

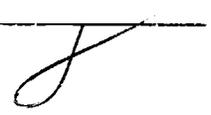
AN ABSTRACT OF THE THESIS OF

Andrew A. Rosenberg for the degree of Master of Science
in Oceanography presented on May 7, 1980

Title: Growth of Juvenile English Sole, *Parophrys vetulus*, in
Estuarine and Open Coastal Nursery Grounds

Redacted for Privacy

Abstract approved: _____

William G. Pearcy 

The growth of English sole juveniles, during 1978-79, is described in detail from estuarine and non-estuarine nursery grounds on the Oregon coast. Counts of fortnightly growth rings on otoliths were used to determine size-at-age. Mean growth rates were similar for the two areas, but variability in size-at-age was much greater among fish captured in the estuary.

Back calculation of individual growth, using radial measurements on the otoliths, showed that growth proceeds linearly during this period. Differences in average growth among individual fish accounts for the high variability in size-at-age for fish using the estuary. Fish from the estuary grew slightly faster, on average, in 1979 compared to 1978.

Settlement of English sole larvae to the benthic habitat, determined from age data, occurred over the winter and spring in the non-estuarine nursery area. In the estuary, settlement was more

concentrated in the early winter.

The implication of these patterns of growth and a suggestion for further research is discussed.

Growth of Juvenile English Sole, Parophrys vetulus,
in Estuarine and Open Coastal Nursery Grounds

by

Andrew A. Rosenberg

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed May 7, 1980

Commencement June 1981

APPROVED:

Redacted for Privacy

Professor of Oceanography
in charge of major



Redacted for Privacy

Dean of the School of Oceanography

Redacted for Privacy

Dean of the Graduate School

Date thesis is presented _____ May 7, 1980

Typed by Larky Hansen for _____ Andrew A. Rosenberg

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. W. G. Pearcy for his patience and strong guidance during the course of this study. Dr. C. B. Miller provided much needed discussion and editorial advice. Dr. A. V. Tyler and Mr. B. Olla suggested many concepts and viewpoints and reviewed the manuscript.

Dr. B. Frey, C. Creech and E. Krygier provided accessory data. Many students and staff of Oregon State University made this study possible with their assistance in the field and continuing encouragement.

Dr. Joanne Laroche assisted, aided and abetted in all phases of this work and deserves my deepest gratitude. Waldo Wakefield shared the work and my thoughts throughout and truly made the completion of this thesis possible. H. Havnevik provided incentive.

Funding was provided by Sea Grant Project No. A/OPF-1.

TABLE OF CONTENTS

I. Introduction.....1
 Determination of Growth Using Otoliths.....2
 An Overview of the Biology of Parophrys vetulus.....3
 A Brief Description of the Study Area.....5

II. Methods.....6

III. Results..... 8
 Biological Data..... 8
 Environmental Data.....12

IV. Discussion.....14
 Growth.....14
 The Distribution of Recruitment to the Benthic Habitat.....20

Bibliography.....22

Tables.....26

Figures.....30

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1 The study area. Sampling stations are indicated by the letters A-G. Station depths are given in Table 1.	30
2 An otolith from a 110 mm SL <u>Parophrys</u> captured in Yaquina Bay. Daily and fortnightly rings are clearly shown. Fourteen daily rings can be counted between the two fortnightly rings indicated by the arrows. There are 21 fortnightly rings on this otolith and the total age is 363 days. Magnification is 200X.	32
3 Size-at-age data for fish captured in the Moolach Beach nursery area.	34
4 Size-at-age data for fish captured in the Yaquina Bay nursery area.	36
5 Backcalculated growth of eight individuals from Moolach Beach during 1978-79.	38
6 Backcalculated growth of 16 individuals from Yaquina Bay during 1978-79.	40
7 Size-at-age data from Yaquina Bay plotted by year of capture.	42
8 Salinity, temperature, and sampled English sole densities for the study areas. Salinity (in parts per thousand) is for Yaquina Bay only. The English sole density data from Yaquina Bay was divided by 10 to obtain the plotted values. Density data is uncorrected for gear efficiency.	44
9 Distribution of recruitment to the benthic habitat (assumed to be 120 days of age) during 1978-79 in the Moolach Beach nursery.	46
10 Distribution of recruitment to the benthic habitat during 1978-79 in the Yaquina Bay nursery.	48
11 Comparison of length frequency modal progression analysis with size-at-age regression for Yaquina Bay fish in 1979. The vertical lines indicate the range in observed lengths. The dots indicate the mode of the distribution selected as the size class with the greatest relative abundance in the samples taken on that date.	50

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1 Sampling dates, stations occupied and station depths.	26
2 Analysis of variance for the least squares multiple regression analysis of size-at-age data from: A. Moolach Beach (Figure 3), B. Yaquina Bay (Figure 4).	27
3 Observed densities of English sole juveniles 20 mm or less in the two nursery grounds during 1978 and 1979.	28
4 Summary of growth estimates from previous studies. The data was recalculated so that direct comparisons can be made.	29

GROWTH OF JUVENILE ENGLISH SOLE, PAROPHRYS VETULUS,
IN ESTUARINE AND OPEN COASTAL NURSERY GROUNDS

I. INTRODUCTION

The life cycle of many marine fishes contains a stage in which the juveniles of the species are concentrated in a specific area or nursery ground where the adults are uncommon. On both the east and west coasts of North America, estuarine areas are extensively used as nursery grounds for a large number of species (Gunter, 1961; Pearcy, 1962; McHugh, 1966; 1967; Haedrich, in press). Many east coast fishes are considered to be dependent on estuaries during early life. On the west coast, estuarine dependence has not been clearly demonstrated (McHugh, 1967; Pearcy and Myers, 1974). The high productivity of estuarine areas, which provide improved growth conditions for juvenile fish, the apparent lack of large predators, and reduction of competition among age groups of a species are frequently invoked explanations for this phenomenon (Haedrich, in press; Kuipers, 1977). Unfortunately, it is difficult to test these hypotheses for most species of fish, since nursery areas for a single species that represent both estuarine and non-estuarine environments in a fairly small geographic range are uncommon.

Parophrys vetulus Girard, off the Oregon coast, is a good subject for a study of this type, since it uses both types of habitats during the first year of life (Laroche and Holton, 1979). This study examines the growth of Parophrys vetulus juveniles from two nursery grounds: Yaquina Bay, an estuary, and the open coastal area off Moolach Beach,

Oregon. Size-at-age data are used to detail growth during the first year.

Determination of Growth Using Otoliths

A description of growth is a prerequisite to calculations of production and recruitment, and is important in estimating mortality. Growth varies with environmental conditions and may provide an index of the physiological and ecological response of the fish to its habitat (Pearcy, 1962; Beyer and Laurence, 1980). Growth and survival during the juvenile period are important determinants of overall stock size and production (Cushing and Harris, 1973).

Determination of growth rates in the field requires some method of aging individual animals, so that size-at-age data may be obtained. Until recently, this was commonly accomplished, for larvae and juveniles, either by following modal progressions through time in length frequency distributions or by laboratory rearing experiments in which the fish are of known age. Some studies of juvenile fishes have also utilized seasonal patterns of otolith growth to describe overall growth of the fish (Pearcy, 1962; Reay, 1972; Scott, 1973). A technique has now been developed which estimates the age of young fish with counts of daily and fortnightly growth rings on their otoliths. Several studies have verified the daily periodicity of growth rings by rearing larvae in the laboratory and examining otoliths from fish of known age (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977). Pannellia (1971) counted small growth increments between successive annual rings on the otoliths of several species of fish. Based on a

mean count of 360 rings per annulus, he concluded that the pattern was daily. In a later paper (Pannella, 1974), he reported that fortnightly growth rings were a consistent pattern on the otoliths of 29 species. Fortnightly banding patterns on mollusc valves are well documented (Rosenberg and Jones, 1976). Daily or fortnightly growth ring counts have only been used in a few studies of natural populations (Methot and Kramer, 1979; Brothers and MacFarland, 1979).

Laroche et al. (in prep.) reared English sole larvae in the laboratory. They found that, although there was a large amount of variability in the time after hatching when the first ring was formed (up to 10 days in the laboratory; J. Laroche, unpub.) there is a good one-to-one correspondence between number of rings and number of days after hatching. Most of the studies cited above report some variability in the correspondence between rings and days. Possibly, some of this variation results from error in counting the rings, rather than in their actual periodicity.

An Overview of the Biology of *Parophrys vetulus*

Parophrys vetulus is a commercially important pleuronectid distributed nearshore from Point Conception to Alaska (Hart, 1973; Alverson et al., 1964). A single spawning stock occurs off the Oregon coast, based on growth studies and some tagging information (Kreuz, 1979; Barss, 1976). Tagging and catch record data (Hewitt, 1980) indicate that the fish move north and inshore to feed and south and offshore to spawn. Hecata and Stonewall Banks, off the central Oregon coast, appear to be major spawning grounds for this species (Hewitt,

1980). The spawning period is protracted and has been reported to vary extensively in timing and duration from year to year (Laroche and Richardson, 1979; Kruse and Tyler, MS).

Larval Parophrys are planktonic and, at times, very abundant in Oregon coastal waters (Laroche and Richardson, 1979). Larval growth from hatching to metamorphosis has been described in detail, using otolith aging, by Laroche et al. (in prep.). The length of larval life has been estimated by combining the length-at-age data for larvae and juveniles (Rosenberg and Laroche, MS). Larvae apparently begin to settle out of the water column and assume the demersal form at about 60 days after hatching. No larvae older than 75 days were found in the bongo samples examined by Laroche et al. (in prep.). A description of growth during the metamorphic period (Rosenberg and Laroche, MS) shows a prolonged plateau in growth in length between 60 and 120 days of age. During this time, the larvae undergo extensive morphological changes and are adapting to the benthic habitat. This plateau occurs when the larvae are 18-22 mm SL, with the majority of individuals 20 mm long.

