GROWTH OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE SEA

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ABSTRACT

Northern anchovy larvae from12 samples collected at 13.0°-16.2° C in the Southern California Bight were aged using daily growth increments in sagittal otoliths, and growth rates were calculated from size at age data. In nine samples, growth rate at 8 mm was very similar, ranging from 0.34 to 0.40 mm per day. Growth in the other three samples ranged from 0.47 to 0.55 mm per day. There was no correlation between growth rate and temperature within this set of field samples, but the range of growth rates was similar to the range expected from laboratory rearing experiments in this temperature domain. In no case was growth in the sea as slow as growth in the laboratory on severely limited rations. Anchovy larvae which obtain enough food to survive apparently obtain enough food to grow rapidly.

The presence of daily growth increments in some hard tissues of various plants and animals has been known for several decades (Neville 1967). Despite the fact that fish otoliths have been examined for annual growth marks throughout this century (Blacker 1974), daily growth increments were only recently identified in fish (Pannella 1971). The daily nature of these increments was verified in the laboratory by Brothers et al. (1976) using marine fish larvae. Taubert and Coble (1977) showed that increment formation in centrarchids is linked to the diel light cycle, not a feeding rhythm. Although studies have been conducted on the gross growth of otoliths (Degens et al. 1969; Mugiya 1974, 1977) the physiological mechanism responsible for daily growth increment formation in fish is unknown (Simkiss 1974). Regardless, daily growth increments provide the ecologist with a tool for determining age and growth of specimens from the field (Struhsaker and Uchiyama 1976).

The objective of this project was to estimate growth of larval northern anchovy, *Engraulis mordax*, in the sea. Many laboratory studies demonstrate that growth of young fish is limited by temperature and ration (Riley 1966; Brett et al. 1969; O'Connell and Raymond 1970; Houde 1975). Because food availability is frequently considered to be one of the major factors controlling larval survival (Cushing and Harris 1973; Jones 1973; May 1974; Lasker 1975; Arthur 1976), growth in the sea may frequently be limited by food. However, when collections of measured larvae are used for indices of spawner abundance or larval mortality studies, growth is assumed to be constant (Houde 1977) or a function solely of temperature (Bannister et al. 1974). Determining growth rates of larval fish in the sea should resolve this contradiction between theoretical and applied fishery science.

Anchovy larvae can be reared to metamorphosis and beyond in the laboratory (Kramer and Zweifel 1970; Hunter 1976; Sakagawa and Kimura 1976). Growth in these experiments was described best by the Gompertz growth equation, equation 1 (Kramer and Zweifel 1970; Zweifel and Lasker 1976). The effect of temperature on embryonic development and larval growth was incorporated by making the Gompertz growth parameters, A_0 and α, increasing functions of temperature (Zweifel and Lasker 1976; Zweifel and Hunter[2]). We compared the size at age of anchovy larvae in each field sample with that predicted by this temperature dependent model of anchovy growth in the laboratory, assuming that the temperature measured at the time of collection represented the temperature experienced by the larvae throughout their lifetimes.

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[2]Zweifel, J. R., and J. R. Hunter. Temperature specific equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval states. (Manuscr. in prep.) Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

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METHODS

Ichthyoplankton samples were collected from the Southern California Bight in March 1976, May 1976, and March 1977 with the NOAA ship *David Starr Jordan*. The sampling gear consisted of a CalCOFI (California Cooperative Oceanic Fisheries Investigations) ring net (1 m mouth diameter), MARMAP (Marine Resources, Monitoring, Assessment, and Prediction Program) Bongo net (60 cm mouth diameters), and a Manta neuston net; all with 505 μm mesh. Oblique tows were made from the depth indicated in Table 1 to the surface. Samples were drained of excess seawater and preserved in 85% ethanol. (Recently we found that preservation is greatly improved if the alcohol is changed at least once after initial preservation; the otoliths may dissolve in poorly preserved samples with large plankton volumes. We change it once within 24 h and again within a few weeks.) Surface temperatures were measured with a bucket thermometer, and vertical temperature profiles were obtained with expendable bathythermographs.

The 12 samples analyzed in this study are from a limited part of the spawning range of the northern anchovy, but the Southern California Bight in March is an important spawning area for the central population of the anchovy (Smith 1972). Samples A1-A3 and B1 were collected near Los Angeles and the Channel Islands in 1976 (Figure 1) and were selected because of the wide size range of anchovy larvae found in each. Samples C1 and C2 were collected in this same region in March 1977. They were selected to represent the widest temperature range possible. Samples D1-D6 were collected in March 1977 along a transect extending seaward from San Diego and were the only samples containing anchovy larvae on this transect. Additional station data are in Table 1.

All fish eggs and larvae were sorted from the plankton samples chosen for analysis and anchovy larvae were processed in a manner similar to that described by Brothers et al. (1976). The standard length, tip of snout to tip of notochord or hypural plates, of each larva was measured to the nearest 0.1 mm. Sagittae were removed and placed on a microscope slide with the lateral (flat) side up. A polarizing filter and analyzer in the dissecting microscope made the otoliths more visible during dissection. The slide was air-dried and the otoliths were mounted under a coverglass with a clear mounting medium (Pro-texx[3]). Daily growth increments were counted in otolith images on a video screen; the total magnification by the microscope and video camera was 600× or 1,500×. Each otolith was counted by 1-3 observers until the range of accepted counts for the two otoliths was ≤2. Accepted counts were averaged over all observers and both otoliths.

