

AGE AND GROWTH OF A PLEURONECTID, *PAROPHRYS VETULUS*, DURING THE PELAGIC LARVAL PERIOD IN OREGON COASTAL WATERS

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ABSTRACT

The age of 331 field-collected English sole, *Parophrys vetulus*, larvae, 3.1-20.0 mm SL, was determined using daily otolith growth increments. Age in days from hatching was estimated by adding 5, the number of days prior to first increment formation in the laboratory, to the number of increments counted on sagittae. Number of otolith growth increments among larvae of known age in the laboratory ranged widely. Yet daily periodicity of increment formation in *P. vetulus* was inferred from the observations that even under poor growing conditions some larvae added one increment each day since first formation and that, unlike the remaining laboratory-reared larvae in which no pattern was evident, increment addition among larvae in the sea appeared to follow a stable and uniform pattern.

Gompertz and von Bertalanffy growth models fitted the resultant size-at-age data equally well; therefore, only the Gompertz model is presented. Larval growth rate decreased from 0.3 mm per day at 8-9 days of age to <0.1 mm per day between 73 and 74 days. The oldest specimen was 74 days old, but most of the larval and transforming specimens collected in plankton samples were <70 days old.

Previous estimates of age at length of larval *P. vetulus*, based on length-frequency modal progression analysis, overestimated the age of larvae >5.5 mm SL by 2-3 times and, correspondingly, the duration of pelagic life was overestimated, 18-20 weeks compared to 8-10 weeks based on otolith-estimated age.

Saccular otoliths grow by addition of layers of material differing in the relative amount of the protein, otolin, and calcium carbonate in the aragonite form (Degens et al. 1969; Pannella 1971). This results in growth units or increments composed of an inner light band and an outer dark band. Once the cycle of formation has been established for a species, otolith growth increments can be used to estimate a fish's age and as a record of its past growth. Daily periodicity of increment formation has been confirmed in numerous species by the number of first-order growth increments within annuli in fish over 1 yr of age (Pannella 1971, 1974), by inspection of otoliths from reared fish of known age (Brothers et al. 1976; Taubert and Coble 1977), or from fish maintained in the laboratory for a known period of time (Struhsaker and Uchiyama 1976). Bands of daily increments are often grouped into fortnightly and monthly growth patterns (Pannella

1974; Rosenberg 1980). Subdaily increments, which appear faint and indistinct, when compared to daily increments, have been found in some species (Taubert and Coble 1977; Brothers and McFarland in press).

The daily increment method of aging larval and juvenile fishes can be used in fishery research to document the timing and duration of spawning, development, and major life history stages and events. The singlemost important application is the accurate determination of growth rates during early life in the sea. This technique has been applied to relatively few species, however, and much remains to be learned about how growth may change during development and under varying environmental conditions. Once specific growth rates are available, age-dependent larval mortality rates can be estimated and used to improve estimates of spawning stock biomass and also, perhaps, provide insight into recruitment success.

This paper documents the existence of daily growth increments in laboratory-reared and field-caught larvae of an eastern North Pacific pleuronectid, the English sole, *Parophrys vetulus*. It provides the first accurate estimates of

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age at length for larvae of this species and describes the growth of larvae collected in Oregon coastal waters during the 1977-78 spawning season. It is the first detailed study of larval growth of a pleuronectid throughout the pelagic period, and further, provides a basis for the documentation of growth during transformation to the adult form (Rosenberg and Laroche 1982) and of juveniles in nursery grounds off the Oregon coast (Rosenberg 1980).

METHODS

Spawning and Rearing Procedures

Ripe adult *P. vetulus* were collected during fall and winter 1978 with a 12 m otter trawl off the Oregon coast in the vicinity of Hecata Head, approximately lat. 44°10'N, long. 124°18'W, 68-77 m water depth. Eggs were artificially fertilized on shipboard (Bagenal and Braum 1971) and transported back to the laboratory in seawater-filled plastic bags.

In the laboratory, eggs were incubated and larvae reared at 12°-13°C and under a 14-h light, 10-h dark photoperiod in filtered seawater taken from the area where the adults were captured. Eggs held in 4 l glass jars hatched in 3-3½ d. The newly hatched larvae were transferred by pipette to new 4 l glass jars or 8 and 9 l plastic tubs in which a bloom of the green flagellate *Tetraselmis* sp. was maintained throughout the rearing period. Approximately every 2 d, one-fourth to one-third of the water in rearing containers was replaced. On day 4 after hatching, *Gymnodinium splendens*, a naked dinoflagellate, and *Brachionus plicatilis*, a rotifer, were introduced into the rearing containers. After 1-2 wk, *G. splendens* was no longer added because larvae did not appear to eat this organism. Prey concentrations were not measured but *B. plicatilis*, the primary food item, was maintained at high levels, i.e., rotifers were readily visible throughout rearing containers. *Artemia salina* nauplii and the harpacticoid copepod, *Tisbe* sp., provided secondary food sources.

One to ten larvae were preserved in ~80% ethanol each day after hatching for the first 35 d; subsequently, older larvae were preserved at irregular intervals. Larvae were reared from two separate spawnings, in early and late fall 1978, but since rearing conditions were identical, age and growth data from the two were combined.

Field and Laboratory Procedures

Parophrys vetulus larvae were collected in the field with 70 cm, 0.505 mm mesh bongo nets in bottom to surface stepped, oblique tows. Samples were taken approximately monthly from November 1977 to June 1978 in Yaquina Bay, Oreg., and 2-7 km offshore (lat. ~44°37'N; long. 124°05'W). Samples were drained and preserved in ~80% ethanol; within 12-18 h the samples were drained again and fresh preservative was added. With each plankton sample surface temperature, surface and bottom salinity were recorded and a bathythermograph cast was made.