The pelagic larvae of P. vetulus are transported inshore and are found, as benthic juveniles, in several types of nursery areas. It is not known whether the larvae settle directly in the nursery areas or swim into the nearshore region after settling farther offshore. Estuarine nursery grounds in Oregon waters have been described by Westrheim (1955), Olson and Pratt (1973), and Percy and Myers (1974), and by other authors for California estuaries (Smith and Nitsos, 1969; Eldridge, 1970; Misitano, 1976). English sole are also reported to

use non-estuarine, nearshore, sandy, protected areas (Ketchen, 1956; Kendall, 1966) and exposed coastal regions (Laroche and Holton, 1979) as nursery grounds during the first year of life.

A Brief Description of the Study Area

The two areas considered in this study are the lower part of Yaquina Bay, Oregon and the area off of Moolach Beach, Oregon between the depths of 9 and 30 meters (Figure 1).

Moolach Beach lies between Yaquina Head to the south and Cape Foulweather to the north. The nearest estuarine embayments are Yaquina Bay, 10 km south and Siletz Bay, 26 km north. The nearshore area itself is sandy and unprotected from the open Pacific.

Yaquina Bay lies 5.6 km south of Yaquina Head. The bay is small, with an area of 11.6 km^2 (Pearcy and Myers, 1974) and is subject to mixed, semi-diurnal tides. The mean tidal range is 1.7 m (Kulm and Byrne, 1967). Temperature and salinity in the bay are very variable, but the lower bay is generally well mixed in summer and partially mixed in winter (Frolander et al., 1973). Winter rains reduce the salinity greatly for short periods of time (Frolander et al., 1971). Seasonal coastal upwelling strongly affects the temperature and productivity of both the estuary and the Moolach Beach area.

II. METHODS

Sampling was conducted from September, 1978 through September, 1979 at Moolach Beach and Yaquina Bay. The sampling stations are shown in Figure 1 and indicated by the letters A through G. Table 1 lists the sampling dates, stations occupied, and the depth of each station.

A tow was made at each station with a 1.5 m wide beam trawl lined with 7 mm stretch mesh. Tows were 5 or 10 minutes in duration in Yaquina Bay and at Moolach Beach, respectively. The beam trawl was equipped with a 1.0 m circumference odometer wheel to measure the distance travelled on the bottom. Measurements of bottom temperature and salinity were also made at each station.

All fish captured were preserved in strongly buffered formaldehyde. In the laboratory, all fish were identified and measured for standard length (SL). Both saccular otoliths were removed from each English sole. In cases where large numbers of P. vetulus were captured, individuals were selected to cover the size range of the sample. The otoliths were mounted on microscope slides in the synthetic mounting medium Pro-Texx.

One otolith from each fish was ground on 600 grit carborundum paper to a thin section along a sagittal plane through the nucleus. The sections were examined under 250x magnification using either brightfield or polarized illumination. Counts of fortnightly rings were made on each bone. No fortnightly rings could be detected in the central area of the otoliths, which apparently represent the time the larvae are in the plankton. Therefore, daily rings were counted from

the nucleus out to the first fortnightly ring. The actual age of each fish is calculated by summing the number of daily rings in the nuclear area, the number of fortnightly rings times 14, and the mean age of first daily ring formation (5; Laroche et al., in prep.).

The count of rings on each otolith was repeated until the same count was obtained three times. As a further check on the accuracy of the counts, a set of 42 otoliths were recounted several months later and a mean error computed. Counts of the number of daily rings between fortnightly rings were made on 40 specimens to check the consistency of the fortnightly pattern. Counts of the number of fortnightly rings between consecutive annual rings were made on 15 otoliths from older fish as a further test of the fortnightly periodicity.

Individual growth curves of 25 fish were backcalculated by making radial measurements to every other fortnightly ring, along the same axis from the nucleus to the anterior edge of the bone. From these measurements and the linear relationship between otolith radius and standard length of the fish¹, length-at-age for various points in the life of an individual were calculated.

Length frequency information for English sole juveniles sampled in 1978 were provided by Krygier and Pearcy (unpub.). Temperature data for Yaquina Bay were obtained from Creech (unpub.). Salinity data were provided by Frey (unpub.).

1. A regression of standard length on anterior otolith radius was performed on 60 data points. The resulting equation was: $Y = 0.86x + 4.5$ where Y is standard length in mm and x is the distance from the nucleus to the anterior edge of the otolith in arbitrary units. $r^2 = 0.98$ for this regression.

III. RESULTS

Biological Data

Counts of daily rings between fortnightly rings yielded a mean of 13.95 with a standard deviation of 0.63. The mean number of fortnightly rings between consecutive annual rings was 26 with a standard deviation of 1.13. The mean difference between repeated counts of fortnightly rings made a substantial period of time was 1.45 rings. Figure 2 clearly shows the daily and fortnightly patterns on a Parophrys otolith. The first fortnightly ring is consistently formed when the fish is 60-75 days old, i.e., the age of metamorphosis and settlement to the benthic habitat.

Basic growth data for the two nursery areas were obtained from size-at-age information. The data for 218 fish captured at Moolach Beach are shown in Figure 3. Two linear portions of the data, with different slopes, can be distinguished and separated by an inflection point. A least squares multiple regression on these data was performed using the following model:

$$Y = B_0 + B_1X + B_2A_1 + B_3A_2 + E \quad (1)$$

where Y is the standard length in millimeters, X is the age in days, A_1 is a dummy variable whose value is zero to the left of the inflection point and one to the right of the inflection point, and A_2 is equal to X times A_1 , i.e., the interaction between the independent variable and the dummy variable. The B terms are the regression coefficients and E indicates the error terms. This regression technique, using a dummy variable, fits lines to the data on either side of the

inflection point with one equation. It is mathematically equivalent to fitting separate regressions to the data above and below the inflection. Use of the multiple regression technique facilitates an iterative search for the point of inflection which produces the smallest residual sum of squares. This point was found to be 140 days of age for the Moolach Beach data. The analysis yielded the equation:

$$\hat{Y} = 16.87 + 0.051X - 32.92A_1 + 0.23A_2$$

An analysis of variance for the regression (Table 2A) shows that a relatively good fit was obtained with this model², and the data set has a fairly low estimated variance. The slopes of the regression below and above 140 days of age were computed as 0.051 and 0.279 respectively. These slopes are estimates of the mean growth rate per day for juvenile Parophrys utilizing the Moolach Beach nursery area. The lower portion of the data, below 140 days of age, shows the plateau in growth attributed to the metamorphic period (Rosenberg and Laroche, MS).

The size-at-age data for Yaquina Bay juveniles are shown in Figure 4. The same multiple regression model (equation 1) was fit to this data set of 186 points. The fitted equation is:

$$\hat{Y} = 13.01 + 0.083X - 33.45A_1 + 0.201A_2$$

The analysis of variance for this model (Table 2B) once again shows that a good fit was obtained, but the estimated variance is much higher than for the Moolach Beach data. The inflection point with

2. A semi-logarithmic transformation was performed on the data in an effort to linearize and stabilize the variance in the data. This transformation did not turn out to be useful, since a better fit could be obtained to the untransformed data.

the smallest residual sum of squares was also 140 days of age for the Yaquina Bay data. The slopes below and above the inflection are 0.083 and 0.284 respectively. The plateau at metamorphosis is not as clear in these data because of a few outlying points just left of the inflection point. This does not affect the slope of the upper portion of the data however.

The first step in comparing the regression lines of growth for English sole from the two nursery grounds was to test for statistical equality of variances. This was done by examination of the ratio of the mean square errors of the fitted regressions. The ratio is distributed as $F(184;216)$ and is significant at the $P = 0.001$ level. This can be seen by inspection of Figures 3 and 4 and the estimated variances: 19.88 for Moolach Beach, and 95.01 for Yaquina Bay data. Since the variances are unequal, statistical tests for equality of slopes or intercepts are not strictly valid (Scheffé, 1959). However, the slopes do not appear to be meaningfully different in any case: 0.284 and 0.279.

The intercepts do appear to be slightly different. Above 140 days of age, the intercepts (-16.05 for Moolach Beach, -20.44 for Yaquina Bay) may indicate that fish at Moolach Beach start their juvenile growth at a younger age than individuals in the estuary. Since the data are far from the origin, the intercepts are difficult to interpret however.

Backcalculated growth data for individuals from both areas are in good agreement with growth estimates from the size-at-age data (Figures 5 & 6). The plots are, in general, linear. Slight changes

in slope do occur in all the lines. This may indicate small variations in individual growth through the juvenile period, changes in the linear nature of the relationship between otolith growth and overall fish growth, or measurement error. By inspection, these variations do not occur at coincident times among individuals. The average slope of each plot was determined by simply comparing successive points on the curve, and taking the mean rate of change in size-at-age for the backcalculated points. For the Moolach Beach data (Figure 5), the average slope of the eight lines ranged from 0.20 to 0.28. A rank sum test was performed to test for differences in growth rate between years. There was no significant difference in growth rate between 1978 and 1979 for this small sample of fish from the open coastal area.

Individual growth backcalculated from the otoliths of 17 fish captured in Yaquina Bay range in average slope from 0.19 to 0.32 (Figure 6). The growth rates of fish collected in 1978 and 1979 were significantly different ($P = 0.005$, non-parametric rank sum test). The range in average slope for the 1978 group is 0.19 to 0.25, and for the 1979 group, 0.21 to 0.32. Since the sample size was small, this test is rather weak, but examination of the size-at-age data by year (Figure 7) tends to support the results of the backcalculations. Only a relatively small number of individuals from 1978 were sampled, because sampling did not begin until the end of the year, and this may influence the data.

