered: a vertebra fashioned into a spool, from the Ozette Village site in Washington). Moreover, scavengers, especially dogs and birds, may have removed or destroyed parts of a carcass so that in the end only a few bones from any given animal are represented in the midden. Finally, only small portions of most large midden deposits are actually excavated by archeologists, further reducing the sample of harvested animals available for archeozoological analysis (Ringrose, 1993, for detailed discussions of these issues; Lyman, 1994). For example, the remains of the 36 individual bluefin tuna recovered from Barkley Sound (Table 6) represent an empirically undeterminable fraction of what was actually harvested and consumed by the aboriginal people in that area. In addition, the number of fish successfully landed constituted a very small proportion of the available population of bluefin tuna. Presumably only a few bluefin tuna would have been actively pursued and some of these would invariably have been lost during the hunt. Thus, even if only one gi-

ant bluefin tuna was successfully harvested every few seasons by native hunters, this could still constitute evidence of a significant population of tuna available as a local resource.

Unfortunately, the time interval between catches of bluefin is not precisely determinable from the dated archeological deposits; it is impossible at this time to determine if catches were made annually, every 10 years, or every 100 years. Although expensive, the use of accelerator  $^{14}\text{C}$ -dating methods on small samples of bluefin tuna remains is the only way to determine a more precise time frame. The remains of bluefin tuna recovered from Barkley Sound during several recent field seasons are perhaps the best candidates for future analysis because there are many vertebral and nonvertebral skeletal elements and the remains appear to represent less than 2,000 years of harvesting activities (McMillan and St. Claire<sup>3</sup>).

### Geographic range of prehistoric bluefin tuna remains

As discussed at greater length previously (Crockford, 1994), it appears probable that the ability to hunt large Pacific bluefin tuna was strongly correlated with native groups who were capable of active whaling. This possible correlation with active whaling rather than with the use of so-called "drift" whales (which die naturally and are fortuitously encountered at sea or as beached carcasses) is important. No other archeological sites in western North America or northeastern Asia appear to contain remains of large bluefin tuna. No large bluefin tuna have been reported from sites in southern California where adult tuna are occasionally taken today, although the remains of other large fish, such as marlin, have been identified and large marine mammals, such as sea lions, were clearly taken (Moratto, 1984; Raab<sup>4</sup>). We cannot assume, however, that large bluefin tuna were not present in southern California waters during prehistoric times because a lack of whaling technology may have prevented aboriginal Californians from harvesting such a resource.

In northern Japan, active whaling is not clearly indicated by the archeological record although hunting of sea lions and other large marine mammals was practiced. Large bluefin tuna remains have not been

reported from archeological sites bordering the Sea of Okhotsk and the Sea of Japan where large bluefin tuna occur today (Niimi, 1994; Otaishi, 1994), but it appears that not many large sites in these areas have been excavated. As in the case for California, it would be inappropriate, given the absence of evidence for an active whaling technology, to suggest that adult bluefin tuna were absent in Japanese waters during prehistoric times.

In contrast, the recovery of large bluefin tuna among dated archeological deposits that span almost 5,000 years is evidence that the occurrence of adult bluefin tuna off the British Columbia coast was longstanding. Clearly, large bluefin tuna were a resource consistently (if sporadically) available to aboriginal people on the central northwest coast until relatively recently. The Nuu-chah-nulth people, in particular, were especially adept at using this resource, and their material culture included large sea-going canoes, detachable harpoon heads, braided ropes, and floats required for the successful hunting of both whales and large tuna (Huelsbeck, 1983; Mitchell and Donald, 1988). Archeological remains are, by inference, invaluable indicators that the environmental conditions that favored the presence (i.e. the inshore surface-feeding behavior) of bluefin tuna must have existed off the coast of British Columbia as a recurring pattern for at least 5,000 years.

### Implications

The lack of reports of adult bluefin tuna off the British Columbia coast since the late 19th century may be due to several factors, including the impact of 20th-century fisheries in both the eastern and western Pacific, the association of large bluefin in northern waters of the eastern Pacific with very specific environmental conditions that have not recurred since the late 19th century, and the misidentification of small schools of large bluefin tuna as marine mammals.

Although relative abundance records over the past 100–150 years are not available for Pacific bluefin tuna, it has been shown for other species that when abundance decreases, the range of a species often contracts (Kawasaki, 1991). In order to investigate how 20th-century fisheries may have impacted abundance and thus the distribution of bluefin tuna, a comprehensive record of the history of the bluefin tuna fishery as conducted by all nations throughout the north Pacific would be needed. This is especially true for Japanese waters because of the use there of large-scale harvesting methods.

It is also possible, however, that short- or long-term (or both) changes in environmental conditions may be affecting bluefin tuna distributions in the east-

<sup>3</sup> McMillan, A. D., and D. E. St. Claire. 1992. The Toquart archaeology project: report on the 1992 excavations. Archaeology Branch, British Columbia Ministry of Small Business, Tourism and Culture, 800 Johnson St. Victoria, British Columbia, Canada V8W 1N3; permit 1991–46. Unpubl. rep., 100 p.

<sup>4</sup> Raab, M. 1994. Anthropology Department, California State University, Northridge, CA 91330. Personal commun.

ern Pacific (Rothschild, 1991). Hubbs (1948) partially addressed this issue in his presentation of evidence that mean water temperatures in southern California were warmer in the mid-to-late 1800's (1850–80). Such water temperatures appeared to be associated with distinctly tropical fauna that no longer occur so far north. This period corresponds roughly to that mentioned in the northwest coast ethnographic accounts as the last time when large tuna were hunted and may reflect a recurring pattern of occasional warm periods along the whole coast of North America.

Because the surface-feeding behavior of large bluefin tuna makes them very conspicuous in inshore waters, it would be extremely unlikely for adult tuna to go totally unnoticed for the last 100 years in British Columbia waters (even if they could not be caught or were indeed mistaken for marine mammals in deeper waters). It seems reasonable to assume under the circumstances that modern records are correct: large adult bluefin tuna have not frequented the northern waters of the eastern Pacific during the last 100 years. The reasons for their absence, however, remain to be determined.

Clearly, more investigation into the history of the distribution and harvesting of all age classes of bluefin tuna within the entire north Pacific will be necessary before we really understand the implications of the archeological remains reported in this study. Complex interactions of changes in ecological conditions and harvesting pressures on various age classes over the last 100 years probably have affected and may have had unexpected repercussions on the population structure of Pacific bluefin tuna. A better understanding of the distribution of adult tuna in the north Pacific through inclusion of archeological records may help document perturbations in the modern fishery.

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**Abstract**—During the summer of 1987 in Coos Bay, Oregon, dietary overlap (Schoener index) between juvenile fall-run chinook salmon, *Oncorhynchus tshawytscha*, and an introduced stock of juvenile hatchery-reared spring-run chinook salmon was high (0.82), indicating the potential for competition for food between these two groups in times of food scarcity. Both groups consumed a variety of prey, including fishes, adult insects, algae, barnacle molts, gammarid and caprellid amphipods, and juvenile decapods. Diets of both salmon groups varied with fish size and capture location. Overlap was low (0.25–0.55) between the smallest juvenile fall chinook salmon ( $\leq 80$  mm FL), for which insects were the predominant prey (26% by weight), and all other length groups of both fall and spring chinook salmon, for which fish were the predominant prey (49%–94% by weight). Dietary overlap between both salmon groups was high in the lower bay (0.82), where fish prey predominated in the diets, and was also high in the mid bay (0.75), where algae and barnacle molts predominated in the diets. Three pieces of evidence suggest that the introduced hatchery-reared spring chinook salmon did not outcompete fall chinook salmon for food: 1) both the median stomach fullness and the percentage of stomachs containing food was higher for fall chinook salmon than for spring chinook salmon, 2) the median stomach fullness of fall chinook salmon was as high in the period following releases of spring chinook salmon into the bay as in the period prior to the releases, and 3) food of high caloric density (i.e. fish prey) formed an equally high proportion of the diets of both salmon groups, indicating that the quality of food eaten by both was similar.

## Dietary overlap of juvenile fall- and spring-run chinook salmon, *Oncorhynchus tshawytscha*, in Coos Bay, Oregon

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Estuaries serve as rich feeding grounds and as refuges from predation for many juvenile subyearling fall-run (hereafter referred to as "fall") chinook salmon, *Oncorhynchus tshawytscha*, that reside in them for weeks or months before entering the ocean (Healey, 1980a, 1982, 1991; Myers, 1980; Kjelson et al., 1982; Myers and Horton, 1982; Simenstad et al., 1982). The survival of subyearling fall chinook salmon may be enhanced by extended residence in estuaries. Reimers (1973) reported that survival was greater among juvenile fall chinook salmon that resided in the Sixes River estuary from early summer through early fall than among those that quickly migrated through the estuary to the ocean in early summer.

Although there is much concern about the interaction between hatchery and wild stocks of salmon (Hilborn and Winton, 1993; Thomas and Mathisen, 1993; Winton and Hilborn, 1994), few reports document possible competition between groups of salmon for food in estuaries or the ocean. Peterman (1984) and Rogers and Ruggerone (1993) found negative correlations between size of sockeye salmon at different ages and their population and suggested that growth of sockeye salmon in the ocean was density

dependent. Reimers (1973) and Neilson et al. (1985) found that the average growth rate of juvenile fall chinook salmon in the Sixes River estuary decreased during mid-summer when the population of juvenile salmon was high. Reimers (1973) attributed this drop in growth rate to intraspecific competition for limited food resources, leading to density-dependent growth, whereas Neilson et al. (1985), noting that the decrease in growth rate occurred during a period of increased abundance of the principal prey (*Corophium* sp.), suggested that lowered conversion efficiencies due to high temperatures in the estuary as well as intraspecific competition may have contributed to the drop in growth rate.

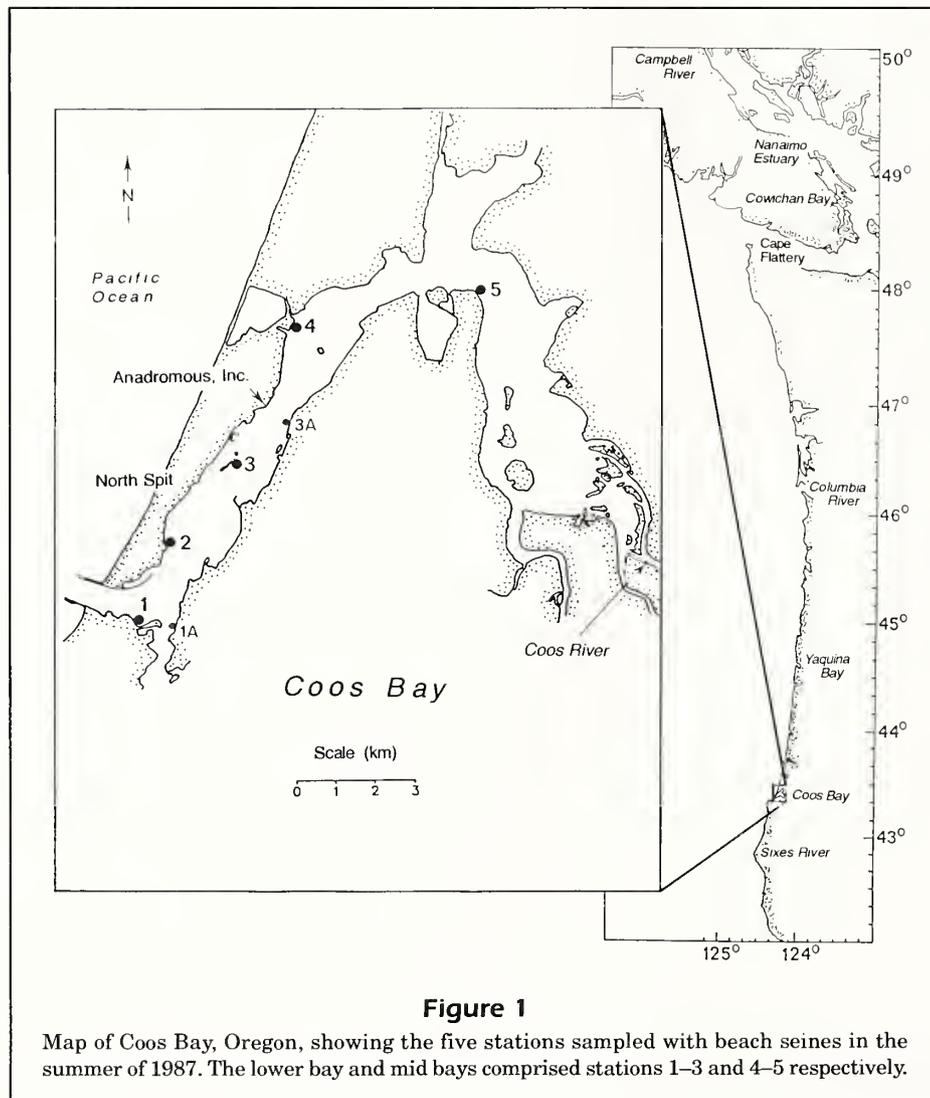
These studies suggest that releases of large numbers of hatchery salmon smolts into an estuarine basin could affect the native salmon in the system through competition for food in the estuary. The effect of competition on growth and survival of native fish would depend on several factors, among them the intensity and duration of the competition between the two groups. If the hatchery-reared fish eat different prey from that eaten by the wild fish, or if they move quickly through the estuary, their impact on the native fish may be relatively small. On the other hand, if the two groups

have similar feeding behaviors and if hatchery fish reside in the estuary for a substantial period, then the effect of hatchery fish on the wild fish may be great.

Anadromous, Inc. operated a salmon-rearing and release facility on the North Spit of Coos Bay, Oregon in the 1980's. From this facility millions of smolts are released into the bay annually, principally large subyearling spring-run ("spring") chinook salmon, thus creating the potential for competition between these hatchery-produced spring chinook salmon and the native runs of fall chinook salmon in the Coos Bay drainage.

During the late spring and summer of 1987 we undertook a sampling program in the lower half of Coos Bay to study the use of the estuary by different groups of juvenile chinook salmon. In 1987 two groups of juvenile chinook salmon were present in Coos Bay: fall chinook salmon from the Coos and

Millacoma River drainages (both wild fish and fish released by the Salmon and Trout Enhancement Program [STEP]) and spring chinook salmon released from the saltwater rearing pens of the Anadromous, Inc. facility, North Spit of Coos Bay (Fig. 1). About 400,000 STEP fall chinook salmon were released in tributaries of the Coos River between 30 April and 28 June at average fork lengths (FL) of between 48 and 94 mm, and over five million spring chinook salmon (123–156 mm FL) were released from the Anadromous, Inc. release facility on North Spit between 19 June and 1 October. In an earlier paper (Fisher and Percy, 1990) we reported on the distributions and residence times of juvenile spring and fall chinook salmon in the bay. In this paper we describe the food habits of these two groups, overlap in their diets, and the potential for competition for food between them.



**Figure 1**

Map of Coos Bay, Oregon, showing the five stations sampled with beach seines in the summer of 1987. The lower bay and mid bays comprised stations 1–3 and 4–5 respectively.

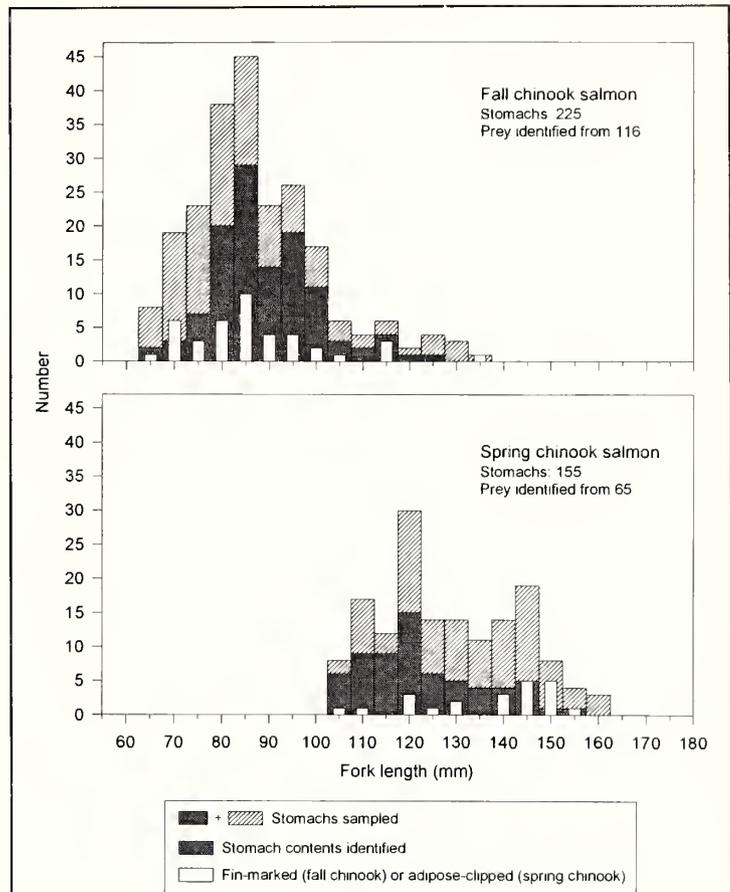
## Methods

Juvenile chinook salmon were caught by beach seine (60 m × 2.5 m with 19- and 13-mm mesh in the wings and bunt, respectively) at five locations on the margins of channels in the lower half of Coos Bay, Oregon, between late May and early October 1987 (Fig. 1). The substratum was sand at all but station 5, where it was a mixture of gravel fill and mud. At stations 2, 3, and 4, portions of eel grass beds were sampled during low tide. The area of Coos Bay we sampled was influenced strongly by the ocean and was highly marine in character with high salinities at all sampling sites, usually greater than 29 psu after mid-June. Water temperature (at 0.3 m depth) was fairly constant between May and October but increased with distance from the mouth, averaging 12.3°C at station 1 and 16.8°C at station 5 (Fisher and Pearcy, 1990).

Subsamples of juvenile chinook salmon caught in beach-seine sets were preserved in approximately 4% formaldehyde solution. Later, these were measured to the nearest mm FL and weighed to the nearest 0.01 g after excess moisture was removed by blotting. Stomachs were removed from 380 juvenile chinook salmon caught between 31 May and 4 September 1987 (Fig. 2). Stomach-content boluses were weighed to the nearest milligram after removing excess moisture by blotting. After weighing, they were preserved in 50% ethanol, then transferred to 75% ethanol.

At the time the stomach samples were obtained, the fish were examined for fin marks or for external parasites that could help to determine their origin. Most fish with clipped adipose fins also contained coded wire tags (CWT's) that identified them as spring chinook salmon produced at Anadromous, Inc. Fish with other fin clips were mainly STEP-reared fall chinook salmon released in freshwater tributaries of Coos Bay (Fisher and Pearcy, 1990).

The encysted metacercarial stage of a strigeoid trematode parasite is common in the skin of juvenile salmonids found in freshwater tributaries of Coos Bay. These cysts are surrounded by a black pigment that can be seen easily without magnification (Amandi<sup>1</sup>). The presence of metacercarial cysts on the skin or fins of juvenile chinook salmon caught in



**Figure 2**

Length-frequency distributions of juvenile fish classified as fall and spring chinook salmon from which stomach samples were taken. Dark shading represents those stomach samples in which prey species were examined and identified. White bars in the upper and lower graphs represent numbers of fin-clipped STEP-reared fall chinook salmon and adipose clipped Anadromous, Inc.-reared spring chinook salmon, respectively.

Coos Bay appeared to be a reliable indicator that the fish originated in the freshwater tributaries of the bay. Cysts were present on 43% of known fall chinook salmon (fin-marked STEP fish or fish caught before the first release of spring chinook salmon) and on 71% of small fish <101 mm FL (>2SD below the mean FL of most release groups of spring chinook salmon by Anadromous, Inc.). Conversely, cysts were absent on adipose-clipped spring chinook salmon and found on only 13% of fish in the size range of the spring chinook salmon released by Anadromous, Inc. (≥101 mm FL). Fish >100 mm FL with cysts were probably native salmon or STEP-reared fall chinook salmon that attained these greater lengths through growth. On the basis of this evidence, we classified fish caught in Coos Bay as fall chinook salmon if they met *any* of

<sup>1</sup> Amandi, T. 1995. Oregon Dep. Fish and Wildl., 516 Nash Hall, Oregon State Univ., Corvallis, OR 97331. Personal commun.

the following criteria: 1) they were caught before the first release of Anadromous, Inc. spring chinook salmon on 19 June; 2) metacercarial cysts were present on their skin or fins; 3) they had one of the STEP fin clips; or 4) they were  $\leq 100$  mm FL. Fish were classified as spring chinook salmon if they were  $\geq 101$  mm FL and did not meet any of the criteria for fall chinook salmon.

Stomach contents were examined and prey items identified to the lowest possible taxon from 116 fall chinook salmon and 65 spring chinook salmon collected between 29 June and 13 August 1987, the period of greatest overlap in the bay of the two groups (Fig. 2). Stomach contents from a single fall chinook salmon caught on 7 June were also examined.

Individual prey taxa in each stomach were weighed to the nearest 0.001 g after removing excess moisture by blotting. Those taxa that were too light to register on the scale (weight  $< 0.0005$  g), were assigned a weight of 0.0004 g. The estimated total weight of all food assigned this arbitrarily small value was only 0.05 g out of a total weight of 60.2 g for all taxa from all stomachs.

In the analyses of stomach contents, juvenile fall and spring chinook salmon were grouped by FL, by two collection areas ("lower bay," stations 1-3, and "mid-bay," stations 4-5) and by two sampling periods: 29 June to 17 July and 3-13 August. Within each class, the percent frequency of occurrence (FO) and percent by weight of each prey category in the diet was calculated. The percent by weight ( $p_i \times 100$ ) of each prey category in each class was calculated as

$$100(p_i) = 100 \left( \frac{\sum_{q=1}^N w_{iq}}{\sum_{q=1}^N \sum_{i=1}^n w_{iq}} \right), \quad (1)$$

where  $w_{iq}$  is the weight of food category  $i$  in fish  $q$ ,  $n$  is the number of food categories, and  $N$  is the number of fish in the class.

Dietary overlap between classes was calculated by using the Schoener overlap index ( $ro$ ; Schoener, 1970; Wallace, 1981; Linton et al., 1981):

$$ro = 1 - \frac{1}{2} \sum_{i=1}^n |p_{ij} - p_{ik}|, \quad (2)$$

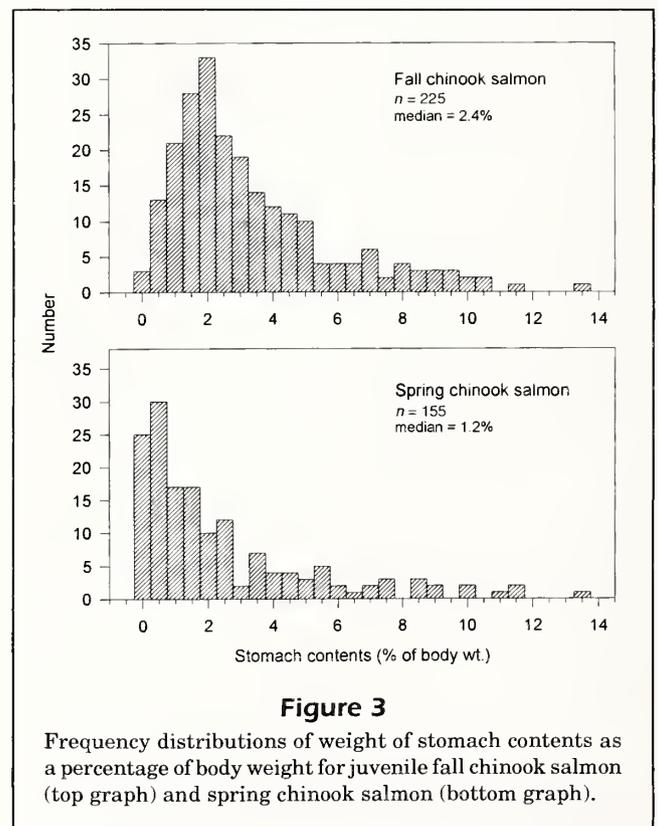
where  $p_{ij}$  and  $p_{ik}$  are the proportions by weight of food category  $i$  (Eq. 1) in the diets of fish in classes  $j$  and  $k$ , respectively, and  $n$  is the number of food cat-

egories. Dietary overlap was calculated by using 14 categories of major prey and, because the overlap index is sensitive to the taxonomic resolution (Brodeur and Pearcy, 1992), it was also calculated by using the 86 lowest taxonomic levels identified (to genus or species in some cases). An overlap of  $\geq 0.60$  was considered significant (Zaret and Rand, 1971; Brodeur and Pearcy, 1992).

## Results

### Stomach fullness

The frequency distribution of stomach-content weight as a percentage of body weight ("stomach fullness") was skewed for both fall and spring chinook salmon (Fig. 3); therefore, nonparametric ranks tests were used to compare stomach fullness among different classes of fish. The median stomach fullness was higher for fall chinook salmon than for spring chinook salmon (2.4% vs. 1.2%, respectively; Mann Whitney (Wilcoxon)  $W$  test,  $W=11,630$ ,  $P<0.0001$ ). Stomachs were empty in a higher percentage of spring chinook salmon than of fall chinook salmon (16% vs. 1%), contributing to the difference in median stomach fullness of these two groups (Fig. 3).



**Figure 3**

Frequency distributions of weight of stomach contents as a percentage of body weight for juvenile fall chinook salmon (top graph) and spring chinook salmon (bottom graph).

Range in stomach fullness was similar among fish of different lengths, and stomach contents weights of 8% of body weight or higher occurred in fish from 69 mm to 145 mm FL (Fig. 4). No significant difference in median stomach fullness was found among four FL classes ( $\leq 80$  mm, 81–100 mm, 101–120 mm, and 121–140 mm) of fall chinook salmon (Kruskal-Wallis test,  $P=0.09$ ). However, a significant difference in median stomach fullness was found among the three FL classes (101–120 mm, 121–140 mm, and  $\geq 141$  mm) of spring chinook salmon (Kruskal-Wallis test,  $P=0.03$ ). Median stomach fullness was lowest (0.4%) for the largest spring chinook salmon ( $\geq 141$  mm FL).

Median stomach fullness of fall chinook salmon was fairly constant during the study period, both before and after spring chinook salmon were released into the bay. No short-term decreases in stomach fullness of fall chinook salmon were associated with individual releases of spring chinook salmon, except for the 4 August release (Fig. 5). Conversely, median stomach fullness of spring chinook salmon was low immediately following releases of large numbers of spring chinook salmon from the Anadromous, Inc.

facility, especially the 4 August and the August 31–3 September releases (Fig 5).

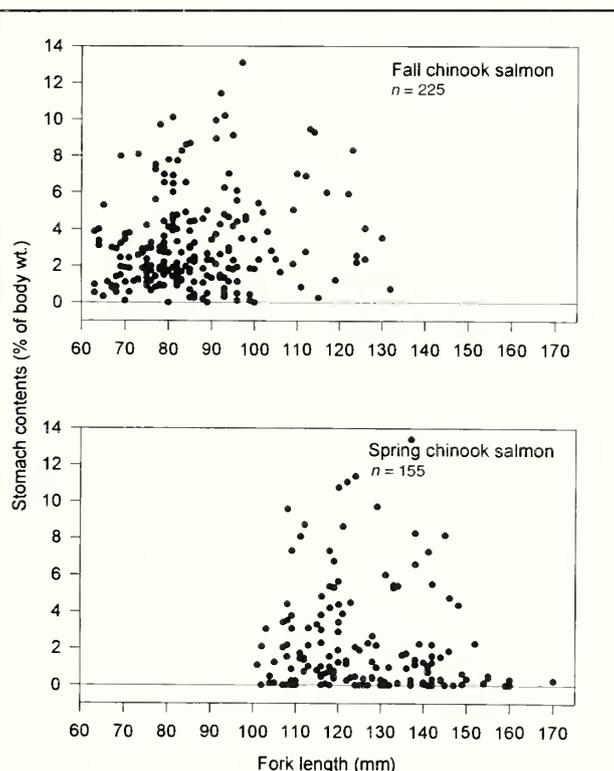
### Diets of fall and spring chinook salmon

Percent FO and percent by weight of fourteen major prey categories from stomachs of juvenile fall and spring chinook salmon are summarized in Table 1. By weight, juvenile or larval fish were dominant prey of both fall and spring chinook salmon, representing 64% and 65% of the total weight of stomach contents, respectively. The fish prey of fall chinook salmon were juvenile smelt, unidentified fish remains, *Ammodytes hexapterus*, juvenile *Sebastes* sp., and an unidentified cottid, representing 41%, 10%, 8%, 6%, and <1% of stomach-content weight, respectively. Fish prey of spring chinook salmon were similar: juvenile smelt, *Ammodytes hexapterus*, unidentified fish remains, and *Sebastes* sp., accounted for 49%, 13%, 3%, and <1% of stomach-content weight, respectively.

Other prey categories accounted for much smaller fractions of stomach-content weights of the two groups of juvenile chinook salmon. Of the nonfish prey, insects and plants (mainly algae) composed the largest fractions by weight in stomachs of fall chinook salmon (8% and 7%, respectively), whereas plants (mainly the algae *Ulva* sp. and *Enteromorpha* sp.) and barnacle molts composed the largest fractions by weight in stomachs of spring chinook salmon (16% and 12%, respectively; Table 1).

The most numerous insects<sup>2</sup> in fall chinook salmon stomachs were adults of terrestrial taxa (61% of the total) and adults of taxa having aquatic or semi-aquatic larvae (36% of the total). Larvae and pupae composed only 3% of the total number of individuals. Adults in the orders Diptera, Hemiptera, Homoptera, Psocoptera, Hymenoptera, Coleoptera, and Trichoptera accounted for 33%, 23%, 15%, 10%, 7%, 6%, and 2% of the total number of insects in fall chinook salmon stomachs, respectively. The most numerous taxa in these insect orders (and their percentages of total insect numbers) were midges (Chironomidae; 25%), plant bugs (Miridae; 22%), aphids (Aphididae; 11%), book and bark lice (10%), parasitoid wasps (5%), rove beetles (Staphylinidae; 4%), and caddis flies (2%), respectively.

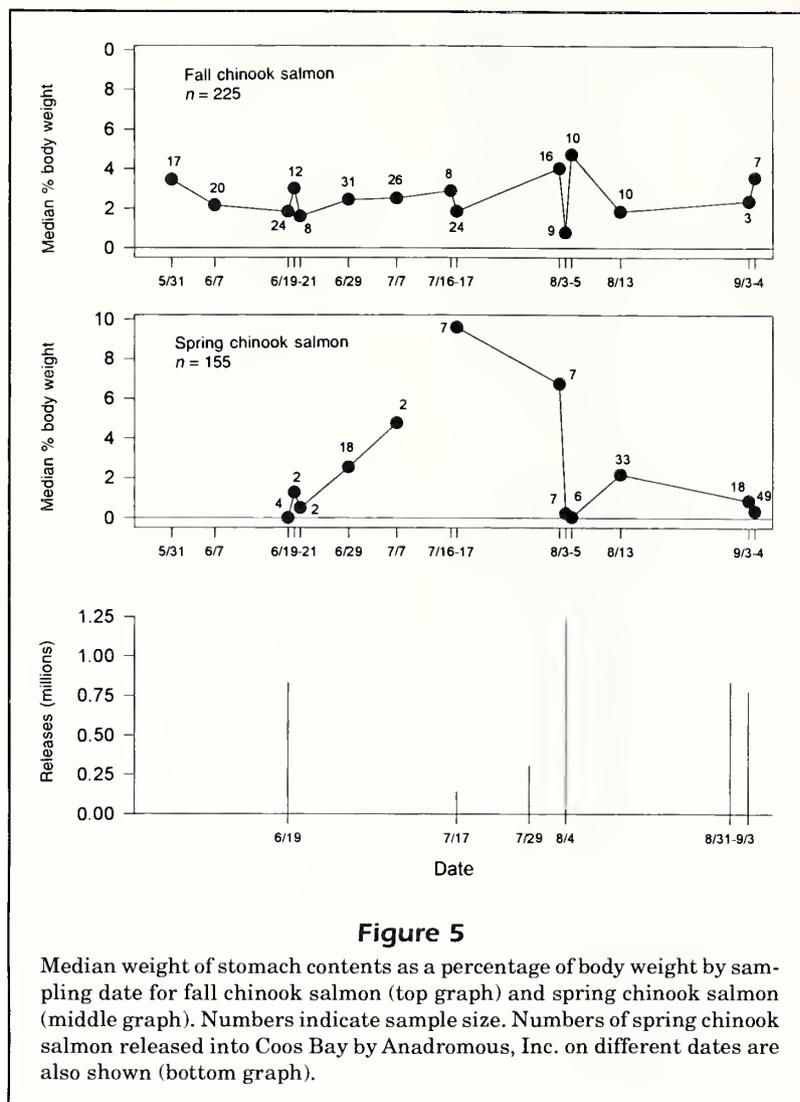
Although insects were a much larger fraction by weight of the diet of fall chinook salmon than of the diet of spring chinook salmon (8% vs. 1%, respectively, Table 1), they occurred frequently in stomachs of both salmon groups (80% and 60%, respectively). Many of the same insect taxa were consumed by both fall



**Figure 4**

Weight of stomach contents as a percentage of body weight versus fish length for juvenile fall chinook salmon (top graph) and spring chinook salmon (bottom graph).

<sup>2</sup> The different insect taxa were not weighed separately, but individuals of each taxon were counted.



**Figure 5**

Median weight of stomach contents as a percentage of body weight by sampling date for fall chinook salmon (top graph) and spring chinook salmon (middle graph). Numbers indicate sample size. Numbers of spring chinook salmon released into Coos Bay by Anadromous, Inc. on different dates are also shown (bottom graph).

and spring chinook salmon. The most numerous insects from spring chinook salmon stomachs were chironomids (31%), book and bark lice (23%), aphids (9%), tipulids (crane flies, 8%), and plant bugs (4%).

Other prey categories that occurred frequently in stomachs of both fall and spring chinook salmon were barnacle molts (47% and 51%, respectively), algae and other plant material (46% and 68%), gammarid amphipods (41% and 43%), fishes (40% and 37%), and crab larvae (27% and 35%). Isopods, caprellid amphipods, nonanomuran or nonbrachyuran decapod larvae, spiders, unidentified arthropods, and molluscs were less common, occurring in 14% or fewer of stomachs

Gammarid amphipods were a moderately important component of the diet of fall chinook salmon (4% by weight), but were less important in the diet of spring chinook salmon (only 1% by weight). A variety of gammarid species were eaten by fall chinook

salmon, the most abundant were *Jassa* spp. unidentified gammarids, *Megalorchestia pugettensis*, *Ischyrocerus* spp., *Atylus tridens*, and *Corophium* spp. (2.0%, 0.6%, 0.3%, 0.2%, 0.2%, and 0.1% of total food weight respectively).

Dietary overlap between juvenile fall and spring chinook salmon, according to the relative weights (Eq. 2) of the 14 major food categories (Table 1), was high (0.82), owing largely to the predominance of fish prey in diets of both groups. Diet overlap based on relative weights of prey identified to the lowest possible taxonomic level (86 categories of varying taxonomic level) was lower but still relatively high (0.66).

### Diets by fish length

Insect prey were relatively more important and fish prey were relatively less important in the diet of the

**Table 1**

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomachs of juvenile fall-run and spring-run chinook salmon caught in 1987 in Coos Bay. Numbers in brackets are sample sizes.

Food category	Fall chinook salmon [116]	Spring chinook salmon [65]
Cirripedia molts	5 (47)	12 (51)
Isopods	<1 (9)	<1 (11)
Caprellid amphipods	1 (14)	<1 (11)
Gammarid amphipods	4 (41)	1 (43)
Brachyuran, anomuran larvae	2 (27)	2 (35)
Other decapod larvae	<1 (8)	<1 (2)
Crustacean fragments	5 (20)	1 (25)
Araneae	<1 (14)	<1 (5)
Insects	8 (80)	1 (60)
Other arthropods	<1 (6)	<1 (2)
Molluscs	<1 (4)	<1 (12)
Teleosts	64 (40)	65 (37)
Algae, plants	7 (46)	16 (68)
Other material	4 (43)	2 (55)

**Table 2**

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomachs of different size groups of fall and spring chinook salmon caught in 1987 in Coos Bay. Numbers in brackets are sample sizes.

Food category	Fall chinook salmon FL (mm)			Spring chinook salmon FL (mm)		
	≤80 [32]	81–100 [73]	≥101 [11]	101–120 [39]	121–140 [19]	≥141 [7]
Cirripedia molts	9 (63)	5 (45)	3 (18)	22 (62)	9 (42)	<1 (14)
Isopods	<1 (9)	<1 (10)	0	<1 (10)	<1 (16)	0
Caprellid amphipods	1 (9)	1 (18)	0	<1 (8)	<1 (16)	<1 (14)
Gammarid amphipods	4 (44)	5 (42)	<1 (18)	1 (51)	1 (37)	<1 (14)
Brachyuran, anomuran larvae	7 (25)	2 (32)	0	1 (28)	2 (42)	3 (57)
Other decapod larvae	<1 (13)	<1 (7)	0	0	<1 (5)	0
Crustacean fragments	11 (22)	6 (22)	0	2 (23)	1 (32)	<1 (14)
Araneae	<1 (13)	<1 (16)	0	<1 (5)	<1 (5)	0
Insects	26 (94)	7 (81)	1 (36)	1 (69)	<1 (63)	0
Other arthropods	<1 (13)	<1 (4)	0	0	<1 (5)	0
Molluscs	1 (6)	<1 (4)	0	<1 (5)	<1 (26)	<1 (14)
Teleosts	18 (9)	62 (45)	94 (91)	49 (31)	68 (32)	91 (86)
Algae, plants	12 (56)	7 (42)	2 (36)	20 (72)	18 (63)	4 (57)
Other material	11 (59)	4 (38)	<1 (27)	4 (59)	<1 (42)	2 (71)

smallest fall chinook salmon (≤80 mm FL) than in the diets of the other length groups of both fall and spring chinook salmon. Insect prey made up 26% of food by weight in stomachs of the smallest fall chinook salmon (Table 2). The insect fraction of the diet dropped to 7% and 1% for larger fall chinook

salmon 81–100 mm FL and ≥101 mm FL, respectively, and was ≤1% for all length groups of spring chinook salmon. Fish made up only 18% by weight of the diet of fall chinook salmon ≤80 mm FL, but 62% and 94% by weight of the diet of fall chinook salmon 81–100 mm FL and ≥101 mm FL, respec-



## Diets by sampling period

Between two sampling periods (29 June–17 July and 3–13 August) moderate changes occurred in the proportions of the 14 major food categories in stomachs of both fall and spring chinook salmon. In stomachs of fall chinook salmon, the percentage by weight of insects, gammarid amphipods, and crab larvae was higher in the earlier than in the later period, whereas the percentage by weight of fish prey was higher in

the later than in the earlier period (Table 6). In spring chinook salmon stomachs, barnacle molts and fish were more abundant in the earlier period than in the later period, whereas algae and crab larvae were more abundant in the later period than in the earlier period.

Despite these shifts in prey composition, diet overlap based on the 14 major prey categories was high for all comparisons of fall and spring chinook salmon caught in the two time periods (Table 7). However,

**Table 4**

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomachs of fall and spring chinook salmon caught in 1987 in the lower (stations 1–3) and mid (stations 4–5) sections of Coos Bay. Numbers in brackets are sample sizes. Mean fork lengths (FL) of fish in each area are also shown.

Food category	Fall chinook salmon		Spring chinook salmon	
	Sta. 1–3 87 mm FL [90]	Sta. 4–5 88 mm FL [26]	Sta. 1–3 123 mm FL [39]	Sta. 4–5 118 mm FL [26]
Cirripedia molts	2 (39)	22 (77)	4 (33)	35 (77)
Isopods	<1 (4)	<1 (23)	<1 (8)	<1 (15)
Caprellid amphipods	1 (14)	1 (12)	<1 (15)	<1 (4)
Gammarid amphipods	4 (42)	2 (35)	<1 (33)	2 (58)
Brachyuran, anomuran larvae	2 (28)	6 (23)	2 (44)	1 (23)
Other decapod larvae	<1 (10)	0	<1 (3)	0
Crustacean fragments	6 (22)	3 (12)	1 (26)	1 (23)
Araneae	<1 (12)	<1 (19)	<1 (3)	<1 (8)
Insects	6 (76)	17 (96)	<1 (49)	1 (77)
Other arthropods	<1 (6)	1 (8)	0	<1 (4)
Molluscs	<1 (2)	1 (12)	<1 (13)	<1 (12)
Teleosts	71 (47)	14 (15)	79 (54)	24 (12)
Algae, plants	3 (37)	31 (77)	11 (56)	32 (84)
Other material	4 (44)	3 (38)	1 (54)	3 (58)

**Table 5**

Dietary overlap of fall and spring chinook salmon caught in the lower (stations 1–3) and mid (stations 4–5) sections of Coos Bay. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values ( $\geq 0.60$ ) are in bold type.

		Fall chinook salmon		Spring chinook salmon		
		Sta. 4–5		Sta. 1–3	Sta. 4–5	
Fall chinook salmon	Sta. 1–3		0.37	<b>0.82</b>		0.38
			<i>0.28</i>	<b>0.68</b>		<i>0.35</i>
	Sta. 4–5		—	0.35		<b>0.75</b>
				<i>0.22</i>		<i>0.47</i>
Spring chinook salmon	Sta. 1–3		—	—		0.43
						<i>0.41</i>

**Table 6**

Percentage by weight and frequency of occurrence (in parentheses) of fourteen major food categories in stomach of juvenile fall and spring chinook salmon caught during two time periods in 1987 in Coos Bay. Numbers in brackets are sample sizes. Mean fork lengths (FL) of fish caught during each time are also shown.

Food category	Fall chinook salmon		Spring chinook salmon	
	29 Jun–17 Jul 85 mm FL [89]	3–13 Aug 95 mm FL [26]	29 Jun–17 Jul 117 mm FL [26]	3–13 Aug 123 mm FL [39]
Cirripedia molts	6 (54)	3 (23)	17 (65)	8 (41)
Isopods	<1 (11)	0	<1 (4)	<1 (15)
Caprellid amphipods	1 (17)	<1 (4)	<1 (12)	<1 (10)
Gammarid amphipods	6 (47)	<1 (19)	1 (38)	1 (46)
Brachyuran, anomuran larvae	2 (29)	<1 (15)	1 (27)	2 (41)
Other decapod larvae	<1 (10)	0	0	<1 (3)
Crustacean fragments	9 (24)	<1 (8)	<1 (15)	2 (31)
Araneae	<1 (17)	<1 (4)	<1 (8)	<1 (3)
Insects	11 (84)	2 (65)	<1 (65)	1 (56)
Other arthropods	<1 (8)	0	<1 (4)	0
Molluscs	<1 (3)	<1 (8)	0	<1 (21)
Teleosts	51 (36)	84 (54)	73 (38)	58 (36)
Algae, plants	6 (45)	7 (50)	6 (62)	24 (72)
Other material	5 (47)	3 (31)	1 (38)	3 (67)

diet overlap based on the lowest identified taxa (86 categories) was low for all comparisons except that between fall and spring chinook salmon caught in the period 3–13 August. Although a variety of fish prey were eaten by both salmon groups during the earlier period, during the later period fish prey were nearly all juvenile osmerids.

## Discussion

### Potential for competition

The high dietary overlap values (Tables 3, 5, 7) between juvenile fall chinook salmon  $\geq 81$  mm FL and hatchery spring chinook salmon suggest that there is the potential for competition for food between these two groups in Coos Bay under conditions of food limitation. However, whether or not the two groups were competing for food in 1987 cannot be determined from dietary overlap alone. In fact, high dietary overlap may sometimes indicate a condition in which abundant food resources are shared between potential competitors rather than a condition in which there is competition for a resource in short supply (Zaret and Rand, 1971; Myers, 1980). Zaret and Rand (1971), in a study of tropical stream fishes, found

that dietary overlap between species was high during the rainy season, when food resources were abundant, and low during the dry season, when food resources were scarce and when the different fish species targeted different prey.

We found little evidence in this study that the introduced hatchery-reared spring chinook salmon outcompeted native and STEP-reared fall chinook salmon for food. One potential result of competition for food between groups is a shift to less desirable prey in the diet of the weaker competitors (Hanson and Leggett, 1986). However, during the period when both fall and spring chinook salmon were in Coos Bay, calorically dense (high-quality) fish prey made up an equally large fraction by weight of the diets of both salmon groups (Table 1); i.e. fall chinook salmon were eating just as nutritious prey as that eaten by spring chinook salmon. Another potential result of competition is a decrease in growth rate (or average stomach fullness) of one or all of the competing groups (Reimers, 1973; Nielson et al., 1985; Hanson and Leggett, 1986). If spring chinook salmon outcompeted fall chinook salmon for food, the average stomach fullness of fall chinook salmon might be expected to drop following releases of the spring chinook salmon; this, however, did not occur. Stomach fullness of fall chinook salmon was equally high in the periods be-

**Table 7**

Dietary overlap of fall and spring chinook salmon during two time periods. Overlap values based on 14 major food categories are in normal type and those based on 86 lower taxonomic categories are in italics. High overlap values ( $\geq 0.60$ ) are in bold type.

		Fall chinook salmon	Spring chinook salmon	
		3–13 Aug	29 Jun–17 Jul	3–13 Aug
Fall chinook salmon	29 Jun–17 Jul	<b>0.66</b>	<b>0.67</b>	<b>0.73</b>
		<i>0.26</i>	<i>0.44</i>	<i>0.32</i>
	3–13 Aug	—	<b>0.83</b>	<b>0.73</b>
			<i>0.49</i>	<i>0.70</i>
Spring chinook salmon	29 Jun–17 Jul	—	—	<b>0.75</b>
				<i>0.56</i>

fore and after spring chinook salmon were released into the bay (Fig. 5). In fact, stomach fullness of fall chinook salmon was usually higher than that of spring chinook salmon throughout the study period (Figs. 3 and 5). The low stomach fullness among spring chinook salmon following releases from the Anadromous, Inc. facility (Fig. 5) may reflect a delay in the start of feeding on natural prey by these hatchery fish. Paszkowski and Olla (1985) suggested that the inability of some hatchery fish to adapt to the natural environment may contribute to the poor survival of some groups of hatchery salmon. We conclude that the high dietary overlap between juvenile fall and spring chinook salmon indicates the potential for competition for food between these salmon groups in Coos Bay, but that in the summer of 1987 there was little evidence of actual food limitation or competition.

Differences between smaller fall chinook salmon and larger hatchery spring chinook salmon in spatial distribution and duration of residence within estuaries may tend to minimize their competition for food. Small fish tend to occur in shallow, nearshore areas or in salt marshes, whereas large fish tend to occur in deeper channel areas (Healey, 1980a, 1991; Kjelson et al., 1982; Levings, 1982; Simenstad et al., 1982; McCabe et al., 1986; Macdonald et al., 1987). Larger juvenile chinook salmon also tend to spend less time in estuaries than do smaller fish (Myers, 1980; Simenstad and Wissmar, 1984; Fisher and Pearcy, 1990). Both these differences may tend to decrease competition for food between hatchery-reared and wild chinook salmon in estuaries if there is a large difference in their size. However, large releases of hatchery salmon smolts into an estuary may affect wild smolts detrimentally by attracting birds and other predators that prey on juvenile salmon (Emlen et al., 1990).

We did not investigate rates of secondary production in the bay, rates of exchange of prey between the adjacent ocean and the bay, the rations required by juvenile salmon to maintain optimum growth rates, or the fractions of available prey in the bay eaten by juvenile salmon and other potential competing species. Without such information it is difficult to assess the likelihood that the growth and survival of juvenile salmon was limited by food in Coos Bay in 1987. The lower half of Coos Bay is strongly influenced by the adjacent ocean (Burt and McAlister, 1959; Fisher and Pearcy, 1990). In a study of Yaquina Bay, an Oregon estuary with physical characteristics similar to Coos Bay, Myers (1980) suggested that much of the food for juvenile salmon residing in the bay was supplied by tidal exchange with the ocean. Undoubtedly, the productivity of the adjacent ocean has a strong influence on the capacity of Coos Bay to support juvenile chinook salmon.

#### Upper-bay and lower-bay gradients in diet

Between the mid and lower sections of Coos Bay the diet of juvenile fall chinook salmon shifted from predominantly drift insects, barnacle molts, and drift algae to predominantly marine fishes (Table 4). A similar increase in piscivory in the lower bay also occurred among spring chinook salmon (Table 4).

Shifts in the diet of juvenile chinook salmon as they move from the river, through the estuary, and to the ocean appear to be related to the changes in habitat and foraging behavior which occur as a consequence of growth and development. Macdonald et al. (1987) observed that large hatchery-reared chinook salmon were often found in deeper, more saline waters of the salt-wedge of the Campbell River estuary, whereas smaller wild chinook salmon were often found in the freshwater layer near the surface. Small

fry and subyearling chinook salmon often use tidal marshes where they eat drift and emergent insects and epibenthic crustaceans (Kjelson et al., 1982; Simenstad et al., 1982; Levings et al., 1991; Shreffler et al., 1992), whereas, larger, yearling chinook salmon spend little time in salt marshes but quickly move to neritic habitats (Simenstad et al., 1982). When subyearling fish move to neritic habitats their diet shifts to fishes, decapod larvae, euphausiids, and drift insects (Simenstad et al., 1982). McCabe et al. (1986) observed that, in the Columbia River estuary, subyearling chinook salmon in pelagic areas were significantly larger than those caught in shallow intertidal habitats and that the prey of juvenile chinook salmon varied with season, habitat, and position in the estuary. Feeding behavior is also influenced by environmental factors, for example turbidity (Gregory and Northcote, 1993).

Diets of juvenile chinook salmon in freshwater reaches of river systems often are dominated by larval, pupal, or adult insects that are captured mainly in the drift at the surface or in the water column (Becker, 1973; Craddock et al., 1976; Sagar and Glova, 1987, 1988; Rondorf et al., 1990; Healey, 1991; Levings and Lauzier, 1991; Smirnov et al., 1994). Depending on season and habitat, both terrestrial insects as well as different developmental stages of aquatic insects can be important prey for chinook salmon in rivers (Rondorf et al., 1990; Levings and Lauzier, 1991). Insects are also important constituents of the diets of juvenile chinook salmon in many estuaries (Healey, 1980, a and b, 1982, 1991; Levings, 1982; McCabe et al., 1986; Kask et al., 1988; this study), particularly in fresh or brackish water tidal marshes (Kjelson et al., 1982; Levings et al., 1991; Shreffler et al., 1992).

Whereas insects are important prey in freshwater and upper estuaries, fishes are important prey of juvenile chinook salmon constituents in the lower reaches of estuaries as well as in marine, neritic or subtidal areas (Healey, 1980a; Myers, 1980; Kjelson et al., 1982; Simenstad et al., 1982; Argue et al., 1986; McCabe et al., 1986; Levings et al., 1991; Reimers et al.<sup>3</sup>; Nicholas and Lorz<sup>4</sup>). Fish prey are also predominant in the diets of juvenile chinook salmon in marine waters off Oregon and Washington (Peterson et

al., 1982; Emmett et al., 1986; Brodeur and Percy, 1990, 1992; Brodeur et al., 1992), in the Gulf Islands area of the Strait of Georgia (Healey, 1980b), and in the Fraser River plume (St. John et al., 1992).

In Coos Bay, the increase in importance of marine fish in the diets of juvenile fall and spring chinook salmon at the lower-bay stations may reflect an upper-bay, lower-bay gradient in the abundance of fish prey. Juvenile osmerids, sandlance, and rockfish were the predominant fish prey of juvenile chinook salmon in Coos Bay. In Yaquina Bay, larval and juvenile stages of these species were present in peak abundances in plankton samples from the extreme lower-bay and offshore stations (Percy and Myers, 1974). Myers (1980) caught more species of fishes in the lower than in the upper section of Yaquina Bay and suggested that much of the food for juvenile chinook salmon residing in the bay was supplied by tidal exchange with the ocean. She also suggested that high temperatures in the upper bay inhibited movement of predominantly marine species into the upper bay. A similar mechanism may be operating in Coos Bay. In our beach-seine samples large juvenile and adult surf smelt were much more abundant at lower than at mid-bay stations (average catch per set was 2,290, 237, 108, 30, and 12 at stations 1, 2, 3, 4, and 5, respectively). If, as was the case in Yaquina Bay, smaller larval and juvenile smelt also are more abundant in lower Coos Bay, the increased consumption by juvenile chinook salmon of these fish prey in the lower bay may be a consequence of their greater density there.

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**Abstract.**—The accuracy and precision of estimates of catch at age from sampled lengths were evaluated for three different methods with simulated red snapper, *Lutjanus campechanus*, data for 1984–94. The methods included a growth curve, age-length keys, and a probabilistic method to classify a known total number of fish into ages from samples of the length frequency of the catch. In the first method, ages were estimated from sample lengths directly from the growth curve. The second method involved expanding the sample length frequency to age frequency by using age-length keys. The probabilistic method incorporated the cumulative frequency distributions of length at age, year-class strength, and estimates of prior survival to build age probability distributions from sampled lengths. The evaluation was based on the error in the assigned catch at age and on the resulting estimates of numbers at age and fishing mortality arising from sequential population analysis. The probabilistic method was the best of the three for the situation evaluated here, and application of the age-length key was better than that of the growth model. However, the probabilistic method requires knowledge of growth, the distributions of size at age, and recruitment that may not be known, or only poorly so. Age-length keys require no such ancillary information and may be more practical in most situations, but the probabilistic method is superior if the data requirements can be met.

## Fish age determined from length: an evaluation of three methods using simulated red snapper data\*

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Age-structured stock-assessment methods require estimates of the age composition of the catch. In stock assessments for Gulf of Mexico red snapper, *Lutjanus campechanus*, age compositions are used that are estimated from the sampled size distribution of the catch with growth models (Goodyear<sup>1</sup>). The application of age-length keys developed from age determinations of length-stratified samples of the catch is a superior method (Ketchen, 1950; Hoenig and Heisey, 1987) that has been recently incorporated into the data collection program for this stock. However, it cannot be readily applied retroactively to improve the estimates of the age composition of historical catch, and it requires significantly more resources than the former method. In this paper, I compare the precision of the estimates of the age composition of the catch from these two methods with an alternative, using simulated red snapper data. The comparisons include both accuracy and precision of the estimates of the age composition of the catch and the consequent estimates of numbers at age and fishing mortality arising from their application to sequential population analysis following the methods of Gavaris<sup>2</sup> and Powers and Restrepo (1992).

## Methods

### Simulated data

The population simulation model used in this analysis (Goodyear, 1989) employed 30 discrete ages with an instantaneous annual natural mortality ( $M$ ) of 0.2 for all ages in the fishery. Each year class was further partitioned into growth platoons (cohorts with identical age but different mean lengths). The position of a growth platoon in the distribution of size at age was fixed so that the larger individuals of a year class at age 1 remained larger throughout their lifetime. Mean lengths ( $L$ ) at age ( $A$ ) at the beginning of January were assumed to be equal to the estimates in the 1994 stock assessment for Gulf of Mexico red snapper (Goodyear<sup>1</sup>) and to correspond to the von Bertalanffy equation,  $L=88.24(1-\exp(-0.159$

\* Miami Laboratory Contribution MIA-94/95-42.

<sup>1</sup> Goodyear, P. 1994. Red snapper in U.S. waters of the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, Miami, Admin. rep. MIA 93/94-63, 150 p.

<sup>2</sup> Gavaris, S. 1988. An adaptive framework for the estimation of population size. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 88/29, 4 p.

( $A+0.458$ )), where  $L$  is total length in cm and  $A$  is age in years. Size at age in the absence of fishing mortality was assumed to be normally distributed with a coefficient of variation of length at age ( $v$ ) of 0.10 based on the observed variability in size at age for red snapper (Goodyear<sup>1</sup>). The mean length of individuals of age  $a$  in growth platoon  $p$ ,  $l_{ap}$ , was determined from mean size at age ( $L_a$ ) by using the normal distribution and the coefficient of variation of length at age as

$$l_{ap} = L_a + L_a z_p v,$$

where:  $z_p$  is the standard normal deviate for the  $p^{\text{th}}$  percentile of the distribution. The simulation considered 101 growth platoons in each age class. The resulting distributions of lengths at the beginning of the year for ages 1–10 are shown in Figure 1. Within-year growth was evaluated as

$$W_{ap} = W_{a-1,p} \exp(G_{ap}),$$

where  $W_{ap}$  is the weight (kg) of an individual in growth platoon  $p$  at age  $a$ , and  $G_{ap}$  = instantaneous growth rate of growth platoon  $p$  at age  $a$ . The  $G_{ap}$  were estimated from lengths at age predicted from the von Bertalanffy growth equation.

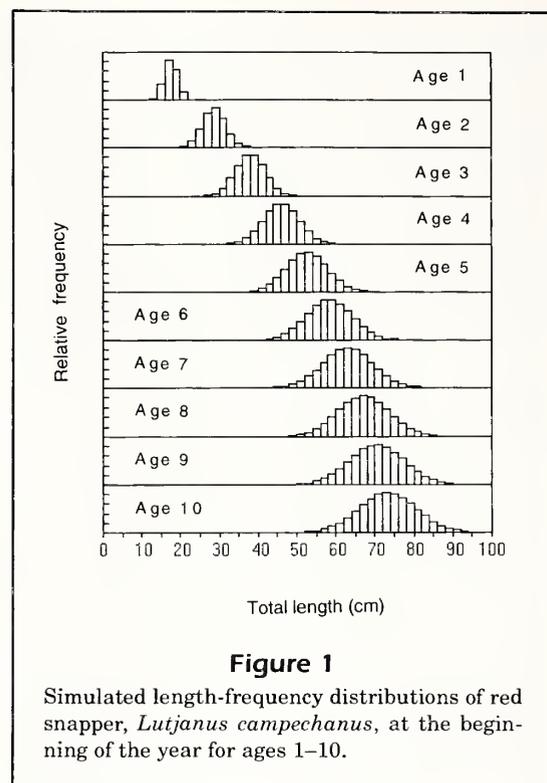
The weight of a fish at capture  $W_c$  was evaluated as

$$W_c = W_{ap} Z_{ap} (\exp(G_a - Z_{ap}) - 1) / ((G_{ap} - Z_{ap})(1 - \exp(-Z_{ap}))),$$

where  $Z_{ap}$  is the total instantaneous mortality for growth platoon  $p$  at age  $a$  during the time period. Weight was converted to length with the length-weight equation ( $W=1.158 \times L^{3.056}$ ,  $r^2=0.985$ ,  $n=25,375$ ) Growth, mortality, and catch were evaluated monthly.

The period simulated was from 1954 to 1994, but catch and sample data were retained and analyzed for 1984–94, which corresponds to the time span of actual data from the fishery. Recruitment in the model was specified by year class from 1954 to 1994 (Fig. 2). The values for 1972–94 follow the recruitment pattern observed in trawl surveys (Goodyear<sup>1</sup>). Earlier values were arbitrarily varied around the level observed at the beginning of the time series because landings from shrimp trawlers (predominantly juvenile fish) during these years were higher than those after 1972.

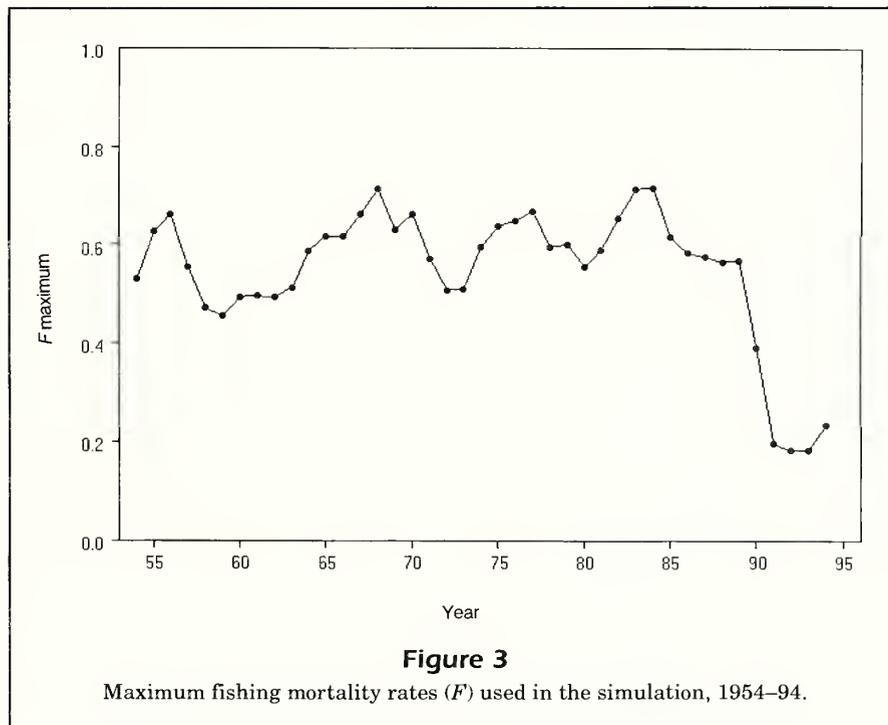
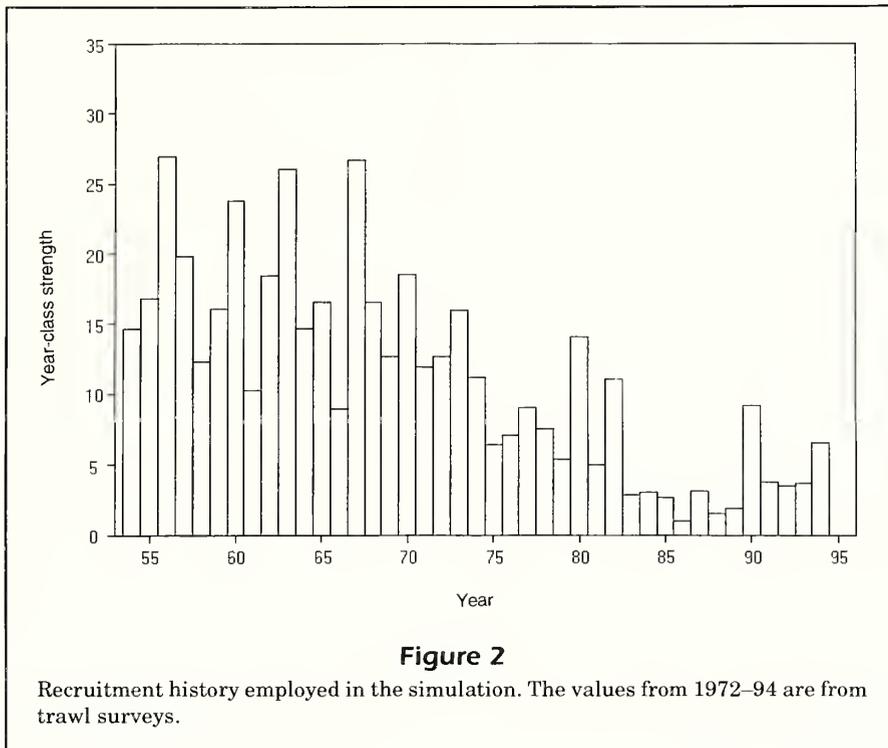
The value of fishing mortality in the model is the product of a maximum potential value for the year and a selectivity value based on the fish's age (Figs. 3 and 4). A dome-shaped selectivity schedule was



**Figure 1**  
Simulated length-frequency distributions of red snapper, *Lutjanus campechanus*, at the beginning of the year for ages 1–10.

selected on the basis of age distribution of the catch (predominantly from handlines) in the 1994 assessment (Goodyear<sup>1</sup>). The value of the annual maximum for 1984–94 also follows the trend in the best estimates from the 1994 assessment, whereas earlier values were arbitrarily varied around the level observed at the beginning of the time series. The reduction in fishing mortality after 1990 was a response to management actions. The selectivity schedule (Fig. 4) was selected to produce a sample length frequency similar to that observed in the fishery (Fig. 5). Samples were truncated below 33 cm after 1990 to include the effects of changes in minimum size regulations at that time.

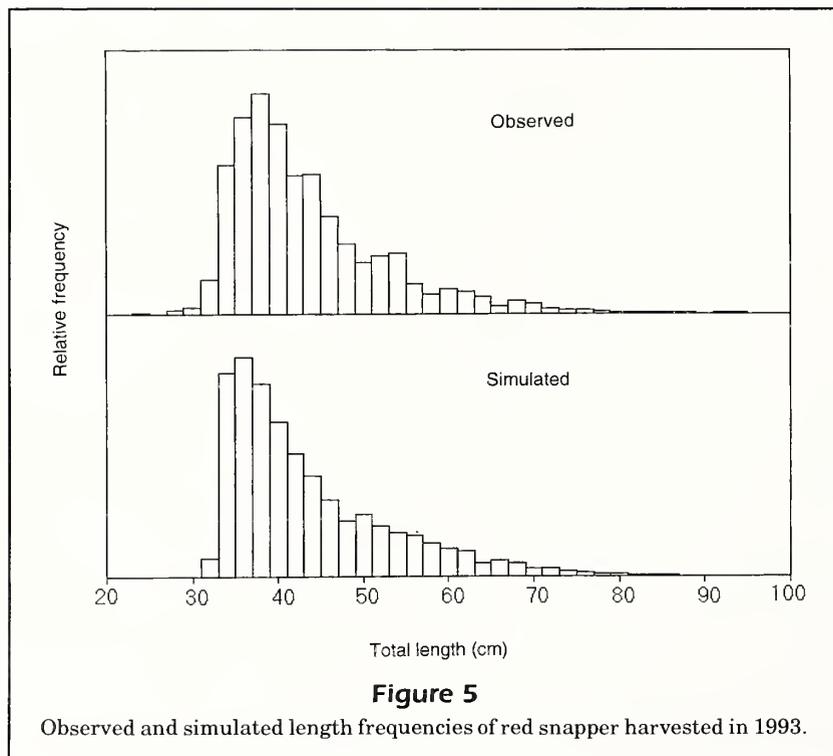
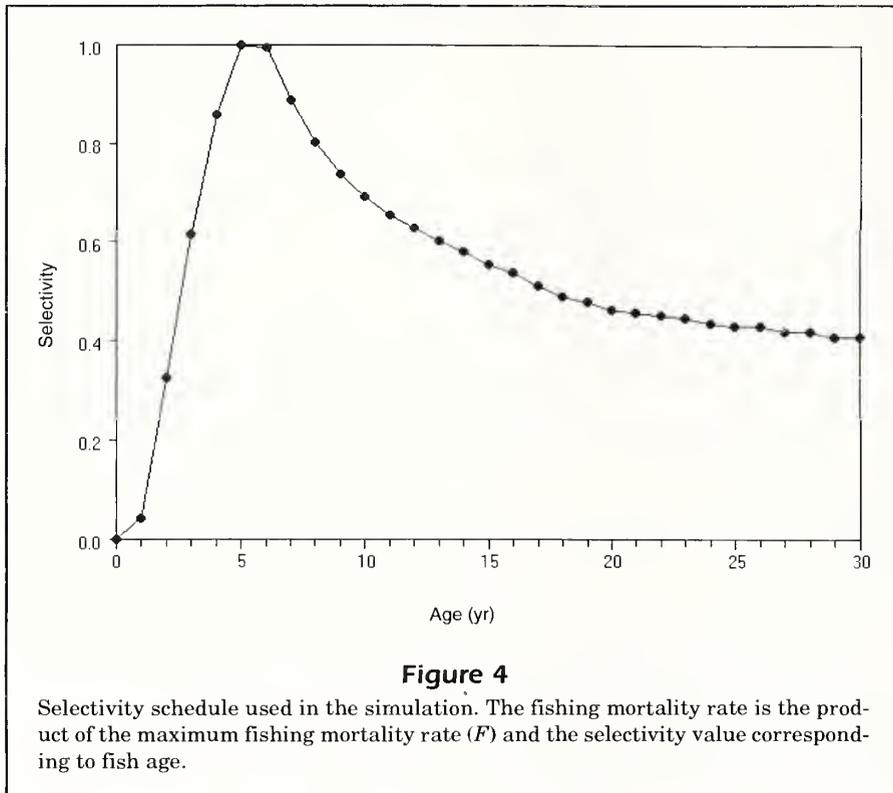
The simulated observations of length (and age) were obtained from the simulated catch. The catch from a growth platoon in the population structure was picked at random. It was evaluated for inclusion as an observation on the basis of the ratio of its magnitude ( $N_p$ ) to the maximum catch from any other growth platoon ( $N_{max}$ ). This was accomplished by drawing a uniform random number ( $R$ ) between 0 and 1.0. If the ratio  $N_p/N_{max} \geq R$ , the length and age attributes of the cell were included as an observation; otherwise, they were discarded. This convention caused the sampled growth platoon to be proportional to their magnitude in the simulated catch. The process was repeated for each month of the simulation until 1,000 samples had been drawn. This provided 12,000 length



samples per year. No error was added to either age or length to simulate measurement error.

The ages of the first two fish sampled in each 1-cm length stratum each month were retained with their lengths to build the age-length key for that month.

This provided a maximum sample size of 24 fish per length stratum or about 4,000 fish per year to construct the age-length key, but sample size varied slightly because of the stochastic nature of the sampling process.



## Age-estimation methods

For all three ageing methods evaluated, the number of fish in the catch at age  $a$ ,  $N_a$ , was estimated as

$$N_a = Cf_a,$$

where  $C$ , the total catch in numbers of fish, was the known value from the simulation, and  $f_a$  was the estimated fraction of catch at age  $a$ . Age frequencies were estimated separately for each year between 1984 and 1994.

With the first method, the von-Bertalanffy growth equation was rearranged to predict age from length,

$$A = -\log_e(1 - L/88.24)/0.159 - 0.458,$$

and the  $f_a$  were estimated as the ratios of the number of sampled fish assigned age  $A$  to the total number of fish in the sample. For this method any sampled fish larger than the asymptotic size was discarded.

With the second method typical age-length keys (Ketchen, 1950; Westrheim and Ricker, 1978) were constructed annually from the monthly age-frequency samples. In this case the  $f_a$  were estimated by multiplying the observed age frequencies for each length stratum by the ratio of length samples in each length stratum to the total number of length samples and by summing over ages.

The third (probabilistic) method is a proposed alternative and requires estimates of prior survival of year classes in the population and independent estimates of year-class strength. In this method

$$f_a = \frac{\sum_{i=1}^j \sum_{a=0}^n P_a}{j},$$

where  $j$  is the number of length samples,  $n$  is the number of ages, and

$$P_a = \frac{W_a R_{y-a} S_a}{\sum_{a=1}^n W_a R_{y-a} S_a}$$

and

$$W_a = \frac{dD_a}{dL_i},$$

where  $D_a$  is the cumulative probability distribution of length for age  $a$ ,  $L_i$  is the observed length of fish  $i$ ,  $R_{y-a}$  is the recruitment strength in year  $y-a$ ,  $y$  is the year of observation, and  $S_a$  is survival probability from recruitment to age  $a$  and is given by

$$S_a = \exp \sum_{i=0}^{a-1} -(F_i + M_i),$$

where  $F_i$  is the fishing mortality of the year class at age  $a$  when it was age  $i$ , and  $M_i$  is the natural mortality of the year class at age  $a$  when it was age  $i$ .

Inspection of the data used in this method reveals that the method requires values for nearly everything one would wish to estimate from the age composition of the catch and consequently seems to place the cart before the horse. However, in many cases ancillary data on year-class strength may be available from research surveys, and estimates of natural and fishing mortalities may be available from earlier assessments. In this investigation, this method was applied in two ways. The first assumed preexisting accurate knowledge of year-class strengths and mortality. The second application assumed knowledge of year-class strengths and natural mortality and proceeded iteratively. In the first iteration, age composition was estimated with the assumption that there was no fishing mortality. This led to a set of estimates of catch at age that were then used through sequential population analysis to estimate fishing mortality at age. With the second iteration the resulting estimates of fishing mortality were added and catch at age was reestimated. This process was repeated several additional times.

Overall, the three methods provided 4 sets of estimates of catch at age that could be compared with the true values from the simulation: those from the growth model, those from the age-length key, those from the probabilistic method given knowledge of survival, and those from the iterated probabilistic method. In addition, numbers at age and fishing mortality for each year were estimated from the catches at age for each set by using sequential population analysis (Powers and Restrepo, 1992). For the purpose of this exercise, the selectivities for the terminal year of the population analysis were the known values from the simulation, and the tuning index was the known number of age-4 individuals alive at the beginning of the year. The methods were compared by correlating the known true values from the simulation to the values estimated by each method. Because there were 31 ages in the model (0–30) and 11 years, these provided a total maximum sample size of 341; however, year-age combinations where the true catch at age was below 100 were dropped. Thus sample sizes for most analyses were reduced to 331. In addition, scattergrams of the logs of the ratios of estimated to true values were constructed for each comparison. The  $r^2$  values for the correlations between true and estimated values are presented with

each of the scattergrams. Although the scattergrams involve transformations to reflect the error more accurately, the correlations themselves are based on the untransformed data.

## Results

The estimates of catch at age from each of the methods were highly correlated with the true values (Fig. 6). But the error in catch at age was clearly highest for the ages assigned with the growth model (Fig. 6A). Catch at age from the age-length key was considerably better than that from the growth model, particularly for the younger more abundant ages in the catch (Fig. 6B). The younger ages in these figures tend to be to the right side of the scattergrams and the older, less abundant ages are on the left.

The probabilistic method, given prior knowledge of fishing mortality and recruitment, provided the best result, with very little difference between true and estimated age compositions except at the oldest ages (Fig. 6C). The bias in the estimates obtained with this method with only natural mortality is evident in Figure 6D, but even so, the estimates for the youngest ages are better than the estimates from the growth model. The bias was reduced by the fifth it-

eration (Fig. 6E) and almost completely removed by the tenth iteration (Fig. 6F).

The estimates of number at age by using an age-sequenced analysis are presented in Figure 7. Again the results were least favorable for the catch-at-age matrix developed from the growth model (Fig. 7A), followed by the age-length key (Fig. 7B) and the probabilistic method (Fig. 7C). The bias in estimated number at age from the probabilistic method, where fishing mortality is not used, is even more pronounced than it was for the catch-at-age matrix (Figs. 5D and 6D). However, the bias was reduced by the fifth iteration by using the fishing mortality rates derived from prior iterations and almost completely removed by the tenth iteration (Fig. 7, E-F). The similarity of  $r^2$  values for the correlations between observed and predicted values for the age-length key and probabilistic methods in Figures 6 and 7 are somewhat misleading because of the very large dynamic range of the numbers and corresponding catches at age used in the analysis. In actuality, the precision of the estimates arising from application of the age-length key was much lower than that for the probabilistic method for age classes that were infrequent in the catch.

The estimates of fishing mortality at age, derived from each set of catch at age by using age-sequenced

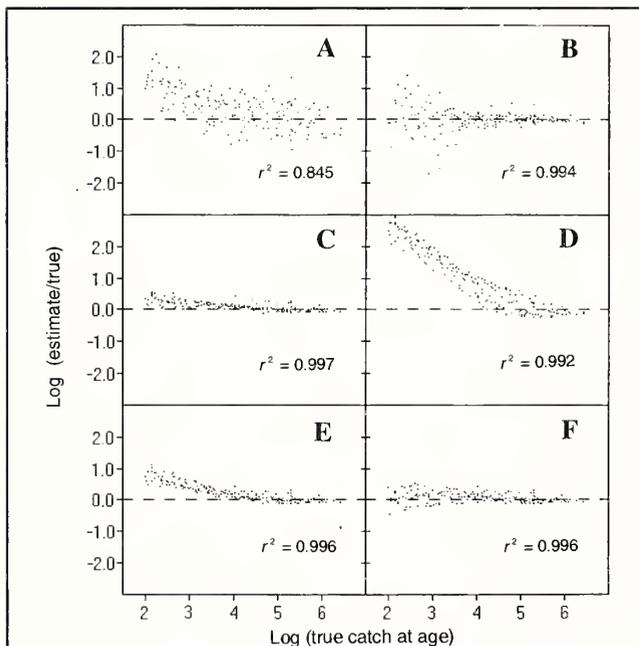


Figure 6

Ratios of estimated to true catch at age from the growth model (A), age-length key (B), and from the probabilistic method with knowledge of prior survival (C), and probabilistic iterations 1, 5 and 10 (D-F).

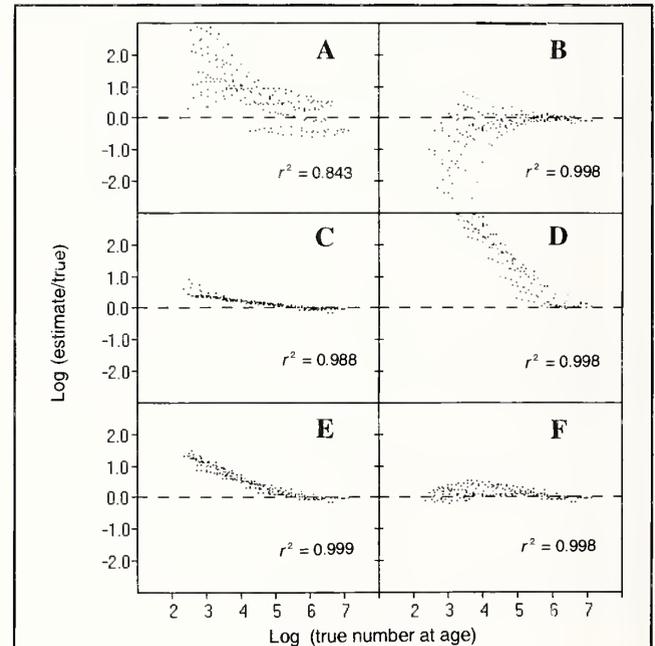


Figure 7

Ratios of estimated to true number at age from analysis of catch at age from the growth model (A), age-length key (B), probabilistic method with knowledge of prior survival (C), and probabilistic iterations 1, 5 and 10 (D-F).

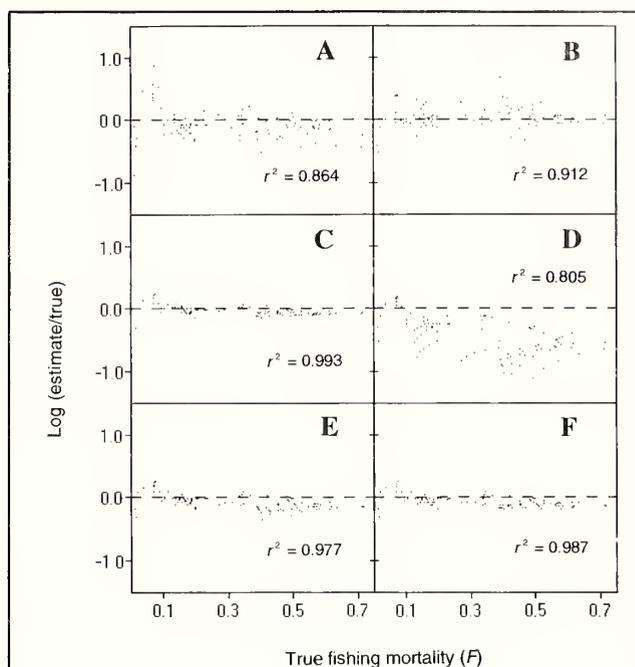
analysis, are presented in Figure 8 for ages up to 10. Again, the results were least favorable for the catch-at-age matrix developed from the growth model (Fig. 8A), followed by the age-length key (Fig. 8B), and the probabilistic method (Fig. 8C). The upward bias in estimated number at age from the probabilistic method in the absence of fishing mortality in Figure 7D led to an underestimate of fishing mortality of Figure 8D. However, the bias was reduced by the fifth iteration and almost completely removed by the tenth iteration (Fig. 8, E–F).

The relatively higher error in the catch at age for older ages estimated by using the growth model and age-length key (Fig. 6, A–B) led to relatively higher error in the estimates of numbers at age from their analysis. This resulted in poor estimation of fishing mortality for the oldest ages in the simulated catch which caused the correlation between true and estimated fishing mortalities to decline when fish older than 10 years were included in the analysis (Fig. 9, A–B). The results from the probabilistic approach also showed a similar trend but were much less sensitive than those for the other two methods (Fig. 9, D–F).

## Discussion

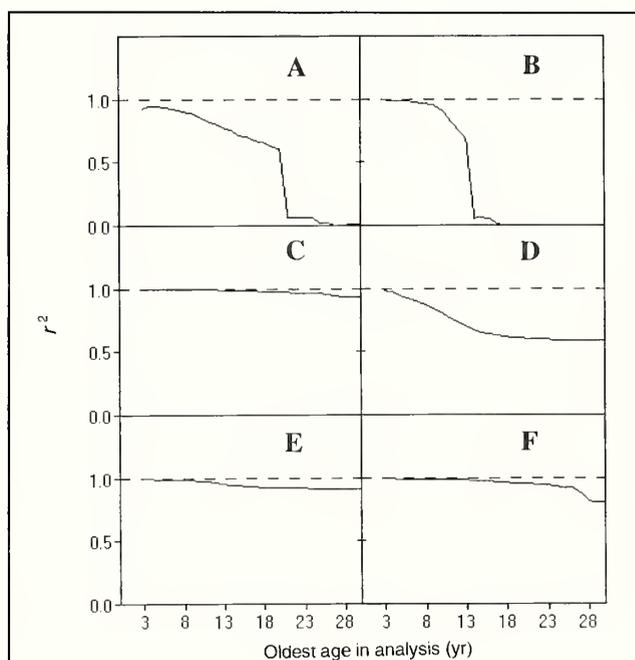
These results indicate that for the situation evaluated here the probabilistic method is superior to age assignment from either a growth model or an age-length key. Factors leading to this conclusion include knowledge of the actual history of year-class strengths and perfect knowledge of growth, natural mortality, and the distribution of size at age. Imperfect knowledge of any of these elements would degrade the performance of the probabilistic method. If there are sufficient data to develop a growth curve then it should be possible to characterize the distribution of size at age, at least for the more abundant ages in the population. Poor knowledge of the growth curve itself would also adversely affect the estimates obtained directly from the growth curve.

The results from the age-length key would be unaffected by poor knowledge of growth, past recruitment, and natural mortality. However, the comparisons among methods in the current analysis assumed no error in age assignments for the age-length key. Experience suggests that there is uncertainty in age assignment from hard-part analysis, an uncertainty that increases with fish age (Beamish and Fournier, 1981). Including such error would have added to the difference between the results of this method and those obtained with the probabilistic method. Nonetheless, the construction and application of age-



**Figure 8**

Ratios of estimated to true fishing mortality ( $F$ ) from analysis of catch at age from the growth model (A), age-length key (B), probabilistic method with knowledge of prior survival (C), and probabilistic iterations 1, 5, and 10 (D–F).



**Figure 9**

Precision of fishing mortality estimates ( $r^2$  from correlations of true and estimated rates) from the growth model (A), age-length key (B), probabilistic method with knowledge of prior survival (C), and probabilistic iterations 1, 5, and 10 (D–F).

length keys involves the fewest assumptions. Where almost certain knowledge of growth and year-class strengths is lacking, and the method for ageing the fish is robust, this method is probably the best choice for monitoring the age composition of a catch.

Where time-series data for year-class strengths are available, where growth and natural mortality are reasonably known, and where there are insufficient age determinations to construct age-length keys, the probabilistic method is clearly superior to age assignments from inverted growth models and also might be as good as, or better than, the age-length keys if they were available. Where growth and year-class strengths are well characterized and natural mortality is reasonably known, the probabilistic method should outperform all the other alternatives. Additionally, this method should be very useful for estimating the age composition of catches for the most recent year of a time series for which sample-age analysis may not yet be complete. It should also provide a reliable method to estimate the age compositions of catches for intermediate years of a time series, for which insufficient age determinations are available to construct age-length keys.

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**Abstract.**—Fishery dependent and fishery independent distribution analyses together reveal that there are three discrete areas of *Argyrosomus inodorus* abundance between Cape Point and the Kei River: one in the southeastern Cape, one in the southern Cape, and one in the southwestern Cape. On the basis of migratory patterns determined from tagging and catch data, differences in growth rates, otolith-dimension and fish-length relationships, growth zone structure, sizes at maturity and sex ratios, and on the fact that each region has nursery and spawning areas, the conclusion has been drawn that these areas of abundance represent three separate stocks. Each stock apparently disperses offshore in winter (to ca. 100 m depth) and concentrates nearshore in summer (<60 m depth) in response to oceanographic patterns. Although there is evidence of spawning activity throughout the year, the main spawning season for silver kob is from August to December, with a peak in spring (Sep–Nov). Size at sexual maturity for silver kob was smaller in the southeastern Cape than in the southern Cape, and in both regions males matured before females. Median sizes at maturity ( $L_{50}$ ) for females and males were 310 mm TL (1.3 yr) and 290 mm TL (1 yr) respectively in the southeastern Cape and 375 mm TL (2.4 yr) and 325 mm TL (1.5 yr) respectively in the southern Cape. East of Cape Agulhas, *A. inodorus* are found just beyond the surf zone to depths of 120 m. Adults occur predominantly on reefs (>20 m), whereas juveniles are found mainly over soft substrata of sand or mud (5–120 m depth). Young juveniles recruit to nurseries immediately seaward of the surf zone (5–10 m depth) but move deeper with growth. Because of lower water temperatures west of Cape Agulhas, the adults in this area are found from the surf zone to depths of only 20 m in summer.

## The life history and stock separation of silver kob, *Argyrosomus inodorus*, in South African waters

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Silver kob, *Argyrosomus inodorus*, is an important commercial and recreational sciaenid fish (max. size 34 kg) that is known from northern Namibia on the west coast of southern Africa to the Kei River on the east coast of South Africa (Griffiths and Heemstra, 1995). It is not common between Cape Point and central Namibia; therefore it is likely that the Namibian populations are not continuous with those off the eastern seaboard of South Africa (Griffiths and Heemstra, 1995). Until recently *A. inodorus* was misidentified as *A. hololepidotus* throughout its distribution; off South Africa it was also confused with a sympatric species, *A. japonicus* (Griffiths and Heemstra, 1995).

The South African line fishery consists of about 2,900 commercial (Kroon<sup>1</sup>) and some 4,000 club-affiliated recreational (Ferreira, 1993) vessels. These vary from 5 to 15 m in length and operate on both east and west coasts. Silver kob is probably the most valuable species caught by the line fishery between Cape Point and East London if market value and annual catch are combined; *A. inodorus* is also landed as a bycatch of the sole- and hake-directed inshore trawl fishery between Cape Agulhas and Port Alfred (Japp et al., 1994) and is caught by rock and surf anglers and commercial beach-seine fishermen in the

southwestern Cape. Although an important species, trawl and line catch per unit of effort for this species has declined substantially during the last three decades, and concern has been expressed over the large contribution of recruits to line catches in the southeastern Cape (Smale, 1985; Hecht and Tilney, 1989).

Knowledge of the life history of fishes "is an almost essential prerequisite to successful identification of stocks" (Pawson and Jennings, 1996) and is fundamental to stock assessment and to the formulation of effective management strategies for their sustainable use. Despite the importance of *A. inodorus* and evidence for declining catches, little has been published on its life history; wise management has therefore not been possible. Smale (1985) investigated the sex ratio and spawning seasonality of "*A. hololepidotus*" based on the catches of lineboat fishermen in Algoa Bay but inadvertently included both *A. inodorus* and *A. japonicus* in his study (established via voucher specimens and otoliths). Griffiths (in press, a) recently described the growth of *A. inodorus* from three geographical regions between Cape

<sup>1</sup> Kroon, W. 1995. Sea Fisheries, Permit Division, P. Bag X2, Roggebaai, 8012, Cape Town, South Africa. Personal commun.

Point and the Kei River. On the basis of grow rate, fish-length and otolith-dimension relationships, and the appearance of growth zones, he concluded that silver kob within this area comprise at least three separate stocks.

The objective of the present study was to provide information on the life history of *A. inodorus* occurring between Cape Point and the Kei River, including reproductive seasonality, spawning grounds, size at maturity, juvenile and adult distribution, and migration. Because the identification of discrete stocks or "management units" is essential for effective management (Pawson and Jennings, 1996), the multiple stock concept is further developed with information on distribution and abundance, life history parameters, and mark-recapture data.

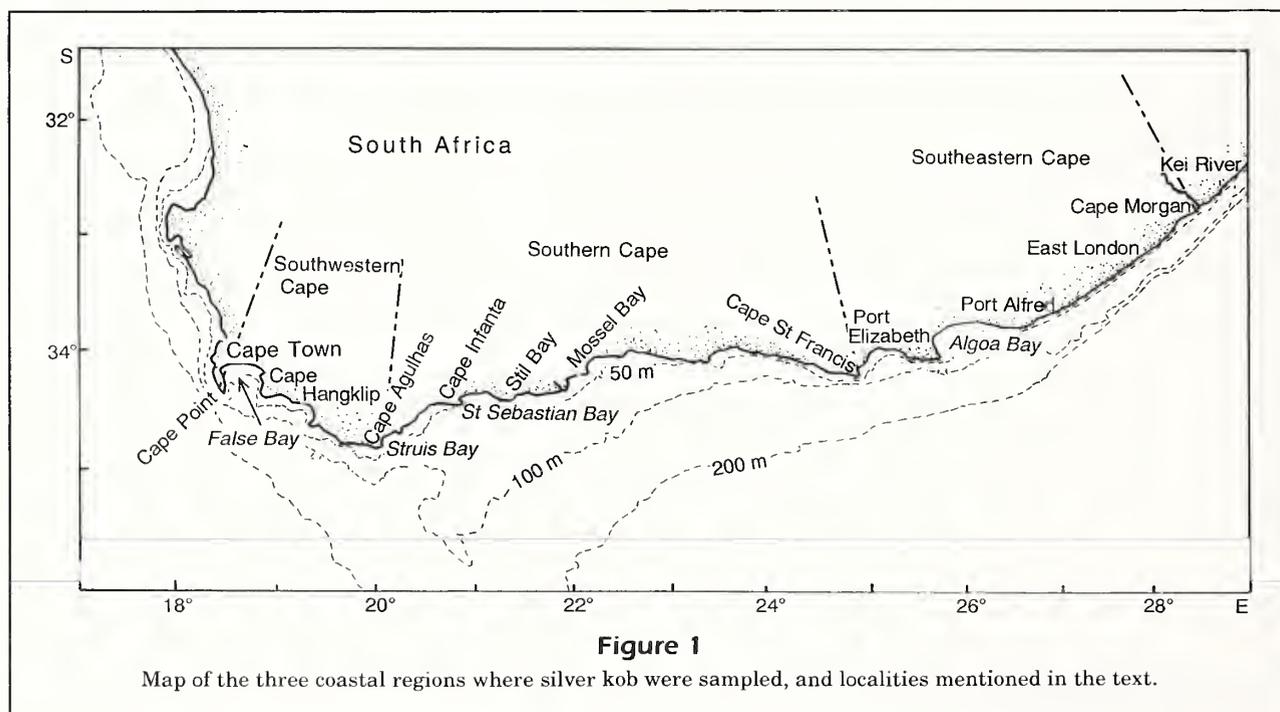
## Materials and methods

The study area (from Cape Point to Kei River) was divided into three regions for sampling purposes (Fig. 1). These regions were identical to those used by Griffiths (in press, a); they were not divided according to political boundaries but rather generated to increase analytical resolution. Biological (March 1990–January 1992) and length-frequency (January 1990–December 1994) data were collected in each region from fish caught 1) by the line fishery, 2) by the inshore trawl fishery, 3) by trawlers during South Coast Biomass Surveys conducted by the Sea Fish-

eries Research Institute, and 4) by research linefishing operations. Biological data were also obtained from silver kob caught by beach seines in False Bay (Oct 1991). Trawled fish were generally caught over sand or mud substrata, and line-caught fish over reef. Owing to the high relief rocky nature of the inshore habitat west of Cape Agulhas, this species is not trawled in the southwestern Cape.

Fish sampled for biological purposes were measured (to the nearest 1 mm [total length]), weighed (to the nearest gram [fish <500 g], the nearest 20 g [fish 500 g–5 kg], or the nearest 100 g [fish 5 kg–25 kg]), cut open, and sexed. Gonads were removed, assigned a visual index of maturity (see Table 1), and weighed to the nearest 0.1 g. Males were assigned an index of drumming muscle development (1=none, 2=partially developed, 3=fully developed). Owing to logistical constraints, monthly biological data were obtained only for the southeastern Cape; in the other two regions biological sampling was limited to the spawning season.

Areas of silver kob abundance were delineated by using returns from the commercial line fishery and data from South Coast Biomass Surveys (SCBS's). Line catches consisted predominantly of adult fish, whereas trawl catches from SCBS's comprised mostly juveniles and young adults (see below). Annual catch-per-unit-of-effort data (catch per outing) were plotted on a subregional basis for the commercial line fishery (an outing did not exceed one day), and the data from 14 SCBS's (Table 2) were used to calculate



**Table 1**Classification and description of the macroscopic gonad maturity stages of *Argyrosomus inodorus*.

Stage	Description
1 <b>Juvenile</b>	This stage is generally only found in fish < 200 mm TL. Testes are threadlike, and the ovaries appear as transparent pinkish flaccid sacs, about half the length of those at stage 2.
2 <b>Immature or resting</b>	Testes are extremely thin, flat, and pinkish white. Ovaries appear as translucent orange tubes. Eggs are not visible to the naked eye.
3 <b>Active</b>	Testes are wider, triangular in cross section and beige. Sperm are visible if the gonad is cut and gently squeezed. Eggs become visible to the naked eye as tiny yellow granules in a gelatinous orange matrix. There is very little increase in the diameter of the ovary.
4 <b>Developing</b>	Testes become wider and deeper and are mottled and creamy beige. They are also softer in texture, rupturing when lightly pinched. Besides the obvious presence of sperm in the main sperm duct, some sperm are also present in the tissue. Ovaries become larger in diameter and opaque yellow in color. Clearly discernible eggs occupy the entire ovary.
5 <b>Ripe</b>	Testes still larger in cross section and softer in texture. They become creamier in color owing to considerable quantities of sperm. The ovaries are larger in diameter as a result of an increase in egg size.
6 <b>Ripe and running</b>	Testes even larger in cross section and uniformly cream in color. They are extremely delicate at this stage and rupture easily when handled. Sperm are freely extruded when pressure is applied to the abdomen of the whole fish. Ovaries amber in color and have a substantial proportion of hydrated eggs.
7 <b>Spent</b>	Testes are shrivelled and a mottled beige and cream. A little viscous semen may still ooze from the genital pore when pressure is applied to the abdomen. Ovaries are reduced in size, similar in appearance to those at stage 2 and have a few remaining yolked oocytes. These yolked oocytes are generally aspherical and appear to be undergoing resorption.

mean numbers of silver kob per 30-min trawl per grid block. The SCBS methods are fully described by Badenhorst and Smale (1991); therefore only a summary is given here. The survey area extended from Cape Agulhas to Port Alfred and seawards to a depth of 500 m. This area was divided into four depth zones (0–50 m, 51–100 m, 101–200 m, and 200–500 m), which were in turn subdivided into blocks of 5 × 5 nautical miles. The blocks trawled during each survey were determined semirandomly according to the ratio of blocks per stratum. Bobbins were not used; therefore trawling was limited to nonreef substrata. The shallowest depth over which the research vessel (*F.R.S. Africana*) could operate was 20 m. A 180-ft German trawler with a 25-mm-mesh (bar) liner attached to the trawl bag was used. Trawl duration was limited to 30 min, and the results of shorter trawls (owing to technical reasons or to hitting the reef) were standardized to that time. Bottom temperature was recorded immediately after most trawls with a Neil Brown MK III-B conductivity, temperature, and depth probe (CTD). Mean numbers of *A. inodorus* per trawl for each 1°C of bottom temperature were plotted to obtain the preferred temperature range of this species.

Migration of *A. inodorus* was studied by using tagging and catch data. A tagging program was initiated in February 1994. Silver kob captured with hook

**Table 2**

Number of trawls in which juvenile *A. inodorus* were caught during South Coast Biomass Surveys between Cape Agulhas (20°E) and Port Alfred (27°E) during the period 1987–95.

Cruise	Total trawls	Trawls with silver kob
9 Sep–4 Oct 1987	88	24
11 May–2 Jun 1988	93	8
11 May–28 May 1989	62	12
24 May–12 Jun 1990	58	12
8 Sep–26 Sep 1990	73	21
8 Jun–1 Jul 1991	91	24
14 Sep–2 Oct 1991	75	30
1 Apr–20 Apr 1992	82	6
3 Sep–20 Sep 1992	87	32
19 Apr–10 May 1993	109	9
2 Sep–28 Sep 1993	106	30
8 Jun–3 Jul 1994	89	11
22 Sep–16 Oct 1994	92	18
23 Apr–15 May 1995	95	9
All cruises	1,200	246

and line were tagged with plastic T-bar tags in False Bay ( $n=1,034$ ), off Struis Bay ( $n=750$ ), and off Stil Bay ( $n=291$ ). The data for recaptured silver kob

( $n=157$ ), predominantly adults, were analyzed according to tagging locality, days free, and the minimum aquatic distance travelled.

Owners of commercial line boats and inshore trawlers are required to submit daily catch returns to the Sea Fisheries Research Institute. The monthly catches of *A. inodorus* made by commercial line-fishermen in each of the three regions and the monthly catches made by the inshore trawl fishery in the southern Cape and the southeastern Cape for the period 1986–94 were expressed as percentages of the respective annual totals.

The median size at first maturity ( $L_{50}$ ) for males and females was estimated by fitting a logistical function (LOGIT) to the fractions of mature fish (gonad stage 3+) per 50-mm length class (midpoint) that were sampled in the southern Cape and the southeastern Cape during the breeding season. Many of the smaller males with active testes lacked drumming muscles. Logistical functions were therefore also fitted to the fractions of males (per 50-mm length class) with fully developed drumming muscles. Because *A. inodorus* are not trawled in the southwestern Cape, few juveniles were sampled and  $L_{50}$  values could not be calculated for that region.

Reproductive seasonality was established in the southeastern Cape by calculating both gonadosomatic indices (GSI's) and the monthly percent frequency of each maturity stage for fish  $>L_{50}$ .

$$\text{GSI} = \frac{\text{gonad weight}}{(\text{fish weight} - \text{gonad weight})} \times 100.$$

The extent of the spawning area was determined by computing the percent frequency of each maturity stage for fish ( $>L_{50}$ ) that were sampled during peak spawning (Oct and Nov 1991) off East London, Port Alfred, Mossel Bay, St Sebastian Bay, and False Bay. Sex ratios were tested statistically for significant deviations from unity with a chi-square test ( $P < 0.05$ ).

Nursery areas were delineated by comparing the length-frequency distributions of silver kob caught 1) during South Coast Biomass Surveys (SCBS), 2) during experimental linefishing expeditions (no minimum size) and 3) by the line fishery (1990–94) as well as by analyzing the catch and effort distributions generated for silver kob during SCBS's (1987–95).

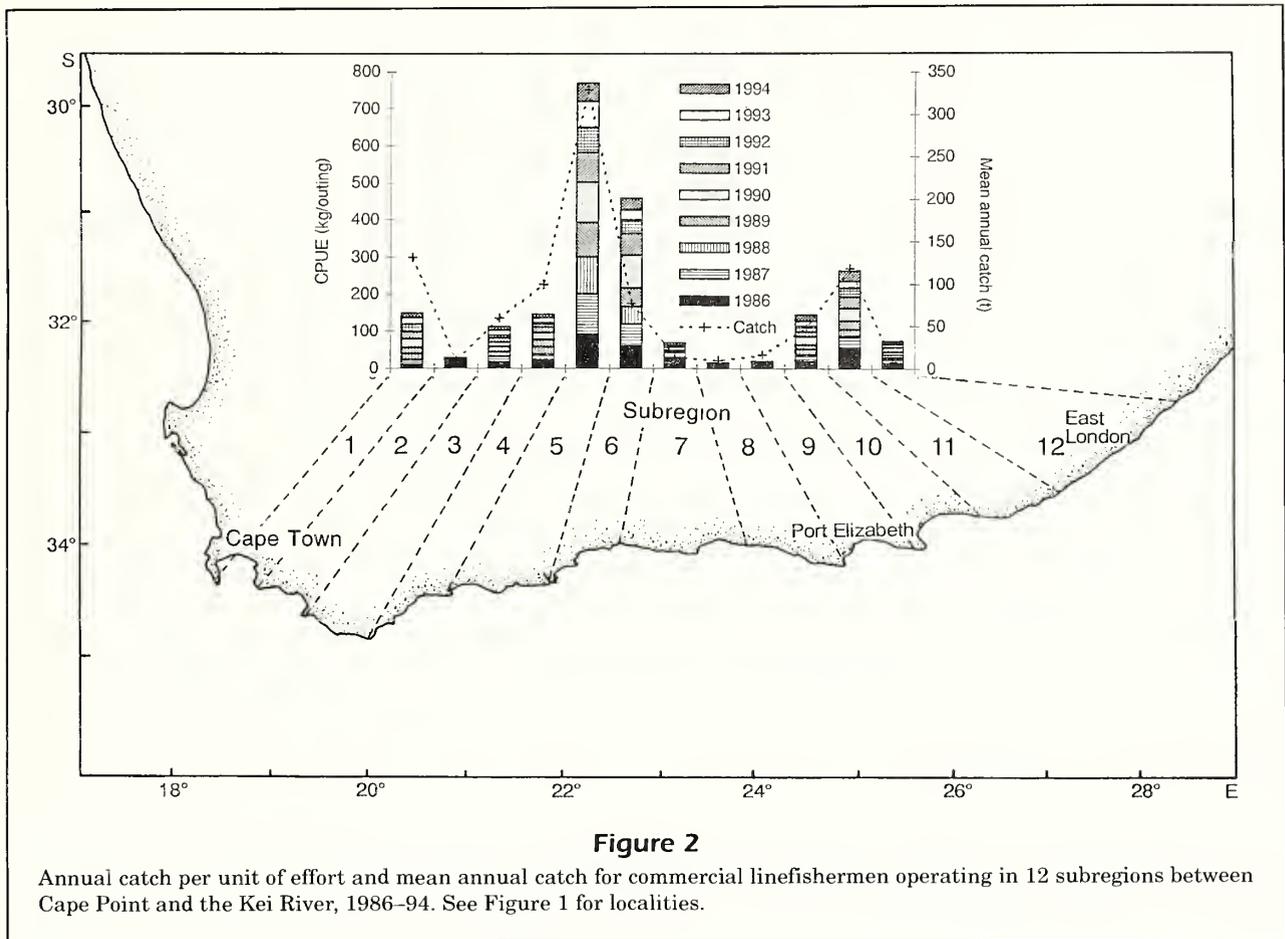
## Results

### Catch distribution and migration

Geographically related catch and CPUE trends for the line fishery consisted of three modal groups

(Fig. 2), indicating that there are three areas of adult abundance between Cape Point and the Kei River (one in each region). Data from SCBS's showed that adult abundance trends were reflected in juvenile distribution, at least for the east coast (Fig. 3). Substantial differences in growth rates, otolith-dimension and fish-length relationships, and growth zone structure (Griffiths, in press, a) suggest that these areas of abundance represent three allopatric stocks. Tag returns from the present study revealed that South African silver kob are capable of migrations of 240 km in six months but that most fish (84%) did not move more than 50 km from their tagging locality (Fig. 4). Only one fish tagged in False Bay was recaptured outside of that bay. Of the silver kob tagged in the Struis Bay vicinity, five (5.3%) had migrated westwards to False Bay, and the rest were recaptured either within 50 km of the tagging locality (77.3%) or had moved eastwards (17%), but only as far as Mossel Bay. None of the tagged fish were recaptured in the southeastern Cape. Tagging data therefore support the three-stock concept but suggest that there is limited exchange between silver kob in the southern Cape and those in the southwestern Cape. Based on catch data, the foci of each stock are apparently False Bay, Stil Bay, and Port Alfred, which are separated by distances of 396 and 630 km, respectively. Struis Bay is situated towards the westerly extreme of the area occupied by the southern Cape stock: therefore it is not surprising that of the recaptured silver kob that had moved substantial distances ( $>50$  km) from this tagging locality, most had moved to the east.

Interviews with commercial linefishermen ( $n=36$ ); also confirmed by author's personal experience indicated that their silver kob catch was made on reefs at depths of 20–60 m to the east and 5–20 m to the west of Cape Agulhas. Inshore trawling between Cape Agulhas and Port Alfred occurs on soft ground at depths of 50–120 m (Japp et al., 1994). Decreases in the line catches of all three stocks during winter (Fig. 5) and corresponding increases in the catches made by inshore trawlers (Fig. 6) suggest that silver kob move farther offshore at this time of the year. Because inshore trawlers fish over substrata that are different from those over which linefishermen fish and since they land mostly juvenile and young adult *A. inodorus* (Fig. 7), it could be argued that trawl catch data do not reflect the winter locality of the adult population. The offshore movement of adults is supported, however, by the recapture of four specimens (435–720 mm) tagged in 30 m of water off Struis Bay in summer 1995 by inshore trawlers operating in 80 m off Stil Bay and off Cape Infanta in the winter and early spring of that year. Presumably, large adults



are also found on predominantly untrawlable rocky substrata during their offshore winter distribution.

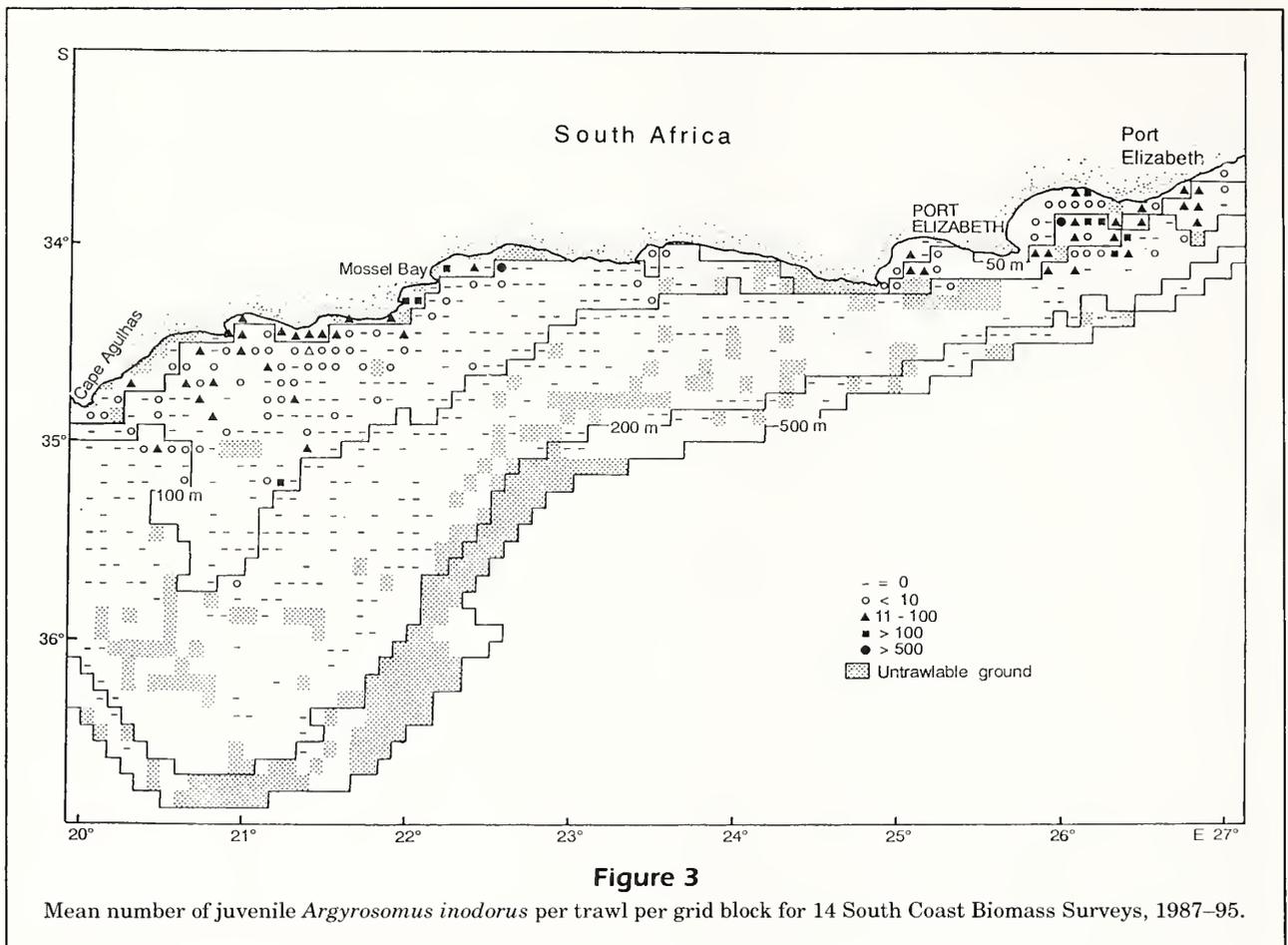
### Size at maturity

Silver kob were found to mature at a smaller size in the southeastern Cape than in the southern Cape, and in both regions males matured at a smaller size than did females. Females began to mature at about 250 mm in both regions, but the percentages of mature fish in consecutive size classes increased more rapidly in the southeastern Cape than in the southern Cape (Fig. 8, A and B). Estimated median lengths at maturity ( $L_{50}$ ) were 310 mm and 375 mm for the two regions respectively. All females in the southeastern Cape larger than 450 mm and all females in the southern Cape larger than 550 mm were mature (Fig. 8, A and B).

A comparison of the testes method with the drumming muscle method for estimating male maturity indicated that, within each region, the two methods produced similar estimates for length at total maturity but that the testes method produced higher es-

timates for the proportions of mature fish in size classes below this length. In the southeastern Cape, males began to mature at 150 mm (testes method) and at 200 mm (drumming muscle method),  $L_{50}$  was calculated at 205 mm (testes method) and 290 mm (drumming muscle method), and total maturity was attained at 400 mm (both methods)(Fig. 8, C and E). In the southern Cape, males began to mature at 200 mm (testes method) and at 250 mm (drumming muscle method),  $L_{50}$  was calculated at 270 mm (testes method) and 325 mm (drumming muscle method), and total maturity was attained at 450 mm (both methods)(Fig. 8, D and F).

Many of the smaller males (<300 mm) classified as mature (i.e. testes contained sperm), had disproportionately smaller gonads and also lacked drumming muscles. Because male drumming plays an important role in sciaenid spawning behavior (Takemura et al., 1978; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Connaughton, 1996), it is not known whether these fish would actually spawn. Even if the small males (without drumming muscles) managed to spawn with a communal spawn-

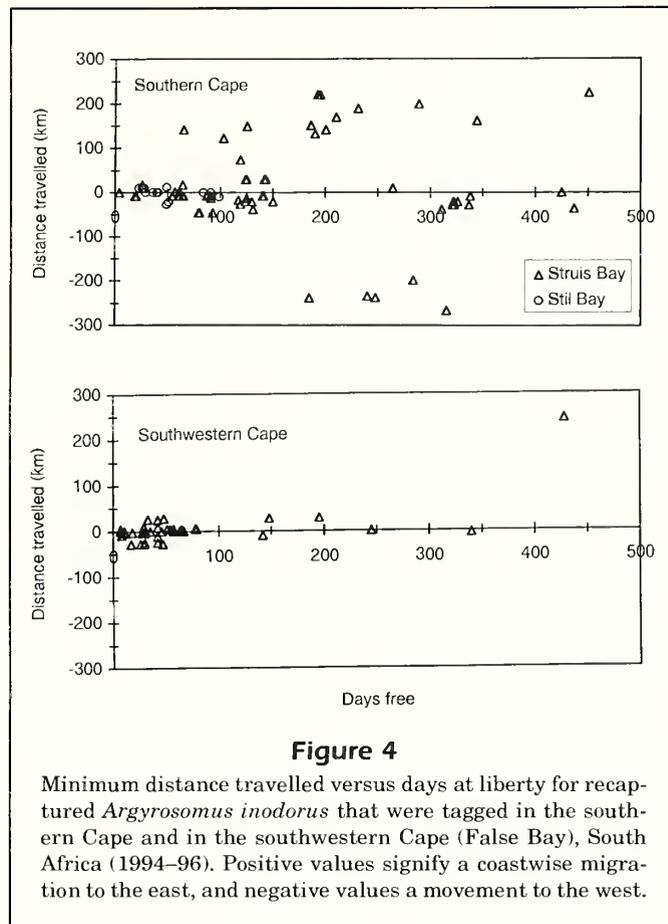


ing aggregation (doubtful as this may be), their contribution to the total reproductive output (of the aggregation), in relation to the small size of their testes, would likely be extremely low. Therefore, from a management view point, the  $L_{50}$  estimates based on drumming muscle development were regarded as more useful than those based on gonad staging.

According to Griffiths (in press, a), there was no difference between the growth rates of *A. inodorus* in the southeastern Cape and those in the southern Cape during 1990-91. The smaller sizes at maturity in the former region were therefore due to earlier maturity and not to slower growth. Female  $L_{50}$  and total maturity are attained at about 1.3 and 3.5 yr in the southeastern Cape and at about 2.4 and 4.7 yr in the southern Cape. Male  $L_{50}$ , based on testes staging and on drumming muscle development, was attained at <1 yr and at 1 yr for silver kob in the southeastern Cape, and at <1 yr (testes staging) and at 1.5 yr (drumming muscle development) in the southern Cape. Total male maturity was attained at about 2.8 yr in the southeastern Cape and at about 3.4 yr in the southern Cape.

## Spawning

Gonadosomatic indices (Fig. 9) and gonad maturity indices (Fig. 10) for silver kob in the southeastern Cape showed that although some spawning occurred throughout the year, there was a clearly defined breeding season from August to December and that peak spawning occurred in spring (Sep-Nov). These results are in general agreement with those of Smale (1985) for Algoa Bay, but his spawning season appears to have been "extended" by about one month, through the inclusion of *A. japonicus*, which spawns from October to January (Griffiths, in press, b) in the southeastern Cape. The low proportion of ripe and running (stage-6) females sampled during the spawning season (Fig. 10; and Smale, 1985) suggests that females feed less and are therefore less prone to capture (with hook and line) after oocyte hydration. This inference is supported by a much higher proportion of stage-6 females in catches of silver kob caught by beach seines in False Bay than in catches made by using hook and line in four other localities



**Figure 4**

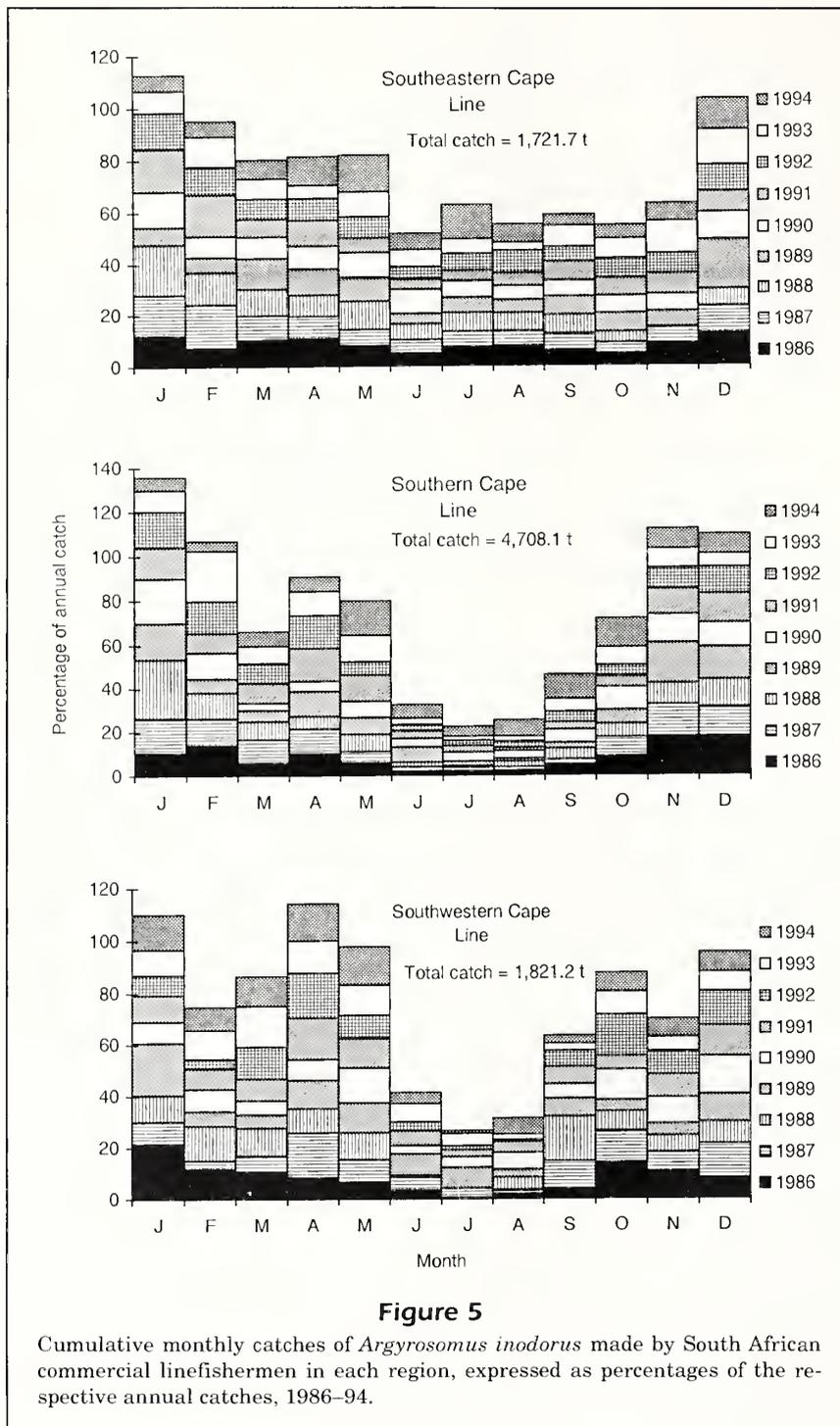
Minimum distance travelled versus days at liberty for recaptured *Argyrosomus inodorus* that were tagged in the southern Cape and in the southwestern Cape (False Bay), South Africa (1994–96). Positive values signify a coastwise migration to the east, and negative values a movement to the west.

(during similar months and times of day)(Fig. 11). Very low numbers of females with hydrated oocytes have also been reported in line catches of other sciaenids, e.g. *Sciaenops ocellatus* (Fitzhugh et al., 1988), *Micropogonias undulatus* (Barbieri et al., 1994), and *Atractoscion aequidens* (Griffiths and Hecht, 1995a); no hydrated oocytes were detected from line catches of *Argyrosomus japonicus* (Griffiths, in press, b). Most silver kob caught during SCBS's were juveniles. Nevertheless, none of the adult females that were trawled had hydrated oocytes, perhaps because these fish were captured on the nursery grounds and not on adult habitat where spawning is expected to occur (see below).

The large proportion of ripe and ripe and running (stages 5 and 6) males and females at each of the five sites between Cape Point and the Kei River (Fig. 11) during October–November suggests that spawning occurs throughout the study area and that peak spawning occurs during spring for all three stocks. The inshore distribution of the adults during spring and summer, the absence of *Argyrosomus* eggs and

larvae in the Agulhas Current (ca. 200 m)(Beckley, 1993), and the occurrence of significant numbers of early stages of *A. inodorus* larvae (identified as "*A. hololepidotus*") in 5–7 m in Algoa Bay (Beckley, 1986) suggest that spawning occurs in less than 50 m depth of water. However, even though early life stages of larvae and juvenile recruits (see "nursery areas" below) are found just seaward of the surf zone (5–7 m), it is not certain whether spawning occurs in this area or whether it occurs in slightly deeper water and the eggs and larvae are transported shorewards by currents.

Although spawning in other sciaenids, including *A. japonicus*, occurs at night (Fish and Cummings, 1972; Takemura et al., 1978; Holt et al., 1985; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Griffiths, in press, b), the fact that large proportions of ripe and running females caught in seine nets in False Bay (Fig. 11) were caught between 11:30 h and 14:30 h, suggests that spawning in *A. inodorus* may occur during the day. The water temperature in which ripe and running females were captured was 18–19°C, but as indicated for other sciaenids (Saucier

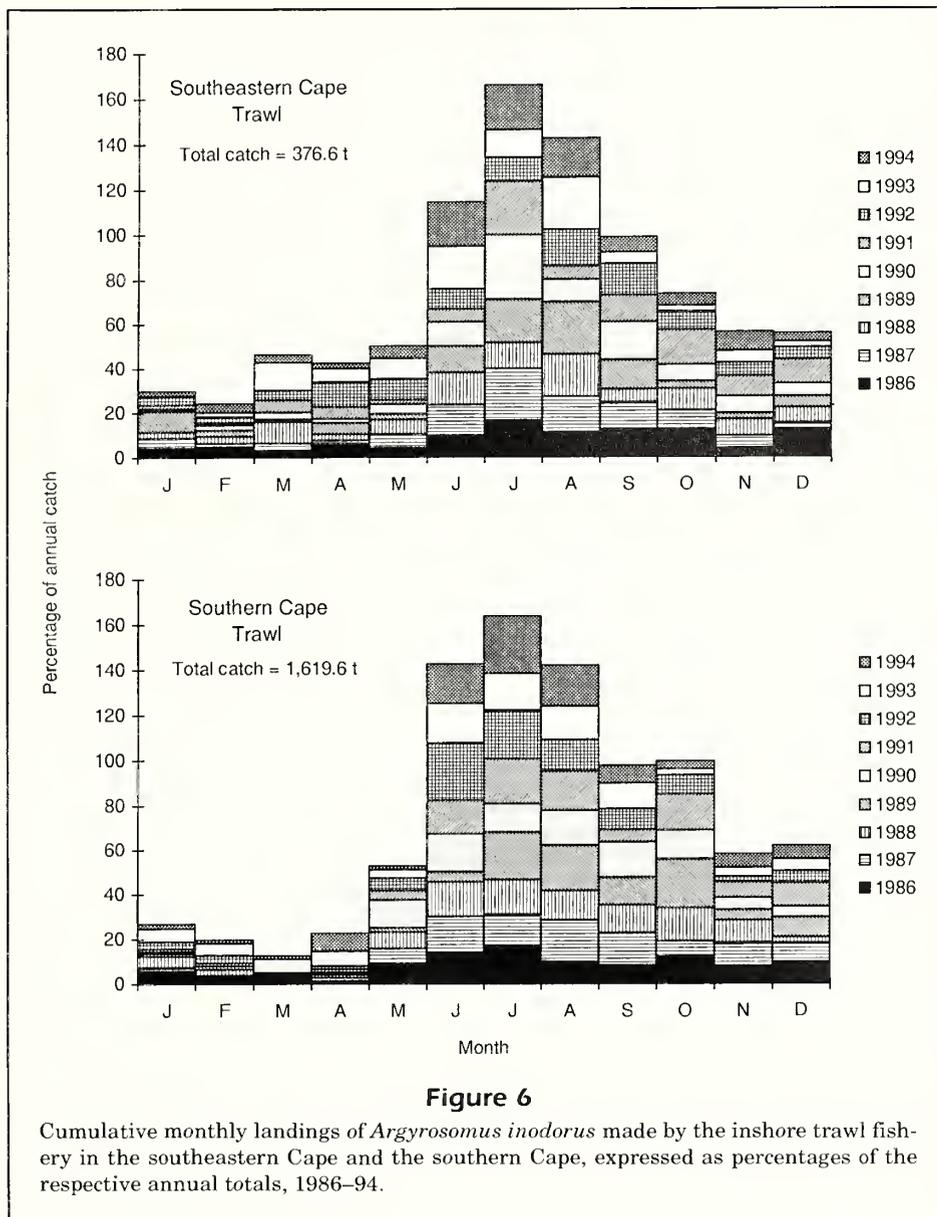


**Figure 5**

Cumulative monthly catches of *Argyrosomus inodorus* made by South African commercial linefishermen in each region, expressed as percentages of the respective annual catches, 1986-94.

and Baltz, 1993; Connaughton and Taylor, 1995), a range of spawning temperatures is expected. Hydrophonic monitoring of drumming levels (Takemura et al., 1978; Saucier and Baltz, 1993; Connaughton and Taylor, 1995) would provide better information on the times, sites, and oceanographic conditions necessary for spawning of silver kob.

Although the ovaries of *A. inodorus* were not examined microscopically, substantial increases in the number of spent gonads towards the end of, and immediately after, the five-month spawning season (Fig. 10), as opposed to throughout the season, suggest that they are multiple spawners. Unfortunately partially spawned fish could not be identified macro-

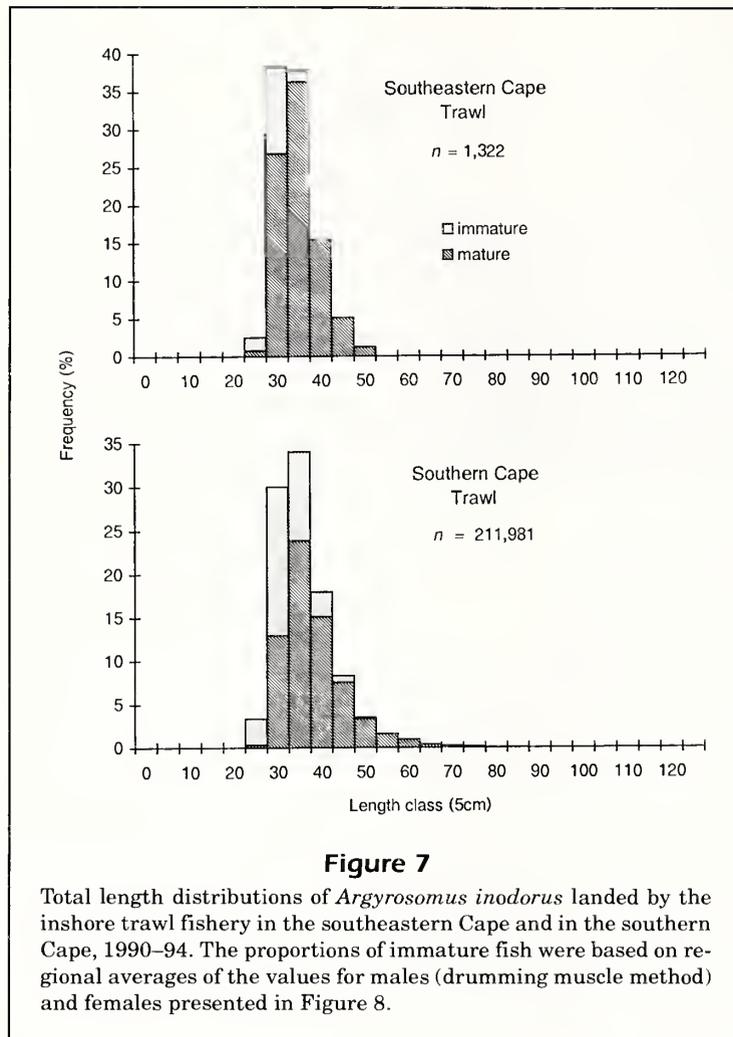


scopically. Multiple-batch spawning has been described for several other species of sciaenids, e.g. *Sciaenops ocellatus* (Fitzhugh et al., 1988), *Seriphus politus* (DeMartini and Fountain, 1981), *Cheilotrema saturnum* (Goldberg, 1981), *Genyonemus lineatus* (Love et al., 1984), *Cynoscion nebulosus* (Brown-Peterson et al., 1988), *Pogonias cromis* (Fitzhugh et al., 1993; Nieland and Wilson, 1993), and *Microgogonias undulatus* (Barbieri et al., 1994).

### Sex ratios

From the total numbers of silver kob sampled, it was evident that there were significantly more females

(1.6×) in the southeastern Cape, more males (1.2×) in the southern Cape, and more females (2.1×) in the southwestern Cape (Table 3). Except for the smallest size class sampled in the southeastern Cape (where males predominated), all other size classes sampled in the southeastern Cape and in the southwestern Cape contained significantly more females. Smale (1985) also recorded consistently higher proportions of female "*A. hololepidotus*" per 100-mm length class for fish sampled in the southeastern Cape (1978–81). Although he included both *A. inodorus* and *A. japonicus* in his study, the latter species recruits to the line fishery only at about 1,000 mm TL (Griffiths, in press, b), therefore his speci-

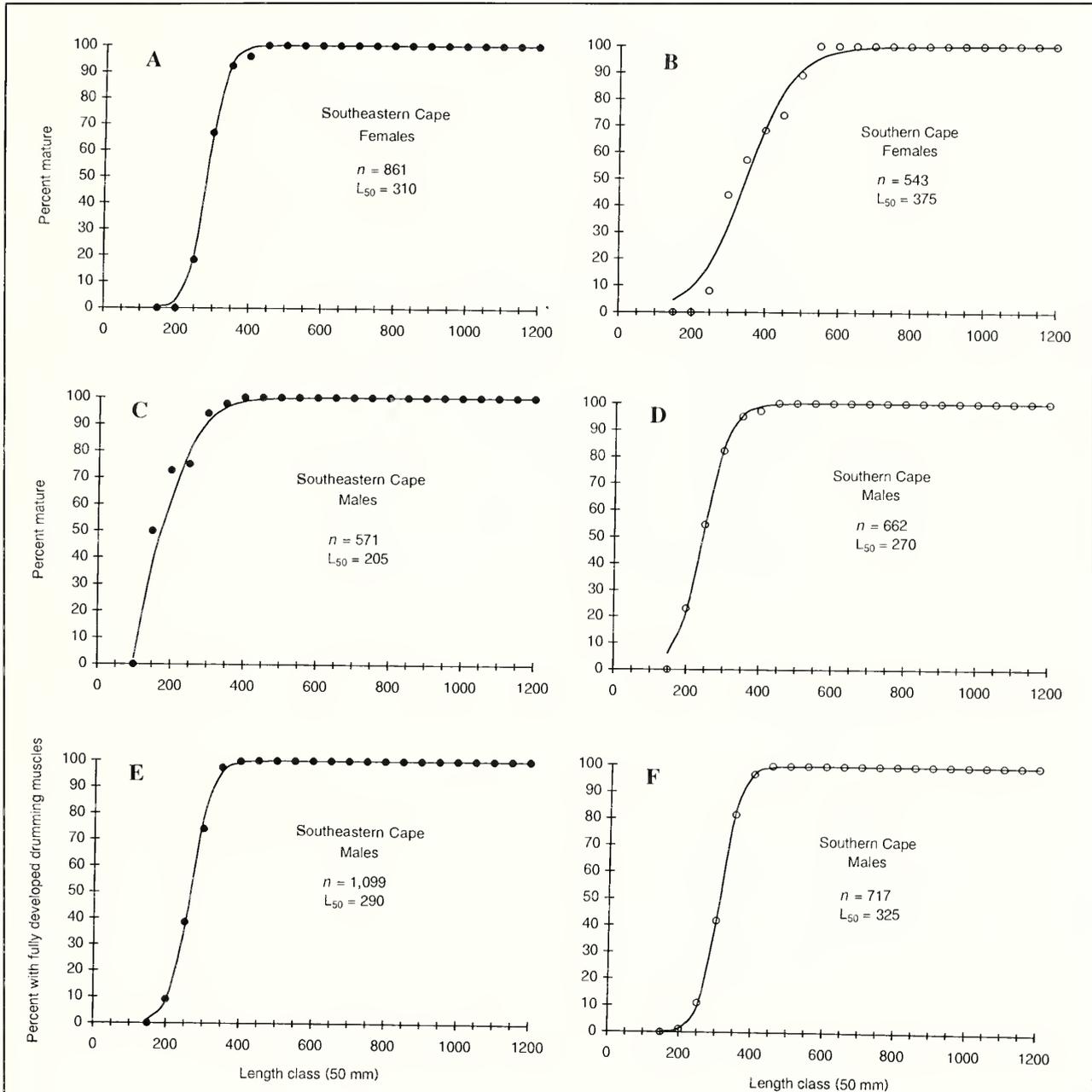
**Table 3**

Sex ratios of *Argyrosomus inodorus* from three regions along the South African eastern seaboard. \* = significant difference at  $P < 0.05$ .

Total length (mm)	Southeastern Cape			Southern Cape			Southwestern Cape		
	M : F	n	$\chi^2$	M : F	n	$\chi^2$	M : F	n	$\chi^2$
100–199	1.4 : 1	188	4.2*	1.2 : 1	114	0.9			
200–299	1 : 1.2	562	4.4*	1.1 : 1	320	1.3			
300–399	1 : 1.7	1,194	72.4*	1.2 : 1	289	2.5	1 : 1.3	72	0.9
400–499	1 : 2.0	541	61.9*	1.3 : 1	544	10.6*	1 : 3.1	49	12.8*
500–599	1 : 2.9	212	49.1*	1.5 : 1	212	9.1*	1 : 1.7	57	4.0*
600–699	1 : 2.0	119	7.1*	1 : 1.2	76	0.8	1 : 2.6	36	7.1*
700–799	1 : 1.8	58	4.4*	1 : 1.2	30	0.1	1 : 1.8	61	13.8*
800–899	1 : 1.5	56	2.6*	1.1 : 1	25	0.0	1 : 2.0	77	8.1*
900–999	1 : 3.2	25	6.8*	1.9 : 1	43	3.9*	1 : 2.8	57	12.8*
1000–1099	1 : 6.3	21	11.6*	1.3 : 1	80	1.0	1 : 2.6	29	5.8*
1100–1199	1 : 1.5	5	0.2	1 : 1.1	30	0.1			
All sizes	1 : 1.6	2,982	158.7*	1.2 : 1	1,764	20.1*	1 : 2.1	446	57.4*

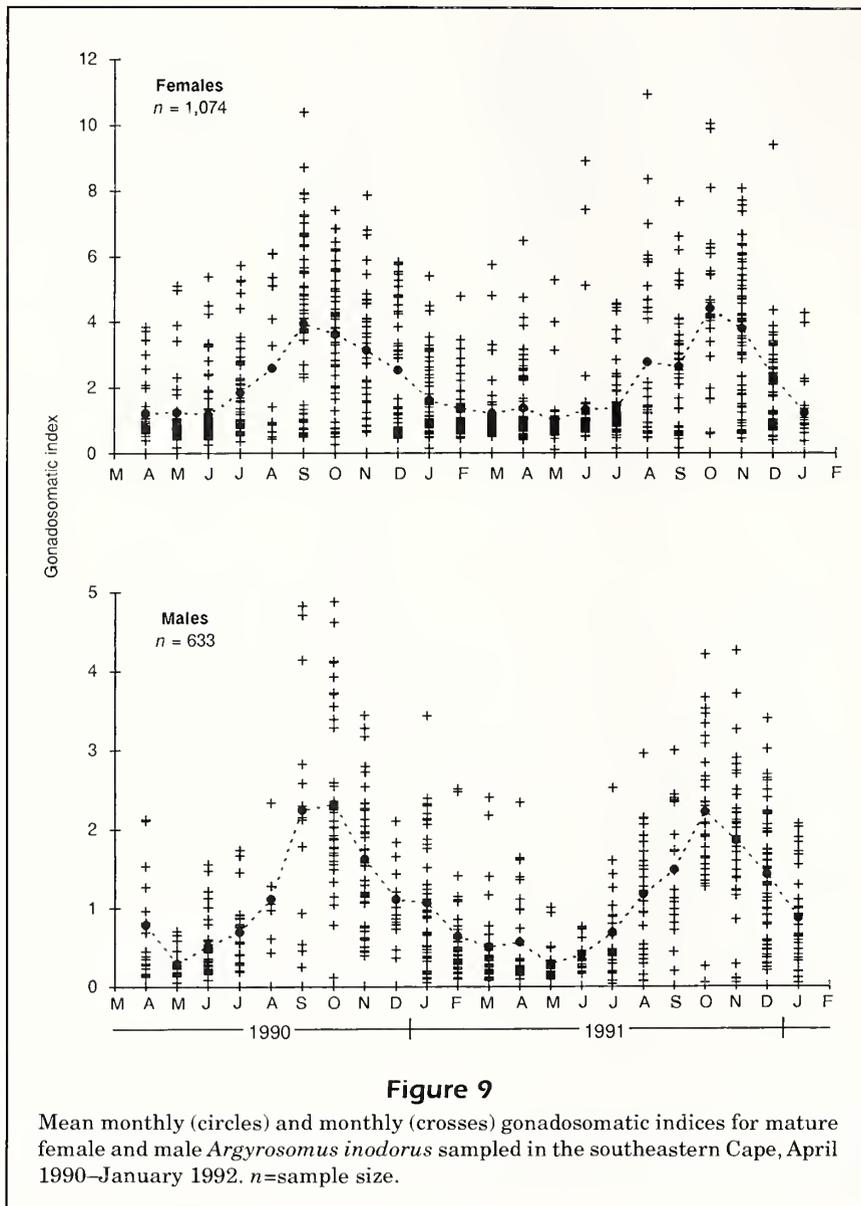
mens below this length were mostly *A. inodorus*. Of the 11 size classes sampled in the southern Cape, eight contained more males and three contained more females (Table 3). However, the ratios of only three of these size classes (each with more males) were significantly different from the expected 1:1. Because more males were sampled within most size classes

in the southern Cape, it would appear that there are more males than females in this region and that the lack of significance for several of the size classes could be due to limitations of the statistical test. The chi-square test is based on absolute differences (between observed and expected) and does not take into account sample size, e.g. although a ratio of 1.2:1



**Figure 8**

Percentage of mature female (gonad stage 3+) and male (gonad stage 3+ and drumming muscle stage 3) *Argyrosomus inodorus* by 50-mm total-length intervals, sampled during the spawning period in the southeastern Cape and in the southern Cape. The solid line describes the fitted logistical function.  $L_{50}$  = median length at first maturity (mm total length);  $n$  = sample size.



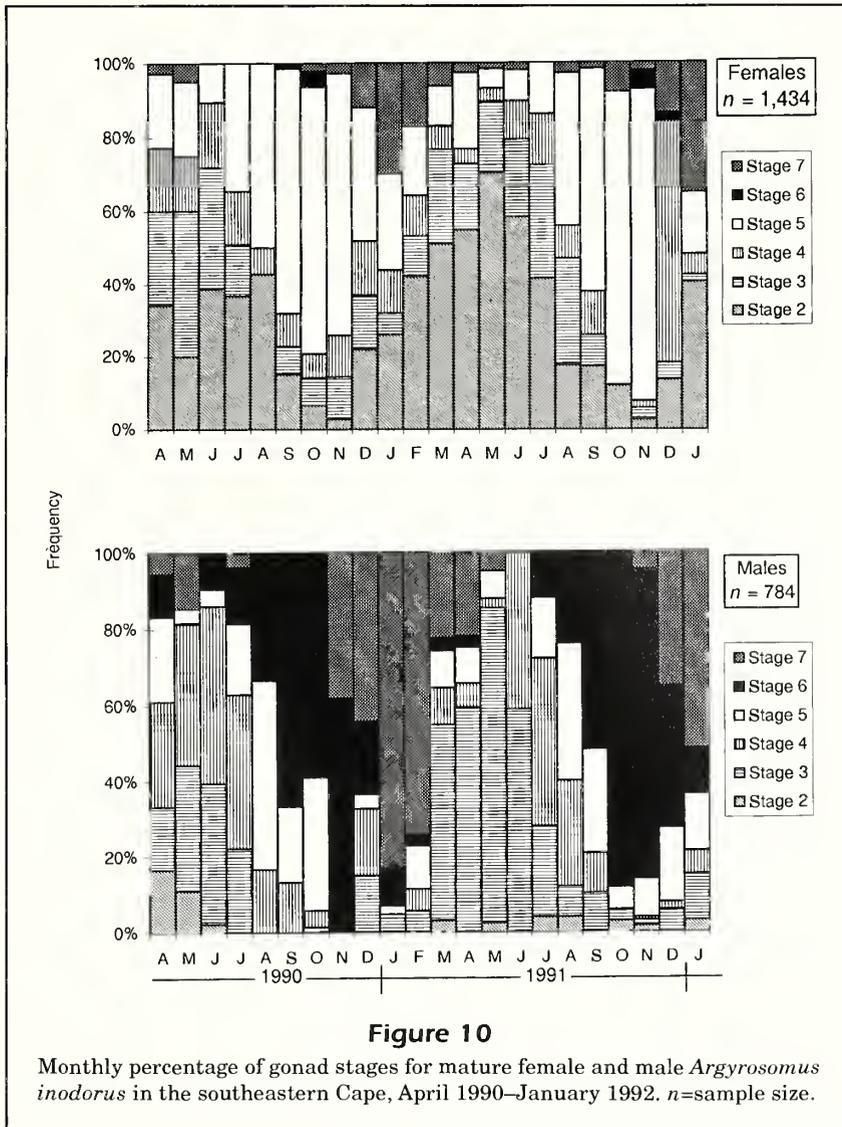
( $n=1,764$ ) was significant (even at  $P<0.001$ ), one of 1.3:1 ( $n=80$ ) was not (Table 3). Thus researchers studying sex ratios should make every effort to obtain large samples, particularly if the chi-square method is to be used as a test for significant difference.

### Nursery areas

*Argysomus inodorus* landed by the line fishery were mostly adult fish between 40 and 120 cm TL (Fig. 12). Although fish <40 cm TL were not represented in the present study owing to the minimum size limit imposed on linefishermen, experimental linefishing indicated that silver kob on the linefishing grounds (reef substrata) were mostly >30 cm TL (Fig. 12) and that in

the southeastern Cape and in the southern Cape they were generally larger than the female  $L_{50}$  estimates.

*Argysomus inodorus* trawled between Cape Agulhas and Port Alfred during SCBS's (nonreef substrata) ranged between 5 and 120 cm TL but were generally <45 cm TL, and largely immature (Fig. 13). The modal length class increased from 20–25 cm at depths of 25–50 m, to 25–30 cm at 50–100 m and 30–35 cm at 100–150 m; and the proportion of mature fish increased accordingly. Although depths <25 m were not sampled during SCBS's, silver kob (identified as "*A. hololepidotus*") trawled in <9 m during an earlier survey of the bays between Mossel Bay and Algoa Bay were mostly 9–18 cm TL (Smale, 1984). Beckley (1984) recorded *A. inodorus* (also iden-

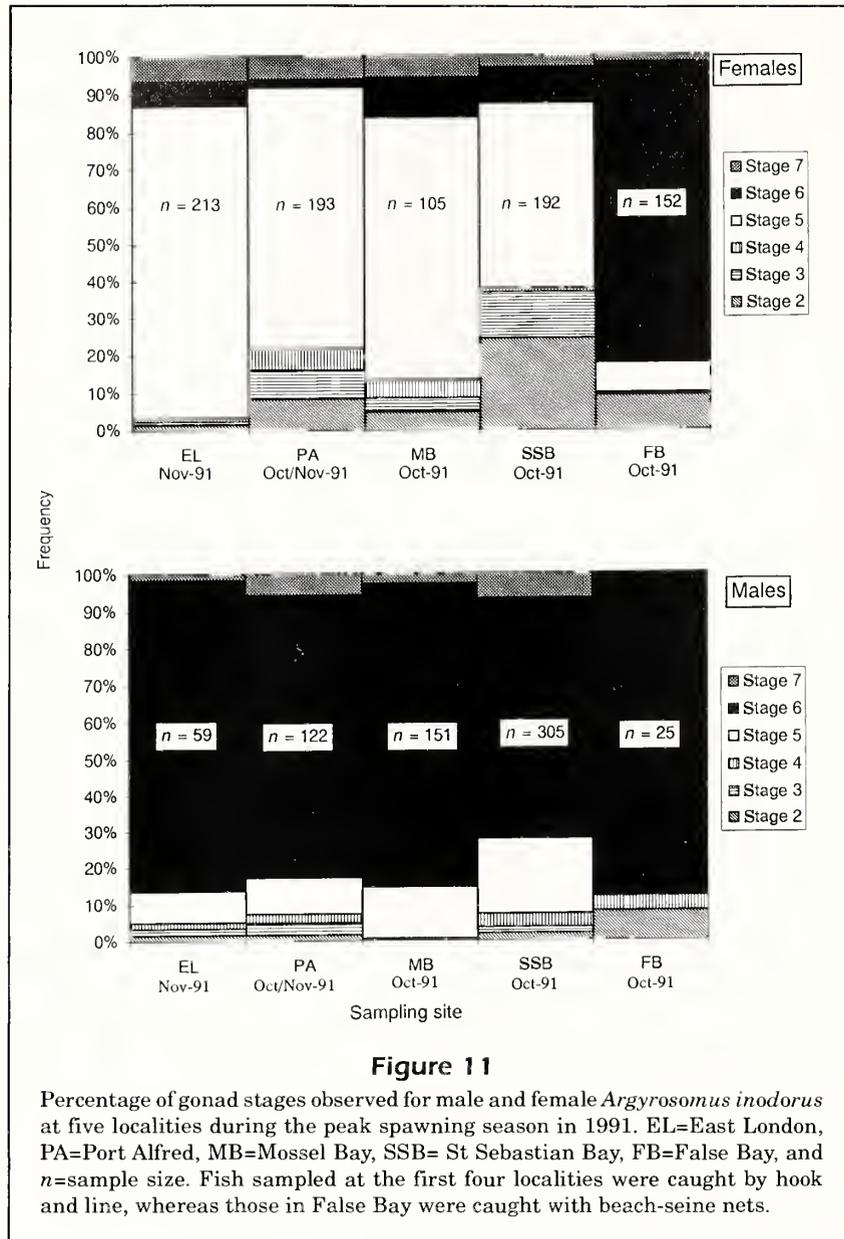


tified as "*A. hololepidotus*") as small as 1.3 cm TL just behind the breakers (5–7 m depth) in Algoa Bay. Voucher specimens (including otoliths) from both of these studies were identified as *A. inodorus*. There is therefore a trend of increasing length with increasing depth and distance from the shore for juvenile silver kob occurring between Cape Agulhas and Port Alfred. This finding suggests that juveniles are recruited to the nursery grounds just seaward of the surf zone and that they move farther offshore as they grow. Silver kob do not enter estuaries, and between Cape Agulhas and the Kei River, they do not occur in the surf zone (Griffiths and Heemstra, 1995). The SCBS CPUE-analyses revealed that juvenile *A. inodorus* were not homogenously distributed over the survey area but were found mostly in <120 m depth and comprised two disjunct distributional ranges, i.e.

Cape Agulhas to Mossel Bay and Cape St Francis to Port Alfred (Fig. 3). Although the inshore areas of the southwestern Cape are not suitable for trawling, analysis of commercial beach-seine catches (Lamberth et al., 1994) revealed that juvenile *A. inodorus* (identified as "*A. hololepidotus*") are also found in False Bay.

## Discussion

The results of this study strongly suggest that silver kob between Cape Point and the Kei River comprise three discrete stocks. The foci of each of these stocks are False Bay in the southwestern Cape, Stil Bay in the southern Cape, and Port Alfred in the southeastern Cape. Tagging evidence indicates that there is lim-



**Figure 11**

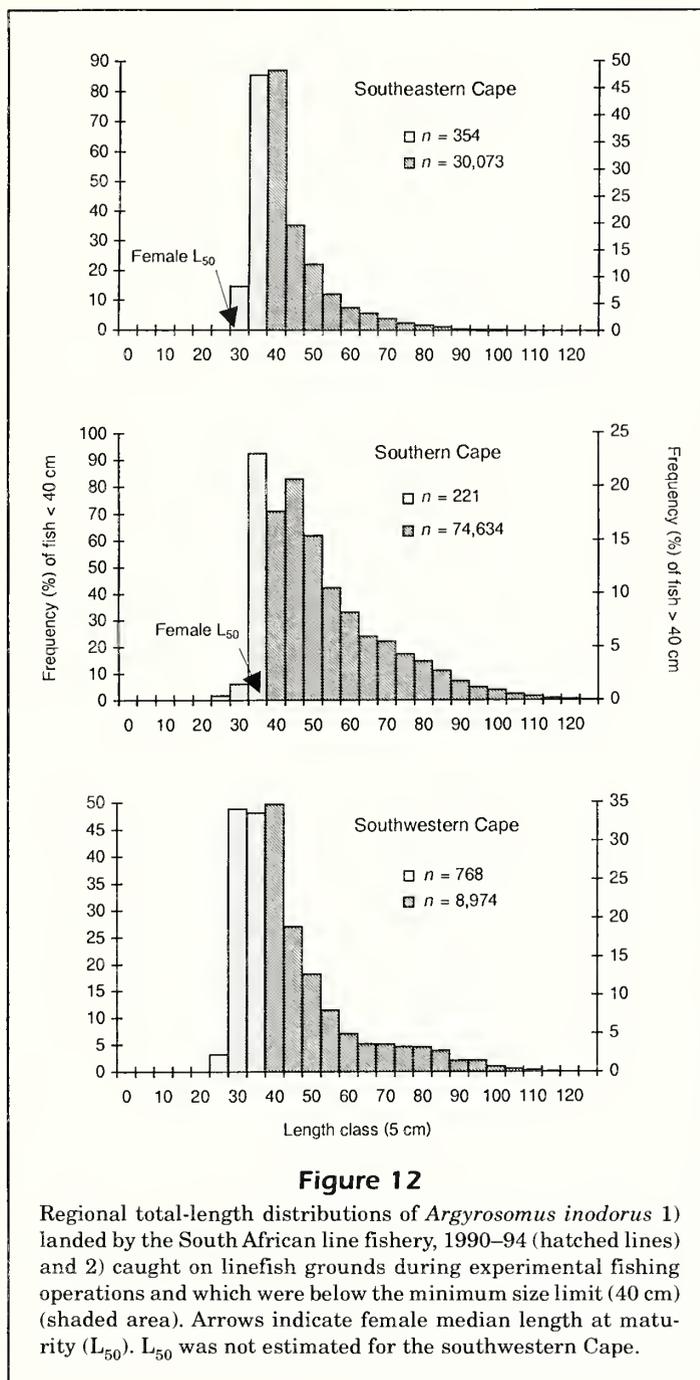
Percentage of gonad stages observed for male and female *Argyrosomus inodorus* at five localities during the peak spawning season in 1991. EL=East London, PA=Port Alfred, MB=Mossel Bay, SSB= St Sebastian Bay, FB=False Bay, and  $n$ =sample size. Fish sampled at the first four localities were caught by hook and line, whereas those in False Bay were caught with beach-seine nets.

ited exchange between the southwestern Cape and the southern Cape stocks but that there is no exchange between either of these two stocks and the one in the southeastern Cape. Analysis of catch and tagging data shows that each of the three stocks is concentrated inshore in summer but disperses seawards in winter.

The distribution of silver kob on the South African eastern seaboard, including the existence of the three stocks and their onshore-offshore movement, is also supported by regional oceanographic patterns. During spring, summer, and autumn, the east coast between Cape Agulhas and the Kei River is characterized by three zones: 1) a warm inshore band (0–20 m) with an average temperature of 21°C (although

in certain areas temperatures can drop to <12°C for brief periods following coastal upwelling); 2) a zone of intermediate temperature (12–19°C) between 20 and 50 m; and 3) a bottom mixed layer of <12°C found below 50 m (Eagle and Orren, 1985; Swart and Largier, 1987; Goschen and Schumann, 1988; Boyd and Shillington, 1994; Greenwood and Taunton-Clark<sup>2</sup>). Silver kob prefer temperatures of 13–16°C (Fig. 14) and are therefore mainly confined to the

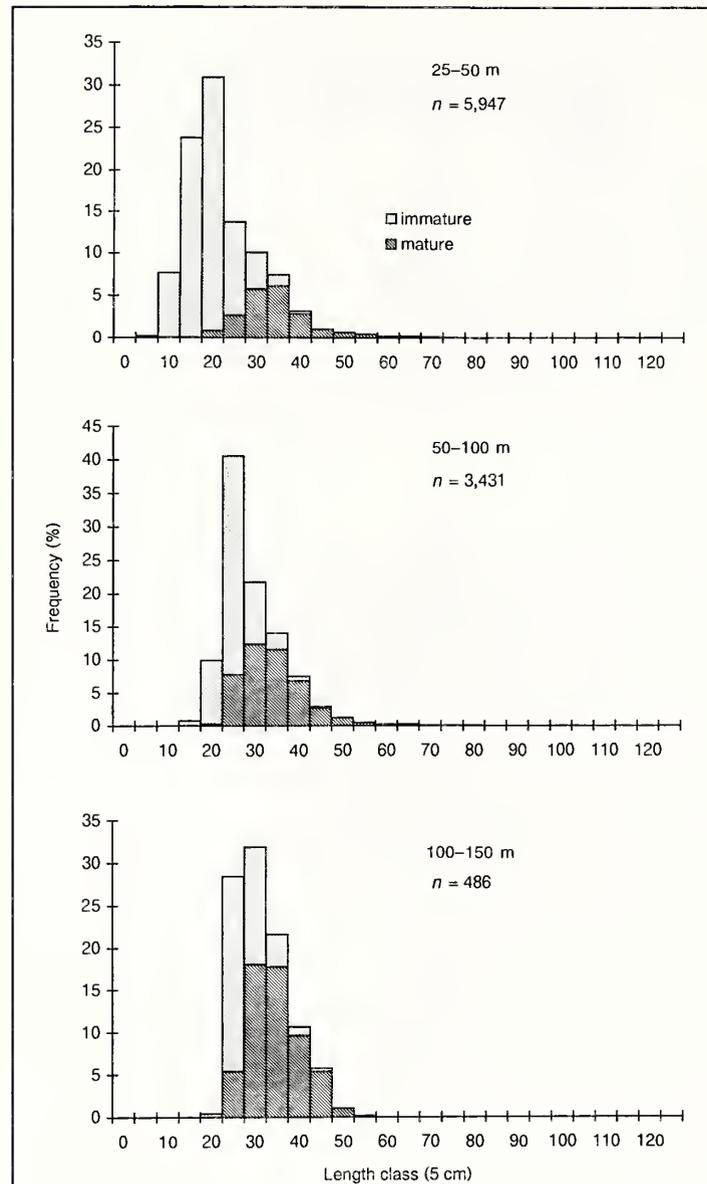
<sup>2</sup> Greenwood, C., and J. Taunton-Clark. 1992. An atlas of mean monthly and yearly average sea surface temperatures around the southern African coast. Sea Fisheries Research Institute, Private Bag X2, Roggebaai 8012, Cape Town, South Africa. Internal report 124, 112 p.



intermediate zone. During spring, summer, and autumn, the intermediate zone is restricted to an area within a few kilometres of the coast and is within easy range of line boats (see 50-m isobath in Fig. 1). In winter the bottom mixed layer retreats down the shelf to about 100 m (Schumann and Beekman, 1984; Eagle and Orren, 1985; Swart and Largier, 1987). As the intermediate zone expands, I propose that *A. inodorus* stocks disperse seaward, moving beyond the

grounds of the linefishery and onto the inshore trawling grounds. Because Agulhas Bank is much narrower in the southeastern Cape than in the southern Cape (Fig. 1), offshore movement would have been more constrained than in the latter region and hence would explain the higher winter line catches in the southeastern Cape (Fig. 5).

Owing to a higher degree of coastal upwelling off the southwestern Cape, the bottom mixed layer

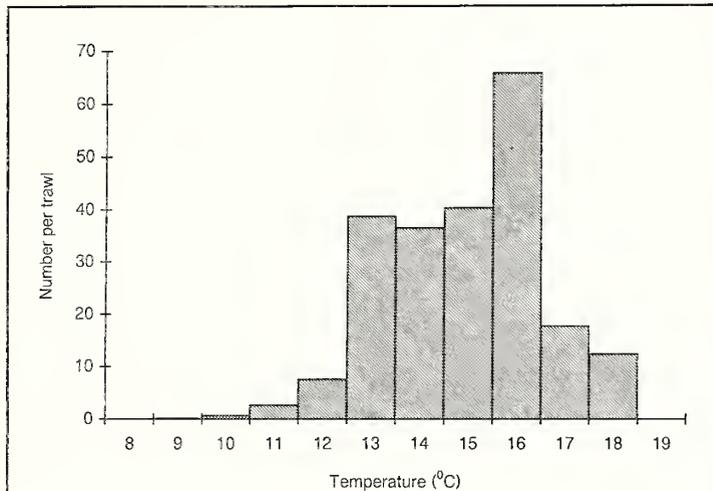


**Figure 13**

Total-length distributions per depth range for *Argyrosomus inodorus* trawled between Cape Agulhas and Port Alfred during South Coast Biomass Cruises, 1990-94. The proportion of immature fish in each length class is an average of the values presented for males (drumming muscle method) and females in the southeastern Cape and the southern Cape in Figure 8.

(<12°C) is shallower (20 vs. 50 m on the east coast) from spring to autumn, and the temperatures above 20 m are generally 13-19°C during this period (Atkins, 1970; Boyd et al., 1985; Largier et al., 1992; Greenwood and Taunton-Clark<sup>2</sup>). Because inshore temperatures are lower than those on the east coast, silver kob are caught by linefishermen from the surf zone to depths of 20 m. As along the east coast, the

bottom mixed layer deepens to about 100 m in winter (Atkins, 1970; Boyd et al., 1985; Largier et al., 1992), and silver kob are expected to move offshore (as indicated by catch trends [Fig. 5]). Because the depth contours broaden east of Cape Hangklip, it is possible that there is also an easterly component to the offshore dispersal of silver kob. A seaward and eastward winter migration has also been postulated



**Figure 14**

Mean number of *Argyrosomus inodorus* per trawl for each 1°C bottom temperature category during South Coast Biomass Surveys, 1987-95.

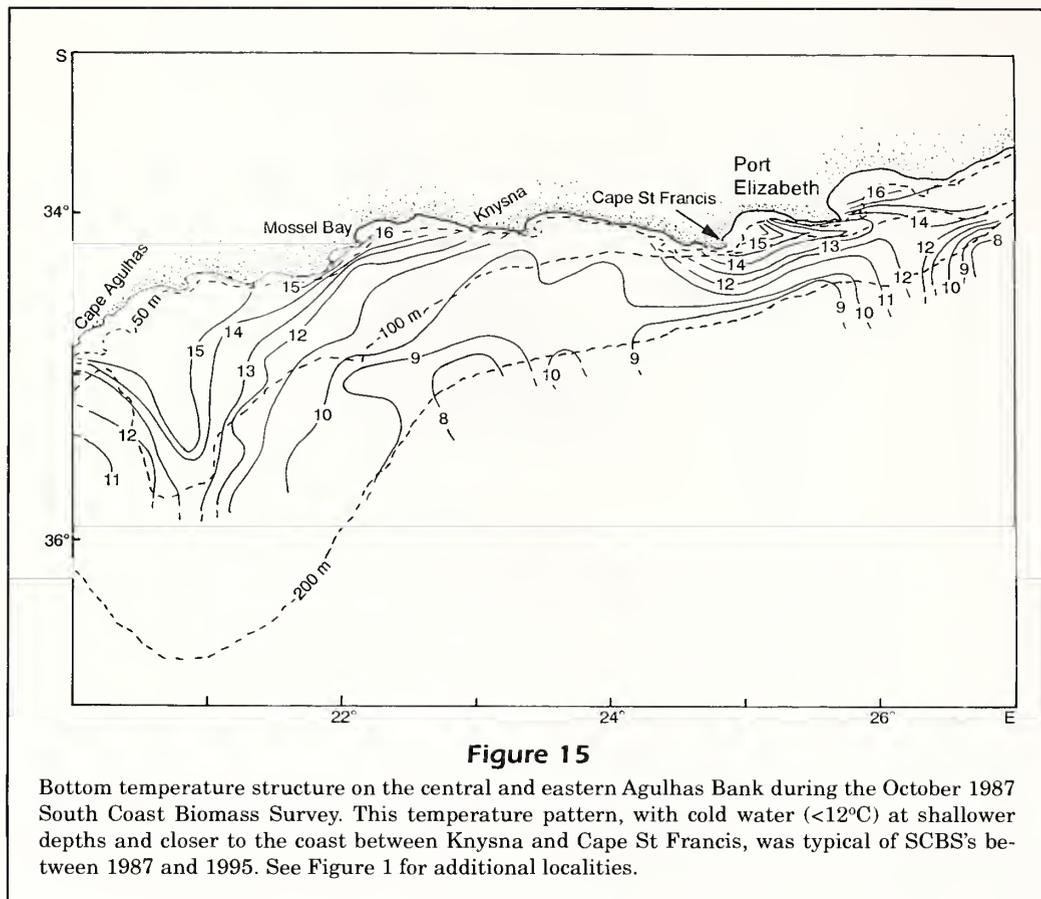
for subadult *Atractoscion aequidens* (Sciaenidae), occurring in the southwestern Cape (Griffiths and Hecht, 1995a).

Data from all 14 SCBS's revealed that the bottom mixed layer (<12°C) extends farther up the shelf (and is closer to the coast) in the area between Knysna and Cape St Francis (Fig. 15; see also Le Clus and Roberts, 1995), thus inhibiting exchange between the silver kob stock in the southern Cape and that in the southeastern Cape. Along the eastern and western sides of False Bay, the 20-m isobath is found <500 m from the shore (van Ballegooyen, 1991). Because suitable temperatures for silver kob are found at depths shallower than 20 m in the southwestern Cape during spring to autumn, the movement of silver kob into or out of False Bay (the focus of the southwestern Cape stock) during this period is therefore restricted. In addition, the upwelled bottom mixed layer frequently extends to the shore between Cape Hangklip and Cape Agulhas, particularly from December to April (Boyd et al., 1985; Largier et al., 1992), thus further limiting exchange between in False Bay and in the southern Cape.

Spawning occurred throughout the distributional ranges of all three stocks and peaked in spring (Sept-Nov) in all regions. Sizes and ages at maturity were, however, substantially smaller in the southeastern Cape than in the southern Cape. Female  $L_{50}$  was 310 mm TL (1.3 yr) in the former and 375 mm TL (2.4 yr) in the latter region. Changes in ages and sizes at maturity have been correlated with exploitation rate for several fish species (Healey, 1975; Borisov, 1978; Ricker, 1981; Beacham, 1983; Wysokinski 1984;

Armstrong et al., 1989). Because fishing mortality is significantly higher in the southeastern Cape than in the southern Cape ( $F=0.67$  vs. 0.42)(Griffiths, in press, c), the smaller sizes at maturity recorded for the southeastern Cape are possibly due to fishing pressure. The mechanisms accounting for the decreases in the size and age at maturity in the southeastern Cape, however, remain to be identified. One explanation is that the younger ages and smaller sizes at maturity for silver kob in the southeastern Cape could be the result of density-dependent effects; higher mortality results in more food for surviving fish, in additional energy for gonad growth, and consequently in earlier maturity. In several other species, ages or sizes (or both) at maturity have been correlated with the amount of accumulated surplus energy within a fish (Armstrong et al., 1989; Rowe et al., 1991; Berglund, 1992; Kerstan<sup>3</sup>). On the other hand, Ricker (1981) stated that "If a fish matures before it is large enough to be vulnerable to fishing, its expectation of contributing to future generations will be greater than that of a sibling of the same size that does not mature until a year later. The result can be a gradual decrease in the mean size at maturity." Female silver kob attain the minimum size limit for the line fishery (400 mm TL) at ca. 2.8 yr in both the southeastern Cape and the southern Cape (Griffiths, in press, a). Approximately 95% of these

<sup>3</sup> Kerstan, M. 1995. Sex ratios and maturation patterns of horse mackerel (*Trachurus trachurus*) from the NE- and SE-Atlantic and the Indian Ocean—a comparison. ICES council meeting H:6, 20 p. (Mimeo.)



new recruits are mature in the southeastern Cape, but only 69% in the southern Cape. Assuming that size at maturity for silver kob in the southeastern Cape was at one time similar to that in the southern Cape, the removal of late-maturing fish, before they had spawned for the first time, could have reduced the sizes and ages at maturity to those recorded in this study. The large contribution of recruits (400–450 mm TL) to the southeastern Cape line catch (ca. 50% by number)(Fig. 12), supports this hypothesis.

Investigation of sex ratios showed that there are substantially more females in the southeastern Cape (1.6×) and southwestern Cape (2.1×) stocks, but more males in the southern Cape (1.2×). Most natural populations tend to stabilize at sex ratios of 1:1 (Conover and Van Voorhees, 1990), including those of other sciaenids (Shepherd and Grimes, 1984; Murphy and Taylor, 1989; Wilson and Nieland, 1994; Ross et al., 1995; Griffiths and Hecht, 1995a). The deviations from this ratio observed for South African silver kob are not easily explained. Basically, the reasons for an observed sex ratio that deviates from unity may be grouped into three categories: 1) more individuals of either sex are produced (e.g. environmental sex determination); 2) equal numbers of both

sexes are produced, but those of one sex are diminished through either emigration or mortality; and 3) sampling methods are biased towards one of the sexes. Although environmental sex determination can temporarily result in skewed sex ratios in some species (Conover and Heins, 1987), frequency-dependent selection is expected to return the ratios of such populations to equality through future generations (Conover and Van Voorhees, 1990). Higher proportions of either sex over most size classes (therefore spanning several age classes) in each region, with consistency over two periods (1978–81 and 1990–91) in the southeastern Cape, render environmental sex determination an unlikely cause of the observed sex ratios. Male emigration from the southeastern Cape and the southwestern Cape to the southern Cape is also unlikely. Because the smallest size class sampled in the southeastern Cape consisted of males without drumming muscles and also consisted of more males than females, it is tempting to suggest that male drumming during the protracted spawning season may have resulted in sex-selective predation in this region and in the southwestern Cape. However, there is no reason to believe that predation rates should be higher in the southeastern Cape and the south-

western Cape than in the southern Cape. Because capture methods were the same in all three regions, increased vulnerability of either sex to capture is not a plausible explanation either. Thus additional research is required before the regionally specific sex ratios observed for *A. inodorus* can be adequately explained.

Silver kob use inshore (<120 m depth) sand and mud substrata as nursery areas. They apparently recruit (ca. 1.5 cm TL) just seawards of the surf zone (5–7 m depth) but move offshore with growth. Upon attaining maturity they recruit to adult populations that are found on reefs. Distributional analyses have revealed that juvenile *A. inodorus* between Cape Agulhas and the Kei River comprise two disjunct distributional ranges, one in the southern Cape and the other in the southeastern Cape. Although the inshore areas of the southwestern Cape are not suitable for trawling, analysis of commercial beach-seine catches (Lamberth et al., 1994) has revealed that juvenile *A. inodorus* (identified as "*A. hololepidotus*") are also found in False Bay. The existence of nursery areas and spawning grounds in each of the three sampling regions, and the differences in size at maturity and sex ratio, lend further credence to the separate stock concept.

## Conclusion

Distributional analyses based on fishery dependant and fishery independent data revealed that there are three areas of silver kob abundance between Cape Point and the Kei River. The fact that each of these "populations" has its own spawning grounds and nursery areas and the fact that there are observed differences in growth rates, otolith-dimension and fish-length relationships, growth zone structure, sizes at maturity, and sex ratios, together indicate that these "populations" represent separate stocks. This three-stock concept is further supported by migratory patterns indicated from catch and tagging data and by the oceanography between Cape Point and the Kei River.

Although genetic differentiation should ideally form the basis of inferences concerning stock distinction, analyses based on protein electrophoresis and mitochondrial DNA have generally been unsuccessful in differentiating between marine stocks (see Campana and Casselman, 1992; Pawson and Jennings, 1996), including those of sciaenids (Ramsey and Wakeman, 1987; Graves et al., 1992; King and Pate, 1992). Although none of the data used to infer separate silver kob stocks necessarily reflect genetic differences (Ihssen et al., 1981), the identification of

three allopatric units of fish with different population parameters indicates that each may respond differently to fishing and that the exploitation of one unit will not affect the size or composition of the other two, thereby supporting separate management of the three units and their stock status (Spangler et al., 1981; Brown and Darcy, 1987; Campana and Gagné, 1995; Edmonds et al., 1995; Pawson and Jennings, 1996).

Recent application of per-recruit models to South African silver kob (based on the results presented in this study) indicates that, owing to their different population parameters, each stock requires a different combination of fishing mortality and age at first capture for optimal exploitation (Griffiths, in press, c). Therefore *A. inodorus* should ideally be managed on a regional and not on a national basis. Studies of the life histories of two other South African sciaenids, *Atractoscion aequidens* (Griffiths and Hecht, 1995a) and *Argyrosomus japonicus* (Griffiths and Hecht, 1995b; Griffiths, in press, b), have revealed that they consist of single stocks with allopatric age or size-determined subpopulations, even though they occur from Cape Point to southern Mozambique and are therefore more widely distributed on the eastern seaboard than are *A. inodorus*. Inferences from stock structure, based on closely related taxa, are therefore not desirable because they could result in erroneous conclusions and consequently in poor management.

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**Abstract.**—Estimates of tag-shedding and tag-reporting rates are required for an estimation of fishing and natural mortality rates from tagging data. For this purpose, double-tagging and tag-seeding experiments were undertaken by the South Pacific Commission, in conjunction with a large-scale tuna tagging program, in the western tropical Pacific Ocean during 1989–1992. Estimates of tag-shedding rates indicated that 89% (95% confidence interval of 82%–94%) of tagged tuna still retained their tags after two years at liberty. Differences in shedding rates among skipjack, yellowfin, and bigeye tuna, and differences in shedding rates among taggers were found not to be statistically significant. Tag seeding carried out on board purse seiners by observers resulted in 342 returns of the 532 tags seeded, for a return rate of 64% (60%–68%). The return rate of seeded tags varied significantly by unloading location (most tags were recovered during unloading), but not by species. The highest return rates of seeded tags occurred from American Samoa, Philippines, and Solomon Islands, whereas Korea and Thailand had the lowest return rates. The overall average reporting rate, weighted by the estimated numbers of tags recovered at each location, was 0.59. A bootstrap procedure was used to estimate a 95% confidence interval of 0.49–0.67. These results implied that, of the 146,581 tags released during the large-scale tagging program, 31,166 (27,208–37,264) were recaptured, of which 18,266 were returned to the South Pacific Commission.

## Estimates of tag-reporting and tag-shedding rates in a large-scale tuna tagging experiment in the western tropical Pacific Ocean

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Tag release-recapture experiments are commonly used to estimate parameters, such as growth, mortality, and population size, of exploited fish stocks (Beverton and Holt, 1957; Seber, 1973). One method used to estimate mortality rates is to fit a tag-attribution model to a time series of tag-return data (Seber, 1973; Kleiber et al., 1987). In its simplest form, the tag attrition model can be expressed as

$$\hat{\phi}_j = (1 - \alpha)T \exp \left[ -(F + M + \lambda)(j - 1) \right] \frac{F}{F + M + \lambda} [1 - \exp(-F - M - \lambda)], \quad (1)$$

where  $\hat{\phi}_j$  is the predicted number of tag returns in time period  $j$ ,  $\alpha$  represents all type-1 tag losses,  $T$  is the number of tag releases,  $F$  is the instantaneous rate of fishing mortality (assumed constant),  $M$  is the instantaneous rate of natural mortality (assumed constant), and  $\lambda$  represents all continuous type-2 tag losses. Type-1 tag losses include immediate tag shedding, immediate tagging-induced mortality, and failure to report recovered tags. Type-2 tag losses include continuous tag shedding, continuous mortality directly attributable to the tag, and emigration of tagged fish away from the area of the fishery. For unbiased estimates of  $F$  and  $M$  to be obtained,

it is clear from Equation 1 that these tag losses must be estimated and included in the tag-attribution model.

In general, type-1 and type-2 loss rates cannot be estimated directly from tag-return data, although estimation of type-1 losses may be possible under circumstances where fishing intensity is highly variable (Beverton and Holt, 1957). More commonly, loss rates are estimated from independent experiments carried out in conjunction with a tagging program. Tag-shedding rates may be estimated from double-tagging (two tags per fish) experiments (Wetherall, 1982) or from direct observation of tagged fish held in captivity. Tag-reporting rates may be estimated from tag-seeding experiments (Youngs, 1974; Green et al., 1983; Campbell et al., 1992), from sequential observations of recoveries at different stages of catch handling and processing (Hilborn, 1988), and by comparing tag return rates from the fishery with those from a control group (such as vessels carrying fisheries observers) assumed a priori to report all tag recoveries (Paulik, 1961; Seber, 1973). Type-1 and type-2 tagging mortality rates may, for some species, be estimated from observations of tagged and untagged fish held in captivity.

The South Pacific Commission (SPC) recently conducted a large-

scale tuna tagging program, the Regional Tuna Tagging Project (RTTP), in the western tropical Pacific. From 1989 to 1992, 146,581 tagged skipjack tuna, *Katsuwonus pelamis*, yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesus*, were released throughout the western tropical Pacific from the Philippines and eastern Indonesia to approximately 170°W. This area is fished by purse-seine, pole-and-line, longline, handline, and troll vessels, which have collectively harvested more than one million metric tons of tuna per year since 1989 (Lawson, 1994). As of 31 May 1995, 18,266 tagged fish had been recaptured and the tags and accompanying recapture information returned to SPC. Tagged tuna were recaptured by all of the fishing methods of the western Pacific fishery. Most tag returns (76%) originated from purse seiners, consistent with the proportion of total catch attributed to that gear (67% for 1990–1993). Few additional tag recoveries are expected.

One of the major objectives of the tagging program was to estimate the rates of fishing-induced and natural mortality by using models similar to Equation 1, so that the impacts of the fishery on the stocks could be assessed. It was therefore necessary to obtain estimates of type-1 and type-2 tag losses. In this paper, I focus on the estimation of tag-shedding rates and tag-reporting rates. Tag-shedding rates were estimated from double-tagging experiments carried out in conjunction with the tag-release program. Differences in shedding rates among species and differences among individual taggers were evaluated. Tag-reporting rates were estimated from tag-seeding experiments in which tuna caught by purse seiners were surreptitiously tagged by fisheries observers prior to the fish being placed in the fish wells. Differences in the rates of reporting seeded tags by species, time, and port of unloading were investigated. An estimate of the overall reporting rate of recovered RTTP tags and its variability, which takes into account the variability in tag reporting among unloading ports, was obtained.

## Materials and methods

### Double-tagging experiments

**Field operations** Tagging was carried out on a pole-and-line vessel from which tuna were captured with standard commercial gear. Only uninjured fish that were cleanly hooked in the jaw were selected for tagging. Fish with excessive mouth damage, eye damage, or gill damage were not tagged. Selected fish were placed in a vinyl tagging cradle and their fork lengths measured to the nearest centimeter. For

single-tagged fish, a Hallprint™ 13 cm dart tag was inserted by using a sharpened stainless steel applicator, into the musculature at an angle of about 45°, 1–2 cm below the posterior insertion of the second dorsal fin. Smaller (10-cm) tags were used for tuna less than 35 cm FL. Ideally, the tag barb was anchored behind the pterygiophores of the second dorsal fin.

Throughout the three-year tag release program, a small sample (approximately 3%) of the tagged tuna were double tagged. Double tagging occurred on particular days chosen in advance by the cruise leader and on such days, most fish were double tagged. The objectives were for each principle tagger to double tag at least 400 tuna, and for the double-tag releases to be as representative as possible of the species and size composition of the single-tag releases. These objectives were largely accomplished (Fig. 1).

The technique for double tagging was identical to that of single tagging, with the exception that a second tag was inserted on the opposite side of the fish, 1–2 cm anterior to the first tag to avoid damaging it with the applicator. For single and double tagging, fish were generally out of the water for less than ten seconds.