The shrinkage of sea-caught larvae in preservative (Blaxter 1971) and the lag between hatching and first increment formation must be considered before comparing the size at age of sea-caught larave with laboratory-reared larvae. Shrinkage of anchovy larvae depends upon the elapsed time between death and preservation (Theilacker[4]). There is no shrinkage when live larvae are placed directly into ethanol but a 5-15 mm larva could shrink about 0.6 mm if dead throughout the 6 min duration of the net tow. No shrinkage correction was applied because the elapsed time between death and preservation probably was <6 min and highly variable. Anchovy larvae tend to stay above the thermocline (Ahlstrom 1959) so are cap-

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

[4]Theilacker, G. H. Preservative shrinkage of larval anchovy, *Engraulis mordax*: laboratory versus field. Paper presented Nov. 1, 1978 at CalCOFI Conference, USC, Idyllwild, Calif.

TABLE 1.—Data on samples of larval northern anchovy taken from the Southern California Bight, spring 1976 and 1977.

Sample	Date	Time	Lat. N	Long. W	Gear	Depth (m)	Temperature (°C)	*N*
A1	29 Mar. 1976	2150	33°35.9′	117°56.6′	Ring	10	15.8	106
A2	31 Mar.	2205	33°43.5′	118°28.0′	Ring	5	15.0	38
A3	1 Apr.	1850	33°42.0′	118°20.5′	Ring	5	15.0	29
B1	8 May	1835	33°27.5′	118°40.0′	Manta	0	16.2	146
C1	20 Mar. 1977	1915	33°30.3′	118°01.5′	Bongo	70	15.1	35
C2	24 Mar.	2320	33°29.4′	117°54.1′	Bongo	70	13.0	112
D6	27 Mar.	0235	32°41.5′	119°01.5′	Ring	70	13.2	18
D1	27 Mar.	1830	32°00.0′	119°12.0′	Ring	70	14.0	13
D2	27 Mar.	2100	32°05.8′	118°55.0′	Ring	70	14.0	25
D3	28 Mar.	0140	32°28.8′	118°35.0′	Ring	70	14.4	18
D4	28 Mar.	0405	32°39.5′	117°59.5′	Ring	70	15.2	22
D5	28 Mar.	0630	32°47.0′	117°38.5′	Ring	70	15.1	25

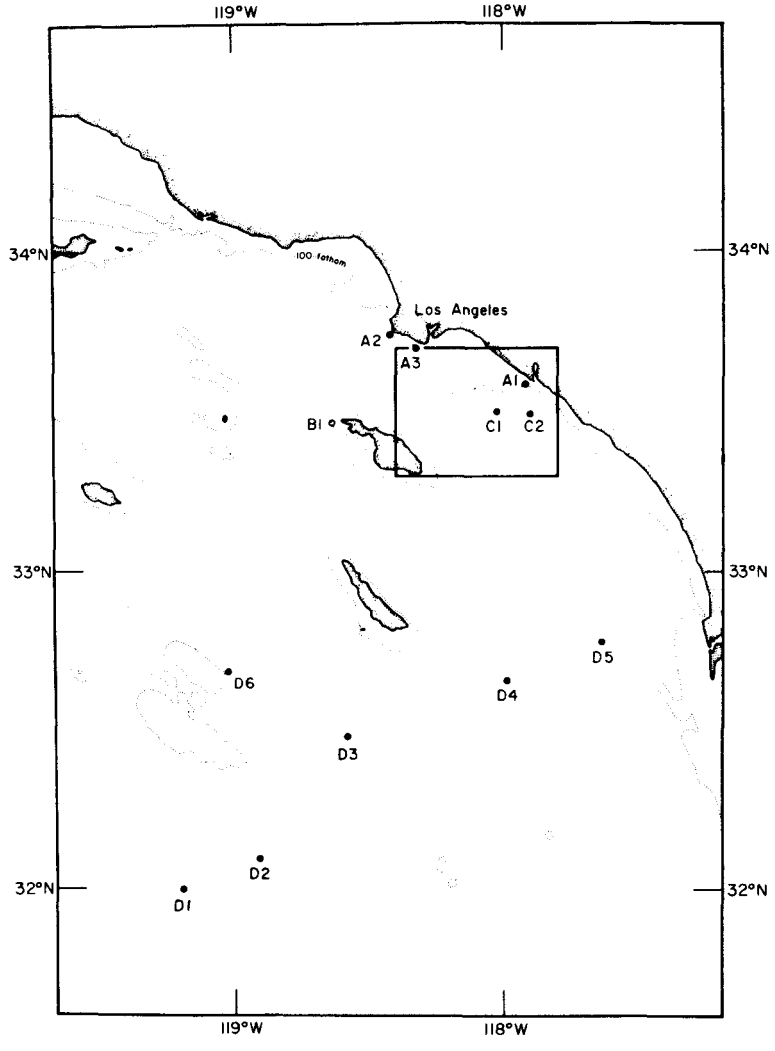


FIGURE 1.—Sampling sites for northern anchovy larvae off southern California. Box indicates the region shown in detail in Figure 4.

tured primarily during the last 1 or 2 min of an oblique tow, and some large larvae were still alive at the time of preservation.

