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SPATIAL COVARIATION OF DAILY GROWTH RATES OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND NORTHERN LAMPFISH, *STENOBRACHIUS LEUCOPSARUS*

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The widths of the outer three daily growth increments in the otoliths of larval *Engraulis mordax* (Engraulidae) and *Stenobrachius leucopsarus* (Myctophidae) were used as a measure of recent growth rate. From 10 samples collected off the coast of Oregon, 367 *E. mordax* and 141 *S. leucopsarus* individuals were analyzed. The overall mean growth rate of *S. leucopsarus* increased from 0.11 mm per day at a length of 5 mm to 0.28 mm per day at 15 mm. For *E. mordax*, growth rate declined from 0.57 per day at 5 mm to 0.41 mm per day at 15 mm. Within-and between-sample variance in growth rate was small, no spatial trends were detected. Correlations between *E. mordax* growth rate and *S. leucopsarus* growth rate among the 10 samples were not significant.

INTRODUCTION

The growth rate of young fish varies greatly in response to temperature and ration (Brett, 1979) and can be accurately measured in wild fish by analyzing daily growth increments in otoliths (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Methot and Kramer, 1979). After correcting for the effect of temperature on growth, the mean growth rate of larval fish in the sea is an indicator of the degree to which growth, and presumably survival, of larval fish is food limited. Variability in growth and condition provides information on time and space scales of ecologically important patchiness in the sea. Anchovy larvae show evidence of variation in growth rate (Methot and Kramer, 1979) and starvation indices (O'Connell, 1980) on scales of 1–100 km while 1–10 m patches of prey can be vital for successful first feeding by anchovy larvae (Lasker, 1975). When variability in larval growth rate of two or more species is compared, one may obtain information on the environmental variables which influence growth and survival of larval fish. Significant positive correlations in growth rate between species, i.e., similar spatial-temporal patterns of deviations from their respective mean growth rates, may indicate that these species respond to some set of environmental variables in the same way. Significant negative correlations suggest that responses to environmental conditions differ between the species. Nonsignificant correlations may mean that growth of each species is limited by different, specific environmental factors and these factors tend not to covary on scales larger than the scale of the sampler. The object of this study is a comparison of the growth rates of northern anchovy, *Engraulis mordax* (Engraulidae), and northern lampfish *Stenobrachius leucopsarus* (Myctophidae), within a specified portion of their distribution. Mean growth rates obtained from this analysis will be the first measure of growth for larval *S. leucopsarus* and for the northern population of *E. mordax*. Covariance in growth rate between species among samples will be examined for clues to relationships between larval fish and their environment.

During the summer along the coast of Oregon, larvae of *E. mordax* and *S. leucopsarus* are the most abundant species in the offshore assemblage of larval fish (Richardson and Pearcy, 1977). Both species inhabit the upper tens of meters of the water column (Ahlstrom, 1959; Richardson and Pearcy, 1977; Fast, 1960). The optimum environmental conditions for the two species may differ for several reasons. Oregon is the center of range for the northernmost of three *E. mordax* populations (Vrooman and Smith, 1971) but is in the south central part of the range of *S. leucopsarus* (Paxton, 1967). July is a prime spawning month for *E. mordax* but is near the end of a

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protracted spawning season for *S. leucopsarus* (Richardson and Pearcy, 1977). *S. leucopsarus* larvae have a larger mouth and will be able to eat prey unavailable to similar length *E. mordax.*

Although good estimates of growth rate have been made by examining the relationship between size at capture and number of daily growth increments in otoliths (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977; Methot and Kramer, 1979), this technique has two limitations. Data on size at age integrates growth rate over the lifetime of each larva and may have little meaning for studying environmental effects because environmental conditions are typically measured only at the time of capture. Second, the otolith morphology of larger larvae such as *S. leucopsarus*, obscures the inner increments. Ages cannot be estimated unless one resorts to the tedious procedure of grinding thin sections of the otoliths. Both problems are solved by using the widths of the outer few increments to measure growth rate a few days before capture. This technique requires the additional assumption that otolith growth mirrors fish growth on a day to day basis. Although this assumption has not been rigorously evaluated, Taubert and Coble (1977) found that otolith size was more closely related to fish size than to age. Correspondence between otolith growth and fish growth is routinely assumed in back calculation of size at age from annual marks in otoliths (Ricker, 1969).

