Growth During the Larval and Juvenile Stages of the Northern Anchovy, *Engraulis mordax*, in the California Current During 1980–84

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ABSTRACT: Increment widths and back-calculated growth rates for northern anchovy, *Engraulis mordax*, did not differ during the years 1980–84. This evidence of stable larval growth rates does not support the theory that it is the variation in larval growth rates that directly affects the magnitude of recruitment. Furthermore, since growth rates remained stable, even though zooplankton volumes in 1983 were well below the long-term mean, it follows that surviving post-first-feeding larval anchovies may not be food limited.

The size of juvenile northern anchovy was reduced during the 1982–83 El Niño "phenomenon" in the California Current. Mean lengths of anchovy juveniles collected in the fall were greatest in 1980, least in 1982, and intermediate in 1981, 1982, and 1984. Growth rates back calculated from otolith increment widths did not differ significantly between the 1980 and 1983 cohort, until 100 days after first feeding. Reduced growth after 100 days largely determined the smaller size of 1983 anchovy juveniles. Condition factor was also reduced in the 1983 cohort. The 1982 cohort was not greatly affected, because El Niño did not have a pronounced effect off the North American coast until well after the 1982 northern anchovy spawning season.

Through the years, the overall abundance of many pelagic fishes varies with the strength of individual year class; changes in mortality rates early in life (Hjort 1914, 1926), rather than parent stock size, may determine the size of individual year classes. Considerable controversy, however, surrounds details of the exact stage and mechanism through which changes in individual year-class strength occur.

The co-occurrence of fish larvae and their food is a mechanism that has been proposed to explain variations in year-class strength (Hjort 1914, 1926). Lasker (1978) has shown that food availability may affect survival of first-feeding north-

ern anchovy, *Engraulis mordax*, larvae in the sea. Food availability may not affect the survival beyond the first-feeding stage; however, Methot (1981) found that early larval anchovy growth rates in the sea were the same as those of well-fed, laboratory-reared larvae. Survival through the larval stage does not determine the magnitude of the northern anchovy recruitment (Peterman and Bradford 1986; Peterman et al. 1988). Thus food availability for larvae may not determine the year-class strength and whether food availability affects juvenile survival are yet to be investigated.

A simulation model of the northern anchovy population indicates that the growth rate of late larvae and early juveniles may affect the magnitude of recruitment (Smith 1985). If mortality rates in the marine environment are size-specific, as predicted by Peterson and Wroblewski (1984), and if growth rates determine the duration of the most vulnerable stages, reduced growth should adversely affect survival. The extent to which growth rates of late larvae and juveniles vary is unknown.

The growth rate of juveniles also affects adult size. Off southern Baja California, the adult size of northern anchovy is entirely determined by juvenile growth, because these fish show no growth after 18 months (Parrish et al. 1985). Analysis of the regional patterns of growth of northern anchovy shows that the average length of fish at a given age increases from south to north. The length at 18 months ranges from 101.1 mm off southern Baja California to 126.6 mm off central California (Parrish et al. 1985).

Because batch fecundity is a function of body size in broadcast spawners, the juvenile and adult growth rates determine the reproductive capacity over the adult lifespan. Competition among juveniles for resources affects adult fertility in other species (Prout and McChesney 1985), and, if growth of juvenile pelagic fishes is food limited, competition among juveniles may

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be a mechanism of density-dependent compensation.

Growth rates of larval and juvenile anchovy during El Niño periods are of particular interest, because the growth rates during an environmental perturbation may reveal details of the processes of growth and survival during normal conditions. During the 1982–83 El Niño event off California, temperatures were elevated (Lynn 1983; Simpson 1983) and zooplankton density was reduced in 1983 (McGowan 1985). If planktivorous fish compete for food, competition should be highest when zooplankton abundance is lowest. Comparison of growth rates throughout the larval and juvenile stages during periods of low and high food abundance may show the size range at which the larval or the juvenile stage is most important. In this paper I examine the interannual variability in growth rates of anchovy larvae and juveniles during periods of low and high food abundance.