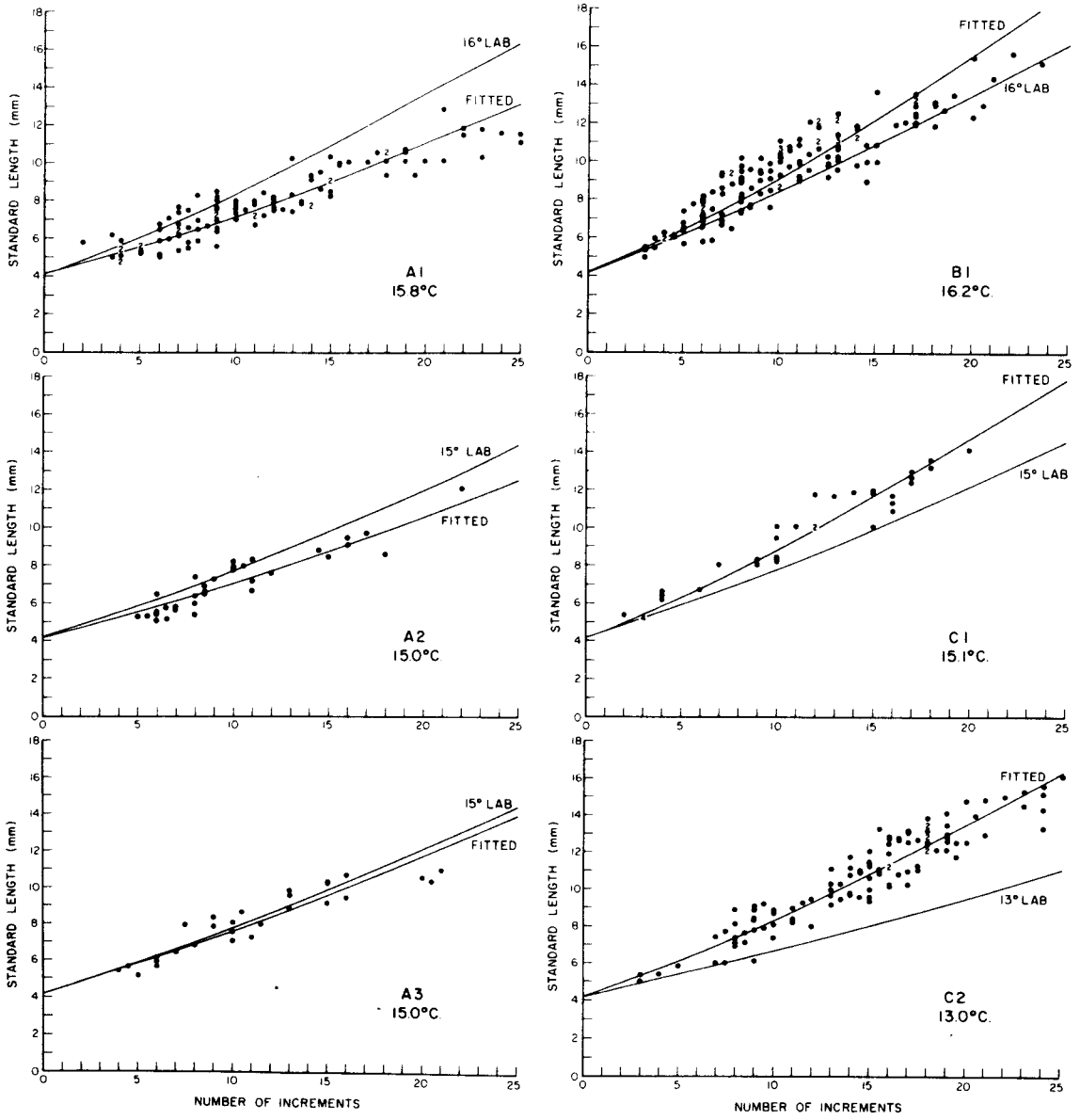
Brothers et al. (1976) found a 5-day difference between posthatch age and number of increments for anchovy larvae reared in the laboratory at 16° C. At 19° C the lag is 3 days and at 12.5° C it is about 9 days (Methot unpubl. data). These lags are very close to the age at completion of yolk absorption (19° C, 2.9 days; 16° C, 4.7 days; 12.5° C, 8 days—Zweifel and Hunter (see footnote 2)); the larvae are about 4.2 mm at this age. Since developmental events, such as a functional jaw, occur at a constant size at all temperatures in this range (Zweifel and Lasker 1976), we assume that increment formation also begins at a constant size of 4.2 mm at all temperatures. The number of increments represents the age in days after yolk absorption.

RESULTS

Standard length of each larvae in a sample was plotted against the mean number of increments (Figure 2). Each data point represents the integral of the growth rate of an individual larva over its lifetime, and a trend line through these points estimates the average growth history of larvae in the region sampled. Possible biases in this estimate of growth rate are discussed below.

According to the null hypothesis, the laboratory growth curve corresponding to the temperature at which the sample was taken should provide the best fit to the data. A suitable parametric procedure for testing this goodness of fit was not available. The nonlinear least-squares method for fitting the Gompertz growth function to size at age data (Zweifel and Lasker 1976) does provide estimates of confidence intervals on the parameters, but the probability levels associated with these intervals are only approximate (Conway et al. 1970). We found these confidence intervals to be rather broad.

