

GROWTH OF LABORATORY-REARED NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, FROM SOUTHERN CALIFORNIA

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ABSTRACT

The northern anchovy, *Engraulis mordax*, was experimentally reared in the laboratory at the Southwest Fisheries Center, La Jolla, Calif. Data from three experiments were used to empirically fit a two-phase Gompertz growth model. The model describes growth from hatching to about 20 mo of age. It was estimated that the average length of laboratory-reared anchovies is 102 mm at 1 yr old and 119 mm at 2 yr old. Growth of laboratory-reared anchovies was comparable to that of anchovies in the wild.

Attempts to rear the northern anchovy, *Engraulis mordax*, at the Southwest Fisheries Center (SWFC), La Jolla, Calif., were begun in 1966 when G. O. Schumann collected anchovy larvae in the ocean off La Jolla and successfully reared them using wild plankton as food in the laboratory (Bardach 1968). Schumann's success was followed by other laboratory experiments in which anchovies were reared from eggs, larvae, and juveniles that were caught in the ocean (Table 1). In 1970, Leong (1971) developed a method for artificially inducing anchovies to spawn by controlling the photoperiod and injecting hormones. This technique is currently used at the SWFC to produce eggs and to rear anchovies for experimental purposes.

One of the purposes of the rearing experiments at the SWFC has been to obtain physiological and biochemical information needed for describing the energy budget of the northern anchovy, and to relate the results to the feeding dynamics of the anchovy population in the California Current, which consists of primarily young fish less than 3 yr old. Growth data are needed for analysis of the budget, and various attempts have been made to measure growth in the laboratory. Kramer and Zweifel (1970) and Lasker et al. (1970) reported growth rates of anchovy larvae. In this report we extend their analyses to include growth from hatching to about 20 mo old. We also present a mathematical model that describes this growth and compare our results with those of other investigators.

SOURCES OF DATA

Data primarily from experiments of G. O. Schumann (Schumann-I; Schumann-II), G. O. Schumann and A. Saraspe (Schumann-III), and R. Leong (pers. commun., SWFC) were used in our study (Table 1).

Schumann-II successfully reared larval anchovies for 22 days at about 22°C water temperature, which is higher than the temperature (15° to 16°C) at which anchovy larvae are frequently found in large numbers in the California Current (pers. commun., P. Smith, SWFC). The larvae were fed wild plankton and samples were taken for length measurement approximately daily.

Schumann-III reared anchovies from the egg stage through the juvenile stage in aquaria for 83 days on a diet of wild plankton, *Artemia salina*, and commercial trout food. The experiment was conducted from March to June and the water temperatures in the aquaria were not recorded. However, during March to June the average water temperature in rearing aquaria at the SWFC is generally about 18° to 22°C.

Leong (pers. commun.) obtained juvenile anchovies from a live-bait dealer and reared the fish to maturity in a 4.6-m diameter pool (13.2 kl) with circulating seawater. The water temperature in the pool was a few degrees higher than the prevailing water temperature off Scripps Pier, La Jolla, site of the water intake for the experimental pool (Lasker and Vlymen 1969). Leong fed the fish a diet of *Artemia salina*, ground squid and anchovies, and commercial trout food. Once a month about 25 fish were sacrificed for length and weight measurements.

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TABLE 1. — Laboratory experiments of rearing the northern anchovy at the Southwest Fisheries Center, La Jolla, Calif.