The growth rate (above 140 days of age) calculated from the Yaquina Bay size-at-age regression falls well within the range of growth rates obtained from the backcalculations. Delayed resumption

of growth after metamorphosis, changes in the growth rate of individuals with age, or simple differences in average growth rate among individuals would result in variability in size-at-age. The back-calculation data from Yaquina Bay (Figure 6) indicate that simple differences in average growth rate among individuals can account for the full range of observed variability in Figure 4.

The ability to accurately determine the age of each fish allows backcalculation of the date of metamorphosis and recruitment to the benthic habitat by individuals. This was done by calculating the month in which each fish was 120 days old, which was taken as the age when juvenile Parophrys become fully vulnerable to the benthic sampling gear. The recruitment of fish using the Moolach Beach nursery ground was distributed over the winter and spring (Figure 9). During the summer, recruitment declined and was zero by July in 1978 and by September in 1979.

For juveniles captured in the estuary, recruitment appeared to be concentrated over a few winter months (Figure 10). A sharp peak is evident in November, December and January. As in the Moolach Beach data, recruitment is reduced in the summer, but it reappears in the fall among Yaquina Bay fish.

Environmental Data

Temperature, salinity, and English sole densities were plotted for 1978-79 (Figure 8). The Yaquina Bay temperatures were obtained from observations taken every three hours at the Coast Guard Station dock in the bay at a depth of 6.7 m (Creech, unpub.). These

observations were averaged over five day periods to obtain the plotted data. The temperature measurements at Moolach Beach were obtained only when sampling was conducted there, so are very scattered in time. The general pattern agrees with the Yaquina Bay data.

The salinity data (Figure 8) are for Yaquina Bay only. A good time series was unavailable for the Moolach Beach area. The data were obtained in 5.5 m of water at the Marine Science Center dock in the bay. Only the general trend in salinity is indicated, but short term fluctuations about this line are a consistent feature of the estuary, especially during the winter months (Frey, unpub.). Salinity at Moolach Beach is probably not very variable (Krygier, unpub.; Huyer, 1977).

Mean juvenile English sole densities in the two nursery grounds as sampled by this study (Figure 8) are uncorrected for gear efficiency, and so only indicate trends in fish densities. Actual biomass data are unavailable. The sampled densities in Yaquina Bay were consistently an order of magnitude higher than at Moolach Beach (note that the values plotted in the figure for Yaquina Bay are the actual values divided by 10).

IV. DISCUSSION

Growth

The various tests performed to verify the technique of counting daily and fortnightly growth rings all indicate that the periodicities are consistent and counts can be made accurately. There are several sources of error, however, which must be recognized in any study of this type. Although there appears to be little variability in the pattern of growth of the otolith, counting variability may be considerable. Consequently, large sample sizes are necessary. Also, the presence of other patterns on the otolith, such as sub-daily rings, may cause problems in some species of fish. Sub-daily rings have been identified in other studies, but are characteristically much weaker and more irregular than daily rings (Taubert and Coble, 1977; Brothers and MacFarland, 1979). Clear sub-daily rings were not noted in Parophrys otoliths. The counting and interpretation of the growth rings definitely involve subjective judgment. This subjectivity introduces an unknown degree of bias in the data, but repeated counts and low variability in the Moolach Beach data especially are arguments for the validity of the technique. There is no reason to suppose that otoliths from Yaquina Bay specimens were more difficult to count than those from Moolach Beach.

Several previous studies have attempted to estimate growth rates for English sole juveniles (Table 4). For the purposes of comparison with the data reported here, the total length measurements used in

other studies were converted to standard length using the relationship given by Laroche and Holton (1979). Also, to make the data more comparable to my data, the fish are assumed to be 20 mm SL at 120 days of age and the growth rates listed in Table 4 are for the juvenile period only. The recalculated daily growth estimates from all of these studies are similar, but are substantially higher than my estimated daily growth rate. Smith and Nitsos (1969) and Van Cleve and El-Sayed (1969) determined growth during the first year of life by backcalculating the size of the fish when the first detectable annulus on the interopercular bone was formed. This method can be quite inaccurate since this first annulus is formed when the fish enters its first slow growth season, which is not necessarily one year after hatching as assumed by these studies. For example, if a fish hatched in the fall, the first detectable annulus would not form until more than a year's time had passed (assuming that the slow growth period begins in winter; Van Cleve and El-Sayed, 1969). The distribution of settlement data (Figures 9 & 10) show that many Parophrys do in fact hatch in the fall, so growth may be overestimated using the first annulus to represent one year of life. Also, growth backcalculations of individual fish (Figures 5 & 6) do not show a clear, slow growth period during the first year.

The other two studies (Westrheim, 1955; Kendall, 1966) utilize the technique of following modal progressions through time in length frequency distributions. These estimates are very strongly influenced by the efficiency of the sampling gear. If the smaller fish are sampled less efficiently than the larger, then the mode will be skewed to the right in the distribution and overestimate growth. Emigration of small

individuals, immigration of large fish, and differential mortality of small fish would all produce overestimates of growth using the length frequency data. Also, length frequency modal progression may give variable results, dependent on the method of choosing the modes. A comparison of the length frequency data from Yaquina Bay for 1979, and the growth curve derived from otolith data is presented in Figure 11. The mode of a frequency distribution (indicated by a dot) is the size class with the greatest relative abundance during that sampling period. Following these modes through time would yield an estimate of growth substantially higher than calculated from the size-at-age data (0.46 mm/day). If the last two sampling dates are excluded however, there is good agreement between the size-at-age regression and the length frequency data. These last two samples are of larger fish. Most fish are leaving the estuary around this size, but the presence of a few residual large fish may strongly affect the position of the mode.

The most striking difference between the size-at-age plots from the Moolach Beach and Yaquina Bay nursery areas is the comparatively high variability shown for fish using the estuary during the first year of life. Little or no difference in mean growth rate could be detected. Since growth is linear during the first year, the growth rate is a progressively smaller proportion of overall size of the fish as it ages. If growth proceeded exponentially, as has often been suggested for juvenile fish, proportionate growth would be constant.

Explanation of differences in growth variability must recognize the fact that individual fish are not identical with respect to their inherent ability to grow. An illustration of this phenomenon among

juvenile European plaice (Pleuronectes platessa) is given by Øiestad et al. (1978). They reared plaice through metamorphosis in the laboratory and then transferred 200 fish between 13 and 20 mm to a concrete basin with a volume of 24 m^3 and a bottom area of 18.5 m^2 . Abundant food was available in the tank. Temperature and salinity were allowed to fluctuate. At the end of the 110 day experiment, the range in length was 29-81 mm, i.e., growth rate ranged from 0.14 to 0.55 mm/day. The mean growth rate was 0.28 mm per day, which is similar to growth in the field for this species (0.20-0.37 mm/day; Steele and Edwards, 1970).

Several physical factors^R may affect growth variability. The physical regime in Yaquina Bay is certainly highly variable with respect to temperature and salinity (Figure 8). Short term variations in both of these parameters are much more extensive than indicated by the figure due to the smoothing effects of the low frequency of sampling and averaging of the data. Frey (unpub.) shows differences of 5 ppt salinity and 2°C between high and low tides in the lower bay. At Moolach Beach, in contrast, a more regular environment may be expected. The open coastal region does not have a large source of fresh water to influence salinity and temperature. Huyer (1977) and Huyer and Smith (1978) report that bottom water salinity off the Oregon coast fluctuates about 1 ppt from winter to summer. Temperature varies from 6.5°C in summer to about 10°C in winter. Seasonal coastal upwelling significantly affects the nearshore area with regard to temperature, salinity, and nutrients (Huyer, 1977; Peterson et al., 1979). Tidal transport causes lower Yaquina Bay to be affected by upwelling also.

The effect of hydrographic variability on growth is difficult to

assess, since studies in the past have examined the overall effects of various types of constant conditions, but do not consider the consequences of short term fluctuations. Williams' (1975) laboratory studies of P. vetulus juveniles found that temperature did not influence growth between 9.5 and 15°C in acclimatized fish. No data were available for temperature effects below 9.5°C, but above 15°C, growth rate decreased. Temperature at both Moolach Beach and Yaquina Bay is within this optimum range on average (Figure 8). Tides, upwelling and storm runoff may increase or decrease temperatures, in the bay in particular, for short periods of time. The response of juvenile Parophrys to these events is likely to be movement away from sub-optimal conditions (Richards et al., 1977; Beitinger and Magnuson, 1979).

The arguments made in connection with temperature variation also apply to salinity. Parophrys juveniles are undoubtedly adapted to the average salinity conditions in the two nursery areas. Salinity does not significantly affect growth in many flatfish species which use estuarine nursery grounds, although a temperature-salinity interaction may be important (Peters and Boyd, 1972).

In general, variability in the environment probably emphasizes the growth differences among individuals. This applies to the diversity of microhabitats in the estuary versus the open coastal region as well as hydrographic variability. Howe (MS) found Parophrys juveniles used three habitat types in Netarts Bay, Oregon: sand flats, shallow channels and deep channels. The lack of hydrographic and microhabitat variability at Moolach Beach (Hogue, pers. comm.) does not explain the suppression of growth variability among English sole there, however.

There are two ways in which growth variability can be reduced. Either outlying individuals have their growth rates altered toward the population mean or they are removed from the population. In the first case, potentially fast growing fish may actually show a growth rate closer to the mean if food were limiting, or growth conditions were poor in general. Limiting or poor conditions presumably affect all individuals in the nursery area though, slow growing individuals included, i.e., the mean growth rate would decrease but variability would remain unchanged or even increase. The opposite is true of improved conditions, which may increase the growth of the slowest growing fish, i.e., the mean would increase.