In the laboratory all fish larvae were removed from plankton samples and stored in ~80% ethanol. Otoliths were removed from *P. vetulus* larvae within 6 mo of initial preservation because longer storage resulted in erosion or complete dissolution of the otoliths.

Prior to otolith removal *P. vetulus* larvae were placed in freshwater for ~1-2 min (somewhat longer for specimens >15 mm) to remove or dilute ethanol in the tissue. A larva was then placed in a drop of water on either a glass slide or large rectangular cover slip under a dissecting microscope fitted with polarizing filter and analyzer. Standard length (SL) was measured with an ocular micrometer to the nearest 0.1 mm and both sagittae were dissected out with fine probes at 25 × or 50 × magnification. The larva was removed from the slide or slip and the otoliths were left to dry concave side up. Sagittae were then permanently mounted under a cover slip with Pro-Texx,³ a clear mounting medium. Rectangular cover slip mounts, which were thought to improve the optical properties of the preparation, were taped for support to a thin piece of brass for viewing under the microscope.

Otolith growth increments, consisting of an inner light band and a narrower, sharply delineated, continuous outer dark band adjacent to it, were counted using a compound microscope with bright field illumination at 800 × or 1,250 × magnification. Faint bands inside the otolith nucleus in reared larvae and "subdaily" or weak rings between well-defined growth increments in some older (>30 d old) field-caught fish were not counted. Counts were made on only one sagitta of the pair and were repeated until a

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

final, "best" count was reached. Successive counts and verification counts which were made by the original reader at a later time usually did not vary by more than ± 2 . Age estimates could not be obtained for 10% of the field-caught larvae because increments were faint and indistinct or the otoliths were misshapen. Maximum otolith and nucleus diameters were measured to the nearest micron. Photomicrographs were taken at $500 \times$ or $1,000 \times$ magnification under a light microscope.

Shrinkage of larvae preserved in 80% ethanol was compared with shrinkage after preservation in 10% seawater-diluted Formalin, the fixative most commonly used to preserve plankton samples. Thirty 7-day-old reared larvae were measured alive and immediately preserved in either 80% ethanol (15) or 10% Formalin (15). The live, mean standard lengths of the two groups of larvae were 4.34 and 4.42 mm. After 4 mo in preservative the mean standard length of the ethanol-preserved group was 4.20 mm and of the Formalin-preserved group, 4.196 mm. Mean percent shrinkage or $100(\text{original SL} - \text{preserved SL}/\text{original SL})$ was 3.2% in the ethanol-preserved group and 5.1% in the Formalin-preserved group. The difference in amount of shrinkage between the two groups was highly significant (ANOVA, $P < 0.01$). Care must be taken, therefore, when comparing estimates of size at age based on measurements of larvae preserved in different fixatives. From this limited investigation it became apparent that Formalin-preserved *P. vetulus* larvae appear to be somewhat smaller at age than ethanol-preserved fish.

Statistical Procedures

Gompertz and von Bertalanffy growth models were fitted to larval *P. vetulus* data because the form of the length-age plot was nonlinear with a distinct upper asymptote. A detailed discussion of the Gompertz function, which is the primary model used in this paper, and methods for obtaining initial parameter estimates are presented by Zweifel and Lasker (1976). The generalized equation of this model is:

$$L_t = L_0 \exp \left[K (1 - e^{-\alpha t}) \right],$$

where L_t = length at age t ; L_0 = length at $t = 0$ (i.e., where the curve intercepts the y-axis); and $K = \frac{A_0}{\alpha}$, or the specific growth rate at $t = 0$

divided by the rate of exponential decay. Untransformed data were used in this model because the standard deviation of larval lengths at age remained relatively constant and did not increase with age, indicating variance homogeneity within the data set. The Gallucci and Quinn (1979) version of the von Bertalanffy equation was employed, utilizing the new parameter, $w = kL_\infty$, where k is the growth constant, and L_∞ , the asymptotic maximum size, which for *P. vetulus* larvae is the maximum size attained in the plankton prior to transformation into benthic juveniles. The general form of this equation is:

$$L_t = \frac{w}{k} \left\{ 1 - \exp \left[-k(t - t_0) \right] \right\},$$

where t_0 is the time when $L_0 = 0$ (i.e., where the curve intercepts the x-axis).

The SPSS NONLINEAR⁴ program employing Marquardt's algorithm was used to fit both models. A measure of goodness of fit was provided by the residual sums of squares (RSS), the standard error of the regression (or standard deviation of the residuals), and approximate 95% confidence limits for each parameter assuming linearity. Linear confidence theory can be applied here because the assumption of linearity at the final (least squares) parameter values is a reasonable one (Conway et al. 1970; Kimura 1980). A comparison of the RSS at the final parameter values to the linear estimate RSS provides a measure of the linearity of the sum of squares (SS) function (SPSS NONLINEAR program).

Absolute growth rate or $\frac{L_2 - L_1}{t_2 - t_1}$ expressed in millimeters per day and specific growth rate or $\frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times 100$ expressed as percent per day of length were calculated (Ricker 1979).

RESULTS

Increment Formation

Parophrys vetulus larvae survived and grew in the laboratory for over 35 d after hatching, with some individuals eventually transforming into juveniles. However, growth after yolk-sac absorption, between days 4 and 5, was retarded and

⁴SPSS NONLINEAR. Statistical Package for the Social Sciences, Vogelback Computing Center, Northwestern University, Evanston, IL 60201.

not comparable to growth in the field. Despite this, growth increments were visible on the otoliths of over 300 reared larvae. Increments, though extremely narrow and crowded, were even visible on the otoliths of larvae as old as 54 d.