METHODS

Samples of juveniles from the central population of northern anchovy were obtained from midwater trawl hauls taken in 1980–84 by the Sea Survey Program of the California Department of Fish and Game. Annual cruises to monitor the strength of the incoming year class of northern anchovy have been conducted during September and October since 1976; Mais (1974) has described the gear and sampling procedures. The surveys extended along the Pacific coast from central Baja California to Point Conception, CA, with the exception of 1982, when the southern limit was the U.S.-Mexican border. Trawl hauls were taken nearshore inside of a 75 fm contour where young of the year are most abundant during the fall (Parrish et al. 1985).

Twenty five juvenile northern anchovy were randomly taken from each positive trawl haul and frozen for age determination. A subsample of 200 juvenile anchovy was randomly taken from the 800 to 1,000 fish collected on each survey for analysis of growth rate using daily increments in the otoliths. Fish were measured from the tip of the snout to the posterior edge of the hypural plate (standard length), and otoliths were removed and mounted on microscope slides using Eukitt[1] mounting medium.

Growth rates and ages of juvenile northern

anchovy were determined by counting and measuring daily increments in the otoliths (Methot 1981). The increment widths were measured and recorded along a transect from the focus to the posterior margin of the otolith (otolith radius), using a video-coordinate digitizer connected to a microcomputer. The otoliths were progressively polished between readings, using 15 and 0.3 μ lapping film, to reveal increments along the entire transect. Data from different areas of the otolith were collected as the increments became visible. During each reading groups of 10 or less (typically five) increments were counted and measured. The number of increments measured was reduced if width varied among increments.

ANALYSIS AND RESULTS

Data from both otoliths and several replicate transects per otolith were combined to calculate age and otolith increment widths (Methot 1981). Mean increment width was calculated at each point along the radius from the focus to the posterior margin of the otolith. In some cases, it was impossible to obtain measurements of all increment widths in the otoliths. In these cases, increment widths were interpolated using linear approximation (see Methot 1983 for details). Data for increment widths and age estimates were not used if more than 5% of age was calculated from interpolated increments.

A direct comparison of the average size of recruits from year to year is inappropriate because their ages may differ from year to year owing to differences in the dates of spawning (Methot 1983) or to dates of collection. To eliminate this bias, the dates of hatching were determined from the dates of sampling and ages, and fish were grouped by year and month of hatching.

Interannual and seasonal differences in length were tested, using an analysis of covariance (Bartlett et al. 1984) with age as the covariate. This analysis adjusted the mean length to the grand mean age of 208 days, approximately the time elapsed from the peak of spawning to the date of capture. Since the relation of length to age is typically nonlinear, some error is introduced using a linear adjustment. The difference in dates of sampling is, however, only about one month and the relation of size to age is approximately linear from two to six months.

Analysis of covariance of these data indicates parallel lines with differences in means (Case 2c

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[1]Reference to tradenames does not imply endorsement by the National Marine Fisheries Service, NOAA.

in Bartlett et al. 1984). Thus, comparison of lengths adjusted by age between years of fish hatched during the same calendar month is reliable. Comparison of lengths of fish hatched at the extremes of the same spawning season may be less reliable than between-year comparisons. Fish hatched in January are four months older than fish hatched in May, and linear extrapolation to a common age may introduce error. However, since growth is decelerating, linear extrapolation overestimates mean lengths of fish hatched at the extremes of the spawning season. The fact that lengths of fish hatched in January and May in all years, except 1983, are less than lengths of fish hatched in March indicates that the error is not great.

The allometric relations of length and weight to otolith radius were estimated using nonlinear regression. These relations were used to back-calculate age-specific size and growth rates for individual fish; not all fish were weighed in 1980 and 1981, and data were pooled from 1980 to 1982 to determine the allometric relations of both length and weight to otolith radius. Individual relations were determined for 1983 and 1984.