In the second case, two removal processes are occurring: mortality and emigration. The size-at-age plot for Moolach Beach (Figure 3) and other data (Laroche and Holton, 1979) indicate that most P. vetulus juveniles move out of the sampling area between 70 and 80 mm SL. Laroche and Holton (1979) showed that English sole move offshore at this size and are subsequently found in 50 m of water or deeper. There is no indication from their data that some proportion of the population (fast growing) move offshore at a smaller size.

Mortality, especially of slow growing fish, would compress observed growth variability. Steele and Edwards (1970) report predation to be the major cause of mortality among juvenile plaice in a nursery area off the Scottish coast. Predation rates on juvenile English sole have not been estimated, but many large fishes, such as the big skate, Raja binoculata, which are known to prey on juvenile flatfish, are common in the very nearshore area (Wakefield, pers. comm.).

In Yaquina Bay, emigration from the nursery appears to be at a larger size (100 mm SL) than from the coastal area (Westrheim, 1955; Olson and Pratt, 1973; Krygier and Pearcy, unpub.). Predation in the estuary is probably low compared to the open ocean. Few large fishes are regularly found in the bay, although birds may be significant predators. Kuipers (1977), in a study of an estuarine nursery for plaice in the Waddensea, reported predation mortality to be low in contrast to the coastal region studied by Steele and Edwards (1970).

A final biological factor to be considered is the effect of intra specific competition on growth. The densities of juvenile English sole captured in the estuary are a consistent order of magnitude higher than at Moolach Beach (Figure 8). Competition, like the effects of physical factors, will emphasize growth differences among individuals and so increase observed variability.

The most plausible mechanism explaining low growth variability at Moolach Beach combines limitation and removal processes. If the population is food limited in the open ocean, and selective predation on slow growers is occurring, the observed variation in size-at-age will be small. Using the otolith aging technique, this hypothesis is testable. It requires a comparison of the size-at-age distribution of fish found in the stomachs of predators with the distribution shown in Figure 3. Otoliths are not usually digested very rapidly, so this comparison is possible.

The Distribution of Recruitment to the Benthic Habitat

Estimation of the distribution of settlement to the benthic habitat

through the year using otolith age data has the advantage of being independent of sampling bias against smaller fish and the distribution of sampling during the year. If the overall sampling effort was low and the number of individuals aged was small, the distribution of settlement estimates would be weak. Using otolith age data for this type of estimate is biased for survivors. If differential mortality or emigration of fish settling at different times occurs the estimate will be inaccurate.

The estimated recruitment distribution from otolith aging data (Figures 9 & 10) and from the relative abundance of individuals 20 mm SL or less in the samples (Table 3) show many of the same features. Both sets of data indicate that settlement is reduced in the summer months. ^{24th March 1979 June 7th 1979} Larger numbers of small fish are present in both nursery grounds in the winter. Fish that enter the estuary in the fall are not indicated in the relative abundance data (Table 3), but show up strongly in Figure 10.

A hypothesis arising from this study is that survival, and not growth, is enhanced in the estuarine nursery ground compared to the open coast. Testing of this hypothesis will be an important step in understanding the role that estuaries play in the life history of many fishes.

BIBLIOGRAPHY

- Alverson, D. L., A. T. Pruter and L. L. Ronholt: A study of demersal fishes and fisheries of the northeastern Pacific Ocean. 190 pp. Vancouver: H. R. MacMillan Lect. Fish. Inst. Fish. Univ. B. C. 1964
- Barss, W. H.: The English sole. Oregon Dept. Fish. Wildl. Inform. Rept. 76-1, 1-7 (1976)
- Beitinger, T. L. and J. L. Magnuson: Growth rates and temperature selection of bluegill, Lepomis machrochirus. Trans. Am. Fish. Soc. 108, 378-382 (1979)
- Beyer, J. E. and G. C. Laurence: A stochastic model of larval fish growth. Ecol. Modelling 8, 109-132 (1980)
- Brothers, E. B., C. P. Mathews and R. Lasker: Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. U. S. 74, 1-8 (1976)
- Brothers, E. B. and W. N. McFarland: Correlations between otolith microstructure, growth and life history transitions in newly recruited French grunts, Haemulon flavolineatum. I. C. E. S. Symp. Early Life History Fish Contrib. P. E. 5, 1-16 (1979)
- Cushing, D. H. and J. G. K. Harris: Stock and recruitment and the problem of density dependence. Rapp. Proc-Verb. Cons. Int. Explor. Mer 164, 142-155 (1973)
- Eldridge, M.: Larval fish survey of Humboldt Bay. 52 pp. Arcata, Calif.: M.S. Thesis Humboldt State Coll. 1970.
- Frolander, H. F., M. J. Flynn, S. C. Spring, S. T. Zimmerman and C. B. Miller: Yaquina Bay zooplankton survey. 27 pp. Corvallis: Oregon State Univ. School Oceanogr. Data Rept. 48 1971.
- Frolander, H. F., C. B. Miller, M. J. Flynn, S. S. Myers and S. T. Zimmerman: Seasonal cycles of abundance in zooplankton populations of Yaquina Bay, Oregon. Mar. Biol. 21, 277-288 (1973)
- Gunter, G.: Some relations of estuarine organisms to salinity. Limnol. Oceanogr. 6, 182-190 (1961)
- Haedrich, R. L.: Estuarine fishes. In: Ecosystems of the world. Vol. 22 Estuaries and enclosed seas. Ed. by B. H. Ketchum. Amsterdam: Elsevier, in press
- Hart, J. L.: Pacific fishes of Canada. Fish. Res. Bd. Canada Bull. 180, 1-740 (1973)

- Hewitt, G. R.: Seasonal changes in English sole distribution: an analysis of the inshore trawl fishery off Oregon. 59 pp. Corvallis: M.S. Thesis Oregon State Univ. 1980
- Howe, K. M.: Habitats, distribution and abundance of the summer ichthyofauna of Netarts Bay, Oregon. manuscript 38 pp.
- Huyer, A.: Seasonal variation in temperature, salinity and density over the continental shelf off Oregon. *Limnol. Oceanogr.* 22, 442-453 (1977)
- Huyer, A. and R. L. Smith: Physical characteristics of Pacific northwestern coastal waters. In: The marine plant biomass of the Pacific northwest coast, pp. 37-55. Ed. by R. Krauss. Corvallis: Oregon State Univ. Press 1978
- Kendall, A. W.: Sampling juvenile fishes on some sandy beaches of Puget Sound, Washington. 77 pp. Seattle: M.S. Thesis Univ. Washington 1966
- Ketchen, K. S.: Factors influencing the survival of the lemon sole, Parophrys vetulus in Hecate Strait, British Columbia. *J. Fish. Res. Bd. Canada* 13, 647-694 (1956)
- Kreuz, K. F.: Long term variation in growth of Dover sole, Microstomus pacificus and English sole, Parophrys vetulus, and its possible relationship with upwelling. 71 pp. Corvallis: M.S. Thesis Oregon State Univ. 1978
- Kruse, G. H. and A. V. Tyler: Influence of physical factors on the English sole, Parophrys vetulus, spawning season. manuscript 20 pp.
- Kuipers, B. R.: On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. *Netherlands J. Sea Res.* 11, 56-91 (1977)
- Kulm, L. D. and J. V. Byrne: Sediments of Yaquina Bay, Oregon. In: *Estuaries*, pp. 226-238. Ed. by G. H. Lauff. Washington: Am. Assoc. Adv. Sci. Publ. 83 1967
- Laroche, W. A. and R. L. Holton: Occurrence of 0-age English sole, Parophrys vetulus, along the Oregon coast: an open coast nursery area? *Northwest Science* 53, 94-96 (1979)
- Laroche, J. L. and S. L. Richardson: Winter-spring abundance of larval English sole, Parophrys vetulus, between the Columbia River and Cape Blanco, Oregon during 1972-1975 with notes on occurrences of three other pleuronectids. *Est. Coast. Mar. Sci.* 8, 455-476 (1979)
- Laroche, J. L., S. L. Richardson, and A. A. Rosenberg: The growth of larval English sole, Parophrys vetulus, in Oregon coastal waters. in preparation.

- McHugh, J. L.: Management of estuarine fisheries. Am. Fish. Soc. Spec. Publ. 3, 133-154 (1966)
- McHugh, J. L.: Estuarine nekton. pp. 581-620. Ed. by G. H. Lauff. Washington: Am. Assoc. Adv. Sci. Publ. 83 1967
- Misitano, D. A.: Size and stage of development of larval English sole, Parophrys vetulus, at time of entry into Humboldt Bay. Calif. Fish and Game 62, 93-98 (1976)
- Øiestad, V., S. A. Iversen and D. S. Danielssen: Growth and survival studies on 0-group plaice, Pleuronectes platessa, in a small basin with a closed ecosystem. Fisk Dir. Skr. Ser. HavUnders. 16, 507-518 (1978)
- Olson, R. E. and I. Pratt: Parasites as indicators of English sole, Parophrys vetulus, nursery grounds. Trans. Am. Fish. Soc. 102, 405-411 (1973)
- Pannella, G.: Fish otoliths: daily growth layers and periodical patterns. Science 173, 1124-1127 (1971)
- Pannella, G.: Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In: Aging of fish, pp. 28-39. Ed. by T. B. Bagnel. London: Unwin Brothers, L. T. D. 1974
- Pearcy, W. G.: Ecology of an estuarine population of winter flounder, Pseudopleuronectes americanus: parts I-IV. Bull. Bingham Oceanogr. Coll. 18, 1-78 (1962)
- Pearcy, W. G. and S. S. Myers: Larval fishes of Yaquina Bay, Oregon: a nursery ground for marine fishes? Fish. Bull. U. S. 72, 201-213 (1974)
- Peters, D. S. and M. T. Boyd: The effect of temperature, salinity and availability of food on the feeding and growth of the hogchoker, Trinectes maculatus. J. Exp. Mar. Biol. Ecol. 7, 201-207 (1972)
- Peterson, W. T., C. B. Miller and A. Hutchinson: Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Res. 26A, 467-494 (1979)
- Reay, P. J.: The seasonal patterns of otolith growth and its application to back-calculation studies in Ammodytes tobianus. J. Cons. Int. Explor. Mer 34, 485-504 (1972)
- Richards, F. P., W. W. Reynolds and R. W. McCauley (editors): Temperature preference studies in environmental impact assessments: an overview with procedural recommendations. J. Fish. Res. Bd. Canada 34, 728-761 (1977)

Rosenberg, A. A. and J. L. Laroche: Age at metamorphosis and duration of the planktonic larval phase of English sole, Parophrys vetulus. manuscript in preparation.