METHODS

The NOAA fisheries RV "David Starr Jordan" surveyed along seven transects off the coast of Oregon 19–26 July 1977. Transects extended from the 50 fathom depth contour to a point 90 miles due west. Direction of survey alternated between transects. During the day the distribution of near surface sonar targets, presumably anchovy schools, along one transect was mapped (Hewitt et al., 1976). During the night, two stations were occupied in regions along the transect with high target density. Each station consisted of a CTD cast, plankton sample, nekton sample, followed by a second plankton sample. Plankton samples were oblique tows from 70 m to the surface using a Bongo net with 60 cm mouth diameters, 0.505 mm mesh on one side and 0.333 mm mesh on the other. The 0.505 mm mesh sample was preserved in formalin and the 0.333 mm mesh sample used for otolith studies was preserved in 80% ethanol. The ethanol was changed within 24 h after initial preservation. All fish eggs and larvae were sorted from the ethanol preserved samples. Size distributions were determined from a subsample containing no more than 150 larvae per species. Larvae less than 5 mm were excluded from subsamples used for otolith analysis. Otoliths were dissected out and prepared for viewing according to Methot and Kramer (1979).

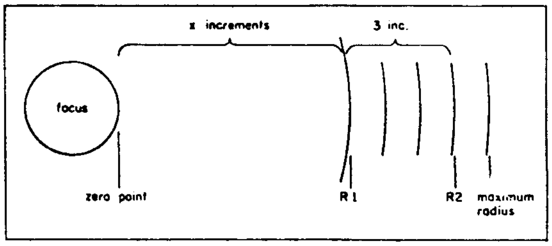

Figure 1. Otolith measurements used to determine otolith size and widths of the outer three complete increments.

Otolith images were viewed on a high resolution TV screen under magnification of 1,500 ×. Total otolith size and width of the outer three complete increments were measured by digitizing the positions of the four points shown in Figure 1 using an electronic cursor (precision ±0.15 μm) and a micro-computer to process the data. All measurements were made along the longest radius of the sagittae (largest otoliths). The data from both otoliths and up to three transects per otolith were combined.

The preserved lengths of *E. mordax* were corrected to live lengths, assuming 5 min elapsed time between capture and fixation (Theilacker, MS). This correction of about 0.8 mm enabled comparisons to other growth studies. No shrinkage correction was applied to the lengths of *S. leucopsarus* larvae.

RESULTS

The distributions of *Engraulis mordax* eggs and larvae and *Stenobrachius leucopsarus* larvae suggest that one mesoscale patch was sampled (Fig. 2a, b, c). Both species occurred in all samples taken at over 15° C and no fish eggs or larvae were found in the colder water nearshore south of 45° N latitude.

Engraulis mordax eggs were most abundant off the mouth of the Columbia River and were not found south of 45° N. Among the 12 positive samples taken north of 45° N the range in mean length was 3.5–7.1 mm for *E. mordax* and 5.1–8.4 mm for *S. leucopsarus.* South of 45° N the range in mean length of *E. mordax* increased to 10.7–14.1 mm and no larvae less than 5 mm were collected; mean lengths of *S. leucopsarus* increased slightly to 8.4–10.0 mm.

Three steps were necessary to convert recent rate of change in otolith size (outer three complete daily growth increments) to range of change in fish length:

1) Define the relation between fish length and otolith radius. Principal component analysis was used rather