Source	Life stage at start	Start of rearing	Rearing duration (days)	Average length (mm)		Food
				Start	Finish	
Hunter (1976)	Eggs	April	74	4.0	35.0	<i>Gymnodinium splendens</i> , <i>Brachionus plicatilis</i> , <i>Tisbe furcata</i> , and <i>Artemia salina</i>
Kramer and Zweifel (1970)	Eggs	August and September	35	3.2	17.4	Wild plankton and <i>A. salina</i>
Lasker et al. (1970)	Eggs	February	50	3.4	21.0	<i>Bulla gouldiana</i> , <i>G. splendens</i> , and <i>A. salina</i>
Leong (unpubl. data) ¹	Juveniles	April	474	88.3	117.7	Squid, anchovy, <i>A. salina</i> , and trout food
Paloma (see text footnote 3)	Juveniles	November	624	75.0	106.2	<i>Artemia salina</i> and trout food
Schumann-I (G. O. Schumann unpubl. data) ²	Larvae	March	97	18.0	81.9	Wild plankton
Schumann-II (Kramer and Zweifel 1970)	Eggs	March	22	2.9	16.2	Wild plankton
Schumann-III (G. O. Schumann and A. Saraspe unpubl. data) ²	Eggs	March	83	3.5	67.1	Wild plankton, <i>A. salina</i> , and trout food
Theilacker and McMaster (1971)	Eggs	—	19	—	12.0	<i>Gymnodinium splendens</i> , <i>B. plicatilis</i> , and <i>A. salina</i>

¹Pers. commun., Southwest Fisheries Center, La Jolla, Calif.

²Data are on file at the Southwest Fisheries Center, La Jolla, Calif.

In all of these experiments the fish were from the southern California stock (Vrooman and Smith 1971), reared at laboratory ambient water temperature, and not subjected to experimental treatment or excessive handling. All fish sampled for measurements were sacrificed. The length measurement is standard length.

TREATMENT OF DATA

The age of anchovies reared by Schumann-II and Schumann-III were known because the anchovies were hatched from eggs at the start of the rearing experiments. In Leong's (pers. commun.) experiment, the exact age of his fish was not known because juvenile fish of average length of 88.3 mm were used at the start of the experiment. We estimated the age of Leong's fish from data from Schumann-I in which anchovies were reared for 97 days from an average length of 18.0 to 81.9 mm (Table 1), and data from Schumann-III which indicated that an 18.0 mm fish, raised from eggs, was about 30 days old. Our age estimate is 4 mo.

Several mathematical models describing growth of organisms are available (e.g., Parker and Larkin 1959; Richards 1959; Laird 1969). The commonly used models in fisheries are the exponential, the von Bertalanffy, and the Gompertz models (Beverton and Holt 1957; Silliman 1969). The Gompertz model was selected for our study because it was shown by Kramer and Zweifel (1970) to be better than the exponential

model for describing growth of laboratory-reared anchovy larvae and because it generally describes the growth of fishes fairly well. Also, preliminary analysis of our data indicated that the von Bertalanffy model poorly described the growth of young fish.

The Laird version of the Gompertz growth model (Laird 1969) describes an asymmetric sigmoid curve of the form.

$$L_t = L_0 \exp \{ C [1 - \exp(-at)] \}$$

where L_0 = length at zero age or hatching
 C = a constant
 a = rate of decay of exponential growth
 t = age in months.

This model was fitted to our data using an iterative least squares procedure (Conway et al. 1970). Our goal was to describe growth on a coarse time scale, i.e., monthly rather than on a fine time scale, i.e., daily.

GROWTH FROM HATCHING TO JUVENILE STAGE

The Gompertz growth model and an exponential growth model were applied to data of Schumann-II by Kramer and Zweifel (1970). Both models described the data from Schumann-II reasonably well, although the Gompertz model de-

scribed the data better. In the Kramer-Zweifel analysis the length at zero age, L_0 , was fixed at 2.5 mm, the average size at hatching. We also applied the Gompertz growth model to data of Schumann-II. Kramer and Zweifel (1970) used data only for 17 days of growth. We used all of the data of Schumann-II, which included sampling through 22 days of growth, and fitted the model first with L_0 fixed at 2.5 mm and again without this constraint, i.e., L_0 was estimated. The results (Figure 1) indicate that there is not much difference in the curves with L_0 fixed or estimated within the range of the data. Outside the range of the data, the curves diverge considerably and there is a substantial difference; the curve with L_0 estimated has a lower asymptotic length (61 mm) than the curve with L_0 fixed at 2.5 mm (asymptotic length of about 696 mm).

Zweifel and Lasker² showed that a two-phase Gompertz curve described the data from Schumann-II better than a single-phase Gompertz curve. The separation of the phases occurred at about 6 days of age, the onset of feeding in anchovy larvae.

