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

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ABSTRACT

The growth of English sole juveniles, during 1978-79, from estuarine and open coastal nursery grounds on the Oregon coast is described in detail. 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 the first year of life. Differences in average growth among individual fish account for the high variability in size-at-age among fish found in the estuary. Fish from the estuary grew slightly faster, on average, in 1979 compared with 1978.

The settlement date of English sole larvae to the benthic habitat, determined from age data, occurred over the winter and spring in the open coastal nursery area. In the estuary, settlement was concentrated in the early winter.

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 1967; Haedrich in press). Many east coast fishes are considered to be dependent on estuarines 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, providing 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 estuarine dependence (Haedrich in press; Kuipers 1977). Unfortunately, it is difficult to test these hypotheses for most species of fish, because it is uncommon to find a species which uses both estuarine and nonestuarine nursery environments in a small geographic area.

The commercially important pleuronectid *Parophrys vetulus* Girard, found off the Oregon coast, uses both estuarine and nonestuarine habitats as nursery areas during the first year of life (Laroche and Holton 1979). This study examines the growth of the English sole, *Parophrys vetulus*, juveniles from two nursery grounds: the Yaquina Bay estuary (Pearcy and Myers 1974) and the open coastal area off Moolach Beach, Oreg. (Laroche and Holton 1979).

Size-at-age data, obtained from daily and fortnightly growth ring counts on otoliths, are used to detail growth during the first year. Daily growth rings on otoliths have been documented in many species of fish (Pannella 1971; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977). Pannella (1974) reported fortnightly banding patterns in several species as well. Laroche et al. (1982) have provided laboratory evidence for the daily periodicity of growth rings on *P. vetulus* otoliths.

METHODS

Sampling was conducted from September 1978 through September 1979 at Moolach Beach and Yaquina Bay. The sampling stations are shown in Figure 1. A tow was made at each station with a 1.5 m wide beam trawl lined with 7 mm stretch mesh. Tows were for 5 min in Yaquina Bay and for 10 min at Moolach Beach. The beam trawl was equipped with a 1.0 m circumference odometer wheel to measure distance travelled on the bottom. Measurements of bottom temperature and salinity were made at each station.

All fish captured were preserved in a strongly buffered 10% solution of Formalin[2] in seawater.

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
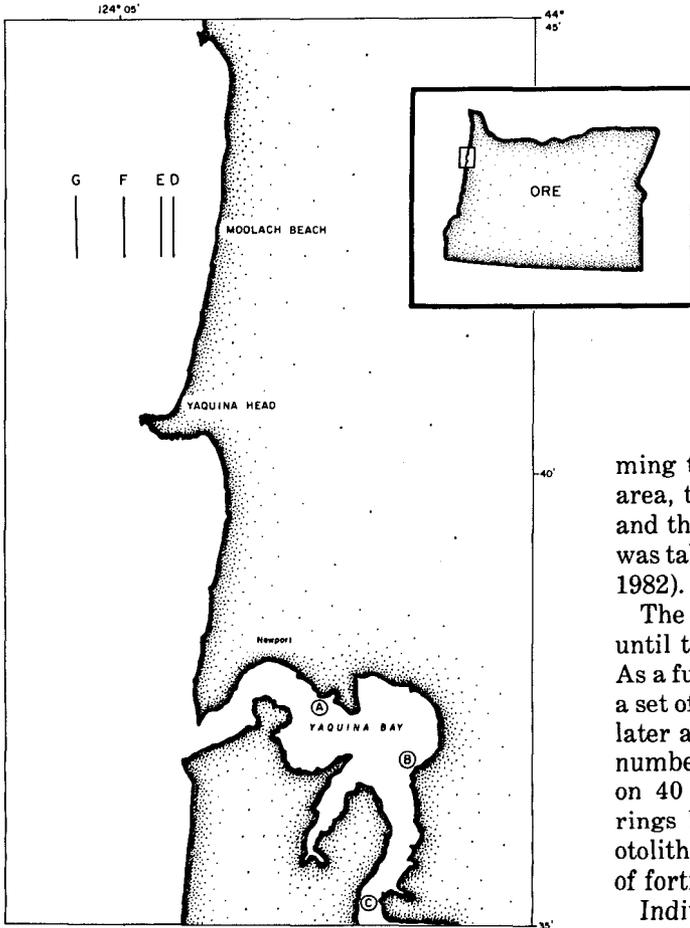
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FIGURE 1.—The study area. Sampling stations are indicated by the letters A through G.