The growth rates in length and in weight were determined from increment widths and the first derivative of the empirical relationship of fish size and otolith radius. The condition factor (dry weight/length cubed) was significantly less in anchovy juveniles collected in 1983 than in anchovy juveniles collected in 1980–82. Therefore, the algorithm to convert otolith increment size to growth in dry weight differed among years. The equation used to calculate growth in length was

$$\Delta L/\Delta t = (\Delta R/\Delta t)(\Delta L/\Delta R); \qquad (1)$$

where $\Delta R/\Delta t$ is rate of change of the width of the daily increments, and $\Delta L/\Delta R$ is the slope of the observed relationship of fish length and otolith radius.

The variance of the product (Y) of two variables (X, Z) is given by

$$\mathrm{Var}(Y) = Z^2\mathrm{Var}(X) + X^2\mathrm{Var}(Z)$$

$$+ 2XZ\,\mathrm{Covar}(XZ) \qquad (2)$$

if the variables are not independent (Goodman 1960). The estimate of the variance of $\Delta R/\Delta t$ was the variance of the measurement of increment width of the fish in each group. If the length, radius relation was linear, the variance of $\Delta L/\Delta R$ was estimated from $S^2_{Y|X}$, the variance of

the slope of the regression of length on otolith radius. If the relation of length to radius was nonlinear, as was often the case, the variance of $\Delta L/\Delta R$ was estimated by partial derivatives. The variance of $\Delta W/\Delta R$ was not calculated; the complex derivative may not be a good estimate of the true variance.

The author tested the assumption that the covariance was equal to zero by comparing the slopes of the relations of juvenile fish length and otolith radius for 70–100 mm, slow- and fast-growing fish collected in October 1984 that were ≥ 1 year old. The slope was 0.0419 for anchovy older than one year and 0.0314 for fish younger than one year old. These slopes were not significantly different $(P > 0.10, \text{ANCOVA})$. Consequently confidence intervals around back-calculated growth rates were calculated ignoring the third term in Equation (1).

Lengths of anchovies were significantly different between months and years $(P < 0.01, \text{ANCOVA})$. Within a spawning season, fish hatched during February, March, and April grew faster than fish hatched in January or May (Fig. 1), although this was not evident for the 1983 or 1984 data. The mean of five fish in January 1982 was not different from that of the April 1982 sample. The adjusted lengths of juveniles collected from the 1983 year class where less than the adjusted lengths of any of those from 1980–82 for all months but May (Fig. 1, Table 1). The adjusted lengths of juveniles from

TABLE 1.—Mean lengths at capture of juvenile northern anchovy hatched in various months of 1980–84, adjusted to a common age of 208 days. SE and N stand for standard error and number of fish, respectively.

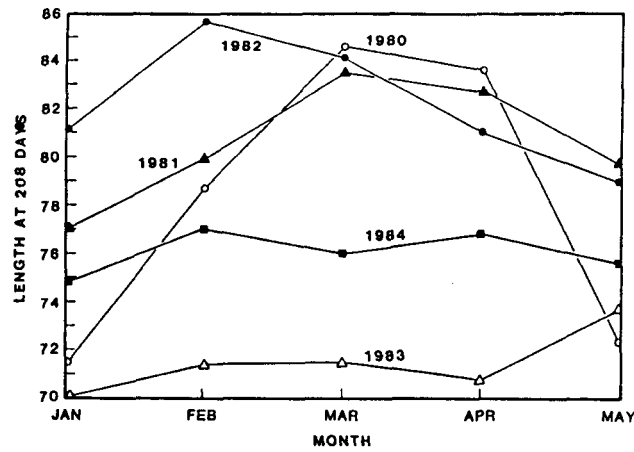| Year | Month of Hatching | | | | |
	Jan.	Feb.	Mar.	Apr.	May
1980	71.4	78.7	84.6	83.6	72.3
SE	3.6	1.6	1.0	1.6	
N	7	30	104	33	2
1981	77.0	79.9	83.5	82.7	79.7
SE	2.2	2.2	1.2	1.5	2.4
N	21	29	42	35	16
1982	81.1	85.79	84.1	81.0	78.9
SE	4.5	1.3	1.1	1.2	1.6
N	2	32	70	53	29
1983	70.0	71.4	71.5	70.8	73.7
SE	2.6	2.1	0.9	0.9	2.7
N	9	17	99	45	8
1984	74.8	77.0	76.0	76.8	75.6
SE	1.5	1.3	1.3	1.9	1.5
N	39	53	42	22	17