Rosenberg, G. D. and C. B. Jones: Approaches to chemical periodicities in molluscs and stromatolites. In: Growth rhythms and the history of the earth's rotation, pp. 223-242. Ed. by G. D. Rosenberg and S. K. Runcorn. London: Wiley Interscience 1976

Scheffe, H.: The analysis of variance. 477 pp. New York: J. Wiley & Sons 1959

Scott, J. S.: Otolith structure and growth in northern sand lance, Ammodytes dubius, from the Scotian Shelf. ICNAF Res. Bull. 10, 107-115 (1973)

Smith, J. G. and R. J. Nitsos: Age and growth studies of English sole, Parophrys vetulus, in Monterey Bay, California. Pac. Mar. Fish. Comm. Bull. 7, 73-80 (1969)

Steele, J. H. and R. R. C. Edwards: The ecology of 0-group plaice and common dabs in Loch Ewe. IV. Dynamics of the plaice and dab populations. J. Exp. Mar. Biol. Ecol. 4, 174-187 (1970)

Struhsaker, P. and J. Uchiyama: Age and growth of the nehu, Stolephorus purpureus, from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull. U. S. 74, 9-17 (1976)

Taubert, B. D. and D. W. Coble: Daily rings in otoliths of three species of Lepomis and Tilapia mossambica. J. Fish. Res. Bd. Canada 34, 332-340 (1977)

Van Cleve, R. and S. Z. El-Sayed: Age, growth and production of an English sole population in Puget Sound, Washington. Pac. Mar. Fish. Comm. Bull. 7, 51-72 (1969)

Westrheim, S. J.: Size composition, growth and seasonal abundance of juvenile English sole, Parophrys vetulus, in Yaquina Bay. Fish. Comm. Oregon Res. Briefs 6, 4-9 (1955)

Williams, S. F.: Rearing conditions and their effects on growth, food conversion and survival of English sole, Parophrys vetulus. 95 pp. Corvallis: Dissertation, Oregon State Univ. 1975

TABLE I. SAMPLING DATES, STATIONS OCCUPIED AND STATION DEPTHS.

<u>Date</u>	<u>Stations</u> ¹
1978	
September 5	D - G
September 28	A - G
October 19	A - G
October 25	D - G
November 14	B - G
November 27	B,C
1979	
January 13	A - C
January 22	A - G
March 10	A - C
April 10	A - C
April 18	D - G
April 22	A - C
May 2	D - G
May 14	B
May 29	B - G
June 30	A - G
July 19	A - G
August 8	A - G
September 14	A - C
September 23	D - G

1. Station Depths: A 6-8m; B 6-8m; C 9-12m; D 9m; E 12m; F 18m; G 27.5m.

TABLE II. ANALYSIS OF VARIANCE FOR THE LEAST SQUARES MULTIPLE REGRESSION ANALYSIS OF SIZE-AT-AGE DATA FROM: A. MOOLACH BEACH (FIGURE 3); B. YAQUINA BAY (FIGURE 4).

A.

Moolach Beach Regression: $Y = 16.87 + 0.051X - 32.92 A_1 + 0.23 A_2$

Multiple R 0.975

R^2 0.950

Analysis of Variance	DF	Sum of Squares	Meansquare
Regression	3	80815.2	26938.4
Residual	214	4253.7	19.9
	F value	1355.2	

B.

Yaquina Bay Regression: $Y = 13.01 + 0.083X - 33.45 A_1 + 0.201 A_2$

Multiple R 0.943

R^2 0.890

Analysis of Variance	DF	Sum of Squares	Meansquare
Regression	3	139575.6	46525.2
Residual	182	17308.1	95.1
	F value	489.3	

TABLE III. OBSERVED DENSITIES OF ENGLISH SOLE JUVENILES 20 MM OR LESS
IN THE TWO NURSERY GROUNDS DURING 1978 AND 1979.

	<u>Jan</u>	<u>Feb</u>	<u>Mar</u>	<u>Apr</u>	<u>May</u>	<u>Jun</u>	<u>Jul</u>	<u>Aug</u>	<u>Sep</u>	<u>Oct</u>	<u>Nov</u>	<u>Dec</u>
Yaquina Bay												
1978	0.013	0.004	0.013	0.198	-	0.001	0	0	0	0	0	0.010
1979	0.009	-	0.002	0.0004	0.0002	0	0	0	0	-	-	-
Moolach Beach												
1978	0.003	0.0004	0.004	0.198	-	0.005	0.001	-	0	0.001	0.006	-
1979	0.010	-	-	0.002	0.032	0.016	0	0	0	-	-	-

TABLE IV. SUMMARY OF GROWTH ESTIMATES FROM PREVIOUS STUDIES.
 THE DATA WERE RECALCULATED SO THAT DIRECT COMPARISONS CAN BE MADE (SEE TEXT).

<u>Location</u>	<u>Size (mm SL) at One Year of Age</u>	<u>Daily Growth Rate (mm/day)</u>	<u>Source</u>
Yaquina Bay, Oregon	117	0.40	Westrheim, 1956
Monterey Bay, California	108-126	0.36-0.43	Smith & Nitsos, 1969
Puget Sound, Washington	128	0.44	Van Cleve & El-Sayed, 1969
Puget Sound, Washington	...	winter 0.48 summer 0.73	Kendall, 1966

Figure 1. The study area. Sampling stations are indicated by the letters A-G. Station depths are given in Table 1.

Figure 1.

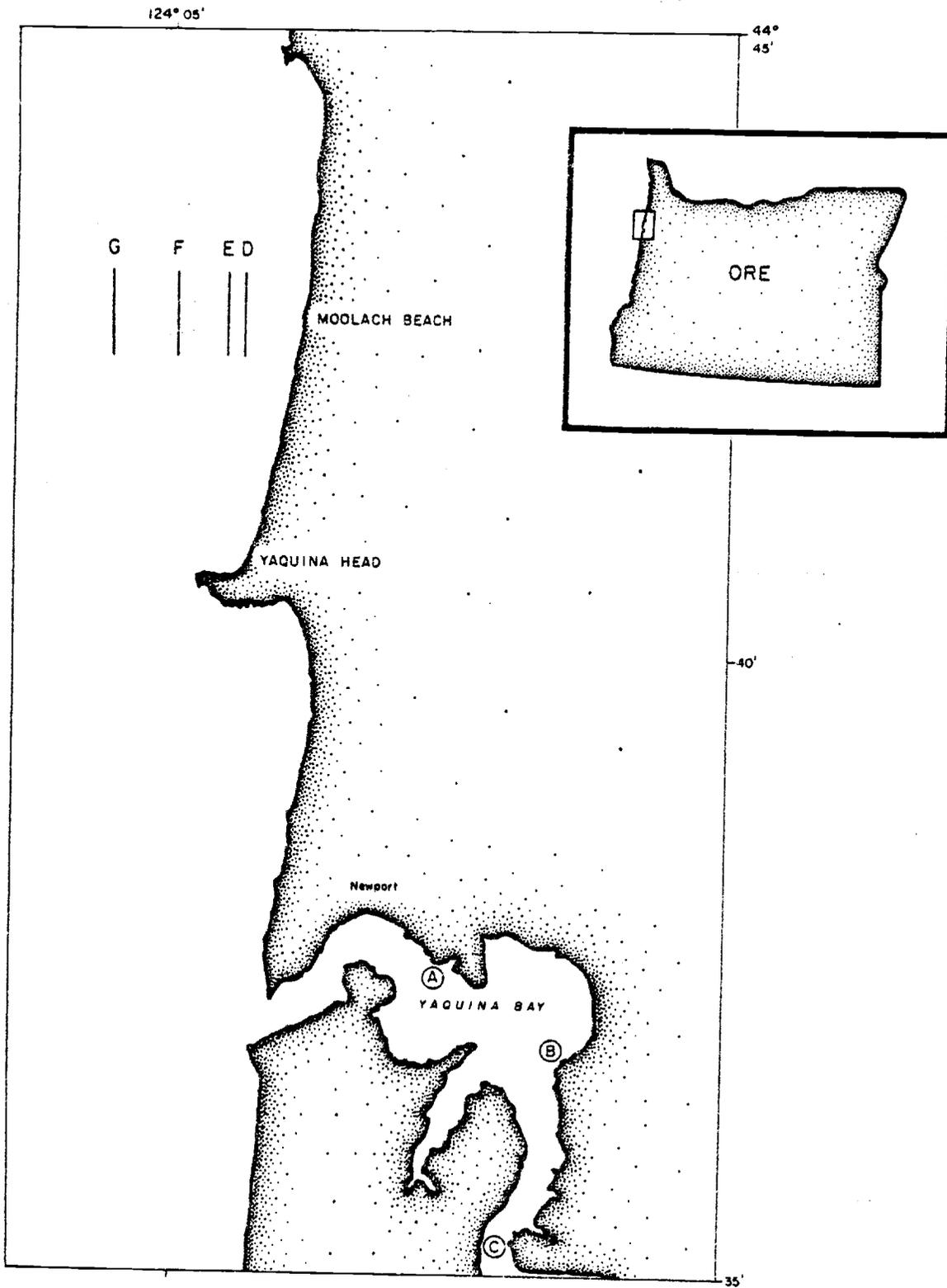


Figure 2. An otolith from a 110 mm SL Parophrys captured in Yaquina Bay. Daily and fortnightly rings are clearly shown. Fourteen daily rings can be counted between the two fortnightly rings indicated by the arrows. There are 21 fortnightly rings on this otolith and the total age is 363 days. Magnification is 200X.