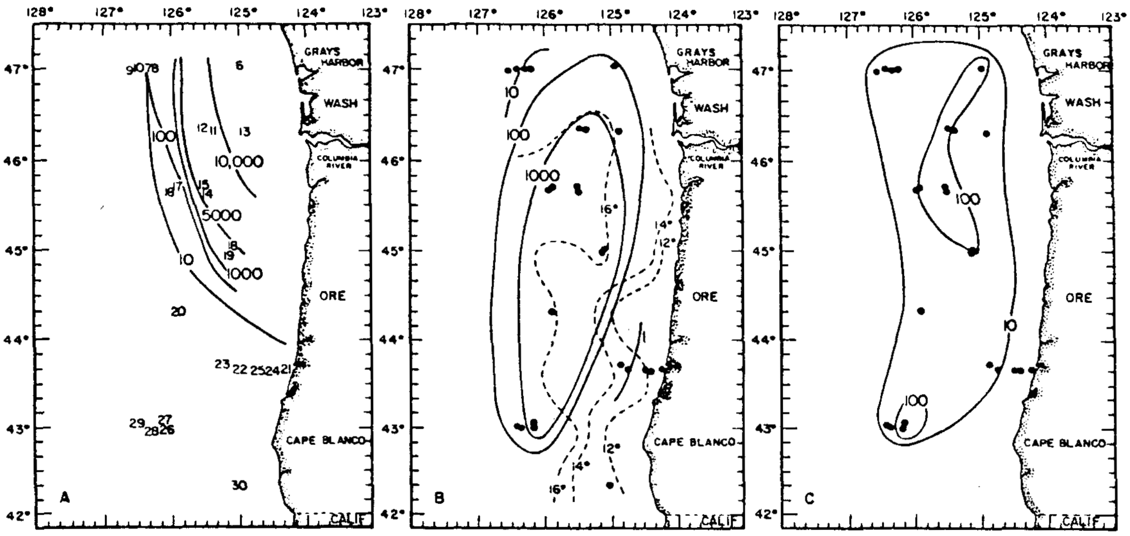

Figure 2. (A) Positions of Bongo samples (number indicates order occupied) and abundance of *Engraulis mordax* eggs (numbers per 10 m^2). (B) Abundance of *Engraulis mordax* larvae (numbers per 10 m^2) and three surface isotherms (dashed line). (C) Abundance of *Stenobrachius leucopsarus* larvae (numbers per 10 m^2).

than linear regression (Harris, 1975; Ricker, 1973) because variable shrinkage and difficulty in measuring bent or decomposing specimens could have introduced over 0.5 mm error in the measurement of fish length.

2) Multiply the two otolith measurements, R1 and R2, (Fig. 1) by the ratio: expected otolith radius/measured otolith meaximum radius. This corrects for the expectation of larger (smaller) increments in otoliths of larvae with larger (smaller) than expected otolith size.

3) Convert the adjusted otolith measurements to estimates of fish length using the principal axis defined in step one above. The assumptions inherent to this technique are discussed below.

The relation between maximum radius and standard length was linear for *S. leucopsarus* and nonlinear for *E. mordax* (Fig. 3). The data for *E. mordax* were linearized by taking the logarithm of both variables. The relationship between the variables was defined by principal component analysis after converting standard length and radius measurements to standard deviation units (Table 1).

For each specimen a first principal component score was calculated from standardized measurements of standard length and otolith radius then used to calculate a predicted otolith radius. Data from a specimen were not used if the ratio of predicted otolith radius to measured otolith radius was greater than 1.25 or less than 0.8. By this criterion 1 *E. mordax* and

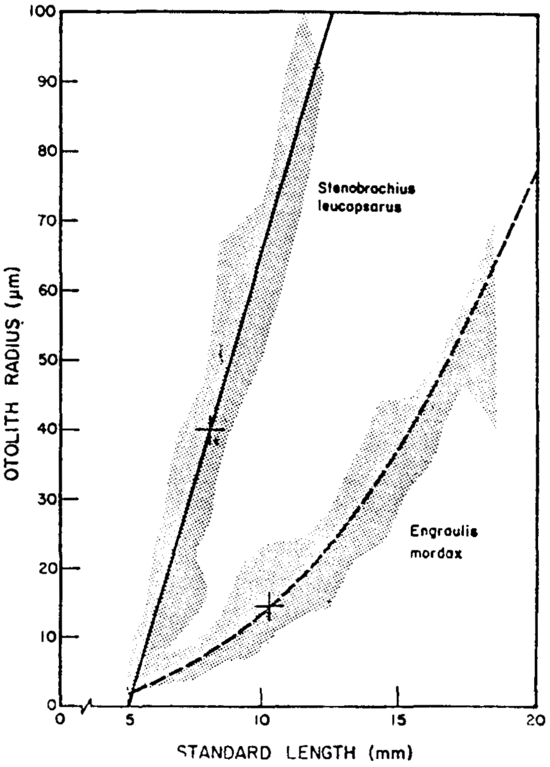

Figure 3. Relationship between maximum radius of otolith and length of larva. Stipled areas are the range of the data.