647

FIGURE 1.—Mean lengths adjusted for age of northern anchovy spawned in 1980–84. For each year, fish are grouped by back-calculated date of hatching, and length at capture is adjusted to mean age of 208 days.

1984 were intermediate between those of 1980–82 and 1983.

Fish hatched during 1983 did not grow more slowly throughout the entire larval and juvenile stage than during other years. Otolith increment widths from 104 juveniles hatched in March 1980 were compared with otolith increment widths from 99 juveniles hatched in March 1983 (Fig. 2). In fish smaller than 40 mm in length, increment width was not different. Above 40 mm, the oto-

lith increment widths were smaller in the 1983 sample than in the 1980 sample ($P < 0.01$); the 95% confidence limits for the two cohorts did not overlap. These results show that the difference in lengths of the two cohorts indicated by the analysis of covariance is largely due to difference in growth rate after a size of 40 mm, rather than to a reduction of growth throughout life.

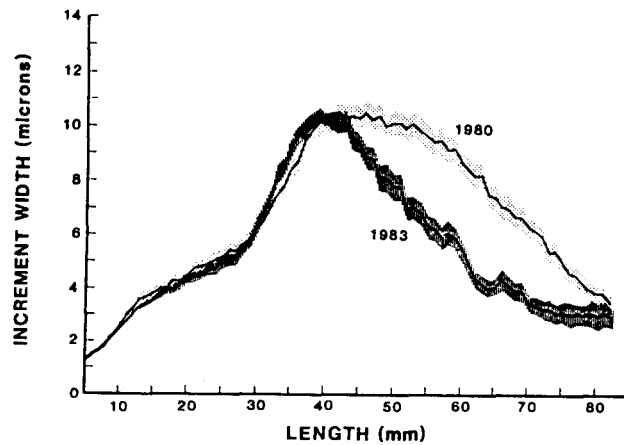Back-calculated lengths and growth rates of 1980 northern anchovy juveniles were greater

FIGURE 2.—Average otolith increment width versus length of 104 northern anchovy spawned in March 1980 and of 99 anchovy spawned in March 1983. Shaded areas are 95% confidence intervals.

648

than those of 1983 (Figs. 3, 4). Cohorts did not differ significantly in growth until approximately 40 mm. The age of the end of the late larval (10 mm) period was 20 days in 1980 and 19 days in 1983. A local minimum for growth rates of 1983 fish occurred at about 35 mm and at about 42 mm for growth rates of 1980 fish. This corresponds, approximately, to metamorphosis from late larval stage to juvenile stage. The duration of the late larval period (10–35 mm) was about 70 days in both 1980 and 1983.