Schumann-III reared anchovies for a longer period than Schumann-II. Fish reared by Schu-

mann-II, however, were larger than those reared by Schumann-III at similar ages. For example, at 0.5 mo of age fish reared by Schumann-II averaged 12.1 mm long and fish reared by Schumann-III, 8.2 mm long. Although the sample size is small, this difference is statistically significant at the 1% probability level. Differences in rearing procedures, i.e., diet and temperature of water, probably produced the difference in growth (Kramer and Zweifel 1970; Lasker et al. 1970).

The Gompertz growth model was applied to data from Schumann-III first with L_0 fixed at 2.5 mm and then with L_0 estimated (Figure 2). As in the case with data from Schumann-II, this model describes the growth data reasonably well, and the curve with L_0 estimated has a lower asymptotic length (81 mm) than the curve with L_0 fixed (asymptotic length of about 93 mm).

GROWTH DURING JUVENILE TO ADULT STAGE

Anchovies reared by Leong (pers. commun.) were juveniles at the start of the experiment and grew to an average size of 117.7 mm in 474 days (Table 2). Growth was in steplike stages characterized by rapid growth followed by a leveling off. The first stage was between 4 and 12 mo of age and the second was between 12 and about 20 mo of age.

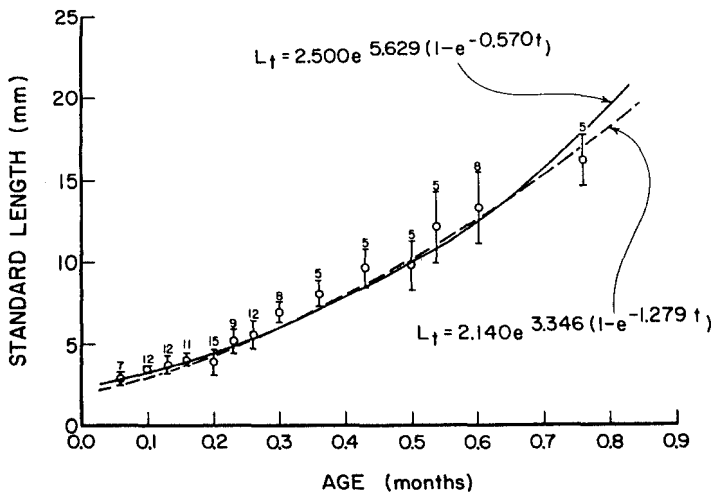


FIGURE 1.—Growth of anchovy larvae reared in the laboratory. The Gompertz growth model of the form, $L_t = L_0 \exp \{C [1 - \exp (-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm and broken line is based on L_0 estimated, 2.140 mm. Data from Schumann-II (Kramer and Zweifel 1970). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

²Zweifel, J. R. and R. Lasker. 1974. Prenatal and postnatal growth of fishes—a general model. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

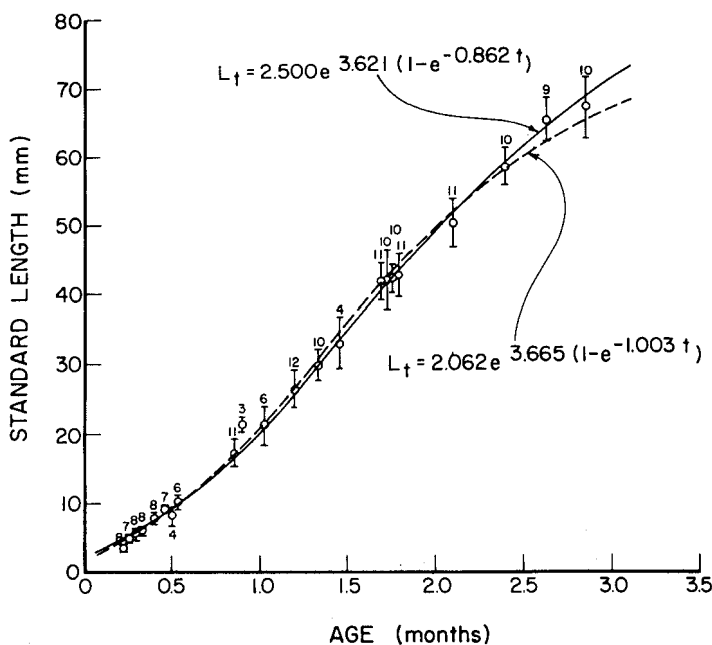


FIGURE 2.—Growth of anchovy reared in the laboratory. The Gompertz growth model of the form $L_t = L_0 \exp \{C[1 - \exp(-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm, and broken line is based on L_0 estimated, 2.062 mm. Data from Schumann-III (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