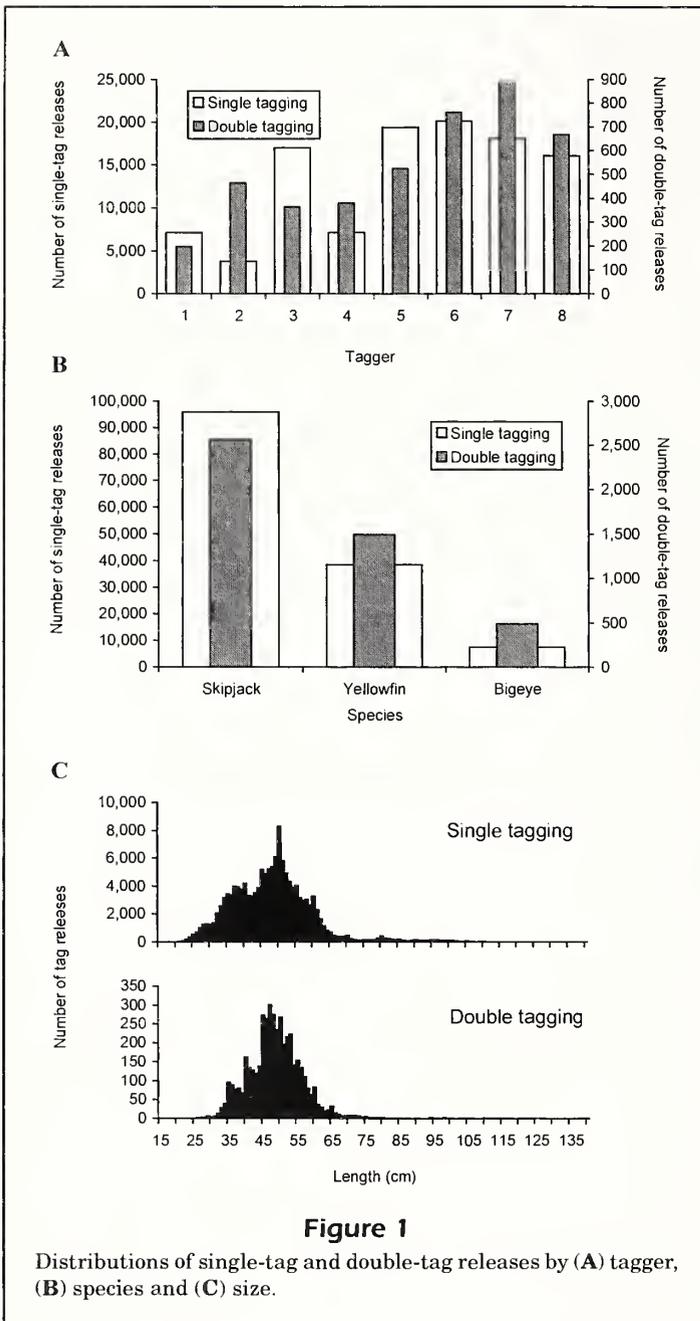
**Data analysis** Observations of the numbers of tags retained by double-tagged tuna at recapture can be used to estimate tag-shedding rates. I used a simple tag-shedding model (Beverton and Holt, 1957; Hampton and Kirkwood, 1990), which defines the probability,  $Q(t)$ , of a tag being retained at time  $t$  after release as

$$Q(t) = (1 - \rho) \exp(-Lt), \quad (2)$$

where  $\rho$  is the immediate type-1 shedding rate and  $L$  is the continuous type-2 shedding rate. These parameters can be estimated from a double-tagging experiment under the assumption that all tags not immediately shed have identical shedding probabilities that are independent of the status of the companion tag. Given this assumption, the probabilities of two, one, and no tags being retained at time  $t$  after release are, respectively,

$$\begin{aligned} P_2(t) &= Q(t)^2, \\ P_1(t) &= 2Q(t)[1 - Q(t)] \\ P_0(t) &= [1 - Q(t)]^2. \end{aligned} \quad (3)$$

Consider a double-tagging experiment resulting in  $m$  recaptures of fish bearing two tags at times  $t_{2i}$  ( $i = 1, \dots, m$ ) and in  $n$  recaptures bearing one tag at times  $t_{1j}$  ( $j = 1, \dots, n$ ). The negative log likelihood of the data  $(\mathbf{t}_2, \mathbf{t}_1)$  given the model parameters  $\rho$  and  $L$  is



$$\Omega(\mathbf{t}_2, \mathbf{t}_1 | \rho, L) = - \sum_{i=1}^m \ln \left[ \frac{P_2(t_{2i})}{1 - P_0(t_{2i})} \right] - \sum_{j=1}^n \ln \left[ \frac{P_1(t_{1j})}{1 - P_0(t_{1j})} \right], \quad (4)$$

where the terms in square brackets represent the probabilities of two tags and one tag being observed for each recapture, given that at least one tag is observed. Maximum-likelihood estimates of  $\rho$  and  $L$  can

therefore be obtained by minimizing  $\Omega$  with respect to the parameters.

The model was fit to pooled recapture data, to data classified by species, and to data classified by tagger. As an approximate indication of the overall losses due to tag shedding for each data set, the proportion of tags retained after two years (99% of RTP tag returns were recaptured within two years of release),  $Q_{2yr}$ , was calculated from Equation 2 by using the estimated parameters. Approximate 95% confidence intervals for  $Q_{2yr}$  were obtained by the percentile method (Efron, 1982) applied to distributions of  $Q_{2yr}$  generated from 1,000 parametric bootstrap (or Monte Carlo) replicates of each data set. The replicates were constructed by using the observed distributions of times at liberty, and the numbers of tags observed for each pseudo-return were determined randomly with the conditional probabilities of a recaptured tuna bearing two tags or one tag, i.e.  $\frac{P_2(t)}{1 - P_0(t)}$  and  $\frac{P_1(t)}{1 - P_0(t)}$ , respectively, given the estimated parameters.

The statistical significance of improvements in fit of models that included species-specific and tagger-specific shedding parameters was determined by using likelihood-ratio tests (Kendall and Stuart, 1961).

### Tag-seeding experiments

**Rationale** Tag seeding was carried out by observers placed on board purse-seine vessels as part of regional and national observer programs. The purse-seine fleet was targeted for tag-seeding experiments for several reasons. First, purse seiners account for most of the tuna catch in the western Pacific (and also recovered most tags); the estimation of reporting rates for this gear type in particular was therefore of critical importance. Second, the large, modern purse seiners typical of the western Pacific fleet handle large quantities of tuna very rapidly, with little opportunity for onboard inspection of individual fish for tags. As a result, tagged tuna recaptured by purse seiners were mostly detected during unloading (when individual fish are handled) or during the initial stages of processing in canneries. The efficacy of tag detection during these periods was unknown prior to the commencement of the tagging experiment; it was feared that delayed detection of tags might result in significant losses which, if ignored, would compromise the objectives of the tagging experiment. Third, the very fact that most tagged tuna recaptured by purse seiners

would be detected during or after unloading of the catch in port offered the opportunity for tagged tuna to be planted in the catches before these detection processes began. Furthermore, the layout of purse-seine vessels and the method of onboard handling of the catch facilitated the opportunity for planting tagged tuna surreptitiously, out of sight of the vessel's crew. Such tag-seeding operations would be more difficult on other types of vessels, e.g. pole-and-liners and longliners, operating in the fishery.

**Field operations** Selected observers on purse seiners were asked to plant up to five tagged tuna in the catch during a voyage. The number of tagged tuna was limited to five so as not to attract undue attention during unloading; it was not unusual during the RTTP for five (and sometimes more) tagged tuna to be recovered from a single unloading. The exact timing of tagging individual fish depended on the circumstances encountered during a cruise, particularly the frequency of successful sets. Therefore, the period over which the five tags were seeded ranged from a few days to several weeks.

Fish were tagged discretely, usually on the well deck (one level below the work deck where the fish are landed), as they passed down the chute just prior to entering the well. The tags and manner of attachment were identical to those used in the tagging program proper. Tag numbers, dates, species, sizes, and well numbers were recorded and the information sent to SPC at the completion of the voyage. Upon recovery, seeded tags were processed in the same fashion as genuine tag recoveries. Tag finders were paid the standard reward for seeded tags and were not informed that the tags were part of a seeding experiment.

**Estimation of return rates of seeded tags** Return rates of seeded tags were calculated for the overall data set, for the three species (skipjack, yellowfin, and bigeye tuna) and for the seven unloading locations represented in the data (American Samoa, Japan, Korea, Philippines, Puerto Rico, Solomon Islands, and Thailand). For one unloading location (American Samoa), there were sufficient returns to estimate reporting rates by time period (year). Differences in seeded tag-return rates among species, unloading locations, and time periods were assessed by using chi-square tests (Sokal and Rohlf, 1981).

Return rates were estimated by assuming that the number of returns,  $r$ , in a given category was a binomial variate. Given the number of tags seeded,  $N$ , the estimated return rate is given by  $\hat{p} = r/N$ . Under these conditions, 95% confidence limits for return rates were also obtained. Lower and upper confidence limits,  $p_A$  and  $p_B$ , for  $p$  were determined by solving the equations

$$\sum_{i=r}^N \binom{N}{i} p_A^i (1-p_A)^{N-i} = \alpha \text{ and}$$

$$\sum_{i=0}^r \binom{N}{i} p_B^i (1-p_B)^{N-i} = \alpha,$$

where  $1-2\alpha$  is the confidence level (0.95 in this instance). Solutions for  $p_A$  and  $p_B$  can be easily obtained using an optimization program, such as the Microsoft Excel Solver.

**Estimation of overall reporting rate for the RTTP** An unbiased estimate of the overall return rate of recovered tags (i.e. the total number of tags returned divided by the total number of tags recaptured) is required for the estimation of fishing and natural mortality rates from the RTTP data. The return rates of seeded tags can be considered as sample means of the overall (population) mean reporting rate. It transpired that seeded tag-return rates varied greatly by unloading location, requiring that the data be stratified by unloading location in the estimation procedure. The parametric bootstrap (or Monte Carlo) approach was used to obtain approximate 95% confidence intervals for the overall reporting rate and its components (with the percentile method), taking account of the different probability distributions of reporting rate by unloading location. One thousand simulations (or bootstrap replicates) were run. In each, the weighted average reporting rate across locations is given by

$$p' = \frac{\sum_j R_j}{\sum_j p'_j},$$

where  $R_j$  is the number of tags returned from location  $j$  and  $p'_j$  is the bootstrap (or pseudo) reporting rate for location  $j$ .

For each replicate, the  $p'_j$  were randomly sampled from probability distributions. For recoveries in locations covered by tag-seeding experiments, beta distributions  $B(x_j, y_j, a_j, b)$  were used to represent the probability distributions of the true reporting rates. These continuous distributions are related to the binomial distributions defined by the tag-seeding data by  $x_j=r_j$  and  $y_j=N_j-r_j+1$  (Mendenhall and Scheaffer, 1973). The limits of the distributions,  $a$  and  $b$ , would normally be 0 and 1, respectively. In this case, we assumed  $b=1$  and set the lower limit of reporting rate for location  $j$ ,  $a_j$ , to the local tag-return rate (i.e. number of local returns divided by the number of local releases), so as to avoid the possibility of estimated recoveries out-numbering releases for any replicate. For two locations, Solomon Islands and Philippines,

there were local tag releases that resulted in most of the tag returns from those locations. These local tag-return rates (0.126 and 0.223, respectively) were used as the lower bounds for the reporting rate distributions for Solomon Islands and Philippines. For the other locations, it was not possible to identify sets of local releases to calculate local tag-return rates because the release locations of the local returns were widely distributed throughout the tag release area, not just in the vicinity of the unloading ports. In these cases, I made the minimal assumption that the "local" releases comprised all tag releases except those returned from other locations. Thus, the shapes of the reporting-rate probability distributions are determined by the tag-seeding data and by this notional minimum possible return rate. Note that the means and medians of such distributions could be quite different from the tag-seeding sample means  $\hat{p}_j$ . In general, the differences will be greatest where  $\hat{p}_j$  is close to 0 or 1 and  $n$  is small.

For returns from locations where no tag-seeding data were available or for tag returns that could not reasonably be pooled with purse-seine returns because the recovery processes were different (14% of all returns), values of  $p'_j$  were sampled from uniform distributions  $U(0.5, 1.0)$ . While somewhat arbitrary, this procedure is meant only to reflect some knowledge of the minimum possible reporting rate from these locations. In fact, this assumption prob-

ably understates the likelihood of tags being reported; almost all of these tags were recovered in Indonesia and in Pacific Island countries, where widespread publicity and the attractiveness of cash rewards are likely to have resulted in high reporting rates.

## Results

### Tag shedding

In all, 4,541 tuna (2,557 skipjack, 1,493 yellowfin, and 491 bigeye) were double-tagged during the RTTP. Return rates of double-tagged tuna were comparable to those of single-tagged tuna.

Returns from 525 double-tagged tuna were available for analysis. Fitting the model specified in Equation 2 to the pooled data provided estimates of  $\rho$  and  $L$  that, according to the model, would result in 89% (95% confidence interval of 82%–94%) of the original tags being retained after two years at large (Table 1). Both  $\hat{\rho}$  and  $\hat{L}$  were significantly different from zero ( $P < 0.001$ ).

Fitting the model to the three species separately, although yielding somewhat different tag-retention rates (Table 1), did not result in an overall statistically significant improvement in fit ( $P = 0.334$ , Table 2). Similarly, there were differences in tag-shedding estimates for the different taggers (Table 1), but over-

**Table 1**

Double-tagging results ( $m$  is the number of returns bearing two tags and  $n$  is the number of returns bearing one tag), tag-shedding parameter estimates, the estimated proportion of tags retained after two years at liberty ( $Q_{2yr}$ ), and likelihood function values ( $\Omega$ ) for fits of the tag-shedding model to the various data sets.

Data set	$m+n$	$m$	$n$	Tag-shedding parameters		$Q_{2yr}$	95% confidence interval for $Q_{2yr}$	$\Omega$
				$\rho$	$L$ (/mo.)			
Pooled data	525	457	68	0.05861	0.002312	0.89	0.82–0.94	201.498
Skipjack tuna	241	211	30	0.03485	0.007179	0.81	0.68–0.93	87.637
Yellowfin tuna	204	176	28	0.06574	0.001532	0.90	0.81–0.95	81.434
Bigeye tuna	80	70	10	0.06667	0.000000	0.93	0.74–0.97	30.142
Total	525	457	68					199.213
Tagger 1	42	40	2	0.01111	0.002788	0.92	0.76–1.00	7.909
2	45	36	9	0.07348	0.009636	0.74	0.42–0.93	22.023
3	45	39	6	0.07143	0.003400	0.86	0.76–0.94	17.670
4	53	47	6	0.06000	0.000000	0.94	0.68–0.98	18.718
5	106	94	12	0.03604	0.004257	0.87	0.73–0.96	36.533
6	68	57	11	0.08800	0.000000	0.91	0.70–0.95	30.096
7	81	67	14	0.00000	0.018460	0.64	0.50–0.85	34.184
8	60	53	7	0.03566	0.007403	0.81	0.55–0.97	21.110
Other taggers	25	24	1	0.00000	0.003059	0.93	0.78–1.00	3.600
Total	525	457	68					191.843

all, classification of the model by tagger did not result in a significant improvement in fit ( $P=0.253$ , Table 2). It is therefore appropriate to use the parameter estimates for the pooled model in models such as that defined by Equation 1.

## Tag reporting

**Return rates of seeded tags by species, unloading location, and time period** Tag seeding was carried out on 111 observer cruises between May 1990 and September 1994. During these cruises, 532 tuna were tagged and placed in fish wells. Of these, 342 (64%) were later recovered during unloading or processing of catches in canneries. The species breakdown of seeded tag releases and returns is given in Table 3. The numbers of returns by species did not differ significantly from those expected from the return rate pooled across species ( $P=0.648$ ). On this basis, reporting of tags can be assumed to be independent of species.

Most tag-seeding cruises (77) were undertaken on United States purse seiners because this fleet had the highest observer coverage during the period of the experiment. Tag-seeding cruises were also undertaken on purse seiners from Japan (18), Taiwan (8), Korea (4), Federated States of Micronesia (3), and

Solomon Islands (1). It was expected that the tag-reporting rate would vary by fleet, not because of variable cooperation by fishing vessel crews, but because different fleets tend to unload their catches in different ports. As tag detection took place during unloading of catches and at later stages of processing, it was suspected that variation in the effectiveness of tag detection and reporting at unloading ports would result in large differences in tag-reporting rates. The individual tag-seeding cruises were therefore classified by unloading location. In several instances, a vessel's catch was transhipped to two or more ports. In these cases, the seeded tags were classified individually according to the destination of fish in the wells into which the seeded tags had been placed.

The numbers of seeded tag releases and returns, by unloading location, are given in Table 4. The return rates vary considerably among unloading locations; for example, the 95% confidence intervals on the return rates for the two unloading locations with the largest numbers of seeded tags, American Samoa and Thailand, do not overlap and are in fact widely separated. Not surprisingly, the observed numbers of returns by unloading location differed significantly from those expected from the return rate pooled across unloading locations ( $P<0.001$ ).

For American Samoa, there were sufficient seeded tags to test the hypothesis of constant return rate of seeded tags over time. The return rate was low in 1990 but was consistently high for 1991 through 1994 (Table 5). The differences in return rates among years were statistically significant ( $P=0.005$ ), but this was due entirely to the lower than expected (on the basis of the return rate pooled across years) number of seeded tags returned in 1990. The differences among years 1991 through 1994 were not statistically significant ( $P=0.706$ ). Other locations (Japan and Thailand) also had highly variable reporting rates across years, but the numbers of seeded tags for these locations were too few to support a statistical treatment of the data.

**Table 2**

Statistical tests of the pooled tag-shedding model versus species-specific and tagger-specific tag-shedding models.

Model	No. of parameters	$\Omega$	$\chi^2$	df	P
Pooled	2	201.498	4.570	4	0.334
Species-specific	6	199.213			
Pooled	2	201.498	19.310	16	0.253
Tagger-specific	18	191.843			

**Table 3**

Numbers of seeded tag releases and returns, by species. The 95% confidence intervals were calculated assuming a binomial distribution.

Tuna species	Number seeded	Number returned	Return rate	95% confidence interval
Skipjack	333	222	0.667	0.613-0.717
Yellowfin	158	94	0.595	0.514-0.672
Bigeye	35	23	0.657	0.478-0.809
Unknown	6	3	0.500	0.118-0.882
Total	532	342	0.643	0.600-0.684

**Table 4**

Numbers of seeded-tag releases and returns, by unloading location. The 95% confidence intervals were calculated assuming a binomial distribution.

Unloading location	Number seeded	Number returned	Return rate	95% confidence interval
American Samoa	324	254	0.784	0.735–0.828
Japan	80	39	0.487	0.374–0.602
Korea	16	0	0.000	0.000–0.206
Philippines	5	4	0.800	0.284–0.995
Puerto Rico	16	9	0.562	0.299–0.802
Solomon Islands	5	5	1.000	0.478–1.000
Thailand	86	31	0.360	0.260–0.471
Total	532	342	0.643	0.600–0.684

**Table 5**

Numbers of seeded tag releases and returns from American Samoa, by year. The 95% confidence intervals were calculated assuming a binomial distribution.

Year	Number seeded	Number returned	Return rate	95% confidence interval
1990	23	3	0.130	0.028–0.336
1991	116	95	0.819	0.737–0.884
1992	50	48	0.960	0.863–0.995
1993	101	83	0.822	0.733–0.891
1994	34	25	0.735	0.556–0.871
Total	324	254	0.784	0.735–0.828

**Estimation of overall reporting rate for the RTTP** The variation in return rates of seeded tags by unloading location (and possibly over time for some locations) means that the simple, pooled return rate of seeded tags may provide a biased estimate of the overall tag-reporting rate for the RTTP. Therefore, the tag-seeding data were stratified by unloading location, and an overall average reporting rate weighted by the estimated numbers of RTTP tags recovered at those locations was determined. I did not attempt to take into account the possible variation in reporting rates by time because of insufficient information for most locations.

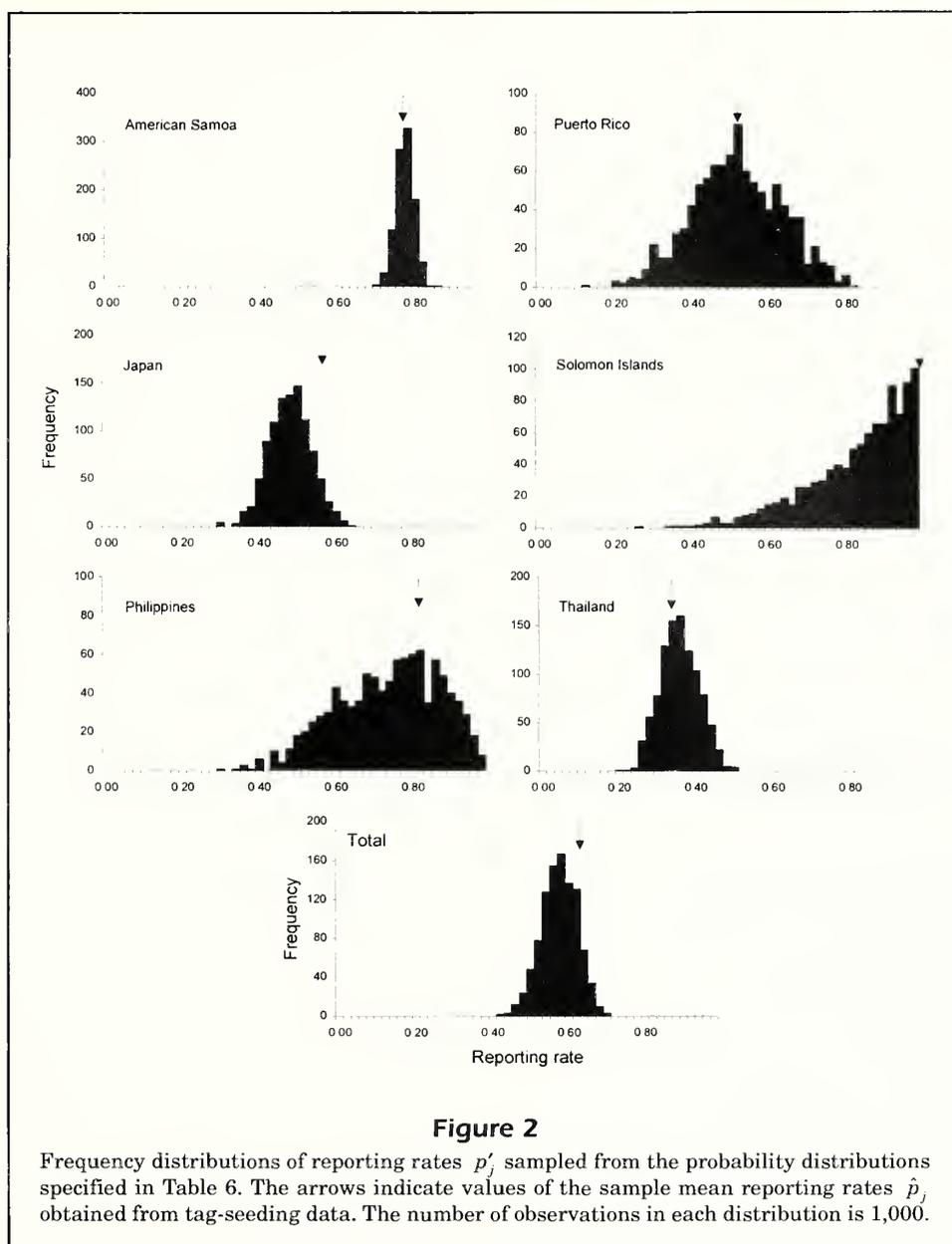
The estimates of the numbers of RTTP tags recovered at various locations and in total are shown in Table 6. Median reporting rates, numbers of tags recovered, and their 95% confidence intervals are based on bootstrap sampling from the reporting-rate probability distributions indicated in Table 6. The relationships between the bootstrap distributions and the sample means  $\hat{p}_j$  from tag seeding are shown in Figure 2. For some locations, notably Philippines and Solomon Islands,  $\hat{p}_j$  overestimates the median of the probability distribution of  $p_j$ . This is due to

the small numbers of seeded tags in these locations and the resulting effect on the shape of the assumed underlying probability distributions.

The estimation of tag recoveries and reporting rates for Korea and Taiwan had to be treated differently because no RTTP tags were returned from Taiwan and only four tags were returned from Korea (which were given to a SPC staff member during a brief visit). Additionally, it was not possible to seed tagged fish into shipments bound for Taiwan. Therefore, there was no basis for estimating tag recoveries and reporting rates in Korea and Taiwan directly from tag-seeding and RTTP tag-return data.

However, other information was available to derive estimates for these locations. During the period of the RTTP, approximately 100,000 t of tuna was processed annually by canneries in Korea, all of which was supplied by Korean purse seiners (Lewis<sup>1</sup>).

<sup>1</sup> Lewis, A.D. 1993. Product flows of tuna in the western Pacific, 1991 with likely trends during 1992. Sixth standing committee on tuna and billfish; 16–18 June 1993, Pohnpei, Federated States of Micronesia, South Pacific Commission, Noumea, New Caledonia. Information paper 2, 7 p.



A similar quantity of the Korean purse-seine catch in the western Pacific was delivered to canneries in Thailand. Assuming a similar occurrence of tagged tuna in these components of the Korean catch, the number of tagged tuna in catches delivered to Korea can be approximated by the tag returns from Korean purse seiners unloading in Thailand (658) divided by the estimated reporting rate for Thailand (0.355). On this basis, 1,798 (95% confidence interval of 1,412–2,386) tagged tuna are estimated to have been landed in Korea, of which only four were returned to SPC under the special circumstances described above. Similarly, the disposition of the Taiwanese purse-seine catch (approximately 20,000 t to Taiwan

and 155,000 t to Thailand annually) and tag returns from Taiwanese purse seiners unloading in Thailand (928) implies that 327 (257–434) tagged tuna were present in catches delivered to Taiwan.

Summing across locations, it is estimated that 31,166 (27,208–37,264) RTTP tags were recovered from all fisheries in the western Pacific, resulting in an overall reporting rate of 0.586 (0.490–0.671).

## Discussion

The objective of this study was to quantify two sources of tag loss, tag shedding and failure to re-

Table 6

Numbers of tags returned and estimates of numbers of tags recovered from various unloading locations. Median reporting rates, median numbers of tags recovered, and their respective 95% confidence intervals, were determined from 1,000 bootstrap replications based on random sampling from the specified beta ( $B$ ) or uniform ( $U$ ) distributions. Parameters for the beta distributions  $B(x,y,a,b)$  are  $x=r$ ,  $y=N-r+1$ , where  $N$  is the number of tags seeded,  $r$  is the number of seeded tags returned,  $a$  is the minimum possible reporting rate (based on the local tag-return rate), and  $b$  is the maximum possible reporting rate (1). The estimations for Korea and Taiwan could not be carried out in the usual way because of zero or very small numbers of seeded or RTTP (or both) tag returns. Estimations for these locations are described fully in the text.

Unloading location	Number of tags returned	Probability distribution	Reporting rate		Number of tags recovered	
			Median	95% confidence interval	Median	95% confidence interval
American Samoa	2,070	$B(254,71,0.016,1)$	0.784	0.739–0.826	2,639	2,505–2,802
Japan	1,969	$B(39,42,0.015,1)$	0.492	0.386–0.595	4,000	3,307–5,104
Korea	4		0.002	0.002–0.003	1,798	1,412–2,386
Philippines	6,671	$B(4,2,0.223,1)$	0.764	0.476–0.961	8,727	6,940–14,003
Puerto Rico	297	$B(9,8,0.002,1)$	0.525	0.301–0.753	565	395–988
Solomon Islands	2,226	$B(5,1,0.126,1)$	0.877	0.526–0.994	2,540	2,239–4,232
Taiwan	0		0.000	0.000–0.000	327	257–434
Thailand	2,218	$B(31,56,0.017,1)$	0.366	0.276–0.466	6,061	4,761–8,043
Tagging vessel	243		1.000	1.000–1.000	243	243–243
Other	2,568	$U(0.5,1.0)$	0.746	0.518–0.987	3,442	2,601–4,956
Total recoveries	18,266		0.586	0.490–0.671	31,166	27,208–37,264

port tags, in a large-scale tuna tagging experiment in the western tropical Pacific Ocean.

Tag-shedding rates were estimated by fitting a tag-shedding model to double-tagging data. The application of a double-tagging experiment to the estimation of the rate at which tags are shed from single-tagged fish requires several assumptions that are discussed in detail by Beverton and Holt (1957). In this study, there are four assumptions that warrant discussion. First, it must be assumed that the shedding rates of tags applied in the double-tagging experiment are the same as those for single-tagged fish. This assumption might fail if, for example, less care was taken with double tagging than with single tagging because of the need to return fish to the water within certain time limits. In the RTTP tagging experiment, taggers were instructed to take as much care in implanting each tag in double-tagged tuna as they would for single-tagged tuna. Although it is not possible to test this assumption with the limited amount of double-tagging data, the similarity in return rates of double- and single-tagged tuna (South Pacific Commission<sup>2</sup>) suggests that there had not

been a gross violation. If the assumption did fail, as described above, the shedding rates as applied to single-tagged tuna would be overestimated.

Second, it is necessary to assume for double-tagged fish that the events potentially resulting in shedding of tags are random and independent with respect to the two tags. If this assumption fails, there will be fewer observations of fish retaining one tag, and consequently shedding rates will be underestimated. This assumption is difficult to test unless it is possible to identify fish that have shed both tags, which of course will not normally be the case under field conditions. The techniques adopted in this experiment (individual tag placement on opposite sides of the fish) were designed to facilitate compliance with this assumption, but the actual extent of compliance remains unknown.

Third, it must be assumed that the first (primary) and second (companion) tags applied to fish in a double-tagging experiment have the same probabilities of shedding. This assumption might fail if, for example, the companion tag is less securely implanted because tagging on the opposite side of the fish is an unfamiliar task. This assumption can be tested by using the frequencies of primary and companion tag retention in fish that were recaptured bearing one tag. In this double-tagging experiment, there were 68 returns that consisted of one tag. Of

<sup>2</sup> South Pacific Commission. 1994. Oceanic Fisheries Programme work programme review 1993–94 and work plan 1994–95. Seventh standing committee on tuna and billfish; 5–8 August 1994, Koror, Palau, South Pacific Commission, Noumea, New Caledonia. Working paper 5, 66 p.

these, 29 returns were of the primary tag and 39 were of the companion tag. The cumulative binomial probability of 29 or less of either the primary or companion tag being found in a sample size of 68 is 0.275, indicating that there is a reasonable chance of the assumption being satisfied.

Fourth, in the analysis carried out here, it was assumed that tag pairs (from fish recovered with two tags) are reported (or not) as a pair—i.e. either both, or none are reported. Furthermore, it was assumed that the probability of reporting a tag pair was the same as that of reporting a single tag. I will refer to this as the dependent hypothesis. An alternative hypothesis is that the reporting of individual tags forming a pair is completely independent; whether or not one tag of a pair is reported has no effect on the probability that the other will be reported. I will refer to this as the independent hypothesis. Under either hypothesis, we can define the probability,  $U(t)$ , that a tag is retained at recapture time  $t$  and is reported as

$$U(t) = pQ(t | \rho, L) = p(1 - \rho)\exp(-Lt). \quad (2a)$$

However, the probabilities of two, one, and no tags being retained at recapture time  $t$ , and, in the case of at least one tag being retained, also reported, are different under the two hypotheses, as follows:

$$\begin{aligned} P_{d2}(t | \rho_d, L_d) &= pQ(t | \rho_d, L_d)^2 \\ P_{d1}(t | \rho_d, L_d) &= 2pQ(t | \rho_d, L_d)[1 - Q(t | \rho_d, L_d)] \\ P_{d0}(t | \rho_d, L_d) &= pQ(t | \rho_d, L_d)^2 - 2pQ(t | \rho_d, L_d) + 1 \end{aligned} \quad (3a)$$

and

$$\begin{aligned} P_{i2}(t | \rho_i, L_i) &= p^2Q(t | \rho_i, L_i)^2 \\ P_{i1}(t | \rho_i, L_i) &= 2pQ(t | \rho_i, L_i)[1 - pQ(t | \rho_i, L_i)] \\ P_{i0}(t | \rho_i, L_i) &= [1 - pQ(t | \rho_i, L_i)]^2, \end{aligned} \quad (3b)$$

where the  $d$  and  $i$  subscripts indicate the dependent and independent hypotheses, respectively.

It can be shown that substitution of the right-hand sides of Equations 3a into the log-likelihood Equation 4 produces an identical result to substitution of Equation 3; the  $p$ 's cancel out and reporting rate has no influence on the estimates  $\hat{\rho}_d$  and  $\hat{L}_d$  when the dependent hypothesis is true. This is therefore equivalent to using Equation 2 as the tag-shedding and reporting model, as I have done in this study.

Under the independent hypothesis, substitution of the right-hand sides of Equations 3b into the log-likelihood Equation 4 does not result in a canceling out of  $p$  terms, and therefore  $p$  must be included in the tag-shedding and reporting model as shown in

Equation 2a. However,  $p$  is totally confounded with  $1 - \rho_i$ , and cannot be estimated from the double-tagging data. If an independent estimate of  $p$  is available (for example, from a tag-seeding experiment), Equation 2a can be applied and  $\rho_i$  estimated free of the effects of  $p$ .

For most double-tagging experiments, it will not be known with any certainty whether the dependent or independent hypothesis is more appropriate. The following procedure may provide some insight in this regard:

- 1 Obtain tag-shedding parameter estimates  $\hat{\rho}_d$  and  $\hat{L}_d$ , assuming that the dependent hypothesis is true (using Equations 2 and 3).
- 2 If an independent estimate of the reporting rate,  $\hat{p}$ , is available, obtain tag-shedding parameter estimates  $\hat{\rho}_i$  and  $\hat{L}_i$ , assuming that the independent hypothesis is true (using Equations 2a and 3b). Small values of  $\hat{p}$  (less than  $1 - \hat{\rho}_d$ ) will usually result in  $\hat{\rho}_i$  entering an unreasonable (negative) domain. Alternatively, if  $\hat{p}$  is constrained to be nonnegative,  $\hat{L}_i$  will differ from  $\hat{L}_d$  and the fit to the data will degrade (i.e.  $\Omega_i > \Omega_d$ ). In either case, this indicates inconsistency between the reporting rate estimate  $\hat{p}$  and the independent hypothesis. In the present study, the estimated reporting rate (0.586) was much smaller than  $1 - \hat{\rho}_d$  (0.941, see Table 1). If  $\hat{p}$  is applicable to the double-tagged tuna, this implies that the independent hypothesis is inappropriate for these data.

In reality, it is likely that the actual situation with respect to the reporting of tag pairs will lie somewhere between completely dependent and completely independent reporting. It is possible to generalize the tag-shedding model with respect to these hypotheses by defining a coefficient of independence,  $c$ , such that

$$U(t) = \frac{p(1 - \rho)\exp(-Lt)}{c(1 - p) + p}.$$

Setting  $c=0$  is equivalent to the dependent hypothesis,  $c=1$  is equivalent to the independent hypothesis, while  $0 < c < 1$  implies partial independence. For the RTTP double-tagging data and  $\hat{p} = 0.586$ ,  $c < 0.088$  allows an unconstrained  $\hat{p}$  to remain nonnegative. This range of possible values of  $c$  implies that the dependent hypothesis is likely to be appropriate for these data.

The tag-shedding model fitted to the double-tagging data assumes that the rate of tag shedding is constant over time. Kirkwood (1981) and Hampton and Kirkwood (1990) found that, in some cases, a model that allowed the probability of shedding to

decrease over time provided a better fit to double-tagging data for southern bluefin tuna, *Thunnus maccoyii*, than the model used in this study. They reasoned that tags might become more securely fixed over time, and thus less likely to be shed, as the fish grows and tissue is built up around the tag shaft. I fitted the three-parameter variable-rate shedding model (model 4 in Hampton and Kirkwood [1990]) to the pooled data set and to the three species-specific data sets and found that the improvement in fit over the constant shedding-rate model was negligible in each case and did not warrant the addition of the extra parameter. There is thus little evidence of a decline in shedding rates over time in these data. This may in part be due to the relatively short periods at liberty (maximum of 2 years) of the double-tagged tuna in this study compared with those for the southern bluefin tuna (up to 18 yr) analyzed by Hampton and Kirkwood (1990).

Given compliance with the assumptions of the experiment and the appropriateness of the model, it can be concluded that losses of tags through shedding are relatively modest (about 11% after two years) for the RTTP. This shedding rate is comparable to those reported by Hampton and Kirkwood (1990) for the more recent southern bluefin tuna double-tagging experiments (16% and 12% after two years for experiments 7 and 8, respectively), where comparable tags and techniques to those used in this experiment were used. Other tuna tagging experiments have reported substantially higher tag losses after two years, e.g. 30%–50% for the early southern bluefin tuna experiments (Hampton and Kirkwood, 1990), 43% for eastern Pacific yellowfin tuna (Bayliff and Mobrand, 1972), and 35% for Atlantic bluefin tuna (Lenarz et al., 1973; Baglin et al., 1980). It is possible that the higher shedding rates observed in some of these experiments were due to inferior tags, in which the streamers were prone to detach from the tag head. The streamers of tags used in this experiment and the recent southern bluefin tuna experiments were heat fused to the tag heads, making detachment impossible under normal conditions.

The analysis of tag-seeding and associated data indicated that, despite extensive publicity and attractive rewards for tag finders, failure to report tags was a significant source of tag loss in the RTTP. Given the diverse nature of the fishery, its spatial extent, and the methods of processing large quantities of fish caught by purse seiners in particular, this is hardly surprising. The estimated overall reporting rate in fact compares more than favorably with those for some tagging experiments carried out on more local scales (e.g. Campbell et al., 1992 for coastal shrimp in the Gulf of Mexico). My estimates of reporting rates

based on tag-seeding data may, if anything, err on the pessimistic side. It is suspected that one cause of failure to report purse-seine-caught tagged tuna may be the detachment of tags (through abrasion) from fish while they are held in the vessels' wells. If this occurs, detached tags would likely be flushed out of the wells into the sea, after which detection would be highly improbable. It is possible that tags placed in dead tuna by observers were more prone to detachment in the well than tags placed in live tuna that had been at liberty for some time. The tag head and the portion of the tag shaft imbedded in the musculature of live tuna were frequently observed to be encased in a fibrous capsule, which would tend to fix the tags more securely than tags placed in dead tuna. "Shedding" of seeded tags could conceivably result in losses of seeded tags of the same order as, or greater than, the immediate tag-shedding rates estimated from the double-tagging experiment on live tuna (about 6%). It may be possible to estimate the extent of this problem by conducting a double-tagging experiment for seeded tags.

The main purpose of estimating tag-shedding and reporting rates is to allow these processes to be incorporated into analyses of the tagging data for the purpose of estimating mortality rates. Typically, this would involve substitution of the point estimates of the parameters into equations such as Equation 1; mortality rates that are free of the effects of these tag losses could then be estimated from the tagging data (e.g. Kleiber et al., 1987). However, where the ultimate objective of the analysis (mortality rate estimation) is stock assessment related, it is important to have not only estimates of the mean rates but also estimates of their precision that are unconditional on estimates of nuisance parameters such as tag-shedding and reporting rates.

In this study, estimates of precision (expressed as 95% confidence intervals) of tag-shedding and reporting rates were obtained by using the percentile method applied to the bootstrap distributions of the parameter estimates. For the tag-shedding analysis, I confined this to estimates of precision of  $Q_{2yr}$ , although confidence intervals for the model parameters could be similarly derived. The advantage of the bootstrap approach as applied to the analysis of tag reporting is that it allowed the precision of the overall reporting rate to be easily determined given some knowledge, or reasonable assumptions, regarding the reporting-rate probability distributions for differing components (in this case, based on unloading location) of the data set. The approach also provided a convenient means of integrating uncertainties in tag-shedding and reporting rates (via the individual bootstrap values) into a similarly structured bootstrap

procedure for the estimation of mortality rates from the overall RTTP tagging data. The precision of the mortality rates estimated with such a procedure will then incorporate uncertainties in the estimates of tag-shedding and reporting rates and not be conditional on point estimates of these parameters.

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**Abstract.**—Gonad weights and results of histological analyses from 85 swordfish, *Xiphias gladius*, were used to develop a validated method for classification of the reproductive activity of female swordfish based on gonad indices (GI's). The validated method provides a significant improvement over previously published (unvalidated) methods. The method was shown to be independent of the length of individual fish, important when length is used as a criterion for selection of individuals from which summary statistics based on GI are being developed. Female swordfish were found to be in a reproductively active condition when  $GI = \ln(\text{gonad weight in gm})/\ln(\text{eye-fork length in cm}) \geq 1.375$ . Classification methods for species with comparable reproductive habits and characteristics may be alike, and it is speculated that results for other billfishes would be similar to those described for swordfish.

## Use of gonad indices to estimate the status of reproductive activity of female swordfish, *Xiphias gladius*: a validated classification method

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We describe a validated classification method that uses gonad indices (GI's) to determine accurately the reproductive condition of female swordfish, *Xiphias gladius*. This study uses previously unpublished data as well as histological analyses detailed in Taylor and Murphy's (1992) study of the reproductive biology of swordfish captured in the Straits of Florida. It is standard practice to use GI's to identify regions and times of active spawning in studies of the distribution and structure of stocks of many species of fish, including swordfish (e.g. Kume and Joseph, 1969; Shingu et al., 1974; Miyabe and Bayliff, 1987; Sosa-Nishizaki, 1990; Nakano and Bayliff, 1992; Arocha and Lee, 1993; Arocha et al., 1994; Gouveia and Mejuto, 1994; Arocha and Lee, 1995; Hinton and Deriso, in press). Data on the reproductive activity of swordfish are costly and difficult to obtain but essential to studies such as those noted; full use should be made of all available information. Our classification method overcomes problems of published methods (e.g. Miyabe and Bayliff, 1987), which have the potential to reduce the information database of the researcher by over 50%. To our knowl-

edge, it is the first method applicable to female swordfish to have been validated with data obtained from histological analyses, which provide a verifiable measure of the reproductive status of individual swordfish.

The standard practice (Gouveia and Mejuto, 1994) in studies using values of GI for female swordfish has been to estimate  $GI = 10^4 \times GW/EFL^3$ , where  $GW$  = gonad weight in grams, and  $EFL$  = length from the posterior edge of the orbit to the fork of the tail in centimeters (we note that without loss of generality, other length measurements, such as lower-jaw fork length (LJFL), have been used) (Kume and Joseph, 1969). The latter assumed that "[females] with gonad indices equal to or greater than 3 are about to spawn." Miyabe and Bayliff (1987) modified their method by assuming that "only females with gonad indices of 7.0 or greater were [about to spawn]." Arocha and Lee (1995) modified the method of Kume and Joseph (1969) when they noted that females with GI's greater than 4.0 were in prespawning condition. In certain applications of these methods, e.g. comparison of average GI's for different regions or time periods,

it is necessary to ensure that the averages being compared are for individuals with comparable reproductive potential or maturity. Thus, it is standard practice to use a minimum length (e.g. Miyabe and Bayliff, 1987; Sosa-Nishizaki, 1990; Nakano and Bayliff, 1992; Arocha et al., 1994; Arocha and Lee, 1995) to decide which data to include in estimates of average values of GI, making it important to document that minimum-length criteria have no impact on methods used to estimate reproductive status (Cayré and Laloë, 1986).

## Data and methods

Details on data collection and histological analyses, other than estimation of the values of individual gonad indices, may be found in Taylor and Murphy (1992). Female swordfish were assigned to eight developmental classes (Murphy and Taylor, 1990) based on the appearance of histological features (Wallace and Selman, 1981). These classes and mean observed oocyte diameters were 1) immature, < 20  $\mu\text{m}$ ; 2) developing, 71  $\mu\text{m}$ ; 3) maturing, 160  $\mu\text{m}$ ; 4) mature, 434  $\mu\text{m}$ ; 5) gravid, 723  $\mu\text{m}$ ; 6) spawning or partially spent, 823  $\mu\text{m}$ ; and 7) spent, 181  $\mu\text{m}$ . Individuals in class 8 (recovering) were observed but not described in Taylor and Murphy (1992). Gonads

of swordfish in class 8 exhibited signs of having spawned in the previous season and were undergoing maturational, prespawning development for subsequent reproductive efforts.

The preferred formulation for GI may be determined by examining the relation of gonad weight to measures of body size (de Vlaming et al., 1982). The formulation chosen should meet the underlying assumptions (de Vlaming et al., 1982) for use of GI as an index of reproductive status. In addition to examining the previously described "standard" expression of GI (hereafter referred to as GI(1)), we examined  $GI = \ln(GW)/\ln(EFL)$ , hereafter referred to as GI(2), and  $GI = GW/EFL$ . Stepwise analysis of covariance (ANCOVA) was used to examine how well these formulations for GI met the underlying assumptions (de Vlaming et al., 1982) for use of GI as an index of the reproductive status of female swordfish. Values of GI were determined for the fish for which histological data had been obtained. For those individuals for which measurements of EFL were not obtained, measurements of LJFL were used to estimate EFL as follows:  $EFL = -8.259 + 0.930 \times LJFL$  [ $n=316$ ,  $r^2=0.996$ ,  $P<0.001$ ] (Taylor and Murphy, 1992). Of the over 400 fish examined by Taylor and Murphy (1992), there were 85 individuals (Table 1) with measurements (40) or estimates (45) of EFL ranging from 73 to 253 cm, for which there were GW's and data from

Table 1

The status of reproductive activity (R) of swordfish determined by histological analyses [Taylor and Murphy, 1992], EFL = eye fork length (cm), and GW = gonad weight (gm).

R	GW	EFL	R	GW	EFL	R	GW	EFL	R	GW	EFL
2	3	77	2	100	113	3	752	169	6	8,740	221
2	13	86	2	110	147	4	530	161	6	8,840	208
2	14	88	2	135	115	4	780	182	6	9,920	206
2	15	94	2	140	118	4	800	187	6	10,180	188
2	30	96	2	140	128	4	1,320	186	6	10,430	227
2	30	95	2	150	121	4	2,140	219	6	11,340	223
2	30	92	2	220	93	4	2,888	201	6	15,140	253
2	35	97	2	225	73	5	2,690	169	8	446	167
2	35	99	2	255	148	5	3,950	184	8	540	172
2	35	106	3	100	121	6	1,240	181	8	600	166
2	35	106	3	105	130	6	1,540	202	8	640	164
2	37	101	3	110	123	6	1,760	174	8	730	183
2	45	114	3	200	137	6	2,270	182	8	800	190
2	50	99	3	240	139	6	3,650	181	8	980	179
2	50	96	3	300	168	6	3,780	171	8	995	197
2	55	104	3	353	166	6	3,850	208	8	1,325	200
2	70	103	3	437	120	6	3,900	155	8	1,340	222
2	70	105	3	470	184	6	4,000	180	8	1,360	249
2	80	104	3	500	181	6	4,700	191	8	1,500	211
2	80	112	3	620	185	6	4,720	197	8	1,790	191
2	90	113	3	680	186	6	6,034	154			
2	100	128	3	680	174						

histological analyses. According to the results of the histological analyses, swordfish were considered to be in spawning condition, i.e. spawning was in progress or imminent in the region in which the fish was captured, if they were either "gravid" or "spawning or partially spent" (classes 5 and 6 of Taylor and Murphy [1992]). Individuals in these conditions were classified as in an active (A) reproductive status. All others were classified as quiescent (Q).

In our study the results of histological analyses represent the known reproductive status of individual swordfish, and the H(i) are various hypothesized classification methods (Table 2) for placing swordfish into categories A or Q. In some cases, these H(i) indicate minimum-length criteria used to determine which data from individual swordfish should be included in estimates of average values of GI. To facilitate the examination of impacts of minimum-length criteria on classification methods, these criteria were treated as a component of the H(i) in our analyses. We do not attempt to define minimum-length criteria for size at maturity in this study (cf. Taylor and Murphy [1992]); our concern was to determine if classification methods based on GI were independent of such criteria. The hypotheses identified in Table 2 as "Present study" are representative of a multitude of hypotheses we examined.

The optimum value (OV) and confidence intervals for the value of GI to be used as criteria,  $GI^*$ , to estimate the reproductive condition of individual female swordfish were determined by using maximum-likelihood estimation procedures and the following model:

Let  $R = 1$  if a swordfish is reproductively active (classes 5 and 6 of Taylor and Murphy [1992]), oth-

erwise  $R = 0$ . Then for individual fish,  $i$ , selected at random,

$$P(\text{a swordfish is reproductively given its gonad index}) = \pi(GI)^R \times (1 - \pi(GI))^{(1-R)}$$

Maximum-likelihood estimates of  $\pi(GI)$  are given by the number of successes in the series of trials determined by the value of  $GI^*$  in the data, divided by the number of trials. Thus, for our data set:  $[GI_1, \dots, GI_k^*, \dots, GI_n]$  and  $[R_1, \dots, R_k, \dots, R_n] =$  [the observed values of  $GI$ ] and [the respective measure of reproductive status determined by histological analyses] for individual fish, these estimates are given by

$$\pi(GI) = \begin{cases} \frac{\text{(number of individuals with } R = 1 \text{ and } GI < GI_k^*)}{k - 1} & \text{for individuals with } GI < GI_k^* \\ \frac{\text{(number of individuals with } R = 1 \text{ and } GI \geq GI_k^*)}{n - k + 1} & \text{for all others} \end{cases}$$

It follows that the optimum value,  $GI^*$ , is that which maximizes the following log-likelihood function (LKLHD):

$$LKLHD = \sum [R \times \ln(\pi(GI)) + (1 - R) \times \ln(1 - \pi(GI))]$$

## Results and discussion

Results of classifying individuals as either A or Q based on the results of the histological analyses and from application of the various H(i) (treated in each test as the null hypothesis) are given in Table 3. It is clear that H(2) and H(3) fail to classify individuals correctly according to reproductive status as determined by histological analyses. Under H(2) and H(3), individuals below the minimum-length criteria are not classified. About 75% of the individuals whose lengths were above the size restrictions stated in these hypotheses were classified correctly, but only 48% of the individuals in this group that were reproductively active were correctly classified which represents a significant type-1 error that may be extremely costly in terms of loss of information on the distributions of reproductively active swordfish. However, this is a result of the value of GI included in the hypotheses and not a result of restrictions placed on lengths of individuals included in the analyses, as is evidenced by the results for the other H(i). We also note that length was not found to be a signifi-

**Table 2**

Levels of gonad indices (GI) used to classify the reproductive activity of female swordfish and minimum eye fork length (EFL) criteria used to standardize statistics for comparison among areas and times, as employed by various researchers. Formulations for GI(1) and GI(2) are given in the text.

H(i)	Classification method	Author
1	GI(1) $\geq$ 3.0	Kume and Joseph
2	GI(1) $\geq$ 7.0 and EFL > 150 cm	Miyabe and Bayliff
3	GI(1) $\geq$ 7.0 and EFL > 160 cm	Sosa-Nishizaki
4	GI(1) $\geq$ 4.0 and EFL > 131 cm <sup>1</sup>	Arocha and Lee
5	GI(1) $\geq$ 6.0	Present study
6	GI(2) $\geq$ 1.37	Present study

<sup>1</sup> Authors used lower-jaw fork length >150 cm.

**Table 3**

Comparison between the correct (from histological analyses [HA] of the ovaries) and estimated (from GI's) classification of reproductive status of female swordfish. Individuals were classified as reproductively active (A) or quiescent (Q). Asterisks designate incorrect classifications based on GI's, IC is the percentage of all individuals [ $n$  determined by H(i)] classified correctly, and AC is the percentage of reproductively active individuals, within the  $n$  individuals, that were classified correctly.

H(i)	$n$	HA	GI	GI	IC	AC
			A	Q		
1	85	A	19	2*	95.3	90.5
		Q	2*	62		
2	48	A	10	11*	77.1	47.6
		Q	0*	27		
3	46	A	10	11*	76.1	47.6
		Q	0*	25		
4	52	A	17	4*	92.3	81.0
		Q	0*	31		
5	85	A	15	6*	92.9	71.4
		Q	0*	64		
6	85	A	21	0*	95.3	100.0
		Q	4*	60		

cant term in logistic regressions that included EFL as a classification variable.

Under H(1) and H(6), 95% of the 85 individuals were classified correctly (Table 3); further, under H(6) all individuals that were reproductively active were correctly classified, which was significantly (see following discussion) more than the 91% of the reproductively-active individuals correctly classified under H(1) and the 71% to 81% correctly classified under H(5) and H(4), respectively. Hypothesis H(6) placed about 4.7% of the individuals that were quiescent in the active category, and H(1), about 2.5%, both of which represent relatively low rates of type-2 error.

Although length-cubed is often the choice to standardize GW, as in the "standard" expression for GI, length is also frequently used. Further, GW may be exponentially related to body size (de Vlaming et al., 1982), in which case log transformation as in GI(2) is indicated. We examined these hypotheses in formulations of GI for female swordfish. The results of ANCOVA revealed significant ( $P < 0.01$ ) heterogeneity among slopes and intercepts of the regressions of GW on EFL and on  $EFL^3$  for reproductive classes (2, 3, 4, [5, 6] and 8) of Taylor and Murphy (1992). At the same time, ANCOVA on the log-transformed data yielded only one significant ( $P < 0.01$ ) coefficient, that for the intercept of class (5, 6); however this coeffi-

cient was only about 28% of the estimated intercept of the overall regression. Thus, the formulation of the gonad index that best conformed to the underlying assumptions (de Vlaming et al., 1982) was GI(2). In addition, the maximum-likelihood test based on the values of LKLHD for the difference between methods showed that model GI(2) provided a significant ( $\chi^2(1), P = 0.033$ ) improvement over model GI(1). The estimate of OV obtained from maximum-likelihood analyses for GI(2) was ( $1.366 < OV < 1.375$ ). Note that although GI(2) has a continuous distribution, the interval estimate of OV is a function of the distribution of values of GI(2) in the sample data, and thus any hypothesized value in this range would yield LKLHD and tabled results identical to those shown for H(6). Further, because the solution for the function LKLHD is so knife-edged, the estimate of OV includes the 90% confidence interval, and the 95% confidence interval for the estimate of OV, ( $1.357 < OV < 1.375$ ), differs only in the lower bound.

Two points should now be clear. First, the classification methods that are based on GI(1) that have been used and published in studies requiring estimates of the reproductive status of female swordfish do not meet the underlying assumptions (de Vlaming et al., 1982) for use as an indicator of reproductive status, and they may also be viewed in some instances as overly restrictive, in that they may have excluded significant amounts of usable data from analyses that were already hampered by limited information. This resulted, at least in part, from using values of GI that corresponded to a fully ripe and running condition of the gonad. Second, the classification methods, both previously published and described herein, were not impacted by minimum-length criteria which may be required to standardize comparisons of statistics that are based on gonad indices.

Our results are conservative in the following respect. We have no knowledge of the frequency of spawning of female swordfish. Thus, because hydration of eggs may occur over a very short period of time, by not including individuals in class 4 ("mature ovaries" of Taylor and Murphy [1992]), some individuals that might be expected to spawn within a short period of time, and thus presumably within the general area of capture, may be excluded from consideration. The question of whether to include these individuals as reproductively active could be addressed by conducting a study of spawning frequency of female swordfish based on the condition of yolk development in the eggs, as has been done for yellowfin tuna, *Thunnus albacares* (Schaefer, 1996). Alternatively, it may be possible to determine whether or not class-4 individuals should be included

by estimating the distribution of spawning using both a classification scheme that considers these individuals as reproductively active, and the classification developed herein, with subsequent testing by comparison of these distributions to other measures of spawning activity, such as distributions of larval fish or of male:female ratios.

Given the interval estimate for OV, and taking a conservative approach with respect to including individuals that are not reproductively active in estimates of the spatial and temporal distributions of spawning, we recommend that researchers requiring an estimate of the reproductive status of female swordfish adopt a method that classifies reproductively active female swordfish as those for which  $GI = \ln(GW)/\ln(EFL) \geq 1.375$ , the upper limit of the interval. When additional information becomes available, further analyses should be undertaken.

The need to develop species-specific classification methodologies has been clearly documented (de Vlaming et al., 1982). However, methods for species with similar characteristics and reproductive habits may be similar (Cayré and Laloë, 1986). Merrett (1970) found that for sailfish (*Istiophorus platypterus*); striped (*Tetrapturus audax*), blue (*T. nigricans*), and black (*T. indica*) marlin; and spearfish (*T. angustirostris*), changes in ovaries through oogenic cycles were similar in all species, as was the shape of the gonads (with the exception of the shape of the spearfish gonad, which was Y-shaped rather than bilaterally symmetrical). These changes are similar to those observed in swordfish (cf. Taylor and Murphy, 1992). Thus, while we concur with de Vlaming et al. (1982) and strongly recommend that classification methods be developed and validated for each species of billfish, we would speculate that results for these species would be comparable to those shown herein.

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**Abstract.**—The annual cycle of abundance and the monthly distributions of the copepod *Centropages hamatus* are described for U.S. northeast continental shelf waters from plankton samples collected approximately bimonthly from 1977 to 1987. The copepod was found distributed throughout the study area with a strong onshore–offshore abundance gradient. After its annual low, *C. hamatus* was found to increase in abundance slowly along the coast and to expand offshore following the northward progression of spring conditions. The highest monthly mean abundance estimates of *C. hamatus* were found on Georges Bank during the month of July. Distribution begins to constrict inshore following peak abundance periods.

Examination of environmental variables revealed that in general *Centropages hamatus* was prevalent when surface temperatures ranged from 12 to 17°C, when water-column chlorophyll levels were high, and where salinity was low on the shelf. The population in the Middle Atlantic Bight sub-area declines sharply as water temperatures rise in summer and does not begin to recover until temperatures decline in the fall. In contrast, populations in the more northern regions decrease slowly from peak abundance and do not increase from their annual low until water temperatures rise in early spring. The pelagic population that survives through low abundance periods is concentrated in shoal or inshore (or both) waters where temperature is low and phytoplankton biomass high. There was no evidence from survey data that predation by ctenophores, chaetognaths, or the copepod *Centropages typicus* has a major effect on *C. hamatus* abundance.

## Persistent spatial and temporal abundance patterns for late-stage copepodites of *Centropages hamatus* (Copepoda: Calanoida) in the U.S. northeast continental shelf ecosystem

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The calanoid copepod *Centropages hamatus* (Lilljeborg, 1853) is one of the dominant members of the zooplankton assemblage found within North Atlantic shelf waters (Davis, 1987; Sherman et al., 1987). The species has a wide latitudinal range that is reported to be as far north as Labrador (Pinhey, 1926) and southward to coastal waters off Florida in the Gulf of Mexico (Marcus, 1989). It occurs primarily in sheltered, coastal, and shoal regions of the continental shelf. This omnivorous copepod produces subitaneous eggs during the breeding season and also can produce diapausal ones in response to an environmental trigger (Pertzova, 1974; Marcus, 1989). McLaren (1978) estimated that generation period is comparatively short, 21–25 days at 12–13°C, and describes *C. hamatus* as a highly productive and ecologically efficient component of the zooplankton community. Sherman et al. (1987) reported that it is a major prey item of larval, juvenile, and adult fish stocks within continental shelf waters.

The National Marine Fisheries Service has monitored the zooplankton populations of the U.S. northeast shelf ecosystem with broad-scale surveys since 1977 as part of the MARMAP (Marine Resources Monitoring, Assessment, and Pre-

diction) program (Sherman, 1980). The resulting historical data set provides the information needed to form a baseline for detection of future changes to the ecosystem. Previous reports on the annual abundance cycle of *Centropages hamatus* within the ecosystem have been limited to specific areas or to comparatively short periods (or both) (Bigelow, 1926; Deevey, 1956, 1960; Judkins et al., 1980; Davis, 1987; Sherman et al., 1987; Grant, 1988; Kane, 1993). No description of the monthly distribution of the copepod in this region has been published from collected data. This report uses information collected during MARMAP surveys from 1977 to 1987 to describe the persistent distribution and abundance patterns of *C. hamatus* throughout the ecosystem. Measurements of salinity, temperature, bottom depth, chlorophyll, and potential predator abundance were considered to gain insight into factors affecting the distribution and annual abundance cycle of *C. hamatus*.

### Methods

#### Sample collection and analysis

The U.S. northeast shelf ecosystem extends from the Gulf of Maine to

Cape Hatteras (Sherman, 1994). Plankton samples were collected within the ecosystem at monthly or bimonthly intervals from 1977 to 1987. Plankton surveys occupied approximately 184 standard station locations that were relatively unchanged during the 11-yr period (Fig. 1). Samples were also collected on trawl and dredge cruises at randomly selected locations that varied yearly. Areal coverage and station spacing on these surveys were similar to broadscale plankton cruises.

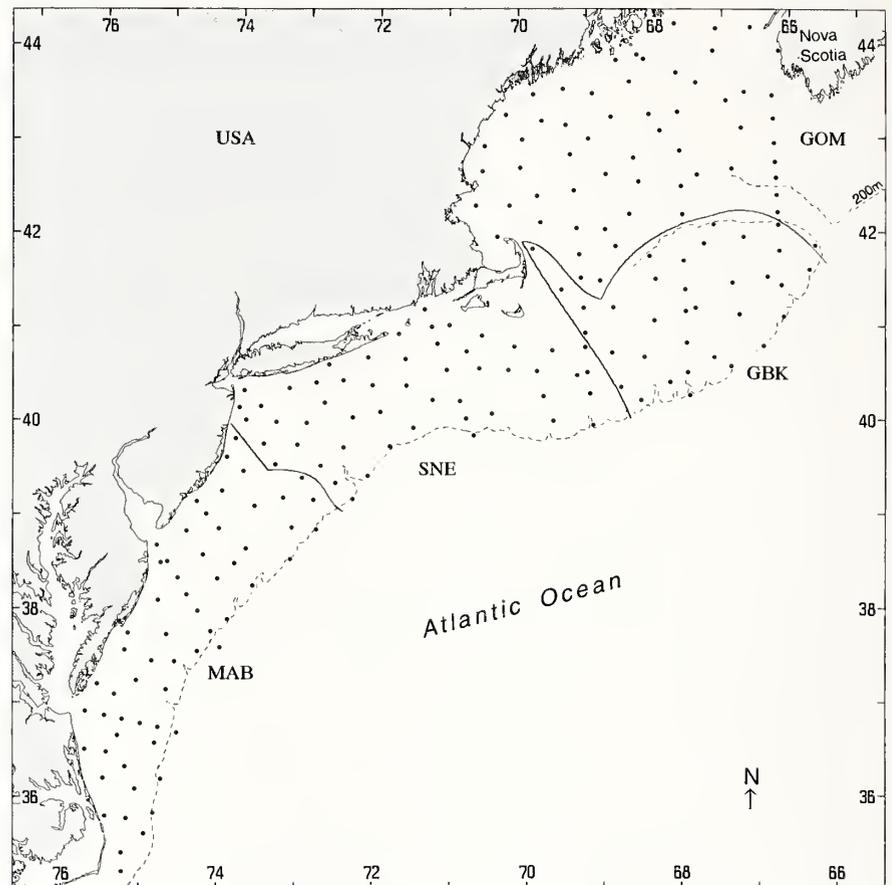
Zooplankton were collected at each station from one side of a 61-cm bongo frame fitted with a 0.333-mm mesh net. The gear was lowered at 50 m/min to within 5 m of the bottom, or to a depth of 200 m maximum, and retrieved at 20 m/min. Ship speed was adjusted to maintain a 45° angle to the towing wire. A digital flowmeter was positioned in the center of the bongo frame to measure the volume of water filtered. All collections were preserved in 5% formalin. Samples were reduced to approximately 500 organisms in the laboratory by subsampling with a modified box splitter. Zooplankton were sorted, identified, and counted at the Plankton Sorting Center, Szczecin, Poland. The total number of samples analyzed for this report was 10,715. The abundance of *Centropages hamatus* is expressed here as numbers/100 m<sup>3</sup> of water filtered and includes only advanced copepodite stages CV and CVI. Earlier copepodite stages were excluded because other copepods of similar size are undersampled by 0.333-mm mesh nets (Anderson and Warren, 1991).

The seasonal abundance cycles of known predators of copepods captured with the nets used during the surveys were examined to determine which might affect *Centropages hamatus* population levels. The three copepod predators examined in this study are: 1) ctenophores, 2) the copepod *Centropages typicus*, and 3) chaetognaths.

Sea-surface temperature was measured at each station to the nearest 0.1°C with a stem thermometer. During plankton surveys from 1977 to 1986,

water bottles with reversing thermometers were used to collect water samples at standard depths in order to measure salinity and temperature. Measurements of bottom temperature were determined by means of the deepest bottle or by means of a special bottom-tripped water-bottle sampler in water less than 75 m. Temperature and salinity data in 1987 were collected with a CTD (conductivity-temperature-depth) probe. Phytoplankton biomass was determined by measuring the concentration of chlorophyll *a* in the netplankton (>20 µm) and the nanoplankton (<20 µm) size fractions from water samples down to 100 m on plankton surveys from 1977 to 1984. These size fractions were summed to generate an estimate of total chlorophyll. The average water-column value of a variable for each station was calculated by arithmetically integrating measurements over depth.

More detailed accounts of sampling procedures and individual cruise tracks are given by Sibunka and Silverman (1984, 1989).



**Figure 1**

Locations of standard MARMAP stations (•) in the U.S. northeast shelf ecosystem and subarea boundaries (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).

## Statistical analysis

Estimates of *Centropages hamatus* and predator abundance were log transformed [ $\log^{10}(\text{no.}/100\text{m}^3 + 1)$ ] prior to contouring and data analysis. Contoured *C. hamatus* distribution maps were made by using Surface III software (Sampson, 1988) on station abundance data from the 11-yr data set grouped by monthly intervals.

Evaluation of species interannual abundance variability was facilitated by subdividing the ecosystem into four subareas: Middle Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GBK), and Gulf of Maine (GOM) (Fig. 1). Each subarea is characterized by distinct patterns of circulation and bathymetry (Sherman et al., 1983). The average annual cycle of abundance and its variation was portrayed for each subarea by plotting the monthly mean abundance of all samples with its 95% confidence interval bar. Individual survey mean abundance and its 95% confidence interval bar were then superimposed on the latter plot. Surveys where the error bar did not overlap the one from the average cycle were judged to be situations where abundance departed substantially from the average cycle. Only surveys, except the one noted below, that covered 75% or more of a subarea were included in the analysis of interannual variability. Statistical analyses, comparing individual survey means with the time series monthly mean were not undertaken because they require the assumption of independence.

Several surveys (see Table 1) prior to 1981 were conducted by foreign vessels that did not have permission to sample east of the U.S.-Canada maritime boundary line in the GBK and GOM subareas. Although areal coverage in these surveys was reduced approximately 40% in relation to complete surveys, I included them in the analysis of this study because the area undersampled was consistent and our surveys still provided adequate coverage of the depth strata found within the two subareas.

Spearman's rank correlation coefficients were calculated for monthly subsets of station data to measure the strength of the relationship within individual months between *Centropages hamatus* abundance and the following variables: surface temperature, bottom depth, and the average water-column values of temperature, salinity, and total chlorophyll. Initial distribution plots of *C. hamatus* revealed that species abundance has a strong onshore-offshore gradient. Thus, to control the effect of depth on the calculation, Spearman's partial correlation coefficients were calculated for monthly subsets where both abundance and the other variable were significantly ( $P < 0.05$ ) correlated to depth.

## Results

### Distribution and abundance

The time-series mean distribution charts by month for *Centropages hamatus* are presented in Figure 2, A and B. Immediately apparent is the persistent onshore-offshore abundance gradient throughout the study area. There are high concentrations of the copepod inshore and within the shoal waters of GBK. Abundance in offshore waters is always much lower. *Centropages hamatus* is found throughout most of the ecosystem at some time during the year, the only exception being certain areas of the eastern offshore waters of the GOM where it is absent year round.

The timing of the annual abundance cycle of *Centropages hamatus* was not consistent throughout the ecosystem. The population in southern reaches of the study area declines through the summer, nearly disappearing from the water column during early autumn (Fig. 3). In December dense concentrations of *C. hamatus* begin to appear close to shore in the MAB subarea. These inshore centers of abundance slowly enlarge and expand along the coast and over the central shoals of GBK with the northward progression of spring (Fig. 2, A and B). Thus, peak times of abundance in the designated subareas vary with latitude (Fig. 3): May in the MAB, June in SNE, July on GBK, and September in the GOM. The population becomes distributed over nearly the entire shelf of each subarea during the annual peak period of abundance. The distribution and monthly abundance figures clearly show that GBK is the area of highest abundance for *C. hamatus* within the northeast shelf ecosystem.

Distribution begins to constrict towards the shore in each subarea during the months approaching the annual period of low abundance (Fig. 2). Abundance estimates in the SNE, GBK, and GOM subareas decline slowly through the autumn and, unlike the MAB region, do not reach the annual low until winter (Fig. 3).

Interannual variation in abundance of *Centropages hamatus* is shown in Figure 4 and individual survey statistics are given in Table 1. Although no long-term temporal trends in abundance were evident within any of the subareas, population estimates in certain years were exceptional. For example, the copepod's abundance in both the MAB and SNE subareas was high for an extended period in 1984 (Fig. 4). Both of these areas also had high abundance during the spring of 1987 and low population estimates in 1982. Departures from the average annual cycle of abundance were not always continuous across these subareas; *C. hamatus* density was low during early

Table 1

*Centropages hamatus* abundance data for each subarea by survey. The asterisk indicates where survey operations were not completed past the US-Canadian maritime boundary. Abbreviation Key: MAB = Middle Atlantic Bight; GBK = Georges Bank; SNE = Southern New England; GOM = Gulf of Maine; Yr = year; no. = number of samples, Mid-day = survey midpoint (jday), Log mean = log (10) mean abundance, SE = standard error of the mean.

MAB					SNE					GBK					GOM				
Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE
77	30	86	2.59	0.33	77	29	74	1.95	0.29	77	19	49	0.16	0.11	77	30	123	0.00	0.00
77	30	140	2.90	0.32	77	46	133	1.89	0.24	77	32	80	0.46	0.15	77	25	308	0.87	0.24
77	30	238	0.16	0.11	77	36	242	1.29	0.27	77	23	114	1.71	0.30	77	27	315	0.18	0.12
77	30	293	0.09	0.09	77	30	300	1.34	0.25	77	31	147	1.18	0.28	78*	25	139	0.09	0.09
78	29	49	1.16	0.27	78	31	60	1.07	0.20	77*	24	219	3.38	0.25	78*	31	193	0.44	0.17
78	28	112	2.00	0.29	78	30	131	1.38	0.25	77	19	307	2.58	0.45	78	29	240	0.46	0.18
78	29	177	2.43	0.30	78	34	188	2.12	0.27	77	22	333	2.47	0.32	78*	31	286	1.49	0.23
78	31	227	0.72	0.25	78	31	233	1.25	0.25	78	28	49	1.33	0.20	78*	31	322	0.44	0.17
79	46	59	1.74	0.24	78	31	294	1.62	0.28	78	29	137	0.46	0.19	79	40	114	0.06	0.06
79	30	129	3.06	0.29	79	40	64	1.64	0.20	78	19	241	3.04	0.42	79	32	147	0.19	0.11
79	49	172	2.74	0.22	79	27	107	1.12	0.29	78	32	287	2.84	0.25	79*	37	240	1.13	0.22
79	46	226	0.59	0.18	79	27	134	2.30	0.29	79	30	94	0.80	0.23	79	32	297	0.51	0.20
79	31	280	0.17	0.12	79	44	188	2.13	0.23	79	20	143	0.80	0.29	79	47	331	0.17	0.10
80	49	64	1.35	0.23	79	37	232	0.59	0.21	79*	18	192	2.38	0.50	80*	34	54	0.29	0.14
80	47	111	2.66	0.23	79	27	290	1.41	0.28	79*	17	238	3.15	0.43	80*	33	178	0.38	0.17
80	48	147	2.52	0.23	80	43	70	1.98	0.18	79	29	296	2.66	0.31	80*	37	217	1.06	0.23
80	45	201	0.97	0.23	80	41	117	2.21	0.21	79	33	349	2.19	0.32	80	51	296	0.34	0.12
80	47	273	0.11	0.08	80	43	157	2.28	0.26	80*	20	62	1.49	0.35	81	53	52	0.13	0.07
80	40	327	0.66	0.22	80	40	207	2.56	0.22	80	29	88	1.32	0.30	81	46	146	0.44	0.14
81	48	82	1.82	0.24	80	43	282	0.38	0.15	80	28	123	1.46	0.34	81	40	339	0.19	0.11
81	43	90	2.08	0.30	80	44	341	1.08	0.23	80*	21	163	3.05	0.40	82	35	49	0.04	0.04
81	42	222	0.99	0.25	81	43	77	1.25	0.18	80*	20	215	3.13	0.36	82	48	124	0.13	0.08
81	43	271	0.00	0.00	81	44	103	1.39	0.23	80	30	293	1.68	0.33	82	37	156	0	0
82	35	80	1.75	0.27	81	35	162	2.07	0.25	80	30	353	1.49	0.29	82	49	302	0.50	0.17
82	44	81	2.60	0.26	81	33	191	2.75	0.29	81	26	66	0.29	0.14	82	52	334	0.44	0.15
82	29	157	1.62	0.31	81	30	228	1.80	0.35	81	20	96	0.92	0.30	83	53	26	0.25	0.09
82	34	214	1.29	0.28	81	38	284	1.43	0.26	81	24	115	1.63	0.32	83	38	116	0.46	0.13
82	38	268	0.55	0.19	82	40	75	1.62	0.19	81	24	157	1.57	0.40	83	55	167	0.68	0.15
83	36	53	1.33	0.28	82	34	100	1.25	0.25	81	31	196	3.34	0.32	83	46	306	0.22	0.11
83	39	78	2.05	0.27	82	44	146	1.44	0.21	81	52	296	2.36	0.25	83	31	349	0	0
83	46	149	2.60	0.18	82	39	198	2.58	0.20	81	32	335	1.71	0.32	84	47	14	0.20	0.10
83	33	212	0.31	0.13	82	24	285	1.86	0.38	82	29	64	0.47	0.18	84	40	112	0.20	0.12
83	43	268	0.07	0.07	82	43	348	1.20	0.21	82	36	109	1.22	0.22	84	54	151	0.36	0.11

continued on next page

spring 1979 in SNE (Fig. 4) and above average in the MAB (Table 1). There were no substantial upward abundance departures recorded on surveys of GBK and only one in the GOM (1978). This is probably due to the limited coverage the areas received during the peak periods of abundance (Fig. 4). There were several years in three of the subareas where survey mean abundance had substantial downward departures from the average annual cycle when *C. hamatus* was at or near its annual low (Fig. 4). These anomalies are probably not significant because log transformation increases the amplitude of low values. Plots of untransformed data

show little interannual variation between survey means during low periods of abundance.

### Correlation of abundance with other variables

**Bottom depth** *Centropages hamatus* abundance is negatively correlated to depth in all the subareas for most or all of the entire year (Table 2). Exceptions occur and correlations weaken during low periods of abundance in the MAB and GOM subareas when the copepod is present only at a few inshore locations.

Table 1 (continued)

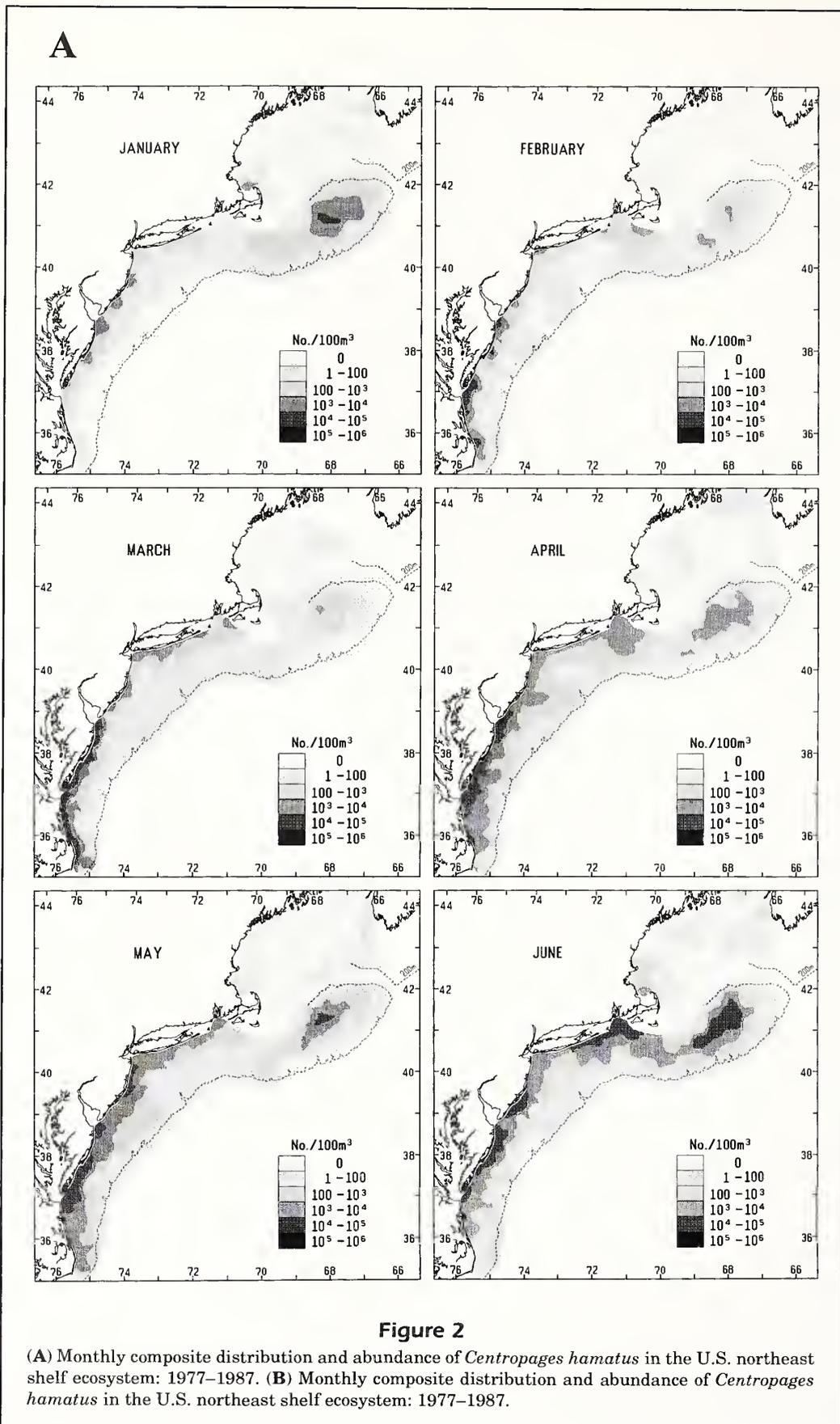
MAB					SNE					GBK					GOM				
Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE
83	48	323	0.75	0.19	83	29	41	1.44	0.27	82	29	140	0.66	0.23	84	50	298	0.59	0.15
84	40	37	1.31	0.26	83	29	91	2.14	0.24	82	34	208	2.82	0.30	85	29	99	0.21	0.13
84	41	71	1.96	0.30	83	41	158	2.84	0.26	82	31	295	2.57	0.29	85	44	260	0.97	0.20
84	48	133	3.32	0.16	83	38	222	2.74	0.28	82	29	323	2.52	0.30	85	37	306	0.29	0.14
84	38	193	2.12	0.31	83	38	278	0.96	0.27	83	28	21	1.55	0.32	85	56	340	0.21	0.09
84	51	198	2.39	0.28	83	42	334	1.28	0.20	83	32	104	1.70	0.33	86	50	39	0.18	0.08
84	31	211	1.24	0.29	84	43	26	1.07	0.20	83	30	163	2.37	0.32	86	44	112	0.23	0.11
84	37	264	0.51	0.20	84	38	83	1.55	0.23	83	36	233	2.69	0.36	86	39	154	0.49	0.17
84	47	309	0.46	0.17	84	42	138	2.75	0.19	83	37	292	1.95	0.29	86	32	262	1.21	0.27
85	38	35	1.22	0.28	84	31	189	3.19	0.23	83	28	340	2.10	0.26	86	45	303	0.59	0.16
85	36	66	1.69	0.30	84	31	205	3.28	0.25	84	29	21	1.88	0.24	87	42	115	0.48	0.14
85	51	110	2.50	0.26	84	35	221	2.07	0.25	84	37	95	0.90	0.21	87	56	155	0.57	0.15
85	51	142	2.64	0.26	84	34	272	0.83	0.26	84	32	146	1.73	0.32	87	55	259	0.92	0.18
85	32	209	0.34	0.14	84	42	318	0.48	0.16	84	25	210	4.95	0.11	87	40	295	0.85	0.21
85	51	245	0.30	0.09	85	50	29	1.00	0.20	84	37	227	3.33	0.27					
85	26	277	0.17	0.12	85	29	79	1.57	0.27	84	35	284	2.37	0.28					
85	47	314	0.21	0.12	85	42	100	1.55	0.24	84	31	334	2.12	0.30					
86	46	12	0.60	0.18	85	43	137	1.93	0.26	85	31	14	2.08	0.25					
86	42	68	1.99	0.27	85	48	214	2.37	0.26	85	27	86	1.56	0.29					
86	46	133	2.37	0.29	85	44	254	1.32	0.24	85	31	94	1.20	0.29					
86	45	175	2.40	0.28	85	33	289	0.97	0.24	85	32	132	2.01	0.35					
86	41	217	0.73	0.20	85	42	323	0.79	0.18	85	45	235	2.78	0.29					
86	47	243	0.15	0.08	86	43	22	0.85	0.17	85	36	258	2.02	0.35					
86	40	263	0.06	0.06	86	31	88	2.41	0.27	85	32	297	1.76	0.34					
86	47	311	0.11	0.08	86	41	138	2.48	0.24	85	29	328	2.00	0.35					
87	47	10	1.45	0.24	86	31	189	2.88	0.31	86	31	35	2.17	0.28					
87	46	87	2.74	0.25	86	37	213	1.51	0.27	86	25	102	1.75	0.37					
87	51	105	3.53	0.15	86	42	252	1.29	0.24	86	31	150	1.95	0.30					
87	58	129	2.90	0.20	86	36	278	0.96	0.24	86	24	197	4.63	0.20					
87	29	193	1.27	0.31	86	43	316	1.56	0.23	86	36	237	3.70	0.23					
87	48	234	0.79	0.19	87	42	28	1.68	0.20	86	31	260	2.62	0.31					
87	37	261	0.27	0.11	87	37	100	2.45	0.24	86	26	293	2.14	0.32					
87	46	311	0.35	0.13	87	38	110	2.97	0.19	86	31	328	1.68	0.29					
					87	53	134	1.55	0.24	87	30	37	1.74	0.24					
					87	46	149	1.84	0.23	87	26	113	1.31	0.29					
					87	37	199	1.23	0.24	87	30	140	1.48	0.30					
					87	43	239	0.98	0.21	87	37	217	2.70	0.31					
					87	36	273	1.39	0.27	87	29	248	3.05	0.35					
					87	43	323	0.75	0.18	87	31	280	1.86	0.30					
										87	29	342	1.17	0.27					

**Temperature** *Centropages hamatus* was found at station locations where surface temperatures ranged from  $-0.5^{\circ}\text{C}$  to  $28.7^{\circ}\text{C}$  and where the average water column temperatures were between  $0.2$  and  $24.6^{\circ}\text{C}$ . Although the copepod can tolerate a wide range of temperatures, abundance was greatest at stations where surface temperature ranged from  $12$  to  $17^{\circ}\text{C}$  (Fig. 5A).

The relationship between surface temperature and the annual abundance cycle is shown in Figure 3. Rising temperatures in the MAB during summer may be responsible for a rapid decline of *Centropages hamatus* there. The population nearly disappears during late

summer as surface temperature reaches annual maximums. The July correlation coefficient between variables indicates a strong inverse relationship ( $P < 0.01$ ). *Centropages hamatus* density remains low until the mean surface temperature falls below  $15^{\circ}\text{C}$  in December. Abundance in the more northern subareas slowly declines after the annual temperature high is reached. Unlike that for the population in the MAB, abundance in these subareas does not increase as temperatures decline in the fall, but only with spring warming (Fig. 3).

Monthly correlations between *Centropages hamatus* station abundance and temperature variables



**B**

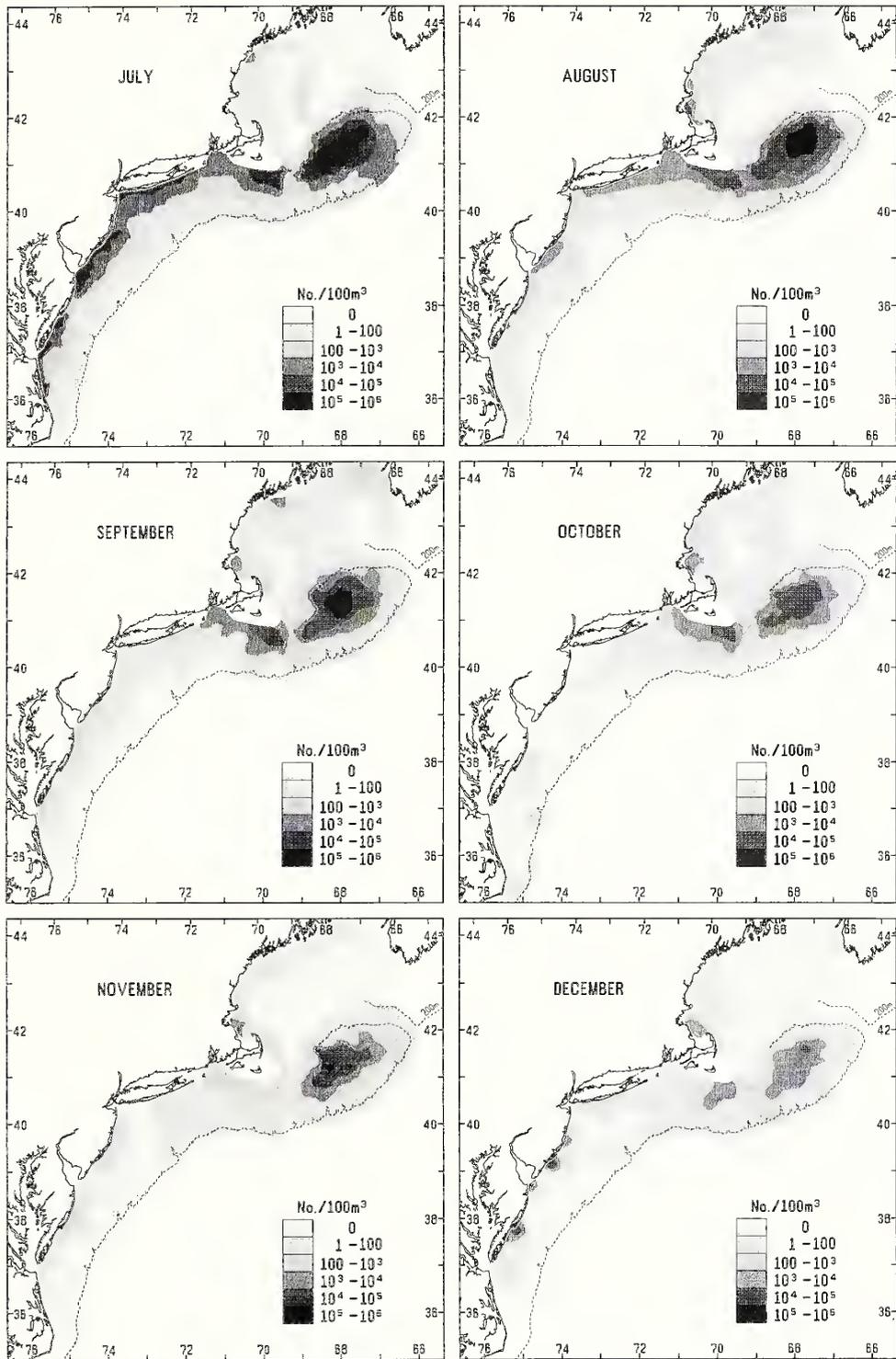
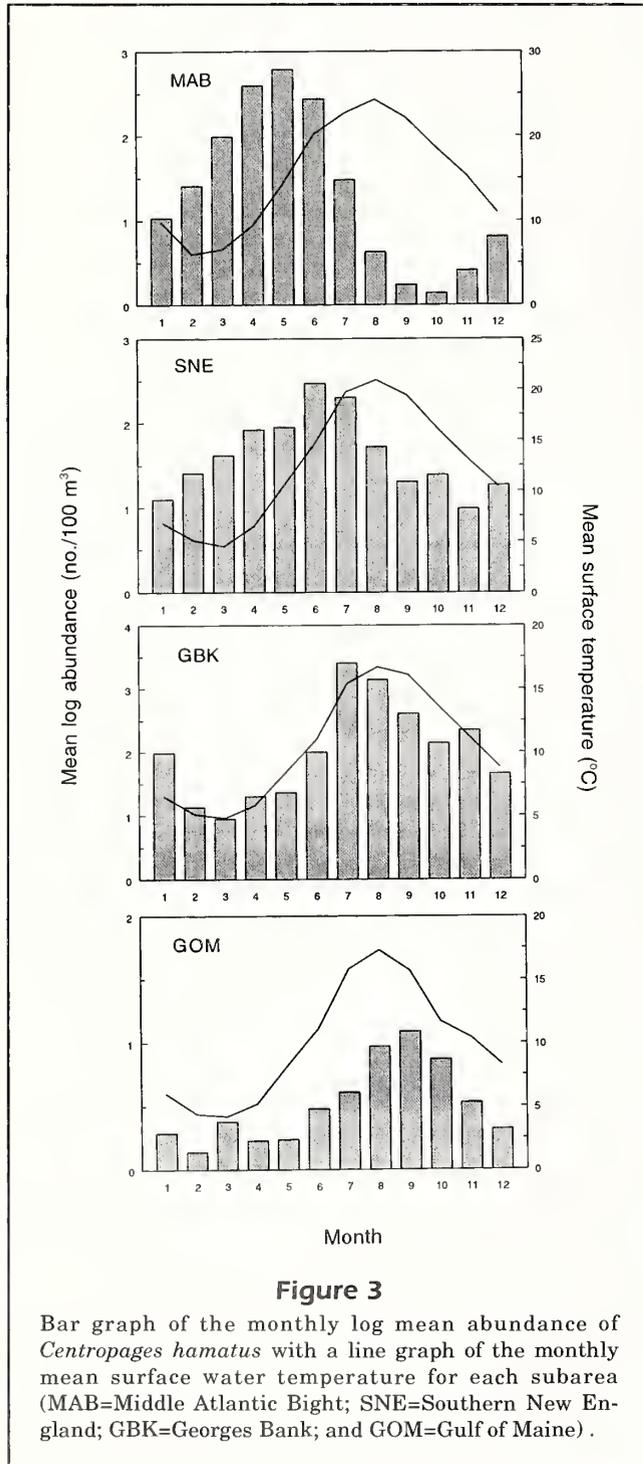


Figure 2 (continued)

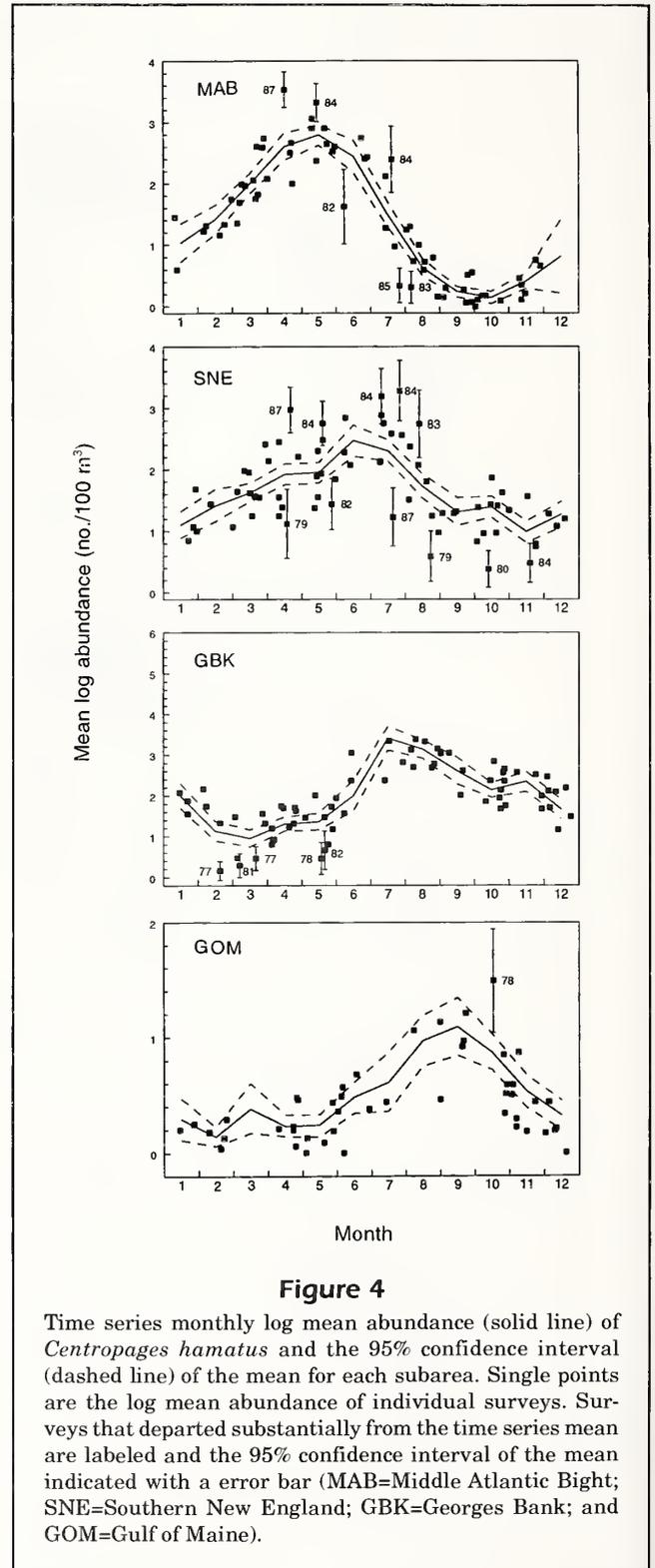
were significant ( $P < 0.05$ ) during certain months in each of the subareas (Table 2). Significant relationships persisted between *C. hamatus* density and a temperature variable for several extended periods. Surface temperature was negatively correlated with abundance from November to March in the MAB subarea and also from June to February in SNE

waters. Abundance in the GBK subarea was positively correlated to average water-column temperatures from May to July and with bottom temperatures from September to December. In the GOM sub-



**Figure 3**

Bar graph of the monthly log mean abundance of *Centropages hamatus* with a line graph of the monthly mean surface water temperature for each subarea (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).



**Figure 4**

Time series monthly log mean abundance (solid line) of *Centropages hamatus* and the 95% confidence interval (dashed line) of the mean for each subarea. Single points are the log mean abundance of individual surveys. Surveys that departed substantially from the time series mean are labeled and the 95% confidence interval of the mean indicated with a error bar (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).

area there were no strong correlations for extended periods between variables.

**Chlorophyll** Estimates of the abundance of *Centropages hamatus* were highest at locations where chlorophyll biomass was also high (Fig. 5B). Total chlorophyll and abundance measures at stations were significantly ( $P < 0.01$ ) correlated during certain times of the year in all subareas (Table 2). In the MAB, variables were posi-

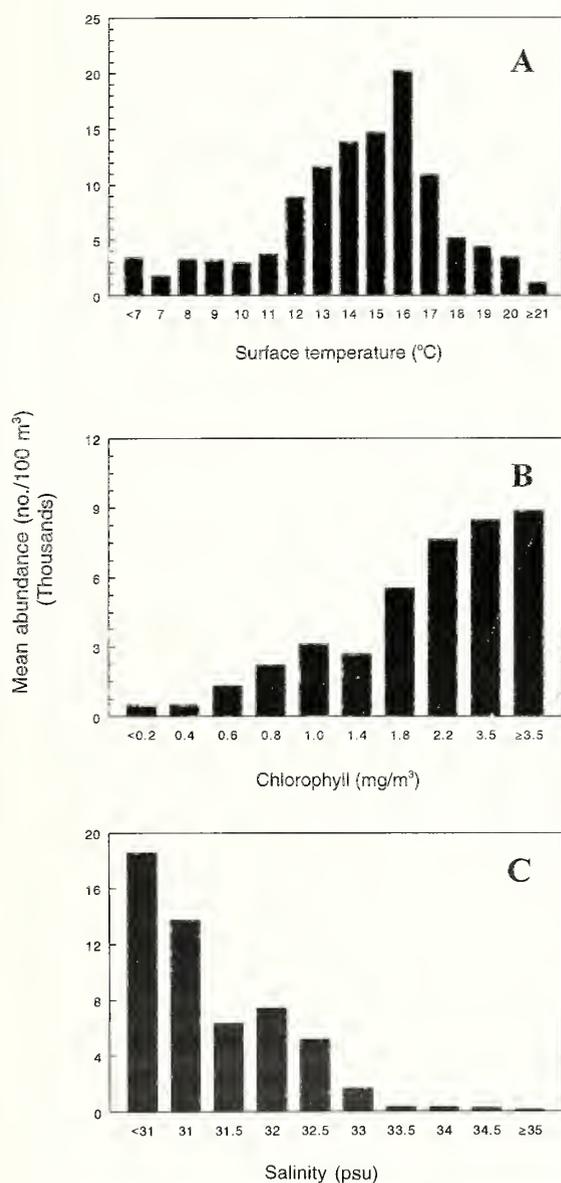
tively correlated from May through July and, in SNE waters, during October and February. Variables on GBK were positively correlated from May through January, except for October. GOM correlations were significantly positive in August, November, and December.

Partitioning of total chlorophyll values into netplankton and nanoplankton size fractions did not typically change the correlation coefficients between *Centropages hamatus* and phytoplankton abundance listed in Table 2. There were a few scattered months in the subareas where coefficients with netplankton were 0.1–0.2 units higher. The most substantial change occurred during October on GBK. The correlation coefficient with netplankton was 0.27 units above the value in Table 2 and was positively correlated ( $P = 0.02$ ).

**Salinity** *Centropages hamatus* was present at stations where integrated water-column salinity ranged from 27.09 to 36.00 psu. Maximum abundance occurred in the lower region of this range (Fig. 5C). Monthly correlation coefficients between station abundance and salinity were usually negative and oftentimes significant during the year (Table 2). Notable were the comparatively high negative correlations found during January in both the MAB and SNE subareas. Values in the MAB were also negatively correlated in February and again in August and September. SNE correlations were also significantly negatively correlated during April, July, and from September through December. GBK correlations, though not always significant, were positive from February through July and negative in the remaining six months. GOM coefficients were generally weak throughout the year.

**Predation Pressure** On average, *Centropages hamatus* and ctenophores both reach peak abundance during June in the SNE subarea (Figs. 3 and 6). During June and July of 1981 a large patch (9–12 stations) of ctenophores occupied inshore waters in the southern region of the subarea offshore of Long Island, New York. This concentration pushed overall mean abundance in the subarea to an 11-year high (Fig. 6). Predation on *C. hamatus* was apparently minimal; its mean abundance in late spring 1981 was slightly above the 11-year average (Table 1; Fig. 3). However, the abundance of *C. hamatus* in June within a ctenophore patch was much lower ( $611/100\text{m}^3$ ) than outside ( $2,712/100\text{m}^3$ ) it. Evidence for predation pressure was also found in the July survey; *C. hamatus* density was  $8,138/100\text{m}^3$  where it co-occurred with ctenophores,  $22,871/100\text{m}^3$  where ctenophores were absent.

In the SNE subarea, the omnivorous copepod *Centropages typicus* is present at relatively high lev-



**Figure 5**

Mean abundance of *Centropages hamatus* by (A) surface temperature, (B) chlorophyll, and (C) salinity interval. All time series data from the entire survey area was used.

Table 2

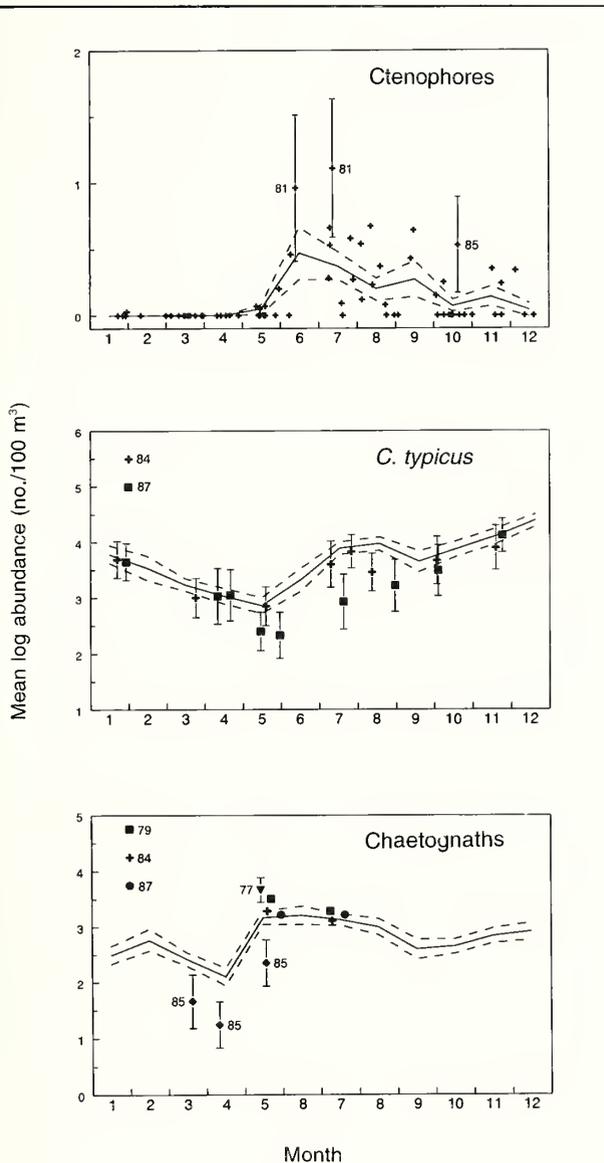
Summary of correlation analysis between abundance and the different environmental variables. An asterisk indicates where partial correlation coefficients were used. Abbreviation key: temp. = temperature; chl. = chlorophyll; no. = number of observations;  $r$  = spearman correlation coefficient;  $P$  = probability that correlation is zero; MAB = Middle Atlantic Bight; SNE = Southern New England; GBK = Georges Bank; GOM = Gulf of Maine.

Area	Month	Bottom Depth			Surface temp.			Column temp.			Bottom temp.			Column salinity			Total chl.		
		no.	$r$	$P$	no.	$r$	$P$	no.	$r$	$P$	no.	$r$	$P$	no.	$r$	$P$	no.	$r$	$P$
MAB	1	93	-0.54	<0.01	89	-0.45	<0.01*	93	-0.47	<0.01*	90	-0.48	<0.01*	93	-0.54	<0.01*	0		
	2	190	-0.63	<0.01	190	-0.23	<0.01*	145	-0.33	<0.01*	139	-0.33	<0.01*	146	-0.40	<0.01*	146	-0.01	0.89*
	3	434	-0.65	<0.01	432	-0.11	0.03*	148	0.05	0.55*	139	0.05	0.60*	148	-0.18	0.03*	161	0.16	0.04
	4	223	-0.65	<0.01	218	-0.02	0.77	67	0.12	0.35	66	0.05	0.68	67	0.09	0.45*	75	0.05	0.64
	5	352	-0.68	<0.01	350	0.01	0.82	278	-0.05	0.41*	266	-0.02	0.78*	278	-0.21	<0.01*	197	0.24	<0.01*
	6	162	-0.64	<0.01	161	-0.03	0.75	75	-0.12	0.29*	73	-0.12	0.31*	75	-0.17	0.16*	79	0.25	0.03*
	7	290	-0.50	<0.01	287	-0.42	<0.01*	19	0.30	0.23*	19	0.30	0.21	19	-0.41	0.09*	70	0.38	<0.01*
	8	354	-0.22	<0.01	352	-0.01	0.98*	146	-0.18	0.04*	143	-0.18	0.04*	146	-0.30	<0.01*	77	0.18	0.12*
	9	313	-0.20	<0.01	306	0.01	0.89	93	-0.09	0.37*	86	-0.24	0.03*	93	-0.28	<0.01*	38	0.20	0.24*
	10	128	-0.04	0.70	127	0.12	0.19	73	0.18	0.14	69	0.17	0.16	73	-0.04	0.76	80	-0.02	0.84
	11	278	-0.36	<0.01	278	-0.24	<0.01	266	-0.23	<0.01	257	-0.20	<0.01	266	-0.08	0.17*	117	0.08	0.38*
	12	27	-0.69	<0.01	27	-0.31	0.12*	26	-0.21	0.32*	25	-0.22	0.31*	26	-0.23	0.27*	27	-0.12	0.56*
SNE	1	146	-0.34	<0.01	146	-0.41	<0.01*	145	-0.44	<0.01*	132	-0.43	0.01*	145	-0.52	<0.01*	64	-0.29	0.02*
	2	92	-0.39	<0.01	92	-0.29	<0.01*	63	0.08	0.56*	57	0.02	0.90*	63	-0.03	0.82*	66	0.25	0.05*
	3	339	-0.33	<0.01	336	-0.01	0.98*	175	-0.11	0.14*	165	-0.09	0.27*	175	-0.09	0.22*	205	-0.04	0.59*
	4	314	-0.42	<0.01	282	0.07	0.24*	61	-0.35	<0.01*	56	-0.35	0.01*	61	-0.49	<0.01*	58	-0.23	0.09*
	5	371	-0.51	<0.01	365	0.08	0.15	245	0.14	0.03*	230	0.23	<0.01*	241	-0.02	0.81*	167	0.17	0.03*
	6	146	-0.56	<0.01	146	-0.30	<0.01*	119	-0.07	0.46	110	0.06	0.55	119	-0.16	0.08*	123	0.01	0.95*
	7	343	-0.66	<0.01	343	-0.27	<0.01*	66	0.22	0.08*	63	0.24	0.06	66	-0.34	<0.01*	107	-0.05	0.63*
	8	289	-0.32	<0.01	286	-0.36	<0.01	89	-0.01	0.90*	89	0.09	0.39*	89	-0.14	0.21*	68	0.09	0.48*
	9	188	-0.33	<0.01	176	-0.44	<0.01*	104	-0.28	<0.01*	101	0.14	0.18*	104	0.28	<0.01*	14	0.52	0.06
	10	354	-0.27	<0.01	327	-0.58	<0.01*	113	-0.33	<0.01*	106	0.10	0.34*	113	-0.24	<0.01*	133	0.20	0.02*
	11	225	-0.15	0.03	224	-0.36	<0.01*	205	-0.31	<0.01*	191	-0.22	<0.01	205	-0.14	0.05*	76	0.11	0.37*
	12	160	-0.22	<0.01	158	-0.22	<0.01*	146	-0.16	0.06*	139	-0.02	0.78*	146	-0.37	<0.01*	141	0.01	0.91*
GBK	1	100	-0.69	<0.01	100	-0.14	0.17	71	0.24	0.05*	61	0.24	0.07*	71	-0.04	0.77*	72	0.28	0.02*
	2	104	-0.42	<0.01	103	0.38	<0.01*	54	0.52	<0.01*	45	0.50	<0.01*	54	0.24	0.08*	12	0	0
	3	152	-0.51	<0.01	148	0.03	0.70*	75	0.01	0.92*	66	-0.16	0.21	75	0.22	0.06*	92	-0.10	0.34*
	4	292	-0.53	<0.01	287	0.13	0.03	53	0.19	0.18*	46	0.22	0.15*	53	0.23	0.10*	28	0.31	0.10
	5	250	-0.61	<0.01	241	0.16	<0.01*	171	0.33	<0.01	153	0.30	<0.01	171	0.27	<0.01*	134	0.45	<0.01*
	6	97	-0.64	<0.01	93	-0.02	0.88*	69	0.40	<0.01*	58	0.45	<0.01*	69	0.14	0.26*	63	0.30	0.02*
	7	163	-0.64	<0.01	161	-0.29	<0.01*	31	0.47	<0.01*	30	0.37	0.05*	31	0.18	0.35*	42	0.36	0.02*
	8	250	-0.67	<0.01	242	-0.19	<0.01*	28	0.04	0.83*	25	0.03	0.91*	28	-0.55	<0.01*	48	0.33	0.03*
	9	124	-0.73	<0.01	108	-0.21	0.03	96	0.19	0.07*	87	0.33	<0.01*	96	-0.16	0.12*	23	0.47	0.03*
	10	393	-0.62	<0.01	388	0.21	<0.01	63	0.12	0.37*	55	0.42	<0.01*	63	-0.41	<0.01*	78	-0.01	0.99*
	11	194	-0.73	<0.01	194	0.11	0.14*	151	0.09	0.29	138	0.21	<0.01	151	-0.13	0.13*	94	0.21	0.04*
	12	165	-0.62	<0.01	152	0.36	<0.01	135	0.31	<0.01	114	0.30	<0.01	135	-0.12	0.16*	95	0.38	<0.01*
GOM	1	95	-0.12	0.26	95	0.01	0.95	59	-0.05	0.70	42	-0.13	0.40	59	-0.06	0.65	8	-0.25	0.55
	2	204	-0.23	<0.01	193	-0.01	0.95*	136	-0.04	0.62*	79	-0.05	0.64*	136	0.06	0.49*	99	0.18	0.07*
	3	70	-0.24	0.05	70	0.06	0.64	48	0.04	0.81	29	-0.05	0.80	48	-0.01	0.96	63	0.12	0.35
	4	288	-0.10	0.08	257	-0.01	0.97	19	-0.13	0.58	10	-0.12	0.74	19	-0.26	0.28	17	-0.22	0.40
	5	278	-0.22	<0.01	251	0.04	0.52*	136	0.17	0.54	84	0.36	<0.01*	136	0.06	0.46*	113	-0.01	0.91*
	6	245	-0.35	<0.01	244	0.10	0.11	189	0.10	0.17	105	-0.31	<0.01	149	-0.13	0.11*	52	-0.16	0.25
	7	75	-0.19	0.10	74	0.07	0.54	37	0.07	0.69	30	0.06	0.75	37	-0.11	0.52	45	0.19	0.20
	8	172	-0.40	<0.01	162	-0.06	0.45*	48	0.25	0.09*	46	0.21	0.17	48	-0.22	0.14*	93	0.25	0.01*
	9	155	-0.28	<0.01	145	<0.01	0.99*	135	-0.09	0.29*	114	-0.20	0.03*	135	-0.12	0.16*	23	-0.06	0.80
	10	307	-0.18	<0.01	302	0.10	0.09*	100	-0.01	0.89*	54	-0.02	0.91*	100	-0.15	0.13*	118	0.08	0.40
	11	274	-0.42	<0.01	272	0.18	0.01*	93	0.20	0.06*	65	0.10	0.42*	93	-0.27	<0.01*	93	0.29	<0.01
	12	274	-0.29	<0.01	269	0.05	0.42*	251	0.05	0.44	167	-0.07	0.38*	251	-0.02	0.72*	107	0.24	0.01

els year round and begins to increase inshore from its annual low in late spring-early summer (Fig. 6) when *Centropages hamatus* is at peak abundance. MARMAP data indicate that it is unlikely that the summer decline or the abundance levels reached by *C. hamatus* are controlled substantially by *C. typicus* predation. There was no strong inverse relationship

between the abundance trends of the two species. For example, in 1987 *C. hamatus* reached peak abundance earlier than usual, in late April, and declined rapidly to below average levels (Table 1). The abundance of *C. typicus* was average in late April 1987 and also declined through the summer to below average levels (Fig. 6). High levels of *C. hamatus* recorded in 1984 (Fig. 4) were not due to the absence of *C. typicus* predators; abundance was close to average for the copepod during spring and summer (Fig. 6). Monthly partial correlation coefficients between station abundance values of the two species during the time series were positive (0.07–0.24) from April through August, further evidence that predation by *C. typicus* is minimal.

Peaks of *Centropages hamatus* abundance and the presence of chaetognaths do coincide in the SNE subarea (Figs. 3 and 6). However, evidence that chaetognathan predation impacts *C. hamatus* abundance could not be found. All of the surveys that had exceptional high or low *C. hamatus* abundance, 1979, 1984, and 1987 (Fig. 4), had near average chaetognath density (Fig. 6). Conversely, *C. hamatus* abundance was close to average when chaetognath density was high in 1977 and low in 1985 (Fig. 6). Monthly partial correlation coefficients between station abundance values of the two species were not significant and very low (–0.10–0.25) throughout the year, indicating that chaetognath predation has little effect on *C. hamatus* abundance.



**Figure 6**

Time series monthly log mean abundance (solid line) and the 95% confidence interval (dashed line) of the mean for the following copepod predators in the Southern New England subarea: ctenophores, the copepod *Centropages typicus*, and chaetognaths. Single points are the log mean abundance of the taxon for individual surveys during certain years. The error bars indicate the 95% confidence interval of the mean.

## Discussion

Temperature affects most processes in marine ecosystems and the life cycle of *Centropages hamatus* is no exception. Opposite extremes in temperature appear to limit the seasonal occurrence of the population at the southern and northern ends of the ecosystem. Warm summer temperatures in the MAB were correlated with the rapid decline of the copepod in this area as values approach or surpass the critical upper thermal level for the species. Similar relationships between temperature and *C. hamatus* were found by Deevey (1960) for the population present near and within Delaware Bay. She reported that the copepod disappears as temperatures rise in summer but is present year round in small numbers during cool summers. Grant (1988) also reported that *C. hamatus* abundance in the MAB declines with increasing temperature and is absent in some years during summer and fall seasons. The MAB population begins to reappear or increase close inshore in late autumn where waters cool faster than those offshore. Populations farther north decline slowly as

winter approaches until only small aggregations of cold-adapted individuals overwinter in the far eastern waters along the SNE coast, on the central shoals of GBK, and within inshore waters in the GOM. Abundance in these areas increase as temperatures rise in spring.

The life cycle of many marine copepods involves the production of resting eggs that allow the species to repopulate areas when environmental conditions again become favorable (Uye, 1985). Evidence that *Centropages hamatus* produce resting eggs has been found in the western North Atlantic (Lindley, 1990), the Gulf coast of Florida (Marcus, 1989), and in the MARMAP survey area on GBK (Davis, 1987). Although this report provides no direct evidence that *C. hamatus* produces resting eggs, it seems unlikely that the small pelagic population that overwinters, or oversummers, could produce the great abundance of the next generation without recruitment from benthic resting eggs. Marcus (1989) found that a *C. hamatus* population residing in a subtropical embayment area produces diapause eggs that allow the species to survive warm summer temperatures. This also likely occurs in the MAB when the population rapidly declines to a few individuals, or disappears entirely during summer, and begins to increase as temperatures decline in winter. Lower maximum temperatures observed on GBK are apparently not sufficiently high to impact populations there dramatically; abundance declines slowly during autumn after peak abundance is reached in summer and does not increase until temperatures rise in early spring. This slow decline in abundance may occur because success of egg hatching decreases as females gradually switch from subitaneous egg production to resting egg production owing to decreasing temperatures and daylengths, as was found for the copepod *Labidocera aestiva* in nearby waters (Marcus, 1982). The resting eggs hatch in the spring to supplement the production of overwintering late-stage copepodites and to ensure the success of the population. Such variation in egg production between well-separated populations has been reported for other species (Marcus, 1984; Uye, 1985). Somewhere in the SNE subarea there is probably a transition zone between adults that are "temperature shocked" to release quiescent eggs and those that slowly change their egg-laying strategy as autumn progresses. Egg-production strategy in the GOM is probably similar to that found in the GBK.

The strongly negative correlation of *Centropages hamatus* abundance to depth and its well-defined inshore-offshore abundance gradient confirm the importance of resting eggs in the life history of this species. Environmental conditions probably do not trigger the release of diapause eggs until after the

population constricts inshore after peak abundance is reached. Evidence for this was found by Lindley (1990) in southern waters of Great Britain where *C. hamatus* eggs were found to be abundant only in depths of less than 50 m. When the eggs hatch, the prevailing westerly winds in the northwest Atlantic slowly spread the pelagic population and the new recruits offshore to establish the characteristic abundance gradient of this species.

Abundance of *Centropages hamatus* appears to be related strongly to the availability of phytoplankton. The copepod's abundance was highest at stations where chlorophyll values were high, and its distribution is similar to phytoplankton gradients in the study area (O'Reilly and Busch, 1984). However, correlation coefficients between variables were weak and inconsistent among subareas, indicating that the species is not particularly sensitive to phytoplankton availability. The low correlation may be because average water-column chlorophyll measurements are static measures that may not reflect the actual food concentrations that are, or were, available to the copepod over the previous 24 hours. Furthermore, it is also possible that late-stage copepodites of this omnivorous species may be more sensitive to zooplankton prey concentrations. Nonetheless, food availability is a key limiting factor throughout nature and certainly has a major role in shaping the life history of this copepod. The maximum mean abundance of *C. hamatus* is greatest on GBK, the ecosystem subarea with the largest estimate of annual primary production (O'Reilly et al., 1987). Conversely, population density is lowest in the GOM where average chlorophyll concentrations are also lowest.

Monthly correlation coefficients between salinity and abundance of *Centropages hamatus* were also weak even though both variables have a strong offshore gradient. Unlike chlorophyll correlations, these coefficients portray accurately the relationship between variables. *Centropages hamatus* is a coastal species with a wide latitudinal range and must tolerate wide environmental fluctuations. It has been reported in areas with salinity as low as 6 psu (Hernroth and Ackefors, 1977), as well as in Mediterranean waters where salinity exceeds 36 psu (Gaudy, 1971). The large numbers of *C. hamatus* associated with low salinity found in this study is probably an artifact of the high phytoplankton concentrations found in a narrow inshore band along the MAB and SNE coasts (O'Reilly et al., 1987). The annual spring increase in precipitation and subsequent river runoff that leads to lowered salinity in the MAB and SNE subareas (Manning, 1991) also introduces nutrient-enriched water that stimulates phytoplankton growth and zooplankton production. Further-

more, the highest mean abundance of *C. hamatus* is found over the central shoals of GBK where salinity usually ranges from 32.2 to 32.7 psu during peak abundance, well above the coastal areas where abundance, on average, is much lower. High salinity offshore may effect *C. hamatus* production there and restrict its distribution, but it is more likely that low offshore abundances are caused by low phytoplankton food stocks that cannot support an overwintering population or the generation that produces resting eggs after peak abundance is reached.

There was no strong evidence from survey data that predation affects interannual variability or causes the seasonal decline of the population in the SNE subarea. Ctenophores appear to lower *Centropages hamatus* abundance when they are plentiful, but this occurred only during one year and in a restricted area. Chaetognaths and the copepod *Centropages typicus* also appear to have little effect on *C. hamatus* density. Clearly, however, a dedicated study analyzing stomach contents and the vertical distribution of the predator-prey field is needed to define the actual food web. Potential predators such as squid, juvenile fish, and populations of planktivorous adult fish must also be considered in order to fully define the role predation has in controlling *C. hamatus* population levels.

Lindley and Hunt (1989) examined the distribution of *Centropages hamatus* to the north and across the Atlantic to the North Sea. They described a life cycle similar to the one reported in this paper and speculated that the autumn decline in abundance is caused by the pressure of competition with *Centropages typicus* for food resources. Dagg and Turner (1982) studied copepod populations in the SNE and GBK subareas during autumn and calculated that copepod grazers may consume entire phytoplankton stocks. If true, high abundance of *C. typicus* could impact population levels of *C. hamatus*. However, MARMAP survey data indicate that high *C. typicus* abundance does not lead to an early decline of *C. hamatus* in either subarea. For example, in 1985 on GBK, median *C. typicus* abundance was 2–3 orders of magnitude above the ten-year average, but *C. hamatus* was also above average and increased in late autumn (Kane, 1993). Data presented in this report also show that the abundance of the two species are not related in the SNE subarea. Although competition pressure between the two species does not appear to cause the decline of *C. hamatus*, laboratory feeding experiments are needed to measure the effect of low food levels on species abundance.

The copepod *Centropages hamatus* has evolved a unique life history to survive and reproduce within the waters of the northwestern Atlantic continental

shelf. The population has a distinct seasonal cycle with peak abundance occurring in shallow areas where phytoplankton food stocks are rich and surface temperature ranges from 12 to 17°C. Predation pressure appears minimal, and *C. hamatus* abundance peaks between the annual maximum of early spring and autumn dominant copepod species (Sherman et al., 1983), thus reducing competition pressure for food resources. *Centropages hamatus* likely produces resting eggs that hatch and help repopulate the ecosystem when environmental conditions are favorable. Comprehensive laboratory and shipboard experiments are needed to distinguish how the above biotic and abiotic factors interact to determine the annual success of the population.

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**Abstract.**—Trawl surveys of hoki, *Macruronus novaezelandiae* (Hector) in the Southland and subantarctic areas (Southern Plateau) of New Zealand's Exclusive Economic Zone were carried out in May 1992 and 1993. The proportion of females of each age that would spawn in the coming spawning season (July–August) was estimated on the basis of histological analysis of gonad samples and ageing data. Comparisons were made between numbers of fish at age in these surveys and numbers of fish at age in surveys in November–December 1991 and 1992 to estimate migration before May.

The results indicate that 66% (standard error [SE] of 3%) of females age 7 and over that were on the Southern Plateau in May 1992 would spawn in winter 1992, compared with 65% (SE 2%) in 1993. If the number of hoki estimated to have already migrated out of the survey area in May are included as prespawners, then up to 67% (SE 5%) of adult females were predicted to spawn in winter 1992 and 82% (SE 3%) in winter 1993.

This study confirms that the proportion of adult hoki that spawn in a given year is substantially less than 1. It is not known how much this varies, whether it is with or without trend, or whether it is correlated with any environmental variables. Fishery indicators such as stock and fishery risk are particularly sensitive to the annual proportion of adult hoki that spawn, and it is possible that its variation could obscure any underlying stock-recruitment relationship.

## Estimating the annual proportion of nonspawning adults in New Zealand hoki, *Macruronus novaezelandiae*

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Hoki (*Macruronus novaezelandiae* Hector) form New Zealand's largest commercial fishery with an annual catch of about 200,000 metric tons (t). The fish are widely distributed throughout New Zealand's 200-mile Exclusive Economic Zone in depths of 50–800 m, but most commercial fishing is at depths of 200–800 m around the South Island (Fig. 1). Fishing effort is greatest during the July–August spawning season off the west coast and in Cook Strait but also occurs on the Chatham Rise and management areas south of Puysegur Point (hereafter referred to as the Southern Plateau) (Fig. 1) throughout the rest of the year.

Although managed as a single stock, hoki are assessed annually as two stocks (Sullivan and Cordue<sup>1</sup>; Sullivan et al.<sup>2</sup>). There is no genetic evidence for a split, but because morphometric and growth rate differences have been found between the two spawning grounds (Horn and Sullivan, 1996; Livingston and Schofield, 1996), a cautious approach in determining yield has been taken. Hoki are assessed as two stocks by using stock reduction models (Sullivan et al.<sup>2</sup>). Abundance indices estimated from acoustic surveys, trawl surveys, and catch-per-unit-of-effort data on the spawning grounds have been the main inputs to the models (Sullivan et al.<sup>2</sup>).

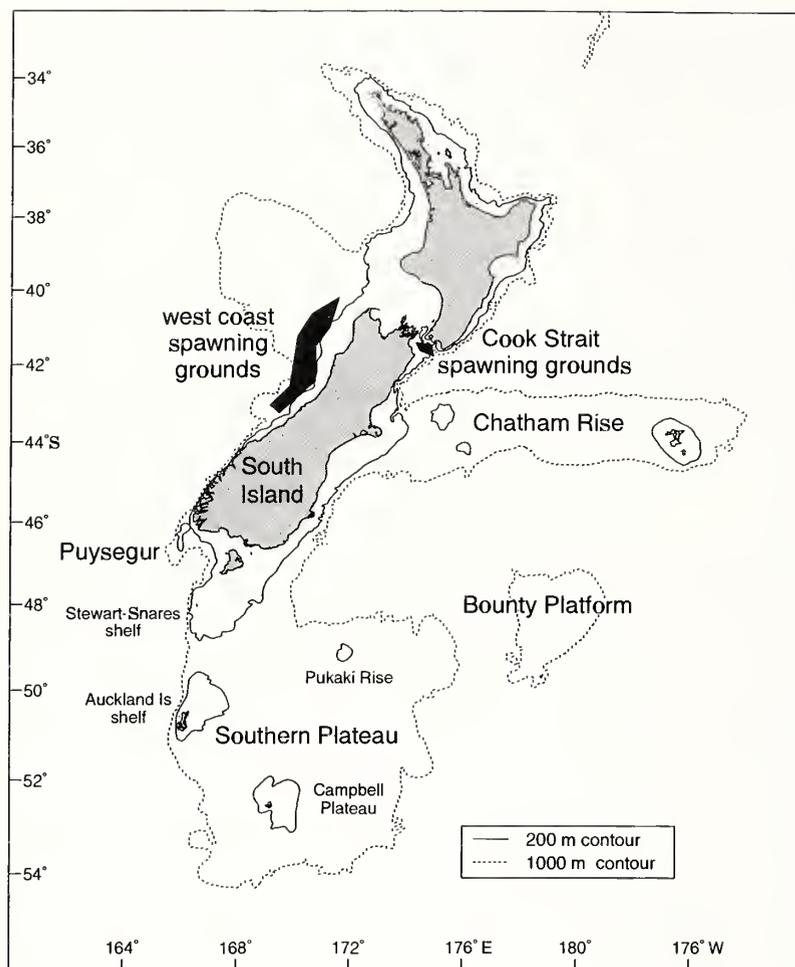
Of the two stocks, the western stock, which resides primarily on the Southern Plateau and spawns off the west coast of the South Island, is substantially larger than the eastern stock, which resides primarily on the Chatham Rise and spawns in Cook Strait. Juvenile hoki (2–5 yr) of both stocks appear to reside and mix together on the Chatham Rise in relatively shallow water. As the fish reach maturity, it is assumed that they recruit to their respective stocks.

Winter surveys of the Southern Plateau and Chatham Rise have shown that significant numbers of mature-size hoki, both males and females, do not partake in the spawning migration in a given year (Livingston et al., 1991; Hurst and Schofield, 1995).

From trawl surveys of the Southern Plateau in July–August and November–December 1990, it was estimated that the ratio of recruited

<sup>1</sup> Sullivan, K. J., and P. L. Cordue. 1992. Stock assessment of hoki 1992. New Zealand Fisheries Assessment Res. Document 92/12, NIWA Greta Point library, Wellington, New Zealand, 43 p.

<sup>2</sup> Sullivan, K. J., P. L. Cordue, and S. L. Ballara. 1995. A review of the 1992-93 hoki fishery and assessment of hoki stocks for 1994. New Zealand Fisheries Assessment Research Document 95/5, NIWA Greta Point library, Wellington, New Zealand, 45 p.



**Figure 1**

Map of New Zealand showing spawning and feeding grounds of hoki, *Macruronus novaezelandiae*.

biomass of western stock hoki present in winter to the recruited biomass of western stock hoki present in summer was 1:2.05 (Hurst and Schofield, 1995). Hurst and Schofield concluded that the total proportion of adult hoki that spawned in 1990 was between 60% and 75%.

The annual proportion of adult hoki that spawn was incorporated into the stock reduction analysis of hoki as a model parameter for the first time in 1992 (Sullivan and Cordue, 1992). A sensitivity analysis of the response of fishery indicators, such as stock and fishery risk to changes in various model parameters, found that they were particularly sensitive to the proportion of hoki that spawn in a given year (Sullivan and Cordue<sup>1</sup>). In view of this sensitivity, a research program, to estimate more accurately the annual proportion of hoki that spawn and the maturity ogive of hoki at age in the western stock, was initiated.

The spawning season for hoki begins in late June and can extend into mid-September (Sullivan et al.<sup>2</sup>).

Large fish tend to spawn earlier than smaller fish, and on the west coast, spawning extends northwards as the season progresses (Langley, 1993). Hoki are not caught in quantity in the vicinity of the west coast outside the spawning season, and there is some evidence from commercial data and trawl survey data to suggest that hoki migrate to the west coast from the Southern Plateau during May–June (Ballara<sup>3</sup>). Female hoki gain up to 40% of their total body weight as their ovaries ripen (Kuo and Tanaka, 1984), but for the remainder of the year, the ovaries are small, weighing less than 1% of total body weight. Ovaries begin to ripen in April before female hoki migrate to their spawning grounds (van den Broek et al., 1981; Kuo and Tanaka, 1984).

Evidence of spawning at other times of the year has not been reported (Kuo and Tanaka, 1984). Preliminary histological work on hoki females collected throughout the spawning season indicates that hoki are either synchronous or group synchronous spawners. That is, their ovaries develop a single set of oocytes in a given season, and these oocytes are released in a single event (synchronous) or over several spawning events (group synchronous) (West, 1990). The same species in Tasmania develops a single set of oocytes in each season (Gunn et al., 1989). It is un-

known whether the proportion of hoki that spawn in a given year is determined by environmental conditions or whether it relates to a shallow recruitment curve or even some nonannual endogenous rhythm.

Our hypothesis was that if hoki develop their oocytes synchronously within each ovary, it should be possible to distinguish developing prespawners from nonspawners prior to the onset of the spawning season and thereby estimate both the proportion of fish that would spawn and a maturity ogive based on histological characterization.

In this study we collected monthly samples to monitor seasonal changes in the ovarian development of hoki prior to spawning. We also used random trawl surveys of the Southern Plateau in December and May in two consecutive years to determine 1) the

<sup>3</sup> Ballara, S. 1995. Natl. Inst. Water and Atmospheric Res., P.O. Box 14-901 Kilbirnie, Wellington, New Zealand. Personal commun.

proportion of female hoki on the Southern Plateau in May that would spawn in the coming season and 2) the proportion of females that already have begun their spawning migration by May. In this paper, we detail 1) the histological basis for classifying hoki as either nonspawners or prespawners and 2) the analyses used to estimate the maturity ogive and the total proportion of fish that would spawn in July or August.

## Materials and methods

### Trawl surveys

Two sets of surveys were completed: 1) 12 November–23 December 1991 and 17 April–21 May 1992; 2) 14 November–22 December 1992 and 1 May–4 June 1993. The survey area (275,356 km<sup>2</sup>) incorporated depths of 300–800 m south of Puysegur Point, excluding rough ground and the Bounty Platform (Fig. 1). The surveys used a two-phase random stratification design (Francis, 1984), and because hoki tend to be near the seabed during daylight, coming up off the bottom to feed at night (Kerstan and Sarhage, 1980), trawling was carried out during daylight hours only. Trawling procedure and standardization of gear, station, and stratum details are reported for each survey individually by Chatterton and Hanchet (1994), Schofield and Livingston (1994, a and b), and Ingerson et al. (1995).

Length-frequency samples of about 200 female hoki were collected from each tow on a random basis. The length-frequency distribution and the total numbers of fish were scaled up to the total stratum area by using the Trawlsurvey Analysis Program, as described by Vignaux.<sup>4</sup> The scaling was done by assuming a catchability and vulnerability of 1.0 in all surveys. Because these assumptions were unlikely to be valid, the numbers of fish were used only in a relative sense.

Additional samples of 20 female hoki were collected from each tow to measure gonad and total body weight, to identify macroscopic gonad stage, and to obtain histological samples from ovaries. Otoliths were also collected from these fish for ageing. Maturing hoki in the later stages of vitellogenesis can be macroscopically distinguished from resting hoki. The ovaries at that point are swollen, and the individual oocytes, visible to the naked eye, are opaque and creamy pink. Resting and immature ovaries are

small and translucent and no oocytes are visible. Previous surveys of hoki in April–May (e.g. van den Broek et al., 1981) reported few hoki that were sufficiently developed to be identified macroscopically as maturing. We therefore obtained histological samples of ovaries as well as recorded their macroscopic appearance. The central portion of the ovary from each sample was preserved at sea in 8%–10% buffered formalin. Samples were later processed to produce thin sections that were stained with standard haemotoxylin and eosin preparations.

### Histological staging

In developing a method to distinguish prespawning hoki from nonspawning hoki, we classified ovaries into the stages given by West (1990). Ovaries were classified according to the most advanced oocyte present in the ovary. A summary of these stages (as given by West) is as follows:

<b>Chromatin nucleolar stage</b>	The oocyte is surrounded by a few follicle cells and contains a large nucleus surrounded by a thin layer of cytoplasm. The nucleus has one large nucleolus and several small nucleoli.
<b>Perinucleolar stage</b>	The nucleus has multiple nucleoli at its periphery. Late perinucleolar oocytes may have vacuoles in the cytoplasm.
<b>Yolk vesicle (cortical alveoli) stage</b>	This stage is characterised by the appearance of large numbers of yolk vesicles in the cytoplasm. They increase in size and number to form several peripheral rows. The chorion is visible at this stage.
<b>Vitellogenic (yolk) stage</b>	Small yolk granules which gradually enlarge until they form fluid-filled spheres are typical. The spheres may eventually fuse to form a continuous mass of fluid yolk.
<b>Ripe (mature) stage</b>	The nucleus may be peripheral or may have disintegrated completely.

Criteria to distinguish prespawners from nonspawners were developed from a subsample of ovary sections from each survey and from some commer-

<sup>4</sup> Vignaux, M. 1994. Documentation of trawlsurvey analysis program. NIWA Greta Point Internal Report 225, NIWA Greta Point library, Wellington, New Zealand, 44 p.

cial samples collected from January through August (see below). These criteria (described in the Results section) were then used by an independent reader to classify May 1992 and May 1993 female hoki as prespawners or nonspawners.

Monthly samples were also collected from commercial vessels to monitor hoki development between January and September. Up to 40 ovary samples from a range of adult-size fish were preserved in 8% buffered formalin at the time of capture. Samples were processed in the laboratory, sectioned, and stained with standard haematoxylin and eosin preparations. Samples were collected mostly from Chatham Rise (Jan–May) and the west coast of the South Island (Jun–Jul) because these were the areas where commercial vessels were operating at that time.

Each fish was staged histologically (as described above) to determine the earliest month in which development began. Five of the most developed fish from each month were then selected for oocyte measurement to confirm that New Zealand hoki are synchronous or group synchronous like their Australian counterparts (Gunn et al., 1989). The mean diameter of 200 oocytes was measured (after Foucher and Beamish, 1980) from each of the five fish.

### Ageing

It is unknown whether recruitment to the spawning fisheries is length-driven or age-driven. Observers from the west coast hoki fishery have found spawning hoki as young as 2 years and as small as 42 cm total length, in some years (Sullivan et al.<sup>2</sup>). Because the model used for stock assessment is an age-structured one (Sullivan et al.<sup>2</sup>), fish were aged as part of this study, and all analyses were carried out by using age data. It was also important to age fish so that comparisons of the numbers of fish in each cohort in December and May could be made.

Otoliths from each fish in the histological samples from the May surveys and from the biological samples in December were aged by using the validated ageing method described by Horn and Sullivan (1996). These data were also used to develop age-length keys. Where there were no fish in the sample of a given length, the age-length key was interpolated with nearby values of age.

### Proportion of each age class developing to spawn

The proportion of fish in each age class that were classified as prespawners was estimated for each age stratum from the aged histological samples. The number of fish at each age in each stratum was esti-

mated from the age-length key and the length-frequency distribution in the stratum. For each age class the total number of prespawners was therefore estimated from the proportion of fish that were developing to spawn and from the total number of fish in each stratum. The standard error of these estimates was estimated by using a resampling technique, whereby in each stratum, a sample, the same size as the original sample, was selected (with replacement) from the original sample. The age-length key and proportion of prespawners were calculated from the combined sample of the 15 strata. This process was repeated 1,000 times. The standard error of the estimates was estimated from the standard deviation of the values in 1,000 replicates.

### Proportion of adult spawning fish

An estimate  $\hat{p}_+$  of the proportion of prespawners in the plus group of adult fish ( $p_+$ ) can be obtained by using the method described above but by considering all adult fish as a single plus group. However, if some fish had already left the Southern Plateau to spawn before the survey in May, they also should be counted as prespawning fish. This means that the proportion of adult prespawners present on the Southern Plateau in May ( $p_+$ ) is an underestimate of the total proportion of fish that will spawn ( $p$ ) as

$$p_+ = \frac{s}{s+ns} \leq \frac{s+g}{s+ns+g} = p, \quad (1)$$

where  $s$  is the number of prespawners on the Southern Plateau in May,  $ns$  is the number of nonspawners on the Southern Plateau in May, and  $g$  is the number of fish that had left the Southern Plateau before May, presumably to spawn.

If we define a migration ratio,

$$x = \frac{g}{s+ns}, \quad (2)$$

to be the ratio of the number of fish which have gone to spawn to the number of fish (both prespawners and nonspawners) that are still in the survey area when the second survey is done, then

$$p = \frac{s+g}{s+ns+g} = \frac{p_+ + x}{1+x}. \quad (3)$$

Thus  $p$  equals  $p_+$  when  $x$  is zero and increases towards an asymptote of 1 when  $x$  is very large.

The migration ratio,  $x$ , cannot be estimated very precisely because both trawl surveys will be subject to measurement error and because an unknown number of fish will have died naturally or have been caught between December and May. But to obtain the best estimate of  $x$ , the numbers of adult fish on the Southern Plateau in December and May were estimated from the total numbers of fish in the surveys and the proportion that were in the adult age group. The age distributions were estimated from the length-frequency distributions and the age-length keys were calculated from the samples collected for age determination.

In determining the number of fish that moved out of the survey area before May, it is necessary to account for fish that died between December and May. Five months of natural mortality was applied to the number of fish observed in the December surveys to estimate the number of fish that would be expected in the May surveys. The catch taken on the Southern Plateau between December and May in these two years was 10,595 t in 1992 and 8,339 t in 1993. Because the estimated size of the stock was 860,000 t in May 1992 and 1.3 million t in May 1993 (Cordue<sup>5</sup>), fishing mortality was considered to be negligible.

The discrepancy between the number of fish expected in the May survey and the number observed was the maximum number of fish that could be considered to have left the Southern Plateau to spawn. This number was used in Equation 2 to obtain an estimate  $\hat{x}$  of the migration ratio  $x$ . An estimate of the total proportion of fish that will spawn ( $p$ ) was calculated by using  $\hat{x}$  and an estimate of  $\hat{p}_+$  of  $p_+$  in Equation 3. Standard errors of these numbers were calculated by a resampling procedure that included uncertainty regarding the total number of fish in the December and May surveys.

### Procedure for estimating the total proportion of adult fish spawning

The estimation procedure for the proportion of adult spawning fish was as follows:

- 1 The total number of fish on the Southern Plateau in December,  $N_1$  was selected from a normal distribution with mean equal to the estimated value for this survey and with standard deviation equal to the standard error of this estimate. This number of fish was then distributed over the length-frequency distribution (assumed to be known exactly).

- 2 An age-length key (including ageing error) was generated by sampling with replacement from the fish in the age-length sample from the December survey and was applied to the December length-frequency distribution to estimate the number of adult fish in December,  $n_1$ . The number of adult fish expected to be alive in May was calculated by applying the natural mortality  $M$  to  $n_1$ , as  $n_1 e^{-M5/12}$ .
- 3 The same procedures described in 1 and 2 above were applied to the May surveys to obtain the total number of fish on the Southern Plateau in May ( $N_2$ ) and the number of adult fish in May ( $n_2$ )

- 4 The number of fish apparently missing ( $n_m$ ) was estimated as

$$n_m = n_1 e^{-M5/12} - n_2.$$

- 5 Taken as a fraction of the number  $n_2$  on the Southern Plateau in May,  $x$  (the migration ratio) was estimated by

$$\hat{x} = \frac{n_m}{n_2}.$$

- 6  $\hat{p}_+$  was calculated by using the simulated age-length key and the histological sample as described above. Hence  $\hat{p}$  was estimated as

$$\hat{p} = \frac{\hat{p}_+ + \hat{x}}{1 + \hat{x}}.$$

This process was repeated 1,000 times. The standard errors of each of the values was calculated from the standard deviation of the distribution of the 1,000 values.

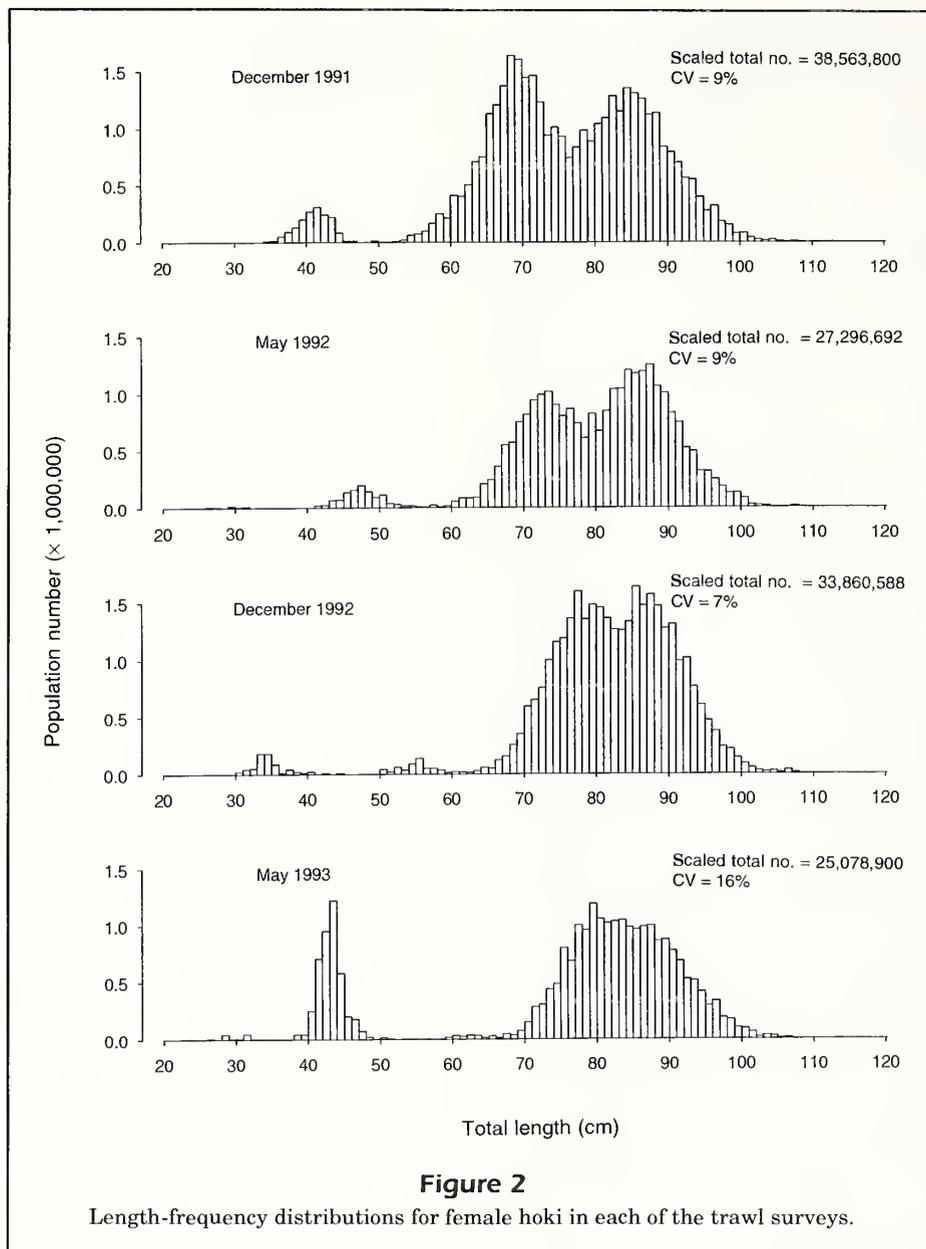
## Results

### Trawl surveys

The four surveys were successfully completed with a combined total of 495 stations sampled. Gear parameters were within the range necessary for survey standardization (Hurst et al.<sup>6</sup>), thereby permitting the direct comparison of survey results used for data analysis (Chatterton and Hanchet, 1994; Schofield and Livingston, 1994, a and b; Ingerson et al., 1995).

<sup>5</sup> Cordue, P. 1996. Natl. Inst. Water and Atmospheric Res. P.O. Box 14-901 Kilbirnie, Wellington, New Zealand. Personal commun.

<sup>6</sup> Hurst, R. J., N. Bagley, T. Chatterton, S. Hanchet, K. A. Schofield, and M. Vignaux. 1992. Standardisation of hoki/middle depth time series trawl surveys. NIWA Greta Point Internal Report 194, NIWA Greta Point library, Wellington, New Zealand, 87 p.



The numbers of hoki observed in the May surveys (26.8 million [1992], 24.4 million [1993]) were considerably less than in the December surveys (38.6 million [1991], 34.8 million [1992]) (Fig. 2). In addition, the length-frequency histograms show a decline in bimodality in the adult part of the distribution between May and December (Fig. 2). In December 1991, 56% of females over 50 cm were in strata west of 170°E. In May 1992, 59% were west of this line. In December 1992, 49% were in the west and in May 1993, 68% were in the west.

There were 541 fish in the histological sample in May 1992 and 1,136 fish in the sample in May 1993 (Table 1). In 1992, stratum 1 (300–600 m depth at

Puysegur) was not sampled and female fish from every second station in the other strata were sampled. In 1993 female fish from every station in all 15 strata were sampled.

### Ageing

There were very few young fish in most strata, and limited numbers of fish in the 1986 cohort, which appeared as age-6 fish in 1992 and as age-7 fish in 1993. Although fish were aged to a maximum age of 19 years, we combined them into a group of age 10+ and above. The ageing data were also used to develop age-length keys.

**Table 1**  
Percentages of each histological stage observed in female hoki sampled from each survey.

Histological stage	Dec 1991	May 1992	Dec 1992	May 1993
Chromatin nucleolar	0	0	0	0.1
Perinucleolar	100	45.4	100	39.7
Yolk vesicle	0	27.1	0	13.6
Vitellogenic	0	27.5	0	43.3
Ripe	0	0	0	3.3
Number in sample	452	541	1,039	1,136

## Histology

Monthly samples of hoki from the Chatham Rise and west coast of the South Island showed little change in oocyte stage in January and February, all being classified as perinucleolar (Table 2). In April, May, and June, larger oocytes of the yolk vesicle and vitellogenic yolk stages were evident. By July and August, females sampled on the west coast of the South Island were vitellogenic or ripe and had hyaline oocytes (Table 2). Oocytes clearly developed as a synchronous group, evidenced by the separation in size of the developing clutch from the reserve fund of chromatin nucleolar and perinucleolar oocytes (Fig. 3).

During the December trawl surveys, most ovaries contained oocytes that could be classified as late perinucleolar (Fig. 4).

By May, however, a significant change in oocyte stage had occurred; many ovaries contained cortical alveoli organized into a ring structure and showed increased oocyte size and oil droplets forming around the nucleus (Fig. 5). Because the oocyte stage observed in summer appeared to be a natural holding point in development, we classified a fish with such a stage as perinucleolar. When we saw the same development in fish in the autumn surveys they were classified as nonspawners. Only those fish with a proliferation of cortical alveoli and oil droplets that had begun to form around the nucleus were classified as being at or beyond the yolk vesicle stage and therefore counted as spawners for the coming season.

Table 1 shows the proportion of fish at each stage in each of the surveys. In both December samples, most or all fish were classified as perinucleolar. In contrast, in the May surveys, only 45.4% and 39.7% were in the perinucleolar stages in 1992 and 1993 respectively.

For fish caught during the trawl survey in May 1993, stage of development of the ovary of each fish in the histological sample was also evaluated mac-

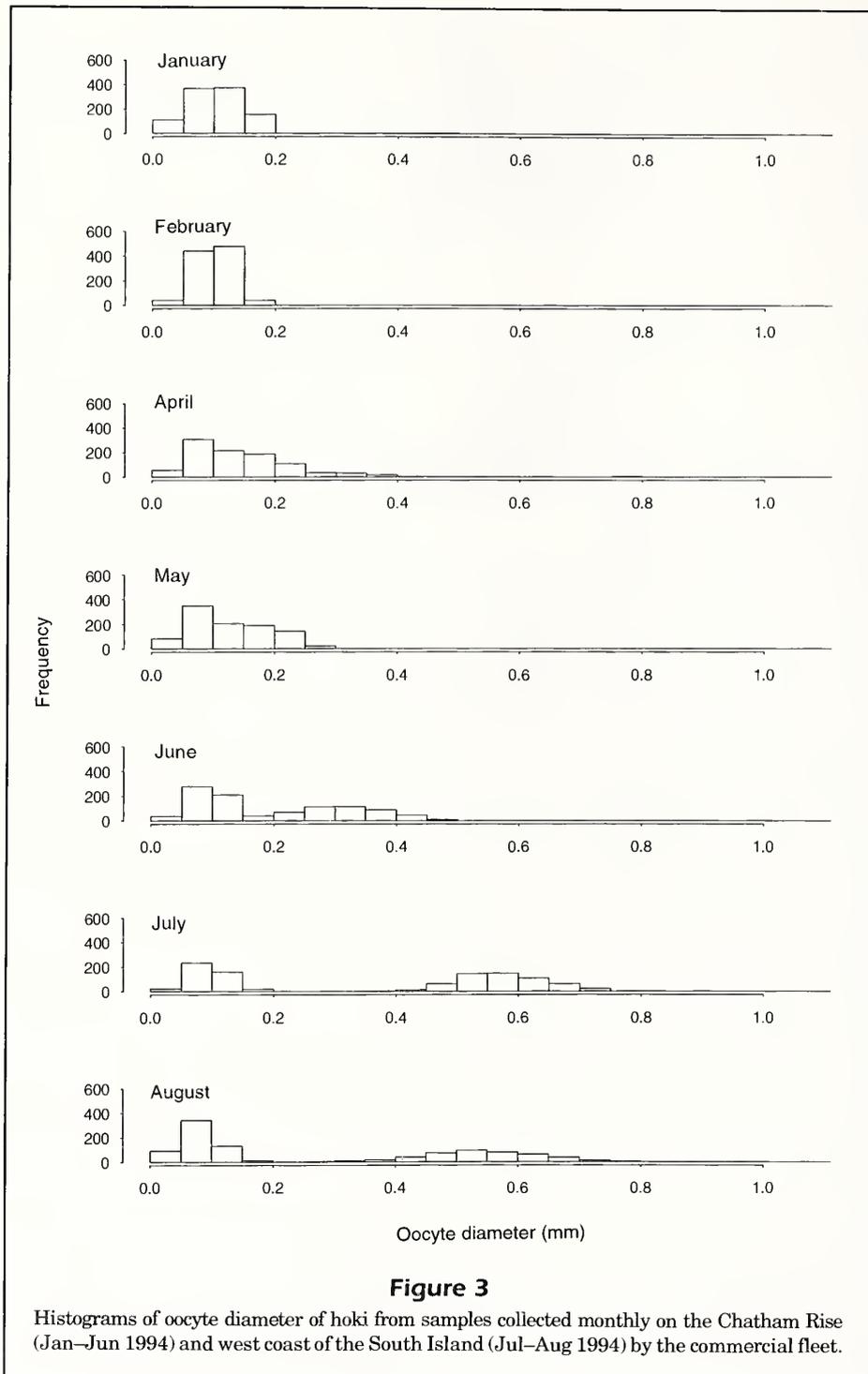
**Table 2**

Numbers of hoki monthly samples showing ovarian development on the Chatham Rise and west coast spawning grounds.

Region and month	Histological stage			
	Perinucleolar	Yolk vesicle	Vitellogenic	Ripe
<b>Chatham Rise</b>				
January	22	—	—	—
February	10	—	—	—
March	no sample			
April	6	9	1	—
May	10	9	1	—
<b>West coast</b>				
June	4	3	13	—
July	—	—	10	5
August	—	—	9	5

roscopically. The number of fish at each histological stage and at each stage of macroscopic gonad development are presented in Table 3. In total, of the 237 ovaries classified as maturing, only two were classified histologically as nonspawners. However, of the 899 ovaries classified as resting, 450 were classified histologically as nonspawners and 449 as prespawners. This finding confirms that physical development for spawning begins before it is apparent macroscopically in the ovaries and reinforces the requirement for histological methods of analysis.

The proportion of prespawners in each stratum was estimated from the aged histological samples from the May surveys (Table 4). If there were not at least two fish in a stratum of a particular age, the proportion was not estimated. Although there were many age-stratum combinations where the proportion of prespawners in a particular age class could not be estimated (mainly for the young fish and for the 1986 cohort), these were not generally found in strata that supported the greatest numbers of hoki of that age class (Table 4).



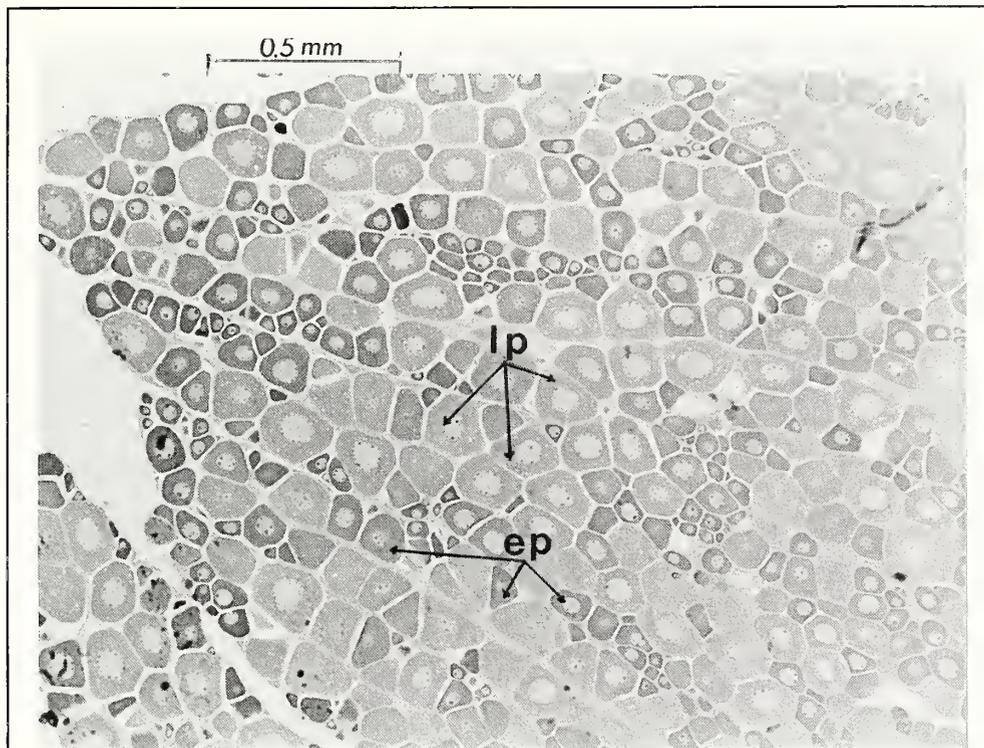
**Figure 3**

Histograms of oocyte diameter of hoki from samples collected monthly on the Chatham Rise (Jan–Jun 1994) and west coast of the South Island (Jul–Aug 1994) by the commercial fleet.

**Proportion of each age class developing to spawn**

Table 4 shows the estimated proportion of pre-spawners in each age class in the 1992 and 1993 May surveys. Table 4 also shows the percentage of fish at each age that were in strata where the proportion of

developing fish could be measured (i.e. had at least two fish in the sample). Where this is less than 50%, the estimate is based on fish from only a small fraction of the population, and should not be used. Where it is less than 66%, the estimate might be considered unreliable. In 1992 there were enough data to make a reliable estimate of the proportion of prespawners



**Figure 4**

Resting ovary with oocytes in the late perinucleolar stage, December 1991. (ep = early perinucleolar stage oocyte, lp = late perinucleolar stage oocyte (some yolk vesicles present)).

for ages 5, 7, 8, 9, and 10<sup>+</sup>, but age 6 (the 1986 cohort) and ages 1, 2, 3, and 4 could not be estimated because the strata with samples contained less than half of the total number of fish in the survey area. In 1993 there were enough data to make a reliable estimate of the proportion of prespawners for ages 5, 6, 8, 9, and 10<sup>+</sup>, but ages 3 and 7 (again, the 1986 cohort) were unreliable and ages 1, 2, and 4 could not be estimated.

The estimates of prespawners in each age class for the two surveys are shown in Figure 6. Although there were too few samples to obtain reliable estimates for fish of age 4 and under, it is clear that this proportion would be small. Only 3 of 42 (7%) fish in the sample that were age 4 or younger were classified as prespawners. It is therefore likely that the ogive increases steeply below age 5 before levelling off.

### Proportion of adult fish spawning

Figure 6 suggests that there may have been some increase in the proportion of prespawners up to age 8 in 1992 but that in 1993 the numbers of prespawners did not increase after age 5.

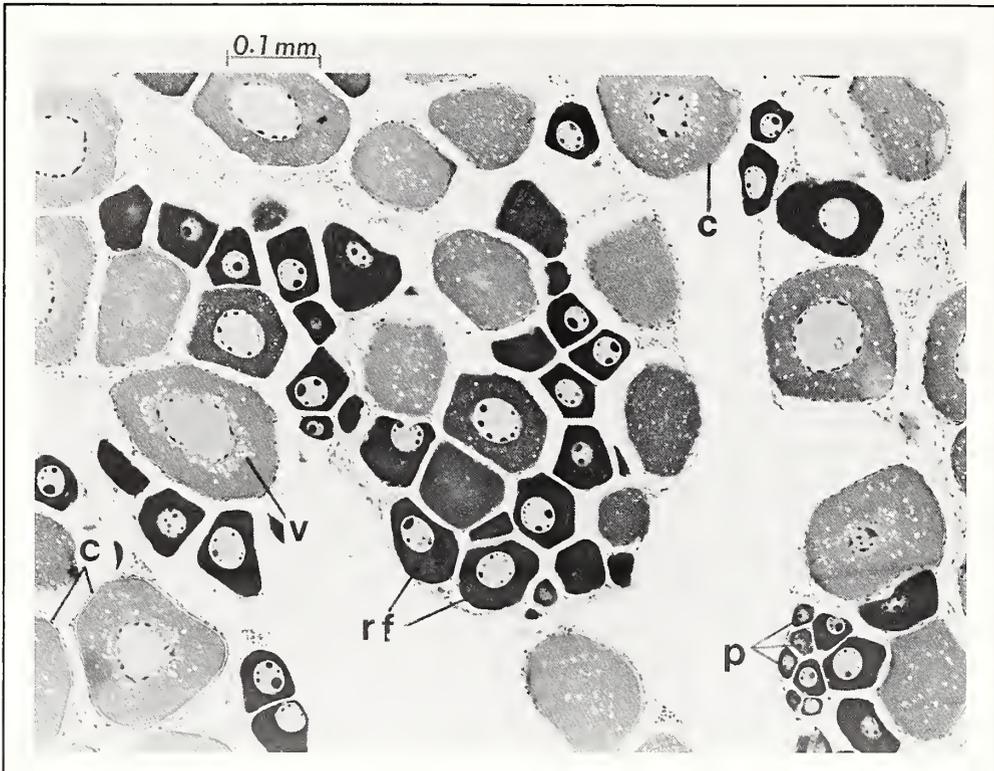
If we assume that any increase after age 7 is not significant, then the asymptotic values of the ogives

**Table 3**

Numbers of hoki classified in each histological stage compared with numbers of hoki classified in each macroscopic stage (May 1993).

Histological stage	Macroscopic stage		
	Resting	Maturing	Total
Nonspawners	450	2	452
Chromatin Nucleolar	1	0	1
Perinucleolar	449	2	451
Prespawners	449	235	684
Yolk Vesicle	154	1	155
Vitellogenic	295	197	492
Ripe	0	37	37
Grand total	899	237	1,136

in Figure 6 represent the measured proportion of adult prespawners ( $p_+$ ) in the years 1992 and 1993. Following a procedure identical to that above, but considering only fish aged 7 and over, the proportion of adult prespawners in the survey area was estimated as 66% in 1992 (SE 3%) and 65% in 1993 (SE 2%).



**Figure 5**

Histological sample from May 1993 showing some oocytes that had developed into the yolk vesicle stage. Note the circumnuclear distribution of the oil droplets that are beginning to form. (c = chorion, p = primary oocytes at chromatin nucleolar stage, rf = nondeveloping reserve fund oocytes at perinucleolar stage, v = vesicle ring around nucleus of yolk vesicle stage oocyte).

**Table 4**

Estimated total numbers of female fish, numbers of female fish in sampled strata, percentage of female fish in strata covered by sampling, numbers of prespawners, proportion of prespawners with standard error (SE), for each age class in the May surveys (NA indicates that the value could not be estimated). SE = standard error.

	Age class									
	1	2	3	4	5	6	7	8	9	10 <sup>+</sup>
<b>May 1992</b>										
Total in survey (× 1,000)	54	1,182	0	1,648	7,645	557	2,101	6,025	3,407	4,150
In sampled strata	0.00	511	0	691	7,458	130	1,478	5,973	3,387	4,132
% in sampled strata	0	43	NA	42	98	23	70	99	99	100
Prespawners (× 1,000)	0.00	0.00	0.00	132	3,333	35	844	4,065	2,323	2,652
Proportion spawning	NA	0.00	NA	0.19	0.45	0.27	0.57	0.68	0.69	0.64
SE	NA	NA	NA	0.10	0.05	0.26	0.08	0.05	0.05	0.05
<b>May 1993</b>										
Total in survey (× 1,000)	95	3,573	142	135	2,614	6,986	338	1,777	4,340	4,447
In sampled strata	0	0	83	29	2,586	6,986	183	1,739	4,304	4,418
% in sampled strata	0	0	59	21	99	100	54	98	99	99
Prespawners (× 1,000)	0	0	0	0	1,649	3,928	123	1,143	2,967	2,782
Proportion spawning	NA	NA	0	0	0.64	0.56	0.67	0.66	0.69	0.63
SE	NA	NA	NA	NA	0.05	0.03	0.18	0.06	0.03	0.03

Table 5

Estimation of total proportion spawning ( $p$ ) of age-7+ hoki based on ( $p_+$ ) the proportion of prespawners on the Southern Plateau and on the number of hoki in the plus group on the Southern Plateau in December 1991, 1992, and May 1992, 1993. ( $n$  = number of hoki  $\times 10^3$ , SE = standard error;  $M$  = natural mortality).

Year	$M = 0$ $n$ (SE)	$M = 0.25$ $n$ (SE)	$M = 0.3$ $n$ (SE)
<b>1992</b>			
Observed, December 1991	17,945 (1,700)	17,945 (1,700)	17,945 (1,700)
Observed, May 1992	15,682 (1,400)	15,682 (1,400)	15,682 (1,400)
Expected, May 1992	17,945 (1,700)	16,170 (1,500)	15,837 (1,500)
Missing, May 1992	2,263 (2,200)	488 (2,100)	155 (2,100)
Migration ratio	0.14 (0.16)	0.03 (0.14)	0.01 (0.14)
Proportion spawning	0.70 (0.05)	0.67 (0.05)	0.66 (0.05)
<b>1993</b>			
Observed, December 1992	23,250 (1,800)	23,250 (1,800)	23,250 (1,800)
Observed, May 1993	10,902 (1,700)	10,902 (1,700)	10,902 (1,700)
Expected, May 1993	23,250 (1,800)	20,950 (1,600)	20,518 (1,600)
Missing, May 1993	12,348 (2,400)	10,048 (2,300)	9,616 (2,300)
Migration ratio	1.13 (0.43)	0.92 (0.39)	0.88 (0.38)
Proportion spawning	0.84 (0.03)	0.82 (0.03)	0.81 (0.04)

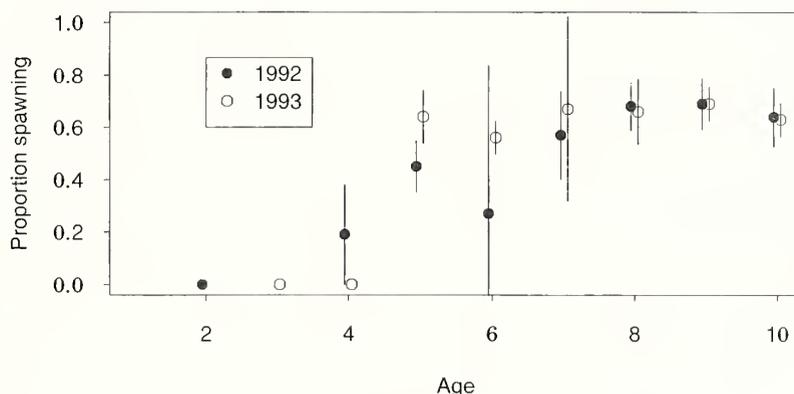


Figure 6

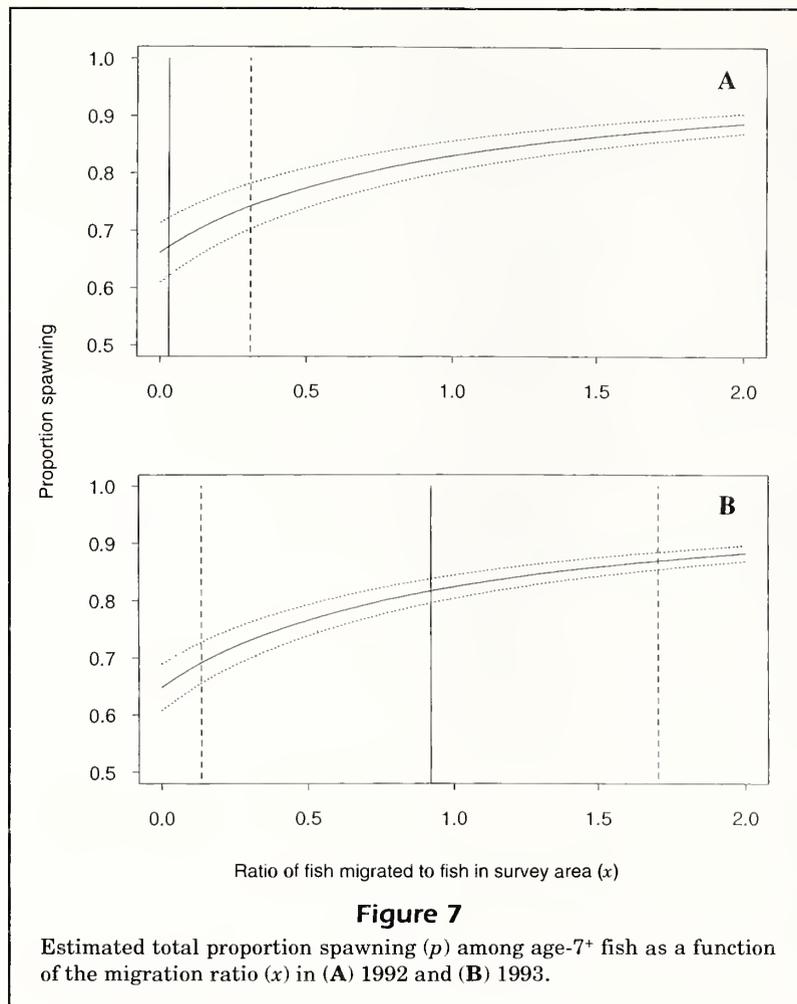
Proportion of prespawners at age from 1992 and 1993 surveys. The error bars indicate two standard errors.

Table 5 shows the estimates of the total proportion of adult fish that will spawn (i.e. including those fish that have already left the area) calculated as above. The calculations were done with three estimates of natural mortality  $M$ , including the best estimate  $M = 0.25$ , and two bounding values  $M = 0$  and  $M = 0.3$  (Sullivan et al.<sup>2</sup>). Table 5 shows that this makes little difference to the estimate of  $\hat{p}$ . Standard errors of the estimates were calculated by using the resampling technique.

The best estimate of the total proportion of adult fish that would have spawned in the 1992 winter sea-

son was 0.67 (SE 0.05, with  $M = 0.25$ ). If  $M$  is as high as 0.3 or as low as 0, the estimate of  $p$  decreases to 0.66 or increases to 0.70 respectively. The best estimate of the total proportion of adult fish that will spawn in the 1993 winter season was 0.82 (SE 0.03). If  $M$  is as high as 0.3 or as low as 0, the estimate of  $p$  is 0.81 or 0.84 respectively.

Figure 7 shows the effect of the estimate of  $\hat{x}$  on the estimate of  $\hat{p}$  for 1992 and 1993. In each plot there are three curves for  $\hat{p}$  as a function of  $\hat{x}$ . The solid curve is the function given the estimated value of  $\hat{p}_+$  (0.66 in 1992 and 0.65 in 1993). The two dot-



ted curves are the functions at plus and minus two standard errors of this value.

The solid vertical lines show the value of  $\hat{x}$  with  $M = 0.25$ . The two dashed vertical lines shown are at plus or minus two standard errors of this value. Clearly the value of  $\hat{x}$  is not at all well known. However, the function is changing slowly over this range; therefore it is still possible to obtain a useful estimate of  $p$ .

## Discussion

The number of studies that have attempted to measure the level of nonspawning in adult fish and to determine its effect on population estimates used for stock assessment appears to be few. It is often assumed that although the steepness of the maturity ogive varies among species, it will always level out at or near 100% spawning (e.g. Hislop, 1984). Species documented to reach less than 100% spawning

include orange roughy, *Hoplostethus atlanticus*, off southeast Australia at 55% (Bell et al., 1992), the brackish water burbot *Lota lota* (L) in the Baltic sea at 70% (Pulliainen and Korhonen, 1990), and the estuarine yellow-fin (surf) bream, *Acanthopagrus australis* at 50% (Pollock, 1984). Although the annual proportion of hoki that spawn is similar to that of these other species, the other studies did not adjust for population size or take migratory movements into account. Our estimates for hoki are close to the range indicated by Hurst and Schofield (1995) who did adjust for population size.

There were some potential sources of error that we could not measure. First, the number of undeveloped fish surveyed on the Southern Plateau in May that were classified as nonspawners, which could have developed late and gone on to spawn, is unknown. This would lead to an underestimate of the proportion of prespawners. Second, if a number of fish remained undeveloped but migrated to the spawning ground anyway, the number of fish that

would leave the Southern Plateau after May would be underestimated. Third, the number of developing fish in May that could have resorbed their eggs and not gone on to spawn after all could lead to an overestimation of the total proportion spawning. Other sources of error concern changes in catchability and vulnerability between surveys and the difficulty of detecting any bias or size selectivity when sampling a population with the trawl.

With regard to the first source of error above, it was encouraging that hoki collected in April showed significant signs of development compared with those collected in February (Table 2). The most likely fish to be affected by late development are the younger, smaller fish because they spawn later in the season compared with the older, larger fish which spawn at the beginning of the season (Langley, 1993). Because we estimated the proportion of hoki age 7 years and above that were spawning, the problem was minimized.

With regard to the second source of potential error, undeveloped hoki of age 4 and greater are not caught on the spawning grounds during the spawning season (Langley, 1993), suggesting that there may be 100% spawning among hoki that migrate to the west coast spawning grounds. We have no data on the number of fish that could resorb their eggs before the spawning season, but none were found in the May samples in this study.

With regard to the trawl survey technique, it is possible that there are systematic changes in catchability or vulnerability between December and May. We considered it more likely, however, that the changes in fish numbers were real, and that some fish had already migrated away from the Southern Plateau before the May survey, particularly in 1993 when the survey took place later than in 1992.

The ratio of the number of missing fish to the number of fish present on the Southern Plateau (the migration ratio,  $x$ ) can also be expressed in terms of the proportion of fish that have already migrated ( $p_m$ )

$$x = \frac{p_m}{1 - p_m}$$

or, equivalently

$$p_m = \frac{x}{1 + x}$$

Both  $x$  and  $p_m$  change as fish leave the Southern Plateau. In December, when no fish have migrated, both  $x = 0$  and  $p_m = 0$ . If a survey were to be done at a point when 33% of the fish had migrated, or  $p_m = 0.33$ , there would be one fish missing for every two fish still in the survey area, and  $x$  would be 0.5. By July 1993, when an estimated 82% of fish have gone

to spawn,  $\hat{p}_m$  is 0.82 and  $\hat{x}$  has increased to 4.6. Therefore, in May 1993, when  $\hat{x} = 0.92$  and  $\hat{p}_m = 0.48$ , we can estimate that more than half (58.5%) of the fish that were going to spawn had already gone.

This is, of course, poorly estimated, as is  $x$ , but it is higher than was expected before the surveys were done. If the survey results are correct, they suggest that in May 1993, fish had already started to migrate in large numbers. The survey in May 1993 began two weeks later in the year than that in 1992, indicating that May is a critical time for the spawning migration of hoki. This interpretation is supported by the change in distribution of fish from the east to the west between December and May in 1993, but not in May 1992. If, however, our estimates of the numbers of fish that have migrated away from the Southern Plateau by May are incorrect (e.g. because of changes in catchability or vertical availability between December and May, or because not all fish have begun to develop by May), then the proportion of prespawners on the Southern Plateau in May could be used as a lower limit of the proportion spawning of the total population. Given that a standardized trawl survey technique was the best method available to us to sample the adult hoki population, we believe that it would be difficult to improve on the estimates of proportion spawning obtained.

The 4–6 yr age classes show different proportions of prespawners in each year, with more 4 year olds but with fewer 5 and 6 year olds developing to spawn in 1992 than those in 1993 (Fig. 6). Differences in the proportion of spawning fish in the younger age classes could also relate to the preceding spawning history of a particular age class.

Although every year many hoki spawn on the west coast of the South Island, it is clear that a large number of individuals do not. Species that exhibit such behavior usually have a major accessory activity that requires a significant amount of energy in addition to spawning itself (Bull and Shine, 1979). Hoki migrate over vast distances of about 1,500 km from the Southern Plateau to the west coast spawning grounds. The energy cost incurred during migration may be so high that there is not enough left for egg production the following year.

Lack of food and migration distance have been suggested as reasons for lack of spawning among orange roughy (Bell et al., 1992) and yellow fin bream (Pollock, 1984). However, Pulliainen and Korhonen (1990) found that nonspawning burbot maintained a condition similar to that of spawning burbot and ruled out low food supplies as an explanation for nonspawning adults.

Within species where different populations show different levels of nonspawning, it has been found

that the lowest frequencies are usually associated with increased stress, such as poorer quality habitat, food shortage, or a shorter growing season (Bull and Shine, 1979). Nonspawning condition has been induced experimentally for several species by reducing their food supply (e.g. haddock [Hislop et al., 1978]; Newfoundland winter flounder [Burton and Idler, 1987]; and plaice [Horwood et al., 1989]).

Nutrients are in good supply and do not limit primary production on the Campbell Plateau (which forms a major portion of the Southern Plateau survey area); however, chlorophyll concentrations over depths of 450 m or greater are generally low (Heath and Bradford, 1980). Heath and Bradford suggest that because of this and other characteristics of the area, there never will be a well-developed zooplankton community with a high biomass on the Campbell Plateau. Areas of higher productivity are found on the island shelves and shallow rises in the area, or downstream from the Campbell Plateau itself. The energetics of the food chain in the study area are not known. It is possible that the lack of high primary and secondary productivity in the area contributes toward nonreproduction in some hoki from year to year.

Whatever the cause, nonspawning among adult hoki has important implications for stock assessment and risk estimation in the management of New Zealand hoki stocks. The proportion of fish that migrate to spawn is a scaling factor that relates the number of fish observed during the spawning season (using tools such as CPUE and acoustics) to the total population. It also provides a buffer between the total stock and the population vulnerable in any one year to the greatest fishing effort that is applied during the spawning season. Further, it reduces the stock size, which is needed for calculating the stock-recruitment relationship used in predicting future recruitment.

The effect of these factors may be minimal if the level of nonspawning fish is constant. If, however, the proportion spawning varies from year to year, as suggested by our study, the implications for modeling may be both complex and important.

It is likely that there are other species not necessarily related to hoki that could also have significant and variable proportions of nonspawning fish. There may therefore be major implications for the stock assessment of those species as well. Any stock assessment tool that is used to obtain an estimate of absolute abundance from a spawning population (e.g. acoustics, egg-production method) should take nonspawning into account. It is also important that the effect of nonspawning on any stock-recruitment relationship (assumed or measured) be taken into account because one of the more serious difficulties

in determining the stock-recruitment relationship of any species is obtaining a reliable measure of the spawning stock size (Hilborn and Walters, 1992). Further, the stock-recruitment dynamics of a population could be masked, particularly if the level of nonspawning is correlated to some environmental factor or autocorrelated because of some inherent life strategy, such as improved longevity or increased egg size.

We have shown that nonspawning among adult hoki is substantial, and it has important consequences for stock assessment. For these reasons, it is clear that a better understanding of its variability, and how widespread its occurrence might be among other species, would be useful for fisheries management worldwide.

## Acknowledgments

We thank Peter Horn for ageing the samples; Kevin Sullivan, Patrick Cordue, and Len Tong for useful discussions; the scientific staff who participated in the trawl surveys; the officers and crew of GRV *Tangaroa*; and the scientific observers for collecting samples from commercial vessels. We also thank three anonymous reviewers for their comments and suggestions.

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**Abstract.**—Florida's rich fisheries are among the state's most valuable resources, attracting the interest of fishermen, divers, and others. Commercial and recreational exploitation of these resources has altered the abundances of some valuable species; consequently fishery regulations and a system to monitor landings have evolved in response.

Until now, the biological structure of the multispecies harvest has not been examined. Landings from commercial trips in Broward County during 1989 were used to describe the structure and seasonal dynamics of that harvest. Cluster analysis classified fishing trips into distinct groups associated with different habitats and gear. Swordfish landings dominated this low-diversity harvest. There were significant seasonal changes in the species assemblages landed. However, most species associations were weak and negative.

The observed structure of the Broward County harvest reflects the selectivity inherent in commercial fishing. It is a balance between the differential availability of various species to the gear used and the market values driving the fishermen to select some species and discard others. Seasonal changes in the harvest structure reflect changes in the availability of various species and in the fishermen's ability to adapt to these changes by switching to alternate target species. The strong biases introduced by the selectivity of this system can obscure events in the natural system and provide little insight into the changes in the natural fish community.

## Structure and dynamics of the fishery harvest in Broward County, Florida, during 1989

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Florida waters are rich in fish and shellfish. Although the greatest diversity is found in coral reef habitats (Starck, 1968), hundreds of species are found throughout Florida's marine waters (Anderson and Gehringer, 1965; Herrema, 1974; Gilmore, 1977). Statewide, commercial landings are reported to the Department of Environmental Protection by using 531 different species codes, some of which represent groups of species. This assemblage is two to three times larger than any other state's marine fishery resource.

Historically, fish communities containing commercially valuable species have been strongly influenced by human activities, especially fishing (e.g. Cushing, 1961; Idyll, 1973; Beddington and May, 1982; Gulland, 1983; Beddington, 1986; Sissenwine, 1986; Laevastu and Favorite<sup>1</sup>). Florida's fishery resource has been intensely exploited both commercially and recreationally for many years (e.g. Nakamura and Bullis, 1979; Newlin, 1991). Bohnsack et al. (1994) have provided a good description of the complexity of Florida fisheries, explored the effects of exploitation, and discussed the difficulties in interpreting available landings data. The effects of exploiting this multispecies resource have been demonstrated for a few valuable species (Spanish mackerel: Williams et al.<sup>2</sup>;

king mackerel: Fable, 1990; spiny lobster: Moe, 1991; red drum: Goodyear<sup>3</sup>; billfishes: Anonymous<sup>4</sup>; swordfish: Anonymous<sup>5</sup>; red grouper: Goodyear and Schirripa<sup>6</sup>). However,

<sup>1</sup> Laevastu, T., and F. Favorite. 1978. The control of pelagic fishery resources in the eastern Bering Sea. Northwest and Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115. Proceedings report. (Manuscript.)