After metamorphosis, growth rates increased in 1980 and 1983 until about 40 mm. At about 40 mm, the growth rates of the two cohorts diverged, and the mean back-calculated growth rate of the 1983 cohort was well below the estimated 95% confidence interval of the 1980 cohort. Growth rates declined steadily in 1983 at sizes larger than 40 mm, while growth rates of about 0.4 mm/d were sustained in 1980 until almost 60 mm. After 60 mm, growth declined at about the same rate as the decline in the 1983
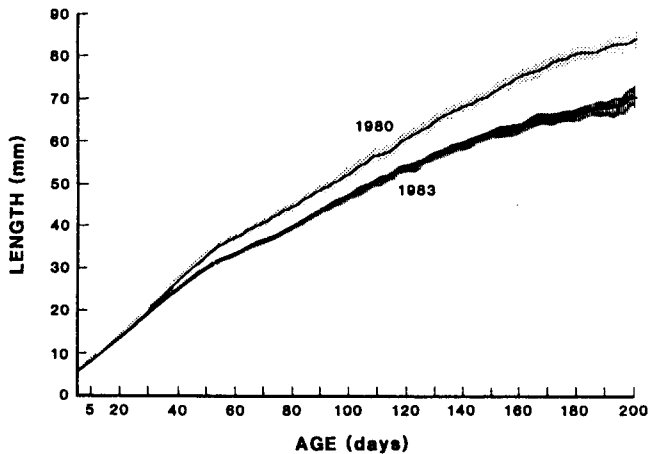

FIGURE 3.—Length versus age of northern anchovy larvae and juveniles of the March 1980 and 1983 cohorts back calculated from daily increments in otoliths.
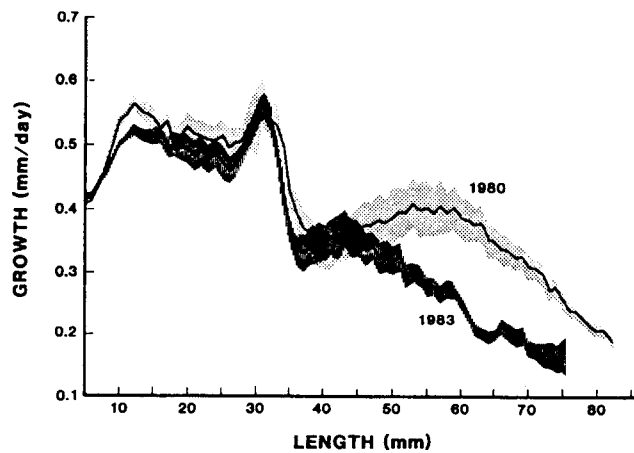

FIGURE 4.—Age-specific growth rates back calculated from daily increment widths of northern anchovy spawned in March 1980 and March 1983. Growth rate of length in mm per day. Shaded areas are 95% confidence intervals.

649

cohort. Growth within cohorts varied most between 40 and 60 mm.

In 1980 and 1983, northern anchovy growth in weight increased rapidly at small sizes (Fig. 5). Back-calculated growth rates for 1983 reached a local maximum of 6.5 mg/d at about 40 mm and then declined before slowly increasing to 7.5 mg/d at 79 mm. Back-calculated growth rates for 1980 showed a steady increase to about 11.5 mg/d at about 65 mm, which was maintained until about 75 mm, after which growth declined. The growth of northern anchovies hatched in March 1983 peaked at an earlier time (about June) in 1983 and at a smaller size (40 mm), whereas the growth of anchovies hatched in March 1980 peaked near the end of July 1980 and at a larger size at (about 65 mm).

geographic shifts in the population or to changes in spawning date and sampling time in 1984.

When size is adjusted for age and date of spawning, growth of juvenile northern anchovy was reduced in fish hatched in February through April of 1984 compared with fish hatched in the same months in 1980–82 (Fig. 1). This result is consistent with the results from studies of other fish populations on the west coast during El Niño. Growth rates and condition factors were also reduced in the Pacific herring, *Clupea harengus pallasi* (Spratt 1987), the blue rockfish, *Sebastes mystinus* (Van Traskie[2]), and in chinook, *Onchorhynchus tshawytscha*, and coho, *Onchorhynchus kisutch*, salmon (Pearcy and Schoener 1987) during El Niño.