We tested the goodness of fit by using a modification of the median regression procedure of Tate and Clelland (1957), replacing their estimated regression line by the laboratory derived Gompertz growth curve specified by our null hypothesis. Only curves at 1° C intervals were considered. Each larva in a sample was classified into a 2 × 2 contingency table, according to whether it was to the left or right of the median age of larvae in the



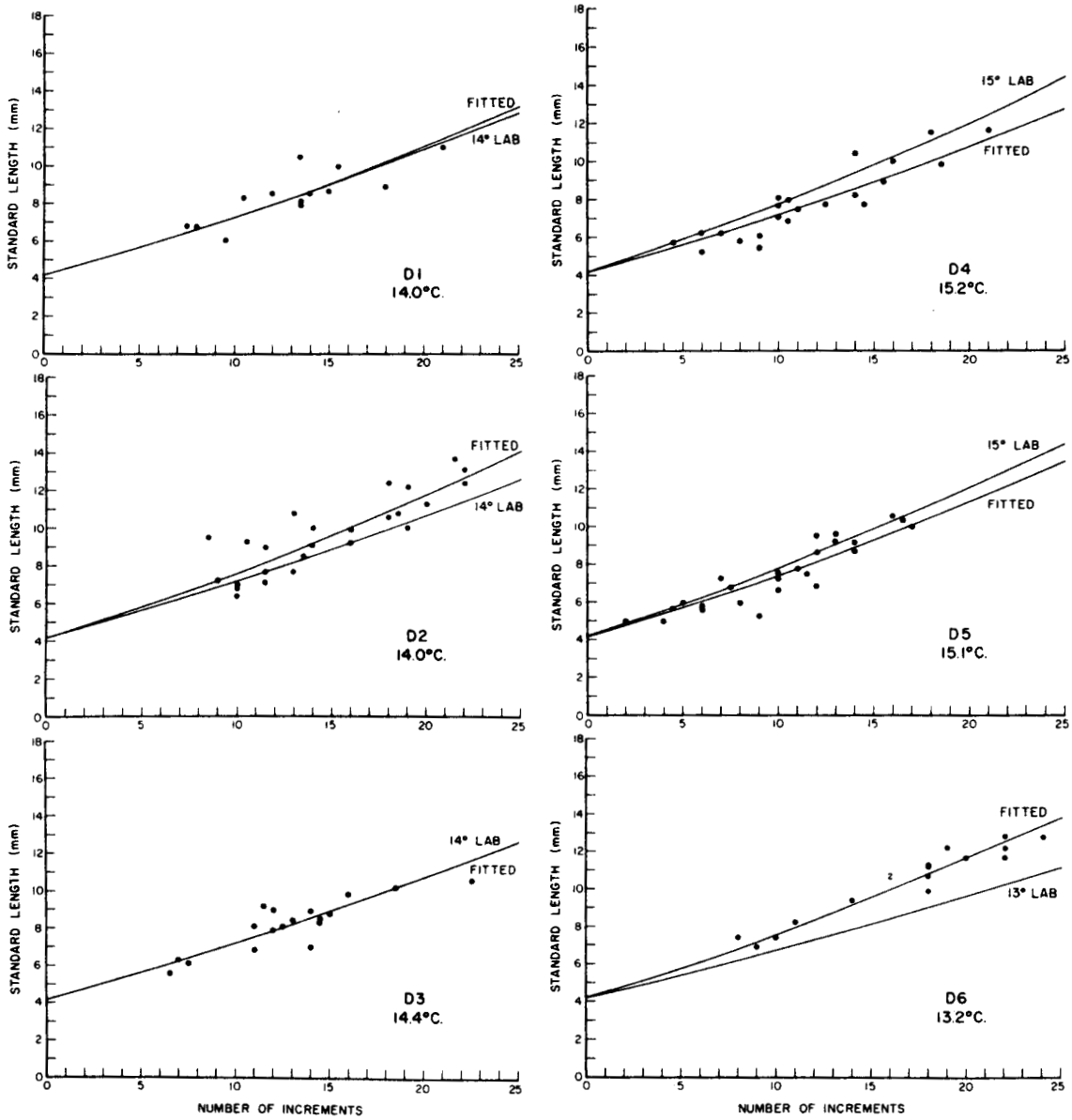


FIGURE 2.—Relationship between standard length of northern anchovy larvae and the number of daily growth increments (age postyolk absorption) in their otoliths. Two growth curves are shown. One (LAB) is the laboratory growth curve which was expected to fit the data because of the temperature at which the sample was collected. The other (FITTED) was fit to the data using a nonlinear least-squares method.

sample and whether it was above or below the laboratory growth curve (line labelled LAB in Figure 2). Points which fell on lines were split equally between the cells on either side of the line. A chi-square statistic with 2 degrees of freedom was calculated using the expectation of equal numbers of larvae in each cell of the table. The results of these tests are in Table 2.

In general, larvae collected between Los Angeles and the Channel Islands in March 1976 (samples A1-A3) grew slower than expected while those collected there in March 1977 (C1, C2) grew

TABLE 2.—Results of chi-square test of the hypothesis (see text) that temperature-specific growth in the northern anchovy is the same in sea and laboratory (A-E) and the parameters of the Gompertz growth curve fit to the data in each sample (F-I). A, sample size; B, surface temperature in degrees Celsius; C, growth curve compared with data; D, probability that growth curve fits data; E, sign of significant deviations (0.05 level) from laboratory curve; F and G, Gompertz parameters, A_0 and α; H, standard error of regression; I, growth rate at 8 mm (in millimeters/day). Last row shows results for combined data (samples with *).