Figure 3. Size-at-age data for fish captured in the Moolach Beach nursery area.

Figure 3.

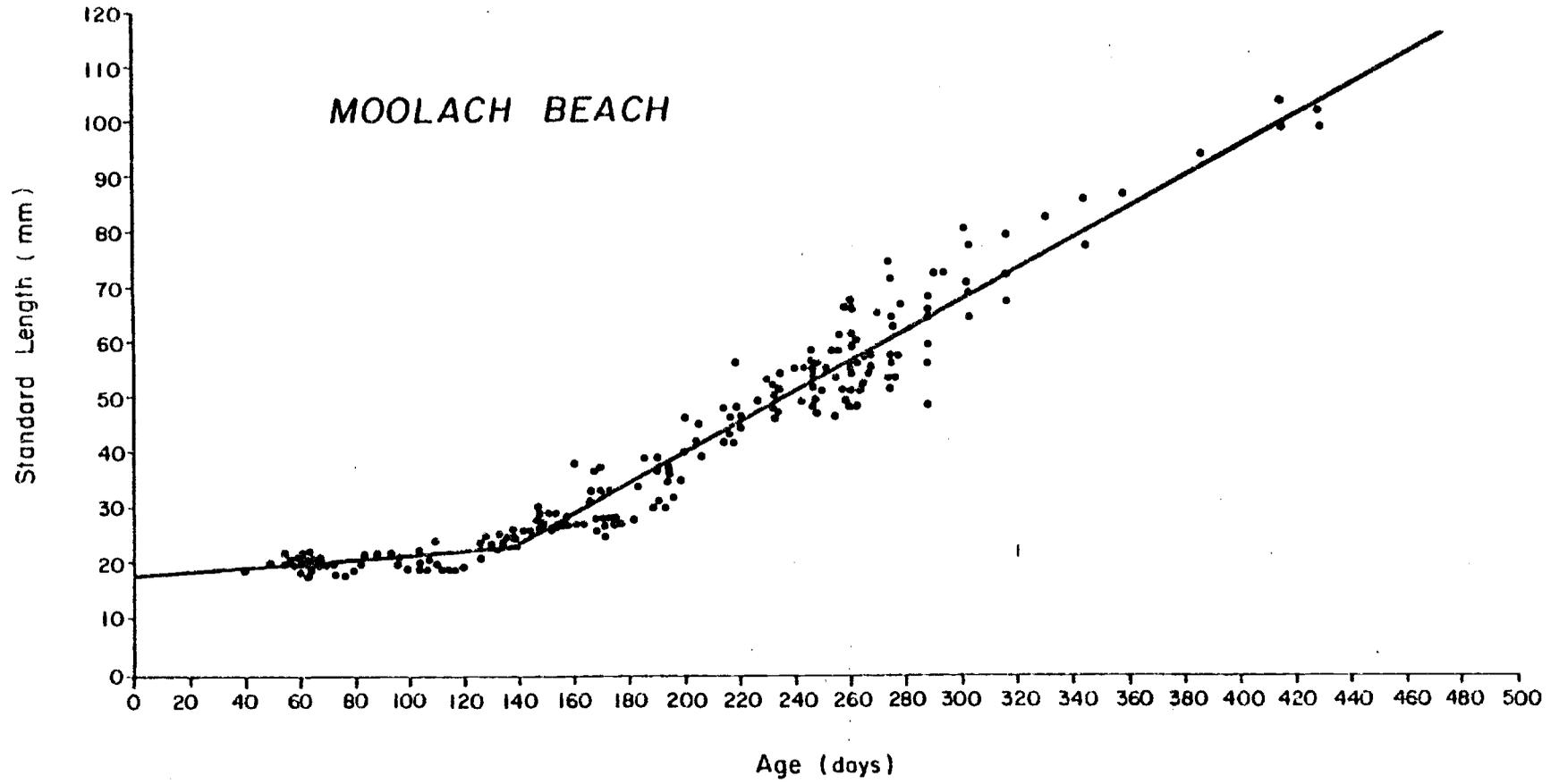


Figure 4. Size-at-age data for fish captured in the Yaquina Bay nursery area.

Figure 4.

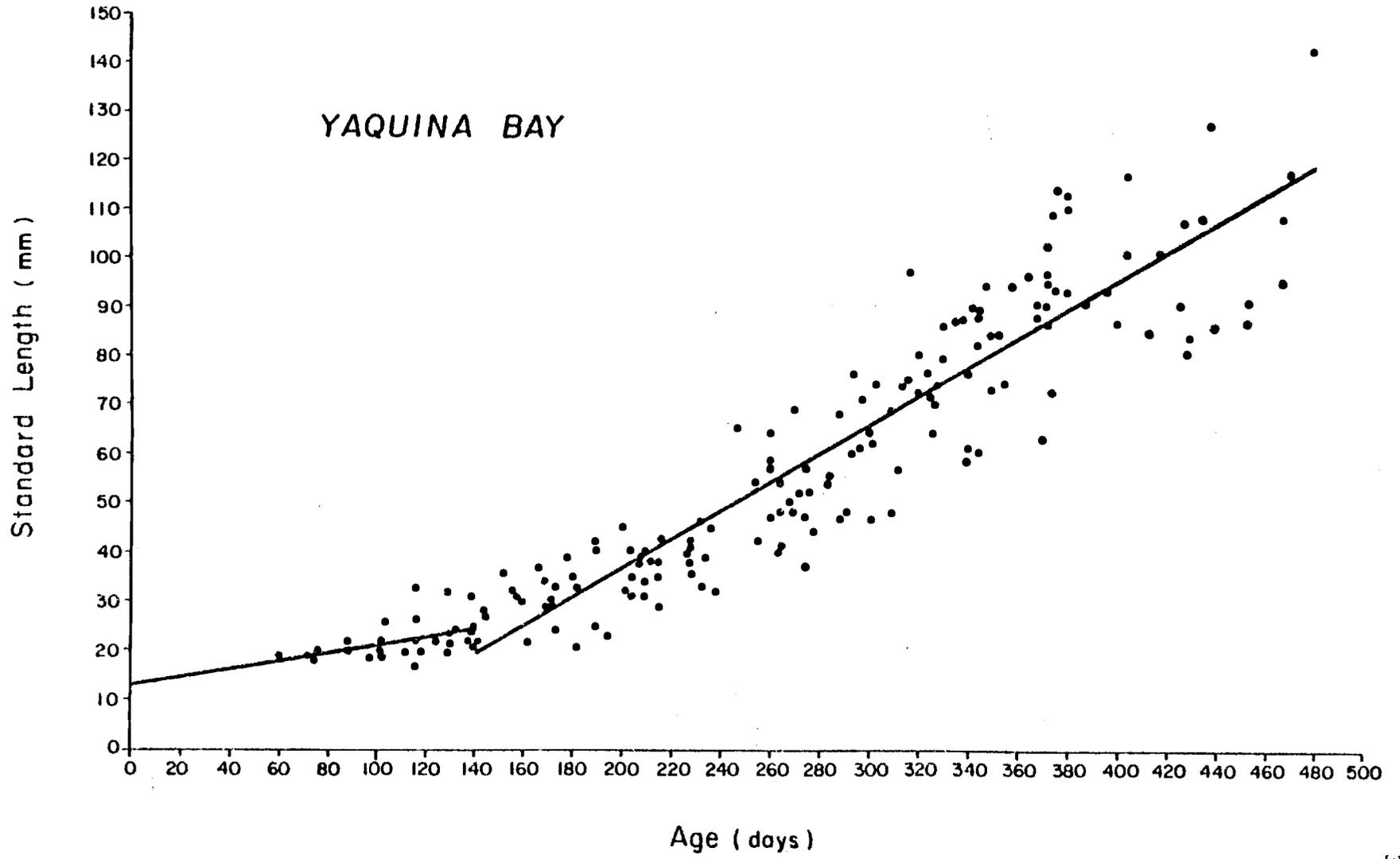


Figure 5. Backcalculated growth of eight individuals from Moolach Beach during 1978-79.

Figure 5.