<sup>2</sup> Williams, R. O., M. D. Murphy, and R. G. Muller. 1985. A stock assessment of the Spanish mackerel, *Scomberomorus maculatus*, in Florida. Unpublished, third draft. Prepared for the Florida Marine Fisheries Commission, 2540 Executive Center, Circle West, Tallahassee, FL 32301, 65 p.

<sup>3</sup> Goodyear, C. P. 1987. Status of red drum stocks in the Gulf of Mexico. Contribution report CRD 86/87-34, Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Dr., Miami, FL 33149, 49 p.

<sup>4</sup> Anonymous. 1982. Draft fishery management plan, draft environmental impact statement, and regulatory impact review for the Atlantic billfishes: white marlin, blue marlin, sailfish and spearfish. South Atlantic Fishery Management Council, 1 South Park Circle, Suite 306, Charleston, SC, report G#27 BF Fmwk 8/82, 64 p.

<sup>5</sup> Anonymous. 1991. Reference paper on 1991 swordfish stock assessments by SCRS swordfish assessment group. Miami Laboratory, Southeast Fisheries Science Center, NMFS, NOAA, Miami, FL, rep. SCRS/91/16, 193 p.

<sup>6</sup> Goodyear, C. P., and M. J. Schirripa. 1991. The red grouper fishery of the Gulf of Mexico. Miami Laboratory, Southeast Fisheries Science Center, NMFS, NOAA, 75 Virginia Beach Dr., Miami, FL 33149. Contribution rep. MIA-90/91-86, 79 p.

only anecdotal reports of associations among harvested species exist.

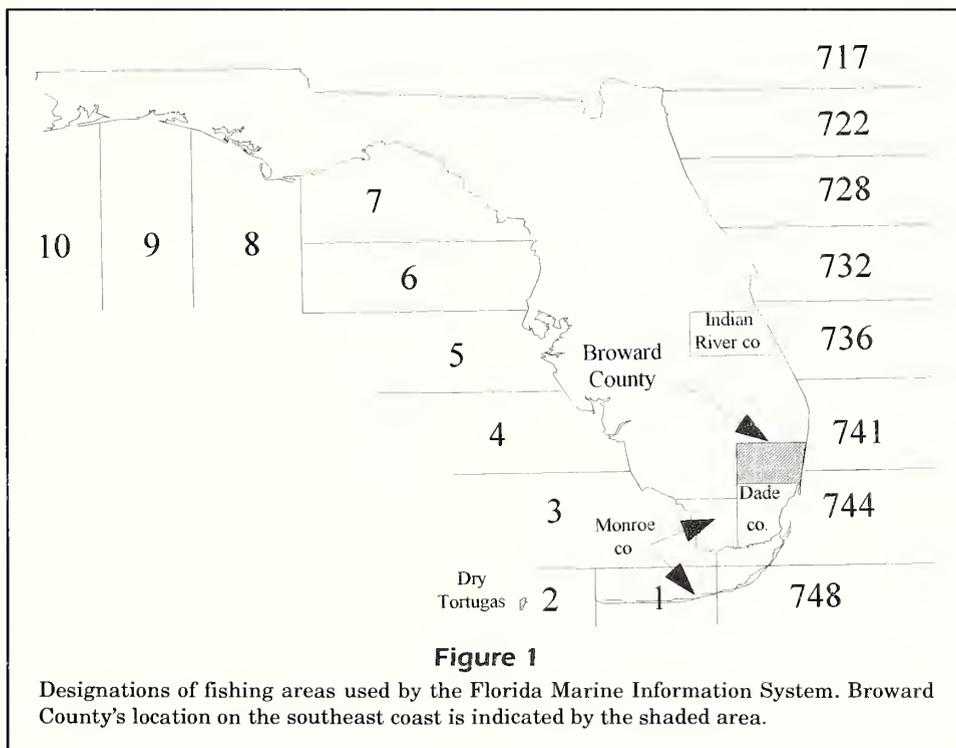
Concern about the effects of harvesting this resource has stimulated research on the structure and dynamics of Florida's marine fish community. Structure of the harvest is related to the structure of the natural community and to the economics influencing fishermen's behavior. It integrates the differential fishing mortality affecting the natural community. In 1984, the Florida Department of Environmental Protection (FDEP) established a trip-ticket reporting system (Marine Fisheries Information System) to monitor the fishery harvest and provide a database of basic information on commercial landings from this resource. All dealers buying fish from fishermen or fishing for themselves must report the amounts of all species landed on each fishing trip. These records normally represent those species brought to shore on a single fishing trip and sold (landed). They do not include species or individuals caught and subsequently discarded, those used as bait, or those brought to shore but not sold. Harvesting occurs in many different ways (e.g. traps, nets, hook-and-line) and can have a variety of effects on the fishery resource and the natural community as a whole. A better understanding of the multispecies resource and the potential effects of the harvest can be gained by relating the structure and its variability to what is known about the natural fish assem-

blage and the harvesting behavior of fishermen. This study uses commercial landings data collected by the Marine Fisheries Information System (MFIS) to examine the structure and temporal dynamics of the harvest in Broward County, Florida (Fig. 1), during 1989.

## Methods

The MFIS database includes, but is not limited to, information on the weight of each species landed from each commercial fishing trip, the date on which those landings occurred, and the time spent fishing. Information on depth and fishing area were provided on a voluntary basis in 1989 but the spaces for reporting such information were often left blank by reporting dealers. Information on gear used was not provided.

All commercial landings reported from Broward County during 1989 were used in this analysis. This subset of the MFIS database was chosen for this study because Broward County fisheries landings are some of the most valuable in the state. Furthermore, because 3,246 landings records (out of more than 2.5 million) exist, it is computationally one of the most manageable data sets available. Each month of data was analyzed separately in an attempt to detect seasonal trends in species assemblage structure. Monthly assemblages were constructed on the basis of total monthly landings of each species.



Diversity was described by using the Shannon-Wiener Information Index ( $H'$ ) (Shannon and Weaver, 1949) and its component parts, richness (number of species) and evenness ( $V'$ ) (Pielou, 1977).

$$H' = - \sum p_i \log_e p_i$$

$$V' = H' / \log_e s^*$$

where  $p_i$  is the proportion of species  $i$  and  $s^*$  is the number of species in the entire community (Pielou, 1977). In this study, the value of  $s^*$  was set to the total number of species landed in a given month when calculating evenness per ticket, and to the total number of species (76) landed over the entire year when calculating evenness per month.

Heterogeneity ratios (HR) (HR actually measures beta diversity, which is an index of dissimilarity, Kobayashi, 1987) were calculated to measure the similarity between all pair-wise comparisons of monthly assemblages. All pair-wise combinations of assemblages were tested for significant differences ( $\alpha=0.05$ ) by using a Monte Carlo simulation technique that compares the observed number of species common to the two assemblages of interest with that expected from randomly extracting two assemblages (each having the same number of species as one of the observed assemblages) from the community as a whole (FAUNSIM) (Raup and Crick, 1979; McKenna and Saila, 1991).

A nonhierarchical cluster analysis (SAS FASTCLUS, SAS, 1985) was applied to classify the trips according to the species assemblage landed each month. A maximum of 3 iterations and 20 clusters were specified. No minimum radius was specified. The REPLACE = option was set to RANDOM so that a simple pseudorandom sample of observations was chosen as initial cluster seeds. The DRIFT option was specified to adjust cluster seeds to their cluster mean each time an observation was added.

Spearman's rank correlation analysis was performed on every pair-wise combination of monthly species landings, on a trip-by-trip basis, to test for significant associations. A Z-test was applied to determine the significance of each correlation at the 0.01 level (Freund, 1970, p. 311–313).

## Results

A total of 1,355,421 kg (2,981,926 pounds) of finfish and shellfish were landed in Broward County during 1989 according to the 3,246 commercial fishing trips reported (Table 1). The monthly average was 112,840 kg (248,247 pounds) ranging from 41,889 kg (92,156 pounds) to 178,489 kg (392,675 pounds) (Fig. 2).

## Geography of the harvest

Florida's commercial fishing fleet is, in general, artisanal (small boats operating near shore). In 1989, 907 saltwater products licenses, 61 wholesale dealer licenses, and 408 retail dealer licenses were issued to residents of Broward County. Most fishermen worked in the waters immediately adjacent to the Broward County coast. The fishing area (Fig. 1) was reported for 76% of the trips landing fish in Broward County. According to those trip-tickets that included fishing area, fishermen harvested from areas 741 (45%) or 744 (37%) on 82% of fishing trips. The number of trips diminished as one moved away from the Broward County coast. Fish were caught from areas as far north as the waters off Indian River County (area 736), as far south and west as the Tortugas (area 2). Rarely, landings were reported from waters of Florida Bay off mainland Monroe County (area 3).

## Diversity

Diversity of landed species was low in comparison with the natural diversity of this subtropical community. A total of 76 species (or groups of species) were landed in Broward County in 1989. Diversity ( $H'$ ) of the total harvest was 1.86; evenness ( $V'$ ) was 0.43. Mean monthly diversity (1.88) was almost identical to that for the total harvest (Table 2). Monthly evenness values varied between 0.31 and 0.62, a mean of 0.43. Diversity and evenness followed roughly sinusoidal patterns throughout the year, with peaks in September ( $H'=2.69$ ,  $V'=0.62$ ) approximately double the minimum value in May ( $H'=1.36$ ,  $V'=0.31$ ). Monthly richness approached 50 species most of the year; June (36) and July (44) had the lowest values, April (54) and November (55) had the highest values. Despite the fact that the waters off Broward County contained a relatively rich (at least 76 species commercially harvested) multispecies fish community, as many as half of all trips in any given month landed only a single species. Mean alpha diversity (defined here as diversity based on landings from a single fishing trip) was low (0.44) and showed little variability (Fig. 3). It was greatest in January and February and dropped to about 60% of those values for the rest of the year. Richness displayed a very small range (2.5–3.5 species per trip).

## Similarity

Beta diversity (HR) among pair-wise comparisons of monthly assemblages ranged from 1.05 to 1.26 (Table 3). The species assemblages landed in March and September were most similar and those landed in

Table 1

Fish and shellfish landed in Broward County, Florida, during 1989. Species groups are identified by the following: BC = blue crab, BF = bait fishes, GS = grouper-snappers, ID = inshore demersals, IP = inshore pelagics, LB = lobsters, OD = offshore demersals, OP = offshore pelagics, SC = stone crab, SH = shrimps, and UM = unidentified miscellaneous fishes. Golden crab landings are included in the category "misc. invertebrates."

Species or complex	Weight (lb)	Group	Species or complex	Weight (lb)	Group
Amberjack	4,315	OP	Sea bass, mixed	327	ID
Bait Fish	246	BF	Shark	59,352	OP
Ballyhoo	23,204	BF	Shark fins	35	OP
Bluefish	38	IP	Sheepshead	120	ID
Bluerunner	813	BF	Hogfish	6,895	ID
Bonito (little tunny)	161	OP	Snapper, lane	833	GS
Bumper, Atlantic	94	BF	Snapper, mangrove	3,335	GS
Cobia	1,350	OP	Snapper, mutton	29,555	GS
Croaker	434	ID	Snapper, red	337	GS
Dolphin	32,704	OP	Snapper, silk	68	GS
Eels	20	ID	Snapper, vermilion	3,358	GS
Goggle eye or scad	1,510	BF	Snapper, yellowtail	23,443	GS
Grouper, black	33,255	GS	Snapper, mixed	11,438	GS
Grouper, gag	6,155	GS	Snapper, other	1,102	GS
Grouper, Nassau	40	GS	Spot	40	ID
Grouper, red	10,612	GS	Swordfish	811,896	OP
Grouper, scamp	194	GS	Tilefish, golden	320	OD
Grouper, snowy	939	GS	Tilefish, gray	800	OD
Grouper, Warsaw	764	GS	Triggerfish	2,289	ID
Grouper, yellowedge	74	GS	Tuna, bigeye	66,437	OP
Grouper, yellowfin	8	GS	Tuna, blackfin	457	OP
Jewfish	232	GS	Tuna, bluefin	2,530	OP
Grouper, mixed	527	GS	Tuna, skipjack	15	OP
Grouper, other	1,496	GS	Tuna, yellowfin	58,626	OP
Grunts	2,700	ID	Tuna, mixed	499	OP
Jack, crevalle	2,304	IP	Wahoo	759	OP
Jack, mixed	1,075	IP	Whiting	37	ID
Jack, other	392	IP	Misc. food fish	57,240	UM
Mackerel, king	25,848	OP	Misc. industrial fish	730	UM
Mackerel, Spanish	723	IP	<b>Total finfish</b>	<b>1,299,945</b>	
Menhaden (pogies)	218	IP	Crabs, blue (hard)	7,564	BC
Mojarra	697	ID	Crabs, stone, large	265	SD
Mullet, black	9	IP	Lobster, Spanish	225	LB
Mullet, silver	1,451	IP	Lobster, spiny	37,068	LB
Permit	1	IP	Octopus	163	ID
Pinfish	2	BF	Shrimp, pink	5,280	SH
Pompano	378	IP	Shrimp, bait	453	SH
Porgies	2,092	ID	Misc. invertebrates	4,458	OD
			<b>Total invertebrates</b>	<b>55,475</b>	
			<b>Grand total</b>	<b>1,355,421</b>	

February and June were least similar. About half (28 out of 66) of all possible unique pair-wise comparisons revealed significantly different assemblages (Table 3). These differences were usually due to changes in the proportion of landings contributed by swordfish and to the prevalence of lobster and baitfish.

The composition of the assemblage landed in a particular month varied considerably. The assemblage landed during any given month was significantly different from those of as few as two to as many

as nine of the other eleven months. Assemblages of adjacent months were not significantly different, with the exception of July–August (owing to a sharp drop in swordfish landings and to a large increase in lobster landings at the beginning of the season) and September–October (owing to a sharp increase in swordfish landings and a general reordering of the dominance of other species) (Table 3). October was different from all months, except November and December, and July was different from all months, except June and September. January was different only

from July and October, whereas December was different only from February and July. Generally, there were significant differences between winter (large

proportion of swordfish and other offshore pelagics) and late summer-fall (relatively small proportions of offshore pelagics with a mix of species from other groups) assemblages.

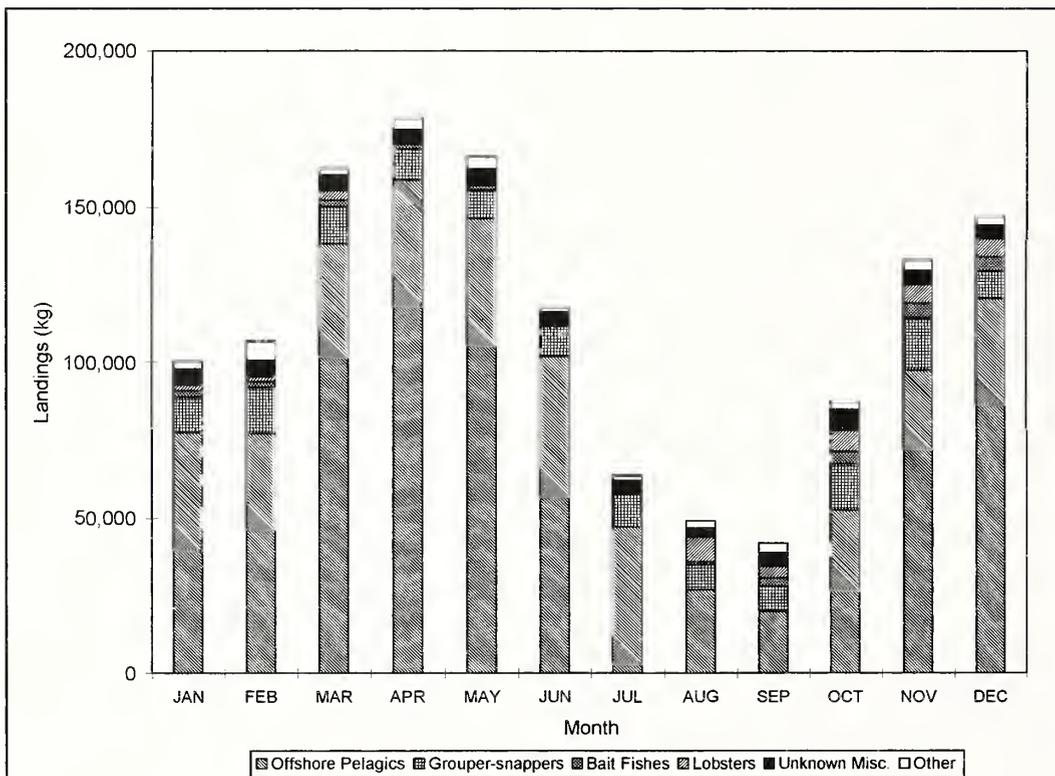
**Table 2**

Monthly diversity of commercial fisheries landings in Broward County, Florida, during 1989.  $H'$  = Shannon-Wiener diversity;  $V'$  = evenness;  $R$  = species richness.

Month	$H'$	$V'$	$R$
Jan	1.73	0.40	48
Feb	2.04	0.47	50
Mar	1.49	0.34	52
Apr	1.49	0.34	54
May	1.36	0.31	51
Jun	1.41	0.32	36
Jul	1.90	0.44	44
Aug	2.66	0.62	48
Sep	2.69	0.62	52
Oct	2.35	0.54	54
Nov	1.90	0.44	55
Dec	1.56	0.36	53
Mean	1.88	0.43	50

**Classification**

Cluster analysis classified trips on the basis of the similarity of the species assemblages landed. I used an artificial, but operational, system of general habitat associations and species complexes to classify species into eleven groups (Table 1). Groupers and snappers inhabit a wide variety of habitats (Smith, 1976; Robins et al., 1986) and were frequently landed together. They were assigned to their own group rather than limited to a single habitat. Similarly, bait fish often formed a unique cluster and thus a "bait fish" group was used. "Miscellaneous food/industrial fish (UM)" was a "catch all" group used by fishermen to report species that were not explicitly given an identification code by the MFIS. It usually included such species as angelfishes (Pomacanthidae), parrotfishes (Scaridae), butterflyfish (*Peprilus* spp.),



**Figure 2**

Total monthly landings in Broward County, Florida, during 1989 and the contribution of each species group. See Table 1 for species within each group. Each segment of each vertical bar represents the portion of total landings attributable to one of the five major groups (offshore pelagics, grouper-snappers, lobsters, bait fishes, and unknown miscellaneous fishes) or other species.

spadefish (*Chaetodipterus faber*), and tripletail (*Lobotes surinamensis*).

The persistence of each group in the harvest varied throughout the year. Offshore pelagics (OP, e.g. swordfish, *Xiphias gladius*) and tuna (*Thunnus* spp.), grouper-snapper (GS), bait fish (BF, e.g. ballyhoo, *Hemiramphus brasiliensis*), and unknown miscellaneous (UM) fishes occurred in each month. Lobsters (LB) occurred during each month of the open season (August–March) but declined steadily from the opening of the season. Blue crabs (BC, *Callinectes sapidus*) occurred in summer and fall (May–September and December). Inshore pelagics (IP, e.g. mullet, *Mugil* spp.) occurred in January, March, April, and August. Stone crabs (SC, *Menippe mercenaria*) and inshore demersals (ID, e.g. sheepshead, *Archosargus probatocephalus*) were landed in November and December. Shrimps (*Penaeus* spp.) occurred in February and April. Offshore demersals (OD, e.g. tilefish [Malacanthidae]) occurred only in July.

Offshore pelagics (OP) accounted for the largest proportion of landings in all months (Fig. 2). They also accounted for the majority of landings on most of the fishing trips from May through July, again in October and November. Groupers and snappers accounted for much of the remaining landings and dominated trips in January and December. Together the offshore pelagics (OP) and the grouper-snappers (GS) accounted for over 80% of landings in all months, except August, September, and October. The addi-

tion of lobster (LB) landings raises the totals for August and October to more than 80%. Inclusion of bait fish landings helps to account for more than 80% of September landings. Unknown miscellaneous (UM) fishes account for most of the remaining landings in each month.

### Species associations

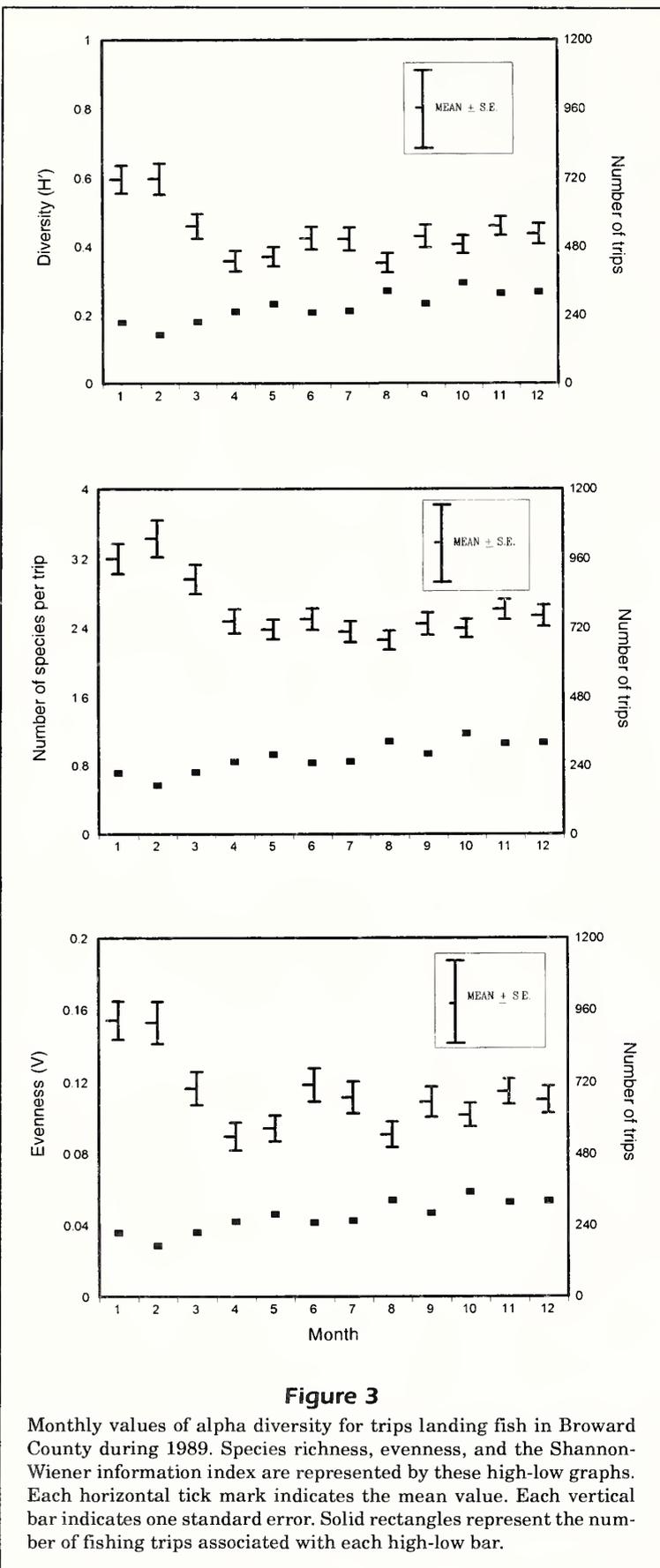
Despite the classification of landings (trip assemblages) into distinct groups of species assemblages, associations between individual species were weak. Less than 4% of the unique pair-wise comparisons of species occurrence in any given month were significant. One fourth to half of these accounted for more than 50% of the variation in their ranked abundances. Four associations accounted for more than 70% and only one association accounted for more than 80% of the variation in correlated species abundances. Roughly half of the significant associations were positive. However, most of these were between two uncommon (landed on less than ten trips per month) species. Only the swordfish-tuna association was consistently strong ( $r' > 50\%$ ) and positive. Mutton snapper (*Lutjanus analis*) was positively associated with black grouper (*Mycteroperca bonaci*), mojarras (Gerreidae), and a number of other species, but these associations were not evident in every month and were usually weak ( $r' < 50\%$ ). Only significant associations are considered in the following discussion.

**Table 3**

Dissimilarity and probabilities in comparing all pair-wise combinations of species assemblages landed in Broward County, Florida, during each month of 1989. The upper half matrix contains the dissimilarity values based on the Heterogeneity Ratio (HR), which is a measure of beta diversity. The lower half matrix contains the associated probabilities, generated by faunal similarity analysis (FAUNSIM), that the number of species observed to be common to each pair was less than that expected. Values in boldface are significant at the 0.05 level or greater.

Month	HR											
	1	2	3	4	5	6	7	8	9	10	11	12
1	—	1.057	1.073	1.107	1.084	1.179	<b>1.186</b>	1.143	1.104	<b>1.181</b>	1.112	1.112
2	0.07	—	1.071	<b>1.141</b>	<b>1.157</b>	<b>1.262</b>	<b>1.201</b>	1.118	<b>1.137</b>	<b>1.176</b>	1.109	<b>1.128</b>
3	0.53	0.40	—	1.069	1.101	<b>1.233</b>	<b>1.149</b>	1.087	1.050	<b>1.150</b>	1.089	1.089
4	0.80	<b>0.99</b>	0.43	—	1.098	<b>1.205</b>	<b>1.182</b>	1.101	1.064	<b>1.163</b>	<b>1.158</b>	1.105
5	0.38	<b>0.99</b>	0.67	0.75	—	1.160	<b>1.161</b>	<b>1.137</b>	1.098	<b>1.124</b>	1.081	1.082
6	0.71	<b>1.00</b>	<b>0.98</b>	0.87	0.47	—	1.161	1.159	<b>1.201</b>	<b>1.245</b>	<b>1.234</b>	1.212
7	<b>1.00</b>	<b>0.99</b>	<b>0.95</b>	<b>1.00</b>	<b>0.99</b>	0.62	—	1.157	1.137	<b>1.229</b>	<b>1.212</b>	<b>1.151</b>
8	0.93	0.80	0.66	0.73	<b>0.99</b>	0.66	1.00	—	1.063	<b>1.187</b>	1.130	1.089
9	0.80	0.97	0.33	0.51	0.86	<b>0.96</b>	0.83	0.10	—	<b>1.148</b>	<b>1.110</b>	1.090
10	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>	<b>0.99</b>	<b>0.95</b>	<b>0.99</b>	<b>1.00</b>	<b>1.00</b>	<b>0.99</b>	—	1.115	1.095
11	0.76	0.88	0.75	<b>1.00</b>	0.58	<b>0.97</b>	<b>1.00</b>	<b>0.94</b>	<b>0.96</b>	0.86	—	1.070
12	0.77	<b>0.96</b>	0.75	0.84	0.50	0.90	<b>0.95</b>	0.66	0.88	0.67	0.44	—

FAUNSIM probability



A strong, positive association between swordfish and both bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*) existed in spring and fall. In December, the association between each of these tunas and swordfish accounted for over 70% of the variations in their landings. Swordfish showed significant negative associations with shark in the early part of the year and with dolphin (*Coryphaena hippurus*) throughout the year.

In 1989, all species of shark landed were reported under the unspecific "mixed shark" code. At least eleven species of shark are landed throughout the state, but blacktip shark (*Carcharhinus limbatus*), sandbar shark (*Carcharhinus plumbeus*), and shortfin mako (*Isurus oxyrinchus*) are most common in the landings from southeast Florida (Brown<sup>7</sup>). Shark landings were negatively correlated with all significant associates in Broward County. There were strong negative associations between sharks and both groupers and snappers throughout most of the year and between sharks and dolphins in spring and fall.

Dolphin landings were negatively correlated with all significant associates except for a few rare positive associations with tunas in mid-summer. They showed strong negative associations with groupers in the early part of the year and with snappers throughout most of the year.

King mackerel (*Scomberomorus cavalla*) is a migratory species and a seasonal member of the offshore pelagics (OP) group (Manooch, 1979; Collette and Russo, 1984). Those caught in the waters off Broward County are considered part of the Atlantic stock from 1 April until 1 November, when they become part of the Gulf-Atlantic stock. The fishery on the Gulf-Atlantic stock is quota-regulated in Florida and usually closes in late December or early January. In 1989, king mackerel landed in Broward County displayed strong, negative associations with dolphin, groupers, and snappers. It also was rarely associated with baitfishes, lobsters, and other offshore pelagics.

Spiny lobster (*Panulirus argus*) landings in Florida occur only during the open sea-

<sup>7</sup> Brown, S. T. 1994. Florida Marine Research Inst., Florida Dep. Environmental Protection, 100 8th Ave SE, St. Petersburg, FL 33701. Personal commun.

son (6 August through 31 March). Broward County lobster landings were consistently negatively associated with yellowtail snapper (*Ocyurus chrysurus*) and "mixed snapper." They were positively associated with grunts (Haemulidae) and "other groupers" in December. A strong positive association with Spanish lobster (*Scyllarides aequinoctialis*) occurred in October.

Black grouper occurred with nine other species and UM. It was negatively associated with lobsters and members of the offshore pelagics group, especially dolphin, king mackerel, and shark. There was a consistent positive association only with mutton snapper.

Hogfish (*Lachnolaimus maximus*) occurred with a dozen other species and UM. This species showed a strong and consistent negative association with sharks and sporadic positive associations with mutton snapper in summer and fall.

Mutton snapper was significantly associated with the largest number of other species (25) but showed consistent associations with only a few. There was a consistent negative association with sharks and dolphin throughout most of the year. Landings of mutton snapper were positively related to those of groupers and mojarra (Gerreidae) in the latter half of the year. This species was frequently associated with hogfish in summer and fall.

Yellowtail snapper was also significantly associated with a large number of other species (18), but showed few consistent associations. Positive associations were rare but negative associations with dolphin, shark, and spiny lobster were common.

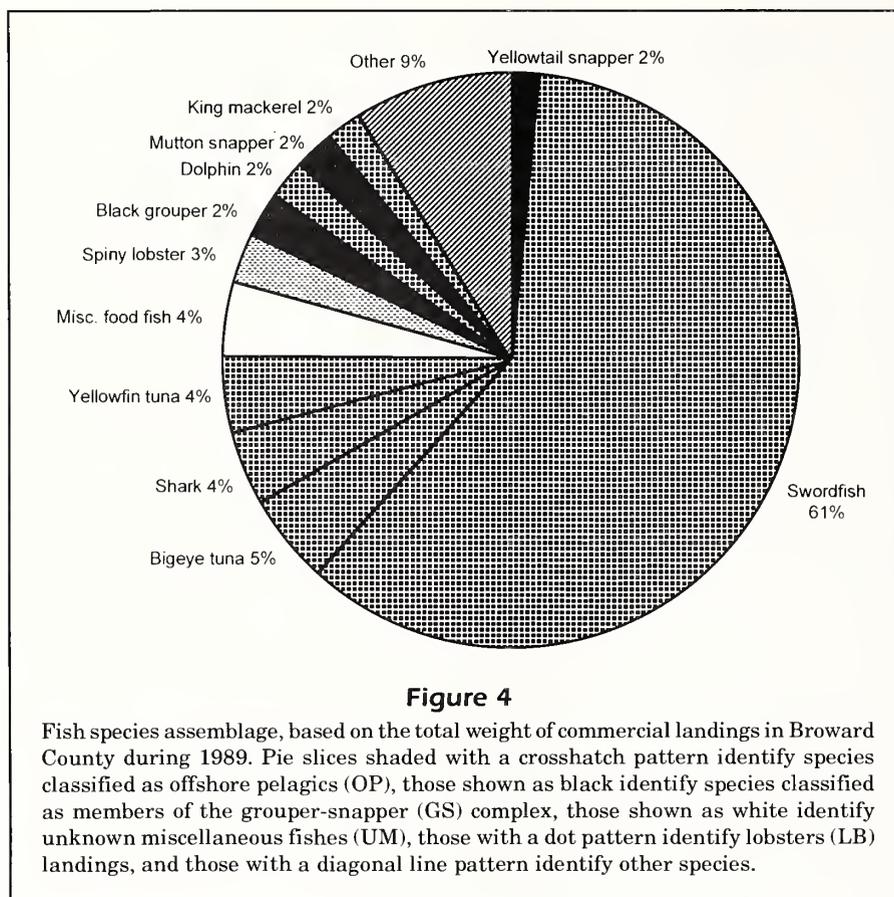
## Species assemblages

Seasonal differences suggested by changes in diversity and similarity were evident in the species assemblages landed each month (Table 4). Offshore pelagic species dominated Broward County landings in 1989 (Fig. 2). Swordfish, shark, and dolphin were listed on at least ten trip tickets every month. Swordfish dominated annual landings as well as those for each month; it accounted for 60% of annual landings (Fig. 4) and more than 50% of landings in all months except August, September, and October. Other offshore pelagics accounted for 18% of annual landings (Fig. 4). Bigeye and yellowfin tunas occurred commonly in nine or more months but were uncommon in the summer. King mackerel occurred commonly in all months except January through March, when the fishing season was closed. Spiny lobster accounted for less than 3% of the annual landings (Fig. 4) but made a large contribution to the landings in the first part of the open season (August: 15% of the landings) and tapered off throughout the fall. Groupers and snappers accounted for more than 6% of the annual landings, but only black grouper, mutton snapper, and yellowtail snapper accounted for more than 1% of annual landings each (Fig. 4). Black grouper, hogfish, mutton snapper, yellowtail snapper, and mixed snappers occurred commonly in every month. Red grouper (*Epinephalus morio*) was common every month, except January. Gag (*Mycteroperca microlepis*) was common only in April, and "other grouper" in winter and September. Unknown mis-

**Table 4**

Species contributions (as a percentage) to monthly landings in Broward County, Florida, during 1989. (See Table 1 for group definitions.)

Group	Species or complex	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GS	Black grouper	3.0	4.3	2.0	1.8	1.7	2.0	3.7	3.8	4.6	3.4	1.6	1.7
	Mutton snapper	1.4	2.3	0.7	0.6	0.9	2.2	3.3	2.5	5.1	5.9	5.1	1.3
	Yellowtail snapper	3.2	2.0	1.0	0.7	0.9	2.2	2.9	4.8	5.2	2.3	1.6	0.4
	Mixed snapper	0.7	0.5	0.3	0.4	0.4	0.6	2.0	1.5	2.1	2.4	1.3	0.7
LB	Lobster	2.0	1.4	1.9	0.0	0.0	0.0	0.0	16.5	9.0	7.8	4.5	4.0
OP	Bigeye tuna	5.0	8.3	5.4	1.9	3.2	2.7	1.8	5.8	1.1	6.8	7.6	7.7
	Dolphinfish	1.8	1.7	1.6	1.0	1.4	5.4	9.7	8.8	4.7	2.0	0.5	0.7
	King mackerel	0.0	0.0	0.0	9.0	1.7	0.4	0.7	2.3	0.7	1.8	0.6	1.0
	Shark	4.3	3.4	5.8	5.7	6.6	4.7	2.3	4.1	5.2	4.0	1.9	2.4
	Swordfish	62.8	53.5	68.2	67.2	71.4	68.2	54.5	25.4	29.5	38.6	55.2	65.2
	Yellowfin tuna	2.3	3.3	1.8	3.6	3.3	5.2	4.4	8.0	5.7	6.8	7.3	4.8
UM	Misc. food fish	5.0	5.0	3.1	2.7	3.3	3.7	6.6	5.7	10.6	7.7	3.4	3.0
	Other species	12.3	13.1	13.2	11.1	10.4	5.8	8.7	14.0	13.6	8.3	12.0	8.3



cellaneous food fish accounted for 4.2% of Broward County landings in 1989.

## Discussion

The diversity of the Broward County harvest in 1989 was relatively low compared with that of a natural marine fish community in Florida. The tropical reef communities of the Florida Keys are some of the richest in the world; more than 500 fish species have been reported on Alligator Reef alone (Starck, 1968). Species-rich fish communities, however, are not restricted to coral reef habitats. Gilmore (1977) and Gilmore and Hastings (1983) reviewed fish collections associated with the Indian River system. They were able to compile a list of 685 species and projected that more than 700 species should be found in that region. The species richness in those studies varied considerably (26–275 species) from habitat to habitat. Grass flats, inlets, and offshore reefs had the richest fish faunas (>200 species). From offshore continental-shelf habitats alone, more than 170 species were found. Anderson and Gehringer (1965) collected 64 species of fish in 94 hours of trawling over the

continental shelf of the Indian River region. Herrema's (1974) marine fish collections from off parts of Broward and Palm Beach counties included 583 species, although many of these are not commercially harvested or are taken in limited number for aquarium collectors. Nevertheless, 76 species of fish and shellfish commercially landed from more than 3,000 fishing trips is a poor representation of the fauna known to be present.

This low species richness is, of course, a reflection of the selectivity of commercial fishing efforts. Only certain sizes of the vulnerable species are available to the gear and only a fraction of these are captured. However, it is unlikely that a catch will be restricted to the two or three species that were landed per trip, on average (Fig. 3) (Fisher et al., 1943). Fishermen keep only the species and sizes that have a market value, discarding all others. The clear seasonal changes in the assemblages landed reflects a balance between changing availability of different fish species to the gear and market values of the various species. Presumably, the commonly landed species were the most valuable. Offshore pelagic species, especially swordfish, were clearly targeted in 1989, as were groupers and snappers. The low summer

landings of offshore pelagics may reflect a decrease in availability as swordfish moved out of the fishing area (Hoey<sup>8</sup>) or a decline in market value, or both. An examination of catch records showed no evidence that fishermen who harvest offshore pelagics had switched to another fishery. However, the increase in landings of lobsters by some fishermen who target grouper-snappers and inshore demersals is indicative of a shift to the more valuable lobster fishery when the season opens.

The grouping of trips into distinct clusters that roughly correspond to different habitats indicates a structure among the fishermen, based on what they target. The use of specific gear and fishing sites restricts the diversity of the catch. The fisherman's ability to use different gear (sometimes on the same trip) and visit different sites is a key characteristic of Florida's fisheries. Twenty-five types of gear were registered by Broward County fishermen in 1989. Such unusual combinations as longlining for swordfish and pulling traps for lobster commonly occur on the same trip. Six hundred and ninety-eight of the 907 fishermen registered rod-and-reel as one of the gear types they possessed (not necessarily used). Each fisherman may register more than one type of gear. The fishing potential of each gear is also different. Only 72 fishermen registered surface long lines, but those 72 lines had a total of 29,445 hooks.

Florida also requires special licenses for use of certain gear and for landing some species. Two hundred and eighty-two lobster (crawfish) licenses were issued to Broward County fishermen in 1989 (207 fishermen registered a total of 32,433 traps). Other special licenses included: blue crab (76), stone crab (123), shrimp (2), and purse seine (1).

Species groups identified by the cluster analysis (Table 1) correspond to those that are vulnerable to different gear types. Species in the offshore pelagic group are caught in offshore surface waters with hook-and-line and surface long lines (Berkely et al., 1981). Most of the common groupers and snappers are caught in shallow, nearshore or shelf waters with hook-and-line. Bait fish are found in all surface waters and are caught with small purse seines and lampara nets. Lobsters and stone crabs are found offshore, whereas blue crabs are harvested from inshore and estuarine waters. All three are caught in traps, but lobster are also landed with shrimp in trawls. By having more than one gear type, a fisherman can simply rerig his vessel (and possibly work a

different site) and partake of a completely different component of the fishery.

The general negative associations among species is another indication of the selective behavior of commercial fishermen. Since the ideal catch for a fisherman is a monocrop of the most valuable targeted species available, landed assemblages are likely to be as close to that ideal as possible. The catch is sorted and filtered such that the vessel's hold capacity is filled with the greatest amount of the most valuable species caught by the gear (Gulland, 1983). Thus, one would expect some trips to be monospecific, others to include a minimum number of other species. Without detailed information on discards and fisherman behavior, it is difficult to determine if negative associations represent an ecological condition whereby the two species avoid each other (or have different, but overlapping habitat requirements) or if they are an artifact of gear selection and fisherman behavior. Most likely they are the result of a combination of these factors.

The selectivity of the commercial fishing process and the nonrandom sampling of the natural environment makes it extremely difficult to use commercial landings data to gain insight into the natural fish community of a region. The commercial data provide only one component of the mortality affecting a fish community. Landings by recreational fishermen can be substantial (Essig et al., 1991) but are often unavailable. Moreover, fish discarded at sea often represent the largest component of fishing mortality in a region (FAO, 1973); the market values that drive the selection process are often not available with the landings data. Nonrandom spatial and temporal distribution of harvest can yield only biased estimates of fish population sizes, and the extent of that bias cannot be determined.

## Conclusions

There was clear structure to the commercial fishery harvest in Broward County during 1989. The low diversity, classification of trips into habitats fished, and negative species associations were clear indications of the selectivity in the system. A rich variety of species were landed by the fishery as a whole, but fishermen focused individual trips on a restricted subset of these species. The multispecies nature of the fishery and the potential for fishermen to exploit different components of the fishery are important features and should be carefully considered when forming management strategies.

These commercial data tell us little about the natural fish community from which the harvest was

<sup>8</sup> Hoey, J. J. 1985. Addendum to the source document for the swordfish fishery management plan, Part I. Prepared by and available from: South Atlantic Fishery Management Council, 1 South Park Circle, Suite 306, Charleston, SC, 132 p.

drawn. All that can be stated with certainty about the biological community is the tautology: the fish that were landed were present at the site where the gear was deployed and were available to the gear used at the time. The biases introduced by the selectivity of this system obscure events in the natural system and provide little insight into the changes in the fish community. However, these data do show a clear structure of the harvest due to fishing behavior and how that structure changes seasonally. The causes of those changes remain unclear. To address this problem, more effort in quantifying discards, recreational fishing mortality, and natural variability is needed, as well as a better understanding of the accessibility and economics driving the social system.

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**Abstract.**—This study compared the hatching season and the actual spawning season of spring- and autumn-spawning herring in the northern Gulf of St. Lawrence as determined by otolith characteristics and maturity stages, respectively, to measure the crossover between the two spawning populations. The growth characteristics of two cohorts that showed significant crossover were contrasted with those of a cohort that did not. It was concluded that variable juvenile growth does influence the adoption of the season of first spawning in these populations, and therefore the progeny of a given seasonal-spawning population may recruit to a local population that has a different reproductive season. It was also shown that the twinning of year-class strength can be explained by the crossover of a large number of individuals from one seasonal spawning population to another. The data presented indicate that the spawning season that is established at the time of first maturation is maintained for the remainder of adult life. The present study therefore does not support the concept of discrete sympatric seasonal-spawning populations in Atlantic herring.

## Year-class twinning in sympatric seasonal spawning populations of Atlantic herring, *Clupea harengus*

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The current theory on Atlantic herring population structure, as it relates to sympatric spring- and autumn-spawning herring, considers them to be discrete populations with independent life histories (Iles and Sinclair, 1982). This concept has largely been based on evidence of significant homing precision to spawning grounds as revealed by tag returns (Hourston, 1982; Wheeler and Winters 1984, a and b; Stevenson et al.<sup>1</sup>; Hart et al.<sup>2</sup>; Stobo<sup>3</sup>) and on studies that have noted significant differences in meristic and morphometric measurements, such as fin-ray counts and otolith characteristics (Messieh, 1972; Parsons, 1973; Postuma, 1974), as well as in life history parameters, such as mean fecundities (Baxter, 1959; Messieh, 1976).

However, several observations are difficult to explain within the discrete population concept: 1) typical spring-type otoliths are often found in autumn-spawning herring and vice versa (Messieh, 1972; Aneer, 1985); 2) "twinning" of recruitment strength between spring- and autumn-spawning year classes (see below); and 3) the lack of genetic divergence between seasonal spawning populations as demonstrated from numerous electrophoretic and mtDNA studies (Grant, 1984; Kornfield and Bogdanowicz, 1987; Safford and Booke, 1992). In light of the conflicting evidence for stock discreteness, an alternative

concept has been proposed whereby seasonal spawning populations are seen as subunits of a larger population, within which there exists a "dynamic balance" characterized by extensive gene flow (Smith and Jamieson, 1986).

Otolith characteristics and maturity stages have been used for many decades to determine the spawning affinity of individual herring from sympatric seasonal-spawning populations. Maturity stages are the preferred method for determining the actual spawning season of mature herring because the state of maturation can be used reliably to ascertain the spawning season throughout the year (McQuinn, 1989). On the other hand, otolith characteristics, being related mainly to environmental conditions at birth, are used to determine the hatching sea-

<sup>1</sup> Stevenson, J. C., A. S. Hourston, K. J. Jackson, and D. N. Outram. 1952. Results of the West Coast of Vancouver Island herring investigation, 1951–52. Report of the British Columbia Provincial Fisheries Department, Victoria, British Columbia, Canada, p. 57–87.

<sup>2</sup> Hart, J. L., A. L. Tester, and J. L. McHugh. 1941. The tagging of herring (*Clupea pallasii*) in British Columbia: insertions and recoveries during 1940–41. Report of the British Columbia Provincial Fisheries Department, Victoria, British Columbia, Canada, p. 47–74.

<sup>3</sup> Stobo, W. T. 1982. Tagging studies on Scotian shelf herring. Northwest Atlantic Fisheries Organization (NAFO) Research SCR Document 82/IX/108. Ser. No. N617, 16 p. P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

son (Einarsson, 1951; Postuma and Zijlstra, 1958; Messieh, 1972). The comparison of hatching season with spawning season as determined by these two methods, respectively, thus provides us with a rare opportunity to study the reproductive interactions between sympatric seasonal-spawning herring populations.

As with most herring populations, herring from western Newfoundland (Canada) are characterized by the periodic appearance of very large year classes followed by several years of relatively poor recruitment. In addition, the sympatric seasonal-spawning populations in eastern Canadian waters often show year-class twinning (Winters et al., 1986; de Lafontaine et al., 1991). This phenomenon is most evident when a strong autumn-spawning year class of a given year coincides with a strong spring-spawning year class of the following year. Twinning is relatively common with seasonal-spawning populations but does not always occur. It is also true that year-class twinning rarely occurs between successive spring- and autumn-spawning year classes of the same year.

Winters et al. (1986) showed a weak, though significant, relationship between year-class strength (natural log scale) of autumn-spawning herring in eastern Newfoundland and that of spring spawners of the following year. An example where year-class twinning occurred in the western Newfoundland herring populations is with the 1979 autumn-spawning and 1980 spring-spawning year classes, both of which were very large (McQuinn and Lefebvre<sup>4</sup>). However, the 1982 spring-spawning year class was also very large but had no large autumn-spawning twin in 1981. Again we observed twinning with the 1986 and 1987 autumn- and spring-spawning year classes. What then are the characteristics that distinguish these year classes and that might explain why twinning occurred in 1979–80 and 1986–87, but not in 1981–82?

Year-class twinning was first reported in herring by Einarsson (1952), who termed it "year-class strength parallelism." He speculated that favorable oceanographic and feeding conditions occurring from the fall of one year until the following summer resulted in a parallelism in larval survival between the two spawning populations. However, an alternative explanation is that year-class twinning is simply a consequence of straying between sympatric spring- and autumn-spawning populations, i.e. significant numbers of individuals from a large cohort of one

seasonal-spawning population subsequently spawn in the other season, creating a strong year class in both populations. Jean<sup>5</sup> and Graham (1962) suggested that the determination of spawning season of sympatric herring populations may be influenced by juvenile growth rates. Winters et al. (1986) presented data in support of their hypothesis that faster-growing spring-spawned juveniles may become autumn-spawners and conversely that slow-growing autumn-spawned juveniles may spawn in the spring. The objective of the present study is to use the otolith characteristics and maturity stage methods to establish whether indeed juvenile growth rates (as represented by size at age) have an effect on the determination of the onset of first maturation and thus the establishment of spawning season in Atlantic herring.

## Materials and methods

Data for this study were collected from the west coast of Newfoundland herring fishery from 1982 to 1990 (after 1990 otolith characteristics of mature herring were no longer determined by our agers). Samples were frozen and shipped to the Fisheries and Oceans laboratories for detailed analyses. Basic biological data (total length, total weight, gonad weight, and otolith characteristics, as well as the number of winter rings from which age was determined) were recorded for all specimens.

The hatching season was ascertained for each fish from otolith characteristics by applying the standard criteria (the size and type—opaque or hyaline—of the nucleus) developed by the Canadian Atlantic Fisheries Scientific Advisory Committee as described by Cleary et al.<sup>6</sup> These criteria were developed from the rationale that rapid growth in the first summer of spring-spawned herring results in a small opaque otolith nucleus. Conversely, the slow first-winter growth of autumn-spawned herring results in a large hyaline otolith center and the first-winter ring is formed only in their second year (Jakobsson et al., 1969; Postuma, 1974). Although the assignment of hatching season is determined subjectively from these criteria, consistency between agers has been shown to be relatively high. A comparative study was

<sup>4</sup> McQuinn, I. H., and L. Lefebvre. 1994. An assessment of the west coast of Newfoundland (NAFO division 4R) herring resource up to 1993. Department of Fisheries and Oceans (DFO) Res. Doc. 94/43, 48 p. Atlantic Stock Assessment Secretariat, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

<sup>5</sup> Jean, Y. 1956. A study of the spring and fall spawning herring *Clupea harengus* L. at Grande-Rivière, Bay of Chaleur, Québec. Contribution 49 of the Department of Fisheries, Québec, Québec, Canada, 76 p.

<sup>6</sup> Cleary, L., J. J. Hunt, J. Moores, and D. Tremblay. 1982. Herring aging workshop; St. John's, Newfoundland, March 1982. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 82/41, 10 p. CAFSAC, Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

conducted involving our ager and several other experienced otolith readers who used otoliths collected from throughout the Gulf of St. Lawrence (Savard and Simoneau<sup>7</sup>). This study showed a high agreement between two agers from our laboratory in Quebec (87%) and agers from the southern Gulf of St. Lawrence and eastern Newfoundland (75 and 76%, respectively) in the assignment of seasonal-spawning type from otoliths.

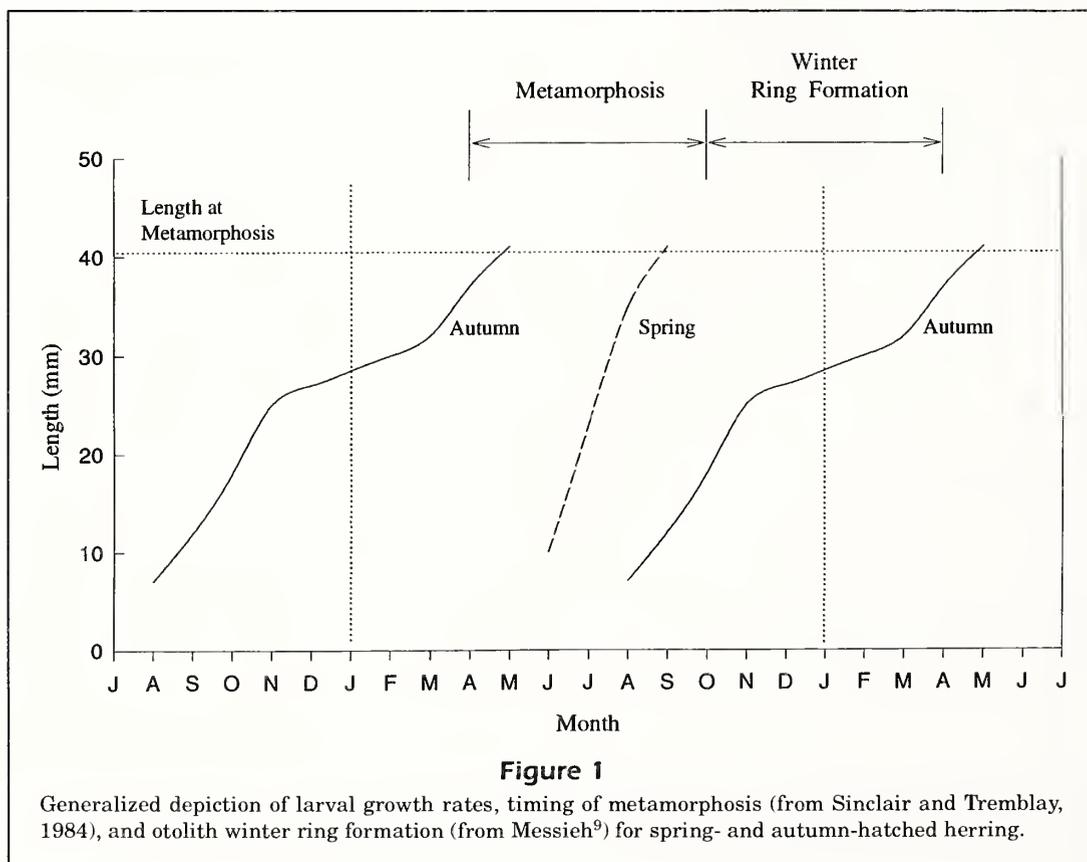
The actual spawning season of the mature individuals was determined from the stage of sexual maturity of each individual by using a temporal gonadosomatic index model (McQuinn, 1989). This model identifies the spawning season by first determining the maturity stage from the ratio of the gonad weight to a power function of the total length and by relating this state of maturation to the month of capture. Although spawning can occur from April

to October, the vast majority of spring herring spawn in May and June, whereas the autumn herring spawn mainly from mid-August to September (Haegele and Schweigert, 1985). The date separating the two spawning seasons was arbitrarily chosen to be 1 July, as relatively little spawning occurs in late June and early July (McQuinn, 1989; Cleary et al.<sup>6</sup>).

Throughout this paper, a distinction is made between the number of rings read from the otoliths and the actual age of the fish because age determination depends upon whether an individual is assigned as a spring spawner or an autumn spawner. Most autumn-spawning herring (August–November) do not produce a winter ring on the otolith in their first year of life (Einarsson, 1951; Jakobsson et al., 1969; Rosenberg and Palmen, 1982; Hunt et al.<sup>8</sup>). The formation of the winter ring takes place between October and April–May in metamorphosed juveniles

<sup>7</sup> Savard, L., and M. Simoneau. 1983. Lecture comparative d'otolithes de hareng et utilisation des stades de maturité sexuelle pour l'attribution du groupe reproducteur. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 83/86, 28 p. Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

<sup>8</sup> Hunt, J. J., L. S. Parsons, J. E. Watson, and G. H. Winters. 1973. Report of the herring ageing workshop; St. Andrews, New Brunswick, 11–13 December 1972. International Commission for the Northwest Atlantic Fisheries (ICNAF) Res. Doc. 73/2, Ser. 2901, 2 p. ICNAF, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.



(Postuma, 1974; Messieh<sup>9</sup>), whereas newly hatched autumn spawners are still larvae (Fig. 1). Thus to assign correctly the age of a herring hatched in the autumn, one must add one year to the number of winter rings read from the otolith. Because spring-hatched herring metamorphose before their first winter and thus produce a winter ring in their first year, their proper age is equal to the number of winter rings. However, for any spring-hatched herring that subsequently reproduces in the autumn, its spawning season would be considered autumn with the maturity-stage method, and one year would be added to the number of rings read from the otolith. Following the same logic in reverse, if an autumn-hatched individual subsequently spawned in the spring, a year would not be added to the number of rings read from the otoliths and it would be assigned an age that was one year younger than its actual age. Therefore, the number of rings will be used when compar-

ing the biological characteristics for a given age between an autumn-spawning year class with the spring-spawning year class of the following year.

## Results

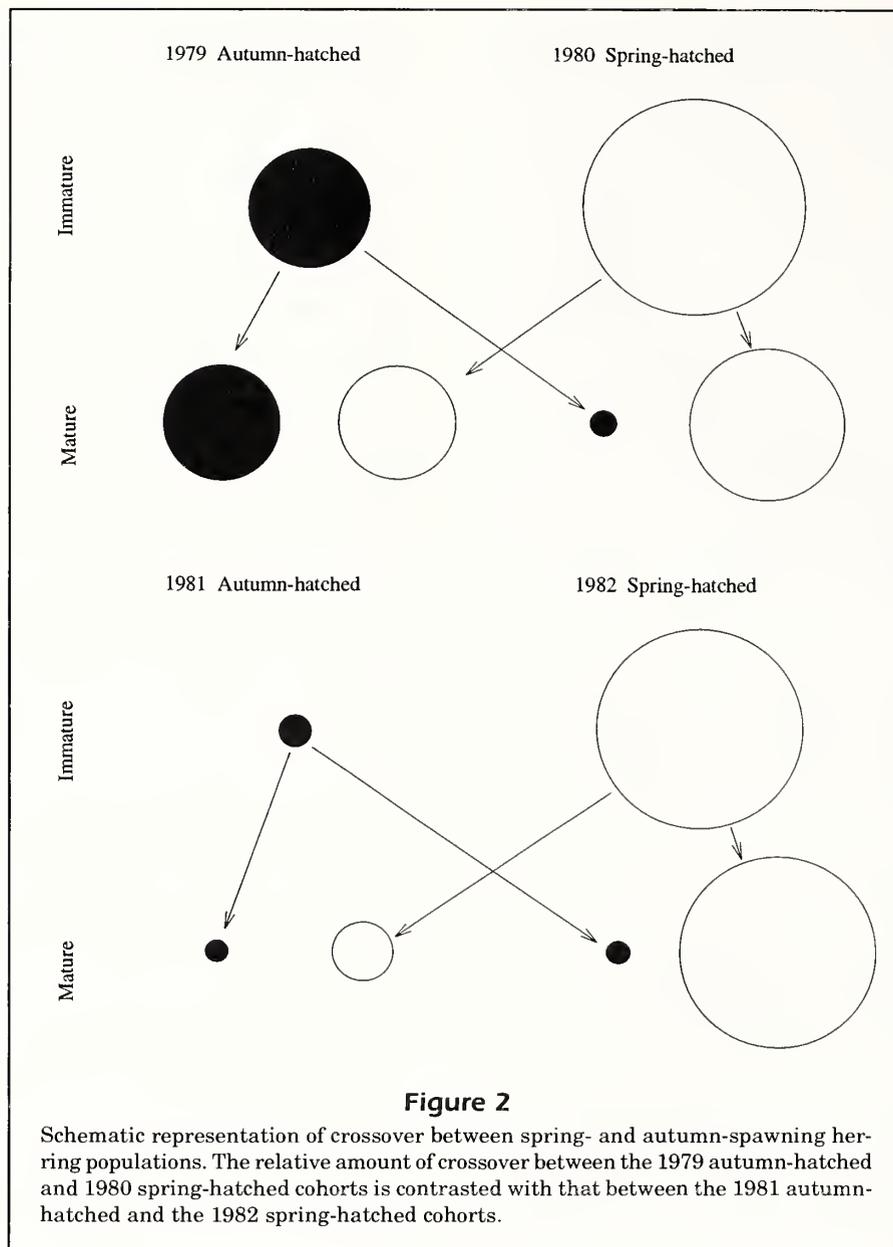
The proportion of spring- and autumn-hatched herring was estimated from the mature members of the 1979–80, 1981–82 and 1986–87 autumn- and spring-spawning year classes, respectively (Table 1). According to their otolith characteristics, the vast majority (>90%) of the 1980 and 1982 spring-spawning herring were also spring hatched. This pattern is consistent from age 3 through age 5 (age=no. of rings). However, a large percentage of the 1979 (40%) and 1981 (77%) autumn-spawning herring were also spring hatched, as judged from their otolith characteristics. Therefore, in both situations, there was a significant crossover from the strong spring-hatched cohort to the autumn-spawning population, in comparison with the number of autumn-hatched individuals. However, because the resulting 1979 autumn-spawning year class was also large, whereas the 1981 autumn-spawning year-class was not, this

<sup>9</sup> Messieh, S. N. 1974. Problems of ageing Atlantic herring (*Clupea harengus harengus* L.) in the ICNAF area. International Commission for the Northwest Atlantic Fisheries (ICNAF) Res. Doc. 74/59, Ser. 3274, 6 p. ICNAF, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

**Table 1**

Percentage of autumn- and spring-hatched herring that became mature autumn and spring spawners within the 1979, 1981, and 1986 autumn-spawning and within the 1980, 1982, and 1987 spring-spawning year classes off western Newfoundland (age is expressed as the number of otolith rings—see text).

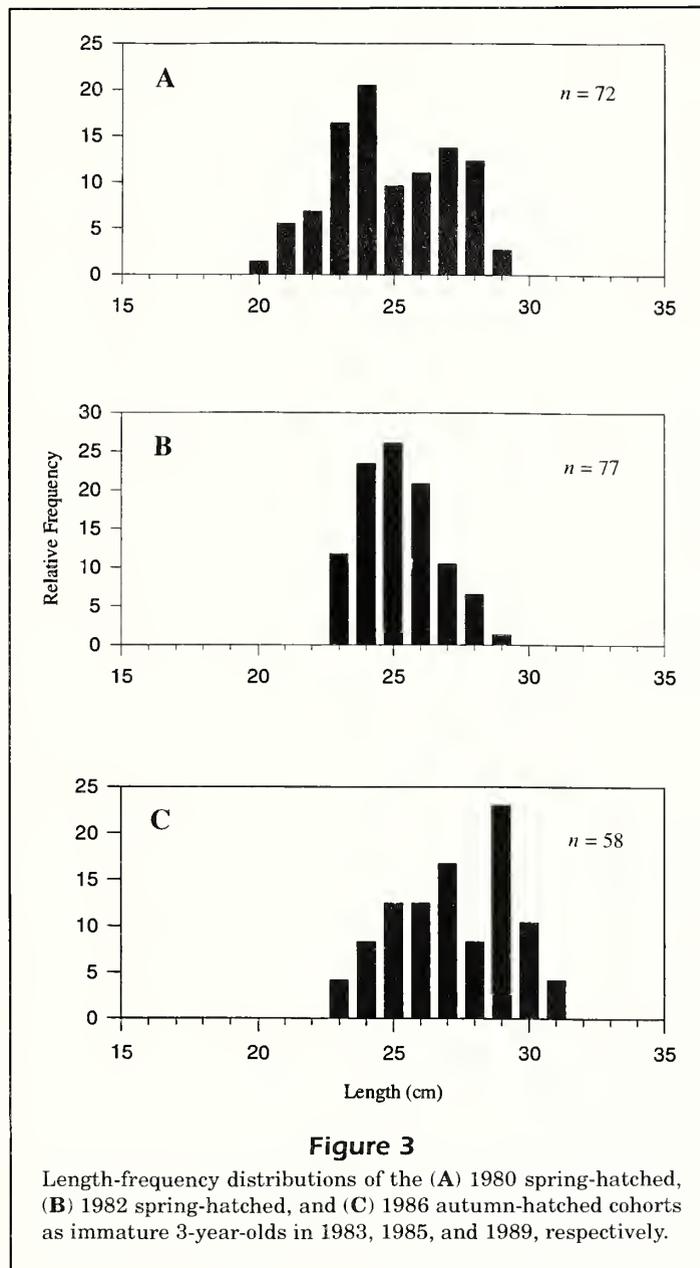
Year	No. of rings	1979 autumn-spawning year class			1980 spring-spawning year class		
		Autumn-hatched (%)	Spring-hatched (%)	<i>n</i>	Spring-hatched (%)	Autumn-hatched (%)	<i>n</i>
1983	3	34.5	65.5	712	90.6	9.4	402
1984	4	55.6	44.4	1923	92.3	7.7	1438
1985	5	60.4	39.6	1760	92.4	7.6	2590
Year	No. of rings	1981 autumn-spawning year class			1982 spring-spawning year class		
		Autumn-hatched (%)	Spring-hatched (%)	<i>n</i>	Spring-hatched (%)	Autumn-hatched (%)	<i>n</i>
1985	3	54.4	45.6	68	92.2	7.8	192
1986	4	30.7	69.3	140	95.2	4.8	481
1987	5	22.6	77.4	186	97.2	2.8	966
Year	No. of rings	1986 autumn-spawning year class			1987 spring-spawning year class		
		Autumn-hatched (%)	Spring-hatched (%)	<i>n</i>	Spring-hatched (%)	Autumn-hatched (%)	<i>n</i>
1990	3	86.0	14.0	57	68.8	31.2	32



crossover was much less important in absolute terms in the latter (Fig. 2). This pattern is different for the 1986 and 1987 autumn- and spring-hatched cohorts (Table 1). There appears to have been a larger net migration (31%) from the autumn-hatched cohort towards the spring-spawners at age 4 (age=no. of rings + 1). Furthermore, the 1979 autumn-spawning year class showed a trend of a decreasing proportion of spring-hatched individuals from age 4 to 6 as more autumn-hatched individuals matured and recruited to the year class (Table 1). Conversely, the 1981 autumn-spawning year class showed an increasing percentage of spring-hatched individuals with age owing to the overwhelming dominance of the large 1982

spring-hatched cohort compared with the small 1981 autumn-hatched cohort (Fig. 2).

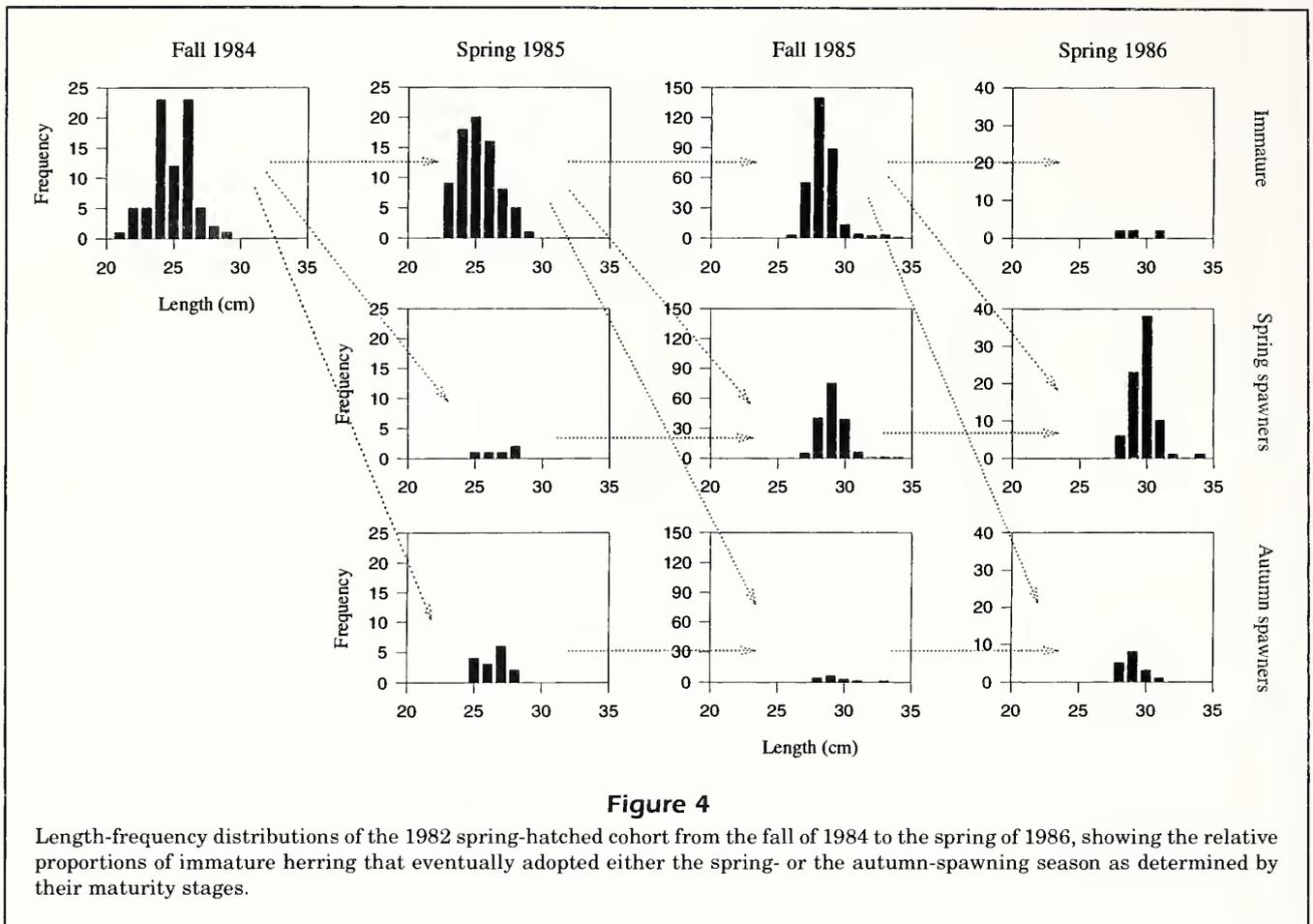
I have also summarized the mean lengths and standard deviations of the immature 1980 and 1982 spring-hatched cohorts to compare their average growth characteristics prior to their first spawning (Table 2). Although the means are similar at similar ages, the standard deviations are quite different, those for the 1980 cohort being 44% to 79% greater than the 1982 cohort from age 2 to age 3. The difference between the two cohorts is even more obvious when their length-frequency distributions at age 3 are compared (Fig. 3, A and B). The length distribution of the 1980 cohort is wider and bimodal. The



**Table 2**

Mean lengths and standard deviations of immature western Newfoundland herring from the 1980 and 1982 spring-hatched cohorts as 2- and 3-year-olds in the spring (April–June) and the fall (October–December) fisheries.

1980 spring-hatched cohort						1982 spring-hatched cohort					
Year	Age	Fishery	Mean length (cm)	SD	n	Year	Age	Fishery	Mean length (mm)	SD	n
1982	2	Spring	—	—	—	1984	2	Spring	187.96	12.87	11
		Fall	248.91	27.23	35			Fall	248.47	15.17	75
1983	3	Spring	247.86	20.87	72	1985	3	Spring	252.11	14.50	77
		Fall	278.80	17.43	585			Fall	283.27	10.56	310



**Figure 4**

Length-frequency distributions of the 1982 spring-hatched cohort from the fall of 1984 to the spring of 1986, showing the relative proportions of immature herring that eventually adopted either the spring- or the autumn-spawning season as determined by their maturity stages.

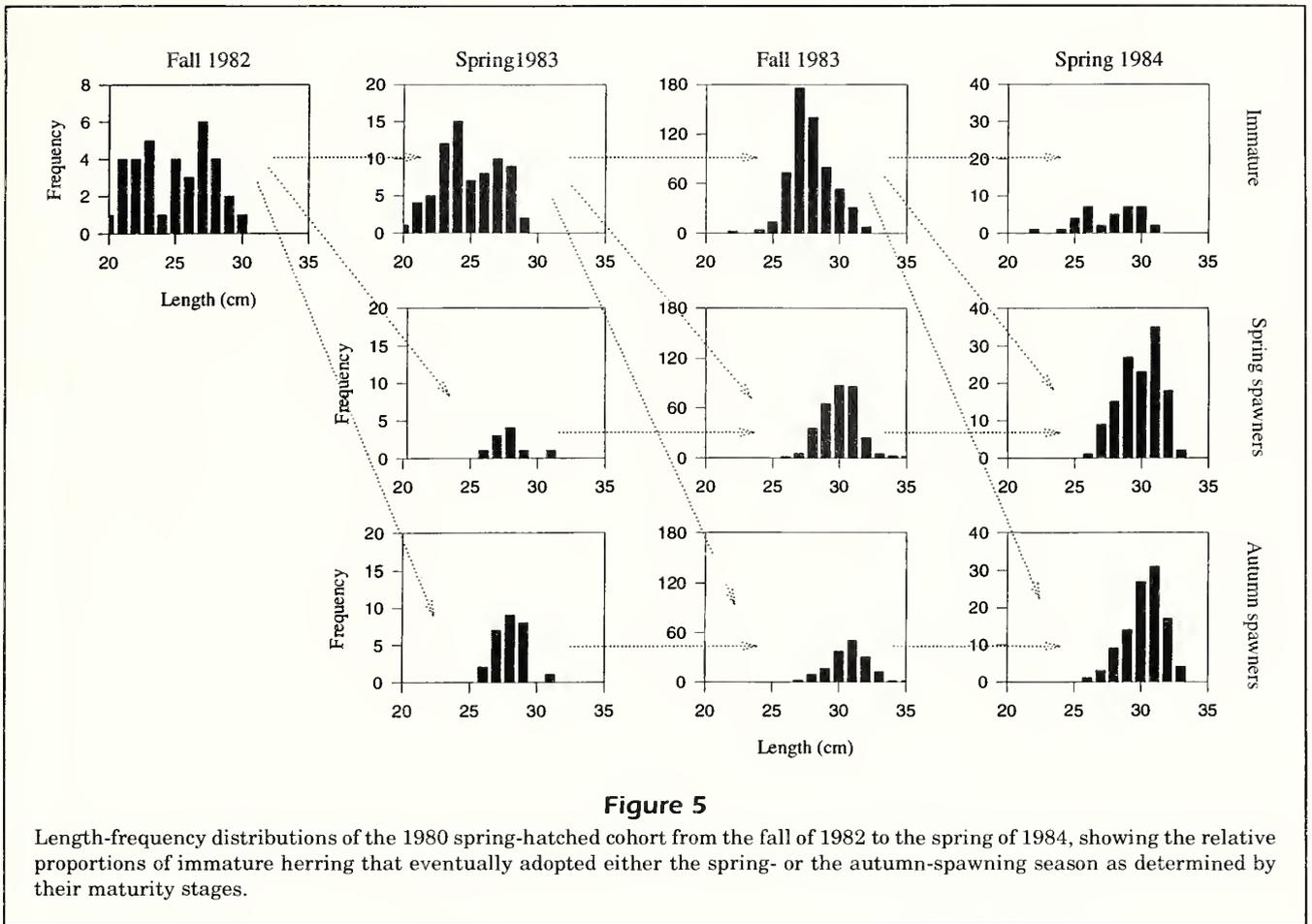
same pattern is evident for the 1986 autumn-hatched cohort, which also showed a large bimodal length-frequency distribution at age 3 (Fig. 3C).

The significance of these differences in length composition is shown by following these cohorts as they became mature and began to spawn. We observed that when the length-frequency distribution of the juvenile spring-hatched herring was unimodal and had a relatively small variance (1982 cohort), the majority of them spawned in the spring of 1986 at age 4 (Fig. 4). Conversely, when the juvenile length-frequency distribution was bimodal and had a relatively large variance (1980 cohort), there was an almost even split between those that became spring spawners and those that eventually became autumn spawners (Fig. 5). In addition, if one follows the 1980 spring-hatched cohort after maturity, those that became spring spawners were significantly smaller ( $t$ -test:  $P < 0.0001$ , SAS Institute Inc., 1985) than those that became autumn spawners (Fig. 6A). This length difference was sustained throughout their early adult life, i.e. from age 3 through age 6. A similar pattern

was also seen with the 1979 autumn-hatched cohort. Those that became spring-spawners were smaller at age (Fig. 6B), although the differences are not significant for certain ages owing to small sample sizes.

## Discussion

Einarsson (1952) hypothesized that year-class parallelism (twinning) in sympatric seasonal-spawning herring populations came about through a correlation between larval survival conditions in the fall of one year with conditions in the spring of the following year, assuming the larval stage to be the critical phase that determines year-class strength. However, given the ontogeny of the larvae of sympatric seasonal-spawning populations, it is difficult to conceive of a single mechanism by which both cohorts would experience similar survival conditions over a 10-month period, especially since twinning does not normally occur with two successive year classes within the same year. If one follows the development



**Figure 5**

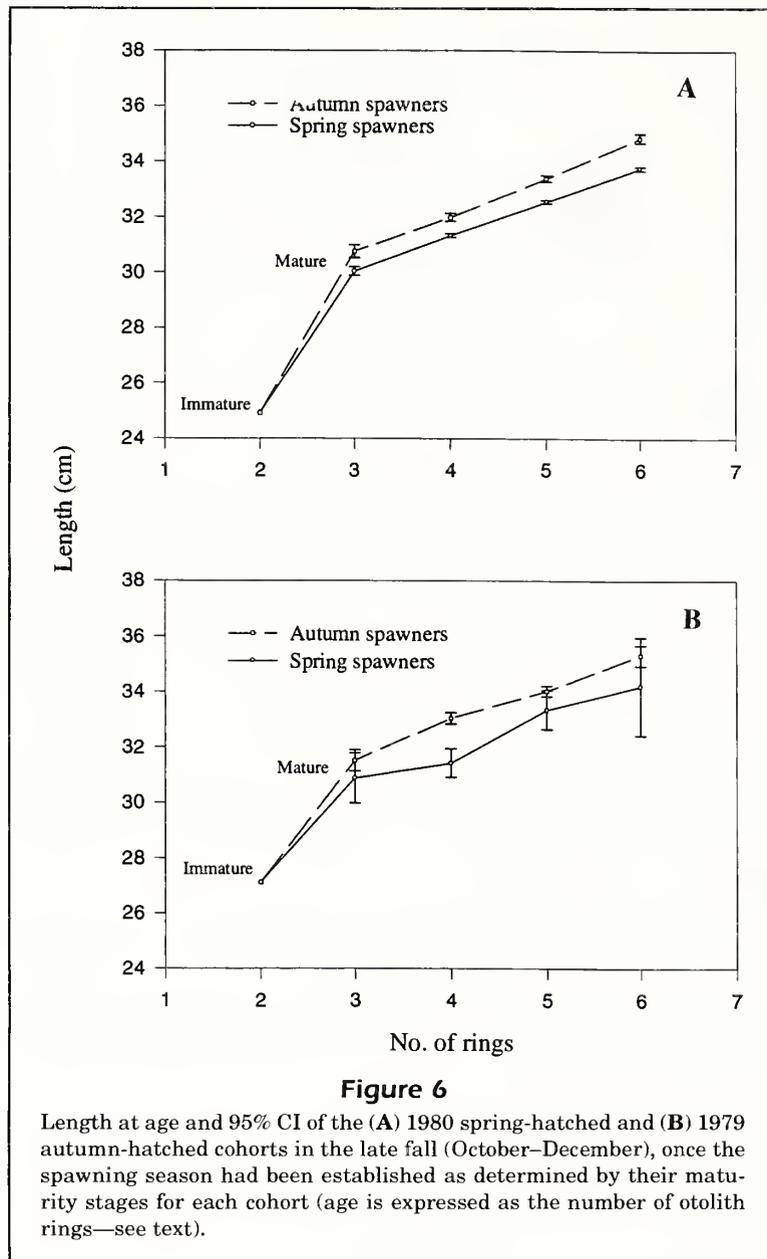
Length-frequency distributions of the 1980 spring-hatched cohort from the fall of 1982 to the spring of 1984, showing the relative proportions of immature herring that eventually adopted either the spring- or the autumn-spawning season as determined by their maturity stages.

of an autumn-hatched cohort and that of the spring-hatched cohort of the following year, from hatching through metamorphosis (Fig. 1), it is apparent that at no time are these two cohorts in the larval stage at the same time, i.e. the autumn spawners have metamorphosed before the spring spawners of the following year have hatched. Autumn-spawned herring in the northwest Atlantic hatch from August to November, remain as larvae throughout the winter (Iles and Sinclair, 1982), and metamorphose within a "window" between March and May (Sinclair and Tremblay, 1984). Larvae hatched in June or July from the spring-spawning event reach the required size for metamorphosis during September or October of their first year. Conditions affecting larval survival would therefore have to be favorable from September of one year to June of the next, but unfavorable between July and August for Einarsson's explanation to be credible.

Einarsson (1952) speculated that a strong standing stock of copepods in the autumn of one year may be correlated with enhanced copepod egg production

the following spring, thus favoring larval herring survival over this extended period, although the data available to him did not show this correlation. In addition, these enhanced survival conditions would not only have to exist over a long, but nonetheless precise period of time (September–June), but would also have to be extremely widespread. Twinning occurs in most if not all sympatric herring populations in the northwest Atlantic (de Lafontaine et al., 1991) and sympatric spring- and autumn-spawners do not necessarily use the same breeding locations nor the same larval retention mechanisms, i.e. spring and autumn spawners along the west coast of Newfoundland (McQuinn and Lefebvre<sup>4</sup>).

The present study supports the alternative hypothesis that the twinning of year classes can be explained by the crossover or straying of a significant number of individuals from one seasonal-spawning population to the other. Our results also support the hypothesis of Jean<sup>5</sup>, Graham (1962) and Winters et al. (1986) that variable growth rates in the juvenile phase lead to this crossover. Results from several



studies have concluded that either density-dependent (Anthony, 1971; Lett and Kohler, 1976) or density-independent factors (Moore and Winter, 1982), or both (Anthony and Fogarty, 1985; Haist and Stocker, 1985), contribute to the significant inter- and intra-annual variations in the growth rates of juvenile herring. There has developed a general consensus among these authors that differences observed in length at age between year classes of adult herring originated in the juvenile phase, before maturation. Further, Toresen (1990) compared the growth of juvenile Norwegian herring from the 1950's with that from the 1970's and concluded that variable growth

rates depended mainly on where the juveniles spent their early years. Large cohorts showed both density-dependent growth when these cohorts were distributed in the fjords, as well as environmentally induced growth variations when components of the cohort were distributed in less productive areas of the Barents Sea. This study demonstrated that different components of a single cohort can encounter different growth conditions before maturation and thus can experience different growth rates.

Density-dependent and environmentally induced variability in growth and condition in the juvenile phase is believed to affect the onset of first maturation.

tion in several teleost species (Lett and Doubleday, 1976; Holdway and Beamish, 1985; Rowe and Thorpe, 1990), including Atlantic herring (Marti, 1959; Raitt, 1961; Anthony and Fogarty, 1985; Haist and Stocker, 1985). Several studies have concluded that length, rather than age, is the "critical" factor determining the onset of first maturation in herring (Burd, 1962; Beverton, 1963; Toreson, 1990). Variations in growth rates within a cohort, whether they are density-dependent or not, will therefore influence the age at which different components of a cohort will reach the critical length.

We have seen in the present study that variable juvenile growth rates do influence the onset of first maturation in herring (the age of maturity) and thus affect which season is adopted for spawning. When the growth characteristics of a cohort were relatively uniform in early life, as represented by the unimodal length distribution of the immature 1982 cohort as 3-year-olds, most of the cohort subsequently matured in synchrony and spawned in the spring of 1986 as 4-year-olds. However, when the immature 3-year-old length-frequency distribution showed signs of differential growth rates, as with the 1980 spring-hatched and 1986 autumn-hatched cohorts, maturation was asynchronous. Those individuals from the 1980 cohort with an advanced length at age matured as autumn spawners in the fall of 1983 at age 3 years and 4 months. A large proportion of this cohort subsequently spawned the following spring at age 4, and the remainder took advantage of an additional growth season before spawning in the fall of 1984 as autumn spawners. The autumn-spawning individuals of this cohort were therefore significantly longer at age than those of the same cohort that remained spring-spawning (Fig. 6A). Winter et al. (1986) also concluded that the faster-growing spring-hatched individuals matured as autumn-spawners. Conversely, the 1979 autumn-hatched individuals that became spring spawners did so the previous spring at age 3 years and 8 months and thus showed a shorter length at age than those that remained autumn spawners and matured at age 4 (Fig. 6B). We also observed that the adopted season was maintained after the initial spawning because this length difference persisted until at least age 6.

This crossover also explains the observed pattern of twinning—that is to say a strong spring-spawning year class matched with a strong autumn-spawning year class from the previous year. The fact that twinning is seldom seen between spring- and autumn-spawning year classes of the same year is due to the ageing convention for herring (Hunter et al.<sup>8</sup>), which does not consider the possibility of crossover between these populations. The present study has demon-

strated that this crossover can occur in both directions, i.e. spring-hatched herring can contribute to an autumn-spawning year class (1980) and vice versa (1986). It should also be mentioned that although the effects of crossover between sympatric herring populations is more striking when large year classes are involved, resulting in year-class twinning, the significant correlation found between subsequent autumn- and spring-spawning year classes in eastern Newfoundland (Winters et al., 1986) indicates that crossover undoubtedly occurs to some extent with all year classes.

The present study therefore does not support the concept of discrete sympatric seasonal-spawning populations in Atlantic herring. The data presented here suggest that the progeny of a given seasonal population do not necessarily recruit to the parental population but may indeed contribute to a local population of another reproductive season. Furthermore, the spawning season that is established at the time of first maturation is maintained for the remainder of adult life.

## Acknowledgments

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**Abstract.**—Densities of juveniles of the Hawaiian deepwater snapper *Pristipomoides filamentosus* were surveyed for 3 years in relation to their demersal environment at an east Oahu study site. Juveniles settled annually to spatially stable aggregations, occupying expanses of uniform sedimentary habitat. Habitat data were collected and used in a logistic regression model to predict correctly 68% of the juveniles' spatial variability. Premium habitat was identified as a sediment bottom, free of relief, and close to focused sources of drainage (reef platforms, embayments, and anthropogenic sources) in adjacent shallows. Surveys for juveniles elsewhere on insular slopes of the Hawaiian Archipelago indicated low juvenile abundance except at infrequent locations close to point sources of coastal drainage. Estimates of recruit production, based on densities of juveniles from other than premium habitat, were a small fraction of the recruits needed (calculated from catch) to account for the fishery's current landings of adult snappers. The 68-fold higher juvenile abundance at premium habitat can reconcile this difference, indicating that such infrequent high-quality habitat is an important (perhaps critical) fishery resource.

## Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus*, in the Hawaiian Archipelago

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Understanding favorable nursery habitat and its contribution to the standing stock of adults provides an important perspective for managing demersal fisheries. In the tropics, such nursery habitat has been studied effectively for many species inhabiting shallower depths (Bardach, 1959; Parrish, 1989; Birkeland<sup>1</sup>). Species using deeper, more remote nursery grounds have received less attention, and as a result, habitat often is not considered adequately in fishery modelling or management planning. In places with limited demersal nursery habitat, such as the minimal shelf area of oceanic islands, this habitat may represent a resource of critical importance to the fishery. Accelerated coastal development on many islands could degrade unrecognized favorable nursery habitat and impact fishery resources. This paper examines the nursery habitat of the deepwater Hawaiian pink snapper, *Pristipomoides filamentosus*, in relation to the spatial variability of its juveniles. A study site at a productive nursery ground was intensively surveyed, and the results compared with surveys made over much of the archipelago. The implications of the variable habitat quality for the stock of adult snappers inhabiting the archipelago were then considered.

The pink snapper accounts for more than 40% of the State of Hawaii's \$3 million annual commercial bottomfish catch<sup>2</sup> and is well represented in the extensive recreational catch. However, study and management of the adult stock has been historically difficult because of its patchy distribution and poorly recorded recreational landings (Ralston and Polovina, 1982). A productive research approach may be to study the juveniles of the species, which are free of fishing pressure and of the factors that affect recruitment to the adult population. Recent discovery (F. A. Parrish, 1989) of a dense, stable aggregation of juveniles in a nursery area has made this approach feasible. Juveniles (7–25 cm fork length [FL]) occupy moderate depths (60–90 m) in patchy aggregations on the insular shelf for less than a year before moving deeper (150–190 m) as they mature

<sup>1</sup> Birkeland, C. 1985. Ecological interactions between mangroves, seagrass beds, and coral reefs. United Nations Environmental Program Regional Series Report and Studies 73, 126 p.

<sup>2</sup> WPRFMC (Western Pacific Regional Fishery Management Council). 1993. Bottomfish and seamount groundfish fisheries of the Western Pacific region. NOAA NA17FC0062-02, Honolulu, HI, 57 p. WPRFMC, 1164 Bishop Street, Suite 1405, Honolulu, HI 96813.

(Moffitt and Parrish, 1996). Sonic tracks of these juveniles indicate a discrete and limited individual home range of 140 m average diameter, suggesting that the locations of these juvenile aggregations could be very stable. Why juvenile aggregations appear spatially stable and how common they are in the rest of the archipelago are the primary focus of this work.

## Methods

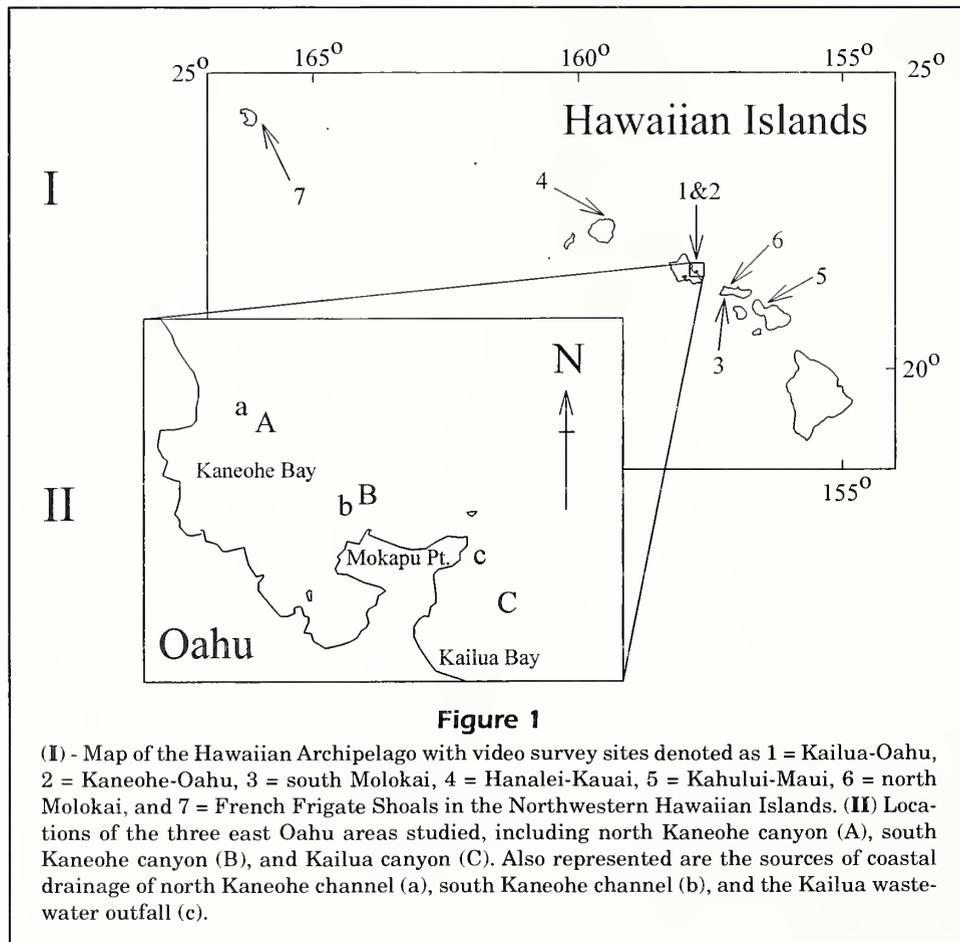
### Survey of the east Oahu study site

The east Oahu study site contains three submarine canyons. Two of the canyons are located just outside Kaneohe Bay, north of Mokapu Point, and the third is located south of Mokapu Point just outside Kailua Bay (Fig. 1, II). Throughout this paper, the three areas will be referred to as the "north Kaneohe," "south Kaneohe," and "Kailua" canyons. Positional data from a Global Positioning System (GPS) were entered and manipulated in a raster-based Geographic Information System (GIS)(IDRISI 4.0 version) (Eastman, 1992).

### Video index of snapper abundance

A baited video camera (Fig. 2) was selected as the primary gear because it provided information on the abundance of snappers and their associated habitat type. In each video drop, the baited camera was placed on the bottom for 10 minutes, where it attracted juvenile snappers in front of the camera lens; the maximum number of snappers seen in a single image was used as the index of abundance. Consecutively deployed video drops were separated by 1,200 m to avoid attraction of fish from previous drops. A description of equipment, method, and validation of the technique for creating a video index of snapper abundance is provided by Ellis and DeMartini (1995).

Selected video stations at the study site were replicated to determine the suitability of unreplicated spatial data for subsequent use in evaluating the persistence of snapper patches over time. Nineteen stations, resampled after 10 days, were used to represent all 3 canyons during February–March 1994. These stations were termed "multicanyon stations."



Interannual fidelity of snapper recruitment to the study site was assessed by using 20 video stations in the north Kaneohe canyon during 4 surveys in May 1992, May 1993, September 1993, and June 1994. These were designated as "multiyear stations" and were compared by using date of survey as a covariate.

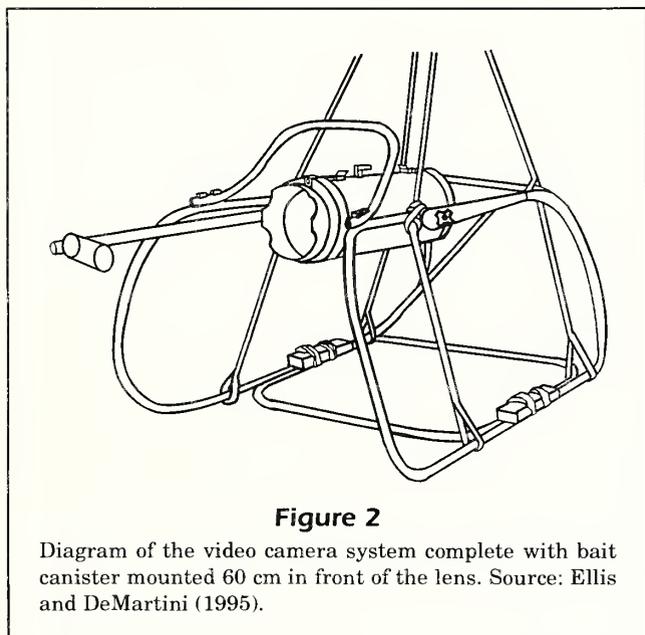
### Habitat characteristics

Slope, substrate type, sediment particle size, and proximity to closest known point sources of focused coastal drainage (channels through reefs and wastewater outfalls) were determined for all areas. The effect of slope on snapper abundance was assessed by using a GIS slope algorithm with collected bathymetry data. At the depths frequented by juvenile snappers, the habitat is typically dominated by a featureless expanse of sediment. To test the effect

of alternative substrates on snapper abundance, types of substrate (as identified in video and chromosome images) were coded as categories: e.g. soft sediments, escarpment-type relief (exposed edges of shelf, about 3 m high), and hard, even bottom. Video drops that recorded alternate substrate, or were within a snapper home range (Moffitt and Parrish, 1996) of such observations, were compared with video drops on soft sediment, presumably away from the influence of the other substrate. Substrate of adjacent shallower (30–60 m) and deeper (90–120 m) habitats, where juveniles have been historically absent (F.A. Parrish, 1989; Moffitt and Parrish, 1996), were surveyed with a longshore transect of 14 video drops in each of the 2 depth ranges.

Ten bottom grab transects perpendicular to the bottom contours, each sampling 3 depths (45, 76, 106 m), were used to assess a possible relationship between snapper abundance and particle sizes in the sedimentary habitat. Replicate grabs were taken in line with and between the axes of the canyons in each area. Samples were wet-sieved into five size categories (>2.0, 0.35–2.0, 0.149–0.35, 0.0625–0.149, and <0.0625 mm).

The effect of some notable sources of natural and anthropogenic drainage present in each of the three canyons was considered. In Kaneohe, bay water drains through narrow channels (one in the north and one in the south, each with maximum depth of ~15 m at the seaward end) in the reef during ebb tide<sup>3</sup> (Fig. 1, II). In Kailua, increased suspended materials are introduced from an island wastewater and sewage outfall.<sup>4</sup> The video index of snapper abun-



**Figure 2**

Diagram of the video camera system complete with bait canister mounted 60 cm in front of the lens. Source: Ellis and DeMartini (1995).

<sup>3</sup> Bathen, K. H. 1968. A descriptive study of the physical oceanography of Kaneohe Bay, Oahu, Hawaii. HIMB Tech. Rep. 14, 353 p. Univ. Hawaii, 2550 The Mall, Honolulu, HI 96822.

<sup>4</sup> City and County of Honolulu. 1993–1994. Discharge monitoring reports. Environmental Protection Agency form 3320-1. Wastewater Division, 650 South King St. Honolulu, HI 96813.

**Table 1**

Depth, mean daily volume, and suspended load of the east Oahu drainage sources. The Kaneohe channels provide tidal drainage; the Kailua discharge is anthropogenic (24 hours).

Source of discharge	Discharge volume (m <sup>3</sup> /day)	Discharge depth (m)	Suspended solids (kg/day)	Source
North Kaneohe channel	18.5 × 10 <sup>6</sup>	0–15	—	Bathen <sup>1</sup>
South Kaneohe channel	12.9 × 10 <sup>6</sup>	0–15	—	Bathen <sup>1</sup>
Kailua wastewater outfall	41,000	30	1,000	City and County of Honolulu <sup>2</sup>

<sup>1</sup>See Footnote 3 in the main body of the text.

<sup>2</sup>See Footnote 4 in the main body of the text.

dance was compared with the volume of each source's discharge (Table 1) divided by the distance separating the video samples from the nearest source of discharge. No attempt was made to sample the nutrients or suspended materials of these discharges. Elevated organics associated with these water masses are documented in the literature (Bromwell, 1992; City and County of Honolulu<sup>4</sup>; Laws and Allen<sup>5</sup>).

### East Oahu statistical analysis

The distribution of the data and the categorical nature of the habitat variables required the use of non-parametric analysis (Siegel and Castellan, 1988). The type-I error for statistical significance was set at 0.05 (2-tailed test). Kruskal-Wallis ANOVA (K-W) was used to assess station effects in both "multicanyon and multiyear" analyses and to assess the effect of substrate type.

Differences in substrate by depth were tested with chi-square analysis. Replicate bottom grabs were compared by using Wilcoxon matched pairs sign ranks (MPSR), and Spearman's correlation was used for association of snappers with slope, sediment fractions, and influence of drainage.

Spatial variation of ranked snapper abundance was related to all habitat variables together by using logistic regression. Snapper abundance was grouped into two categories, aggregation present ( $n \geq 5$ ) and aggregation absent ( $n < 5$ ), and assessed relative to the habitat variables that significantly influenced snapper abundance in the previously described univariate analyses (Norusis, 1992). Models of the variables and their plausible interaction effects were explored with the simple logistic regression model (Kleinbaum, 1992):

$$\pi = \frac{e^{\sum B_i X_i}}{1 + e^{\sum B_i X_i}}, \quad (1)$$

where  $\pi$  is the probability of detecting snappers with the linear combination of the habitat variables  $X_i$  in a given location. The coefficients estimated with the nonlinear regression by using maximum likelihood are represented by  $B_i$ . The base of the natural logarithm is  $e$ . The  $P$ -value for retention of independent variables in the model was set at 0.01.

### Survey of the archipelago

Conventional fishing gear (e.g. trawls, longlines, traps, handlines) was used to survey a total of 332 km of longshore habitat dispersed over seven islands of the archipelago (1989–94). The effectiveness of each gear at catching juvenile snappers was tested at the east Oahu study site. Sites surveyed included areas outside of embayments, places with large shelf areas at snapper depths, and sites of previous research fishing where juveniles had been documented incidentally (Struhsaker, 1973). Sites where snappers were found were then reassessed with longshore baited video surveys (range 5.5–42.6 km) to permit comparison with snapper abundance at the east Oahu study site. Numbers of juvenile snappers observed at each site were standardized by effort. The distance of each video drop from the coastal reef edge (15-m isobath) and the type of substrate seen in the video image were tabulated for each site; these variables were then compared with the respective video index of juvenile snapper abundance. Catch-per-unit-of-effort (CPUE) data from sets of conventional fishing gear at these coastlines were included to provide an independent index of snapper abundance.

In comparing video data from other coastlines with those of east Oahu, data for the two Kaneohe areas were pooled. Coastlines with point sources of drainage were identified, and the distance between sources of discharge and the video drops (weighted for maximum depth of discharge) were calculated. Importance of proximity to drainage sources to snapper abundance was then evaluated for these archipelago sites.

### Snapper production estimates

To assess the importance of the contribution of juveniles from a site with premium habitat (e.g. Kaneohe) to the adult fishery, the adequacy of recruit production from other habitat areas was estimated. The density of snappers at habitat without snapper aggregations was compared with the density of snappers needed to explain the catch from the main Hawaiian Islands (MHI) commercial snapper fishery. Derived from mandatory reporting from the commercial fishery, the estimate is based on the catch of ~3-year-old snappers (termed "immature") just entering the MHI adult snapper fishery (Ralston, 1981; DeMartini et al., 1994). Based on the years 1989–92, the estimated mean annual catch,  $C$  (i.e. the commercial catch [WPRFMC<sup>2</sup>]) was ~22,000 immature (1.3 kg) snapper/year. Recreational fishing produces a significant additional catch in Hawaii, but it is poorly documented and was not considered in this estimate.

<sup>5</sup> Laws, E. A., and C. B. Allen. 1993. Impact of land runoff on water quality in Kaneohe Bay, a subtropical Hawaiian estuary. Proceedings of the first biennial symposium for main Hawaiian islands marine resources investigation, November 17–18. Hawaii Department of Land and Natural Resource Technical Report 95-01, p. 232–248. Hawaii Dep. Land Natl. Resources, 1151 Punchbowl, Honolulu, HI 96813.

By using the estimated growth coefficient,  $k$ , of 0.25/yr derived for juvenile snappers (DeMartini et al., 1994) in the mortality relationship of  $M/k=2$  (Ralston, 1987a), the instantaneous natural mortality coefficient,  $M$ , was estimated as 0.50/yr, and a range for the instantaneous fishing mortality coefficient,  $F$ , was calculated. The low end of the range assumes  $M = F$ , on the basis of the fishery operating at maximum sustainable yield (Ralston and Polovina, 1982), providing an instantaneous  $F$  of 0.50/yr. The high end of the range assumes that fishing mortality is twice natural mortality,  $F = 2M$  (Ralston, 1987b), resulting in an  $F$  of 1.0/yr. The two estimates of  $F$  were used independently to represent the extremes of the probable range. The mean standing stock of immature snappers,  $N_3$ , can be calculated by use of the conventional formula for the annual rate of exploitation (Everhart and Youngs, 1981; Gulland, 1983):

$$N_3 = \frac{C}{\frac{F}{F+M} (1 - e^{-[F+M]})}, \quad (2)$$

resulting in estimates of 42,500–69,600 fish. Because these immature snappers have been exposed to natural mortality for 2 years since the time  $t_1$  that they inhabited nursery depths, a back calculation provides  $N_1$ , an initial estimate of juveniles supported on the MHI grounds. The formula (Gulland, 1983)

$$N_1 = \frac{N_3}{e^{-M(t_3-t_1)}}, \quad (3)$$

yielded values of  $N_1$  between 115,600 and 189,200 fish. With this estimate of  $N_1$ , divided by the amount of bottom area in the MHI between the 60 and 90 m isobaths (2,600 km<sup>2</sup>, NOS bathymetric charts), an estimate of the overall density of juvenile snappers required to support the current fishery was derived.

## Results

### The east Oahu study site

Two-hundred and eleven video camera drops with standard bait were dispersed throughout the insular slope (60–90 m depth) of the Oahu study site. Abundance data from the video drops were nonnormally distributed (33% zero observations) (Fig. 3). Snappers were found at each of the 3 east Oahu canyons. Snapper abundance differed significantly among the multicanyon stations (K-W,  $\chi^2=35.6$ ,

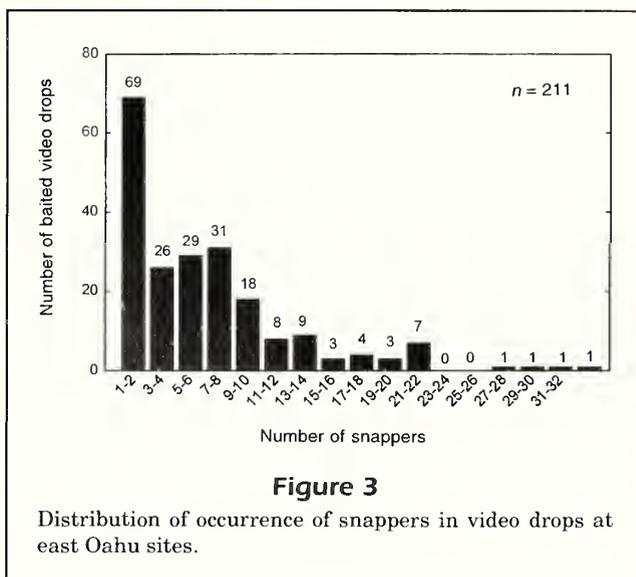
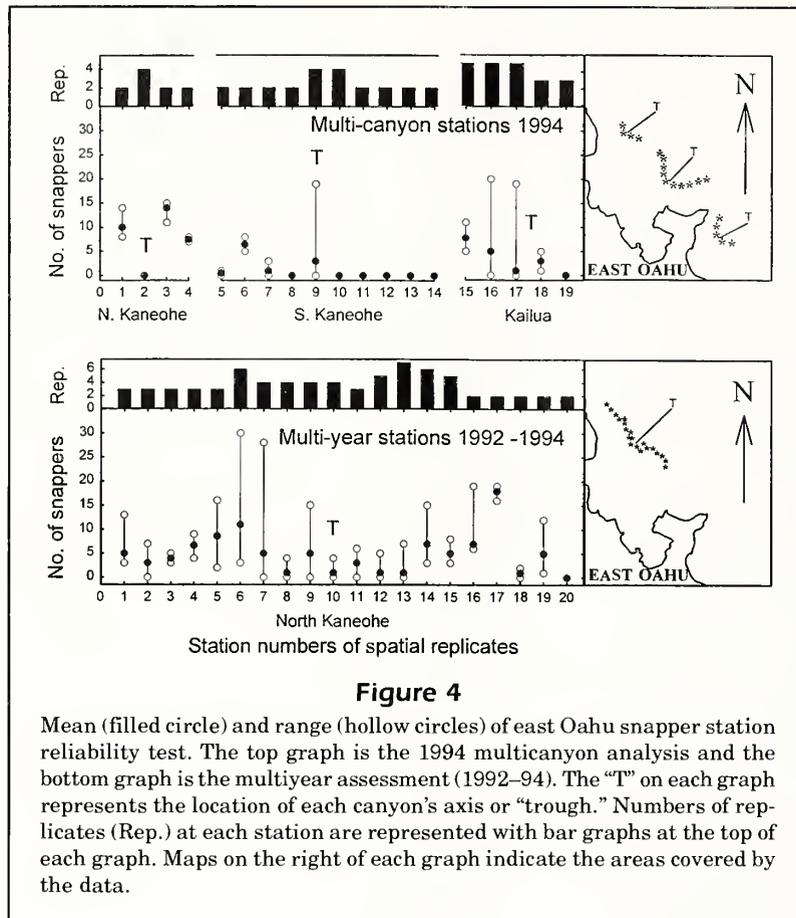


Figure 3  
Distribution of occurrence of snappers in video drops at east Oahu sites.

$P < 0.01$ ), confirming that relative spatial differences in snapper distribution remain stable (Fig. 4). In the multiyear stations at north Kaneohe canyon, essentially similar spatial differences persisted (K-W,  $\chi^2=37.3$ ,  $P < 0.01$ ); this finding suggests that successive years of juvenile snappers settle spatially according to habitat quality. Because the effect of station was significant for both the multicanyon and multiyear comparisons, the abundances of snappers at unreplicated video drops were considered representative of the habitat quality at those locations.

Bottom slope was unrelated to the video indices of snapper abundance (Spearman's  $r_s=0.013$ ,  $P=0.72$ ). Substrate at 95% of the video drops (60–90 m) was composed of uniform, smooth sediment. High, escarpment-type relief was detected in only 3% of the drops. A significantly lower abundance of snappers occurred in the area surrounding escarpment-type relief than in the even sediment bottom ( $\chi^2=11.48$ ,  $P < 0.001$ ). The 95% confidence intervals of snapper densities at sites with relief (0–1 snappers) versus sites with sediment bottom (3–4 snappers) did not overlap. A similarly low abundance of snappers was associated with areas near exposed hard substrate ( $\chi^2=10.50$ ,  $P < 0.01$ ; 95% CI=0–2 snappers). Snapper grounds (60–90 m) and the adjacent deeper (90–120 m) area did not differ in the occurrence of soft sediment substrate ( $\chi^2=0.44$ ,  $P=0.43$ ). However, the adjacent shallow grounds (30–60 m) had significantly more hard bottom and relief ( $\chi^2=11.36$ ,  $P < 0.001$ ); soft sediment occurred in fewer (71%) of the shallow video images.

The duplicate sediment grabs did not differ, suggesting that the sediment sampling effectively represented the soft bottom habitat (Wilcoxon MPSR,  $P=0.93$ ). Of the 5 sediment fractions, snapper abun-



**Figure 4**

Mean (filled circle) and range (hollow circles) of east Oahu snapper station reliability test. The top graph is the 1994 multicanyon analysis and the bottom graph is the multiyear assessment (1992-94). The "T" on each graph represents the location of each canyon's axis or "trough." Numbers of replicates (Rep.) at each station are represented with bar graphs at the top of each graph. Maps on the right of each graph indicate the areas covered by the data.

dance was significantly correlated with only the clay-silt (<0.0625 mm) fraction (Spearman's  $r_s = 0.35$ ,  $P < 0.001$ ) (Table 2). The greatest abundance of clay-silt occurred in an area just northwest of the north Kaneohe canyon trough; at Kailua the abundance was less than half that at Kaneohe, and high concentrations spread southeast of the canyon trough.

Proximity of point sources of drainage was associated with snapper abundance, i.e. video index of snapper abundance and distance to discharge were significantly negatively correlated ( $r_s = -0.18$ ,  $P < 0.05$ ). The weakness of the relationship resulted from the failure to consider the effect of bottom relief in the comparison. This result indicated the need for a model that considered the variables together.

### Modeling of snapper aggregations.

The stepwise backward regression evaluated the relative importance of the 3 habitat variables found significant in the univariate analysis: 1) escarpment-type relief; 2) clay-silt (<0.0625 mm) sediment fraction; and 3) proximity of coastal discharge. The interaction of discharge with the presence of clay-silt

**Table 2**

Spearman rank order correlation coefficients and probability values for snapper abundance with sediment particle size. In all comparisons sample size = 211.

Sediment size fraction (mm)	Correlation coefficient $r_s$	Probability value $P$
>2.000	-0.0426	0.54
0.350-2.000	-0.0932	0.178
0.149-0.350	-0.0922	0.184
0.063-0.149	0.0809	0.244
<0.063 (clay-silt)	0.3555	<0.001

was also assessed. All variables except clay-silt were retained by the model ( $P < 0.01$ ; Table 3). Reasons for the model's exclusion of clay-silt will be discussed later. The model correctly predicted overall presence ( $\geq 5$ ) or absence ( $< 5$ ) of snapper aggregations for 68% of the video drops. The model predictions of presence (79% [ $\geq 5$ ]) were roughly balanced by those for absence (60% [ $< 5$ ]) (Table 4). Ranked snapper abundance was interpolated by using all video drops to

**Table 3**

Statistical specifics associated with the regression for presence ( $\geq 5$ ) or absence ( $< 5$ ), of snapper aggregations at east Oahu. Model chi-square ( $\chi^2$ )=54.11,  $P < 0.0001$ ,  $df=3$ .

Name of variable	Estimated coefficient	Standard error	Probability value $P$
Cross product of clay-silt with proximity of drainage source	$1.45 \times 10^{-6}$	$3.47 \times 10^{-7}$	$< 0.0001$
Distance to drainage	$-7.5 \times 10^{-7}$	$1.58 \times 10^{-7}$	$< 0.0001$
Escarpment relief	-1.586	0.435	0.0003

provide an image of snapper distribution at east Oahu (Fig. 5).

### Abundance of juveniles in the archipelago

Fishing surveys at insular slopes other than east Oahu (total 332 km) detected few juveniles (Table 5). Five of these sites (with snappers) were surveyed with video camera to compare with the east Oahu aggregations. Significant numbers of snappers were found only at a site off the southwest end of the island of Molokai (Sept 1993). A repeat video survey indicated that the significant between-station differences in snapper abundance initially reported at South Molokai, persisted 7 months later (K-W,  $\chi^2=50.8$ ,  $P < 0.05$ ) (Fig. 6).

The video index and CPUE of the conventional fishing gear were roughly consistent for all sites (Table 6). Snapper abundance was found unrelated to substrate type ( $r_s=0.59$ ,  $P=0.40$ ,  $n=7$ ) or distance from the 15-m isobath ( $r_s=-0.84$ ,  $P=0.15$ ,  $n=7$ ). However,

distance/depth of discharge at the four sites with known sources of coastal drainage (Kaneohe, Kailua, S. Molokai, and Hanalei) were associated with snapper abundance ( $r_s=-1.0$ ,  $P < 0.001$ ,  $n=4$ ).

### Video- and catch-based production estimates

Video abundance data from MHI sites at N. Molokai, Hanalei, and Kahului yielded a mean estimated den-

**Table 4**

Two by two table of presence ( $\geq 5$ ) or absence ( $< 5$ ) of snapper aggregations predicted by the model versus presence or absence observed from baited video drops. Includes all 211 drops at east Oahu.

Observed	Predicted by model		
	Aggregations absent ( $< 5$ )	Aggregations present ( $\geq 5$ )	Percent correct
Aggregation absent	73	48	60
Aggregation present	19	71	79
			68 overall

**Table 5**

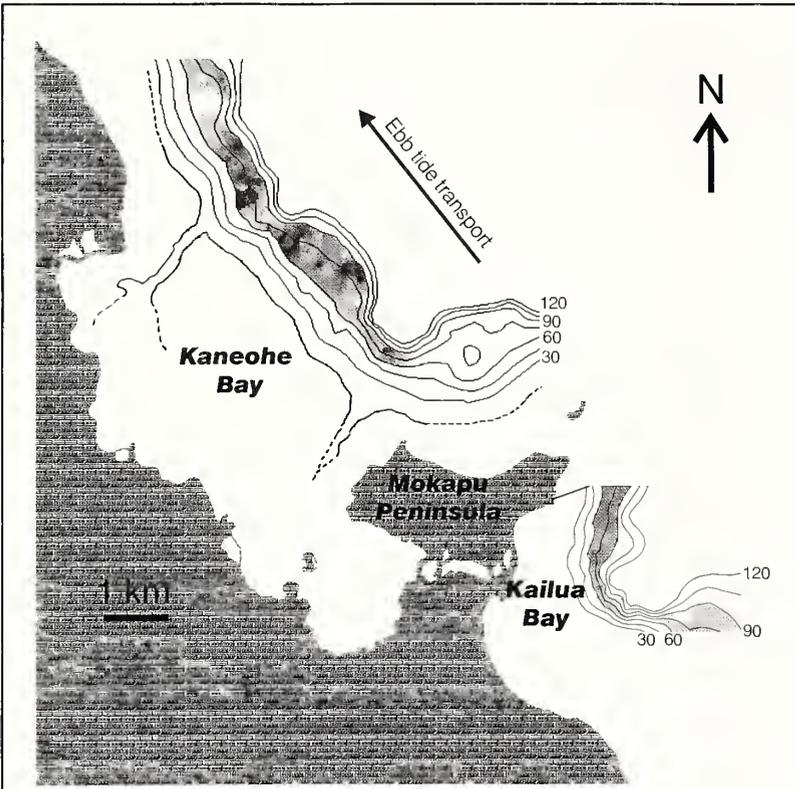
Fishing effort, length of slope fished, and total snappers caught on surveys of Hawaiian insular slopes for juvenile snappers.

Island	Bottom trawls	Bottom longlines	Fish traps	Handlining	Length of slope fished	Total snapper caught
	1990 (no.)	1992 (no. hooks)	1989-94 (no.)	1993-94 (line-hr)	(km)	(no.)
Oahu <sup>1</sup>	16 (5) <sup>2</sup>	— (150)	27 (53)	60 (50)	164 (14)	16 (828)
Molokai	26	—	101	87	60	256
Maui	6	150	—	—	16	4
Lanai	6	—	—	—	16	0
Kauai	—	150	—	—	18	3
Necker	—	—	25	—	16	0
FFS <sup>3</sup>	—	—	63	—	42	5
Total	54	300	216	147	332	284

<sup>1</sup> The east Oahu study site values are not included in any of the figured totals.

<sup>2</sup> Numbers in parentheses represent additional values from gear validation test done at the east Oahu site.

<sup>3</sup> FFS = French Frigate Shoals.



**Figure 5**

Interpolation of snapper abundance from all video deployments at the east Oahu study site (north Kaneohe, south Kaneohe, and Kailua). Increasing snapper abundance is signified by darker shading. Both north and south channels of Kaneohe Bay are contoured on the map, and a line is used to indicate the eastward extension of the Kailua outfall from the Mokapu peninsula. Isobaths are in 15-m intervals.

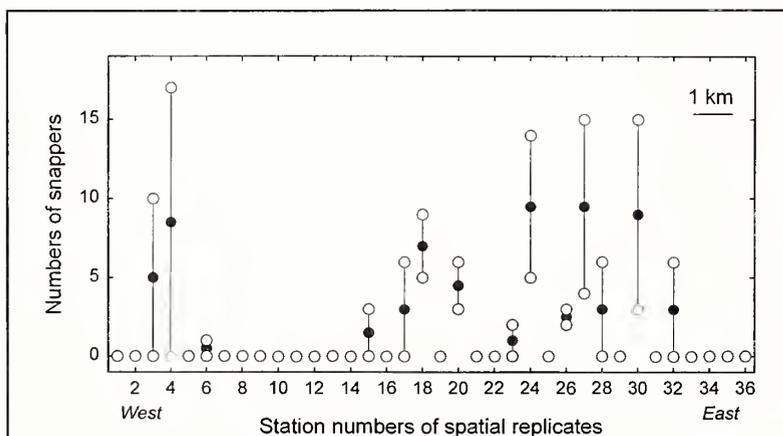
sity of 6.6 snappers/km<sup>2</sup>, which was taken as representative of routine “nonpremium” habitat. Assuming this density and a uniform distribution of snappers at a large scale, we estimated that the 2,600 km<sup>2</sup> of available habitat at 60–90 m depth in the MHI is equivalent to 17,200 juvenile snappers. This video-based estimate is no more than 15% of the 115,600–189,200 juvenile snappers (44–72 snappers/km<sup>2</sup>) backcalculated from catch in the commercial fishery. A pilot study of recreational fishing<sup>6</sup> suggests that if recreational catch was included in the back calculation, the difference between video and catch estimates could be as high as one order of magnitude.

## Discussion

### Premium nursery habitat

Persistence of specific snapper aggregations on east Oahu was supported by both the multicanyon and multiyear analyses. However, because no multi-year surveys extended beyond the north Kaneohe site, we can only assume that year-to-year variability in the other east Oahu sites was similar. A strong year class of snappers might be expected to force some individuals to occupy marginal habitat, making the distinction between snapper aggregations less clear. Results of the multiyear survey indicated that 1993 and 1994 were relatively poor years for recruitment of young snappers, suggesting that the observed snappers in the multicanyon stations occupied favorable habitat.

Slope showed no significant effect on the distribution of snappers, but relief did. The deep sediment deposits on the terraces preclude any undetected small-scale relief features to which juveniles might orient. The few areas where escarpment features protruded from the sediment layer were associated with ab-



**Figure 6**

Mean (filled circle) and range (hollow circles) of number of snappers seen per video drop on south Molokai coastline survey. Each station received two video deployments. The drainage from the Kahanui swamp enters the ocean ~1 km to the east of extreme right of the graph.

<sup>6</sup> Hamm, D. C., and H. K. Lum. 1992. Preliminary results of the Hawaii small-boat fisheries survey. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Sci. Cent. Admin. Rep. H-92-08, 35 p.

sence of snapper aggregations in the logistic model. This finding supports the hypothesis that structural relief or its associated community represents conditions less favorable or more hazardous to the snappers (greater interspecific competition, risk of predation, etc.) (Johannes, 1978; F. A. Parrish, 1989). Expanses of uniform sediment bottom are obviously an important substrate feature. The relative scarcity of this habitat observed at depths <60 m at least partly explains the absence of snappers on the shallower (30–60 m) grounds.

Proximity to point sources of drainage and its relationship with the presence of clay-silt sediment can explain much of the snappers' longshore distribution. Work with first-year juveniles of species of *Pagrus* has demonstrated that substrate and associated water flow are important to habitat selection (Francis, 1995). Improved availability of food has been proposed as a reason for fish demonstrating habitat preferences (Sudo et al., 1983). Distributions of sediment particle sizes such as clay-silt have been shown to enhance the localized distribution of certain benthic invertebrate infauna (Fegley, 1988). A favorable localized sediment composition might contribute to an enhanced forage base for juvenile fish (Tito de Moraes and Bodiou, 1984). However, these longshore variations in clay-silt abundance are simply indicative of the longshore differences in coastal water flow that disperse the flocculent clay-silt. The highest fraction of clay-silt is found at the seaward end of the north Kaneohe channel, where snapper abundance is high and bay drainage is most concentrated. The density of fish in Kailua is greatest near the wastewater outfall, where the clay-silt fraction is lowest. The outfall introduces and increases the frequency of drifting materials to the area, similar to the flow of natural drainage sources, but without creating a clay-silt dispersion field. For this reason, the logistic model excluded the variable

**Table 6**  
Characteristics and results of longshore coastal surveys for snappers at 7 sites.

Location (year) and "figure ID number"	Longshore distance surveyed (sampling interval) (km)	Index of abundance			Uniform sediment seen in survey (%)	Mean distance of video drops from 15 m isobath and range (km)	Source of coastal drainage (max. depth of source in meters)
		Video sampling mean no./ video drop	Conventional research fishing (mean no.)	Trap set			
Kailua, Oahu (1994) "1"	4.6 (1)	24.8	—	—	88	1 (0.61–1.3)	Kailua wastewater outfall (30)
Kaneohe, Oahu (1992–94) "2"	13.8 (0.5)	4.5	3.8	5.78	95	1.24 (0.64–1.6)	Kaneohe Bay, north and south channels (15)
South Molokai (1993–94) "3"	16.6 (0.5)	1.97	—	2.0	81	1.6 (0.87–3.9)	Kahanui swamp and fringing reef drainage (15)
Hanalei, Kauai (1992) "4"	18.5 (1.5)	0.22	0.20	—	52	1.5 (0.77–4.2)	Hanalei estuary
Kahului, Maui (1992) "5"	15.7 (1.5)	0.03	0.01	—	92	4.3 (1.6–10.5)	None known
North Molokai (1994) "6"	5.5 (0.5)	0	—	0.007	92	0.87 (0.64–1.2)	None known
French Frigate Shoals (1993) "7"	42.6 (1.5)	0	—	0.037	40	1.3 (0.92–2.3)	None known

Figure ID numbers listed in first column correspond with survey sites shown in Figure 1, I.

clay-silt. This finding suggests that the distribution of juveniles within the preferred uniform sediment habitat is related more closely to water flow than to sediment particle size. Similar enhanced abundances of fish associated with anthropogenic sources have been proposed elsewhere (Mearns, 1974; Monaco et al., 1992) and in Hawaii (Henderson, 1992; Grigg, 1994).

In video deployments at many study sites, snappers were observed routinely picking at items in the lower water column and mouthing the substrate. DeMartini et al. (1996) determined that juvenile snappers at the north Kaneohe canyon eat a mixture of gelatinous drift, demersal crustaceans (amphipods, etc.), and benthos (micromollusks, annelids, etc.). The majority of prey were <1 cm, of low motility, and bottom associated.

Habitats receiving drainage from shallower environments might have their food supply enhanced in at least two ways. First, fish may encounter and feed more frequently on suspended organisms and other materials flushed from shallower reef and estuarine environments (Gerber and Marshall, 1974). Second, the flow from shallow sources may elevate the organics in sediments, thereby enhancing production of the benthos that snappers eat. Changes in benthic fauna at comparable depths (50–200 m) have been documented in relation to the flux of organics in the water column—both in natural (Buchanan and Moore, 1986) and anthropogenic situations (Nichols, 1985). Benthos may also become enriched during large episodic movements of nutrient-rich bay sediment to localized areas in the snapper grounds. The significant interaction, identified by the logistic model, of clay-silt with proximity to drainage sources supports the notion of enhanced organic input to the benthic community provided by such drainage.

### Distribution of juveniles in the archipelago

Conventional fishing on the insular slopes of the archipelago (332 km) identified few sites with juvenile snappers; the mode and median of the catch of juveniles from all the gear was zero. Except for aggregation sites at Oahu and Molokai, catches of juveniles occurred only in token numbers. In a 1967–68 demersal trawl survey ( $n=62$ ), Struhsaker sampled ~90 km of relevant depths in the main Hawaiian Islands and similarly found the occurrence of juveniles to be infrequent and patchy. His catches of juvenile snappers had a mode of zero and median of one (Struhsaker, 1973).

The 5 sites other than east Oahu that were surveyed by video (Table 6) each had substrate and depths consistent with those at east Oahu; 2 had

sources of drainage; but only 1, south Molokai, supported a snapper aggregation. South Molokai's Kahanui swamp, located within the island's extensive fringing reef complex, has a drainage channel similar in width and depth (15 m) to north Kaneohe Bay (U.S. Army Corps of Engineers, 1984). Its associated snapper aggregation is well situated to exploit the tidal drainage of the reef platform and swamp dispersed by westbound currents of the area<sup>7</sup> (Fig. 6). The Hanalei estuary, on the island of Kauai, probably fails to influence snapper depths because it discharges at a zone of high-energy mixing (~1 m depth) too far inshore from juvenile snapper grounds.<sup>8</sup> The site at Kahului, Maui, would have to have a very large coastal drainage feature to aggregate snappers; the distance between the snapper grounds and such a source would be twice that of the other sites surveyed. Presumably, any source of increased suspended materials (embayments, reef platforms, or atoll lagoons) could enhance snapper aggregations if depth, distance, and circulation characteristics focused water and increased the frequency of suspended materials close to juvenile grounds (Cyrus and Blaber, 1983; Birkeland, 1984).

Struhsaker, during his 1967–68 trawl survey, identified one location (north coast of Oahu) with catches as high as 180 individuals in one haul. The substrate at the site was composed of uniform sediment and received discharge from two north Oahu rivers. However, according to the surveys from the present work, the snapper depths at this site seem almost too far offshore (mean=4.5 km) to support an aggregation. Numerous attempts in 1990 (Table 5) to relocate this north Oahu aggregation with the same gear that was used in 1967–68 did not yield any snappers. Many changes that could have modified the suitability of this habitat for juveniles (e.g. heavy exploitation of the snapper stock [WPRFMC<sup>2</sup>]; collapse of the coast's large-scale irrigation-based agriculture and its drainage; effects of increasing relief on juvenile grounds from the accumulation of incidental ocean dumping) have occurred in the 22 years between the surveys.

### Implications for the fish stock

Regardless of what factors create premium habitat, the implications for the snapper stock of the archi-

<sup>7</sup> Wyrski, K., V. Graefe, and W. M. Patzert. 1969. Current observations in the Hawaiian Archipelago. Hawaii Institute of Geophysics HIG-69-15, 27 p. Hawaii Inst. Geophysics, 2525 Correa Rd., Honolulu, HI 96822.

<sup>8</sup> U.S. Geological Survey. 1993. Water resources data Hawaii and other Pacific areas, water year 1993. Water-data Report HI-93-1:78-79. U.S. Geological Survey, 677 Ala Moana Suite, Honolulu, HI 96813.

pelago are intriguing and potentially important. It is not clear how widespread such habitat (and associated high densities of juvenile snappers) may be in Hawaii; present surveys and those of 1967–68 suggest that it represents a minor fraction of all habitat at appropriate depths. Use of the observed mean density of snappers on other habitats (6.6 snappers/km<sup>2</sup>) produced an estimate of juvenile standing stock much lower than that derived from catch records. A possible explanation for the discrepancy is that an abundance of snappers use unidentified habitats significantly shallower or deeper than 60–90 m. However, extensive diving in shallower waters, observations from submersibles (Moffitt et al., 1989; Haight et al., 1993), and systematic trawl surveys of deeper waters (Struhsaker, 1973) have not disclosed juveniles in other depth ranges. Conceivably, areas at depths with less than prime habitat for juvenile snappers may support loose, mobile aggregations with large home ranges that are difficult to relocate. As of yet, no such aggregations have been documented.

According to the Kaneohe GIS data (Fig. 5), juvenile snappers occurred within an area of 8 km<sup>2</sup> and showed a median video-based density index of 7; therefore, Kaneohe is likely to support 450 snappers/km<sup>2</sup> (68-fold above mean estimated density) or a total of 3,600 snappers. This finding suggests that recruits from premium habitats like Kaneohe can produce a significant percentage of the MHI juveniles. If Kaneohe snapper abundance values are applied to reconcile the difference between the estimates generated by video densities in nonpremium habitats and those obtained by fishery catches, between 9% and 15% of the MHI habitat would have to be of the premium type to account for the current commercial snapper catch. If recreational catch is considered, a larger fraction of total habitat must be of a premium type. Exploring the actual extent of this habitat and the adult stock's dependence on it should be a management priority and a major focus for future work.

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**Abstract.**—Many tuned assessment models, such as sequential population analysis and nonequilibrium production models, are cast in the form of least-squares minimization routines. It is well known that outliers can substantially alter the results of least-squares methods. Indeed, in the process of conducting stock assessments, much time and effort are often spent in discussing the merits of individual data points and in evaluating the impact that including or excluding them has on the perceived stock status. Unfortunately, straight-forward statistical tests for detecting outliers have been developed only for univariate statistics or for the simplest of linear models and are generally useful to test for a single outlier only. In this paper, we apply a high-breakdown robust regression technique, least trimmed squares, to two assessment models using North Atlantic swordfish and West Atlantic bluefin tuna as examples. We illustrate how robust regression can be used as an initial step in statistically detecting outliers before the more efficient least-squares minimization can be used.

## Application of high-breakdown robust regression to tuned stock assessment models

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Tuned stock assessment models are statistical methods that analyze time series of fishery catch data in conjunction with auxiliary information (indices of relative abundance, fishing effort, etc.) to yield estimates of stock abundance and exploitation rates over time. Such methods are widely used today by stock assessment working groups throughout the world because they provide an objective and statistically defensible way to assess the status of stocks and to derive management advice. The two primary methods are sequential population analysis (SPA: Fournier and Archibald, 1982; Deriso et al., 1985; Pope and Shepherd, 1985; Kimura, 1989; Methot, 1990; Powers and Restrepo, 1992; Gavaris<sup>1</sup>) and nonequilibrium production models (Pella and Tomlinson, 1969; Hilborn, 1990; Hilborn and Walters, 1992; Prager, 1994). SPA's are typically age structured and production models are not, although there are exceptions to this generalization in the references just cited. Both types of methods, however, share the commonality of often being cast as nonlinear least-squares minimization problems.

Despite efforts to standardize all steps involved in a stock assessment (from data collection, preparation of

model inputs, to running the models), stock assessments are rarely automated and, more often than not, generate controversy. In our experience with different fora, a common cause for controversy is as follows: various data sets are presented to a working group and then the group collectively decides on the sets of data and model assumptions to be used. The consensus selection is typically termed the "base case." Individual data points are then scrutinized for exclusion from further analyses to determine the robustness of the overall assessment to the sensitivity changes. This partial "sensitivity analysis" can, in practice, be undesirable because perceptions of what results ought to be like may influence which data or data points are scrutinized and thus generate controversy; not every working group participant has the same perception. The lack of an a priori objective selection process could lead working groups astray (Restrepo and Powers, 1995). A so-

<sup>1</sup> Gavaris, S. 1988. An adaptive framework for the estimation of population size. Can. Atl. Fish. Sci. Adv. Comm. (CAFSAC) Res. Doc. 88/29, 12 p. Biological Station, Department of Fisheries and Oceans, St. Andrews, New Brunswick, Canada EOG 2X0.

lution to this problem lies in a method that would objectively identify—and deal with—“outliers.”

Statistical tests have been developed for identifying outliers (see Barnett and Lewis, 1994), but most of the straight-forward approaches can only deal with a few outliers in univariate analyses or in linear regression. High-breakdown robust regression methods (Rousseeuw, 1984; Rousseeuw and Leroy, 1987) hold promise for addressing the issue, as suggested by several recent papers in fisheries literature (e.g. Chen et al., 1994; Chen and Paloheimo, 1994). The goal of high-breakdown robust regression is to provide model estimates that are insensitive to contamination (up to 50%) by outliers and thus will serve to identify outlying observations. However, most robust regression applications in fisheries science (Chen et al., 1994; Chen and Paloheimo, 1994) and in statistics literature have been developed for linear problems (but, see Stromberg, 1993). In this study we seek to illustrate the application and usefulness of this tool by using two nonlinear examples: a nonequilibrium production model for North Atlantic swordfish, *Xiphias gladius*, and a sequential population analysis for West Atlantic bluefin tuna, *Thunnus thynnus*. Both stocks are assessed by the Standing Committee on Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT). The analyses presented here are illustrative and are not intended to replace those of the SCRS.

## Methods

### Assessment models

Assuming a normal (Gaussian) error structure, the typical tuned assessment method minimizes the squared deviations (residuals,  $r$ ) between observed and predicted indices of abundance:

$$\min \sum_{i=1}^m \sum_{j=1}^{n_i} (I_{ij} - \hat{I}_{ij})^2 = \min \sum_{i=1}^m \sum_{j=1}^{n_i} (r_{ij}^2), \quad (1)$$

for  $m$  indices, each with  $n_i$  observations. The prediction of each index,  $\hat{I}_{ij}$ , comes from a population model, such as a surplus production model or a sequential population analysis. Alternatively, the minimization can be made in terms of observed and predicted catches or in terms of observed and predicted fishing effort. Note that some maximum-likelihood approaches do not make the normal error assumption (e.g. Fournier and Archibald, 1982); we focus on those approaches that are in a least-squares framework or

that can be transformed to one, which include iteratively reweighted least squares and some forms of maximum likelihood.

In this paper, we give robust regression examples using two population models. A detailed explanation of these methods is beyond the scope of this paper and readers are referred to the citations given below. The surplus production model corresponds to a Schaeffer (logistic) form, fitted as nonequilibrium time series by using the continuous time method presented by Prager (1994). This method estimates parameters describing the carrying capacity, rate of intrinsic population growth, initial biomass, and catchability coefficients that best explain observed time series of relative abundance according to the criterion in Equation 1. The sequential population analysis corresponds to a tuned virtual population analysis method known as ADAPT, an age-structured assessment framework popular in the east coast of North America. Details on ADAPT can be found in Powers and Restrepo (1992, 1993), Punt (1994), and Gavaris.<sup>1</sup> ADAPT estimates age-specific fishing mortality rates in the last year of data and catchability coefficients that satisfy Equation 1, while forcing cohorts to conform to exponential survival through time:

$$N_{a+1,y+1} = N_{a,y} e^{-Z_{a,y}},$$

where  $N$  denotes stock size in numbers,  $Z$  denotes instantaneous total mortality, and  $a$  and  $y$  are subscripts for age and year.

### Data sets

The data set used with the nonequilibrium production model is for North Atlantic swordfish as employed by ICCAT in its 1994 assessment (ICCAT, 1995). This data set consists of total landings (in weight) for the period 1950–93 and of a single standardized longline series of catch per unit of effort (CPUE, used as a measure of relative abundance), spanning the period 1963–93 (Table 1). After a series of sensitivity tests, ICCAT assumed in its “base case” analysis that the initial biomass in 1950 was a known quantity, equal to 0.875 times the stock’s carrying capacity. Thus, 3 parameters were estimated: carrying capacity, intrinsic rate of growth, and a constant of proportionality ( $q$ ) relating the series of relative abundance ( $X$ ) to absolute biomass units ( $B$ ). The minimization of Equation 1 was done in log scale, i.e.  $I_{ij} = \ln(X_{ij})$  and  $\hat{I}_{ij} = \ln(qB_j)$ .

The data for the SPA is for West Atlantic bluefin tuna, also as employed by ICCAT in its 1994 base case assessment (ICCAT, 1995). It consisted of catch

Table 1

North Atlantic swordfish, *Xiphias gladius*, data used for the nonequilibrium production model (from ICCAT, 1995). Relative abundance is in Kg/1,000 standard hooks, standardized from Canadian, Japanese, Spanish, and U.S. longliners. t = metric tons.

Year	Landings (t)	Relative abundance	Year	Landings (t)	Relative abundance
1950	3,646	—	1973	6,001	—
1951	2,581	—	1974	6,301	—
1952	2,993	—	1975	8,776	421.69
1953	3,303	—	1976	6,587	353.66
1954	3,034	—	1977	6,352	393.92
1955	3,502	—	1978	11,797	649.61
1956	3,358	—	1979	11,859	338.57
1957	4,578	—	1980	13,527	430.69
1958	4,904	—	1981	11,138	310.18
1959	6,232	—	1982	13,155	356.96
1960	3,828	—	1983	14,464	287.88
1961	4,381	—	1984	12,753	286.12
1962	5,342	—	1985	14,348	265.94
1963	10,189	1,258.10	1986	18,447	255.54
1964	11,258	467.29	1987	20,234	217.30
1965	8,652	294.86	1988	19,614	207.62
1966	9,338	273.50	1989	17,299	196.90
1967	9,084	320.22	1990	15,865	199.20
1968	9,137	269.55	1991	15,224	194.02
1969	9,138	233.95	1992	15,593	182.55
1970	9,425	274.25	1993	16,977	172.27
1971	5,198	—			
1972	4,727	—			

at age from 1970 to 1993 for ages 1 to 10<sup>+</sup> (Table 2), and of 7 indices of relative abundance assumed to track different segments of the population (Table 3; see Fig. 4). A number of assumptions were made and these can be found in Appendix BFTW-2 of ICCAT (1995). The parameters estimated were 7 constants of proportionality relating each index of relative abundance to absolute biomass or numbers and 4 fishing mortalities in 1993 (for ages 2, 4, 6, and 8).

We reiterate that we chose the same data sets and model structures as those in ICCAT (1995) for illustrative purposes. It may be worthwhile to investigate the results of robust regression techniques applied to alternative data (e.g. indices obtained with a different standardization procedure) or to formulations (e.g. different assumptions about known quantities and other constraints).

### Robust regression

Several robust minimization criteria discussed in Rousseeuw and Leroy (1987) have been applied to fisheries data (see Chen et al., 1994). In contrast with the method of least squares, the goal of these techniques is to moderate the influence of outliers in the parameter fitting process (Eq. 1). Of particular interest to us are the so-called "high-breakdown" meth-

ods that are insensitive to up to 50% contamination by outliers, because they can effectively be used as an objective method to identify outliers.

Two high-breakdown robust regression methods are least median squares (LMS) and least trimmed squares (LTS). LMS minimizes the median of the squared residuals and LTS minimizes the sum of the lowest  $xn$  squared residuals, where  $x$  is a fraction (less than 1.0 to 0.5) defined by the user. The results of an LMS regression and an LTS regression with a 50% trim are essentially very similar, although the LTS one is statistically more efficient (Rousseeuw and Leroy, 1987). In our initial experimentation with fisheries assessment models, we found that the LTS minimum was somewhat easier to find (the LMS could sometimes not converge, indicating that a large number of restarts may be required). Therefore, we limited our investigation to the LTS minimization criteria discussed below. This can be either

$$LTS_1 = \sum_{i=1}^m \min \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i} \quad (2)$$

or

$$LTS_2 = \min \sum_{i=1}^m \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i}, \quad (3)$$

Table 2

West Atlantic bluefin tuna, *Thunnus thynnus*, catch at age data (in numbers) used for the sequential population analysis (from ICCAT, 1995).

Year	Age									
	1	2	3	4	5	6	7	8	9	10+
1970	64,886	105,064	127,518	21,455	3,677	914	176	172	535	3,726
1971	62,998	153,364	38,360	46,074	672	1,673	2,109	1,350	1,133	5,957
1972	45,402	98,578	33,762	3,730	3,857	118	569	576	261	5,519
1973	5,105	74,311	30,482	7,161	2,132	1,451	953	1,544	555	4,444
1974	55,958	20,056	21,094	6,506	3,170	683	916	913	1,081	12,508
1975	43,556	148,027	8,328	11,963	821	547	317	671	1,651	9,472
1976	5,412	19,781	72,393	2,910	2,899	344	206	1,168	558	14,033
1977	1,274	22,419	9,717	32,139	4,946	3,633	957	513	1,109	13,532
1978	5,133	10,863	20,015	6,315	10,530	4,061	655	472	341	11,982
1979	2,745	10,552	16,288	14,916	3,448	3,494	2,612	599	557	12,283
1980	3,160	16,183	11,068	8,881	2,866	2,982	5,533	3,454	1,061	12,213
1981	6,087	9,616	16,541	5,244	6,023	3,721	2,884	3,211	2,764	10,621
1982	3,528	3,729	1,654	498	342	751	477	519	896	3,077
1983	4,173	2,438	3,268	894	866	911	1,402	1,353	1,039	5,628
1984	868	7,504	1,848	2,072	2,077	1,671	594	759	1,091	4,574
1985	568	5,523	12,310	2,814	4,329	4,019	1,024	612	698	5,603
1986	563	5,939	7,135	3,442	1,128	1,726	931	520	345	5,335
1987	1,513	13,340	9,137	5,491	4,385	2,318	1,566	1,251	1,014	3,856
1988	4,850	9,149	11,745	3,933	4,144	4,220	2,258	1,631	1,600	4,555
1989	787	12,877	1,679	3,815	1,713	2,082	2,677	1,864	1,461	5,356
1990	2,368	4,238	17,958	1,947	2,747	1,825	1,629	2,388	1,522	4,253
1991	3,327	14,533	10,761	2,924	1,650	2,166	2,347	1,946	1,915	4,485
1992	420	5,985	1,997	711	1,425	737	1,916	1,870	1,323	4,383
1993	329	1,130	5,215	3,689	2,089	1,883	1,598	2,456	1,479	2,922

where the notation  $j:n_i$  indicates that the squared residuals are sorted in ascending order from  $j=1$  to  $n_i$ ; note that  $n_i/2 + 1$  is actually an integer value equal to  $n_i/2$  when  $n_i$  is even and equal to  $n_i/2 + 1$  when  $n_i$  is odd. Equations 2 and 3 are two different minimization objectives that differ in the way they treat multiple series of relative abundance data. In Equation 2, the trimmed sums of squared residuals are computed separately for each index and then added to the objective function being minimized. Thus, the individual indices are de facto given equal weighting. In Equation 3, the trimming is done over all available data points, regardless of which relative abundance series they belong to. Thus, the  $LTS_1$  formulation forces each available series to contribute to the objective function, whereas the  $LTS_2$  formulation could plausibly eliminate indices that fit very poorly in comparison with the others. An analogous distinction can be made for the LS fit by giving either equal weight to all available data series (as in Eq. 1) or by assigning weights to each series in proportion to their mean squared errors. The latter has often been accomplished by means of iterative reweighting (Powers and Restrepo, 1992) or maximum likelihood (Punt, 1994).

Algorithms for high-breakdown robust regression are notoriously computation-intensive, even in the simplest univariate linear regression case (Rousseeuw, 1984; Rousseeuw and Leroy, 1987; Steele and Steiger, 1986). A typical algorithm for a linear robust regression with  $p$  parameters goes like this: For a large number of times,  $s$ , select  $p$  data points, do a least-squares regression (LS) and compute the corresponding robust objective function (e.g. sum of trimmed squares) for the complete data set. The LTS solution is given by the parameter estimates and results in the lowest robust objective function value. In the linear case, the value of  $s$  is chosen such that, for a given fraction of data contamination and a given  $p$ , at least one of the  $s$  subsamples is not contaminated (Rousseeuw and Leroy, 1987). The choice of  $s$  in the nonlinear case is not clearcut. However, in the linear case the values of  $s$  grow very rapidly with  $p$  and percent contamination; therefore many available algorithms set  $s = 3,000$  for  $p > 9$  (Rousseeuw and Leroy, 1987). Similar values were used here for the nonlinear case.

Algorithms for nonlinear robust regression are rare, owing partly to the increased computational

Table 3

West Atlantic bluefin tuna, *Thunnus thynnus*, relative abundance indices (from ICCAT, 1995). The larval index is in relative biomass units, while all others are in relative numbers. The numbers below each index label are the ages or range of ages that each index is assumed to represent. TL = tended line, LL = longline, RR = rod and reel, GOM = Gulf of Mexico, NWA = Northwest Atlantic.

Year	Canada TL 10 <sup>+</sup>	Japan LLGOM 10 <sup>+</sup>	Japan LLNWA 1-9	Larval GOM 8 <sup>+</sup>	US LLGOM 8 <sup>+</sup>	US RR 8 <sup>+</sup>	US RR 1-5
1974	—	1.4670	—	—	—	—	—
1975	—	1.0200	—	—	—	—	—
1976	—	0.8960	0.8134	—	—	—	—
1977	—	0.6700	1.7822	1.7704	—	—	—
1978	—	0.9350	1.4621	4.2341	—	—	—
1979	—	0.9380	0.5476	—	—	—	—
1980	—	1.5130	1.0327	—	—	—	1.2109
1981	2.3489	0.5610	1.4812	0.9575	—	—	0.1274
1982	2.1095	—	0.7121	1.1008	—	—	1.3417
1983	1.5621	—	0.5022	0.8977	—	2.4703	0.7816
1984	1.0718	—	0.8527	0.4750	—	1.0949	—
1985	0.5131	—	0.9967	—	—	1.0483	0.5366
1986	0.6157	—	0.5725	0.1897	—	0.7324	0.9995
1987	0.3991	—	1.1490	0.3236	1.7544	0.6933	1.2138
1988	0.6271	—	0.8773	1.4146	0.6842	1.3195	1.6059
1989	0.4561	—	0.7417	0.5803	1.0526	0.6808	1.3339
1990	0.2965	—	0.7754	0.3446	1.1404	0.6204	0.7331
1991	—	—	0.7523	0.2652	1.5614	0.7694	1.3277
1992	—	—	1.8813	0.4464	0.5263	0.8727	0.7968
1993	—	—	1.0675	—	0.2807	0.6981	0.9912

requirements. Although the LS solutions for the linear case (as described in the previous paragraph) can be accomplished with simple matrix manipulations, nonlinear LS solutions require iterative computations. Stromberg (1993) presented a multistage algorithm for nonlinear regression that is similar to the one outlined above, succeeded by a direct minimization of the robust objective function by using the simplex search of Nelder and Mead (1965). Building upon Stromberg's ideas, we reviewed algorithms for an LTS<sub>1</sub> solution to the bluefin tuna SPA. On the basis of these results and the work of Stromberg (1993), we adopted the algorithm below but acknowledge that there are many other possible fruitful options to be explored, such as "simulated annealing" (Corana et al., 1987). Our algorithm uses the fact that the simplex search of Nelder and Mead (1965) requires  $p+1$  starting guesses, denoted by  $v$  vertices, for each of the  $p$  parameters being estimated.

- 1 Find the LS estimate for the entire data set. The estimates  $(p)_{LS}$  are used as starting guesses for step 2.
- 2 Repeat  $s$  times:
  - a) Set initial parameter guesses at random from within 10 times the  $(p)_{LS}$  estimates from step 1.

- b) Find the LTS estimates for the complete data set by using the starting values from step 2a.
  - c) Restart step 2b until the objective function (either Eq. 2 or Eq. 3) does not change appreciably.
  - d) Save the parameter estimates corresponding to the  $(p+1)_{LTS}$  parameter sets with the lowest objective function value.
- 3 Initialize the  $v$  vertices for the simplex search with the best  $(p+1)$  parameter sets from the  $s$  solutions from step 2 and find the LTS estimate for the entire data set. As in step 2, carry out restarts as needed.

This algorithm is a direct robust minimization search that is initialized  $s$  times from a Monte Carlo grid centered around the LS solution. It is computationally intensive, but this seems necessary given the multi-modal nature often encountered in the LTS or LMS objective function. For this study we used  $s = 500$ . For both the swordfish nonequilibrium production model and the bluefin tuna SPA analyses, step 2 involved 5 restarts on average and thus made the total number of minimizations greater than 2,500. It should be noted that this search algorithm does not guarantee that a global minimum LTS solution is going to be found. Therefore, we favor mul-

tiple replicates and restarts so that there is some confidence that the solution is globally minimal. At this point we have no firm guidance about the tradeoffs between the number of replicates (*s*) and the number of restarts other than to say that replicates are probably more important than restarts. For example 500 replicates with 5 restarts seems preferable to 25 replicates with 100 restarts.

### Dealing with outliers

Aside from biological or fishery considerations, statistical outliers are data points whose residuals, scaled by the dispersion of errors,

$$\frac{r_{ij}}{\sigma}$$

are far from the mean scaled residual. For the simple LS minimization (Eq. 1), the overall dispersion of the residuals is the mean squared error (MSE),

$$\sigma = \sqrt{\frac{1}{\sum_{i=1}^m n_i} \sum_{i=1}^m \sum_{j=1}^{n_i} (r_{ij}^2)}$$

For the LTS regression, the dispersion is similarly computed as a robust measure of average dispersion ( $\sigma_i$  for index *i* in Eq. 2 or  $\sigma$  for all data points in Eq. 3):

$$\sigma_i = 3.7444 \sqrt{\frac{1}{n_i} \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i}}$$

for  $LTS_1$ , Eq. 2, or

$$\sigma = 3.7444 \sqrt{\frac{1}{\sum_{i=1}^m n_i} \sum_{i=1}^m \sum_{j=1}^{n_i/2+1} (r^2)_{j:n_i}}$$

for  $LTS_2$ , Eq. 3.

The constant 3.7444 is a correction factor used to achieve consistency with normal error distributions (Rousseeuw and Leroy, 1987). As a rule of thumb, Rousseeuw and Leroy (1987) suggest that absolute values of scaled residuals larger than 2.5 can be treated as statistical outliers. Owing to the small number of observations in some of our data series, we use a threshold based on the *t*-distribution with  $\alpha = 0.01$  and *n*-1 degrees of freedom. After obtaining the LTS estimates, we carried out a new least-squares minimization excluding from the analyses any absolute scaled residuals greater than the corresponding critical value. We refer to this final result as the "trimmed LS" solution.

## Results

### Swordfish nonequilibrium production model

The swordfish data represent a simple example with a single index. Nevertheless, there are several very large deviations between the observed and predicted index values, when the traditional least-squares (LS) solution to the nonequilibrium production model fit is computed (Fig. 1). Indeed, these deviations have generated considerable debate (ICCAT, 1995). Therefore, we applied the robust regression techniques of the LTS algorithm and the trimmed LS method of outlier detection to this example. The LTS solution (with a 50% trim) was computed 500 times with 5 restarts each. There did not appear to be problems of multiple minima with this example because vir-

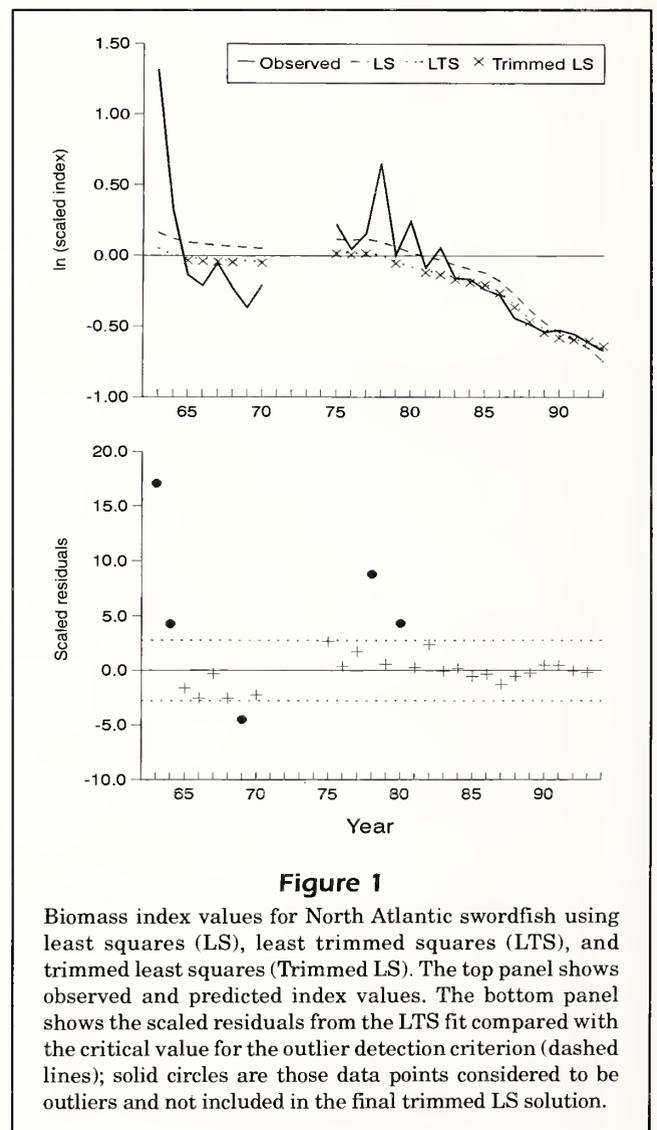


Figure 1

Biomass index values for North Atlantic swordfish using least squares (LS), least trimmed squares (LTS), and trimmed least squares (Trimmed LS). The top panel shows observed and predicted index values. The bottom panel shows the scaled residuals from the LTS fit compared with the critical value for the outlier detection criterion (dashed lines); solid circles are those data points considered to be outliers and not included in the final trimmed LS solution.

tually all of the 500 solutions converged to the same value. The outlier detection criteria identified five of the original 27 data points (19%), all of which occurred before 1981 (Fig. 1). Predicted index values with both the LTS and trimmed LS solutions were higher than the LS predictions prior to the late 1980's and lower than LS predictions in recent years (Fig. 1).

Predicted relative biomass values with either the LTS or trimmed LS solutions are higher than the initial LS solution (ICCAT, 1995), particularly in the 1990's (Fig. 2) and suggest less of a decline in the population. Absolute biomass predictions with the LTS method were generally higher than those from the initial LS solution, whereas trimmed LS solutions were lower (Fig. 2). The trimmed LS solution results in biomass levels

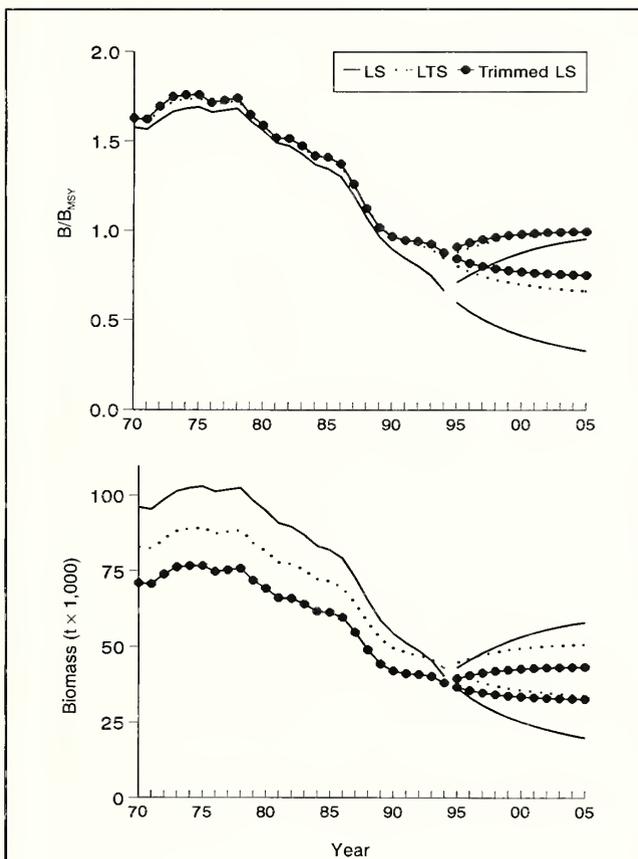
that are lower than those in the other two methods; however, the decline over the time series is less. Biomass projections were made under two strategies: 1) a recovery strategy in which future fishing mortality rate was fixed at the value that would produce maximum sustainable yield and 2) a status quo strategy in which the fishing mortality would be fixed at the 1993 level. The LTS and trimmed LS projections indicate that both recovery and decline is not as rapid as that predicted from the initial LS solution (Fig. 2).

The robust regression techniques applied here tend to provide a better fit to the index data points in recent years at the expense of the data points in the earlier years of the series. Indeed, several of the points identified through the outlier detection process were those data points for which there was much debate regarding variability and bias (ICCAT, 1995). However, some of the data points identified here were not identified by ICCAT (1995); therefore, we reemphasize the point that the selection of outliers should be based on objective criteria.

### Bluefin tuna SPA

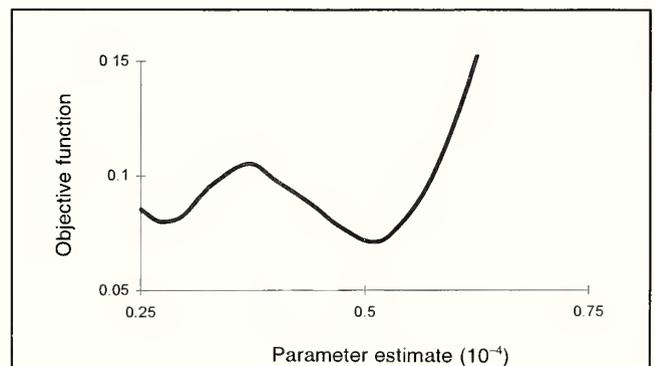
As mentioned before, a high-breakdown robust regression objective function can possess multiple minima. Figure 3 illustrates this point with the  $LTS_1$  objective function plotted around  $\pm 50\%$  of the final estimate for one of the parameters, while all other parameter values were fixed at their solution. The figure highlights the need for an exhaustive search owing to the multimodal nature of the response surface.

Figure 4 shows the observed indices of relative abundance in the first column, the scaled residuals



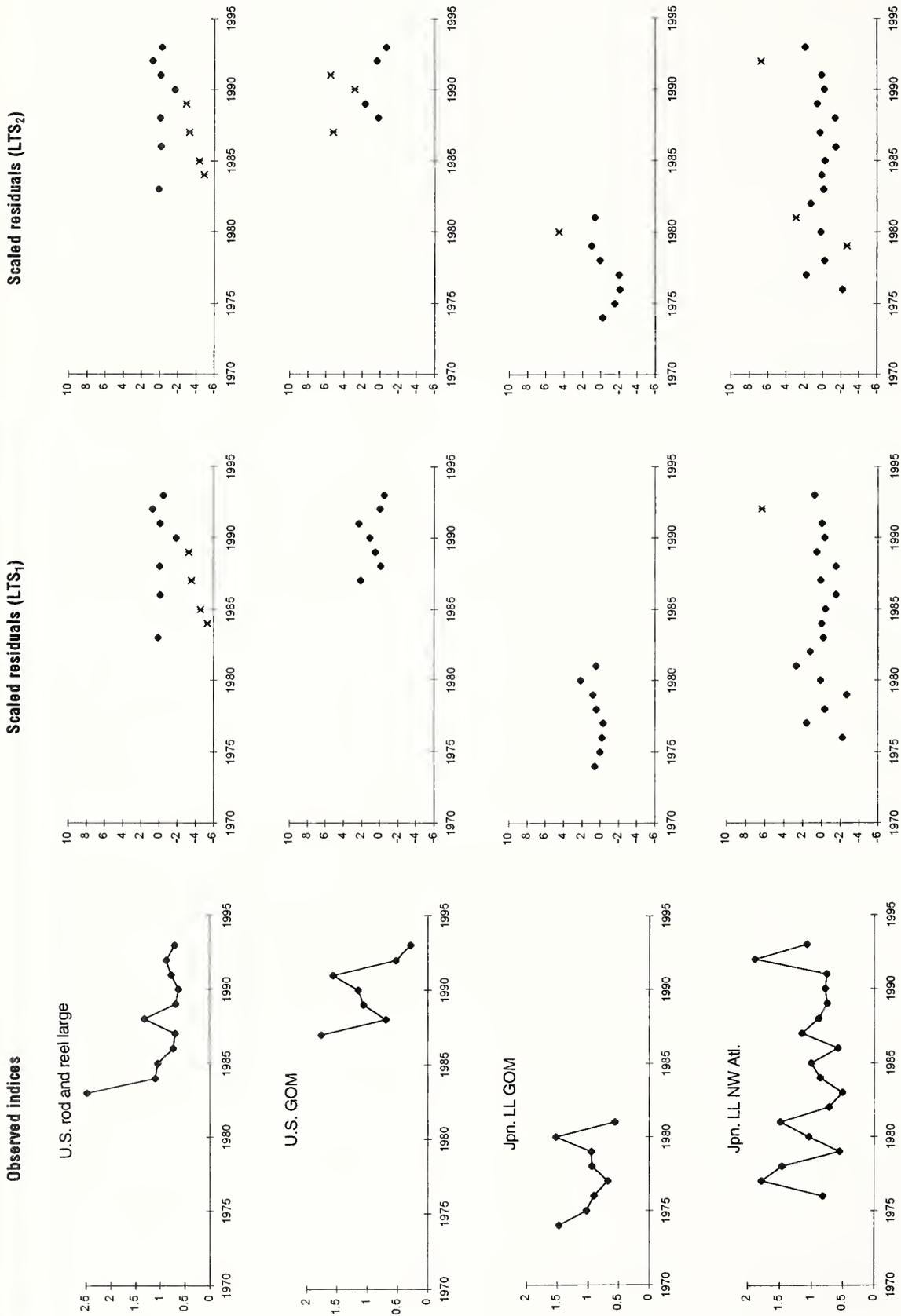
**Figure 2**

Predicted biomass relative to biomass at maximum sustainable yield ( $B/B_{MSY}$ , top panel) and absolute biomass (bottom panel) resulting from LS, LTS, and trimmed LS solutions. The left side of the graphs show the production model estimates. The right sides of the graphs are projections made with the fishing mortality rate at maximum sustainable yield ( $F_{MSY}$ ) and with the fishing mortality rate in 1993 ( $F_{93}$ ). Ascending limbs were projected by using  $F_{MSY}$ , descending limbs by using  $F_{93}$ .



**Figure 3**

Trimmed squares objective function (Eq. 2) plotted around the solution for one of the parameters estimated in the bluefin tuna sequential population assessment (catchability for the U.S. rod and reel large fish index, Table 3). The plot shows that multiple local minima can occur in robust regression problems.



**Figure 4**

Results from the bluefin tuna sequential population analyses using least trimmed squares (LTS) regression. The left-hand column shows the seven available indices of relative abundance (see Table 3). The middle and right-hand side columns show the scaled residuals resulting from the minimizations with Equations 2 and 3, respectively. Crossed symbols identify statistical outliers at the 1% significance level.

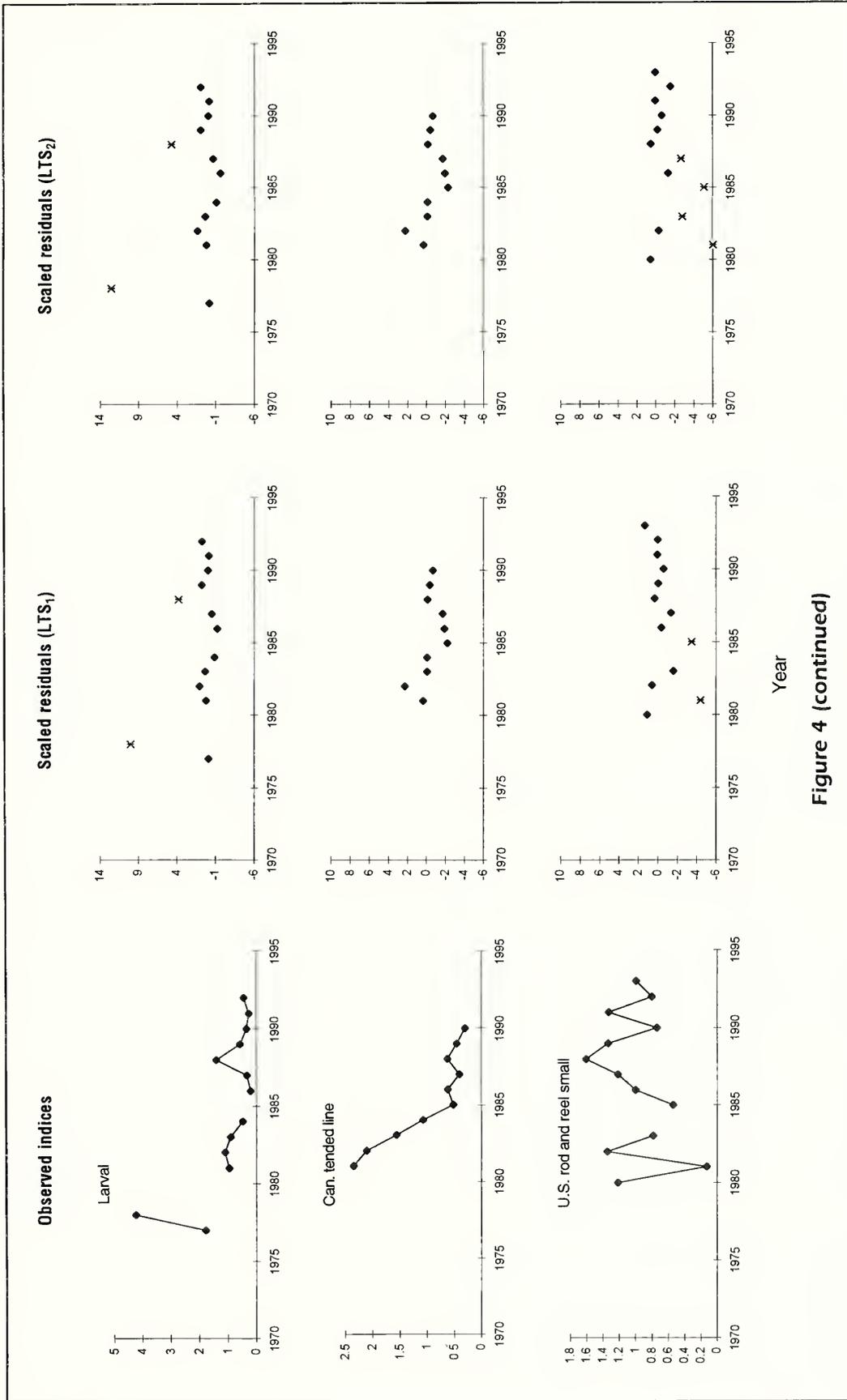


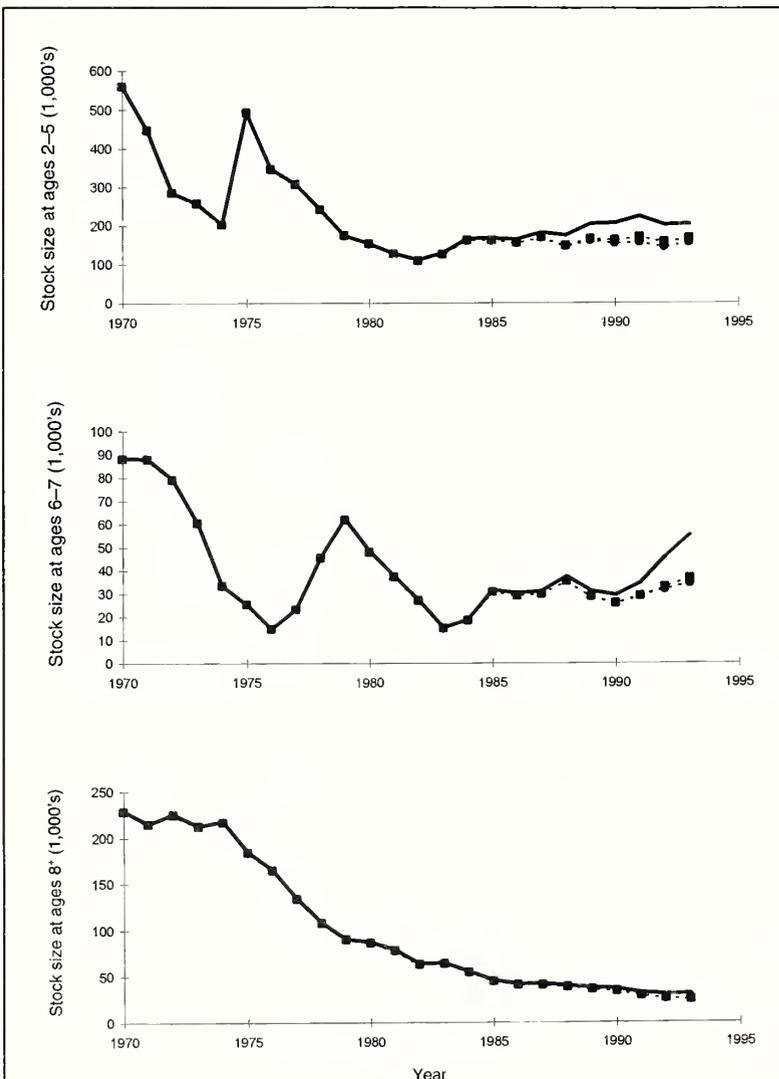
Figure 4 (continued)

from the  $LTS_1$  fit (second column), and the  $LTS_2$  fit (last column). The open symbols indicate which data points were identified as outliers according to the  $t$ -test criterion mentioned previously. The  $LTS_1$  regression, which gives equal consideration to all index series, identified 9 outliers (11% of the total index data points). The  $LTS_2$  approach, which gives more weight to the better-fitting series, identified the same 9 observations as outliers, and an additional 8 (21% of the total number of data). The 1978 estimate from the larval index stands out as a particularly large

outlier (Fig. 4). But perhaps more importantly in terms of the effect on the SPA results, the 1992 data point for the Japanese Northwest Atlantic longline index, is also identified as a large outlier. That is, because of the convergence properties of the ADAPT approach, the more recent data tend to have a larger impact on the estimates of current stock status.

Figure 5 shows the estimated stock size trajectories for 3 age groupings that ICCAT assessments focus on: small fish (ages 2 to 5), medium fish (ages 6 and 7), and spawners (ages 8 and older). The solid line without symbols represents the initial LS solution (Eq. 1), as in the 1994 ICCAT assessment. The 2 dashed lines with symbols (virtually indistinguishable from each other) represent the final trimmed LS solutions, i.e. after removal of the outliers identified in Figure 4. Note that all the stock size estimates are identical in the first half of the time series, owing to the convergence properties of the SPA. Differences in 1990's stock size estimates before and after trimming are most notable for small and medium bluefin tuna (Fig. 5). For this example, the final trimmed LS solutions estimate lower current stock sizes (Fig. 5) and correspondingly higher current exploitation rates (not shown).

The impact that these differences in the estimates have on management recommendations can be appreciated in Figure 6, which shows a 10-year projection of the stock's spawning biomass at two levels of constant landings considered by ICCAT. These projections were made by using the same assumptions as those in the assessment (Appendix BFTW-2 in ICCAT, 1995): essentially, that recruitment is constant after a certain parental biomass level and that the 3 most recent recruitment values from the SPA are poorly estimated and are replaced by the geometric mean recruitment from past years. The top panel in Figure 6 is a projection made by assuming 2,000 metric tons (t) landings after 1993: the lower panel assumes 2,660 t landings after 1993. The solid lines represent the LS solution as in the ICCAT assessment, and the dashed lines represent the LS solutions after trimming (squares for results from the  $LTS_1$  solution and circles for results from the  $LTS_2$  solution). The projections made without removing outliers



**Figure 5**

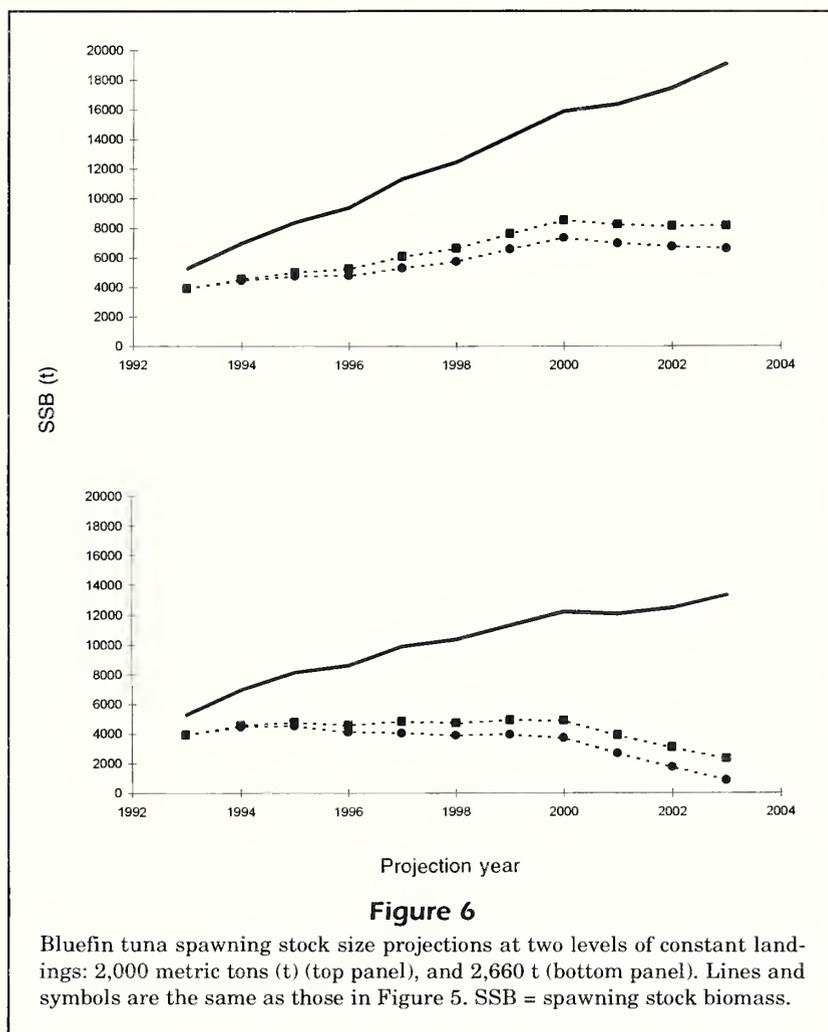
Bluefin tuna stock size estimates for 3 groups of ages. The solid line represents the estimates from the least-squares solution with all the available data, as in the ICCAT assessment. The dashed lines show the least squares estimates after removal of the data points identified as outliers in Figure 4. Squares = after minimization with Equation 2; circles = after minimization with Equation 3. Squares and circles overlap.

are optimistic and suggest a continued increase in parental biomass even at the higher level of landings. The projections made after trimming, on the other hand, are less optimistic. These suggest a more modest increase in spawning biomass at the 2,000 t level of landings, or a decline in spawning biomass after 7 years of 2,660 t landings (Fig. 6).

## Discussion

The robust regression methods as applied to tuned population assessment models may be helpful in several ways. The methods can be used as an alternative minimization criterion to obtain estimates of the population parameters. They can also be used to identify outliers for elimination from subsequent fitting. In either case, much of the subjectivity that can enter discussions about individual data points during working group meetings would be eliminated. The latter aspect (identification and elimination of outliers) is especially useful because, after elimination of the outliers, one can then go on and conduct the normal bootstrap (Punt, 1994) or Monte Carlo (Restrepo et al., 1992) analyses used to evaluate uncertainty in the estimates. The robust regression methods could be used to screen the outliers, and then the other methods could be used to estimate variability and to project the population status under different management scenarios. Presently, computation time would preclude incorporating bootstrap or Monte Carlo techniques directly into the LTS search. Removing outliers should, also, have a moderating effect on the so-called retrospective patterns (Sinclair et al., 1990), some of which are caused by outliers in the indices (ICES, 1995).

It is important to keep in mind a point of caution when removing statistical outliers from an assessment. Observations that appear to be outliers are so in the overall context of data-model. That is, it is possible that a data point is considered as either an outlier or not, depending on the model formulation, constraints, etc. For example, if the bluefin tuna indices of abundance had been considered to be log-normally distributed instead of normally-distributed,



**Figure 6**

Bluefin tuna spawning stock size projections at two levels of constant landings: 2,000 metric tons (t) (top panel), and 2,660 t (bottom panel). Lines and symbols are the same as those in Figure 5. SSB = spawning stock biomass.

the LTS regression may have identified more or fewer observations as outliers. A related point is that we do not advocate rushing to eliminate outliers automatically from stock assessments. Instead, a first step should be to look into reasons why such observations may seem like outliers, e.g. undetected transcription errors or environmental influences that were not accounted for in the analysis. Additionally, the outlier detection would identify candidates for sensitivity analysis in an objective manner. Instead of determining data points that are influential on the results and trying to determine if those points could be considered outliers, we are advocating the converse.

The outlier detection procedures outlined here inherently assume symmetry in the response surface. Thus, it is expected that the trimmed LS technique will provide results similar to those coming from bias correction procedures used in bootstrapping methods (e.g. Prager, 1994). Both methods assume that the underlying distributions are symmetrical and

adjust the results in order to maintain that symmetry. However, if model constraints or other features of the model or data force the response surface to have an underlying (but unknown) skewed distribution, then the outlier selection process outlined here might falsely identify some data points as outliers. Conversely, the least trimmed squares (LTS) solutions make no assumptions about the shape of the response surface. Therefore, we expect that the LTS method could be robust to those situations where the distribution is skewed. Nevertheless, with judicious application, robust regression is expected to be a useful tool for evaluating and selecting data appropriate for tuning stock assessment models.

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**Abstract.**—Growth and mortality rates of 0<sup>+</sup> English sole were estimated from field data collected from estuarine and nearshore nursery areas off Washington during 1985–88. Growth of 0<sup>+</sup> English sole was approximately linear over time and was estimated with the length modal progression method. Point estimates of growth rates during May through September were in the range of 0.33 to 0.49 mm/day. Statistical analysis with a general linear model showed significant year and settlement time effects on growth of 0<sup>+</sup> English sole but failed to detect any density or temperature effect. Instantaneous mortality rate varied significantly with season, declining from 0.0175 per day in July and August to 0.0075 per day in September. Changes in population density appeared to play a minor role in causing this decline.

## Growth and survival of 0<sup>+</sup> English sole, *Pleuronectes vetulus*, in estuaries and adjacent nearshore waters off Washington

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Fish growth depends on numerous factors, e.g. supply of suitable prey items, ambient temperatures, and oxygen concentration. Laboratory studies have shown that growth of juvenile plaice (*Pleuronectes platessa*), sole (*Solea solea*), and English sole (*Pleuronectes vetulus*) depends strongly on ambient temperature (Williams and Caldwell, 1978; Fonds, 1979; Yoklavich, 1981).