In the laboratory, the highest incidence of larvae with one growth increment occurred on days 5 and 6 (Table 1; Fig. 1a, b). This coincided with the time that larvae first began to swim actively near the surface of rearing containers and search for food. By day 5 larvae had also acquired darkly pigmented, iridescent eyes and functional mouths, and had utilized all or almost all their yolk. Age at first increment formation in the field was ascertained by comparing mean otolith diameter (μm) of field-caught larvae with a single increment, to mean otolith diameter of laboratory-reared larvae of known age (Table 1). The otolith diameter, $23.8 \mu\text{m}$, of field-caught larvae with only one growth increment ($\overline{\text{SL}} = 3.7 \text{ mm}$) fell between the mean values for laboratory-reared larvae at 5 d, $23.1 (\overline{\text{SL}} = 4.2 \text{ mm})$, and at 6 d, $24.2 (\overline{\text{SL}} = 3.9 \text{ mm})$. Age of all field-caught larvae with one otolith growth increment was, therefore, taken to be 6 d. Age at first increment formation varied among individuals in the laboratory and may, likewise, vary in the field; however, for the purpose of developing a generalized growth model, a single, best estimate of this event was made. The apparent smaller size of field-caught larvae with one increment most likely resulted from shrinkage during capture prior to preservation (Theilacker 1980). Larvae sampled in the laboratory were pipetted alive directly into preservative, thus reducing the amount of handling-induced shrinkage.

Although laboratory results were somewhat ambiguous, daily periodicity of otolith growth increment formation in *P. vetulus* was inferred from the following observations: 1) despite less than optimum rearing conditions some 14-, 17-, and 20-d-old larvae had added one increment each day since first formation on day 4 (Table 2); 2) no other periodical pattern in increment formation (i.e., other than daily) was observed among laboratory-reared larvae; 3) increment addition among larvae in the sea appeared to follow a stable and uniform pattern. The wide range in number of otolith increments among reared larvae of known age may have been caused by poor growing conditions which resulted in stunted body and otolith growth (Table 2). Reared larvae of northern anchovy also failed

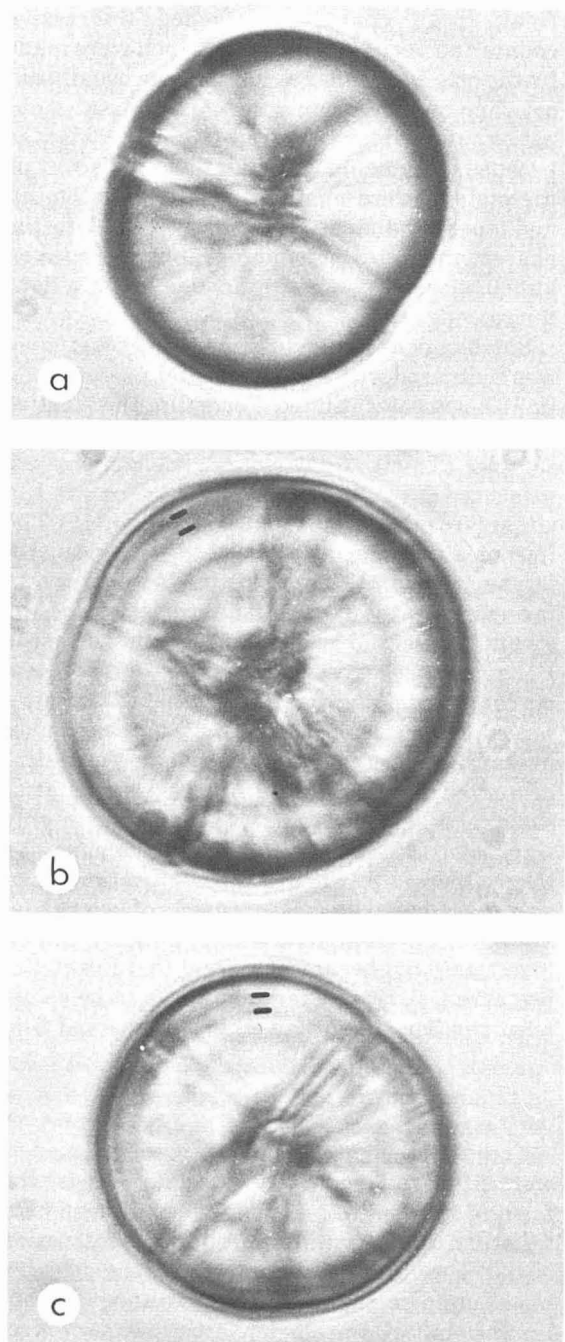


FIGURE 1.—Photomicrographs of *Parophrys vetulus* otoliths ($\times 1,000$). a. Sagitta ($22 \mu\text{m}$ in diameter) prior to first increment formation from a 4-d-old, laboratory-reared larva; b. Sagitta ($24 \mu\text{m}$ in diameter) with two complete increments (highlighted with black lines) from a 6-d-old, laboratory-reared larva; c. Sagitta ($22 \mu\text{m}$ in diameter) with two complete increments (highlighted with black lines) from a 7-d-old, field-caught larva.

TABLE 1.—Comparison of mean otolith diameters (OD) of laboratory-reared and field-collected *Parophrys vetulus* larvae. Age of reared larvae represents days from hatching.