TABLE 2.—Estimated age and average standard length of northern anchovies reared in the laboratory by R. Leong (pers. commun., Southwest Fisheries Center, La Jolla, Calif.)

Age		Number of fish	Average length (mm)	Standard deviation
Days	Months			
120	4.00	10	88.30	6.34
153	5.10	23	92.35	4.90
189	6.30	24	94.63	5.85
231	7.70	25	97.68	6.40
270	9.00	25	96.48	6.19
301	10.03	23	99.30	5.14
351	11.70	25	101.52	4.59
385	12.83	25	105.72	5.26
413	13.77	25	109.16	5.75
444	14.80	26	109.23	6.07
471	15.70	26	110.58	6.82
503	16.77	25	114.56	6.57
533	17.77	24	117.38	6.11
562	18.73	25	116.32	7.07
594	19.80	25	117.68	6.69

The Gompertz growth model was applied, but did not adequately fit the data. This is characteristic of asymptotic models like the Gompertz model when all the data points are for a segment of the growth curve where growth is relatively slow and the plot of the data exhibits little curvature.

GROWTH FROM HATCHING TO ADULT STAGE

Growth Curve

As indicated earlier, anchovies reared by Schumann-III grew slightly faster than those of Schumann-II, probably due to slight differences in the rearing environment and procedures. Because our goal was to construct a general growth curve and the differences in the data were relatively slight, we elected to disregard the difference and pooled the data from the three experiments (Schumann-II, Schumann-III, and Leong). The Gompertz growth model was applied to the pooled data. The results (Figure 3) indicate that the model does not adequately describe the data. For example, the model overestimates the sizes of fish at about 4 to 12 mo old and underestimates the sizes of fish older than about 13 mo. These biases are caused by the steplike growth pattern which produces plateaus at about 6 mo and 19 mo of age.