Sample	A	B	C	D	E	F	G	H	I
A1*	106	15.8	16	<0.001	–	0.060	0.024	0.094	0.356
A2*	38	15.0	15	<0.01	–	0.059	0.025	0.089	0.341
A3*	29	15.0	15	<0.25	0	0.067	0.029	0.086	0.387
B1	146	16.2	16	<0.001	+	0.093	0.037	0.111	0.552
C1	35	15.1	15	<0.001	+	0.089	0.038	0.074	0.515
C2	112	13.0	13	<0.001	+	0.080	0.033	0.083	0.471
D6*	18	13.2	13	<0.001	+	0.067	0.029	0.059	0.389
D1*	13	14.0	14	<0.25	0	0.061	0.024	0.109	0.358
D2*	25	14.0	14	<0.025	+	0.068	0.029	0.120	0.397
D3*	18	14.4	14	<0.25	0	0.059	0.025	0.092	0.348
D4*	22	15.2	15	<0.10	0	0.061	0.027	0.105	0.348
D5*	25	15.1	15	<0.25	0	0.064	0.027	0.103	0.371
*						0.063	0.027	0.097	0.370

faster than expected. The larvae collected in March 1977 along the transect extending seaward from San Diego (D1-D6) grew about as fast as expected, given the surface temperature at which the sample was collected.

Since the data in 7 of 12 samples deviated significantly from the predicted Gompertz growth curve, we fit the Gompertz growth function (Zweifel and Lasker 1976)

$$\log_e (SL) = \log_e (SL_0) + \frac{A_0}{\alpha} (1 - e^{-\alpha t}) \quad (1)$$

where SL = standard length in millimeters
t = number of increments = age in days postyolk absorption
SL_0 = initial size, fixed at 4.2 mm
A_0, α = parameters to be estimated

to each using a nonlinear least-squares method (Conway et al. 1970).

The parameters of the fitted curves (Table 2) were used to calculate a linear approximation of the growth rate of 7.5-8.5 mm anchovy larvae (Figure 3). The range of growth rates among the 12 samples collected at 13°-16.2° C was bounded by the growth rates of anchovy larvae grown in the laboratory at 14° and 17.5° C. Growth was very similar in all but three samples (B1, C1, C2) although the temperatures associated with these nine samples spanned a range of 2.5° C. The growth rate of 8 mm larvae calculated from a Gompertz curve fit to the combined data of the nine similar samples was 0.37 mm/day. The mean

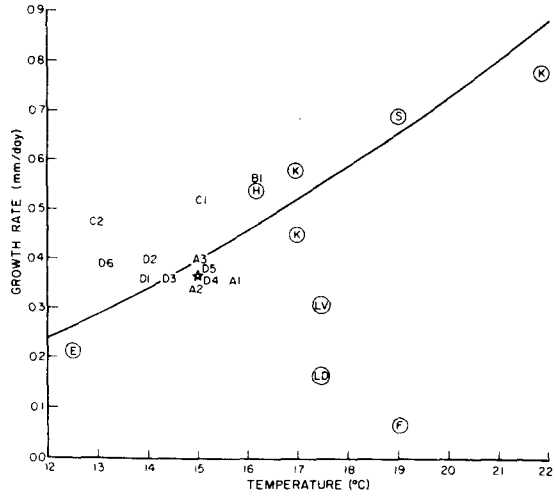


FIGURE 3.—Relationship between growth rate (millimeters/day at 8 mm) and temperature for northern anchovy larvae from the field (bare symbols) and in the laboratory (circled symbols). Field samples, this study, A1-D6; composite of nine field samples, B1, C1, and C2 not included, ☆; Hunter 1976, laboratory-reared prey, H; Kramer and Zweifel 1970, wild plankton for food, K; Lasker et al. 1970, dinoflagellates only, LD, dinoflagellates plus veliger, LV; Sakagawa and Kimura 1976, S; unpubl. data available at Southwest Fisheries Center, low temperature experiment, E, periodic starvation experiment, F. Curve was derived from the model of Zweifel and Hunter (see text footnote 2); it was not fit to the growth rate data presented here.

temperature of these nine samples (weighted by number of larvae) was 15.04° C. The model of Zweifel and Hunter (see footnote 2) predicts that 8 mm larvae reared at 15° C would grow at 0.395 mm/day.

Standard deviation of $\log_e$ (size) at age, calculated from the set of combined data, ranged from 0.045 at 4 increments to 0.144 at 19 increments with a mean of 0.0904. The standard error of regression (standard deviation of residuals) of the Gompertz curves fit to the data (Table 2) were similar to these estimates of standard deviation of size at age. Any difference in growth rate between these samples, small scale environmental heterogeneity integrated by our nets, or random error in the aging of the larvae causes the standard error of regression to overestimate variability in the growth process. Over the same age range in a laboratory experiment (Hunter 1976), standard deviation ranged from 0.064 to 0.153 with a mean of 0.115.

EVALUATION OF POTENTIAL BIASES

The conditions under which larvae are reared and growth is measured in the laboratory may differ sufficiently from conditions in the sea to bias the comparison of growth in the sea with growth in the laboratory. In the laboratory, growth is estimated from a time series of samples from a cohort. The exact age of each larva is known; temperature rarely varies >1°C; prey concentration is rather constant; and mortality is low (about 3%/day in Hunter 1976) and except for cannibalistic species, not influenced by size-selective predation. Growth of sea-caught larvae is estimated from one sample containing larvae of several ages. The age of each is estimated from the number of daily growth increments in its otoliths, the environmental conditions are measured only when the sample is taken, mortality is over 10%/day (Smith and Lasker 1978) and probably size selective, and large larvae avoid the net disproportionately.