Age (days)	Mean OD (μm)	No. larvae	No. growth increments					Mean OD (μm)	No. larvae	No. growth increments
			0	1	2	3	4			
0	14.6	10	10							
1	16.6	12	12							
2	18.8	10	9	1						
3	20.5	11	10		1					
4	21.6	14	13		1		21.3	7	0	
5	23.1	24	10	10	4		23.8	4	1	
6	24.2	19	4	4	8	2	24.6	10	2	

to consistently form growth increments when maintained on low rations (Methot and Kramer 1979). In *P. vetulus*, delayed inception of increment formation, up to 8 d after hatching, may also have accounted for some of the apparent irregularity in increment formation in the laboratory (Table 2). Another factor contributing to ambiguity of laboratory results was the difficulty in counting otolith increments in older larvae. Increments in most laboratory-reared fish after 16-25 d were exceedingly faint and, in some fish, no increments could be discerned (Fig. 2a, b). Growth increments were, in general, clearer and more distinct on the otoliths of field-caught *P. vetulus* larvae than on otoliths of laboratory-reared fish (Figs. 1c, 2c). The steady increase in number of increments with increasing otolith diameter and length of pretransformation larvae in the field is evidence that the irregularity in increment formation observed in the laboratory did not occur under natural feeding conditions (Figs. 3, 4).

Age and Growth

Age of field-caught *P. vetulus* larvae in days from hatching was estimated by adding 5, the number of days prior to appearance of the first

otolith growth increment, to the number of increments counted on sagittae. Counts of growth increments were obtained from 338 larval and transforming, pelagic specimens ranging from 2.4 to 20.0 mm SL (Fig. 4). But age could be estimated for only 331 larvae because increment formation had not yet begun in seven small specimens, 2.4-3.7 mm SL (Fig. 5). The oldest *P. vetulus* taken in plankton samples during 1977-78 was 74 d (2.4 mo) old and 17.8 mm SL. The next oldest larvae ranged from 65 to 70 d old and were 19-20 mm SL. The length of pelagic life of *P. vetulus* can be estimated directly from these data to be 2-2.5 mo. Few *P. vetulus* larvae >20 mm SL, the size at which larvae transform to benthic juveniles (Ahlstrom and Moser 1975; Rosenberg and Laroche footnote 3), were taken in extensive plankton collections off Oregon during the spring months in 1972-75 (Laroche and Richardson 1979). The largest larva taken in those collections was 22 mm SL.

Behavior of reared *P. vetulus* larvae further supports a pelagic phase of 2+ mo. At approximately 60 d of age, larval *P. vetulus* maintained in the laboratory first exhibited the tendency to rest on their sides on the bottom and to swim with their bodies at an angle to the vertical (J. L. Laroche unpubl. data).

TABLE 2.—Summary of growth in body length (SL) and otolith diameter (OD), and counts of growth increments on otoliths of laboratory-reared *Parophrys vetulus* larvae. *N* = number of larvae from which growth increment counts were taken; (*N*) = number of larvae used in mean otolith diameter calculation.

Age (days)	<i>N</i>	Mean SL (mm)	Range SL (mm)	Mean OD (μm)	Range OD (μm)	No. growth increments	
						Mean	Range
4	14	4.1	3.7-4.4	21.6	20-25	0	0-2
5	24	4.2	3.8-4.5	23.1	20-25	1	0-2
6	19(17)	3.9	3.1-4.2	24.2	23-27	2	0-4
9	9	4.0	3.7-4.1	24.7	23-26	3	2-4
10	13	4.2	3.7-4.6	25.7	25-27	4	3-6
14	13	4.9	5.8-4.2	28.7	27-33	8	5-10
17	13	5.4	4.5-6.3	29.6	28-33	10	5-13
20	7(6)	5.7	5.1-6.4	31.8	30-36	10	5-16
21	6	5.9	5.4-6.6	31.2	30-34	13	10-16
26	18(17)	7.0	5.6-8.6	33.4	30-37	14	10-20