ming the number of daily rings in the nuclear area, the number of fortnightly rings times 14, and the mean age of first ring formation, which was taken to be 5 d for this species (Laroche et al. 1982).

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 was recounted several months later and a mean error computed. Counts of the number of daily rings between fortnightly rings on 40 otoliths and the number of fortnightly rings between consecutive annual rings on 15 otoliths from older specimens were made as tests of fortnightly periodicity.

Individual growth curves of 25 fish were back calculated by making radial measurements to every other fortnightly ring along the same axis from the nucleus to the anterior edge of the otolith. From these measurements and the linear relationship between otolith radius and standard length of the fish,[3] lengths-at-age for the various points in the life of an individual were calculated.

RESULTS

Counts of daily rings between fortnightly rings yielded a mean of 13.95 with a standard deviation of 0.68. 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 apart was 1.45 rings. Figure 2 shows the daily and fort-

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 Protexx.

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 250× magnification, using either bright-field or polarized illumination. Counts of fortnightly rings were made on each otolith. No fortnightly rings could be detected in the central area of the otoliths, which apparently represents 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 was calculated by sum-

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[3]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 for this regression is 0.98.
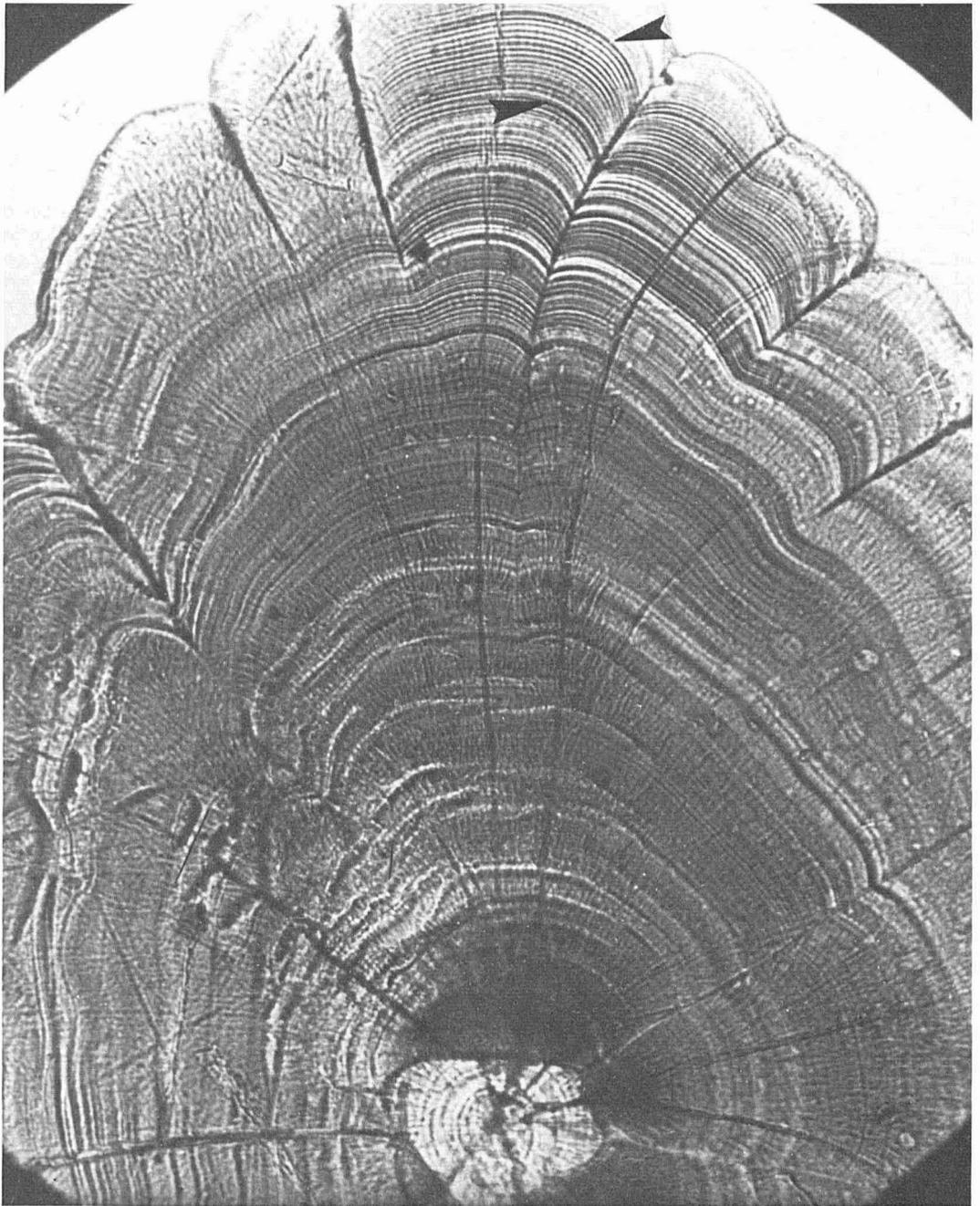
FIGURE 2.—An otolith from a 110 mm SL *Parophrys vetulus* captured in Yaquina Bay. Arrows indicate clear fortnightly rings. There are 21 fortnightly rings on this otolith. The actual age was calculated to be 363 d (see text).