Although the 1982–83 El Nino was fully devel-
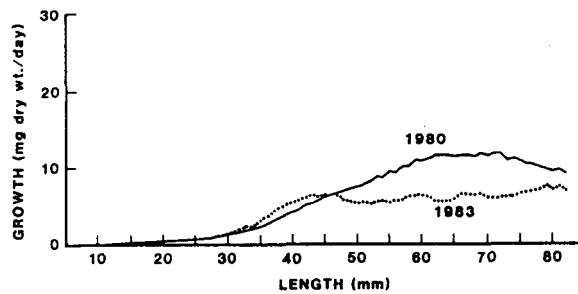

FIGURE 5.—Mean back-calculated growth rates of northern anchovy spawned in March 1980 and March 1983. Growth rate of mass in mg dry weight per day.

DISCUSSION

Growth rates of late larval northern anchovy did not vary in two otherwise extreme years, 1980 and 1983. Methot (1981) found little variance in early larval growth in the sea. Smith (1985) postulated that major changes in recruitment would result from changes in growth rates in the late larval period (10–35 mm) from 0.227 to 0.559 mm/d, a difference of 0.3 mm/d. In this study, however, growth rates of the late larval stage varied by <0.05 mm/d between 1980 and 1983.

Northern anchovy juveniles grew less during 1983 and 1984, compared with the previous three years. Fiedler et al. (1986) also reported reduced growth of anchovy in 1983, but the mean size of 1 yr old fish indicated a dramatic recovery in 1984. This apparent recovery may be in part due to

oped by October 1982 along the coast of Peru, full development of large scale warming off the North American coast did not occur until January 1983 (Lynn 1983). Positive temperature anomalies (>1°C) were evident both at the surface and at depth throughout the California Current (McGowan 1985; Norton et al. 1985). Negative salinity anomalies associated with subsurface temperature anomalies indicated intrusion of low salinity water from the south and west into the Southern California Bight (Simpson 1983).

These temperature anomalies represent a large change in the heat content of the ocean but are small relative to the thermal range of northern anchovy. Thus the small size of juvenile

[2]Van Traskie, D. 1985. Growth of blue rockfish (*Sebastes mystinus*) during El Niño. (Abstr.) Calif. Coop. Fish. Invest. Conf., Idyllwild, CA, Oct. 22–25, 1985.

anchovies during 1983 may be a direct result of reduced food availability at the same time that the rapidly growing juveniles experienced higher metabolic rates due to the elevated environmental temperatures. Zooplankton volumes on CalCOFI line 90 (line 90 intersects the coast at lat 33°29.9'N, long. 117°44.4'W and proceeds seaward on a bearing 240° clockwise from North) were lower than the 95% confidence limit of the 30 year CalCOFI time series (McGowan 1985).

Growth rates were not, however, depressed over the entire early life history. The growth rates of larval stages (5–35 mm) were not significantly different between the two years 1982–83 (Figs. 3, 4). Growth rates in 1983 were reduced in the early juvenile stage, and in particular after 40 mm, compared with growth rates in 1980.

Thus food was not growth limiting until the fish reached a certain size. As fish larvae grow, the ration necessary to sustain growth increases. Since the density of food particles decreases with size (Sheldon and Parsons 1967; Sheldon et al. 1972), at some stage food must become growth limiting. Based on this analysis, food-limited growth is unlikely in anchovies <40 mm during conditions that existed in the Southern California Bight in 1983, and unlikely in anchovies <65 mm during "normal" years such as 1980.

The similarity of back-calculated larval growth rates between years may be a result of the interaction of growth and mortality. A wide range of growth rates are possible at this stage (Hunter 1980), but variable growth rates are not observed in the field. Mortality of slow-growing individuals may reduce the range of growth rates in survivors to metamorphosis.

While the 1957–58 El Niño had a dramatic effect on northern anchovy recruitment in 1958, the numbers of fish in the 1983 and 1984 year classes were not appreciably lower than the previous years (Methot 1988). Thus, although the juvenile period was prolonged in 1983, recruitment was not affected. The major effect of El Niño on the anchovy population was to reduce the size of recruits as well as perhaps the size of adults and the reproductive potential of the 1983 and 1984 cohorts.

ACKNOWLEDGMENTS

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