Age Determination

Anchovy larvae deprived of food at the normal time of first feeding may delay deposition of daily growth increments until food is provided and growth resumes (Theilacker[5]), but if larvae are still about 4.2 mm when the first increment appears, estimates of the growth rate of larger larvae will be unaffected. Taubert and Coble (1977) found that increment formation in late larval and juvenile centrarchids stopped if growth was slowed sufficiently by low temperature. We examined the otoliths of some anchovy larvae whose growth was drastically retarded by a reduction in rations (Methot unpubl. data) (F in Figure 3). The slowest growing of these larvae had fewer increments than expected, so increment formation can stop before the point of no return is reached. However, if we use number of increments rather than known age to estimate growth rate of these laboratory-reared larvae, the resulting overestimated growth rate is still slower than that observed in any field samples used in this study. We conclude that the sea-caught larvae were growing fast enough to deposit a growth increment every day.

[5]G. H. Theilacker, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1978.

Temperature Determination

Anchovy larvae usually remain above the thermocline (Ahlstrom 1959), so surface temperature probably accurately represents the temperature they experience. Growth was slower than expected in March 1976, but it is unlikely that the surface temperature overestimated the temperature experienced by the larvae because these samples were all collected shallower than 10 m (Table 1). Positive deviations in growth rate, equivalent to a temperature change of up to 3° C, were observed in March 1977, but additional temperature data collected at that time indicate that the measured surface temperature accurately represented the temperature experienced by the larvae throughout their lifetimes. The relative surface temperature field determined from satellite observations of infrared radiation (Bernstein et al. 1977), taken just before and after this 2-wk cruise, was entirely consistent with the temperature field measured during the cruise; there was no cooling trend. The resolution of the satellite observations was insufficient to distinguish details of the eddy structure in the region of samples C1 and C2, but here the greater intensity of surface temperature determinations allowed contouring of isotherms for the first 4 days of the cruise and the next 5 days (Figure 4). Samples C1 and C2 were taken within persistent water masses of about 10 km width, not in regions with steep horizontal gradients in temperature. Because of the shallow thermocline in this region (<5 m at some stations), we may have overestimated the temperature experienced by the larvae but this would cause a negative deviation from the model, not the observed positive deviations.

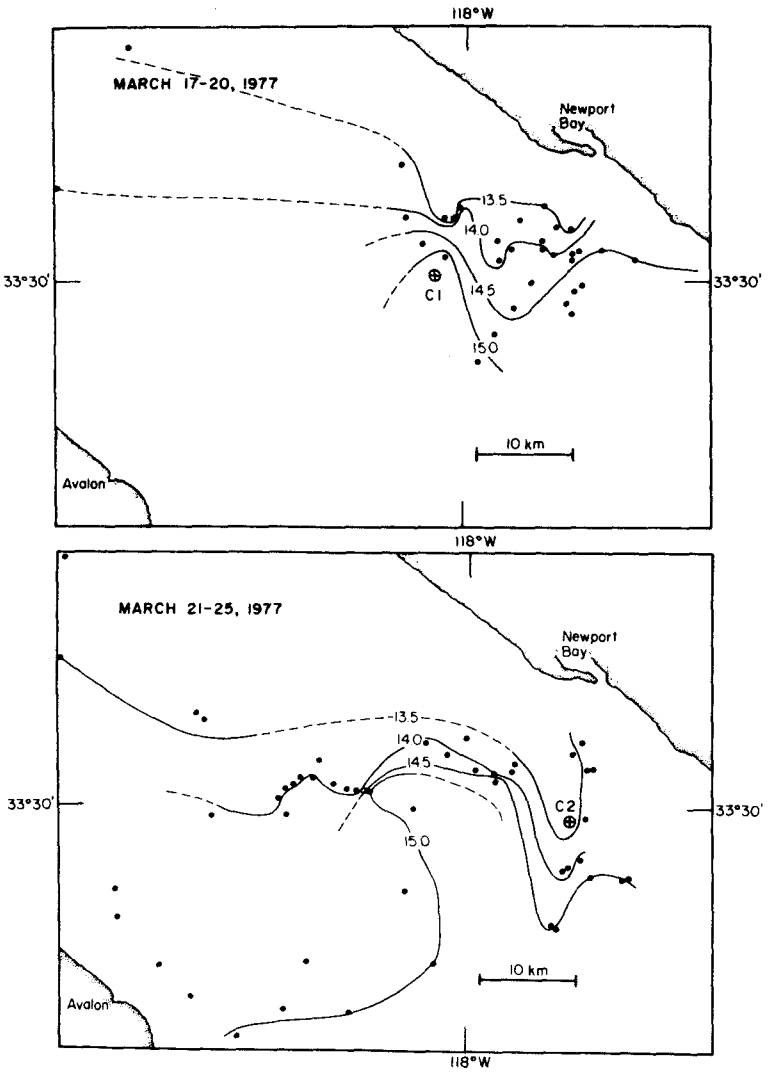


FIGURE 4.—Surface isotherms in degrees Celsius between Los Angeles and Santa Catalina Island, Calif., in March 1977.