nightly patterns of a *P. vetulus* otolith. The first fortnightly ring is formed consistently when the fish is 60 to 75 d old, i.e., the beginning of the metamorphic period (Rosenberg and Laroche 1982).

Basic growth data for the two nursery areas were obtained from size-at-age information. The data for 218 fish captured at Moolach Beach (Fig. 3) show that there are two linear portions of the data, with different slopes, separated by an
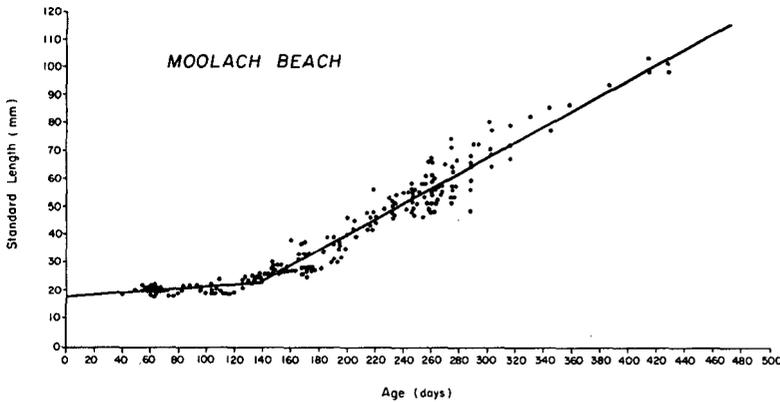
FIGURE 3.—Size-at-age data for *Parophrys vetulus* captured in the Moolach Beach nursery area.