Field observations also show that growth of flatfishes is regulated by ambient temperature. Applying a model based on Fonds's (1979) laboratory experiment and observed temperature data for predicting monthly growth of North Sea plaice, van der Veer et al. (1990) showed a close overall agreement between predicted growth increments and those observed in the field. Simulated growth rates, however, were consistently lower than field-observed growth rates in June, and this tendency was reversed in August (Fig. 7 in van der Veer et al., 1990). This finding suggests that in addition to temperature there are other factors that also affect the growth of plaice.

Laboratory studies of juvenile English sole (Williams and Caldwell, 1978; Yoklavich, 1981) have

shown that food limitation can significantly reduce growth. Edwards and Steele (1968) suggested that food limitation was the controlling factor for the growth of North Sea plaice in Loch Ewe. Bergman et al. (1988) reported that growth reduction of 0-group plaice occurred in specific areas of the Wadden Sea where there was low food abundance, although this phenomenon was restricted to only a small part of the population.

Isolating the effects of fish density, food supply, and ambient temperature on growth is difficult with field data. Within a certain range of population density or food abundance, growth may be regulated primarily by temperature and, within a certain range of temperature, population density may have a dominant influence.

Survival is the key element in determining success of recruitment. Early research was largely focused on the "critical period" theory (Hjort, 1913), i.e. survival of small first-feeding larvae is critical to subsequent year-class strength. More recent studies have shown that low

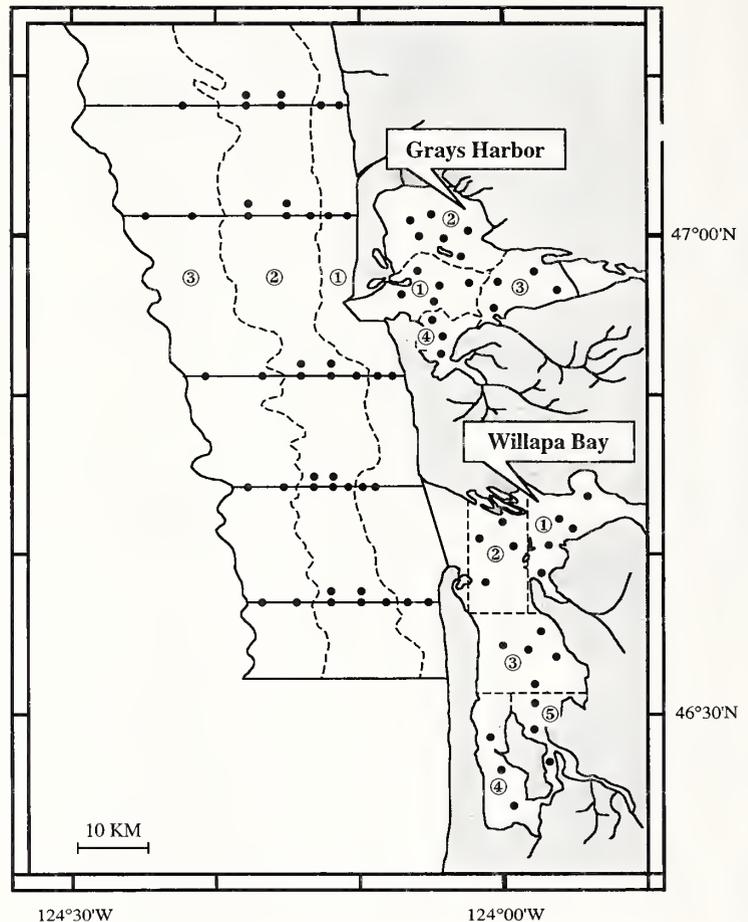
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larval abundance may indicate poor year-class strength, but high larval abundance will not guarantee a strong year class (Bailey and Spring, 1992; Bradford, 1992). Survival during the juvenile stage is critical to year-class success. On the basis of simulation, Bradford (1992) concluded that correlation between recruitment and abundance at early life stages increases monotonically with age, especially during the first 100 days of life, because variation in survival weakens the relationship between recruitment and abundance of early life stages. Although monthly or annual instantaneous mortality is usually higher during the larval stage than that at the juvenile stage, the cumulative mortality might be higher, and more variable, during the juvenile stage because it usually lasts much longer. Therefore any variation in mortality at this stage would induce much greater variation in recruitment.

English sole spawn in offshore areas. Timing of spawning is variable and duration of the spawning period is protracted (August to May, Shi, 1994). The egg and larval stages last from two to two-and-a-half months, and survival and transport of eggs and larvae are dependent on oceanographic conditions (Boehlert and Mundy, 1987, 1988; Shi, 1994). Once metamorphosis and benthic settlement have occurred, English sole actively seek out estuarine nursery areas, and oceanographic influence becomes less important. Analyses of tagging data, distribution of adults, available spawning habitat, and egg distribution (Shi, 1994) suggest that the Grays Harbor and Willapa Bay estuaries serve as nursery areas for English sole that spawn as far south as central Oregon.

This study summarizes results from a series of trawl surveys of Grays Harbor, Willapa Bay, and the adjacent nearshore, 1985–88. Previous work (Gunderson et al., 1990; Shi et al., 1995) has shown that these estuaries provide critical nursery habitat for juvenile English sole during their first year of life.

The abundance of 0+ English sole in our study area (Fig. 1) was relatively stable during September, showing only a threefold difference during 1985–88, despite great variation in settlement in May (Shi et al., 1995). If survival is density dependent, then density could function to stabilize recruitment. In this paper, growth and survival rates will be estimated by using data from field surveys, and we will investigate statistically the effects of population size and ambient temperature on the growth and survival of juvenile English sole.



**Figure 1**

The study area along the southern Washington coast. Shown are subsystem boundaries, nearshore transect lines, trawl stations (filled circles), and stratum numbers (open circles). Dashed lines indicate survey stratum boundaries.

## Methods

### Study area and field methods

Grays Harbor (8,545 ha) and Willapa Bay (11,200 ha) are two major Washington coastal estuaries characterized by numerous channels, sandflats, and eelgrass beds that provide excellent habitat for 0+ English sole. The nearshore portion of the study area is bounded to the north at 47°15'N, and to the south at about 46°30'N, and extends from the shoreline seaward to 60 m. It encompasses an area of nearly 146,600 ha.

A stratified random trawl survey was performed to estimate population sizes for English sole in both estuaries (Fig. 1) with the area-swept method:  $P = A\bar{d}$ , where  $P$  = population size,  $A$  = area of survey stratum (ha), and  $\bar{d}$  = mean density (no. of fish caught/

ha) (Shi et al., 1995). Within each stratum, stations were randomly selected from sampling units superimposed on nautical charts, with the constraint that no two stations were immediately adjacent to one another. The effort (number of stations) allocated to each stratum was proportional to the abundance of English sole in that stratum (Shi et al., 1995).

The nearshore area was sampled along fixed transects oriented east–west and trawl stations were located at discrete depths (Fig. 1). Five transects were established, and sampling stations were located at depths of 5, 9, 18, 27, 36, 46, and 55 m. The 55-m station was not sampled on the northernmost transect because of frequent gear damage at this location. Additional effort was allocated to the intermediate stratum; two trawl samples were taken at all 27- and 36-m depths. Sampling stations were stratified according to depth to obtain population estimates. The outer boundary for the nearshore study area was the 59-m (32.5-fm) isobath, and the mean low low water (MLLW) mark was the inner boundary. The boundary separating the inner and middle strata followed the 14-m (7.5-fm) isobath, whereas the boundary between the middle and outer strata was located at 41 m (22.5 fm). The northern and southern limits of the survey area were positioned 5 km beyond the northernmost and southernmost transects.

Each of the three areas was visited once a month. Sampling in estuaries was planned during low spring tides of the month (April or May through September) so that we could navigate among unmarked channels, which otherwise are difficult to see. Stations in close proximity to intertidal areas were sampled preferentially at low tide to minimize bias associated with fish movement onto the tideflats at higher stages of tide. More exposed sites were typically sampled at high water. Trawling operations ceased when tidal currents were judged sufficiently strong that the trawl gear would not tend the ocean bottom properly. Nearshore sampling trips were usually made between the two estuary trips in that month.

Survey samples throughout the study area were collected with a 3-m beam trawl specifically developed for this study (Gunderson and Ellis, 1986). Effective width of the net was 2.3 m, whereas the estimated vertical opening was 0.6 m. The body of the net was composed of 7–9 mm (lumen) knotless nylon, and the codend was lined with 4-mm stretch mesh. A double tickler chain array was attached to a 9.5-kg wingtip weight at each corner of the net. The tickler chain array, together with the turbulent zone it creates, dislodges small animals from the substrate, thus promoting capture by the net.

Nearshore sampling was conducted from the 17-m stern trawler F/V *Karelia*. Tows in the nearshore were taken parallel to isobaths. Scope was routinely 5:1, except at the 5 and 9 m stations where it was 8:1 and 9:1, respectively. Time on the ocean bottom was estimated by using a trigonometric relationship between water depth and wire out, whereas the linear distance towed (mean: 750 m) was determined from LORAN-C readings. Tow duration was routinely 20 minutes at a mean towing speed of 2.6 km/hr (1.4 knots), except at the 5- and 9-m stations, which often yielded excessive quantities of sand dollars (*Dendraster excentricus*) and gravel; tows in these areas were limited to 5 or 10 minutes.

A 6.4-m Boston whaler with a 150-hp outboard engine was used for estuarine trawling. Buoys were deployed at the points where the net first contacted the bottom and subsequently left bottom upon retrieval. The distance towed (mean: 260 m) was estimated with an optical rangefinder. Mean towing speed was 2.8 km/hr (1.5 knots), comparable to that used in the nearshore area.

## Data analysis

**Length** Growth rate estimates were obtained by regressing the mean length of a recruitment influx (indicated by a mode in the length-frequency distribution [Shi et al., 1995]) against the time when samples were taken. There was a linear relationship between modal length and time, as was the case in previous growth studies on juvenile English sole (Ketchen, 1956; Kendall, 1966; Rosenberg, 1982). Because size-dependent migration between nearshore and estuarine systems occurs, with smallest juveniles migrating into estuaries and larger fish moving offshore (Gunderson et al., 1990; Shi et al., 1995), separate estimates of growth rates for nearshore and estuarine fish would be inappropriate. To minimize the effect of interregional migrations, the mean lengths at each mode (defined on the basis of visual inspection of monthly length frequency plots [Shi et al., 1995]) were calculated from the estimated size composition of the overall population. The length statistic used was the mean modal length (MML), which is defined as the mean length within a mode, weighted by the estimated population size for each size group:

$$MML = \frac{\sum_{l=l_{low}}^{l_{up}} l \hat{P}_l}{\sum_{l=l_{low}}^{l_{up}} \hat{P}_l}, \quad (1)$$

where,  $\hat{P}_l$  = estimated population (millions) of fish in length group  $l$ ;  $l_{up}$  and  $l_{low}$  = length (mm) at upper and lower limits of the mode, which are so defined that  $l_{up}$  and  $l_{low}$  are the length groups at which abundance has declined to half that at the modal size (Fig. 2). If length is normally distributed,  $l \sim N(\bar{l}, s^2)$ , the population within the upper and lower limits of the mode so defined would account for about 75% of the total population of that cohort (Shi, 1994).

**Date** The dates used in growth and mortality estimation were also population-weighted means. The dates when the samples were taken cannot be used directly in growth and mortality estimation without being standardized. Estuarine samples had to be taken during low low tide (LLT) periods, and we were often forced to take estuarine samples at unequal time intervals.

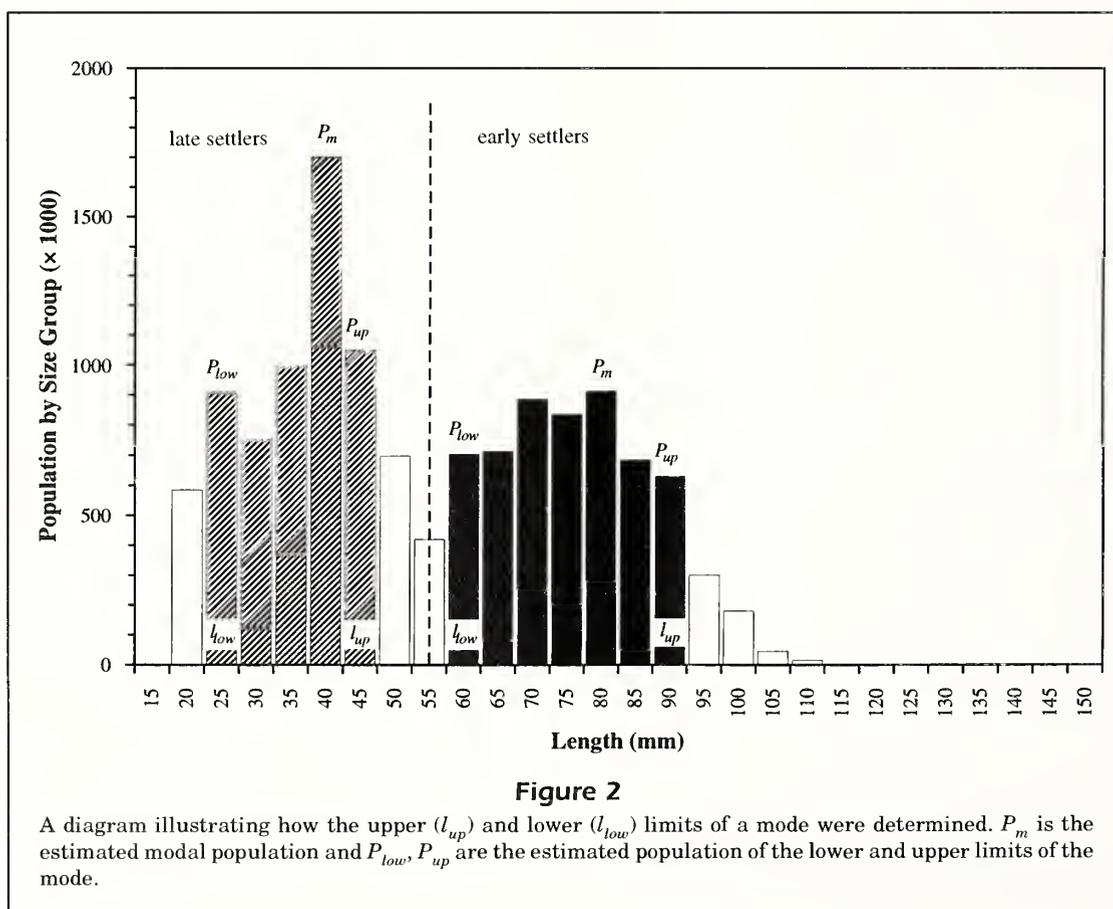
We made every effort to carry out the monthly nearshore surveys during the intervals between the Grays Harbor and Willapa Bay surveys, but they sometimes had to be done either before or after the estuarine trips owing to logistic difficulties. This made the time between the first and last surveys for

a given month more than a half-month apart. The population-weighted mean date (PWMD) was chosen to standardize the "date" of monthly surveys and is the best estimate of the average sampling date for the total population in our study area. The PWMD was computed from

$$PWMD_{jm} = \frac{\sum_{i=1}^3 P_{ijm} \overline{date_{ij}}}{\sum_{i=1}^3 P_{ijm}}, \quad (2)$$

where,  $PWMD_{jm}$  = population-weighted mean date in month  $j$  (May, June, July, August, and September) for mode  $m$  (1 or 2);  $P_{ijm}$  = population of mode  $m$  in system  $i$  (GH, WB, NS), month  $j$ ;  $\overline{date_{ij}}$  = mean date of a survey carried out in month  $j$  and system  $i$ , i.e. number of days from 1 May.

**Temperature** A population-weighted mean bottom temperature (PWMBT) was developed in this study because of extensive seasonal ontogenetic migrations



between estuarine and nearshore areas and because of differences in mean bottom temperatures between estuarine and nearshore systems (2–8°C, Fig. 3).

$$PWMBT_{jm} = \frac{\sum_{i=1}^3 \sum_{s=1}^{s_i} P_{isjm} \bar{T}_{isj}}{\sum_{i=1}^3 \sum_{s=1}^{s_i} P_{isjm}}, \quad (3)$$

where,  $PWMBT_{jm}$  = population-weighted mean bottom temperature in month  $j$  for mode  $m$ ;  $P_{isjm}$  = population of mode  $m$  in system  $i$ , stratum  $s$ , month  $j$ ;  $\bar{T}_{isj}$  = mean bottom temperature in system  $i$ , stratum  $s$ , and month  $j$ ; and  $s_i$  = number of strata in system  $i$ .  $PWMBT_{jm}$  is the best estimate of the average temperature experienced by the population in our study area.

**Growth rates** A linear model was developed to determine competing factors that had significant effects on the growth of 0+ English sole.

$$l_{ji} = \alpha + \alpha_1 c + \alpha_2 y_j + \beta t_i + \beta_1 c t_i + \beta_2 y_j t_i + \beta_3 d_i t_i + \beta_4 T_i t_i + \varepsilon_{ji}, \quad (4)$$

where,  $l_{ji}$  = mean modal length (MML) at time  $t_i$  and year  $j$ ;  $y_j$  and  $c$  are dummy variables for year and settlement time;  $t_i$  = population weighted mean date (PWMD);  $d_i$  = density (no/ha), monthly mean density from May through September;  $T_i$  = population weighted mean bottom temperature ( $PWMBT$ ); and  $\varepsilon_{ji}$  = residual. The  $d_i$  and  $T_i$  terms were used to examine whether or not there were density or temperature effects (or both) on the growth of 0+ English sole in the study areas. The dummy variable  $y_j$  (year) was defined as follows:

$$y_1 = \begin{cases} 1 & 1986 \\ 0 & \text{otherwise} \end{cases}, \quad y_2 = \begin{cases} 1 & 1987 \\ 0 & \text{otherwise} \end{cases},$$

$$y_3 = \begin{cases} 1 & 1988 \\ 0 & \text{otherwise} \end{cases}.$$

Since, settlement time obviously differed between cohorts (Fig. 4), the dummy variable ( $c$ ) was used to denote early (1) and the late (0) settlement groups:

$$c = \begin{cases} 1 & \text{early settlements (1985, 1986 - 1, 1988)} \\ 0 & \text{late settlements (1986 - 2, 1987)}. \end{cases}$$

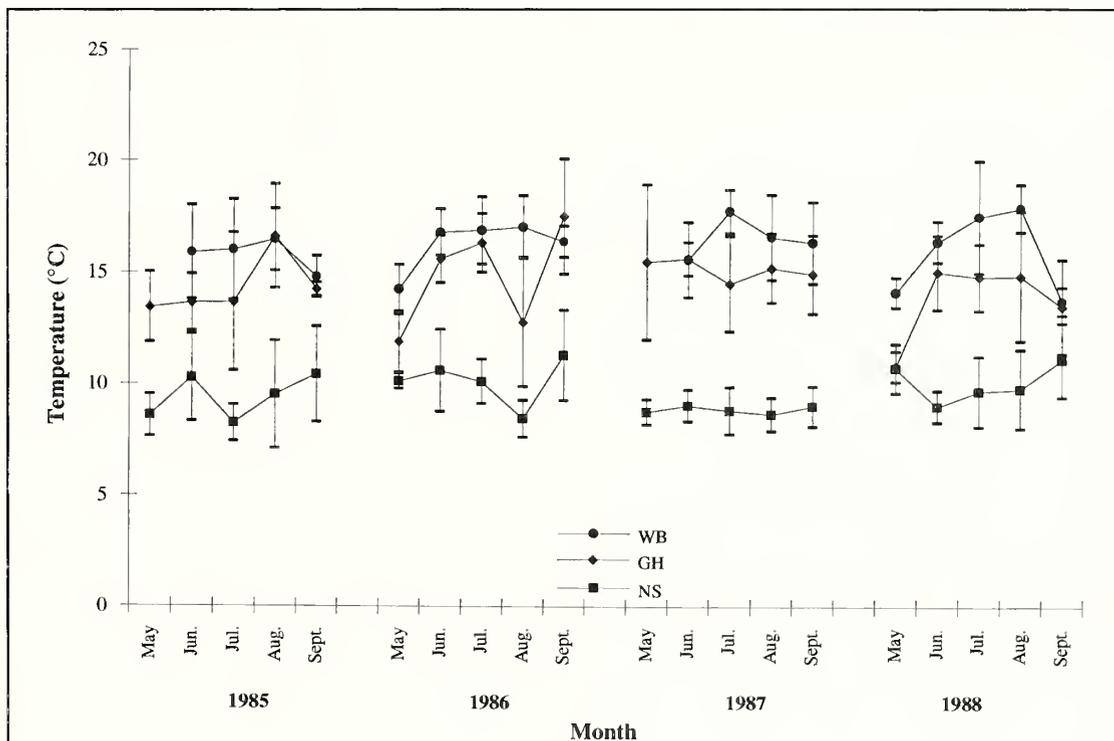
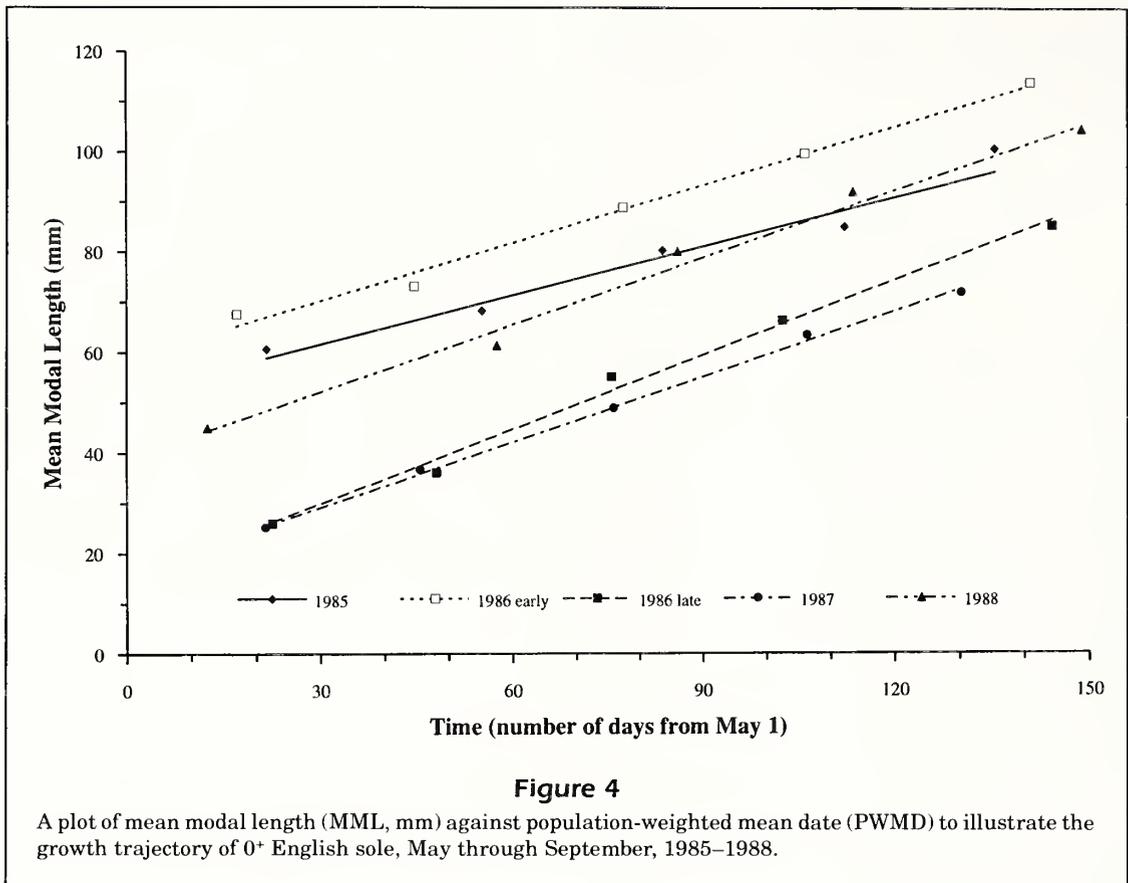


Figure 3

Monthly unweighted mean bottom temperature (°C) by area from years 1985 to 1988. Bars indicate one standard deviation. WB = Willapa Bay; GH = Grays Harbor; NS = nearshore.



Early and late settlement was defined by visual inspection of length frequency (Shi et al., 1995). A recruitment influx with mean modal length less than 40 mm during the May survey was defined as late settlement, and that with mean modal length greater than 40 mm in May was defined as early settlement. A multiple-partial *F*-test was used here to test the significance of settlement time ( $\beta_1c$ ), year ( $\beta_2y_j$ ), density ( $\beta_3d_i$ ), and temperature ( $\beta_4T_i$ ) effects on growth. The computer program MGLH (SYSTAT [Wilkinson, 1989]) was used to carry out all calculations.

**Mortality rates** The significance of density and season effects on mortality was examined by using the restated Beverton-Holt equation (Beverton and Iles, 1992):

$$\frac{dP}{Pdt} = -(\mu_1 + \mu_2 \ln P), \quad (5)$$

where *P* is the population of juvenile English sole in our study area;  $\mu_1$  is the density independent coefficient, as defined in Beverton and Iles (1992), and  $\mu_2$  is the density-dependent coefficient.

Population estimates from the surveys were fitted to the following three competing models, by using nonlinear least-squares regression (Wilkinson, 1989):

- 1) By integrating Equation 5 with  $\mu_2 = 0$ , the density-independent mortality model is

$$P_{t_i} = P_{oi}e^{-\mu_1 t_i}. \quad (6)$$

- 2) Integrating Equation 5 over the time period from  $t = 0$  to  $t = t_i$  without any constraint on  $\mu_1$  or  $\mu_2$ , the full model is

$$P_{t_i} = e^{\frac{\mu_1(e^{-\mu_2 t_i} - 1)}{\mu_2}} P_{oi}e^{-\mu_2 t_i}. \quad (7)$$

- 3) Integrating Equation 5 with  $\mu_2 = 0$ , and allowing  $\mu_1$  to vary, the model becomes

$$P_{t_i} = \begin{cases} P_{oi}e^{-\mu' t_i} & t_i = 0 \text{ to } 31 \text{ (July)} \\ P_{oi}e^{-\mu'(32)}e^{-\mu''(t_i-32)} & t_i = 32 \text{ to } 62 \text{ (August)} \\ P_{oi}e^{-\mu'(32)}e^{-\mu'''(62-32)}e^{-\mu''(t_i-62)} & t_i > 62 \text{ (September)} \end{cases} \quad (8)$$

where  $t_i$  = time, number of days elapsed since 1 July for surveys conducted in year *i* (1985-88);  $P_{t_i}$  = the observed total population size (0+ group) for all areas combined at time  $t_i$  in year *i*; and  $P_{oi}$  = initial total population size on 1 July in year *i*.  $P_{oi}$  was estimated as a parameter along with the coefficients  $\mu_1$  and  $\mu_2$ .  $\mu'$ ,  $\mu''$ , and  $\mu'''$  are the density-independent mortality

Table 1

Monthly population-weighted mean date (PWMD), mean modal length (MML), population-weighted mean bottom temperature (PWMBT) and overall mean densities of 0<sup>+</sup> English sole, 1985–88.

Year	Settlement time	Month	PWMD (days)	MML (mm)	PWMBT (°C)	Density <sup>1</sup> (No./ha)
1985	Early	May	21.66	60.56	13.07	55.03
		Jun	55.34	68.08	14.66	130.95
		Jul	83.75	79.95	12.94	200.60
		Aug	112.39	84.55	14.34	132.69
		Sep	135.72	99.96	12.24	96.42
1986	Early	May	17.05	67.54	13.61	118.25
		Jun	44.71	72.97	16.24	77.06
		Jul	77.54	88.58	14.66	96.75
		Aug	106.18	99.17	12.07	72.55
		Sep	141.32	112.98	12.49	65.80
1986	Late	May	22.51	25.99	12.33	118.25
		Jun	48.11	36.09	15.31	77.06
		Jul	75.63	55.01	15.43	96.75
		Aug	102.64	66.10	14.63	72.55
		Sep	144.51	84.67	14.81	65.80
1987	Late	May	21.47	25.17	10.48	188.77
		Jun	45.58	36.64	13.70	219.35
		Jul	76.00	48.83	15.28	346.38
		Aug	106.47	63.19	12.48	186.98
		Sep	130.45	71.49	13.65	200.48
1988	Early	May	12.48	45.01	13.21	269.44
		Jun	57.61	61.24	15.20	193.18
		Jul	86.10	79.77	14.91	182.15
		Aug	113.75	91.58	14.78	116.13
		Sep	149.10	103.72	12.26	90.31

<sup>1</sup>The estimated densities are combined densities of early and late recruits.

coefficients during July, August, and September, respectively. Model selection was based on the Bayesian Information Criterion (BIC) proposed by Schwarz (1976).

## Results

The mean modal length (MML), population-weighted mean date (PWMD), population-weighted mean bottom temperature (PWMBT), and overall mean densities of 0<sup>+</sup> English sole from May through September are shown in Table 1.

## Growth

Growth of 0<sup>+</sup> English sole was linear over time (Fig. 4). A general linear model pooled all data together and considered the effects of year, time of settlement, density, and temperature on growth. The final, best-fitted ( $R^2 = 0.99$ ,  $P < 0.001$ ) model was

$$l_{ji} = 8.44 + 43.48c + 6.76y_1 + 7.79y_2 - 13.06y_3 + 0.43t_i - 0.11ct_i + 0.06y_1t_i + 0.12y_3t_i + \varepsilon_{ji}$$

The results of partial *t*-tests (used in all comparisons unless specified otherwise), indicated there was a significant settlement time effect on growth ( $P < 0.01$ ), late-settling cohorts growing the fastest. The year effect was also significant (multiple partial *F*-test  $P < 0.05$ , Table 2). Multiple-partial *F*-tests indicated that there were no density ( $P = 0.80$ ) or temperature ( $P = 0.37$ ) effects on the growth of 0<sup>+</sup> English sole.

The date of settlement was estimated by fitting separate regression equations to each cohort in Figure 4, then by backcalculating to a length of 20 mm TL (Table 3), or by inverse prediction (Neter et al., 1985). We estimated that settlement of the 1985 and 1986 group-1 cohorts peaked in January, with 95% prediction intervals ranging from 27 November to 22 March. Settlement of the 1986 group-2 and 1987 cohorts peaked in May (with 95% prediction intervals ranging from 21 April to 29 May), and that of the 1988 cohort peaked in March (ranging from 17 February to 16 April).

**Mortality** The following equations were obtained from nonlinear least-square regression:

**Table 2**  
A summary of effects of year and settlement time on the growth of 0+ English sole.

	Variable	Parameter	Coefficient	Partial- <i>t</i>	<i>P</i> (2-tail)
Intercept	Constant	$\alpha$	8.44	3.19	< 0.01
	Settlement Time (c)	$\alpha_1$	43.48	17.03	< 0.01
	Year ( $y_1, y_2, y_3$ )	—	—	—	< 0.01 <sup>1</sup>
	$y_1$	$\alpha_{21}$	6.76	2.61	< 0.05
	$y_2$	$\alpha_{22}$	7.79	3.58	< 0.01
	$y_3$	$\alpha_{23}$	-13.06	-4.19	< 0.01
Slope (Growth)	PWMD ( $t_i$ )	$\beta$	0.43	18.45	< 0.01
	Settlement time (c)	$\beta_1$	-0.11	-4.04	< 0.01
	Year ( $y_1, y_2, y_3$ )	—	—	—	< 0.05 <sup>2</sup>
	$y_1$	$\beta_{21}$	0.06	2.13	< 0.05
	$y_2$	$\beta_{22}$	0.12	3.66	< 0.01
	$y_3$	$\beta_{23}$			

<sup>1</sup> Based on the result of an *F*-test,  $F_{3,15} = 4.35$ .

<sup>2</sup> Based on the result of an *F*-test,  $F_{3,15} = 13.25$ .

$$\text{Model 1: } \mu_2 = 0, P_{t_i} = P_{oi} e^{-0.0123t_i}; \quad P_{oi} = \begin{cases} 42.82 & 1985 \\ 21.02 & 1986 \\ 66.63 & 1987 \\ 40.40 & 1988 \end{cases}$$

$$\text{Model 2: } P_{t_i} = e^{\frac{-0.0066}{0.0056}(e^{-0.0056t_i} - 1)} P_{oi} e^{-0.0056t_i}; \quad P_{oi} = \begin{cases} 43.80 & 1985 \\ 18.62 & 1986 \\ 73.33 & 1987 \\ 40.46 & 1988 \end{cases}$$

$$\text{Model 3: } P_{t_i} = \begin{cases} P_{oi} e^{-0.0175t_i} \\ P_{oi} e^{-0.0175 \times 62} e^{-0.0075(t_i - 62)} \end{cases}$$

$t_i = 0$  to 62 (July and August)  
 $t_i > 62$  (September)

$$P_{oi} = \begin{cases} 49.60 & 1985 \\ 23.23 & 1986 \\ 74.33 & 1987 \\ 47.28 & 1988 \end{cases}$$

The estimated instantaneous mortality rates of 0+ English sole in July and August were equal, therefore model 3 was reduced from a three-step to a two-step model. The data fitted model 3 best (Fig. 5) with instantaneous mortality rates of 0.0175 per day in July and August and 0.0075 per day in September. The value of the Bayesian information criterion was 3.68 for model 1, 4.04 for model 2, and 2.65 for model 3. As a result, we concluded that model 3 was the best for estimating mortality.

**Table 3**

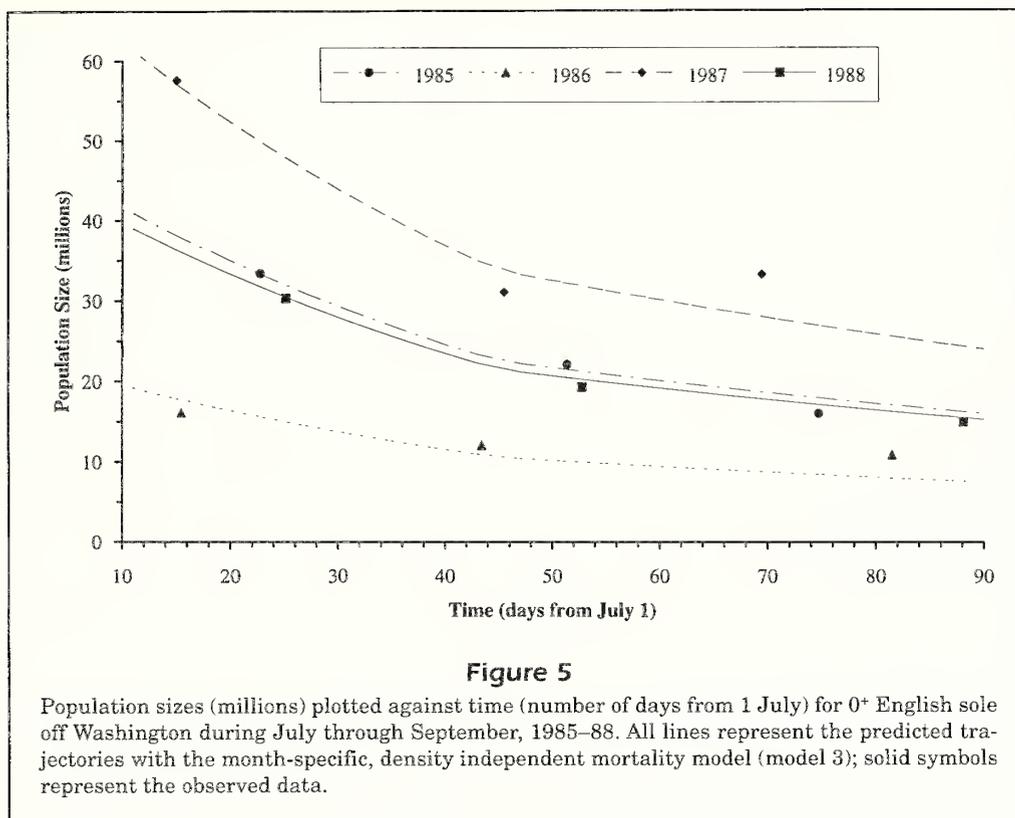
Back-calculated settlement dates with their ranges, assuming average length at settling,  $l_{\text{settlement}} = 20$  mm TL.

Year	Settlement cohort	Date of settlement	95% prediction interval
1985	1	24 Jan	27 Nov–22 Mar
1986	1	16 Jan	17 Dec–16 Feb
	2	10 May	21 Apr–29 May
1987	2	8 May	30 Apr–16 May
1988	1	18 Mar	17 Feb–16 Apr

## Discussion

### Gear efficiency

Our estimates of growth and mortality might be biased if gear selectivity varied with size. Edwards and Steele (1968) suggested that beam trawl efficiency depends on a number of factors, such as towing speed, bottom type, and fish size. At a speed of 35 m/min, the efficiency of their 2-meter beam trawl was 25–35%, depending on fish size. They point out that their results apply only to their particular gear and the special conditions in Loch Ewe. Kuipers (1975) found that the efficiency of a 2-m beam trawl in the Dutch Wadden Sea declined from 100% at lengths below 70 mm to 15–30% for plaice larger than 150 mm. Our gear was a 3-m beam trawl with effective fishing width of 2.3 m, wider than the gear used by either Kuipers or Edwards and Steele, and was towed faster (41–47 m/min vs. 30–35 m/min). Also the ratio of fish-



ing line out to bottom depth used in our survey (10–15 in shallow waters) was greater than that in Kuipers' experiment (4–8), resulting in better bottom contact and reduced vessel avoidance.

During a series of 15 pairs of day–night comparative tows, for which gear and operating procedures were the same as those described in this paper, Gunderson and Ellis (1986) failed to detect any significant net avoidance by either butter sole (*Pleuronectes isolepis*) over the length range from 40 to 280 mm, or Pacific tomcod (*Microgadus proximus*) over the length range from 60 to 220 mm. In the present study, the data for English sole did not show any decline in estimated growth with size (Fig. 4). We conclude that the efficiency of the gear used in this study does not decrease with fish size over the length range from 20 to 150 mm and has little influence on estimates of growth or mortality.

### Growth

It has been shown that English sole juvenile migration in and out of estuaries is size dependent (Gunderson et al., 1990; Shi et al., 1995), and our approach to the length modal progression method (LMP), namely pooling length data from coastal and estuarine areas to estimate growth, accounts for the

effect of such migrations. Our nearshore survey area covered the outer limit of 0+ English sole bathymetric distribution; less than 1% of the total population was found in the deepest nearshore stratum (Shi et al., 1995). To minimize the effects of inter-area migration, we pooled data from all three areas surveyed (Fig. 1), which cover a major portion of waters available to English sole juveniles along the Washington coast. The resulting estimates fall between faster growth rates estimated from previous LMP analyses (Westrheim, 1955; Smith and Nitsos, 1969; Krygier and Percy, 1986) and slower growth rates estimated from fortnightly ring counts by Rosenberg (1982) (Table 4). Gunderson et al. (1990) and Shi et al. (1995) suggested that the population of English sole juveniles in this study may not be closed, however, and that some migrations, especially during May and June each year, involve areas outside the study area shown in Figure 1. Continuous recruitment of young juveniles from outside the study area would result in an underestimation of growth rates, as could emigration of larger juveniles. Our data do not show any decline in growth at either the beginning or end of the survey season (Fig. 4); thus the influence of continuous recruitment of small fish or emigration of larger fish on growth estimation appeared to be minimal.

Table 4

A summary of daily growth rate estimates from field studies.

Location	Size at age 1-yr (mm TL)	Daily growth rate (mm/day)	Data source
Willapa Bay, Grays Harbor, and adjacent neashore, WA	≤150	0.33–0.49 (May–Sep)	This study, 1985–88
Yaquina Bay, OR	130–160	0.49 (May–Oct)	Westrheim, 1955
Monterey Bay, CA	130–150	0.55 (May–Oct)	Smith and Nitsos, 1969
Yaquina Bay, OR	100–140	0.33	Rosenberg, 1982 <sup>1,2</sup>
Moolach Beach, OR	100	0.34	
Yaquina Bay, OR	≤150	0.46–0.49 (Mar–Oct) 0.26–0.32 (Dec–Apr)	Krygier and Percy, 1986 <sup>2</sup>
Moolach Beach, OR	≤150	0.28–0.42 (Apr–Oct)	

<sup>1</sup> The original daily growth rates were estimated from fortnightly ring counts.

<sup>2</sup> Length at age 1 and daily growth rates were converted from standard length (SL) to total length (TL) by using the relationship:  $SL = -0.205 + 0.848 TL$  (senior author, unpubl. data).

Several previous studies with the LMP technique have attempted to estimate growth rates for English sole juveniles from estuaries and open coast but failed to consider the effect of interarea migration on the growth estimates. As a consequence, their results often show significant differences between coastal and estuarine populations (Westrheim, 1955; Smith and Nitsos, 1969; Krygier and Percy, 1986). In contrast, growth estimated from fortnightly ring counts showed no differences between coastal and estuarine populations (Rosenberg, 1982).

Previous laboratory studies where ration was held constant (Williams and Caldwell, 1978) showed that ambient temperature had no statistically significant effect on English sole growth rate between 9.5 and 15.0°C but significantly reduced growth between 15.0 and 18.0°C. The artificial food pellets used in that study may have been nutritionally inadequate, however, making it difficult to extrapolate the results to field conditions. Laboratory studies by Yoklavich (1981), where live polychaetes were used as food, showed a significant decline in the mean growth rate of 0<sup>+</sup> English sole (from 1.87% to 1.17% of body weight per day) between 13.0 and 17.5°C. Our results do not indicate any statistically significant interannual effect of temperature on the growth of English sole juveniles over the range of population-weighted mean temperatures (10.5–16.2°C) observed under field conditions. Higher temperatures presumably result in increased benthic productivity (Johnson and Brinkhurst, 1971) and in more food available to juveniles. On the other hand, metabolic requirements increase at high temperatures. Whether the juveniles grow faster or slower under field conditions probably depends on the bioenergetic balance at higher temperatures.

Peterman and Bradford (1987) found that density had a significantly negative effect on the growth of 1<sup>+</sup> English sole off the Oregon and Washington coasts ( $P=0.024$ , one-tailed  $t$ -test); therefore it would be reasonable to expect that growth of 0<sup>+</sup> English sole is also density dependent. Nevertheless growth rate and mean population size varied over relatively narrow ranges in this study, and we were unable to detect any statistically significant density effect.

The spawning season for English sole can extend from September to April (Kruse and Tyler, 1983), and recruitment processes are also protracted. Multiple peak recruitments are common (Kendall, 1966; Boehlert and Mundy, 1987; Gunderson et al., 1990; Shi et al., 1995), and peak recruitment occurs at different times each year, depending on ocean temperature and transport mechanisms (Ketchen, 1956; Boehlert and Mundy, 1987). Kendall (1966) reported that for Puget Sound English sole juveniles that were recruited earlier, growth was slower than that of later recruits during the same period. Our results led to the same conclusion, that is, timing of settlement influences the growth trajectory (Fig. 4).

Different size groups of English sole have different prey requirements and suffer from different degrees of food limitation (Gunderson et al., 1990). Off the Oregon coast, English sole 17–35 mm standard length (SL) fed primarily on polychaete palps, juvenile bivalves, and harpacticoid copepods, whereas 35–82 mm fish fed on larger prey such as amphipods and cumaceans (Hogue and Carey, 1982). In the Humboldt Bay estuary, English sole smaller than 50 mm TL fed almost exclusively on harpacticoid copepods whereas the diet of 66–102 mm fish was dominated by polychaetes (Toole, 1980).

Winberg (1956) found that individual metabolic requirements and food consumption increase as a function of  $W^{0.8}$  (where  $W$ =body weight), and Fonds (1979) showed a similar relation for young sole, *Solea solea*. The larger sizes attained by the early-settlement cohorts of English sole would probably also entail increased food requirements for those fish during May–September. The lower growth rates observed for early-settlement cohorts in comparison with those that settled later probably resulted from a combination of higher metabolic demands and reduced availability of suitable prey. Growth of 0+ English sole does not appear to be strictly linear if a sufficiently long period of time is examined.

### Mortality

Estimates of mortality rates were subject to some of the same sources of error and bias that the growth estimates were. Previous work (Gunderson et al., 1990; Shi et al., 1995) has shown that migrations of 0+ English sole are size dependent. Typically, larger fish emigrate from estuaries and perhaps out of our nearshore survey area, whereas smaller fish immigrate into our survey area. Immigration of small fish would cause underestimates of mortality. Previous analysis indicated that most immigration probably occurred near the settling period, i.e., May and June or earlier (Shi et al., 1995). Therefore, it is unlikely that immigration had much effect on the mortality estimates because only population estimates for July through September were used in this analysis.

Emigration of large 0+ fish would cause overestimation of mortality rates. Although we cannot completely ignore the possibility of emigration, previous analysis of length increment patterns in estuarine and nearshore areas has indicated that net emigration of large fish from the study area is minor during July–September (Shi et al., 1995). In addition, had substantial emigration occurred during July through September, estimated mortality rates would be consistently higher during September than during July and August, rather than the opposite (0.0075 per day vs. 0.0175 per day).

Seasonally differentiated daily mortality could be related to differences in temperature, individual size, or population density. Water temperatures, however, remained relatively stable in the study area during July through September (Fig. 3). Size-dependent mortality may have occurred, because 0+ English sole grow rapidly during the summer, with increases in individual size of 0+ English sole ranging from 20 to 30 mm TL from July to September. Kramer (1991) estimated the mortality rates for each 5-mm size group of California halibut, *Paralichthys californicus*,

on the basis of daily production by size group, and found that mortality was size specific for fish less than 70 days old (< 30 mm SL), smaller fish suffering higher mortality than larger ones. For older 0+ California halibut (70–115 days of age or 31–70 mm SL), mortality varied little (0.011–0.014 per day, with mean=0.0124 per day and SD=0.001 per day) and no trend was observed. Beverton and Iles (1992) found a significant density-dependent mortality ( $\mu_2$ ) effect for North Sea plaice ranging from ≤15 mm to 35 mm, although this effect was not significant for fish larger than 35 mm. Both Kramer (1991) and Beverton and Iles (1992) found that mortality of juvenile flatfish is highest during and immediately after settlement, and our results for English sole suggest the same.

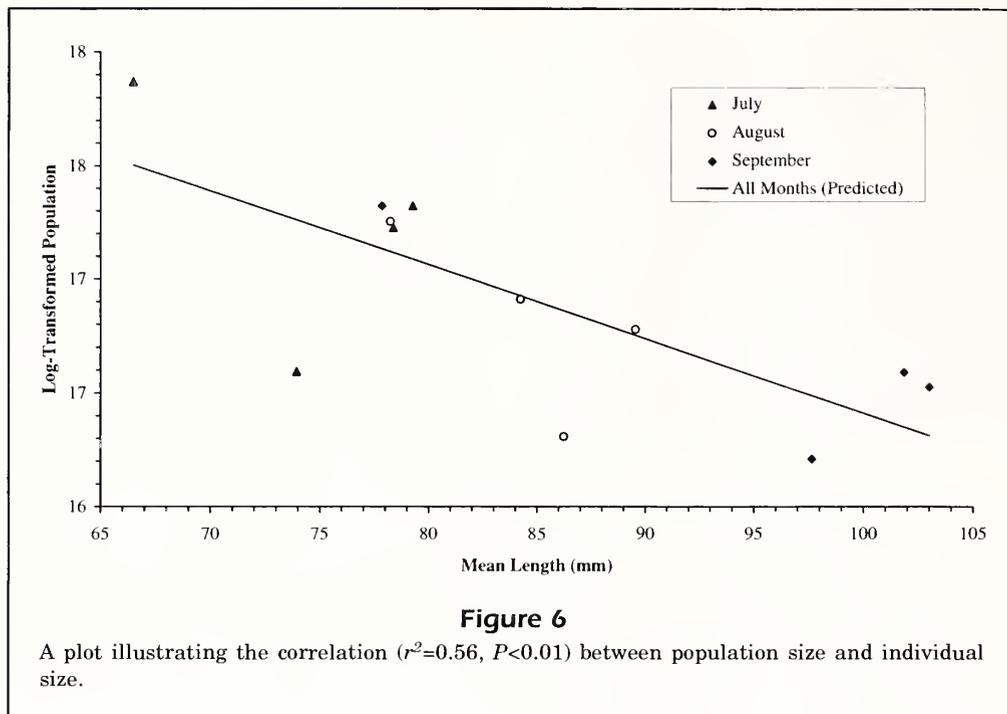
The effects of density and individual size were clearly confounded in our study (Fig. 6). An empirical relation between population size in the survey area ( $P_t$ ) and mean length ( $l_t$ ) was fitted as

$$\ln P_t = A + Bl_t,$$

where,  $P_t$  = the estimated total population size at time  $t$ ;  $l_t$  = the mean length of all 0+ English sole at time  $t$  (July through September); and the correlation between the two confounding factors was highly significant ( $r^2=0.56$ ,  $P<0.01$ ). It should always be borne in mind that it is very difficult, if not impossible, to isolate these two confounding factors in field observations; controlled enclosure experiments would probably be required to disentangle them. There is both a theoretical (Peterson and Wroblewski, 1984) and an empirical (McGurk, 1986; Kramer, 1991) basis for assuming that mortality decreases with individual size, and if this is the case,  $\mu_2$  (the density-dependent mortality coefficient) would have been overestimated. If mortality of 0+ English sole is density dependent, it appears that this dependence is weak because adding a density-dependent term to the model (model 2) did not improve the fit to the data.

Our surveys showed only a threefold difference in abundance of 0+ English sole during 1985–88, but stock synthesis analysis of commercial fisheries data indicates this was a period of relatively stable recruitment (Sampson<sup>1</sup>). The estimated recruitment of age-2+ females to the commercial fishery varied by no more than a factor of 1.8 for the 1985–88 year classes, whereas it varied by a factor of 6.5 for the

<sup>1</sup> Sampson, D. B. 1993. An assessment of the English sole stock off Oregon and Washington in 1992. Appendix H in Status of the Pacific coast groundfish fishery through 1993 and recommended allowable biological catch for 1994. Pacific Fish. Management Council, 2000 SW 1st Ave., Suite 420, Portland, OR, 43 p.



1975–90 year classes. Although our results apparently did not encompass periods of poor recruitment, they show that surveys of the nursery areas of 0<sup>+</sup> English sole have the potential to provide estimates of year-class strength several years in advance of the commercial fishery, as well as provide insight into the processes that generate recruitment variability.

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# Mitochondrial DNA diversity in and population structure of red grouper, *Epinephelus morio*, from the Gulf of Mexico\*

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Red grouper, *Epinephelus morio*, is a protogynous hermaphrodite found exclusively in the Atlantic Ocean from the coast of Massachusetts southward to Brazil (Smith, 1961). It is most abundant along the western Florida shelf and off the north coast of the Yucatan Peninsula, Mexico (Brulé and Canché, 1993). Studies on the biology of red grouper are few. Adults are known to be associated with rocky reef bottoms and caverns, ledges, and crevices formed by limestone outcroppings (Moe, 1969). Other available data include food habits and some aspects of early life history and patterns of migration (Moe, 1969; Brulé and Canché, 1993).

Red grouper are important to both commercial and recreational fisheries in the United States (U.S.) and Mexico (Moe, 1969). In recent years, declines in recreational and commercial landings have led to regulation of both fisheries in U.S. waters. The Mexican red grouper fishery, reportedly working above maximum sustainable yield (Solís Ramírez, 1970; Arreguín-Sánchez, 1987), however, remains essentially unregulated. Important in formulating management plans for marine fish species such as red grouper is information on population structure or stocks and on levels of genetic variation. This information

is critical for both stock assessment and adjustment of fishery regulations within regions.

In a previous study (Richardson and Gold, 1993), we examined mitochondrial (mt)DNA variation among a sample of red grouper from the west coast of Florida. Estimated within-population mtDNA diversity in this sample was among the lowest reported for a marine fish species. In this note, we report mtDNA variation within a sample of red grouper from the Campeche Banks, Mexico (Fig. 1). The main objectives were 1) to determine whether red grouper from Florida and Mexico represent different genetic stocks and 2) to compare levels of mtDNA diversity in red grouper from Campeche Banks, Mexico, with those from west Florida.

## Materials and methods

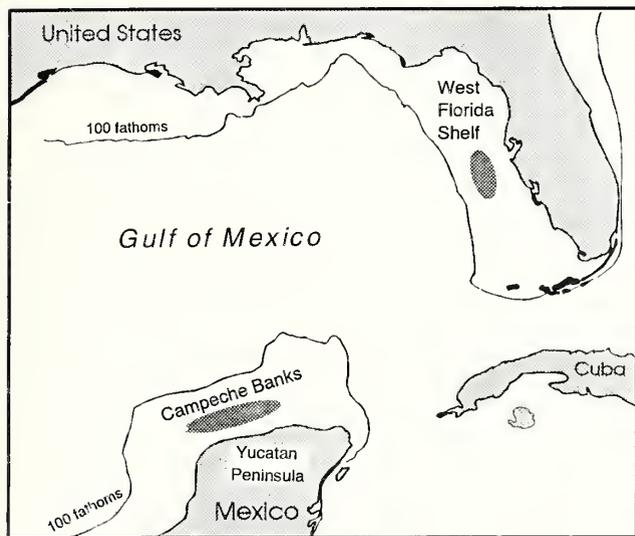
Specimens were obtained from commercial fishermen in Celestún and San Felipe, Mexico, during November, 1991 (Fig. 1). Heart and muscle tissue were removed from each individual, stored at  $-20^{\circ}\text{C}$  in a fish house in Merida, Mexico, and transported on wet ice to Houston, Texas, where they were frozen in liquid nitrogen. Upon arrival at Texas A&M, tissues were stored at  $-80^{\circ}\text{C}$ .

Details of DNA isolation, storage, restriction enzyme digestion, agarose electrophoresis of DNA fragments, and Southern blot hybridization with a mtDNA probe may be found in Gold and Richardson (1991). The mtDNA probe used ( $\lambda\text{Em-mt2}$ ) was an entire red grouper mtDNA genome cloned into lambda bacteriophage (Richardson and Gold, 1993). The ten restriction endonucleases used in this study were those previously identified to be polymorphic in red grouper (Richardson and Gold, 1993) and included *ApaI*, *KpnI*, *NcoI*, *NdeI*, *NheI*, *NsiI*, *PvuII*, *SspI*, *XbaI*, and *XmnI*.

Within-sample mtDNA diversity was assessed by nucleon diversity (probability that any two individuals drawn at random will differ in mtDNA haplotype) and by intrapopulation nucleotide sequence diversity (average nucleotide difference between any two individuals drawn at random). Both estimates of mtDNA diversity were generated by using equations in Nei and Tajima (1981).

Geographic partitioning of mtDNA variation was assessed by homogeneity testing of mtDNA haplotype frequencies and by searching for phylogeographic cohesion or structure of mtDNA haplotypes with a parsimony approach. Homogeneity tests included 1) a log-likelihood ( $G$ ) test and 2) a Monte Carlo randomization procedure developed by Roff and Bentzen (1989). Analyses were carried out with the BIOM-PC (a package of statistical programs, Applied Biostatistics Inc.; Rohlf, 1987) and REAP (restriction en-

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**Figure 1**

Sampling localities of red grouper (*Epinephelus morio*).

zyme analysis package; McElroy et al., 1992) computer software packages. A minimum-length parsimony network of mtDNA haplotypes was constructed by connecting haplotypes in increments of (inferred) single site gains and losses.

## Results

Digestion patterns of the ten restriction enzymes revealed 16 mtDNA haplotypes among all red grouper assayed to date (exclusive of the five individuals from the Dry Tortugas sampled by Richardson and Gold [1993, Table 1]). Of the 16 mtDNA haplotypes, one (haplotype 1) accounted for 77% of all individuals sampled. Four haplotypes were present in both geographic regions. The remaining 12 haplotypes were unique to a geographic region (Table 1). Percentage nucleotide sequence divergence between individual haplotypes ranged from 0.09 to 0.59 (mean  $\pm$  SE =  $0.27 \pm 0.01$ ).

MtDNA nucleon diversity among individuals from the Campeche Banks was 0.365. This value is lower than that found among individuals from the west coast of Florida (0.457). Percentage intrapopulation nucleotide sequence diversity among individuals from the Campeche Banks was  $0.042 \pm 0.001$  (mean  $\pm$  SE), as compared with  $0.078 \pm 0.003$  among individuals from the west coast of Florida. Nucleon and intrapopulation nucleotide sequence diversities among all red grouper assayed to date are  $0.389$  and  $0.059 \pm 0.001$ , respectively. Values obtained are based

on the 28 restriction enzymes surveyed by Richardson and Gold (1993) and on the assumption that the restriction enzymes previously found to be monomorphic among red grouper from the west coast of Florida are monomorphic among red grouper from Mexico as well.

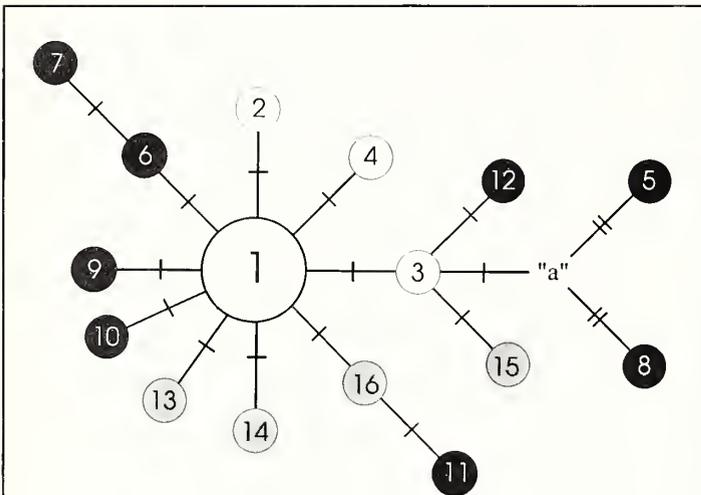
Results of tests for homogeneity of mtDNA haplotype frequencies between the two localities were nonsignificant ( $G=20.02$ ,  $P=0.21$  and  $\chi^2=14.71$ ,  $P=0.55$ ). The parsimony network (Fig. 2) included a single "assumed" haplotype (i.e. one not detected in the survey). All the haplotypes in the network, including the "assumed" haplotype, could be derived from adjacent haplotypes by one or two restriction site changes. The most common haplotype (haplotype 1) was considered to be central, and nine of the remaining 14 haplotypes were derived from the central haplotype by a single restriction site change. Haplotypes 5 and 8 are most divergent and are separated from the common haplotype by 4 restriction site changes. Except for haplotypes 5 and 8, and 6 and 7 (all from Campeche Banks, Mexico) which are grouped by a single restriction site change, no geographic partitioning was evident.

**Table 1**

Distribution of 16 mitochondrial DNA composite genotypes (haplotypes).

Haplotype number	Composite MtDNA genotype <sup>1</sup>	Locality	
		Campeche Banks	West Florida Shelf
1	AAAAAAAAAA	43	34
2	AAABAAAAAA	1	1
3	AAAAAAAAAAB	3	2
4	AAAABAAAAA	1	1
5	ABAAAABAAC	—	1
6	AAAAAABAAA	—	1
7	AABAAAABAAA	—	1
8	ABAAAABCAB	—	1
9	CAAAAAAAAAA	—	1
10	AAAAAABAAAA	—	1
11	AAAAAAAABBA	—	1
12	BAAAAAAAAB	—	1
13	AAAACAATAAA	2	—
14	ACAAAAATAAA	2	—
15	AAAAAADAB	1	—
16	AAAAAABAA	1	—

<sup>1</sup> Letters (from left to right) are digestion patterns for *Apa*I, *Kpn*I, *Nco*I, *Nde*I, *Nhe*I, *Nsi*I, *Pvu*II, *Ssp*I, *Xba*I, and *Xmn*I. Restriction fragment sizes may be found in Richardson and Gold (1993). Fragment sizes for three restriction fragment patterns not previously identified are as follows: (in base pairs) *Kpn*I(C): 16800; *Nhe*I(C): 6800, 3200, 2950, 2450, 1300, 50; and *Ssp*I(D): 6000, 5400, 2900, 1700, 800.



**Figure 2**

Minimum-length parsimony network of red grouper mitochondrial DNA haplotypes. Numbers refer to mtDNA haplotypes listed in Table 1. Hatch marks represent the number of restriction site changes among individual haplotypes. The haplotype designated by "a" refers to a haplotype assumed to exist, but not detected in the survey. Shaded and solid circles refer to haplotypes unique to a locality (West Florida Shelf and Campeche Banks respectively). Open circles are haplotypes found in both localities.

## Discussion

Homogeneity in mtDNA haplotype frequency and absence of phylogeographic structure among haplotypes are consistent with the hypothesis that red grouper from the west Florida shelf and the Campeche Banks represent a single unit stock. There are caveats to this hypothesis. First, genetic homogeneity does not unequivocally establish occurrence of a unit stock, in part because proof of a null hypothesis is impossible. Genetic homogeneity in this case is simply consistent with the hypothesis that samples are drawn from a single population with the same parametric haplotype frequencies. In addition, small amounts of gene flow are sufficient to homogenize populations genetically (Allendorf and Phelps, 1981), even though geographic samples may be discontinuous demographically. Another caveat is that observed homogeneity may reflect historical rather than current events. Present-day populations could be isolated spatially but have had enough contact in the recent past such that haplotype frequencies are overshadowed by historical gene flow. Examination of a more rapidly evolving nuclear marker (e.g. microsatellite loci) may provide data that suggest such a scenario.

Within-population mtDNA diversity among red grouper from the Campeche Banks was lower than

that reported previously for red grouper from the west Florida shelf, and overall, red grouper have among the lowest levels of mtDNA diversity reported for marine fish species (Table 2). Levels of intrapopulation mtDNA diversity are thought to reflect evolutionary-effective population sizes of females (Avice et al., 1988), although there is some evidence (Gold et al., 1994) that intrapopulation mtDNA diversities may also reflect contemporary (female) population sizes as well. The latter is of interest given that some of the species with low intrapopulation mtDNA diversities (e.g. weakfish, orange roughy) have experienced significant reductions in population sizes over the past several years (Graves et al., 1992b; Smolenski et al., 1993). The mtDNA diversity observed in red grouper may thus indicate that red grouper warrant immediate attention in terms of management regulation. Alternatively, red grouper and black sea basses, the species with the lowest reported mtDNA diversities (Table 2), are protogynous hermaphrodites (Manooch, 1988), and it is possible that this mode of reproduction may affect estimates of mtDNA diversity. Estimates for black sea bass (Bowen and Avice, 1990), however, may be somewhat compromised

by the low sample sizes, given that a significant proportion of the sampling variance for estimates of nucleotide diversity stems from population sampling (Lynch and Crease, 1990). Further study of mtDNA diversity in other hermaphroditic fishes and in sea bass is clearly warranted.

## Present-day gene flow

The observed genetic homogeneity in *E. morio* from west Florida and Mexico was surprising because, a priori, we expected gene flow between the two areas to be minimal and the two populations to be divergent in mtDNA haplotypes. This expectation was based on available information about the life history of red grouper and on reported discontinuity in red grouper distribution. Observations from divers and aquaria personnel have shown that juvenile red grouper are fairly sedentary, preferring to hide in crevices or shells of shallow nearshore habitat (Moe, 1969). Adult red grouper also are important members of the benthic community, frequently occupying crevices, ledges, and caverns formed by rugged limestone reefs. There is, however, evidence that red grouper do migrate at least to some extent, and tagging data suggest "developmental" migration from shallow coastal waters to depths greater than 36 m at approximately 5 years of age (Moe, 1966, 1967;

**Table 2**

Comparison of estimates of intrapopulation mtDNA diversity in various species of marine fishes.

Species	Number of individuals surveyed	Number of mtDNA haplotypes	Nucleotide sequence diversity (%)
Bluefish <sup>1</sup>	372	40	1.23
Atlantic herring <sup>2</sup>	69	26	1.09
Gulf Menhaden <sup>3</sup>	16	16	0.99
Red drum <sup>4</sup>	693	99	0.88
Spanish sardine <sup>5</sup>	73	24	0.52
Red snapper <sup>4</sup>	421	68	0.50
Black drum <sup>4</sup>	300	37	0.48
Greater amberjack <sup>6</sup>	59	23	0.34
Spotted seatrout <sup>7</sup>	384	73	0.31
Orange roughy <sup>8</sup>	244	22	0.13
Weakfish <sup>9</sup>	370	11	0.13
Red grouper	105 <sup>10</sup>	16	0.05 <sup>11</sup>
Atlantic black sea bass <sup>2</sup>	19	3	0.03
Gulf black sea bass <sup>2</sup>	9	2	0.03

<sup>1</sup>Graves et al., 1992a.<sup>2</sup>Kornfield and Bogdanowicz, 1987.<sup>3</sup>Bowen and Avise, 1990.<sup>4</sup>Gold et al., 1994.<sup>5</sup>Tringali and Wilson, 1993.<sup>6</sup>Richardson and Gold, 1993.<sup>7</sup>Gold, J. R. 1995. Dep. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX 77843-2258. Unpubl. data.<sup>8</sup>Smolenski et al., 1993.<sup>9</sup>Graves et al., 1992b.<sup>10</sup>Number of individuals includes 5 additional specimens from the Dry Tortugas surveyed by Richardson and Gold (1993).<sup>11</sup>Value obtained by using 28 restriction enzymes surveyed in Richardson and Gold (1993). Value obtained from the ten polymorphic restriction enzymes surveyed here is 0.15.

Beaumariage<sup>1</sup>). Presumably, this migration corresponds to the onset of sexual maturity. Other tagging data (Moe, 1966) suggest that adult red grouper may move as much as 18 to 50 miles over a period of time from several months to a year. Finally, on the basis of data from other species of *Epinephelus* (Mito et al., 1967), the pelagic larval stage in *E. morio* is presumed to last 30–40 days, during which larvae are dispersed by ocean currents along a great portion of the Florida shelf (Moe, 1969). However, despite the evidence suggesting that individual red grouper could move considerable distances, consistent patterns of migration in red grouper are not re-

ported, and it is generally presumed that adult red grouper do not undergo large-scale movements offshore.

Gene flow between the west Florida shelf and the Campeche Banks via migration of adults would have to occur either 1) along the north-central and western Gulf or 2) across the Florida Straights. Rivas (1970) noted circumstantial evidence suggesting that there may be seasonal migration of red grouper between the northern and southern Gulf, most probably via a western route. Red grouper, however, are rarely taken in the Gulf west of the Mobile Basin (Springer and Bullis, 1956), and virtually no landings of red grouper occur along most of the Texas coast (Osburn<sup>2</sup>; Campbell<sup>3</sup>). The apparent paucity of red grouper in the northwestern Gulf may reflect either the absence of suitable habitat along the Texas–Louisiana shelf or be a result of some other extrinsic barrier (McEachran<sup>4</sup>). These observations suggest that movement of adult red grouper through the western Gulf is unlikely, if it occurs at all. With respect to movement across the Florida Straights, Rivas (1970) considered it unlikely that red grouper, a bottom dwelling fish, would cross great depths. The Florida Straights are characterized by 100 to 2,000 fathom depths that separate the Campeche Banks from the west Florida shelf (Rezak et al., 1985). This range also suggests limited movement, if any, of red grouper from west Florida to the Campeche Banks.

Alternatively, present-day gene flow among red grouper could occur through dispersal of larvae by ocean currents. Shulman and Bermingham (1995) recently examined variation in mtDNA data among eight species of reef-associated fishes and searched for correlations between gene flow and egg type (pelagic and nonpelagic) and length of planktonic (usually larval) life, two life history traits which could potentially affect dispersal capability. Although surface currents that might explain observed genetic homogeneity in five of the species were identified, neither egg type nor length of larval stage appeared to be an adequate predictor of geographic structure in reef associated fishes (Shulman and Bermingham, 1995). Therefore, even though red grouper may have

<sup>1</sup> Beaumariage, D. S. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results. Fla. Dept. Nat. Resources, Mar. Res. Lab., Tech. Ser. No. 59:1–38. Div. of Mar. Resources, Dep. of Environmental Protection, Florida Mar. Res. Inst., 100 Eighth Ave. SE, St. Petersburg, FL 33701.

<sup>2</sup> Osburn, H. R. 1988. Trends in finfish landings by sport-boat fishermen in Texas marine waters, May 1974–May 1987. Texas Parks Wildl. Dep., Manag. Data Ser., no. 150, Austin, TX. Fisheries and Wildlife Div., Coastal Fisheries Branch, Texas Parks and Wildlife Dep., 4200 Smith School Road, Austin, TX 78744.

<sup>3</sup> Campbell, R. P. 1993. Trends in Texas commercial fishery landings, 1972–1992. Texas Parks Wildl. Dep., Manag. Data Ser., no. 106, Austin, TX. Fisheries and Wildlife Div., Coastal Fisheries Branch, Texas Parks and Wildlife Dep., 4200 Smith School Road, Austin, TX 78744.

<sup>4</sup> McEachran, J. D. 1995. Dep. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX 77843-2258. Personal commun.

a lengthy pelagic larval stage, there is no reason to assume a priori that gene flow occurs via dispersal of red grouper larvae. Nonetheless, it cannot be ruled out as a contributing factor.

### Historical bottleneck

In a general sense, genetic homogeneity and absence of phylogenetic structure are compatible with limited gene flow under models where isolated populations (or subpopulations) have recently diverged from a panmictic population that possessed low levels of genetic variation and where each subpopulation has a small effective population size. An example of isolated subpopulations that are genetically homogeneous and also genetically depauperate are African cheetahs, where subspecies in east and south Africa are essentially monomorphic for the same alleles at numerous genetic loci (O'Brien et al., 1987). To account for both genetic homogeneity between, and low genetic variability within, subpopulations, O'Brien et al. (1987) hypothesized the past occurrence of at least two genetic bottlenecks. Their hypothesis was based on the premise that genetic homogeneity of isolated subpopulations was consistent with a historical event; whereas low genetic variability in extant populations was consistent with a more recent event.

Red grouper fit the cheetah model in that the subpopulations surveyed are genetically homogeneous and each possesses limited genetic variation. We suggest the possibility that red grouper from west Florida and Mexico are isolated genetically, but that recurring genetic bottlenecks continue to generate high frequencies of the most common genotype. In addition, we suggest that red grouper from these two regions were not isolated historically and that the historical population underwent a severe bottleneck that reduced much of the extant genetic variation. These suggestions account for the observed genetic data and how isolated populations can be genetically homogeneous. A historical bottleneck could have occurred during late Pleistocene times when environmental fluctuations impacted the biota of the region (Rezack et al., 1985; Graham and Mead, 1987). Our suggestions could be tested, in part, by asking whether rare haplotypes found in both locals are identical by descent (i.e. independently derived). In red grouper, two of the three haplotypes shared between west Florida and Campeche Banks are the result of a site loss from the common haplotype and could be the result of a nucleotide substitution at any one of six nucleotide positions. Examination of a more rapidly evolving nuclear marker in individuals from each locality that share these rare haplotypes would address this issue.

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# Entanglement of California sea lions, *Zalophus californianus californianus*, in fishing gear in the central-northern part of the Gulf of California, Mexico

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The range of the California sea lion, *Zalophus californianus californianus*, extends from British Columbia south to Mazatlan, Mexico, and includes the Gulf of California. The population of sea lions in Mexico has been estimated at 74,467 individuals along the Pacific coast (Lowry et al.<sup>1</sup>), 28,220 in the Gulf of California (Zavala, 1990). Little is known about the Pacific coast population, but there are probably 8 breeding colonies (Lowry et al., 1992). In the Gulf there are 40 rookeries: 13 breeding colonies and 27 haulouts (Zavala et al., in press). Strong tidal forces cause a constant upwelling condition in the central-northern part of the Gulf of California that sustains high nutrient and phytoplankton concentrations, especially around the Midriff Islands in the central Gulf (Alvarez-Borrego, 1983; Alvarez-Borrego and Lara-Lara, 1991). This upwelling condition allows the existence of large populations of fish, marine mammals, and marine birds.

Between the 1960's and the 1980's, the population at some breeding colonies of California sea lions in the Gulf of California increased 30% (Le Boeuf et al., 1983). During the 1980's and early 1990's, the yearly increase in those populations was between 2% (Morales,

1990; Zavala et al., in press) and 4.7% (Aurióles and Arizpe<sup>2</sup>). After 1991 some populations experienced a slight reduction in size and later a partial recovery (Heath et al., 1994; Zavala et al.<sup>3</sup>).

Since 1985, we have censused annually 10 of the 11 reproductive sea lion colonies that account for 94.9% of all sea lions in the Gulf of California (Fig. 1 in Aurióles and Zavala, 1994). In 1991 we commenced seeing more sea lions with pieces of fishing gear entangled around their head and neck than we had remembered seeing during previous years (Zavala and García<sup>4</sup>) and began documenting the incidence of entanglement. We report the numbers of entangled sea lions observed between 1991 and 1995 in the central-northern part of the Gulf of California and comment on the effect this may have on the conservation of the species.

## Methods

Ten of 11 breeding colonies in the central-northern Gulf of California were studied (Fig. 1). Only Roca Consag (31°12'N, 114°29'W) was excluded. Between 1991 and 1995, we made eight cruises to the 10 breeding colonies: 16 Jun–19 Jul

1991, 8 Jul–4 Aug 1992, 16–25 Jun 1993, 10–29 Jul 1993, 16–25 Jun 1994, 11–20 Jul 1994, 1–4 Aug 1994, and 15–28 Jun 1995. San Jorge and El Coloradito were visited only once each year whereas Los Cantiles and San Pedro Mártir were not surveyed in 1991 and 1992, respectively. All other islands were surveyed on every trip.

All cruises were made on patrol ships of the Mexican Navy, leaving from Guaymas, Sonora. Surveys around the islands were made aboard small (7 m in length) fiberglass boats with 35–55 hp outboard motors. We cruised at about 2 knots, 30–50 m from the coast, to census the animals. They were classified as adult males, subadult males, females, juveniles, or pups (sensu LeBoeuf et al., 1983; Aurióles and Zavala, 1994).

Entanglement frequencies were calculated by dividing the total number of entangled animals (those animals with pieces of fishing gear around head and neck) by the total number of adult, subadult, and

<sup>1</sup> Lowry, M. S., P. Boveng, R. J. DeLong, Ch. W. Oliver, B. S. Stewart, H. DeAnda, and J. Barlow. 1992. Status of California sea lion (*Zalophus californianus californianus*) population in 1992. Admin. Rep. LJ-92-32, 35 p. Southwest Fisheries Science Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

<sup>2</sup> Aurióles, D., and O. Arizpe. 1989. Unpubl. data. Departamento de Pesquerías y Biología Marina. Centro Interdisciplinario de Ciencias Marinas. Apdo. Postal 592, La Paz, B.C.S., México.

<sup>3</sup> Zavala, A., H. de la Cueva, and E. Mellink. 1991. Unpubl. data. Departamento de Ecología, Centro de Investigación Científica y Educación Superior de Ensenada, Apdo. Postal 2732, Ensenada, B.C., México.

<sup>4</sup> Zavala, A., and M. C. Garcia. 1991. Departamento de Ecología, Centro de Investigación Científica y Educación Superior de Ensenada, Apdo. Postal 2732, Ensenada, Baha California, México. Personal obs.

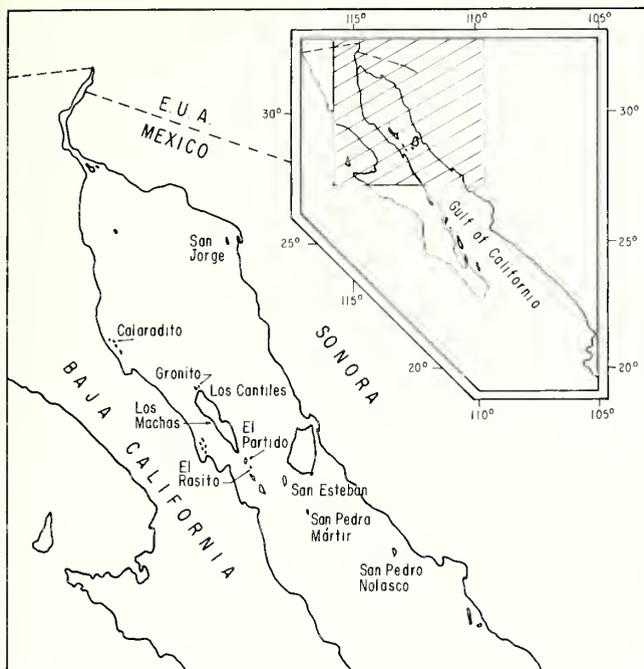


Figure 1

Central-northern Gulf of California, showing the study localities.

young animals. We excluded dead animals because time since death could not be assessed. Pups spend most of their time on land and have virtually no interaction with fishing gear during the survey periods. When we made more than one survey per year, we considered the highest rate of entanglement as the best estimator.

We used the "differences-between-proportions" test (Zar, 1974) to compare the proportions of age and sex classes between the entangled animals and the population. Differences between sea lion colonies and years were compared by using a two-factor Analysis of Variance (ANOVA) and Newman-Keuls (N-K) tests (Zar, 1974) on the basis of the number of entangled animals (adjusted by a square-root transformation) and entanglement rates (adjusted by an arcsine transformation). Variation in the number of entangled animals and in the average transformed entanglement rates over time, as well as the relationship between number of entangled animals and colony size, were analyzed with simple linear regressions (Zar, 1974).

In the two cases where we lacked data, we used the eight colonies, for which we had complete information, to calculate the relationship between the year with missing data (1991 or 1992) and the average of the remaining four years, and then used the average of the problem colony (Los Cantiles or San Pedro Mártir) to estimate the missing value. This was done

in order to perform the statistical tests on a standard basis.

Types of fishing gear involved were recorded from dead entangled animals. This information was completed with records about the size and characteristics of the fishing gear used by fishermen working in the islands. Similarly, fishing gear debris found on sea lion rookeries and showing evident signs of having been associated with a sea lion (bites, sea lion fat,) was noted. We also interviewed local fishermen about their problems with sea lions.

## Results and discussion

### Sea lion entanglement

During the study, we counted 237 entangled animals (Table 1), 207 of which could be assigned to a particular sex and age class: 46.4% were young animals (1–3 yr), 41.5% females, 7.2% subadult males, and 4.8% adult males. The percentage of young animals among the entangled animals was statistically higher than their proportion in the censused population (25.8%,  $Z=6.70$ ,  $P=7.13 \times 10^{-11}$ ), whereas that of females was lower (60.5%,  $Z=-5.53$ ,  $P=0.913 \times 10^{-8}$ ). This is probably a result of young animals being more curious, less experienced, and weaker, in addition to foraging closer to the surface (senior author, personal observation [1994–95]). In other species (northern fur seals, *Callorhinus ursinus*) high rates of juvenile mortality might have caused a decrease in the population (Trites, 1992). Our data are not sufficient to establish or discard any such links. Percentages of entanglement of subadult and adult males were not different from percentages of proportion of subadult and adult males in the population (6.3%,  $Z=0.78$ ,  $P=0.294$  and 7.4%,  $Z=1.5$ ,  $P=0.13$ , respectively).

Between 1991 and 1995, the number of recorded entangled sea lions for all 10 rookeries combined varied from 34 ( $\pm 2.27$ , 95% CI) (adjusted to 36) to 72, with a low of 24 ( $\pm 4.02$ , 95% CI) (adjusted to 27) in 1992 (Table 1). Regression analysis between number of entangled animals and year was significant ( $n=5$ ,  $r^2=0.79$ ,  $F=11.05$ ,  $P=0.045$ ). Significant differences were found only between 1992 and 1995: the other years were not different from one other ( $F=3.09$ ,  $P=0.027$ ).

In 1992, there were not only fewer entangled animals, but also there were fewer sites with entangled animals. This year saw the worst recent fishing season in the central Gulf according to information at the Bahía de Los Ángeles fishing office, and this finding is likely a reflection of the prevailing El Niño Southern Oscillation conditions, which had strong

Table 1

Number of entangled and total (in parentheses, including entangled) California sea lions, except pups, in 10 breeding colonies in the central-northern Gulf of California, 1991–95.

Rookeries	Locations		Year				
	Lat.	Long.	1991	1992	1993	1994	1995
San Jorge	31°01'N	113°15'W	8 (4,536)	14 (2,915)	10 (2,183)	4 (2,208)	24 (3,200)
Coloradito	30°03'N	114°29'W	4 (2,100)	2 (1,610)	7 (1,662)	3 (1,749)	13 (1,688)
Granito	29°34'N	113°33'W	2 (609)	1 (603)	6 (390)	2 (923)	4 (631)
Los Cantiles	29°32'N	113°29'W	—	1 (712)	3 (620)	1 (602)	6 (916)
Los Machos	29°18'N	113°31'W	0 (718)	0 (601)	1 (718)	4 (659)	1 (512)
El Partido	28°53'N	113°02'W	5 (463)	2 (524)	4 (798)	3 (311)	1 (402)
El Rasito	28°49'N	113°00'W	1 (353)	0 (326)	1 (101)	5 (223)	0 (198)
San Esteban	28°43'N	112°35'W	10 (4,758)	4 (3,135)	10 (2,610)	20 (3,859)	14 (3,396)
S.P. Mártir	28°23'N	112°20'W	1 (1,379)	—	11 (676)	8 (770)	7 (937)
S.P. Nolasco	27°58'N	111°23'W	3 (1,009)	0 (338)	1 (517)	3 (340)	2 (358)
Total			34 (15,925)	24 (10,764)	54 (10,275)	53 (11,644)	72 (12,238)

effects in the Gulf (Hamman et al., 1995). Entanglement rate did not exhibit any tendency through time ( $n=5$ ,  $r^2=0.44$ ,  $F=2.35$ ,  $P=0.223$ ), and the ANOVA detected only 1992 as statistically inferior to 1993 and 1994, whereas 1991 and 1995 were not different from any other year ( $F=4.20$ ,  $P=0.007$ ).

San Jorge and San Esteban exhibited the largest overall numbers of sea lions (>2,000 California sea lions) (Table 1); El Coloradito had intermediate values (>1500, <2200), and the other colonies  $\leq 1400$  sea lions. The ANOVA indicated that the first two sites had statistically more entangled sea lions than did El Partido, Granito, Cantiles, San Pedro Nolasco, El Rasito, and Los Machos, whereas San Pedro Mártir and El Coloradito were not different from any other site ( $F=7.67$ ,  $P<0.001$ ). This pattern corresponds to differences in the size of the colonies; a regression linking total number of entangled animals at each colony and size of the different colonies was highly significant ( $n=10$ ,  $r^2=0.92$ ,  $F=89.71$ ,  $P<0.001$ ).

We have no detailed records of differences in the fishing effort throughout the study area, although it seems to be larger in the Midriff region than in the northern Gulf (E. Mellink, personal obs. [1995]). The ANOVA did not show differences in the entanglement rates between colonies ( $F=0.64$ ,  $P=0.76$ ), and the number of incidents seemed to be more a function of the size of the colony than of local and yearly variations in fishing effort, although, as suggested by the 1992 data, these effects cannot be neglected.

Entanglement rates in our region varied between 0% and 2.24%. These values are substantially lower than the 3.9–7.9% detected in Los Islotes, Bahía de La Paz, in the southern Gulf of California (24°35'N, 110°23'W; Harcourt et al., 1994). In the latter local-

ity, high values may have been due to the proximity of Los Islotes to a moderate-size city (La Paz, approx. 250,000 inhabitants) and to abundant sport and commercial fishing. However, our entanglement values are higher than those at California islands (0.08%, Stewart and Yochem, 1987) and, again, this could be due to differences in the intensity and type of fishing practiced.

The main fishing gear involved in sea lion entanglement in the study area were nets and, to a lesser degree, lines and ropes. The nets included monofilament, purse seine, and gill nets (with stretched mesh sizes 3", 3.2", 4.5", 5", and 8"), cotton gill nets (1.5" and 5.1" mesh size), and trammel nets (either cotton or nylon monofilament with 14" to 16" mesh size). These nets originally measure 120–180 fathoms long and 7 fathoms high. The lines involved were all nylon of different thickness and, in most cases, were found tied around the animal. In only one case did we see a hook in a sea lion's mouth, or a line coming out of it.

Most entanglement occurs during fishing, either when the net and the catch are hauled out or when a net is deployed during 24–48 hr periods. In other regions of the North Pacific, in addition to entanglement during events involving active fishing, entanglement occurs because marine mammals encounter drifting debris, especially when they are foraging or migrating (Fowler, 1987). In the central-northern Gulf of California it is rare to encounter fishing gear debris drifting in the water. Artesanal fishermen, who carry out most of the fishing in the area, cannot afford to lose nets; therefore nets are usually fixed, not drifted. When part of a net or a complete net is no longer usable, it is usually discarded in a local gar-

bage dump. When a fisherman finds a lost drifting net at sea, he takes it for his own use. Unlike other areas of the world (Croxall et al., 1990) and the southern Gulf of California (Harcourt et al., 1994), the central-northern portion of the Gulf of California did not provide evidence of sea lions entangled in nonfishing plastic debris.

### Sea lion conservation

In addition to accidental entanglements reported here, there is a deliberate (although illegal) killing of sea lions in the region for baiting shark longlines. At Isla San Pedro Mártir, Thomson and Mesnick<sup>5</sup> found 14 sea lions entangled in a gill net in a cave about 15–20 m from a breeding site, in July 1993. They concluded that the net had been set to intentionally capture sea lions. In December 1993, about 20 sea lions were captured in a gill net in San Pedro Nolasco (El Imparcial, Hermosillo, Sonora, 25 December 1993). The fishermen involved argued that the capture had been accidental, resulting from their lack of expertise. In addition to their intentional capture, sea lions are sometimes shot with firearms because fishermen believe that they interfere with fishing gear (Delgado-Estrella et al., 1994).

Our data were limited to a single season in each year of a 5-yr span and did not include animals that died without us having seen them on the islands. However, according to our assessment, the current entanglements rate of 0.49% does not seem to pose a threat to the conservation of California sea lions in the central-northern Gulf of California. We believe, however, that entanglement should be routinely monitored and studied in further detail.

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**Zavala G. A., A. Aguayo L., D. Aurióles G., and M. C. García R.**

**In press.** Distribución y abundancia del lobo marino *Zalophus californianus californianus* (Lesson 1828), en el Golfo de California, México. Biótica.

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# Erratum

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Quinn, T. P., J. L. Nielsen, C. Gan, M. J. Unwin,  
R. Wilmot, C. Guthrie, and F. M. Utter.

1996. Origin and genetic structure of chinook salmon,  
*Oncorhynchus tshawytscha*, transplanted from Cali-  
fornia to New Zealand: allozyme and mtDNA evi-  
dence. Fish. Bull. 94:506-521.

## Corrections:

In Table 1 (p. 509) and Table 3 (p. 514):  
Locus *PEP-B2\**, Allele \*108 should be  
Locus *PEP-B1\**, Allele \*103

In Table 4 (p. 516)  
Locus *PEP-B2\** should be  
Locus *PEP-B1\**



# Fishery Bulletin

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# Fishery Bulletin



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U.S. Department  
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Volume 95  
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**Abstract.**—The ages of 217 juveniles from the Atlanto-Iberian sardine (*Sardina pilchardus*) stock were determined by means of counts of daily growth rings in otoliths. These juveniles were caught by the commercial purse-seine fleet off Galicia (NW Spain) between June and November 1992. The back-calculated hatching period was 13 December 1991 to 2 April 1992, with a mean date of 2 February and a standard deviation of  $\pm 17$  days. The original aim of the study was to relate the birthdate distribution of the recruits to environmental, biological, and physical data taken during a series of oceanographic cruises. Oceanographic cruises, carried out between March and July 1992, covered the spring-spawning area of the stock (Cantabrian Sea and coasts of Galicia, the supposed area of origin for the recruits) but such a relationship was not documented because the results of the study showed that most surviving juveniles were spawned before the period considered during the oceanographic cruises. However, the observed birthdate distribution of the recruits, together with hydrographic data, does suggest that a larval drift from the northern Portuguese coasts to the Galician coast took place. Thus, at least in 1992, there is evidence to suggest that the winter-spawning zone, located along the coast of northern Portugal, may have been the area of origin for recruits off Galicia, in contrast to the previous assumption that these fish were spawned in the Cantabrian Sea.

## Birthdate analysis and its application to the study of recruitment of the Atlanto-Iberian sardine *Sardina pilchardus*

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The Atlanto-Iberian sardine *Sardina pilchardus* (also known as European pilchard [Robins et al., 1991]) is the dominant coastal pelagic fish species along the Atlantic coasts of the Iberian peninsula, as much for the biomass of the stock as for its importance in the pelagic fisheries of Spain and Portugal. Landings, carried out by purse seiners, reached a maximum value for the period 1975–92 of 214,000 metric tons (t) in 1981, and a minimum of 126,000 t in 1992. In the same period, the estimated biomass of the spawning stock varied between 160,000 t in 1976 and 510,000 t in 1985 (Anonymous<sup>1</sup>). An analysis of the abundance trend of the stock (Pestana, 1989) suggests that, in the short term, catches are dependent on recruitment, characteristic of short-lived pelagic species (Ulltang, 1980).

In recent years more intensive work has been done on documenting the oceanographic characteristics for the area of distribution of the Atlanto-Iberian sardine stock. Among these, the most noticeable is the seasonal upwelling that affects the west coast of the Iberian peninsula (Fiuza, 1984; Lavín et al., 1991; Cabanas et al., 1992). Numerous studies have also been carried out on the biological aspects of the species, such as areas and periods of reproduction (Ré et al., 1990; López-Jamar et al., in press; Cunha and Figueiredo<sup>2</sup>; García et al.<sup>3</sup>; Solá

et al.<sup>4</sup>), frequency of spawning (Pérez et al., 1992a), batch fecundity (Pérez et al., 1992b), and larval growth (Ré, 1983; Alemany and Álvarez<sup>5</sup>), as well as the spatial distribution by age classes, of which the latter suggests a northward displacement of early age groups as they grow (Porteiro et al.<sup>6</sup>). In this area, the sardine has a protracted spawning season that can last prac-

<sup>1</sup> Anonymous. 1993. Report of the Working Group on the assessment of mackerel, horse mackerel, sardine and anchovy. ICES Council Meeting 1993/H:19, 274 p. (mimeo).

<sup>2</sup> Cunha, E., and I. Figueiredo. 1988. Reproductive cycle of *Sardina pilchardus* in the central region off the Portuguese coast (1970/1987). ICES Council Meeting 1988/H:61, 54 p. (mimeo).

<sup>3</sup> García, A., C. Franco, A. Solá, and M. Alonso. 1988. Distribution of sardine *Sardina pilchardus* egg and larval abundance off the Spanish North Atlantic coast (Galician and Cantabrian areas) in April 1987. ICES Council Meeting 1988/H:27, 8 p. (mimeo).

<sup>4</sup> Solá, A., L. Motos, C. Franco, and A. Iago de Lanzós. 1990. Seasonal occurrence of pelagic fish eggs and larvae in the Cantabrian sea (VIIIc) and Galicia (IXa), from 1987 to 1989. ICES Council Meeting 1990/H:25, 15 p. (mimeo).

<sup>5</sup> Alemany, F., and F. Álvarez. 1992. Regional growth differences in sardine *Sardina pilchardus* larvae from Cantabrian and Galician coasts. ICES Council meeting, 22 p. (mimeo).

<sup>6</sup> Porteiro, C., F. Alvarez, and J. A. Perreiro. 1986. Sardine (*Sardina pilchardus* Walb.) stock differential distribution by age class in Divisions VIIIc and IXa. ICES Council Meeting 1986/H:20, 13 p. (mimeo).

tically all year. The main spawning periods, however, are in the spring (April–May) along the northern coast of Spain (Cantabrian Sea) (Solá et al.<sup>4</sup>) and in winter (December–January) off the northern Portuguese coast (Ré et al., 1990). Thus, in a given year, a wide range of likely birthdates exist. Depending on the particular biotic and abiotic conditions that affect survival during the prerecruitment period, the abundance and the age composition (birthdate distribution) of recruits will be restricted, however, to a relatively short period.

An important part of the present study was initiated through Spanish-USA collaboration (Anonymous, 1990) within the framework of the Sardine Anchovy Recruitment Project (SARP). The work carried out in this program continued for the next 3 years under the auspices of a European program that also sponsored research on the sprat *Sprattus sprattus* in the German Bight and the anchovy *Engraulis encrasicolus* within Portuguese estuaries. The original aim of this project was to identify the biological and environmental factors affecting interseasonal larval mortality of short-lived coastal pelagic fish. Birthdate analysis is one of the more relevant tools for the study of recruitment processes (Campana and Jones, 1992). Birthdates of juvenile fishes were first calculated by Methot (1983) who showed that the data can be used to determine periods of high survival. This technique is a key element in the work of SARP, i.e. to test the critical survival-period hypothesis (Hjort, 1914 and 1926) and its later variants

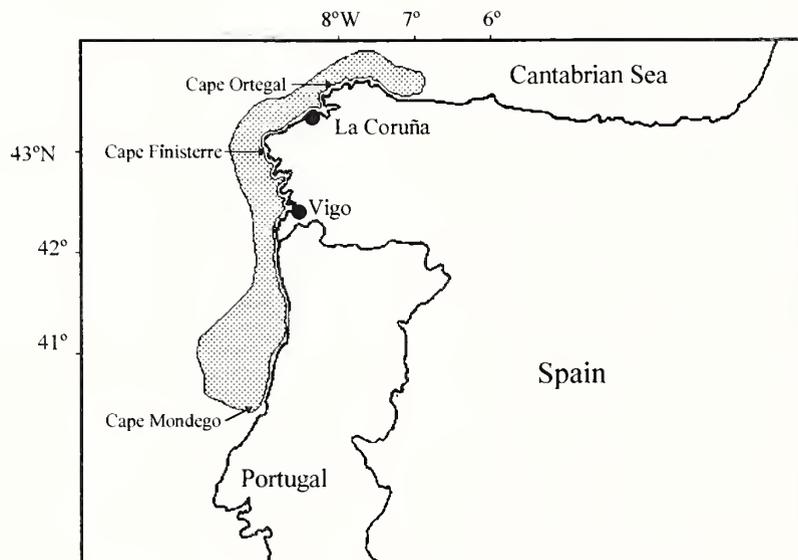
(Cushing, 1975; Lasker, 1981; Parrish et al., 1981). Only one paper, in which this technique was applied, is available for the area studied (Alvarez and Butler, 1992). It shows that birthdates of surviving fish occurred at the beginning of a period of calm weather in May and is consistent with Lasker's (1981) stable-ocean hypothesis.

The aims of the present work were 1) to calculate the birthdate distribution of recruits in the stock of the Atlanto-Iberian sardine in 1992, as inferred from daily otolith growth increment analysis; 2) to relate the birthdate distribution of recruits to environmental conditions during earlier development stages; and 3) to verify the previous hypothesis that sardine recruits in the Galician area originate in the Cantabrian Sea.

## Material and methods

### Age determination

Juvenile sardines were sampled fortnightly, 30 June–19 November 1992, from landings of the commercial purse-seine fleet at the ports of Vigo and La Coruña (Fig. 1), providing a total of 22 samples, each of 50 specimens. These ports are located in the area of recruitment of the Atlanto-Iberian sardine (age-0 fish) (Anonymous<sup>1</sup>). A subsample of ten individuals was taken at random from each sample for birthdate analysis from counts of the daily growth-ring incre-



**Figure 1**

Map of the northwestern Iberian peninsula showing sampling ports (dots) and area of distribution of age-0 sardines, *Sardina pilchardus* (shaded), during the 3rd and 4th quarters in 1992 (redrawn from Anonymous, 1993).

ments (Methot, 1981). The length ranges by sample of the analyzed specimens ( $n=220$ ) are given in Table 1. Fish were measured (standard length and total length by 1-mm size classes), weighed (0.1 g), and their otoliths were removed and mounted on microscope slides with Eukitt mounting medium. It is possible to determine the ages of juveniles and their daily growth rates because the daily deposition of growth increments has been validated for sardine (Ré, 1984), the time of formation of the first daily growth ring is known (Alemany and Álvarez, 1994), and because it is possible to distinguish false or subdaily increments from true daily growth rings. It should be pointed out that no gaps were observed in the daily growth rings in the sagittal otoliths of the analyzed specimens. Each daily ring was counted and its width was measured, along a transect located at  $\pm 5^\circ$  of the longest radius from the focus to the posterior margin of the otolith, with a video coordinated digitizer connected to a microcomputer (Methot, 1981). To reveal increments, the otoliths were progressively polished between readings by using 30-, 9-, and 0.3-micron lapping film. Magnifications of  $\times 60$ ,  $\times 640$ , and  $\times 1,000$  were used. Data from several replicate transects per otolith, at different magnifications, were combined

to estimate age. Occasionally, daily increments were difficult to resolve within short (<60 microns) segments of the otoliths. In these cases, widths of rings, and hence their number, were interpolated by using linear approximation based on the widths of previous and later clearly visible daily rings. Data from an otolith reading were rejected as unreliable if the interpolation process affected more than 5% of the readings.

**Environmental conditions**

During the main sardine spawning season off the northern and northwestern coasts of the Iberian peninsula, 5 cruises were conducted between March and July 1992 (López-Jamar et al., in press). The protocols established during a pilot cruise carried out in April 1991 (López-Jamar et al.<sup>7</sup>) were followed. The

<sup>7</sup> López-Jamar, E., S. Coombs, F. Alemany, J. Alonso, F. Álvarez, C. Barrett, J. M. Cabanas, B. Casas, G. Díaz del Río, M. L. Fernández de Puelles, C. Franco, A. García, N. C. Halliday, A. Lago de Lanzós, A. Lavín, A. Miranda, D. Robins, L. Valdes, and L. M. Varela. 1991. A SARP pilot study for sardine *Sardina pilchardus* off north and northwest Spain in April/May 1991. ICES Council Meeting 1991/L:69, 36 p. (mimeo).

**Table 1**

Summary statistics for the Atlanto-Iberian sardine *Sardina pilchardus* by port and sampling date in 1992. TL=total length (mm), SD=standard deviation, BD=birthdate, Age=days.

Port and sampling date	Mean TL	SD	Min. TL	Max. TL	Mean BD	Mean age	SD	Min. age	Max. age
<b>La Coruña</b>									
7 Jul	90	6	82	103	18 Jan	173	11	156	193
24 Jul	113	7	105	127	13 Jan	194	13	172	215
9 Sep	116	3	111	122	23 Jan	231	8	216	246
17 Sep	130	3	125	133	21 Jan	243	13	225	265
1 Oct	128	9	121	155	20 Jan	256	19	231	294
6 Oct	126	6	118	135	1 Feb	249	19	228	295
13 Oct	118	11	105	139	1 Feb	254	22	215	298
28 Oct	133	6	121	140	30 Jan	273	13	241	291
4 Nov	115	2	112	120	14 Feb	265	22	217	293
13 Nov	109	3	105	113	13 Feb	275	21	256	290
<b>Vigo</b>									
30 Jun	83	3	77	87	26 Jan	157	5	151	169
8 Jul	89	5	80	97	25 Jan	165	5	154	173
16 Jul	97	3	94	105	22 Jan	177	13	162	207
8 Sep	104	3	92	102	9 Feb	212	11	193	224
22 Sep	112	6	107	127	3 Feb	235	13	218	254
1 Oct	104	5	93	111	11 Feb	234	10	220	247
9 Oct	107	6	99	122	10 Feb	243	7	238	260
14 Oct	113	5	103	120	30 Jan	259	11	240	279
22 Oct	131	6	121	141	8 Feb	259	9	249	273
27 Oct	138	13	101	145	1 Feb	270	14	254	292
11 Nov	122	4	117	132	1 Mar	258	17	231	280
19 Nov	121	8	112	137	23 Feb	271	11	247	287

seasonal production and distribution of sardine larvae and their nutritional condition were determined during these cruises as were the spatial and temporal distributional patterns of larvae in relation to hydrographic and biological parameters. During the first 3 cruises, additional transects were located in French waters to estimate the extension of spawning in the northeastern area of the Cantabrian Sea. In the western area, spawning during these months is very low from Cape Finisterre southwards (García et al., 1992); therefore sampling was curtailed at the Portuguese border. The sampling design for the present study did not cover, either spatially or temporally, spawning along the entire Iberian peninsula, because sampling on the Portuguese shelf during winter was not possible owing to logistical reasons. Sampling of this area was not considered important because other studies (Robles et al., 1992; Cabanas et al.<sup>8</sup>; Roy et al.<sup>9</sup>) have suggested that recruitment

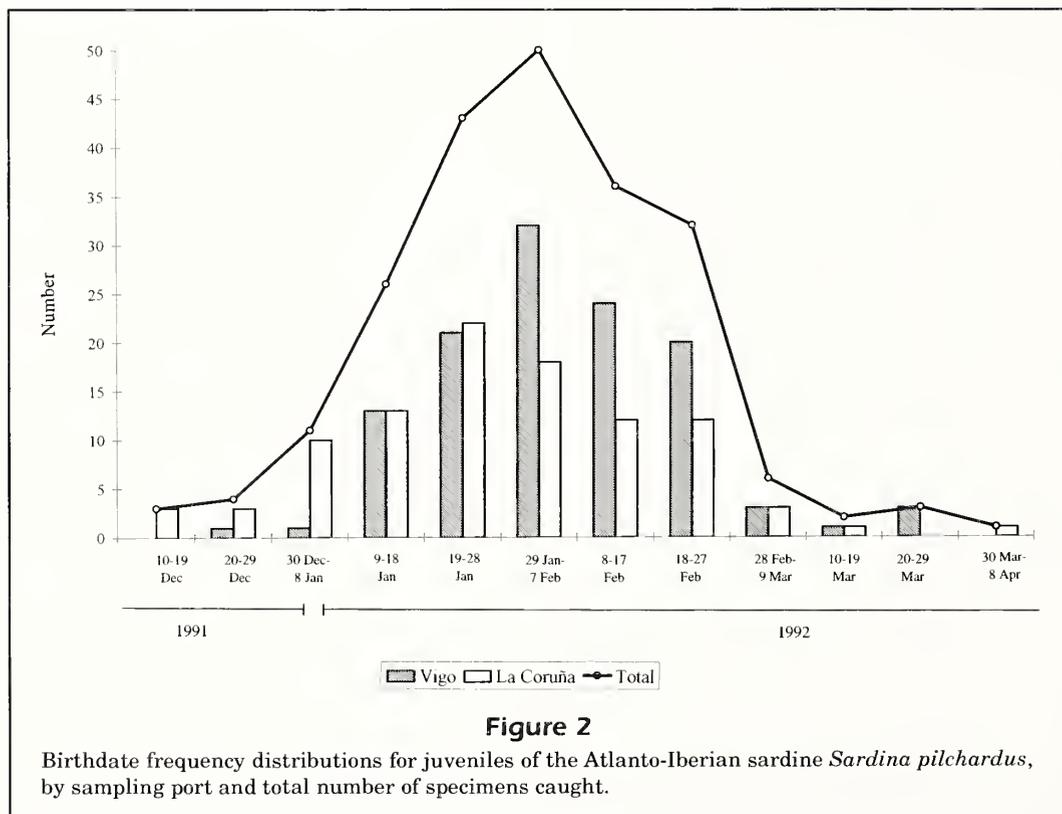
of the Atlanto-Iberian sardine stock depends mainly on spring spawning in the Cantabrian Sea, as well as on upwelling features along the west coast of the Iberian peninsula.

## Results

The length distribution of a subsample of 220 juveniles used for the birthdate analysis was not significantly different from that of the entire sample of 1,100 juveniles (Kolmogorov-Smirnov test,  $P>0.2$ ). Of these 220 juveniles, 3 were rejected because daily rings were not visible in more than 5% of the transect readings. The age of the remaining 217 fishes ranged from 151 to 298 days, with birthdates from 13 December 1991 to 2 April 1992 (Fig. 2). Data by sample date are shown in Table 1. The average birthdate of juveniles from La Coruña was 28 January 1992 ( $n=98$ ,  $SD=19$  d, birthdate range: 13 December 1991 to 2 April 1992), and the average birthdate of juveniles from Vigo was 6 February 1992 ( $n=119$ ,  $SD=16$  d, birthdate range: 23 December 1991 to 26 March 1992). The observed differences between the two birthdate distributions (Fig. 2) were significant (Kolmogorov-Smirnov test,  $P<0.001$ ). Specimens younger than 5 months were not caught by the fish-

<sup>8</sup> Cabanas, J. M., C. Porteiro, and M. Varela. 1989. A possible relation between sardine fisheries and oceanographic conditions in NW Spanish coastal waters. ICES Council Meeting 1989/H:18, 12 p. (mimeo).

<sup>9</sup> Roy, P., C. Porteiro, and J. M. Cabanas. 1993. The optimal environmental window hypothesis in the ICES area: the example of the Iberian sardine. ICES Council Meeting 1993/L:76, 13 p. (mimeo).



ery (see Table 1; Robles et al., 1992). Thus, no corrections for cumulative mortality were made because the corrected birthdate distribution would be quite similar to the uncorrected distribution (Methot, 1983). The most significant aspect of these results is that they indicate a period of birthdates outside the main period of larval production in the Cantabrian Sea.

The relationship between the estimated age and length of the sampled recruits from Vigo and La Coruña are shown in Figure 3. In both cases, the relationship was linear, and significant (ANOVA,  $P < 0.000$ ). The slopes ( $t = 1.26$ ,  $P > 0.10$ ,  $df = 213$ ) and the intercepts ( $t = 0.96$ ,  $P > 0.20$ ,  $df = 214$ ) were not significantly different. Thus, a regression from pooled data was fitted (ANOVA,  $P < 0.000$ ).

The precision of ageing within each sample and within each 1-cm length range was assessed with the calculated coefficient of variation, CV (standard deviation divided by the the mean estimated age). The precision was good ( $CV < 20\%$ ), stabilizing at a level of about 5–10% as fish grew in length (Fig. 4). The within-sample CV did not show any trend and remained at values less than 10% across all ages (Fig. 5). These results suggest that the intrinsic variability that may exist between otoliths of different fish of the same length range is low and that the precision of the age estimates is not affected by age.

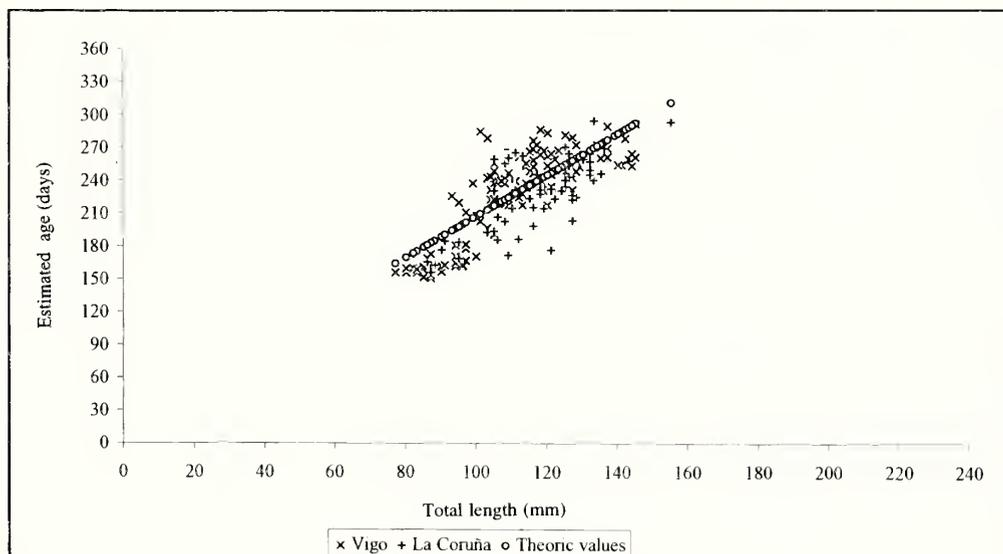
To assess seasonal changes in the estimated birthdate distribution, we performed a test to compare birthdate distribution from early samples (June–September,  $n = 89$ ) with a distribution calcu-

lated from late samples (October–November,  $n = 128$ ). There was no significant difference (Kolmogorov-Smirnov test,  $P > 0.05$ ), which indicated that the samples came from the same cohort and that mortality during the period was not age selective.

### Discussion

The juvenile birthdate distribution, which shows that the 1992 recruits were winter spawned, does not support the hypothesis that sardine recruits in the Galician area are mainly spawned during spring in the Cantabrian Sea, as was suggested by a previous study on the birthdate distribution of juveniles in this area (Álvarez and Butler, 1992). In fact, the surviving juveniles observed in our study were spawned earlier than the time when the sampling cruises were carried out in 1992. Thus, it was not possible to draw any detailed conclusions on the relationship between larval survival and environmental factors from otolith data. This was a significant obstacle for the achievement of the objectives of SARP because the “within year” exercise relies on a comparison of the birthdate distribution of juveniles with environmental conditions that occur during their larval development (Bakun et al.<sup>10</sup>).

<sup>10</sup> Bakun, A., J. Alheit, and G. Kullenberg. 1991. The sardine-anchovy recruitment project (SARP): rationale, design and development. ICES Council Meeting 1991/L:43, 17 p. (mimeo).

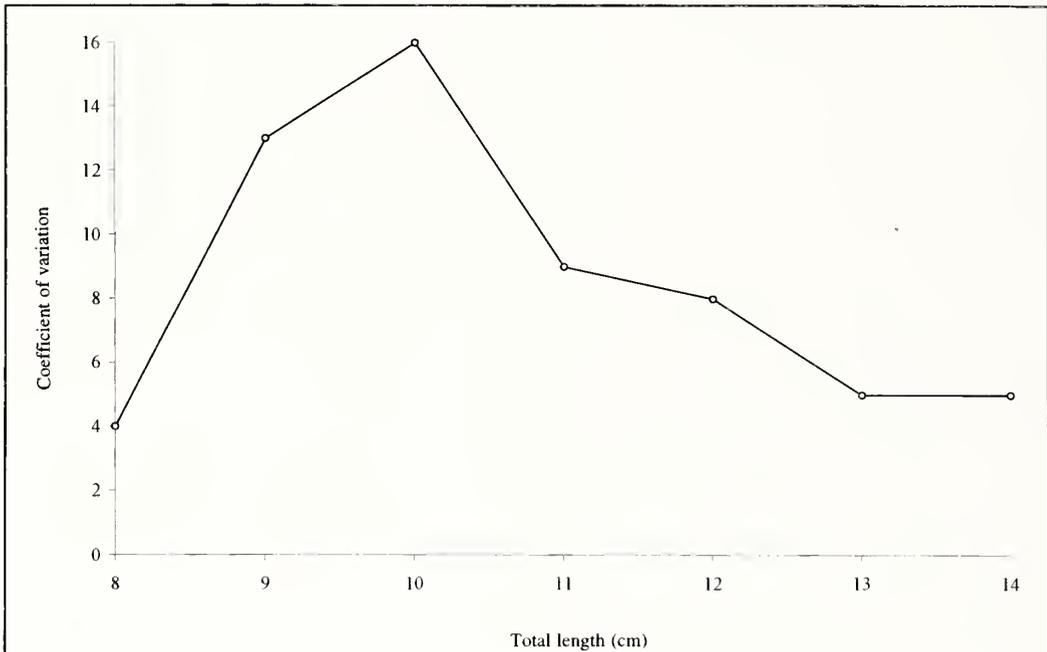


**Figure 3**

Age-length relationship and fitted regression for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus*. Data are indicated by sampling port.

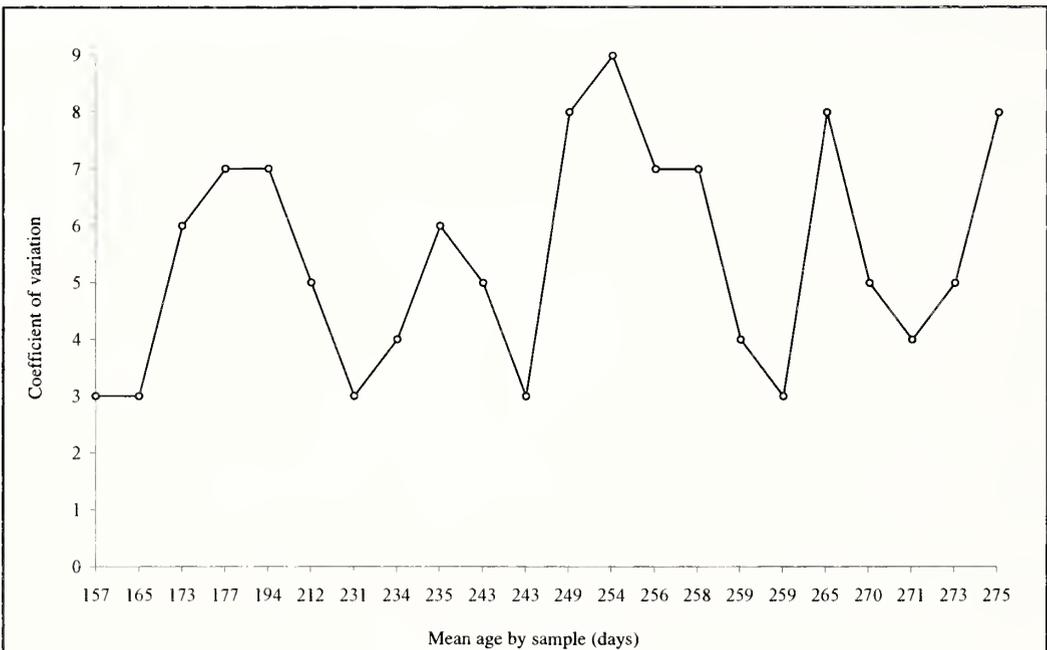
However, if the spatial-temporal features of spawning of this species in this area are taken into account, the results of Álvarez and Butler (1992), cited above,

cannot be considered to be based on an unbiased sampling of the 1988 recruitment because they were derived from two samples only.



**Figure 4**

Ageing precision for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus* within 1-cm length ranges. Precision is defined as the standard deviation divided by the mean (CV).



**Figure 5**

Ageing precision for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus* within each sample. Precision is defined as the standard deviation divided by the mean (CV).

An alternative area of origin for the 1992 recruits is the coastal waters off northern Portugal, where eggs are presumably spawned during the winter. Relatively large larvae were found in March–April in southern and western Galicia. These larvae may not have been locally spawned, because spawning is low in this area (García et al., 1992; López-Jamar et al., in press), but rather spawned during the winter off the coasts of north Portugal where high winter spawning has been observed (Ré et al., 1990). Supporting evidence for such an area of spawning was deduced by López-Jamar et al. (in press) from the results of a 1992 sampling, where the progressive northwards and westwards displacement (around Galicia) of a group of larger larvae (mean length >13 mm) was documented. Using a larval growth-rate estimate of 0.59 mm/day in March off Galicia (Alemany and Álvarez<sup>5</sup>), we found that the length range of this group of larvae is in accordance with a February birthdate. Moreover, such a spawning area is consistent with the poleward flow of winter circulation in the coastal ocean off southwest Europe (Frouin et al., 1990).

The significant differences between the mean birthdates of recruits sampled at Vigo and those sampled at La Coruña are also consistent with the hypothesis of a larval drift from the south. The larvae that were produced at the beginning of the period, when the displacement northwards took place, would reach areas farthest from the spawning zone. Thus, the mean birthdate of specimens at La Coruña would be earlier than that of specimens at Vigo, as was observed. It is suggested from the evidence of the overall distribution pattern of sardine larvae in the Cantabrian Sea that, during the 1992 spawning season, most larvae drifted westwards and were dispersed offshore in northern Galicia (López-Jamar et al., in press). This pattern could be explained by the hydrographically dynamic area observed off northwestern Galicia in spring (López-Jamar et al., in press; Chesney and Alonso-Noval<sup>11</sup>). On the other hand, several studies have also suggested that recruitment of the Atlanto-Iberian sardine stock depends mainly on spring spawning in the Cantabrian Sea and on upwelling features along the west coast of the Iberian peninsula. These studies have been based on empirical relationships (Dickson et al., 1988; Cabanas et al.<sup>8</sup>) and a qualitative approach (Robles et al., 1992; Roy et al.<sup>9</sup>). Possible mechanisms associated with physical factors that could influence early

life-stage larvae from spring spawning in the Cantabrian Sea are suggested in these works. However, the present study is a process-oriented approach, which accounts for intraseasonal effects of the biotic and physical environment on the survival of a fish cohort.

There is a possibility that spring-spawned recruits could exist off Galicia, but owing to their later incorporation into the juvenile fishery, they may not have been present before the sampling of recruits was finished in November 1992, when the March–June larvae may not have yet recruited to the fishery. However, on the basis of the age range given in Table 1, these spring-spawned recruits would be caught by the fishery from August and should be distinguishable in birthdate distribution. Moreover, the routine sampling of sardine length-frequency distributions carried out for stock assessments at the same area from January 1993 onwards has not revealed the presence of smaller sizes,<sup>12</sup> which would be an indication of recruitment from spring-spawned larvae in the Cantabrian Sea.

In summary, our results reinforce the suggestion of an alternative origin for the Atlanto-Iberian sardine recruits of the Galician area, at least in some years. The particular hydrological conditions along the northern coast of Portugal would favor either spring- or winter-spawned recruits, as outlined by López-Jamar et al. (in press). If upwelling in spring is weak, larvae spawned at this time in the Cantabrian Sea could be transported to the Galician area. On the other hand, if upwelling is intense, they may drift offshore at Cape Ortegal, as was postulated by López-Jamar et al. (in press) for the 1992 spawning in the Cantabrian Sea. In this latter case, the recruits in the Galician area would come from winter-spawned larvae in northern Portugal, which could reach the Galician area by northward-flowing surface currents during the winter. The influence of these mechanisms on year-class abundance remains to be investigated.

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<sup>11</sup> Chesney, E. J., and M. Alonso-Noval. 1989. Coastal upwelling and the early life history of sardine *Sardina pilchardus* along the Galician coast of Spain. ICES Council Meeting 1988/H:61, 54 p. (mimeo).

<sup>12</sup> Porteiro, C. 1994. Instituto Español de Oceanografía, P.O. Box 1552, 36280 Vigo, Spain. Personal commun.

Fischereiwissenschaft) and involved in the larval sampling cruises, especially to E. López-Jamar, S. H. Coombs, A. García, R. Knust, and W. Nellen. We are also grateful for the contribution and the support of J. M. Cabanas and C. Porteiro, and we would like to thank E. Moksness and two anonymous reviewers who offered useful suggestions for improvement of the manuscript. This work was carried out with partial funding from the Consejo Interministerial de Ciencia y Tecnología (CICYT) of Spain, contract 91.0089, and from the Fisheries Aquaculture Research (FAR) programme of the European Union, contract MA196.

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**Abstract.**—We documented the distribution and abundance of demersal fishes in the northeastern Chukchi Sea, Alaska, in 1990 and 1991, and described 1990 demersal fish assemblages and their relationship to general oceanographic features in the area. We collected samples using an otter trawl at 48 stations in 1990 and 16 in 1991, and we identified a total of 66 species in 14 families. Gadids made up 83% and 69% of the abundance in 1990 and 1991, respectively. Cottids, pleuronectids, and zoarcids together made up 15% of the species in 1990, 28% in 1991. The number of species, species diversity ( $H$ ), and evenness ( $V'$ ) generally were greater inshore than offshore and greater in the south than in the north. There were significant differences in ranks of species, species diversity, and evenness at 3 of 8 stations sampled both years. From data collected in 1990, 3 nearshore and 3 offshore station groupings were defined. The northern offshore assemblages had the fewest species, lowest diversity and evenness, and least abundance, whereas two southern assemblages had the most species, highest diversity and evenness, and greatest abundance. We determined that bottom salinity and percent gravel were probably the primary factors influencing assemblage arrangement.

## Demersal fish assemblages of the northeastern Chukchi Sea, Alaska

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The distribution and abundance of commercially important demersal fishes inhabiting temperate and tropical seas are relatively well studied (e.g. Percy, 1978; Mahon and Smith, 1989; Weinberg, 1994). Results from such studies have been used to examine relationships between environmental factors and fish assemblage distributions. Important environmental variables that have been identified include sediment type, water depth, bottom temperature, and bottom salinity.

Overholtz and Tyler (1985) found that six species assemblages on Georges Bank, northwestern Atlantic, remained consistent over depth for a number of years. Fargo and Tyler (1991), sampling at depths of 18–240 m in Hecate Strait off British Columbia, found four species assemblages separated by depth. Percy (1978) described shallow and deep demersal fish assemblages in the northeast Pacific Ocean off the coast of Oregon at depths ranging from 70 to 102 m. Although there was an interaction between depth

and sediment type, he concluded that depth was a primary factor and that sediment type was of secondary importance. Mahon and Smith (1989) looked for interactions between sediment characteristics, water depth, bottom temperature, and bottom salinity but concluded that assemblages were related more to depth than to other attributes. Scott (1982) reported that although fish distributions were related to sediment types, the latter was related to depth. Studies of other fishes indicated that temperature and salinity are important; Jahn and Backus (1976), using salinity and temperature to characterize slope waters, the Gulf Stream, and northern and southern Sargasso Sea waters in the Atlantic Ocean, concluded that mesopelagic fishes associated with slope and Gulf Stream waters were distinct and different from fish assemblages associated with the other two water masses. Bianchi (1992, a and b) determined that water depth, bottom temperature, bottom salinity, and

dissolved oxygen content determined benthic fish assemblages observed off the west coast of central Africa.

Relatively few fisheries resource surveys have been conducted in Arctic waters off Alaska; only three have been conducted in the northeastern Chukchi Sea (Alverson and Wilimovsky, 1966; Frost and Lowry, 1983; Fechhelm et al.<sup>1</sup>). These were limited in geographic coverage and not designed to address questions on environmental factors influencing fish distribution. The studies were, however, important first steps in determining factors influencing the distribution and abundance of fishes in Arctic waters.

The goal of our study was to determine the distribution and abundance of demersal fishes, the presence of species assemblages, and the relationship of such assemblages to oceanographic features in the northeastern Chukchi Sea, Alaska. Results from investigations of the distribution and relative abundance of infaunal and epifaunal mollusks in the eastern Chukchi Sea suggest that invertebrate assemblages may be associated with differences in hydrographic conditions and sediment types (Feder et al., 1994, Feder et al.<sup>2</sup>). On the basis of these findings, we hypothesized that there would be onshore-offshore and north-south differences in demersal fish abundance, biomass, and assemblages, and that these differences would be related to hydrographic conditions and sediment type.

## Materials and methods

Our study area was north of 68°N (Point Hope, Alaska), east of 168°58'W, and limited in northward extent by weather and sea ice (Fig. 1).

The shelf of the northeastern Chukchi Sea is relatively shallow, gently sloping offshore to depths of 30–50 m in the study area. Bottom sediments in the region are poorly sorted, trending to relatively coarse sediments on the inner shelf between Point Hope and Point Barrow, and shifting offshore to muds containing various proportions of gravel and sand (Sharma, 1979; Naidu, 1988). Sediments in the more northerly offshore region contain a higher percentage of water and a lower percentage of gravel than sediments found in the more southern offshore area (Feder et al.<sup>2</sup>).

The Chukchi Sea consists of several water masses (Weingartner, in press): Alaska Coastal Water (ACW) and the Resident Chukchi Water (RCW) commonly dominate the study area. The ACW is relatively warm, low-salinity water lying nearshore. It is a mixture of Bering Shelf water and freshwater that comes from western Alaskan rivers, primarily the Yukon. The RCW is relatively cold, high-salinity water that lies seaward of the ACW. The RCW is either advected onshore from the upper layers of the Arctic Ocean or is remnant ACW from the previous winter. The ACW and RCW masses are separated by a hydrographic front that tends to be located between the 25-m and 40-m isobaths and that intersects the coast between Icy Cape and Point Franklin (Johnson, 1989; Weingartner, in press; Feder et al.<sup>2</sup>).

Sampling occurred during August and September in 1990 and 1991. In 1990, 48 stations were occupied along 11 transects perpendicular to shore; 16 stations were occupied in 1991, including 8 that were sampled in 1990 (Fig. 1; station locations, water depths, bottom temperatures, and bottom salinities are given in Smith et al., in press, b). In 1990, nearshore stations were established closer to one another than were stations farther offshore in order to increase the probability of having two stations in each transect inshore of the historical position of the "bottom (hydrographic) front." Weather and ice conditions dictated the sequence of stations sampled. Stations were numbered to reflect the sampling sequence.

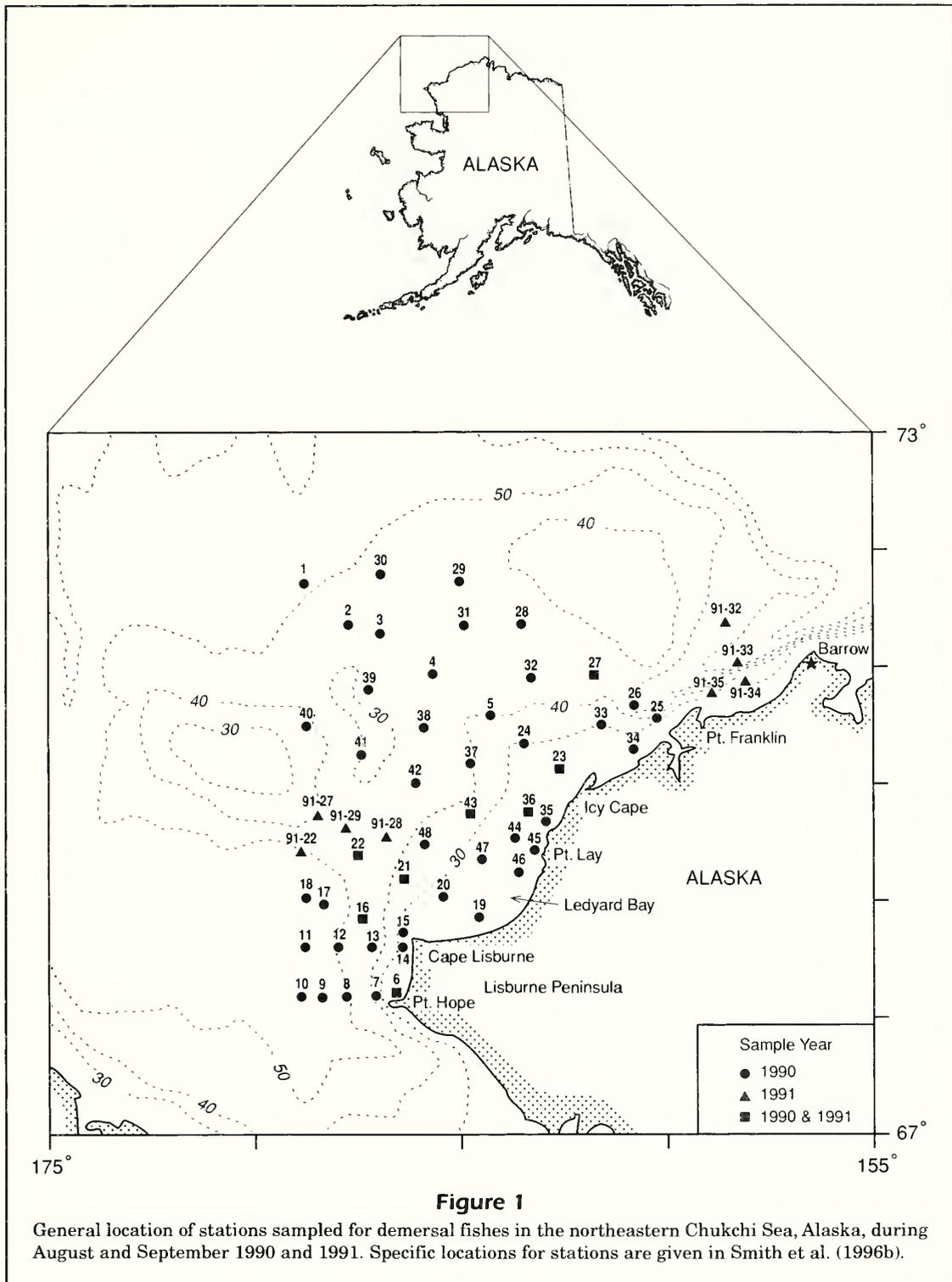
Two samples for each category (fishes and invertebrates) were collected at each station by towing a standard 83–112 survey otter trawl<sup>3</sup> for 30 minutes. However, because of weather condition and torn nets, only one haul was made at station 31 in 1990 and at stations 16, 91–33, 91–34, and 91–35 in 1991. The trawl had a 25.2-m head rope, 34.1-m footrope, tickler chain, and codend of 8.9-cm stretched mesh with a 3.2-cm stretched mesh liner. The area swept by the trawl was calculated by multiplying the length of each trawl haul (beginning and ending location of each tow was determined with "Global Positions System") by the width of the trawl during fishing (the trawl width at the wings and height of the headrope above the footrope were determined with a Scanmar<sup>TM</sup> electronic mensuration unit).

Upon retrieval of the trawl, the entire catch was either weighed in the net with an electronic load cell or in baskets on a mechanical platform. Fish were sorted to the lowest taxa possible, counted, and weighed with a mechanical platform scale. Fish abundance (fish/km<sup>2</sup>) and biomass (g/km<sup>2</sup>) were deter-

<sup>1</sup> Fechhelm, P., C. Craig, J. S. Baker, and B. J. Gallaway. 1985. Fish distribution and use of near shore waters in the northeastern Chukchi Sea. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 32, p. 121–297.

<sup>2</sup> Feder, H. M., A. S. Naidu, M. J. Hameedi, S. C. Jewett, and W. R. Johnson. 1990. The Chukchi Sea continental shelf: benthos-environmental interactions. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 68:25–311.

<sup>3</sup> Sample, T. E. 1994. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Seattle, WA. Personal commun.



mined by the area-swept method (Wakabayashi et al., 1985).

Following the last trawl at each station, bottom temperature and bottom salinity were measured with a Seabird™ SBE 19 internally recording conductiv-

ity-temperature-depth recorder. Owing to a malfunction, however, salinity and temperature could not be recovered for 7 of 48 stations sampled in 1990.

The total number of unique species captured at each station was determined by pooling results from

the 2 trawl hauls. Mean abundance and biomass of each species at each station were determined by averaging the results from the 2 trawl hauls, except at the few stations where only 1 sample could be collected.

To investigate diversity, we used the number of species for richness ( $S$ ) and calculated Shannon's Index ( $H$ ) (Pielou, 1977). Abundance and total unique species of both samples were combined for each station. Shannon's index was calculated as

$$H = \frac{n \log n - \sum_{i=1}^k f_i \log f_i}{n},$$

where  $n$  = total number of fish;

$f_i$  = number of individuals in species  $i$ ; and

$k$  = the number of species (Zar, 1984).

By using Shannon's Index ( $H$ ), "evenness" was estimated with the equation

$$v' = \frac{H}{\ln s},$$

where  $v'$  = measure of evenness; and

$s$  = the number of species present.

Fish assemblages were identified and their relationship to physical oceanographic conditions determined in a two-stage process. The first stage used cluster analysis of species abundance by station, followed by discriminant function and principal coordinate analyses of environmental data. Cluster analysis based on species abundance at each station was used to determine fish assemblages. Following the recommendation of Clifford and Stevenson (1975), the most commonly occurring species (21 species, each of which made up >0.1% of abundance) were chosen on the basis of a preliminary examination of abundance data. These species made up 99.6% of the total abundance, 98% of the biomass. Prior to calculating similarity indices, abundance ( $X$ ) was transformed ( $\ln [X+1]$ ) to normalize the data (Clifford and Stevenson, 1975). Similarity indices were calculated as  $1 - D$ , where  $D$  is the Bray-Curtis dissimilarity index (Clifford and Stevenson, 1975) adapted from Lance and Williams (1967).

The algorithm for  $D$  is

$$D = \frac{\sum_{i=1}^n |x_{1j} - x_{2j}|}{\sum_{i=1}^n (x_{1j} + x_{2j})},$$

where  $n$  = number of individuals in species  $i$ ; and  
 $j$  = number of stations.

Similarity index values range from 0 to 1; a value of 1 indicates identical species composition between 2 stations and a value of 0 indicates no common species between stations. Following Clifford and Stevenson (1975), a range of similarity indices was used to determine major groupings. From preliminary inspection of the data, it appeared that groupings could be distinguished with indices of 0.5–0.6. These indices were used as our reference for examining the resulting dendrograms.

Relationships between environmental conditions and fish assemblages were evaluated by using the following data subsets: 1) environmental (water depth, bottom temperature, and bottom salinity); 2) sediment type (arcsine-transformed percent of mud, sand, and gravel); and 3) abundance of infaunal and epifaunal mollusks. Sediment type and mollusk data values for those stations nearest ours were taken from Feder et al. (Footnote 1, sediment type) and Feder et al. (1994, mollusks).

Multiple discriminant function analysis (DFA) and principal coordinate analysis (PCA) were used to evaluate the relationship between fish assemblages and environmental parameters. Mud, bottom temperature, epifaunal biomass, and invertebrate infaunal biomass were not included in the analyses because they were highly correlated with gravel, bottom salinity, epifaunal abundance, and infaunal invertebrate abundance, respectively. PCA was used to validate the results of the DFA and to determine whether other variables were influencing assemblages. To control for multicollinearity, we discarded one of any pair of variables with  $-0.8 < r > 0.8$ .

Abundance, commonality in species occurrence, ranks, and diversity were used to determine whether there was congruity between years at stations sampled in 1990 and 1991. Species ranks were compared by using the Wilcoxon signed-ranks test (Siegel and Castellan, 1988).

## Results

### Abundance and biomass

A combined total of 66 species of 14 families were collected in 1990 and 1991 (Table 1). In 1990, two species of gadids, *Boreogadus saida* and *Eleginus gracilis*, made up 82% of the abundance and 69% of the biomass. Cottids, pleuronectids, and zoarcids made up an additional 15% of total abundance and 24% of total biomass in 1990. On the basis of percent

Table 1

Estimated mean abundance (no. of fish/km<sup>2</sup>), biomass (g/km<sup>2</sup>), and the percent (%) of each demersal fish species collected in the northeastern Chukchi Sea, Alaska, during 1990 and 1991. The 21 most abundant species are labeled in parentheses according to a decreasing scale of abundance from 1 (most abundant) to 21 (less abundant).

Species	1990		1991	
	Abundance (%)	Biomass (%)	Abundance (%)	Biomass (%)
<b>Cottidae (sculpins)</b>				
<i>Icelus spatula</i> <sup>1</sup>	2 3	12 3	0.00 0.00	0.00 0.00
<i>I. spiniger</i> <sup>1</sup>	2 3	10 3	0.00 0.00	0.00 0.00
Cottidae sp.	0.00 0.00	0.00 0.00	5 (0.05)	272 (0.20)
<i>Artediellus</i> sp. (21)	26 (0.10)	280 (0.06)	0.00 0.00	0.00 0.00
<i>A. pacificus</i>	2 (0.01)	47 (0.01)	0.00 0.00	0.00 0.00
<i>A. scaber</i> (7)	141 (0.55)	583 (0.12)	197 (2.28)	704 (0.51)
<i>Blepsias bilobus</i>	1 3	169 (0.03)	0.00 0.00	0.00 0.00
<i>Enophrys diceraus</i>	5 (0.02)	188 (0.04)	130 (1.50)	1,106 (0.81)
<i>Eurymen gyrinus</i>	2 3	31 (0.01)	1 (0.01)	17 (0.01)
<i>Gymnocanthus tricuspis</i> (4)	783 (3.06)	9,070 (1.84)	494 (5.71)	5,228 (3.81)
<i>Hemilepidotus papilio</i> (20)	28 (0.11)	571 (0.12)	9 (0.11)	414 (0.30)
<i>Megalocottus platycephalus</i>	15 (0.06)	944 (0.19)	10 (0.12)	944 (0.72)
<i>Microcottus sellaris</i> <sup>1</sup>	2 3	12 3	0.00 0.00	0.00 0.00
<i>Myoxocephalus</i> sp. (3)	1,573 (6.15)	49,167 (9.99)	90 (1.05)	1,295 (0.94)
<i>M. polyacanthocephalus</i>	1 (.01)	167 (0.03)	0.00 0.00	0.00 0.00
<i>M. quadricornis</i>	6 (0.02)	442 (0.09)	0.00 0.00	0.00 0.00
<i>M. verrucosus</i> (6)	238 (0.93)	12,604 (2.56)	1,033 (11.95)	35,017 (25.51)
<i>Myoxocephalus</i> sp. 2	0.00 0.00	0.00 0.00	108 (1.25)	4,550 (3.31)
<i>Myoxocephalus</i> sp. 1	0.00 0.00	0.00 0.00	2 (0.02)	318 (0.23)
<i>Nautichthys pribilovius</i> <sup>1</sup>	2 3	12 3	4 (0.05)	15 (0.01)
<i>Triglops forficatus</i> <sup>1</sup>	2 3	20 3	0.00 0.00	0.00 0.00
<i>T. pingeli</i>	137 (0.54)	1,698 (0.35)	131 (1.52)	1,294 (0.94)
	(11.56)	(15.46)	(25.61)	(37.29)
<b>Pleuronectidae (flounders)</b>				
<i>Hippoglossoides robustus</i> (5)	486 (1.90)	17,406 (3.54)	25 (0.29)	940 (0.68)
<i>Pleuronectes aspera</i>	20 (0.08)	746 (0.15)	101 (1.17)	1,505 (1.10)
<i>P. proboscideus</i>	5 (0.02)	181 (0.04)	0.00 0.00	0.00 0.00
<i>P. sakhalinensis</i> <sup>1</sup>	2 3	12 3	0.00 0.00	0.00 0.00
<i>P. quadrituberculatus</i>	18 (0.07)	2,467 (0.50)	16 (0.19)	2,016 (1.47)
<i>Platichthys stellatus</i>	2 (0.01)	1,365 (0.28)	0.00 0.00	0.00 0.00
<i>Reinhardtius hippoglossoides</i>	2 (0.01)	85 (0.02)	0.00 0.00	0.00 0.00
<i>Hippoglossus stenolepis</i> <sup>1</sup>	2 3	256 (0.05)	0.00 0.00	0.00 0.00
	(2.11)	(4.59)	(1.65)	(3.25)
<b>Zoarcidae (eelpouts)</b>				
<i>Lycodes palearis</i> (11)	133 (0.52)	4,802 (0.98)	24 (0.27)	536 (0.39)
<i>L. polaris</i> (14)	83 (0.33)	7,780 (1.58)	0.00 0.00	0.00 0.00
<i>L. raridens</i> (15)	67 (0.26)	8,078 (1.64)	71 (0.82)	5,241 (3.82)
<i>L. turneri</i>	8 (0.03)	580 (0.12)	0.00 0.00	0.00 0.00
<i>L. rossi</i>	4 (0.02)	137 (0.03)	0.00 0.00	0.00 0.00
<i>Lycodes</i> sp. 1	0.00 0.00	0.00 0.00	8 (0.09)	92 (0.07)
<i>Lycodes</i> sp. 2	0.00 0.00	0.00 0.00	8 (0.09)	92 (0.07)
<i>Lycodes</i> sp.	0.00 0.00	0.00 0.00	4 (0.04)	112 (0.08)
<i>Gymnelis hemifasciatus</i> <sup>1</sup>	2 3	12 3	0.00 0.00	0.00 0.00
<i>G. viridis</i>	1 3	30 (0.01)	30 (0.35)	72 (0.05)
	(1.16)	(4.37)	(1.66)	(4.48)
<b>Agonidae (poachers)</b>				
<i>Aspidophoroides bartoni</i> <sup>1</sup>	1 3	24 3	0.00 0.00	0 (0.00)
<i>A. olriki</i>	2 (0.01)	85 (0.02)	0.00 0.00	0 (0.00)
<i>Podothecus acipenserinus</i> (16)	57 (0.22)	1,077 (0.22)	24 (0.28)	147 (0.11)
<i>Ocella dodecaedron</i> <sup>1</sup>	2 3	11 3	0.00 0.00	0 (0.00)
<i>Pallasina barbata</i>	0.00 0.00	0.00 0.00	2 (0.02)	9 (0.01)

continued on next page

Table 1 (continued)

Species	1990		1991	
	Abundance (%)	Biomass (%)	Abundance (%)	Biomass (%)
<b>Stichaeidae (pricklebacks)</b>				
<i>Chirolophis snyderi</i>	0.00	0.00	1 (0.01)	57 (0.04)
<i>Lumpenus fabricii</i> (13)	90 (0.35)	1122 (0.23)	52 (0.61)	102 (0.07)
<i>L. medius</i> <sup>1</sup>	1	38 (0.01)	0.00	0.00
<i>Stichaeus</i> sp.	0.00	0.00	2 (0.02)	48 (0.03)
<i>S. punctatus</i>	2 (0.01)	107 (0.02)	1 (0.01)	28 (0.02)
<i>Eumesogrammus praecisus</i>	1 (0.01)	61 (0.01)	3 (0.04)	151 (0.11)
<b>Gadidae (cods)</b>				
<i>Boreogadus saida</i> (1)	19,456 (76.06)	301,878 (61.34)	5,728 (66.27)	63,913 (46.56)
<i>Eleginus gracilis</i> (2)	1642 (6.42)	38,769 (7.88)	255 (2.95)	7150 (5.21)
<i>Gadus macrocephalus</i> (17)	44 (0.17)	1869 (0.38)	0.00	0.00
<i>Theragra chalcogramma</i> (8)	138 (0.54)	1883 (0.38)	0.00	0.00
	(83.19)	(69.98)	(69.22)	(51.77)
<b>Cyclopteridae (snailfishes)</b>				
<i>Eumicrotremus andriashevi</i> <sup>1</sup>	2	3	11	3
<i>E. orbis</i>	4 (0.02)	116 (0.02)	2 (0.02)	112 (0.08)
<i>Liparis</i> sp.	1	3	34 (0.01)	4 (0.05)
<i>L. tunicatus</i>	10 (0.04)	373 (0.08)	0.00	0.00
<i>L. gibbus</i> (18)	44 (0.17)	442 (0.90)	17 (0.20)	2408 (1.75)
<b>Osmeridae (smelts)</b>				
<i>Osmerus mordax</i> (19)	32 (0.13)	1903 (0.39)	13 (0.15)	129 (0.09)
<i>Mallotus villosus</i> (10) <sup>4</sup>	133 (0.52)	710 (0.14)	1 (0.01)	6
				3
<b>Hexagrammidae (greenlings)</b>				
<i>Hexagrammos stelleri</i>	4 (0.01)	151 (0.03)	0.00	0.00
<b>Clupeidae (herring)</b>				
<i>Clupea harengus pallasii</i> (12)	126 (0.49)	17,469 (3.55)	1 (0.01)	57 (0.04)
<b>Ammodytidae (sand lances)</b>				
<i>Ammodytes hexapterus</i>	0.00	0.00	5 (0.06)	10 (0.01)
<b>Anarhichadidae (wolffish)</b>				
<i>Anarhichas orientalis</i> <sup>1</sup>	1	3	61 (0.01)	0.00
			0.00	0.00

<sup>1</sup> Found at only one station in 1990.

<sup>2</sup> Less than 0.49.

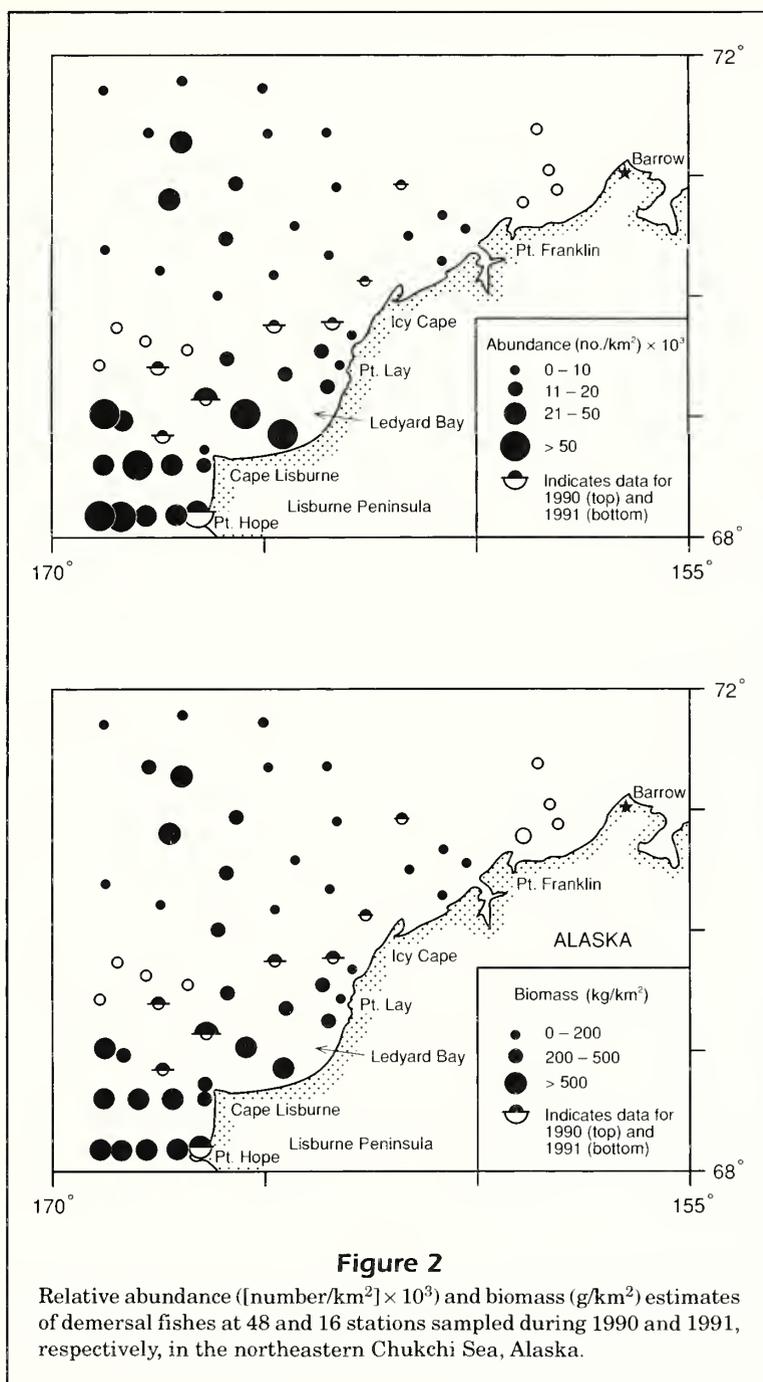
<sup>3</sup> Less than 0.01%.

<sup>4</sup> Found at only one station in 1991.

of total abundance, the 45 species captured in 1990 fell into four general categories: category 1 (extremely abundant) consisted only of *B. saida* and made up 76.1% of total abundance and 61.3% of total biomass; category 2 included five moderately abundant species (*Myoxocephalus verrucosus*, *Myoxocephalus* sp., *E. gracilis*, *Gymnocanthus tricuspis*, and *Hippoglossoides robustus*) and made up 18.4% and 25.8% of total abundance and biomass, respectively (Table 1); category 3 included 13 occasional species and made up 5.9% and 13.7% of total abundance and biomass, respectively; and category 4 included 26 rare species that accounted

for only 0.46% of the abundance and <5.0% of the biomass in 1990 (Table 1). The fish in the first two categories accounted for more than 94.4% and 87.1% of the total abundance and biomass, respectively. This pattern was generally reflected in the 1991 catches.

In 1990, there was a tendency for abundance and biomass of all species combined to be greatest in the southern part of the study area and lowest in the northern part of the study area (Fig. 2). Seven stations south of Ledyard Bay yielded more than 50,000 fish/km<sup>2</sup>. In contrast, many stations off and north of Icy Cape had fewer than 10,000 fish/km<sup>2</sup>.



In 1991, abundance and biomass estimates were low over the entire study area and there was no trend towards greater abundance or biomass in the southern area (Fig. 2). At the eight stations sampled in both 1990 and 1991, biomass and abundance estimates differed widely between years (Table 2). For example, at station 22, *B. saida* was 2.4 times as abundant in 1990 as in 1991, and *H. robustus* was 23 times as abundant in 1991 as in 1990.

### Species richness and diversity

Families contributing the most species were Cottidae (21), Zoarcidae (10), Pleuronectidae (8), Stichaeidae (6), and Agonidae (5) (Table 1). Ten families contributed only 16 additional species. Fifty-five percent of the species were represented by less than 10 individuals and some 45% were represented by a single specimen.

Table 2

Estimated mean abundance (fish/km<sup>2</sup>) of demersal fishes collected at stations sampled during both 1990 and 1991 in the north-eastern Chukchi Sea. Species sequence is based on the overall abundance of 1990 (Table 1), and the probability value (*P*) is from the Wilcoxon signed-ranks test. Species diversity was calculated from Shannon's Index (*H*).

Species	Station 6		Station 16		Station 21		Station 22		Station 23		Station 43		Station 36		Station 27	
	1990	1991	1990	1991	1990	1991	1990	1991	1990	1991	1990	1991	1990	1991	1990	1991
<i>Boreogadus saida</i>	56,373.8	14,183.5	22,386.5	2,273.4	32,184.6	393.0	20,475.3	8,527.7	318.0	2,379.4	13,684.7	5,090.2	19,104.8	2,139.4	3,017.3	2,180.3
<i>Gymnocanthus</i>																
<i>tricuspis</i>	207.3	3,047.0	157.6	0	386.8	0	494.5	124.8	778.3	2,041.0	160.2	244.5	728.4	969.1	0	0
<i>Myoxocephalus</i>																
<i>verrucosus</i>	324.7	0	0	27.0	630.5	0	0	568.8	1,163.1	1,016.2	170.6	189.8	246.7	702.2	0	0
<i>Enophrys diceraus</i>	59.4	1,932.8	11.6	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Myoxocephalus</i> sp.	0	0	712.2	0	599.4	0	608.9	0	6	55.9	0	11	0	0	0	0
<i>Pleuronectes aspera</i>	400.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hippoglossoides</i>																
<i>robustus</i>	0	37.5	1,113.5	0	229.7	0	254.8	10.8	0	0	66.8	88.2	0	33.4	0	0
<i>Lycodes raridens</i>	0	102.4	0	54.1	0	0	1,061.0	0	0	0	550.5	22.0	0	0	0	34.6
<i>Myoxocephalus</i> sp.2	0	1,621.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lycodes palearis</i>	0	37.5	492.1	162.4	199.8	0	416.1	0	0	0	0	0	0	0	0	0
<i>Lumpenus fabricii</i>	22.1	651.8	147.3	0	129.8	0	124.0	0	0	0	43	111.0	0	11.1	0	0
<i>Triglops pingeli</i>	0	519.1	0	0	27.4	0	0	0	57.8	111.8	375.4	22.2	49.1	11.1	0	0
<i>Clupea harengus</i>	221.8	0	10.7	0	804.1	0	26	0	0	0	34.1	0	0	0	0	0
<i>Gadus</i>																
<i>macrocephalus</i>	830.6	0	102.7	0	0	0	62.5	0	6	0	0	0	0	0	0	0
Number of other species	2,853.2	6,807.0	492.1	0	376.5	0	551.6	135.6	28.9	86.3	178.0	99.2	49.0	100.3	0	251.1
<i>P</i>	0.562		0.003		0.001		0.004		0.444		0.42		0.975		0.498	
Number of species	19	24	15	4	15	1	17	8	7	9	14	13	8	10	1	5
Total number of species, both years combined	32		17		15		19		10		18		14		5	
Percent in common both years	40.6		17.6		6.7		42.1		60		50		28.6		20	
Species diversity	0.47	1.83	0.62	0.4	0.52	—	0.74	0.4	1.01	1.25	0.53	0.54	0.38	1.18	—	0.37

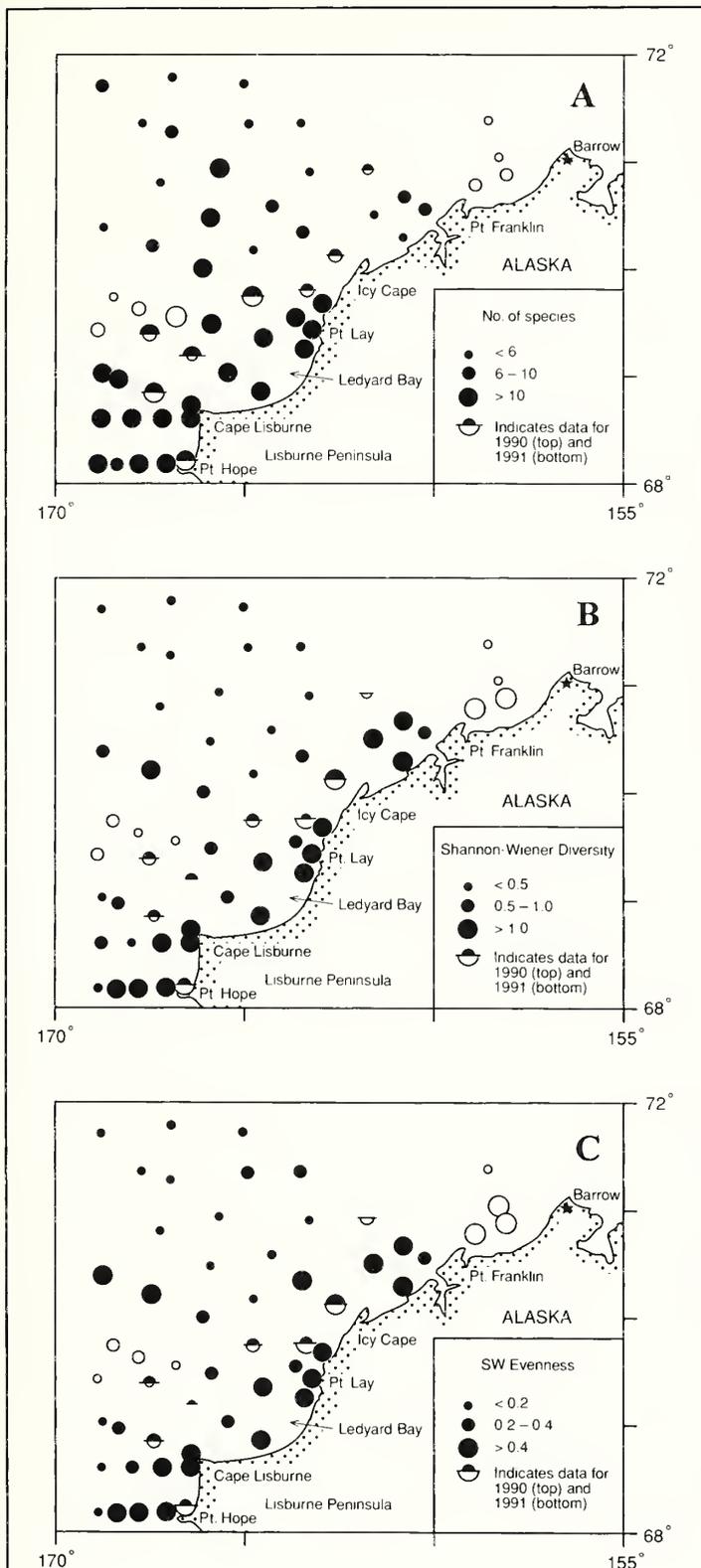
There was a trend towards higher species richness in the southern and offshore areas than in the northern and inshore areas (Fig. 3). The greatest numbers of species per station (19) were recorded at stations 6 (Point Hope), 45 (Point Lay), and 48 (Ledyard Bay) in 1990 and at station 6 (23 species) in 1991 (Fig. 3). The fewest species (2 or 3) occurred at four stations in the more northern area (stations 28 through 32). There was a tendency for the stations south of Icy Cape to have 11 or more species and those stations to the north to have 10 or less; the majority of the latter had fewer than 8 species.

The number of species at stations sampled during both 1990 and 1991 differed considerably (Table 2). For example, catches at three stations northeast of Cape Lisburne consisted of 15 and 17 species in 1990 but in 1991 comprised 1 to 8 species. In contrast, farther north at station 21, 1 species was collected in 1990 and 5 species in 1991.

Those stations with a species diversity of >0.90 occurred south of a line extending south-westward from Point Franklin. The greatest species diversity (1.99) occurred at station 45 off Point Lay; species diversity at two stations off Cape Lisburne (15 and 14) was nearly as large (1.56 and 1.87, respectively). Nearly all stations with a diversity of >1.0 occurred alongshore from Point Franklin to Point Hope. Lowest species diversity occurred at station 39 (0.02). Evenness followed the same pattern as species diversity indices (Fig. 3).

### Assemblages

Fishes collected in 1990 formed, at a similarity level of 0.5–0.6, three nearshore (I, III, and V) and three offshore (II, IV, and VI) associations (Fig. 4). One station (15) was not classifiable (Fig. 4). Two clusters of stations formed an association (I) off the Lisburne



**Figure 3**

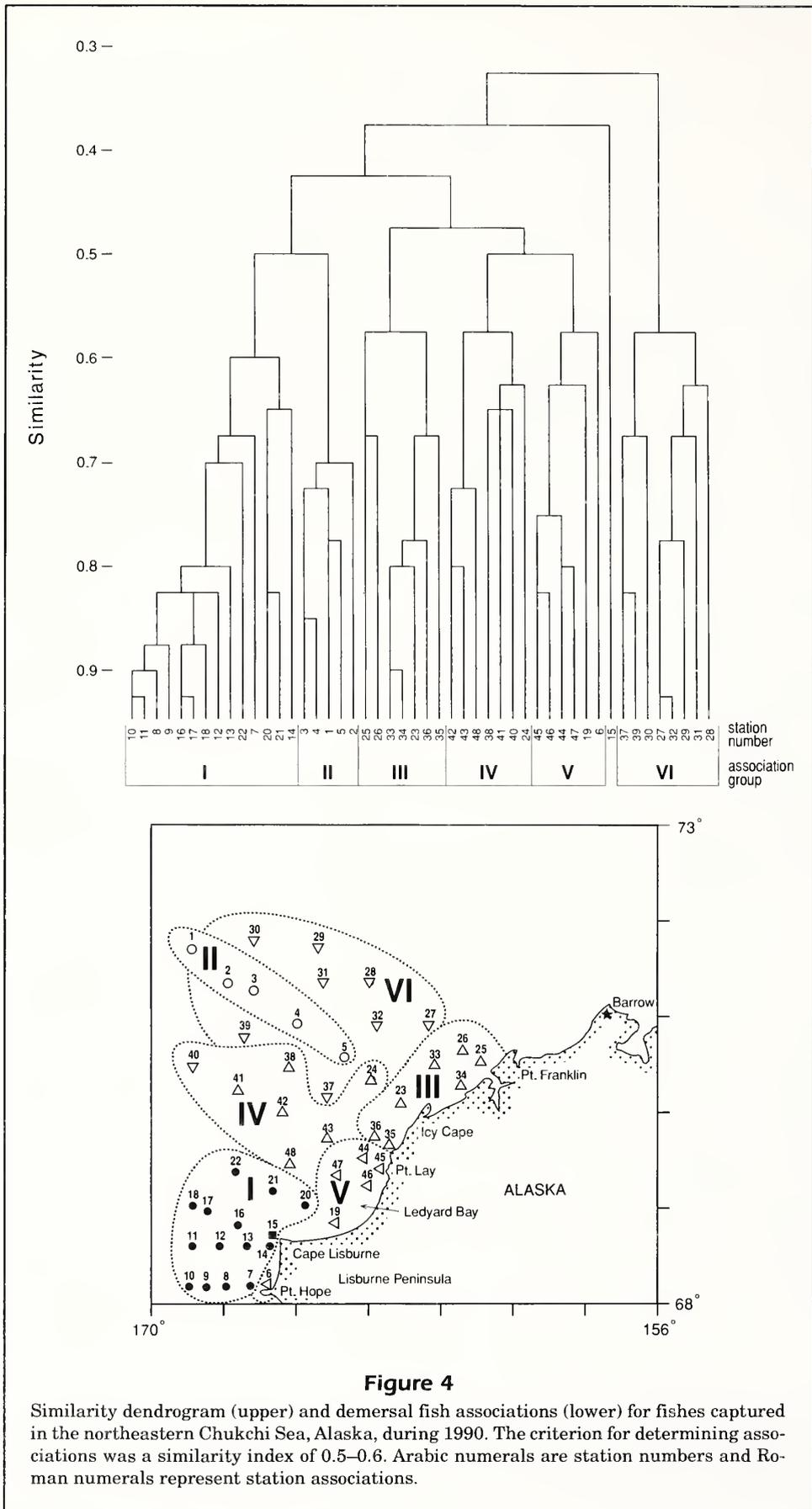
Relative richness (number of species), species diversity (Shannon index), and evenness of demersal fishes at 48 and 16 stations sampled during 1990 and 1991, respectively, in the northeastern Chukchi Sea, Alaska. SW = Shannon Wiener.

Peninsula. A second association (II) was formed near a station cluster that bisected the northern offshore association (VI) but was more closely related to association I. The northern offshore association (VI) consisted of two relatively distant clusters, whereas the northern inshore association (III) consisted of two closely related clusters, one made up of two stations. The central offshore association (IV) was formed by two clusters. Finally, there was the central onshore association (V) in Ledyard Bay, which consisted of four closely related and two distantly related stations. The cluster analysis yielded similar results when *B. saida* was not included in the analysis. In all associations, *B. saida* made up over 90% of the abundance (Table 3).

The most distinctive assemblage was VI, which had the fewest species, lowest abundance, and least diversity and evenness (Table 3). In comparison, associations I and V had much greater values for all these measures. Association I had the greatest number of species; the top five species in order of abundance were *B. saida*, *Myoxocephalus* sp., *H. robustus*, *G. tricuspis*, and *Lycodes palearis*. Association II had the second most abundant species; the top five species in order of abundance were *B. saida*, *L. raridens*, *M. verrucosus*, *G. tricuspis*, and *Clupea harengus pallasii*.

Bottom salinity and percent gravel were identified through discriminant analysis as key factors separating assemblage groups. The first axis accounted for 72%, the second axis for 28% of the variation (Table 4). Bottom salinity showed the strongest association with axis 1, whereas percent gravel was strongest in axis 2. The lines superimposed on Figure 5 enclose stations of similar environmental conditions. There is relatively little overlap of groups III and V; the former is characterized by low bottom salinity and high gravel, whereas the latter is intermediate in salinity and gravel (Fig. 5). Stations 14 and 15 were classified together, with lowest salinity and percent gravel. There is overlap at the boundaries of groups I and VI, which suggests that there is a gradation in environmental conditions. Group VI is associated with more saline water but includes a wide range of percent gravel.

A principal component analysis, which included all environmental data, supports the discriminant analysis but suggests that other variables are also important determinants of fish associations (Table 5). This analysis indicated that bottom salinity, water depth, and



**Figure 4**

Similarity dendrogram (upper) and demersal fish associations (lower) for fishes captured in the northeastern Chukchi Sea, Alaska, during 1990. The criterion for determining associations was a similarity index of 0.5–0.6. Arabic numerals are station numbers and Roman numerals represent station associations.

gravel accounted for 37.1% of the variance among stations, that epifaunal and infaunal abundances and gravel accounted for 27.8% of the variation, and that gravel and sand accounted for an additional 15.6% of the variation.

## Discussion

The northeastern Chukchi Sea lies between the Arctic Ocean and the Bering Sea and serves as a conduit for water flowing between these two bodies of water. In terms of oceanographic flow, this is a dynamic region, with a net water transport from the Bering Sea into the Arctic Ocean. Flow reversals occur in response to regional storm events (primarily during the seasonal ice-forming period). Therefore, oceanographic information used in this study represents but a short-term snapshot of environmental conditions within the region. Information on sediment distribution and associated invertebrate fauna was considered to provide a long-term integration of oceanographic conditions within the region. Even though invertebrate fauna may be influenced by hy-

drographic conditions in much the same way as ichthyofauna are influenced by these conditions, in this study they were used as independent variables. This designation was made in part because invertebrates tend to be less mobile than fishes and because, in ecological terms, invertebrates provide habitat and food for many fish species.

During this study, 66 species representing 14 families were collected, 56 in 1990 and an additional 10 in 1991. This number is similar to the number of species (52) collected in the Chukchi Sea by Alverson and Wilimovsky (1966) and is greater than the 29 species taken in the nearshore Chukchi Sea by Fehelm et al.<sup>1</sup> and the 19 species captured west of Point Barrow by Frost and Lowry (1983). As in our study, *Boreogadus saida* was the dominant species captured during each of these surveys. Other important species reported by these authors that were important in our study included *Mallotus villosus*, *Liopsetta glacialis*, *Lycodes polaris*, and *Icelus bicornus*.

The number, diversity, and biomass of fish species documented during our study are comparable to those in more southerly areas of the North Pacific Ocean. Day and Pearcy (1968) found 67 species represent-

**Table 3**

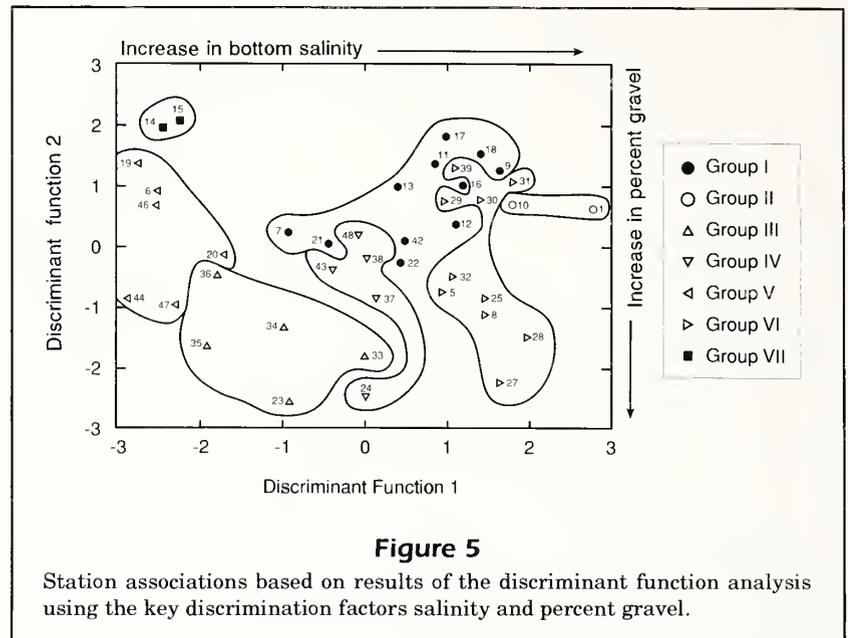
Estimated mean abundance (fish/km<sup>2</sup>), number of species, Shannon Wiener diversity, and evenness found in the six assemblages for the 21 most abundant demersal fish species determined from the cluster analysis with the Bray-Curtis dissimilarity index.

Species	Assemblage					
	1	2	3	4	5	6
<i>Boreogadus saida</i>	43,733	16,419	5,280	8,172	16,096	6,100
<i>Eleginus gracilis</i>	684	2	170	19	10,956	0
<i>Myoxocephalus</i> sp.	3,391	49	44	2	4,492	0
<i>Gymnocanthus tricuspis</i>	1,005	87	889	156	2,618	7
<i>Hippoglossoides robustus</i>	1,599	72	0	61	15	3
<i>Myoxocephalus verrucosus</i>	178	0	429	177	773	9
<i>Artediellus scaber</i>	20	0	0	11	1,061	4
<i>Theragra chalcogramma</i>	69	0	0	26	861	0
<i>Triglops pingeli</i>	70	3	120	59	722	0
<i>Mallotus villosus</i>	437	0	0	40	0	0
<i>Lycodes palearis</i>	453	0	0	7	0	0
<i>Clupea harengus pallasii</i>	195	0	0	139	323	0
<i>Lumpenus fabricii</i>	235	18	2	14	141	0
<i>Lycodes polaris</i>	260	64	2	0	6	0
<i>L. raridens</i>	76	7	4	284	13	5
<i>Podothecus acipenserinus</i>	60	0	18	5	280	0
<i>Gadus macrocephalus</i>	21	0	1	6	273	0
<i>Liparis gibbus</i>	129	2	0	15	29	0
<i>Osmerus mordax</i>	0	0	0	0	258	0
<i>Hemilepidotus papilio</i>	89	0	0	13	0	0
<i>Artediellus</i> sp.	80	0	0	0	20	0
Number of species	20	10	11	18	18	6
Shannon Wiener diversity	0.35	0.05	0.37	0.25	0.72	0.02
Evenness	0.27	0.05	0.35	0.20	0.57	0.02

ing 21 families offshore of central Oregon at depths of 40–1,829 m. Fargo and Tyler (1991) reported more than 50 species of demersal fish in Hecate Strait, British Columbia. Species diversity seems to be somewhat lower in our study area than off Oregon, where diversity indices varied from 0.7 to 2.47 (Pearcy, 1978).

As noted, in terms of biomass and abundance, *B. saida* was the most common species in our study area; however, this species varied extensively between stations and years. For example, at station 15 (off Cape Lisburne), *B. saida* accounted for 0.23% of the number and 0.18% of the biomass. In contrast, at station 27 (northwest of Point Franklin), 100% of the catch comprised *B. saida*.

Observed trends of fish distribution, abundance, biomass, and assemblages were qualitatively similar to those of epifaunal mollusks found by Feder et al. (1994) but not to those of infaunal mollusks. These qualitative similarities suggest that common variables are influencing the distribution of fishes and epifaunal mollusks in the study area. Feder et al. (1994) found epifaunal mollusk abundance and biomass to be highest along the coast, with very high values adjacent to Point Hope and north of Cape Lisburne. Additionally, the 5 epifaunal mollusk assemblages described by Feder et al. were configured in the same way as the fish assemblages described in our study. However, in contrast to results from our study, abundance and distribution of infaunal mollusks were highest north of and adjacent to the hydrographic front associated with the Alaska Coastal Current (ACC) and along the coast north of Icy Cape and adjacent to or north of Cape Lisburne. The multivariate, cluster,



**Figure 5**

Station associations based on results of the discriminant function analysis using the key discrimination factors salinity and percent gravel.

discriminant, and principal component analyses yielded similar results: stations tended to be grouped by bottom salinity and percent gravel.

Because of the relatively shallow (30–50 m) depth of the northern Chukchi Sea and its gradual, featureless northward slope (Fig. 1), it seems surprising that the principal component analysis identified depth as a significant variable. Depth may have been significant because it acted in concert with other factors, such as sediment (which tends to be relatively coarse, grading to muds containing various proportions of gravel and sand) on the inner shelf between Point Hope and Point Barrow (Sharma, 1979; Naidu, 1988).

Fargo and Tyler (1991) found assemblages related to depth and sediment type, where sediment type

**Table 4**

Discriminant function analysis of environmental factors with Chukchi Sea demersal fish abundance as the class criterion. Significant relationships are underlined.

Independent variable	Standardized discriminant function coefficients	
	1st axis	2nd axis
Bottom salinity	<u>0.94189</u>	0.48469
Percent gravel	-0.14688	<u>1.04905</u>
Percent variance	71.81	28.19
Eigen value	1.887	0.741

**Table 5**

Results of the principal component (PC) analysis using both environmental factors and infaunal and epifaunal abundance. Significant relationships are underlined.

Variable	PC1	PC2	PC3
Percent sand	0.563	<u>-0.451</u>	<u>-0.643</u>
Percent gravel	<u>0.663</u>	-0.421	<u>0.771</u>
Depth	<u>-0.796</u>	0.398	-0.238
Bottom salinity	<u>-0.882</u>	0.118	0.105
Epifaunal abundance	0.461	<u>0.861</u>	0.060
Infaunal abundance	0.318	<u>0.880</u>	0.040
Cumulative variance	0.371	0.649	0.805
Eigenvalue	2.596	1.951	1.095

was different for each species assemblage. Their species assemblages and sediment types, however, did not coincide exactly; two sediment types were found in the same depth range of species assemblages. They suggested that faunal similarities were maintained in regions of sediment transition and that factors other than sediment type governed distribution of assemblages. Similarly, Pearcy (1978) found a clear separation in the effects of depth but not in the effects of sediment for two assemblages, one shallow and one deep. There was, however, an interaction between depth and sediment type where the shallow assemblages showed a high similarity between stations of different sediment types.

In respect to the hydrography of this area, the ACC sweeps through the area in a general northwest flow. However, change in wind conditions may cause periodic and persistent reversals in the southerly flow of the ACC (Johnson, 1989; Weingartner<sup>4</sup>). Flow reversals tend to be more common during winter ice cover. A review of long-term ice records suggests that in summer, an oceanographic front (as represented by the southern ice edge) may exist to the south and east of Point Franklin. However, there is much interannual variation in the location of this front, in related flow patterns, and in potential transport of adult and larval fishes into the area from the south.

Variations in hydrographic conditions, coupled with differences in catches and changes in year-class strength, strongly suggest that there are interannual changes in abundance and distribution of fishes within the study area. How, or if, the dynamics of oceanographic parameters are translated into distributions and relative abundances of fishes and fish assemblages is unknown. Differences in catches at stations sampled in 1990 and 1991 may have been due to interannual changes in fish distribution and abundance, or even to sampling error. However, differences in the age-class structure of fishes captured during the two years are striking. In 1990 approximately 42% of *G. tricuspis* (Smith et al., 1996b) were older than 4 years, but in 1991 only 9% were older than 4 years. Similarly, ages of *H. robustus* in 1990 ranged from 1 to 11, and age class 5 was most abundant (Smith et al., 1996a), whereas ages reported by Pruter and Alverson (1962) for this species were 6 to 13, and ages 7 through 9 accounted for 90% of the fish samples.

Interannual change in the distribution and relative abundance of fish species may not lead to different associations or result in a change in the locations of these fish within the study area. Overholtz

and Tyler (1985) concluded that, even though some assemblages changed dramatically in species richness and relative abundance, the spatial integrity of each complex remained constant over time. Similarly, there were seasonal changes in species associations on the Scotian Shelf, but these were relatively constant over 9 years within seasons (Mahon and Smith, 1989). Colvocoresses and Musick (1984) examined 9 years of trawl data from the Middle Atlantic Bight, and the distributional patterns that were found were largely structured by temperature on the innershelf and midshelf and by depth on the outer shelf and shelf break. They also found that there was sedimentary and topographical uniformity for both the innershelf and midshelf and that there were no strong relationships between species group and sediment. Like Mahon and Smith (1989), Colvocoresses and Musick (1984) found good geographic definition in both autumn and spring groups and overlap between groups. The groups that made up the communities had much in common but differed between seasons. Colvocoresses and Musick (1984) also found relationships between groups and depth, and shifts in the groups with changes in temperature. For example, the geographic extent of assemblages varied between years depending on the southward extent of the cooler 8°C water. The fish apparently behave as a group in response to environmental variation.

The fish assemblages in our study were depicted as having clear assemblage boundaries related to sediment type and oceanographic features. Results from a principal coordinate analysis, however, indicate that these boundaries are related to other features as well. Therefore, the assemblages shown in the ordination plots should more appropriately be thought of as transitional species abundances and proportional compositions. This conclusion is similar to that reached by McKelvie (1985), namely that assemblages of mesopelagic fishes were best interpreted as gradations between faunas associated with different water masses. Consequently, our study area may be viewed as a transition zone between fish communities of the southern Chukchi Sea and those of the Arctic Ocean. In this view, the presence of different species assemblages in the northeastern Chukchi Sea represents a mixture of 2 fish communities whose abundance and biomass vary, shifting somewhat offshore–onshore or northerly–southerly, according to variations in the oceanographic structure of the area.

## Acknowledgments

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<sup>4</sup> Weingartner, T. J. 1994. Institute of Marine Sciences, Univ. Alaska Fairbanks, Fairbanks, AK 99775-7220. Personal commun.

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**Abstract.**—Several bycatch-reducing devices (BRD's) were compared for their effectiveness in reducing bycatch while maintaining catches of prawns in an estuarine prawn-trawl fishery in New South Wales (NSW), Australia. A solid separator-panel (the Nordmøre grid), a soft separator panel (the commercially used blubber chute), and four secondary BRD's (the fisheye, extended mesh funnel, Allerio Brothers grid, and square-mesh panel) each attached to a Nordmøre grid, were compared against each other in a series of paired comparisons in the Hunter River prawn-trawl fishery. The results showed that the Nordmøre grid and all secondary BRD's caught less bycatch and more prawns than the commercially used blubber chute. Most bycatch seemed to escape with use of the Nordmøre grid, and there was no significant advantage in adding a secondary BRD to this design. The efficiency of the Nordmøre grid has led to its voluntary adoption by many commercial prawn-trawl fishermen throughout NSW estuaries.

## Evaluations of the Nordmøre grid and secondary bycatch-reducing devices (BRD's) in the Hunter River prawn-trawl fishery, Australia

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In New South Wales (NSW), Australia, estuarine prawn-trawling occurs in five localities and is valued at approximately A\$7 million per annum. Like the majority of the world's prawn-trawl fisheries, significant numbers of nontarget organisms, or bycatch, are captured incidentally with targeted prawns (for reviews see Sails, 1983; Andrew and Pepperell, 1992; Alverson et al., 1994; Kennelly, 1995).

In recent years, bycatch from these fisheries has become of increasing concern to a broad cross section of the fisheries community. As a result, a 3-yr observer-based study was undertaken from 1990 to 1992 to quantify the distributions and abundances of bycatch species (Liggins and Kennelly, 1996; Kennelly<sup>1</sup>). The results from these studies showed that, despite large spatial and temporal variabilities in the bycatches of many species, some juveniles of commercially and recreationally important species were caught in large numbers throughout the trawling seasons. The quantities involved raised concerns over the potential impacts of prawn-trawling on subsequent

stocks of these species. These concerns led to the current investigation, which examines various modifications to trawling gear and trawling practices that minimize undesirable bycatches while maintaining catches of prawns.