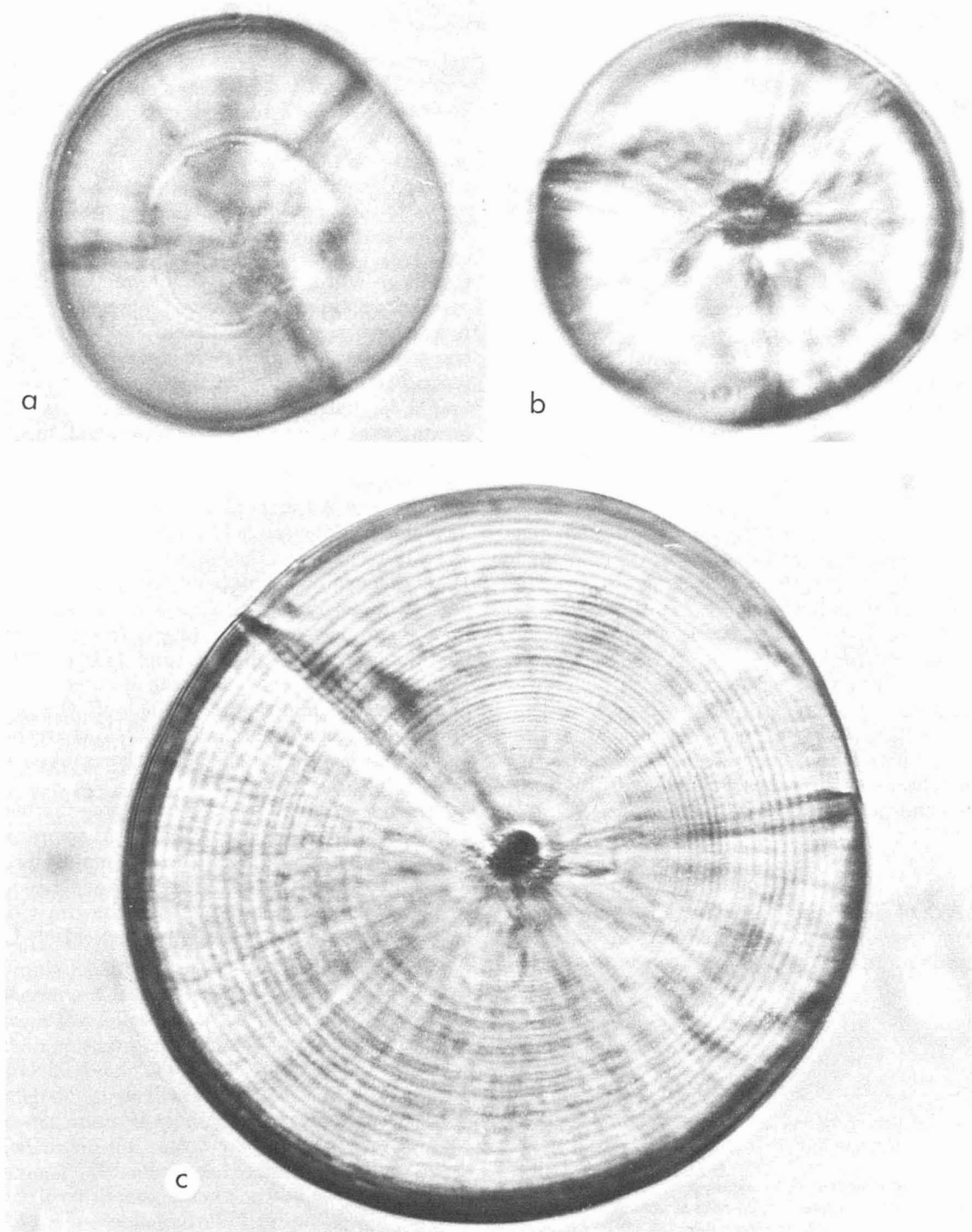


FIGURE 2.—Photomicrographs of *Parophrys vetulus* otoliths ($\times 1,000$). a. Sagitta ($30\ \mu\text{m}$ in diameter) with 16 complete increments from a 21-d-old, laboratory-reared larva; b. Sagitta ($32\ \mu\text{m}$ in diameter) with no discernible increments from a 22-d-old, laboratory-reared larva; c. Sagitta ($102\ \mu\text{m}$ in diameter) with 42 complete increments from a 47-d-old, field-caught larva.

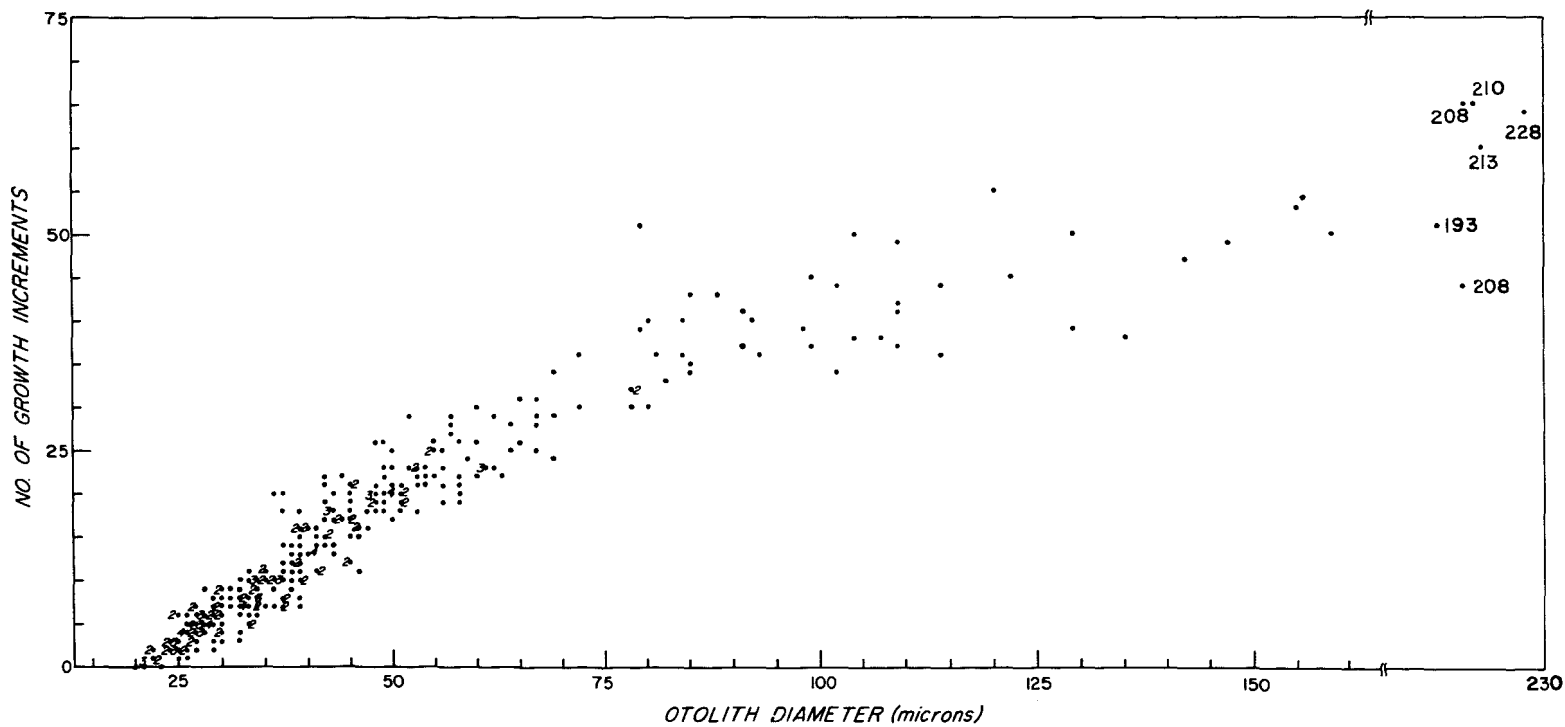


FIGURE 3.—Number of otolith growth increments related to otolith diameter of 338 larval and transforming, field-caught *Parophrys vetulus*.