Selective Mortality

If mortality rate is a function of size, then growth rates determined from size at age data will provide a biased estimate of the true growth rate of the survivors which are sampled (Ricker 1969). The effect of size selective mortality on our estimates of growth is difficult to assess. Few sets of data are extensive enough to even consider the question of ontogenetic changes in mortality rate of larval fish. All available estimates are based upon sized but not aged specimens. They depend upon an assumed growth curve (Farris 1960) and are susceptible to bias by size selective avoidance of the sampler. Smith (1973) found a difference in mortality rate between sardine eggs and young sardine larvae, but mortality in plaice was essentially constant through the egg and larval stages (Bannister et al. 1974). Laboratory experiments show that older, more active yolk-sac anchovy larvae are less susceptible than newly hatched larvae to some invertebrate predators (Lillelund and Lasker 1971; Theilacker and Lasker 1974). As a rough estimate of the magnitude of the maximum effect of size selective mortality on our growth estimates, we examined the interaction between variable growth and size selective mortality and determined the effect of this mortality on mean size of anchovy larvae at 25 days after yolk absorption.

Suppose variation in growth is such that individuals of age 25 days range in size from 11.4 to 16.6 mm and that the exponential growth rate parameter which gives rise to this variation has an uniform statistical distribution. If mortality during this 25-day period is random with respect to size, the mean size of individuals which survive to age 25 days will be 13.86 mm. However, if the instantaneous daily mortality rate is related to size by $M = 3.5 L^{-2}$ (this is consistent with current estimates of egg, young larvae, and adult mortality rates for anchovy (MacCall 1974; Smith and Lasker 1978)), the mean size of individuals which survive to age 25 days will increase only slightly to 14.08 mm. We conclude that an overestimate of growth because of size selective mortality is unlikely to occur.

Another possibility is that mortality is related to growth rate rather than size, the mortal fraction being that portion of the population which is slow growing and weak and therefore more susceptible to predators (Isaacs 1964). If we make the extreme assumption that the daily mortal fraction is the slowest growing 10% of the cohort, the survivors at age 25 days will be the fastest growing 7% of the original cohort, but this extreme model unrealistically predicts that variations in size at age would decline as the slow growing larvae die. Some intermediate degree of growth rate selective mortality could affect estimates of growth rate in the sea, especially if mean growth rate is slow and the slower growing individuals are near starvation.

Net Avoidance

Avoidance of the ring net by anchovy larvae in daylight begins at a length of about 5 mm and increases with size (Lenarz 1973; Murphy and Clutter 1972). The Bongo net catches larvae more effectively but avoidance still occurs in the larger size classes. The degree to which we underestimated mean size at age depends upon how rapidly avoidance increases with increasing size. We attempted to minimize this bias by only considering larvae with fewer than 25 increments (lengths less than about 15 mm) and samples taken at twilight or dark. There was no difference in size at age between the twilight samples (D1, D5) and the night samples (D2-D4) along the transect. Although fast growth was observed only in samples taken with the Bongo or neuston net (B1, C1, C2), we do not believe this was an artifact caused by size-selective avoidance of the ring net. If this were an artifact, then ranges in size at age in samples taken by the less selective gear would have been broader and overlapped the distribution of size at age in samples taken with gear which allowed larger larvae to escape. This was not observed.

DISCUSSION

Growth rates of larval northern anchovy <1 mo old were determined with size at age data. In 9 of 12 samples, growth rates at 8 mm were very similar, ranging from 0.34 to 0.40 mm/day. The growth rate estimated from the combined data of these samples was 0.37 mm/day. Growth in the three other samples was faster, 0.47-0.55 mm/day. Variation in size at age between individuals was small. A typical 95% confidence interval for larvae with 12 daily growth increments was 6.5-9.5 mm.

When the trend of growth rate on temperature, obtained from several rearing experiments, was compared with the field results (Figure 3) it was obvious that growth in the sea was similar to growth in the laboratory. The range in growth rate between field samples at the same temperature was similar to the range in growth rate between laboratory rearing experiments conducted at the same temperature (Kramer and Zweifel 1970). Variation of size at age was also similar in the sea and the laboratory. In no case were sea-caught larvae growing as slowly as larvae reared in the laboratory on inadequate rations (LV, LD, F in Figure 3). At 17.5° C (Lasker et al. 1970) anchovy larvae fed only a dinoflagellate grew at about 0.15 mm/day (LD) and larvae fed dinoflagellate and veligers (LV) grew still slower than larvae fed wild plankton (K) (Kramer and Zweifel 1970). Although the availability of suitable prey may limit the feeding success rate of first feeding anchovy larvae (Lasker 1975), larvae which get enough food to survive apparently get enough food to grow rapidly.

There was no obvious relationship between growth rate and temperature. This is not surprising considering the narrow temperature range considered, the variation in growth rate between laboratory experiments at the same temperature, and the uncertainty in our measurement of the temperature experienced by the larvae in the sea. The samples we examined came from near the center of distribution of northern anchovy larvae with respect to space, time, and temperature. As samples from the periphery of this species range

become available, we expect to find increased variation in growth rate.

Correlations between the spatial-temperature pattern of variation in growth rate and environmental parameters may provide clues to the events which control larval survival. This analysis will require that the measured growth rates reflect the larvae's response to the environmental factors measured at the time the sample was collected. We estimated the growth rate of larvae in a sample by determining the relationship between size (L) and age (T). This technique is susceptible to several biases discussed above and is not sensitive to changes in growth conditions occurring a few days before the sample is taken. If the instantaneous growth rate of each individual could be measured, then the same growth rate parameters could be estimated from the relationship between dL/dT and L. This alternative method would reflect growth conditions at the time of sampling and would be independent of changes in growth conditions during the lifetime of the older larvae in the sample. Ottaway and Simkiss (1977) developed a relative measure of the instantaneous growth rate of adult fish using the in vitro rate of incorporation of ^{14}C labelled glycine into scales, but this technique may not be adaptable to larval fish. Another approach is to correlate the width of a daily growth increment with the growth of the fish on that day. A measurement of the width of the outer increments could provide an absolute measure of growth rate during the few days before capture.