inflection point. There is no evidence of an upper asymptote in the data, so the use of growth models such as the Gompertz or von Bertalanffy equations is inappropriate. 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 term. The B terms are the regression coefficients and E indicates the error terms. The point of inflection which produced the smallest residual sum of squares was found to be 140 d for the Moolach Beach data. The fitted equation is:

$$Y = 16.87 + 0.051X - 32.92A_1 + 0.23A_2.$$

An analysis of variance for the regression (Table 1A) shows that a good fit was obtained with this model, and the data set has a relatively low estimated variance. The slopes of the regression below and above 140 d were computed as 0.051 and 0.279, respectively. These slopes are estimates of the mean growth rate per day for juvenile *P. vetulus* utilizing the Moolach Beach nursery area. The lower portion of the data, below 140 d of age, shows a plateau in growth attributed to the metamorphic period (Rosenberg and Laroche 1982).

Regression of the size-at-age data for Yaquina Bay juveniles (Fig. 4: 186 data points) yields the fitted equation:

$$Y = 13.01 + 0.083X - 33.45A_1 + 0.201A_2.$$

The analysis of variance for this model (Table 1B) 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 the smallest residual sum of squares was also 140 d of age for the Yaquina Bay data. The slopes below and above the inflection are 0.083 and 0.284, respectively.

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, 19.88 for the Moolach Beach data and 95.01 for the Yaquina Bay data. The ratio is distributed as F(184:216) and the variances are significantly different at the $P = 0.001$ level. Since the variances are unequal, statistical tests for equality of slopes or intercepts are not strictly valid (Scheffe 1959). However, the slopes are similar, 0.279 and 0.284.

Back-calculated growth for individuals from both areas are in good agreement with growth

TABLE 1.—Analysis of variance for the least squares multiple regression analysis of size-at-age data.

A. Moolach Beach regression:

$$Y = 16.87 + 0.015X - 32.92\ A_1 + 0.23\ A_2$$

Multiple R = 0.975
R^2 = 0.950

Source	DF	Sum of squares	Mean square
Regression	3	80815.2	26938.4
Residual	214	4253.7	19.9

F value = 1355.0

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

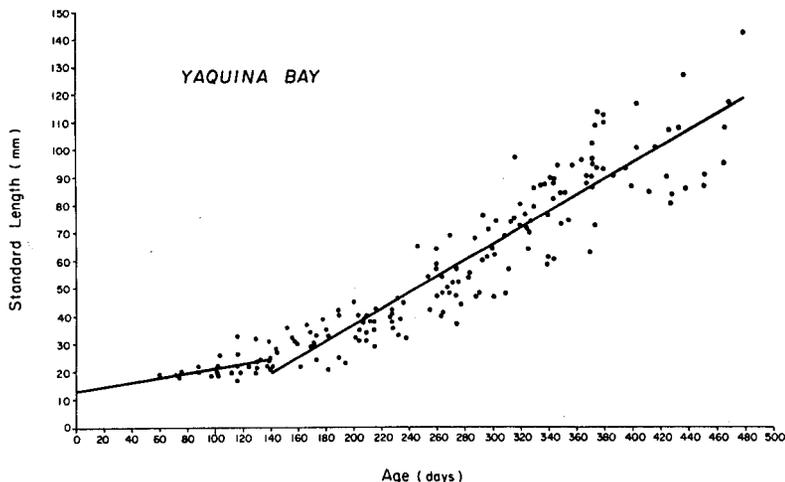| Source	DF	Sum of squares	Mean square
Regression	3	139575.6	46525.2
Residual	182	17308.1	95.1

F value = 489.3

FIGURE 4.—Size-at-age data for *Parophrys vetulus* captured in the Yaquina Bay nursery area.

estimates from the size-at-age data (Figs. 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. For the Moolach Beach data (Fig. 5), the average slope of the eight lines ranged from 0.20 to 0.28. Average growth was not significantly different in the 2 yr (nonparametric rank sum test).