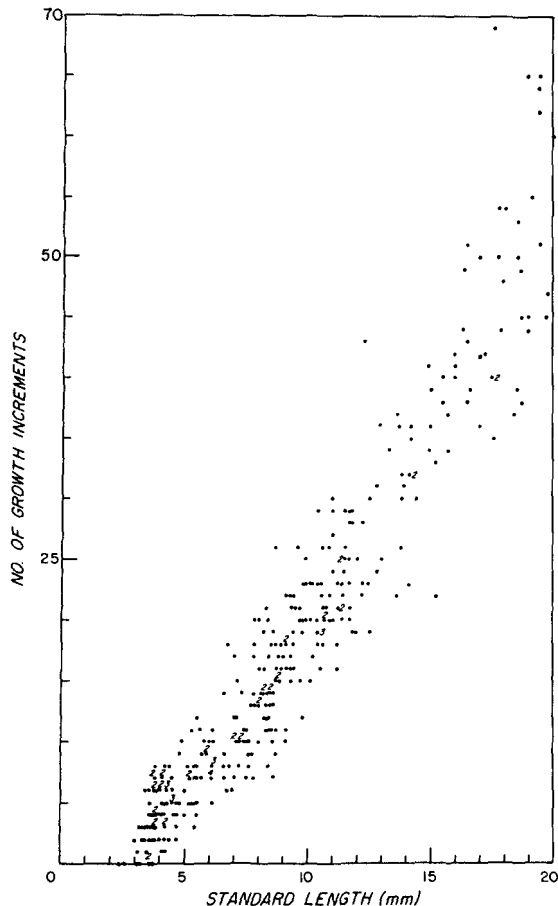


FIGURE 4.—Number of otolith growth increments related to standard length of 338 larval and transforming, field-caught *Parophrys vetulus*.

Our description of early growth of *P. vetulus* in Oregon coastal waters at temperatures ranging from 9° to 11°C is based on the ages and lengths of 331 specimens, 3.1-20.0 mm SL, with otolith growth increments. Gompertz and von Bertalanffy models yielded good and nearly identical fits to the data and similar estimates of growth rate; therefore, the results of only one model (Gompertz) are presented (Table 3; Fig. 5). RSS and linear estimate RSS of the Gompertz growth parameters were very similar; thus, the assumption of linearity in computing 95% confidence limits is reasonable, and the computed limits indicate relatively narrow confidence regions around the parameters (Table 3).

Previous estimates of age at length of larval *P. vetulus* were derived from the progression of

modes in length-frequency distributions of larvae from a time series of (10% Formalin preserved) plankton samples (Laroche and Richardson 1979). A comparison of those results with age at length estimated by the Gompertz equation (Zwiefel and Lasker 1976) indicates that the length-frequency method overestimated the age of larvae >5.5 mm SL by 2-3 times (Table 4).

Estimates of specific and absolute rates of growth were calculated from length at age for various ages as predicted by the Gompertz model (Table 5). Specific growth rate steadily decreased between 8 and 74 d. Absolute growth rate was fairly uniform between 8 and 31 d, slowed somewhat between 31 and 41 d, but was more drastically reduced between 73 and 74 d, at which time larvae undergo transformation, a

TABLE 3.—Gompertz equation and estimated parameters describing the growth of 331 *Parophrys vetulus* larvae in Oregon waters during the 1977-78 spawning season. RSS = residual sum of squares; SE = standard error of the regression; S² = variance; CL = confidence limits.

Equation				RSS	SE
$L_t = 2.073 \exp[2.354(1 - e^{-0.045t})]$				520.83	1.256
Parameters	S ²	RSS	Linear est. RSS	Approximate 95% CL	
L ₀ = 2.073	0.023	564.892	564.892	L ₁ = 1.779, L ₂ = 2.367	
K = 2.354	0.003	535.762	536.093	L ₁ = 2.245, L ₂ = 2.462	
α = 0.045	0.00001	533.854	533.635	L ₁ = 0.040, L ₂ = 0.050	

TABLE 4.—Age of *Parophrys vetulus* larvae; (A) estimated from modal progression in length-frequency distributions of larvae caught during 1971 in biweekly and weekly Formalin-preserved plankton samples (Laroche and Richardson 1979), (B) estimated by the Gompertz equation based on otolith increment counts from ethanol-preserved larvae caught in 1977-78.

SL (mm)	Estimated age (weeks)	
	(A)	(B)
5.5	2.3	1.7
7.5	4.1	2.5
9.5	5.9	3.3
11.5	8.7	4.1
13.5	13.4	5.0
15.5	17.6	6.1
17.5	21.9	7.5

TABLE 5.—Growth rates of *Parophrys vetulus* larvae predicted from the Gompertz equation at various times from hatching.

Age (days)	Specific growth rate (% per day SL)	Absolute growth rate (mm per day)
8-9	7.3	0.32
15-16	5.3	0.36
19-20	4.4	0.36
24-25	3.5	0.35
30-31	2.7	0.33
40-41	1.7	0.25
73-74	0.4	0.08