A number of recent attempts to exclude bycatch from prawn-trawls have concentrated on modifications that incorporate bycatch-reducing devices (BRD's) (Christian and Harrington, 1987; Averill, 1989; Kendall, 1990; Isaksen et al., 1992; Rulifson et al., 1992; Broadhurst et al., 1996). In previous experiments (Broadhurst and Kennelly, 1994, 1995, 1996; Broadhurst et al., 1996) we showed that the successful application of various BRD's is specific to individual fisheries and depends upon several factors, including the type of species to be excluded. Further, to promote acceptance by industry, BRD's should be designed so that they do not adversely influence normal commercial operations.

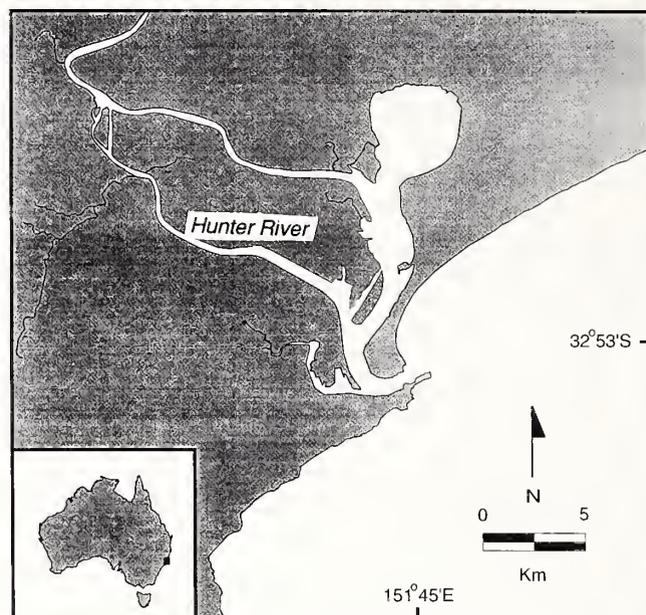
<sup>1</sup> Kennelly, S. J. 1993. Study of the bycatch of the NSW east coast trawl fishery. Final rep. to the Fisheries Research and Development Cooperation. Project 88/108, ISBN 0 7310 2096 0, 520 p.

In estuarine prawn-trawl fisheries in NSW, many of the individual fish in bycatch are larger than the targeted prawns and include organisms such as jellyfish or jelly "blubber"—*Catostylus* spp. For the past 30 years, many of the estuarine prawn-trawlers in NSW have routinely used a BRD designed specifically to exclude these individuals. Commonly called "blubber-chutes," these BRD's consist of a funnel of soft mesh inserted into the aft belly of the trawl. Organisms larger than the mesh in the funnel are guided through an opening in the top of the trawl, while prawns and smaller individuals pass through the mesh into the codend (see Broadhurst and Kennelly, 1996). In the Hunter River (HR) prawn-trawl fishery (Fig. 1), the abundance of jellyfish means that commercial fishermen use blubber chutes throughout most of the trawling season.

In a series of experiments that examined the performance of several types of BRD's (Broadhurst et al., 1996; Broadhurst and Kennelly, 1996), we showed that a rigid separator-panel (the Nordmøre grid) significantly reduced the mean weight of bycatch in two estuaries and had no effect on the catches of prawns. Compared with the commercially used blubber chute, the Nordmøre grid also retained significantly less bycatch but caught more prawns.

Bycatch-reducing devices, such as the Nordmøre grid and the blubber chute, function by mechanically partitioning the catch according to size (see Broadhurst et al., 1996), and therefore are generally not as effective in excluding unwanted individuals that are of a similar size or that are smaller than the targeted prawns. Previous studies have shown, however, that it may be possible to exclude these smaller individuals by exploiting behavioral differences between some species of fish and prawns (Watson et al., 1986; Broadhurst and Kennelly, 1994, 1995; Broadhurst et al., 1996). For example, studies by Watson et al. (1993) in the Gulf of Mexico showed that small individuals of red snapper (*Lutjanus campechanus*), Atlantic croaker (*Micropogon undulatus*), Atlantic bumper (*Chloroscombrus chrysurus*) and whiting (*Menticirrhus* sp.) were passively excluded from trawls by various BRD designs comprising strategically placed panels of netting and escape exits. These designs were located posteriorly to a larger mechanical separating grid (designed to exclude turtles) and effectively functioned as secondary BRD's.

It is apparent that several options exist for ways of excluding bycatch from prawn trawls. In the present study we wanted to determine which of these various devices (i.e. the Nordmøre grid, blubber chute, or some type of secondary BRD) is most appropriate for use in the HR prawn-trawl fishery. Our



**Figure 1**

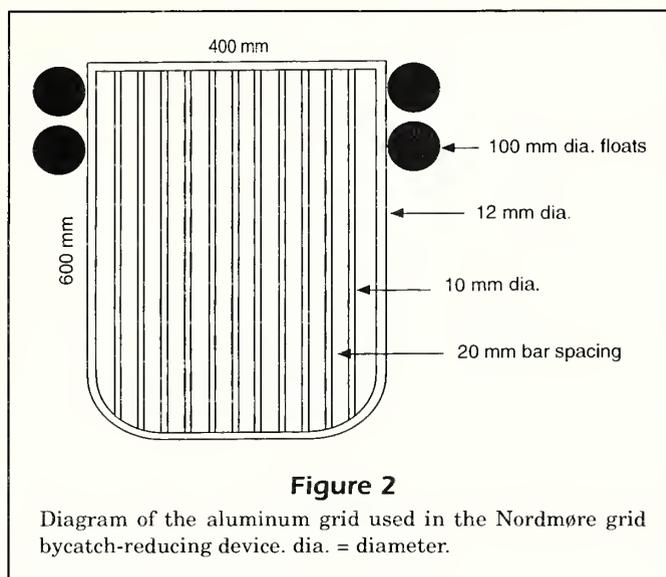
The location of the Hunter River in New South Wales.

specific goals, therefore, were 1) to assess the performance of four secondary BRD's located behind the Nordmøre grid (including designs previously tested in the Gulf of Mexico by Watson et al., 1993) in reducing smaller unwanted individuals in the HR prawn-trawl fishery; 2) to compare the two most appropriate secondary BRD's from 1) against a standard Nordmøre grid and the commercially used blubber chute; and 3) to test a standard Nordmøre grid (with no secondary BRD) against the commercially used blubber chute.

## Materials and methods

Two experiments were performed on commercial prawn-trawl grounds in the Hunter River (32°53'S, 151°45'E, Fig. 1), between November and December 1995 with a chartered commercial prawn-trawler (12.72 m). Three Florida flyers (mesh size=40 mm), each with a headline length of 9.14 m, were rigged in a standard triple gear configuration (see Andrew et al., 1991, for details) and towed at 2 knots across a combination of sandy and muddy bottoms in depths ranging from 2 to 8 m. Each of the identical outside nets were rigged with zippers to facilitate changing the codends (see Broadhurst et al., 1996). Because the middle net was not rigged in an identical manner to that used on the outside nets, its catch was excluded from analysis.

The codends used in the experiments measured 50 meshes long (2 m) and were constructed from 40-



mm netting. They comprised two panels. The anterior panel was 100 meshes in circumference, 25 meshes in length, and constructed of 400/36 ply, UV-stabilized, high-density polyethylene twine. The posterior panel was 150 meshes in circumference, 25 meshes in length, and constructed of 3-mm diameter braided polyethylene twine. Two standard Nordmøre grids (each measuring 600 × 400 mm and weighing 1.9 kg, Fig. 2) were constructed and located in 2-m extension pieces (made from 400/36 ply, UV-stabilized, high-density polyethylene twine, mesh size = 40 mm) immediately anterior to each codend (Fig. 3A, see also Broadhurst and Kennelly, 1996, for details).

### Experiment 1 (comparisons of secondary BRD's)

Four designs of secondary BRD's were constructed and installed into the codends described above, behind the Nordmøre grids. The first design (termed the fisheye) consisted of a stainless steel pyramid-shaped frame inserted 12 meshes to the left of the center of the top anterior section of the codend (Fig. 3B, see also Watson and Taylor<sup>2</sup>; Watson<sup>3</sup>). The second design (termed the square-mesh panel) had a panel of 50-mm knotless netting, hung on the bar and inserted into the top anterior section of the codend (Fig. 3C). The third design (termed the ex-

tended mesh funnel or EMF) comprised a guiding funnel surrounded by larger square-shaped mesh (see Watson and Taylor<sup>2</sup>; Watson<sup>3</sup>) and was located in the anterior section of the codend (Fig. 3D). The fourth design (termed the Allerio Brothers grid, Watson<sup>4</sup>) was constructed like the Nordmøre grid but included additional lateral fish escape windows posterior to the aluminium grid (Fig. 4).

All four designs were compared against each other, one pair of each design on the outside nets of the triple-rigged gear (i.e. 6 separate paired comparisons). The position and order of each secondary BRD was randomly determined, and during 6 days in the trawling season in the Hunter River, we completed a total of 12 replicate 30-min tows for each paired comparison. The location of each tow was randomly selected from the available prawn-trawl locations that were possible under the particular conditions. Prior to the trials, we rigged both nets with normal commercial codends to ensure that there were no differences in fishing characteristics.

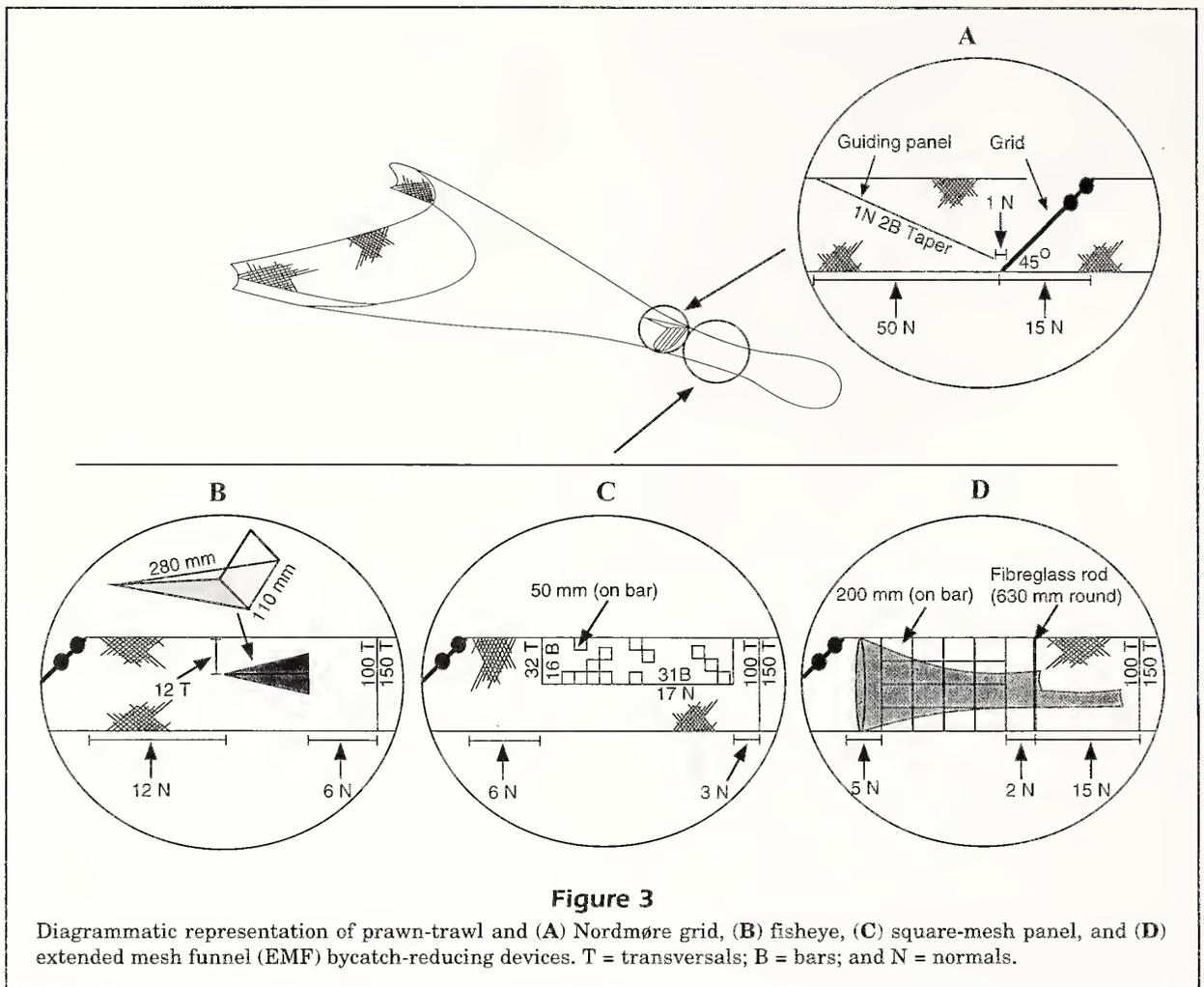
### Experiment 2 (comparison of two secondary BRD's, standard Nordmøre grid and blubber chute)

In this experiment, the fisheye and EMF, each attached to a Nordmøre grid, were compared against a standard Nordmøre grid (with no secondary BRD) and the commercially used blubber chute. The standard Nordmøre grid and blubber chute were also compared against each other (providing a total of five

<sup>2</sup> Watson, J. W., and C. W. Taylor. 1996. Technical specifications and minimum requirements for the extended funnel, expanded mesh and fisheye BRDs. Mississippi Laboratory, NMFS, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567.

<sup>3</sup> Watson, J. W. 1996. Summary report on the status of bycatch reduction devices development. Mississippi Laboratory, NMFS, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567.

<sup>4</sup> Watson, J. W. 1995. Mississippi Laboratory, NMFS, NOAA, P.O. Drawer, 1207, Pascagoula, MS 39567. Personal commun.



**Figure 3**

Diagrammatic representation of prawn-trawl and (A) Nordmøre grid, (B) fisheye, (C) square-mesh panel, and (D) extended mesh funnel (EMF) bycatch-reducing devices. T = transversals; B = bars; and N = normals.

paired comparisons). The blubber chute comprised a panel of netting (36-ply, UV-stabilized, high-density polyethylene with a mesh size of 90 mm) sewn into a funnel (with an anterior circumference of 100 meshes) located in a 2-m panel of mesh (mesh size of 40 mm) measuring 150 meshes in circumference (see Broadhurst and Kennelly, 1996, for details). The posterior point of the blubber chute was attached five meshes from the end of the 2-m panel. A 30-mesh opening (termed the escape exit) was cut immediately anterior to this point of attachment.

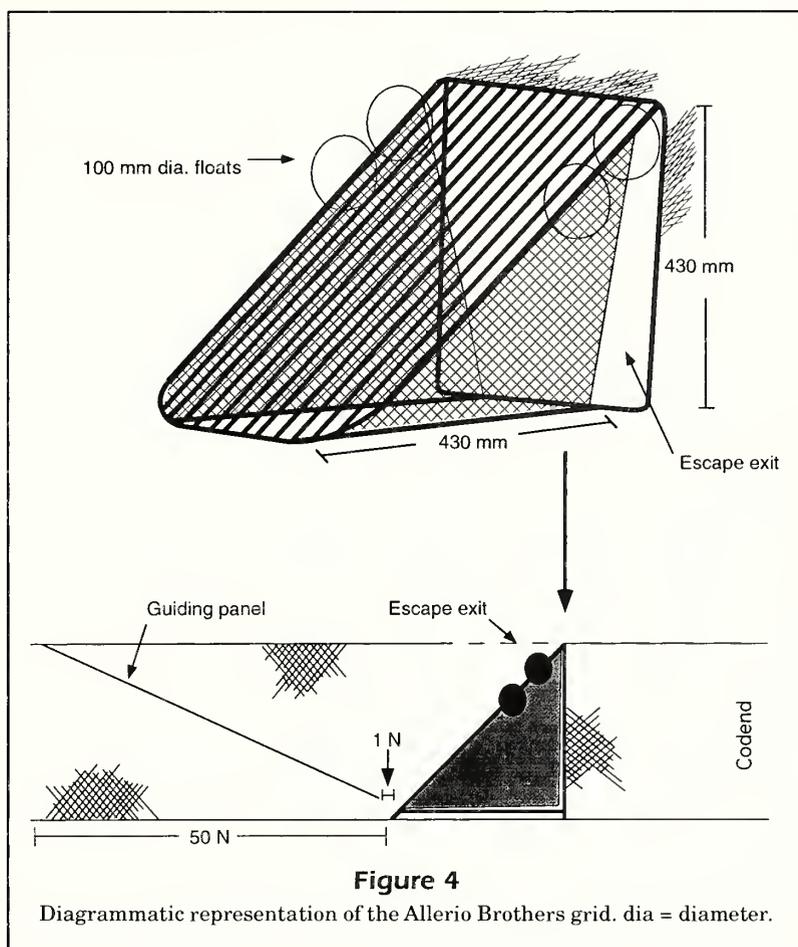
As was the case for experiment 1, the position and order of each design was randomly determined and used in normal commercial tows of 30-min duration. Over 8 days, we completed a total of 23 replicate tows for each of the five paired comparisons.

### Data collected

After each tow in each paired experiment, the two codends were emptied onto a partitioned tray. All

organisms were sorted according to species. The following data were collected from each tow: the total weight of prawns; the total weight of bycatch; the weights; numbers and sizes of commercially or recreationally (or both) important finfish (to the nearest 0.5 cm); the numbers of noncommercial or nonrecreational species; and the total numbers of noncommercial and commercial species in the assemblage. All prawns in a subsample of the total prawn catch from each tow in experiment 2 were measured in the laboratory (to the nearest 1-mm carapace length). Several species were caught in sufficient quantities to provide meaningful analyses. These were the commercially important school prawns (*Metapenaeus macleayi*) and large tooth flounder (*Pseudorhombus arsius*) and the commercially unimportant fortesque (*Centropogon australis*), narrow banded sole (*Synclidopus macleayanus*), bridle goby (*Arenigobius bifrenatus*), and catfish (*Euristhmus lepturus*).

Data from all replicates that had sufficient numbers of each variable (defined as >2 fish in at least 8



replicates) in experiment 1 were analyzed by using two-tailed, paired *t*-tests. Because a previous experiment in the Clarence River prawn-trawl fishery showed that the Nordmøre grid caught more prawns than the blubber chute (Broadhurst and Kennelly, 1996), in experiment 2 we tested the hypothesis that each of the three designs incorporating a Nordmøre grid caught more prawns but less bycatch than the commercially used blubber chute. These data were analyzed by using one-tailed paired *t*-tests. Size frequencies of prawns from experiment 2 were graphed and compared by using two-sample Kolmogorov-Smirnov tests ( $P=0.05$ ).

## Results

### Experiment 1 (comparisons of secondary BRD's)

Apart from a significant reduction in the number of noncommercial species caught as bycatch by the Allerio Brothers grid, compared with the number

caught with the square-mesh panel, there were no other detectable differences between any of the secondary BRD's tested (Table 1). However, because previous studies in the Gulf of Mexico showed that the EMF and fisheye were most effective in excluding small fish from the codend (Watson and Taylor<sup>2</sup>; Watson<sup>3</sup>), these two designs were tested further in experiment 2.

### Experiment 2 (comparison of two secondary BRD's, standard Nordmøre grid and blubber chute)

Compared with the commercially used blubber chute, the standard Nordmøre grid, EMF, and fisheye all significantly increased the weight of prawns caught (means increased by 24%, 41%, and 23%, respectively) and decreased the weight of total bycatch (means reduced by 58%, 45%, and 55%, respectively) and number of noncommercial species in bycatch (Fig. 5, A, B, and H; Table 2). The fisheye also significantly reduced the mean number of catfish caught by 79.5% (there were insufficient catfish from the

**Table 1**

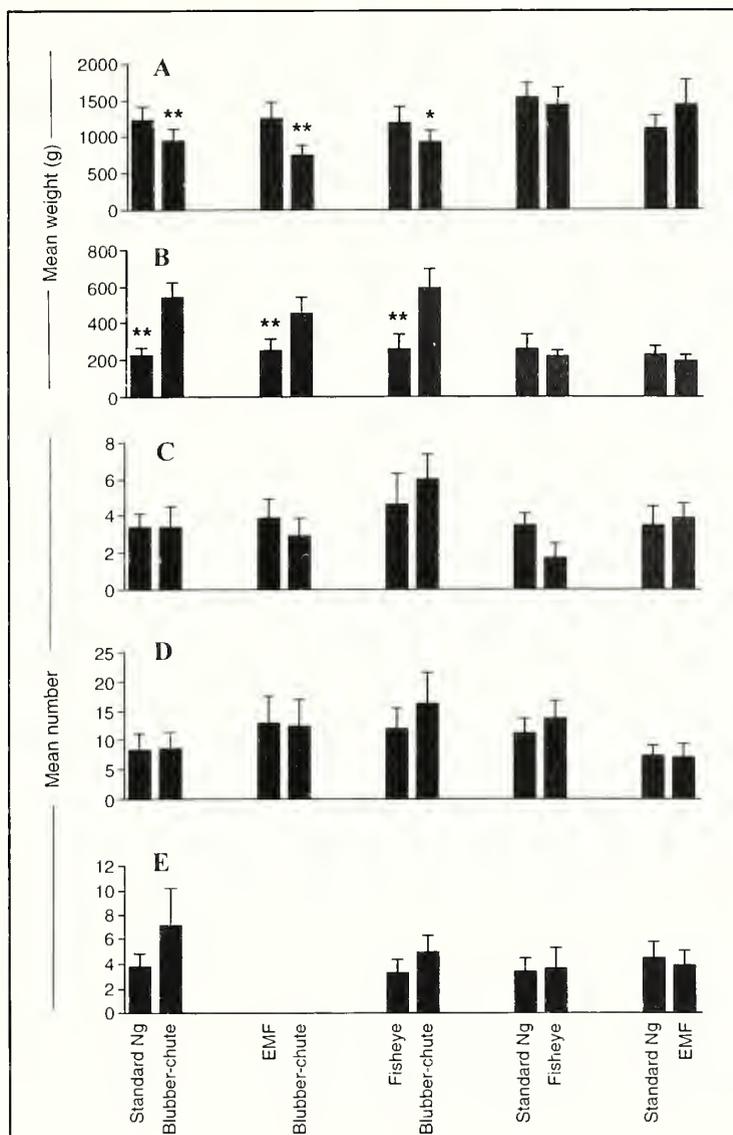
Summaries of two-tailed paired *t*-tests in a series of comparisons of various secondary BRD's in experiment 1. \*\* = significant ( $P < 0.01$ ); \* = significant ( $P < 0.05$ ); *n* = the number of replicates that had sufficient data available for analysis (i.e. >2 fish in 8 replicates).

	Allerio Bros. vs. EMF			Allerio Bros. vs. square-mesh			Allerio Bros. vs. fisheye		
	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>
Wt. of prawns	-0.602	0.559	12	0.193	0.850	12	0.689	0.505	12
Wt. of total bycatch	-0.967	0.354	12	-1.827	0.095	12	0.958	0.358	12
No. of fortesque	0.000	0.999	9	0.886	0.398	10	2.200	0.052	11
No. of noncommercial sp.	-0.860	0.407	12	-2.46	0.031*	12	-1.146	0.276	12
No. of commercial sp.	-0.232	0.821	12	1.517	0.157	12	-1.698	0.120	12
	Square-mesh vs. EMF			Fisheye vs. square-mesh			Fisheye vs. EMF		
	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>
Wt. of prawns	-0.225	0.826	12	-1.36	0.200	12	-1.795	0.100	12
Wt. of total bycatch	-0.318	0.756	12	-1.821	0.095	12	-0.513	0.618	12
No. of fortesque	0.808	0.440	10	-0.683	0.544	8	-0.455	0.659	10
No. of noncommercial sp.	1.216	0.249	12	-1.431	0.180	12	-1.383	0.194	12
No. of commercial sp.	-0.890	0.392	12	-0.364	0.722	12	-1.190	0.256	12

**Table 2**

Summaries of one-tailed paired *t*-tests in a series of comparisons of various BRD's in experiment 2. Ng = Nordmøre grid. \*\* = significant ( $P < 0.01$ ); \* = significant ( $P < 0.05$ ); *n* = the number of replicates that had sufficient data available for analysis (i.e. >2 fish in 8 replicates).

	Standard Ng vs. blubber chute			EMF vs. blubber chute			Fisheye vs. blubber chute		
	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>
Wt. of prawns	2.864	0.004**	23	3.764	0.0005**	23	2.020	0.027*	23
Wt. of total bycatch	3.515	0.001**	23	2.930	0.003**	23	3.306	0.002**	23
Wt. of large tooth flounder	0.979	0.173	14	0.729	0.239	14	1.394	0.103	8
No. of large tooth flounder	0.061	0.476	14	-0.879	0.802	14	0.747	0.239	8
No. of fortesque	0.286	0.389	19	-0.261	0.601	20	0.761	0.228	18
No. of narrow banded sole	1.064	0.164	8	—	—	—	1.440	0.090	10
No. of bridled goby	-0.414	0.654	8	—	—	—	-0.078	0.531	11
No. of catfish	—	—	—	—	—	—	3.490	0.003**	10
No. of noncommercial sp.	2.626	0.007**	23	2.040	0.026*	23	1.931	0.033*	22
No. of commercial sp.	-1.190	0.876	23	0.000	0.500	23	0.282	0.390	23
	Standard Ng vs. fisheye			Standard Ng vs. EMF					
	Paired <i>t</i> -value	<i>P</i>	<i>n</i>	Paired <i>t</i> -value	<i>P</i>	<i>n</i>			
Wt. of prawns	0.618	0.271	23	-1.418	0.914	23			
Wt. of total bycatch	0.721	0.239	23	0.512	0.307	23			
Wt. of large tooth flounder	0.410	0.346	9	-0.507	0.689	13			
No. of large tooth flounder	1.835	0.052	9	-0.456	0.672	13			
No. of fortesque	-0.647	0.736	16	-0.128	0.449	19			
No. of narrow banded sole	-0.147	0.556	9	0.741	0.241	8			
No. of bridled goby	—	—	—	3.468	0.004**	8			
No. of catfish	—	—	—	—	—	—			
No. of noncommercial sp.	0.530	0.300	23	2.688	0.007*	23			
No. of commercial sp.	1.156	0.130	23	0.755	0.229	23			

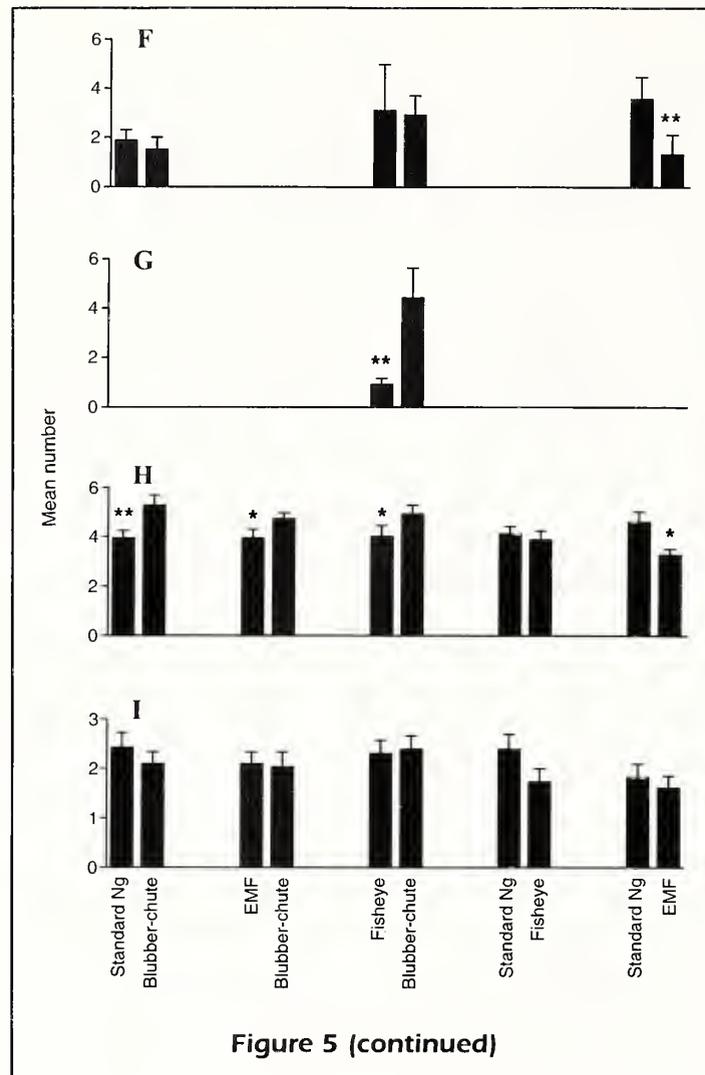


**Figure 5**

Differences in mean catch ( $\pm$  SE) between the various designs of (A) the weight of prawns (*Metapenaeus macleayi*), (B) the weight of total bycatch, (C) the number of large tooth flounder (*Pseudorhombus arsius*), (D) the number of fortesque (*Centropogon australis*), (E) the number of narrow banded sole (*Synclidopus macleayanus*), (F) the number of bridled gobies (*Arenigobius bifrenatus*), (G) the number of catfish (*Euristhmus lepturus*), (H) the number of noncommercial species, and (I) the number of commercial species. \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ . Ng = Nordmøre grid; EMF = extended mesh funnel.

standard Nordmøre grid and EMF for meaningful analyses) (Fig. 5G; Table 2). There were no significant differences detected between the standard Nordmøre grid and fisheye, whereas the EMF caught significantly fewer bridled gobies and noncommercial species than did the standard Nordmøre grid (Fig. 5, F and H; Table 2).

Two sample Kolmogorov-Smirnov tests comparing the size-frequency distributions for school prawns showed that, apart from a significant difference between the standard Nordmøre grid and the EMF (Fig. 6E), there were no other differences in the relative size-compositions between any of the codends tested in experiment 2.



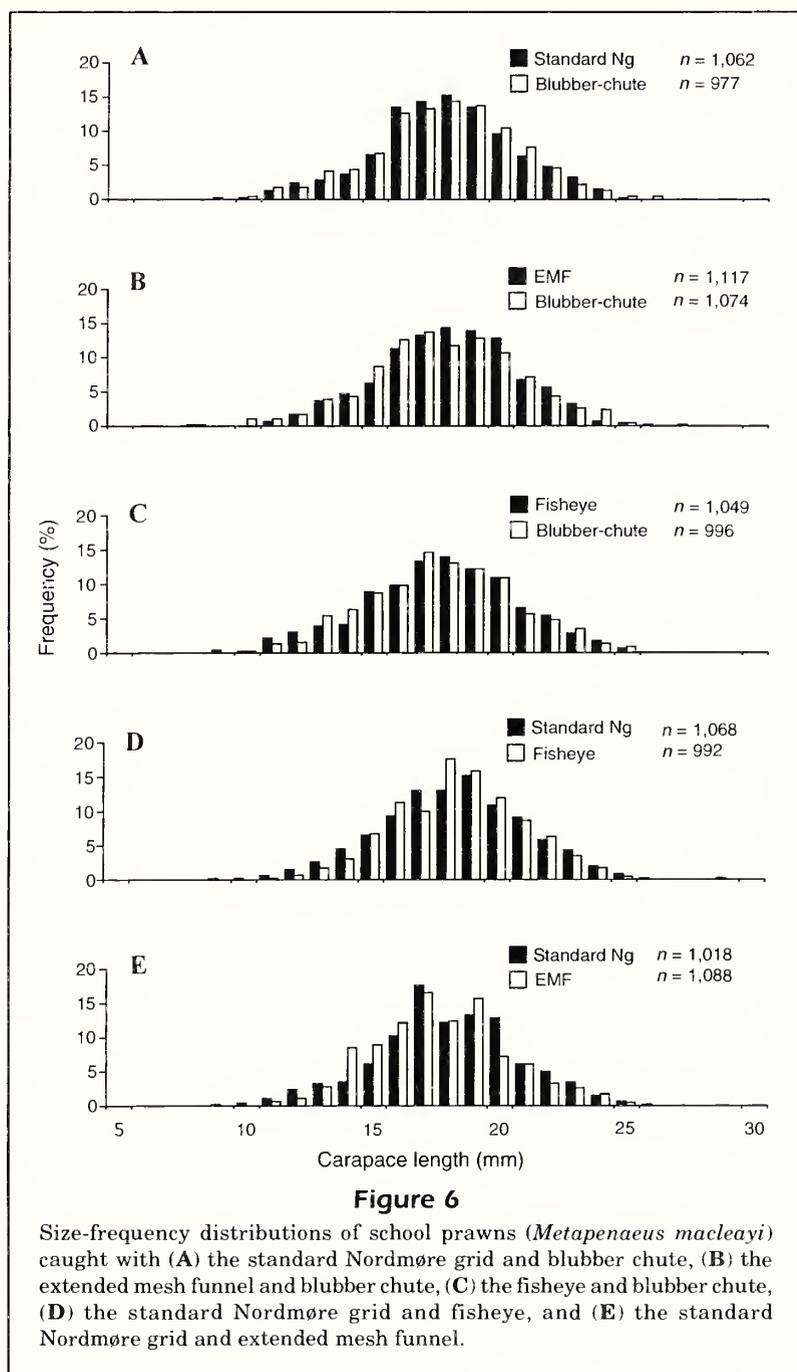
## Discussion

This study has confirmed the effectiveness of the Nordmøre grid in reducing bycatch while maximizing catches of prawns in NSW estuarine prawn-trawl fisheries (see also Broadhurst and Kennelly, 1996; Broadhurst et al., 1996). By comparing several secondary BRD's attached to a Nordmøre grid, we have also provided information on the relative effectiveness of these designs and their suitability in the HR prawn-trawl fishery.

The results from experiment 1 showed that apart from a significant reduction in the number of non-commercial species with the Allerio Brothers grid, compared with the square-mesh panel, there were no detectable differences in the relative performance of any of the secondary BRD's tested (Table 1).

Compared with the commercially used blubber chute, all three designs incorporating Nordmøre grids

in experiment 2 (the standard Nordmøre grid and the Nordmøre grid incorporating the EMF and fisheye) significantly increased the catches of prawns (by 24%, 41%, and 23%, respectively) while significantly reducing the total bycatch (by 58%, 45%, and 55%, respectively) (Fig. 5; Table 2). In earlier papers (Broadhurst and Kennelly, 1996; Broadhurst et al., 1996), we concluded that the prawn-retention characteristics of the Nordmøre grid were attributed to its ability to remove seaweed and debris more effectively. In the present study we observed that, at the end of each tow, those designs incorporating the Nordmøre grid were observed to be relatively free of seaweed and debris, whereas the blubber chute often had large quantities entangled between the meshes, which may have decreased the lateral openings between the meshes in the blubber chute and contributed towards the escape of prawns with this design. Further, because Kolmogorov-Smirnov tests



on the size-frequency compositions of school prawns failed to detect any difference between the standard Nordmøre grid and the blubber chute (Fig. 6A), such escapees were probably of all sizes. Another hypothesis to explain the loss of prawns from the blubber chute is that some prawns became entangled within the tentacles and large subumbrella of captured jelly fish and were directed, along with the jellyfish, out through the escape exit. In contrast, the long guiding panel and smooth contours of the Nordmøre grid

may have allowed the prawns to detach from the jellyfish and thus enabled them to pass into the codend.

Apart from a significant reduction in the numbers of bridle goby and noncommercial species caught by the EMF compared with the number caught by the standard Nordmøre grid in experiment 2, there were no other significant differences between the relative performance of the secondary BRD's and the standard Nordmøre grid (Fig. 5; Table 2). Given these results, therefore, it is likely that most of the fish

escaped at the standard Nordmøre grid. While the relatively small bar spacings (20 mm) may have been sufficient to exclude a large number of individuals simply because of their size, it is also possible that smaller fish were able to escape passively. For example, in a previous paper (Broadhurst et al., 1996) we provided evidence that some small bream (*Acanthopagrus australis*) detected the grid in advance (either visually or by means of their lateral lines). These fish may have then orientated away from the grid into an area of reduced water flow behind the guiding panel. The geometric attitude of the grid possibly directed some of these fish out of the codend without mechanical separation through the bars.

Whatever the mechanism of escape, we conclude that, given the effectiveness of the Nordmøre grid in excluding large quantities of bycatch, there appears to be little advantage in attaching secondary BRD's behind grids in the HR prawn-trawl fishery. Because of this, the additional labor and time involved in the manufacture, maintenance, and deployment of these secondary BRDs is clearly unwarranted.

Like several recent studies, this study has shown that there is great utility for the Nordmøre grid in many of NSW estuarine prawn-trawl fisheries. The increases in prawn catches and reductions in bycatch shown in our work in these fisheries have already led many commercial fishermen to use the standard Nordmøre grid in preference to the traditional blubber chute. Such independent and voluntary adoption of the Nordmøre grid by industry may eventually lead to further refinements in design and should facilitate widespread acceptance of this bycatch-reduction gear throughout most of NSW's estuarine prawn-trawl fisheries.

## Acknowledgments

This work was funded by the Australian Fishing Industry Research and Development Corporation (Grant No. 93/180). The authors are grateful to Gerry O'Doherty for his valuable expertise and for construction of the BRD's, Chris Hyde for the use of his vessel, the *Diane Mildred*, and Chris Paterson and Daniel Foster for providing technical support.

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**Abstract.**—Trawl surveys conducted at index sites off the northern Washington coast between 1968 and 1992 indicate that rockfish stocks respond to fishing over very small spatial scales. The abundance of Pacific ocean perch, rougheye rockfish, and total *Sebastes* (all species combined) remained roughly constant between 1968 and 1992, whereas catch rates in an experimental management area only 28 km to the north declined 76–91%, depending on species. Declines in the abundance of Pacific ocean perch in the index area appear to be less drastic than those reported for the U.S. Vancouver–Columbia management area during this same time period. Substantial differences in the abundance, species composition, and status of rockfish stocks can exist over relatively small spatial scales, a characteristic that must be carefully considered in their management. Pacific ocean perch off northern Washington appear to have matured considerably earlier (age 8) in 1992 than they did during 1968–72 (age 10), but growth rate did not change appreciably during the same period.

## Spatial patterns in the dynamics of slope rockfish stocks and their implications for management

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The rockfish assemblage along the Vancouver Island–Oregon continental slope is dominated by Pacific ocean perch (*Sebastes alutus*), rougheye rockfish (*Sebastes aleutianus*), darkblotched rockfish (*Sebastes crameri*), splitnose rockfish (*Sebastes diploproa*), and shortspine thornyhead (*Sebastes alascanus*) (Leaman and Stanley, 1993; Weinberg, 1994). It is typically assumed that these species undertake only limited migrations after they have recruited to the adult stock. Because these fish are difficult to tag successfully, this supposition is based primarily on observations of abundance and age composition over area and time. Parasite studies on Pacific ocean perch (Leaman and Kabata, 1987) also indicate that adult migrations are quite limited.

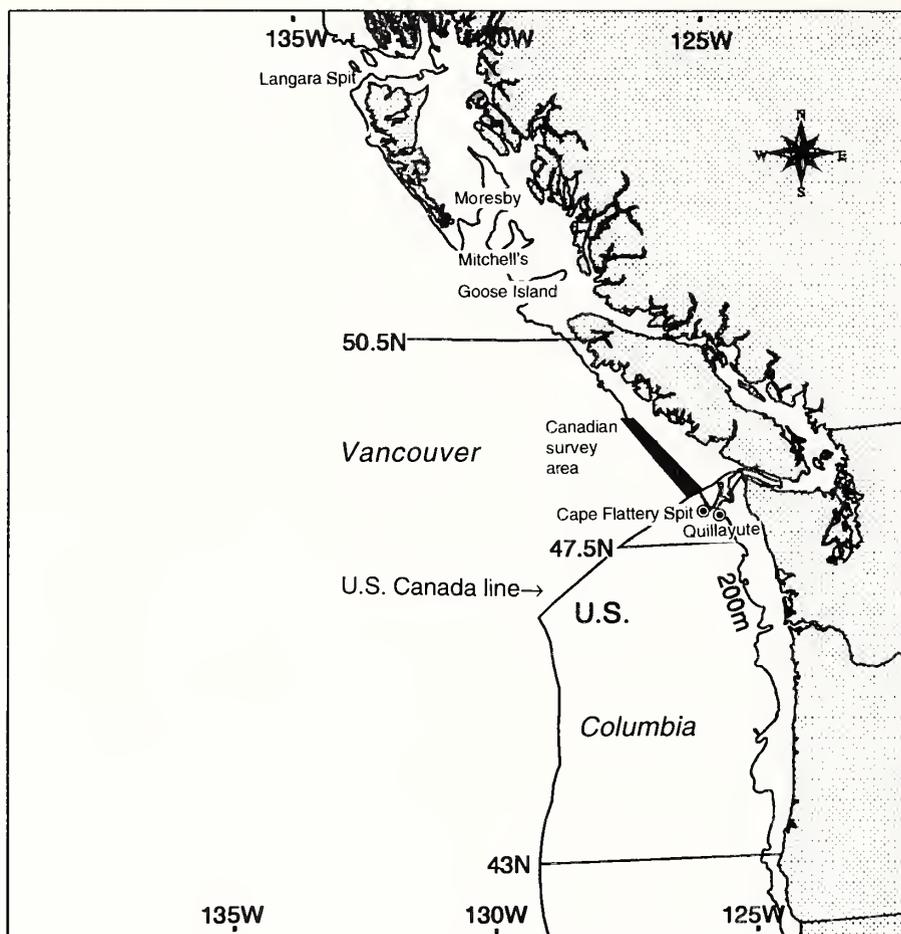
Pacific ocean perch stocks in the Washington–southern Vancouver Island area were heavily exploited by Soviet and Japanese fleets during 1966–68, effectively removing the 1951–53 year classes. Catch per hour in the Washington trawl fleet declined 61% between 1966 and 1968 (Gunderson, 1977). An experimental overfishing program was carried out in Canadian waters off Vancouver Island in 1980–84 (Leaman and Stanley, 1993), resulting in 76–91% reductions in the catch rates for the species dominating the slope rockfish complex in the Canadian trawl survey area (Fig. 1) between 1979 and 1985 (Table 1). That

portion of the survey area lying immediately north of the U.S.–Canada line experienced particularly intensive fishing during 1980–84 (Leaman<sup>1</sup>). From 1986 to 1992, annual slope rockfish catches in Canadian waters off southwest Vancouver Island (Richards, 1994) often exceeded those reported during the overfishing experiment, and it is unlikely that the abundance of these stocks increased during this period.

Exploitation rates for slope rockfish in the U.S. Fisheries Conservation Zone were much lower than those off Canada during 1980–92. Pacific Ocean perch are the dominant member of the slope rockfish community and have been managed under a stock rebuilding program in U.S. waters since 1981. This program has attempted to discourage directed Pacific ocean perch fishing and to restrict landings of Pacific ocean perch to levels that would allow incidental catches and yet allow the stock to rebuild over a 20-yr period. In 1994, for example, Pacific ocean perch landings could not exceed 3,000 lb (1,361 kg) per vessel-trip, or 20% of all fish on board, whichever was less, in Pacific ocean perch landings greater than 1,000 lb (454 kg).

<sup>1</sup> Leaman, B. M. 1995. Dep. Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, British Columbia, Canada V9R 5K6. Personal commun.

<sup>2</sup> Butler, J. L. 1995. Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038. Personal commun.



**Figure 1**

Locations of the northern Washington index sites (Cape Flattery Spit, Quillayute) and the Canadian survey area. Goose Island, Mitchell's, and Moresby Gullies, Langara Spit, and the Vancouver and Columbia management areas are also shown.

In effect, the differential exploitation rates in waters bordering the line separating the U.S. and Canadian Fisheries Conservation Zones (Fig. 1) constitute an unplanned experiment that allows an evaluation of the discreteness of local rockfish stocks and of the spatial impact of intensive removals. If any intermingling takes place between stocks immediately north and south of the U.S.-Canada line, the 1980-84 experimental overfishing program in Canadian waters would also have impacted U.S. stocks.

Two sites off the northern Washington coast, immediately south (28 km) of the experimental overfishing area (Fig. 1), were monitored intensively during 1968-70 (Gunderson, 1974). The principal objective of this study was to resurvey them in 1992 and evaluate the impact of intensive rockfish fishing in adjacent Canadian waters. The 1992 survey also provided an opportunity to see how well abundance trends in the index sites off northern Washington reflected overall changes in the abundance of Pacific

**Table 1**

Catch rates (kg/h) from 1979 and 1985 Canadian trawl surveys in the Vancouver Island experimental fishing area (Leaman and Stanley, 1993).

Species	1979 183-365 m depth	1985 160-439 m depth	Relative change in catch rate (%)
<i>S. alutus</i>	1,149.7	241.5	-78.9
<i>S. diploproa</i>	343.5	35.7	-89.6
<i>S. aleutianus</i>	93.7	8.8	-90.6
<i>S. crameri</i>	31.1	7.5	-75.8
Total <i>Sebastes</i>	1,917.2	378.1	-80.3

ocean perch in the U.S. Vancouver and Columbia management areas and to examine long-term changes in age composition, size at maturity, and growth at the index sites.

## Methods

The Washington State Department of Fisheries carried out a series of trawl surveys during 1968–70 aimed at monitoring the abundance and age composition of Pacific ocean perch stocks. A 400-mesh eastern otter trawl (28.7-m footrope) of uniform 3.5-inch (8.9-cm) mesh and with a 1.5-inch (3.8-cm) codend liner was used, with roller gear attached to the footrope in the manner shown in Gunderson (1969). The net was fished with 1.5 m × 2.1 m steel “vee” doors, 18.3-m bridles, and 27.5-m sweepnet lines. The 20.4-m research vessel *Commando* was used during each survey, which comprised a sampling design of two index sites (Fig. 1) and three depths (219 m, 293 m, and 366 m) at each site. Four 45-min hauls were made at each of these site-depth strata, and an attempt was made to make each haul during a different part of the day (morning, mid-morning, afternoon, or evening). A total of 24 hauls were planned during each cruise, although this target was exceeded in 1969 (Table 2). The trawl, bridles, sweepnet lines, and doors used in the 1992 survey were nearly identical to those used in the 1968–70 surveys although there were minor differences in the roller gear and in the mesh sizes used in the net (4 inch; 10.2 cm) and codend liner (1.25 inch; 3.2 cm). However, the 30.5-m research vessel *Alaska* was used during 1992, and comparisons of the distance covered during each 45-min haul showed that the average distance traveled by the *Alaska* was 11% greater than that covered by the *Commando*. Effort data for the 1992 survey were consequently adjusted upward by this amount.

Sampling design and gear deployment in 1992 were similar to the 1968–70 protocol although it was not possible to complete the 24 hauls planned in the time allotted (Table 2). The trawl was monitored during fishing operations with a SCANMAR acoustic monitoring system, and the mean horizontal spread (between wingtips) was 13.9 m and the vertical opening was 3.0 m.

**Table 2**

Cruise dates and number of hauls at each depth for surveys of the northern Washington index sites, 1968–92.

Cruise dates	No. of hauls		
	219 m	293 m	366 m
17 July–28 July 1968	8	8	8
1 July–10 July 1969	9	10	9
27 Sep–4 Oct 1970	8	8	8
7 Oct–10 Oct 1992	7	7	7

An index of abundance for each survey was estimated by weighting each of the six site-depth strata separately (Eq. 5.1, Cochran, 1977):

$$\bar{y}_{st} = \sum_{h=1}^L W_h \bar{y}_h,$$

where  $\bar{y}_{st}$  = mean catch rate (kg/h);  
 $W_h$  = stratum weight (=1/6 for all strata);  
 $\bar{y}_h$  = sample mean (kg/h) for stratum  $h$ ; and  
 $L$  = number of strata (6).

The variance of this index was estimated by using Equation 5.7 of Cochran (1977):

$$V(\bar{y}_{st}) = \sum_{h=1}^L W_h^2 s_h^2 / n_h,$$

where  $s_h^2 = \frac{1}{n_h - 1} \sum_{i=1}^{n_h} (y_{hi} - \bar{y}_h)^2$ ;

$n_h$  = number of hauls in site-depth stratum  $h$ ; and

$y_{hi}$  = catch rate (kg/h) for haul  $i$ .

All rockfish were sorted and weighed by species during the surveys, and all other species were also sorted and weighed in 1992. Sex and length data were obtained for each catch of Pacific ocean perch. For large catches, sex and length data were obtained by sampling an equal portion of the first, middle, and last part of the sorted catch (Westrheim, 1967). All fish were measured to the nearest cm (FL), and otoliths were extracted from random subsamples of the length-sex samples at each depth (Table 3). Ages were determined during 1968–70 by using surface readings of the otoliths, whereas broken and burned cross sections were used in 1992. Because comparative ageing experiments have shown that surface ages are biased for fish older than 17 (Tagart, 1984), all surface-aged fish older than this were pooled. Age-length keys were used to estimate age composition from length data, and separate keys were constructed for each cruise depth-sex stratum. Within a given stratum, size composition data for each haul were weighted by the catch per hour (catch per nmi in 1992) prior to combining them.

The age-length relation for Pacific ocean perch varies with depth so that there is an inverse relation between depth and apparent growth rate (Westrheim, 1973; Gunderson, 1974). As a result, separate curves were fitted for the age-length data at each depth by using a nonlinear least-squares algorithm (EXCEL) to fit the data to the Bertalanffy growth model:

Table 3

Number of Pacific ocean perch sampled for length, sex, and otoliths during surveys of the northern Washington index sites, 1968–92.

	Depth (m)	Length and sex	Otoliths
1968	219	1,316	486
	293	868	392
	366	800	241
	Total	2,984	1,119
1969	219	592	584
	293	2,016	1,518
	366	1,837	1,258
	Total	4,445	3,360
1970	219	1,663	1,120
	293	1,761	1,144
	366	589	564
	Total	4,013	2,828
1992	219	1,432	355
	293	1,366	412
	366	453	391
	Total	3,251	1,158

$$l_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where  $l_t$  = fork length (cm) at age  $t$  years;  
 $L_\infty$  = theoretical asymptotic length;  
 $K$  = constant expressing rate of approach to  $L_\infty$ ; and  
 $t_0$  = theoretical age at which  $l_t = 0$ .

A total of 453 Pacific ocean perch females were classified as to state of maturity during the 1992 survey, following the criteria described in Gunderson (1977). Maturity observations were obtained from all index site-depth strata, and emphasis was placed on obtaining as many observations as possible from fish less than 38 cm, the size at which the transition from juvenile to adult occurs. A maximum-likelihood algorithm (SYSTAT) was used to fit these data to the logistic model:

$$P_l = \frac{1}{1 + e^{-(\alpha + \beta l)}},$$

where  $P_l$  = proportion mature at length  $l$  (cm);  
 $\alpha, \beta$  = constants; and

$$\frac{-\alpha}{\beta} = l_{0.5} = \text{length at which 50\% of the females are mature.}$$

The variance of  $-\alpha/\beta$  was estimated with the delta method (Gunderson, 1977), and the variance estimates for  $\alpha$  and  $\beta$  were provided by SYSTAT.

## Results

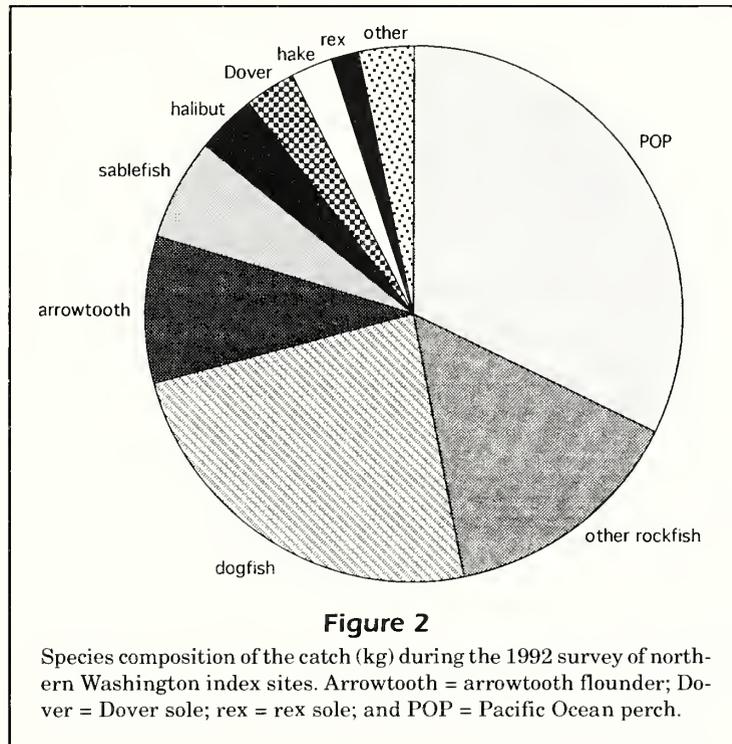
Rockfish dominated the catches in the northern Washington index sites during the 1992 survey (Table 4; Fig. 2), and Pacific ocean perch was the most abundant species present. In contrast to the sharp reductions in rockfish abundance in the Canadian portion of the Vancouver area (Table 1), catch rates for rockfish in the northern Washington index sites (Table 4) indicated little change in abundance between 1968 and 1992. Overlapping approximate 95% confidence intervals ( $\pm 2\text{SE}$ ) indicated nonsignificant interannual differences in the catch rates for most species, including Pacific ocean perch and rougheye rockfish, the two most abundant species of rockfish (Fig. 3A). Both of these mature relatively late in life and are quite long-lived. The median age at maturity ( $t_{0.50}$ ) for females is about 10 years for Pacific ocean perch (Gunderson, 1977) and about 20 years for rougheye rockfish (McDermott, 1994). Pacific ocean perch can live to be 90, rougheye rockfish to 140 years (Chilton and Beamish, 1982). As a result, reductions in abundance would be expected to be sharp and of long duration if stocks off northern Washington had experienced the same level of fishing as that observed off Canada (Table 1). One species, shortspine thornyhead, actually showed a statistically significant increase in abundance over the period covered by the surveys (Fig. 3B) despite the fact that this species appears to be long-lived (otolith counts indicate that some individuals live at least 100 years; Butler<sup>2</sup>).

Comparison of trends in abundance within the index sites and within the U.S. Vancouver–Columbia area as a whole (as estimated by Stock Synthesis analysis, Ianelli et al.,<sup>3</sup>) are also possible in the case of Pacific ocean perch (Fig. 4). This comparison suggests that the abundance of Pacific ocean perch at the index sites remained at comparable levels between 1968 and 1992, at a time when most stocks in the Vancouver–Columbia area continued to decline from 1962 levels.

Nevertheless, stocks within the index area showed evidence of significant fishing during 1970–92 because the strong 1961 year class present during 1968–70 (Fig. 5) was no longer apparent (as 31-year-olds) in 1992 (Fig. 6). In a lightly exploited stock of

<sup>2</sup> Butler, J. L. 1995. Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038. Personal commun.

<sup>3</sup> Ianelli, J. N., D. H. Ito, and M. E. Wilkins. 1995. Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1995. App. B in Status of the Pacific coast groundfish fishery through 1995, and recommended acceptable biological catches for 1996. Pacific Manage. Council, Portland, OR, 39 p.

**Table 4**

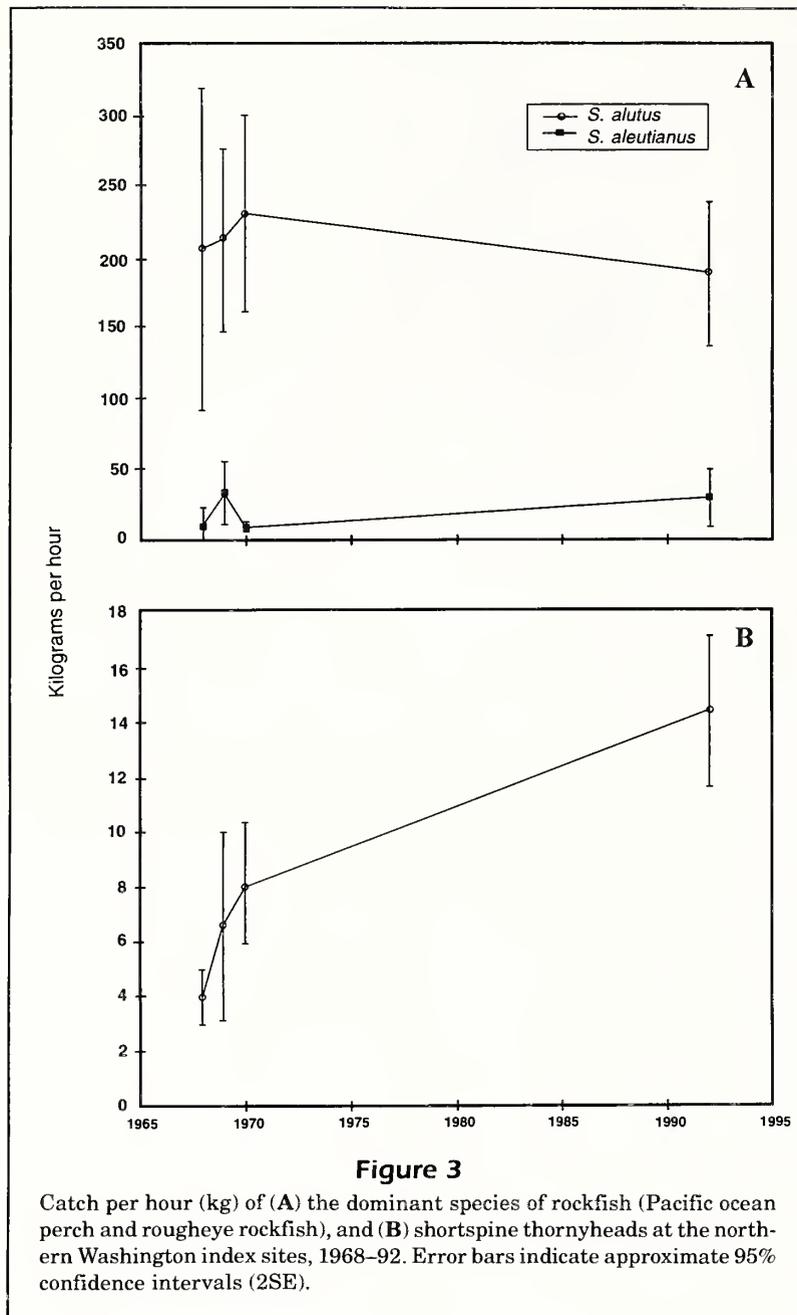
Mean catch rates (kg/h) and their standard error (SE) for surveys of the northern Washington index sites, 1968–92.

	1968		1969		1970		1992	
	kg/h	SE	kg/h	SE	kg/h	SE	kg/h	SE
<i>S. alutus</i>	205.3	56.8	211.6	32.6	230.0	34.8	186.9	25.4
<i>S. aleutianus</i>	9.5	6.6	32.8	11.1	9.0	1.6	28.9	10.1
<i>S. diploproa</i>	19.9	5.9	15.7	4.6	9.8	2.0	16.6	6.7
<i>S. crameri</i>	4.8	0.9	12.6	2.7	13.3	3.2	6.7	1.6
Total <i>Sebastes</i>	247.0	59.7	348.5	65.2	276.7	37.0	257.5	35.6
<i>S. alascanus</i>	4.0	0.5	6.6	1.7	8.1	1.1	14.4	1.4
Total catch							592.5	68.0

Pacific ocean perch in Moresby Gully, Leaman (1991) found that the 1952 year class still dominated survey catches as 30-year-olds in 1982 (Fig. 6). A comparison of the 1992 age composition in the northern Washington index area with that of lightly (Moresby Gully) and heavily (Langara Spit) exploited stocks off British Columbia (Fig. 6) suggests that Pacific ocean perch stocks in the index areas still showed signs of heavy exploitation. Although the catch curve for the index area does not show the truncation at age 40 that characterized the heavily exploited Langara Spit stock, stocks in this area can hardly be classified as lightly exploited. The size composition of stocks at the index sites (Fig. 7) reflects little of

the rather substantial interannual changes in age composition seen in Figure 5. This is due to the uninformative nature of the length data in relation to age composition, characteristic of slow-growing fish in general.

Mean length at age declined with depth (Fig. 8), a phenomenon previously reported in a number of studies (Westrheim, 1973; Gunderson, 1974). The results are summarized in terms of predicted length at age 15 with the Bertalanffy growth model, following Gunderson (1974). Age 15 was taken as the reference age because this was generally the oldest age group for which age-length data were available from all sampling depths and reflects the accumulated



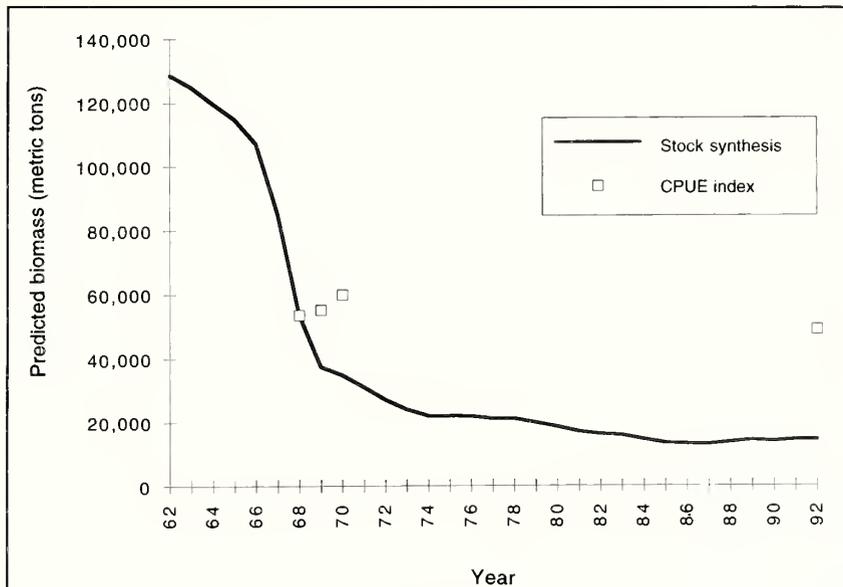
differences in annual growth in all ages younger than 15. The magnitude of interannual differences in size at age 15 for a given depth and sex were relatively minor (Fig. 8), particularly when differences in age determination technique are considered.

The length-maturity curve for 1992 (Fig. 9) indicates a significant shift toward maturation at a smaller length than was the case in 1968–72 (Table 5; Fig. 9). Both a Z-test (Table 5) and logistic regression analysis (SPSS) showed that the year effect was highly significant ( $P < 0.001$ ) statistically. Age at 50% maturity, as predicted from the Bertalanffy growth

model presented in Gunderson (1977, Table 3) decreased from 10.1 to 8.1 years over this same period.

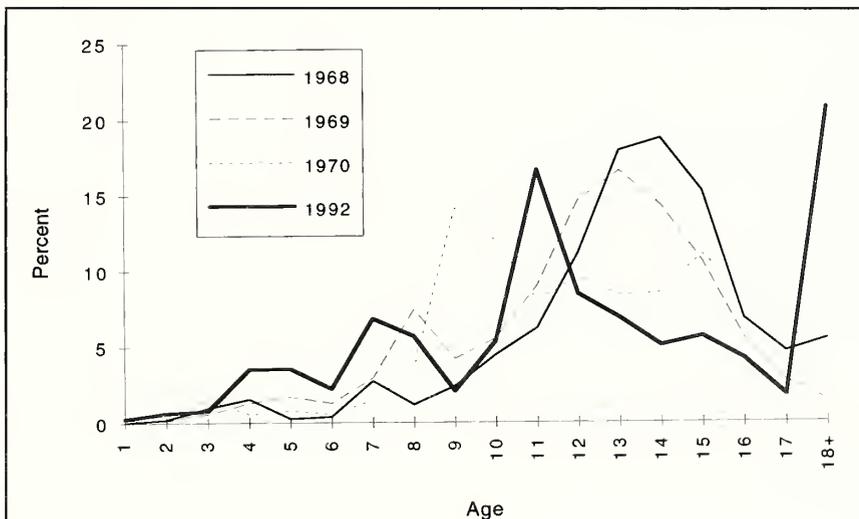
## Discussion

Although members of the genus *Sebastes* are viviparous and retain their larvae for varying periods prior to releasing them, the larvae can still be transported considerable distances during their 3–6 month pelagic phase, resulting in broad spatial synchrony in recruitment trends (Ralston and Howard, 1995). In



**Figure 4**

Estimated biomass (t) of Pacific ocean perch in the U.S. Vancouver–Columbia management area based on Stock Synthesis analysis (Ianelli et al.<sup>3</sup>) and extrapolated CPUE (1968 CPUE =  $q \times$  1968 Stock Synthesis biomass, where  $q$  is the catchability coefficient) at the northern Washington index sites for the years 1968–92.



**Figure 5**

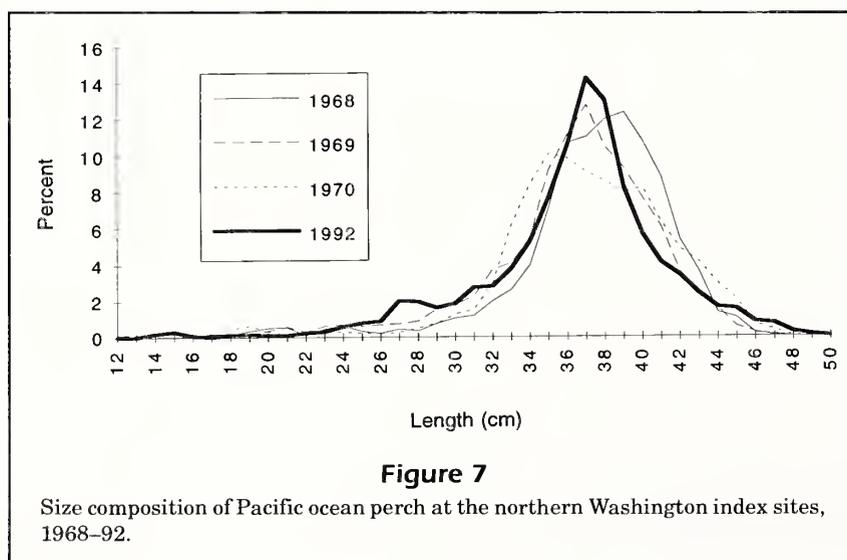
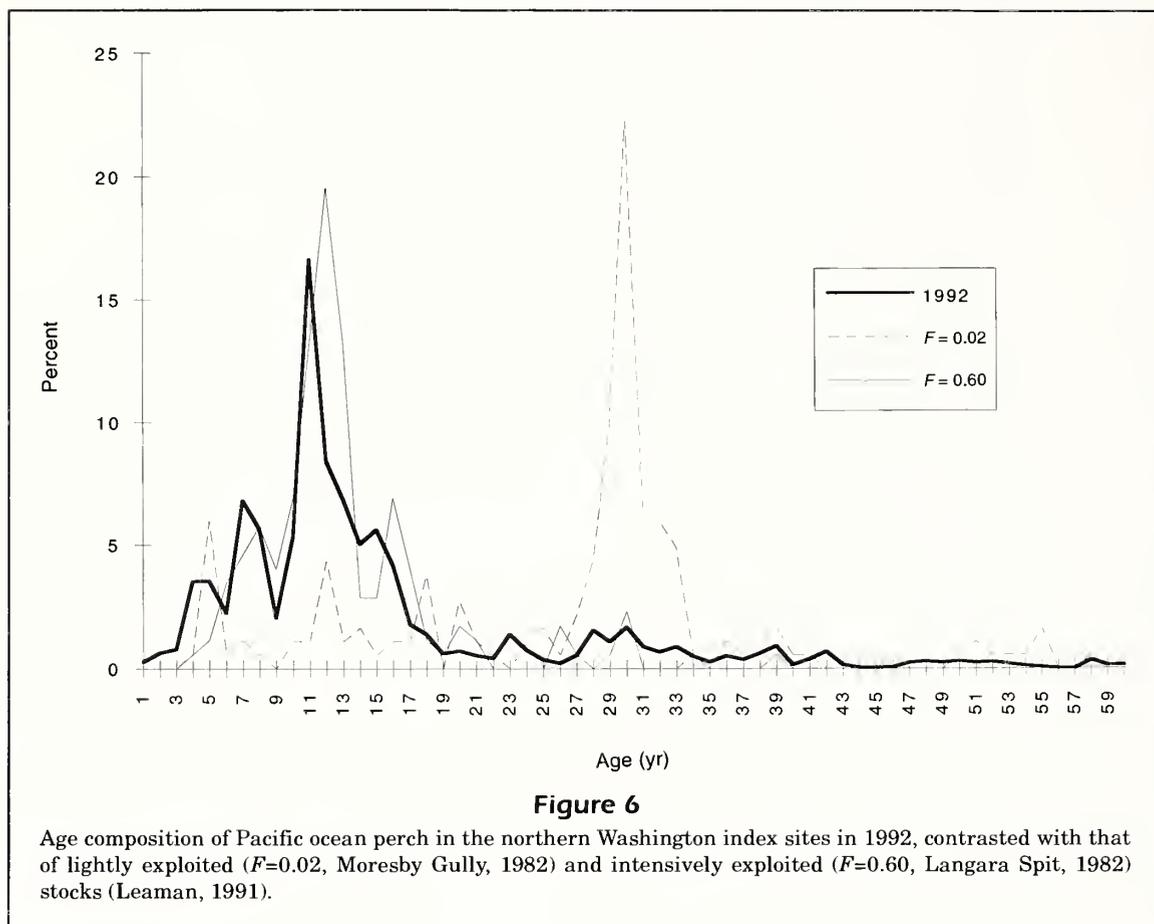
Age composition of Pacific ocean perch in the northern Washington index sites, 1968–92.

the case of Pacific ocean perch, allozyme differences follow a cline from the Washington coast to the Bering Sea rather than show discrete differences between stocks (Seeb and Gunderson, 1988). Strong year classes of Pacific ocean perch tend to occur synchro-

nously throughout the Oregon–British Columbia region (Gunderson, 1977; Hollowed, et al., 1987), indicating recruitment strength is determined by oceanographic conditions operating over broad spatial scales.

However, migrations of adult Pacific ocean perch appear to be quite limited. For example, Westrheim et al. (1974), documented a virtually unexploited stock of Pacific ocean perch in Moresby Gully, B.C.,

located immediately north of heavily fished stocks in Mitchell's Gully, also within Queen Charlotte Sound (Fig. 1). Pacific ocean perch habitat in Moresby Gully is contiguous with that of Mitchell's Gully at



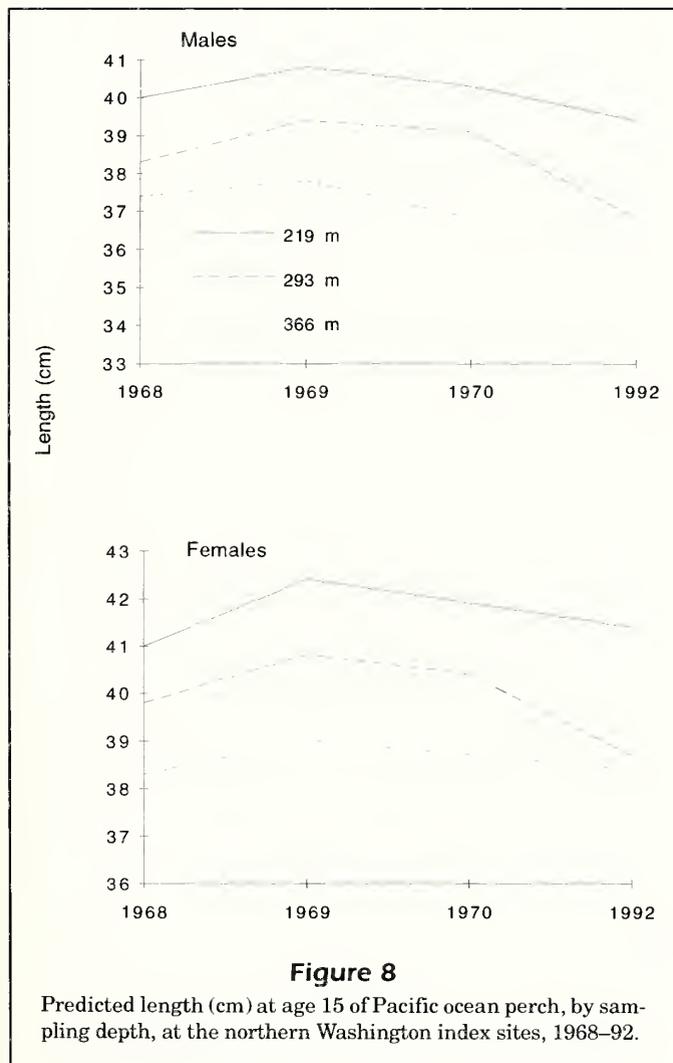
the shallower extremes, and the 200-m contours are separated by only about 30 km. Nevertheless, the size and age composition in these two areas differed sharply (Gunderson et al., 1977). The composition of the parasite fauna on adult Pacific ocean perch in Moresby Gully has also been shown to differ significantly from that found on adult ocean perch in Goose Island Gully (immediately south of Mitchell's) (Leaman and Kabata, 1987). It seems clear that, whereas spawner-recruit processes probably operate over broad geographic scales, adult migrations are limited, and changes in abundance and age composition for this species in response to fishing are highly localized.

The results of this study indicate that responses to fishing also occur over very small spatial scales off Oregon–southern Vancouver Island as well as in Queen Charlotte Sound, and that this is true for rougheye, splitnose, and darkblotched rockfish as well as for Pacific ocean perch. The index areas off

the northern Washington coast were only 28 km south of the Canadian experimental overfishing zone (Fig. 1), yet rockfish stocks in this area appear to have experienced little change in abundance between 1968 and 1992. Shortspine thornyhead abundance within the 219–366 m depth interval actually increased between 1968 and 1972, although these fish represent only the shallowest part of the range and the younger age groups in a stock that can extend to depths greater than 1,100 m (Ianelli et al.<sup>4</sup>).

Although the rockfish assemblage in the northern Washington index sites was not depleted to the same extent as its counterpart in Canadian waters during 1970–92, it is far from being at pristine abundance. The effects of the overfishing during 1966–68 are still evident because the abundance of fish older than age 15 is still much lower than that characteristic of lightly exploited stocks (Fig. 6). Pacific ocean perch stocks in the index areas appear to have undergone significant exploitation between 1970 and 1992 but have not declined to the same extent as those in Canadian waters to the north (Tables 1 and 4) or in U.S. waters to the south (Fig. 4).

The size and age at maturity for Pacific ocean perch in the northern Washington index areas appear to have declined significantly between 1968 and 1972 (Gunderson, 1977) and 1992. Length at 50% maturity declined from 34.4 cm to 31.6 cm (Table 5), whereas age at 50% maturity declined from 10.1 years to 8.1 years. This shift in size and age at maturation should be viewed with some caution, however, because most adult fish examined in 1992 were still in the "maturing" stage. Only one of the 382 adults examined was in a more advanced



<sup>4</sup> Ianelli, J. N., R. Lauth, and L. D. Jacobson. 1994. Status of the thornyhead (*Sebastolobus* sp.) resource in 1994. App. D in Status of the Pacific coast groundfish fishery through 1994, and recommended acceptable biological catches for 1995. Pacific Manage. Council, Portland, OR, 58 p.

**Table 5**

Estimated length and age at maturity for female Pacific ocean perch off the northern Washington coast, 1968–72 versus 1992.

	1968–1972	1992
$\alpha$	-29.0258	-20.3196
$\beta$	0.8439	0.6428
$l_{0.5}$ (cm)	34.40	31.61
Var ( $l_{0.5}$ )	0.0437	0.1498
Z-statistic <sup>1</sup>		6.33
$t_{0.50}$ (years) <sup>1</sup>	10.1	8.1

<sup>1</sup> See Gunderson (1977).

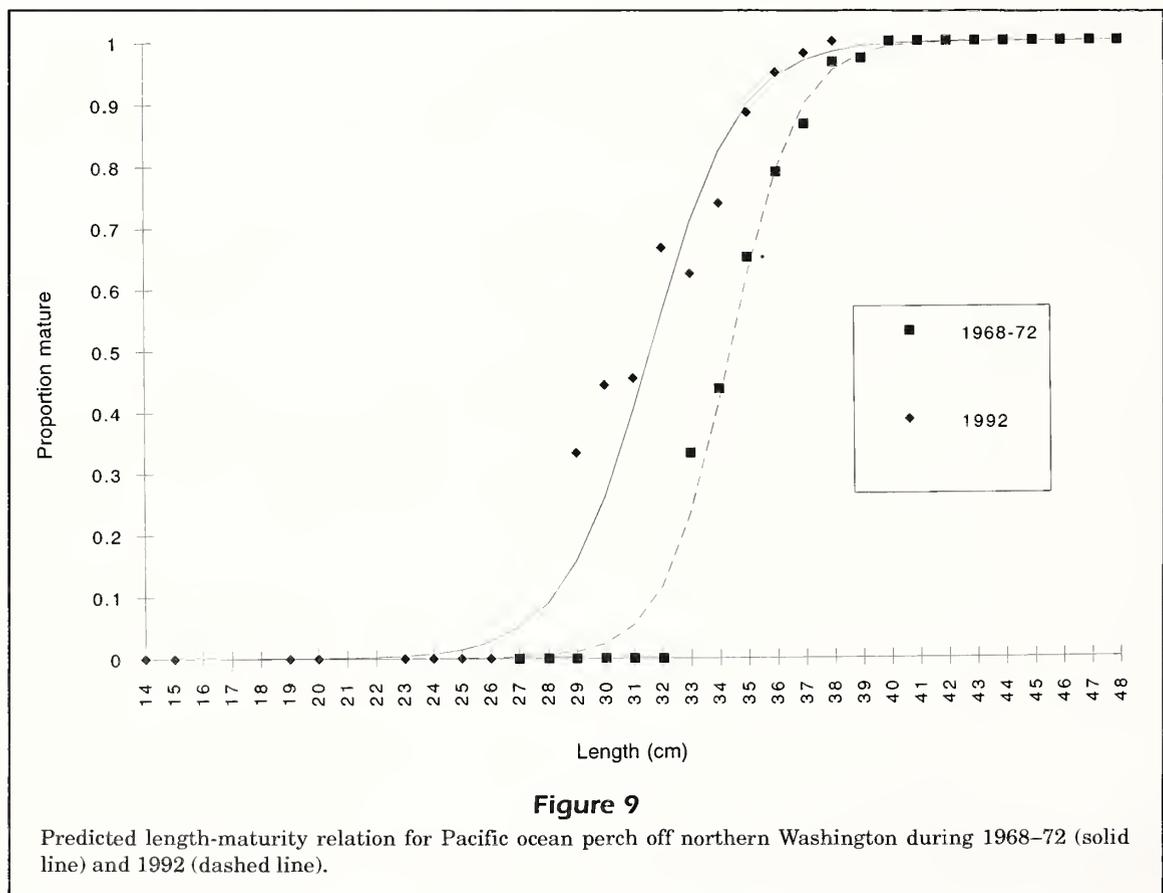
maturation stage, i.e. "fertilized." In contrast, the fish used in constructing the length-maturity curve for 1968–72 were collected during February–June, when Pacific ocean perch are closer to the embryo-release period.

Nevertheless, it appears that after 20 years in a depleted state, the stocks of Pacific ocean perch off Washington have partially compensated for a loss in reproductive potential by reducing their age at maturity from 10 years to 8. Comprehensive studies have shown long-term declines in age at maturity from 10.5 years (1923) to 8 years (1976) in a heavily fished stock of Northeast Arctic cod (Jørgensen, 1990), and from 5–7 years (early 1900's) to 4–5 years in North Sea plaice (Rijnsdorp, 1989). Although a genetic basis for such changes has been documented in some species (Policansky, 1993), disentangling genetic changes and phenotypic plasticity is often difficult. Given the long generation time of Pacific ocean perch and the relatively short time span involved, these changes probably reflect reaction norms of phenotypic plasticity rather than changes in genotype.

In contrast, growth, as reflected in size attained at age 15, showed no substantial changes between 1968–70 and 1992. Although monitoring length-age

relationships at fixed bathymetric locations allows the depth effect to be controlled for, it is difficult to maintain the sampling depth within a range of less than about 18 m with trawls on the continental slope. Aggregations of Pacific ocean perch often have different growth characteristics and vary interannually in their availability (Gunderson, 1974), and further sources of bias and variability are inherent in using different age-determination techniques. All of these factors make it difficult to detect changes in growth rates unless they are substantial. Nevertheless it should be kept in mind that interannual variations in food availability can often be more influential than changes in population density in determining growth rates (Rijnsdorp et al., 1991; Rijnsdorp and van Leeuwen, 1992).

Most adult rockfish in the Oregon–Vancouver Island region probably migrate to a very limited extent, and stocks within these regions represent a mosaic of small, highly localized stocks. Nevertheless, practical considerations in terms of data collection, data assessment, and management enforcement often force the geographic scale of fishery management to be relatively broad. For example, although the Pacific Fishery Management Council has at-



tempted to eliminate directed fishing on Pacific ocean perch in the U.S. Vancouver–Columbia management area, fishermen have been observed fishing for this species in the northern Washington index areas, where Pacific ocean perch and other rockfish are the most abundant fish in catches (Fig. 2). Only distance and time act as disincentives for fishermen, who have yet to achieve their “incidental” allotment of Pacific ocean perch, from moving to areas such as these to “top off” their catch. It is not surprising then that stocks in the index area have failed to rebuild as the Council had hoped. While often ignored in management considerations owing to a lack of information, other species in the slope rockfish assemblage (notably rougheye and splitnose rockfish) have probably experienced the same pattern of overfishing as Pacific ocean perch and should be considered when contemplating future rebuilding plans.

One possible solution to many of the problems that currently exist in managing slope rockfish stocks is to delineate areas such as the index sites, where rockfish dominate the exploitable fish biomass (Fig. 2), and to eliminate all fishing within them. A variety of questions remain as to the optimal size and spatial dispersion of such closed areas (or “refugia”), as well as the enforcement problems associated with maintaining them, but it seems clear that if managers cannot rebuild rockfish stocks in areas of prime habitat, it is unlikely that they will be able to rebuild them over broader scales.

## Acknowledgments

This research was supported in part by grants from the U.S. National Marine Fisheries Service and Washington Sea Grant. Assistance by the scientists and staff at the NMFS Alaska Fisheries Science Center in constructing the trawl gear, implementing the 1992 survey, and ageing the otoliths collected is gratefully acknowledged. I also thank Dan Ito and Bruce Leaman for their comments on an earlier draft of this paper.

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**Abstract.**—Differences in fecundity and egg weight were evaluated in English sole, *Pleuronectes vetulus*, from four sites in Puget Sound (the Duwamish Waterway, Eagle Harbor, Sinclair Inlet, and Port Susan) with differing concentrations and types of sediment contamination. Duwamish Waterway sediment has high concentrations of both polychlorinated biphenyls (PCB's) and polycyclic aromatic hydrocarbons (PAH's), Eagle Harbor sediment has high concentrations of PAH's, and Sinclair Inlet sediment has low concentrations of PAH's and moderate concentrations of PCB's, whereas sediments at Port Susan, the reference site, are minimally contaminated. Fish from the Duwamish Waterway and Eagle Harbor had significantly higher levels of fluorescent aromatic compounds (FAC's) in bile than sole from Port Susan and Sinclair Inlet, and fish from the Duwamish Waterway had significantly higher concentrations of PCB's in ovary and liver tissue than fish from the other sampling sites. Fecundity and egg weight were compared in fish of equivalent size, age, and reproductive maturity from the four sites; fish from the Duwamish Waterway showed significantly higher relative fecundity and lower egg weight than fish collected from the three other sites. Production of more and smaller eggs in fish from the Duwamish Waterway site was associated with elevated hepatosomatic indices, elevated plasma triglyceride levels, and elevated levels of PCB's in liver and ovarian tissue, and reduced plasma vitellogenin levels (as estimated from alkali-labile protein (ALP) concentrations). Fish from the Duwamish Waterway and Sinclair Inlet also had higher age-specific fecundity than animals from other sites because of their larger size at age. On an individual fish basis, elevated tissue PCB concentrations were significantly correlated with low plasma ALP, reduced egg weight, and increased egg number, whereas elevated biliary FAC's were associated with increased ovarian atresia, increased egg weight, and reduced egg number. The results of this study suggest that English sole exposed to chemical contaminants may experience alterations in egg development; however, nutritional or other environmental factors may also contribute to the observed intersite differences in egg weight and fecundity.

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## Fecundity and egg weight in English sole, *Pleuronectes vetulus*, from Puget Sound, Washington: influence of nutritional status and chemical contaminants

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Reproductive impairment is potentially one of the most damaging effects of aquatic pollution on marine fish and shellfish because of its impact on population growth and consequently on the abundance of marine resources (Hose and Guillette, 1995; Grosse et al., in press). Environmental contaminants exert their effects on reproductive function through a variety of mechanisms: they may have direct toxic effects on germ-cell tissue or may disrupt the endocrine mechanisms that regulate reproduction and early development, causing inhibited or abnormal gonadal development or reduced fertility (Donaldson, 1990; Colburn et al., 1993; Kime, 1995).

Sediments from several areas of Puget Sound, Washington, are polluted with xenobiotic compounds such as polychlorinated biphenyls (PCB's), and polycyclic aromatic hydrocarbons (PAH's) (Malins et al., 1984, 1985; PSWQA<sup>1</sup>). These compounds are known or suspected disruptors of endocrine function (Colburn et al., 1993) and, as such, pose a potential threat to the reproduc-

tive health of marine fish that reside in these areas. In previous studies, we examined the effects of these contaminants on several aspects of reproductive function in English sole, *Pleuronectes vetulus*, a commercially important bottom-fish species that is widely distributed in Puget Sound (Johnson et al., 1988, 1993; Casillas et al., 1991; Collier et al., 1992). These investigations revealed that sole from two heavily polluted sites, Eagle Harbor and the Duwamish Waterway, exhibited various types of reproductive dysfunction, including inhibited gonadal development (Johnson et al., 1988), depressed plasma estradiol levels and reduced ovarian estradiol production in vitro (Johnson et al., 1988, 1993), and reduced spawning success (Casillas et al., 1991). In contrast, fish from Port Susan and Sinclair Inlet, two sites

<sup>1</sup> PSWQA (Puget Sound Water Quality Authority). 1994. Puget Sound update: fifth annual report of the Puget Sound ambient monitoring program. Puget Sound Water Quality Authority, Seattle, WA, 122 p.

with low to moderate levels of sediment contamination (Malins et al., 1984), showed little evidence of reproductive dysfunction. Although the causative agents were not definitively identified, aromatic and chlorinated hydrocarbons present in sediments at the Duwamish Waterway and Eagle Harbor sites were shown to be significant risk factors for the development of these reproductive abnormalities (Johnson et al., 1988; Casillas et al., 1991). The present study extends our previous work by examining egg weight and fecundity in English sole from the same four sites in Puget Sound.

Fecundity and egg size are important determinants of reproductive output in fish (Bagenel, 1973). Fecundity provides a measure of the potential number of offspring a female can produce, whereas egg size is an indicator of the nutritional reserves available to developing embryos and may strongly influence the growth and survival of larval fish (Blaxter and Hempel, 1963; Miller et al., 1988). Both egg size and fecundity vary considerably among stocks, species, and individuals. However, in most marine teleosts, fecundity within a stock or species is highly correlated with fish size or weight. Egg size is generally more constant but may vary with factors such as fish age or spawning time or with genetic, nutritional, or environmental factors (Hempel and Blaxter, 1967; Bagenel, 1971; Gall, 1974; Zastrow et al., 1989; Zamaro, 1992).

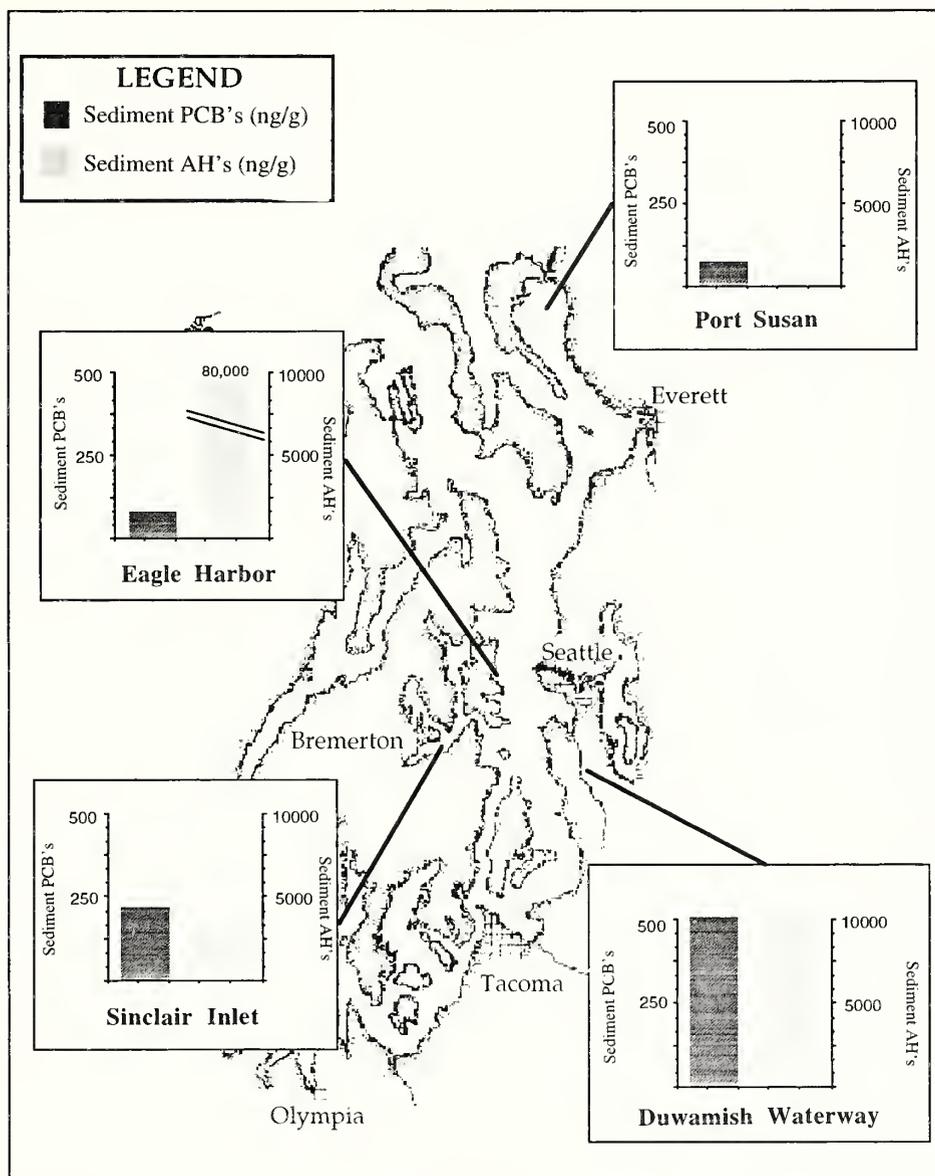
Teleost fish may have either determinate fecundity, in which egg production is set before the spawning season, or indeterminate fecundity, in which egg production can be increased, by recruiting additional oocytes into vitellogenesis during gonadal development, or reduced through atresia (Hunter and Macewicz, 1985a). In Puget Sound English sole populations, potential fecundity appears to be determined several months before the spawning season because these fish recruit a single clutch of oocytes in late summer or early fall and no additional oocytes enter vitellogenesis prior to spawning in February or March (Johnson et al., 1991). However, the extent to which fecundity declines as a result of atresia of developing oocytes is unclear.

In most fish species, both egg size and fecundity can be influenced by environmental conditions such as water temperature, salinity, and food supply. In herring (*Clupea* sp.), for example, water temperature 60 to 90 days before spawning may be critical in determining the balance between egg size and number. Unusually warm temperature leads to high fecundity and smaller eggs (Tanasichuk and Ware, 1987). Other stressors, such as handling or crowding, may also be associated with alterations in egg size and number; typically, stressed animals produce

more and smaller eggs than do controls (Contreras-Sanchez et al., 1995; Short et al., 1995).

Field and laboratory studies have demonstrated that fish exposed to certain chemical contaminants exhibit alterations in both egg size and fecundity. Contaminant-associated declines in egg size, fecundity, or in both, have been noted in several marine fish species collected from urban embayments, including white croaker and kelp bass from the Los Angeles area (Hose et al., 1989), striped bass from San Francisco Bay (Setzler-Hamilton et al., 1988), and winter flounder from Boston Harbor and Long Island Sound (Nelson et al., 1991; Johnson et al., 1994). Similarly, white sucker exposed to pulp mill effluent in a contaminated lake of Ontario, Canada, showed a decrease in egg size and fecundity (McMaster et al., 1991). Reductions in egg size and fecundity have also been observed in a number of other fish species in conjunction with controlled exposure to chlorinated and aromatic hydrocarbons and to other organic pollutants (reviewed in Kime, 1995). These compounds may have direct toxic effects on oocytes and supporting cells (Armstrong, 1986), or alternatively, may disrupt normal hormonal regulation of gonadal growth (Donaldson, 1990; Thomas, 1990).

Egg production is strongly influenced by the nutritional status of fish; if this status is extremely poor, animals may not reproduce at all (e.g. Burton and Idler, 1987), or fecundity may be reduced (Penzak, 1985; Springate et al., 1985; Chappaz et al. 1987; Rozas and Odum, 1988). Studies also suggest that egg size and number may change seasonally or as environmental conditions vary, thus maximizing the larvae's probability of survival as food availability changes (Buckley et al., 1991). Interactive effects of toxicant exposure and nutrition may also occur. For example, toxicants may influence reproductive output indirectly, by reducing food quality, food abundance, or the ability of animals to digest food or to forage effectively. In some studies where fish were exposed to oil or other organic compounds, declines in fecundity were associated with reduced food intake and weight loss; thus the contaminants were likely affecting reproductive success by reducing the animal's condition (e.g. Ghatak and Konar, 1991). In order to account, more precisely, for possible effects of nutritional status on egg weight and fecundity in English sole from contaminated Puget Sound sites, we measured several indicators of nutritional status (i.e. condition, plasma glucose and triglyceride levels, and hepatosomatic index [HSI]) in sampled fish, as well as parameters associated with reproductive development and contaminant exposure. Our objective in this paper is to describe age and size-specific



**Figure 1**

Chart of Puget Sound, showing locations of sampling sites and concentrations of aromatic hydrocarbons (AH's) (ng/g dry weight) and polychlorinated biphenyls (PCB's) (ng/g dry weight) in sediments collected from these areas. Data from Malins et al. (1984, 1985); contaminant levels in the same range have been observed in more recent samplings (see Footnote 1 in the main text).

patterns of egg production in Puget Sound English sole and to examine how these patterns vary in relationship to collection site, chemical contaminant exposure, and nutritional status.

## Materials and methods

### Collection of samples

Vitellogenic female English sole (greater than 250 mm total length [TL]) were collected by otter trawl

from Eagle Harbor, Sinclair Inlet, Port Susan, and the Duwamish Waterway in Puget Sound, Washington (Fig. 1). Sampling was conducted during the winters of 1986–87 and 1989–90 in mid-December and from mid to late January, to coincide with the period in which vitellogenesis normally occurs in this species, before substantial migration to spawning areas has taken place (Johnson et al., 1991). Aside from a relatively brief spawning migration, sole are relatively territorial and reside at these sites throughout the year (Day, 1976). It should be noted that because these animals were not actively spawning, fecundity determi-

nations estimated potential rather than actual fecundity. However, we chose to collect animals at this earlier stage of development to ensure that specimens came from resident subpopulations at sites with known sediment contaminant concentrations. This selection would not have been possible if animals had been collected on their spawning grounds.

Fecundity determinations were carried out on 5 to 10 animals from each site at each sampling time. Fish sampled in 1986–87 were collected as part of a study on gonadal development in English sole (Johnson et al., 1988); ovary samples were preserved for fecundity determination and archived, but not analyzed, at that time. Fish collected in 1989–90 were sampled specifically for fecundity determination.

Fish were caught by otter trawl in 5-min tows and held in aerated saltwater in holding tanks on the deck of the research vessel until they could be processed. Within an hour of capture, fish were weighed and measured. From each animal, a 1-mL blood sample was collected with a heparinized syringe from the caudal vessel. Blood samples for measurement of plasma estradiol concentrations were centrifuged at 3,000  $\times$ g, and the plasma was stored at  $-20^{\circ}\text{C}$ . Fish were sacrificed by severing the spinal cord. Ovaries from vitellogenic females were removed and weighed; one ovary was slit longitudinally and preserved in modified Gilson's fluid (Simpson, 1951) for later determination of fecundity and egg weight. Ovarian tissues for histological examination were preserved in Davidsons' fixative (Mahoney, 1973). Additionally, tissue samples for determination of PCB concentrations were collected from the liver and ovary and stored at  $-20^{\circ}\text{C}$ . Bile for measurement of fluorescent aromatic compounds (FAC's) was collected and stored at  $-0^{\circ}\text{C}$ .

### Analysis of samples

Ovaries collected for histology were embedded in paraffin, stained with hematoxylin and eosin (Luna, 1968), and examined microscopically to confirm their developmental stage and to record ovarian atresia and related lesions by using criteria outlined in Hunter and Macewicz (1985b) and Johnson et al. (1991). Ovarian lesion severity was ranked on a subjective scale of 1 to 7, with 1 being minimal and 7 being severe.

Fecundity was determined by using the gravimetric method described by Bagenal and Braum (1971). Ovaries were preserved in Gilson's fluid for at least 3 months to allow eggs to harden and ovarian connective tissue to disintegrate. Preserved eggs were washed with water, filtered to separate them from residual ovarian connective tissue fragments, and

dried at  $60^{\circ}\text{C}$  for 24 hours. All eggs were weighed, and then 3 subsamples of 200 eggs each were weighed. Fecundity, relative fecundity, and reproductive rate were subsequently determined by using the formulas below:

$$\text{Fecundity} = 2 \frac{[(\text{total weight of eggs}) (\# \text{ of eggs in subsample})]}{(\text{mean weight of eggs in subsample})}$$

*Relative fecundity* = [Fecundity/gutted body weight (g)]; and

*Reproductive rate* (g of eggs/year) = [Fecundity  $\times$  egg weight in (g)].

Additionally, gonadosomatic index (GSI), hepatosomatic index (HSI), and condition factor were calculated as follows:

$$\text{GSI} = \left[ \frac{\text{ovary weight (g)}}{\text{gutted body weight (g)}} \right] \times 100$$

$$\text{HSI} = \left[ \frac{\text{liver weight (g)}}{\text{gutted body weight (g)}} \right] \times 100$$

Condition factor = gutted body weight (g)/length<sup>3</sup> (cm).

Levels of fluorescent aromatic compounds (FAC's) in bile were measured according to the method of Krahn et al. (1987), which provides a semiquantitative determination of the concentrations of metabolites of PAH's (Krahn et al., 1993). Bile sampled from fish was injected directly into a Spectra-Physics Model 8800 high performance liquid chromatograph (HPLC) equipped with a Phenomenex reversed-phase C18 analytical column. The polar analytes (primarily metabolites of AH's) in bile were eluted with a linear gradient from 100% water containing 5 mL of acetic acid/L to 100% methanol and monitored by two fluorescence detectors connected in series. Fluorescence of metabolites was measured at two wavelengths: 290/335 nm, where metabolites of naphthalene (NPH) and related two-ring aromatic compounds from petroleum fuels fluoresce; and 380/480 nm, where metabolites of benzo[a]pyrene (BaP) and related multi-ring AH's from combustion sources fluoresce (Krahn et al., 1987). Levels of biliary FAC's were reported as equivalents of known concentrations of BaP or NPH standards on the basis of biliary protein because recent studies (Collier and Varanasi, 1991) have shown that such normalization can account for variation in FAC levels associated with the feeding status of

sampled fish. Concentrations of biliary protein were determined by the method of Lowry et al. (1951) with bovine serum albumin (BSA) as the standard.

Liver and ovary tissue were analyzed for PCB's by following the method described by MacLeod et al. (1985) and modifications later described in Stein et al. (1987). Tissue samples (approximately 2 g) were ground with 10 g of silica and then added to a column (270 × 23 mm) containing 3 g of activated silica gel (Amicon Corp., Danvers, MA) held in place by a glass wool plug. PCB's were eluted with pentane:methylene chloride (90:10, V/V). The first 50 mL of eluant were collected, concentrated, and exchanged with 1 mL of hexane prior to analysis by gas chromatography with electron capture detection (GC/ECD) (MacLeod et al., 1985). Selected samples of ovary tissue required the removal of lipids by size-exclusion HPLC (Krahn et al., 1988) prior to analysis with GC/ECD.

Plasma estradiol-17 $\beta$  concentrations were determined by radioimmunoassay as described by Sower and Schreck (1982). Plasma glucose and triglycerides were determined as described by Casillas et al. (1983) and Casillas and Ames (1986), respectively.

Fish age was estimated from length by using site-specific age-length curves calculated from length and age data collected from female English sole sampled during previous studies in Puget Sound. Fish ages were determined from otolith analysis (Chilton and Beamish, 1982). Site-specific growth relationships were fitted by using the von Bertalanffy growth curve (Ricker, 1987), and age was then estimated with the formula

$$age = t - ((\ln(1 - length/L_{\infty}))) / K,$$

where  $t$  = time at which length = 0;

$L_{\infty}$  = asymptotic length; and

$K$  = Brody's growth coefficient.

Substituting site-specific values for  $t$ ,  $L_{\infty}$ , and  $K$  into the general formula, age-length equations for female sole from the specific sites were as follows:

$$age_{\text{Port Susan}} = -3.41 - ((\ln(1 - length/487))) / 0.096;$$

$$age_{\text{Sinclair Inlet}} = -1.82 - ((\ln(1 - length/445))) / 0.200;$$

$$age_{\text{Duwamish Waterway}} = -2.87 - ((\ln(1 - length/586))) / 0.085;$$

$$age_{\text{Eagle Harbor}} = -2.41 - ((\ln(1 - length/394))) / 0.209.$$

## Statistical analyses

Data were initially analyzed to identify the major biological factors affecting fecundity and egg weight

so that potential confounding factors could be adjusted before evaluating the impacts of sampling site and contaminant exposure on these endpoints. Analysis of variance (ANOVA), and Fisher's protected least-significant difference multiple-comparison test (Fisher's PLSD) were used to examine the effects of site, year, and month of capture on fecundity and egg weight. Intersite differences in ovarian atresia severity, an ordinal variable, were compared by using the nonparametric Kruskal-Wallis test. Linear regression analysis was used to examine the relationships of fecundity and egg weight with biological variables (i.e. fish size, condition, and gonadosomatic index (GSI)). Stepwise multiple-regression analysis was subsequently used to assess the relationships of fecundity and egg weight with indicators of contaminant exposure (e.g. tissue PCB levels, biliary FAC's, and site of capture) after adjusting for relevant biological factors identified in initial regression analyses. Data were log-transformed as necessary prior to statistical analyses to normalize data and reduce heteroscedasticity. These standard statistical analyses are described in detail in Sokal and Rohlf (1981) and Dowdy and Wearden (1991). For all statistical tests,  $\alpha$  was set at 0.05.

## Results

### Biological factors affecting egg production

The number of eggs produced by sole from our sampling sites ranged from approximately 120,000 in a 28-cm TL fish to approximately 1.2 million in a 43-cm TL fish. In multiple regression analysis (Table 1), fish length was the strongest predictor of fecundity, but GSI (an indicator of the level of gonadal development) also showed significant associations with fecundity. Fish length explained the highest proportion (48%) of variation in fecundity; GSI accounted for 8% of variation in fecundity. Fish age was also positively correlated with fecundity ( $r^2=0.41$ ,  $P=0.0001$ ,  $n=47$ ), but the association was not as strong as the association between fecundity and length because of the high variability in size, and consequently, in egg production, among fish of the same age class. After the influences of fish length and GSI had been accounted for, fish age and sampling time had weak but significant negative relationships with fecundity, a finding that suggests a tendency for fecundity to decline in older animals and at the end of the sampling season. Sampling time and age accounted for approximately 3% and 4% of variation in fecundity, respectively.

In contrast to fecundity, egg weight was not highly correlated with either fish size or age but was re-

Table 1

Results of multiple regression analysis examining effects of biological factors (length, age, GSI, sampling year, and sampling time in Julian day) on egg weight and fecundity. Factors that did not contribute significantly to the model are not included in the table.

Model variables	Regression results				
	df	F-test	r <sup>2</sup>	t-value	p-value
<b>Fecundity</b>					
Overall model	98	42.25	0.63	—	<0.0001
length			0.48	8.31	<0.0001
+GSI			0.56	5.98	<0.0001
+sampling time			0.59	-3.41	0.0010
+age			0.63	-3.13	0.0023
<b>Egg weight</b>					
Overall model	98	154.23	0.76	—	<0.0001
GSI			0.73	8.674	<0.0001
+sampling time			0.76	3.164	0.0004

lated primarily to the degree of gonadal development (i.e. GSI), and increased as vitellogenesis progressed. In vitellogenic sole sampled in December, mean egg weight was  $4.6 \pm 0.4 \mu\text{g}$  ( $n=66$ ), whereas in January, it was  $13.0 \pm 0.9 \mu\text{g}$  ( $n=34$ ) ( $P<0.0001$ , 1-way ANOVA). In multiple regression analysis, the best predictors of egg weight were GSI (73% of variation) and sampling time (3% of variation), both of which were positively correlated with egg weight (Table 1).

Because of their strong influence on fecundity and egg size and because of their high degree of individual variability, the basic parameters included in Table 1 were adjusted for in subsequent analyses to assess the effects of contaminant exposure, nutritional factors, and site of capture on fecundity and egg size.

### Site-specific patterns of egg production

Mean fecundity, relative fecundity, egg weight, and reproductive output for English sole from Port Susan, Sinclair Inlet, the Duwamish Waterway, and Eagle Harbor are shown in Table 2, along with results of 2-way ANOVA examining the effects of site and sampling time on these parameters. Overall, fecundity did not change significantly with sampling time, and no significant site-month interactions were seen for fish from Port Susan, the Duwamish Waterway, or Eagle Harbor. Fish from Sinclair Inlet, however, had significantly higher fecundity in December than in January ( $t=2.613$ ,  $P=0.0105$ ). Site of capture had a significant effect on fecundity; fish from the Duwamish Waterway exhibited higher fecundity than fish from the Port Susan reference site ( $t=2.016$ ,  $P=0.0467$ ). Like fecundity, relative fecundity did not show any consistent overall change with sampling

time, but significant site-month interactions were seen for fish from Sinclair Inlet, Port Susan, and Eagle Harbor. Relative fecundity of fish from Sinclair Inlet was significantly higher in the December than in the January sampling ( $t=2.829$ ,  $P=0.0058$ ), whereas in fish from Eagle Harbor ( $t=-2.747$ ,  $P=0.0072$ ) and Port Susan ( $t=-4.232$ ,  $P=0.0001$ ), relative fecundity was significantly lower in December than in January. There was also a significant effect of site on relative fecundity, which was lower in Sinclair Inlet than in Port Susan sole ( $t=-3.46$ ,  $P=0.0006$ ).

Egg weight increased significantly, by 2- to 3-fold, between December and January at all sampling sites. No significant site-month interactions were seen. Site of capture did not have a significant effect on egg weight, although Duwamish Waterway fish tended to exhibit lower egg weights than fish from Port Susan ( $t=-1.878$ ,  $P=0.0635$ ). Like egg weight, reproductive rate was significantly higher in January than in December. However, no significant intersite differences or month-site interactions were seen for reproductive rate.

The effects of site of capture on egg weight and fecundity were also evaluated by using multiple regression, after adjusting for the influence of fish length, age, GSI, and sampling time (see Table 1). Results showed that even after fish length, sampling time, and GSI had been accounted for, Duwamish Waterway fish had significantly higher fecundity ( $t=4.52$ ,  $P=0.0001$ ) than comparable animals from the Port Susan reference site (see Fig. 2A). Age and fecundity relationships were also analyzed by using multiple regression (excluding fish length from the model); the results showed that Duwamish Water-

**Table 2**

Mean values ( $\pm$  SE) of fecundity, egg weight, relative fecundity, and reproductive rate in English sole from four sites in Puget Sound, and results of 2-way analysis of variance (ANOVA) assessing effects of site and month of collection on these variables. All variables were normalized by log transformation prior to statistical analysis. EH = Eagle Harbor, DW = Duwamish Waterway, SI = Sinclair Inlet, and PS = Port Susan. ns = not significant.

Site	Fecundity (egg no. $\times 10^5$ )		Egg weight ( $\mu$ g)		Relative fecundity (eggs/g gutted wt)		Reproductive rate (g eggs/yr)	
	Dec	Jan	Dec	Jan	Dec	Jan	Dec	Jan
Port Susan	2.34 $\pm$ 0.25 (n=19)	2.65 $\pm$ 0.28 (n=9)	5.3 $\pm$ 0.2 (n=19)	16.7 $\pm$ 1.8 (n=10)	770 $\pm$ 50 (n=19)	1,250 $\pm$ 126 (n=9)	1.4 $\pm$ 0.40 (n=19)	4.2 $\pm$ 0.70 (n=9)
Sinclair Inlet	5.44 $\pm$ 0.70 (n=15)	2.78 $\pm$ 0.27 (4)	4.1 $\pm$ 0.5 (n=15)	13.9 $\pm$ 2.2 (n=4)	1,080 $\pm$ 82 (n=15)	670 $\pm$ 62 (n=4)	2.4 $\pm$ 0.45 (n=15)	3.7 $\pm$ 0.27 (n=4)
Duwamish	4.74 $\pm$ 0.38 (n=17)	3.92 $\pm$ 0.43 (n=10)	4.4 $\pm$ 0.7 (n=17)	10.7 $\pm$ 1.4 (n=10)	1,190 $\pm$ 57 (n=17)	1,220 $\pm$ 106 (n=10)	2.2 $\pm$ 0.41 (n=17)	4.0 $\pm$ 0.64 (n=10)
Eagle Harbor	3.22 $\pm$ 0.32 (n=15)	3.64 $\pm$ 0.46 (n=10)	4.6 $\pm$ 0.9 (n=15)	11.4 $\pm$ 1.2 (n=10)	760 $\pm$ 64 (n=15)	1,020 $\pm$ 73 (n=10)	1.7 $\pm$ 0.44 (n=17)	4.3 $\pm$ 0.74 (n=10)
<b>2-way ANOVA results</b>								
Month	ns	ns	$F = 94.42$	$P = 0.0001$	ns	ns	$F = 36.57$	$P = 0.0001$
			Dec < Jan				Dec < Jan	
Site	$F = 8.83$	$P = 0.0001$	ns	ns	$F = 6.22$	$P = 0.0004$	ns	ns
	DW > PS, $t = 2.02, P = 0.047$		DW < PS, $t = -1.88, P = 0.064$		SI < PS, $t = -3.55, P = 0.0006$			
Month*Site	$F = 3.23$	$P = 0.026$	ns	ns	$F = 8.86$	$P = 0.0001$	ns	ns
	SI: Dec > Jan, $t = 2.61, P = 0.011$				SI: Dec > Jan, $t = 2.83, P = 0.0058$ EH: Dec < Jan, $t = -2.78, P = 0.0078$ PS: Dec < Jan, $t = -4.23, P = 0.0001$			

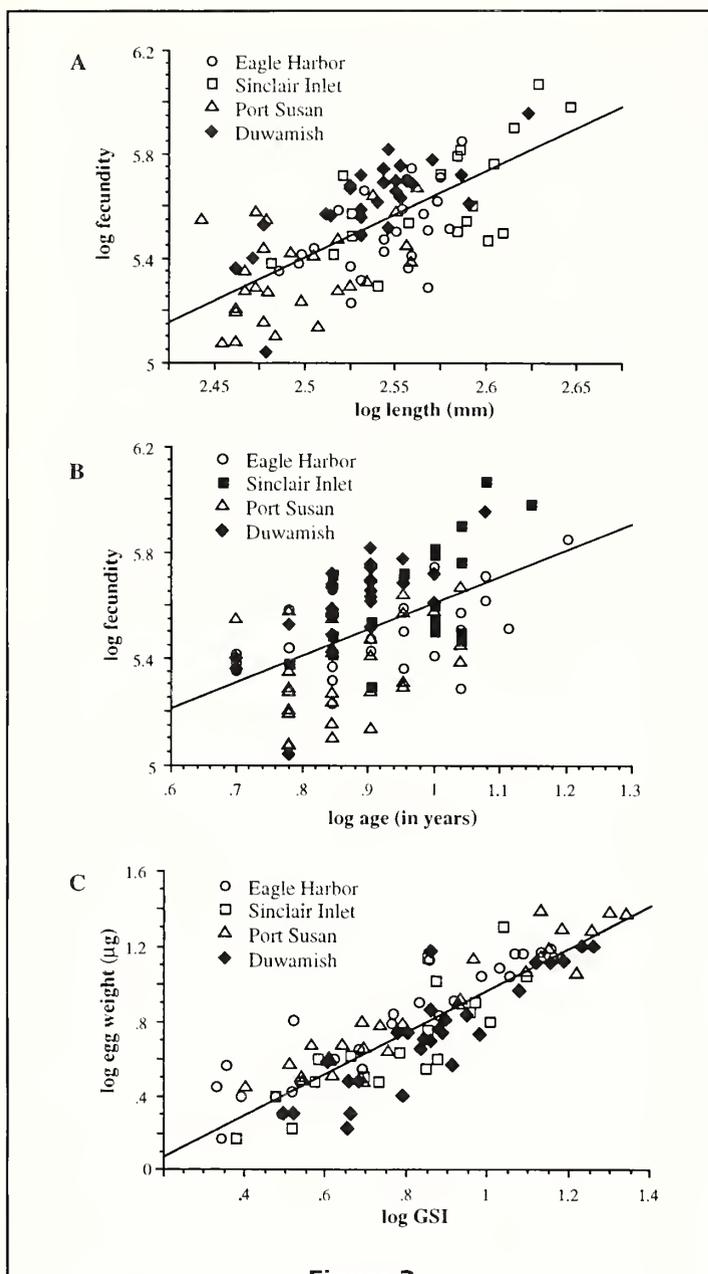
way ( $t = 6.23, P = 0.0001$ ) and Sinclair Inlet sole ( $t = 4.33, P = 0.0001$ ) had significantly higher age-specific fecundity than Port Susan reference fish (see Fig. 2B). Mean age-specific fecundity in sole from the four sampling sites is shown in Table 3. Similarly, results of multiple regression analysis indicated that intersite differences in egg weight were only partially explained by variation in the degree of gonadal development (i.e. GSI) or sampling time. Even after adjusting for these factors, Duwamish Waterway fish exhibited significantly lower egg weight ( $t = -4.070, P = 0.0001$ ) than comparable fish from the other sites (Fig. 2C).

### Intersite differences in biological and chemical factors

**Indicators of contaminant exposure** Mean levels ( $\pm$  SE) of biliary FAC's in English sole from Port Susan, Sinclair Inlet, the Duwamish Waterway, and Eagle Harbor are shown in Fig. 3A; mean concentrations of PCB's ( $\pm$  SE) in liver and ovary tissue are shown in Fig. 3B. English sole from Eagle Harbor had significantly higher biliary FAC-BaP levels than fish from any of the other sampling sites, including

the Duwamish Waterway, and significantly higher FAC-NPH levels than fish from either Port Susan or Sinclair Inlet. Duwamish Waterway fish had significantly higher biliary FAC-BaP and FAC-NPH levels than Port Susan or Sinclair Inlet fish. No significant differences were found between biliary FAC concentrations in Port Susan and Sinclair Inlet fish. Duwamish Waterway fish had significantly higher liver PCB concentrations than fish from any of the other sampling sites and significantly higher ovarian PCB concentrations than fish from either Port Susan or Eagle Harbor. Concentrations of PCB's in liver and ovary tissues of fish from Sinclair Inlet, although not as high as those observed in Duwamish fish, were significantly elevated in comparison with those found in Port Susan and Eagle Harbor fish. Tissue PCB concentrations in Port Susan and Eagle Harbor fish were not statistically different.

**Size and nutritional status** Mean values ( $\pm$  SE) of length, age, condition factor, HSI, plasma triglyceride levels, and plasma glucose levels for sole collected from the four sampling sites are shown in Table 4. Port Susan fish were significantly smaller (in length) and Sinclair Inlet fish significantly larger than ani-



**Figure 2**

(A) Linear regression of log fecundity vs. log length in gravid English sole from Port Susan, Sinclair Inlet, Eagle Harbor, and the Duwamish Waterway. Multiple regression analysis indicated that fecundity was significantly higher in fish from the Duwamish Waterway than in fish of comparable size from the other sites ( $t=3.601$ ,  $P=0.0005$ ). (B) Linear regression of log fecundity vs. log age (in years) in gravid English sole from Port Susan, Sinclair Inlet, Eagle Harbor, and the Duwamish Waterway. Multiple regression analysis indicated that fecundity was significantly higher for a given age in fish from the Duwamish Waterway ( $t=6.23$ ,  $P=0.0001$ ) and Sinclair Inlet ( $t=4.33$ ,  $P=0.0001$ ) than in animals from other sites. (C) Linear regression of egg weight vs. GSI in gravid English sole from Port Susan, Sinclair Inlet, Eagle Harbor, and the Duwamish Waterway. Multiple regression analysis indicated that egg weight was significantly lower for given GSI in fish from the Duwamish Waterway than in animals from other sites ( $t=-3.218$ ,  $P=0.0018$ ).

mals collected from the other sites; fish age (as estimated from length) was significantly lower in fish from the Duwamish Waterway and Port Susan than in fish from Sinclair Inlet and Eagle Harbor. No significant intersite differences were found in either condition factor or length-weight relationship. In contrast, other indicators of nutritional status showed significant intersite differences. Duwamish Waterway fish had significantly higher HSI than fish from other sites, as well as significantly higher triglyceride levels in plasma. Plasma glucose levels, on the other hand, were significantly lower in Eagle Harbor fish than in those from the other sampling sites. Moreover, condition factor and the other proposed indicators of nutritional status were not consistently correlated. A significant positive correlation was found between condition factor and plasma triglyceride concentrations ( $r=0.312$ ,  $P=0.014$ ,  $n=62$ ), but no significant relationship was found between condition factor and either HSI ( $r=0.093$ ,  $P=0.356$ ,  $n=100$ ) or plasma glucose concentrations ( $r=0.036$ ,  $P=0.773$ ,  $n=65$ ).

**Reproductive indicators** Mean values ( $\pm$  SE) of GSI, plasma  $17\text{-}\beta$  estradiol, and plasma ALP (vitellogenin) for sole collected from the four sampling sites are shown in Table 5, along with results of 2-way ANOVA examining the effects of site and sampling time on GSI and plasma estradiol concentrations, and 1-way ANOVA examining the effects of sampling site on plasma ALP (measured in December only). Both GSI and plasma estradiol concentrations increased significantly between December and January at all sites; no significant month-site interactions were observed. Site of capture also influenced both GSI and plasma estradiol concentrations. Fish from Eagle Harbor exhibited significantly lower GSI ( $t=-2.566$ ,  $P=0.0115$ ) and Duwamish Waterway fish exhibited significantly lower plasma estradiol concentrations ( $t=2.464$ ,  $P=0.0156$ ) than fish from the Port Susan reference site. Plasma ALP concentrations were significantly lower in sole from Sinclair Inlet ( $t=-3.004$ ,  $P=0.0058$ ) and higher in sole from Eagle Harbor ( $t=2.860$ ,  $P=0.0039$ ) than in fish from the Port Susan reference site.

**Ovarian atresia** Ovarian atresia was also assessed in fish sampled for fecundity analysis. The prevalence of atresia of yolked oocytes was significantly higher in sole from Eagle Harbor than in sole from the other sampling sites ( $G$ -

**Table 3**

Age-specific fecundity in thousands of eggs (mean  $\pm$  SE) for English sole from Port Susan, Duwamish Waterway, Sinclair Inlet, and Eagle Harbor.

Fish age (yr)	Sampling site			
	Port Susan	Sinclair Inlet	Duwamish Waterway	Eagle Harbor
5	351 (1)	—	240 $\pm$ 12 (2)	242 $\pm$ 11 (3)
6	191 $\pm$ 29 (8)	243 (1)	223 $\pm$ 113 (2)	331 $\pm$ 54 (2)
7	215 $\pm$ 31 (7)	368 $\pm$ 58 (4)	406 $\pm$ 25 (8)	277 $\pm$ 51 (5)
8	218 $\pm$ 35 (4)	271 $\pm$ 74(2)	489 $\pm$ 29 (10)	284 $\pm$ 16 (2)
9	301 $\pm$ 60 (4)	531 (1)	542 $\pm$ 58 (2)	364 $\pm$ 59 (4)
10	377 (1)	468 $\pm$ 71 (1)	464 $\pm$ 58 (2)	410 $\pm$ 153 (2)
11	330 $\pm$ 70 (3)	499 $\pm$ 122 (4)	—	298 $\pm$ 53 (3)
12	—	1,180 (1)	901 (1)	467 $\pm$ 49 (2)
13	—	—	—	—
14	—	970(1)	—	—
15	—	—	—	—
16	—	—	—	708 (1)

**Table 4**

Mean values ( $\pm$  SE) for length (mm), age, condition factor, hepatotoxic index (HSI), plasma triglyceride, and plasma glucose levels in English sole from four sites in Puget Sound. Plasma triglyceride and glucose concentrations were normalized by log-transformation prior to statistical analysis; other variables were already normally distributed. Values with different superscripts are significantly different (Fisher's PLSD multiple range test,  $P \leq 0.05$ ).

Site	Length (mm)	Age (yr)	Condition	HSI	Triglycerides	Glucose
Port Susan	314 $\pm$ 28 <sup>a</sup> (n=29)	7.6 $\pm$ 0.3 <sup>a</sup> (n=28)	0.0083 $\pm$ 0.0013 (n=29)	1.82 $\pm$ 0.07 <sup>a</sup> (n=18)	74 $\pm$ 9 <sup>a,b</sup> (n=18)	52 $\pm$ 9 <sup>a</sup> (n=18)
Sinclair Inlet	376 $\pm$ 37 <sup>b</sup> (n=19)	9.4 $\pm$ 0.5 <sup>b</sup> (n=19)	0.0088 $\pm$ 0.0007 (n=19)	2.01 $\pm$ 0.09 <sup>a,b</sup> (n=15)	101 $\pm$ 11 <sup>b</sup> (n=15)	42 $\pm$ 3 <sup>a</sup> (n=15)
Duwamish	346 $\pm$ 29 <sup>c</sup> (n=27)	7.7 $\pm$ 0.3 <sup>a</sup> (n=27)	0.0088 $\pm$ 0.0013 (n=27)	3.06 $\pm$ 0.07 <sup>c</sup> (n=17)	187 $\pm$ 17 <sup>c</sup> (n=17)	53 $\pm$ 5 <sup>a</sup> (n=17)
Eagle Harbor	350 $\pm$ 22 <sup>c</sup> (n=25)	8.8 $\pm$ 0.6 <sup>b</sup> (n=25)	0.0091 $\pm$ 0.0010 (n=25)	2.22 $\pm$ 0.10 <sup>b</sup> (n=15)	73 $\pm$ 21 <sup>a</sup> (n=15)	25 $\pm$ 41 <sup>b</sup> (n=15)
	P=0.0001	P=0.0076	P=0.1016	P=0.0001	P=0.0001	P=0.0005

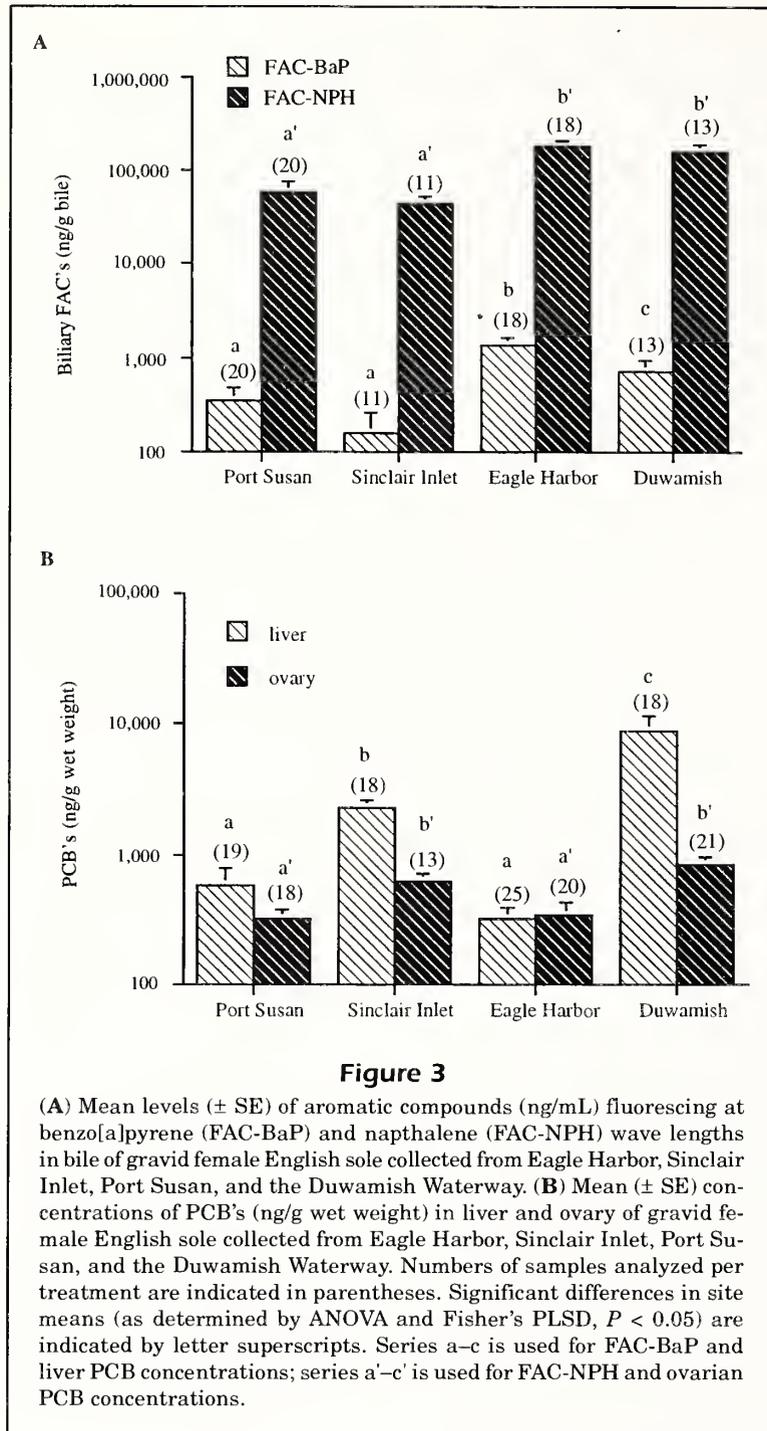
statistic,  $P < 0.05$ ). At Eagle Harbor, 43% of sampled fish exhibited atresia, in comparison with 28%, 21%, and 17% of fish at Sinclair Inlet, Port Susan, and the Duwamish Waterway, respectively. Atresia severity also tended to be greatest at Eagle Harbor (average rankings were 1.33 at Eagle Harbor, 1.00 at Sinclair Inlet, 0.759 at Port Susan, and 0.542 at the Duwamish Waterway), but intersite differences in severity were not statistically significant ( $P = 0.2659$  in the nonparametric Kruskal-Wallis test).

#### Chemical and nutritional parameters as predictors of egg production patterns

Results of multiple regression analysis examining associations of egg weight, fecundity, and relative fecundity with biomarkers of contaminant exposure

and nutritional factors are shown in Table 6 (reproductive rate was not included in this analysis because no significant intersite differences were seen in this variable). As noted above, potentially confounding biological factors (i.e. fish length, age, sampling time, and GSI in the case of fecundity, and GSI and sampling time in the case of egg weight; see Table 1) were incorporated into the regression analyses along with bioindicators of exposure in order to adjust for their contribution to the observed variation in fecundity and egg weight.

Both fecundity and relative fecundity were found to be significantly and positively associated with PCB concentrations in liver. Egg weight showed a significant positive association with biliary FAC's-BaP; the relationship with FAC's-NPH was also positive, but not statistically significant. Additionally, a near-sig-



**Figure 3**

(A) Mean levels ( $\pm$  SE) of aromatic compounds (ng/mL) fluorescing at benzo[a]pyrene (FAC-BaP) and naphthalene (FAC-NPH) wave lengths in bile of gravid female English sole collected from Eagle Harbor, Sinclair Inlet, Port Susan, and the Duwamish Waterway. (B) Mean ( $\pm$  SE) concentrations of PCB's (ng/g wet weight) in liver and ovary of gravid female English sole collected from Eagle Harbor, Sinclair Inlet, Port Susan, and the Duwamish Waterway. Numbers of samples analyzed per treatment are indicated in parentheses. Significant differences in site means (as determined by ANOVA and Fisher's PLSD,  $P < 0.05$ ) are indicated by letter superscripts. Series a-c is used for FAC-BaP and liver PCB concentrations; series a'-c' is used for FAC-NPH and ovarian PCB concentrations.

nificant negative association ( $P=0.0617$ ) was found between liver PCB concentrations and egg weight. A significant negative association was also observed between fecundity and atresia severity of yolked oocytes, and a positive association between atresia and egg weight. Vitellogenin concentration showed significant or near-significant negative associations with fecundity ( $P=0.0579$ ) and relative fecundity ( $P=0.0164$ )

and was significantly positively correlated with egg weight ( $P=0.0164$ ). Plasma estradiol concentration showed a similar relationship with fecundity, relative fecundity, and egg weight, but the associations were not statistically significant at  $\alpha = 0.05$  ( $0.06 < P < 0.18$ ).

In addition to bioindicators of contaminant exposure and reproductive condition, fecundity and rela-

**Table 5**

Mean values ( $\pm$  SE) of gonadosomatic index (GSI), plasma estradiol concentration and plasma vitellogenin concentrations (as estimated from plasma alkali-labile phosphate (ALP)) in English sole from four sites in Puget Sound, and results of 2-way analysis of variance (ANOVA) assessing effects of site and month of collection on these variables. All variables were normalized by log-transformation prior to statistical analysis. No significant month-site interactions were observed for either GSI or plasma estradiol concentration, so the interaction term was suppressed in the final model. EH=Eagle Harbor, DW=Duwamish Waterway, SI=Sinclair Inlet, and PS=Port Susan. nd=not determined.

Site	GSI		Plasma estradiol 17- $\beta$ (pg/mL)		Plasma ALP (vitellogenin) (mg/mL)	
	Dec	Jan	Dec	Jan	Dec	Jan
Port Susan	5.5 $\pm$ 0.7 (n=19)	15.0 $\pm$ 1.4 (n=9)	5000 $\pm$ 600 (n=19)	12000 $\pm$ 1700 (n=10)	35 $\pm$ 3 (n=19)	nd
Sinclair Inlet	5.8 $\pm$ 0.6 (n=15)	9.4 $\pm$ 0.1.3 (n=4)	5300 $\pm$ 400 (n=15)	11000 $\pm$ 2100 (n=4)	24 $\pm$ 8 (n=19)	nd
Duwamish Waterway	6.4 $\pm$ 0.7 (n=17)	11.4 $\pm$ 1.3 (n=10)	3300 $\pm$ 400 (n=17)	9000 $\pm$ 900 (n=10)	29 $\pm$ 2 (n=17)	nd
Eagle Harbor	4.5 $\pm$ 0.6 (n=15)	9.6 $\pm$ 1.1 (n=10)	4900 $\pm$ 700 (n=13)	8500 $\pm$ 800 (n=10)	49 $\pm$ 3 (n=15)	nd
<b>2-way ANOVA Results</b>						
Month	F=65.9 Dec < Jan		P=0.0001 Dec < Jan		F=49.4 P=0.0001 nd	
Site	F=3.05 EH < PS, t=-2.57, P=0.012		P=0.032 F=3.57 DW < PS, t=-2.46, P=0.016		F=11.25 P=0.0001 EH > PS, t=2.86, P=0.006 SI < PS, t=-3.00, P=0.004	

tive fecundity were significantly related to several indicators of nutritional status. Fecundity was positively associated with condition factor ( $P=0.0006$ ) and showed a near-significant tendency ( $P=0.0603$ ) to increase with increasing plasma triglyceride levels. Relative fecundity was significantly positively associated with plasma triglyceride levels. These relationships were also observed when only sole from the least contaminated sites (Port Susan and Sinclair Inlet) were examined (e.g. for fecundity vs. condition factor,  $t=3.177$ ,  $P=0.0028$ ,  $n=47$ ; for fecundity vs. plasma triglyceride concentration,  $t=1.923$ ,  $P=0.0647$ ,  $n=32$ ). In addition, significant positive associations were observed between both fecundity and relative fecundity and HSI ( $P=0.0011$ ) when fish from all sites were included in the analysis. These associations were not apparent when only reference fish were examined (e.g. for fecundity vs. HSI,  $t=0.776$ ,  $P=0.4423$ ,  $n=47$ ). None of the nutritional factors examined were significantly associated with egg weight.

Significant correlations were found between indicators of contaminant exposure and several of the factors related to fish nutritional status (Table 7). Hepatosomatic index showed strong positive correlations with both biliary FAC and tissue PCB concentrations ( $0.0001 < P < 0.0002$ ), and plasma triglyceride and glucose levels were significantly posi-

tively correlated with PCB concentrations in the liver. Plasma triglyceride and glucose levels also tended to increase as ovarian PCB concentrations increased and to decrease as biliary FAC levels increased ( $0.05 < P < 0.07$ ), but the correlation was not statistically significant at  $\alpha = 0.05$ . Condition factor was not significantly correlated with any biomarker of contaminant exposure. No significant correlations were seen between either GSI or plasma estradiol concentrations and either tissue PCB levels or biliary FAC's. However, significant negative correlations were found between plasma vitellogenin (ALP) concentrations and both hepatic and ovarian PCB concentrations.

## Discussion

Significant intersite differences in both egg weight and fecundity were detectable in English sole sampled in this study, even after variation in fish size and sampling time had been taken into account. One notable finding was the tendency for Duwamish Waterway and Sinclair Inlet fish to exhibit higher age-specific fecundity in comparison with fish from Eagle Harbor and Port Susan. This difference appeared to be due, at least in part, to a larger size at age in the Duwamish and Sinclair Inlet fish. Although additional data, particularly on older fish,

Table 6

Associations between bioindicators of contaminant exposure, atresia severity, and nutritional factors in English sole and egg weight, fecundity, and relative fecundity as determined through multiple regression, while adjusting for effects of fish size, GSI, and sampling time. For each independent variable, *t*-value, *P*-value, and sample number (*n*) are shown. The sign of the *t*-value indicates the direction of the association (positive or negative). Statistically significant associations ( $P \leq 0.05$ ) are indicated in bold.

Independent variable	Fecundity <sup>1</sup>	Egg weight <sup>2</sup>	Relative fecundity <sup>2</sup>
Biliary FAC-BaP	-1.379 <i>P</i> =0.1733 ( <i>n</i> =62)	<b>2.314</b> <i>P</i> = <b>0.0242</b> ( <i>n</i> =62)	-1.083 <i>P</i> =0.2835 ( <i>n</i> =62)
Biliary FAC-NPH	0.842 <i>P</i> =0.4032 ( <i>n</i> =61)	1.593 <i>P</i> =0.1165 ( <i>n</i> =62)	-0.029 <i>P</i> =0.9767 ( <i>n</i> =61)
Liver PCB's	<b>2.402</b> <i>P</i> = <b>0.0187</b> ( <i>n</i> =79)	-1.897 <i>P</i> =0.0617 ( <i>n</i> =72)	<b>2.350</b> <i>P</i> = <b>0.0214</b> ( <i>n</i> =79)
Ovary PCB's	0.933 <i>P</i> =0.3544 ( <i>n</i> =72)	-0.105 <i>P</i> =0.9166 ( <i>n</i> =72)	1.641 <i>P</i> =0.1054 ( <i>n</i> =72)
Atresia severity <sup>3</sup> (yolked oocytes)	<b>-2.162</b> <i>P</i> = <b>0.0334</b> ( <i>n</i> =91)	<b>2.901</b> <i>P</i> = <b>0.0047</b> ( <i>n</i> =92)	-1.852 <i>P</i> =.0674 ( <i>n</i> =91)
Plasma estradiol	-1.907 <i>P</i> =0.0598 ( <i>n</i> =96)	1.340 <i>P</i> =0.1834 ( <i>n</i> =97)	-1.775 <i>P</i> =0.0792 ( <i>n</i> =96)
Vitellogenin	-1.934 <i>P</i> =0.0579 ( <i>n</i> =65)	<b>2.462</b> <i>P</i> = <b>0.0164</b> ( <i>n</i> =65)	<b>-2.468</b> <i>P</i> = <b>0.0164</b> ( <i>n</i> =65)
Condition factor	<b>3.552</b> <i>P</i> = <b>0.0006</b> ( <i>n</i> =99)	-1.440 <i>P</i> =0.1531 ( <i>n</i> =100)	0.330 <i>P</i> =0.7419 ( <i>n</i> =99)
HSI	<b>3.381</b> <i>P</i> = <b>0.0011</b> ( <i>n</i> =99)	-1.440 <i>P</i> =0.1531 ( <i>n</i> =100)	<b>4.350</b> <i>P</i> = <b>0.0001</b> ( <i>n</i> =99)
Glucose	1.722 <i>P</i> =0.0902 ( <i>n</i> =65)	0.896 <i>P</i> =0.3735 ( <i>n</i> =65)	1.355 <i>P</i> =0.1803 ( <i>n</i> =65)
Triglycerides	1.917 <i>P</i> =0.0603 ( <i>n</i> =62)	1.680 <i>P</i> =0.0983 ( <i>n</i> =62)	<b>2.629</b> <i>P</i> = <b>0.0109</b> ( <i>n</i> =62)

<sup>1</sup> Adjusted for fish length, age, GSI and sampling time.

<sup>2</sup> Adjusted for GSI and sampling time.

<sup>3</sup> Ranked on a scale of 1-7, where 1 is minimal and 7 is severe.

are needed to confirm that Duwamish and Sinclair Inlet fish do in fact have a higher growth rate or longer period of growth than fish from the other sampling areas, the present results suggest that intersite differences in growth rate may have a significant effect on age-specific egg production in Puget Sound

English sole. This problem deserves further investigation because of its potential impact on sole population dynamics.

Another notable finding was the tendency of English sole from the Duwamish Waterway to produce more and smaller eggs than fish of comparable size

Table 7

Associations between nutritional and reproductive factors and biomarkers of contaminant exposure in English sole as determined through multiple regression, while adjusting for effects of sampling time. *T*-value for regression factor, *P*-value, and sample number are shown. The sign of the *t*-value indicates the direction of the association (positive or negative). Statistically significant associations are indicated in bold.

Exposure biomarkers	Nutritional and reproductive factors						
	Condition	HSI	Glucose	Triglycerides	Estradiol	Vitellogenin	GSI
Biliary FAC-BaP	1.701 <i>P</i> =0.0942 ( <i>n</i> =62)	<b>6.297</b> <b><i>P</i>&lt;0.0001</b> <b>(<i>n</i>=62)</b>	-1.902 <i>P</i> =0.0654 ( <i>n</i> =37)	-1.880 <i>P</i> =0.0699 ( <i>n</i> =33)	-0.739 <i>P</i> =0.4628 ( <i>n</i> =59)	0.493 <i>P</i> =0.6248 ( <i>n</i> =37)	-0.237 <i>P</i> =0.8133 ( <i>n</i> =62)
Biliary FAC-NPH	1.287 <i>P</i> =0.2032 ( <i>n</i> =62)	<b>6.660</b> <b><i>P</i>&lt;0.0001</b> <b>(<i>n</i>=62)</b>	-1.692 <i>P</i> =0.0994 ( <i>n</i> =37)	-0.851 <i>P</i> =0.4041 ( <i>n</i> =33)	-0.636 <i>P</i> =0.5274 ( <i>n</i> =59)	-0.280 <i>P</i> =0.7809 ( <i>n</i> =37)	-0.262 <i>P</i> =0.7939 ( <i>n</i> =62)
Liver PCB's	0.143 <i>P</i> =0.8870 ( <i>n</i> =80)	<b>3.905</b> <b><i>P</i>=0.0002</b> <b>(<i>n</i>=80)</b>	<b>2.357</b> <b><i>P</i>=0.0228</b> <b>(<i>n</i>=47)</b>	<b>3.786</b> <b><i>P</i>=0.0005</b> <b>(<i>n</i>=43)</b>	-1.209 <i>P</i> =0.2305 ( <i>n</i> =77)	<b>-2.717</b> <b><i>P</i>=0.0093</b> <b>(<i>n</i>=47)</b>	0.096 <i>P</i> =0.9328 ( <i>n</i> =80)
Ovary PCB's	0.132 <i>P</i> =0.8956 ( <i>n</i> =72)	<b>5.279</b> <b><i>P</i>=0.0001</b> <b>(<i>n</i>=72)</b>	1.997 <i>P</i> =0.0534 ( <i>n</i> =38)	1.920 <i>P</i> =0.0630 ( <i>n</i> =34)	0.066 <i>P</i> =0.9476 ( <i>n</i> =69)	<b>-2.603</b> <b><i>P</i>=0.0133</b> <b>(<i>n</i>=38)</b>	0.676 <i>P</i> =0.5010 ( <i>n</i> =72)

and maturity from other sites. Although this intersite difference in egg production pattern could represent a genetic adaptation of the Duwamish sole stock to its particular habitat, this is not likely on the basis of current knowledge of the population structure of English sole in Puget Sound. Sole populations residing at our sampling sites do not appear to constitute discrete breeding populations but migrate to common breeding areas, such as University Point or Duwamish Head in central Puget Sound, for spawning (Collier et al., 1992). Moreover, their eggs and larvae are pelagic and therefore are transported from the breeding area to nearshore nursery ground settling sites in accordance with current patterns (Lassuy, 1989). Site-specific genetic adaptation would be unlikely in animals with such a breeding system, although some genetic divergence between subpopulations in northern and southern Puget Sound with distinct spawning areas is a possibility. Overall, marine fish show relatively little geographic diversity (Gyllensten, 1985), and their genetic structure is thought to be determined largely by the dispersal potential of the pelagic stages, rather than by adaptation to local environmental conditions (Waples, 1987). Studies of marine flatfish, such as the common sole (*Solea vulgaris*), turbot (*Scophthalmus maximus*), and flounder (*Platichthys flesus*) in the north-eastern Atlantic and Mediterranean (Galleguillos and Ward, 1982; Blanquer et al., 1992; Kotoulas et al., 1995), indicate that these species exhibit some geo-

graphic isolation or differentiation due to temperature gradients that inhibit larval transport and survival but that they show fairly substantial gene flow on a regional level. In the common sole, for example, a species with a life history strategy similar to that of English sole, the geographic unit of population structure appears to lie within a radius of approximately 100 km (Kotoulas et al., 1995).

Changes in egg weight and number could also be associated with alterations in habitat characteristics, such as water temperature, food supply, and food quality, all of which have been shown to influence egg development in English sole or other fish species. Winters et al. (1993), for example, demonstrated that winter temperature 2 to 3 months before spawning can affect fecundity and egg size in herring from the northwest Atlantic. Temperature can also affect the rate of gonadal development in English sole, and consequently egg size at a particular sampling time (Kruse and Tyler, 1983). In general, however, bottom temperature in Puget Sound is not highly variable over the geographic range encompassed by this study (Collias et al., 1974; Malins et al., 1980, 1982), and water temperatures in the Duwamish Waterway are comparable to those from sites in the main basin (Collier, 1988). Consequently, it is unlikely that temperature is a major contributing factor to the intersite differences in patterns of egg development that we observed in this study.

The present findings suggest, on the other hand, that contaminant exposure and nutritional variables,

or their interaction, could be important contributing factors to the observed changes in fecundity and egg weight. Although indicators of chemical contaminant exposure were not among the strongest predictors of fecundity and egg weight in the sole examined in this study, some significant associations were observed between tissue PCB and biliary FAC concentrations in individual fish and patterns of egg production. Elevated concentrations of PCB's in liver or ovarian tissue, which were characteristic of fish from the Duwamish Waterway, were associated with reduced plasma ALP (vitellogenin) concentrations, as well as with production of more but smaller eggs. These data suggest that exposure to PCB's might affect egg development, perhaps by inhibiting either the production or uptake of vitellogenin. However, reports of the effects of PCB's on vitellogenin production in fish are somewhat inconsistent. In the larger set of fish sampled in our earlier study (Johnson et al., 1988), a correlation between elevated tissue PCB concentrations and reduced plasma ALP in vitellogenic fish was also observed ( $n=60$ , Spearman's  $\rho=-0.30$ ,  $P=0.023$ ), as well as a tendency for plasma ALP concentrations to be lower in fish from the Duwamish Waterway and Sinclair Inlet, although intersite differences were less pronounced than in the smaller set of fish for which fecundity and egg weight determinations were performed. In other studies such compounds have proved to be estrogenic and have enhanced vitellogenin production in fish and reptiles (von der Decken et al., 1992; Guillette et al., 1994) or have exerted little effect on plasma vitellogenin concentrations (Monosson et al., 1994). The impact of PCB exposure on egg development might be better clarified through congener-specific analysis of PCB's because the various coplanar and noncoplanar PCB congeners present in complex PCB mixtures are known to differ in toxicity (Safe, 1990), as well as in their ability to enhance or inhibit vitellogenin synthesis (Anderson et al., 1996). Exposure to PAH's also appeared to have some influence on egg development because we found that elevated biliary FAC-BaP levels were correlated with both increased atresia of yolked oocytes and a trend toward increased egg weight and lowered fecundity. Interestingly, atresia tended to be most prevalent and of greatest severity at Eagle Harbor, where biliary FAC concentrations in fish were particularly high.

In earlier studies of reproductive function in English sole (Johnson et al., 1988), we observed reduced plasma estradiol concentrations in female fish from both Eagle Harbor and the Duwamish Waterway. These differences were partially associated with inhibited ovarian development in significant proportions of adult fish from these sites, but differences persisted even when only vitellogenic fish were examined. A similar trend was

observed in the fish examined in this study, all of which were vitellogenic, although the intersite difference was statistically significant only for fish from the Duwamish Waterway. Depressed plasma estradiol concentrations tended to be associated with increased fecundity but were not strongly correlated with changes in egg production patterns.

Nutritional status appeared to have a significant effect on fecundity in English sole because a strong correlation was found between condition factor and fecundity in fish from minimally to moderately contaminated sites. Similar relationships between fecundity and food supply, condition factor, and other indicators of nutritional status have been observed in other fish species, including winter flounder (Tyler and Dunn, 1976), temperate and tropical clupeids (Hay and Brett, 1988; Milton et al., 1994), plaice (Horwood et al., 1986, 1989), and rainbow trout (Bromage et al., 1992). When sole from the contaminated sites (Eagle Harbor and the Duwamish Waterway) were included in the analyses, additional nutrition-related factors showed correlations with fecundity in English sole. Of these factors, HSI showed a particularly strong relationship with fecundity and was significantly higher in Duwamish Waterway fish than in animals from the other sampling sites. Animals from the Duwamish Waterway also exhibited elevated plasma triglyceride levels, which, like increased HSI, appeared to be associated with production of more and smaller eggs. Milton et al. (1994) also observed production of more, but smaller, eggs in tropical clupeids with increased HSI, and interpreted the alteration in egg size and number as a response to the good nutritional status of the female and a possible adaptation to environmental conditions in which food was abundant. It is possible that elevated HSI and plasma triglyceride levels in Duwamish Waterway fish could be related to favorable feeding conditions. Previous studies have, in fact, shown that benthic invertebrates such as mollusks and polychaetes, which form a significant proportion of the diet of English sole (Varanasi et al., 1989), are relatively abundant in the Duwamish Waterway (Malins et al., 1980, 1982). However, the Duwamish Waterway fish did not have a significantly higher mean condition factor than that of animals from the other sampling sites, and although plasma triglyceride concentrations showed some correlation with condition factor, HSI did not. Both HSI and plasma triglyceride concentrations, however, showed strong correlations with bioindicators of contaminant exposure. Increased HSI in association with exposure to toxicants, particularly agents that induce cell proliferation, is well documented in a number of fish species (Heath, 1987), and toxicant-related increases

in serum triglycerides have also been observed in previous studies. For example, English sole showed increased serum triglyceride levels in response to laboratory exposure to model toxicants bromobenzene and *o*-bromophenol (Casillas and Myers, 1989). Consequently, elevated levels of these parameters in Duwamish Waterway fish could be a reflection of toxicant exposure rather than good nutritional status. Moreover, the contaminants may affect fecundity or egg size indirectly through their impact on liver function, lipid disposition, or lipid metabolism. Results of this study suggest the possibility of such interactive effects of contaminants and nutritional factors on egg development.

In addition to PCB's and PAH's, other contaminants, such as heavy metals and organotins, which are present in the Duwamish Waterway and to a lesser extent at Sinclair Inlet (Krone et al., 1989; PSWQA, 1994; Dutch et al.<sup>2</sup>), could affect egg weight or other aspects of gonadal development in English sole. Previous studies have shown that a number of toxic trace elements, including copper, lead, mercury, and cadmium (Kaviraj, 1983; Munkittrick and Dixon, 1988; Dethlefsen, 1989), as well as tributyl tin (TBT) (Walker et al., 1990), can affect egg size or gonadal development in fish. Previously, Krone et al. (1989) showed increased tissue concentrations of TBT in English sole from the Duwamish Waterway. However, many of these trace elements in their organic form do not bioaccumulate in English sole (Meador et al., 1994) and indicate low bioavailability.

Increased egg production or production of more but smaller eggs is not the most commonly observed response in fish exposed to environmental contaminants, but such trends have been observed in some previous studies. Slooff and DeZwart (1983) reported increased fecundity in bream exposed to a mixture of chlorinated and aromatic compounds in the Rhine River, and Walker et al. (1990) reported a similar finding for medaka exposed to TBT. Reduced egg size, although not necessarily in conjunction with increased egg production, has been reported in a number of studies in which fish were exposed to PAH's, PCB's, or both (Kime, 1995). Interestingly, since 1900, North sea plaice have also exhibited a trend toward production of more but smaller eggs (Rijnsdorp, 1991). The causes of these changes are unknown, but it is suspected that they are most likely related to changes in environmental conditions, which could

include environmental degradation associated with anthropogenic activities.

In summary, the results of this study suggest that egg weight and number in English sole are influenced by a variety of factors, including exposure to organic chemical contaminants such as PCB's and PAH's, nutritional status, and growth rate. Although chemical contaminant exposure did not appear to have a major impact on egg development in English sole, high concentrations of contaminants in tissues or body fluids showed significant associations with certain potentially detrimental changes: elevated PCB concentrations in liver were correlated with reduced plasma vitellogenin levels and reduced egg weight, and high levels of biliary FAC's were associated with increased ovarian atresia and reduced fecundity. The impact of these alterations in egg weight and number on the reproductive fitness of affected fish is not clear. It is likely that smaller eggs will tend to produce smaller larvae, and reduced larval size has been associated with lower growth and survival rates in other flatfish species (Buckley et al., 1991). However, the detrimental effects of reduced egg weight could be offset by increased egg production, or, at least in the case of the Duwamish Waterway fish, by a relatively fast growth rate and high age-specific fecundity. In order to gain a better understanding of the relationships between chemical contaminants, nutritional factors, and alterations in gonadal development and egg production, we are currently investigating the effects of PCB's, AH's, and food supply on egg weight and fecundity in further laboratory studies with English sole.

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**Abstract.**—By analyzing annual ichthyoplankton survey data from 1983 to 1988, I found a significant positive correlation in distribution and abundance between larval *Cubiceps pauciradiatus* and the Loop Current in the Gulf of Mexico. The data indicate that *C. pauciradiatus* is a species whose adult spawning grounds and larval habitat are tied to sharp temperature gradients. These gradients occur along the edge of the Loop Current in the eastern Gulf of Mexico and along the anticyclonic-cyclonic rings in the western Gulf of Mexico. Transects made across the Loop Current, in 1987 and 1988, show that larval *C. pauciradiatus* is found close to the frontal interface and that peak abundance occurs before peak SST (sea surface temperature).

Variation in the extent of the frontal systems in the Gulf of Mexico would be expected to affect annual recruitment of a species that is tied to a frontal habitat. Annual abundance of *C. pauciradiatus* varied considerably but was similar to that of other pelagic species. This finding suggests that the physical processes in the Gulf of Mexico may affect a wide range of species.

## The Loop Current and the abundance of larval *Cubiceps pauciradiatus* (Pisces: Nomeidae) in the Gulf of Mexico: evidence for physical and biological interaction

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Bigeye cigarfish, *Cubiceps pauciradiatus*, is a member of the family Nomeidae (suborder Stromateoidei) characterized by Haedrich (1967) as "oceanic fishes of tropical and subtropical waters." Fishes of this family are widely distributed across the Gulf of Mexico, in Caribbean waters, and in the tropical Atlantic, Pacific, and Indian Oceans (Butler, 1979). The family Nomeidae comprises three genera: *Cubiceps*, *Psenes*, and *Nomeus*. *Nomeus* is monotypic, *Cubiceps* has seven species, and *Psenes* six (Haedrich, 1967, 1972; Butler, 1979). *Cubiceps pauciradiatus* Günther is a worldwide tropical species and an important forage fish for porpoises (Perrin et al., 1973) and tuna (Alverson, 1963). Because of their oceanic habitat, cigarfishes are poorly known, and only limited information is available on their distribution. Ahlstrom et al. (1976) described the larval stages of five species of this suborder, including *C. pauciradiatus*. All identifications in this study are based upon their work.

In the central and South Atlantic, Oven et al. (1984) found that *Cubiceps pauciradiatus* was always present in the upper sound-scattering layer. It was also the dominant species in the Gulf of Guinea, accounting for 46–85% of the catch (Salekhov, 1989). Like many fishes,

*C. pauciradiatus* migrate to the surface waters at night, concentrating in the upper 70 m. Salekhov (1989) reported that they were abundant and at times the dominant species in night-collected samples where surface-water temperatures were 26.2–28.30°C. Juveniles do not migrate but remain in the 30–90 m stratum. *Cubiceps pauciradiatus* is an intermittent spawner and has a life span of 1 to 2 years. Peak spawning occurs from December to April in tropical waters.

The distribution of this fish in the North Atlantic and Gulf of Mexico is poorly known. In a 1979 study by Houde et al.,<sup>1</sup> *C. pauciradiatus* were the most abundant nomeid in the eastern Gulf. Richards (1984) found this species widely distributed in the eastern Caribbean Sea. In the central and South Atlantic, Salekhov (1989) showed that largest catches of *C. pauciradiatus* occurred in tropical waters along the periphery of cyclonic gyres, the Equatorial Counter Current, and the upwelling region of the Sierra-Leone Ridge. The Gulf of Mexico contains similar frontal areas, such as the Loop

<sup>1</sup> Houde, E. D., J. C. Leak, C. E. Dowd, S. A. Berkeley, and W. J. Richards. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Contract Report to the Bureau of Land Management, rep. AA550-ct7-28, 546 p.

Current in the eastern Gulf and the large warm-core anticyclonic and smaller cold-core cyclonic eddies in the western Gulf. These features form frontal zones across a wide area of the Gulf of Mexico and may be areas in which adult *C. pauciradiatus* are abundant. If *C. pauciradiatus* are abundant around the edges of gyres and upwelling areas, the Gulf of Mexico could be expected to support an extensive population.

This relationship between larval fish and frontal zones has been an area of intense research since Iles and Sinclair (1982) first proposed the existence of larval retention zones caused by oceanographic features. Thermal fronts are defined as a boundary between two water masses that usually have a sharp temperature gradient over short (<10 km) distances (Brandt and Wadley, 1981; Owen, 1989). The biological implications of these features have been recognized by several authors (Brandt and Wadley, 1981; Le Feure, 1986; Richardson et al., 1986, 1989). Thermal fronts are often associated with abrupt changes in salinity, color, turbidity, primary productivity, and phytoplankton species composition and abundance. Fronts may also be considered ecotones and may pose a zoogeographic barrier to both adult and larval fish (Brandt and Wadley, 1981; Richards et al., 1993).

Changes in the distribution and abundance of phytoplankton species across frontal zones have been reported by Seliger et al. (1981), Holligan et al. (1984), Richardson et al. (1985), and Richardson et al. (1986). These authors have reported increased abundance across these features, but the duration and long-term effect of increased phytoplankton abundance on trophic levels have yet to be determined. In a series of papers examining larval herring patches in the Buchan area of Scotland, Richardson et al. (1986) found phytoplankton biomass was highest at a transition zone created by warming waters and tidal mixing. Increased zooplankton abundance across fronts has also been reported (Tranter et al., 1983; Kiørboe and Johansen, 1986; Richards et al., 1989). Tranter et al. (1983) and Kiørboe and Johansen (1986) both reported increased zooplankton biomass concurrent with increased phytoplankton abundance. In a series of transects across the Loop Current, Richards et al. (1989) found increased zooplankton volumes in thermally mixed water close to the outer perimeter of highest surface-current velocity. This occurrence coincided with increases in surface chlorophyll measurements.

The purpose of this paper is to describe the large-scale (Gulf-wide) distribution and abundance of larval *C. pauciradiatus* and their interaction with meso-scale oceanographic features in the Gulf of Mexico. I will show that *C. pauciradiatus* are retained on the cool side of thermal fronts in areas of high produc-

tivity. I hypothesize that the temporal persistence of northern excursions of the Loop Current directly affects the abundance and probably the survival of this species. Because this study focuses on larval, rather than adult, *C. pauciradiatus*, the results of this study will help define the role that these oceanographic features play in larval distribution and may help to determine the size of future year classes.

## Physical oceanography of the Gulf of Mexico

The Gulf of Mexico is a semi-enclosed body of water, the circulation of which is dominated by the Loop Current. Water enters through the Yucatan Channel and exits through the Straits of Florida. The Loop Current is very dynamic and unstable, pushing as far as 29 degrees north latitude into the Gulf of Mexico and at other times flowing almost directly out through the Straits (Vukovich et al., 1979). These characteristics have caused considerable confusion over the years, and only recently have we begun to understand the dynamics of this system (Leipper, 1970; Behringer et al., 1977; Maul, 1977; Vukovich et al., 1979; Vukovich, 1988; Maul and Vukovich, 1993).

Among the more significant features of the Loop Current are the large (200–300 km at formation) anticyclonic rings generated when the northward intrusion separates from the rest of the Current. These rings are pinched off from the Loop Current and move into the western Gulf shelf where they eventually spin down and break up (Merrell and Vazquez, 1983; Lewis and Kirwan, 1987; Lewis, 1992). The exact mechanism of ring genesis is unclear, but it seems to involve the formation of a narrow intrusion of cold water between the ring and the remainder of the Loop Current (Cochrane, 1972; Vukovich and Maul, 1985; Vukovich, 1986). Hurlburt and Thompson (1980, 1982) used numeric models that showed that inherent instabilities exist within the flow field and eventually result in ring separation. Ring separation occurs every 6–17 months (on average every 11 months [Maul and Vukovich, 1993]).

As these warm-core anticyclonic rings move westward, adjacent mesoscale (20–80 km) cyclonic circulations may develop (Elliot, 1979; Merrell and Morrison, 1981; Merrell and Vazques, 1983; Lewis and Kirwan, 1985). These cyclonic rings may be important biologically; Biggs (1992) found elevated nitrate concentrations just below the mixed layer. Cyclones such as these exist for 6 months or more, during which time they may move tens to hundreds of km (Hamilton, 1992). However, their cold surface

expression is limited, and generally these rings can be recognized better by direct sampling from ships or aircraft than from satellites (Hamilton, 1992).

## Materials and methods

Collections in this study were gathered from the NOAA Ship *Oregon II*. Annual surveys were conducted that covered most of the U.S. Exclusive Economic Zone (Richards, 1984). These surveys followed a grid pattern with stations at every 30 minutes of latitude and longitude. Each station consisted of conductivity-temperature-depth (CTD) casts to 200 meters or consisted of an expendable bathythermograph (XBT) drop. Biological samples were collected with 60-cm paired bongo nets of 0.333-mm mesh towed to 200 m or to within 5 m of the bottom at stations <200 m. The nets were towed at a speed of approximately 1.5 kn with a wire angle of 45° and retrieved at a rate of 20 m per minute. A neuston-net tow of 10-min duration (vessel speed approximately 2.5 kn) was also conducted at each station. In 1983 and 1984 only one survey of the northern Gulf of Mexico was completed (Table 1). In the following years, two surveys were completed (1986, 1987, and 1988), each about two weeks apart, although with fewer stations and reduced geographic coverage. There was no survey in 1985. In addition to the normal survey, six transects across the Loop Current were made in 1987. The transect locations were selected on the basis of real-time satellite imagery and frontal analysis and the frontal positions were radioed to the vessel (Richards et al., 1989). Transects 1–6 consisted of stations 2 km apart, and transects 7–8 were 3.6 km apart.

In 1988, a line of stations was sampled along 86°W running from 29.5°N to 27.6°N. All stations except

the first two were 8.3 km apart. Biological samples were taken until the 22°C isotherm rose to 100 m. The XBT drops were continued in order to provide a more detailed definition of the water mass. A 1-m Tucker trawl, with three nets and two opening and closing bongo nets, was deployed in addition to the standard gear. Samples were fixed in buffered formalin and transferred to 70% ethanol within 48 hours.

Bulk zooplankton biomass was estimated from wet displacement volume (dv) (Ahlstrom and Thraillkill, 1960). Samples from the annual surveys were processed at the Plankton Sorting and Identification Center, Szczecin, Poland. The samples from the transects in 1987 and 1988 were processed at the Southeast Fisheries Science Center, Miami, Florida. Fish were identified from the descriptions of Ahlstrom et al. (1976). Catches of larvae were standardized to number under 10 m<sup>2</sup>. Bulk plankton standing stocks were standardized to mL of wet displacement volume per 1,000 m<sup>3</sup>.

To test the relationship between larval *C. pauciradiatus* and the close proximity (<5 km) of a frontal feature, a chi-square ( $\chi^2$ ) test for one-dimensional count data was performed. Because the sampling grid was held constant, the total number of stations <5 km from a zone of surface-temperature gradient varied in relation to the spatial location and size of the frontal features present in that year. To account for the fact that in some years most of the stations were within 5 km of a frontal zone and in other years few were, the analysis was performed to test whether the percentage of stations with *C. pauciradiatus* <5 km from a frontal feature was greater than the percentage of stations with *C. pauciradiatus* >5 km from a frontal feature. This procedure has the added benefit of accounting for random distribution; i.e. if 90% of the stations are within 5 km of a feature, then expectations are such that 90% of the stations with *C. pauciradiatus* would be within 5 km. Pearson correlation coefficients (*r*) were also obtained from the relationship between larval *C. pauciradiatus* and plankton volume and between total larvae (number under 10 m<sup>2</sup>) and plankton volume from the transects.

The frontal edge of the Loop Current and anticyclonic rings was defined as 22°C at 100 m depth following Leipper, (1970) and Maul and Herman (1985).

## Results

### Physical oceanography

The circulation patterns preceding and during the 1983–88 April–May ichthyoplankton cruises varied

**Table 1**

NOAA ship *Oregon II* cruise dates covering the period 1983–88.

Cruise	Leg	Date	Year	No. of bongo stations
OT-134		25 April–16 May	1983	99
OT-143		23 April–7 May	1984	98
OT-159	1	22 April–6 May	1986	36
	2	9 May–22 May	1986	37
OT-166	1	15 April–2 May	1987	35
	2	7 May–20 May	1987	35
OT-173	1	15 April–2 May	1988	34
	2	12 May–26 May	1988	35

considerably from year to year and within years (cruises) in both the eastern and western Gulf of Mexico. A brief synopsis of the circulation patterns present throughout this study are presented below.

Figure 1 shows the position of the 22° isotherms (Loop Current frontal edge) in the eastern Gulf of Mexico for each of the 5 years covered in this study. In 1983, 1984, and 1988, the Loop Current extended north to 27°N. However, in 1986, the Loop barely penetrated into the sample area, and in 1987, a broad front stretched from 88°W to 84°W, although not as far north as in other years. The positions of the Loop Current and cyclonic-anticyclonic rings are detailed in Figures 2–11.

Although Figure 1 indicates the position of the Loop current at the time of the survey, it does not reflect the dynamics of the system nor the formation of warm-core eddies. The northward penetration and stability of the Loop Current front is directly impacted by formation and separation of warm-core eddies. In 1983, a ring began to form in January but did not separate until March and left the Loop Current extended to the northeast with the northern boundary at 27°N (Fig. 2). It remained in that position throughout most of the spring. In contrast, the Loop Current underwent ring-shedding events in January 1984 and 1986, and the front remained farther south and with a much narrower frontal area

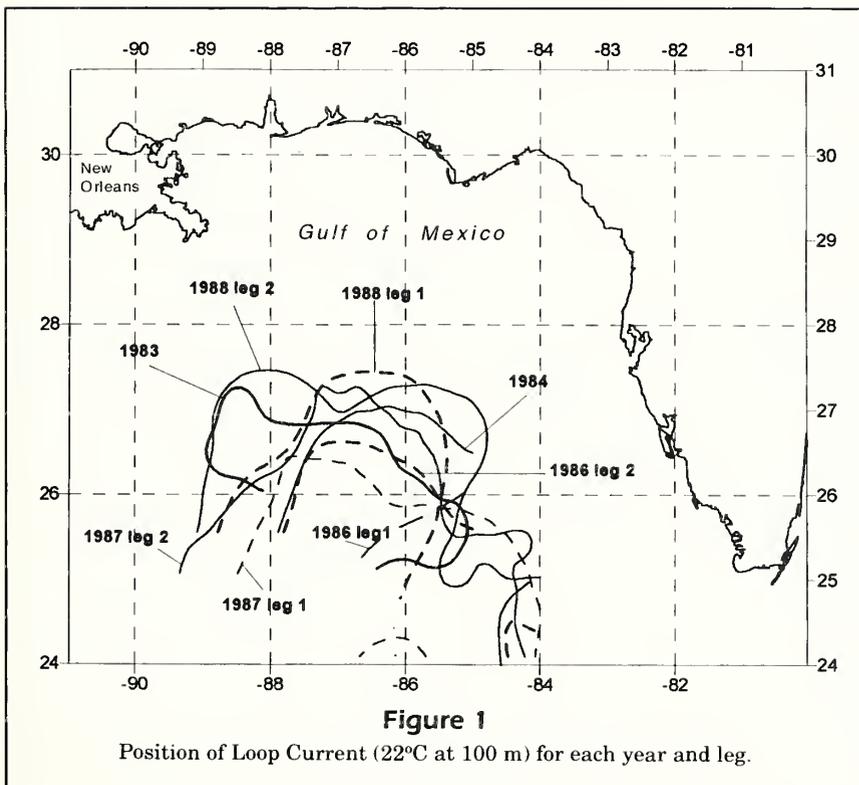
(Figs. 3–5). In 1987, and 1988, ring formation had taken place in September–November of the previous year. However, the Loop Current did not push north until the spring of the following year.

The presence or absence of the anticyclonic (warm-core) rings and their companion cyclones (cold-core) also strongly influences the circulation in the western Gulf of Mexico. Anticyclonic rings were present in the western Gulf of Mexico in all years, although their influence on the area sampled varied considerably. In 1983, 1984, and 1986, warm-core rings were present in the western Gulf. In 1987, and 1988, their influence was restricted to the southern part of the survey area, and in 1988, the temperature signature was evident only at 200 m. Cyclones were also present, although the number and position varied considerably from year to year. However, in some years it was not possible to resolve the circulation patterns because of difficulty in obtaining sufficient sample density.

### Distribution and abundance

In each year of this study, larval *C. pauciradiatus* were most abundant in temperature gradients: in the Loop Current front between the the 22° and 20° isotherms and in the gradients of 16–20°C associated with cold cyclonic rings. Abundance varied considerably from year to year and between

the eastern and western Gulf. Overall, abundance was greatest in 1983 and lowest in 1987. In 1983, *C. pauciradiatus* were present at 41 of 99 stations, with peak catches in the southeast of 162 and 188 individuals under 10 m<sup>2</sup> (Fig. 2). Thirty six of the 41 stations were in the eastern Gulf. In succeeding years, abundance was greatly reduced. In 1984, *C. pauciradiatus* were present at only 9 stations in the eastern Gulf (Fig. 3). This pattern continued through 1988, when *C. pauciradiatus* was found at no more than 9 stations and at as few as 4 (leg 2, 1988). Although *C. pauciradiatus* were present at a few stations inshore, most were found concentrated around the Loop Current, but not in its interior. Peak catches often occurred when a station coincided with a cyclonic meander at the Loop Current or in areas associated with cyclonic rings and cold water intrusions.



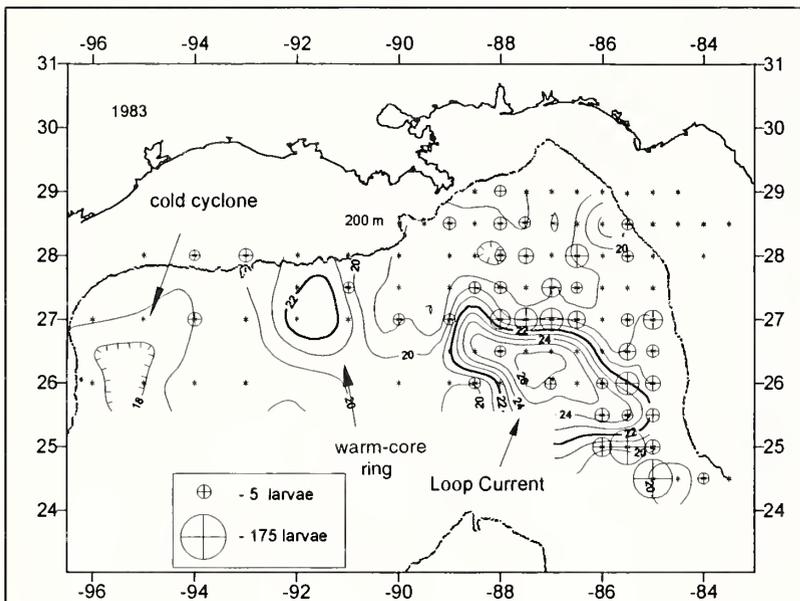
Distribution and abundance were considerably different in the western Gulf than in the eastern. Lar-

val *C. pauciradiatus* were found at few stations (except in 1984), and generally in smaller numbers. They tended to be found around the edge of rings (warm and cold) when present. The number of stations occupied in the western Gulf varied considerably from year to year and created difficulties for evaluating the available data and for constructing a meaningful interpretation of the physical oceanography. Both interannual and east-west differences, however, were evident. In 1983, *C. pauciradiatus* was abundant in large numbers at 36 stations in the eastern Gulf of Mexico but were present in only five stations west of 90°W. The following year they were taken at only 9 stations in the eastern Gulf but were found at 17 stations throughout the western Gulf, although in fewer numbers. They were found infrequently in the following years.

Total larvae (number under 10 m<sup>2</sup>) and plankton displacement volumes showed similar trends in abundance. Larval abundance and plankton displacement volumes were generally highest inshore and along the 100-m curve. However, at stations along the edge of the Loop Current and around the cold core rings, numbers of larvae and plankton were often equal to and sometimes exceeded values at the inshore stations.

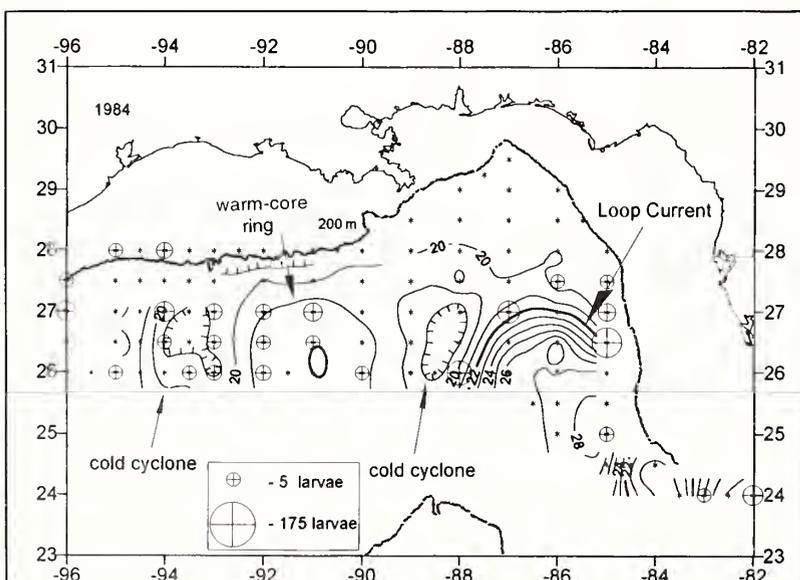
### Transects

Measurements at each station and satellite sea-surface temperatures indicate that in 1987, transects I, II, III, V, VI, and VII crossed surface fronts (Figs. 12 and 13), as did the only transect in 1988 (Fig. 14). Transect I crossed a warm filament extending north from the eastern edge of the Loop. Transect II was south of the origin of the warm filament. Transect III was made in a north-south direction, and transect V was the only transect to cross a cold-core cyclonic ring. Transect VI was on the cool side of the front and is discussed in detail by Richards et al. (1989). Transect VII began on the cool side of the Loop Current along longitude 87°W and crossed south into the northern edge of the Loop. Sea-surface temperatures increased from



**Figure 2**

NOAA ship *Oregon II* cruise 134, 25 April–16 May 1983. Temperature (°C) of northern Gulf of Mexico at 100 meters. ⊕ indicates stations where *C. pauciradiatus* was found. Number of larvae under 10 m<sup>2</sup> ranged from 4 to 188 individuals per station. Asterisk (\*) indicates CDT/XBT and bongo or neuston stations.



**Figure 3**

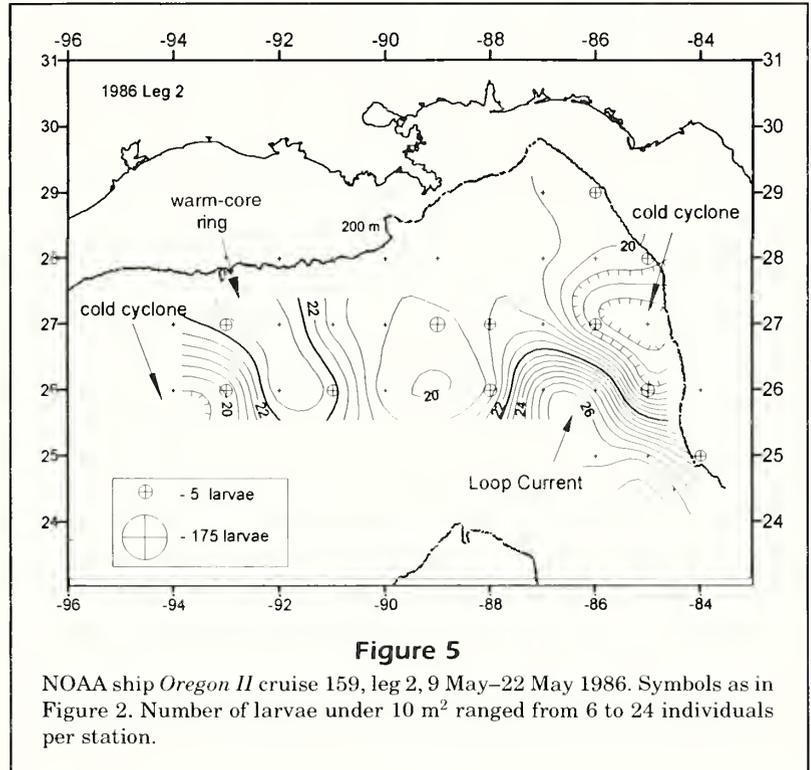
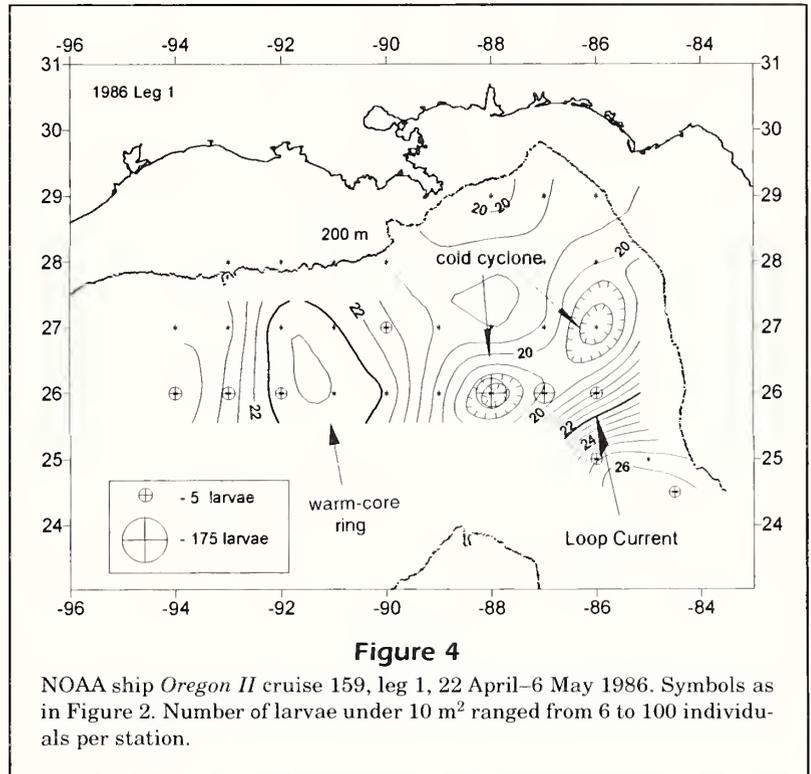
NOAA ship *Oregon II* cruise 143, 23 April–7 May 1984. Symbols as in Figure 2. Number of larvae under 10 m<sup>2</sup> ranged from 5 to 53 individuals per station.