To account for this steplike growth pattern, a

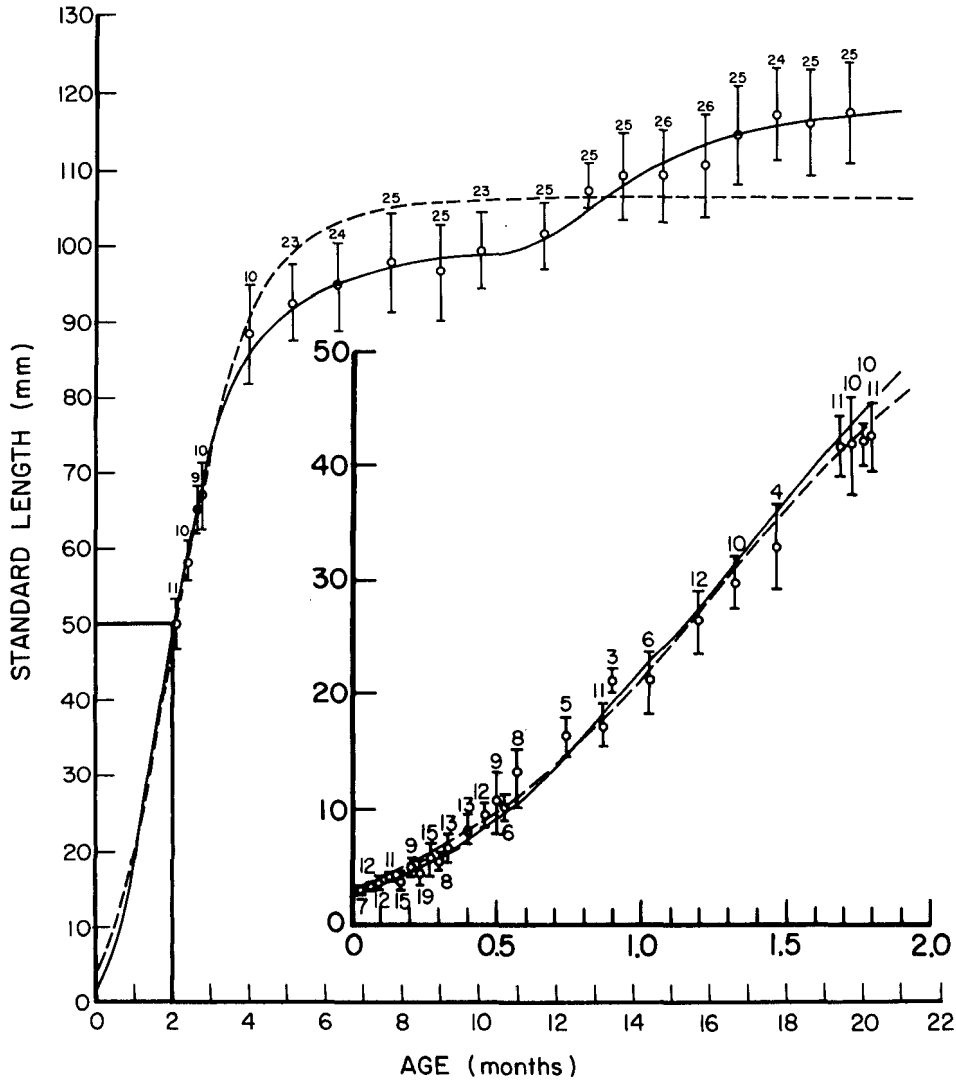


FIGURE 3.—Growth of northern anchovy reared in the laboratory. One-phase (broken line) and two-phase (solid line) Gompertz growth models are used to describe the data. Data from Schumann-II (Kramer and Zweifel 1970), Schumann-III, and Leong (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown. Broken line is described by $L_t = 2.825 \exp \{3.623 [1 - \exp (-2.877t)]\}$ and solid line by $L_t = 2.745 \exp \{3.563 [1 - \exp (-0.848t)]\}$ for $t \leq 11$ mo, and $L_{(t-11)} = 96.782 \exp \{0.213 [1 - \exp (-0.258 \{t - 11\})]\}$ for $t > 11$ mo.

two-phase Gompertz model (Zweifel and Lasker see footnote 2) was fitted to the data. The two-phase model is essentially two separate Gompertz equations that describe different segments of the growth curve. The equations were fitted simultaneously and the convergence point of the equations was determined on the basis of least squares analysis. Our best fit of the data was with the

equation, $L_t = 2.745 \exp \{3.563 [1 - \exp (-0.848t)]\}$ for growth from hatching to 11 mo of age and the equation, $L_{(t-11)} = 96.782 \exp \{0.213 [1 - \exp (-0.258 \{t - 11\})]\}$ for growth from 11 to 20 mo of age (Figure 3). From the equations, the estimated average length of anchovies after 1 yr of life is 101.6 mm and after 2 yr of life, 118.9 mm (Table 3).

TABLE 3.—Estimated growth for the first 24 mo of life of the northern anchovy reared in the laboratory. Estimates are based on a two-phase Gompertz growth curve (see text).

Age (mo)	Standard length (mm)	Age (mo)	Standard length (mm)
hatching	2.7	13	105.5
1	21.0	14	108.6
2	50.4	15	111.0
3	73.2	16	112.9
4	85.9	17	114.5
5	92.0	18	115.6
6	94.7	19	116.6
7	95.9	20	117.3
8	96.4	21	117.8
9	96.6	22	118.3
10	96.7	23	118.6
11	96.8	24	118.9
12	101.6		

General Remarks

The steplike growth pattern is commonly found in fishes. Gerking (1967) reviewed the literature on this subject and noted that many temperate species have seasonal, sigmoid growth curves. Lockwood (1974) recognized this feature in the growth of plaice and brown trout and applied a multiphase von Bertalanffy growth model to describe the data mathematically. His results were satisfactory but because the von Bertalanffy growth equation does not describe a sigmoid curve, his analysis was confined to growth for part of the season only.