Table 1. First principal component of standard length and otolith radius. Variables were converted to normal deviations before analysis.

		Standard length		Otolith radius		Percent variance in 1st principal component
		Mean	Variance	Mean	Variance	
Engraulis mordax	linear	10.76	10.08	18.64	169.43	97.2
	log-log	2.335	0.0921	2.672	0.5959	98.2
Stenobrachius leucopsarus	linear	9.12	4.57	39.83	782.28	99.8

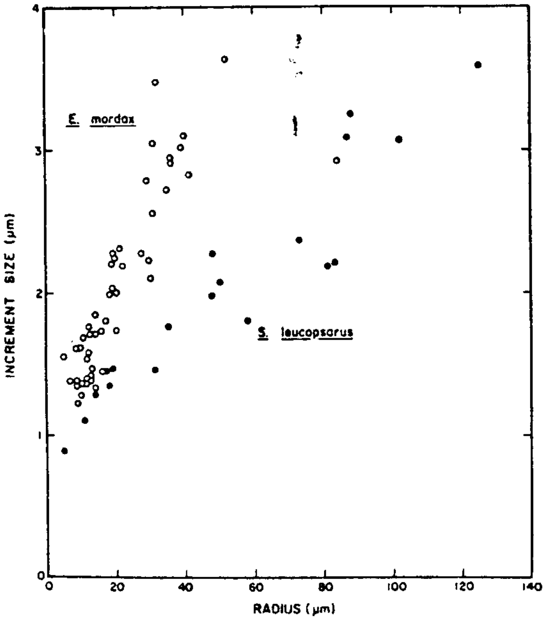

Figure 4. Distribution of mean size of the outer three complete increments with respect to the radial distance to the midpoint of these three increments. Increment size is otolith growth rate in µm per day. Data are from sample 27.

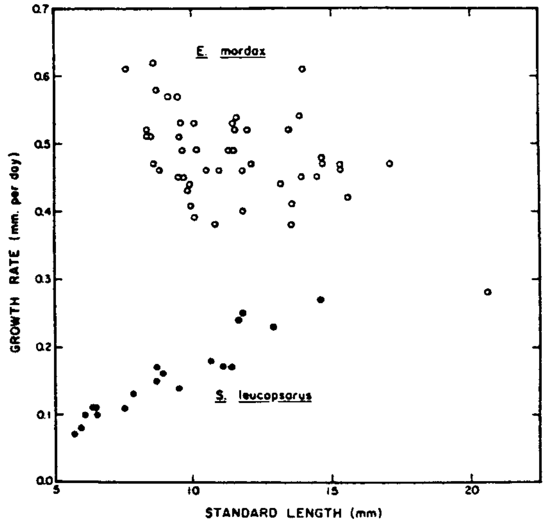

Figure 5. Same data as in Figure 4 but otolith measurements were transformed to fish lengths.

32 *S. leucopsarus* were not considered in the growth rate analysis. The two otolith measurements, R1 and R2, were multiplied by this ratio.

Mean increment size (R1-R2)/3, is presented as a function of radius to the center of the measurement interval, (R1+R2)/2, for one sample in Figure 4. Otolith growth is faster in larger specimens of both species. When these same data are transformed from otolith size to fish length the pattern of growth with respect to size differs between the two species (Fig. 5). Wider increments deposited by larger *E. mordax* did not necessarily reflect increased fish growth rate because of the non-linear relation between otolith size and fish length. In other samples the same trends were apparent (Table 2). *E. mordax* grew 2–3 times faster than *S. leucopsarus*. Large *S. leucopsarus* grew faster than small *S. leucopsarus*. Large *E. mordax* grew at the same rate or slightly slower than small individuals.

These data on size-specific growth rates were summarized into a single indicator of the quality of each species environment at each sample site by calculating the linear, least-squares regression of growth rate on size (Table 2) then using these equations to estimate growth rates at the overall mean lengths analyzed (10 mm for *E. mordax* and 8.5 mm for *S. leucopsarus*) (Fig. 6). The error bars shown in Figure 6 are not sufficiently conservative because they do not account for error in the adjustment ratios applied to the data, but the high incidence of non-overlap does suggest some significant between-sample variation in growth rate. However, the absolute magnitudes of the deviations (Fig. 6) were small compared to the scope for growth in anchovy larvae (Fig. 7), the two members of a pair of samples were often dissimilar in growth (compare samples 26 and 27 in Fig. 6), and correlation between growth rate of *E. mordax* and *S.*

Table 2. Relationship between growth rate (mm per day) and length of larva (mm) in each sample.