Individual growth back calculated from the otoliths of 16 fish captured in Yaquina Bay range in average slope from 0.19 to 0.32 (Fig. 6). The growth rates of fish collected in 1978 versus 1979 were significantly different ($P = 0.05$, nonparametric 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 inconclusive, but examination of the size-at-age data by year (Fig. 7) tends to support the results of the back calculations.

The influx of fish to the Moolach Beach nursery ground, determined by back calculating the date of recruitment to the sampling gear for each fish, was distributed over the winter and spring (Fig. 8). During the summer, recruitment declined and was zero by July 1978 and by September 1979.

For juveniles captured in the estuary, recruitment appeared to be concentrated over a few winter months (Fig. 9). A sharp peak is evident
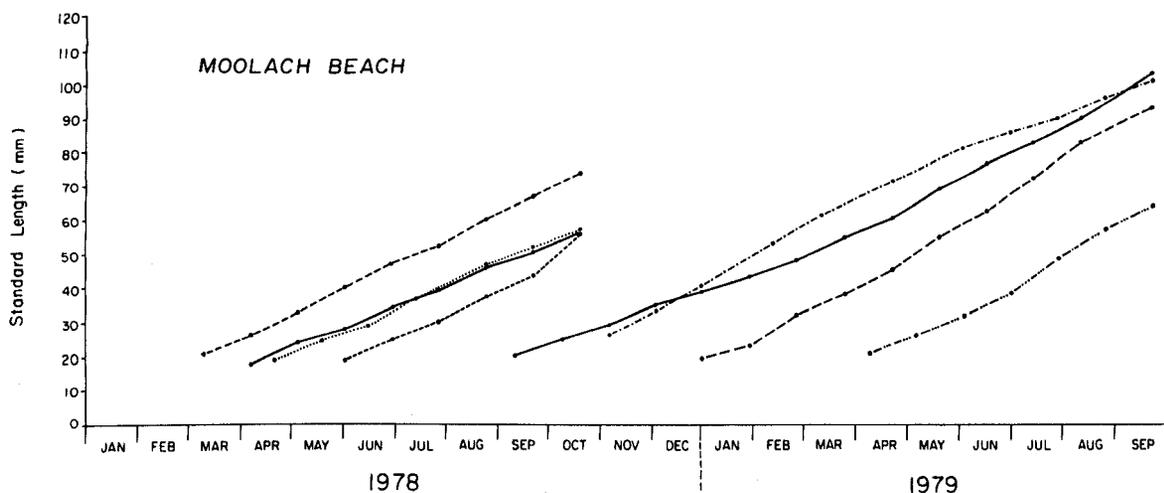

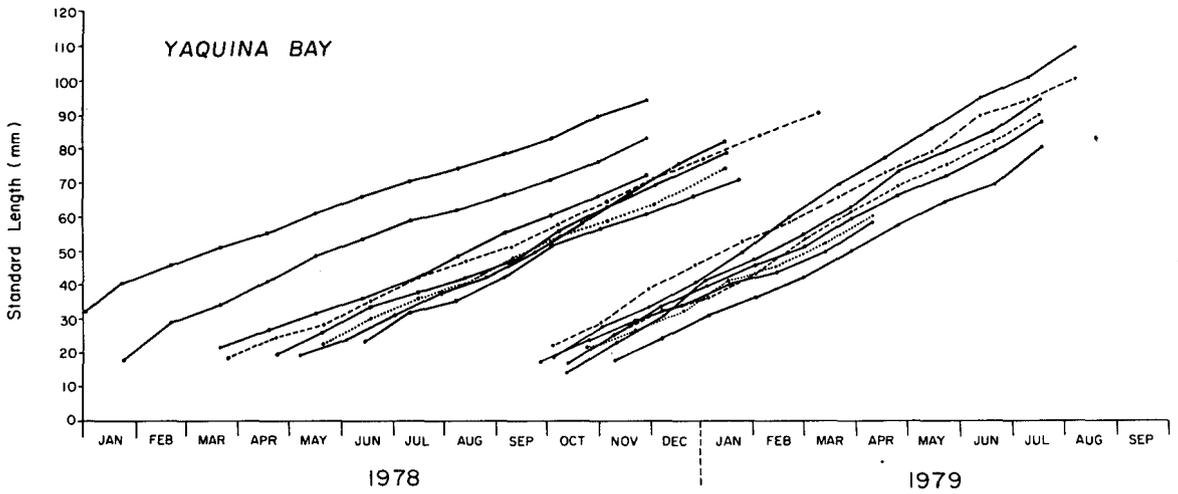FIGURE 5.—Back-calculated growth of eight individual *Parophrys vetulus* from Moolach Beach during 1978-79.