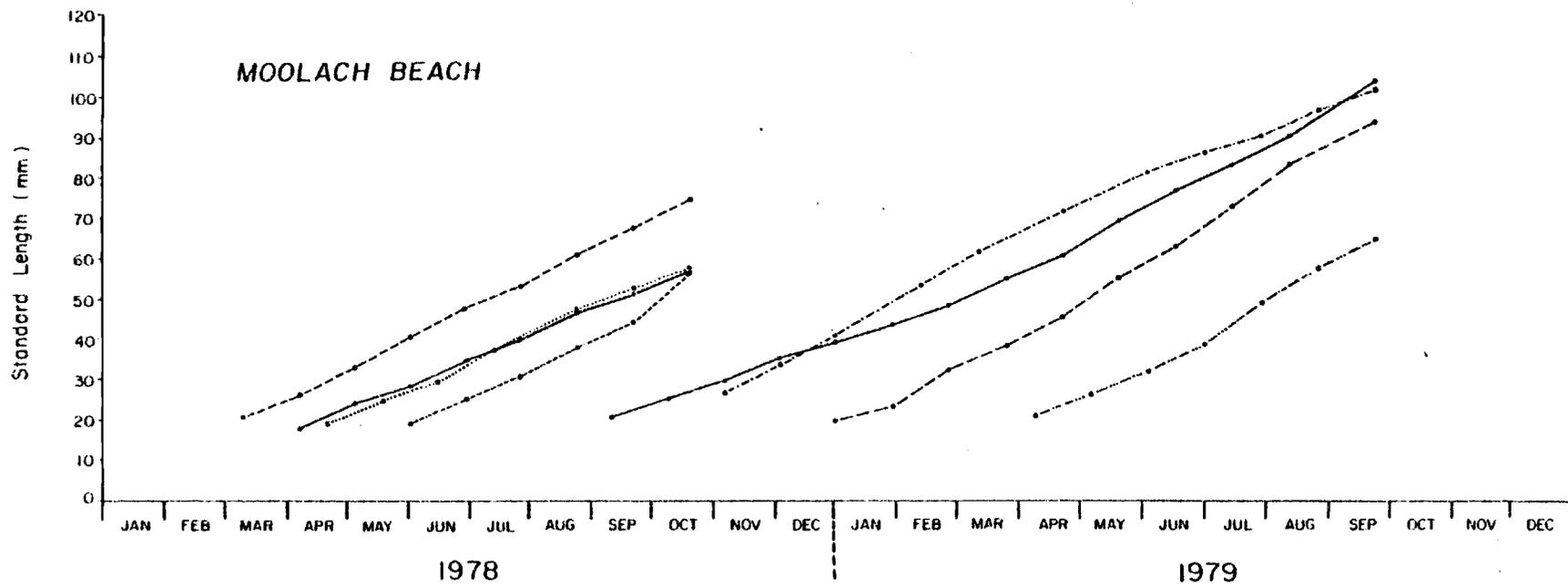


Figure 6. Backcalculated growth of 16 individuals from Yaquina Bay during 1978-79.

Figure 6.

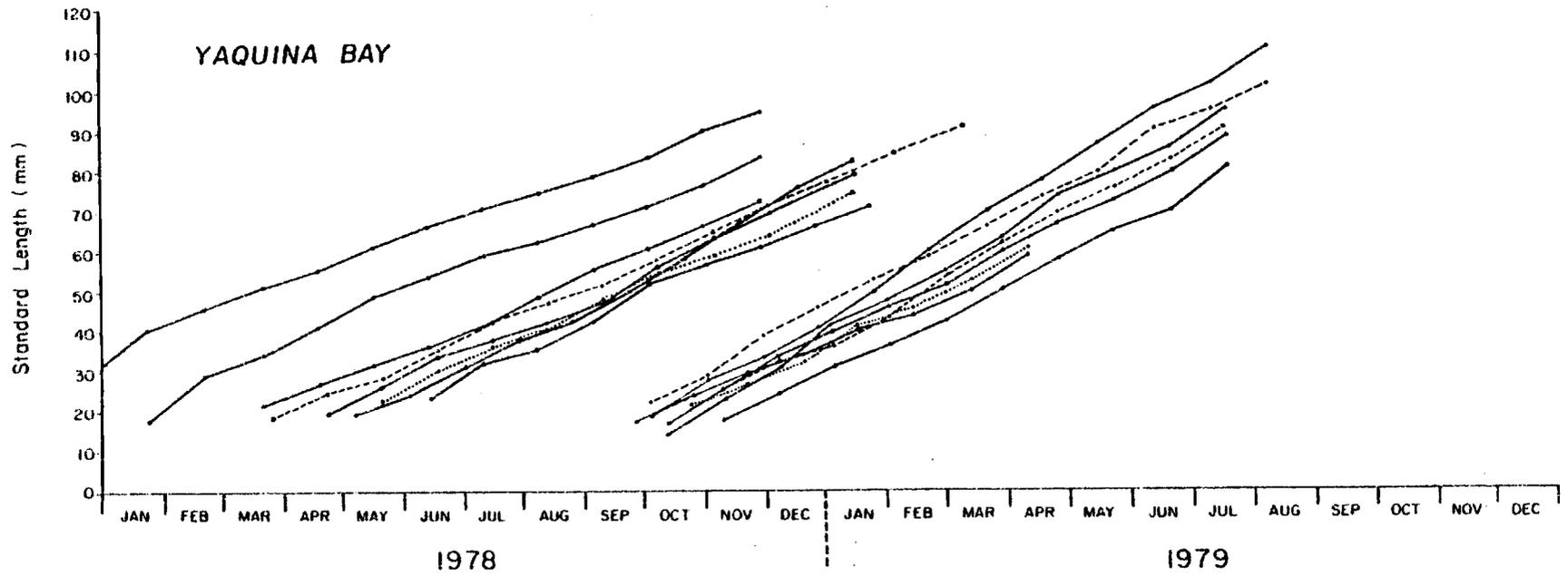


Figure 7. Size-at-age data from Yaquina Bay plotted by year of capture.

Figure 7.

YAQUINA BAY

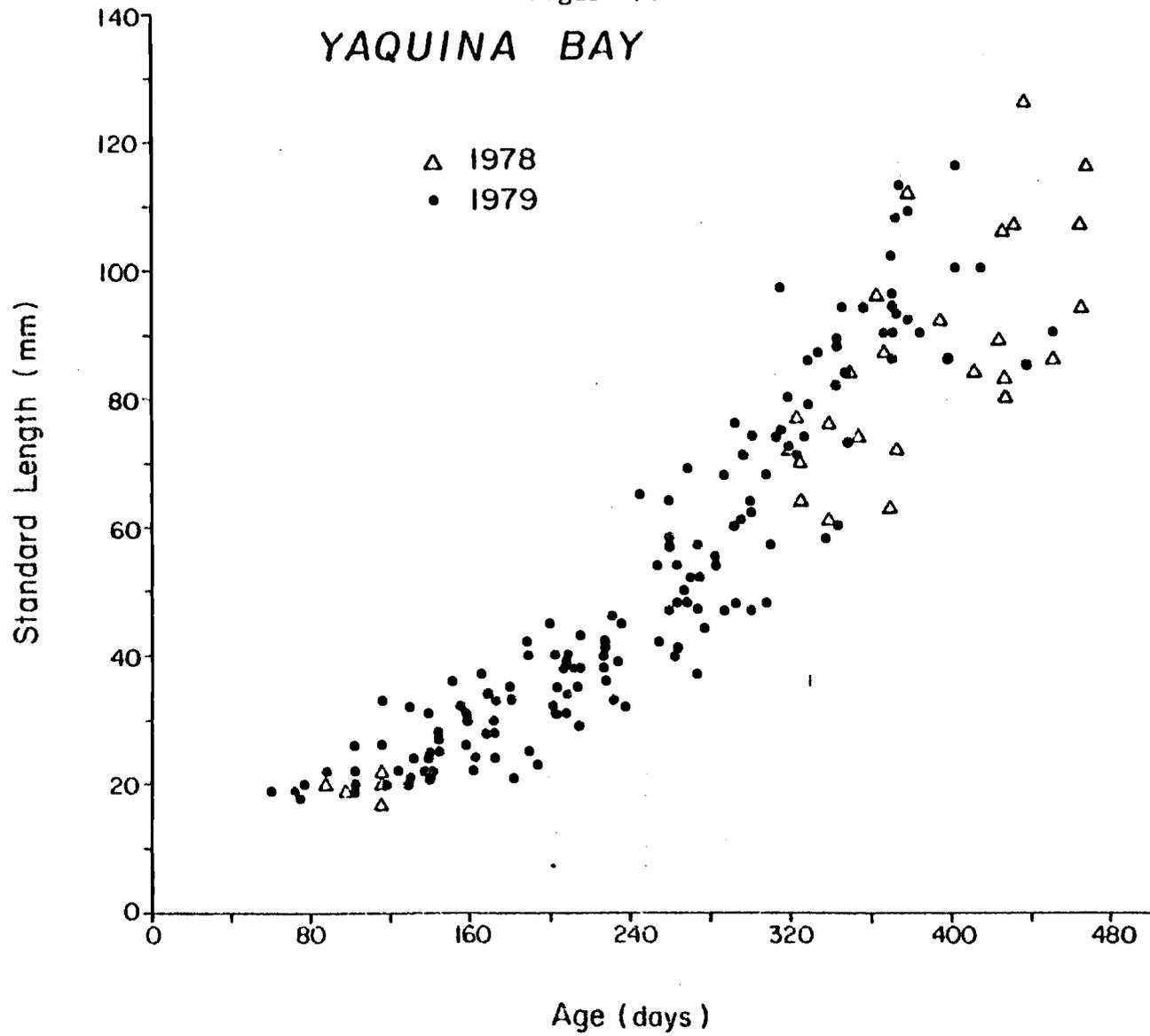


Figure 8. Salinity, temperature, and sampled English sole densities for the study areas. Salinity (in parts per thousand) is for Yaquina Bay only. The English sole density data from Yaquina Bay was divided by 10 to obtain the plotted values. Density data is uncorrected for gear efficiency.

Figure 8.