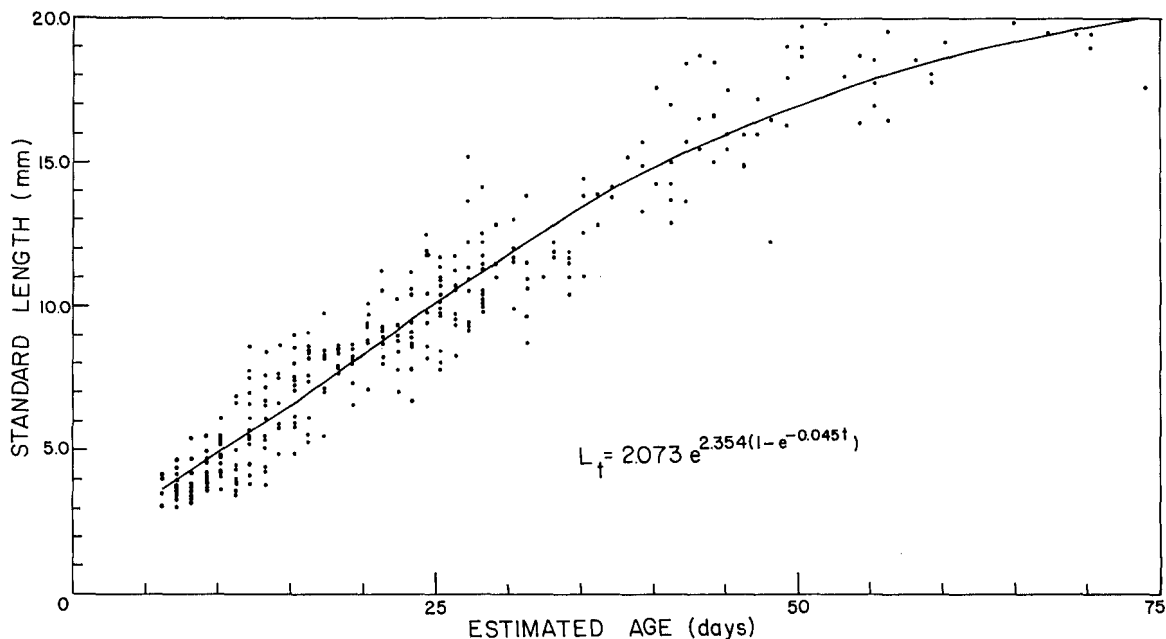


FIGURE 5.— Gompertz curve and equation fitted to length at age of 331 larval and transforming, field-caught *Parophrys vetulus* with at least one otolith growth increment.

period characterized by reduced growth in length (Rosenberg and Laroche 1982).

The plot of otolith diameter on standard length of pelagic larval and transforming *P. vetulus* revealed an allometric relationship (Fig. 6). A distinctive feature of this plot was the apparent continued, even accelerated growth of sagittae as *P. vetulus* larvae reached the size of transformation, 18-20 mm SL, when rate of growth in body length slows down. Physical evidence of accelerated growth in otolith diameter relative to body length can be seen by the increased width of the outermost increments on otoliths of larvae older than 30 d (e.g., outer 9-10 increments on sagitta in Fig. 2c). The otolith diameter to standard length relationship, once a mathematical formulation has been computed, can be used to back-calculate individual growth histories of larvae and juveniles (Rosenberg 1980; Methot in press), as has been done for adult fishes (Tesch 1968; Ricker 1969).

DISCUSSION

As in numerous other temperate and some tropical species of fishes, growth increments on the otoliths of *P. vetulus* larvae appear to be formed daily after yolk-sac absorption when larvae become capable of exogenous feeding.

Counts of these increments provide more precise and accurate estimates of larval age and growth rates throughout the larval period than have previously been available. This information, when combined with abundance data, allows computation of age-dependent mortality rates resulting in more accurate estimates of larval mortality in the sea.

Empirically, both the Gompertz and von Bertalanffy growth models fit the larval *P. vetulus* data well. Both yielded similar values for length at age and growth rates from which age-dependent mortality estimates can be made. There has been much disagreement, on theoretical grounds, as to the appropriateness of either model for describing growth in fishes, although they are mathematically quite similar (e.g., Zweifel and Lasker 1976; Ricker 1979). Despite numerous attempts to attribute biological significance to mathematical models of growth, the best criterion available for choosing a particular model is still goodness of fit to the data (Ricker 1979). In that respect, both models were appropriate to this data set.

A practical measure of the appropriateness of mathematical models is the relative accuracy and stability of pertinent parameter estimates (Gallucci and Quinn 1979). In the Gompertz