In this study we used the Gompertz growth equation to describe the sigmoid curve. The two-phase model satisfactorily described our data for laboratory-reared anchovy, and a cycle that occurs at 12-mo intervals is evident in our results. This is quite similar to the seasonal growth patterns described by Gerking (1967), Mann (1971), Kroger et al. (1974), and others. The cycle indicates that for the northern anchovy, about 95% of the first year's growth is completed by the 8th month of life and about 91% of the second year's growth is completed by the 20th month of life.

If this cyclic pattern in growth also occurs in anchovies in the wild, then it may have a considerable impact on yield models, such as yield-per-recruit models, and on management decisions. It might be that the best harvesting strategy in terms of maximum yield-per-recruit is during the period of the cycle when growth is relatively slow, i.e., period of plateau. It seems important, therefore, that a multiphase growth function be considered for use in yield models for northern anchovy.

We point out the possibility that the cyclic pat-

tern could have been artificially created because our data were from three cohorts that were reared under different laboratory conditions during different periods of the year and the ages of fish reared by Leong (pers. commun.) were estimated. However, we discount that possibility because the cyclic pattern persists even if our age estimates of Leong's fish were off by 1 or 2 mo. Rearing conditions, on the other hand, could have produced the cyclic pattern if the pattern is influenced primarily by environmental factors, e.g., temperature, length of day, and food density and quality.

WEIGHT-LENGTH RELATION

Weight-length relations for the northern anchovy were reported by several investigators (Table 4). Only Lasker et al. (1970), however, reported on estimates for laboratory-reared anchovies, and their estimates were for anchovy larvae.

Length and weight data were collected by Leong (pers. commun.) and Paloma³ from fish reared in their experiments. We used their data from 757 fish to estimate the weight-length relation of laboratory-reared anchovies of 70 to 131 mm long. Data from Paloma were only from fish in their first year of life, in which growth was somewhat similar to that of fish reared by Leong. Separate estimates were made for males and females (Table 4), and the results subjected to covariance analysis (with log transformed data) to test whether the relation could be represented by a single line. The analysis indicated that the separate lines were parallel and not significantly different from a common line. The data were, therefore, pooled and a weight-length relation estimated for the combined (all sexes) data (Table 4).

Our estimates are compared with those of Collins (1969) for anchovies from southern California (Figure 4). Collins based his estimates on data from anchovies caught in the reduction fishery off southern California. For a given length, fish examined by Collins were lighter than the laboratory-reared fish. This phenomenon appears common for fishes (Kramer 1969; Kimura and Sakagawa 1972). Kimura and Sakagawa (1972) mentioned that for Pacific sardines, differences in diet and reduced amount of exercise because of confinement were some possible causes for

³Paloma, P. 1971. Annulus formation in the scale of marked anchovy *Engraulis mordax* Girard. Unpubl. manusc. Southwest Fisheries Center, La Jolla, CA 92038.

TABLE 4. —Coefficients of the weight-length relation for the northern anchovy as reported by various investigators. The coefficients are for the equation, $\text{weight} = a \times \text{length}^b$.

Origin of sample	Source	Rearing environment		Sex	Number of fish	b	a	Unit of measure		Range of length (mm)
		Ocean	Laboratory					Length	Weight	
Southern California	Clark and Phillips (1952)	X		Combined sexes	(¹)	3.453	2.7×10^{-4}	mm	ounce	56-134
	Collins (1969)	X		Male	926	3.049	8.1×10^{-6}	mm	gram	97-161
	Collins (1969)	X		Female	1,513	2.984	1.1×10^{-5}	mm	gram	
	Lasker et al. (1970)		X	Combined sexes	63	3.324	1.5×10^{-4}	mm	mg	3-25
	Present study ²		X	Male	257	3.521	1.0×10^{-6}	mm	gram	73-126
	Present study		X	Female	500	3.433	1.5×10^{-6}	mm	gram	70-131
Central California	Present study		X	Combined sexes	757	3.461	1.4×10^{-6}	mm	gram	70-131
	Clark and Phillips (1952)	X		Combined sexes	(¹)	3.252	7.2×10^{-6}	mm	ounce	114-160
	Collins (1969)	X		Male	270	2.805	2.7×10^{-5}	mm	gram	80-171
	Collins (1969)	X		Female	407	2.743	3.6×10^{-5}	mm	gram	

¹Clark and Phillips (1952) used data from 17 samples from southern California and 77 samples from central California but they did not specify the number of fish in each sample.