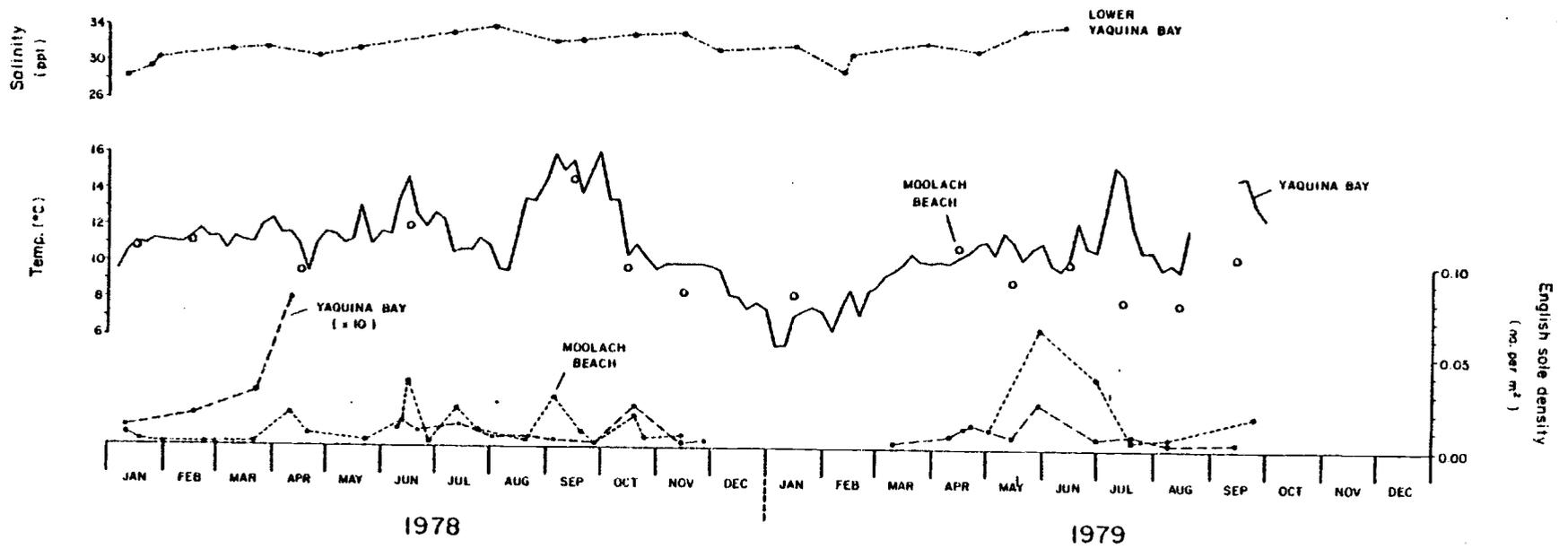


Figure 9. Distribution of recruitment to the benthic habitat (assumed to be 120 days of age) during 1978-79 in the Moolach Beach nursery.

Figure 9.

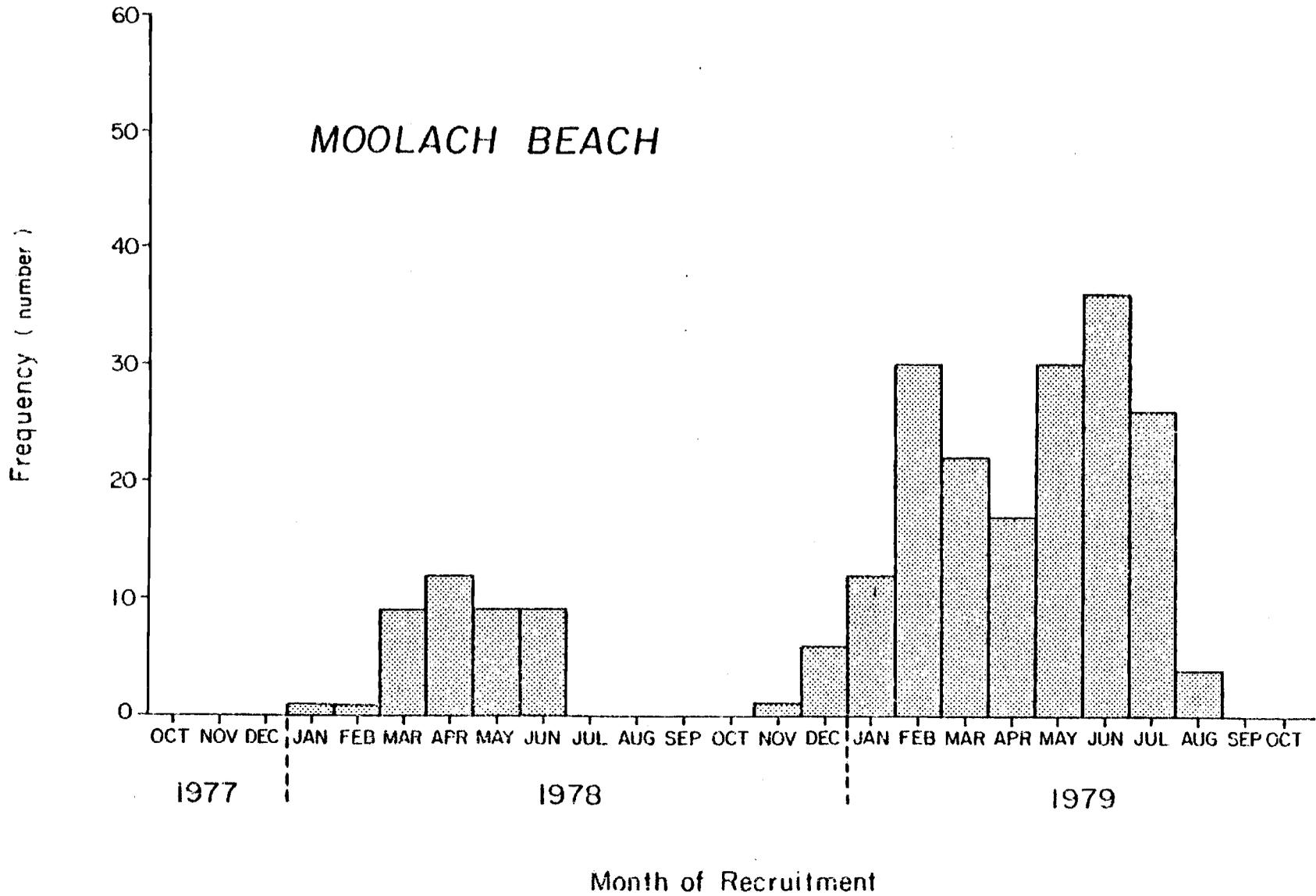


Figure 10. Distribution of recruitment to the benthic habitat during 1978-79 in the Yaquina Bay nursery.

Figure 10.

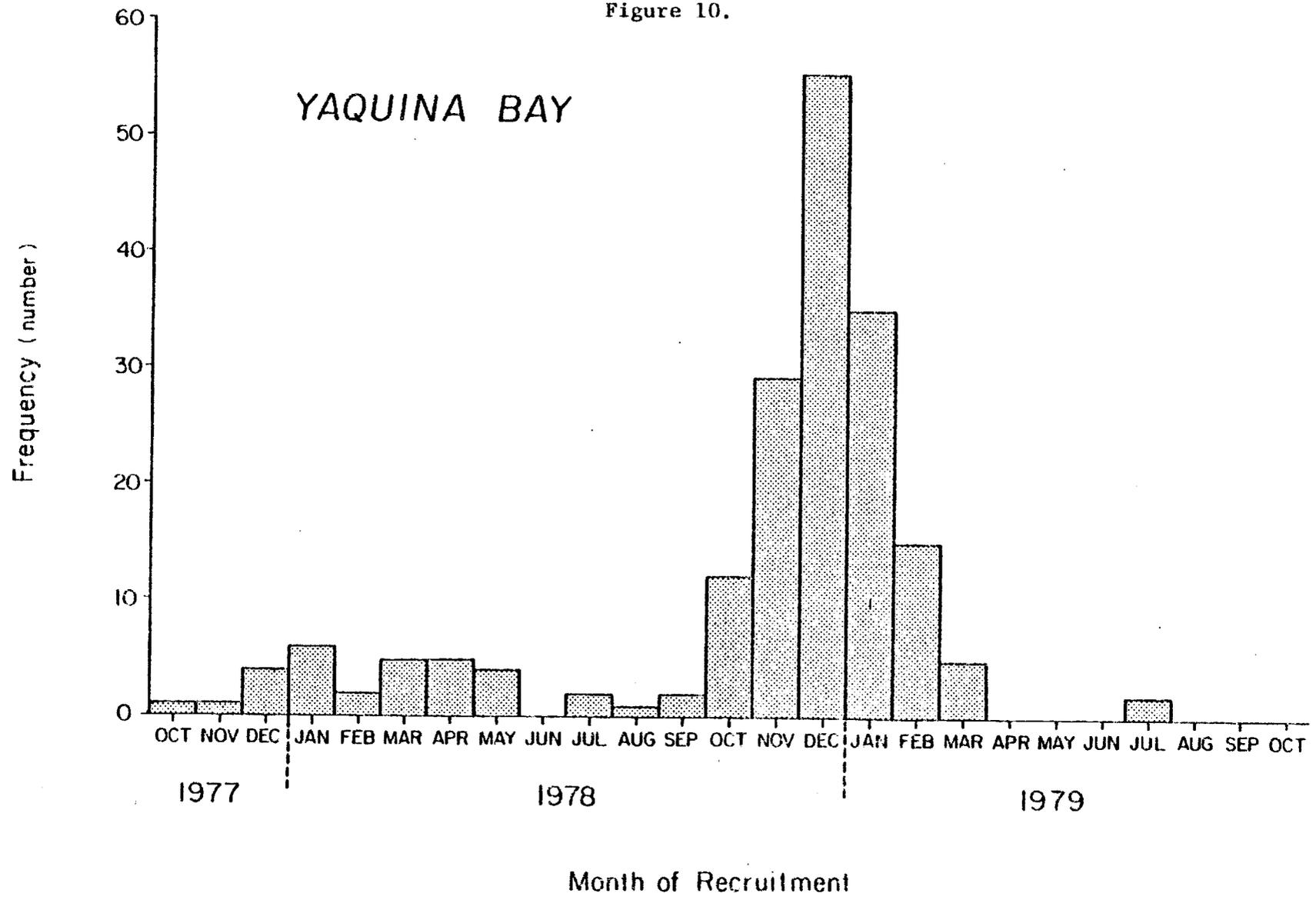


Figure 11. Comparison of length frequency modal progression analysis with size-at-age regression for Yaquina Bay fish in 1979. The vertical lines indicate the range in observed lengths. The dots indicate the mode of the distribution selected as the size class with the greatest relative abundance in the samples taken on that date.

Figure 11.