FIGURE 6.—Back-calculated growth of 16 individual *Parophrys vetulus* from Yaquina Bay during 1978-79.
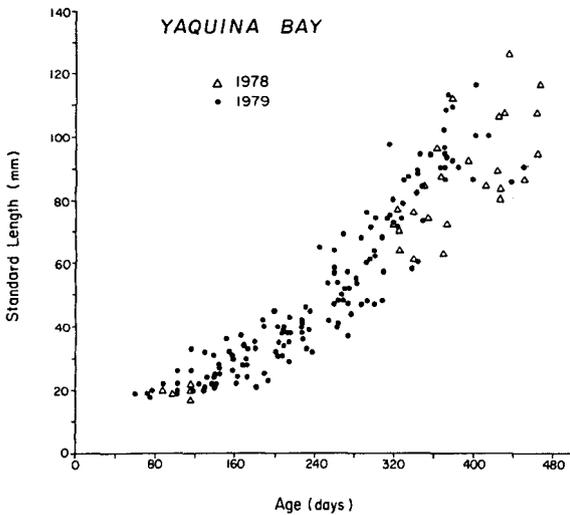

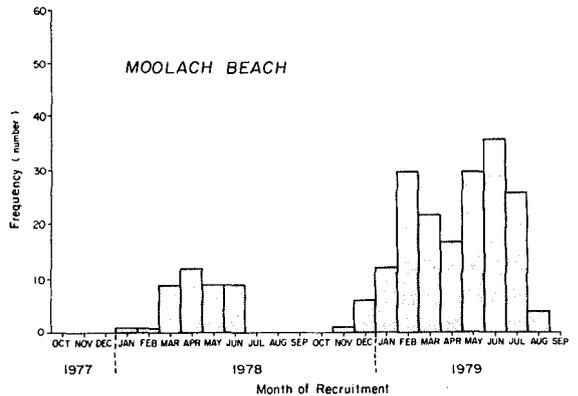FIGURE 7.—Size-at-age data plotted by year of capture of *Parophrys vetulus*.

FIGURE 8.—Distribution of *Parophrys vetulus* recruitment to the sampled population at Moolach Beach during 1978-79. Full recruitment to the sampling gear was estimated to occur at 120 d of age.

in November, December, and January. As in the Moolach Beach data, recruitment goes to zero in the summer, but reappears in the fall among Yaquina Bay fish.

DISCUSSION

Several previous studies have attempted to estimate growth rates for English sole juveniles (Table 2). 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). The recalculated daily growth estimates from all of these other studies are similar, but are substantially higher than my estimated daily growth rates. Smith and Nitsos (1969) and Van Cleve and El-Sayed (1969) determined growth during the first year of life by back calculating the size of the fish when the first detectable annulus on the interopercular bone was formed. This occurs during the fish's first slow growth season, which may be at various ages due to the protracted spawning period of this species. Growth back calculations of individual fish (Figs. 5, 6) do not show a clear slow growth period during the first year.
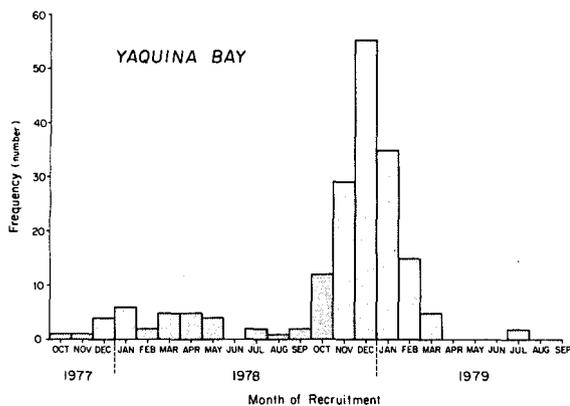
FIGURE 9.—Distribution of *Parophrys vetulus* recruitment to the sampled population in the Yaquina Bay estuary during 1978-79. Full recruitment to the sampling gear was estimated to occur at 120 d of age.