	Engraulis mordax				Standard error (reg)	*Stenobrachius leucopsarus*				Standard error (reg)
Sample	N	Mean length	Slope	Intercept		N	Mean length	Slope	Intercept	
6	5	8.1	−0.0324	0.707	0.090					
11	22	7.3	−0.0252	0.690	0.102	6	6.0	0.0072	0.075	0.021
12	14	8.3	−0.0282	0.753	0.088	11	6.3	0.0030	0.129	0.029
13	7	7.0	−0.0474	0.898	0.031					
14	26	9.2	−0.0256	0.7'5	0.072	13	8.1	0.0151	0.083	0.048
15	29	9.2	−0.0297	0.729	0.075	20	7.0	0.0328	−0.075	0.036
16	27	8.3	−0.0200	0.681	0.066	19	8.6	0.0239	−0.031	0.020
17	39	8.6	−0.0212	0.735	0.075	6	8.1	0.0144	0.021	0.018
18	30	7.0	−0.0236	0.684	0.080					
26	49	12.4	−0.0060	0.490	0.059	33	9.4	0.0165	0.022	0.026
27	49	11.5	−0.0137	0.644	0.067	19	9.1	0.0207	−0.032	0.020
28	47	12.3	−0.0109	0.607	0.071	3	10.3	0.0418	−0.246	0.024
29	23	12.7	−0.0049	0.497	0.062	9	10.3	0.0310	−0.065	0.065
Combined	367	10.0	−0.0167	0.654	0.078	141	8.4	0.0185	0.016	0.039

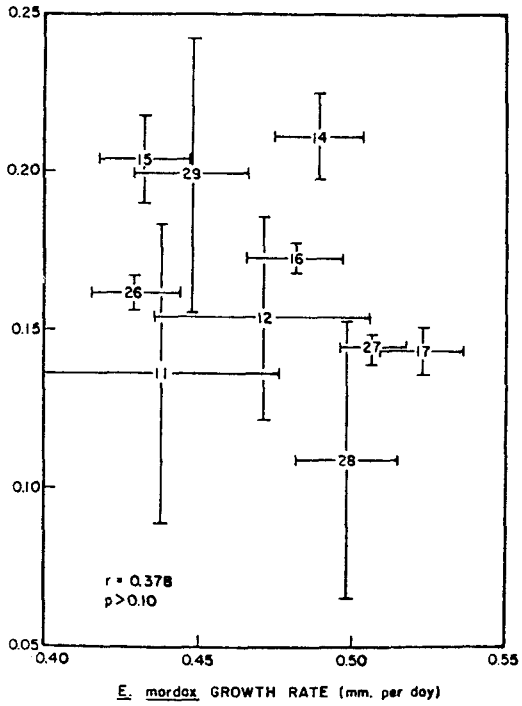

Figure 6. Growth rates of *E. mordax* (mm per day at 10 mm) and *S. leucopsarus* (mm per day at 8.5 mm) estimated from the regression equations in Table 2. Plotted points are the sample numbers (see Fig. 2A). Error bars are ±1 standard error. Correlation between growth rate of *E. mordax* and growth rate of *S. leucopsarus* was not significant.