²Unpublished data from R. Leong and P. Paloma (pers. commun.), Southwest Fisheries Center, La Jolla, Calif. The coefficients with the more appropriate functional regression (Ricker 1973) are: 1) male, $a = 7.0 \times 10^{-7}$, $b = 3.608$; 2) female, $a = 1.0 \times 10^{-6}$, $b = 3.518$; 3) combined sexes, $a = 9.2 \times 10^{-7}$, $b = 3.547$.

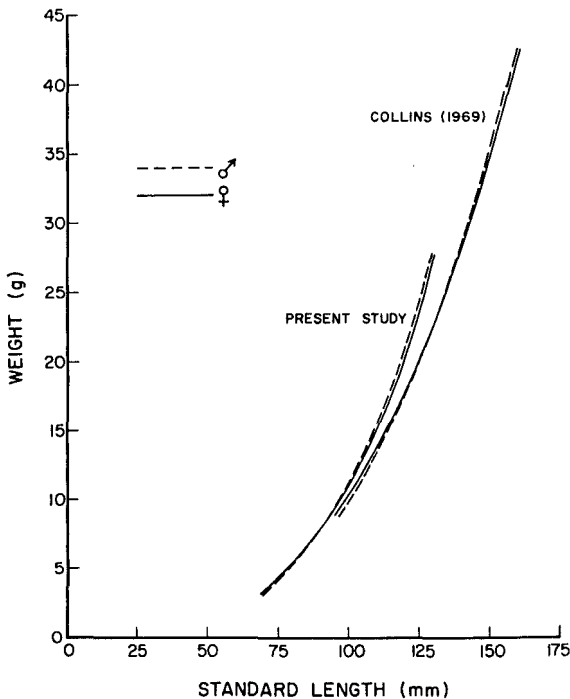


FIGURE 4. — Weight-length relation for northern anchovy from southern California. Laboratory-reared fish were used in present study, and fish caught in the California reduction fishery were used by Collins (1969).

laboratory-reared fish being heavier than fish in the wild. Zweifel and Lasker (see footnote 2) mentioned the possibility that the differences arise when the curves are based on fish in different phases of their growth cycle.

COMPARISONS OF GROWTH

Growth of anchovies reared in the laboratory

was studied by Kramer and Zweifel (1970), Lasker et al. (1970), Theilacker and McMaster (1971), Hunter (1976), and Paloma (see footnote 3). Kramer and Zweifel and Lasker et al. studied the effects of diet and water temperature on growth of anchovy larvae. They concluded that larval growth was best at 22°C with wild plankton as a food source. The growth curve of Figure 3 for the larval stage is for fish reared on wild plankton and *Artemia salina* at about 22°C. It is the best so far attained in the laboratory.

Theilacker and McMaster (1971) and Hunter (1976) reared anchovy larvae on cultured foods. Results of their studies show that growth of anchovies on cultured food diets is about the same as that on wild plankton.

Paloma (see footnote 3) obtained juvenile anchovies from a live-bait dealer and reared the fish in the laboratory for 624 days (Table 1). He injected oxytetracycline hydrochloride into the fish at various times to label the body structures for ageing. At 2-wk intervals, scales and data on body measurements were collected. Fish reared by Paloma started at a smaller average size (75 mm long) than fish reared by Leong (pers. commun.) (88 mm long) and grew at a much slower rate (21 mm in about 470 days versus 30 mm in about 470 days for Leong's fish) without a noticeable step-like pattern. Perhaps the frequent handling, injection of tetracycline, and small size of the rearing pool (2.74-m diameter) contributed to the slow growth and eliminated the steplike pattern.