The other two studies (Westrheim 1955; Kendall 1966) utilize the technique of following modal progressions through time in length-frequency distributions. These estimates are strongly influenced by the efficiency of the sampling gear. If the smaller fish are sampled less efficiently than the larger, growth will be over-estimated. Emigration of small individuals, immigration of larger fish, and differential mortality of small fish would all produce overestimates of growth using this method. Also, length-frequency modal progression may give variable results dependent on the method of choosing the modes.

Variability in the size-at-age data was much higher for fish sampled in the estuary compared with those sampled in the open coastal area, but the mean growth rates for fish from the two areas were similar. Physical factors may affect growth variability. Yaquina Bay has highly variable temperature and salinity. Frey[4] found differences of up to 5‰ salinity and 2°C between high

and low tides in the lower bay. Bottom temperature in the estuary ranges between 5° and 15°C through the year, and salinity from virtually 0 to 34‰. At Moolach Beach in contrast, a more constant environment may be expected. The open coastal region does not have a large source of freshwater to influence salinity and temperature. Huyer (1977) and Huyer and Smith (1978) reported that bottom water salinity off the Oregon coast fluctuates about 1‰ from winter to summer. Temperature varies from 6.5°C in summer, due to seasonal upwelling, to about 10°C in winter.

There are two ways in which growth variability can be reduced. Either outlying individuals have their growth rates altered towards the mean or they are removed from the population. Particularly good or bad growth conditions in an area would affect the growth of all individuals, and alter the mean. Emigration and mortality are the two possible removal processes. The size-at-age plot for Moolach Beach (Fig. 3) and other data (Laroche and Holton 1979) indicate that most *P. vetulus* juveniles move out of the near-shore area at between 70 and 80 mm SL. Emigration from the estuary appears to be at a larger size, approximately 100 mm SL (Westrheim 1955; Olson and Pratt 1973).

Predation in the estuary is probably low compared with the open coast. 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 Wadden Sea, reported predation mortality to be low in contrast to a coastal nursery area studied by Steele and Edwards (1970).

Finally, intraspecific competition may affect growth. The estimated densities of juvenile English sole in the estuary are a consistent order of magnitude greater than at Moolach Beach (Krygier and Pearcy[5]). Competition may potentially

TABLE 2.—Summary of growth estimates from previous studies: the data has been recalculated so that direct comparisons can be made (see text).

Location	Size at 1 yr of age (mm SL)	Daily growth rate (mm/d)		Source
Yaquina Bay, Oreg.	117		0.40	Westrheim 1956
Monterey Bay, Calif.	108-126		0.36-0.43	Smith and Nitsos 1969
Puget Sound, Wash.	128		0.44	Van Cleve and El-Sayed 1969
Puget Sound, Wash.	—	winter	0.48	Kendall 1966
		summer	0.73	

emphasize differences among individuals and increase observed variability.

The most plausible mechanism for 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 smaller, slower growing individuals is occurring, the observed variability 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.

A hypothesis arising from this study is that survival, not growth, is enhanced in the estuarine nursery ground compared with 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.

ACKNOWLEDGMENTS

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