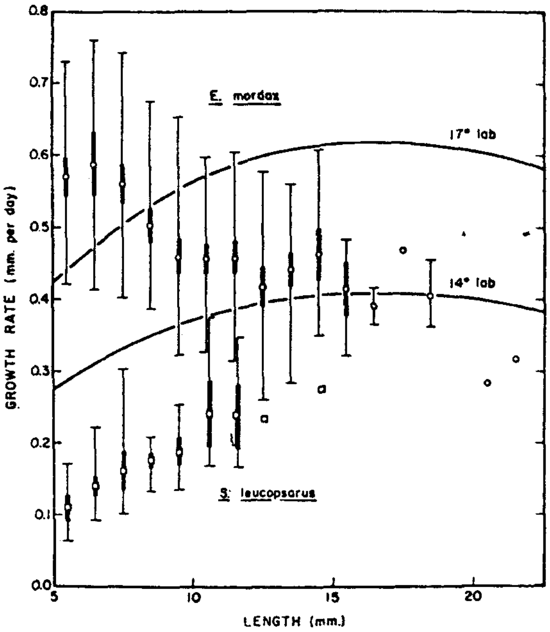

Figure 7. Distribution of growth rate (heavy vertical bars are ±2 standard errors, narrow vertical bars are the range) in each 1 mm size interval. Data from all samples were combined. Also shown are the relationships between daily growth rate and size at two temperatures in the laboratory (derived from model in Zweifel and Hunter, pers. comm.).

leucopsarus among these 10 samples was not significant. Since some of the regression equations in Table 2 were not significant the estimates of growth rate at a standard size were also calculated using the mean growth rate for each species in each sample and a relation between growth and size derived from all data for that species. This shifted the points displayed in Fig. 6 by an amount less than the standard errors shown in that figure. The correlation in growth rate between the two species was still not significant.

ASSUMPTIONS

1) One growth unit is deposited per day. This was confirmed for *E. mordax* using laboratory-reared larvae (Brothers et al., 1976). No confirmation is available for *S. leucopsarus* but the growth units appeared similar to those in *E. mordax* and other species examined in the laboratory. Sub-daily growth increments were occasionally observed in both species and distinguished from the daily growth units (Taubert and Coble, 1977).

2) Otolith increment size is a function of growth rate. This relation is assumed from the close correlation between otolith size and fish size.

3) Outer increment size should be adjusted by the ratio, expected otolith size/measured otolith size, before interpreting increment size as an absolute measure of growth rate. This assumes that this ratio was constant over the lifetime of the larva. The method of calculating expected otolith size was critical. When calculated from a linear regression of otolith radius on fish length the resulting adjustment ratio tended to over-correct the otolith measurements. Recognizing that mismeasurement of fish length was not trivial, the relation between otolith radius and fish length was defined by principal component analysis. This resulted in an expected otolith size that was a function of measured otolith size as well as fish length. The bias introduced by mismeasured fish was reduced. For larvae with otolith radii less than about 10 μm, error in measuring otolith radius also introduced some error in the adjustment ratio.

DISCUSSION

Within the region sampled, *Engraulis mordax* and *Stenobrachius leucopsarus* larvae were abundant and had similar distributions (Fig. 2b, c). Each species showed little variation in growth rate and the null hypothesis, no correlation in growth rate between species could not rejected. However, the null hypothesis certainly cannot be accepted until samples from a larger domain of environmental conditions with greater range in growth rate are examined. In this study, the surface temperature ranged less than 1° C in the set of 13 samples analyzed and the sample mean growth rates of 10 mm *E. mordax* ranged from 0.42 to 0.52 mm per day. A wider range, 0.34–0.55 mm per day, was found among 12 samples in the more heterogeneous waters off southern California (Methot and Kramer, 1979). In the laboratory the range of growth rates obtained when temperature and ration are manipulated is greater than 0.5 mm per day (several experiments are summarized in Methot and Kramer, 1979).

These data are the first estimates of growth rate for larval *Stenobrachius leucopsarus* and for the northern population of *Engraulis mordax*. The mean growth rate of *S. leucopsarus* larvae increased from 0.11 mm per day at 5 mm to 0.28 mm per day at 15 mm (Fig. 7). *E. mordax* larvae grew more rapidly (0.57 mm per day at 5 mm to 0.41 mm per day at 15 mm).

Although ages of individual larvae usually were not determined, the distributions of size at age were estimated by simulating growth curves using distributions of growth rate in each 1 mm size category (Fig. 7). In these simulations age 0 was defined as the onset of daily otolith increment formation (approximately at completion of yolk absorption, 5 days past hatch in *E. mordax*) and size at age 0 was 4.2 mm in *E. mordax* and 4.5 mm in *S. leucopsarus*. Simulations were run using the mean, minimum, maximum and ±2 standard errors of growth rate in each 1 mm size category (Fig. 8). Methot and Kramer (1979) determined growth rates of *E. mordax* by counting daily growth increments. Within samples, larvae 15 days old typically had a 3 mm range in size. In the present study, using data from all samples, simulated size at age 15 days had a range of 4 mm.