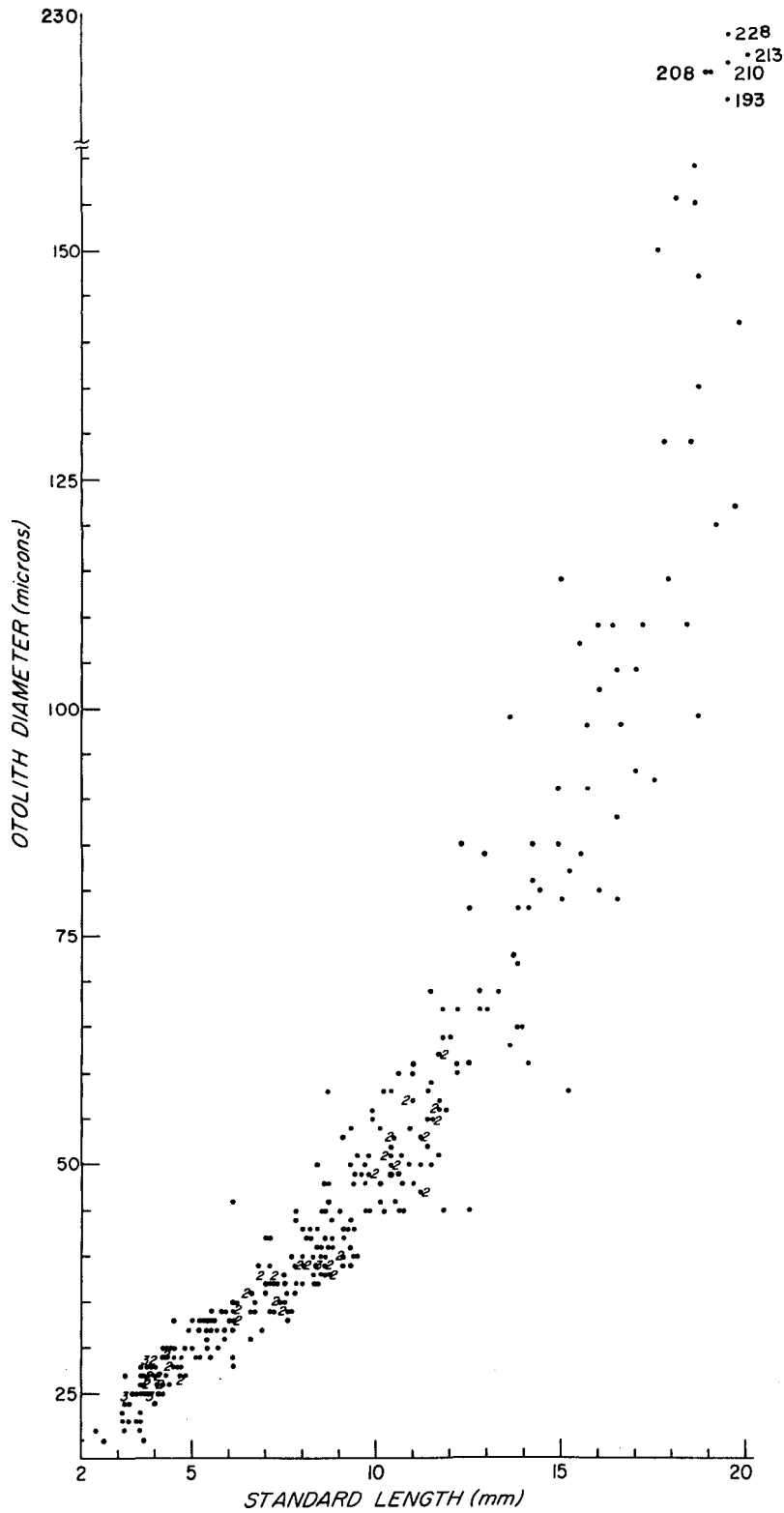


FIGURE 6.—Otolith diameter related to standard length of 338 larval and transforming, field-caught *Parophrys vetulus*.

model, the parameter L_0 or the y-intercept has been used as an estimator of length at hatching (Zweifel and Lasker 1976). However, the value of this parameter, 2.07 mm SL, for the *P. vetulus* data set was low compared to mean hatching lengths of reared larvae: 2.60 ($N = 11$) and 2.91 ($N = 10$) mm SL at 12°-13°C (Laroche unpubl. data); and 2.85 ($N = 25$) mm TL at 10°-11°C (Orsi 1968). Net-caught larvae on which the growth model is based would appear smaller at age because of increased shrinkage during capture (Theilacker 1980). This may account for some of the difference in predicted and observed hatching lengths. Another probable cause of this discrepancy is the lack of data points in the <6 d of age region of the plot, i.e., before growth increment formation begins. The value of L_0 is based on extrapolation beyond the actual data and may be, therefore, of questionable use as a measure of the appropriateness of this model.

Comparison with larval growth in the field at similar temperatures of another pleuronectid, *Pseudopleuronectes americanus*, provided evidence that growth rates predicted by the Gompertz model for *Parophrys vetulus* are realistic. Larval *Pseudopleuronectes americanus* between the ages of 28 and 42 d, growing in large enclosures in Narragansett Bay at 10°-15°C, had a specific growth rate of 1.9% per day of standard length (Laurence et al. 1979). The predicted specific growth rate of *Parophrys vetulus* of the same age, growing at 9°-11°C, was 2.2%. Larval *Pseudopleuronectes americanus* between 28 and 42 d of age grew from 6.6 to 8.6 mm SL, while *Parophrys vetulus* larvae grew from 11.2 to 15.3 mm SL. Although these two species differ in size at age, both transform at approximately the same age, 8-10 wk, and appear to grow at similar rates between 4 and 6 wk of age. Since length at hatching, ~2-3 mm SL, is similar for both species, higher rates of growth prior to and after 4-6 wk probably accounts for the greater size at age of *P. vetulus* and greater size at transformation, >18 mm SL in *P. vetulus* versus <10 mm for *Pseudopleuronectes americanus*.

A comparison of otolith-estimated and length-frequency derived age-at-length data indicated that the latter method overestimated age of *Parophrys vetulus* larvae >5.5 mm SL by 2-3 times. This resulted in a gross overestimate of duration of the pelagic life of this species, 18-22 wk (Laroche and Richardson 1979) compared to 8-10 wk based on the age data presented here. It

is unlikely that these large differences are solely the result of different preservatives. Such a large discrepancy between the two methods demonstrates the serious inaccuracies that could result from attempts to estimate age and growth rates from length-frequency data. Such data predictably yield low estimates of growth, especially for species with protracted spawning, because of continual recruitment of small larvae to the population. Problems of net avoidance by larger specimens further bias length-frequency distributions.

The otolith aging method developed in this study could be used further to investigate growth and survival among different cohorts of *P. vetulus* larvae. Spawning in this species is highly variable in both frequency and timing (Laroche and Richardson 1979). Peak spawning can be bimodal in some years with a 2-4 mo separation between peaks (Kruse and Tyler⁵). Larvae produced in those two peaks could develop and grow under very different temperature regimes and feeding conditions, which could result in two distinct groups of larvae differing in rates of growth, mortality, and relative contribution to that year class.

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⁵Kruse, G. H., and A. V. Tyler. 1980. Influence of physical factors on the English sole (*Parophrys vetulus*) spawning season. Unpubl. manuscr., 25 p. Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331.

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