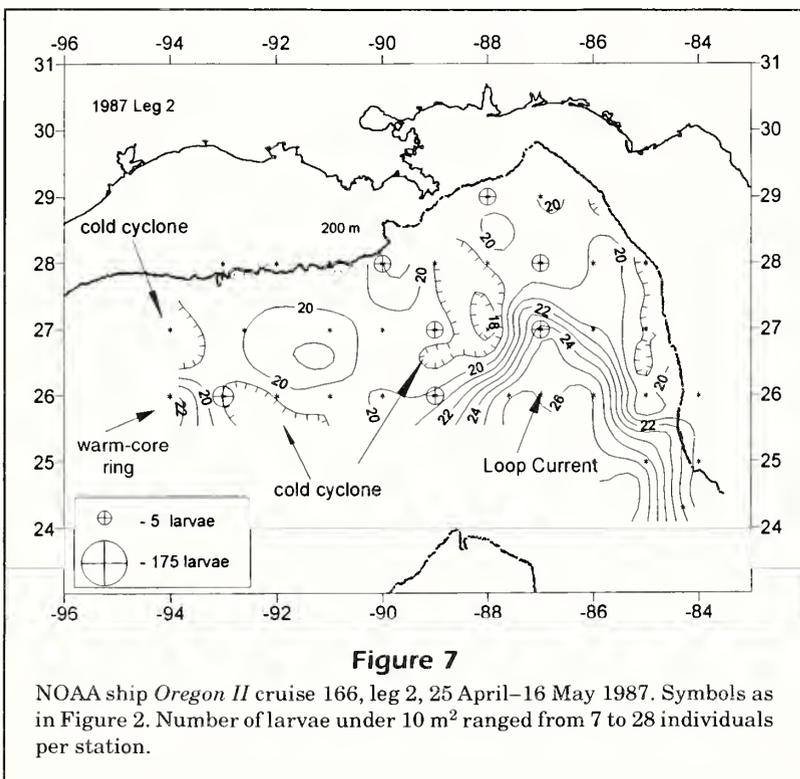
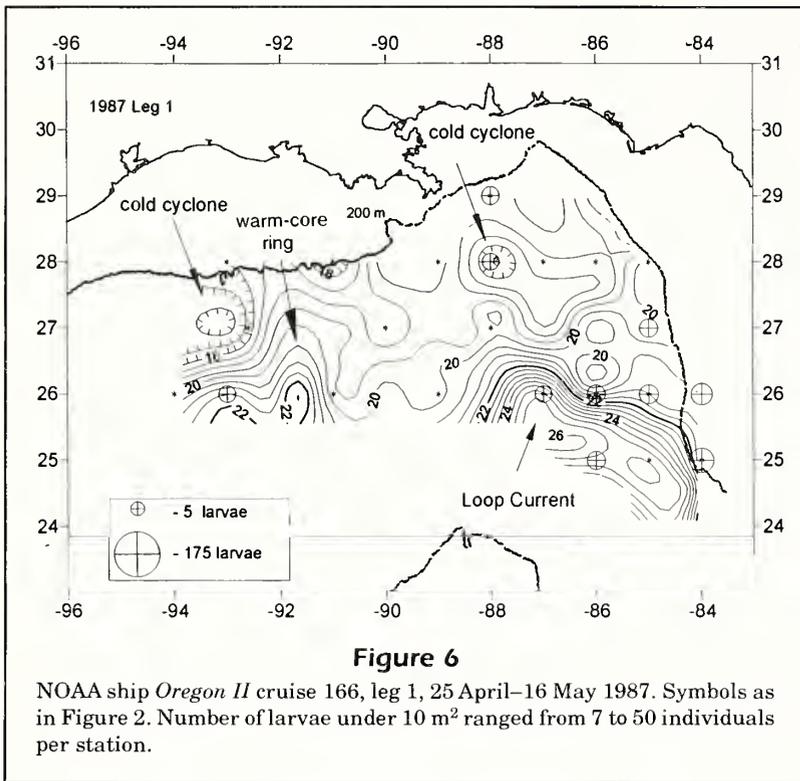
25.1°C to a high of 29°C in the middle of the transect. The transect in 1988 (Fig. 14) bisected a northward intrusion of the Loop Current between a cyclonic ring to the west and cooler shelf water to the east.

Figures 15 and 16 show the distribution of *C. pauciradiatus* in relation to SST fronts. Few were found in areas of peak temperatures, and the larvae were generally more abundant on the cool side, although SST was not as important as spatial orientation to the front. Peak abundances occurred at a variety of temperatures (21.5°C–28.7°C) but were always greatest in regions of greatest horizontal temperature gradients. This pattern can best be seen at transect III in 1987 and at the single transect completed in 1988. In transect III, *C. pauciradiatus* were found on both sides of the temperature front but were concentrated around the steepest slope. In 1988, the transect was much longer, and stations were 5 nautical miles apart (Fig. 16). *Cubiceps pauciradiatus* were absent until sea-surface temperatures began to increase significantly and peaked prior to maximum SST temperatures. Few *C. pauciradiatus* were found in the warm Loop Current waters or in the cooler continental shelf waters.

Plankton volumes, total larvae (under 10 m<sup>2</sup>), and larvae in the neuston net showed similar patterns (Fig. 17). Perhaps the most important of these is plankton volume because this may show an abundance of the potential prey of larval *C. pauciradiatus*. There was no significant correlation between abundance of larval *C. pauciradiatus* and plankton volume across all transects. However, few larvae were found in the second series of transects (V, VI, VII). When each transect was examined separately, II and III showed high correlations between *C. pauciradiatus* and plankton volume (0.829,  $P=0.0410$ , and 0.896,  $P=0.0002$ , respectively). In both these transects, larval *C. pauciradiatus* were present in consecutive stations, and the frontal features were well defined. Total larvae (number under 10 m<sup>2</sup>) were correlated with plankton volume when examined across all transects (0.236,  $P=0.0349$ ) but not when com-

pared transect by transect. Within each transect, correlations were highest in III and VII (0.822,  $P=0.0019$ , 0.697,  $P=0.017$ ). The results of the test be-





tween larval *C. pauciradiatus* and the close proximity of a temperature front across all cruises yielded a value of 34.128 with a *P*-value of <0.01, indicating

a very strong correlation between the presence of *C. pauciradiatus* and frontal zones. Of stations with *C. pauciradiatus*, 84.7% occurred at <5 km, and 15.3% were >5 km from a front. For all stations, the values were 51.8% and 48.2%, respectively.

Such tight spatial correlations with frontal zones are best seen by comparing the abundance of *C. pauciradiatus* in the transects with that in the surveys. In both legs of the 1987 survey a combined mean of 207 (under 10 m<sup>2</sup>) larval *C. pauciradiatus* were caught at 14 grid stations. Mean abundance averaged 2–3 fold higher in frontal zones, for 70% of these larvae (160) were taken at nine stations that were on or near a front. Only five stations with 47 larvae (30%) were not associated with an identifiable frontal structure.

In the same 1987 survey, 6 dedicated transects across the Loop Current caught a combined mean of 693 larvae (number under 10 m<sup>2</sup>). Larval *C. pauciradiatus* were caught at 22 bongo stations and another 91 were taken in neuston tows. If these numbers are combined, 94.5% were caught along frontal zones.

Results were similar in 1988. During the grid survey, 13 stations contained 343 *C. pauciradiatus*, only one of which was not associated with the front. This station accounted for only 1.7% of the larvae. In the one transect, 330 *C. pauciradiatus* larvae (under 10 m<sup>2</sup>) were found at 9 of 16 stations.

Further examination of these transects across the Loop Current and the grid stations shows that *C. pauciradiatus* occur primarily on the cold side of the temperature gradient. When the temperature gradient is well defined and *C. pauciradiatus* are present across the front, abundance is highly correlated with bulk plankton standing stocks (displacement volume maxima). The pattern can be clearly seen in transect III and in the transect completed in 1988 (Figs. 15 and 16). In transect III, *C. pauciradiatus* were not

present until sea surface temperature (SST) started to increase, and their abundance peaked just before an SST maximum. Bulk plankton displacement vol-

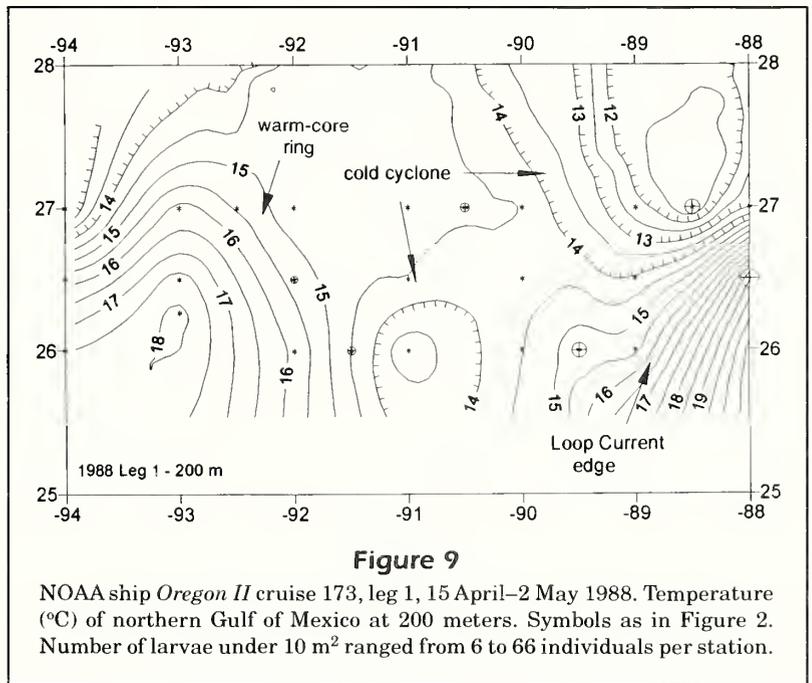
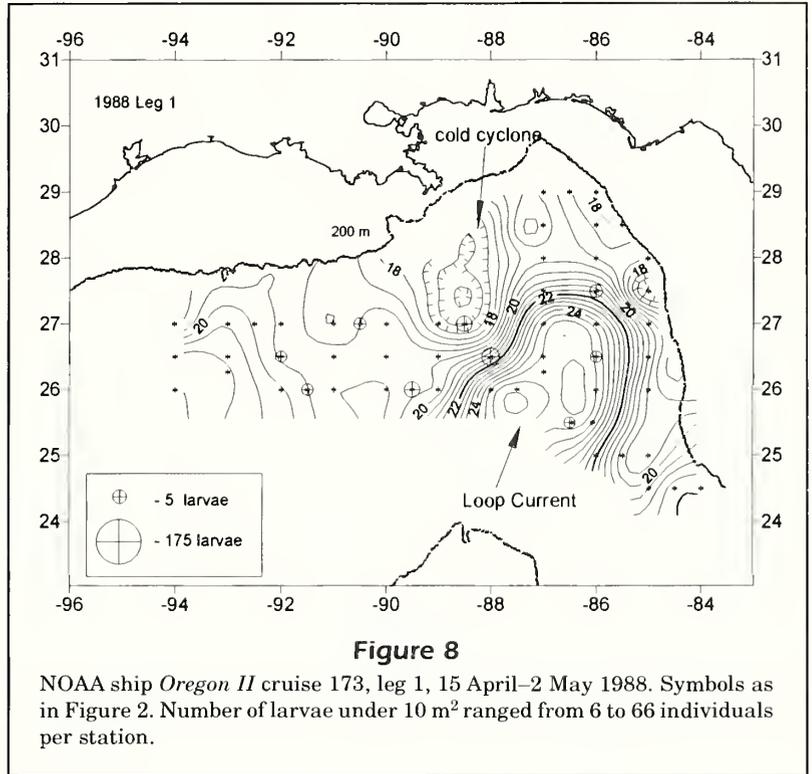
umes were also at or near maxima at the same stations where *C. pauciradiatus* were abundant. In the 1988 transect, with stations 8 km apart, the patterns of abundance clearly showed that *C. pauciradiatus* prefer the frontal interface between the Gulf common water over the continental margin and the subtropical underwater of the Loop Current. Larvae were not present until the SST began to increase, rose to a peak after the initial temperature increase, then declined sharply in the warmer waters. Bulk plankton displacement volumes did not follow an identical pattern but nonetheless peaked in mid-transect, just before those stations where *C. pauciradiatus* were most abundant. Such patterns may be a spatial consequence of the fact that this transect had stations 8 km apart rather than 3.2 km apart.

**Discussion**

In this study, the abundance and distribution of larval *C. pauciradiatus* were examined over five yearly surveys and seven transects. Analyses of survey data and transects depict a species whose adult spawning grounds and larval habitat are tied to sharp temperature gradients associated with the Loop Current in the eastern Gulf and to anticyclonic-cyclonic rings in the western Gulf of Mexico. Larval *C. pauciradiatus* were most abundant near a temperature front. It is apparent from these data and the transects made in 1987 and 1988 that this frontal environment is the preferred habitat and probable spawning area for the adult population of *C. pauciradiatus* in the Gulf of Mexico. Salenkov (1989) found that areas of highest density of juvenile and adult *C. pauciradiatus* in the tropical Atlantic Ocean were situated in zones of high production such as the edge of cyclonic gyres, the equatorial countercurrent, and the upwelling regions of the Sierra Leone Ridge.

In general, fish are often found aggregated at fronts (Brandt and Wadley, 1981; Nero et al., 1990). Currently there are two competing theories to explain this relationship: 1) that fish have thermal require-

ments and are attracted to temperature gradients, and 2) that fish are attracted to fronts because of the increased concentration of prey (Brandt, 1993). A third explanation may be that spawning in a frontal area may also provide optimal conditions for survival and growth of larvae and that increased concentra-



tion of prey may be beneficial for both larvae and adults.

The concentration of biomass at a front may be caused by advection (Olson and Backus, 1985) or by new production. Claustre et al. (1994) found evidence that suggested that the increased biomass found

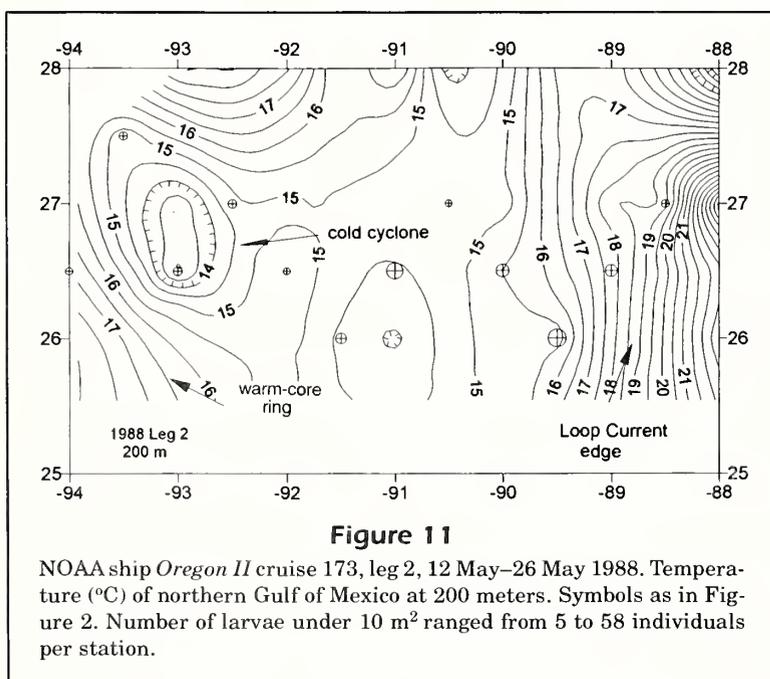
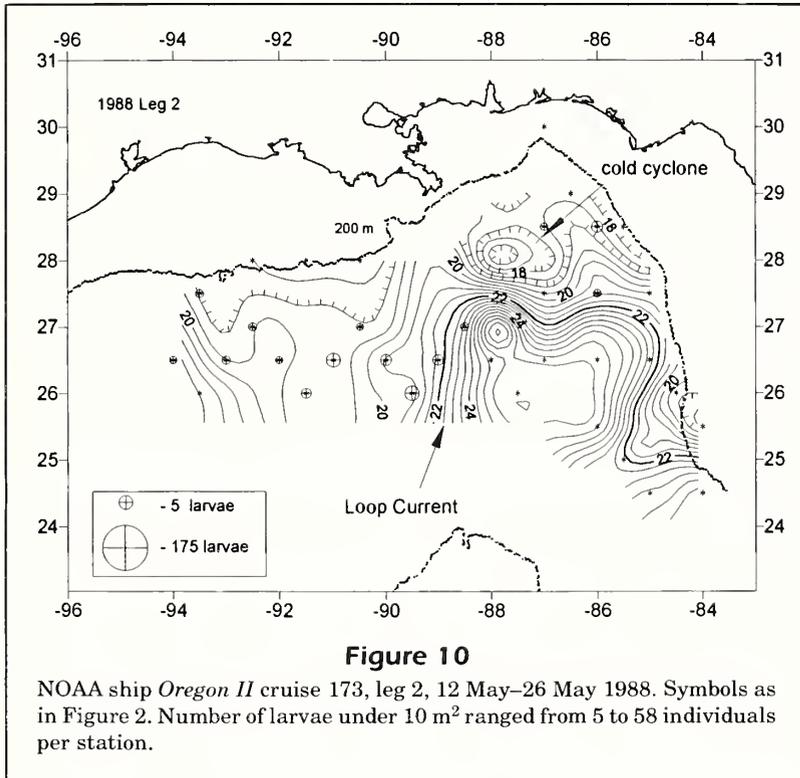
along a frontal region is due to new production. In the Mediterranean they found that frontal stations had phytoplankton biomass levels much higher than those at adjacent zones. These areas of high biomass were dominated by diatoms as opposed to flagellates and cyanobacteria found in typical Atlantic and Mediterranean waters. They concluded that the high biomass levels found at the front are not the result of purely passive accumulation but are the result of physically driven new production.

The Loop Current and the anticyclonic-cyclonic gyres found in the Gulf of Mexico provide an extensive (and dynamic) frontal habitat, and new production, coupled with coastal production advected off the shelf by ring-ring dipoles (Biggs and Muller-Karger, 1994), may play an important role in maintaining the productivity of these areas. It follows that stability and position of these mesoscale physical features may have a profound impact upon the spawning success of *C. pauciradiatus* and on subsequent recruitment to the stock.

Examination of the survey and transect data indicates considerable within- and among-year variation both in the position, shape, and intensity of the dominant physical oceanographic features as well as in the abundance of larvae and plankton along the front.

Variation in the distribution of larvae along the Loop Current is evident and is the result of the interaction of physical and biological processes. As Loop water flows north, it makes an anticyclonic turn to the east and south. The meanders and eddy separations that result can be thought of as forcing mechanisms for ecology and population structure through divergence and upwelling; likewise convergence results in passive accumulation of plankton and larvae and in the formation or dispersion of micro patches of prey.

Cold-core submesoscale (~50 km) cyclonic rings that form along the northern edge of the Loop Current would also be expected to affect both the physical and biological component. In the eastern Gulf, these closed cyclonic domes apparently form as a cold perturbation on the northern boundary of the Loop Current and move south along the Florida shelf (Vukovich and Maul, 1985; Vukovich,



1986). Large filaments of warm Loop Current water are advected north as much as 300 km in the flow confluence of cold-ring and Loop Current interactions. These cyclonic rings were noted in every survey and the biologically fine structure of one of these was sampled in transect V. Analysis of satellite SST images shows that at least one and often two cold perturbations are generally present along the northern edge of the Loop Current and along the west Florida shelf.

The formation and circulation patterns are not completely understood, but other authors have examined similar features elsewhere. In the western North Atlantic, Pollard and Regier (1990) described the structure and variability of the upper 300-m of fronts. They found that small-scale eddies, tens of kilometers in width, may have vertical velocities as large as tens of meters a day and may approach 50 m/d. Trantor et al. (1983) suggested that in the Tasman Sea, an upwelling-downwelling circulation cell existed at the interface between a cyclonic crescent of cool water and an anticyclonic ring. They reported high concentrations of surface chlorophyll, surface nitrate, and the copepod *Calinoides carcinatus* often associated with upwellings along the edge of a warm core eddy in the cool crescent. Both of these mechanisms act to inject nutrients into the photic zone. However, whether there is a direct effect of these cold-core eddies on larvae and zooplankton of Gulf of Mexico stocks is not clear. Plankton displacement volume and larval abundances are larger, especially in the area between the ring and Loop Current.

Transect V, which apparently bisected a cyclonic ring, had plankton displacement volumes higher than those of any of the other five transects (202 mL/1,000 m). The cold-core rings found to the south are usually associated with increased abundances of both zooplankton and larvae. Maul et al. (1984) found that a

cold ring that persisted for several months off the Dry Tortugas was associated with a 3-fold increase in catch per unit of effort of Atlantic bluefin tuna. A cyclonic ring was present in this position in 1983, 1984, and 1988. In fact, in 1983 the highest catches of *C. pauciradiatus* (188 under 10 m<sup>2</sup>) were found near this feature along with elevated plankton displacement volume and larval abundance.

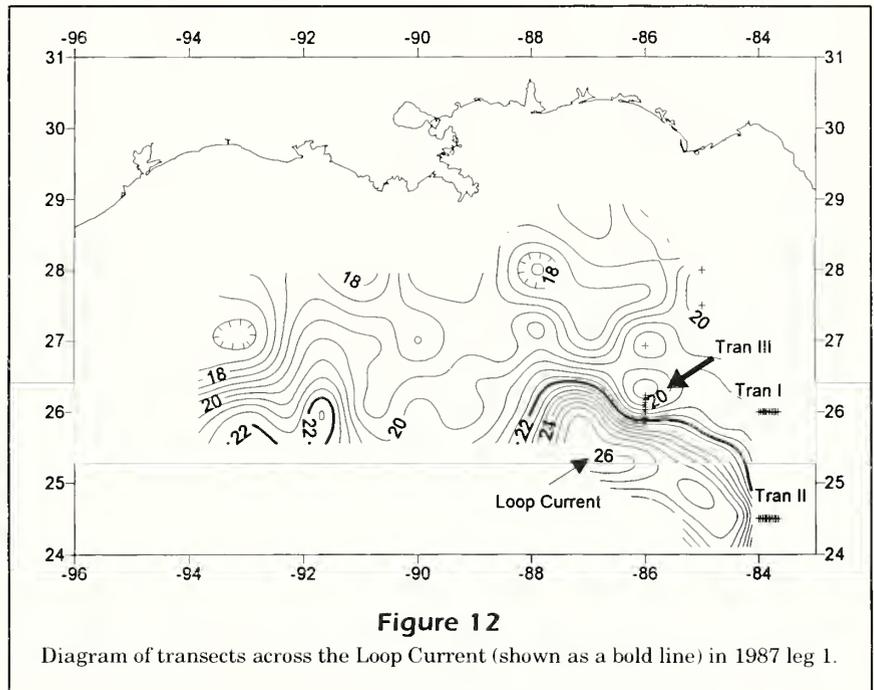


Figure 12  
Diagram of transects across the Loop Current (shown as a bold line) in 1987 leg 1.

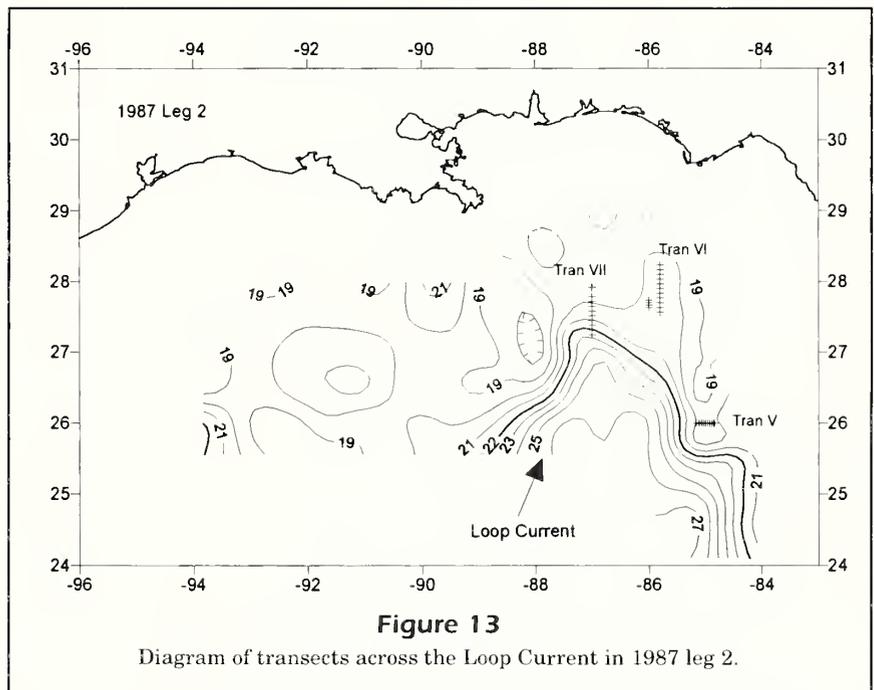
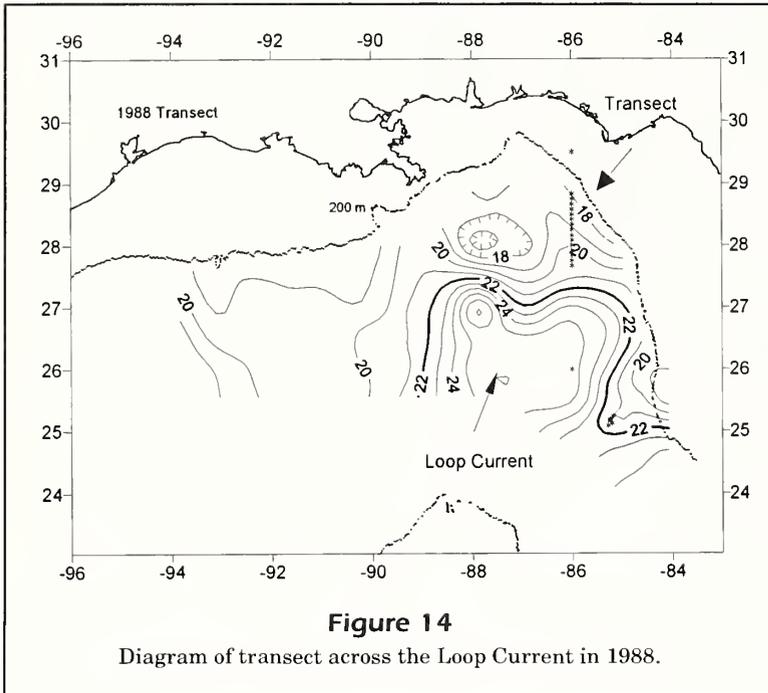


Figure 13  
Diagram of transects across the Loop Current in 1987 leg 2.

**Western Gulf of Mexico**

The situation in the western Gulf of Mexico is less clear owing to the complexity of the physical regime

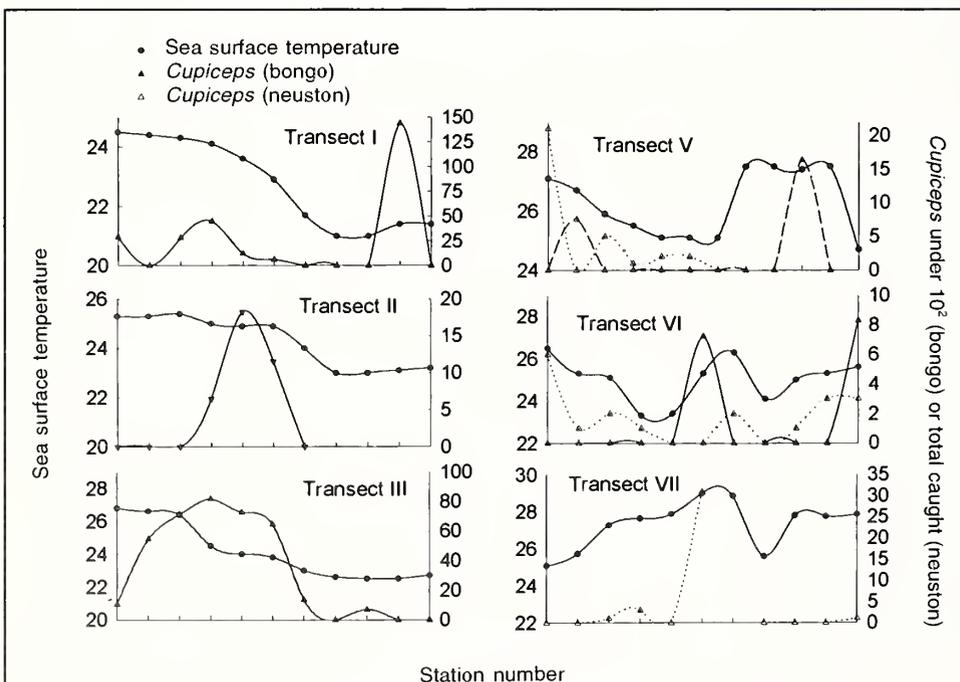


**Figure 14**  
Diagram of transect across the Loop Current in 1988.

on mesoscales of 10–100 km, coupled with the fact that fewer ichthyoplankton stations were made in this region. In this region there was no systematic effort to define the features that were present and to sample densely enough in a way that defined coarse scale (<10 km) distributions of larvae. Because surface thermal fronts associated with the warm-core rings are much more diffuse, they were difficult to characterize on the scale of this survey. Several research efforts have been directed to this area in an attempt to understand the complexities of the interaction among large anticyclonic rings generated by the Loop Current, cold dome cyclonic rings, and the continental shelf in the western Gulf of Mexico (Lewis, 1992). Only a few research scientists have dealt with biological components, but they suggest that the cyclonic circulation regions, similar to shelf waters, have a level of primary productivity much greater than that in surrounding oceanic waters (Biggs, 1988). Wormuth (1982) found 1.5–3 times more bulk plankton volume in cyclonic rings than in warm-core rings.

By comparison, the near surface waters of warm-core rings are oligotrophic and depleted in nutrients; therefore only near the ring edge were there significant concentrations of nitrate at 100 m and elevated primary production in the upper 100 m (Biggs, 1992). Because large anticyclonic rings are oligotrophic, it is unlikely that mobile oceanic predators, such as *C. pauciradiatus* or scombrids, would be found within its interior where prey is presumably scarce.

Despite the paucity of ichthyoplankton stations west of 89° in the Gulf, trends are evident. Foremost of these is that larval *C. pauciradiatus* appear more frequently in collections along the edges of both anticyclonic and cyclonic rings than in tows made inside warm eddies or over the adjacent continental margin. This find-



**Figure 15**

Plots of transects across the Loop Current in 1987. Figure shows SST and number of *C. pauciradiatus* in bongo nets (under 10 m<sup>2</sup>) and total number of larvae in the neuston net. Stations were two nautical miles apart.

ing can be seen in 1984 when there were two warm anticyclonic rings separated by a cold cyclonic ring at 26.5°N, 93.5°W (Fig. 3). *Cubiceps pauciradiatus* were distributed primarily around the edge of this cyclone and the leading edge of the incoming warm-core ring to the east.

In 1988 the situation was similar. Most *C. pauciradiatus* larvae were found west of 89°W. Although at 100 m, the Gulf waters west of the Mississippi River seem fairly homogeneous, at 200 m there was considerable structure evident in the water column (Figs. 8 and 10): in leg 1, the edge of a warm-core ring was evident at 26.5°N, 93°W with cooler water to the east (Fig. 9); by leg 2 there was a cold-core ring centered at 26.5°N, 93°W, approximately

83 km in diameter as defined by the 14°C isotherm at 200 m (Fig. 11). These cold-core cyclonic rings may have a life span of 6 months or more, and it is not unusual for there to be a weak temperature signature in the upper 100 m (Hamilton, 1992). In both legs of the 1988 survey west of 89°W, *C. pauciradiatus* were distributed around the edges of the two cold-core rings and in the cooler waters to the east of these features.

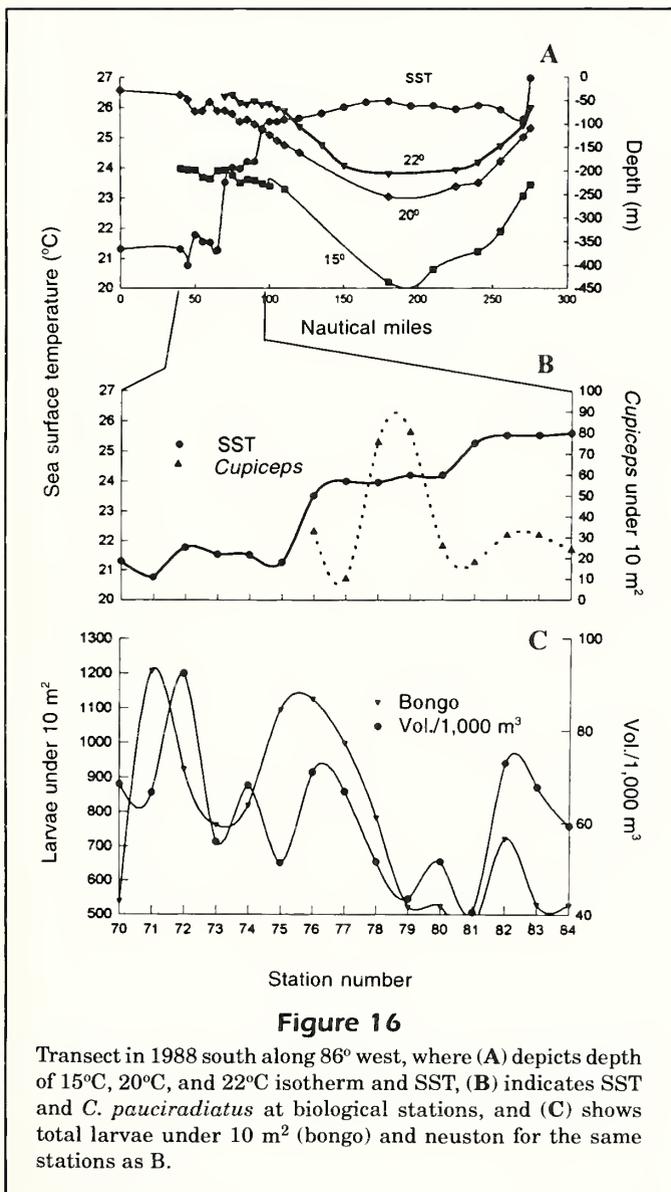
The basic pattern was the same in other years, but oceanographic features could not be as well defined as they were in 1984. First, the large anticyclonic rings often pass south of the survey area and thus are incompletely sampled. Second, after 1984, the number of stations in the western Gulf was reduced, and therefore the physical features could not be as densely sampled as they were the first two years. For a species such as *C. pauciradiatus*, the western Gulf of Mexico may at times provide a variety of frontal habitats, such as those that occurred in 1984. In other years the oceanographic conditions may be less favorable.

### Abundance

This year-to-year change in the number and position of mesoscale oceanographic features occurred in both the eastern and western Gulf of Mexico, both within years and between years; the abundance of *C. pauciradiatus* changed similarly. (Fig. 18). *Cubiceps pauciradiatus* larvae were abundant in 1983 but declined thereafter. These changes in abundance are the result of natural mortality because there is no fishery for this species; owing to their pelagic nature, they are taken only occasionally as bycatch by longliners.

Iles and Sinclair (1982) and Sinclair (1988) argued that the existence of a population "depends on the ability of the larvae to remain aggregated during the first few months of life," and that absolute abundance was a function of the physical oceanographic processes of the spawning areas. Population abundance depended on the horizontal size scale of the physical system underlying larval retention. Rothschild et al. (1989) suggested that the physical environment underlies the processes acting on recruitment variability. *Cubiceps pauciradiatus* do not spawn at a specific geographic location as do herring populations, but instead have spawning sites that appear to be tied to dynamic oceanographic features, namely to the Loop Current and its associated rings. Larvae are spawned at the frontal zones regardless of geographic position.

The physical oceanographic processes acting on the spawning sites of *C. pauciradiatus* change im-



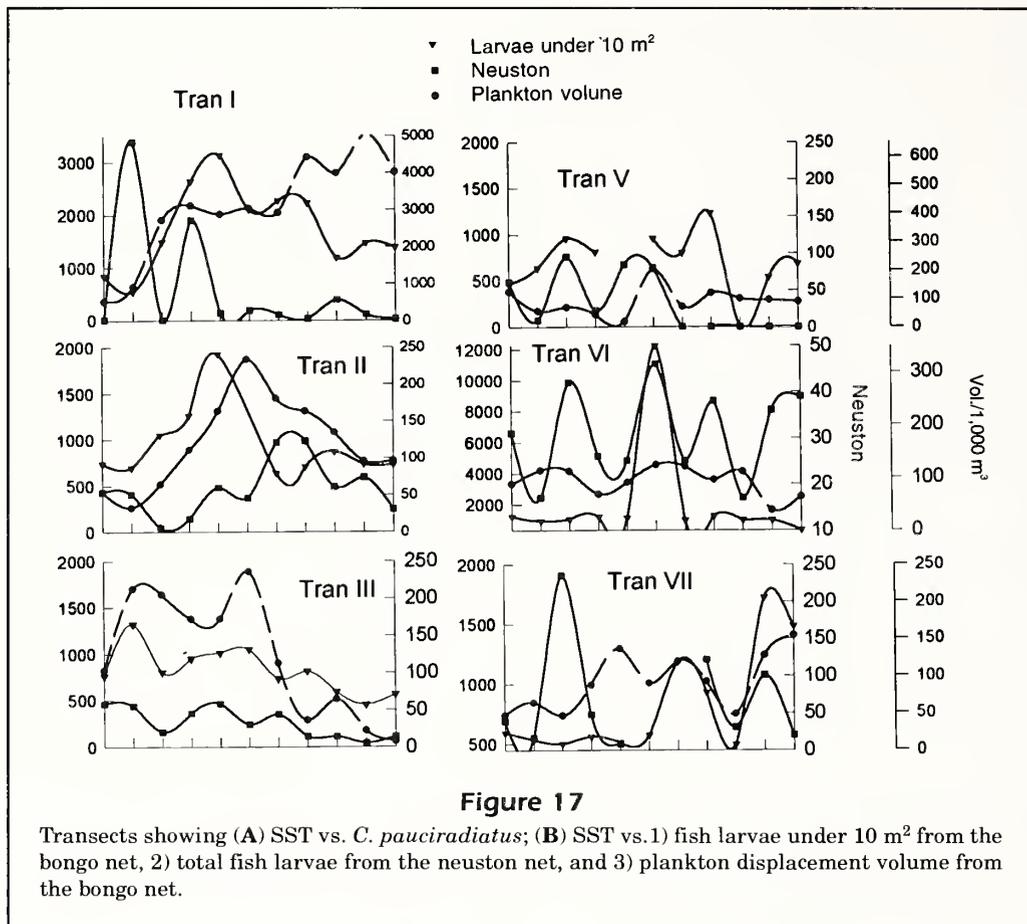


Figure 17

Transects showing (A) SST vs. *C. pauciradiatus*; (B) SST vs. 1) fish larvae under 10 m<sup>2</sup> from the bongo net, 2) total fish larvae from the neuston net, and 3) plankton displacement volume from the bongo net.

mensely from year to year and within time scales on the order of weeks. Figure 1 shows the range in variability of the northern perimeter of the Loop Current over the period studied. Not only do the size and north-south position of the front vary, but stability, length, shape, and intensity of the frontal system vary as well.

Major changes in position may occur within time scales of weeks. In 1986 and 1987, the Loop Current was positioned south of 26°N during the first leg of the survey. In both years the front pushed north before the second leg. In 1987 it moved almost 100 km north in 2 weeks. In other years, 1983, 1984, and 1988, the Loop Current was already at 27°N when the survey began. Over the years studied, the length of the northern perimeter of the Loop Current front ranged from 880 km in 1988 to 182 km in 1986 (as measured along the 22°C isotherm in the area sampled). Length of this front in each year is summarized in Table 2. However, length and position in itself says little about the frontal interface and biological response to hydrodynamic processes.

Larval *C. pauciradiatus* were most numerous in both the eastern and western Gulf of Mexico in 1983. In this year the Loop Current had pushed north in

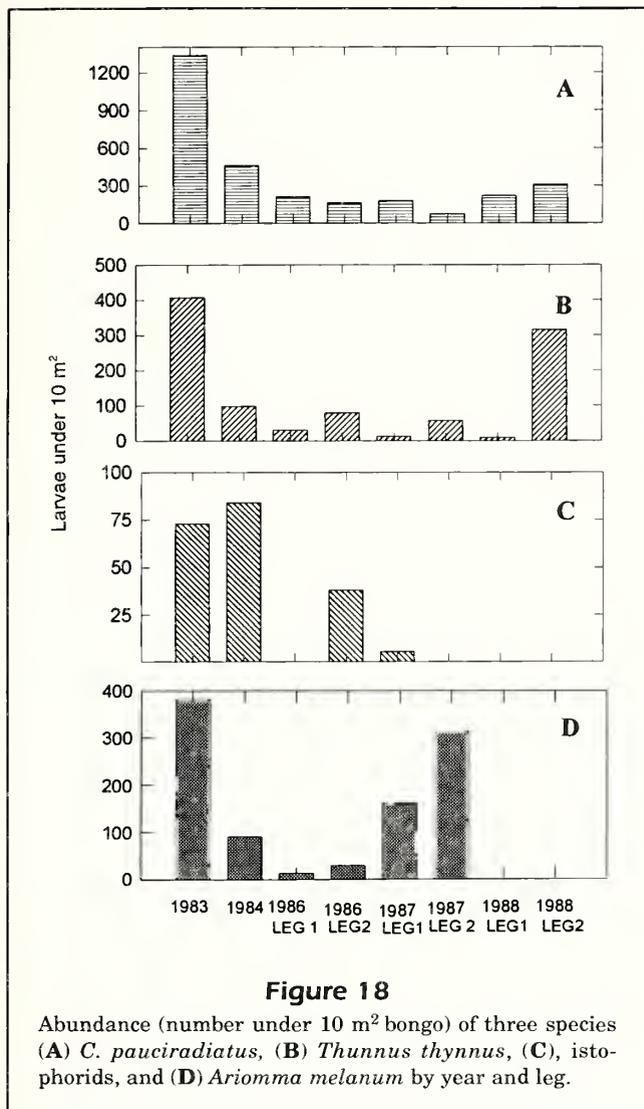
Table 2

Length of the Loop Current as measured at the 22° isotherm at 100 m and number of *C. pauciradiatus* larvae caught at grid stations (under 10 m<sup>2</sup>).

Date	Leg	Length in kilometers	No. of larvae under 10 m <sup>2</sup>
1983		647	1,445
1984		332	258
1986	1	182	179
1986	2	299	124
1987	1	564	170
1987	2	681	44
1988	1	697	219
1988	2	880	307

the winter and despite shedding a ring, had been stable for almost 6 months prior to the survey. Plankton displacement volumes were also high, averaging 100 mL/1,000 m<sup>3</sup> in the eastern Gulf and 130 mL/1,000 m<sup>3</sup> in the western Gulf.

By remaining in a relatively stable position, the biological components have time to respond to physi-



cal input of upwelling regions, and adults will be concentrated by increased abundances of prey (Atkinson and Targett, 1983). Turbulent mixing is increased at frontal areas; therefore, formation and dissipation of prey patches will also be affected. A recent model by Davis et al. (1991) shows that formation and abundance of microscale patches (<10 m) of prey can change the growth rate of larvae by up to 25%. Frontal regions, with convergent and divergent zones that result in biological gradients such as those found in the transects across the Loop Current, could be expected to lead to patchiness both across and along the front. This model predicts that even small variation in growth rates due to turbulence and patchiness can lead to large fluctuations in recruitment.

In contrast, the years following 1983 were characterized by a less stable Loop Current structure, and fish abundances were considerably reduced. In 1984

the Loop Current did not move north of 27°N until late March, only one month before the survey began (Fig 3). In 1986 the Loop was positioned well to the south, and little frontal habitat was available in the Gulf of Mexico to the spawning population (Figs. 4 and 5). The pattern was similar in 1987 and 1988 (Figs. 6–10). In both years the 22°C isotherm at 100 m began well to the south of 27°N, before pushing north in the spring.

It is not clear what factors are the important ones in driving such variations in abundance. Variance of fish populations is a natural occurrence and the subject of many studies on recruitment. However, the pattern of abundance during these five years was not unique to *C. pauciradiatus*. Aggregation of bluefin tuna (*Thunnus thynnus*), and billfish (Istiophoridae) are also closely tied to the location of thermal fronts (Roffer, et al., 1994). These unrelated pelagic species showed similar trends in larval abundance with peaks in 1983 and with decreases thereafter. *Thunnus thynnus* larval abundance closely paralleled *C. pauciradiatus* abundance, even showing an increase in 1988. *Ariomma melanum*, another stromateoid, showed similar trends in larval abundance (Fig. 18). These fish are benthopelagic over the continental margin, and most adults are taken in bottom trawls at depths of 225–480 m. This certainly indicates that the variation in the Loop Current position and stability may impact the abundance of a wide range of species and not just large pelagic predators such as bluefin and billfish.

Although stability and size of the frontal system are important to frontal species, other physical-biological interactions take place within the system on a variety of scales. The importance of each interaction will vary on time scales ranging from months to days because of the inherent nature of frontal systems. Rothschild et al. (1989) states that it is necessary to consider the “mechanisms of population stabilization at each phase of the life history.” Although it has sometimes been possible to tie population fluctuations to a certain physical event (Harris et al., 1992), it is more often the case that we are faced with a much more multidimensional problem.

That large-scale oceanographic processes have a major influence on the abundance of fish stocks has been recognized by a variety of authors. Harris et al. (1988) reported on several species and presented evidence that large-scale changes in the distribution of southern bluefin tuna result from large-scale changes in SST. Koslow (1984) argued that large-scale physical forcing rather than ecological and biological interactions is the dominant factor controlling the recruitment of several northwest Atlantic fisheries. Basin-scale circulation patterns may be the driving

influence on the distribution of larval *C. pauciradiatus* and other pelagic species.

In conclusion, this study indicates that larval *C. pauciradiatus* are a frontal species, concentrated at temperature fronts throughout the Gulf of Mexico. This is an important concept that needs to be recognized. Fronts and eddies are fundamental to the world oceans, and they are the only coherent feature in the Gulf of Mexico. The Loop Current itself acts as a zoogeographic barrier separating the oceanic and shelf species (Richards et al., 1993). Although it is not surprising that certain species have evolved to take advantage of this environment, it means that frontal species must be recognized as such in order to sample and manage these stocks effectively.

Spawning-stock biomass estimates are an important consideration in the management of pelagic species. These are inferred from the abundance of larvae taken at fixed stations (CalCofi, SEAMAP). If the target species is tied by life history parameters to a frontal system, then its apparent abundance will be affected by the extent of the frontal system found within the sampled area. For instance, if the frontal system within the area sampled is extensive, higher numbers of larvae are expected. Likewise, if only a small portion of the frontal system is sampled, then numbers are expected to be low, as was the case in 1986. Thus, the lower abundance estimates do not necessarily mean that there were fewer fish spawned that year but, rather, may indicate that they were spawned along the front outside the area sampled.

Accurate abundance estimates are a problem in the Gulf of Mexico because only the northern and eastern Gulf are sampled. The boundaries of the Loop Current pass through the Exclusive Economic Zone of the United States, Mexico, and Cuba, and the large anticyclonic rings often pass south of the area sampled. In addition, there is considerable variation in abundance along a temperature front. It is important to note that the presence of a frontal region in itself does not necessarily constitute a favorable habitat, but favorable spatial and temporal patterns of the front may determine the abundance of the larvae on a basin scale.

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**Abstract.**—The concept that depleted populations of marine fishes can be revitalized by releasing cultured fish is being tested in Hawaii. In this study we evaluated effects of interaction between release season and size-at-release on recapture rates of cultured striped mullet, *Mugil cephalus*, released into Kaneohe Bay, Hawaii. Over 90,000 cultured *M. cephalus* fingerlings, ranging in size from 45 to 130 mm total length, were tagged with binary coded-wire tags. Half were released in spring, the remainder in summer. In both seasons, releases were made in three replicate lots. In each replicate, five size intervals of fish were released at two nursery habitats in Kaneohe Bay. Monthly cast-net collections were made in 6 nursery habitats over a 45-week period to monitor recapture rates, growth, and dispersal of cultured fish.

Recapture rate was directly affected by the seasonal timing of releases. Greatest recovery of the smallest fish released (individuals <60 mm) occurred following spring releases and coincided with peak recruitment of similar-size wild *M. cephalus* juveniles. In contrast, recovery of fish that were <60 mm at release was very poor after summer releases. Overall survival was similar at both release sites. We hypothesize that survival of released cultured fish will be greater when releases are timed so that fish size-at-release coincides with modes in the size structure of wild stocks. To optimize effectiveness of stock enhancement as a fishery-management tool, pilot release-recapture experiments should be conducted to evaluate effects of release season on size-dependent recovery of released animals.

## Influence of release season on size-dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary

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With world fisheries yields in steady decline (FAO, 1992, 1994; WRI, 1996), renewed interest in stock enhancement based on marine hatchery-releases is growing worldwide. This interest follows the demonstrated impact of stock enhancement in freshwater systems (e.g. Foerster, 1936; Solazzi et al., 1991) and is coupled with rapidly expanding marine aquaculture technology (Colura et al., 1976; Roberts et al., 1978; Øiestad et al., 1985; Lee and Tamaru, 1988; Eda et al., 1990; Forés et al., 1990; Tilseth and Blom, 1992; Honma, 1993; Main and Rosenfeld, 1994; Ostrowski et al., 1996).

An experimental and careful approach is needed to ensure that hatchery releases in marine systems result, at best, in successful supplementation or replenishment of marine fish populations, or, at least, in a better understanding of system uncertainty (Peterman,

1991; Blankenship and Leber, 1995). This approach should involve an initial research phase with pilot releases to explore the effectiveness of release strategies. Before initiating a test release to evaluate stock-enhancement potential in Hawaiian coastal environments, initial research was focused on a series of release experiments to determine which release strategies yielded greater survival of hatchery fish in the wild. This approach provided a more powerful field test of the marine stock-enhancement concept by using prior knowledge about the effects of 1) fish size-at-release, 2) release habitat, and 3) release season on growth and survival (Cowx, 1994; Blankenship and Leber, 1995; Leber et al., 1996).

Evidence is mounting that release habitat, season, and size-at-release, can substantially affect success of marine hatchery releases (e.g. Tsukamoto et al., 1989; Svasand

and Kristiansen, 1990; Stoner, 1994; Leber, 1995; Willis et al., 1995). Pilot releases have shown that survival rates following hatchery releases of striped mullet, *Mugil cephalus*, in Hawaii (Leber and Arce, 1996; Leber et al.<sup>1</sup>) and of queen conch, *Strombus gigas*, in the Caribbean (Stoner, 1994) were strongly affected by release habitat. Pilot releases with *M. cephalus* have also shown differential survival based on size-at-release. Pilot releases conducted during summer and fall in Maunaloa Bay, Hawaii, (southern exposure) and during summer in Kaneohe Bay (eastern, windward exposure) have shown poor survival of cultured *M. cephalus* smaller than 70 mm total length (TL) at the time of release, compared with survival of larger-size individuals (e.g. 70 to 130 mm TL, Leber, 1995). In this study, we document a substantial effect of the seasonal timing of releases upon size-at-release-dependent recapture rates (number recaptured/number released) of cultured *M. cephalus*.

## Materials and methods

### Hatchery releases

Striped mullet were spawned at The Oceanic Institute in 1991 and reared to fingerling size. Batches of striped mullet eggs were hatched approximately every 5–6 weeks over a 5-month period and reared through three stages in cylindrical tanks. Larvae from each batch were hatched and cultured in 5,000-L conical-bottom tanks for 45 days. Stage-1 juveniles (i.e. postlarvae 45 days old, 20 mm total length [TL]) were transferred to 8,000-L tanks and reared for 40 days to stage-2 juveniles (i.e. the age and size at which we typically transfer fish out of nursery tanks into larger growout tanks, 85 days old, around 40 mm TL). Stage-2 juveniles were transferred to 30,000-L tanks and reared to tagging size (45 to 130 mm TL).

A factorial-design release-recapture experiment was performed to compare interactive effects of release season and fish size-at-release upon growth and survival of about 90,000 cultured striped mullet in the wild. During the period 5 May through 17 May 1991, and again from 12 July through 26 July 1991,

juvenile striped mullet, ranging in size from 45 to 130 mm TL, were harvested from culture tanks and transferred to 40,000-L holding tanks. These fish were graded into five size groups, tagged, then released into Kaneohe Bay; half were released in May, the other half in July.

To identify experimental treatment conditions, all released fish were tagged with binary coded-wire tags (Jefferts et al., 1963). Tags identified release season, release site, size-at-release (SAR), release lot (date), and number of fish per treatment condition. Fish were tagged in batches, with a different code for each season-site and SAR-lot combination ( $2 \times 2 \times 5 \times 3 = 60$  batch codes). The five size groups released were 45–60 mm; 60–70 mm; 70–85 mm; 85–110 mm; and 110–130 mm TL.

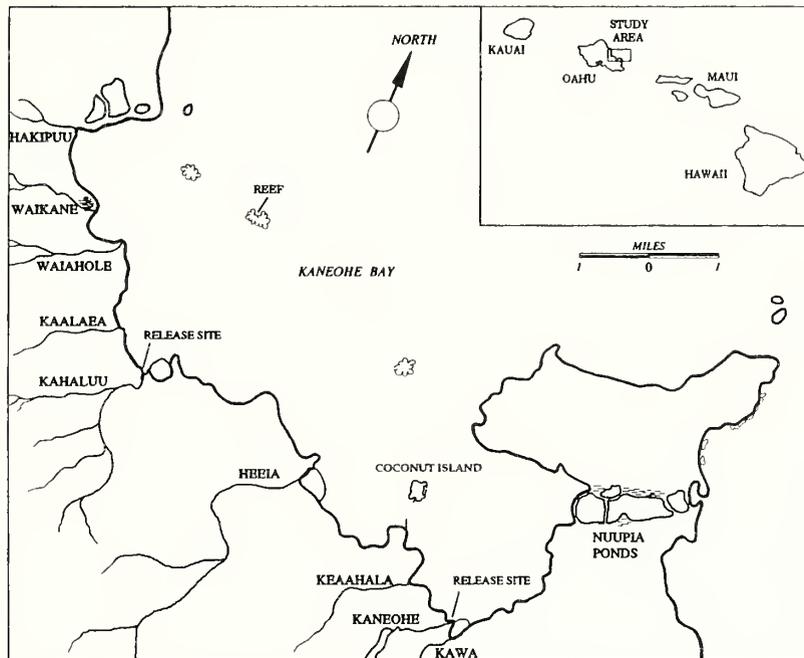
Tags were implanted in the snout area with an automatic injector with head molds designed specifically for striped mullet. Previous studies have shown a coded-wire tag retention rate of 97% for striped mullet over a 6-month period (Leber, 1995). To verify tag-retention rates in this study, at least 5% of the fish tagged for each release lot were randomly subsampled prior to each release. The subsamples were retained in tanks for up to 6 months to check tag retention. Subsampled fish were not released.

### Release statistics

During May and July 1991, 90,817 juvenile striped mullet were tagged and released into Kaneohe Bay. Numbers of fish released varied among size groups but were held nearly constant among release lots and between release sites and seasons (Table 1). At least 7,500 tagged fish were released in each of 12 release lots. There was size variation in all batches of mullet reared for this study. However, the primary difference among size-at-release groups was fish age.

For each season and SAR treatment combination, the experiment was replicated at two sites in Kaneohe Bay, and within each site, three replicate release lots were made (Table 1). The release lots were introduced into the bay over a 3-week period during both seasons (spring and summer). In each season, releases were made simultaneously at the inlets of two primary striped mullet nursery habitats, Kahaluu Stream and Kaneohe Stream. Kahaluu Stream is located in the north end of Kaneohe Bay (Fig. 1). This tributary is fed by several stream systems that originate in the Ko'olau mountain range. Kahaluu Stream expands into a lagoon about 300 m upstream. The mouth of Kaneohe Stream is 11.6 km southeast of Kahaluu Stream. Kaneohe Stream is also a Ko'olau mountain drainage system. Selection of release habitats in the vicinity of fresh-water tribu-

<sup>1</sup> Leber, K. M., D. A. Sterritt, R. N. Cantrell, and R. T. Nishimoto. In press. Contribution of hatchery-released striped mullet, *Mugil cephalus*, to the recreational fishery in Hilo Bay, Hawaii. In K. Lowe (ed.), Proceedings of the first biennial symposium for the Main Hawaiian Islands Marine Resources Investigation. Technical Rep. 96-01. Hawaii Department of Land and Natural Resources, Division of Aquatic Resources, Honolulu, HI.



**Figure 1**

Map of the study area in Kaneohe Bay. Releases were conducted near the mouths of Kahaluu Stream and Kaneohe Stream. Recapture collections were conducted in streams throughout the Bay and on reef flats in the vicinity of stream mouths.

**Table 1**

Summary statistics for 90,817 striped mullet, *Mugil cephalus*, tagged and released in the 1991 pilot experiment to evaluate release-season effects on hatchery releases in Kaneohe Bay. Unique batch codes were used to identify fish from each cell in the matrix. Spring release lot 1 occurred on 3 May, lot 2 on 10 May, and lot 3 on 17 May. Summer release lot 1 occurred on 12 July, lot 2 on 19 July, and lot 3 on 26 July.

Release site	Size at release	Release season							
		Spring				Summer			
		Release lot			Total	Release lot			Total
1	2	3	1	2		3			
Kahaluu Stream	45-60 mm	2,090	2,090	2,088	6,268	2,081	2,058	2,084	6,223
	60-70 mm	2,090	2,089	2,087	6,266	2,082	2,090	2,085	6,257
	70-85 mm	2,054	2,090	2,090	6,234	2,084	2,088	2,085	6,257
	85-110 mm	1,119	959	990	3,068	1,128	956	1,296	3,380
	110-130 mm	150	323	386	859	151	323	76	550
	Subtotal	7,503	7,551	7,641	22,695	7,526	7,515	7,626	22,667
Kaneohe Stream	45-60 mm	2,065	2,087	2,089	6,241	2,281	2,088	2,001	6,370
	60-70 mm	2,070	2,089	2,088	6,247	2,044	2,086	2,086	6,216
	70-85 mm	2,088	2,090	2,088	6,266	2,047	2,088	2,090	6,225
	85-110 mm	1,127	958	990	3,075	1,152	959	1,298	3,409
	110-130 mm	147	323	386	856	151	323	76	550
	Subtotal	7,497	7,547	7,641	22,685	7,675	7,544	7,551	22,770
Grand total		15,000	15,098	15,282	45,380	15,201	15,059	15,177	45,437

taries was based upon results from earlier releases (Leber, 1995; Leber and Arce, 1996; Leber et al.<sup>1</sup>) where release habitat appeared to be critical to survival.

All releases were conducted at about noon or early afternoon. The successive weekly release lots spanned the rising tide (lot 1 on a low tide; lot 2 on a rising tide; lot 3 on a low tide in both seasons). Releases were made near the shoreline in water from 0.5 to 1.5 m deep. There was a wider range of salinities at the southernmost site (Kaneohe Stream; Table 2).

## Monitoring

Beginning 21 May 1991, we monitored abundances of hatchery-released and wild *Mugil cephalus* in Kaneohe Bay monthly for 11 months by sampling with cast nets. Recaptured tagged fish were removed from collections and returned to the laboratory for tag analysis. The first field collection after spring and summer releases began 2 weeks after the middle release lot (lot 2) was planted.

Each monthly collection was conducted over approximately a 2-week period. Collections were made at six nursery sites (sampling stations) within Kaneohe Bay. Collections were made for about an 8-hr period during the day at each sampling station. Stations were established in the vicinity of documented striped mullet nursery habitats at various tributaries located throughout the bay (Leber, 1995; six streams in Fig. 1: Waiahole, Kaalaea, Kahaluu, Heeia, Kealahala, and Kaneohe Streams).

To standardize collection effort, at each station two substations were sampled—one substation was established upstream, the other near the mouth of the tributary. Within substations, 15 cast net throws were made. To broaden the range of microhabitats and fish size-ranges sampled, two sizes of cast nets were employed. Ten of the 15 casts per substation were made with a 5-m diameter, 10-mm mesh net, and 5 casts were made with a 3-m diameter, 6-mm mesh net. Thus, a total of 180 casts were made each month.

Placement of net samples was stratified over observed schools of striped mullet juveniles. Completely random sampling in preliminary collections yielded few wild striped mullet and very few tagged individuals. Striped mullet schooled in fairly low densities within these clear-water nursery habitats, and our stratified-random collections targeted those schools. Nevertheless, the sample data used to determine proportions of tagged versus untagged mullet were randomly distributed because we had no a-priori indication that schools, once sighted, contained tagged individuals.

All striped mullet sampled were measured and checked for tag presence with a field-sampling detector (Northwest Marine Technology, Inc., Shaw Island, WA). Tagged fish were placed on ice and returned to the laboratory where the tags were recovered, and each fish was weighed and measured. Untagged fish were held at the field site in oxygenated water and then released after the 30 cast-net samples were completed.

Treatment identifications were made on the basis of the tags retrieved from recaptured fish. In the labora-

**Table 2**

Physical data recorded at the two release sites in Kaneohe Bay, Kahaluu Stream and Kaneohe Stream, for each release lot (release date) of striped mullet, *Mugil cephalus*. IN = incoming.

Season and release site (stream)	Release date	Tide stage	Secchi (cm)	Depth (cm)	Temperature (°C)		Salinity (‰)		
					Top	Bottom	Top	Bottom	
<b>Spring</b>									
Kahaluu	5/03/91	IN 0.2'	51	59	33	32	11	12	
Kaneohe	5/03/91	IN 0.5'	110	120	27	27	6	32	
Kahaluu	5/10/91	IN 0.8'	70	75	29	26.5	15	27	
Kaneohe	5/10/91	IN 1.6'	92	92	26	27	4	35	
Kahaluu	5/17/91	IN 0.0'	25	40	29	29	24	26	
Kaneohe	5/17/91	IN 0.0'	55	80	28	28.2	3	15	
<b>Summer</b>									
Kahaluu	7/12/91	IN 0.8'	57	57	27.5	28	11	28	
Kaneohe	7/12/91	IN 0.8'	75	122	27	27	11	35	
Kahaluu	7/19/91	IN 1.6'	85	100	25.3	27	10	19	
Kaneohe	7/19/91	IN 1.7'	115	115	26	27	4	35	
Kahaluu	7/26/91	IN 0.7'	40	70	27.6	28	12	20	
Kaneohe	7/26/91	IN 0.9'	65	90	26.2	26.5	6	34	

tory, tags were located and extracted with a field-sampling detector. Tags were decoded by using a binocular microscope (at 40×). To verify tag codes, each tag was read twice (once each by two different research assistants).

Data were analyzed with Systat (Wilkinson, 1990). A randomized-block factorial analysis of variance (ANOVA) was used to compare means. Systat Basic was used to write tag decoding algorithms. For each recaptured fish, the algorithms identified batch size, release date (lot), release site, size-at-release, and release season from the tag codes identified in the laboratory. An error-check algorithm was also written to help identify errors that may have been made in reading tag codes. Variance estimates are expressed throughout as standard errors (with  $n$ =number of release lots).

## Results

### Tag retention

Tag retention in 4,799 individuals subsampled and held in tanks for six months averaged 98.6% (0.4% SE). With one exception (92.4%), all retention rates within release lots exceeded 97%. No significant tag loss was observed in any group later than 1 month after tagging. This is a normal tag loss rate for coded-wire tags (Blankenship, 1990).

### Recapture summary

Of the fish released, 2,511 cultured striped mullet were recaptured in monthly cast-net samples at nurs-

ery habitats. Based on the 98.6% average tag retention rate, the number of cultured fish recaptured can be extrapolated to 2,546, or 2.8% of the fish released. About 6.6% (166) of the tags taken from the 2,511 recaptured fish were lost during extraction.

Total number of tagged fish in samples decreased over the 11-month monitoring (Table 3) but was fairly constant during the last 7 months of the study (when numbers of tagged fish ranged from 49 to 134 individuals). Total number of tagged fish collected was greater at Kaneohe Stream. However, this pattern varied considerably from month to month, and most of those fish were collected within 1 month after the May and July releases.

Tagged fish represented between 8% and 48% of the striped mullet captured in monthly samples (from all stations combined; Table 3). Percentage of cultured fish in samples was greatest at Kaneohe Stream, where contribution rates declined from 76% following the May release to 41% by the end of the study. Although numbers of tagged fish collected at Kahaluu Stream were often similar to those for Kaneohe Stream, there were always greater numbers of wild fish in collections at Kahaluu Stream (Table 3).

### Impact of release season

**Recapture rates and contribution rates** When size-at-release was not considered, the contribution of cultured fish to recruitment appeared to be unaffected by release season. Release season had no significant effect on mean recapture rates over time (ANOVA,  $P>0.54$ , data from all size-at-release intervals combined). After 3 months in the wild, mean numbers of cultured fish in samples varied between

**Table 3**

Numbers of wild and hatchery-released striped mullet, *Mugil cephalus*, recovered in cast-net samples made in Kaneohe Bay. Proportions of hatchery fish were determined by the presence of a coded wire tag.

Collection site	Source	1991								1992			Total	Mean	Standard Error
		May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar			
All stations in Kaneohe Bay	Wild	985	1,099	1,439	453	659	722	952	550	824	864	310	8,857	805.2	95.7
	Hatchery	912	194	551	184	101	117	134	76	116	77	49	2,511	228.3	79.9
	% Hatchery	48.1	15.0	27.7	28.9	13.3	14.0	12.3	12.1	12.3	8.2	13.6		18.7	3.5
Kahaluu Stream (Release site in N. Kaneohe Bay)	Wild	265	201	303	137	260	318	331	158	350	184	134	2,641	240.1	24.3
	Hatchery	184	122	237	25	20	56	91	25	46	15	18	839	76.3	22.7
	% Hatchery	41.0	37.8	43.9	15.4	7.1	15.0	21.6	13.7	11.6	7.5	11.8		20.6	4.1
Kaneohe Stream (Release site in S. Kaneohe Bay)	Wild	207	87	264	88	44	85	115	52	85	87	41	1,155	105.0	20.9
	Hatchery	653	64	270	135	43	52	35	45	55	45	28	1,425	129.5	56.5
	% Hatchery	75.9	42.4	50.6	60.5	49.4	38.0	23.3	46.4	39.3	34.1	40.6		45.5	4.2

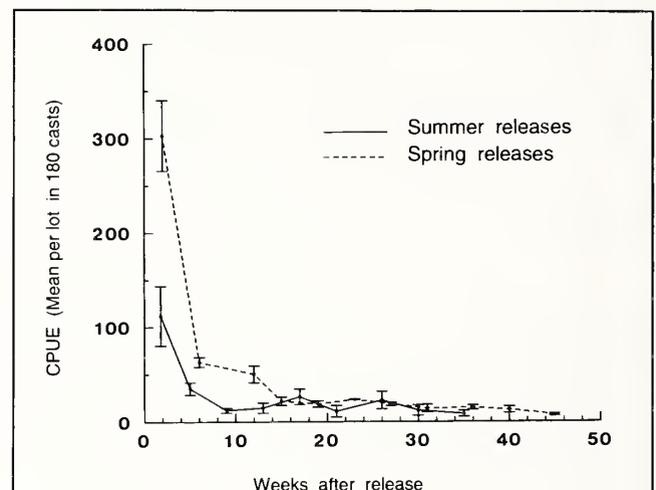
about 10 and 27 individuals per release lot throughout 36 weeks (Fig. 2). However, as shown below, recapture rate was in fact dependent upon the interactive effect of release season and size-at-release. (Note: for evaluating the effect of release-season, data can be compared only through weeks 35 or 36 following releases, the length of time fish were monitored after summer releases; by the end of the study, fish released in the spring had been in the wild for an average of 45 weeks, 10 weeks longer than those released in summer.)

**Dispersal patterns** There were no clear seasonal trends in dispersal patterns. Cultured striped mullet showed a strong tendency to remain in the vicinity of release sites, regardless of release season or size-at-release. Few of the 2,511 tagged fish recovered in samples had moved into other nursery habitats in the bay. The only significant movements observed were from release habitats into the streams located immediately to the north of each release site (Table 4). This pattern was repeated after spring and summer releases. There were isolated cases of fish moving from one release habitat to the other, as well as movement from release habitats into other nursery habitats in the bay. But the magnitude of dispersal out of release habitats and beyond the streams immediately north of those sites was negligible. Overall,  $90.8\% \pm 3.1\%$  (SE) of the cultured fish collected through 36 weeks in the wild were recovered at the nursery habitats into which they had been released.

**Growth** Growth after spring releases was similar to growth following summer releases. Length in-

crease following releases is plotted in Figure 3 for fish from the 70–85 mm treatment group, which was representative of all 5 size-at-release groups. There was little change in mean length during winter months (from September 1991 through February 1992; weeks 20–45 following spring releases in Fig. 3).

**Release season effect on recapture frequencies among size-at-release groups** Recapture frequencies ( $[\text{number recaptured} / \text{number released}] \times 100\%$ ) within size-at-release intervals revealed an obvious



**Figure 2**

Mean number of tagged cultured fish in samples following spring and summer releases into Kaneohe Bay. Data are means per release lot ( $\pm$  standard error [SE];  $n = 6$  lots per season [3 at each release site]).

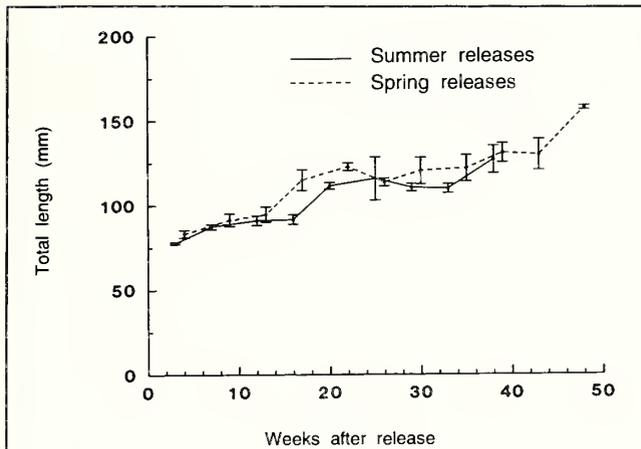
**Table 4**

Movement patterns following 1991 releases in Kaneohe Bay. Release season and release site are identified for tagged fish recovered at the various collection (recapture) sites throughout the Bay. Recapture sites (and distances travelled) are ordered geographically within collection dates, from the northernmost site (Waiahole Stream) to the southernmost site (Kaneohe Stream) at which tagged fish were collected (see Fig. 1). Totals for spring releases represent those through week 36; totals for summer releases are those through week 35. To compare results between release seasons over a similar time frame, data are excluded for weeks 40 and 45 after spring releases.

Release season and recapture site	Kahaluu Stream		Kaneohe Stream		Release season and recapture site	Kahaluu Stream		Kaneohe Stream	
	<i>n</i>	Distance (km)	<i>n</i>	Distance (km)		<i>n</i>	Distance (km)	<i>n</i>	Distance (km)
<b>Spring release</b>					<b>Summer release</b>				
Waiahole	1	3.05	0	15.00	Waiahole	0	3.05	0	15.00
Kaalaea	92	0.98	0	12.59	Kaalaea	14	0.98	0	12.59
Kahaluu	509	0	1	12.04	Kahaluu	298	0	0	12.04
Heeia	0	5.55	1	5.88	Heeia	0	5.55	0	5.88
Keaahala	0	10.61	31	1.08	Keaahala	1	10.61	57	1.08
Kaneohe	1	11.58	947	0	Kaneohe	0	11.58	392	0
Total	603		980		Total	313		449	

and direct relationship between size-at-release and recapture rate (Fig. 4)—when fish were released in summer, recapture frequency was almost directly

proportional to size-at-release within 1 month after release. This pattern was evident throughout the rest of the study. In contrast, size-at-release had much less effect on recapture frequencies for fish released 10 weeks earlier, in the spring (Fig. 5).

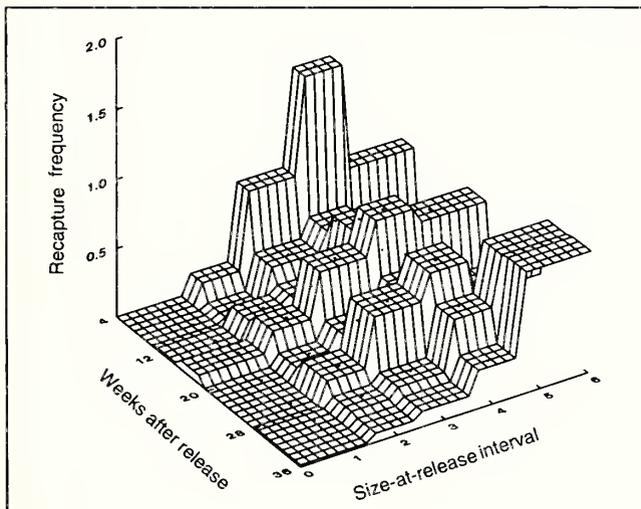


**Figure 3**

Mean total length ( $\pm$  SE) of cultured fish recaptured in collections made following spring and summer releases into Kaneohe Bay. Data are for the 70–85 mm size-at-release interval. Length was averaged within replicate release lots. Standard errors were based on replication established by release lots ( $n=6$  lots per season [3 at each release site], not total number of individuals recaptured).

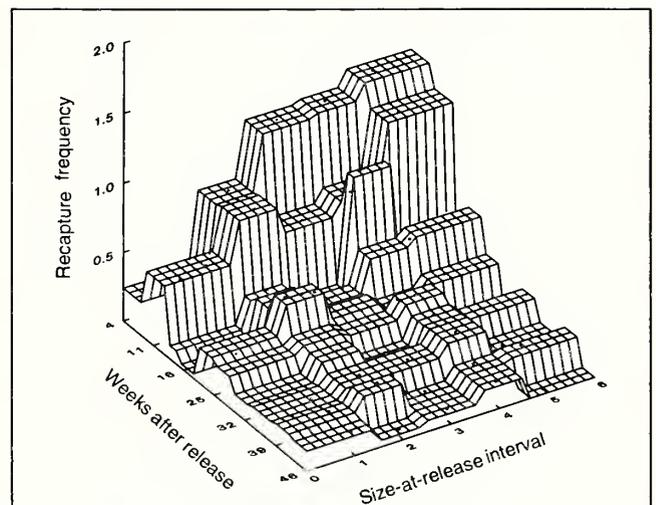
Recapture frequencies of small tagged fish (<70 mm TL) were clearly greater throughout collections made following spring releases than in those after summer releases. After 45 weeks in the wild, fish from the smallest size classes released in spring remained abundant in net samples. The relative impact derived from the smallest fish released in spring (45–60 mm) corresponded to impacts of some of the larger sizes released. In contrast, on the majority of collection dates following summer releases, not a single individual (released in summer) was collected from the 45-mm to 60-mm size-at-release group. After a few months in the wild, the larger fish released (>85 mm) generally were more abundant in samples when they were liberated in summer rather than in spring.

To compare recapture frequencies statistically among size-at-release intervals, values per release lot were summed across weeks for the period between 16 and 36 weeks after releases. After summer releases, mean recapture frequencies of fish <70 mm when released were substantially less than frequencies for fish > 85 mm when released (Fig. 6; ANOVA,  $P < 0.001$  in a posteriori orthogonal contrasts [Sokal and Rohlf, 1981] of intervals 1 and 2 combined versus intervals 4 and 5 combined).



**Figure 4**

Recapture frequencies of tagged cultured *Mugil cephalus* recaptured in cast-net samples after summer releases into Kaneohe Bay. Data are presented for each of the five size intervals released (size-at-release: 1=40–60 mm total length, 2=60–70 mm, 3=70–85 mm, 4=85–110 mm, and 5=110–130 mm). Data are given as percent recaptured fish of the total fish released per size-at-release interval.



**Figure 5**

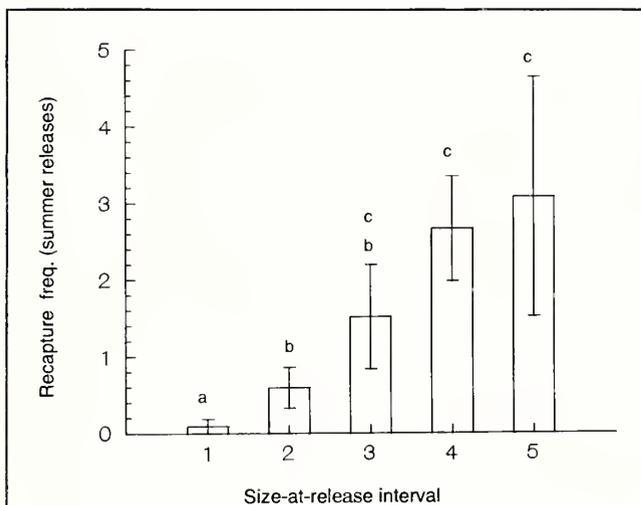
Recapture frequencies of tagged cultured *Mugil cephalus* recaptured in cast net samples after spring releases into Kaneohe Bay. See Figure 4 for description of fish size-at-release. Data are given as percent recaptured fish of the total fish released per size-at-release interval.

However, with the data from spring releases, mean recapture frequency of the smallest fish released (45 to 60 mm) was statistically similar to frequencies of some of the larger fish released (70 to 85 mm and those >110 mm) (Fig. 7;  $P=0.33$ ). Fish from groups 2 and 4 (60 to 70 mm and 85 to 110 mm when released) had marginally greater recapture frequencies than those for small fish ( $P < 0.03$ ; spring releases). Fish from the two largest size intervals (fish >85 mm) released in summer exhibited mean recapture frequencies about twice as high as those for any size fish from spring releases ( $P < 0.02$ ).

Interaction between size-at-release effects and release season effects was statistically significant ( $P=0.01$ , season  $\times$  size interaction term, Table 5). A significant interaction term indicates dependence of one factor upon the other; in this case, size-at-release affected recapture rate ( $P < 0.001$ ), but the degree of that effect depended upon release season.

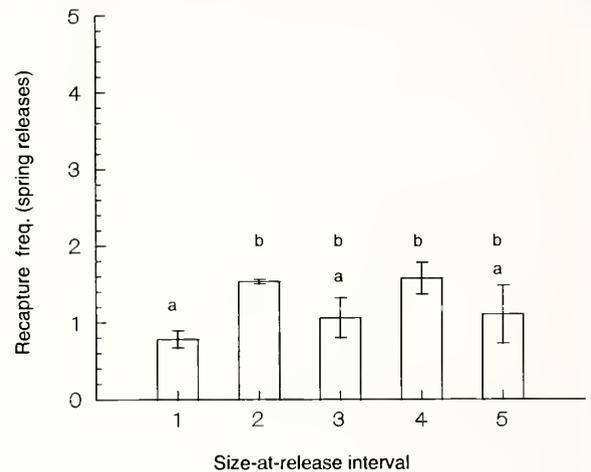
**Size structures of released cultured *Mugil cephalus* and wild recruits** A comparison of the sizes of fish in cast-net samples revealed that similar-size individuals schooled together. One month after spring releases, most of the smaller tagged striped mullet collected were schooling with relatively large num-

bers of wild *M. cephalus* similar in size to the tagged individuals. However, the larger cultured fish released found relatively few counterparts in size among wild individuals at that time (Fig. 8). The size structure of cultured fish released in spring was clearly out of phase with the wild recruitment pulse at that time. Whereas we had timed spring releases



**Figure 6**

Mean recapture frequencies ( $\pm$  SE,  $n=6$  lots) for the five sizes of fish released into Kaneohe Bay during summer releases (see Fig. 4 for description of fish size-at-release). Data are mean recapture frequencies per release lot ( $[\text{number recaptured}/\text{number released}] \times 100\%$ ) summed over collections made between 16 and 36 weeks after release. See Figure 4 for description of fish size-at-release codes. Letters above bars indicate results of multiple comparisons of means; size-at-release intervals that share the same letter were not significantly different.



**Figure 7**

Recapture frequencies ( $\pm$  SE,  $n=6$  lots) for the five sizes of fish released into Kaneohe Bay during spring releases (see Fig. 4 for description of fish size-at-release). Data are mean recapture frequencies per release lot ( $[\text{number recaptured}/\text{number released}] \times 100\%$ ) summed over collections made between 16 and 36 weeks after release. Letters above bars indicate results of multiple comparisons of means; size-at-release intervals that share the same letter were not significantly different.

**Table 5**

ANOVA table (randomized-block design, lots=blocking variable) for evaluation of release season and size-at-release effects on recapture frequencies after 4 months in the wild. Data (means per release lot) were combined here over the 20-week period following 4 months in the wild (weeks 16 to 36). Recapture frequencies are percent of the total number of fish released that were recovered during this period; these proportions were arc-sin square-root transformed prior to analysis.

Source of variation	Sum of squares	df	Mean square	F-ratio	P
Release lot	0.009	2	0.004	4.309	0.030
Release season	0.000	1	0.000	0.021	0.886
Size-at-release	0.030	4	0.007	7.173	0.001
Season $\times$ size	0.019	4	0.005	4.577	0.010
Error	0.019	18	0.001		

to coincide with peak abundances of young-of-the-year recruits in these nursery habitats, the modal size of cultured fish led that of the wild recruitment pulse by around 30 mm at one month after spring releases. In contrast, the size structures of wild young-of-the-year and cultured fish were nearly identical 1 month after summer releases (Fig. 9).

## Discussion

### Recapture rates and release impact

Release impact on striped mullet abundance was comparable to contributions from experimental releases of cod in Norway (e.g. Kristiansen and Svasand, 1990; Nordeide et al., 1994), red drum in Florida (Willis et al., 1995), and to proportions of cultured flounder in commercial landings in Japan (Kitada et al., 1992). Cultured striped mullet amounted to no less than 7% of the fish in monthly samples throughout the 11-month study period at both release sites. By the end of this study, cultured fish represented about 12% of the striped mullet sampled at Kahaluu Stream, over 40% of those sampled in Kaneohe Stream, and 13.6% of the total collected in Kaneohe Bay.

There was clearly an improvement in this study in recapture frequencies compared with initial releases into the Bay in 1990 (Leber, 1995). The improvement was largely due to adjusting release strategy in this study to avoid releases outside of streams, the nursery habitats preferred by striped mullet. Recovery rates (number recaptured/number released)

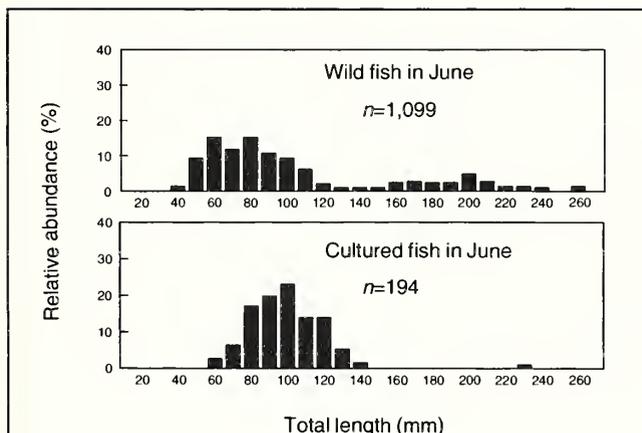
× 100%) of fish released at Kahaluu Stream in 1991 (this study) were similar to rates following a release of 10,000 fish at the same site in 1990; whereas, considerably fewer striped mullet were recovered following 1990 releases of 30,000 fish into more marine conditions near Coconut Island in the southern portion of the bay (authors' unpubl. data for juveniles; and see Leber and Arce, 1996, for data on adults).

### Temporal changes in abundance of released fish

Reduction in abundance of cultured fish over time at release sites was likely a result of 1) mortality, 2) emigration from nursery habitats into adjacent reef habitats in the bay, and 3) sampling bias as fish grew to larger sizes and moved out of shallow water. Mortality appeared to be more important than emigration as the cause for reduction over time in recapture rates.

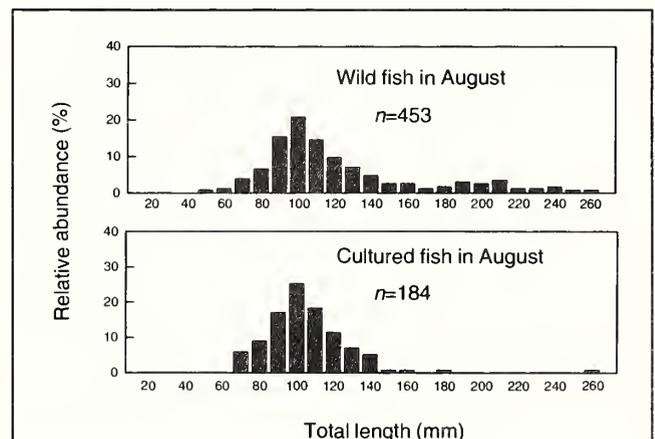
Juvenile striped mullet have a relatively strong affinity for brackish water during the nursery stage of their life cycle (Major, 1978; Blaber, 1987). After earlier pilot releases, when cultured striped mullet were released into more marine conditions (surface salinities >25 ppt), they schooled in both directions along the shore and rapidly occupied nearly all striped mullet nursery habitats (streams and tributaries) in those bay systems (Leber, 1995). In contrast, when striped mullet were released into habitats with lower surface salinities, as in this study, the majority of individuals recaptured were caught at or near the release site (Leber et al., 1995, 1996).

Had emigration out of release habitats remained high in this study after fish had had time to accli-



**Figure 8**

Size structures of wild and cultured *Mugil cephalus* collected in samples made about 1 month following spring releases into Kaneohe Bay.



**Figure 9**

Size structures of wild and cultured *Mugil cephalus* collected in samples made about 1 month following summer releases into Kaneohe Bay.

mate in the wild, then cultured individuals should have occupied several of the other tributaries sampled. However, few tagged fish were collected farther than 1 km away from either release site, and the difference in proportions of cultured fish retrieved outside of release sites, compared with proportions collected at release sites, did not increase over time. These data (Table 4) provide circumstantial evidence that, following 2 weeks of acclimation in the wild, cultured striped mullet then tended to stay at or near the stream they occupied for the duration of the study. Strong site fidelity (during the juvenile stage) has also been documented in marine nursery habitats following hatchery releases of lobster (Bannister and Howard, 1991; Latrouite and Lorec, 1991) and cod (e.g. Nordeide et al., 1994).

### Impact of release season

Fish size-at-release is clearly an important mediator of the effect of hatchery releases on stock abundance (Hager and Noble, 1976; Bilton et al., 1982; Tsukamoto et al., 1989; Liu, 1990; Svasand and Kristiansen, 1990; Ray et al., 1994; Leber, 1995; Wahl et al., 1995; Willis et al., 1995). At all of the release sites tested in Hawaii, size-at-release has been an important factor affecting recapture probability of cultured striped mullet (Leber, 1995; Leber et al.<sup>1</sup>). In previous studies with striped mullet, where releases were conducted in summer and fall, recapture rate was directly related to size of fish at the time of release.

As expected (Leber, 1995), in this study recapture rates after summer releases of small fish (individuals <60 mm long) approached zero and were an order of magnitude less than recapture rates of the larger fish released. Thus, when releases are made in summer in Kaneohe Bay, small (<60 mm) cultured striped mullet do not significantly affect juvenile recruitment in Kaneohe Bay. It is important to note that the fish in the different size intervals released were produced from multiple rearings and that the smallest fish released in summer were not merely the slowest growing individuals; rather, size-at-release was related primarily to age.

A new finding revealed by this study was that the seasonal timing of striped mullet releases can substantially alter size-at-release effect on recapture rate. Compared with recapture rates after summer releases, recovery of the smallest individuals released was significantly greater when releases were timed to coincide with peak recruitment of small wild individuals (in the spring). This was the first evidence that releases of relatively small (45 to 60 mm TL) individuals could make any lasting contribution to

striped mullet abundances in nursery habitats on Oahu. Subsequently, Leber and Arce (1996) showed that some of the small fish released in spring did survive to adult size and contribute to the commercial fishery catch in Kaneohe Bay. The latter study also revealed that the smallest individuals in summer releases from this study apparently suffered total mortality. Because of the obvious economic importance of our findings, we replicated part of this study in a follow up study, with spring releases of the same size groups studied here; the results were identical—small fish (<60 mm) did contribute to juvenile recruitment when releases were made in spring (Leber et al., 1996).

It is not clear how one is to interpret the lack of a strong correlation between size-at-release and recapture rates following the spring releases. On the basis of cast-net samples alone, we cannot rule out the possibility that a direct relation existed between size-at-release and survival after spring releases. Cast nets are biased in favor of collecting small individuals (Leber et al.<sup>1</sup>). Thus, a weak size-at-release effect following spring releases could be masked by sampling bias. Indeed, for fish from the spring releases, data from subsequent samples of adult cultured fish caught in the Kaneohe Bay mullet fishery revealed a (nonsignificant) trend towards a direct size-at-release effect (Leber and Arce, 1996). As in this study of juveniles, the data for adults revealed a highly significant effect of size-at-release on recovery rates when releases were made in summer.

On the basis of this study and on subsequent data on adult recruitment to the commercial fishery (Leber and Arce, 1996), striped mullet < 60 mm should not be released during summer in Kaneohe Bay. However, early (spring) releases of 45–60 mm striped mullet can make a contribution both to juvenile recruitment (this study) and to adult recruitment (Leber and Arce, 1996). Maximum recovery from summer releases will occur when individuals are >85 mm at the time of release. To determine optimal size-at-release, an economic analysis is needed to evaluate benefits and costs of releasing larger individuals.

Bilton et al. (1982) showed an interaction between release timing and size of juvenile coho salmon, *Oncorhynchus kisutch*, released in British Columbia. In that study, returns would be maximized from early release of large juveniles. The effect of the seasonal timing of releases on size-dependent recapture rates may not be universal (e.g. Willis et al., 1995); nevertheless, release season could be a key factor in successful enhancement of many marine species.

What processes could account for the seasonal change in size-at-release dependent recapture rates? Size structures of cultured and wild fish suggest that

schooling behavior of striped mullet may partly control the release-season effect. Schools of juvenile striped mullet are usually aggregated according to size (Leber, 1995). Because of the difference in size structures between wild and cultured fish in the spring, schools of larger striped mullet, after spring releases, contained mostly cultured fish and few wild fish. We hypothesize that at the time of spring releases, the large individuals were more susceptible than smaller ones to mortality from predation. We reason that, because the smallest fish released in spring had merged with relatively large numbers of small wild striped mullet, the smallest fish should have been afforded greater refuge from predators than that provided the large fish in our spring releases, because there were more small wild fish than large ones (i.e. refuge effect from schooling behavior; e.g. Parrish, 1989, 1992; deVries, 1990; Ranta et al., 1994).

This pattern was reversed following summer releases, when size structures of the larger cultured and wild individuals were equivalent. By summer, most wild juveniles had grown larger than the size range of the smallest cultured individuals released. Thus, few small wild juveniles were available to form schools with small cultured fish and thus the advantage of refuge that such schooling behavior would provide to small cultured fish was reduced.

The results of this study are consistent with the hypothesis that size-selective predation is a primary mechanism controlling recapture rates following hatchery releases in Kaneohe Bay (Leber, 1995). Although, after summer releases, large wild fish were not as abundant as small wild fish in the spring (thus reducing the advantage gained by cultured fish from schooling with large wild fish), larger cultured fish would have the added advantage of size in escape from predators. Whatever the cause(s) of size-at-release impact on recovery rates, it was clear from this study that release season can influence the underlying mechanism.

## Conclusions

The importance of conducting test releases to evaluate release strategies prior to conducting full-scale hatchery releases cannot be overemphasized. This study documented that release season can have a significant effect upon recovery of cultured striped mullet in the wild by affecting size-at-release dependent recapture rates. To optimize the impact of full-scale releases, marine stock-enhancement programs should perform test releases to evaluate interaction of release season with size-at-release effects.

We hypothesize that survival of cultured fish will be greater when releases are timed so that size-at-release coincides with modes in population size structures of wild stocks. A corollary to this is that the fewer cultured fish there are in a particular size interval at the time of release, the lower survival will be for wild fish in that interval.

These results need to be related to the hatchery costs of rearing fingerlings to various sizes and also to the increased production allowed by releasing small fingerlings in the spring, because spring releases would make nursery tanks or ponds available to grow more fish for summer releases.

Although the mechanism underlying the direct relationship between survival and size-at-release is not well understood, it is clear that in Hawaii, fish size-at-release can determine release success following summer releases of striped mullet. Based on this study, critical release size (CSAR, the size-at-release below which probability of survival approaches zero; Leber, 1995) for enhancing striped mullet in Kaneohe Bay appears to be lower when releases are made in spring (CSAR <45 mm) than when releases are made in summer (CSAR <60 mm).

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**Abstract.**—The catch equation used in virtual population analysis (VPA), and most annual age-structured methods, assumes a constant fishing mortality rate ( $F$ ) throughout the year even though many, if not most, fisheries are seasonal. Breaking this assumption of a constant  $F$  creates a bias in the resulting population-size estimates when the observed catch is used as input in VPA. The bias can be reduced by changing the time step in the analysis to quarters or months, as has been suggested in the past, but this change is not always easy or practical. This paper presents an alternative method for reducing the bias: correction of the catch values to meet the assumption of a constant fishing mortality rate. A simple algorithm is presented that gives the number of fish that would have been caught from a given population if the observed fishing mortality rate had been spread evenly throughout the year. An iterative process improves the required guess for the population size such that the bias is eliminated.

## Correcting annual catches from seasonal fisheries for use in virtual population analysis

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Nelson M. Ehrhardt

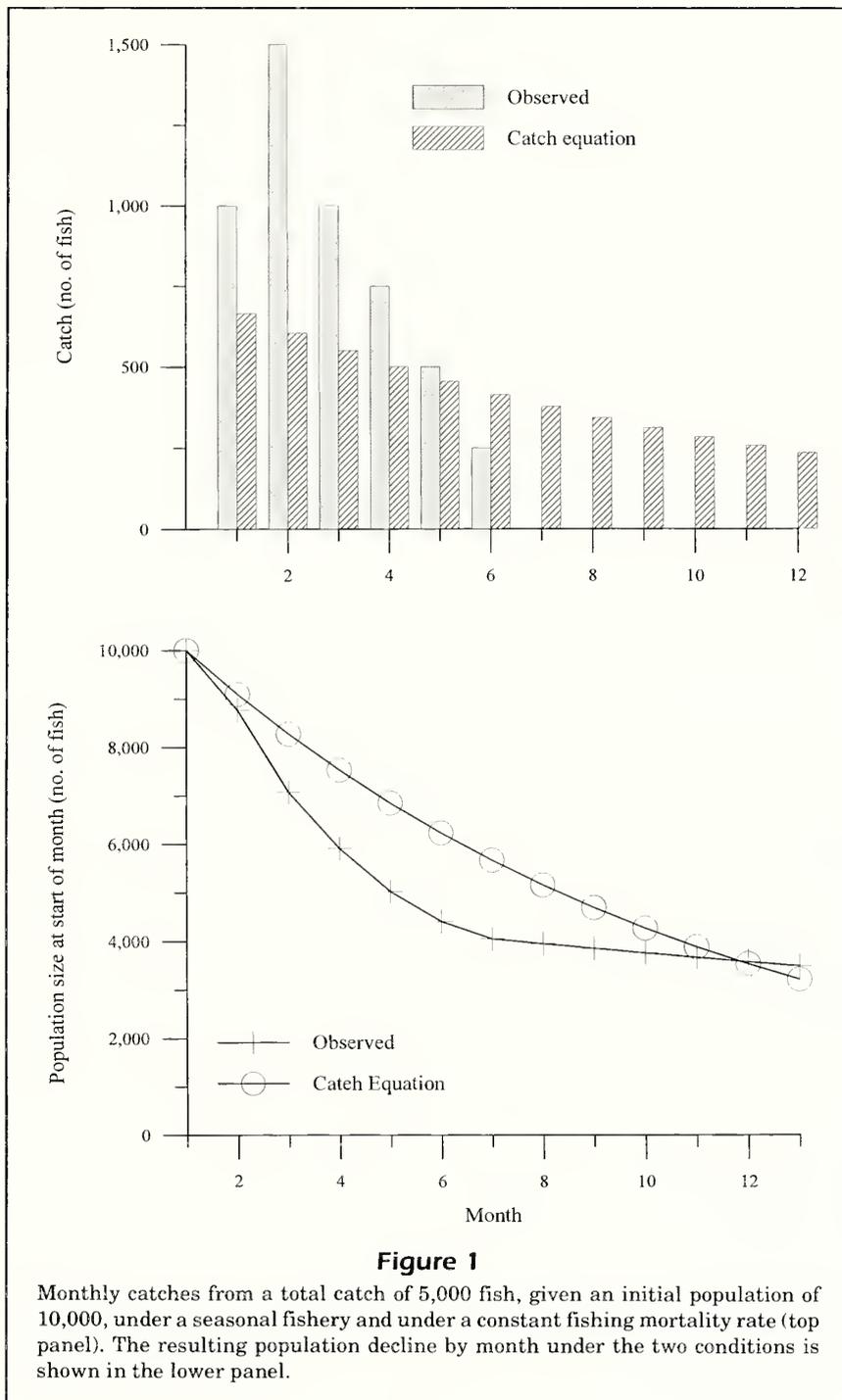
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Many, if not most, fisheries operate during only part of the year. The seasonal nature of fisheries is caused by quota and regulatory limitations, weather conditions, and fish availability among other reasons. The catch equation used in virtual population analysis (VPA) and in other annual age-structured analyses, assumes that a constant fishing mortality rate is applied continuously throughout the year. Under this assumption, a bias will be introduced into the analysis when the fishery is in fact seasonal. With the catch equation, the total catch is assumed to be distributed throughout the year, such that it follows the exponential decline of the population. The resulting total mortality rate inferred from the decline of the population with the catch equation is different from what actually occurred in the population. For example, given a total catch of 5,000 fish distributed unevenly during the first half of the year (Fig. 1, top panel), the population numbers at the end of the year would be negatively biased with the assumption inherent in the catch equation (Fig. 1, lower panel).

This bias has been examined in the past and found to be at a low level for most situations; exceptions occur for heavily exploited fisheries that occur during either the first or last quarter of the year. The fact that seasonal catches cause the es-

timated exploitation rate to be biased was described by Youngs (1976). The impact of seasonal catches on population-size estimates from cohort analysis was explored by Ulltang (1977), who recommended using smaller time units than a year to overcome the errors. Sims (1982) used both analytic methods and simulation to demonstrate the effects of seasonal catches on cohort analysis, concluding that the relative errors in population-size estimates are not severe unless the natural mortality rate is large or the fishery is heavily exploited, or both. The traditional recommendation for seasonal fisheries is to change the time scale from year to quarter or month so that the fishing mortality rate will be approximately constant within the time unit. The conversion from annual to monthly or to some other time step is not always simple, either in the coding of programs or in the collection of data. For example, the creation of adequate age-length keys for ageing the catch under monthly or even quarterly time steps could require prohibitively expensive sampling schemes and would be technically challenging.

A more recent approach to deal with the problem of seasonal fisheries is the generalization of the equations used in virtual population analysis. An attempt to remove the



bias caused by seasonal fisheries was made by MacCall (1986) who provided a family of approximations to virtual population analysis based on Pope's (1972) cohort analysis. Hiramatsu (1995) generalized the equations to allow for a constant catch rate within a season, and Mertz and Myers (1996) reformulated the equations to allow for any seasonal pattern of catches. Most current software available for virtual

population analysis and other age-structured analyses are designed for constant fishing mortality rates and annual time steps, however. Reformulating the basic equations used in virtual population analysis may not be practical for situations where a given algorithm is used that is already quite complex.

An alternative to changing the time scale or modifying the equations for the analysis of a seasonal fish-

ery is to correct the catch values to reflect the assumption of a constant fishing mortality rate ( $F$ ). The catch matrix for VPA would no longer contain the observed numbers of fish caught, but rather the numbers of fish that would have been caught under the assumption of an annual  $F$ . This paper presents a simple method for this conversion along with examples of the reduction of bias due to the method and a discussion of further applications. The Fortran source code and the executable program for this correction process are available from the authors.

## Methods

The algorithm for correcting annual catches from seasonal fisheries to meet the assumption of a constant fishing mortality rate during the year is as follows:

Let  $i = 1, 2, \dots, K$  index time intervals (not necessarily of equal length) during the year;

$\Delta t_i$  = the length of time in years for interval  $i$ ;

$M$  = annual natural mortality rate;

$C_i$  = observed catch in numbers during interval  $i$ ;

$N_i$  = population numbers at the start of interval  $i$ ;

$F_i$  = fishing mortality rate during interval  $i$ ; and

$F_A$  = annual fishing mortality rate.

For each year, age cell in the VPA catch matrix:

- 1 Assume a value for  $N_{K+1}$ .
- 2 For each time interval progressing backwards from  $K$  to 1.
- 2a Solve for  $F_i$  given  $C_i$ ,  $N_{i+1}$ ,  $M$ , and  $\Delta t_i$  from the catch equation:

$$C_i = \frac{N_{i+1} e^{M\Delta t_i + F_i} F_i (1 - e^{-M\Delta t_i - F_i})}{M\Delta t_i + F_i}.$$

- 2b Compute  $N_i$  given  $N_{i+1}$ ,  $M$ ,  $\Delta t_i$  and  $F_i$  from the exponential decline equation:

$$N_i = N_{i+1} e^{M\Delta t_i + F_i}.$$

- 3 Compute  $F_A$  that reduces  $N_1$  to  $N_{K+1}$  given  $M$  as

$$F_A = -M - \ln \left[ \frac{N_{K+1}}{N_1} \right].$$

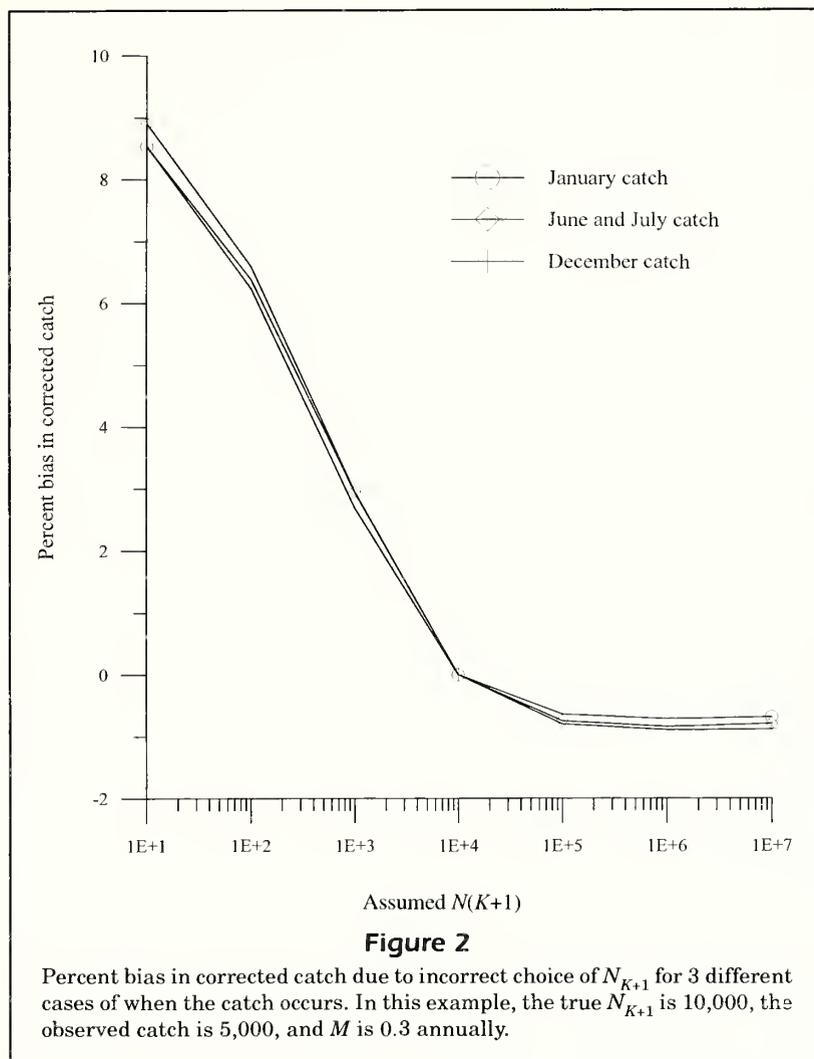
- 4 Compute annual catch ( $C_A$ ) under  $F_A$ , given  $N_1$  and  $M$  from catch equation:

$$C_A = \frac{N_1 F_A (1 - e^{-M - F_A})}{M + F_A}.$$

$C_A$  is the corrected catch to be used in VPA for the given year and age. Once all years and ages in the catch matrix have been corrected, the population abundance matrix can be estimated through virtual population analysis with the corrected catch values in place of the observed catches. The resulting population abundances at the end of the year can be used as the assumed values for  $N_{K+1}$  in step 1 and the process repeated to generate a recorrected catch matrix. Note that the observed catches are still used in step 2a of the algorithm; it is only the  $N_{K+1}$  values that change from computing the corrected to computing the recorrected catch. The recorrected catch matrix can again be used in virtual population analysis to estimate the population abundance matrix, and this iterative procedure can be repeated until the corrected catches do not change value.

This iterative process will produce population numbers from virtual population analysis that are consistent with the assumption of a constant fishing mortality rate during the year. Each annual catch in the VPA matrix is treated individually for the correction and then all the corrected catches used as input for VPA. The purpose for the iteration is to give a more solid basis for the choice of  $N_{K+1}$  for each observed catch (step 1 in algorithm) because the corrected catch value depends on the choice of  $N_{K+1}$  (Fig. 2). Guessing too high a value for  $N_{K+1}$  results in an underestimation of the corrected catch and vice versa, although, in general, the magnitude of bias is less for choosing  $N_{K+1}$  too large than too small. The timing of the catch also impacts the amount of bias in the corrected catch; earlier catches are slightly less biased than later catches (Fig. 2). The high biases found with low guesses for  $N_{K+1}$  correspond to extremely high values of the fishing mortality rate (Fig. 3, top panel) and are due to the catch removing a large portion of the population (>90%). When the catch is not removing such a large proportion of the population, a wide range of guesses for  $N_{K+1}$  will result in similar corrected catches (Fig. 3, bottom panel). The direction of the change between observed and corrected catch depends more upon the time of the catch than the  $N_{K+1}$  though (Fig. 4). It should be noted that the apparent linear relationship between corrected catch and time of the catch shown in Figure 4 is due to the values of  $N_{K+1}$  and  $M$  used in the example and will not always occur. The use of VPA results for values of  $N_{K+1}$  ensures a reasonable corrected catch value.

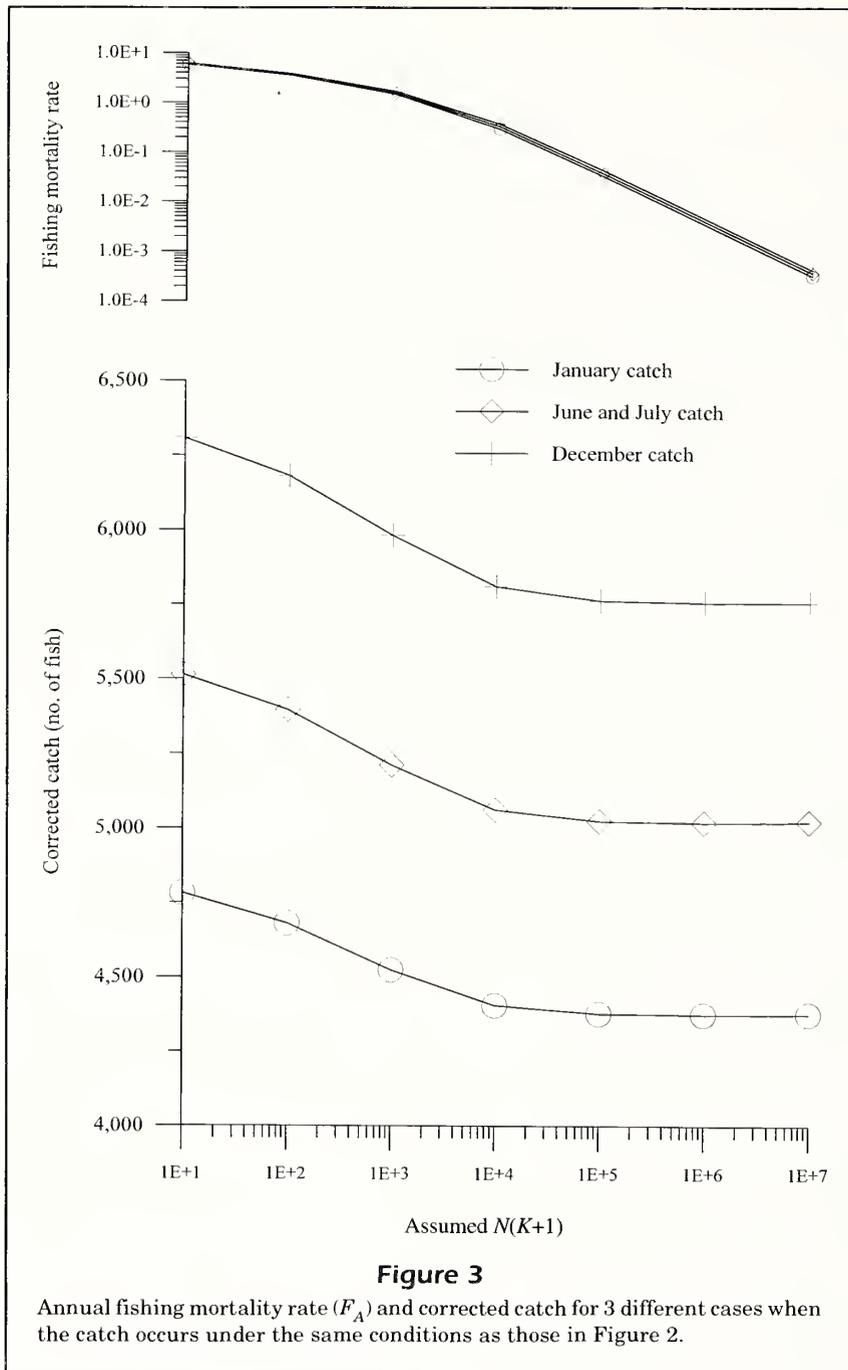
Once a value of  $N_{K+1}$  is chosen for an age cell of a given year in the VPA catch matrix, either from a



guess or from results of VPA, the corrected catch can be computed from the observed catch, the time sequence of the accumulation of this observed catch, and the natural mortality rate. Each cell in the catch matrix can have its own timing pattern. For example, if two gears operate in the fishery during different times of the year and target different-size fish, the timing of the catch will be different among ages. The observed catch for each time interval ( $C_i$ ) is used to solve for the fishing mortality rate during the interval ( $F_i$ ), given the population numbers at the start of the next interval ( $N_{i+1}$ ), the annual natural mortality ( $M$ ), and the length of the time interval ( $\Delta t_i$ ) (step 2a of the algorithm). The fishing mortality rate cannot be solved for directly in the equation and thus a search routine or iterative solution must be employed. A simple bisection algorithm will suffice, although quicker methods are available (see e.g. Press et. al., 1989). Once the fishing mortality rate for the

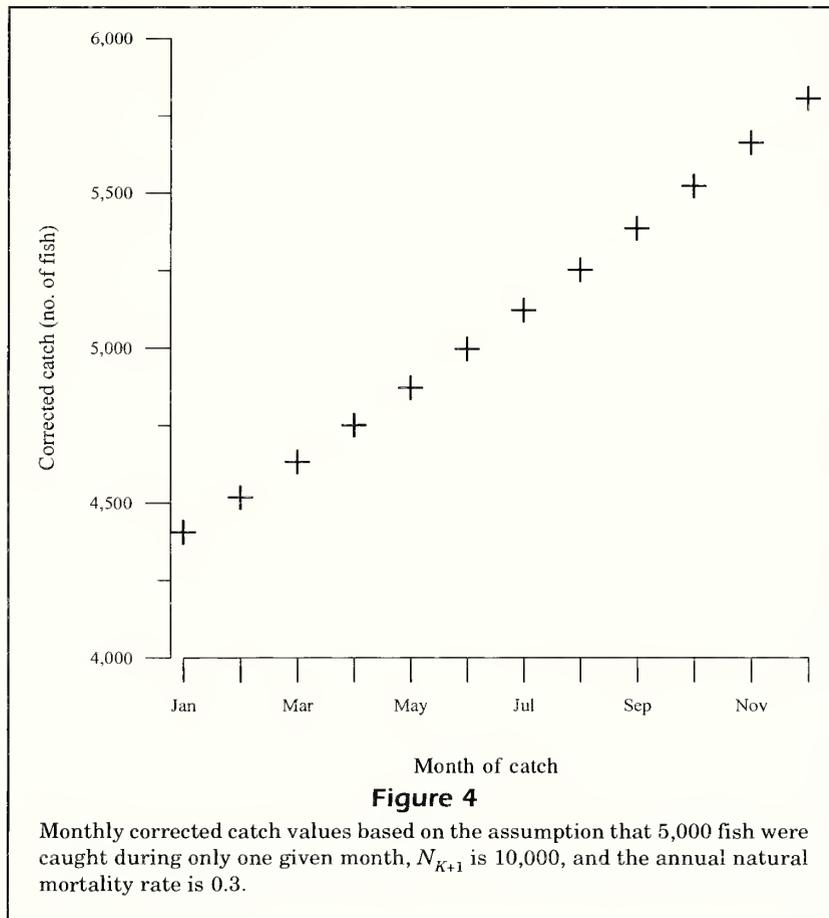
time interval ( $F_i$ ) is estimated, the population size at the start of the time interval ( $N_i$ ) can be computed directly with the equation in step 2b of the algorithm. Thus the natural and fishing mortality rates are assumed constant during each time interval, and the year should be split into time intervals accordingly. In most cases, monthly time steps should be sufficient unless the fishing season is extremely short and intense or the natural mortality rate is extremely high (or both situations occur).

The algorithm progresses backwards in time, from 31 December to 1 January, to minimize the propagation of errors, in the same manner that virtual population analysis follows a cohort backwards in time (Pope, 1972). When all the time intervals are completed, the corresponding annual fishing mortality rate ( $F_A$ ) can be computed from the equation given in step 3 of the algorithm. The population size at the start of time interval  $K+1$  is equivalent to the popu-



lation size for that cohort at the start of the next year and thus the annual  $F$  will reduce  $N_1$  to  $N_{K+1}$ . The annual  $F$  is then applied in the catch equation to generate the corrected catch ( $C_A$ ) (step 4 in the algorithm). The resulting catch is distributed throughout the year according to a constant  $F$  and thus reflects a smooth population abundance decline (see Figs. 5 and 6). In both Figures 5 and 6, the sum of the observed monthly catches are different from

the sum of the corrected monthly catches, whereas the observed and corrected population numbers follow different paths to the same endpoint. Figures 1 and 5 have the same observed catch, but the population numbers (and resulting fishing mortality rates) under the assumption inherent in the catch equation are different owing to the corrected catch value used in Figure 5. It is exactly the nonalignment of endpoints in Figure 1 that causes the bias in virtual



population analysis when catches from seasonal fisheries are used directly without correction.

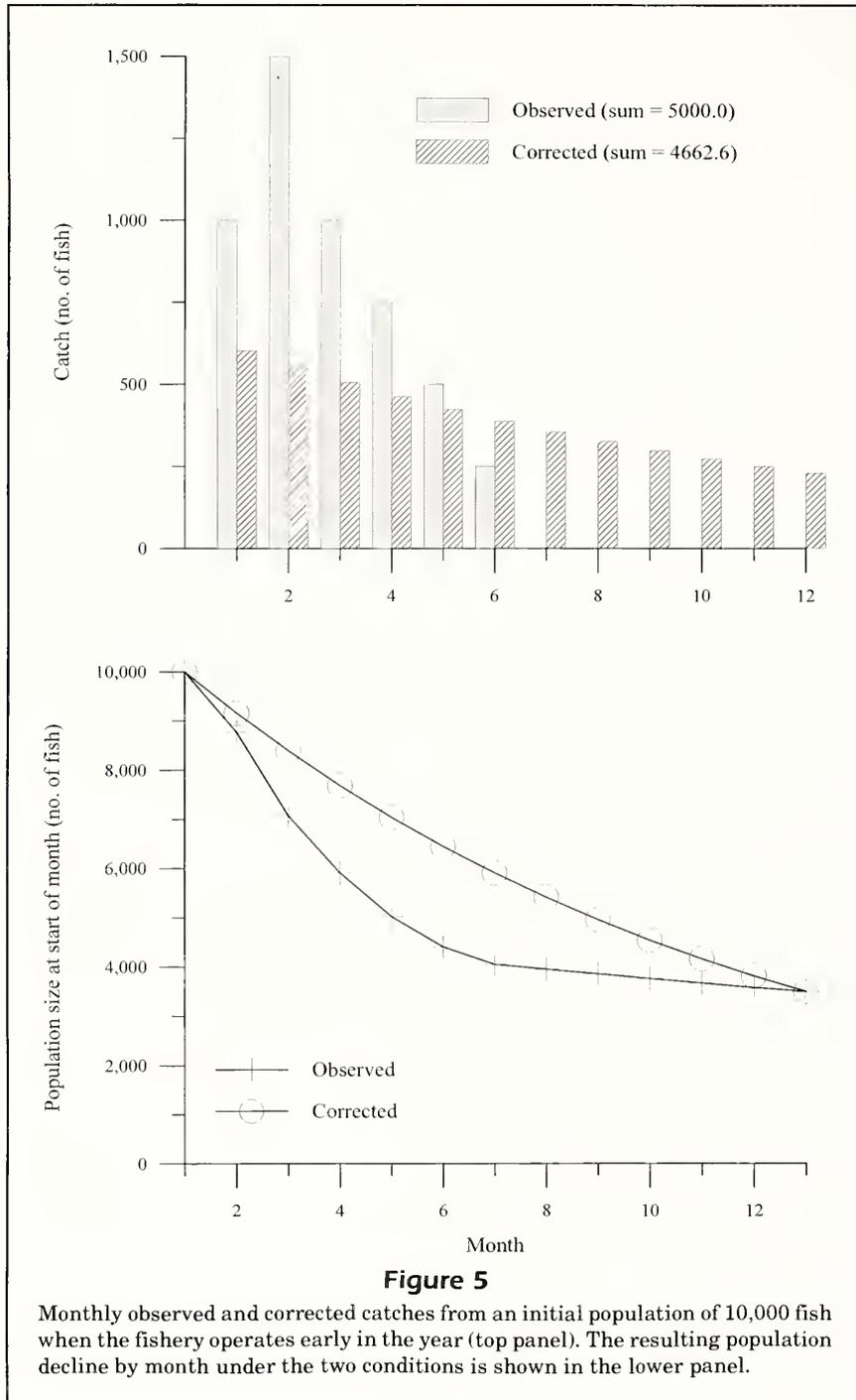
## Examples

Three scenarios were examined by means of simulation to demonstrate the algorithm. An initial population structure and recruitment pattern were set, and a given catch was removed at a constant fishing mortality rate under three scenarios: 1) the catch occurred only in January, 2) the catch was split evenly between June and July, and 3) the catch occurred only in December. The natural mortality rate was constant for all ages and years at 0.5 per year. The selectivity curve was sigmoid to follow a trawl-type pattern. A tuning index was collected from the population without error for use in calibrated virtual population analysis (VPA). The VPA used in the examples was FADAPT3 (Restrepo<sup>1</sup>). Any sequential popula-

tion analysis program could be used for these simulated examples because of a lack of error distributions for the data. Seven years were simulated for each scenario by applying the catch during the appropriate month(s) and the observed catch at age recorded for each year. For each scenario, 3 different sets of catch data were used as input for the VPA: 1) the observed catch-at-age data, 2) the corrected catch-at-age data with guesses for the  $N_{K+1}$  values, and 3) the recorrected catch-at-age data with the population numbers at age taken from the results of the corrected catch-at-age VPA. The resulting population numbers at age from the three VPA's were compared with the true values, and the percent bias in the estimates was computed. The true population numbers, 3 catch matrices, and 3 bias matrices are given for the January, June and July, and December catch scenarios in Tables 1, 2, and 3, respectively.

Although each scenario had the same initial population, recruitment pattern, and annual catches, the populations became quite different, depending upon when the catch was removed. The earlier the catch was taken in the year, the lower the resulting fishing mortality and the larger the remaining popula-

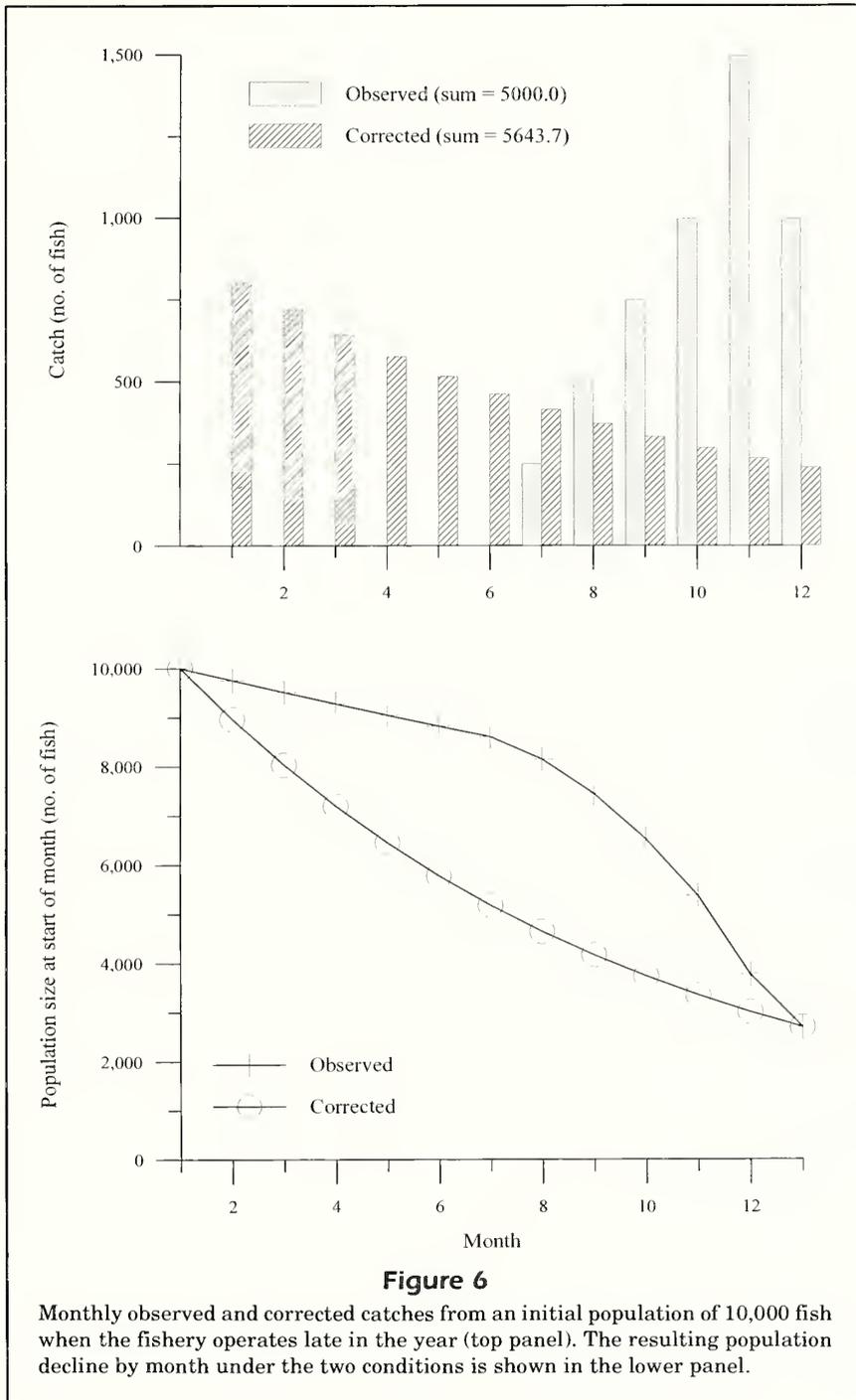
<sup>1</sup> Restrepo, V. 1996. Cooperative Unit for Fisheries Education and Research, Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, 4600 Rickenbacker Causeway, Miami, FL 33149. Personal commun.



**Figure 5**  
 Monthly observed and corrected catches from an initial population of 10,000 fish when the fishery operates early in the year (top panel). The resulting population decline by month under the two conditions is shown in the lower panel.

tion. The differences are most clearly seen in the older ages late in the simulated time span (Tables 1–3). The January catches were corrected to lower values than those of the observed catch, but the values for December corrected catches were higher than those for observed catches in order to reflect more accurately these changes in the fishing mortality rate caused by the timing of the catch.

In each scenario the recorrected catch matrix gave the lowest bias in estimated population size, whereas the observed catch resulted in the highest bias in two of the three scenarios (Table 4). The bias was largest for the observed catches that occurred in January and December. Use of observed January catches in the VPA overestimated the true population size, and use of observed December catches un-



derestimated the true population size. The June and July observed catches produced low bias, demonstrating the validity of Pope's cohort analysis approximation (Pope, 1972). The increasing bias at age for all three scenarios with corrected catch data was due to a choice of a small constant  $N_{K+1}$  value for all ages and years. This method of choosing  $N_{K+1}$  is not recommended during normal application of the algo-

rithm but was done to demonstrate the increased or decreased bias relative to observed catches, depending upon the timing of the catch. Much better guesses of  $N_{K+1}$  for the corrected catch would be the results of VPA with the observed catch matrix. In this case the re-corrected catches will usually be so similar to the corrected catches that no further iterations are required.





Table 3

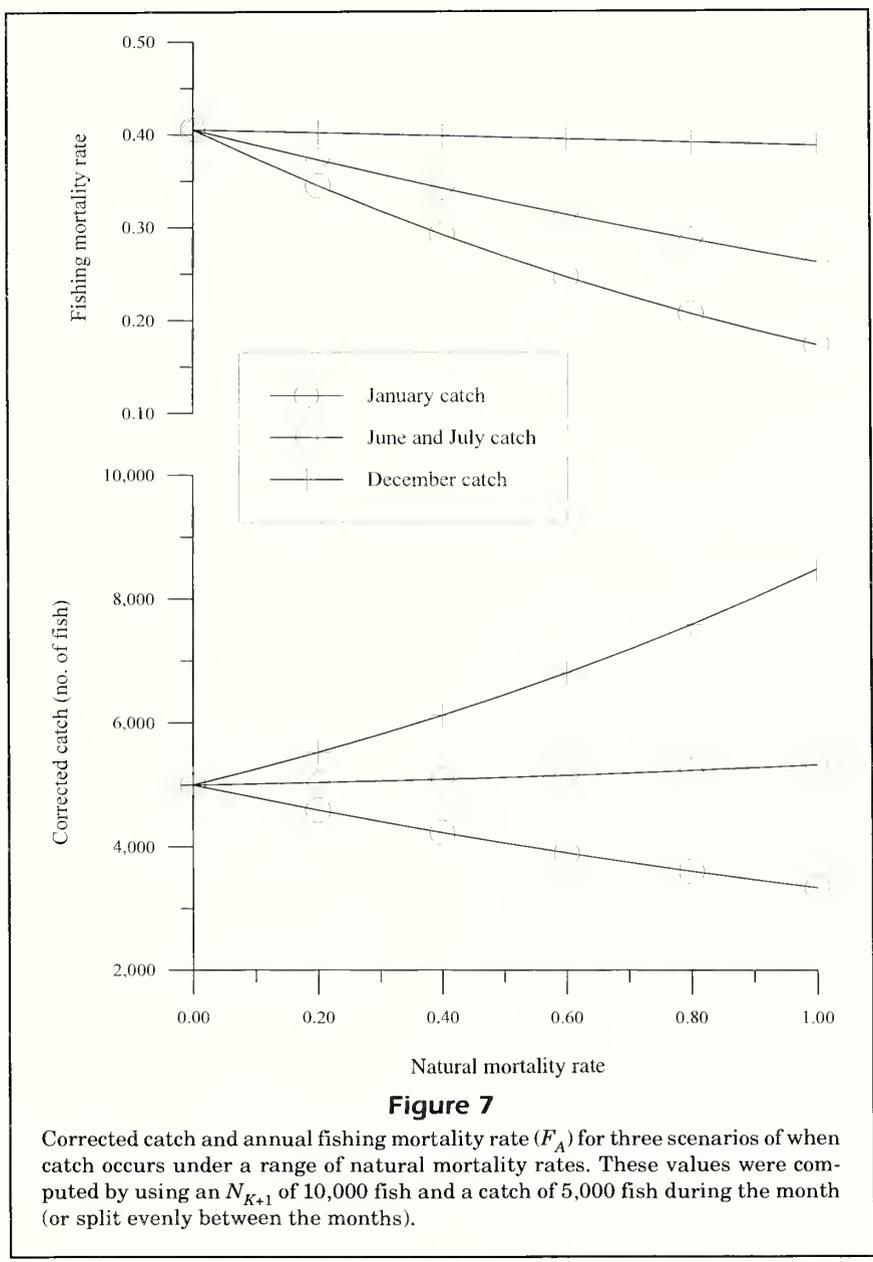
True population numbers, observed catch, corrected catch, recorrected catch, and percent bias in population numbers output by VPA with the three catch matrices as input for scenario 3. Catch occurred only in December. Years are in columns and ages are in rows.

Catch data for December							
True population numbers							
1,000,000	2,000,000	4,000,000	1,000,000	3,000,000	1,000,000	1,000,000	1,000,000
563,368	468,980	986,837	2,044,458	532,809	15,944,22	489,054	489,054
288,839	229,497	206,672	459,258	1,014,679	263,412	693,044	693,044
144,699	95,547	85,574	83,737	205,232	450,766	96,185	96,185
77,637	47,574	35,453	34,531	37,305	90,887	163,755	163,755
Observed catch							
140,582	231,169	389,959	75,314	230,032	120,048	137,635	137,635
114,731	79,510	142,362	230,269	61,058	280,134	97,654	97,654
81,495	54,848	42,555	74,950	168,329	65,040	192,120	192,120
41,126	23,014	17,764	13,784	34,340	112,163	26,861	26,861
22,066	11,459	7,360	5,684	6,242	22,615	45,731	45,731
Corrected catch							
184,448	306,692	524,132	97,697	305,147	157,007	180,502	180,502
149,922	103,228	186,832	305,469	78,960	373,391	127,228	127,228
105,848	70,827	54,785	97,218	221,702	84,184	253,787	253,787
52,927	29,468	227,09	17,598	44,113	146,503	34,433	34,433
28,246	14,619	9,376	7,237	7,949	28,953	58,922	58,922
Recorrected catch							
180,390	296,049	498,706	96,173	293,745	153,805	176,580	176,580
148,011	102,273	182,738	294,826	78,198	360,493	125,966	125,966
105,966	71,003	54,919	96,365	216,452	84,285	249,728	249,728
53,491	29,800	22,930	17,726	44,172	145,367	34,941	34,941
28,703	14,838	9,500	7,310	8,030	29,319	59,482	59,482
% bias in population numbers from observed catch							
-22.3	-22.3	-22.3	-22.4	-22.4	-21.9	-21.5	-21.5
-22.5	-22.4	-22.4	-22.4	-22.5	-22.5	-21.9	-21.9
-22.8	-22.6	-22.5	-22.5	-22.6	-22.7	-22.6	-22.6
-22.8	-22.6	-22.5	-22.5	-22.6	-22.7	-22.6	-22.6
-22.8	-22.6	-22.5	-22.5	-22.6	-22.7	-22.6	-22.6
% bias in population numbers from corrected catch							
-0.4	-0.1	0.9	-1.5	0.6	-1.3	-1.1	-1.1
-0.6	-1.2	-0.9	0.1	-1.9	0.2	-2.1	-2.1
-1.2	-1.6	-2.0	-1.8	-0.7	-2.5	-1.2	-1.2
-1.8	-2.1	-2.4	-2.9	-2.8	-1.9	-4.1	-4.1
-2.3	-2.5	-2.7	-3.1	-3.7	-3.8	-3.6	-3.6
% bias in population numbers from recorrected catch							
0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0
0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

ary and the catch occurs. Larger  $M$  will cause a large population size to be present at the start of February, and thus the fishing mortality rate needed to generate a given catch will be lower. In contrast, the December fishing mortality rates are nearly constant

over the range of  $M$  because the value of  $M$  does not change the population-size value used in step 2 of the algorithm as it did for the January catch.

These examples assume a constant natural mortality rate, which may be false in reality. If  $M$  varies dur-



**Figure 7**

Corrected catch and annual fishing mortality rate ( $F_A$ ) for three scenarios of when catch occurs under a range of natural mortality rates. These values were computed by using an  $N_{K+1}$  of 10,000 fish and a catch of 5,000 fish during the month (or split evenly between the months).

ing the year, then the expected amount of bias removed by the catch correction algorithm may in fact be incorrect. The actual amount of bias between the true state of the population and the estimated values also depends upon the amount and type of error in the observed catch estimates and tuning indices. The reduction in bias produced by this algorithm may be insignificant relative to the level of bias produced by other sources in the analysis, but it should at least be in the correct direction.

The direction of change between observed and corrected catches has implications for quota projections and biological reference-point determination, such as  $F_{0.1}$  or  $F_{\%SPR}$ . Catches from early in the year are

corrected to lower values than those for the observed catch, and thus use of the observed catch in VPA results in overestimates of the population size, if unbiased indices are used to tune the VPA. The overestimated population size would then be used to predict a quota for the upcoming year which would be too large. When this quota was filled, observed catch, which is larger than the corrected catch in the VPA, would again be used in the following year's stock assessment and would thus predict a larger population size than was present. This feedback cycle could cause problems if the tuning indices do not adequately reflect the decline of the population.

**Table 4**

Unweighted average percent bias in population numbers for the three scenarios when catch occurs and the three catch matrices input in VPA (summary of Tables 1, 2 and 3).

Catch matrix	January	June and July	December
Observed	23.4	-2.1	-22.5
Corrected	-2.7	-2.2	-1.7
Recorrected	0.1	0.1	0.1

The determination of current stock health in relation to a biological reference point will also be affected by the timing of the catch, especially spawning potential ratios. If the catch is taken before spawning, a much lower spawning potential ratio will result in relation to the catch being taken after spawning (compare observed population numbers for June in Figures 5 and 6). Thus the timing of the catch must be incorporated into the prediction or reference point algorithms, whereas the population numbers at the start of the year can be derived from annual VPA's or from other techniques when the constant  $F$  is assumed, if the corrected catch values are input.

All the examples and discussion so far have been in terms of numbers of fish, but the quotas used by management are most often given in weight. The average weight at age for the catch and population has a confounding effect on the correction algorithm that can either reduce or increase the bias. The use of average weight of a fish at the midpoint of the year, combined with the assumption of a constant fishing mortality rate, can lead to highly biased quotas in relation to the true timing of the catch and the average weight at age of the fish at that time. A quota in weight, for fish caught early in the year, will cause more fish to be caught than the same quota filled late in the year when the fish have increased in weight. Thus particular attention must be paid to the growth of the fish during the year in relation to the timing of the catch in cases where management advice is based on weight data.

## Summary

Use of observed catch values from seasonal fisheries directly in virtual population analysis or in other

analyses, where a constant annual fishing mortality rate is assumed, will bias the population-size estimates. If the catch occurs at the beginning of the year, the population size will be overestimated, whereas catch late in the year will cause underestimation of the population size. The observed catches can be easily corrected to reflect the assumption of a constant fishing mortality rate and to eliminate bias through the algorithm presented in this paper.

## Acknowledgments

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**Abstract.**—Between 1986 and 1988, 10,545 double-tagged sablefish were released off California, Oregon, and Washington. Tags recovered from these fish have provided one of the best sets of data available for estimating tag-shedding rates. We developed a new model and a maximum-likelihood procedure to estimate the rates. Both initial and long-term shedding rates were low, but posteriorly placed tags were shed at about twice the rate of anteriorly placed tags. Bootstrapping indicated that the estimates were precise and accurate. Shedding rates for sablefish were considerably lower than most published estimates for other species. Although the rates were low, the extra tag increased recoveries by nine percent over a six-year period.

## Estimates of tag loss from double-tagged sablefish, *Anoplopoma fimbria*

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The sablefish, *Anoplopoma fimbria* (Pallas, 1811), is a long-lived species (Beamish and McFarlane, 1987) of considerable commercial importance (Kinoshita, 1987; Korson and Kinoshita, 1989; Kinoshita et al., 1996) and is found in the north Pacific Ocean from Baja California, north to the Bering Sea, and south to Japan in the western Pacific (Sasaki, 1985). Scientists have used tagging to study population size, mortality, migration, and movement of this species for more than four decades (Holmberg and Jones, 1954; Wespestad et al., 1983; Beamish and McFarlane, 1988; Fujioka et al., 1988; Heifetz and Fujioka, 1991).

Estimates of mortality and exploitation rates, along with estimates of population size, can be biased owing to loss or shedding of tags (Wetherall, 1982). Estimated rates of tag loss are used to correct the bias. The placement of two tags in the same fish (double-tagging) is the most common technique used to obtain data for estimation of tag loss rates (Beverton and Holt, 1957; Gulland, 1963; McFarlane et al., 1990). In this study we estimate the rate of tag loss from sablefish, using results from a double-tagging experiment.

## Methods

Sablefish were captured with fish traps (Parks and Shaw, 1994), double tagged, and released by the Alaska Fisheries Science Center (AFSC) during 1986, 1987, and 1988. The Southwest Fisheries Science Center (SWFSC) used bottom trawl gear (Butler et al., 1989) to capture additional sablefish for double tagging in 1987. Identical tags and tagging procedures were used during the three years.

Captured sablefish were routinely put into "live" tanks supplied with fresh-running seawater immediately after the catch was brought on board (Shaw, 1984). No anesthetic was used. Usually within 15 minutes of the completion of each haul, sablefish were dip-netted from the live tank and placed in a padded tagging cradle. Each sablefish was tagged with two identical anchor tags (Floy FD-68). Tags were 60 mm long, 2 mm in diameter, yellow in color, and labeled with a unique number and with instructions on where to return the tag. The primary tag was placed below the anterior end of the first dorsal fin, and the secondary or extra tag was placed near the posterior end of the same fin. Each tag was in-

serted between and engaged behind the pterygiophores of the dorsal fin. Fork length, tag number, and the geographical position and date of release were recorded for each fish. Only fish judged to be in viable condition were tagged.

Wetherall (1982) reviewed literature on analytical methods for estimating tag-shedding rates. For mathematical convenience, tag shedding is usually described by tag-retention models. Following Wetherall (1982) and common practice, we assume that the retention rate of a tag of type  $i$  through the mid-point of the  $j$ th recovery period ( $ret_{ij}$ ) is

$$ret_{ij} = \rho_i e^{-L_i t_j}, \tag{1}$$

where  $\rho_i$  = retention rate during initial brief time after tagging for tag type  $i$ ;

$L_i$  = instantaneous tag shedding rate for tag type  $i$ ;

$i = 1$  for anterior tag;

$i = 2$  for posterior tag; and

$t_j$  = time at liberty at midpoint of  $j$ th recovery period.

We used a weighted linear regression approach, as suggested by Wetherall (1982) for multiple releases, for an exploratory analysis of the data. The results indicated that  $\rho_i$  did not vary with tag type, but that  $L_i$  did. The regression approach assumed that the error terms were independent and normally distributed. We believed that these assumptions may not be valid and that it would be more appropriate to use a maximum-likelihood procedure for the analysis. We also decided to assume that  $\rho$  is independent of tag type. Because the linear regression approach was used only for an exploratory analysis of the data, we neither describe it nor present the results from using it in this paper.

We developed a new model and used maximum-likelihood principles to estimate the parameters, following the suggestions of Wetherall (1982). We combined recoveries from the three release periods and estimated confidence bounds for the parameters ( $\rho$ ,  $L_1$ , and  $L_2$ ) by bootstrapping (Efron and Tibshirani, 1993).

The probability that a tag of type  $i$  is shed by the  $j$ th recovery period is

$$J_{ij} = 1 - \rho e^{-L_i t_j}. \tag{2}$$

Then the probability that a recovered tag-bearing fish has only tag type 1 during the  $j$ th recovery period is

$$P_{1j} = \frac{J_{2j}(1 - J_{1j})}{1 - J_{1j}J_{2j}}.$$

The probability that a recovered tag-bearing fish has only tag type 2 during the  $j$ th recovery period is

$$P_{2j} = \frac{J_{1j}(1 - J_{2j})}{1 - J_{1j}J_{2j}}.$$

The probability that a recovered tag-bearing fish has both tags is

$$P_{3j} = \frac{(1 - J_{1j})(1 - J_{2j})}{1 - J_{1j}J_{2j}}.$$

We assumed that the proportions of tag recoveries among recovery type followed a multinomial distribution. After terms not affected by the parameter estimates were dropped, the log likelihood of the observed recoveries is

$$\mathcal{L} = \sum_{j=1}^T [r_{1j} \ln(J_{2j}) + r_{2j} \ln(J_{1j}) + (r_{1j} + r_{3j}) \ln(1 - J_{1j}) + (r_{2j} + r_{3j}) \ln(1 - J_{2j}) - (r_{1j} + r_{2j} + r_{3j}) \ln(1 - J_{1j}J_{2j})];$$

where  $T$  = number of recovery periods;

when  $i = 1$  or 2,

$r_{ij}$  = number of fish recovered with only a type  $i$  tag during  $j$ th recovery period; and

when  $i = 3$ ,

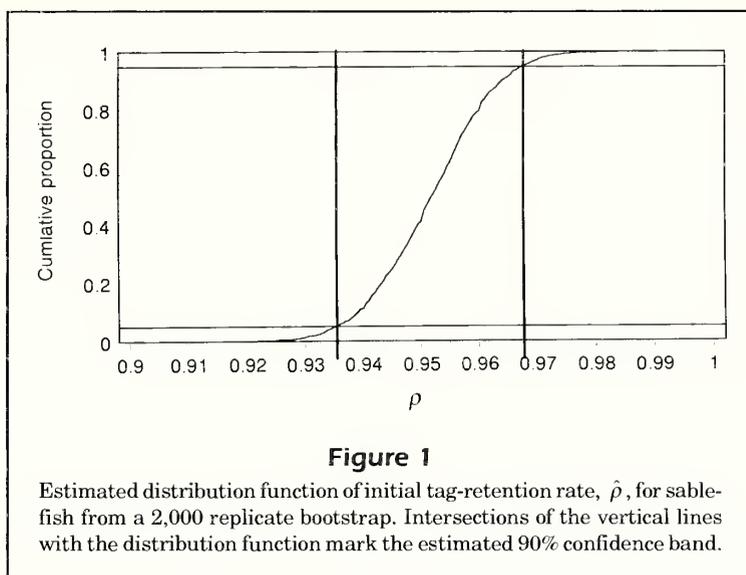
$r_{ij}$  = number of fish recovered with both tags.

We used the NLIN procedure (SAS Institute Inc., 1990) with the Gauss-Newton method, which requires derivatives of the log likelihood with respect to the parameters, to estimate the parameters of the model. The derivatives are

$$\frac{\delta \mathcal{L}}{\delta \rho} = \sum_{j=1}^T [r_{1j} / (\rho - e^{-L_1 t_j}) + r_{2j} / (\rho - e^{-L_2 t_j}) + (r_{1j} + r_{2j} + 2r_{3j}) / \rho - (r_{1j} + r_{2j} + r_{3j}) (1/\rho - 1/\text{div}) e^{(L_1 + L_2) t_j}],$$

$$\frac{\delta \mathcal{L}}{\delta L_1} = \sum_{j=1}^T [r_{2j} \rho t_j / (e^{-L_1 t_j} - \rho) - (r_{1j} + r_{3j}) t_j - (r_{1j} + r_{2j} + r_{3j}) t_j e^{-L_1 t_j} (\rho e^{-L_2 t_j} - 1) / \text{div}],$$

$$\frac{\delta \mathcal{L}}{\delta L_2} = \sum_{j=1}^T [r_{1j} \rho t_j / (e^{-L_2 t_j} - \rho) - (r_{2j} - r_{3j}) t_j - (r_{1j} + r_{2j} + r_{3j}) t_j e^{-L_2 t_j} (\rho e^{-L_1 t_j} - 1) / \text{div}],$$



where  $div = e^{-L_1 t_j} + e^{-L_2 \rho t_j} - \rho e^{-(L_1 + L_2) t_j}$ .

We employed Mathematica (Wolfram, 1991) as an aid in deriving the derivatives.

We programmed a parametric bootstrap with 2,000 replicates in SAS to estimate confidence limits and bias. Since the bias estimates were very low, we used the uncorrected percentile method to estimate 90% confidence limits (Efron and Tibshirani, 1993).

## Results

The SWFSC double tagged 229 fish during its egg-production survey cruise in early 1987. These fish were caught by bottom trawl and represented what was left over after needs for extensive biological samples were satisfied. The AFSC double tagged 10,316 fish during its sablefish abundance-indexing surveys in the fall of 1986, 1987, and 1988. The fish were caught by fish traps and represented a significant portion of the catches by the AFSC. There were five recoveries of trawl-caught fish and 1,552 recoveries of trap-caught fish through the end of March 1995. Because there was an insufficient number of recoveries from trawl-caught fish to allow for examination of recoveries by release gear types, we combined trawl and trap releases of tagged sablefish. We used recoveries of tag-bearing fish that were at liberty for no more than six years so that each release would have the same number of full years at liberty. Recoveries of tag-bearing fish were summarized by year of release and years at liberty (Table 1).

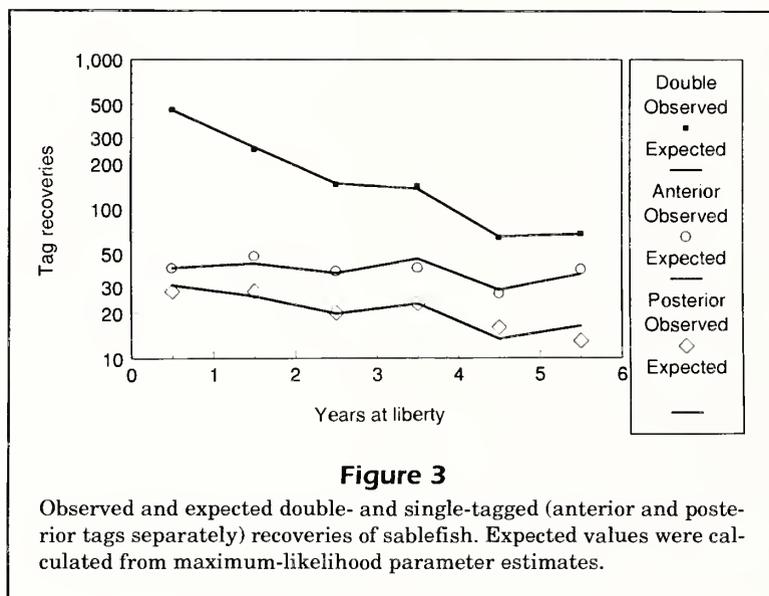
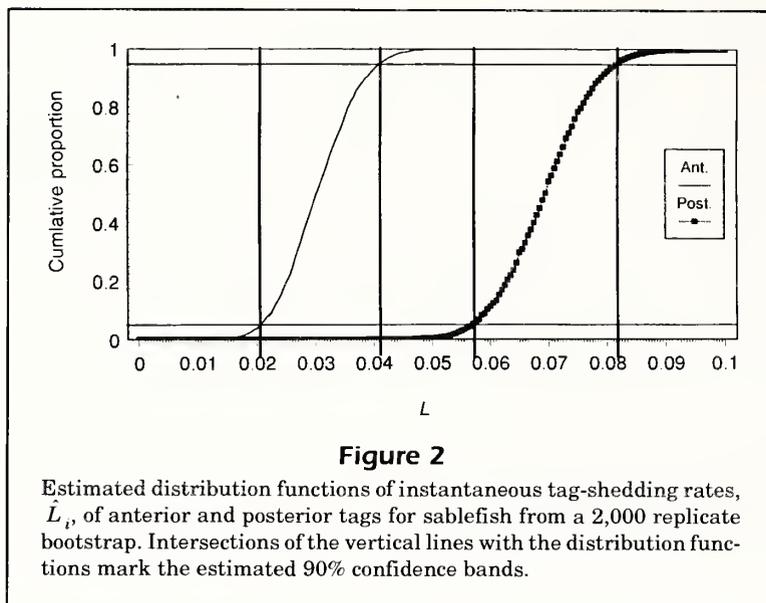
Bootstrap estimates of the averages and medians of the parameters,  $\rho$  and  $L_i$ , were very close to the

maximum-likelihood estimates, indicating that the estimation procedure was unbiased (Table 2). The bootstrap-estimated distribution functions indicated that the density functions were unimodal, smooth, and symmetrical (Figs. 1 and 2). The 90% confidence band for  $\rho$  does not overlap with 1 (Fig. 1), indicating that although initial shedding is low, it is greater than 0. The 90% confidence bands for  $L_1$  and  $L_2$  do not overlap (Fig. 2), indicating that the instantaneous shedding rate is greater for posterior tags than for anterior tags. The model provided an excellent fit to the observed pattern of tag recoveries (Fig. 3).

## Discussion

The double-tagging experiment with sablefish revealed that both immediate ( $1-\rho$ ) and long-term instantaneous ( $L_i$ ) tag loss rates were low and that long-term loss rates were higher for the posterior tagging position. The model fitted the recovery data very well, indicating that loss rates did not change with time at liberty during the first six years. Loss rates may have been higher for tags from the first release year because the ratio of single to double tag recoveries was higher than that during the other years (Table 1). Since tags and tagging procedures were identical in all three years, we assumed that any differences in loss rates were random.

Fishermen may have occasionally reported only one tag from recaptures of fish bearing two tags (Lauris et al., 1976; Wetherall, 1982). A reward was given for each tag returned to encourage complete reporting of tags, and single tags were checked to determine if the other tag of the pair had been reported at



another time. Although we believe that most, if not all, reports of single tag recaptures were accurate, misreporting may have caused underestimation of  $\rho$ .

Tag-loss rates in this study are similar to those of Beamish and McFarlane (1988) for sablefish. They used two types of tags (anchor and suture) and did not find a significant difference in the rate of loss by tag type. From a line fitted by eye through the data, they found a loss rate of approximately 10% during the first year and 2% per year thereafter. Examination of Figure 2 of their paper indicated that  $\rho$  was about 0.95.

We present tag-loss rates from sablefish and other species in Table 3. Values were taken from the lit-

erature and standardized, as much as was feasible within limitations, owing to the variety of models used and plethora of reporting styles. The median estimate of  $L$  was 0.15, and the range was 0.00 to 3.93. Estimates of  $L$  for most species were higher than that for sablefish. The distribution of  $L$  estimates had a relatively long upper tail. Only a few of the other studies provided estimates of  $\rho$ , and the estimates for sablefish were in the middle of the range of the other estimates.

Although tag-shedding rates for sablefish were low, it still appears worthwhile to double tag. During the six-year recovery period, 128 sablefish were recovered with only a posterior tag. Thus, by double tag-

**Table 1**

Double-tag releases and recoveries of sablefish, *Anoplopoma fimbria*, during first six years at liberty. Number of releases are shown in parentheses.

Years at liberty (Midpoint)	Recoveries			
	Single tag			Total
	Both tags	Anterior	Posterior	
<b>1986 releases (2,652)</b>				
0.5	116	21	12	49
1.5	77	10	13	100
2.5	29	8	6	43
3.5	37	11	5	53
4.5	16	18	3	37
5.5	31	17	8	56
Total	306	85	47	438
<b>1987 releases (1,872)</b>				
0.5	74	3	5	82
1.5	16	4	1	21
2.5	19	7	2	28
3.5	19	3	4	26
4.5	11	5	2	18
5.5	11	6	1	18
Total	150	28	15	193
<b>1988 releases (6,021)</b>				
0.5	272	16	11	299
1.5	159	34	14	207
2.5	98	23	12	133
3.5	86	26	14	126
4.5	37	4	11	52
5.5	26	16	4	46
Total	678	119	66	863
<b>Total releases (10,545)</b>				
0.5	462	40	28	530
1.5	252	48	28	328
2.5	146	38	20	204
3.5	142	40	23	205
4.5	64	27	16	107
5.5	68	39	13	120
Total	1,134	232	128	1,494

ging the fish, the total recoveries appeared to be increased by 9%. The cost of the double tagging was low compared to the cost that would have been incurred by increasing time at sea by 9%.

The parameter estimates of this study indicated that by the middle of the sixth recovery period, 19% of the anterior tags ( $\hat{J}_{1,6}$ ) and 35% of the posterior tags ( $\hat{J}_{2,6}$ ) had been shed, and 7% of the fish had lost both tags ( $(\hat{J}_{1,6})(\hat{J}_{2,6})$ ). Thus, even though shedding rates are low for sablefish, these rates are sufficiently high to affect analysis of tag-return data from this long-lived species.

Tag-shedding rates were high enough in many of the reviewed studies to warrant incorporation of tag-loss rates in analysis of tag-return data. Double tag-

**Table 2**

Maximum-likelihood estimates of rates of immediate tag retention ( $\hat{\rho}$ ) and tag-shedding rates for anterior tags ( $\hat{L}_1$ ) and posterior tags ( $\hat{L}_2$ ) for sablefish. Also shown are estimates of the averages, medians, standard deviations, and ranges of the rates from 2,000 bootstrap replicates.

	Parameter		
	$\hat{\rho}$	$\hat{L}_1$	$\hat{L}_2$
Maximum-likelihood estimate	0.9516	0.0304	0.0694
Bootstrap average	0.9517	0.0304	0.0693
Median	0.9519	0.0302	0.0694
Standard deviation	0.0098	0.0062	0.0075
Minimum	0.9176	0.0108	0.0457
Maximum	0.9855	0.0515	0.0968

ging is necessary to estimate tag-loss rates. Thus we recommend that double tagging be considered, when feasible, for at least a portion of any tagging study. The number of fish released in our study was not affected by double tagging. It is possible, however, that in some situations double tagging could increase the time required to process fish so as to decrease the number of fish released. The tradeoff between the potential reduction in number of fish released and the potential increase in number of fish recovered should be considered when designing a tagging program.

In summary, analysis of returns from double-tag releases indicates that initial shedding of tags was 0.048. The long-term instantaneous rates of shedding were 0.030 and 0.069 for the anterior and posterior positions, respectively. Because there was a difference in the long-term instantaneous rates and because fish released with single tags are only tagged in the anterior position, corrections made for single-tagging experiments should be done only with the anterior tag loss rates.

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Table 3

List of immediate ( $1-\hat{\rho}$ ) and long-term instantaneous ( $L$ ) tag-loss rates found in the literature. Some authors did not estimate  $\hat{\rho}$ .

Species (and tag type)	Authors	Immediate $1-\hat{\rho}$	Annual $\hat{L}$
Plaice (silver wire)	Gulland, 1963		0.162
Plaice (stainless steel)	Gulland, 1963		0.025
Pacific yellowfin tuna	Chapman et al., 1965		0.814
Pacific yellowfin tuna	Bayliff and Moberand, 1972	0.087	0.278
Southern bluefin tuna	Hynd, 1969		0.26
Southern bluefin tuna	Kirkwood, 1981		0.205
Southern bluefin tuna (60's and 70's)	Hampton and Kirkwood, 1990		0.173-0.301
Southern bluefin tuna (80's)	Hampton and Kirkwood, 1990		0.056
Atlantic bluefin tuna	Lenarz et al., 1973	0.027	0.310
Atlantic bluefin tuna	Baglin et al., 1980	0.042	0.186
North Pacific albacore	Laurs et al. 1976	0.12	0.086-0.098
Australian salmon	Kirkwood and Walker, 1984		0.29
Stripey sea perch (dart)	Whitelaw and Sainsbury, 1986		2.116
Stripey sea perch (anchor)	Whitelaw and Sainsbury, 1986		0.415
Sablefish	Beamish and McFarlane, 1988	0.05	0.020
Sablefish (anterior)	This study	0.048	0.030
Sablefish (posterior)	This study	0.048	0.069
Rig (anterior )	Francis, 1989		0.039
Rig (posterior )	Francis, 1989		0.013
Largemouth bass (anterior)	Hightower and Gilbert, 1984		3.977
Largemouth bass (posterior)	Hightower and Gilbert, 1984		1.370
Striped bass (anchor)	Waldman et al., 1991		0.229
Striped bass (internal anchor)	Waldman et al., 1991		0.004
White bass	Muoneke, 1992	0	0.285
Lingcod	Smith et al., 1990		0.137
Black rockfish	Lai and Culver, 1991		0.131
Brown trout	Faragher and Gordon, 1992		0.181
Rainbow trout	Faragher and Gordon, 1992		0.201
Cutthroat trout (coded wire)	Blankenship and Tipping, 1993		0.000
Cutthroat trout (visible impl)	Blankenship and Tipping, 1993		0.035
Northern pike (anchor)	Pierce and Tomcko, 1993		0.015
Northern pike (Dennison)	Pierce and Tomcko, 1993		0.015
White sturgeon (anterior)	Rien et al., 1991		0.041
White sturgeon (posterior)	Rien et al., 1991		0.128
Channel catfish (spaghetti)	Timmons and Howell, 1995		0.286
Channel catfish (anchor)	Timmons and Howell, 1995		0.252
Blue catfish (spaghetti)	Timmons and Howell, 1995		0.177
Blue catfish (anchor)	Timmons and Howell, 1995		0.083
Smallmouth buffalo (spaghetti)	Timmons and Howell, 1995		0.489
Smallmouth buffalo (anchor)	Timmons and Howell, 1995		0.036
Bigmouth buffalo (spaghetti)	Timmons and Howell, 1995		0.611
Bigmouth buffalo (anchor)	Timmons and Howell, 1995		0.000
Paddlefish (spaghetti)	Timmons and Howell, 1995		0.036
Paddlefish (anchor)	Timmons and Howell, 1995		0.022

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**Abstract.**—Aerial surveys were conducted daily from 19 May to 9 June 1995 to document the apparent abundance and migration behavior of giant bluefin tuna, *Thunnus thynnus*, over the Great Bahama Bank region of the Straits of Florida. Our objectives were to conduct an aerial assessment of giant bluefin tuna in this region and to compare our results with previous aerial surveys conducted in the 1950's and 1970's. Two professional bluefin spotter pilots flew 70-nmi transect surveys along "Tuna Alley" as well as surveys into adjacent areas in search of bluefin tuna. The present study area was broader than that surveyed in the 1970's, which consisted of repeated flight tracks, each 1 nmi, across Tuna Alley at a point just south of South Cat Cay. Spotter aircraft carried a data acquisition system consisting of a global positioning system (GPS), a laptop computer, and a 35-mm camera to photograph schools. A total of 839 giant bluefin tuna were documented, within range of totals counted in the 1974–76 surveys (368–3,125 bluefin tuna). Single fish and loosely aggregated schools of up to 100 fish were seen travelling steadily north along the western flank of the Great Bahama Bank. They did not engage in feeding, smashing, or cartwheeling behaviors that are exhibited in New England waters. All bluefin tuna appeared to be "large giants," weighing an estimated 227 kg and over. There is little information documenting the origins and previous locations of giant bluefin tuna travelling along the Great Bahama Bank; therefore the use of direct counts of bluefin tuna in this region as an index of spawning biomass would require further documentation.

## Aerial survey of giant bluefin tuna, *Thunnus thynnus*, in the Great Bahama Bank, Straits of Florida, 1995

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In the 1950's, and later in 1974–76, the U.S. National Marine Fisheries Service conducted aerial surveys for bluefin tuna, *Thunnus thynnus*, migrating along the Great Bahama Bank region (Rivas, 1954, 1978). It is generally believed that large bluefin tuna travel along the Straits of Florida from late April through mid-June on their way to feeding grounds at higher latitudes where they are usually resident from June through October. The bluefin tuna found on the Great Bahama Bank are giants (over 185 cm/107 kg) and are believed to have recently spawned in the Gulf of Mexico or in the Straits of Florida (Rivas, 1978; Mather et al., 1995). Sport fishermen since the 1930's and researchers alike believe that these fish are members of the seasonal assemblage occurring off New England and maritime Canada (Farrington, 1939; Rivas, 1954; Mather et al., 1995). Fish tagged and released on the Great Bahama Bank have been recovered primarily in the northeastern U.S., Canadian, and Norwegian waters.

Recreational fishermen and researchers have identified a narrow region of the Great Bahama Bank off South Cat Cay as Tuna Alley (Fig. 1) because travelling schools

seem to concentrate in this region and are easily visible by air (Rivas, 1954, 1978; Anonymous<sup>1</sup>). In three surveys conducted from May through June 1974–76, survey aircraft flew a 1-mi long transect across Tuna Alley, at 25°31'N and 79°18'W, for about 60 minutes (Rivas, 1978). Flights were conducted on days when weather was suitable for flying for a total transect effort ranging from 38 to 52 hours per survey period (Rivas, 1978). The number of bluefin tuna encountered was multiplied by the number of minutes in a day to derive a daily abundance estimate. This estimate was then multiplied by the assumed 50-d migration interval to derive an estimate of spawning population size. Over the three-year survey period this estimate ranged from 9,630 to 99,360 fish. Rivas (1978) linked the presence and apparent abundance of bluefin tuna in the area with environmental factors, such as increased wind speed and (less strongly) with

<sup>1</sup> Anonymous. 1975. A study of the application of remote sensing techniques for detection and enumeration of giant bluefin tuna. Southeast Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, Miami FL. Contribution rep. 437, 48 p.

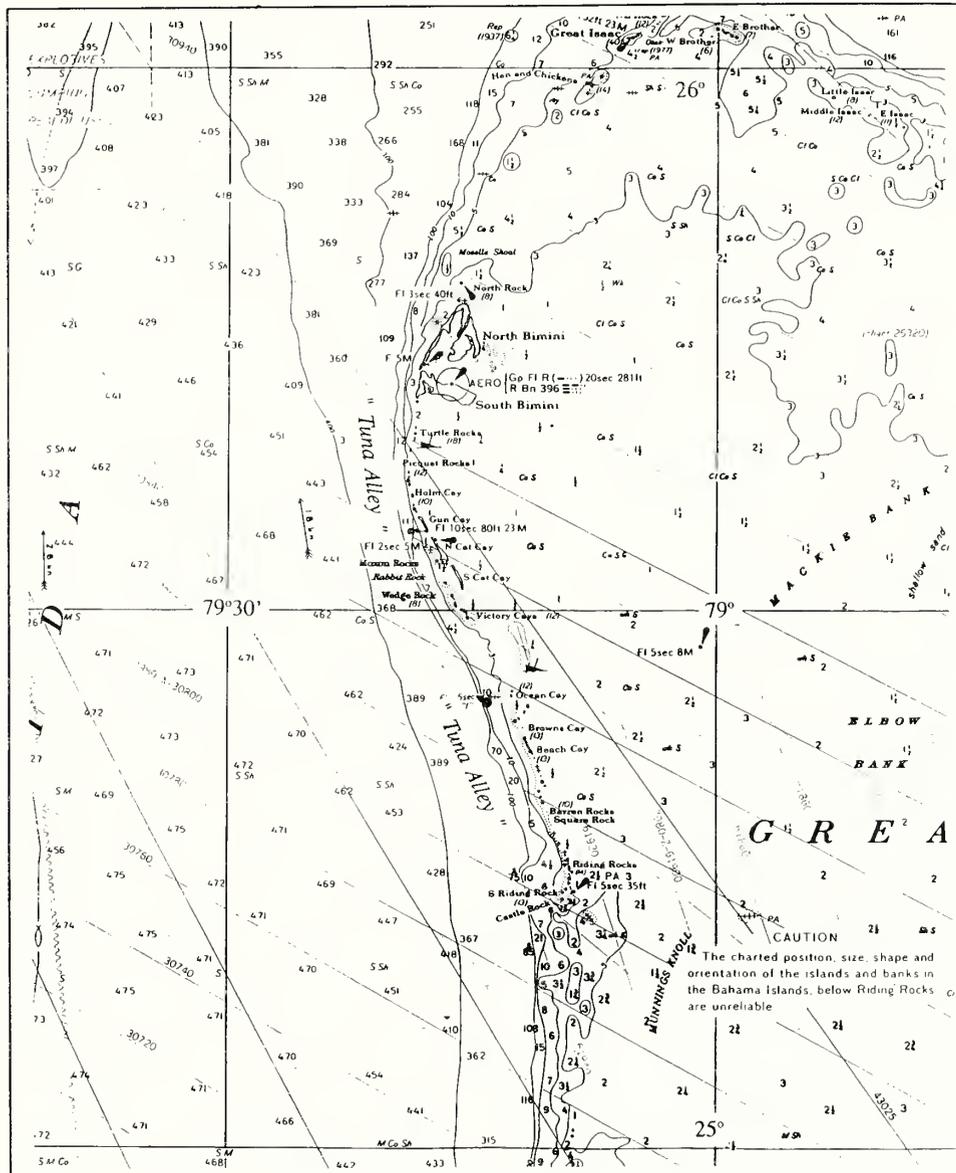


Figure 1

View of the study region showing the location of "Tuna Alley" along the western margin of the Great Bahama Bank, Straits of Florida.

wind direction, lunar phase, and tide. He tentatively concluded that the difference in magnitude of the annual population estimates might be attributed to differences in wind speed across Tuna Alley and, consequently, to changes in the visibility of bluefin tuna to aircraft and fishing vessels.

The decline of North Atlantic bluefin tuna stocks since the 1970's has heightened efforts to obtain more accurate indices of abundance, particularly for spawning biomass. Despite documented changes in

bluefin tuna stocks and commercial fishing practices, there have been no aerial surveys or direct assessments of giant bluefin tuna transiting the Great Bahama Bank for over 20 years. From 19 May to 9 June 1995, we conducted an aerial survey of giant bluefin tuna transiting the Great Bahama Bank region in the general vicinity of the Bimini islands and sand cays. Our objectives were to document their apparent abundance and behavior and to compare the results of the present study with those obtained

in previous aerial surveys conducted by the National Marine Fisheries Service.

## Methods

Bluefin tuna were sighted and counted by two tuna spotter pilots each having over 20 years of experience in the commercial bluefin tuna, yellowfin, and tropical tunas purse-seine fisheries. It is standard practice for spotters to identify species and to estimate average size, weight, and total tonnage before a set is made. The two spotter pilots, having participated in the 1994 New England bluefin tuna aerial survey (Lutcavage and Kraus, 1995), flew a single-engine aircraft (Supercub, tailnumber 344Z, and Cessna 172, tailnumber 270Q) that had viewing access from both sides. Flights originated from Executive Airport, Fort Lauderdale, FL, and required approximately a 40–55 min transit to reach the Great Bahama Bank area near Bimini. The two pilots began spotting fish when they reached the Florida Straits. The survey was targeted to occur between 11:00–13:00 h, similar to the time of day covered by the 1974–76 surveys. The data acquisition system (Tunalog, Cascadia Research, Inc.) consisted of a global positioning system (GPS), a laptop computer with mouse (for event marking), and a 35-mm camera, identical to that used in the New England bluefin tuna spotter survey (Lutcavage and Kraus, 1995), to photograph schools. Position was automatically logged every 15 seconds, and daily flight tracts were reconstructed and bluefin tuna positions plotted with OPCPLOT, version 7.0.

Each day the transect aircraft (Supercub 344Z, except on 28 May) surveyed a zigzag transect line of approximately 70 nmi in length along Tuna Alley, beginning at a southernmost point near 24°45'N and following a zigzag pattern north to approximately 25°48'N. The starting point was set far enough south to incorporate the southernmost limit of the presumed migration route on the Great Bahama Bank where bluefin tuna are visible from the air (Rivas, 1954; Mather et al., 1995). On the first survey day (19 May) the transect aircraft 344Z carried an observer (Hoggard) to establish and verify survey protocol. The starting point of the transect was staggered slightly so that daily transects were not identical. Surveys were conducted at an altitude of 750–1,000 feet and at a true airspeed of 80 knots. The transect legs forming the zigzag were flown to points approximately 3 nmi west of Tuna Alley and were bounded on the east by the shallows of the Great Bahama Bank. The transect was repeated unless rain squalls and strong winds greatly reduced visibility.

The spotter conducting the transect noted any bluefin tuna encountered during transit to the starting point.

The "discovery" aircraft Cessna 270Q did not fly dedicated transects, (except on 28 May). Its mission was to search Tuna Alley and adjacent areas between N. Bimini and Orange Cay in order to identify the general limits of bluefin tuna travel patterns, and to locate, photograph, and observe the behavior of any bluefin tuna encountered. The spotter was free to determine his own search patterns and carried an observer on six survey days. There were two aircraft present in the study area on 14 out of 17 survey days. Pilots remained in radio contact with one another, except for the period of time when the Supercub 344Z was conducting the transect. At the beginning of each survey and at the end of each transect leg pilots recorded their estimation of wind strength and direction, visibility, cloud cover, and water color. During surveys they were instructed to mark the location of all sighted bluefin tuna with the mouse event marker and to document them with photographs when possible. Radio contact with local sport fishing boats targeting bluefin tuna allowed the spotters and observer to collect general information on sea surface temperature, sizes of landed fish, and additional sightings.

## Results

Spotters flew a total of 11,910 nmi (158 hr, including time in transit), encountering bluefin tuna on 10 out of 17 survey days. Approximately 7,126 nmi (115 h) were flown over the Great Bahama Bank. Of these, 1,502 nmi were trackline distance (usually 2 transects/day). Spotters documented 53 bluefin tuna schools overall and estimated a total count of 839 fish (Table 1). No bluefin tuna were sighted on any transits over the Florida Straits; turtles, sharks, delphinids, and flying fish, however, were sighted on numerous occasions. Most bluefin tuna sightings occurred north of 24°30'N, and within the presumed migratory route identified by Rivas (1954) and Mather et al. (1995). Other sightings on or adjacent to the Great Bahama Bank near Tuna Alley included loggerhead sea turtles (*Caretta caretta*), unidentified dolphins, tiger (*Galeocerdo cuvier*) and other sharks, a single sperm whale (*Physeter macrocephalus*), schools of skipjack tuna (*Katsuwonus pelamis*), Bermuda chub (*Kyphosus sectatrix*), permit (*Trachinotus falcatus*), and other unidentified fish.

Sightings ranged from individual bluefin tuna to loosely aggregated schools from 20 to 100 individuals, all judged by spotters to be large giants (> 226 kg, or about 196 cm), similar in size to giants landed

**Table 1**

Giant bluefin tuna aerial survey, 19 May–9 June 1995, over the Great Bahama Bank. Sea water temperatures provided by charter boats. Wind speed and direction estimated by pilots based on sea state.

Sea water temp (°C)	Date	Total no. of bluefin	Total no. of sightings	Winds (knots)	
				North end	South end
	19 May	0	0	S 15–20	
	21 May	0	0	SSW 10–15	
	22 May	0	0	WNW <10	WNW 10–15
	23 May	0	0	WNW 8	
26.4	25 May	0	0	ENE 10–15	
	26 May	0	0	CALM	
26.7	28 May	8	1	ENE 8	SSE 10–12
28.6	29 May	8	2	E 15	E 12–15
29.2	30 May	45	4	CALM	ESE 8–10
28.9	31 May	75	9	CALM	SE <10
28.9	1 June	181	3	E 10–12	ESE 15–20
	2 June	125	9	ESE 20	SE 20–30
29	3 June	149	10	SSE 20	ESE 25–30 (squalls)
27.9	4 June	186	8	ESE 12–15	S/E 25+ (squalls)
28.5	7 June	59	5	WSW 15	W 5–8
29	8 June	1	1	NNW 8–10	WSW 8 (squalls)
	9 June	1	1	CALM	
	Totals	839	53		

by anglers (Beare<sup>2</sup>). Bluefin tuna were first observed in Tuna Alley on 24 May from a sport fishing boat but were not observed from the air until 28 May. Sightings peaked in the first week of June (Table 1) and declined gradually to the last survey day (9 June) when only one giant was seen. According to interviews conducted with charter boat captains, aerial sightings were consistent with the timing and general location of bluefin tuna sightings by recreational vessels. However, aerial sightings were more extensive and covered a much broader area than that covered by charter boats, which tended to limit their fishing on Tuna Alley to a strip of approximately 12 nmi between Bimini and Victory Cay. The last bluefin tuna was sighted in Tuna Alley on 11 June, and all fishing ended by 12 June. Surface seawater temperatures taken by charter boats during the survey ranged from 26 to 29°C, and the prevailing winds were primarily from the E/SE sectors (Table 1).

A general account of sightings per unit of effort (SPUE) and search mileage is given in Table 2. Daily transects were conducted by the Supercub 344Z on all but one survey day (28 May), and the 4 June transect was abandoned because of squalls at the starting point (Table 3). Three out of 53 sightings (with counts of 100, 6, and 1 bluefin tuna, respectively) occurred on transect.

Although our analyses of environmental conditions occurring during the survey are limited, some general conclusions can be drawn. Tropical storm Allison in the Gulf of Mexico generated strong winds and squalls that affected the survey region beginning on 1 June. General SPUE was highest from 1 to 4 June, associated with strongest winds, although fish were also seen on completely calm days with light and variable winds. Peak sightings occurred in the six days following the new moon on May 29. Although the majority of search effort occurred between 11:00 and 13:00 h, the largest school of an estimated 100 bluefin tuna was sighted on 1 June at 09:53 h. On this day pilots had an early start because wind conditions (ESE 15–20 kn) were expected to be especially suitable for the appearance of bluefin tuna. According to interviews with charterboat captains, a total of no more than 10–20 bluefin tuna were sighted over the survey period on Tuna Alley by recreational vessels before survey aircraft had arrived in the morning at the study site.

## Discussion

The total number of bluefin tuna seen in the 1995 survey (839) was generally within the range of bluefin tuna counted in the 1974–76 surveys (368–3,125). Upon examination of school positions for possible re-

<sup>2</sup> Beare, Captain D. 1995. 2462 Lighthouse Point, FL 33064. Personal. commun.

Table 2

A summary of sightings of giant bluefin tuna during an aerial survey, 19 May–9 June 1995 over the Great Bahama Bank.

Aircraft	T/D	Date	Start time	Total time (h)	Est. time on Banks	Total nmi	Nmi. on banks	Number of sightings	No. of bluefin	Sight. per 100 nmi	Bluefin per 100 nmi
344Z	T*	19 May	9:14:0	4.9	3.4	340	230	0	0	0.00	0.00
344Z	T	21 May	9:15:0	3.7	2.2	249	139	0	0	0.00	0.0
270Q	D	22 May	9:48:0	6.2	4.7	441	331	0	0	0.00	0.0
344Z	T	22 May	9:47:15	5.9	4.4	388	278	0	0	0.00	0.0
270Q	D*	23 May	9:17:25	6.6	5.1	424	314	0	0	0.00	0.0
344Z	T	23 May	9:18:15	6.5	5.0	440	330	0	0	0.00	0.0
270Q	D	25 May	9:52:15	6.1	4.6	438	328	0	0	0.00	0.0
344Z	T	25 May	9:42:30	6.4	4.9	406	296	0	0	0.00	0.0
270Q	D	26 May	9:23:15	3.6	2.1	268	158	0	0	0.00	0.0
344Z	T*	26 May	9:23:45	3.6	2.1	244	134	0	0	0.00	0.0
270Q	T	28 May	9:46:0	7.5	6.0	540	430	1	8	0.23	1.9
344Z	T	29 May	9:9:15	5.9	4.4	383	273	2	9	0.73	3.3
270Q	D	30 May	9:21:45	5.7	4.2	364	254	3	37	1.18	14.6
344Z	T	30 May	9:20:0	5.7	4.2	372	262	1	8	0.38	3.1
270Q	D	31 May	9:23:15	5.6	4.1	345	235	3	30	1.27	12.7
344Z	T*	31 May	9:17:15	5.7	4.2	374	264	6	45	2.27	17.0
270Q	D	1 June	7:13:0	5.9	4.4	348	238	2	81	0.84	34.1
344Z	T	1 June	7:13:30	6.0	4.5	399	289	1	100	0.35	34.7
270Q	D	2 June	8:51:15	5.5	4.0	316	206	6	93	2.91	45.2
344Z	T	2 June	8:44:30	5.6	4.1	341	231	3	32	1.30	13.8
270Q	D	3 June	9:11:30	5.1	3.6	297	187	4	84	2.14	44.9
344Z	T	3 June	9:5:15	5.2	3.7	298	188	6	65	3.19	34.6
270Q	D*	4 June	9:54:15	3.2	1.7	206	96	4	90	4.18	94.0
344Z	T**	4 June	9:53:15	3.2	1.7	188	78	4	96	5.10	122.4
270Q	D*	7 June	9:8:15	6.5	5.0	464	354	2	29	0.57	8.2
344Z	T	7 June	9:2:15	7.1	5.6	445	335	3	30	0.90	9.0
270Q	D*	8 June	9:34:30	5.9	4.4	425	315	1	1	0.32	0.3
344Z	T	8 June	9:38:15	5.8	4.3	384	274	0	0	0.00	0.0
270Q	D	9 June	9:54:15	4.0	2.5	268	158	1	1	0.63	0.6
344Z	T	9 June	9:54:15	4.2	2.6	262	152	0	0	0.00	0.0
		Totals		162.9	117.9	10,656	7,356	53	839		

Abbreviations: nmi=nautical miles; T=transect aircraft; D=discovery aircraft; \*=Observer present. Great Bahama Bank mileage was estimated as total flight miles minus 110 (distance over land/Straits of Florida). Estimated time on Bank is total time minus 1.5 h. Transect aircraft mileage includes survey miles spent off transect. \*\*=Transect abandoned due to squalls.

dundant counts, a school of 100 fish recorded by Supercub 344Z and one of 80 fish recorded by Cessna 270Q (Table 4) were judged to be the same, giving an adjusted estimated total count of 759 bluefin tuna. Bluefin tuna were most abundant adjacent to the region west of and between South Bimini and Castle Rock, with sighting concentrations near Victory and Gun Cays (Fig. 2A) similar to distributions described in the past by anglers (Farrington, 1939) and noted by Rivas (1954; 1978).