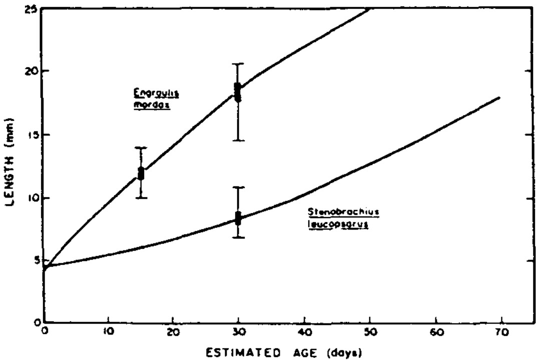

Figure 8. Simulation of size at age using size specific growth rate data in Figure 7. Trajectories are the result when mean growth rate in each 1 mm size category is used. Wide vertical bars show range of size at age with ±2 standard errors of growth rate and narrow vertical bars show range with minimum and maximum growth rates.

Thus, growth rates from widths of outer increments seem as precise as those obtained from a trend of size at age. For *S. leucopsarus* it was not possible to count the total number of increments, consequently the outer increment method was invaluable.

Although *E. mordax* larvae were growing 2–3 times faster than *S. leucopsarus* larvae on the basis of length, their growth rates may be nearly the same on a weight basis. Unfortunately, the appropriate length-weight conversions are not available. Using the length-dry weight relation of Hunter (1976) for laboratory reared *E. mordax* larvae and extrapolating the length-dry weight relation for juvenile and adult *S. leucopsarus* of Smoker and Pearcy (1970), I estimated that 10–20 mm *S. leucopsarus* are 3.5–4.0 times heavier than *E. mordax* in the same size range. This approximately offsets the difference in growth based on length. In the future more precise estimates of weight should be made so we can compare the absolute growth rates of various larval fish species.

No other estimates of the growth rate of larval *Stenobrachius leucopsarus* are available. Larvae in the 5–15 mm size range are found for several months (Fast, 1960; Richardson and Pearcy, 1977) so modal progressions cannot be used to estimate growth rates. Smoker and Pearcy (1970) found recruitment of juveniles into the 20–25 mm size class beginning in August–October. If the 10 mm larvae collected in this study continued growing at 0.2 mm per day they would be in the 20–25 mm size range in September.

Mean growth rates of *E. mordax* larvae in the 8–12 mm size range were 0.52–0.45 mm per day and the mean surface temperature at which specimens were collected was 16.1° C. Larvae in the same size range in a laboratory rearing experiment at 16.2° C (Hunter, 1976) were growing 0.54–0.60 mm per day. In general, larvae larger than 8 mm were growing at the same rates as larvae reared in the laboratory at about 15° C (curves in Fig. 8 were derived from parameters of a growth model prepared by Zweifel and Hunter, pers. comm.). Although the growth rates of 5–8 mm larvae may have been over-estimated they still are within reasonable limits; similar to the growth of 5–8 mm larvae at 18° C in the laboratory. Considering the uncertain relation between surface temperature and the temperature experienced by the larvae, these data support the general conclusion of Methot and Kramer (1979) that growth of anchovy larvae is similar in the laboratory and in the sea.

SUMMARY

1) Larvae of northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobrachius leucopsarus*, were abundant off the coast of Oregon in July 1977. Both occurred in all samples taken at 15° C or warmer.

2) The growth rates of 367 *Engraulis mordax* and 141 *Stenobrachius leucopsarus* were determined by measuring the widths of recent daily growth increments of otoliths.

3) Very little variation in growth rate was observed between samples and the correlation in growth rate between species was not significant.

4) The mean growth rate of *Stenobrachius leucopsarus* increased from 0.11 mm per day at a size of 5 mm to 0.28 mm per day at 15 mm. This is the first growth rate estimate for larvae of this species.

5) The mean growth rate of *Engraulis mordax* larvae declined from 0.57 mm per day at 5 mm to 0.41 mm per day at 15 mm. This is very similar to the growth rate of anchovy reared in the laboratory at similar temperatures (15°–16.3° C).

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