In addition, the radius of each increment in an individual's otoliths could be used to back calculate its growth history (Ricker 1969). The difference between the back calculated growth histories of older individuals, the survivors captured with nonselective gear, and the distribution of size at age of all younger individuals supplies information on differential mortality and size dependent net avoidance by the larvae. Ultimately, analysis of daily growth increments in the otoliths of larval fish may provide a means of determining whether larval survival is limited primarily by predation or food and how these two factors interact.

ACKNOWLEDGMENTS

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LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.

BANNISTER, R. C. A., D. HARDING, AND S. J. LOCKWOOD.
1974. Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa* L.). *In* J. H. S. Blaxter (editor), The early life history of fish, p. 21-37. Springer-Verlag, Berl.

BERNSTEIN, R. L., L. BREAKER, AND R. WHRITNER.
1977. California Current eddy formation: ship, air, and satellite results. Science (Wash., D.C.) 195:353-359.

BLACKER, R. W.
1974. Recent advances in otolith studies. *In* F. R. Harden Jones (editor), Sea fisheries research, p. 67-90. John Wiley and Sons, N.Y.

BLAXTER, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 160:128-136.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP.
1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363-2394.

BROTHERS, E. B., C. P. MATHEWS, AND R. LASKER.
1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1-8.

CONWAY, G. R., N. R. GLASS, AND J. C. WILCOX.
1970. Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51:503-507.

CUSHING, D. H., AND J. G. K. HARRIS.
1973. Stock and recruitment and the problem of density dependence. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:142-155.

DEGENS, E. T., W. G. DEUSER, AND R. L. HAEDRICH.
1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berl.) 2:105-113.

FARRIS, D. A.
1960. The effect of three different types of growth curves on estimates of larval fish survival. J. Cons. 25:294-306.

HOUDE, E. D.
1975. Effects of stocking density and food density on survival, growth and yield of laboratory-reared larvae of sea

bream, *Archosargus rhomboidalis* (L.) (Sparidae). J. Fish. Biol. 7:115-127.

1977. Abundance and potential yield of the round herring, *Etrumeus teres*, and aspects of its early life history in the eastern Gulf of Mexico. Fish. Bull., U.S. 75:61-90.

HUNTER, J. R.

1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.

ISAACS, J. D.

1964. Night-caught and day-caught larvae of the California sardine. Science (Wash., D.C.) 144:1132-1133.

JONES, R.

1973. Density dependent regulation of the numbers of cod and haddock. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:156-173.

KRAMER, D., AND J. R. ZWEIFEL.

1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as inflenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.

LASKER, R.

1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.

LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.

1970. Feeding, growth, and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. (Berl.) 5:345-353.

LENARZ, W. H.

1973. Dependence of catch rates on size of fish larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:270-275.

LILLELUND, K., AND R. LASKER.

1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull., U.S. 69:655-667.

MACCALL, A.

1974. The mortality rate of *Engraulis mordax* in southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 17:131-135.

MAY, R. C.

1974. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, Berl.

MUGIYA, Y.

1974. Calcium-45 behavior at the level of the otolithic organs of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 40:457-463.

1977. Effect of acetazolamide on the otolith growth of goldfish. Bull. Jpn. Soc. Sci. Fish. 43:1053-1058.

MURPHY, G. I., AND R. I. CLUTTER.

1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.

NEVILLE, A. C.

1967. Daily growth layers in animals and plants. Biol. Rev. (Camb.) 42:421-441.

O'CONNELL, C. P., AND L. P. RAYMOND.

1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.

OTTAWAY, E. M., AND K. SIMKISS.

1977. "Instantaneous" growth rates of fish scales and their use in studies of fish populations. J. Zool. (Lond.) 181:407-419.

PANNELLA, G.

1971. Fish otoliths: daily growth layers and periodical patterns. Science (Wash., D.C.) 173:1124-1127.

RICKER, W. E.

1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479-541.

RILEY, J. D.

1966. Marine fish culture in Britain. VII. Plaice (*Pleuronectes platessa* L.) post-larval feeding on *Artemia salina* L. nauplii and the effects of varying feeding levels. J. Cons. 30:204-221.

SAKAGAWA, G. T., AND M. KIMURA.

1976. Growth of laboratory-reared northern anchovy, *Engraulis mordax*, from southern California. Fish. Bull., U.S. 74:271-279.

SIMKISS, K.

1974. Calcium metabolism of fish in relation to ageing. *In* T. B. Bagenal (editor), Ageing of fish, p. 1-12. Unwin Bros. Ltd., Old Woking Surrey.

SMITH, P. E.

1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.

1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164:282-292.

SMITH, P. E., AND R. LASKER.

1978. Position of larval fish in an ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.

STRUHSAKER, P., AND J. H. UCHIYAMA.

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

TATE, M. W., AND R. C. CLELLAND.

1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

TAUBERT, B. D., AND D. W. COBLE.

1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. J. Fish. Res. Board Can. 34:332-340.

THEILACKER, G. H., AND R. LASKER.

1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 287-299. Springer-Verlag., Berl.

ZWEIFEL, J. R., AND R. LASKER.

1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.