The Cessna 270Q's search area included broad search tracks extending to North Rock and west of Tuna Alley (Fig. 2B), but no bluefin tuna were sighted in these areas. In comparison with the 1970's surveys, the two survey aircraft produced a 2–3 fold increase in effort hours but had only 33–45% of the number of observation days in comparison with the 1974–76 surveys,

which began almost three weeks earlier and ran 7–11 days later in June (Table 5). In the 1974 and 1975 surveys, no bluefin tuna were observed after 11 June and 2 June, respectively. Although it is possible that bluefin tuna entered the region without being detected by recreational vessels, nevertheless, according to aerial and charter boat sightings, the 1995 migration period of about 20 days was considerably shorter than the presumed 50 day migration period noted in the 1950's and the 1970's (Rivas, 1978). Although SPUE values are not strictly comparable in the present and 1974–76 surveys because of differences in survey protocols and platforms (Table 5), there are resemblances in the general appearance and behavior of giant bluefin tuna.

In the present survey the majority of bluefin tuna (50 out of 53 sightings) were documented off transect; therefore the longitudinal transect along the Great

**Table 3**  
Transect of the giant bluefin tuna aerial survey, 19 May–9 June 1995 over Great Bahama Bank.

Date	Start time	End time	Trackline nmi	Sighting	Bluefin tuna	Sightings per 100 nmi	Bluefin tuna per 100 nmi
19 May	10:51:0	11:50:0 <sup>3</sup>		0	0	0	0
19 May	12:35:0	13:15:0 <sup>3</sup>		0	0	0	0
21 May <sup>1</sup>	11:07:30	12:09:15	72	0	0	0	0
22 May	11:28:0	12:42:45	80	0	0	0	0
22 May	13:33:0	14:50:45	75	0	0	0	0
23 May	10:57:15	12:11:0	77	0	0	0	0
25 May	11:44:0	12:46:0	71	0	0	0	0
25 May	13:40:15	14:43:15	70	0	0	0	0
26 May	11:06:30	12:05:45	71	0	0	0	0
28 May	11:46:45	12:47:29	80	0	0	0	0
29 May	11:06:45	12:15:14	74	1	1	1.3	1
29 May	13:04:29	04:15:00	74	1	1	1.3	1
30 May	11:06:30	12:11:15	71	0	0	0	0
30 May	13:05:0	14:10:30	71	0	0	0	0
31 May	11:11:30	12:10:45	69	1	1	1.46	1
31 May	13:07:15	14:07:15	69	0	0	0	0
1 June	09:06:15	10:06:0	68	1	100	1.47	147
1 June	10:59:45	11:58:15	66	0	0	0	0
2 June	11:13:0	12:08:30	68	0	0	0	0
3 June	11:24:45	12:22:45	69	0	0	0	0
4 June <sup>2</sup>							
7 June	11:28:50	12:52:45	95	0	0	0	0
7 June	13:19:15	13:46:15	28	1	6	3.54	21
8 June	11:25:0	12:31:0	70	0	0	0	0
8 June	13:25:0	14:40:30	78	0	0	0	0
9 June	11:45:0	13:09:15	84	0	0	0	0
		Totals	1,650	5	109		

<sup>1</sup> Trackline altered to avoid local storm squalls.

<sup>2</sup> Transect abandoned because of squalls. All transects, except that flown on 28 May, were conducted by Supercub 344Z.

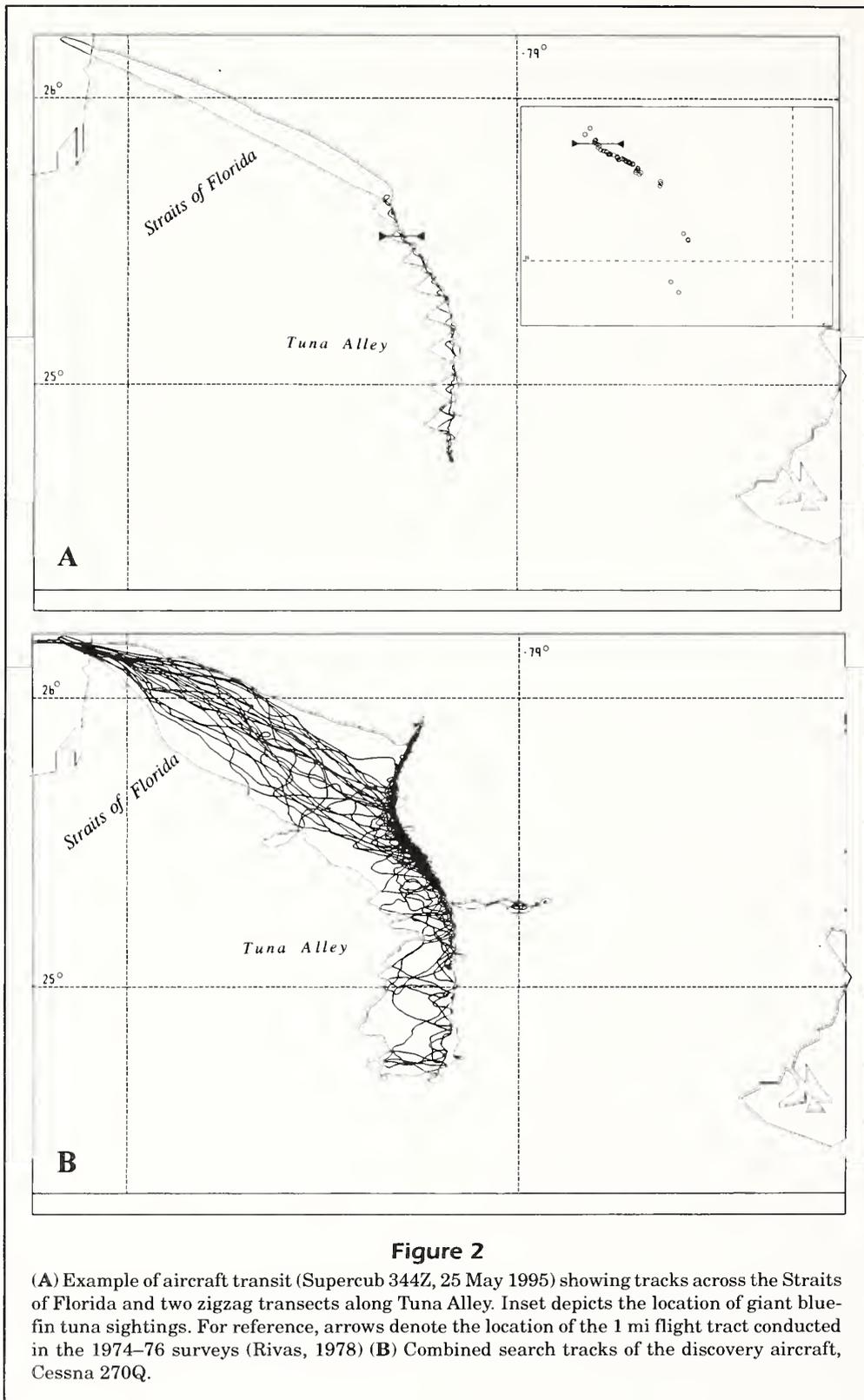
<sup>3</sup> We experienced GPS problems on 19 May 1995; therefore times were estimated, not actual.

Bahama Bank and Tuna Alley may be less effective than other survey methods. On days when fish were present on the banks, general sightings per search mile (i.e. schools or bluefin tuna per nmi of spotter pilot search effort) were within the same order of magnitude for the Cessna 270Q and the Supercub 344Z (which spent nearly half its search time off transect).

In general, the schooling behavior of bluefin tuna travelling adjacent to the Great Bahama Bank differed substantially from what we have observed in the Gulf of Maine aerial surveys (Lutcavage and Kraus, 1995). On the Great Bahama Bank, giant bluefin tuna were much less tightly aggregated and did not exhibit cartwheeling and milling formations or smashing behaviors that indicate feeding, although they are said to "smash" on rare occasion farther offshore (Mather et al., 1995). In contrast with prolonged surface "shows" and the appearance of densely packed schools in New England, the Great Bahama Bank schools spent very little time at the

surface, making it difficult for pilots to photograph the school in entirety. As in previous surveys, schools were most readily detected and successfully photographed while swimming over white sand in shallow water. Photographs of schools in the deeper blue water usually depicted only a few fish visible at the surface. Because of the lack of color contrast between the tuna and the water and because of their deeper position in the water column, these schools were more difficult to detect and photograph, but experienced spotters use several cues including color contrast and surface disturbance to identify bluefin tuna.

Singles and loosely aggregated groups swam steadily north at an estimated speed of 6–8 knots, similar to speeds reported by Mather et al. (1995), with the exception of one school, which we followed for 36 minutes in the air (Fig. 3). As two fishing boats approached from opposite sides, the school of ten fish changed spatial conformation several times, turned west, and disappeared into deeper water.



In general, spotters estimated that all the bluefin tuna they had encountered were large giants ranging from 227 kg to over 295 kg (approximate length:

225–250 cm straight fork length [SFL]). Three fish landed by anglers during the survey period ranged from 264 to 280 cm SFL (250–317 kg), equivalent to

Table 4

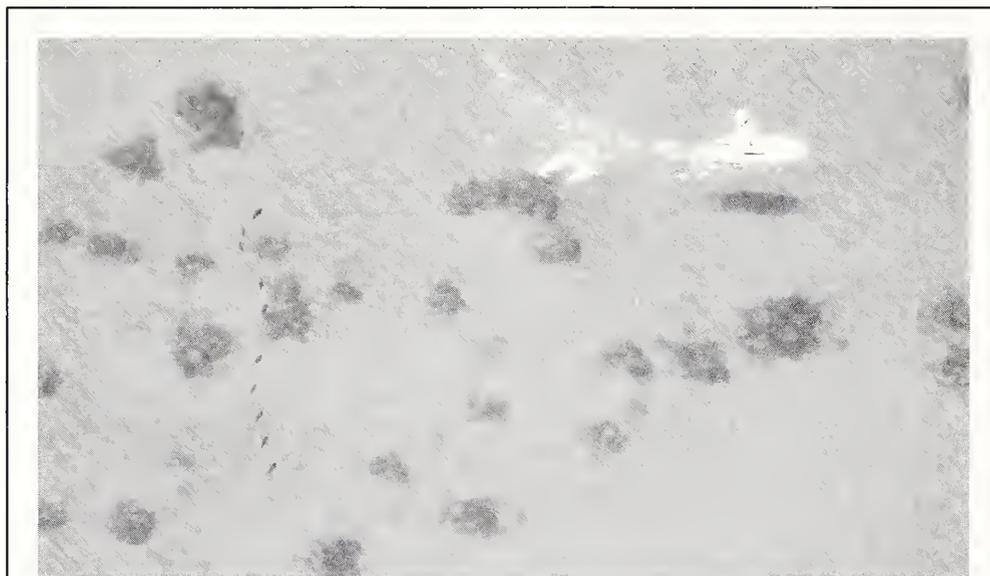
Giant bluefin tuna aerial survey, 19 May–9 June 1995, over the Great Bahama Bank. Sighting positions.

Aircraft	Date	Time	Latitude	Longitude	Count
270Q	28 May	16:10:30	N25:24.60	W079:14.93	8
344Z	29 May	10:50:42	N25:03.50	W079:09.68	8
344Z	29 May	11:16:24	N24:52.97	W079:10.30	1
344Z	30 May	12:28:0	N25:24.73	W079:14.15	8
270Q	30 May	11:17:20	N25:25.47	W079:14.42	15
270Q	30 May	12:32:19	N25:26.04	W079:14.45	10
270Q	30 May	12:39:48	N25:25.87	W079:14.43	12
270Q	31 May	11:10:1	N25:36.93	W079:18.94	10
344Z	31 May	12:47:27	N25:05.97	W079:09.72	1
344Z	31 May	10:52:30	N25:05.76	W079:09.71	8
270Q	31 May	13:7:15	N25:27.35	W079:15.17	10
344Z	31 May	10:28:42	N25:29.94	W079:17.04	7
270Q	31 May	10:35:13	N25:33.75	W079:18.40	10
344Z	31 May	10:17:24	N25:34.92	W079:19.50	25
344Z	31 May	11:20:0	N24:54.18	W079:11.33	1
270Q	1 June	08:30:29	N25:32.09	W079:18.06	1
344Z	1 June	09:52:42	N25:28.17	W079:15.65	100
270Q	1 June	09:53:40	N25:28.53	W079:15.94	80
270Q	2 June	10:34:41	N25:29.17	W079:16.36	7
270Q	2 June	12:39:10	N25:30.49	W079:17.37	7
270Q	2 June	12:2:38	N25:29.70	W079:17.02	27
270Q	2 June	11:14:47	N25:29.63	W079:16.73	17
270Q	2 June	13:5:52	N25:32.93	W079:18.48	27
344Z	2 June	12:23:29	N25:32.52	W079:18.22	12
270Q	2 June	12:15:29	N25:28.30	W079:16.24	8
344Z	2 June	13:14:06	N25:31.65	W79:18.18	10
344Z	2 June	10:26:12	N25:28.10	W079:15.54	10
344Z	3 June	12:33:00	N25:34.15	W079:19.16	12
344Z	3 June	12:56:00	N25:22.33	W079:12.31	14
344Z	3 June	12:43:15	N25:29.69	W079:17.21	3
344Z	3 June	10:54:59	N25:07.61	W079:10.14	6
344Z	3 June	11:15:47	N24:51.24	W079:10.59	5
344Z	3 June	10:37:44	N25:20.97	W079:12.35	25
270Q	3 June	12:55:51	N25:30.92	W079:17.93	5
270Q	3 June	12:26:57	N25:30.55	W079:17.38	35
270Q	3 June	11:59:11	N25:24.77	W079:14.62	17
270Q	3 June	13:10:5	N25:25.24	W079:14.60	27
344Z	4 June	12:09:59	N25:30.59	W079:17.58	15
270Q	4 June	12:1:59	N25:28.80	W079:16.36	35
270Q	4 June	11:35:26	N25:27.84	W079:15.54	13
270Q	4 June	11:24:0	N25:29.77	W079:17.07	35
344Z	4 June	11:18:0	N25:27.88	W079:15.51	25
344Z	4 June	11:14:45	N25:28.34	W079:16.13	30
270Q	4 June	12:7:30	N25:27.25	W079:14.91	7
344Z	4 June	11:48:28	N25:27.53	W079:15.31	26
270Q	7 June	11:2:6	N25:28.58	W079:15.90	25
270Q	7 June	14:10:22	N25:30.77	W079:17.70	4
344Z	7 June	14:40:00	N25:27.00	W079:14.92	12
344Z	7 June	11:08:30	N25:28.97	W079:16.35	12
344Z	7 June	13:28:29	N25:24.24	W079:14.37	6
270Q	8 June	14:40:00	N25:27.82	W079:15.29	1
270Q	9 June	12:08:14	N25:08.88	W079:11.53	1

the highest range of values given in the length histogram of fish captured previously in the Bahamas from 1939 to 1966 (Mather et al., 1995). Rivas (1976) noted that the mean length of Bahama bluefin tuna increased by 20–25 cm over a 20-yr period dating back to the 1950's. Bluefin tuna documented in New England aerial surveys spanned a much broader range of size classes and include small medium (145–178 cm SFL, 61<107 kg), large medium (178–196 cm,

107<141 kg), and a broader range within the giant bluefin tuna size class (>196 cm, >141 kg).

As in previous Bahamas surveys, the majority of sightings occurred under conditions of strong winds, but 121 out of 839 (759 adjusted total) bluefin tuna were sighted under calm or variable wind conditions. Experienced tuna guides emphasized that bluefin tuna do not appear on the Bank until winds are of sufficient strength from the southern sector or when



**Figure 3**

A school of ten giant bluefin tuna photographed on the Great Bahama Bank (N25:27.35, W79:15.17) on 31 May 1995 from discovery aircraft Cessna 270Q. The school was arrayed in "soldier formation" as swimmers from the boat approached.

**Table 5**

Comparison of giant bluefin tuna aerial surveys conducted in the Straits of Florida and the Great Bahama Bank region.

	1974 <sup>1</sup>	1975 <sup>1</sup>	1976 <sup>1</sup>	1995
Survey dates	9 May–16 June	1 May–16 June	2 May–20 June	19 May–9 June
Survey type	1-mi transect across Tuna Alley	1-mi transect across Tuna Alley	1-mi transect across Tuna Alley	70-nmi transect and discovery flts.
Aircraft used	not given	not given	not given	2, single engine
Time of day (h)	11:00–13:00	12:00–14:00	09:30–14:00	11:00–13:00
Total observation days	37	46	42	17
Total survey hours	37.7	48.6	51.6	117.9
Date of first sighting	9 May	1 May	6 May	28 May
Date of last sighting	11 June	2 June	15 June	9 June
Total bluefin	3,125	368	1,120	839

<sup>1</sup> 1974–76 surveys are taken from Rivas, 1978.

the Gulf Stream's edge intercepts the Bank (or both), producing stronger northerly flow. Previous reports have also noted the bluefin tuna's apparent avoidance of the "dirty water" tidal flow from the Bank, which varied a good deal over the survey period. However, on at least two occasions we observed bluefin tuna in turbid water. In the present study, the period of highest sightings occurred in the six days following the new moon. Although aerial sightings were not given in relation to lunar phase for the 1974–76 surveys, this period coincided with the lowest catch per boat day for 11 Cat Cay bluefin tuna tournaments from 1941 to 1960 (Rivas, 1978).

It is possible that the apparent relation of strong winds with appearance of bluefin tuna on Tuna Alley may be driven by oceanographic conditions occurring in adjacent staging areas. In general, flow over the Great Bahama Bank in the Bimini area is weak and driven by wind and tide (Lee<sup>3</sup>). Although the Bank constitutes a topographic wall, it is not associated with strong upwelling. Much stronger flow and upwelling occurs where the Loop Current leaving the Gulf of Mexico impinges on the north coast of Cuba. The dynamics of eddy systems near Cay Sal Bank and northern Cuba could conceivably influence travel routes of bluefin tuna, a concept that is reinforced by the reports of giant bluefin tuna on Cay Sal Bank and the Old Bahama Channel by anglers and fish spotters (Rivas, 1954; 1978; Mather et al., 1995), and one that would explain the large variability in numbers of bluefin tuna sighted on Tuna Alley from year to year (e.g. an order of magnitude difference in sightings between 1974 and 1975 (Rivas, 1978).

During the survey, surface sea water temperatures in the Straits of Florida and adjacent to the Great Bahamas Bank, obtained from advanced high-resolution radiometer (AVHRR) satellite imagery, ranged from 26° to 30°C, nearly 10°C higher than the mean sea surface temperature associated with bluefin tuna schools in the New England region (Lutcavage et al.<sup>4</sup>). However, our opportunity to examine additional environmental conditions that might have influenced bluefin tuna occurrence on the Great Bahama Bank region in 1995 was limited. Sea surface temperatures across the Straits of Florida are somewhat uniform in the late spring and summer, and to our knowledge there were no current meters or buoy data re-

flecting the precise boundary of the Gulf Stream edge. This information, along with tide and wind stress records, might have provided a more specific relation between environmental conditions and the appearance of bluefin tuna on the Great Bahama Bank.

There are numerous reports of giant bluefin tuna in other areas of the Bahamas and Straits of Florida beyond Tuna Alley, particularly to the east and northeast off Walkers Cay, the Abacos, and also in deep water regions west and southwest of the Great Bahama Banks and off Cuba (Rivas, 1978; Mather et al., 1995; Murray<sup>5</sup>). Recent longline captures also corroborate the presence of bluefin tuna in the eastern areas, well before and concurrent with the assumed migration period of fish that transit Tuna Alley (Turner<sup>6</sup>). In addition, giant bluefin tuna were landed in the first week of June in the Gulf of Maine, nearly coincident with our first sightings on the Great Bahama Bank. At present there is little information that would identify whether fish travelling in this region are members of the same assemblage, and further, whether they had recently exited the Gulf of Mexico, or had travelled from areas to the south and east, or from the Windward Passage, as suggested by Mather et al. (1995).

Mather et al. (1995) reported that the Great Bahama Bank migration area continues along the western edge of the Little Bahama Bank, and they sighted giant bluefin tuna travelling north between the Great and Little Bahama Banks in May–June 1968. It is clear that without complementary oceanographic surveys, the sporadic appearance and diffuse aggregation behavior of giant bluefin tuna on the Great Bahama Bank present serious problems for direct aerial assessment in this region. Although fish can be seen and enumerated under suitable conditions during daylight hours, there is no way of determining how many fish transit the Straits of Florida in deeper water, or determining their presence and abundance in other regions of the Bahama islands. Lacking this information, the use of direct counts of bluefin tuna in this region as an index of spawning biomass seems unwarranted. Alternatively, aerial surveys on the Great Bahama Bank, in conjunction with direct sampling of landings, may provide an index of regional abundance and information on the size classes and reproductive status of bluefin tuna transiting the area. In the future, examination of oceanographic conditions occurring in the Loop

<sup>3</sup> Lee, T. 1995. Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, Miami, FL. Personal commun.

<sup>4</sup> Lutcavage, M., J. Goldstein, and S. Kraus. 1996. Sustaining tuna fisheries—issues and answers. Proceedings of the 47th tuna conference; Lake Arrowhead, CA, 20–23 May 1996.

<sup>5</sup> Murray, Captain E. 1996. 8101 Nashua Dr., Palm Beach Gardens, FL 33418. Personal commun.

<sup>6</sup> Turner, S. 1995. Southeast Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, Miami, FL. Unpubl. data.

Current, Cay Sal Bank, and north Cuban coast might provide information that could be used to forecast the appearance and relative abundance of bluefin tuna across the western Bahama Banks and the Straits of Florida. A direct hydroacoustic count of all bluefin tuna transiting the Straits of Florida would provide additional information on the numbers of bluefin tuna exiting the Gulf of Mexico, and possibly, regions of the Caribbean.

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Spotter pilots George Purmont (Little Compton, RI) and Dave Thompson (Chatsworth, NJ) provided their considerable skills and aircraft for this survey. We thank Gerry Scott, Steve Turner, and Rosemary Sullivant for logistical support, Dennis Lee for bluefin tuna longline capture locations, and Captains Edward Murray, Danny Beare, and Richard Wright for helpful discussions on the Bahamas bluefin tuna sport fishery.

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**Abstract.**—Populations of Atlantic hagfish, *Myxine glutinosa* (L.), are found throughout the Gulf of Maine in soft-bottom substrates at depths greater than 50 m. This report presents data on the sizes, weights, morphometric characters, and reproductive states for specimens collected at a study site approximately 50 km offshore in the Gulf of Maine. Limited comparisons with data from specimens collected elsewhere suggest that this data set is representative of hagfish populations within the inner Gulf of Maine. The small number of eggs produced (less than 30 per female), the large number of animals without macroscopically visible gonadal tissue (25% of the population), and the small number of males (<6% of the population), gravid females (<1%), and postovulatory females (<5%) suggest that hagfish have limited reproductive potential. This raises serious questions about the long-term viability of the New England eelskin fishery.

## A population profile for Atlantic hagfish, *Myxine glutinosa* (L.), in the Gulf of Maine. Part I: Morphometrics and reproductive state

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The hagfishes, or Myxinoidea, are worldwide in distribution, with 59 species recognized at present (Fernholm<sup>1</sup>). Hagfishes are noteworthy from an evolutionary standpoint because they represent the oldest extant clade among the craniates. A better understanding of their anatomical and physiological characters may thus reveal information about an early stage in vertebrate evolution. Although eel-like in general body form, hagfish lack jaws, paired fins, vertebrae, bone, and a variety of other gnathostome characteristics.

All known species of hagfish live in close association with the bottom, resting on the substrate or occupying burrows within soft sediments (Gustafson, 1935; Adam and Strahan, 1963, a and b; Foss, 1963; Fernholm, 1974; Neira, 1982; Martin and Heiser, 1989; Cailliet et al., 1992; Barss, 1993). They are generally described as predators on invertebrates and as opportunistic scavengers on both invertebrate and vertebrate remains. There are two major groups of living hagfishes

united under the family Myxinidae: the Eptatretinae, typified by the genus *Eptatretus* (30–35 species), and the Myxiniinae, typified by the genus *Myxine* (19 species) but also including the genera *Nemamyxine*, *Neomyxine*, and *Notomyxine* (Nelson, 1994). The characteristics of the *Myxine* appear to be more derived than those of the *Eptatretus*. For example, hagfishes of the genus *Eptatretus* have multiple efferent gill openings on each side of the pharynx, vestigial eyes beneath a pale skin patch, and traces of a cephalic lateral line complex. In contrast, hagfishes of the genus *Myxine* have a single common efferent duct opening on each side of the pharynx, even smaller eyes covered by undifferentiated integument, and no traces of any lateral line components. In general, the genus *Eptatretus* has a more widespread distribution than the genus *Myxine*, whose center of diversity appears to be the New World, where 14 of 19

species have been identified (Wisner and McMillan, 1995).

Only one myxinid, *Myxine glutinosa* L., is found on both sides of the Atlantic Ocean, and this is the only hagfish reported within the Gulf of Maine. There are several reasons why *Myxine glutinosa* is an important species for the Gulf of Maine:

- 1 The substantial numbers present and their ongoing energetic requirements suggest that they play a significant role in the benthic ecosystem throughout the Gulf of Maine (Lesser et al., in press).
- 2 This species has both direct and indirect effects on commercial fisheries in the Gulf of Maine. In areas of abundance their opportunistic feeding habits can reduce the value of the catches made by longline or fixed gillnet fisheries. Hagfish have been known to feed on restrained or moribund cod, herring, haddock, hake, mackerel, spiny dogfish, and mackerel sharks caught in fisheries gear (Gustafson, 1934; Bigelow and Schroeder, 1953; Strahan, 1963). Equally important, feeding studies by Shelton (1978) suggest that hagfish predation could have a significant impact on *Pandalus borealis* populations within the Gulf of Maine.
- 3 *Myxine glutinosa* populations are now targeted by American and Canadian fishermen in the Gulf of Maine to meet the South Korean demand for "eelskin" used to manufacture expensive leather goods. In 1990, the sale of eelskin leather goods, all produced from hagfish skin, brought South Korea revenues of approximately US\$100 million (Gorbman et al., 1990). The value of eelskin products imported into the U.S. alone in 1992 was US\$70 million (Melvin and Osborn<sup>2</sup>). So large is this market that Korean processors, unable to supply the demand from overexploited eastern Asian fisheries, have begun sampling and purchasing hagfish from several other regions, including North and South America (Gorbman et al., 1990). During 1993 and 1994, Gulf of Maine fishermen harvested roughly 1600 metric tons (3.6 million pounds) of hagfish, and there were unknown effects on the ecology of the region (Kuenstner, 1996).

Part 1 of this report presents morphological data and a population profile generated in a study of a hagfish population in the Gulf of Maine. Part 2 of this report, published separately, will relate these and other data to the proposal made by Wisner and McMillan (1995) to reserve *M. glutinosa* for the east-

ern Atlantic, and to give western Atlantic populations, including those of the Gulf of Maine, separate status as *Myxine limosa*.

## Materials and methods

The primary study site was adjacent to a small rock ledge known locally as "the Nipper" (near 42°57'N, 70°17'W). This site is within the Bigelow Bight, approximately 25 km west of Jeffrey's Ledge and 50 km east of the New Hampshire coast. The Bigelow Bight and Jeffrey's Ledge are both important groundfishing areas. Hagfish in the study area inhabit a superficial zone of fine, organic sediment covering a layer of grainy clay that overlies a thick layer of silty clay. Individual hagfish are usually found in shallow, sinusoidal, temporary burrows, with nose and barbels exposed to passing currents. The bottom temperature year-round is 4–6°C, and the salinity is 32 ppt or higher at all times. The superficial biotic community includes representatives from several families of tube worms, Cerianthid anemones, tunicates, sponges, and shrimp (*Pandalus borealis*). Comparable habitats that could support hagfish populations cover 60–70% of the floor of the Gulf of Maine (National Ocean Service<sup>3</sup>).

Hagfish were collected with baited traps set on the bottom in depths of 130–150 m. The traps consisted of garbage cans with holes punched in the side and with an internal screen that funneled hagfish toward the enclosed bait. The baited traps were left on the bottom for periods of 30 minutes to 1 hour and then retrieved. The animals were then placed in seawater chilled to approximately 4°C for transport to the Shoals Marine Laboratory on Appledore Island, Maine. After being held in refrigerated aquaria for a period of hours to days, animals were sacrificed and measurements were taken. The aquarium complex was monitored daily, and animals dying in captivity were measured immediately, prior to disposal. Morphometric data were collected from fresh specimens from the primary site between June 1989 and August 1992.

Methods of measuring and counting followed those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). All measurements were recorded in millimeters. For descriptive purposes, after total length (TL) was recorded, the body axis was divided into 3 regions (*snout-pcd*, *trunk*, and *tail* regions;  $n=143$ ) or 4 regions (*prebranchial*, *branchial*, *trunk*,

<sup>2</sup> Melvin, E. F., and S. A. Osborn. 1992. Development of the west coast fishery for Pacific hagfish. Seattle, WA. Natl. Mar. Fish. Serv., NOAA. Final Rep. NA90AA-H-SK142.

<sup>3</sup> National Ocean Service, Coast and Geodetic Survey. 1995. Gulf of Maine and George's Bank, Chart No. 13009. National Ocean Service, Silver Springs, MD.

**Table 1**  
Morphological measurements for the sample population of Atlantic hagfish, *Myxine glutinosa*.

Character	Mean	SD	Range	%TL <sup>1</sup>	SD	Range	n
Total length (mm)	509	104	195–724	100			202
Snout–pcd <sup>2</sup>	135	27	54–200	27.0	1.6	24–37	143
Prebranchial	82	20	34–130	17.0	1.9		67
Branchial	46	14	16–75	9.3	2.1	5–21	67
Trunk	311	72	107–459	61.4	3.8	42–83	143
Tail	64	14	25–106	12.6	1.1	9–17	143
Width	14	7	4–35	2.7	1.1	2–6	91
Depth (trunk)	22	7	8–35	4.2	0.7	2–7	87
Depth (cloaca)	19	5	6–28	3.7	0.5	2–5	198
Depth (tail)	20	5	8–30	4.0	0.5	2–5	97
Weight (g)	136	67	8–290				80
Total cusps	35	2	28–40				97
Multicusps							
outer	2	0.3	1–3				97
inner	2	0.1	1–2				97
Unicusps							
outer	7	0.7	5–9				97
inner	7	0.7	6–9				97
Total slime pores (left side)	114	7	91–128	%TL <sup>3</sup>	SD	Range	94
Snout–pcd	33	4	20–45	29	3.0	21–40	94
Trunk	67	4	51–77	59	2.9	51–69	94
Tail	13	2	8–19	11	1.3	9–15	94

<sup>1</sup> %TL = Percentage of total length.

<sup>2</sup> pcd = pharyngocutaneous duct.

<sup>3</sup> % TP = Percentage of total slime pore counts.

and tail regions;  $n=67$ ). The snout-pcd measurement extends from the tip of the snout to the anterior margin of the pharyngocutaneous duct (pcd), the trunk continues to the anterior margin of the cloaca, and the caudal region extends from that point to the tip of the tail. The sum of these measurements is equal to the total length.

For one series of animals, prebranchial and branchial measurements were taken within the snout-pcd length. The prebranchial region extends from the tip of the snout caudally to the rostral margin of the first gill pouch, the branchial region extends from that point to the anterior margin of the pharyngocutaneous duct.

Width is the maximum width of the trunk; depth (trunk) is the body height, exclusive of fin fold, at that site. Cloacal depth, measured at mid-cloaca, excludes the dorsal fin fold, whereas tail depth spans the entire tail, including dorsal and ventral fin folds. Cusp counts (unicusps and multicusps on outer and inner rows) were recorded for the left side; then the right side was counted to obtain the total cusp count. When slime pores were counted, the first two axial regions were combined and recorded as the snout-

pcd count, which corresponds to the prebranchial count of Wisner and McMillan (1995). This distinction was made to maintain consistency with the length data, where prebranchial and branchial lengths together constitute the snout-pcd length. Reproductive state was determined by visual inspection, rather than histological analysis. If present, ova were measured and the maximum length recorded.

## Results

Table 1 summarizes pertinent morphometric data for this population of *Myxine glutinosa*. Hagfish species in general show remarkable variation in number of gill pouches. Table 2 presents data on the total number of gill pouches in our sample population. The range of gill pouch data (range:10–14,  $n=94$ ) is greater than that reported for *M. glutinosa* in the eastern Atlantic by Fernholm and Hubbs (1981) (range: 11–13,  $n=8$ ).

Despite the size of the landings (over 1,400 metric tons in 1994 [Kuenstner, 1996]), there are relatively few available data concerning the lengths and

**Table 2**Number of gill pouches in *Myxine glutinosa* (n=94).

	No. of gill pouches (total)				
	10	11	12	13	14
Incidence (%)	1.1	1.1	74.5	7.4	15.9

weights of the harvested hagfish. This may in part reflect the effort required to immobilize and weigh individual hagfish. To address this problem we reviewed the morphometric data for a relatively quick and reliable method of estimating sizes and weights in the field. The easiest and most accurate method found involved measuring the depth of the body at the cloaca, excluding the dorsal fin fold. The fin fold was excluded to make the measurement easier to perform at sea with unanesthetized animals. (A caliper measurement of cloacal depth can be taken quickly, with minimal stress to the animal.)

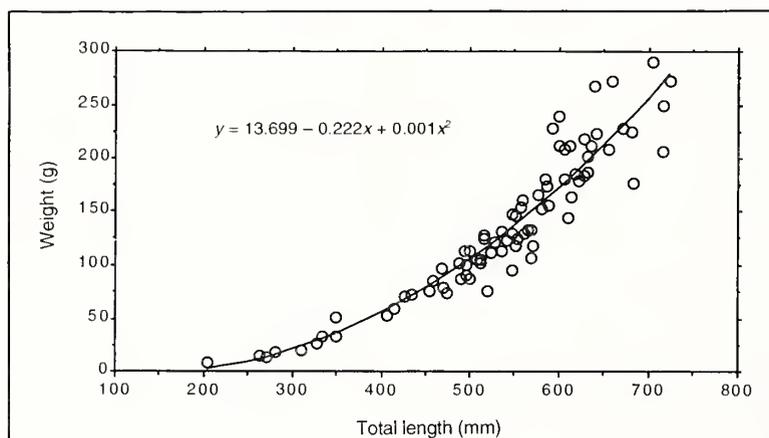
Figure 1 presents the relationship between total length and weight for a sample population of  $n=83$ . Figure 2A is a length histogram for the entire sample population ( $n=306$ ) which comprised 202 animals whose lengths were measured directly (see Table 1) and 104 lengths calculated on the basis of cloacal depth using the formula shown in Figure 2B.

Figure 3A is a weight histogram for the entire sample population which comprised 80 direct measurements (see Table 1), 122 weights calculated on the basis of total length (see Fig. 1), and 104 weights calculated on the basis of cloacal depth with the formula shown in Figure 3B.

Note the preponderance of adult specimens and the absence of juveniles smaller than 195 mm (7.6 in.) at this collection site. No smaller individuals have been seen with ROV's or manned submersibles in this area, either on the soft bottom or over the associated rocky ledges (Martini and Heiser, 1989; 1991). Data on 1,172 animals from other locations in the Gulf of Maine (details below) indicate animals as small as 170 mm TL. However, the size of *M. glutinosa* at hatching has been estimated to be approximately 50 mm (Fernholm, 1969), and there has long been a general consensus that hagfishes, including *Myxine*, do not have a larval stage (Putnam, 1874; Dean, 1900; Worthington, 1905; Walvig, 1963). The absence of animals of 50–170 mm TL from traps at widespread locations and in visual surveys of bait stations suggests that newly hatched *M. glutinosa* may target different feeding resources from those targeted by older animals. Juveniles may, for example, feed solely on invertebrates within the substrate.

No data are available concerning the reproductive cycle and behavior of *M. glutinosa*. The sampled population contained a mixture of sexually immature and sexually mature individuals (Fig. 4). The following patterns can be recognized:

- 1 Individuals shorter than 400 mm TL are sexually immature. These animals either lack macroscopically visible gonads altogether or have granular tissue in the gonadal mesentery that cannot be identified as either testicular or ovarian in nature.
- 2 Approximately 59% of the population is classified as females on the basis of egg development. Testicular tissue is usually rudimentary in these animals.

**Figure 1**

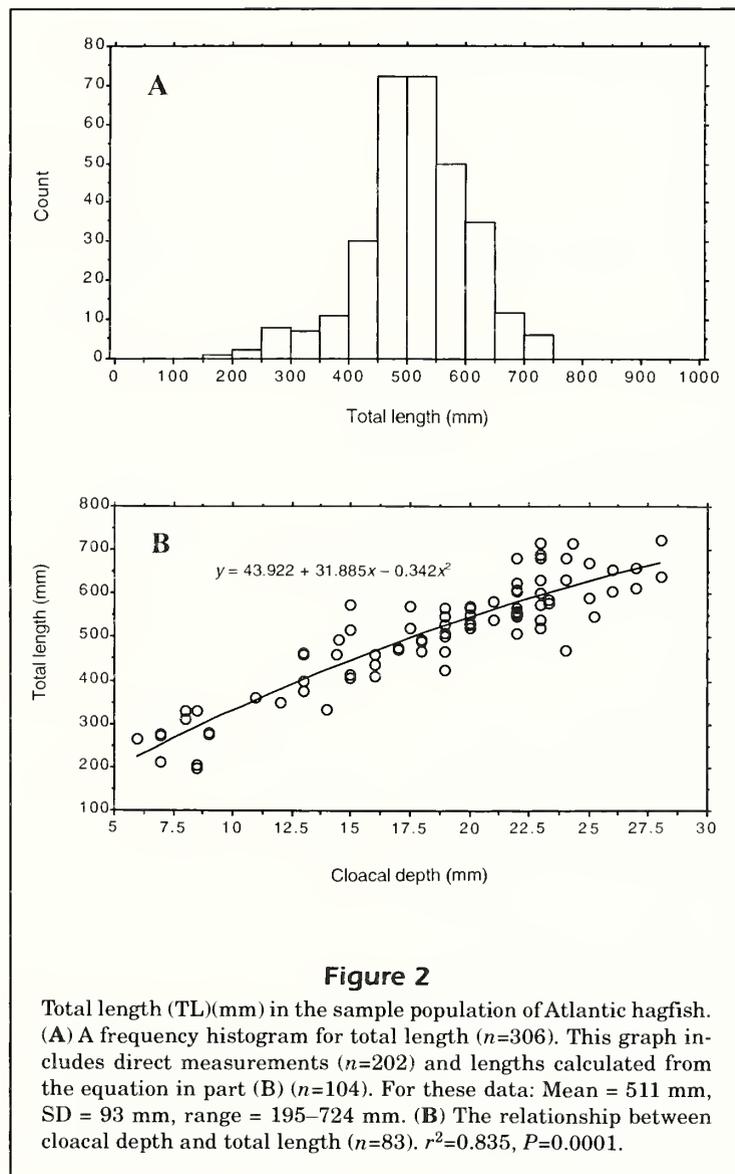
Total length (mm) versus body weight (g) in a sample population of Atlantic hagfish, *Myxine glutinosa* ( $n=80$ ).

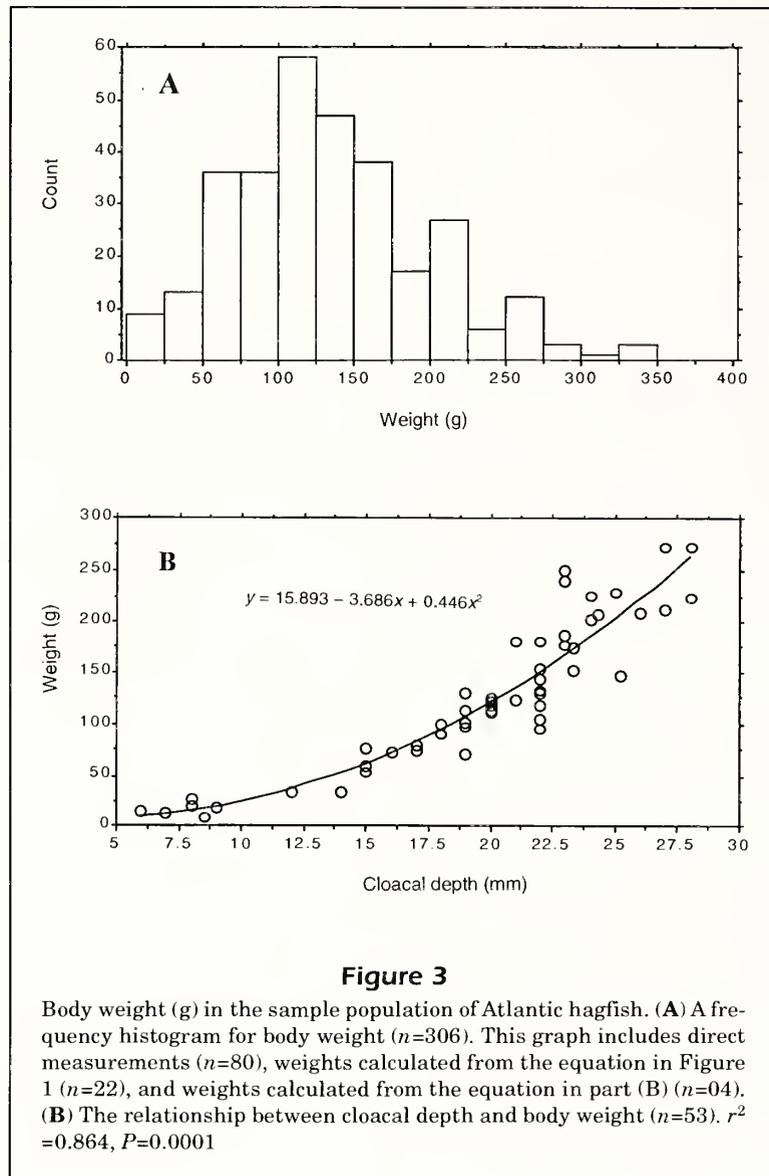
- 3 Males represent a very small percentage of the population (less than 6%).
- 4 Roughly 25% of the adult population does not have macroscopically identifiable gonadal tissue; the presence of large numbers of sterile individuals has also been reported for populations in the eastern North Atlantic (Schreiner, 1955; Jespersen, 1975).
- 5 The overlap in sizes between males and females suggests neither protandry nor protogyny.

Regression analyses were performed on morphological data sets to detect significant trends. No relationships were found between total slime pores, snout-pcd slime pores, or tail slime pores versus total length. This finding indicates that the number of

slime pores is fixed for each individual and that additional slime pores are not added as growth occurs. However, with growth, the prebranchial region forms a significantly smaller percentage of the total length. The feeding apparatus, consisting of the tooth cusp plates and the dental muscle complex (Dawson, 1960), is therefore relatively large in smaller individuals. No data are available concerning the life span or growth rates for this species.

To determine whether or not our data were representative of the Gulf of Maine as a whole, we began by comparing the morphological data from our study site with data from eight specimens collected at Stellwagen Bank in Massachusetts Bay (42°20'N, 70°17'W), roughly 36 km from our primary study site. The size range (460–600 mm TL; average: 523 mm





TL) was comparable to that found at the Nipper (range: 195–724 mm TL; average: 509 mm TL). Although the small size of the Stellwagen sample constrains the power of statistical comparison, the only statistically significant differences found between these groups were that the maximum depth and width (in percent of body length) of animals from Stellwagen Bank were greater than those from the original study site. This may reflect differences in the substrate and food availability between the two locations, or it may be an artifact of the small sample size.

We next compared our length distribution data with catch statistics collected between 19 May and 28 July 1994 by the New England Fisheries Development Association (Kuenstner, 1996). The close

agreement between the data sets (Fig. 2A vs. Fig. 5) suggests that the sampling reported here is representative of hagfish populations throughout the Gulf of Maine.

## Discussion

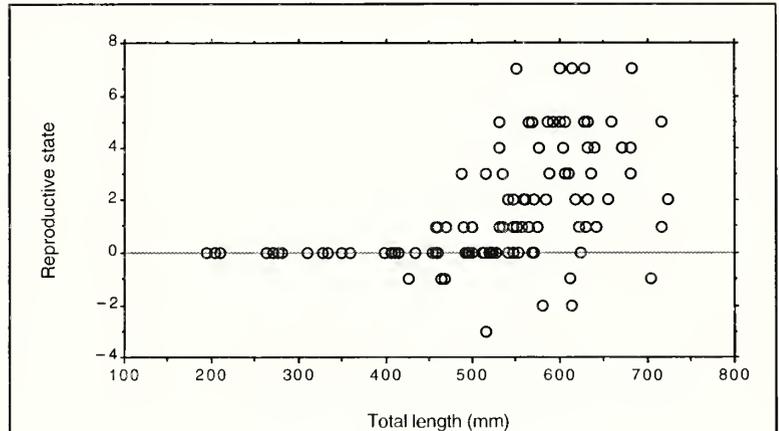
The gonads in hagfishes develop within a mesenterial fold located to the right of the dorsal mesentery that supports the gut. The anterior 2/3 of the gonad may develop into ovarian tissue, and the posterior 1/3 may develop into testicular tissue. Details of sexual differentiation are known for only a few species, notably the Pacific hagfish, *Eptatretus stouti*. Gorbman (1990) reported that *E. stouti* are protogynous her-

maphrodites: sexually immature animals are found at some stage of female differentiation, and mature animals are usually differentiated as either males or females. Mature females are longer than 200 mm TL and males are longer than 280 mm TL. The largest animals are usually females. The incidence of hermaphroditism in animals over 230 mm TL is very low (0.3% [Gorbman, 1990]), but there is evidence that this condition may persist throughout the life of the individual (Johnson, 1994).

In our study of *M. glutinosa*, animals at any size above 400 mm TL, the minimum size at which gonadal tissues become macroscopically identifiable, may have no discernible gonads or possess an immature ovary and immature testis, a mature ovary and immature testis, an immature ovary and a mature testis, or a mature ovary only. Animals with only mature testes were not seen, and only one animal was observed with what appeared to be a mature ovary and a mature testis. There was no apparent relation between total length and sex of the individual, nor between length and the lack of visible gonadal tissue. An incidence of sterility of 25% in animals over 400 mm TL is higher than the 13% incidence reported by Schreiner (1955) for mature eastern Atlantic *M. glutinosa*.

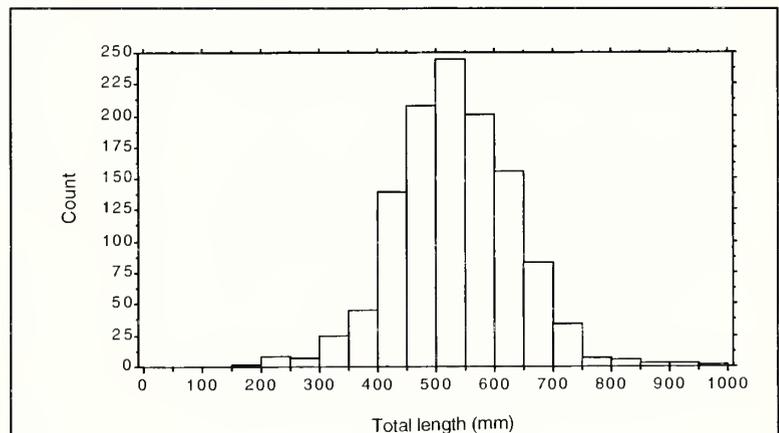
The sex ratio of females to males in many *Eptatretus* species has been reported to be skewed, from slightly to strongly in favor of females. For example, Johnson (1994) reported a sex ratio for *E. deani* of 2.58:1 and for *E. stouti* a sex ratio that gradually decreased from 1.8:1 at small sizes to roughly 1:1 for animals near 380 mm TL. Because sizes and sexes are unevenly distributed over the depth range where *E. stouti* is abundant (100–400 m), the sex ratio can vary widely depending on the depth of and season at the collection site. This may explain the broad range of sex ratios (0.58:1 to 4.38:1) reported for *E. stouti* above 200 mm TL collected from a single area in British Columbia (Leaman<sup>4</sup>).

The sex ratio of females to males in our sample of *M. glutinosa* was highly skewed, at 9.8:1. This highly



**Figure 4**

A scattergram of the reproductive state of the population of Atlantic hagfish as a function of total body length ( $n=122$ ). Key: -3 = male, swollen testicular follicles; -2 = male, testicular follicles containing fluid; -1 = male, testicular tissue present; 0 = no macroscopically visible gonadal tissue; 1 = female, eggs <5 mm; 2 = female, eggs 5–9 mm; 3 = female, eggs 10–14 mm; 4 = female, eggs 15–19 mm; 5 = female, eggs >20 mm; 6 = female, shelled eggs in coelom; and 7 = female, postovulatory follicles.



**Figure 5**

A length (total length) histogram for Atlantic hagfish, prepared from data provided by the New England Fisheries Development Association ( $n=1,172$ ). For these data: Mean=529 mm, SD=104 mm, range=170–950 mm. Compare with Figure 2A,  $P=0.000$ .

skewed sex ratio is typical for the species as a whole. The paucity of males in populations on both sides of the Atlantic has long been recognized, but it remains unexplained (Schreiner and Schreiner, 1904; Conel, 1931; Holmgren, 1946; Schreiner, 1955; Walvig, 1963; Cunningham, 1886–87). Males whose testes contain mature spermatozoa are even more unusual. Jespersen (1975) collected 1,000 specimens at a fjord

<sup>4</sup> Leaman, B. M., ed. 1992. Groundfish stock assessments for the west coast of Canada in 1991 and recommended yield options for 1992. Biological Sciences Branch, Dep. Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia.

reputed to contain a relatively high proportion of males. Of 200 animals identified as male, only one contained a testis with motile sperm. Holmgren (1946) suggested that either ripe males may have a different distribution or that the ripe males do not feed. The latter suggestion appears more plausible in view of the broad areas sampled by investigators over the last 100 years.

Among hagfish, only *Eptatretus burgeri* has been shown to have an annual breeding cycle (Fernholm, 1975; Patzner, 1977; Tsuneki et al., 1983). Our data, collected during the summer months (June–August), indicate that there is no correlation between the size of a female and the size of the eggs within the ovary. Thus at any given time, one can collect females with ova at any stage of maturation. This is consistent with the contention that *M. glutinosa*, like most other hagfishes studied, have no specific breeding season (Cunningham, 1886–87; Nansen, 1887; Walvig, 1963).

The location of egg deposition also remains a mystery. Over the last 150 years, fewer than 200 eggs of *Myxine glutinosa* have been recovered. Only 4 of these eggs were fertilized, and none of the embryos were in an ideal state of preservation when examined. A trawled and damaged embryo, described by Dean (1899), has been the only report of a fertilized hagfish egg recovered in the western Atlantic. The great majority of the *Myxine* eggs—fertilized or not—described in the literature were collected in the eastern Atlantic, primarily from the nets of trawlers working soft bottom substrates. Three embryos of *M. glutinosa*, in somewhat better condition than Dean's specimen, served as the basis for papers by Holmgren (1946) and Fernholm (1969). Despite concerted efforts, no egg clusters were seen during winter and summer ROV surveys or summer submersible dives in an area supporting a large hagfish population, nor on the adjacent ledges (Martini and Heiser, 1989).

It is not known where or when mating takes place, nor how males locate females (or vice versa). Although at least one species (*Eptatretus burgeri*) has an annual reproductive season and migrates to reproductive sites that are used year after year (Tsuneki et al., 1983), such is not the case for *M. glutinosa*. The population at our primary study site appears to remain in place throughout the year; ROV work in June–September and December–January did not reveal any obvious differences in abundance at our study site.<sup>5</sup> However, these observations need to be supported by additional collections and tagging studies.

Although our picture of reproduction in this species remains incomplete, it is clear that the population reproduces very slowly. Of 122 animals surveyed in the summers of 1989–90, only five were females with postovulatory follicles, and only one had fully developed shelled eggs loose in the coelom. In animals with postovulatory follicles, the remaining ovarian tissue did not contain eggs in advanced stages of development; there must therefore be a significant time period between reproductive cycles for a given individual. The time required for a female *M. glutinosa* to produce a clutch of eggs is not known, but it is probably longer than a year (Patzner and Adam, 1981). This makes good sense because the synthesis of large (25 mm × 10 mm) yolky eggs is a substantial energetic investment. It appears likely that the reproductive potential of the population as a whole is relatively low, because 1) many of the individuals have no discernible gonads, 2) each mature female produces only 20–30 eggs at a time, and 3) a relatively small proportion of the females contain mature eggs at any given time. This low reproductive potential has obvious implications for the development of a sustainable fishery for these animals.

Given the evidence, there is considerable risk that the Gulf of Maine industry will prove to be another boom-and-bust fishery. The processors accept only fish greater than 350 mm in length (Kuenstner, 1996), which corresponds to a weight of more than 43 g (see Fig. 1). Because the average weight for Gulf of Maine specimens greater than 350 mm was 140 g, the fishing years of 1993–94 probably represented a harvest of roughly 11 million individual hagfish. The actual impact on the population is considerably greater, however, because 1) smaller hagfish are caught in the traps and are discarded into the surface waters and 2) hagfish of all sizes escape from the trap as it ascends. Except in winter, when the fishery is relatively inactive, hagfish released or escaping in this manner are unlikely to survive. The oceanographic conditions where these hagfish are collected are extremely stable, with summer temperatures of 4–6°C and a salinity of 33–34 ppt. Hagfish held in aquaria at the Shoals Marine Laboratory survive at 0–4°C but become increasingly agitated and soon die if the temperature rises above 10°C. Surface temperatures in the inner Gulf of Maine reach 16–18°C or more in the top 25–50 m during July and August, and at least one other warm-water mass covers the cold bottom water (Appollonio and Mann, 1995). When suddenly exposed to salinities below 31 ppt, individuals will struggle violently, produce copious slime, and then become moribund (Martini et al., pers. obs., and Adam and Strahan, 1963a). Surface salinities are often below 30 ppt in

<sup>5</sup> This conclusion is based on visual surveys only. Weather conditions and equipment problems made it impossible to collect specimens during the winter trips.

surface waters of the Gulf of Maine (Bigelow, 1914). This combination of factors suggests that hagfish released at the surface or escaping from a trap within superficial water layers are unlikely to reach the bottom alive.<sup>6</sup>

On some commercial hagfishing trips, up to 70% of the catch (by weight) was discarded as unmarketable (Gryska<sup>7</sup>; the average for late 1995 was estimated at 41.1% (Kuenstner, 1996). The number of escaping animals cannot be estimated. It is therefore possible that the number of individuals removed from the environment may be twice the number landed onshore. Although the hagfish population present in the Gulf of Maine as a whole might well support such a harvest for a time, this level of fishing pressure could not be sustained. Because the fishing effort is not randomly distributed throughout the Gulf of Maine, the populations at sites targeted by this fishery can be expected to decline much more precipitously. There are already anecdotal reports suggesting that after only two years the catch per trap set has declined, and the average size of caught hagfish is decreasing (Hall-Arber, 1996).

It is not known what effects a decline in hagfish abundance will have on benthic ecology. However, from a regulatory perspective it is obviously difficult to set politically viable quotas or guidelines for a fishery when virtually nothing definitive is known about 1) the size of the population, 2) reproductive potential, 3) individual growth rates, or 4) longevity. There is therefore an urgent need for increased research on the basic biology and ecology of this interesting species.

## Acknowledgments

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<sup>6</sup> For release of live hagfish, the Shoals Marine Laboratory uses special gear that holds the animals in a volume of chilled, full-salinity sea water until the apparatus contacts the bottom.

<sup>7</sup> Gryska, A. 1994. New England Fish. Development Assoc., 451 D St., Boston, MA. Personal obs.

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**Abstract.**—The reproductive biology and sexual maturity of Atka mackerel (*Pleurogrammus monopterygius*) in Alaskan waters were examined with data collected from commercial fishing vessels and National Marine Fisheries Service research surveys. The female reproductive system and ovarian development over time were described by using histological methods. The reproductive cycle is characterized by a period of slow development from January until May, a rapid growth period of vitellogenesis in June, and a protracted spawning period, July until October, during which three batches of eggs are spawned on average.

Length and age at maturity were calculated and compared for different subareas of the Aleutian Islands and Gulf of Alaska region. Size at 50% maturity was significantly different among the subareas, decreasing from east to west.

Lengths at 50% maturity were 38.24, 35.91, 33.55, and 33.64 cm in the Gulf of Alaska, eastern Aleutian Islands, central Aleutian Islands, and western Aleutian Islands, respectively. Age at maturity was not significantly different by area; Atka mackerel were found to reach 50% maturity at 3.6 years. Therefore, it was assumed that different sizes at sexual maturity were reflections of different growth rates in the respective geographic subareas.

## The reproductive cycle and sexual maturity of Atka mackerel, *Pleurogrammus monopterygius*, in Alaska Waters

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Atka mackerel, *Pleurogrammus monopterygius*, is a member of the greenling family (Hexagrammidae). It is distributed in Alaskan and Russian waters from the Gulf of Alaska to Kamchatka and is most abundant in the North Pacific Ocean, southern Bering Sea, and along the Aleutian Archipelago (Rutenberg, 1962). It has been of increasing commercial importance to the United States, with Alaskan catches averaging about 80,000 metric tons (t) in the last 3 years (valued at \$14 million [ex-vessel] in 1993).

Recent information suggests that Atka mackerel play an important role in the Aleutian Islands and Gulf of Alaska ecosystems as forage for other groundfish, seabirds, and marine mammals, including the Steller sea lion (*Eumetopias jubatus*) which has been listed as a threatened species under the U.S. Endangered Species Act (Kajimura, 1984; Livingston et al., 1993; NMFS<sup>1</sup>). Despite the value of the species to commercial fisheries and other piscivores, many aspects of its life history and ecology are poorly understood. Furthermore, information and data available suggest behav-

iors and distribution patterns unique among Alaska groundfish.

During much of the year, Atka mackerel are pelagic but migrate annually from the lower edge of the continental shelf to shallow coastal waters where they spawn demersally. In eastern Kamchatka waters, the spawning migration begins at the end of May and peaks in the middle of June (Zolotov, 1993). Spawning peaks June through September, but may occur intermittently throughout the year (Gorbunova, 1962; Zolotov, 1993). Atka mackerel spawn their eggs in rock crevices or among stones, which are guarded by brightly colored males until hatching occurs (Gorbunova, 1962; Zolotov, 1993). Females are reported to spawn an average of three batches per season with at least a 2-week hiatus between subsequent spawnings (Zolotov, 1993). Batches of eggs in different phases of development were found inside one nest, suggesting a promiscuous mating system

<sup>1</sup> NMFS. 1995. Status review of the U.S. Steller sea lion (*Eumetopias jubatus*) population. Natl. Mar. Mamm. Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, 61 p.

with polygyny in the males and polyandry in the females (Zolotov, 1993). The adhesive eggs hatch in 40–45 days, releasing planktonic larvae that have been found up to 800 km from shore (Gorbunova, 1962). Preliminary analyses of fishery and survey data suggest evidence of sex segregation during the spawning period. Males presumably remained on the spawning grounds guarding the nests, whereas females were found in exploitable concentrations farther offshore in high current areas such as island passes.<sup>2</sup>

The Atka mackerel resource in the Aleutian Islands appears to be in excess of 0.5 million t.<sup>3</sup> Owing to a lack of a strong market for the product, and insufficient biological information that prompted conservative catch recommendations, it was lightly exploited through the 1980's. Catch recommendations depend on an accurate knowledge of abundance which is based on the biology, distribution, and population dynamics of the species. The expansion of the fishery has greatly intensified the need for accurate estimates of life history parameters. However, to date most of the life history information available on Atka mackerel has been obtained in Russian waters (Gorbunova, 1962; Rutenberg, 1962; Zolotov, 1993); there is little or no information on the reproductive cycle, behavior, and ecology of Atka mackerel in U.S. waters. Because its distribution appears to be closely related to its reproductive life history, information on the reproductive cycle and spawning behavior of Atka mackerel off Alaska could lead to a better understanding of its localized movement patterns. This information is necessary to improve surveys for biomass estimates which will result in more accurate stock assessments and provide better long-term management of the fisheries. Of particular importance are parameters governing the reproductive potential of the stock, i.e. maturity at age, which is a direct input into the stock assessment model and is required to estimate female spawner biomass.

This paper presents the results of a study that was undertaken to examine the reproductive biology of Atka mackerel. Female gonads and otoliths were collected, gonads examined histologically, egg stages and maturity stages defined, and the reproductive cycle was described. Ages were estimated from otoliths. The gonad somatic index (GSI) and the mean

egg stage per month were used as indicators of ovarian development over time. Population parameters such as length and age at 50 % maturity were determined and compared between different geographical areas.

## Methods

Few opportunities existed for the collection of biological samples of Atka mackerel other than aboard commercial fishing boats or National Marine Fisheries Service (NMFS) research surveys. Consequently, sample collection was restricted to periods when the fishery was open and when the NMFS surveys were conducted.

### Data and sample collection

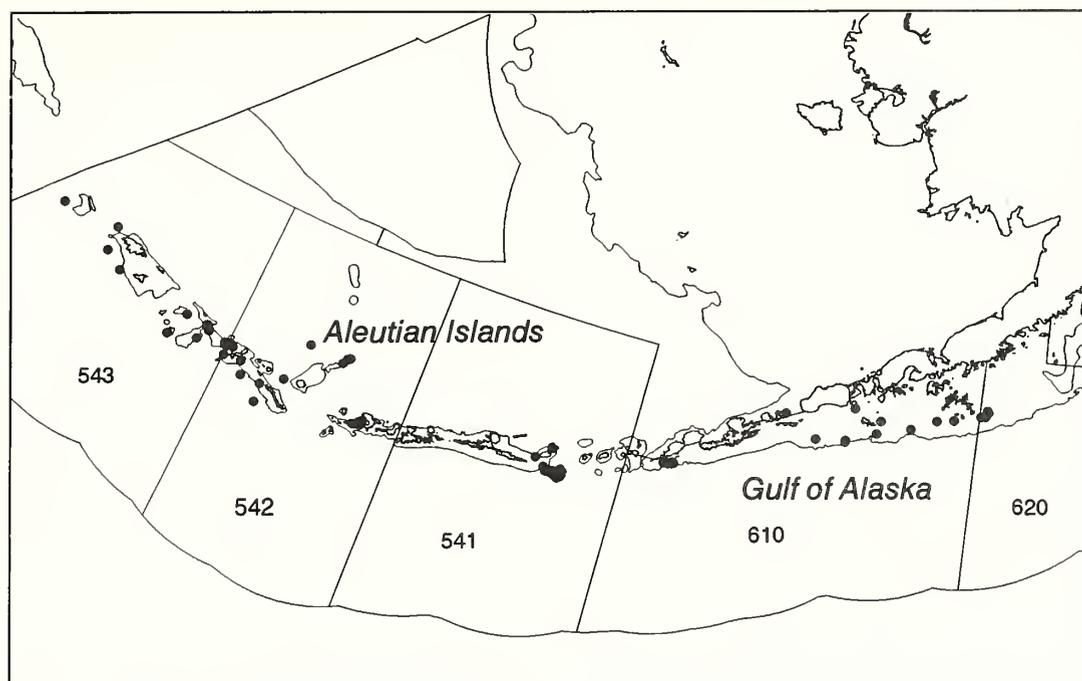
The data and samples analyzed in this study were collected from 1992 through 1994 in 1) the Gulf of Alaska and 2) the Aleutian Island Region by observers and research scientists aboard commercial fishing vessels and NMFS research boats, respectively (Fig. 1). For purposes of collection and analysis, the study region was subdivided into four geographical subareas: western Aleutians, central Aleutians, eastern Aleutians, and the Gulf of Alaska.

The total number of gonad samples collected was 978. Monthly sample sizes ranged from a low of 30 in August to a high of 196 in June (Table 1). Otoliths were also collected from 537 of the sampled fish. Overall sampling effort by area was fairly even. However, sampling effort in each area by month was strongly dependent on the location of the seasonal fishing effort in winter, spring, and fall. Winter samples were available only from the eastern Aleutians, whereas spring and summer sampling took place in all areas. The only fall samples taken were in October from the Gulf of Alaska. Samples collected on research cruises were taken from June through August throughout most of the areas. Since the sampling scheme for samples on commercial vessels did not differ from the sampling scheme on research boats, all data were combined. However, commercial catches were obtained by directly targeting certain locations or schools, whereas the survey catches were obtained by sampling at randomly stratified stations. Therefore the age and size composition of the commercial catch may reflect a more uniform population structure because most commercial boats target schools of adult fish.

There were insufficient samples to distinguish annual differences, therefore all samples were pooled by month and subarea for the determination of length

<sup>2</sup> Fritz, L. W. 1995. Alaska Fish. Sci. Center, Natl. Mar. Fish. Serv., Seattle, WA 98115. Personal commun.

<sup>3</sup> Lowe, S. A., and L. W. Fritz. 1995. Atka Mackerel. In Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Bering Sea/Aleutian Island Regions as Projected for 1996. North Pacific Management Council, P.O. Box 103136, Anchorage, AK 99510.



**Figure 1**

Haul locations for Atka mackerel ovary samples; 541 = eastern Aleutians, 542 = central Aleutians, 543 = western Aleutians, 610 and 620 = Gulf of Alaska.

**Table 1**

Number of samples of Atka mackerel, *Pleurogrammus monopterygius*, collected from 1992 to 1994 by month and area.

Month	Eastern Aleutians	Central Aleutians	Western Aleutians	Gulf of Alaska	Total
January	85	0	0	0	85
February	55	0	0	0	55
March	68	1	9	71	149
April	0	12	71	0	83
May	0	52	45	0	97
June	62	0	72	62	196
July	0	84	83	16	183
August	0	20	10	0	30
September	0	38	0	0	38
October	0	0	0	62	62
Total	270	207	290	211	978

and age at maturity and pooled by month only for the description of the reproductive cycle (Table 1).

Atka mackerel were collected from subsamples of individual trawl tows. Collections were stratified by size of individual fish. No more than five fish per sex in each 1-cm size group were collected within each subarea during a sampling cruise. Each selected fish was measured to the nearest centimeter and weighed to the nearest 0.1 kg. In most cases, the stomach was emptied before weighing the individual fish. The ovaries were excised and placed in labeled cloth bags

in a 10% buffered formalin solution. Sodium acetate (20 g per liter of formalin solution) was used as a buffer. Weights of fresh ovaries were taken and recorded to the nearest gram for 254 specimens collected during the 1994 bottom trawl survey of the Aleutian Islands. In addition to the ovary samples, otoliths were collected opportunistically from sampled specimens. Ages were determined from otoliths by the Alaska Fisheries Science Center Age and Growth Unit using the surface-reading and break-and-burn technique (Chilton and Beamish, 1982).

**Table 2**  
Definition of oocyte stages of Atka mackerel based on major histological characteristics.

Oocyte stage	Mean oocyte size ( $\mu\text{m}$ ) (range)	Major histological characteristics
1 Early perinucleus	55 (30–80)	Small oocyte with hematoxylin-positive cytoplasm. Nucleoli on the outer margin of nucleus.
2 Late perinucleus	147 (117–176)	Oocyte becoming larger, cytoplasm lighter, nucleoli still present.
3 Cortical alveoli	230 (216–255)	Cortical alveoli present as a ring on the outer margin of the cytoplasm. Cortical alveoli appear as white droplets since they do not stain in H&E. The zona radiata can be seen developing as a thin, pink layer. Cytoplasm in center of oocyte appears granular.
4 Oil droplet stage	490 (313–628)	Oil droplets appear first on inner margin of cytoplasm and then start to fill out the inner half of the oocyte. Zona radiata thickens, nucleoli are still present in nucleus, granulosa cells in tight circle around zona radiata.
5 Yolk globule stage	677 (549–843)	Eosin-positive yolk droplets appear between the inner layer of oil vesicles and the outer layer of cortical alveoli, giving the oocyte a three-layered appearance. Vacuoles appear in oil droplet or cortical alveoli layer. Cytoplasm around nucleus granular, staining eosin-positive. With further development, yolk droplet zone and oil droplet zone may fuse together. Zona radiata thickens and oocyte increases in size.
6 Migratory nucleus	944 (686–1,294)	Yolk platelets form by the fusion of smaller yolk droplets. Oil droplet and yolk platelet zone have fused, with cortical alveoli still on the margin of the oocyte. Nucleus in the center loses its shape (nuclear membrane gets dissolved) and migrates towards the micropyle.
7 Early hydration	1,277 (999–1529)	Zona radiata thickens to almost twice the thickness characterizing migratory nucleus stage. Oocyte increases rapidly in size. Yolk fuses to uniform, pink mass (H&E stain) in center of oocyte, with still some large yolk platelets surrounding it. The margin of the cytoplasm does not stain, nucleus is no longer visible.
8 Late hydration	1,932 (1,646–2,195)	Yolk fused to one mass in the center of oocyte, surrounded by nonstaining area. Oocyte still within follicle.
9 Ovulation	Same as in stage 8	Oocyte same as in stage 8, but oocyte no longer inside follicle and usually found within lumen of ovary.

### Histological preparation

After storage for several months in formalin, the ovary pairs were reweighed and sections from the middle of one ovary were taken and processed for histological examination. The tissue samples were embedded in Paraplast and sectioned with a microtome to a thickness of 5  $\mu\text{m}$ . All samples were routinely stained with hematoxylin and eosin (H&E). Selected samples were stained with Periodic Acid Schiff reagent (PAS) to identify carbohydrate complexes in cortical alveoli while other samples were sectioned frozen and stained with Sudan black in order to demonstrate the presence of oil droplets (Galigher and Kozloff, 1971). Oocytes in each ovary

were subsequently classified into histological oocyte stages (Table 2). Postovulatory follicles and atretic oocytes were also recorded and classified according to the categories defined by Hunter and Macewicz (1985).

### Mean oocyte stage per month

Each ovary was classified to the most advanced oocyte stage present using the histological criteria summarized in Table 2. Mean oocyte stage per month was determined by summing the individual specimen's oocyte stages (most advanced) by month and dividing the sum by the number of specimens collected in that month as follows:

$$\bar{e}_j = \frac{\sum_{i=1}^{n_j} e_{ij}}{n_j},$$

where  $\bar{e}_j$  = mean oocyte stage in month  $j$ ;  
 $e_{i,j}$  = the most advanced oocyte stage of specimen  $i$  in month  $j$ ; and  
 $n_j$  = number of specimens in month  $j$ .

The estimated variance ( $s^2$ ) of the mean egg stage was determined using the formula:

$$S\bar{e}_j^2 = \frac{\sum_{i=1}^{n_j} (e_{ij} - \bar{e}_j)^2}{n_j(n_j - 1)}.$$

### Size measurement of oocytes

Oocyte diameters were measured from histologically prepared ovary sections using a compound microscope with an ocular micrometer. Random measurements were taken by measuring oocytes along multiple transect lines across the section. Only oocytes that touched the transect line and which had been sectioned through the nucleus were measured. For each oocyte stage a minimum of 15 oocytes per fish were measured from at least two individuals.

### Length and age at 50% maturity

To minimize confusion between immature and resting fish (mature females with oocytes smaller than oocyte stage 4; see Table 2), only samples in which the oocytes of mature fish were in advanced oocyte stages (oocyte stages 4–9, Table 2) were used for the calculation of length and age at maturity, except for some samples collected in the Gulf of Alaska as discussed below.

The proportion of fish mature at length or age was estimated by fitting a logistic model to the observed proportion mature. The logistic equation used was:

$$Y = \frac{1}{1 + e^{-(\alpha + \beta x)}},$$

where  $Y$  = proportion mature at length or age  $x$ ;  
 $\alpha, \beta$  = model parameters to be estimated; and  
 $x$  = fork length (cm).

Length or age at 50% maturity ( $L_{50}$ ;  $Age_{50}$ ) was calculated as  $-\alpha/\beta$ . The statistical program used was S-plus (Venables and Ripley, 1994). A general linear model with a binomial error distribution was applied

with geographical area as a factor. The variance for the estimated  $L_{50}$  or  $Age_{50}$  was calculated using the delta method (Seber, 1982):

$$S^2(Age_{50}, L_{50}) = \frac{S^2(\hat{\alpha})}{\hat{\beta}^2} - \frac{2\hat{\alpha}S(\hat{\alpha})S(\hat{\beta})r}{\hat{\beta}^3} + \frac{\hat{\alpha}^2 S^2(\hat{\beta})}{\hat{\beta}^4},$$

where  $S^2(L_{50}; Age_{50})$  = variance of the length or age at 50% maturity;

$\hat{\alpha}$  = estimate of  $\alpha$ ;

$\hat{\beta}$  = estimate of  $\beta$ ;

$r$  = correlation coefficient;

$S(\hat{\alpha})$  = standard error of  $\hat{\alpha}$ ; and

$S(\hat{\beta})$  = standard error of  $\hat{\beta}$ .

### Calculating gonad somatic index

Relative reproductive effort was expressed as a gonad somatic index (GSI), defined as the ratio of gonad weight to somatic body weight. In all cases the gonads were weighed after they had been preserved in formalin. For the samples that did not have weights for fresh gonads, fresh gonad weight was estimated with a linear regression using the samples for which both fresh weight and formalin-preserved weight of the gonads had been measured ( $n=254$ ). The regression line was forced through the origin using:

$$y = cx,$$

where  $y$  = fresh weight of ovary;

$x$  = formalin preserved weight of ovary; and

$c$  = constant.

The GSI was calculated as:

$$GSI = \frac{G}{B} \times 100,$$

where GSI = gonad somatic index;

$G$  = fresh gonad weight; and

$B$  = somatic body weight (stomach empty, gonads removed).

## Results

### Definition of oocyte stages and maturity stages

Oocyte development was classified into nine oocyte stages based on major histological characteristics (Fig. 2, Table 2). The oocyte stages were then used to determine maturity stages.

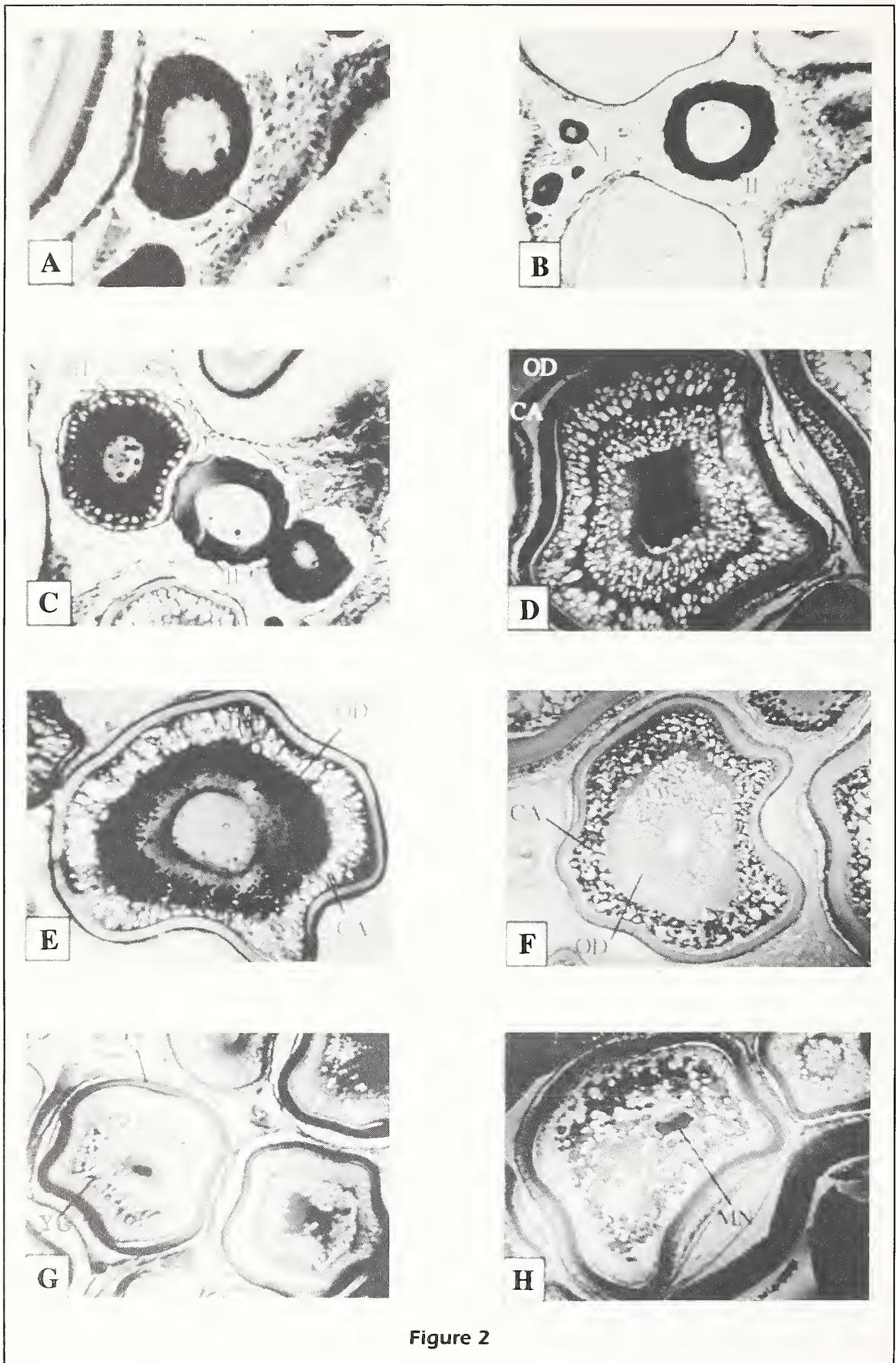
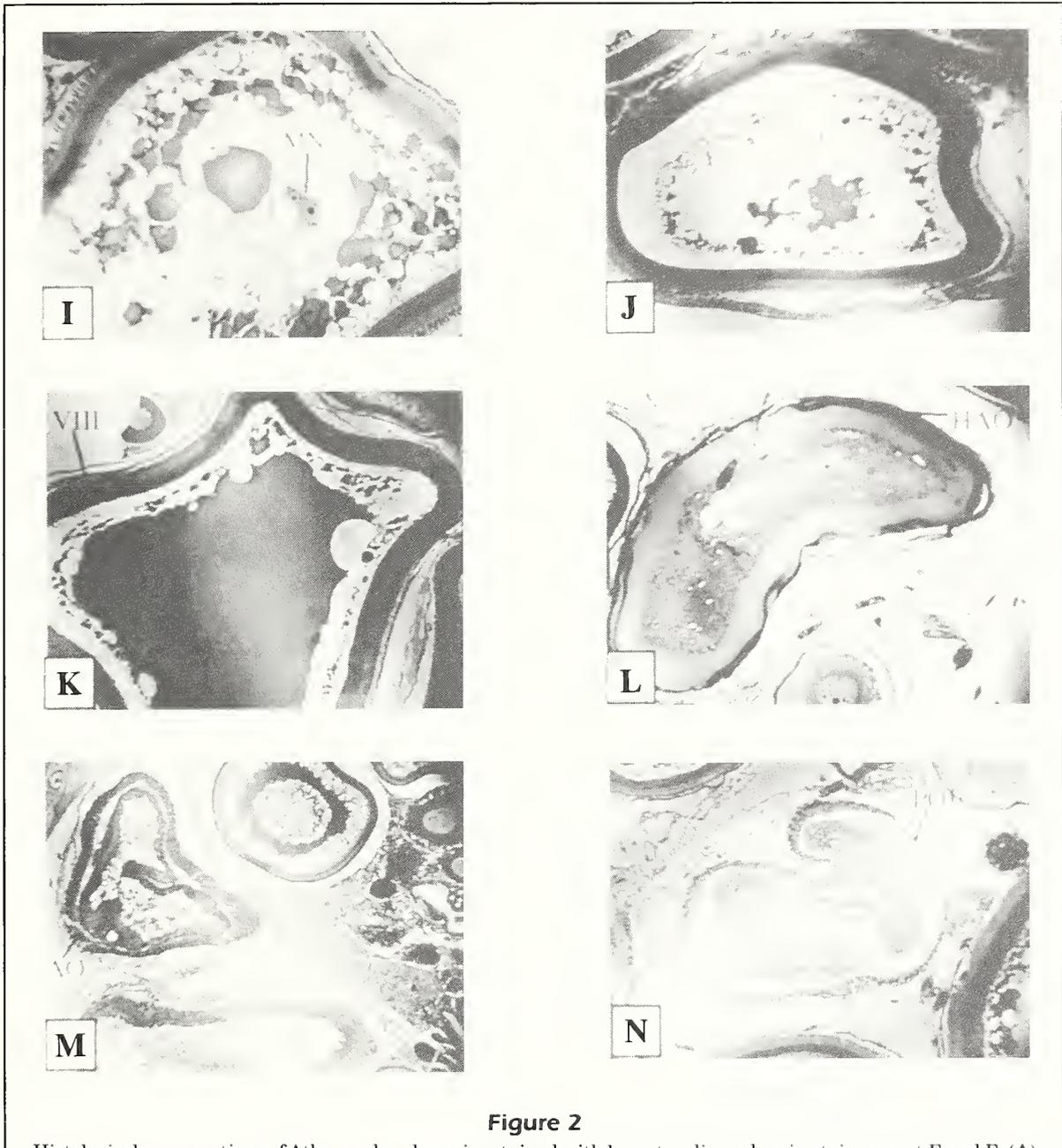


Figure 2



**Figure 2**

Histological cross sections of Atka mackerel ovaries stained with hematoxylin and eosin stain, except E and F: (A) cross section of ovary with early perinucleus oocyte (egg stage 1) ( $\times 200$ ); (B) cross section of ovary with late perinucleus oocyte (egg stage 2) ( $\times 79$ ); (C) cross section of ovary with late perinucleus oocyte (egg stage 2) and cortical alveoli stage (egg stage 3) ( $\times 79$ ); (D) cross section of ovary with oil droplet oocyte (egg stage 4), both cortical alveoli and oil droplets appear as clear droplets ( $\times 200$ ); (E) cross section of ovary with oil droplet oocyte (egg stage 4), oil droplets are staining deep black, cortical alveoli are clear (Sudan black) ( $\times 200$ ); (F) cross section of ovary with oil droplet oocyte (egg stage 4), cortical alveoli are staining PAS positive, oil droplets appear clear (PAS) ( $\times 200$ ); (G) cross section of ovary with vitellogenic oocyte (egg stage 5), yolk is staining eosin-positive ( $\times 79$ ); (H) cross section of ovary with early migratory nucleus stage (egg stage 6), yolk droplets fuse to yolk platelets ( $\times 79$ ); (I) cross section of ovary with late migratory nucleus oocyte, nuclear wall is disintegrated ( $\times 200$ ); (J) cross section of ovary with early hydrated oocyte (egg stage 7) ( $\times 79$ ); (K) cross section of ovary with late hydrated oocyte (egg stage 8) ( $\times 79$ ); (L) cross section of ovary with atretic hydrated oocyte ( $\times 79$ ); (M) cross section through ovary showing alpha atresia in a yolked oocyte ( $\times 79$ ); (N) cross section through ovary with post-ovulatory follicle ( $\times 79$ ). Roman numerals I–VIII=oocyte stages 1–8. AO=atretic oocyte; CA=cortical alveoli; HAO=hydrated atretic oocyte; MN=migratory nucleus; OD=oil droplets; POF=postovulatory follicle; and YG=yolk globules.

In order to define maturity stages, the most advanced oocyte stage in each specimen was used (Table 3). In most cases, oocytes in all stages up to the most advanced stage observed were present. For some of the spawning fish, however, stage 5 oocytes (vitellogenic) were absent. Since Atka mackerel are batch spawners (Zolotov, 1993), the number of advanced oocytes (egg stage 5 and larger) decreased with the number of batches spawned.

For the Aleutian Islands region, the ovaries of the mature females were far enough advanced to distinguish mature from immature fish by the presence of advanced oocyte stages (stages 5–9). Because of the timing of the collection of samples for the Gulf of Alaska, some of the maturity classification was done by comparing GSI values. Certain Gulf of Alaska samples showed a GSI that was almost an order of magnitude smaller than the GSI of the mature fish even though the oocytes appeared to be in a similar oocyte stage (stage 4, cortical alveoli and oil globules present). Because the GSI value was not continuous but showed a distinctive gap and because there was

no evidence of yolk in the presumably immature ovaries, fish that belonged in the group with the lower GSI value were classified as immature. This GSI value coincided with the GSI value of the immature fish in the Aleutian Island region, and the age at maturity calculated also coincided with the age at maturity determined for the samples in the Aleutian Island region. However, until year-round samples for the Gulf of Alaska can be obtained, the possibility of the presumably immature fish spawning later in the year cannot be excluded.

### Reproductive cycle

Since data were not available throughout the year in all of the areas, the data were pooled and compared by month only. Mean oocyte stage did not increase substantially from January until June, when most females possessed ovaries with stage 5 oocytes (vitellogenesis) (Fig. 3). Mean oocyte stage started to increase rapidly in June, peaked in August, and declined slightly in September. The mean GSI value

**Table 3**  
Definition of maturity stages of Atka mackerel.

Maturity stage	Description	Most advanced oocyte stages
Stage 1: Immature	Ovary small with small oocytes. Oogonial nests, early and late perinucleus stages and cortical alveoli stage present. In some ovaries early oil droplet stage present.	Oocyte stages 1–3; early oocyte stage 4
Stage 2: Developing	Ovary increasing in size. Oocytes show oil droplets in advanced stage. Ovary wall thickens. Vascularization increases.	Oocyte stage 4
Stage 3: Vitellogenesis	Large visible eggs undergoing yolk development. Yolk globules present in oocytes. Wide range in oocyte diameter since oocytes from stage 1 through stage 5 are present.	Oocyte stage 5
Stage 4: Early hydration	Most advanced yolked oocytes are in migratory-nucleus and early hydration stage. Yolk is not completely coalesced in hydrated oocytes. Oocytes are present in stages 1–7	Oocyte stages 6 and 7
Stage 5: Spawning	Large oocytes visible at 2 mm. In advanced oocytes, yolk is completely coalesced. Number of yolked oocytes decreases as multiple batches are spawned. After first spawning, postovulatory follicles (POF) are present. In ovaries of fish that have spawned more than one batch, different stages of POF are distinguishable. In some cases proportion of vitellogenic oocytes decreases with the increase of hydrated oocytes. Ovaries are highly vascularized. Ovulated oocytes are found free-flowing in the center of the ovary.	Oocyte stages 8 and 9
Stage 6: Spent	Ovary appears flaccid and highly vascularized. Ovary shows abundance of late POF, and atretic hydrated oocytes. Healthy oocytes are all in early developing stage.	Oocyte stage 3 and 4, presence of post-ovulatory follicles and atretic hydrated oocytes. Atresia of oocyte stages 5–8.

reflected a similar pattern (Fig. 3), although a slight increase was noted from February through June, reflecting slow growth of oocytes during that time. The rapid increase from June through August suggests a rapid period of oocyte growth during vitellogenesis and hydration. The decrease in GSI after August reflects the loss of ovary weight due to spawning single batches, but it should be noted that the GSI in October is still higher than the GSI value in June, which suggests, that the fish might be still spawning their last batches. High variance in GSI and mean egg stage during the spawning period (July through October) could be attributed to batch spawning since most females were not spawning synchronously and the ovary weight and oocyte stages differed accordingly.

Examination of maturity stages over time indicated the same cycle with a long period of initial oocyte development, the appearance of vitellogenesis in June, and peak spawning in August (Fig. 4). Vitellogenesis progressed rather rapidly and was observed almost exclusively in June. However, vitellogenic eggs were found throughout most of the early hydration stage and during the spawning in some ovaries. It should be mentioned that in one

cruise a few spawning fish were found in the central Aleutians in March and April 1992. While this was an oddity not observed in other years, it suggests that under certain circumstances fish can spawn as early (or late) as March.

In general, Atka mackerel develop their oocytes slowly in the oil droplet phase from at least January until May, with a gradual increase in oocyte size and ovary weight. Vitellogenesis starts in June and early migratory nucleus and early hydration is observed in July. Spawning individuals were observed from July until October with the peak in August, when the highest mean egg stage and GSI values were observed. Fish with ovaries having hydrated eggs in October were clearly spawning their last batch as they had many atretic hydrated oocytes, no vitellogenic, and few early hydrated oocytes present. Spent ovaries were found in September and October. Since no samples were collected in November and December, it is not clear how long the spawning season could last. However, by January all fish collected were in the early developing phase for the next year's cycle.

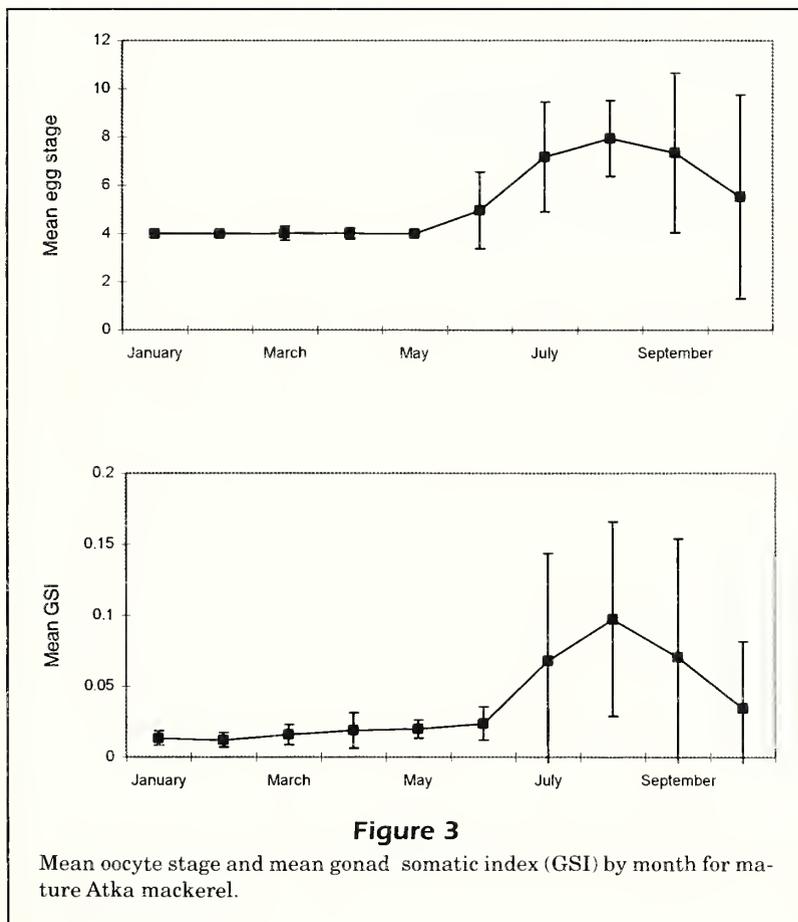
### Size and age at 50% maturity

Size at 50% maturity ranged from 33 cm to 38 cm (Table 4). However, subarea was a highly significant factor ( $P < 0.001$ ), exhibiting a cline in the size at 50% maturity from east to west (Table 4, Fig. 5). Samples from the eastern areas reached 50% maturity at larger sizes. Length at 50% maturity in the Gulf of Alaska was 38.24 cm, while in the eastern Aleutian subarea the fish matured at 35.91 cm. Samples from the central and western Aleutian subareas matured at essentially the same size, 33.55 cm and 33.64 cm, respectively.

Age at maturity was not significantly different among the different Aleutian subareas ( $P = 0.66$ ) or between the Gulf of Alaska versus the Aleutian subareas combined ( $P = 0.69$ ), therefore the data were pooled. The age at 50% maturity (all areas combined) was 3.6 years for Atka mackerel (Table 4, Fig. 6).

### Discussion

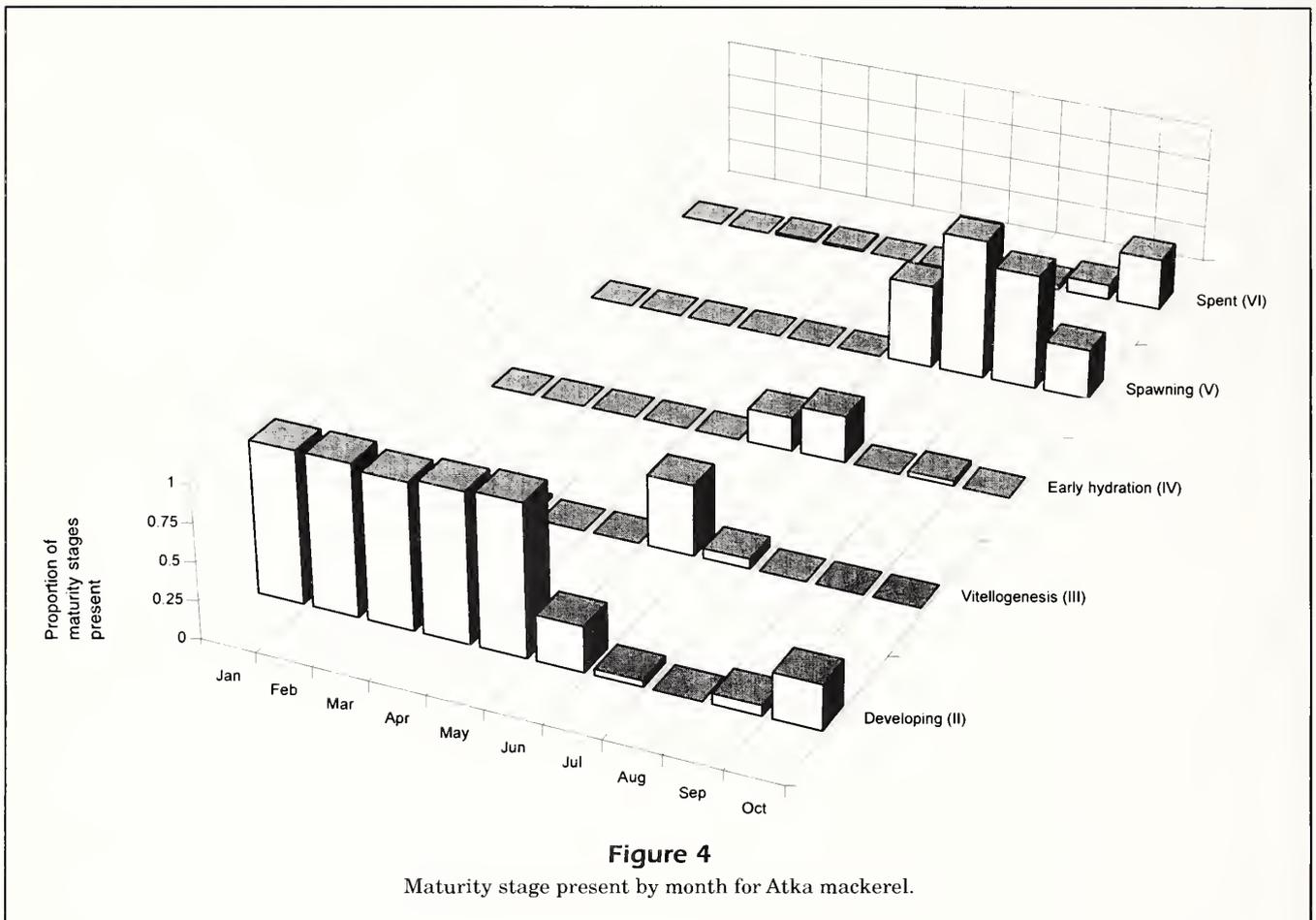
In order to make inferences about population parameters and biology, it is necessary to take representative samples of the population's true age and size



composition and sex ratio throughout their distribution. Due to the opportunistic nature of obtaining samples, only the portion of the population available to fisheries and research vessels was sampled. These are likely the larger animals, i.e. the mature individuals of the population. Therefore the results of length and age at maturity could be overestimated. Additionally, during the time of sex segregation the samples may be biased towards more females, since the males

may be unavailable for sampling. Until the population distribution over time and space is better understood, it will be difficult to design sampling schemes that will yield unbiased population parameters.

Egg stage development for Atka mackerel is similar to that described for the masked greenling (*Hexagrammos octagrammos*) (Munehara et al., 1987; Munehara and Shimazaki, 1989). Oogenesis in Atka mackerel exhibited the following sequence:



**Table 4**  
Length and age at maturity for Atka mackerel.

Area	$\hat{\alpha}$	$S(\hat{\alpha})$	$\hat{\beta}$	$S(\hat{\beta})$	L 50%	95% CI (low)	95% CI (upper)	Var (L 50%)
Gulf of Alaska	-27.16	3.69	0.71	0.09	38.24	36.27	40.21	1.00
Eastern Aleutians	-25.50	3.57	0.71	0.09	35.91	33.94	37.90	1.01
Central Aleutians	-23.83	3.67	0.71	0.09	33.55	31.12	36.57	1.54
Western Aleutians	-23.89	3.68	0.71	0.09	33.64	31.20	36.69	1.55
Area	$\hat{\alpha}$	$S(\hat{\alpha})$	$\hat{\beta}$	$S(\hat{\beta})$	Age 50%	95% CI (low)	95% CI (upper)	Var (Age 50%)
Areas combined	-7.33	0.87	2.03	0.22	3.60	3.40	3.81	0.01

the formation of cortical alveoli, followed by oil droplets, yolk accumulation, nuclear migration, and hydration (Fig. 2). The appearance of oil droplets after the formation of cortical alveoli and the coalescence of yolk before or during nuclear migration are features that have also been described for masked greenling (Munehara et al., 1987). Another feature that is similar to the masked greenling is that hydrated atretic oocytes were reabsorbed very slowly and could be found in the ovary for over 1 year.

The early maturation of the Atka mackerel ovary is characterized by an accumulation of oil droplets in the developing oocytes with a gradual increase in oocyte size over several months from January until May. Vitellogenesis is completed within 1 month, similar to the duration of vitellogenesis in masked greenling, but uncommonly short for most subarctic fishes (Munehara and Shimazaki, 1989).

The spawning period for Atka mackerel is extended and can last up to 4 months, from July through October. This relatively long spawning period can be attributed to the duration of time spent between the spawning of individual batches. Zolotov (1993) stated that the greater number of batches and the longer interval between their spawning corresponds to the longer duration of the reproductive period of Atka mackerel as compared with the arabesque greenling (*Pleurogrammus azonus*). The average spawning duration of 3 months found in this study is in agreement with the spawning duration reported for Atka mackerel in Kamchatka waters (Zolotov, 1993). However, the beginning of spawning in Alaska waters was observed in July lasting until October, whereas the spawning period in Kamchatka waters was described as starting in June and lasting until September (Zolotov, 1993). These differences may be attributed to year-to-year variations; however, different oceanographic conditions in Alaska versus Kamchatka waters may also be a contributing factor. There are not enough data to substantiate a seasonal cline in the timing of the reproductive cycle ranging from Kamchatkan waters to the Gulf of Alaska. The observation of a few spawning fish in March and April indicates that spawning times may be more variable than previously assumed. Data from several years were pooled in this study as the number of samples was insufficient to distinguish annual differences.

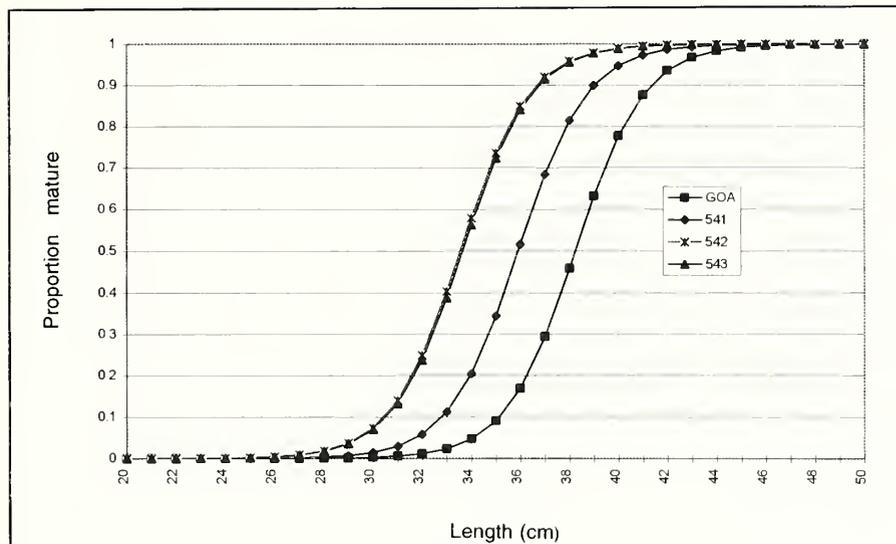


Figure 5

Length at maturity by geographical area for Atka mackerel; 541 = eastern Aleutians, 542 = central Aleutians, 543 = western Aleutians, GOA = Gulf of Alaska.

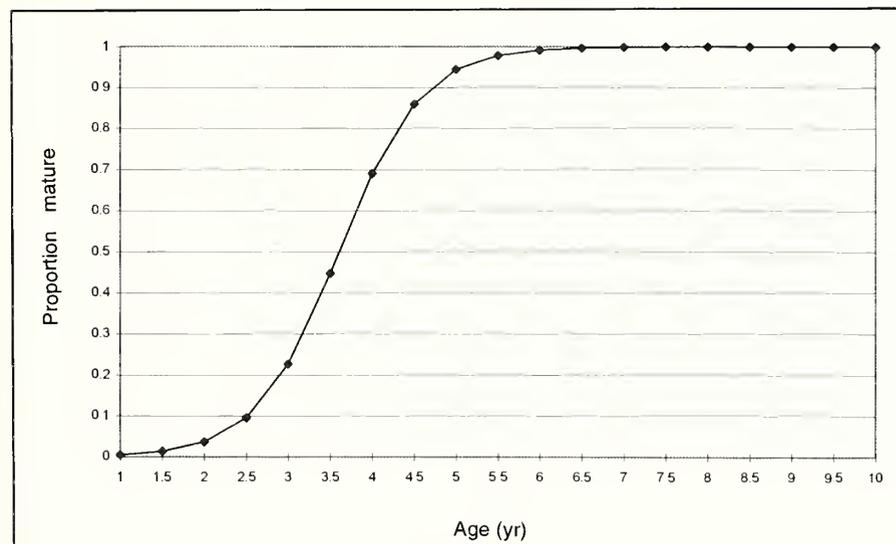


Figure 6

Age at maturity (all geographical areas pooled) for Atka mackerel.

Reproductive timing and parameters can vary from year to year; this might be reflected in increased variance and range of the results in this study.

The spawning period during late summer and fall for Atka mackerel is earlier than that observed for the masked greenling (September through October; Munehara and Shimazaki, 1989), but later in the year than most other Alaska groundfish of commercial importance. Sablefish (*Anoplopoma fimbria*), Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*), and flathead sole (*Hippoglossoides elassodon*) are reported to spawn in winter and early spring in the Gulf of Alaska, whereas walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific ocean perch (*Sebastes alutus*), and rock sole (*Pleuronectes bilineatus*) were reported to have their spawning peak from spring to early summer in the Gulf of Alaska (NPFMC<sup>4</sup>). The life history feature of summer and fall spawning for Atka mackerel and other greenling species might be an adaptation to spawning large demersal eggs, the larvae of which enter the plankton at a larger size than larvae from pelagic eggs (Kendall and Dunn, 1985).

The differences by subarea for length at 50% maturity can be attributed to different growth rates by subarea, given that no age-at-maturity differences among geographical areas were found. Length-at-age curves in each management area revealed an increasing size at age from west to east (Lowe and Fritz<sup>3</sup>). The reasons for these different growth rates are unknown. It is not clear whether more favorable conditions such as food availability, or a more favorable temperature regime are contributing to a higher growth rate in the Gulf of Alaska and eastern Aleutian Islands subarea, or whether there are genetic differences in the populations. However, initial genetic studies suggest that there is little or no stock differentiation in Alaska (Winans<sup>5</sup>).

Analysis of fisheries data (Fritz<sup>2</sup>) indicated that in late summer and fall commercial hauls in many locations had a larger proportion of females than males. Sex segregation coincided with the spawning season (July through October) and supported the hypothesis that males were unavailable to the fishery, presumably guarding nests close to shore. Segregation of the Atka mackerel population by sex during the spawning season could also affect the results of summer trawl surveys used to assess population

size if only a portion of the population is surveyed. More information on the location of nesting sites, behavior, and spawning distribution is necessary to understand the implications of population segregation on resource assessments.

Future research should be conducted on a more long-term basis for collection of maturity information, and larval and juvenile biology and distribution. Time and area gaps should be filled to understand the spatial and seasonal distribution patterns linked to spawning, crucial for assessing and managing this species appropriately.

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**Abstract.**—Identified prey of pantropical spotted dolphins, *Stenella attenuata*, include 56 species of fish and 36 species of cephalopods. Species identifications were made from fish otoliths and cephalopod beaks recovered from 428 stomachs collected throughout the eastern tropical Pacific between 1989 and 1991. The most frequently found fish were lanternfish (family Myctophidae) at 40%, and the most frequently found cephalopods were flying squids (family Ommastrephidae) at 65%. The dominance of these primarily mesopelagic prey species and a significantly higher stomach fullness index for stomachs collected during the morning hours ( $\chi^2=112.99$ ,  $df=6$ ,  $P<0.0001$ ) suggest that pantropical spotted dolphins feed at night when many mesopelagic species migrate toward the surface. Significant differences in prey composition by season and geographic region indicate that pantropical spotted dolphins are flexible in their diet and may be opportunistic feeders. Comparison of the diets of pregnant and lactating female dolphins revealed that lactating females increase both the proportion of squid in their diet and quantity of food consumed.

## Prey occurrence in pantropical spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific

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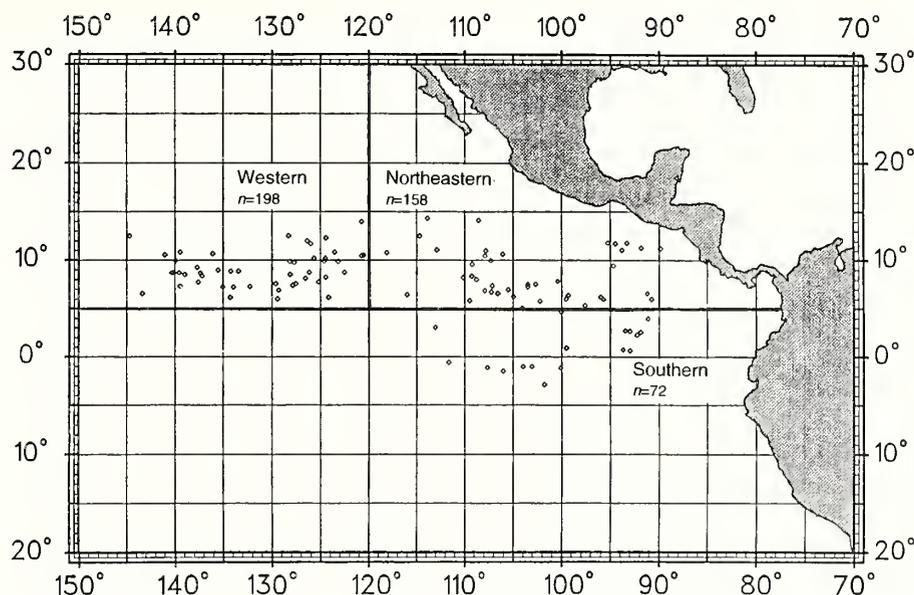
Previously published analyses of the prey of pantropical spotted dolphins in the eastern tropical Pacific (ETP) have reported that many species are consumed and that the species composition and importance varies. Three previous studies reported that epipelagic species are the dominant prey and included species belonging to the families Ommastrephidae (flying squid), Onychoteuthidae (hooked squid), and Exocoetidae (flying fish) (Fitch and Brownell, 1968; Perrin et al., 1973; Bernard and Hohn, 1989). However, mesopelagic species in the families Myctophidae (lantern fish) and Euprolaetidae (enope squid) were also identified in high numbers (Fitch and Brownell, 1968; Perrin et al., 1973). A more recent study by Roberts (1994) examined only cephalopod prey and found that primarily mesopelagic squid species in the family Ommastrephidae were dominant. Another study reported on the prey of a spotted dolphin caught off Hawaii. The prey were predominantly mesopelagic species belonging to the families Myctophidae and Euprolaetidae (Shomura and Hida, 1965). All these studies were based on either a small number of samples or samples that were collected from a restricted area of the Pacific Ocean and, therefore, may be limited in their representation of the prey of pantropical spotted dolphins.

In this paper, we describe the prey of pantropical spotted dolphins collected throughout their range in the ETP. We calculate the percent number and percent frequency of occurrence for each prey species identified to quantify the relative importance of prey species. Variability in the diet due to geographic region, oceanographic season, and, for females, due to reproductive condition are examined. We also present the size distribution of prey consumed for species for which data were available in order to convert otolith and beak measurements to prey size.

### Methods

Stomachs were collected from 428 pantropical spotted dolphins in 103 net sets by biological technicians placed aboard U.S. tuna purse-seine vessels fishing in the ETP between 1989 and 1991 (Fig. 1; see Jefferson et al., 1994, for collection procedures).

Only the contents in the esophageal (fore) stomach were examined for our analyses because this stomach compartment contains the most recent meal and thus the most identifiable remains (Harrison et al., 1967). The forestomach of each specimen was weighed full and empty to the nearest 0.1 g with a Mettler PC4400 balance. The contents were sorted and recovered by



**Figure 1**

Distribution of net-sets ( $n=103$ ) from which 428 pantropical spotted dolphin stomachs were collected between 1989 and 1991. For analysis of geographic variability in prey composition, the sample was divided into areas which correspond to recognized stock boundaries and different oceanographic regions: northeastern, southern, and western.

rinsing them through a series of sieves with mesh sizes of 12.5 mm, 1.4 mm, and 500  $\mu$ . Fish otoliths and other skeletal remains, cephalopod beaks, crustaceans, gastropods, and parasitic nematodes were collected and enumerated.

Left and right fish otoliths for each species were separated and counted. The highest count of either was used as the minimum number of fish present for that species. Fish species were identified to the lowest possible taxon by using voucher collections of otoliths at the Los Angeles County Museum of Natural History (Lavenberg<sup>1</sup>), the Southwest Fisheries Science Center (SWFSC) (Pitman and Carretta<sup>2</sup>), and otolith identification keys published by Fitch and Brownell (1968), Fitch (1969), and Butler (1979). Frigate mackerel (*Auxis thazard*) were identified from vertebral characteristics rather than from otoliths (Clothier, 1950; Uchida, 1981). For cephalopods, upper and lower mandibles were separated and counted for each species; the highest count of either represented the minimum number present in the stomach. Species identifications to the lowest possible taxon were made with the voucher collection of

beaks at the Santa Barbara Museum of Natural History<sup>3</sup> and identification keys published by Wolff<sup>4</sup> and Clarke (1986a). The relative importance of prey was determined by calculating the percent number and percent frequency of occurrence (Hyslop, 1980) for each individual species and family.

### Prey size

For analysis of prey size, maximum length of otoliths (tip of the rostrum to the posterior margin) and lower rostral length (LRL) of beaks were measured with an ocular micrometer disc accurate to 0.1  $\mu$ , only for those items that showed little sign of erosion. Regression equations and ratios of standard length to otolith length were used to convert measurements to prey lengths and weights (Butler, 1979; Clarke, 1986a; Hecht, 1987; Wolff,<sup>4</sup> Pitman and Carretta<sup>5</sup>). Length measurements of *A. thazard* were obtained by estimating total length from whole fish and skeletons recovered from the stomachs. We used the prey

<sup>1</sup> Lavenberg, R. 1993. Los Angeles County Mus. Natl. History, Ichthyology Dep., 900 Exposition Blvd., Los Angeles, CA 90007.

<sup>2</sup> Pitman, R., and J. Carretta. 1993. Southwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.

<sup>3</sup> Hochberg, E. 1992. Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

<sup>4</sup> Wolff, G. A. 1982. A study of feeding relationships in tuna and porpoise through the application of cephalopod beak analysis. Final Tech. Report for DAR-7924779, 231 p.

<sup>5</sup> Pitman, R., and J. Carretta. 1993. Southwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038. Unpubl. data.

size data to test the hypothesis that dolphins of all size classes eat prey of the same size. To do this, we fitted a linear regression to prey size versus the total body length of the dolphins (Norris, 1961). We also tested the null hypothesis of no correlation between size class of prey consumed and number of items consumed by using a Pearson Correlation Matrix (SYSTAT, 1992; unless otherwise noted, all statistical tests are interpreted with  $\alpha=0.05$ ).

### Geographic and seasonal variability

To test for variability in diet, we stratified the sample by season and area. For season, we used the two oceanographic seasons characteristic of the ETP: winter (January–June) and summer (July–December; Reilly, 1990). For area, we stratified the sample by the two recognized management stocks: northeastern and western-southern (Perrin et al., 1994). However, we divided the western-southern stock into a western and a southern section at the equator (Fig. 1) because biological differences in pantropical spotted dolphins have been noted between the western and southern sections of the western-southern stock (Perrin et al., 1976, 1979; Barlow, 1985; Hohn and Hammond, 1985; Myrick, et al., 1986; Chivers and Myrick, 1993; Bright and Chivers<sup>6</sup>). With the 10 most numerous species of fish and squid, we used  $\chi^2$  to test the null hypothesis that there was no difference in prey consumed by season or area.

### Stomach fullness index (SFI)

A relative index of stomach fullness (SFI) was calculated for each stomach with the method of Bernard and Hohn (1989) to estimate when pantropical spotted dolphins were feeding. With this method, the SFI can never equal 100% because the initial weight of the contents includes the weight of the forestomach. To compensate for this method, we adjusted the scale of the SFI to range from 0% to 100% by dividing the index for each stomach by the maximum index value in our sample (Eq. 1):

$$SFI_{adj} = \frac{(w_c / w_i)}{SFI_{max}} \times 100, \quad (1)$$

where  $SFI_{adj}$  = adjusted stomach fullness index;  
 $SFI_{max}$  = maximum stomach fullness index;

$w_i$  = initial weight of the forestomach with contents (g); and  
 $w_c$  = weight of the forestomach contents (g).

Using a  $\chi^2$ , we tested the hypothesis of no difference in the SFI during the course of the day (all stomachs were collected between 0600 and 1800 h). The data were stratified by time-of-day collected: 0600–0900, 0901–1200, 1201–1500, and 1501–1800 h and by SFI categories: 0–30%, 31–60%, and 61–100% full.

### Reproductive condition

The reproductive condition of female pantropical spotted dolphins was determined by microscopic examination of the ovaries and macroscopic examination of the uteri and mammary glands (Perrin et al., 1976; Akin et al., 1993). Using the mean number of fish and squid consumed by lactating ( $n=57$ ) and pregnant ( $n=37$ ) females, we used Student's  $t$ -test to test the null hypothesis that there was no difference in consumption of fish and squid between the two groups. We also compared the SFI of lactating and pregnant females by time-of-day as described in the SFI analysis section.

### Results

Our sample of 428 stomachs contained 49,798 prey items, representing 56 fish species and 36 cephalopod species (Table 1). Thirty-eight (38) of the species identified had not been previously reported as prey of pantropical spotted dolphins (Shomura and Hida, 1965; Fitch and Brownell, 1968; Perrin et al., 1973; Bernard and Hohn, 1989; Roberts, 1994). Some species identifications could not be positively confirmed and were designated as species 1, 2, etc. of the lowest identifiable taxon. One crustacean, *Pleuroncodes planipes*, accounted for 2.4% of the crustacean remains (Table 1). The parasitic nematode *Anisakis simplex* was found in 38% of the stomachs.

Cephalopods occurred in 354 (82.7%) of the stomachs and fish occurred in 270, or 63.1%, of the stomachs. However, the percent number of fish (66.6%) was higher than that for cephalopods (32.6%). Of the 56 species of fish identified, 27 belonged to the family Myctophidae (lanternfish). As a family, myctophids had the highest percent by number of all prey (49.7%) and accounted for 74.6% of all fish prey. Myctophids occurred in 40.2% of all stomachs (Table 1).

The cephalopod species identified belonged to two orders: 1) Teuthoidea (squids; 32 species) and 2) Octopoda (octopuses; 4 species). Squids from the family

<sup>6</sup> Bright, A. M., and S. J. Chivers. 1991. Post-natal growth rates: a comparison of northern and southern stocks of the offshore spotted dolphins. Southwest Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-30, 24 p.

Table 1

Number and frequency of occurrence for prey recovered from pantropical spotted dolphins, *Stenella attenuata*, ( $n=428$ ) from the eastern tropical Pacific. "No." represents the total number of a species recovered from all stomachs and "Frequency of occurrence" represents the number of stomachs in which that species was found.

Prey	Number		Frequency of occurrence	
	No.	%	No.	%
Class Osteichthyes	33,176	66.6	270	63.1
Order Myctophiformes				
Family Myctophidae	24,747	49.7	172	40.2
<i>Symbolophorus</i> spp.	4,052	8.1	151	35.3
<i>Myctophum aulolaternatum</i>	1,379	2.8	81	18.9
<i>Myctophum nitidulum</i>	182	0.4	11	2.6
<i>Myctophum asperum</i>	160	0.3	16	3.7
<i>Myctophum spinosum</i>	109	0.2	14	3.2
<i>Myctophum</i> spp.	43	<0.1	8	1.9
<i>Lampanyctus parvicauda</i>	6,834	13.7	130	30.4
<i>Lampanyctus omostigma</i>	900	1.8	31	7.2
<i>Lampanyctus festivus</i>	848	1.7	29	6.8
<i>Lampanyctus idostigma</i>	264	0.5	35	8.2
<i>Lampadena luminosa</i>	1,358	2.7	36	8.4
<i>Lampadena</i> sp.	7	<0.1	5	1.2
<i>Diaphus splendidus</i>	1,889	3.8	57	13.3
<i>Diaphus mollis</i>	175	0.4	32	7.5
<i>Diaphus</i> sp. 1 close to <i>chrysorhynchus</i>	125	0.3	25	5.8
<i>Diaphus</i> sp. 2 close to <i>effulgens</i>	13	<0.1	5	1.2
<i>Diaphus</i> sp. 3	1,533	3.1	62	14.5
<i>Hygophum proximum</i>	331	0.7	46	10.7
<i>Hygophum reinhardtii</i>	2	<0.1	2	0.5
<i>Diogenichthys laternatum</i>	372	0.7	55	12.9
<i>Triphoturus mexicanus</i>	195	0.4	25	5.8
<i>Tarletonbeania crenularis</i>	6	<0.1	3	0.7
<i>Notoscopelus resplendens</i>	23	<0.1	4	0.9
<i>Ceratoscopelus warmingii</i>	254	0.5	13	3.0
<i>Taaningichthys</i> spp.	276	0.6	14	3.2
<i>Parvilux ingens</i>	21	<0.1	8	1.9
<i>Benthoosema panamense</i>	16	<0.1	1	0.2
Unidentified myctophids (worn)	3,380	6.8	145	33.8
Order Perciformes				
Family Nomeidae	3,053	6.1	108	25.2
<i>Cubiceps pauciradiatus</i>	2,961	5.9	101	23.6
<i>Cubiceps baxteri</i>	51	0.1	18	4.2
<i>Cubiceps</i> c.f. <i>paradoxus</i>	41	<0.1	8	1.9
Family Acropomatidae				
<i>Howella</i> sp.	81	0.2	5	1.2
Family Scombridae				
<i>Auxis thazard</i>	27	<0.1	11	2.5
Family Stromateidae				
<i>Hyperglyphe</i> sp.	6	<0.1	4	0.9
Order Beloniformes				
Family Exocoetidae	858	1.7	82	19.2
<i>Exocoetus volitans</i>	446	0.9	63	14.7
<i>Exocoetus monocirrhus</i>	58	0.1	17	4.0
<i>Cheilopogon</i> sp.	26	<0.1	13	3.0
Family Hemiramphidae				
<i>Oxyporhamphus micropterus</i>	328	0.7	40	9.3

Continued on next page

Table 1 (continued)

Prey	Number		Frequency of occurrence	
	No.	%	No.	%
Order Gadiformes				
Family Bregmacerotidae				
<i>Bregmaceros bathymaster</i>	1,838	3.7	24	5.6
Order Aulopiformes				
Family Scopelarchidae	30	<0.1	12	2.8
<i>Scopelarchus guentheri</i>	24	<0.1	11	2.5
<i>Benthalbella</i> sp.	6	<0.1	2	0.5
Family Notosudidae				
<i>Scopelosaurus</i> c.f. <i>harryi</i>	56	0.1	6	1.4
Family Paralipididae				
<i>Stemonosudis</i> sp.	41	<0.1	14	3.2
Order Beryciformes				
Family Melamphidae				
<i>Scopelogadus bispinosus</i>	906	1.8	19	4.4
Order Stomiiformes				
Family Phosichthyidae	835	1.7	40	9.3
<i>Vinciguerria lucetia</i>	830	1.6	38	8.9
<i>Ichthyococcus</i> sp.	5	<0.1	4	0.9
Family Gonostomatidae				
<i>Gonostomatid</i> spp. close to <i>Diplophus proximus</i>	3	<0.1	2	0.5
Order Salmoniformes				
Family Microstomatidae				
<i>Xenophthalmichthys</i> sp.	9	<0.1	2	0.5
Unidentified species				
Unknown no. 1	5	<0.1	3	0.7
Unknown no. 2	20	<0.1	5	1.2
Unknown no. 3	41	<0.1	13	3.0
Unknown no. 4	47	<0.1	6	1.4
Unknown no. 5	9	<0.1	4	0.9
Unknown no. 6	2	<0.1	1	0.2
Unknown no. 7	2	<0.1	2	0.5
Unknown no. 8	1	<0.1	1	0.2
Unknown no. 9	7	<0.1	1	0.2
Unidentified otoliths (worn)	475	0.1	36	8.4
Class Cephalopoda	16,258	32.6	354	82.7
Order Teuthoidea	16,217	32.5	354	82.7
Family Ommastrephidae	4,594	9.2	280	65.2
<i>Ommastrephes bartrami</i>	2,040	4.1	212	49.5
<i>Eucleoteuthis luminosa</i>	713	1.4	174	40.7
<i>Sthenoteuthis oualaniensis</i>	499	1.0	117	27.3
<i>Dosidicus gigas</i>	384	0.7	109	25.5
<i>Hyaloteuthis</i> c.f. <i>pelagica</i>	310	0.6	35	8.2
<i>Nototodarus</i> c.f. <i>hawaiiensis</i>	7	<0.1	5	1.2
<i>Ommastrephid</i> sp. no. 1	7	<0.1	4	0.9
<i>Ommastrephid</i> sp. no. 2	512	1.0	71	16.6
<i>Ommastrephid</i> sp. no. 3	2	<0.1	2	0.5
<i>Ommastrephid</i> sp. no. 4	120	0.2	28	6.5
Family Onychoteuthidae	1,151	2.3	177	41.4
<i>Onychoteuthis banksi</i>	1,029	2.1	168	39.3
<i>Onychoteuthis</i> sp. no. 1	116	0.2	26	6.1
<i>Onychoteuthis</i> sp. no. 2	6	<0.1	3	0.7

Continued on next page

Enoploteuthidae (enope squids) accounted for most of the cephalopod prey by number (31.8%) and represented 10.5% of all prey (fish and squid) by num-

ber. The next most numerous squids belonged to the family Ommastrephidae (flying squids), which accounted for 28.2% of all cephalopod species by num-

Table 1 (continued)

Prey	Number		Frequency of occurrence	
	No.	%	No.	%
Family Enoploteuthidae	5,175	10.4	235	54.9
<i>Abraliopsis affinis</i>	4,880	9.8	199	46.5
<i>Ancistrocheirus lesueuri</i>	183	0.4	78	18.2
<i>Pterygioteuthis giardi</i>	112	0.2	40	9.4
Family Mastigoteuthidae				
<i>Mastigoteuthis dentata</i>	1,163	2.3	188	43.9
Family Cranchiidae	2,057	4.1	214	50.0
<i>Leachia dislocata</i>	1,075	2.3	133	31.1
<i>Megalocranchia</i> sp.	628	1.3	87	20.3
<i>Liocranchia reinhardtii</i>	354	0.7	81	18.9
Family Pholidoteuthidae				
<i>Pholidoteuthis boschmai</i>	225	0.5	57	13.3
Family Thysanoteuthidae				
<i>Thysanoteuthis rhombus</i>	129	0.3	66	15.4
Family Octopoteuthidae	103	0.2	56	13.1
<i>Octopoteuthis deletron</i>	102	0.2	56	13.1
<i>Octopoteuthis</i> sp.	1	<0.1	1	0.2
Family Ctenopterygidae				
<i>Ctenopteryx sicula</i>	64	0.1	31	7.2
Family Grimalditeuthidae				
<i>Grimalditeuthis bomplandi</i>	8	<0.1	7	1.6
Family Architeuthidae				
<i>Architeuthis</i> sp.	3	<0.1	1	0.2
Family Histiototeuthidae	3	<0.1	3	0.7
<i>Histiototeuthis dofleini</i>	1	<0.1	1	0.2
<i>Histiototeuthis meleagroteuthis</i>	2	<0.1	2	0.5
Unidentified squid species				
Unknown no. 1	1	<0.1	1	0.2
Unknown no. 2	7	<0.1	5	1.2
Unknown no. 3	1	<0.1	1	0.2
Unidentified upper beaks	1,533	3.1	183	42.8
Order Octopoda	37	<0.1	19	4.4
Family Argonautidae				
<i>Argonauta</i> sp. (Type A)	16	<0.1	14	3.3
Family Tremoctopodidae				
<i>Tremoctopus violaceus</i>	10	<0.1	5	1.2
Family Bolitaenidae				
<i>Japatella heathi</i>	8	<0.1	5	1.2
Family Alloposidae				
<i>Alloposus mollis</i>	3	<0.1	3	0.7
Unidentified octopus beaks	4	<0.1	4	0.9
Class Gastropoda	31	<0.1	10	2.3
Class Crustacea				
Order Decapoda	333	0.7	60	14.0
Family Galatheididae				
<i>Pleuroncodes planipes</i>	8	<0.1	7	1.6
Unidentified shrimp	26	<0.1	12	2.8
Order Isopoda	299	0.60	52	12.1
Total	49,798			

ber and represented 9.2% of all prey consumed. However, the family Ommastrephidae had the highest percent frequency of occurrence at 65.2%, followed by the family Eupoloteuthidae at 54.9%. Octopus accounted for only 0.23% of cephalopod prey and occurred in 4.4% of the stomachs examined (Table 1).

## Prey size

The beaks of 18 out of 32 squid species could be converted to mantle length and weight (Table 2). The average mantle length of squid was 75.8 mm (SE=0.54) and ranged in size from 2.4 to 321 mm. The largest species of squid, on average, was *Dosidicus gigas* at 181 mm (SE=2.9), and the smallest species of squid was *Pterygioteuthis giardi* (mean=22 mm, SE=0.41). The otoliths of only eight fish species could be converted to total length (TL) (Table 3). The average size fish consumed was 92.9 mm TL (SE=1.41) with a range of 34–260 mm TL. The largest species of fish, on average, was *A. thazard* (mean=211.5 mm TL, SE=8.08) and the smallest was *Ceratoscopelus warmingii* (mean=49.3 mm TL, SE=0.45).

We found that the size of fish and squid consumed increased significantly with dolphin length (Fig. 2; fish:  $r^2=0.648$ ,  $P<0.001$ ; squid:  $r^2=0.791$ ,  $P<0.0001$ ).

We also found that the number of prey consumed was negatively correlated with the size of prey (squid:  $r^2=-0.555$ ,  $P<0.001$ ; fish:  $r^2=-0.624$ ,  $P<0.003$ ). If a prey species was small, more were consumed by the dolphins.

## Geographic and seasonal variability

To test the hypotheses of variability in prey composition between areas and seasons, 10 species that accounted for 55% of the sample by number were selected for the analyses (Table 1). These included five species of fish: *Symbolophorus* spp., *Myctophum aurolaternatum*, *Lampanyctus parvicauda*, *Diaphus splendidus*, *Cubiceps pauciradiatus*, and five species of squid: *Ommastrephes bartrami*, *Onychoteuthis banksii*, *Abraliopsis affinis*, *Mastigoteuthis dentata*, and *Leachia dislocata*. A significant difference was found in the prey composition by area and season ( $\chi^2=13,373$ ,  $df=45$ ,  $P<0.0001$ ).

Fish were the dominant prey species of *S. attenuata* in the winter: *L. parvicauda* was found in the highest numbers in the northeast, *M. aurolaternatum* in the south, and *Symbolophorus* spp. in the west. Squid were the dominant prey species in the summer; *A. affinis* was found in highest numbers in both the northeast and west, and *O. bartrami* in the south (Fig. 3).

**Table 2**

Mean, standard deviation, and range of mantle length and weight of cephalopod species consumed by spotted dolphin, calculated with regression equations (Clarke, 1986a; Wolff<sup>4</sup>). 'Number' represents the total number of cephalopod beaks that were measurable, without being broken or worn.

Species of prey	Number	Estimated prey length		Estimated prey weight (g)			
		Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Total	% weight
<b>Cephalopods</b>							
<i>Ommastrephes bartrami</i>	1,158	129.2 $\pm$ 35.3	69.7–273.5	63.9 $\pm$ 69.6	2.3–463.0	74,048	31.90
<i>Eucleoteuthis luminosa</i>	475	112.7 $\pm$ 33.9	51.6–219.4	40.4 $\pm$ 38.5	2.5–226.9	19,186	8.30
<i>Sthenoteuthis oualaniensis</i>	287	144.2 $\pm$ 42.1	73.4–320.9	136.5 $\pm$ 147.1	11.8–1,248.2	39,165	16.90
<i>Dosidicus gigas</i>	207	180.8 $\pm$ 43.1	99.2–319.4	177.9 $\pm$ 134.3	15.7–853.2	36,822	15.90
<i>Hyaloteuthis pelagica</i>	141	75.3 $\pm$ 12.7	50.6–117.9	11.9 $\pm$ 5.3	3.7–34.0	1,688	0.70
<i>Nototodarus hawaiiensis</i>	5	70.8 $\pm$ 9.9	65.0–87.9	16.3 $\pm$ 9.9	10.9–33.6	82	0.03
<i>Onychoteuthis banksii</i>	646	74.3 $\pm$ 20.0	8.6–139.9	14.9 $\pm$ 11.3	0.2–77.3	9,676	4.20
<i>Abraliopsis affinis</i>	3,671	30.0 $\pm$ 4.9	18.7–45.4	2.3 $\pm$ 1.2	0.4–7.0	8,424	3.60
<i>Ancistrocheirus lesueurii</i>	139	46.9 $\pm$ 29.6	8.8–203.1	21.9 $\pm$ 50.7	0.3–484.7	3,043	1.30
<i>Pterygioteuthis giardi</i>	65	21.8 $\pm$ 3.4	16.4–31.7	0.7 $\pm$ 0.4	0.2–2.5	50	0.02
<i>Mastigoteuthis dentata</i>	870	69.1 $\pm$ 14.2	20.6–132.4	17.4 $\pm$ 10.7	0.6–98.3	15,166	6.50
<i>Leachia dislocata</i>	628	127.9 $\pm$ 33.4	49.6–248.1	12.4 $\pm$ 7.6	0.8–52.3	7,782	3.40
<i>Liocranchia reinhardtii</i>	238	125.4 $\pm$ 34.4	42.2–199.6	18.3 $\pm$ 10.6	1.2–48.0	4,363	1.90
<i>Megalocranchia</i> sp.	479	109.1 $\pm$ 54.2	2.4–253.9	15.4 $\pm$ 12.2	0.4–63.8	7,296	3.10
<i>Pholidoteuthis boschmai</i>	150	97.3 $\pm$ 25.5	42.9–181.9	26.5 $\pm$ 23.0	1.3–149.2	3,978	1.70
<i>Octopoteuthis deletron</i>	63	45.6 $\pm$ 23.5	10.3–130.2	15.8 $\pm$ 20.2	0.4–125.4	996	0.40
<i>Ctenopteryx sicula</i>	39	34.7 $\pm$ 6.3	21.7–51.6	3.9 $\pm$ 2.5	0.5–12.5	153	0.06
<i>Architeuthis</i> sp.	2	62.9 $\pm$ 25.8	44.7–81.2	4.8 $\pm$ 4.2	1.9–7.7	10	<0.01

**Table 3**

Mean, standard deviation, and range of fish length (total length) and weight of fish species consumed by spotted dolphin, calculated with regression equations (see Footnote 2 in the main text) and ratios of otolith length to fish length (Butler, 1979; Hecht, 1987). 'Number' represents the total number of otoliths that were measurable, without being broken or worn. For *A. thazard*, '8' represents the number of fish measured.

Prey species	No.	Estimated prey length		Estimated weight (g)		
		Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Total
Fish						
<i>Symbolophorus</i> spp.	273	66.6 $\pm$ 7.0	40.9–82.4	4.1 $\pm$ 1.3	0.8–7.9	1,105
<i>Myctophum nitidulum</i>	14	56.4 $\pm$ 5.2	46.7–63.1			
<i>Ceratoscopelus warmingii</i>	114	49.3 $\pm$ 4.8	33.8–61.5			
<i>Exocoetus volitans</i>	68	158.7 $\pm$ 22.2	90.9–187.4			
<i>Exocoetus monocirrhus</i>	19	164.7 $\pm$ 16.8	136.9–193.7	50.9 $\pm$ 8.3	37.2–65.2	967
<i>Oxyporhamphus micropterus</i>	40	143.4 $\pm$ 15.1	122.2–180.1			
<i>Cubiceps pauciradiatus</i>	233	109.1 $\pm$ 9.8	74.6–129.8			
<i>Cubiceps baxteri</i>	3	140.9 $\pm$ 4.9	136.1–145.8			
<i>Auxis thazard</i>	8	211.5 $\pm$ 22.9	190.0–260.0			

### Stomach fullness index (SFI)

The SFI ranged from 0.4% to 86.4% (average: 29.4%) after all measures were scaled to the maximum SFI. A statistically significant difference was found in the SFI between quarters of the day ( $\chi^2=112.99$ ,  $df=6$ ,  $P<0.0001$ ). A SFI >60% was calculated for 42.0% of the animals collected between 0600 and 0900 h, whereas only 1.0% of the sample collected between 1501 and 1800 h had a SFI >60% (Fig. 4).

### Reproductive condition

The mean number of squid differed significantly between pregnant and lactating females (Student's  $t$ -test = -2.65,  $P=0.010$ ); however, no significant difference was found in the mean number of fish consumed (Student's  $t$ -test = 0.25,  $P=0.803$ ). When stratified by time-of-day, the mean SFI was significantly higher for lactating dolphins during all time periods ( $\chi^2=46.98$ ,  $df=6$ ,  $P<0.0001$ ; Table 4).

### Discussion

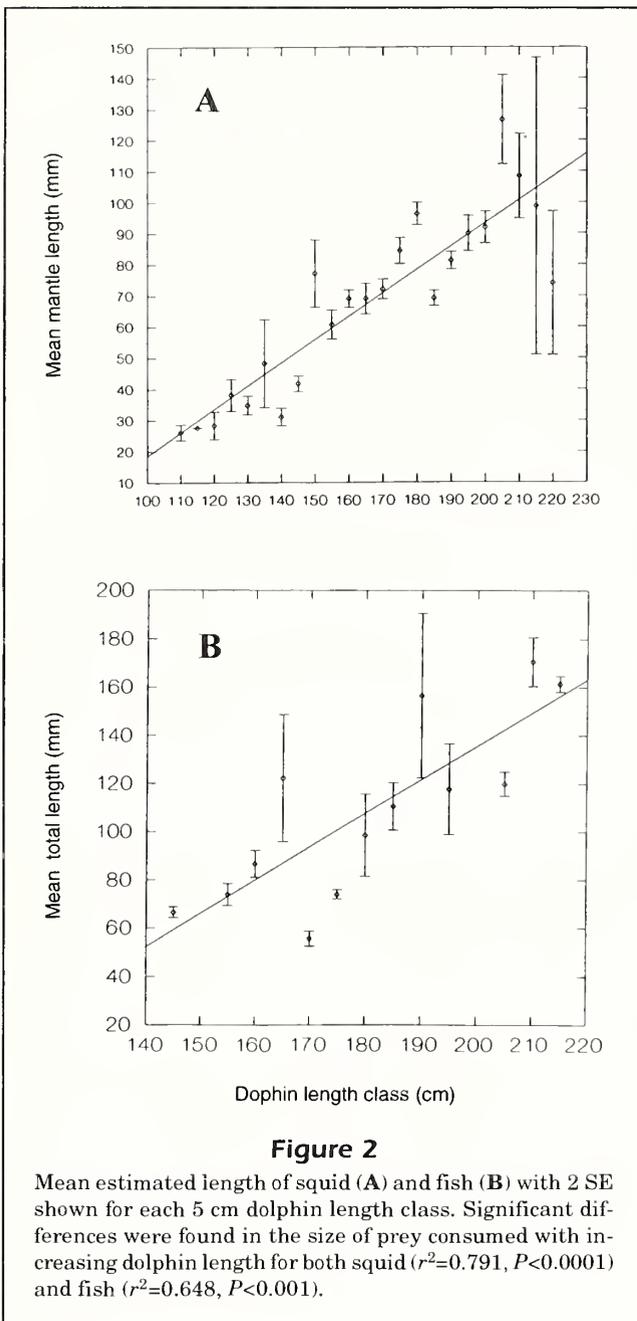
Mesopelagic prey were found to dominate the diet of pantropical spotted dolphins; myctophid fish, and enoploteuthid and ommastrephid squid accounted for 69% of all prey consumed (Table 1). These mesopelagic species are associated with the deep scattering layer and most undergo diel vertical migration, moving into the upper 200 m at dusk to feed and retreating to depth at dawn to avoid predation (Gibbs and Roper, 1971; Clarke, 1973, 1978; Wisner, 1974; Roper

**Table 4**

The average stomach fullness (%) for lactating and pregnant spotted dolphins throughout the day. The day is divided into three hour increments from 0600 h to 1800 h. 'No.' is equal to the number of stomachs in each time category.

Time (h)	Average stomach fullness			
	Lactating		Pregnant	
	%	No.	%	No.
0600–0900	52.7	15	38.6	6
0901–1200	37.3	18	23.1	10
1201–1500	27.2	15	15.2	7
1501–1800	26.1	9	10.9	14
Overall average	44.3	57	19.5	37

and Young, 1975; Roper et al., 1984; Smith and Heemstra, 1986). The SFI, which we found to be highest in the morning hours (i.e. 0600–0900 h, Fig. 4), suggests that pantropical spotted dolphins feed during the night when these prey are nearest to the surface. In fact, Shomura and Hida (1965) hypothesized that the spotted dolphin caught off Hawaii fed just before dawn, prior to descent of the deep scattering layer, because fresh mesopelagic prey were found in its stomach (enoploteuthid squid and myctophid fishes). Evidence of nighttime feeding by pantropical spotted dolphins has also been presented by Scott (1991), who reported that the highest proportion of undigested prey was recovered from spotted dolphin stomachs collected between 0700 and 0930 h and that



schooling size of prey, and bioluminescence of prey (Clarke, 1973; Crawford, 1981; Clarke, 1986b). The top three prey families in our study (Myctophidae, Enoploteuthidae, Ommastrephidae) are all abundant in the ETP and have bioluminescent organs (Clarke, 1973, 1978; Wisner, 1974; Okutani, 1974; Clarke, 1977; Crawford, 1981; Roper et al., 1984; Harman and Young, 1985; Clarke, 1986b). Myctophids, which accounted for 49.7% of all prey recovered in our sample, are the most abundant deep scattering layer species, representing 25% of the biomass of all mesopelagic fishes (Karnella, 1987). Myctophids are small in size, school in large numbers, and have bioluminescent organs, all characteristics that might facilitate detection by dolphins (Crawford, 1981).

### Prey size

There does appear to be some selectivity of prey by size because larger dolphins tend to eat larger prey (Fig. 2). Our results support the supposition that because most dolphins have been observed to consume their prey whole, the size of prey ingested is limited by the size that can be swallowed (Fiscus and Kajimura, 1981; Fiscus and Jones, 1990; Wolff<sup>4</sup>). The size of prey in our study indicated that prey consumed by juveniles through adults ranged from 2.4 to 320.9 mm (Okutani, 1974, Butler, 1979; Uchida, 1981; Roper et al., 1984; Clarke, 1986a; Smith and Heemstra, 1986; Karnella, 1987; Murata and Hayase, 1993; Welch and Morris, 1993). Most of our size ranges corresponded with those reported by Wolff,<sup>4</sup> who examined the squid prey of spotted dolphins from the Perrin et al. (1973) study, except for *A. affinis*, which had a narrower size range in our study, and *O. banksii*, which encompassed a broader size range. Wolff<sup>4</sup> also showed an increase in the size of squid consumed by spotted dolphins; there was a 30-mm mantle length increase for squid found in dolphins from 140 to 205 cm in length. He also found that a broader size range of squid was consumed for larger dolphins, which was also the case in our study.

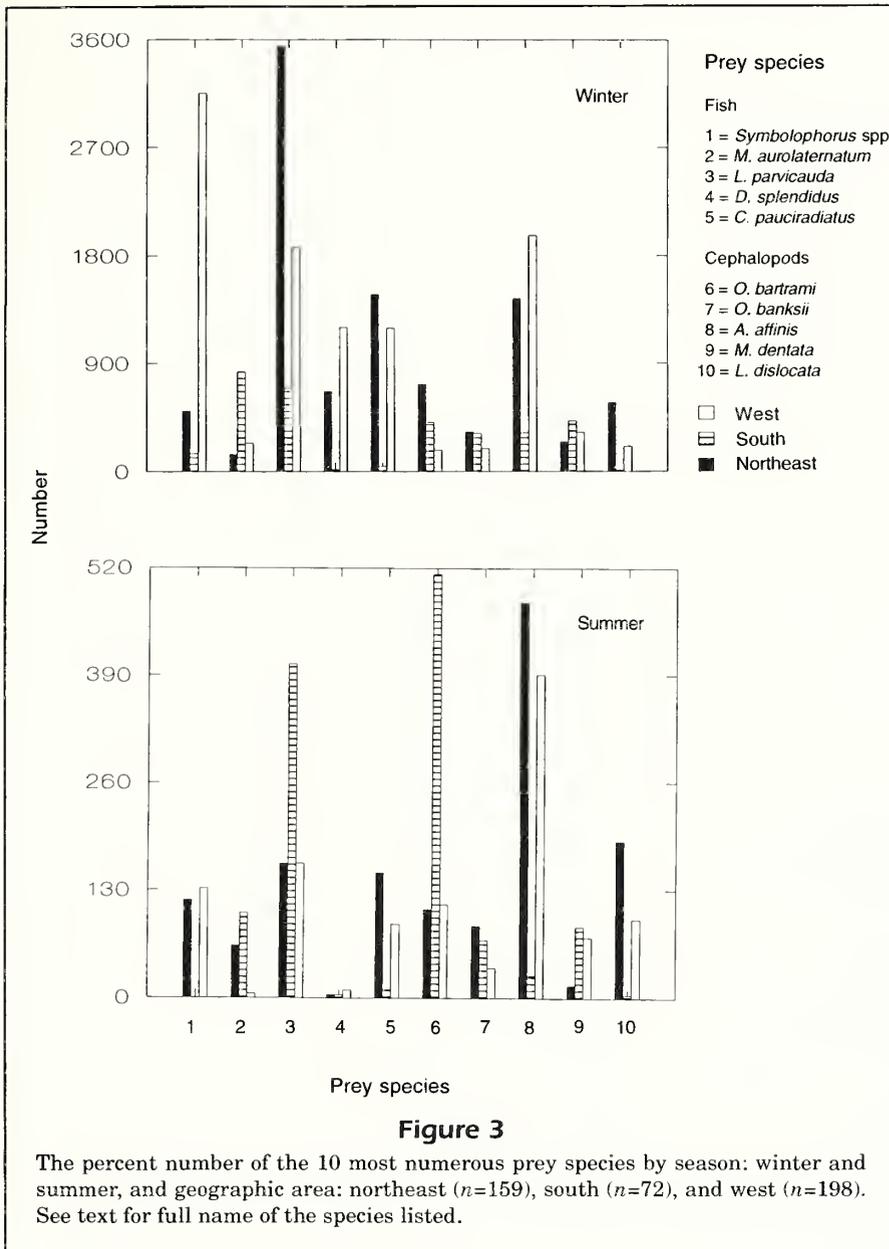
### Geographic and seasonal variability

The composition of prey species consumed by pantropical spotted dolphins changed both temporally and spatially (Fig. 3), suggesting that they are opportunistic feeders, as is the case with many other

no fresh prey was recovered from stomachs collected after 1200 h. More recently, the collection of data on dive patterns has provided additional evidence of nighttime feeding by spotted dolphins. The dive patterns show marked diurnal changes and both deeper and longer dives at night. In particular, the dawn-dusk diving patterns suggest that dolphins were following the ascent and descent of the deep scattering layer (Scott et al.<sup>7</sup>).

The capture of prey by dolphins in the deep scattering layer may be facilitated by abundance of prey,

<sup>7</sup> Scott, M. D., S. J. Chivers, H. Rhinehart, M. Garcia, R. Lindsey, R. L. Olson, W. Armstrong, and D. A. Bratten. 1997. Movements and diving behavior of pelagic spotted dolphins. Inter-Am. Tropical Tuna Comm., c/o Scripps Institution of Oceanography, Univ. Calif., San Diego, CA 92037.



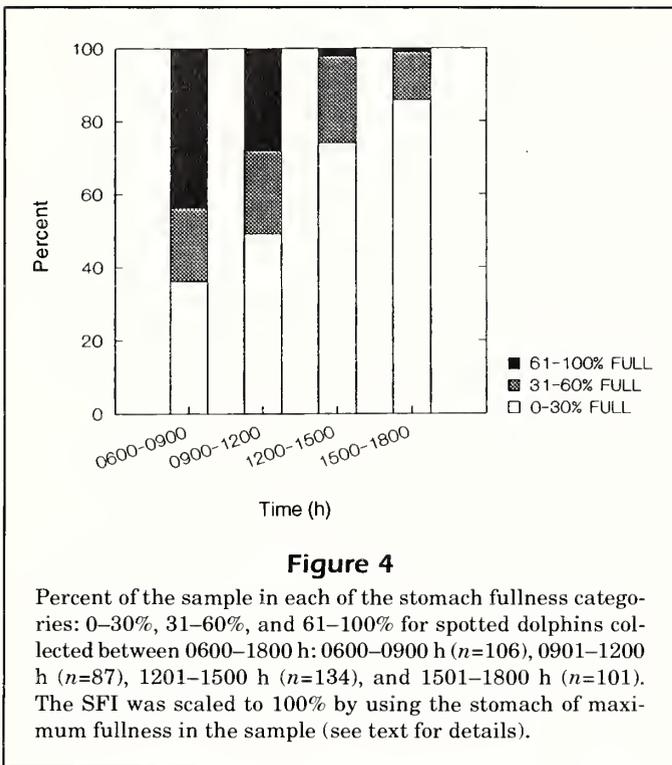
dolphin species (Brown and Norris, 1956; Ross, 1979; Jones, 1981; Fiscus, 1982; Gaskin, 1982; Leatherwood et al., 1983; Evans, 1987; Young and Cockcroft, 1995). Geographic and seasonal changes in prey composition could be a result of migration of prey into or out of an area, prey spawning seasons, or simply distributional boundaries of prey. It has been suggested that the movements of dolphin may correspond to the movement or availability of prey (Jones, 1981; Reilly, 1990; Young and Cockcroft, 1994). There is evidence that the distribution of pantropical spotted dolphin shifts westward along the 10°N latitude as the summer season progresses, and it has been hypothesized that this change in distribution is due to

changes in prey distribution resulting from the equatorial currents (Au and Perryman, 1985; Reilly, 1990). Unfortunately, information on precise distributions and seasonal movements of identified prey species in the ETP is limited; therefore this hypothesis cannot be addressed properly (Clarke, 1973; Okutani, 1974; Wisner, 1974; Clarke, 1977; Roper et al., 1984; Clarke, 1986, a and b).

### Reproductive condition

Changes in diet composition between lactating and pregnant dolphins have been documented in a number of species (Perez and Mooney, 1986; Bernard and Hohn, 1989; Recchia and Read, 1989; Cockcroft and Ross, 1990; Young and Cockcroft, 1994, 1995). The physiological energy required to maintain lactation is quite high for mammals and may require a change in diet composition to include food with a higher caloric content (Clutton-Brock et al., 1982; Perez and Mooney, 1986; Recchia and Read, 1989; Iverson, 1993). In fact, Bernard and Hohn (1989) presented evidence for a shift in diet between pregnant and lactating pantropical spotted dolphins and suggested that it was due to the physiological demands of lactation. They found a higher

proportion of flying fish (family Exocoetidae) in the diet of lactating females and a higher proportion of ommastrephid squid in the diet of pregnant females. We tested the same hypothesis for our sample, but our results were different. Although the proportion of fish (family Myctophidae) in the diet was higher than the proportion of squid (family Ommastrephidae) for both pregnant and lactating females, the proportion of squid was significantly higher in the diet of lactating females. Fish may provide most of the caloric intake for both lactating and pregnant females because both lanternfish and flying fish have a high caloric and lipid content in comparison with squid (Childress and Nygaard, 1973; Sidwell et al.,



1974; Sidwell, 1981; Croxall and Prince, 1982). A possible explanation for increased consumption of squid by lactating spotted dolphins is that milk production increases the demand for metabolic water (Croxall and Prince, 1982; Young and Cockcroft, 1994) and most squid have a higher water content than fish (Sidwell, 1981; Croxall and Prince, 1982). Cetacean milk has been estimated to be 40–60% water (Eichelberger et al., 1940; Gregory et al., 1955; Slijper, 1966; Best, 1982; Lockyer, 1984).

Rather than by a change in diet composition, the high metabolic demands of lactation could be met by increasing the amount of food consumed (Baldwin, 1978; Millar, 1979; Clutton-Brock et al., 1982; Yasui and Gaskin, 1986; Perez and Mooney, 1986; Kastelein et al., 1993). Estimates of food intake for lactating versus nonlactating females have been estimated to increase by 75–86% for lactating minke whales (*Balaenoptera acutorostrata*) and fin whales (*Balaenoptera physalus*) (Lockyer, 1978, 1981), by 500 g for lactating harbor porpoise (*Phocoena phocoena*) (Recchia and Read, 1989), and by 30% for captive Commerson's dolphins (*Cephalorhynchus commersoni*) (Kastelein et al., 1993). For spotted dolphins, Bernard and Hohn (1989) reported a SFI that was 24% higher for lactating females (Mann-Whitney,  $0.05 < P < 0.10$ ). Similarly, we found that the SFI of lactating females was 16% higher than that for pregnant females and that a higher SFI was maintained

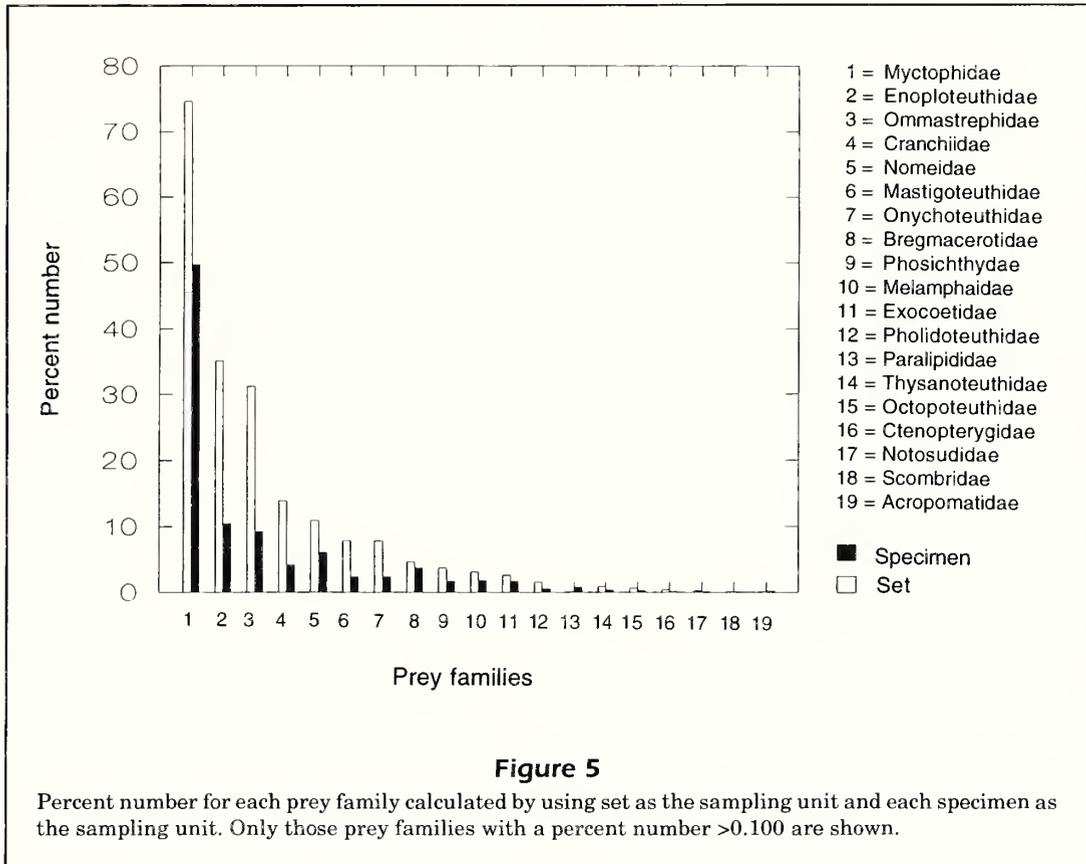
by lactating females throughout the day (Table 4). This finding parallels those of Cockcroft and Ross (1990) in which they estimated that lactating bottlenose dolphins (*Tursiops truncatus*) would need to consume 3 or 4 stomachfuls of food per day to keep up with energetic demands, whereas males and resting females (not pregnant or lactating) had to consume only 2 stomachfuls to maintain their energetic requirements. Our results also suggest that lactating spotted dolphins may consume more food throughout the day to meet the higher energetic and nutritional demands of lactation.

### Biases associated with analyses

As in every food-habit study, there are inherent biases associated with the analyses. Differential prey digestibility and secondary prey can bias all measures. The importance of small prey species can be overestimated by methods that determine both the percent number and the percent frequency of occurrence. Furthermore, infrequently consumed species may be overemphasized by the percent frequency-of-occurrence method (Hyslop, 1980; Bigg and Fawcett, 1985; Bigg and Perez, 1985).

Analysis of only hard parts can be biased through differential passage, retention, and degradation rates of beaks and otoliths (Hyslop, 1980; Bigg and Fawcett, 1985; Bigg and Perez, 1985; Pierce and Boyle, 1991). The importance of squid can be exaggerated by using only hard parts because beaks tend to get stuck in the stomach rugae and accumulate (Ross, 1979; Shroud et al., 1981; Clarke, 1986a). There are few data available on the passage and retention rates of various prey in cetaceans, although work on captive bottlenose dolphins (*Tursiops aduncus*) has indicated that fish otoliths were retained for up to 48 h and squid beaks for up to 72 h (Ross, 1979). Similarly, Clarke (1980) reported that sperm whales (*Physeter macrocephalus*) retained squid beaks for 36–60 h. The only way to avoid biases introduced by using hard parts is to use only fresh or whole prey recovered from stomachs. Although this method can tremendously limit the sample size and underestimate the importance of squid because squid flesh digests more quickly than fish flesh (Bigg and Fawcett, 1985).

Another source of bias may have affected the interpretation of our results. Ninety-six percent (96%) or 411 of the stomachs were recovered from net sets from which more than one stomach was collected. We tested whether multiple samples per set would bias our interpretation of important prey species by calculating the percent number for prey families,



using each set as a sampling unit. The percent numbers, for set as the sampling unit and specimen as the sampling unit, were then compared by using a Mann-Whitney rank test, and no significant difference was found in the rank order of prey families between the set and specimen methods (Zar, 1984, p. 141-143;  $P=0.05$ , Fig. 5). Therefore, we conclude that for our data set, there was no bias introduced by using multiple specimens collected from the same set.

## Summary

Based on the analysis and identification of fish otoliths and cephalopod beaks, our results provide evidence that pantropical spotted dolphins feed primarily at night on mesopelagic fish and squid. The dominant prey species belong to the families Myctophidae, Enoploteuthidae, and Ommastrephidae. Composition of the diet differed by season and area; thus pantropical spotted dolphins are likely opportunistic feeders. Prey included a wide range of sizes of both fish and squid, with the largest prey consumed by the largest dolphins, and the smallest prey consumed in the largest numbers. Furthermore,

the diet of female dolphins differed by reproductive condition. Lactating females consumed more food and a higher proportion of squid than did pregnant females.

## Acknowledgments

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**Abstract.**—Seventy-five shovelnose guitarfish, *Rhinobatos productus*, were collected between November 1988 and January 1991 near Long Beach, California, to determine age, growth, and sexual maturity. Thirteen guitarfish were kept in captivity and injected with Terramycin to provide a time mark for growth analysis. Later, vertebral centra were examined for opaque band formation, and there were positive results in two individuals. Outer margin analysis of centra from captive and field-collected guitarfish indicated that opaque bands formed between August and December. Guitarfish were aged to 11 years, and growth appeared to be best represented by a linear growth equation,  $TL = 43.33 + 6.90x$ , where  $TL$  = total length and  $x$  = estimated age in years. Analysis of reproductive tracts showed that female guitarfish matured at 99 cm (estimated age at seven years). Clasper length and width indicated that males matured at 90–100 cm (estimated age at eight years).

## Age, growth, and sexual maturity of shovelnose guitarfish, *Rhinobatos productus* (Ayres)

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Recently, a Federal fishery management plan was initiated for some large coastal and pelagic species of sharks of the eastern seaboard of the United States (NMFS<sup>1</sup>). Regulations on shark fisheries are important not only because they affect fisheries but because they set an example to be followed by other coastal areas. Many species of elasmobranchs are highly migratory; thus regulations are necessary on a broader scale if they are to be effective management tools.

Elasmobranchs tend to have slow growth and low fecundity (Holden, 1973); thus, overexploitation of a species is possible. Fortunately, recent collection of age, growth, and reproductive data on elasmobranchs has helped provide some of the baseline information necessary to manage many species.

The shovelnose guitarfish, *Rhinobatos productus*, is a common coastal ray found in temperate waters along the Pacific coast of the United States from Baja California to San Francisco (Miller and Lea, 1972). Although not a highly prized commercial catch, it is edible and is often found in fish markets labeled as generic "shark steak" and sold on piers in Santa Barbara, California, as "fish n' chips." Guitarfish

is not sold as "guitarfish" on restaurant menus; however it may become a popular fare in the future as a substitute for shark. Furthermore, dried guitarfish are sold in large numbers as curios in shell shops from central California to Baja California. The majority of guitarfish sold for human consumption are the larger, mature individuals; however, curio and shell shops tend to sell all sizes, especially newborn pups. Congeners of *Rhinobatos* are particularly targeted for commercial sale in other areas of the world including Peru (Tresierra et al., 1989) and Brazil (Lessa and Vooren, 1986). Currently, in southern California, commercial landings of guitarfish are grouped under benthic shark species and not recorded as guitarfish.<sup>2</sup> Most literature on *R. productus* is contained in field guides and California Fish and Game publications (Roedel, 1953; Miller and Lea, 1972; Lane and Hill, 1975; Eschmeyer et al. 1983; Talent, 1982, 1985) usually with no more than brief mention of some of

<sup>1</sup> NMFS. 1993. Fishery management plan for sharks of the Atlantic Ocean. Prepared for the U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, 167 p.

<sup>2</sup> Vojkovich, M. 1994. Dep. Fish and Game, Long Beach, CA 90807. Personal commun.

its life history aspects, such as maximum size and food preferences. One particular aspect of guitarfish behavior is that large numbers of them are often found in shallow embayments, such as Elkhorn Slough and Mugu Lagoon, California, and Almejas Bay, Baja California, México. In these areas, they are easily captured with a seine net and are thus particularly susceptible to fishing pressure.

Because elasmobranchs tend to be exploited before regulatory measures are in effect (Pratt and Casey, 1990), it is necessary to determine age and growth relationships and size at sexual maturity of *R. productus* prior to increases in fishing pressure. The results of this study provide basic information for management of guitarfish, should it become more popular as a food item.

We have incorporated the following methods of age determination into this study of the age, growth, and sexual maturity of guitarfish: 1) a laboratory analysis of the vertebral bands and their outer margin state (translucent or opaque) in order to assign ages to individuals; 2) a study of growth in captivity to verify estimated growth from the laboratory analysis; and 3) a determination of age at sexual maturity. The main focus of this age and growth study is based on an examination of vertebral centra and their use in ageing guitarfish.

## Methods

### Age and growth

Seventy-five guitarfish were collected between November 1988 and January 1991 from the waters between Seal and Redondo Beaches, California (Fig. 1). Guitarfish were captured by hook and line, gill net, otter trawl, long line, or beach seine, and then frozen. Lengths were measured with a tape measure to the nearest centimeter over the contour of the dorsal portion of the guitarfish and included total length (TL), disc width (DW), first dorsal fin length (1D), and second dorsal fin length (2D) (Fig. 2). The contour measurement over the dorsal portion provided a more precise measurement of the first and second dorsal fin lengths. This method will increase the total length measurement and should be taken into consideration if comparisons are made with lengths of guitarfish in this study.

The only portion of the guitarfish that is available in fish markets is the trunk and tail or loin region, which includes the two dorsal fins. Therefore, we included the measurement of the distance from the origin of the first dorsal fin to the origin of the second dorsal fin (2D) to facilitate future predictions of

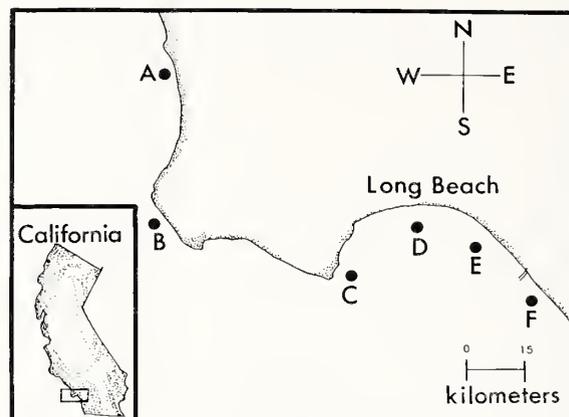
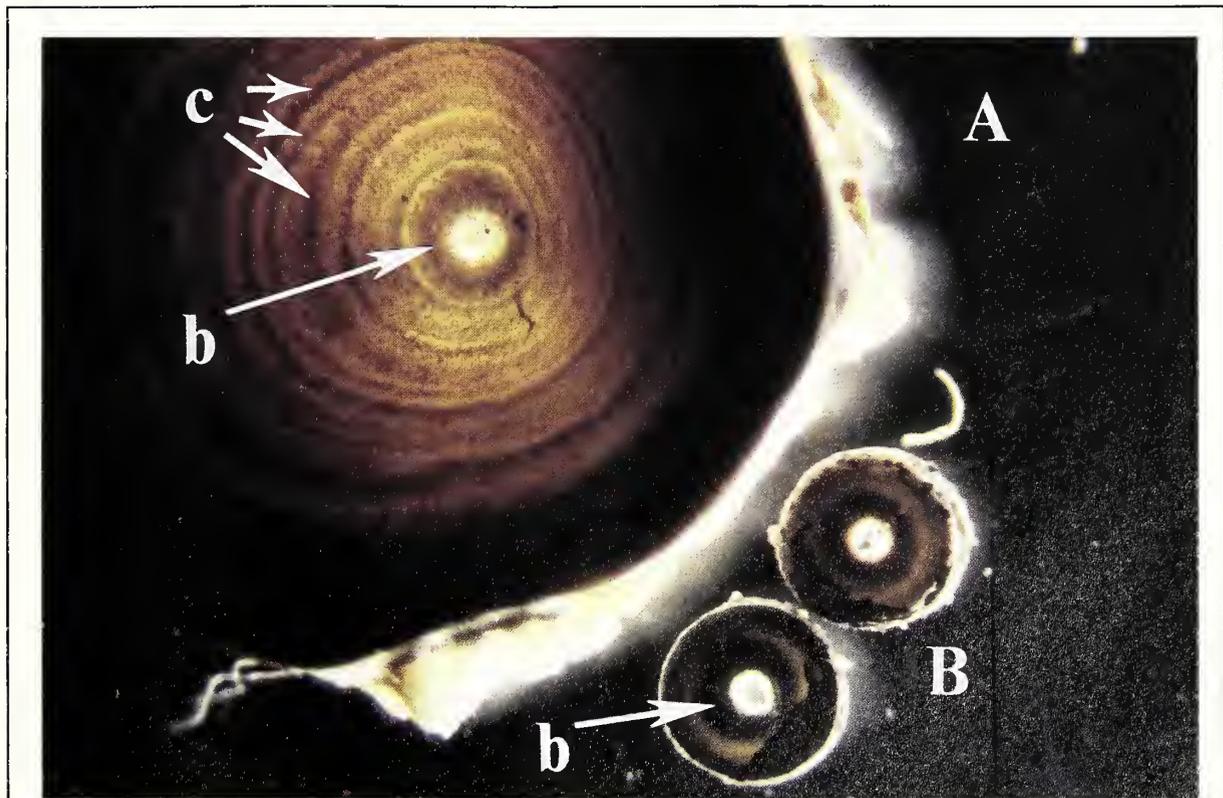
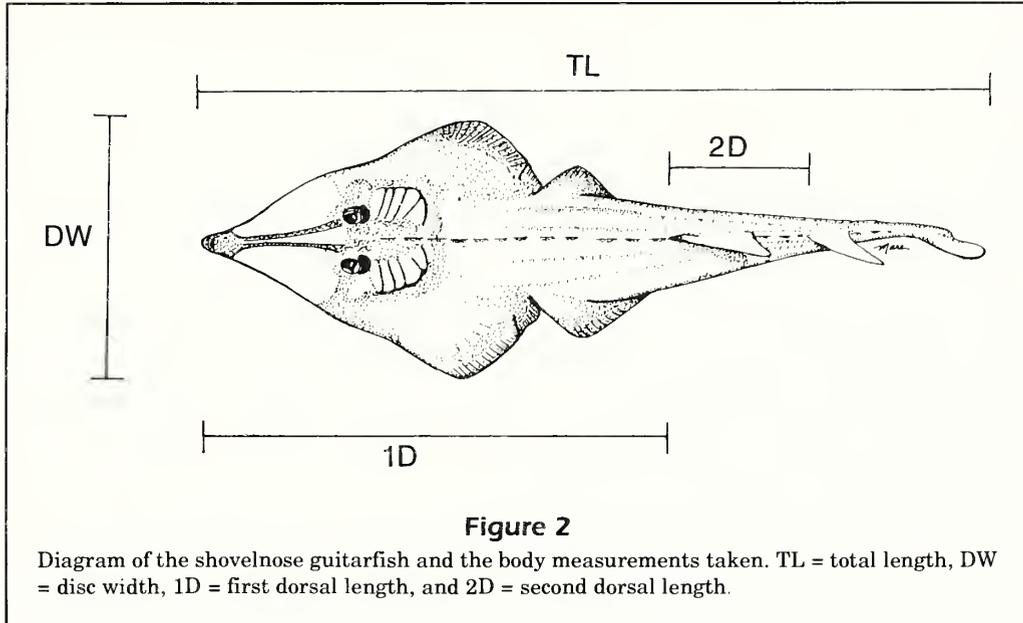


Figure 1

Study sites where guitarfish, *Rhinobatos productus*, were collected along the coast of southern California. A = Redondo Beach, B = Palos Verdes, C = San Pedro, D = Long Beach, E = Belmont Shores, and F = Seal Beach.

total length from market fish. Damp weight was measured for all guitarfish with a spring balance. Ten vertebrae were removed from each guitarfish just anterior to the first dorsal fin for analysis. The larger vertebrae were located just posterior to the eyes; however, they were not used because removal of these vertebrae would have interfered with dissection of the female reproductive tract. Each guitarfish was assigned a code number and this became the only identifying feature for each guitarfish for the remainder of the study. Vertebrae were cleaned by placing them in a dermestid beetle colony. The beetles consumed almost all muscle and connective tissue; the only remaining tissue was a cone-shaped membrane (membrane elastica externa) on the centrum that was easily removed from the dry vertebrae with fine forceps. Cleaned and dried vertebral centra were viewed whole with a Wilde dissecting scope with transmitted light within a dark field. Ten vertebrae from each guitarfish were examined to determine consistency of band formation within an individual. If all vertebrae for an individual guitarfish contained the same number of bands, then two of those vertebrae were used for three separate readings. Those having variable band counts or unreadable vertebrae among the ten vertebrae were discarded. Opaque bands present beyond the birth mark were counted (Fig. 3). Rings within bands were not always discernible as separate rings; therefore, bands were determined to be the most useful increment. The birth mark was defined here as the centermost opaque portion (first band) of the centra. It was present in the smallest of the guitarfish and was in the same position in all larger specimens. This birth mark is similar in place-



**Figure 3**

Examples of band formations in the vertebra of a 125.5-cm guitarfish (A) and a 28.8-cm guitarfish (B). The birth mark (b) appeared in all three vertebrae. Band formations (c) were poor towards the outer edge of the centra of the larger individual (A), and this individual was not used in the age study. Poor band formations were indicative of individual guitarfish with deformed vertebral columns.

ment to that found by Cailliet et al. (1983) in the blue shark, *Prionace glauca*, and Casey et al. (1985) in the sandbar shark, *Carcharhinus plumbeus*. Diameters of vertebral centra were measured with an ocular micrometer at 12× magnification. Each vertebra was read three times, one month apart, and those vertebrae in which all three readings agreed were used in the final analysis. To determine periodicity of band formation, the condition of the outermost band was recorded as either translucent, opaque, or undetermined. Ages were assigned to guitarfish on the basis of the number of opaque bands.

Statistical analyses included least squares regression analysis to provide predictive equations for estimates of TL from centrum diameter, TL from band counts, TL from second dorsal fin length (2D), and age from TL. Regression parameters were obtained with SAS PC software (SAS, 1985). Male and female growth curves were constructed from von Bertalanffy's growth curve equation (von Bertalanffy, 1938):

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

where  $L_t$  = total length at time  $t$ ;  
 $L_\infty$  = maximum theoretical length of species;  
 $k$  = growth constant;  
 $t_0$  = theoretical age at zero length; and  
 $t$  = estimated age.

The von Bertalanffy growth equation was fitted by using FISHPARM (FISHPARM software [Prager et al., 1989]) to estimate the growth constant  $k$  and was compared to a linear least squares regression by using the same data.

### Growth rate of guitarfish in captivity

The main purpose of the captivity study was to determine if Terramycin (manufactured by Pfizer Agricultural Division) produced a readable time mark in vertebral centra of guitarfish. The study was designed to maintain guitarfish in captivity for at least one year to determine the temporal periodicity of band formation and growth rate of guitarfish in captivity.

Over a two-year period, 13 guitarfish (five males and eight females) were taken live and placed in an outdoor saltwater tank at California State University, Long Beach, California. Before guitarfish were introduced into the tank, we repeatedly measured TL, DW, 1D, and 2D until we obtained consistent, repeatable measurements. Guitarfish were first weighed, and then injected with Terramycin (dosage=0.5 mg/kg). Terramycin was injected with tuberculin-type syringes in the epaxial musculature, within two centimeters of the skin surface. Guitar-

fish were fed every other day a diet of anchovy, mackerel, mud shrimp, ghost shrimp, and squid.

When a guitarfish died in captivity, it was used for vertebral and reproductive analysis. Vertebral growth (beyond the time mark) was measured with the aid of a Wilde dissecting scope and ultraviolet flashlight (Fig. 4). Because time marks could be seen only under ultraviolet light and the opaque band formation could not be seen under ultraviolet light, transmitted light was used immediately after the ultraviolet light to compare the time mark with the opaque band position. This method allowed determination of whether a translucent or opaque band had formed after the time mark.

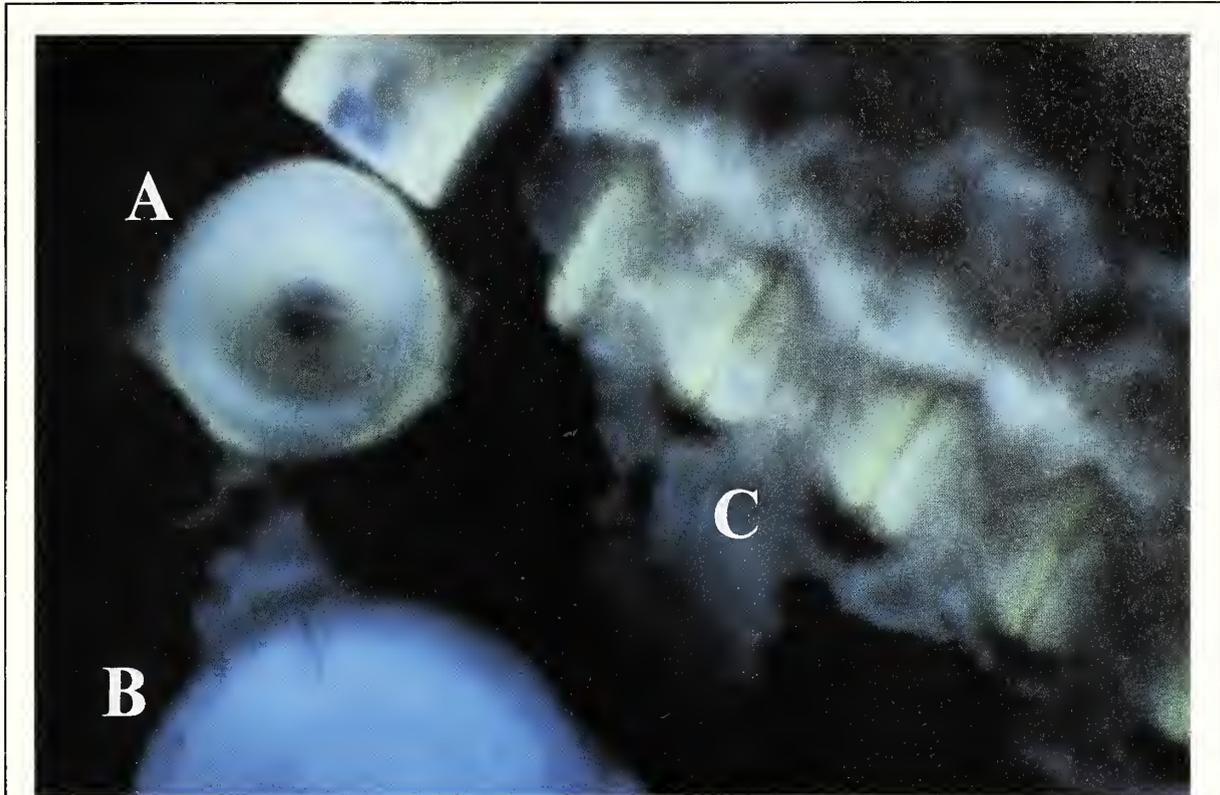
### Reproductive maturity

Thirty-six female guitarfish were dissected for examination of their reproductive tract. Mature individuals were categorized into one of three visual stages: Stage 1—shell gland not differentiated from uteri, uteri empty, small follicles present; Stage 2—shell gland and characteristic diagonal white band pattern within it forming, large Graafian follicles present, uteri thick; and Stage 3—uteri full, large Graafian follicles present. Immature individuals had no visible egg follicles, uteri were thin and transparent, and shell glands consisted only of a slight bulge in the upper portion of the uteri. These stages were distinct; any female guitarfish, upon dissection, could be categorized by using these criteria. No dissections were made for male guitarfish. The maturity of male guitarfish was determined by measuring the clasper width and length and by comparing the clasper length to total length, as well as by visual examination.

## Results

### Age and growth

Growth of the vertebrae was proportional to the growth of the guitarfish, as evidenced by the significant positive relation between centrum diameter and total length for females and males (females:  $r^2=0.98$ ,  $n=27$ ,  $P=0.0001$ ; males:  $r^2=0.96$ ,  $n=31$ ,  $P=0.0001$ ; Fig. 5). The number of bands per vertebra correlated strongly ( $r=0.92$ ,  $n=42$ ,  $P=0.0001$ ) with the diameter of the centra, indicating that individuals having more bands had larger centra. Similarly, the number of opaque bands present in any individual was higher in larger guitarfish; the regressions were significant for females and males (females:  $r^2=0.95$ ,  $n=19$ ,  $P=0.0001$ ; males:  $r^2=0.78$ ,  $n=24$ ,  $P=0.0001$ ). A Pearson correlation matrix analysis of total length, centrum



**Figure 4**

Comparison of Terramycin-injected guitarfish vertebrae (A and C) with control (B). The guitarfish vertebral column (C) was removed from a 27-cm individual that had been injected with Terramycin one month prior to its death in captivity. Note the yellow Terramycin band on the outer edge of the vertebra (A), and the Terramycin incorporation on the entire outside of the vertebral column (C). The control vertebra (B) was from a 37-cm guitarfish sacrificed immediately after capture.

diameter, and number of opaque bands further emphasized the strong relation between the three variables for males and females combined (opaque bands and TL:  $r=0.92$ ,  $n=43$ ,  $P=0.0001$ ; centrum diameter and TL:  $r=0.99$ ,  $n=60$ ,  $P=0.0001$ ; for opaque bands and centrum diameter see above).

Growth zones formed at approximately the same time each year, as was evident from examination of centra of two captive guitarfish. One of these guitarfish was injected with Terramycin in December 1989 and in July 1990 and was held in captivity for 13 months. The first Terramycin mark (closest to the focus of the centrum) was found at the peripheral edge of an opaque band (Fig. 6A). We do not know if the opaque band had formed prior to the injection or during the same month as the injection because the Terramycin may have diffused into the opaque band region. It was clear, however, that the mark was the same distance (0.07 cm) from the outer margin of the centrum as the peripheral edge of the opaque band. From the periphery of the opaque band to the

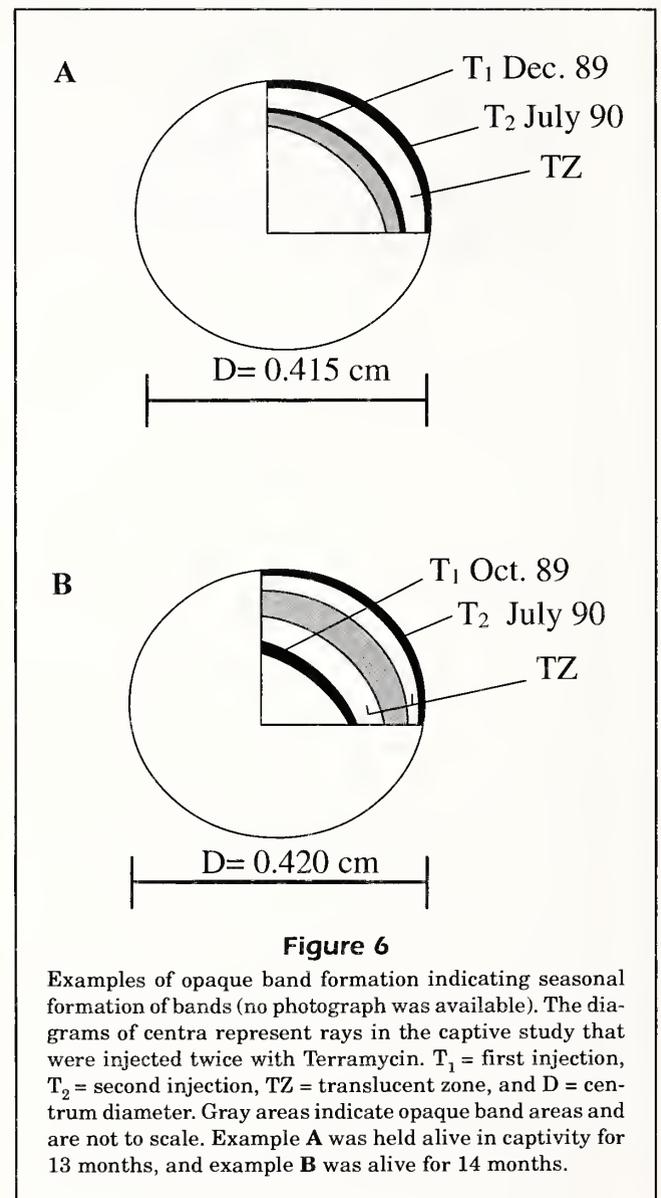
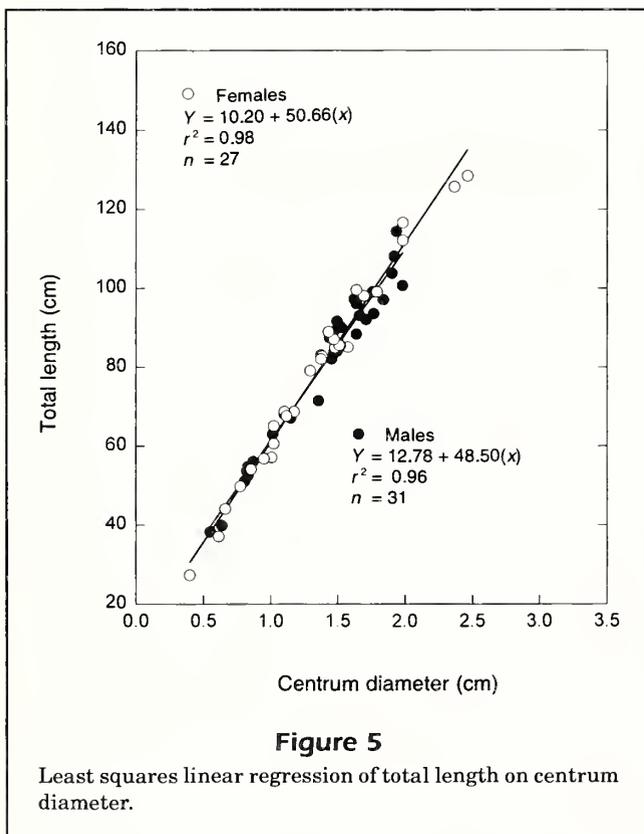
outer margin of the centrum, a translucent band was present; and the outer margin of the centrum contained the other Terramycin mark. The predicted growth (0.029 cm) of this centrum (with the formula in Fig. 5) was lower than the actual growth of 0.07 cm and shows that individuals probably vary in growth, especially in more optimal laboratory conditions. A second guitarfish was first injected in October 1989 and again in July 1990. This guitarfish lived for 14 months and had completely formed one opaque band during this period (Fig. 6B). This opaque band was formed after the October injection, and a translucent band was present beyond the opaque band to the outer margin of the centrum. The outer margin of the centrum showed the second injection mark at the periphery of the translucent zone at the time of death in January 1991. For this guitarfish, the predictive equation (Fig. 5) estimated centrum growth to be 0.062 cm; it was actually 0.053 cm. In both guitarfish, opaque band formation occurred sometime between the months of October and December fol-

lowed by translucent band formation. The remaining eleven guitarfish were held in captivity for six months or less. Eight of the eleven were injected with Terramycin and did not show any growth beyond the Terramycin mark on the vertebrae and each had grown less than one centimeter in total length. Three control guitarfish (no injections) lived 10, 50, and 72 days in captivity and showed no gain in length.

Analysis of the outer edges of the centra with regard to periodicity of band formation provides further evidence for opaque band formation between October and December. Eight out of 17 guitarfish collected between October and November had opaque outer margins, whereas none of the 34 other guitarfish collected during the other months (excluding August) had opaque outer margins. Three guitarfish caught in August showed opaque formation on the outer margins. A two-way test of independence indicated rejection of the null hypothesis that opaque band formation was independent of month (group 1=January–June, group 2=August–November;  $G(\text{adjusted})=18.94$ ,  $df=1$ ,  $P=0.00003$ ). Therefore, it appears that opaque bands form from late summer (August) into fall (November). There was no pronounced relation between outer margin width and months of the year, probably indicating variation of growth within individual guitarfish. Another way to

interpret these findings is to suggest that guitarfish lay down opaque bands bi-yearly (every other year). If this is the case, then the guitarfish were twice as old. However, the band formations found in the two captive guitarfish led us to assume that opaque bands were formed once per year.

Assigning ages under the assumption of the annual formation of one opaque and one translucent band, we found that both males and females ranged in age from one to 11 years. Females ranged from 25 to 130 cm TL. Males ranged from 23 to 114 cm TL. Percent agreement in band counts from three separate readings of two vertebrae from each guitarfish showed 73.8% in total agreement (43 guitarfish), 16.4% disagreement  $\pm 1$  band (10 guitarfish), 6.5% disagreement  $\pm 2$  bands (4 guitarfish), and 3.3% dis-

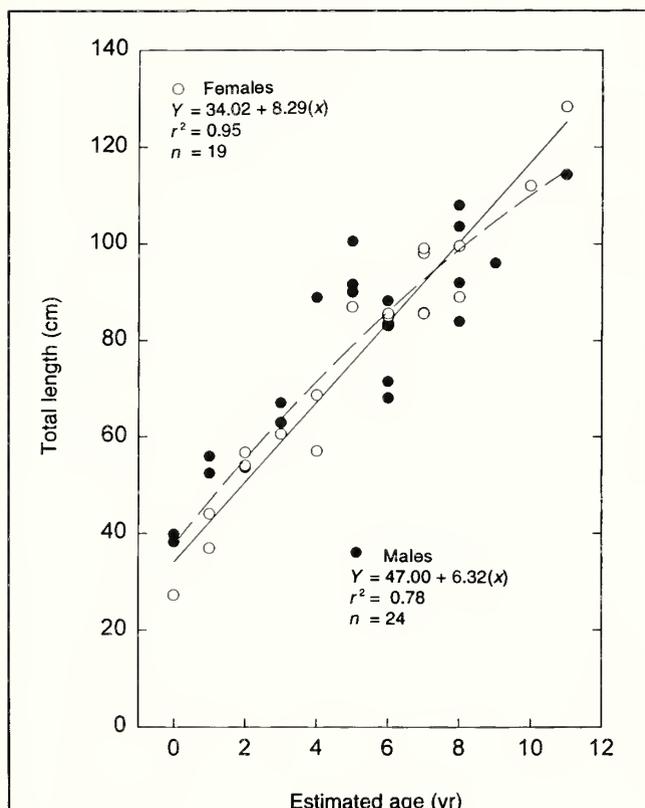


agreement  $\pm 3$  bands (2 guitarfish). Only bands in total agreement (from 43 guitarfish) were used in the final analysis.

The linear model best represented growth of combined sexes of guitarfish because the coefficient of determination was 0.90 for the linear regression, and 0.81 for the nonlinear von Bertalanffy curve (Fig. 7; Table 1). For females only, the linear regression and the von Bertalanffy curve produced similar values

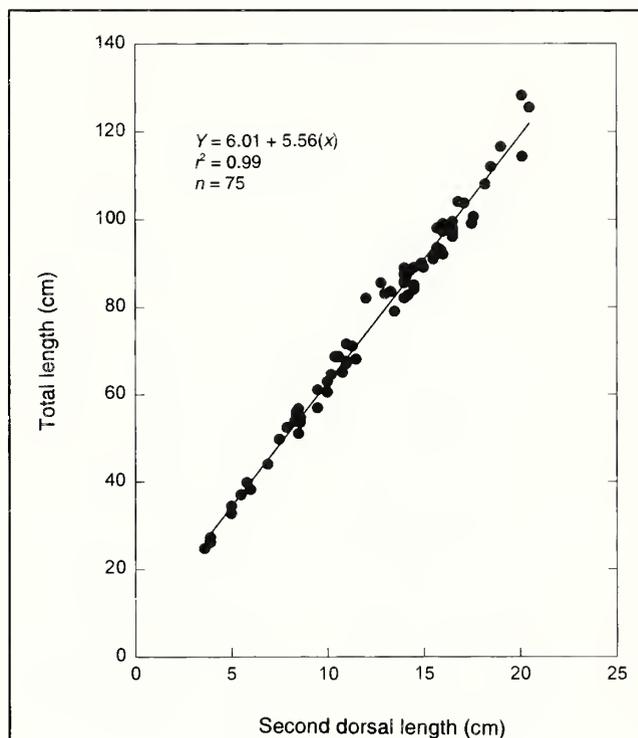
for the coefficient of determination ( $r^2=0.95$ , and  $r^2=0.94$ , respectively). For males, the linear regression also appeared to be a better predictor ( $r^2=0.78$ ) than the von Bertalanffy curve ( $r^2=0.70$ ; Table 1). Residuals for both the linear regression and the von Bertalanffy model (females and males) clustered evenly about both sides of the prediction lines. There was no reason to suggest any violation of homoscedasticity in either model.

If it is necessary to predict the total length of a specimen from fish markets using only the tail region of the guitarfish, the following equation is suggested (Fig. 8):



**Figure 7**

Growth of the guitarfish predicted by a linear regression (dotted line). The solid line represents a von Bertalanffy growth curve for the data. Equations are those used to calculate the regression.



**Figure 8**

Predictive relationship for total length of guitarfish based on their second dorsal fin length.

**Table 1**

A comparison of linear regression parameters and von Bertalanffy parameters for male (n=24) and female (n=19) guitarfish and for combined sexes (n=43).

	Linear regression parameters			von Bertalanffy parameters			
	Y-intercept	Slope	$r^2$	$L_{\infty}$	$k$	$t_0$	$r^2$
Female	34.02	8.29	0.95	594	0.016	-3.80	0.94
Male	47.00	6.32	0.78	142	0.095	-3.942	0.70
Female and male	43.33	6.90	0.90	228	0.047	-4.030	0.81

$$TL = 6.01 + 5.56(2D),$$

where  $TL$  = estimated total length of the guitarfish;  
and

$2D$  = second dorsal length (when  $2D > 3.5$  cm  
and  $< 20$  cm).

### Reproductive maturity

The smallest sexually mature female guitarfish was 99 cm TL and was estimated to be seven years old, based on vertebral band counts. Developing ovaries were present in 26 specimens from 40 to 99 cm TL. These individuals showed no evidence of previous birthing or egg follicles: uteri were thin walled and shell glands were not distinguishable from surrounding oviducts. Immature female guitarfish accounted for the majority of specimens taken (27 of 36).

A well-developed shell gland (nidimental gland) was present in mature shovelnose. Females with full uteri contained a case as described by Cox (1963) for *Rhinobatos*. In four individuals with full uteri, no developing embryos were seen in any of the specimens. These specimens contained either four or five yolks within the right or left egg case and, with the exception of one specimen, had nine total yolks per mature female. These four fish were captured in February (one), April (one), and June (two).

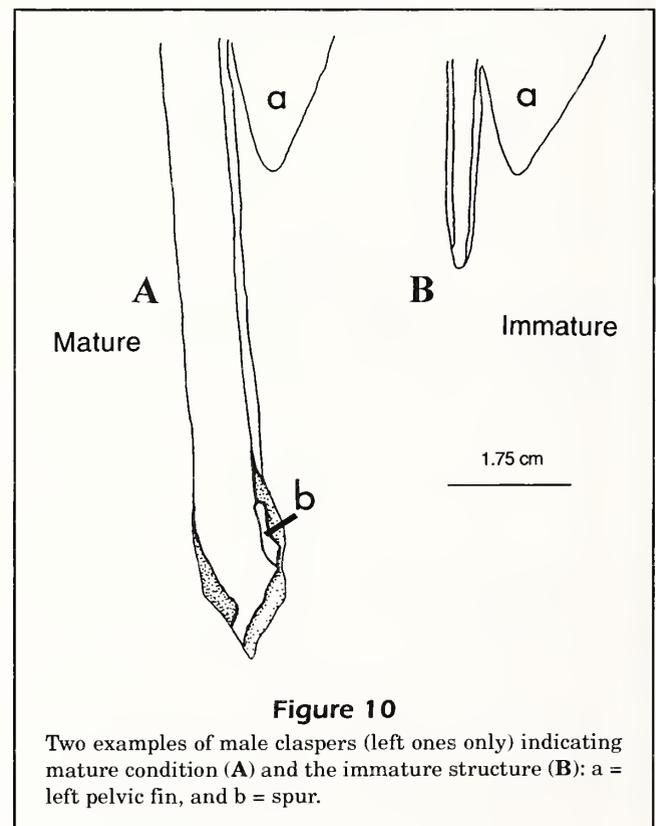
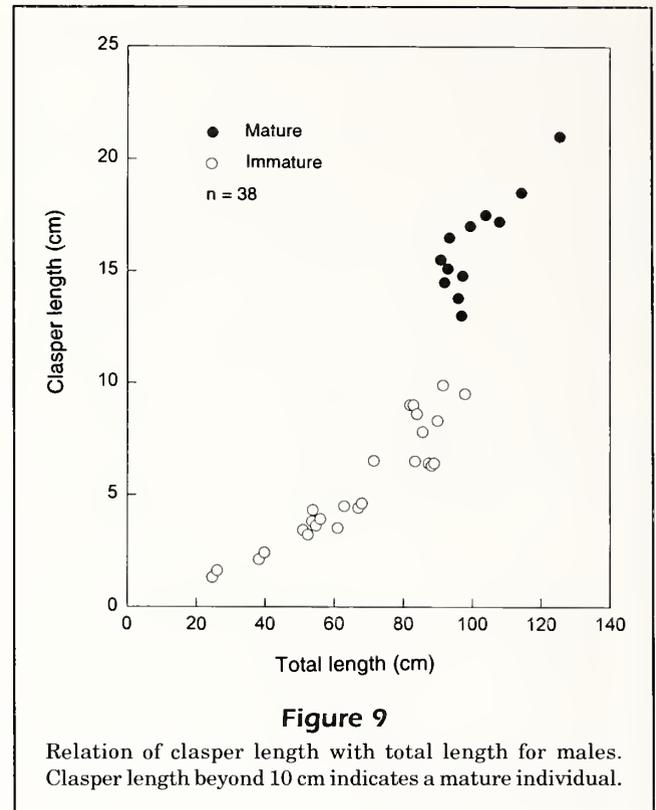
Male guitarfish reached maturity between 90 and 100 cm TL. At maturity there was an abrupt increase in clasper length and claspers extended well beyond the pelvic fin (Fig. 9). Claspers of mature males were at least 13 cm in length, and clasper width at maturity was at least 1 cm. A well-developed spur was present on both claspers in mature males and was not present in immature males (Fig. 10). Immature male squaloid sharks also lack spines (Applegate, 1967). Twelve of the 38 sampled were mature and 26 were immature.

### Discussion

#### Age and growth

The shovelnose guitarfish is best described as a slow-growing species typified by linear growth after parturition. Our total estimated age range (one to 11 years) for *R. productus* was the same that Lessa (1982) found for *R. horkelii*. Her specimens were also in the same size range as *R. productus* (20 to 120 cm). Rossouw (1984) found ages 0 to 6 years in *R. annulatus*, and his largest specimen was 99.3 cm.

Age estimates in this study were based on the assumption that one opaque and one translucent band



are formed annually. One verification procedure, examination of individuals held in captivity, provided support for the outer margin analysis; however, this analysis was based on only two specimens. The second verification procedure, outer margin analysis of field-caught specimens, indicated that band formation was dependent on season; however, there was no correlation between width of the outer margin and month. Early band formations at the margin can be difficult to detect with whole centra. To avoid this difficulty we tried sectioning the centra; however, we were unable to obtain readable sectioned centra. Others, such as Tanaka (1990) and Gruber and Stout (1983) have had success in sectioning vertebrae to view band formations. Therefore, we do not consider our verification procedure to be complete. It is evident that guitarfish have linear growth which might be somatic and not correlated with age of the guitarfish, as was suggested by Natanson et al. (1984) for *Squatina californica*. Further studies should be attempted to answer this question. Specifically, we suggest more tagging and injection studies to validate laboratory data.

### Reproductive maturity

We encountered a problem collecting large (>90 cm) females; it has been suggested by Baxter (1980) and Lane and Hill (1975) that individuals of this size are uncommon. Our largest female was 130 cm. In Almejas, Baja California Sur, México, Villavicencio-Garayzar (1993) reported that his largest captured female *R. productus* was 137 cm. Females in the present study were mature at  $\geq 99$  cm TL, whereas Villavicencio-Garayzar (1993) suggested that maturity of *R. productus* was at >70 cm TL. The youngest free-living guitarfish obtained was 23 cm TL, and it appears that the estimate of 15 cm (Eschmeyer et al., 1983) for newborn pups might be low. Melouk (1949) reported 16-cm specimens of *R. halavi* that still had sizable yolk attachments in utero. It is possible that Eschmeyer's measurements of 15 cm were taken from expelled premature pups. Expulsion of embryos can occur from stressed females (Pratt and Casey, 1990). Another possibility is that mortality is high in postpartum pups and many do not survive. Perhaps the smallest specimens that we sampled were first-year survivors. Rossouw (1984) suggested that the average length of *Rhinobatos annulatus* at birth was 23 cm TL and Dubois (1981) stated that embryos of *R. productus* at parturition were 23 cm. Villavicencio-Garayzar (1993) reported a free-swimming *R. productus* at 24 cm and suggested neonates are 20–24 cm. The first year class we collected (presumably represented as the smallest guitarfish we obtained) did not have any bands present beyond the birth mark. Many of the

young guitarfish were captured by otter trawls in the Belmont Shores area in Long Beach, CA.; it appears that this is a nursery ground for guitarfish.

Our estimates of nine offspring per female were also the mean number of offspring found by Villavicencio-Garayzar (1993) for *Rhinobatos productus* in Almejas, Baja California Sur, México. He found that *R. productus* females had a minimum of six pups and a maximum of 16. Additionally, Villavicencio-Garayzar (1995) found that *Zapterix exasperata* females contained a minimum of 4 and a maximum of 11 embryos (the most common numbers of embryos per individual were between 6 and 9).

Males showed the same size at maturity as males sampled by Dubois (1981). His males were all mature when TL exceeded 92 cm. No males in his study had clasper lengths in the range of 11 to 15 cm, indicating a definite size break in clasper length between immature and mature males. Our male guitarfish showed this same break between clasper lengths of 11 and 13 cm, and all males in our study were mature when TL exceeded 100 cm. Our smallest mature male was 91 cm. Both of our studies indicated a lack of individuals with clasper lengths in the 10–13 cm range, and Martin and Cailliet (1988) found a similar break in clasper lengths (between approximately 22–37 cm) in *Myliobatis californica*. This indicated to us that sexual maturity occurred within a distinct size range (TL) for males. Visual examinations of the claspers confirmed maturity; they were well developed and occasionally contained semen. Villavicencio-Garayzar (1993) found male *Rhinobatos productus* with sperm in their vasa deferentia at 63, 68, and 69 cm TL, but did not indicate a length at first maturity. For *Zapterix exasperata*, Villavicencio-Garayzar (1995) found males at 69 cm with semen.

Information from this research will provide a starting point for persons who may be interested in regulating guitarfish catch in the future. The information on size at first maturity for both males and females and the equation for estimating total length of guitarfish from tails sold to markets by fisherman will be useful management tools. Although the age estimates of the guitarfish are preliminary, total length (TL) at sexual maturity is most valuable. This information provides a starting point for evaluation of possible future size limitations for catches of guitarfish. We suggest further studies in order to attempt to age guitarfish over its entire population range.

### Acknowledgments

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# Food habits and energy values of prey of striped marlin, *Tetrapturus audax*, off the coast of Mexico

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The waters off the tip of the Baja California peninsula are good fishing grounds for striped marlin, *Tetrapturus audax* (Squire and Suzuki, 1990) because they offer a shallow thermocline and an abundant food supply (Hanamoto, 1974). Although striped marlin are an important game fish, few biological studies have been done on them. Most trophic studies on marlin species have simply identified and determined the relative importance of food consumed in a given geographic region and were based on few samples (Morrow, 1952; Hubbs and Wisner, 1953; Yabuta, 1953; La Monte, 1955; de Sylva, 1962; Williams, 1967; Koga, 1968).

Only two studies have been done off the coast of Mexico in the Pacific Ocean. Evans and Wares (1972) described the stomach contents of striped marlin caught at three locations off southern California and Mexico (San Diego, Mazatlan, and Buenavista) from 1967 to 1969. They found in Buenavista, the site closest to our study area, that the food for marlin consisted mainly of squid and fish, particularly red-eye round herring (*Etrumeus teres*) and chub mackerel (*Scomber japonicus*). In the second

study, Eldrige and Wares (1974) described food habits, seasonal abundance, and parasites of striped marlin caught in 1970 near the same locations. The differences found, in comparison with the first study were the absence of *S. japonicus* and a greater importance for three fish species: *E. teres*, black skipjack (*Euthynnus lineatus*), and oceanic puffer (*Lagocephalus lagocephalus*).

This paper provides information on food habits and energy content of the principal prey consumed by striped marlin in waters off the coast of the Baja California peninsula, Mexico.

## Materials and methods

Striped marlin were caught by trolling with live chub mackerel, *S. japonicus*, and jacks, *Caranx* spp., as bait or by jigs used by the sport fishing fleet. All fish were collected at approximately 22° 53'N, 109° 54'W (Fig. 1) near Cabo San Lucas, Baja California Sur (B.C.S.), Mexico. Stomachs were sampled in port, May 1988 to December 1989, by personnel of the Centro Interdisciplinario de Ciencias Marinas (CICIMAR), La Paz, B.C.S. Each

fish was weighed to the nearest kg and its length (eye fork length) measured to the nearest cm. Stomach contents were removed and fixed in 10% formalin. Prey were identified to the lowest possible taxon. Vertebral characteristics (e.g. number, position) were used to identify fish with the help of taxonomic keys (Clothier, 1950; Monod, 1968; Miller and Jorgensen, 1973). The fish collection of CICIMAR was also used for comparison and validation of identifications. For complete, undigested fish, the keys of Jordan and Evermann (1896–1900), Meek and Hildebrand (1923–28), Miller and Lea (1972), and Thomson et al. (1979) were used for identification. Crustacean prey were identified from exoskeleton remains with keys provided by Garth and Stephenson (1966) and Brusca (1980). Cephalopods were identified from mandibles with the keys of Clarke (1962, 1986), Iverson and Pinkas (1971), and Wolff (1982, 1984).

The stomach contents were enumerated ( $N$ ) and the volume ( $V$ ) measured to the nearest mL. These two measures and frequency of occurrence ( $FO$ ) were combined to calculate the index of relative importance ( $IRI$ ) of Pinkas et al. (1971) as

$$IRI = (\%N + \%V) \%FO.$$

$IRI$  is a commonly used measure that provides a more representative summary of dietary composition (Caillet et al., 1986).

A multivariate analysis of variance (MANOVA) was made on  $IRI$  values to examine differences in the relative importance of prey by season and between species. The treatment included only five seasons because the data in two seasons (summer and fall 1989) had too few values for statistical analysis (Table 1). The data were standardized following the formula

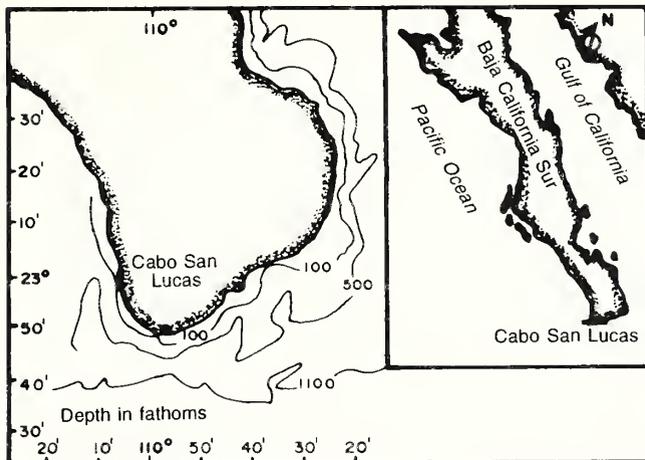


Figure 1

Map showing the location of the study area off the tip of Baja California.

$$x_i - X / SD,$$

where:  $x_i$  = the absolute IRI value of each prey species;  
 $X$  = the mean value of the IRI; and  
 $SD$  = standard deviation.

The caloric content of each prey, based on three samples obtained from stomach contents, was measured with a Parr 1241 adiabatic calorimeter and expressed as calories per gram of dry weight, wet weight, and ash-free dry weight following Phillipson (1964). One-way analysis of variance was used to evaluate differences between ash-free dry weight caloric values of particular prey. Also a post-hoc test  $T$ -method (Sokal and Rohlf, 1981) was used to compare the means of dry-weight caloric values.

The calories provided by each prey species were calculated by multiplying the values (calories/g wet weight) of each prey by the sum of their total contribution (weight) in the diet. To convert prey volumes to calories we assumed a density of 1.0 g/mL.

## Results

### Food habits

Striped marlin (403) were sampled. The mean postorbital length was  $177 \pm 15$  cm (standard deviation) and the mean weight was  $58.4 \pm 12.8$  kg. Of those specimens sampled, 27 (6.7%) had empty stomachs and 26 (6.5%) had regurgitated their stomach contents. A total of 33 prey taxa were identified that comprised fish, cephalopods, and crustaceans. Only 17 prey types could be identified to species (Table 2).

The most important prey by volume were fish (86.2%), including *S. japonicus* (25.7%), California pilchard, *Sardinops caeruleus*, (18.8%), and *E. teres* (10.2%). Cephalopods made up 12.8% of the total volume, and jumbo flying squid, *Dosidicus gigas*, was particularly important (11.3%). Crustaceans, mainly red crab, *Pleuroncodes planipes*, represented only 1% of the total volume.

A total of 2,679 organisms were enumerated, 68.6% of which were fish, 21.3% cephalopods, and 10.2% crustaceans. The dominant fish prey by number were *S. caeruleus* (18.9%), *S. japonicus* (14.3%), and Pacific hake, *Merluccius productus*, (9.6%). The cephalopod *D. gigas* represented 14.9%, and *Argonauta* spp. 3.0% of the total stomach contents by number. *Pleuroncodes planipes* was the most abundant crustacean, representing 7.2% of the total number of food items.

In frequency of occurrence, fish were the most important food in the diet of striped marlin (93.4%), particularly *S. japonicus* (45.4%), *S. caeruleus* (27.7%), and *E. teres* (12.6%). Cephalopods occurred in 32.9% of the samples; and *D. gigas* was the most common species (28.3%). Crustaceans, mainly *P. planipes*, occurred in 6.3% of samples.

According to the IRI, fish were the most important prey (80.7%) of striped marlin, followed by cephalopods (18.5%), and crustaceans (0.8%). *Scomber japonicus*, *S. caeruleus*, and *D. gigas* were the most important fish prey (Fig. 2).

Relative importance of several prey varied seasonally (Table 1). During 1988, fish were the most important prey in spring and fall, cephalopods the most important prey in summer. In spring 1988, *S. caeruleus* was the most important fish in the diet, followed by *S. japonicus* and *E. teres*. In summer 1988, the most important species was *D. gigas*, followed by the fish *Selar crumenophthalmus*, *S. japonicus*, and *E. teres*. In fall 1988, the highest IRI values were for *S. japonicus*, *D. gigas*, *E. teres*, and *M. productus*.

During 1989, fish were the most important prey in all seasons, followed by cephalopods and crustaceans. In winter, the dominant species were *S. japonicus*, *M. productus*, and *S. caeruleus*. In spring, *S. japonicus*, *D. gigas*, *S. caeruleus*, and *E. teres* were the most important species. In summer, *Caranx caballus* was the most important prey. In fall, the highest IRI values were for *S. caeruleus*, *S. japonicus*, and *Decapterus hypodus*. The MANOVA showed no significant differences among seasons in the IRI values of food groups consumed ( $F=1.96$ ;  $df=4$ ;  $P=0.11$ ). However, when we considered taxa consumed (33 recorded), we found significant differences ( $F=17.6$ ;  $df=32$ ;  $P<0.005$ ), probably caused by the greater

Table 1

Summary of food categories in stomach contents of striped marlin from Cabo San Lucas, B.C.S., Mexico, expressed as percentages based on frequency of occurrence (FO), number (*n*), volume (Vol.), and index of relative importance (IRI).

Prey	FO	% FO	<i>n</i>	% <i>n</i>	Vol.	% Vol.	IRI	% IRI
<b>Mollusca</b>								
Cephalopoda								
Teuthoidea								
Enoploteuthidae								
<i>Abraliopsis affinis</i>	12	3.43	46	1.72	1,254	0.65	8.13	0.19
Ommastrephidae								
<i>Dosidicus gigas</i>	99	28.3	399	14.9	21,866	11.3	740.37	17.8
<i>Stenoteuthis oualaniensis</i>	15	4.28	34	1.27	688	0.35	6.93	0.17
Octopoda								
Octopodidae								
<i>Octopus</i> spp.	4	1.14	11	0.41	131	0.07	0.55	0.01
Argonautidae								
<i>Argonauta</i> spp.	13	3.71	80	2.99	819	0.42	12.65	0.3
Total			570	21.29	24,758	12.79	768.63	18.47
<b>Arthropoda</b>								
Crustacea								
Amphipoda	2	0.57	22	0.82	13.5	0.01	0.47	0.01
Isopoda	3	0.86	8	0.3	3	0	0.26	0
Stomatopoda								
Squillidae								
<i>Squilla</i> spp.	1	0.28	1	0.04	15.1	0	0.01	0
Euphausiacea	3	0.86	48	1.79	11	0.05	1.55	0.04
Decapoda								
Galatheidae								
<i>Pleuroncodes planipes</i>	14	4	193	7.2	1,929	0.99	32.76	0.79
Total			272	10.15	1,971.6	1.05	35.05	0.84
<b>Chordata</b>								
Osteichthyes								
Clupeiformes								
Clupeidae	30	8.57	12	0.44	3,206	1.65	17.99	0.43
<i>Etrumeus teres</i>	44	12.57	199	7.42	19,681	10.16	220.98	5.31
<i>Ophistonema libertate</i>	10	2.86	27	1.01	4,985	2.57	10.24	0.25
<i>Sardinops caeruleus</i>	97	27.7	507	18.92	36,492	18.83	1,046.05	25.15
Gadiformes								
Merluccidae								
<i>Merluccius productus</i>	19	5.43	257	9.59	16,619	8.58	98.66	2.37
Cyprinodontiformes								
Belonidae								
<i>Strongylura</i> spp.	1	0.28	1	0.04	340	0.17	0.06	0
Syngnathiformes								
Fistulariidae								
<i>Fistularia</i> spp.	16	4.57	38	1.42	5,065	2.61	18.42	0.44
Scorpaeniformes								
Triglidae								
<i>Prionotus</i> spp.	1	0.28	1	0.04	10	0.01	0.01	0
Perciformes								
Serranidae	1	0.28	2	0.07	245	0.13	0.06	0
Carangidae	10	2.86	15	0.56	2,111	1.09	4.72	0.11
<i>Caranx caballus</i>	11	3.14	15	0.56	1,988.5	1.02	4.96	0.12
<i>Caranx hippos</i>	9	2.57	10	0.37	796	0.41	2	0.05
<i>Decapterus hypodus</i>	18	5.14	87	3.25	8,365	4.32	38.91	0.93
<i>Selar crumenophthalmus</i>	16	4.57	31	1.16	3,337	1.72	13.16	0.32
Coryphaenidae								

continued on next page

Table 1 (continued)

Prey	FO	% FO	n	% n	Vol.	% Vol	IRI	% IRI
<i>Coryphaena hippurus</i>	1	0.28	1	0.04	180	0.09	0.04	0
Mugilidae								
<i>Mugil</i> spp.	1	0.28	1	0.04	290	0.15	0.05	0
Sphyraenidae								
<i>Sphyraena ensis</i>	1	0.28	2	0.07	680	0.35	0.12	0
Scombridae								
<i>Auxis</i> spp.	10	2.85	83	3.09	7,870.5	4.06	20.38	0.49
<i>Scomber japonicus</i>	159	45.43	382	14.26	49,778.5	25.69	1,814.93	43.63
Tetraodontiformes								
Balistidae								
<i>Balistes polylepis</i>	18	5.14	164	6.12	4,844.5	2.5	44.31	1.06
<i>Xanthichthys mento</i>	1	0.28	1	0.04	110	0.06	0.03	0
Diodontidae								
<i>Diodon</i> spp.	1	0.28	1	0.04	27	0.01	0.01	0
Total			1,837	68.55	167,021	86.18	3,356.09	80.66
Unidentified organic matter	1	0.28			145	0.07	0.02	0

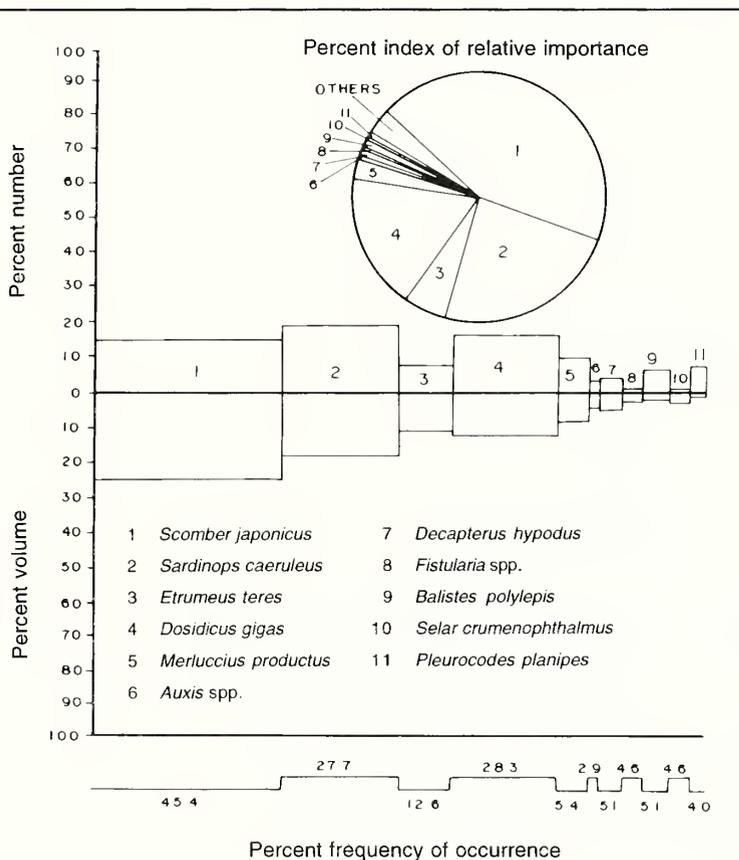


Figure 2

The major prey species found in the stomachs of striped marlin presented as percentages of number of individuals, volume, frequency of occurrence, and IRI.

number of five prey species: *D. gigas*, *S. japonicus*, *S. caeruleus*, *E. teres*, and *M. productus*.

### Calorimetric analysis

The energy content of the most important prey of striped marlin as wet, dry, and ash-free dry weights, is given in Table 3. Values ranged from 3.42 kcal/g dry weight for red crab, *P. planipes*, to 6.14 kcal/g dry weight for the cornet fish, *Fistularia* spp. The ANOVA showed that the caloric values of the 11 most important prey were significantly different ( $F=904.3$ ;  $df=10$ ;  $P=2.3E-26$ ). When the means of the caloric values were compared by *T*-method, a significant difference was obtained ( $\alpha=0.05$ ) (Fig. 3).

Caloric percentages of the 11 major prey types (Fig. 4), indicate two species, *S. japonicus* (32.4%) and *S. caeruleus* (21.2%), contributed 53.7% of the total calories to the diet of striped marlin.

### Discussion

#### Food habits

Previous studies have shown that striped marlin mainly consume prey that school near the surface. Such prey are generally

fish of the families Engraulidae (Hubbs and Wisner, 1953; de Sylva, 1962; Evans and Wares, 1972; Holts and Bedford, 1990), Clupeidae (Hubbs and Wisner, 1953; Koga, 1968), Scombridae (Backer, 1966; Evans and Wares, 1972), Scomberesocidae (Morrow, 1952; Hubbs and Wisner, 1953), and Carangidae (de Sylva, 1962; Backer, 1966; Evans and Wares, 1972), and some cephalopods (Morrow, 1952; Yabuta, 1953; La Monte, 1955; de Sylva, 1962; Williams, 1967; Eldrige and Wares, 1974).

We also found that striped marlin feed on demersal species, such as *M. productus* and searobins,

*Prionotus* spp, as well as on benthic species, such as mantis shrimp, *Squilla* spp. Other authors have found occasional prey from benthic or reef habitats in striped marlin (Morrow, 1952; Backer, 1966; Williams, 1967; Evans and Wares, 1972; Eldrige and Wares, 1974); thus, it appears that striped marlin move to the bottom to prey on benthic organisms.

Our results show the importance of seasonal prey availability off Cabo San Lucas. During spring 1988, *S. caeruleus* was the main prey of striped marlin, whereas in fall and winter, *S. japonicus* was more important. The latter is probably more abundant in

**Table 2**

Seasonal absolute values of the index of relative importance (IRI) of the stomach contents of striped marlin from Cabo San Lucas, B.C.S., Mexico (WI = Winter, SP = Spring, SU = Summer, FA = Fall).

Species	1988 SP n = 55	1988 SU n = 34	1988 FA n = 92	1989 WI n = 56	1989 SP n = 67	1989 SU n = 11	1989 FA n = 35
<b>Cephalopoda</b>							
<i>Abraliopsis affinis</i>	0	0	6.13	160.62	0.82	0	0
<i>Dosidicus gigas</i>	21.08	2,637.22	480.66	59.48	1,031.04	0	672.83
<i>Stenoteuthis oualaniensis</i>	12.21	8.58	24.28	0.97	1.79	0	0
<i>Octopus</i> spp.	1	1.99	0.31	0	2.49	0	0
<i>Argonauta</i> spp.	4.14	42.34	38.08	2.04	0	0	0
<b>Crustacea</b>							
Amphipoda	0	0	0	0	0	0	33.57
Isopoda	0	0	1.05	0	0	0	0
<i>Squilla</i> spp.	0	0	0	0	0.45	0	0
Euphausiacea	10.32	21.49	0	0	3.04	0	0
<i>Pleuroncodes planipes</i>	22.56	3.09	104.10	16.99	13.50	628.17	0
<b>Osteichthyes</b>							
Clupeidae	49.08	27.96	9.59	18.31	33.27	0	0
<i>Etrumeus teres</i>	368.43	346.57	357.95	67.47	369.22	0	51.76
<i>Sardinops caeruleus</i>	8,049.39	30.58	102.05	473.74	739.77	644.94	2,072.04
<i>Opisthonema libertate</i>	0	0	0	0	295.76	0	0
<i>Merluccius productus</i>	0	0	203.19	855.85	49.07	0	0
<i>Strongylura</i> spp.	0	0	0	2.27	0	0	0
<i>Fistularia</i> spp.	0	0	83.03	40.63	0	0	51.76
<i>Prionotus</i> spp.	0	0	0	0.50	0	0	0
Serranidae	0	0	0.81	0	0	0	0
Carangidae	0	74.97	1.97	27.56	1.55	0	0
<i>Caranx caballus</i>	25.30	27.81	4.17	0	0	780.10	0
<i>Caranx hippos</i>	4.48	0	0.59	2.86	0	0	19.88
<i>Decapterus hypodus</i>	54.50	58.56	1.62	0	0	0	1,036.23
<i>Selar crumenophthalmus</i>	1.60	446.19	28.31	2.17	0	0	0
<i>Coryphaena hippurus</i>	0	0	0	1.41	0	0	0
<i>Mugil</i> spp.	1.87	0	0	0	0	0	0
<i>Sphyrna ensis</i>	0	0	0	0	0	586.04	0
<i>Auxis</i> spp.	2.69	8.76	131.51	22.63	0	0	0
<i>Scomber japonicus</i>	1,299.15	351.06	1,957.42	4,324.37	2,117.20	0	1,073.73
<i>Balistes polylepis</i>	0	0	115.06	0	0	0	864.20
<i>Xanthichthys mento</i>	0	0	0.37	0	0	0	0
<i>Diodon</i> spp.	0	2.09	0	0	0	0	0
Unidentified organic matter	0	0	0.07	0	0.03	0	0

the area, as happens in waters off southern California where fall and winter catches present large numbers of chub mackerel (Roedel, 1952). Both *S. japonicus* and *S. caeruleus* were found in some stomachs, but this finding is not surprising because *S. japonicus* is abundant off Baja California and in the Gulf of California (MacCall, 1973), where mixed populations of *S. japonicus* and *S. caeruleus* are often found (Kramer, 1969). During summer, the

greater numbers of the jumbo squid *D. gigas* in striped marlin stomachs are not surprising because this squid is very common in waters from 200 to 2,000 m in depth off Cabo San Lucas (Sato, 1976). This species, from subtropical and tropical waters, undergoes long, large seasonal migrations. The presence of *D. gigas* can be associated with tropical water masses at the entrance of the Gulf of California (25° to 29°C) and with the occurrence of prey species (pilchards and mackerels) in this area (Erhardt et al., 1986).

Our results, compared with those of studies in other areas, showed similar types of prey consumed by striped marlin. Previous studies found that striped marlin commonly feed on clupeids, scombrids, jacks, and cephalopods. Striped marlin in New Zealand ate saury and squid (Morrow, 1952). Baker (1966), in the same area, found that jacks and cephalopods were the main prey. In Peru and Chile, La Monte (1955) and de Sylva (1962) found cephalopods, engraulids, and jacks in the stomach contents of striped marlin. In East Africa, Williams (1967) found cornet fish (*Fistularia* sp.), bullet mackerel (*Auxis thazard*), and unidentified squid. Fish of the families Alepisauridae and Clupeidae are common in the Tasman Sea (Koga, 1968). Around the Bonin Islands, striped marlin ate *Gempylus* sp., *Pseudoscopelus* sp., *Alepisaurus* sp., *Ostracion* sp., cephalopods, and crustaceans (Yabuta, 1953). In the eastern Pacific Ocean, Hubbs and Wisner (1953) found that striped marlin consumed saury, anchovy, and sardine.

Evans and Wares (1972) and Eldrige and Wares (1974) found that the most important prey of striped marlin off Buenavista, Mexico, included the fish *E. teres*, *Euthynnus lineatus*, *Lagocephalus lagocephalus*, and *S. japonicus*, as well as the squid *D. gigas*. These findings are similar to those of our study, even though the relative importance of the main species differed; e.g. in our study *S. japonicus* and *S. caeruleus* were more important than *E. teres*, and squid were less important. These results indicate that the prey composition of striped marlin probably has not changed drastically off the coast of

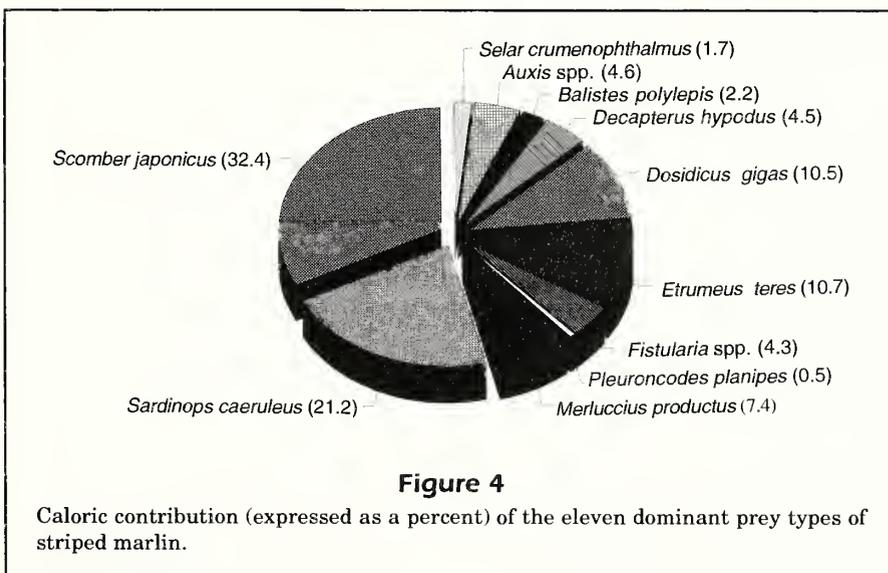
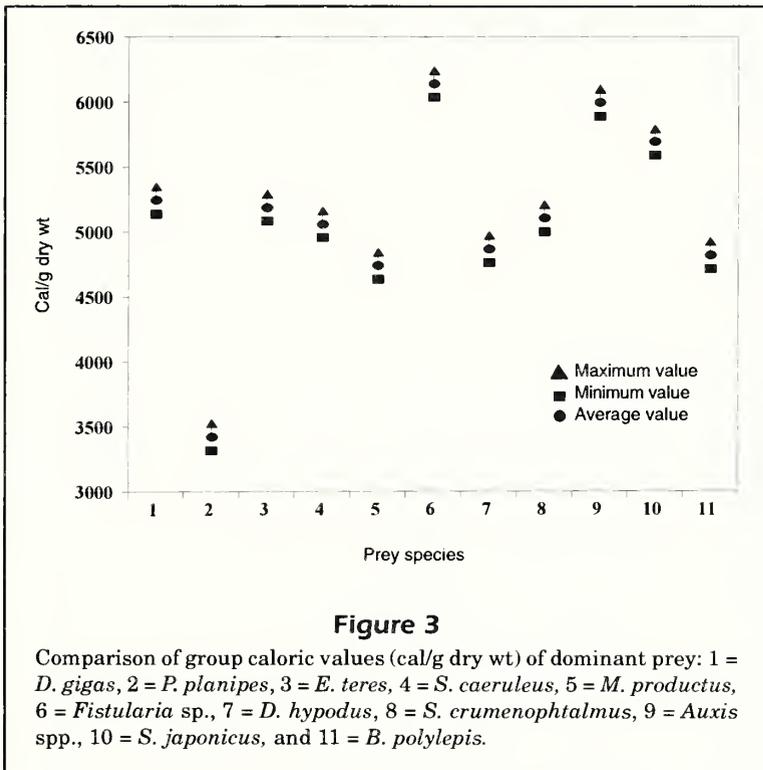


Table 3

Mean and standard deviation (SD) caloric values, water content, and ash content of prey in the diet of striped marlin.

Prey	% Water	SD	% Ash	SD	Kcal/g wet wt	SD	Kcal/g dry wt	SD	Kcal/g ash-free dry wt	SD
<b>Cephalopoda</b>										
<i>Dosidicus gigas</i>	70.02	0.97	2.95	0.04	1.57	0.08	5.24	1.20	5.40	0.13
<b>Crustacea</b>										
<i>Pleuroncodes planipes</i>	72.66	0.05	4.67	0.03	0.94	0.01	3.42	0.11	3.59	0.01
<b>Osteichthyes</b>										
<i>Etrumeus teres</i>	64.34	1.10	3.78	0.04	1.80	0.05	5.06	0.03	5.26	0.01
<i>Sardinops caeruleus</i>	65.92	0.38	2.71	0.01	1.77	0.02	5.19	0.09	5.33	0.01
<i>Merluccius productus</i>	68.92	1.01	5.60	0.01	1.47	0.06	4.74	0.57	5.02	0.06
<i>Fistularia</i> spp.	64.44	0.72	13.05	0.07	2.18	0.04	6.14	0.11	7.06	0.01
<i>Decapterus hypodus</i>	64.95	0.34	6.09	0.03	1.79	0.01	5.11	0.12	5.44	0.01
<i>Selar crumenophthalmus</i>	68.64	0.60	7.00	0.01	1.53	0.03	4.87	0.02	5.24	0.00
<i>Auxis</i> spp.	66.31	0.83	1.53	0.03	1.92	0.05	5.69	0.28	5.78	0.03
<i>Scomber japonicus</i>	63.90	0.10	3.16	0.03	2.16	0.01	5.99	0.01	6.19	0.00
<i>Balistes polylepis</i>	69.38	0.54	2.83	0.15	1.48	0.02	4.83	0.14	4.97	0.01

Mexico in the last two decades. Cabo San Lucas appears to be an area with stable prey populations, probably the result of prevailing oceanographic conditions (Roden and Groves, 1959; Alvarez, 1983).

In waters off Baja California, the thermocline is generally shallow and there is a correspondingly high standing crop of zooplankton (Brandhorst, 1958). Laevastu and Rosa (1963) suggested that the shallow thermocline promotes a high standing crop of zooplankton and thus increases the production of small foraging organisms, which in turn may result in the aggregation of top predators. It is likely that the seasonal shifts in good fishing areas for striped marlin coincide with shallow thermocline areas. Feeding ecology, however, may play a major role in determining the distribution and abundance of striped marlin in some areas.

### Calorimetric analysis

Of the eleven most important prey analyzed, *P. planipes* had a significantly low caloric content, common in crustaceans (Golley, 1961; Slobodkin and Richman, 1961; Thayer et al., 1973). Paine (1964) concluded that the presence of calcium carbonate and calcium phosphate in cuticle and valves was the cause of their low caloric value.

We found our results agree well with values from other studies. Thayer et al. (1973) found a caloric value of 5.74 kcal/g dry weight and 1.05 kcal/g wet weight for the squid *Loligo brevis*. For crustaceans, caloric values ranged between 2.12 and 6.03 kcal/g dry weight (average value: 5.74 kcal/g dry weight,

range: 0.80–1.48 kcal/g wet weight). They also found fish contained 4.39 to 6.0 kcal/g dry weight and 0.67 to 1.57 kcal/g wet weight. Cortes and Gruber (1990) estimated the energy content of prey of lemon shark, *Negaprion brevirostris*, and found caloric values of 4.81 kcal/g dry weight and 0.68 kcal/g wet weight for cephalopods, *Octopus* spp. Crustaceans of the genus *Callinectes* yielded 3.2 kcal/g dry weight and 1.04 kcal/g wet weight. For fish, Cortes and Gruber found values that ranged from 3.38 to 4.73 kcal/g dry weight and 0.96 to 1.86 kcal/g wet weight.

Our results show that pelagic fishes and cephalopods yielded more than 80% of the caloric content in the diet of striped marlin. However, if we take into account that more than 70% of the stomachs were less than full and that the predatory capacity of striped marlin allows them to consume large quantities of prey in a short time, as is the case with yellowfin tuna, *Thunnus albacares* (Olson and Boggs, 1986), a pelagic species with feeding habits similar to those of marlin in the eastern Pacific Ocean, we believe the estimated caloric values underestimated actual energy intake.

In summary, we consider that striped marlin is a generalist as a predator and has a high predatory capacity, foraging mainly on schools of epipelagic organisms in neritic and oceanic zones.

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# Note on plankton and cold-core rings in the Gulf of Mexico

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Data from ship and aircraft hydrographic surveys, supplemented with data from current meter moorings and drifters, have demonstrated that one or more cyclonic circulation features, 100–200 km in diameter, are often present in the Gulf of Mexico. In the eastern Gulf, these cold-core rings (CCR's) occur in close association with the Loop Current (LC) (Lee et al., 1994), and in the central and western Gulf, they are companions of the anticyclonic eddies that are shed during northern excursions of the LC (Hamilton, 1992). Cyclone-anticyclone dipoles and cyclone-anticyclone-cyclone triads have been described (Lewis and Kirwan, 1985; Rouse et al., 1994; Vidal et al., 1994). Temperature-salinity relationships document that cyclones and anticyclones in the Gulf of Mexico form from the same water types, but convergence flow within the anticyclones causes the surface waters of these gyres to be regions of low production. The upper 100 m are depleted in nitrate and chlorophyll concentrations, primary productiv-

ity, and zooplankton biomass are generally extremely low (Biggs, 1992). In contrast, the companion cyclones are mesoscale regions of divergence flow. From nutrient-chlorophyll data collected during several cruises when Gulf of Mexico CCR's were tracked, Biggs et al. (1988) hypothesized that cyclones were regions of locally high primary productivity which could support elevated stocks of zooplankton.

In March 1993, a CCR was detected by remote sensing of the western central Gulf of Mexico, and the opportunity arose to study its hydrographic and biological signature as RV *Gyre* transited this feature while proceeding along a TOPEX ground track. This mesoscale cyclonic circulation was visible in remote sensing data as a region of surface temperatures 1–2°C cooler than the adjacent oceanic surface waters (Fig. 1; Table 1) and as an elliptical local depression in sea surface height (SSH) (–15 to –20 dyn cm of SSH anomaly; see Table 1). Expendable bathythermographs (XBT's), dropped to

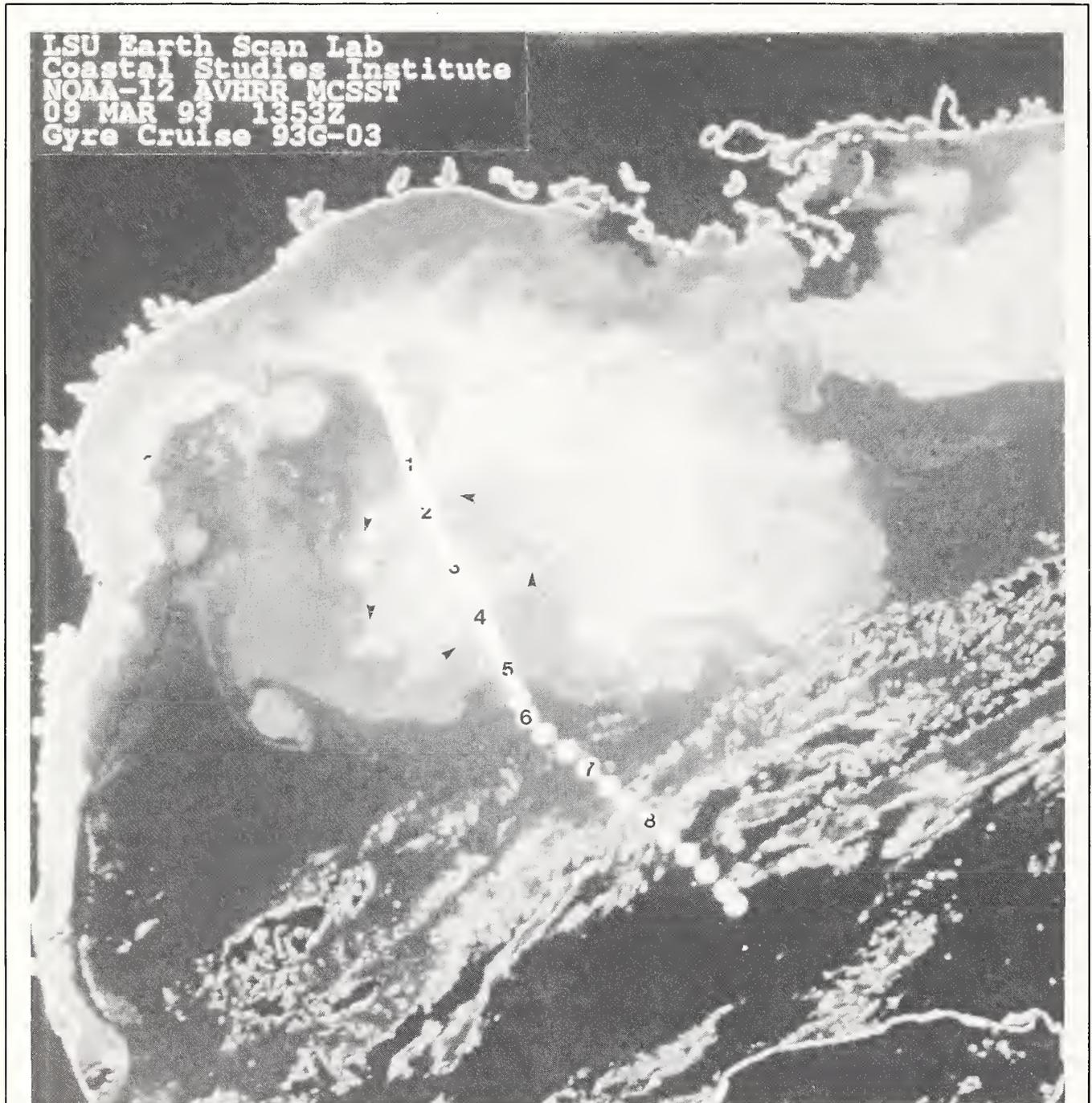
profile isotherm depths in the upper 760 m, resolved strong doming of subsurface isotherms within this CCR (Fig. 2), and *Gyre*'s hull-mounted 153 kHz acoustic Doppler current profiler (ADCP) confirmed that cyclonic near-surface currents were associated with this feature. Both the amplitude and direction of these ADCP-measured currents were found to be in close agreement with those computed from the along-track horizontal geopotential gradient in relation to a reference level of 800 db: a low of 88 dyn cm in the interior of the CCR, versus  $\geq 102$  dyn cm to the north and south (Table 1). This –14 cm SSH gradient between interior and periphery of the CCR over a distance of 100 km should have driven a cyclonic transport (relative to 800 db) of 6–7 Sverdrup, with mixed-layer velocities of 40–60 cm/s (see p. 165–166 in Texas A&M<sup>1</sup>). Altimeter-derived dynamic height anomalies from TOPEX Cycle 18, which flew over the ship's track just as *Gyre* completed the XBT survey, showed agreement with the hydrographic estimates to better than 2 cm residual mean squares difference with respect to a corrected along-track mean surface, which is within the generally accepted error range for altimeter measurements (Leben et al., 1993). A comparison with TOPEX Cycle 17 data from 10 days earlier also demonstrates the presence of this cyclone (see Fig. 2 in Leben et al., 1993).

Time constraints did not allow us to divert the ship to make a more detailed hydrographic survey of the CCR or to stop to make time-series measurements. However, we were

<sup>1</sup> Texas A&M University. 1993. Ship-of-opportunity hydrographic data from R/V *Gyre* cruise 93G-03. Tech. Rep. 93-04-T, Dep. Oceanography, TAMU, College Station, TX, 216 p. Available from NTIS, Springfield, VA: PB94-123957.

able to slow the vessel eight times for 15–20 min periods for net tows in order to collect zooplankton at three stations within and five outside the CCR for comparison with ADCP acoustic backscatter inten-

sity data logged while these tows were made. The ADCP acoustic backscatter intensity data were collected according to the methods described by Flagg and Smith (1989) and Zhou et al. (1994).



**Figure 1**

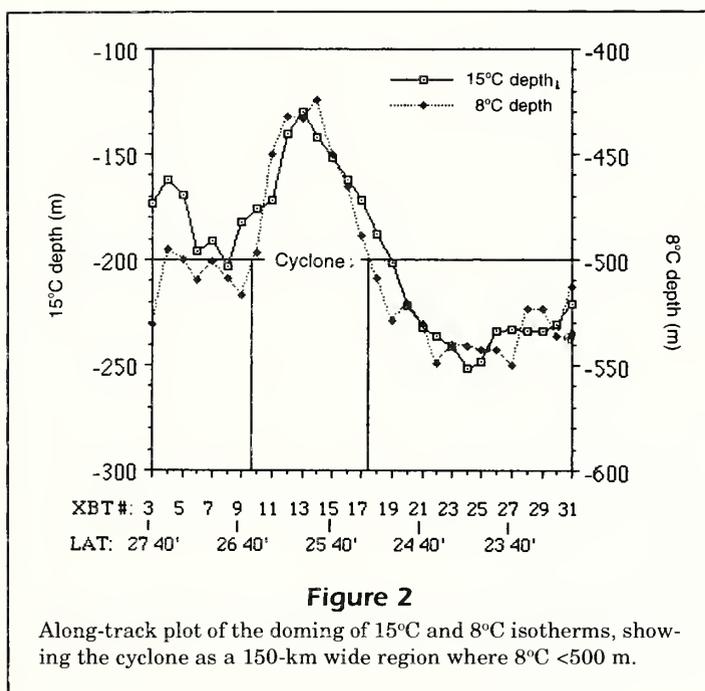
Analysis of NOAA-12 advanced very-high-resolution radiometer satellite imagery of sea surface temperatures (SST) processed by Louisiana State University. Circles give the location of the 33 XBT stations; the numbers inside these circles designate where zooplankton tows 1–8 were made. Lighter grey shades represent lower SST; the CCR is visible as a region of locally cooler surface temperatures encircling XBT's 10–17 (zooplankton tows 2–4). Arrowheads show the expected counter-clockwise circulation in CCR periphery.

The plankton tows were made with an open net of 333- $\mu\text{m}$  mesh and 1 m in diameter, at every 3rd XBT site beginning at 27°00'N. The net was outfitted with an impeller-type flowmeter (General Oceanics) that allowed the volume of water fished to be determined upon recovery of the net. In 15–20 min oblique tows to 100 m depth, volumes of water fished ranged from 450 to 800  $\text{m}^3$ . Collections were preserved in a 4% formaldehyde solution buffered with borax, and then bulk sample displacement volume was measured according to the method of Ahlstrom and Thraillkill (1960). Four of the 8 tows were made during daylight hours and the other 4 were made at night. Tow 1 was made in daylight outside and to the northwest

of the CCR, whereas tows 2–4 were at night, within the CCR. Tows 5–7 were daylight tows outside and to the southeast of the CCR, and tow 8 the following night was also outside and to the southeast of the CCR. Because only nighttime tows were able to be made in the CCR, we chose to enumerate the taxonomic composition of all eight samples for three groups of macrozooplankton that are well known to exhibit diel vertical migration (Gasca et al., 1995). Each sample was split 1:4 with a Folsom plankton splitter and then euphausiids, thecosome pteropods, and siphonophores were enumerated to species at the Centro de Investigaciones Quintana Roo.

## Results

Zooplankton biovolume averaged 2.4-fold higher in nighttime tows than in daytime tows (90 versus 38  $\text{mL}/1,000 \text{ m}^3$ ; see Table 2). This elevation of stock at night reflects greatly increased numbers of euphausiids at night, for most of the euphausiid species present in the western Gulf of Mexico perform vertical migratory patterns during a day-night cycle. During the night hours, these euphausiid species can be collected in the upper 200 m (Mauchline, 1980). However, the numbers and kinds of euphausiids present at night inside versus outside the CCR were quite different: 56% of the number of euphausiids inside the CCR were species of the genus *Euphausia*, whereas 63% of the individuals in the night tow outside the CCR belonged to two species of the smaller-size genus *Stylocheiron*. Moreover, euphausiid species of the genus *Euphausia* at night were, on average, 1.8-fold more abundant within the CCR than outside (321 individuals/ $1,000 \text{ m}^3$  inside,



**Table 1**

Surface temperature, mixed layer (ML) depth, temperature at 100 m, and the calculated dynamic height (relative to 800 db) for stations where plankton tows were made.

Plankton Tow	Local Time	XBT station	Temp (°C) at surface	Depth (m) to reach surface temp. minus 1°C (= ML depth)	Temp (°C) at 100 m	Dynamic height (cm)
1	15:52–16:09	7	23.24	54	19.7	102
2	19:23–19:38	10	22.34	72	19.2	97
3	23:11–23:27	13	21.50	75	17.8	88
4	03:08–03:23	16	21.75	71	19.0	94
5	07:08–07:19	19	22.50	99	21.4	106
6	12:11–12:26	22	23.62	98	22.4	115
7	16:08–16:25	25	23.39	112	22.5	113
8	21:17–21:34	28	23.36	95	21.9	111

versus 179 individuals/1,000 m<sup>3</sup> outside), the most abundant being *E. tenera*, *E. mutica*, and *E. americana*. Species richness of euphausiids was also greater inside the CCR than outside: five species (*Euphausia pseudogibba*, *E. brevis*, *Nematoscelis atlantica*, *Thysanopoda monoacantha*, and *Nematobrachion flexipes*) were found only in collections made inside the CCR. Details are available from the authors in a 3-page table. We speculate that the presense of the later three mesopelagic euphausiid species within the CCR, but not recorded outside the CCR, reflects the extension of their upper vertical distribution limits: where cold water domed shallower than 100 m, these mesopelagic species reached up into the zone where our nets collected samples at night.

We have calculated a mean acoustic backscatter intensity (ABI) 0–200 m by time-averaging ADCP data from the 15–20 minute periods when net tows were made. The ADCP was calibrated, as explained by Zimmerman (1993), with mean ABI expressed as dB re(M $\times$ 4 $\pi$ )<sup>-1</sup>. We also computed the integrated ABI (IABI): the amount of backscatter that was greater than the grand mean of -74 dB for the upper 200 m, bin by bin, from the 8–12 m bin to the 96–100 m bin) to provide a summary number for comparison with wet displacement volume of zooplankton collected from 0 to 100 m in the net tows. Figure 3 summarizes the mean ABI during the ensembles when net collections were being made. These acoustic data have been corrected for sound attenuation with depth, which was modeled from the *T/Z* relationship at each XBT station. Sub-surface regions of locally intensified return (locally higher backscatter) are presumed to be local concentrations of biological scatterers. Although these regions of locally enhanced backscatter were concentrated into the vertical range of 60–100 m during the day, they reached closer to the surface and occurred over a greater vertical range of the water column at night. The ABI data, however, are not sufficient to distinguish whether at night euphausiids were more abundant and more species rich within the CCR than without.

## Discussion

In the decade since Iles and Sinclair (1982) recognized the existence of larval retention zones caused by oceanographic features, the relations between stocks of phytoplankton, zooplankton, larval nekton, and frontal zones have been an area of intense research. For example, it is now well known that local aggregations of phytoplankton can develop along and within week-long meanders and eddies in the Gulf Stream (Lee et al., 1991) and that elevated fish stocks often co-occur in these frontal disturbances (Atkinson and Targett, 1983). In the Gulf of Mexico, frontal zones at the periphery of meanders and eddies that are seaward of the continental margin are typically expressed as sharp gradients in temperature. These may have secondary expression as gradients in salinity, particularly in local convergences that can entrain low-salinity water and transport it off shelf as plumes or jets. For example, Biggs and Muller-Karger (1994) reported that some cyclone-anticyclone geometries in the Gulf of Mexico create flow confluence zones that can transport high-chlorophyll shelf water seaward several hundreds of kilometers. Sharp frontal zones may also be created during periods of northern extensions of the Loop Current. Lamkin (1997) found a significant positive correlation between the abundance of larval nomeid fish and the location of the northern edge of the Loop Current by analyzing NOAA annual ichthyoplankton survey data from 1983 to 1988. Lamkin's data indicate that *Cubiceps pauciradiatus*, in particular, is a species whose adult spawning grounds and larval habitat are tied to sharp temperature gradients. Peak larval abundance was found close to the frontal interface, and peak abundance occurred just above the region of peak sea surface temperature (SST) gradient. Lamkin went on to speculate that the extent of the frontal systems in the Gulf of Mexico would be expected to impact annual recruitment of a species that is tied to a frontal habitat.

**Table 2**

Comparison of net-collected with acoustic characterization of zooplankton stocks. See text for explanation of how Acoustic Backscatter was calculated. CCR = cold-core ring; IABI = integrated acoustic backscatter intensity.

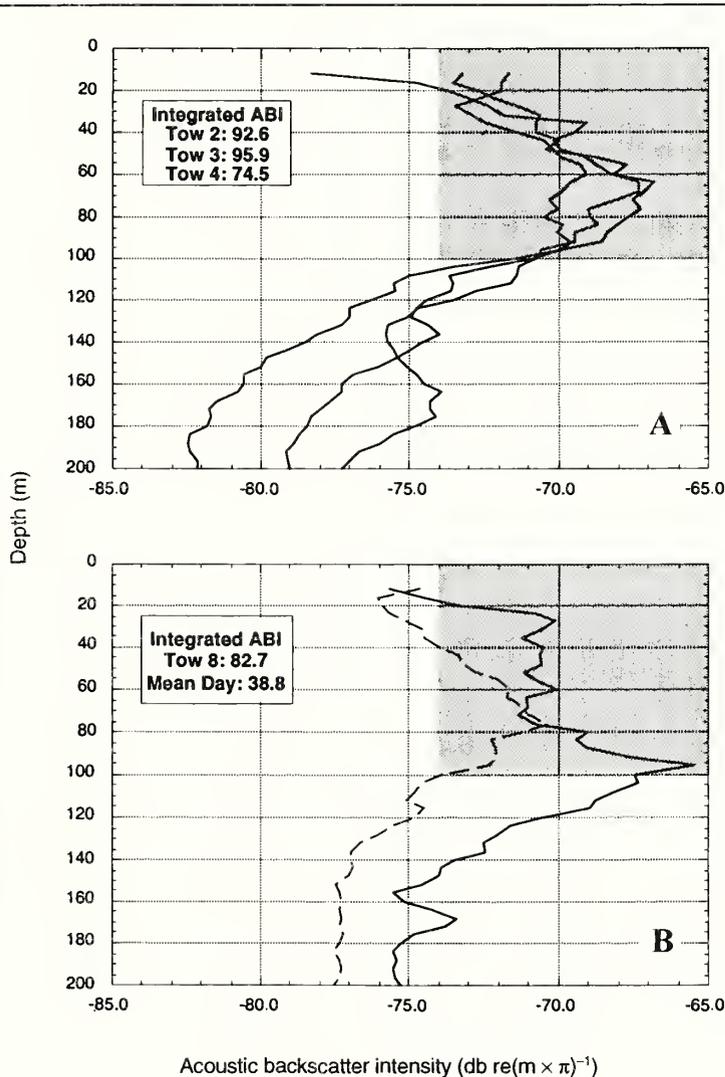
Plankton Tow (0-100-0 m)	Total wet displaced volume (mL/1,000 m <sup>3</sup> $\pm$ SD)	Acoustic Backscatter (db) (IABI, 10–100 m $\pm$ SD)	Euphausiids	Pteropods	Siphonophores
			(numbers per 1,000 m <sup>3</sup> $\pm$ SD)		
1 (day: NW of CCR)	36	46.3	112	93	212
2–4 (night: inside CCR)	90 $\pm$ 12	87.7 $\pm$ 11.5	574 $\pm$ 138	204 $\pm$ 19	580 $\pm$ 78
5–7 (day: SE of CCR)	39 $\pm$ 6	36.2 $\pm$ 31.2	154 $\pm$ 56	104 $\pm$ 48	453 $\pm$ 253
8 (night: SE of CCR)	67	82.7	806	198	840

On shorter time scales, the biological implications of thermal fronts in the Gulf of Mexico are widely recognized by fishermen: many of them now direct their boats to selected fishing areas where SST imagery shows sharp temperature gradients over short (<10 km) distances. Skipjack, blackfin tuna, swordfish, and blue marlin have been reported by fishermen to be locally abundant in these frontal zones (Roffer<sup>2</sup>). Also, on seven research cruises of the GulfCet program 1992–94, there were frequent

sightings of family groups of sperm whales, *Physeter catodon*, and periodic sightings of pods of killer whales, *Orcinus orca*, in association with thermal fronts over the continental slope of the northern Gulf of Mexico (Davis and Fargion<sup>3</sup>). Clearly, populations of apex predators like these are not likely to be sustained by low or infrequent episodes of enhanced secondary productivity.

One explanation for the fact that elevated stocks of biomass were not found in the CCR during the March 1993 transect is that biomass may “grow in” only when cyclones are “spun up” into surface waters. That is, if “new” nitrate is but episodically injected into the photic zone of cyclones, there may be lag times of days or weeks between what we hypothesize should be pulses of new production and secondary production. Alternatively, as these cyclones spin up, nitrate levels may be slowly domed and then decrease as the ring spins down and loses its cold-core surface expression.

Because Gulf of Mexico cyclones contain water of the same temperature-salinity properties as the rest of the Gulf of Mexico, only when they are well “spun up” will they have colder surface as well as colder interior temperatures. In fact, the cyclone of the present study was one of the few that has been visible in SST as well as in altimeter imagery; it may have spun up to have locally cool surface temperatures in response to cyclonically favorable wind curl from the passage of a strong atmospheric cold front. This strong “norther” passed through Texas and out across the Gulf of Mexico 36 hours before the cruise; the cloud banks that stretch NE to SW along the trailing edge of this norther can be seen in Figure 1. Rapid (hours-to-days scale) and intense cyclogenesis has been reported to occur after cold front passage in the northern Gulf of Mexico, especially when the cold fronts stall over deep water off the edge of the continental margin (Lewis and Hsu, 1992).



**Figure 3**

Acoustic backscatter intensity versus depth for time-averaged ADCP (acoustic Doppler current profiler) records (mean of three ensembles of 5-min duration each) that were concurrent with times of plankton net tows: (A) three nighttime tows in the cold-core ring (CCR); (B) night tow southeast of CCR (solid line) and mean of four day tows outside CCR (dashed line). The region 10–100 m where acoustic backscatter intensity (ABI) >74 db is shaded; the inset at top left summarizes this integrated ABI >74 db (IABI).

<sup>2</sup> Roffer, M. 1994. Ocean Fishing Forecasting Service, Miami, FL. Personal commun.

<sup>3</sup> Davis, R. W., and G. A. Fargion (eds.). 1996. Distribution and abundance of cetaceans in the north-central and western Gulf of Mexico. Outer Continental Shelf Study (OCS) Study MMS 96-0027. U.S. Dep. Interior, Minerals Manage. Serv., Gulf of Mexico OCS Region, New Orleans, LA, 357 p.

Clearly, we need additional information on how and when the biological productivity of Gulf of Mexico cyclones may "spin up." As a corollary, however, we need to remember that Gulf of Mexico cyclones are analogous but not homologous to Gulf Stream cold-core rings. As a consequence of their cyclonic nature, Gulf of Mexico cyclones are regions of elevated near-surface nutrients but unlike Gulf Stream cold-core rings, they are not regions of biological expatriation. Studies of the fauna within Gulf Stream cold-core rings have documented that because these rings are "oases" of temperate slope water that are transported into an oligotrophic subtropical central gyre, some of their resident fauna succumb to thermal stress as the cold-core of temperate origin dissipates by mixing with the surrounding subtropical water (Wiebe et al., 1976; Boyd et al., 1978). In contrast, populations of plankton and nekton in Gulf of Mexico cyclones should be sustained (rather than stressed) by mixing with surrounding subtropical water and so persist as local aggregations of enhanced food supply for apex predators that feed on krill-size food.

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# Physical environment and recruitment variability of Atlantic herring, *Clupea harengus*, in the Gulf of Maine

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Recruitment is generally recognized as a complex ecological process determined by the interrelation of many biological and environmental variables and has always been one of the most difficult terms to estimate in fisheries science (Russell, 1931). Methods for forecasting fisheries yields with time-series analyses (Saila et al., 1980; Mendelsohn, 1980), surplus production models (Schaaf et al., 1975), and models employed to relate recruitment to egg production (Koslow et al., 1987), larval abundance (Lett and Kohler, 1976; Lough et al., 1981; Smith, 1981), or spawning stock size (Sissenwine, 1984) have had limited success. Factors dominating recruitment appear to operate on local scales (Cohen et al., 1991); changes in physical factors operating through marine food webs are a major force affecting the abundance of fish stocks (Mann, 1993).

*Clupea harengus*, are an important component of the fisheries of the Northwest Atlantic and show great variability in recruitment. Spawning usually begins in the eastern part of the Gulf of Maine (Fig. 1) during August (Graham, 1982; Stevenson et al., 1989) and over the Nova Scotian shelf (MacKenzie, 1964), and occurs as late as November or December (Graham, 1982; Lazzari and Stevenson, 1992).

Eggs are deposited on the bottom (Boyar et al., 1973; Caddy and Iles, 1973; Stevenson and Knowles, 1988) and hatch in one to two weeks depending on temperature. Larvae are transported to estuaries and embayments along the central and western Maine coast (Graham, 1982; Graham and Townsend, 1985) or remain offshore for the winter (Townsend, 1992). The planktonic larval stage lasts until spring when larvae undergo metamorphosis into the juvenile form. Recruitment to the fishery occurs primarily in the following spring (at age 2) when juveniles reach a size appropriate for canning (150–200 mm).

The recruitment success of herring may be associated with various physical environmental factors, including sea surface temperature (SST) (Sutcliffe et al., 1977; Cushing, 1982; Anthony and Fogarty, 1985; Murawski, 1993), residual surface currents (Norcross and Shaw, 1984), winds (Corten<sup>1</sup>; Christensen et al.<sup>2</sup>), or atmospheric-pressure gradients (Carruthers, 1938), or a combination of the last two. Theoretical models for predicting variations in juvenile herring production in the Gulf of Maine were developed by using sea surface temperature from the late-larval to early-juvenile period (Anthony and Fogarty, 1985), first quarter (Janu-

ary–March) sunshine (Ezzy, 1988), and by using either food supply and spawning distribution when year-class strength was established during the larval stage or predation for those years when year-class strength was established in the brit stage (Campbell and Graham, 1991).

In addition, several hypotheses concerning wind events or larval dispersal may help us to understand herring recruitment in the Gulf of Maine. Ridgway (1975) proposed a conceptual model of recruitment variability based on changes in the dispersal of herring larvae by ocean currents from spawning areas to nursery areas. Water column stability and its impact on the availability of food resources for larval fish at some critical life stage also has been proposed to affect recruitment (Lasker, 1975). Periodic winds that produce moderate turbulence may enhance larval survival by increasing the probability of encounter between larvae and their prey (Sundby et al., 1989; MacKenzie et al., 1994).

The purpose of this study was to associate physical environmental factors with size estimates of age-2 herring of the coastal Atlantic herring stock in order to identify the important environmental factors underlying recruitment variability and to examine the importance of the wind and dispersal hypotheses

<sup>1</sup> Corten, A. 1984. The recruitment failure of herring in the central and northern North Sea in the years 1974–78 and the mid-1970s hydrographic anomaly. ICES Mini-Symposium. Council Meeting 1984/Gen., 12 p.

<sup>2</sup> Christensen, V., M. Heath, T. Kiorboe, P. Munk, H. Paulsen, and K. Richardson. 1985. Investigations on the relationship of herring larvae, plankton production and hydrography at Aberdeen Bank, Buchan Area, September 1984. ICES Council Meeting 1985/L, 23 p.

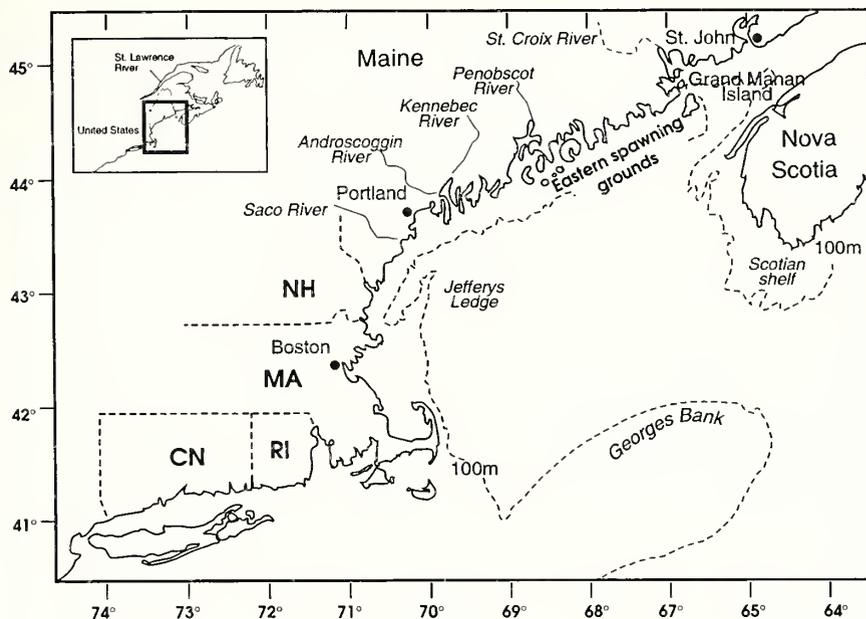


Figure 1

Map of the Gulf of Maine showing the spawning grounds of Atlantic herring, *Clupea harengus*.

as subjects for future research. Through examination of time-series data and the use of exploratory correlations, contingency tables, and *t*-tests, a search was made for those environmental factors that related positively or negatively with size estimates of age-2 herring populations.

## Methods

The method of exploratory correlation (Sutcliffe et al., 1977; Hayman, 1978) was used to determine relationships between monthly means of environmental factors along the Maine coast. Records were analyzed for the larval year 1 August through 31 July for years 1965 through 1990 (Table 1). The herring recruitment index used was the virtual population

analysis (VPA) estimation of two-year-olds from 1967 to 1991 in the coastal Atlantic stock (NEFC,<sup>3</sup> Fig. 2). For purposes of our analysis, we assumed predation to be constant and that spawning stock biomass was not a major factor affecting recruitment. Sea surface temperature (SST) records were supplied by the Maine Department of Marine Resources Laboratory, Boothbay Harbor, ME. Sunshine was measured as percent possible sunshine from observations of cloud cover conditions at the Portland, ME, airport. Long-term sunshine, atmospheric pressure, wind direction, and velocity data records were compiled for Portland as 12 monthly averages per year and archived by the National Climatic Data Center.

Wind speed and direction were measured at the Portland airport,

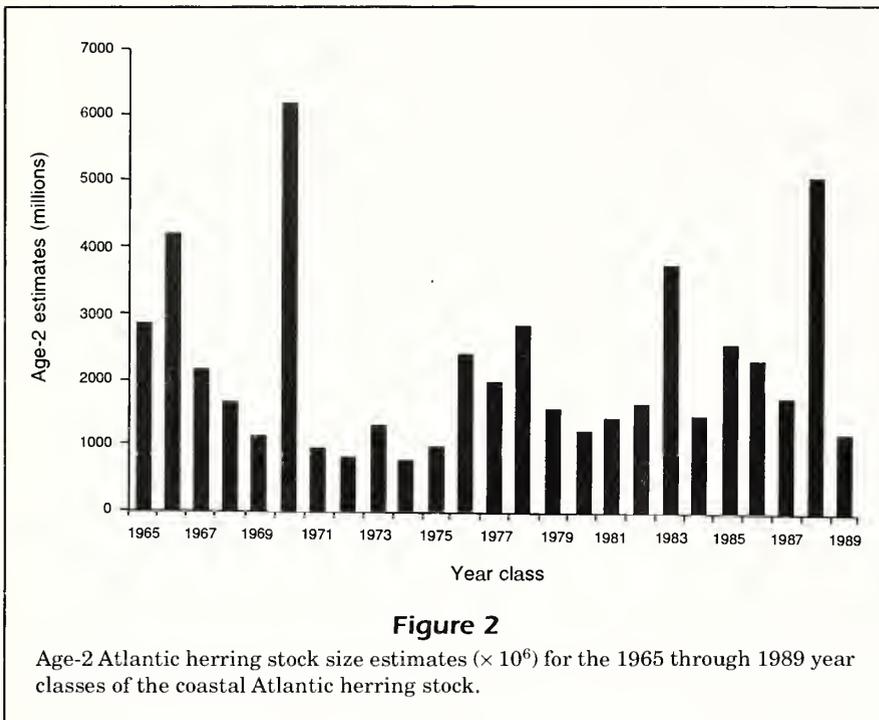
8 km inland, where an anemometer is situated 7 m above the ground at an elevation of 25 m. Storm frequency was also compiled as days with mean winds in excess of 5 m/s. Daily average wind speed and direction were further analyzed for the period August–December when the influence of wind-driven surface currents on the dispersal of newly hatched herring larvae would be greatest. The daily resultant wind direction (a vector variable) was separated into one of four directions on the basis of compass headings of northeasterly (1–90°), southeasterly (91–180°), southwesterly (181–270°), and northwesterly (271–

<sup>3</sup> NEFC (Northeast Fisheries Center). 1991. Assessment of the coastal Atlantic herring stock. Thirteenth Northeast Regional Stock Assessment Workshop. Northeast Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, 111 p.

Table 1

The location and origin of environmental factors tested for association with the age-2 Atlantic herring abundance estimates. ME DMR = Maine Department of Marine Resources; NCDC = National Climatic Data Center; NEFC = Northeast Fisheries Center.

Environmental factor	Location	Years	Source
Sea surface temperature	Boothbay Harbor	1965–90	ME DMR
Wind speed and direction	Portland, ME	1965–90	NCDC, Asheville, NC
Storm index (no. of days > 5 m/s)	Portland	1965–90	ME DMR
Sunshine	Portland	1965–90	NCDC, Asheville, NC
Barometric pressure	Portland	1965–90	NCDC, Asheville, NC
Herring abundance estimates	Gulf of Maine	1967–91	NEFC, 1991



368°) for each month from 1965 to 1989. The number of storm days, determined by daily average wind speeds greater than 5 m/s from each direction were also tabulated monthly. The number of major storms, defined as the number of periods of three or more consecutive days with mean wind speeds greater than 5 m/s were tabulated monthly. The number of major storms, defined as the number of periods of three or more consecutive days with mean winds in excess of 5 m/s were tabulated monthly and for the August–December period. The number of Lasker events, defined as the number of consecutive days when mean winds were less than 5 m/s for four or more consecutive days (Pauly, 1989) were tabulated monthly for August–September and for the August–December period.

We examined SST, percent sky cover, relative humidity, air temperature, solar radiation, and wind speed and direction at several locations in the Gulf of Maine to determine the similarity of environmental conditions within the Gulf. Wind data recorded at the Portland, ME, and Boston, MA, airports every 3 hours from August through December 1980–89 were compared for direction with contingency tables. Winds were converted from vector variables into one of four directions from compass headings of northeasterly, southeasterly, southwesterly, and northwesterly for each 3-h period. Monthly means of environmental variables including percent sky cover, relative humidity, air temperature, solar radiation, and wind velocity recorded by the National Weather Ser-

vice, Logan Airport, Boston, MA, were compared by using Pearson correlation analyses and *t*-tests with those recorded at the Portland airport for the period 1961–90 ( $n=30$ ).

Similarity of historic seawater temperature data between several sites along the Maine coast, in Massachusetts Bay, and in waters off New Brunswick (Canada) were tested by using Pearson correlation analyses. Monthly and yearly mean sea surface temperatures recorded at Boothbay Harbor (BBH) were compared with similar temperatures recorded in St. Andrews, New Brunswick, between 1921 and 1969, in Eastport between 1930 and 1971, Bar Harbor between 1947 and 1971, and in Portland between 1922 and 1971.

The 25 years of environmental data and age-2 population estimates for the Gulf of Maine were

partitioned into three clusters with the KMEANS cluster analysis procedure from SYSTAT (Wilkinson, 1991). This analysis is used to divide a series of data into a selected number of clusters in order to reduce the within-group sums of squares to a minimum value. The independence of periods of low, medium, and high values of the environmental variables were tested against the observed versus the expected age-2 population estimates with  $3 \times 3$  contingency tables.

As a selection criterion to identify important variables, we used a significant ( $P < 0.05$ ) result for the  $3 \times 3$  contingency tables. The existing low, medium, and high cells were then combined to form  $2 \times 2$  contingency tables from these results. All environmental factors of interest and the age-2 abundance estimates were tested again in four ways. To test the hypothesis that high estimates were associated with low values of an environmental factor, low and medium age-2 estimates and medium and high values of the factor were combined. To test the hypothesis that high estimates were associated with high values of an environmental factor, low and medium age-2 estimates and low and medium values of the environmental factor were combined. To test the hypothesis that low estimates were associated with high values of an environmental factor, medium and high age-2 estimates and low and medium values of the factor were combined. To test the hypothesis that low estimates were associated with low values of an environmental factor, medium and high age-2 estimates

and medium and high values of the environmental factor were combined. The  $2 \times 2$  tables were tested for independence by using Fisher's exact test because one cell often had zero observations (Zar, 1984).

A *t*-test for unequal variances (Zar, 1984) was used to determine whether the mean environmental factors differed between years of good and poor recruitment. The hypothesis that the mean environmental factor was higher (or lower, depending on the relationship with the age-2 estimates) during higher than expected recruitment years (1966, 1970, 1983, 1988,  $n=4$ ) than during lower than expected recruitment years (1971, 1972, 1974, 1978,  $n=4$ ) was tested.

## Results

Our examination of SST, percent sky cover, relative humidity, air temperature, solar radiation, and wind speed and direction revealed widespread coherence at several locations in the Gulf of Maine. The null hypotheses of independence were rejected in all months for the wind directions recorded every 3 hours between Portland and Boston, August through December 1980–89 ( $P < 0.001$ ,  $n > 2,200$ ). Wind direction at both locations showed a definite seasonal trend from May into September when more southerly winds predominated. Monthly mean wind speeds for the period 1961–90 between Portland and Boston were always significantly greater at Boston in all months (*t*-test,  $P < 0.001$ ,  $n = 30$ ), except in January and October. In addition, significant Pearson correlations ( $P < 0.001$ ,  $n = 30$ ) were found for all monthly means of solar radiation ( $r^2 = 0.80$ ), total sky cover ( $r^2 = 0.79$ ), air temperature ( $r^2 = 0.95$ ), relative humidity ( $r^2 = 0.68$ ), and precipitation ( $r^2 = 0.91$ ) between Portland and Boston for the same period.

The null hypothesis of independence was rejected for the age-2 Atlantic herring abundance estimates and ten environmental factors with  $3 \times 3$  contingency tables. These environmental factors were November storms, March sunshine, and October sea surface temperature, October and first quarter (January–March) barometric pressure, December and August–September Laker events, the number of days of southwesterly winds in September, the total number of days of southeasterly winds between August and December, and the number of storm days with southeasterly winds in November.

Five environmental factors were associated with either high or low age-2 abundance in the  $2 \times 2$  contingency table analyses (Table 2). Low abundance was associated with reduced sunshine in March and with fewer days of southeasterly winds from August to December. Associations with high age-2 abundance

**Table 2**

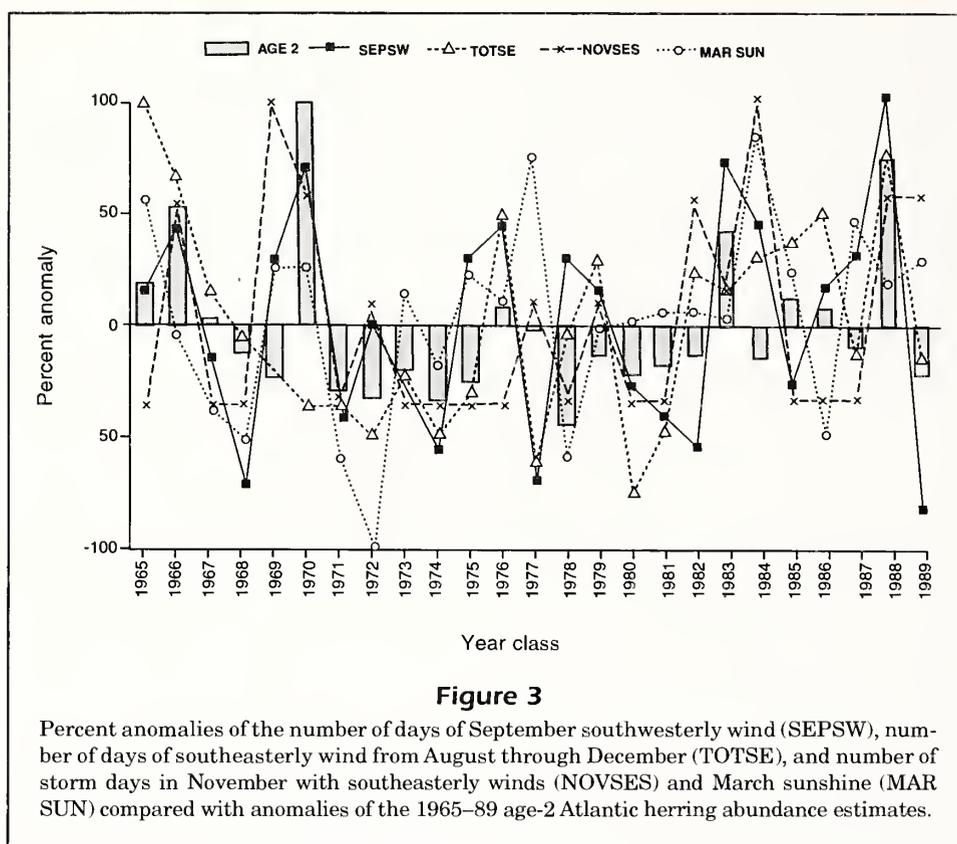
Probabilities of  $2 \times 2$  contingency table (Fisher's exact chi-square test) results for the environmental factors associated with the age-2 Atlantic herring estimates. ns = not significant.

Environmental factor	2x2 contingency tables			
	Low age-2 estimate		High age-2 estimate	
	High factor	Low factor	High factor	Low factor
November storms	ns	ns	0.020	ns
March sunshine	ns	0.012	ns	ns
September SW wind	ns	ns	0.002	ns
Aug–Dec SE wind	ns	0.005	ns	ns
November SE storms	ns	ns	0.026	ns

occurred with more November storms, with more days of southwesterly winds in September, and with more days of southeastern storms in November.

Comparison of environmental factors (mean values) between the four best and four worst recruitment years revealed only March sunshine and three southern wind direction factors were significantly different. The amount of monthly March sunshine and the number of days of southwesterly winds in September, the number of days of southeasterly winds from August to December, and the number of storm days with southeasterly winds in November were all significantly higher during good recruitment years than during lower recruitment years (Table 3). The four strongest year classes (1966, 1970, 1983, 1988) were associated with greater than 50% of the possible March sunshine and were associated in eleven out of twelve cases with above average September southwesterly, August–December southeasterly winds and November southeasterly storms (Fig. 3). In eight cases, conditions were greater than 50% above normal for the entire period. The only exception during the four years of above average recruitment occurred in 1970 when August–December southeasterly winds were extremely low.

The four worst year classes (1971, 1972, 1974, 1978) were associated with less than half of the possible March sunshine and with average or below average September southwesterly, August–December southeasterly winds and November southeasterly storms in 9 of 12 cases. In eight of these cases, conditions were at least 25% below normal for the entire period. However, two below average year classes (1979 and 1984) were produced despite the fact that all three of the significant wind factors were above



**Figure 3**

Percent anomalies of the number of days of September southwesterly wind (SEPSW), number of days of southeasterly wind from August through December (TOTSE), and number of storm days in November with southeasterly winds (NOVSES) and March sunshine (MAR SUN) compared with anomalies of the 1965–89 age-2 Atlantic herring abundance estimates.

**Table 3**

Mean and standard deviation (in parentheses) and *t*-test results assuming unequal variances for the environmental factors associated with the high and low age-2 Atlantic herring estimates. ns = not significant.

Environmental factor	Low age-2 estimate (n=4)	High age-2 estimate (n=4)	<i>t</i> -test probability
November storms	7.20 (1.64)	7.00 (5.23)	ns
March sunshine	40.75 (6.94)	57.00 (3.16)	0.012
September SW wind	11.40 (2.79)	17.00 (1.63)	0.008
Aug–Dec SE wind	14.40 (2.30)	19.75 (3.30)	0.039
November SE storms	0.20 (0.451)	1.75 (0.50)	0.003

normal in those years. Average year classes were much more common during the 25-yr period and, in 14 of these 17 years, August–December southeasterly winds were also below average. September southwesterly winds and November southeasterly storms, on the other hand, were below average during about half of these years.

## Discussion

In our study, we observed associations of sunshine, wind direction, and velocity with the number of age-2 herring estimated to recruit to the coastal Atlantic

stock. Strong year classes were produced in years with more days of southerly fall (September) winds and storms (November), and weak year classes were produced in years with less sunshine in March and fewer days of southeasterly fall (August–December) winds. However, because southwest wind velocities are lower than velocities from other directions in the Gulf of Maine in fall, it is not possible to differentiate between the effects of wind direction and strength in this study. We believe that our results, without specifically addressing how wind events influence herring larval survival, show that recruitment success and, therefore, larval survival are related to wind events. In general, wind-driven transport and tur-

bulence are two processes hypothesized to affect the survival of marine fish larvae (Lasker, 1975; Norcross and Shaw, 1984), but strong evidence linking larval survival to wind conditions remains inconclusive. Wind-related transport is believed to influence the recruitment of many species of marine invertebrates (Roughgarden et al., 1988; Farrell et al., 1991) and fishes (Bailey, 1981; Heath, 1989).

For Atlantic herring in the Gulf of Maine, the eastern Maine–Grand Manan Island spawning ground presents a unique case in how southwesterly winds enhance larval transport and survival. Bigelow (1927) found that winds from the southwest tend to “build up” surface waters in the Bay of Fundy causing an “overflow” in the shape of a westerly drift that increases the flow of the coastal current along the eastern Maine coast, i.e. against the prevailing winds. Herring larvae depend on these currents for dispersal to more productive nursery areas (Graham, 1982; Graham and Townsend, 1985; Townsend et al., 1986, 1987) because the area of extensive tidal activity in the Bay of Fundy and off eastern Maine (Garrett et al., 1978) leads to pronounced vertical mixing and less stratification of the water column off eastern coastal Maine (Yentsch and Garfield, 1981). As a result, primary production is much lower in the northeastern Gulf of Maine because the mixed layer extends deeper than the critical depth for plankton production (Townsend et al., 1987). Zooplankton prey organisms that support larval growth and survival are extremely rare on this spawning ground in the fall, only reaching adequate densities about 100 km “downstream” from the spawning ground (Townsend et al., 1986, 1987); therefore, increased dispersal of recently hatched larvae that originate on the eastern Maine–Grand Manan Island spawning ground is a mechanism that could enhance the recruitment of juveniles to the coastal herring stock.

This study generally supports the Campbell and Graham (1991) theory that release of larvae from the eastern Maine–Grand Manan spawning ground is mediated by wind events that generate horizontal flows and can carry larvae out of retention areas into the counterclockwise residual flow that moves from northeast to southwest along the Maine coast. Bigelow and Schroeder (1953) thought that this circulation is set in motion by wind and freshwater inflow and that it influences the availability of two-year-old herring because the fish follow the drifting planktonic animals on which they feed. Furthermore, Chenoweth et al. (1989) observed that larvae hatched in this spawning area at the same time had different horizontal displacements away from the spawning area; some larvae remained in the area for up to a month after spawning, whereas others were trans-

ported up to 100 km southwestward down the coast during the same time period. Townsend (1992) attributes this variable release of larval herring from the eastern Maine retention area to the intrusion of slope water into Jordan Basin (a deep offshore basin located in the northeastern Gulf of Maine), the timing of hatching (to coincide with lunar periodicity and the intensity of tidal mixing), and the location of egg beds in relation to the front between the area of tidal mixing and more stratified water offshore, where the geostrophic flow that would pull larvae out of the retention area is greatest (Brooks and Townsend, 1989). In addition, Brooks (1990) found a relation between wind stress and currents that suggested the action of a density-modulated coastal upwelling mechanism in which the deep inward currents over Lindenköhl sill respond directly to northeastward alongshore wind stress at times of weak stratification, such as occurs in fall.

Once entrained within the coastal current, the larvae are dispersed to an overwintering area that has not been conclusively determined as yet. Greater advection of larvae from the eastern Maine–Grand Manan Island spawning area to the southwest as hypothesized by Graham (1982) would distribute larvae among more coastal overwintering areas. This distribution would improve recruitment success by lessening density-dependent mortality within the estuarine and nearshore waters shallower than 100 m that act as a nursery area and would establish a carrying capacity for larvae on the Maine coast for a given year. Research has shown that larvae from this spawning ground reach at least as far south as the Sheepscot River in mid-coastal Maine (Graham, 1982; Graham and Townsend, 1985; Stevenson et al., 1989). However, recent research shows that larval herring overwintering “offshore” may have a higher survival rate than those wintering in nearshore waters (Townsend et al., 1989; Townsend, 1992) and that dispersal associated with southerly winds could enhance offshore transport. In either case, dispersal of larvae away from the eastern Maine–Grand Manan Island spawning area is critical for good larval survival (Graham, 1982; Campbell and Graham, 1991; Townsend, 1992). Wind-induced effects on transport have been shown to affect the distribution and recruitment of other marine fishes (Stevenson, 1962; Checkley et al., 1988; Fechtel and Griffiths, 1990; Koutsikopoulos et al., 1991; Castillo et al., 1993).

Therefore, we propose that more southwesterly wind conditions in September increased dispersal of eastern Maine–Grand Manan Island larvae in 1966, 1970, 1983, and 1988, setting up an initial situation of high larval survival, which, when combined with more southerly wind conditions through December

and more sunshine in March, resulted in the success of these year classes. A continuation of a more summer-like (southwesterly) wind pattern through September may result in better larval herring survival in the Gulf of Maine during these years. Average frequencies of southwest winds off Nova Scotia can vary between 10% and 39% for the months of July–September, 1955–1980 (Hudon, 1994), and summer (June–August) wind stress over the eastern continental shelf is generally toward the northeast and about 0.25 dyn/cm; whereas in fall (September–November), wind stress shifts toward the southeast and can be twice as strong (Saunders, 1977).

Effects of turbulent mixing on food encounter rates must be considered because southwesterly winds are lower in velocity in the Gulf of Maine during the early (August–December) larval phase. The effects of turbulence on the availability of zooplankton prey for larvae are related to those biological processes (primary production) that are disturbed by physical processes, i.e. turbulence generated by wind mixing (Rothschild and Osborn, 1988; Sundby et al., 1989; MacKenzie and Leggett, 1991). Recently, the overall probability of larval feeding has been described as a dome-shaped function of turbulent velocity with maximum feeding, depending on turbulence level and behavioral characteristics of predator and prey (MacKenzie et al., 1994). Calmer wind conditions through September when most first-feeding larvae are present, could enhance larval survival and result in the success of these year classes. Strong recruitment to walleye pollock, *Theragramma chalcogramma*, stocks in the Gulf of Alaska (Megrey et al., 1994) and Bering Sea (Bailey et al., 1986) has been linked to initially calm wind conditions and is associated with calm periods preceded and succeeded by periods of stronger mixing (Bailey and Macklin, 1994). For Atlantic herring in the Gulf of Maine, these conditions would result from periods of calm southwesterly winds in conjunction with stronger southeasterly winds. However, strong mixing can disrupt layers of prey (Lasker, 1975; Wroblewski and Richman, 1987; Owen 1989) and has also been linked to reduced growth of Atlantic herring larvae (Heath, 1989).

Three other environmental variables, the amount of March sunlight, August–December southeasterly winds, and November southeasterly storms, were related to herring year-class size. Dispersal associated with the latter two southeasterly wind factors could result in a positive effect on recruitment by transporting larvae spawned in the western Gulf of Maine and on Jeffreys Ledge toward inshore larval overwintering and juvenile nursery areas along the Maine coast (Lazzari and Stevenson, 1992). Because

herring larvae feed on zooplankton, spring phytoplankton production and, ultimately, sunshine should be positively related to larval survival. The timing of plankton blooms in the Gulf of Maine was highly influenced by the amount of sunshine available early in the year (Townsend and Spinrad, 1986). Therefore reduced sunshine in March would have a detrimental effect on the spring bloom, resulting in fewer food resources for herring larvae and reducing recruitment as seen in Ezzy's (1988) model using first quarter sunshine.

Recruitment of animals with planktonic stages is a complex process; we would not expect any single factor affecting the early larval stage to dominate the entire survival process (Wooster and Bailey, 1989; Campbell and Graham, 1991). In our study, although more days of southerly winds were generally associated with higher than expected age-2 recruitment, this was not always the case. For example, in two of the six years (1976 and 1984, Fig. 3) when southwesterly winds averaged > 25% higher than normal, strong year classes were not produced. Other factors may have reduced year class size (e.g. predation on larvae or age-1 juveniles) during these periods of lower abundance, or some other conditions may not have been suitable for prey production or feeding. We would have been surprised if the relation of any environmental factor and recruitment had always been consistent, because a high larval survival rate appears to be a necessary, but not sufficient, condition for strong recruitment. Year-class strength can instead be determined by conditions that prevail during the juvenile life stage in some years (Campbell and Graham, 1991; Bailey and Spring, 1992). The environment does not act alone in affecting recruitment success; biotic effects, competitive interaction between species, and the removal of adults caused by fishing mortality, should be considered (Drinkwater, 1987). The results of our analyses to date are interesting and worth expanding, with more research and analyses, to other Atlantic herring stocks to determine the effects of the environment, particularly the wind-driven transport of larvae, on their recruitment variability.

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# In vitro digestibility of some prey species of dolphins

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Studies of dolphin (Cetacea, Odontoceti) food habits are conducted by examining stomach contents because it is difficult to observe feeding behavior directly. It is rare, however, to find prey items intact in stomachs; often only fragments of muscle and some hard parts remain. Identification of prey species and estimation of their original size are usually carried out with trace remains, such as cephalopod beaks (Clarke, 1980) and fish otoliths (Fitch and Brownell, 1968), because of their species-specific shapes and allometric relationships with body size (Clarke, 1962; Jobling and Breiby, 1986).

There are several problems with using cephalopod beaks and fish otoliths in dietary studies. Otoliths are composed of calcium carbonate and can be eroded by stomach acids (McMahon and Tash, 1979; da Silva and Neilson, 1985; Murie and Lavigne, 1985, 1986; Jobling and Breiby, 1986; Harvey, 1989). Reduction in otolith size depends on the length of time they are exposed to stomach acids. Because otoliths are located inside the skull, the length of time they are exposed to acids may differ depending on the overall digestibility of the fish species concerned. Some species are identifiable even after their otoliths have been eroded and reduced in size. For such species, it may be difficult to tell if the otolith is of a

reduced or original size (McMahon and Tash, 1979). Because estimation of fish prey size is usually based on a regression between otolith size and the weight or length of the prey, any reduction in otolith size that is not detected may cause prey size to be underestimated.

The use of cephalopod beaks may create different problems. Although Bigg and Fawcett (1985) reported that soft-bodied squids (*Loligo opalescens*) decreased in weight faster than herring (*Clupea harengus pallasi*) in an artificial digestion solution, cephalopod beaks were not dissolved by gastric acids. Cephalopod beaks may, therefore, accumulate in cetacean stomachs. It has been observed that some marine mammals occasionally regurgitate squid beaks (Clarke, 1980; Pitcher, 1980). Cephalopod beaks present in a stomach may, consequently, represent the remains of more than one meal and thus may result in overestimations of the proportion of squid to fish in the predator's diet.

Bigg and Perez (1985) introduced the "modified volume" method to avoid the problem of the accumulation of cephalopod beaks. This method uses the frequency of occurrence of nontrace remains to calculate the ratio between cephalopods and fish in a meal. However, if all prey remnants come from the same meal, any difference in digestibil-

ity between prey items will affect the relative frequency of occurrence of nontrace remains when the stomach is examined. As an extreme case, prey items that are digested very rapidly would not be represented by "nontrace remains" in the stomach soon after feeding.

Differentials in digestion rates between *Loligo* squid and herring in an artificial digestion solution, as demonstrated by Bigg and Fawcett (1985), may apply to other prey species. For example, Jackson et al. (1987) could not detect differences in the rates that fish and squid were completely digested in vitro but noted that exoskeletons of intact crustaceans resisted digestion. Thus, it is possible that digestion rates for each prey species, or prey type, could be used as "correction factors" in dietary analysis.

The present study investigates the differences in digestion rates of major prey species of dolphins in artificial digestion solutions. In addition, digestion rates of different sizes of the same prey species are considered. Digestion rates are then calculated to establish the basis for a revised method of dietary analysis.

## Materials and methods

The following fish and squid species were used in a set of six experiments: 1) 5 lanternfishes (Myctophidae), 5 large and 5 small Cape anchovies (*Engraulis capensis*, Engraulidae); 2) 5 large and 5 small round herrings (*Etrumeus whiteheadi*, Clupeidae); 3) 5 large and 5 small pilchards (*Sardinops sagax*, Clupeidae); 4) 5 hakes (*Merluccius* sp., Merlucciidae) and 5 chokka squids (*Loligo vulgaris reynaudii*, Loliginidae); 5) 5 maasbankers (horse mackerel) (*Trachurus trachurus capensis*, Carangidae) and

5 red squids (*Todaropsis eblanae*, Ommastrephidae); and 6) 5 pelagic gobies (*Sufflogobius bibarbatus*, Gobiidae) and 5 lanternfishes. These taxa are commonly found in stomachs of dolphins (including common dolphins, *Delphinus delphis*, dusky dolphins, *Lagenorhynchus obscurus*, and Heaviside's dolphins, *Cephalorhynchus heavisidii*) along the west coast of southern Africa (Sekiguchi et al., 1992). Table 1 shows the sizes of sample species used: all were collected in trawls by the RV *Africana*, November 1987 or January 1988, and frozen at  $-20^{\circ}\text{C}$ .

For the first experiment, the procedure followed that of Jackson et al. (1987). Four liters of a digestion solution of 0.15% HCl, 0.05%  $\text{Na}_2\text{CO}_3$  (buffer) and 1.0% pepsin (pepsin A powder, BDH Chemicals Ltd.) were adjusted to an initial pH of 2.30, near the midpoint of the range of that recorded for cetacean stomachs (pH=1.4 to 3.0, Ishihara, 1960; pH=1.8 to 3.0, Smith, 1972; pH=1.5 to 3.5, Jobling and Breiby, 1986). A Beckman expanded scale pH meter was used to monitor pH. The solution was then divided into

240-mL portions in each of seven 600-mL beakers, and 1,150 mL portions in each of two 5-L beakers.

The beakers were placed in two water baths continuously agitated (rocked) 20–30 times per minute at  $38^{\circ}\text{C}$ . Each fish was put in a small fiber glass bag (mesh size  $0.5 \times 0.5$  mm) and then suspended in the solution. Four samples were placed in each of the 5-L beakers and a single sample in each of the 600-mL beakers. The pH for each beaker was maintained between 1.90 and 3.37; pH increased with time and was adjusted by adding HCl.

Owing to the effort required to maintain pH in individual beakers, one large PVC container ( $40 \times 28 \times 20$  cm) made specifically to fit in the water bath was used in subsequent experiments. Ten liters of digestion solution, consisting of 0.50–0.56% HCl, 0.27–0.29%  $\text{Na}_2\text{CO}_3$ , and 1.0% pepsin, were maintained at  $36.0$  to  $39.1^{\circ}\text{C}$  in the PVC container. A Beckman expanded-scale pH meter was placed in the corner of the container to monitor pH constantly. The pH was maintained between 2.25 and 2.51 by occasional

Table 1

The species used in the artificial digestion experiments; their total length (TL, cm) or dorsal mantle length (DML, cm) and corresponding weight (WT, g). (L=large size and S=small size groups.)

Sample species		Length (cm) and weight (g)				
Cape anchovy (L)	TL	13.6	12.7	12.7	12.8	11.7
	WT	19.48	17.28	21.25	18.09	16.45
Cape anchovy (S)	TL	9.9	9.6	9.6	9.4	9.6
	WT	8.25	8.05	8.01	7.81	7.56
Round herring (L)	TL	19.5	18.7	19.5	21.0	19.8
	WT	68.95	63.49	79.03	96.27	79.47
Round herring (S)	TL	14.4	14.8	14.8	14.8	15.2
	WT	28.28	33.47	34.88	36.77	34.69
Pilchard (L)	TL	20.8	20.0	20.8	20.0	20.3
	WT	108.70	104.55	105.27	103.11	103.72
Pilchard (S)	TL	13.7	13.0	14.0	14.1	13.5
	WT	31.0	27.88	30.59	30.89	30.65
Hake	TL	17.0	17.4	17.3	17.5	16.5
	WT	46.1	51.2	48.4	52.2	41.5
Maasbanker	TL	18.8	19.4	18.9	19.1	16.5
	WT	79.5	83.3	80.2	80.4	53.6
Goby	TL	8.7	7.8	8.2	8.5	8.6
	WT	10.2	7.1	8.6	8.9	10.0
Lanternfish	TL	5.3	5.1	3.5	3.9	4.5
		4.4	4.4	4.2	4.1	4.6
	WT	1.85	1.64	0.61	0.93	1.16
		1.1	1.1	0.8	1.0	1.0
Chokka squid	DML	16.0	18.5	16.5	15.8	15.8
	WT	118.3	152.9	120.7	104.4	98.8
Red squid	DML	10.4	9.6	10.7	9.9	9.2
	WT	60.6	55.8	61.2	49.1	40.8

addition of 10% HCl (45 to 655 mL per experiment in total). The water bath rocked the container about 40 times per minute. As in the first experiment, each sample item was placed in a small mesh bag and suspended in the digestion solution.

Every hour, each bag was lifted from the container, all excess liquid was wiped off with a paper towel, and the bag with sample weighed to the nearest 0.1 g. The physical appearance of each sample was also recorded. Weighings were made at 1-h intervals until the sample mass (i.e. measured weight minus weight of the empty mesh bag) had decreased to 5–10% of its original mass.

To compare digestion rates between each species, the mean time to reach 20% of original weight ( $T_{20}$ ) was calculated for each sample species. This percentage was chosen because the rate of decline in mass decreased when the sample reached this point. This decrease probably resulted from inaccuracies in weighing smaller masses as well as from the accumulation of less digestible remains. The  $T_{20}$  values for different size groups of the same prey species were compared first with a *t*-test. Then, one-way ANOVA and the Newman-Keuls test were applied to compare all sample species (Zar, 1974). A digestion rate ratio was calculated from the  $T_{20}$  values for each species, expressed as a proportion of that for lanternfish.

## Results

Samples were digested almost completely in the pepsin solution. Although digestion rates were quite different among species, the sequences of digestion of particular tissues were similar among species (Table 2). Although the head of a fish usually disintegrated when about half the body had been digested, otoliths were not always visible through the mesh bag at this stage. In the case of hake and maasbanker, the dorsal surface of the head began to be digested at an earlier stage (15% digested at 2–3 h for hake, 5–6 h for maasbanker) than that found for other fish species. Otoliths became visible (through the mesh bag) at 5–8 h for hake and at 19 h for maasbanker. Hake otoliths fell through the mesh at 9–13 h. Most otoliths were dissolved completely when the experiments with hake terminated at 20 h

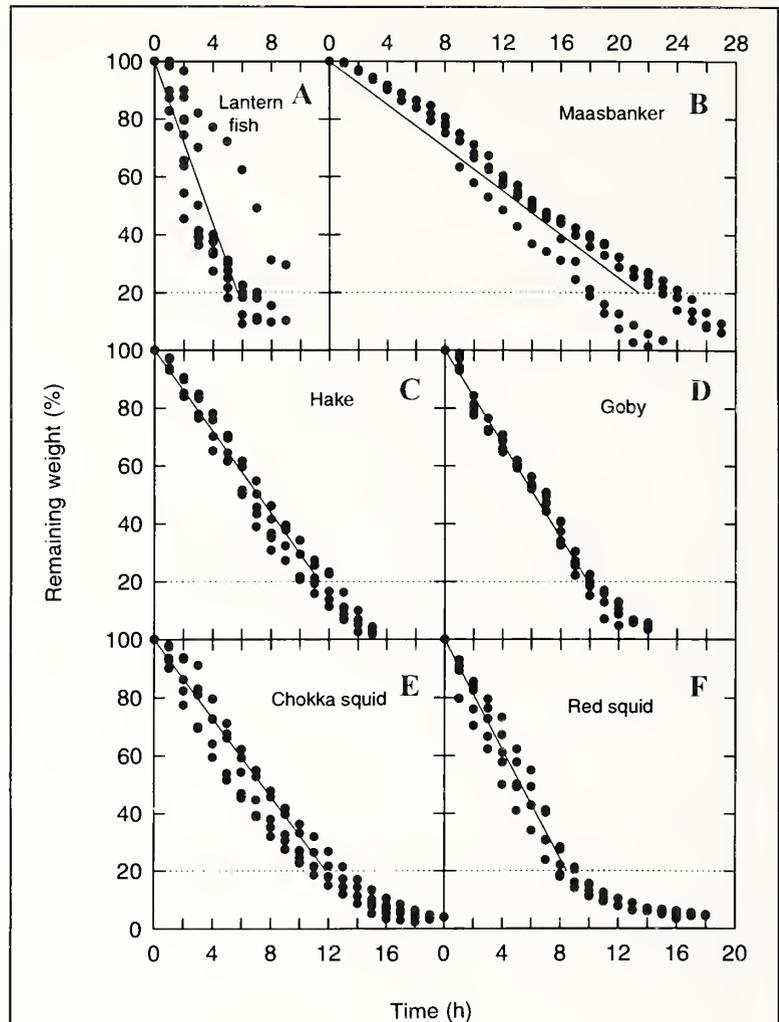


Figure 1

The rate of digestion of fish and squid species in an artificial digestion solution, expressed as the percentage of their original weight remaining at hourly intervals. The slope shown is the digestion rate to the mean time to 20% of the initial weights ( $T_{20}$ ). (A) 10 lanternfish (*Myctophidae* sp.), (B) 5 maasbanker (*Trachurus t. capensis*), (C) 5 hake (*Merluccius* sp.), (D) 5 pelagic goby (*Sufflogobius bibarbatus*), (E) 5 chokka squids (*Loligo v. reynaudii*), and (F) 5 red squids (*Todaropsis eblanae*).

(except one otolith), and at 27 h (except for five otoliths) with maasbanker. Some otoliths of reduced size were recovered in experiments involving other species (i.e. 16 from anchovy, 8 from herring, and 10 from goby). All squid beaks recovered at the termination of the experiments showed no obvious signs of having been digested.

All samples decreased in weight over time (h), each species having different rates of digestion (Figs. 1 and 2). Lanternfish were digested very quickly, and were almost completely gone within 9 hours. Hake

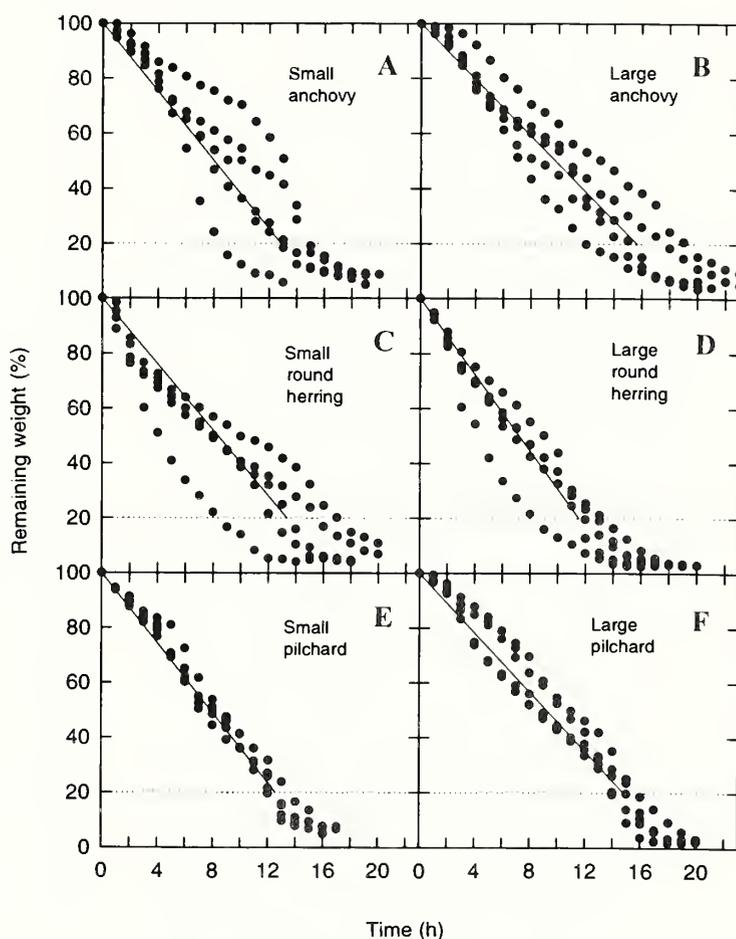
**Table 2**  
The generalized sequence of digestion for fish and squid in the artificial digestion experiments.

Weight remaining (%)	Squid	Fish
95–85	Begins to lose skin and viscera	Abdomen breaks up; begins to lose skin and viscera
85–60	Loses fins; muscle reduced	Most of skin and viscera are gone; loses eyes and tail; head begins to be digested
60–40	Tentacles featureless; mantle splits, exposing the pen	Head is gone; muscle reduced; releases otoliths
40–30	Flesh reduced further	Muscle disintegrates; backbone exposed
30–10	Beaks, eyes, and pen released	Muscle reduced further
<10	Beaks, eyes, part of pen, and a little flesh remain	Pieces of muscle and skin, and some vertebrae remain

and goby were also digested quickly and reduced to less than 10% of their original weight within 15 hours. Most species, however, took longer for complete digestion (about 20 h); maasbanker took as long as 27 hours to be reduced to less than 10% of its original weight.

Table 3 lists the  $T_{20}$  values for each sample species. The  $T_{20}$  values varied between species sampled (from 5.68 h to 21.35 h), but for most species, the  $T_{20}$  value was roughly 13 h. Among the 12 species and size groups sampled, maasbanker had the slowest rate of digestion and lanternfish the highest, being digested about 3.8 times faster than maasbanker. Red squid was digested faster than most fish species except lanternfish, whereas the digestion rate of chokka squid was slower than that of large round herring, hake, goby, red squid, and lanternfish.

There appeared to be differences between digestion rates of different sizes of the same species (Table 3). Smaller anchovy and pilchard were digested about 1.2 times faster than larger ones, but round herrings showed the opposite pattern. However, for anchovy and round herring, the  $T_{20}$  values for large and small fish were not significantly different ( $t=1.65$ ,  $df=8$ ,  $P=0.1381$ , for large fish;  $t=1.05$ ,  $df=8$ ,  $P=0.3256$ , for small fish). The two size groups of pilchard had significantly different  $T_{20}$  values



**Figure 2**

The rate of digestion of two different size groups of fish species in an artificial digestion solution, expressed as the percentage of their original weight remaining at hourly intervals. The slope shown is the digestion rate to the mean time to 20% of the initial weights ( $T_{20}$ ). (A) 5 small and (B) 5 large specimens of anchovy (*Engraulis capensis*), (C) 5 small and (D) 5 large round herring (*Etrumeus whiteheadi*), (E) 5 small and (F) 5 large pilchard (*Sardinops sagax*).

Table 3

The list of calculated mean times and standard deviations for each species in the artificial digestion experiments when remaining weights reach 20% of the original weight ( $T_{20}$ ). The digestion rate ratio shows the  $T_{20}$  value for each species in relation to that of lantern fish. (L=large size and S=small size groups—see Table 1).

Sample species	<i>n</i>	Time (h) to reach 20% of original wt. ( $T_{20}$ )		Digestion rate ratio	
		Mean	SD		
Maasbanker	<i>Trachurus t. capensis</i>	5	21.35	3.09	3.76
Cape anchovy (L) <sup>1</sup>	<i>Engraulis capensis</i>	5	15.67	2.81	2.76
Pilchard (L)	<i>Sardinops sagax</i>	5	14.82	0.80	2.61
Round herring (S) <sup>2</sup>	<i>Etrumeus whiteheadi</i>	5	13.35	3.33	2.35
Cape anchovy (S) <sup>1</sup>	<i>Engraulis capensis</i>	5	12.85	2.60	2.26
Pilchard (S)	<i>Sardinops sagax</i>	5	12.57	0.62	2.21
Chokka squid	<i>Loligo v. reynaudii</i>	5	11.82	1.04	2.08
Round herring (L) <sup>2</sup>	<i>Etrumeus whiteheadi</i>	5	11.54	1.96	2.03
Hake	<i>Merluccius</i> sp.	5	11.36	0.98	2.00
Goby	<i>Sufflogobius bibarbus</i>	5	9.88	0.39	1.74
Red squid	<i>Todaropsis eblanae</i>	5	8.44	0.70	1.49
Lanternfish	Myctophidae	8	5.68	0.66	1.00

<sup>1</sup>  $T_{20}$  for large and small anchovy = 14.26 ± 2.95 h.

<sup>2</sup>  $T_{20}$  for large and small round herring = 12.45 ± 2.75 h.

( $t=5.02$ ,  $df=8$ ,  $P=0.001$ ). Because there was no significant difference between the two size groups of anchovy and round herring, data were combined for one-way ANOVA on all sample species.

The  $T_{20}$  values for 10 sample groups (maasbanker, large and small pilchard, anchovy, round herring, hake, goby, lanternfish, chokka squid, and red squid) showed a significant difference (one-way ANOVA,  $F=27.3$ , total  $df=62$ ,  $P<0.0001$ ). The Newman-Keuls test indicated maasbanker, goby, red squid, and lanternfish had different  $T_{20}$  values from other species ( $P<0.05$ ).

## Discussion

Compared with previous digestion experiments, complete digestion of samples took longer than expected (Figs. 1 and 2). Bigg and Fawcett (1985) reported that whole herring and squid were digested within 10 h in an artificial solution of 1% HCl and 1% pepsin. Jackson et al. (1987) found that about 10–15 h were required to digest whole anchovies in vitro (pH=1.25–1.35). These time differences are probably the result of differences in acidity of the digestion solutions. In the present experiments, the solutions had a pH of ~2.3. The pH of the solution used by Bigg and Fawcett (1985) can be calculated as about 1.1. Therefore, their solution was far more acidic than ours, resulting in more rapid digestion of fish and squid tissues.

As noted, there was a general tendency for the digestion rate to decline when the remaining weight was less than 20% of the original weight. This was more pronounced for cephalopods than fish (Figs. 1 and 2). Bigg and Fawcett (1985, Fig. 16.1) reported similar trends: declines in rates of digestion can be caused by the accumulation of less digestible material, i.e. squid beaks and pens (Table 2; also Table 16.3 in Bigg and Fawcett, 1985).

Although their procedure was different from that used in the present study, the digestion experiment of Nordøy et al. (1993) for herring (*Clupea harengus*) also showed a rapid decline in digestion rate after about 70% of "dry matter disappearance" (DMD), and stated that the maximum DMD of herring is about 80%. The digestion rate decline at 80% in the present study may also be related to the digestibility of prey species of dolphins, or cetaceans in general. Undigested prey remains may be voided via gastric evacuation or, possibly, by regurgitation, as proposed for squid beaks (Clarke, 1980; Pitcher, 1980).

The validity of in vitro experiments in representing in vivo situations remains a matter of debate, but technical and other considerations make in vivo digestion experiments with dolphins impractical at this stage. Although not engaging strictly in a digestion experiment, Kastelein et al. (1993) fed captive Commerson's dolphins (*Cephalorhynchus commersonii*) on North Atlantic herring (*Clupea harengus*) and Columbia river smelt (*Thaleichthys pacificus*),

into which gelatine capsules containing red dye were inserted. They found that only 40 to 155 minutes elapsed before dye appeared in feces, but it is not clear how this relates to the full digestion times of the fish. In vivo experiments with pinnipeds (another marine mammal feeding largely on cephalopods and fish) suggest somewhat faster digestion rates than those in our study. Murie and Lavigne (1985) found no fish hard parts remaining in seal stomachs 18 hours after feeding. However, stomachs could have been voided by regurgitation and gastric evacuation, whereas "hard parts" in our experiments could escape from the digestion bags only if they were reduced to less than mesh size. Thus, their results are not necessarily inconsistent with those of the present study, although mechanical break-down actions of stomachs are likely to produce faster digestion in vivo.

The in vitro digestion speeds recorded in the present study differed between species (Table 3), but there was no consistent correlation with the taxonomic position of the prey. Three fish species in the order Clupeiformes (round herring, pilchard, and anchovy) had digestion-rate ratios in the range 2.03–2.76, although large and small size groups of pilchard had significantly different  $T_{20}$  values. However, maasbanker and goby, both in the order Perciformes, showed very different digestion-rate ratios (3.76 and 1.74). While both squid species were digested faster than most fish species, chokka squid was digested more slowly than large round herring, hake, goby, and lanternfish. Bigg and Fawcett (1985) found that the squid *Loligo opalescens* was digested much faster than herring (*Clupea harengus pallasii*), both in vitro and in vivo (i.e. in a seal stomach). On the other hand, Jackson et al. (1987) found no difference in the digestion rate between fish (hake and anchovy) and squid (*Loligo*) in vitro. LeBrasseur and Stephens (1965) reported that fish (salmonids, myctophids, and hexagrammids) were digested faster than squid (gonatids) in their pepsin-hydrochloric acid solution (0.2 g pepsin/1 L, 1.5% HCl, pH 1.8). These in vitro differences quite possibly are the result of variations in the acidity of the solutions used and differences in experimental procedures.

It is possible that digestion rates are related to muscle structure. Because pepsin is an enzyme that dissolves protein, the protein composition of a body will have an effect on digestion rate. Greer-Walker and Pull (1975) found that active pelagic fish had higher proportions of red muscle than coastal or deep-sea fish species. They reported that the mean red muscle proportion was 19.8% for Clupeidae, 18.3% for Carangidae, 4.5% for Gobiidae, and 4.5% and 0.6% for the deep-sea fish families Macrouridae and Chimaeridae, respectively. The digestion rates of fish

prey found in the present study (Table 3) appear to fit a pattern in which the prey species digested most slowly tend to have the highest proportions of red muscle. Red muscle, containing greater quantities of mitochondria, myoglobin, fats, and glycogen than white muscle, may have stronger resistance to pepsin in the digestion process.

Fish otoliths recovered in the present study were reduced in size, and most hake and maasbanker otoliths completely dissolved within 8–12 h after exposure. McMahon and Tash (1979) reported that otoliths in a 0.01 N HCl solution (pH=2.0–2.5) at 25°C were dissolved completely in 24 h, and a herring otolith in a pH 1.09 to 3.09 solution disappeared in 7 h (Jobling and Breiby, 1986). However, the erosion rate of otoliths of different species in acid varies (Jobling and Breiby, 1986), possibly depending on the ratio of surface area to volume (da Silva and Neilson, 1985). On the other hand, using otoliths recovered from fecal samples of captive harbor seals (*Phoca vitulina*), Harvey (1989) found no significant relation between the robustness (length/weight) of the otolith and the degree to which the resultant estimate of fish length was reduced. In seal stomachs, all otoliths were released from herring skulls within 6 h and no otoliths were found 12 h after feeding (Murie and Lavigne, 1986; Murie, 1987). In the present experiments, only fragile, somewhat eroded otoliths were recovered after about 20 h of digestion in vitro. Consequently, it would be likely that any intact otoliths that are found in dolphin stomachs are from recently ingested fish.

Walker et al. (1986) reported the recovery of anchovy (*Engraulis mordax*) otoliths from the stomach of a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) that had been held in captivity for 8 days without being fed anchovy; this finding suggested the possibility that otoliths can be retained over a period of one week. In the present experiments, a total of 16 anchovy otoliths (80%) were recovered after 20 h; these otoliths were too eroded, however, to estimate original sizes. Because the forestomach of a dolphin contains no glands, gastric juice must be refluxed from the main stomach (Harrison et al., 1970), so that the retention of otoliths for as long as 8 days should be viewed as exceptional.

The digestion sequences were similar for all experimental species (Table 2). Because otoliths are located inside a fish skull, their size reduction depends on when they are initially exposed to stomach acids. In most cases, heads of fish had disintegrated when about 40–60% of the body had been digested (Table 2), usually some 4 to 15 h after digestion began (Figs. 1 and 2), when most otoliths were probably exposed to the acids and began to erode. Harvey

(1989) found that lengths of prey estimated from the sizes of otoliths in seal feces were underestimated by an average of 27.5%. Although the erosion rate of otoliths may be different for each species (Jobling and Breiby, 1986), it should be possible to apply correction factors to avoid underestimating fish size. The stage of digestion of fish prey in a stomach, for instance, could be used as an index to suggest how much time has passed since feeding.

A significant difference in  $T_{20}$  values for different size groups of a particular prey species was only found in pilchard. Smaller anchovy were digested about 1.2 times faster than larger ones. On the other hand, larger round herring were digested about 1.2 times faster than smaller ones (Table 3). These differences were not significant, however, although there was more variation among samples for anchovy and round herring than for pilchard (Fig. 2). Larger sample sizes may be required to test for differences in digestion rates between different-size individuals of a prey species.

Although it has not been possible to calibrate these in vitro experiments with in vivo information, this paper indicates interspecific differences in relative digestion rates for several prey items taken by dolphins. It should, therefore, be possible to apply "correction factors" to estimate the original amount of particular prey consumed when prey of different digestibility occur together in a stomach. However, the wider application of such a method would require the examination of digestion rates for additional prey species.

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# Development of laboratory-reared sheepshead, *Archosargus probatocephalus* (Pisces: Sparidae)\*

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Twenty-two sparid species are known from the western Atlantic and 15 from eastern coastal waters of the United States and Canada, including two in the genus *Archosargus*: *A. probatocephalus*, sheepshead, and *A. rhomboidalis*, Caribbean sea bream (Johnson, 1978; Robins et al., 1991). Two previous publications have provided partial descriptions of mid- to late larval and juvenile sheepshead based on wild specimens. Hildebrand and Cable (1938) described wild sheepshead larvae and juveniles, beginning with 6-mm-TL larvae. Mook (1977) described osteology of 2–25 mm wild sheepshead, with notes on pigmentation and illustrations of mid- to late larvae and a juvenile. Rathbun (1892) reported a diameter of about 800  $\mu\text{m}$  for sheepshead eggs. Houde and Potthoff (1976) gave a comprehensive description of Caribbean sea bream reared from collected eggs. For other genera in this region, partial descriptions exist for scup (*Stenotomus chrysops*) eggs and larvae (Kuntz and Radcliffe, 1917; Hildebrand and Schroeder, 1928; Wheatland, 1956) and pinfish (*Lagodon rhomboides*) eggs, larvae, and juveniles (Hildebrand and Cable, 1938; Cardeilhac, 1976). This paper describes the size and shape, morphometrics, pigmentation, feeding, and growth for a series of sheepshead reared from eggs to 67-day-old juveniles.

## Materials and methods

### Specimens

Eggs and milt were stripped from a pair of running ripe adults caught in the Indian River just west of Fort Pierce Inlet on 4 April 1984 (398-g female, 367-g male). Larval and juvenile specimens were reared from 14,000 eggs stocked in a 2.4-m diameter cylindrical fiberglass tank holding 3,500 L of water. Filtered estuarine water was supplied from the Indian River, and exchange was increased from zero at day 5 to 300% per day by day 30. During the culture period, water temperature was 22.1–33.2°C (mean 27.0°) and salinity, 27–36 ppt. For the first 7 days, temperature was 23°C and salinity 34–36 ppt. The tank was in a greenhouse that admitted 35% diffuse natural light. The fish were fed cultured rotifers, *Brachionus plicatilis* (days 3–31); cultured artemia nauplii to adults (days 14–47); cultured and wild copepods, *Tigriopus japonicus* and *Acartia tonsa* (days 18–67); bay scallop and penaeid shrimp meal (days 24–77); commercial dry salmon starter feed (days 27–100); wild crab larvae (occasionally during days 28–45); and commercial soft-moist salmon feed (days 36–80). Details of spawning, culture conditions, and foods are given in Tucker (1987). Specimens were preserved in 5% formalin buffered with

sodium acetate; 145 of the preserved specimens and several live specimens were used for the description.

### Measurements and counts

Measurements were made with an ocular micrometer in a stereomicroscope, except that standard and total length of postflexion larvae longer than 9 mm SL were determined with a millimeter scale. Mean diameters of the yolk and oil globule were determined and volumes calculated for ten specimens of each age from 2.5 haf (hours after fertilization) until yolk and oil were exhausted. Notochord length (NL), standard length (SL), total length (TL), snout length, horizontal eye diameter, predorsal length (snout to first dorsal spine [snout-DSp1]), snout to first dorsal ray (snout-DRa1), snout to pelvic spine (snout-PvSp1), preanus length (snout-anus), and body depth at anus were measured as in Houde and Potthoff (1976). Other measurements were upper jaw length—snout tip to posterior margin of maxillary; head length (HL)—horizontal distance from tip of snout to anterior margin of cleithrum at body midline; head depth—greatest vertical depth of head; body depth at pelvic fin—vertical distance from dorsal to ventral body margin at base of second pelvic ray (body at Pv); and caudal peduncle depth—least vertical distance from dorsal to ventral body margin.

Most specimens were fairly transparent, and internal structures such as myomeres were visible during preflexion without clearing and staining. Vertebrae were not counted. The following counts were taken

\* Contribution 1142 from Harbor Branch Oceanographic Institution, Fort Pierce, Florida.

from larvae and juveniles with a stereomicroscope: caudal rays, dorsal spines and rays, anal spines and rays, pectoral rays, and pelvic spine and rays.

## Results and discussion

### Egg development

The planktonic eggs were spherical. The chorion was transparent and smooth; the yolk clear, homogeneous, and unpigmented; and the single oil globule yellow. The perivitelline space was very narrow (12–39  $\mu\text{m}$  before fertilization, 10–48  $\mu\text{m}$  at 5 haf, and 31–77  $\mu\text{m}$  at 28 haf). Diameter of live eggs at 2.5 haf was in the range of 806–865  $\mu\text{m}$  (mean 824  $\mu\text{m}$ ) and was constant until hatching; oil globule diameter range was 187–241  $\mu\text{m}$  (mean 206  $\mu\text{m}$ ). At 2.5 haf, mean yolk volume was 254 nL and oil globule volume was 4.58 nL (Fig. 1). Just before hatching (Fig. 2A), the embryo had sparse pigmentation on the snout and behind the eye. Several punctate melanophores were present on the oil globule. At 23°C, about 90% of the eggs hatched at 28  $\pm$  0.5 haf.

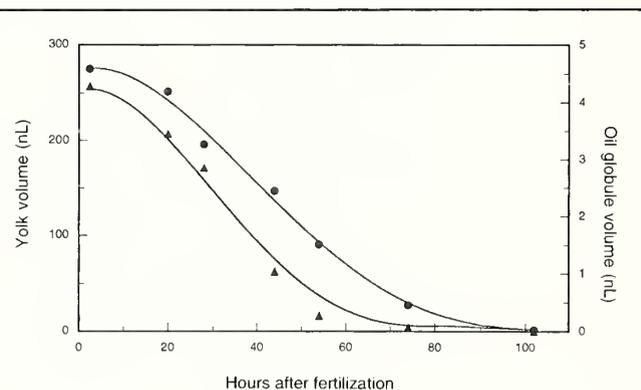
### Larval development

Hatchlings had unpigmented eyes, undeveloped mouths, and clear finfolds (ranges 1.58–1.70 mm NL, 1.68–1.78 mm TL, Fig. 2B). The pigmented oil globule was near the posterior margin of the unpigmented yolk sac, close to the anus. Distinct melanophores were visible on the ventral midline, halfway between the anus and the notochord tip. Several small contracted melanophores were on the body, but no distinct pattern was seen in the examined material. Sixty-seven percent of the yolk remained and 70% of the oil (Fig. 1). At 15 hah (h after hatching), pigmentation was not visible. At 25 hah, live larvae had five distinct vertical bands of yellow pigment, one above the yolk sac, three between the anus and the notochord tip, and one at the notochord tip (Fig. 2C; yellow pigment not shown here, but see photograph in Tucker, 1986). Six percent of the yolk remained and 33% of the oil (Fig. 1). At 45 hah, eyes were only partly pigmented, and the mouth was not yet open. Except for the eyes, no pigmentation was visible in preserved specimens. Two percent of the yolk remained and 10% of the oil (Fig. 1). Between 3 and 4 dah (d after hatching), nearly all larvae developed functioning digestive systems and fully pigmented eyes and began to feed on rotifers. Lower jaw length averaged 0.29 mm. Pigmentation was present on the ventral surface of the gut and anus. Some melano-

phores were visible along the ventral midline. At 73 hah, only 0.2% of the yolk remained and 0.4% of the oil (Fig. 1). At 4.0 dah, larvae were feeding efficiently (Fig. 3A). Rayless pectoral fins were present at 2.37 mm NL. Pigmentation was sparse. Melanophores on the head had disappeared, and those on the gut had contracted. Dendritic melanophores were visible on the surface of the gut and were densest on the dorsal surface. Several distinct melanophores were on the ventral midline. No fin rays were visible. In at least half the specimens, yolk and oil were exhausted; the rest had a trace. At 5.0 dah, shape and pigmentation had not changed appreciably, but by 6 dah, all larvae had melanophores on the gut, as well as preanal and postanal pigmentation on the ventral midline.

At 9 dah, nine larvae (2.78–3.24 mm NL) were still in preflexion (Fig. 3B), and one (3.50 mm NL) had begun notochord flexion. Pigmentation was as for 6 dah. Number and position of branching melanophores on the ventral midline were variable. The larva undergoing notochord flexion also had internal melanophores in the center of the auditory vesicle, one branched melanophore on the forehead, and melanophores on the lower jaw angle and throat. At 14 dah, two larvae (4.16–4.66 mm NL) were in preflexion and eight (4.66–5.36 mm NL) in flexion. Four of the flexion specimens were in early flexion and four in midflexion. Rays began forming above the center of the pectoral fin at 4.66 mm NL and just below the center of the caudal fin at 4.91 mm NL (Table 1).

At 17 dah, all 10 specimens were in midflexion. Caudal rays continued to develop. Rays began forming in the posterior part of the soft dorsal fin at 5.29 mm NL and in the posterior part of the anal fin at 5.36 mm NL. Larvae had two melanophores on the forehead, four



**Figure 1**

Yolk and oil globule depletion in sheephead, *Archosargus probatocephalus*, eggs and larvae. Triangles represent yolk and dots represent oil.

melanophores along the ventral midline, and one large melanophore on the posterior part of the anus. At 21 dah, all larvae were in late flexion (Fig. 3C) and were characterized by a more rounded head and increased pigmentation. Large dendritic melanophores spread over the gut and along the ventral midline. One distinct dendritic melanophore was visible on the forehead and another behind the eye. Small punctate melanophores were visible on the ventral abdomen. In live larvae, reddish chromatophores were scattered over the body but mainly between the developing dorsal and anal fins (not shown in Fig. 3C, but see photograph in Tucker, 1986).

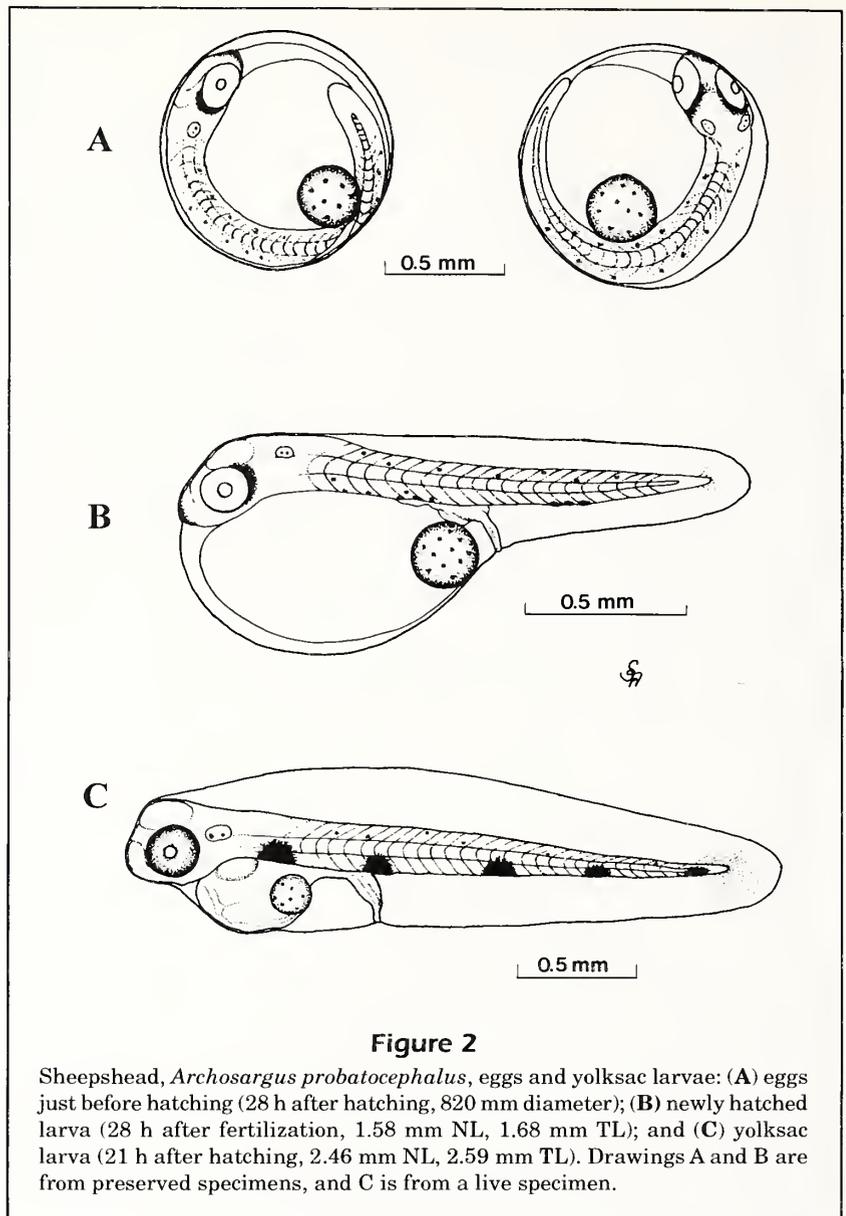
At 28 dah, five larvae had completed flexion. The finfold was gone, and caudal, dorsal, anal, and pectoral fin spines and rays were well developed (Table 1). Caudal rays numbered 21–29 and pelvic rays 0–3. Ten dorsal spines were present in all larvae; the last one was yet to form. Rays began forming at the center of the pelvic fin at 6.24 mm SL. The first and second anal spines were present in all specimens. Punctate melanophores were scattered over the entire body.

### Prejuvenile development

By 28–30 dah, transformation was nearly complete. Adult counts of spines and rays were reached in all fins except for a lack of 0–2 caudal rays, the last dorsal spine, the lowermost 1–2 pectoral rays, and the last pelvic ray (Table 1). Coloration was similar to that of adults, and 5–6 of the characteristic lateral black bars had formed, but the fish were more slender than adults. This could be considered a prejuvenile phase. At 28 dah, two specimens (8.54 and 8.81 mm SL) had become prejuveniles (Fig. 3D). By 38 dah, the adult complement of fin elements was present except for 1–2 caudal rays, one anal spine, and one pectoral ray in some specimens; 1–2 pelvic rays still were missing. Ten of 14 specimens were fully scaled.

### Juvenile development

Between 38 and 53 dah, all specimens reached the juvenile stage and had adult counts for fin elements.



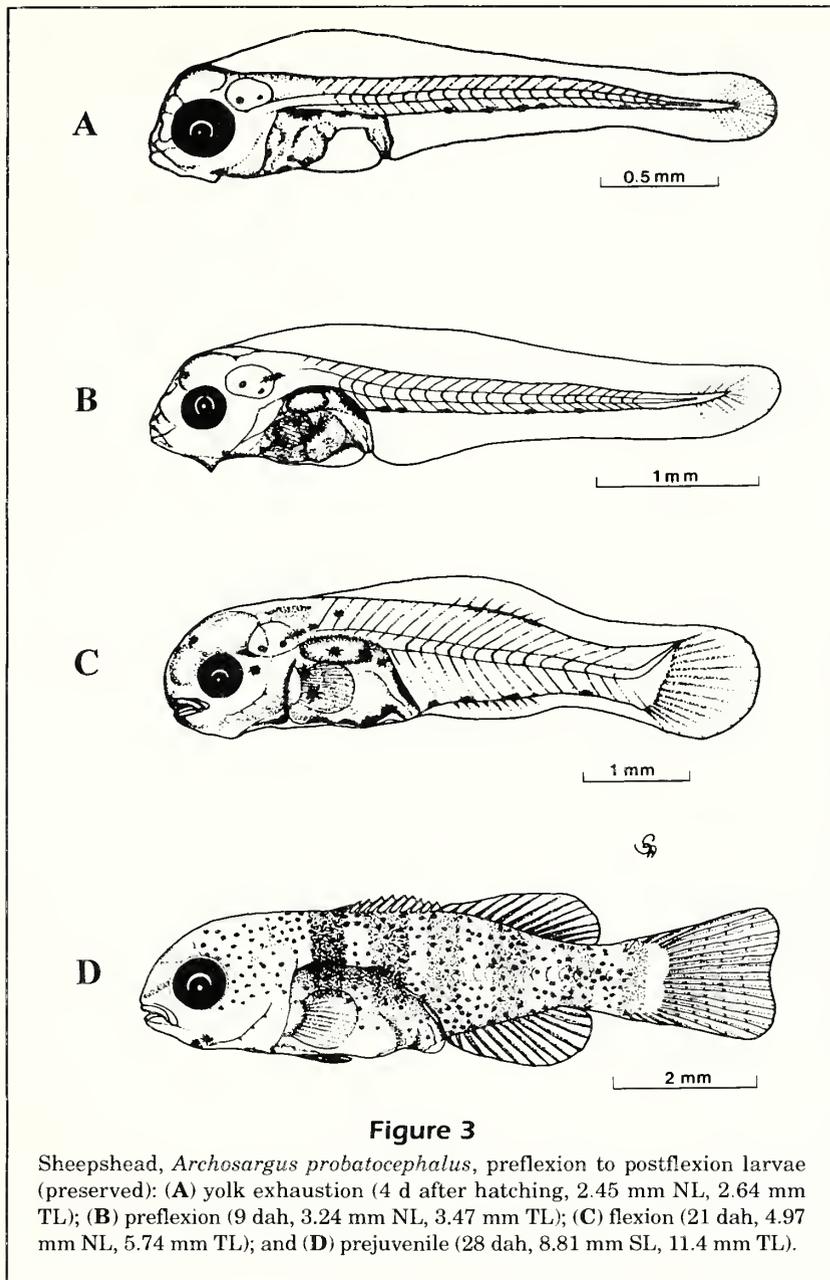
**Figure 2**

Sheepshead, *Archosargus probatocephalus*, eggs and yolksac larvae: (A) eggs just before hatching (28 h after fertilization, 820 mm diameter); (B) newly hatched larva (28 h after fertilization, 1.58 mm NL, 1.68 mm TL); and (C) yolksac larva (21 h after hatching, 2.46 mm NL, 2.59 mm TL). Drawings A and B are from preserved specimens, and C is from a live specimen.

By 42 dah, the body had deepened, but the eye was relatively large. By 67 dah, body proportions of the juveniles were similar to those of adults.

### Proportions

Snout length:head length (HL) varied slightly until 53 dah, then increased to 28% at 67 dah (Table 2). Eye diameter:HL was largest at 0.6 dah (69%) and decreased to 36% at 67 dah. Upper jaw length:HL was greatest at 17 dah and least at 67 dah. HL:body length (BL) was least at 0.6 dah and most at 38 dah, then decreased at 53–67 dah. Snout to first dorsal spine:BL, snout to first dorsal ray:BL, and snout to first pelvic spine:BL were greatest at 38 dah. Snout



**Figure 3**

Sheepshead, *Archosargus probatocephalus*, preflexion to postflexion larvae (preserved): (A) yolk exhaustion (4 d after hatching, 2.45 mm NL, 2.64 mm TL); (B) preflexion (9 dah, 3.24 mm NL, 3.47 mm TL); (C) flexion (21 dah, 4.97 mm NL, 5.74 mm TL); and (D) prejuvenile (28 dah, 8.81 mm SL, 11.4 mm TL).

to anus:BL was minimal at 5–9 dah and greatest at 38 dah. Total length:BL and head depth:BL were least at hatching and most at 38 dah. Body depth at pelvic fin:BL increased between 28 dah and 38–67 dah. Body depth at anus:BL decreased from 17% at 0.6 dah to 14% at 5–6 dah, then rose to 35–36% for 28- and 38-day-old prejuveniles. Caudal peduncle depth:BL increased between 9 dah and 28–38 dah.

At 28 dah, prejuveniles were slightly deeper than postflexion larvae at the pelvic fin and anus. All lengths and depths divided by BL were highest at about 38 dah. Thereafter, postanal length increased relatively faster than the other lengths and depths,

leading to a decrease in proportional measurements, except for body depth at pelvic fin:BL, which was constant during 38–67 dah.

### Growth and survival

Growth of sheepshead to 27.5 mm TL at 67 dah (Fig. 4) was similar to that of Caribbean sea bream (Houde and Potthoff, 1976). Mean dry weight rose from 14.5  $\mu\text{g}$  (about 69 ( $\mu\text{g}$  wet) at 7 dah to 88  $\mu\text{g}$  (464  $\mu\text{g}$  wet) at 67 dah (Fig. 4); mean wet weight was 7.6 g at 101 dah. Survival was 40% from fertilization to 101 dah, and 100% thereafter to 3 years.

### Comparison with other sparids

Our specimens up to 9 dah (Fig. 3B) were younger than previously described sheepshead; most larvae were longer than those at the same stage illustrated by other authors (Hildebrand and Cable, 1938; Mook, 1977), until 6 mm. The 3.9-mm TL larva in Fig. 3B corresponded to the 2-mm specimen illustrated by Mook (1977). The 6.1-mm specimen in Fig. 3C fitted between Mook's (1977) 4- and 4.5-mm specimens and corresponded with Hildebrand and Cable's (1938) ca. 6-mm specimen. The 8.9-mm specimen in Fig. 3D fitted between Mook's (1977) 8- and 11-mm specimens. As Riley et al. (1995) have discussed, net damage to field-caught larvae can shrink and distort them to different degrees, depending on species and stage.

At 23°C, sheepshead hatched at ~28 haf, first fed at ~84 haf (~112 haf) and exhausted their yolk and oil by ~96 haf (~124 haf). At 26°C, Caribbean sea bream hatched by ~22 haf, first fed at about 35 haf (~57 haf), and exhausted yolk by 50 haf (~72 haf) (Houde and Potthoff, 1976). Eggs of gilthead sea bream, *Sparus aurata* (native to the Mediterranean region), with a mean diameter of 1,020  $\mu\text{m}$ , are larger than those of sheepshead and Caribbean sea bream (Table 3) and contain about twice as much yolk and oil (Ronnestad et al., 1994). At 25 haf, gilthead sea bream eggs had 430 nL yolk and 5.8 nL oil, but sheepshead had only 184 nL yolk and 3.6 nL oil. At 18°C (first 6 h at 15–18°C), gilthead

**Table 1**  
Meristic ranges for 65 reared sheepshead, *Archosargus probatocephalus*, larvae and juveniles.

Days after hatching	No. of specimens	Caudal rays	Dorsal spines	Dorsal rays	Anal spines	Anal rays	Pectoral rays	Pelvic spines	Pelvic rays
Preflexion									
9	5	0	0	0	0	0	0	0	0
14	2	0-7	0	0	0	0	0	0	0
Flexion									
9	1	0	0	0	0	0	0	0	0
14	8	7-11	0	0	0	0	2-3	0	0
17	10	9-17	0	5-10	0	3-9	5-7	0	0
21	2	15-16	0	0-6	0	6-9 <sup>2</sup>	7-9	0	0
Postflexion									
28	5	21-29	10 <sup>2</sup>	11-12 <sup>2</sup>	2-3 <sup>1</sup>	10	11-13	0	0-3
Prejuvenile									
28	2	30-32 <sup>1</sup>	10	11-12	3	10-11	13-14	1 <sup>1</sup>	4
38	10	30-34	11	11-13	2-3	10-11	14-15 <sup>1</sup>	1	3-4
Juvenile									
53	10	32-34	11	12-13	3	10-12	15	1	5 <sup>1</sup>
67	10	32-34	11	12-13	3	10-11	15	1	5

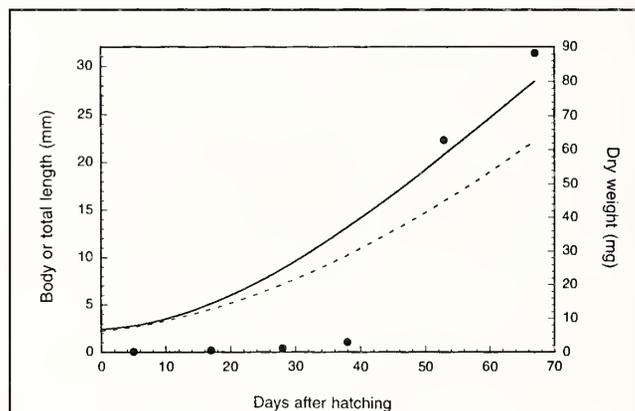
<sup>1</sup> First reached adult number.

<sup>2</sup> First reached adult number, but one more will be added.

sea bream hatched at ~55 haf, first fed at ~100 hah (~155 haf) and exhausted their yolk at ~115 hah (~170 haf) and their oil slightly later. Also at 18°C, pinfish (with similar sized eggs) hatched at ~48 haf and were ready to feed sooner, by ~76 hah (~124 haf)(Cardeilhac, 1976). Oil of unfed pinfish was exhausted at ~150 hah (~198 haf) and yolk at ~165 hah (213 haf).

### Distinguishing characteristics

Between hatching and full eye pigmentation, Caribbean sea bream had little coloration, but sheepshead had five large ventral melanophores and scup three large ventral melanophores. In both sheepshead and scup, one melanophore was over the gut and the second over the anus. In sheepshead, the remaining three were evenly spaced between the anus and notochord tip. In scup, the third melanophore was about halfway between the anus and notochord tip, and each of the three areas of pigment formed more of a lateral band than in sheepshead. From about 2.7 mm to at least 10 mm TL, both sea bream and scup had a ventral row of postanal melanophores associated with myosepta; sheepshead had scattered ventral melanophores, rather than an evenly-spaced row. By about 9 mm TL, prejuvenile sheepshead had five or six distinct lateral black bars on the body; all juveniles had six. Sheepshead from the Atlantic typically have six complete bars, whereas those from the Gulf of Mexico typically have five (Johnson, 1978). By about 15 mm



**Figure 4**

Growth of sheepshead, *Archosargus probatocephalus*, larvae and early juveniles. The dashed curve represents mean body length and the solid curve represents mean total length. Dots represent mean dry weight.

TL, Caribbean sea bream had six indistinct bars (Houde and Potthoff, 1976). By about 25 mm TL, scup had six irregular bars (Johnson, 1978). By about 30 mm TL, pinfish had five or six indistinct bars (Hildebrand and Cable, 1938).

Meristics are only slightly helpful for identification. Western North Atlantic sparids usually have 10 precaudal vertebrae and 14 caudal vertebrae (Jordan and Evermann, 1896-1900; Miller and Jorgenson, 1973; Hoese and Moore, 1977; Johnson, 1978).

Table 2

Summary of proportional measurements of 145 reared sheepshead, *Archosargus probatocephalus*, larvae and juveniles. Except for body length, values are in percentage of head length (HL) or body length (BL). Mean  $\pm$  standard deviation is on the first line, and range on the second. A zero means  $\leq 0.5\%$ . For BL, notochord length (NL) was used through flexion and standard length (SL) after flexion. DSp1 = first dorsal spine, DRa1 = first dorsal ray, PvSp1 = first pelvic spine, and Pv = pelvic fin.

Events and days after hatching	n	Body length (mm)	Percent of head length			Percent of body length									
			Length			Length					Depth				
			Snout (%)	Eye (%)	Upper jaw (%)	Head (%)	Snout-DSp1 (%)	Snout-DRa1 (%)	Snout-PvSp1 (%)	Snout-anus (%)	Total (%)	Head (%)	Body at Pv (%)	Body at anus (%)	Caudal peduncle (%)
<b>Hatching</b>															
0	10	1.65 $\pm$ 0.03	24 $\pm$ 5	58 $\pm$ 5		19 $\pm$ 1					104 $\pm$ 1	13 $\pm$ 1			
		1.58-1.70	14-29	52-67		18-20					103-106	11-15			
0.6	10	2.21 $\pm$ 0.03	22 $\pm$ 4	69 $\pm$ 4		14 $\pm$ 1			47 $\pm$ 1	105 $\pm$ 1	14 $\pm$ 1		17 $\pm$ 1		
		2.16-2.25	19-30	64-77		13-14			46-49	103-106	12-14		16-19		
1.0	10	2.42 $\pm$ 0.01	22 $\pm$ 1	50 $\pm$ 1		17 $\pm$ 0			43 $\pm$ 1	106 $\pm$ 1	14 $\pm$ 0		16 $\pm$ 1		
		2.34-2.47	20-24	47-52		16-18			41-46	105-107	13-15		15-18		
1.9	10	2.59 $\pm$ 0.02	24 $\pm$ 1	50 $\pm$ 1		18 $\pm$ 0			41 $\pm$ 1	106 $\pm$ 0	17 $\pm$ 0		15 $\pm$ 0		
		2.55-2.60	21-26	49-51		17-18			39-43	105-107	16-18		15-17		
<b>Eye pigmentation and first feeding</b>															
3.0	10	2.55 $\pm$ 0.06	21 $\pm$ 2	48 $\pm$ 2		20 $\pm$ 0			41 $\pm$ 1	107 $\pm$ 0	19 $\pm$ 1		15 $\pm$ 0		
		2.45-2.65	19-24	46-51		19-20			40-44	106-107	18-20		14-15		
<b>Yolk and oil exhaustion</b>															
4.0	10	2.46 $\pm$ 0.16	22 $\pm$ 2	46 $\pm$ 2		21 $\pm$ 1			40 $\pm$ 2	107 $\pm$ 1	20 $\pm$ 2		15 $\pm$ 2		
		2.20-2.65	20-26	43-50		20-24			38-44	106-108	17-24		13-17		
5.0	10	2.49 $\pm$ 0.04	22 $\pm$ 2	45 $\pm$ 2		20 $\pm$ 1			38 $\pm$ 1	107 $\pm$ 0	19 $\pm$ 0		14 $\pm$ 1		
		2.43-2.56	19-25	42-48		19-22			37-40	107-108	18-20		12-15		
6	10	2.43 $\pm$ 0.09	20 $\pm$ 1	42 $\pm$ 1	37 $\pm$ 4	22 $\pm$ 0			40 $\pm$ 1	107 $\pm$ 1	20 $\pm$ 1		14 $\pm$ 1		
		2.25-2.54	19-22	40-44	29-41	21-22			38-42	103-108	18-20		12-17		
9	5	3.10 $\pm$ 0.12	22 $\pm$ 5	43 $\pm$ 4	36 $\pm$ 6	22 $\pm$ 1			39 $\pm$ 1	107 $\pm$ 2	21 $\pm$ 2		16 $\pm$ 2	3 $\pm$ 1	
		2.78-3.24	17-31	39-48	30-43	21-24			38-42	105-111	18-23		14-17	2-4	
14	2	4.41 $\pm$ 0.35	20 $\pm$ 2	40 $\pm$ 0	36 $\pm$ 8	25 $\pm$ 1			49 $\pm$ 1	105 $\pm$ 1	25 $\pm$ 1		24 $\pm$ 1	7 $\pm$ 1	
		4.16-4.66	18-22	40	28-43	24-25			48-50	104-106	24-27		23-24	6-8	
<b>Flexion</b>															
9	1	3.50	21	40	31	23			40	106	22		18	4	
14	8	5.06 $\pm$ 0.21	21 $\pm$ 3	38 $\pm$ 2	38 $\pm$ 6	26 $\pm$ 1			51 $\pm$ 1	106 $\pm$ 2	26 $\pm$ 1		24 $\pm$ 1	8 $\pm$ 1	
		4.66-5.36	18-26	36-42	34-51	24-27			49-52	103-110	25-27		23-25	8-9	
17	10	4.92 $\pm$ 0.51	23 $\pm$ 5	37 $\pm$ 5	41 $\pm$ 3	28 $\pm$ 2			54 $\pm$ 4	114 $\pm$ 5	27 $\pm$ 2		26 $\pm$ 3	11 $\pm$ 3	
		3.90-5.41	14-35	26-43	36-44	24-30			49-59	104-124	26-30		21-31	4-13	
21	2	4.95 $\pm$ 0.05	22 $\pm$ 4	38 $\pm$ 0	35 $\pm$ 2	28 $\pm$ 0			54 $\pm$ 0	116 $\pm$ 1	28 $\pm$ 1		25 $\pm$ 0	10 $\pm$ 0	
		4.92-4.97	19-24	38	33-36	28-29			54	115-117	28-29		25-26	10	
<b>Postflexion</b>															
28	5	6.60 $\pm$ 0.79	22 $\pm$ 2	41 $\pm$ 2	32 $\pm$ 3	34 $\pm$ 2	40 $\pm$ 1	65 $\pm$ 2	37 $\pm$ 2	59 $\pm$ 2	124 $\pm$ 2	34 $\pm$ 2	33 $\pm$ 3	31 $\pm$ 3	14 $\pm$ 1
		5.83-7.93	20-25	38-43	27-36	30-36	39-42	63-67	35-39	57-61	122-126	29-35	29-36	26-35	13-15
<b>Prejuvenile</b>															
28	2	8.68 $\pm$ 0.19	23 $\pm$ 1	39 $\pm$ 0	28 $\pm$ 7	35 $\pm$ 2	39 $\pm$ 3	64 $\pm$ 3	40 $\pm$ 1	59 $\pm$ 0	124 $\pm$ 1	34 $\pm$ 1	35 $\pm$ 1	36 $\pm$ 2	15 $\pm$ 1
		8.54-8.81	22-24	39	23-33	33-36	37-41	62-66	39-40	59	123-124	33-35	34-36	34-37	14-15
38	10	7.22 $\pm$ 0.64	21 $\pm$ 1	39 $\pm$ 1	26 $\pm$ 1	40 $\pm$ 1	44 $\pm$ 2	77 $\pm$ 2	44 $\pm$ 1	68 $\pm$ 2	132 $\pm$ 3	35 $\pm$ 1	37 $\pm$ 2	35 $\pm$ 2	15 $\pm$ 1
		6.05-10.3	19-23	37-40	24-29	38-42	42-47	74-79	42-46	65-71	126-134	34-38	35-38	30-37	13-16
<b>Transformation</b>															
53	10	18.6 $\pm$ 3.2	22 $\pm$ 1	38 $\pm$ 1	26 $\pm$ 1	33 $\pm$ 1	34 $\pm$ 1	63 $\pm$ 1	36 $\pm$ 1	61 $\pm$ 1	129 $\pm$ 1	28 $\pm$ 0	38 $\pm$ 2	33 $\pm$ 2	13 $\pm$ 0
		13.7-24.7	21-24	35-40	25-27	30-35	33-36	62-66	34-39	60-63	128-130	27-29	36-42	31-36	12-14
67	10	21.5 $\pm$ 5.2	28 $\pm$ 3	36 $\pm$ 2	24 $\pm$ 2	33 $\pm$ 1	36 $\pm$ 2	65 $\pm$ 2	40 $\pm$ 2	62 $\pm$ 2	128 $\pm$ 0	29 $\pm$ 1	37 $\pm$ 1	32 $\pm$ 2	13 $\pm$ 0
		15.9-33.7	22-34	33-39	20-26	31-35	34-38	62-68	37-42	59-65	126-130	27-31	36-40	31-35	12-14

Dorsal ray, anal spine, anal ray, pectoral ray, and caudal ray counts of sheepshead overlap with those of most other sparids (Table 4). For most species of *Archosargus*, *Calamus*, *Diplodus*, *Lagodon*, *Pagrus*, and *Stenotomus*, 11 or 12 dorsal spines are typical, with a range of 10–13. Dorsal rays mostly number

10–12, with a range of 9–16, and anal rays mostly are 10–11, with a range of 8–15. Caudal rays usually are in the range of 32–38, with 9+8 principal rays. For sheepshead, typical counts followed by ranges in parentheses are caudal rays 32–33 (8–9+9+8+7), dorsal spines 12 (10–12), dorsal rays 11 (10–13), anal

**Table 3**

Spawning, egg, and hatchling data for sheepshead, *Archosargus probatocephalus*; Caribbean sea bream, *Archosargus rhomboidalis*; pinfish, *Lagodon rhomboides*; and scup, *Stenotomus chrysops*.

	Sheepshead	Sea bream	Pinfish	Scup
Location	Florida	Florida	Florida	Northeastern U.S.
Spawning season	Feb–Apr	Sep–May	Oct–Mar	May–Aug
Egg diameter (µm)	806–865	800–940	990–1,050 <sup>1</sup>	800–1,150
Oil globule diameter (µm)	187–241	210–260	~200 <sup>1</sup>	140–280
Hatching temperature (°C)	23	24	18	22
Incubation time (h)	28	~<22	48	≤40
Hatchling length (mm TL)	1.7–1.8	2.1–2.3		~2
References	Present study	Houde and Potthoff, 1976	Caldwell, 1957 Cardeilhac, 1976	Kuntz and Radcliffe, 1917 Hildebrand and Schroeder, 1928 Wheatland, 1956

<sup>1</sup> Unfertilized.

**Table 4**

Comparison of selected larval and juvenile characters of sheepshead, *Archosargus probatocephalus*, reared at a mean temperature of 23°C and Caribbean sea bream, *Archosargus rhomboidalis*, reared at 26°C (Houde and Potthoff, 1976): size and age from first development to completion in all specimens. Less common counts are in parentheses. Because specimens were not taken every day, age ranges are approximate. BL = body length; dah = days after hatching.

	<i>Archosargus probatocephalus</i>			<i>Archosargus rhomboidalis</i>		
	Adult number	BL (mm)	Age (dah)	Adult number	BL (mm)	Age (dah)
Hatchling		1.6–1.7			2.0–2.2 <sup>1</sup>	
Flexion		3.5–5.0	9–21		4.2–4.9	9–11
Pectoral rays	15	4.7–10.3	14–38	14(15)	5.0–8.0	11–15
Caudal rays	(8)9+9+8+7–8(9)	4.9–13.7	14–53	(10)8–9+9+8+7–8(9)	4.1–10.2	7–16
Dorsal rays	12–13	5.3–13.7	17–53	10–11	5.0–5.7	11–13
Anal rays	10–11(12)	5.4–6.4	17–28	10(11)	5.0–5.7	11–13
Pelvic rays	5	6.2–13.7	28–53	5	6.6–15.6	26–37
Dorsal spines	11	7.2–8.5	28–38	(12)13(14)	5.7–8.2	13–16
Prejuvenile <sup>2</sup>		≥6.0, <13.7	≥28, <53			
Pelvic spines	1	8.5–9.5	28–38	1	6.6–15.6	26–37
Anal spines	3	8.5–13.7	28–53	3	5.4–7.1	13–26
Juvenile <sup>3</sup>		13.7	>38, ≤53		20.0	~35

<sup>1</sup> Smallest specimens described.

<sup>2</sup> Juvenile coloration attained; all fin elements present except last dorsal spine, last pectoral ray, and last one or two pelvic rays.

<sup>3</sup> All fin elements present, and fish fully scaled.

spines 3, anal rays 10–11 (9–11), pectoral rays 15–17, pelvic spine 1, pelvic rays 5 (Miller and Jorgenson, 1973; Johnson, 1978). Caribbean sea bream usually have 13 dorsal spines, whereas sheepshead, pinfish, and most other sparids usually have 12. *Diplodus* spp. have slightly higher counts than most sparids: 11–13 dorsal spines, 13–16 dorsal rays, and 13–15 anal rays. *Pagrus* species have fewer anal rays, usually 8.

Stage of development at a given size could be useful for distinguishing larvae. At the same stage, scup tended to be much longer than sheepshead (Fig. 4) and Caribbean sea bream. Kuntz and Radcliffe's (1917) 25-mm TL scup (their Fig. 36) corresponds with Houde and Potthoff's (1976) 12.8-mm TL sea bream (their Fig. 5a) and our 8.9-mm TL sheepshead (Fig. 3D).

The proportions snout length:BL (3–8%), eye diameter:BL (7–14%), predorsal length:BL, snout to first dorsal ray:BL, snout to pelvic spine:BL, preanus length:BL, and body depth at anus:BL (Table 2) all were similar during development of sheepshead and Caribbean sea bream (Houde and Potthoff, 1976). Eye diameter and body depth are relatively small in scup at 10 mm TL. At that size, eye diameter:HL was about 32% in scup, 37% in sea bream, and 39% in sheepshead; depth at pelvic fin:SL was 27% in scup, 34% in sea bream, and 37% in sheepshead.

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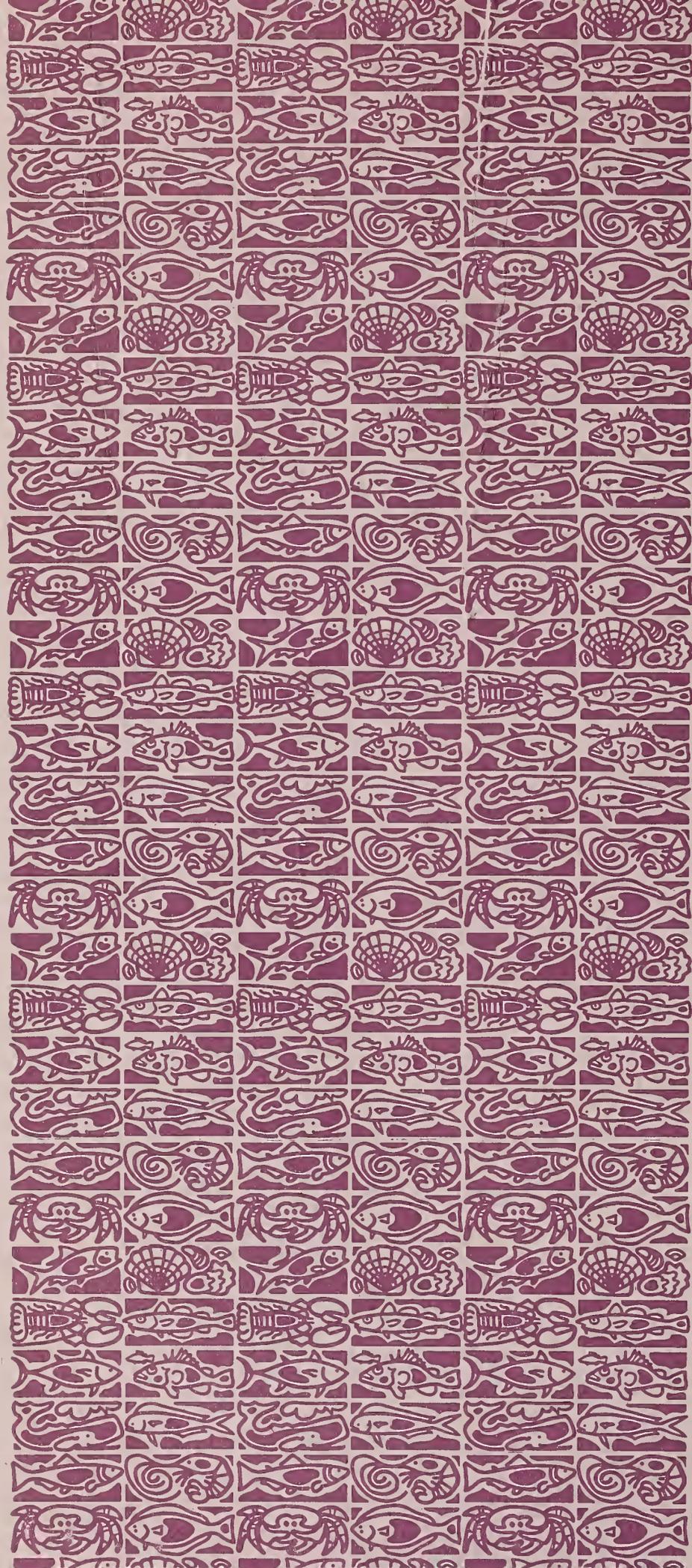
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