Clark and Phillips (1952), Miller et al. (1955), Collins (1969), and Collins and Spratt (1969), studied growth of anchovies caught in the California fisheries. They used scales and otoliths for ageing fish to the nearest whole year. Clark and Phillips reported their results for the combined

southern and central California fisheries. Miller et al., Collins, and Collins and Spratt, on the other hand, reported their results separately for each fishery.

To compare growth of anchovies in the wild with that of laboratory-reared anchovies, we limited the comparison to fish from southern California to eliminate possible regional biases in growth. We also adjusted Miller et al.'s (1955) data upward by 1 yr to make them comparable to those of Collins (1969) and Collins and Spratt (1969) (Figure 5). This was necessary because Miller et al. did not correct their age readings for date of capture (August to March) and growth on the margin of the scale relative to the birthdate (April 1); hence, they underestimated the age of their fish by approximately 1 yr.

The growth curves in Figure 5 indicate that anchovies in the wild are 95 to 115 mm long at about 1 yr old and 115 to 125 mm long at about 2 yr old and possibly growth was slower in the 1960's than in the 1950's owing to the dramatic increase in the northern anchovy population (Spratt 1975). Our growth estimates for laboratory-reared anchovies are 102 mm for 1 yr olds and 119 mm for 2 yr olds; hence, growth of laboratory-reared fish seems to be similar to that of anchovies in the wild. However, we note that this direct comparison is not entirely valid because inherent biases exist in the growth curves in Figure 5. The biases exist because: 1) larger fish are generally more available to the reduction fishery than the live-bait fishery (Messersmith 1969) and thus are over-represented in the data for the reduction fishery; 2) live-bait fishermen "consciously avoid taking large anchovies, since they are less desirable for bait than smaller anchovies" (MacCall 1973:5-6) and thus large fish are underrepresented in the data for the live-bait fishery; 3) the true birthdate of anchovies aged by otolith or scale readings is not known although it is known that the birth date varies (Kramer and Smith 1971; Smith 1972), the ages, therefore, are not exact ages; and 4) growth of several year classes are averaged and consequently, variability in growth is reduced.

Spratt (1975), who also studied growth of the northern anchovy from otoliths, accounted for some of these biases by using back-calculated lengths and fish from the reduction fishery, live-bait fishery, and catches of a research vessel. He estimated that the mean standard length of anchovies in the wild is 92 and 112 mm at the end of the first and second year of life, respectively. These

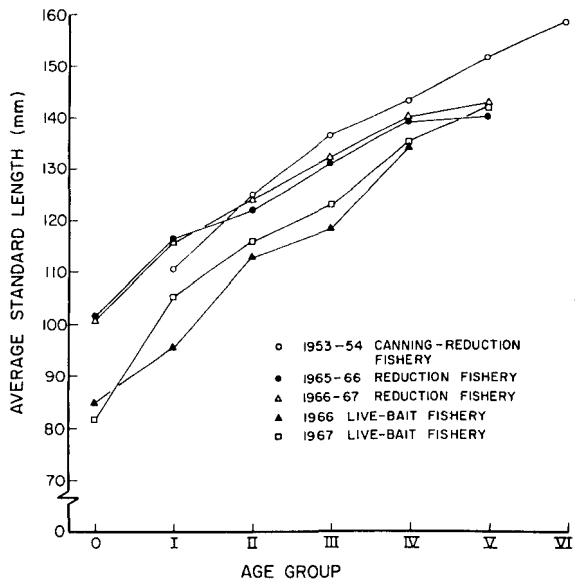


FIGURE 5.—Growth curves for northern anchovy caught off southern California in the fisheries for reduction (Collins 1969), live-bait (Collins and Spratt 1969), and canning-reduction (Miller et al. 1955).

estimates are somewhat less than ours for laboratory-reared fish but they are close.

It appears that growth of anchovies in the wild is similar to that estimated, on an annual basis, from our growth curve. We have not demonstrated, however, whether there is a cyclic pattern in growth of anchovies in the wild similar to that revealed in our results for laboratory-reared fish. On the other hand, studies on growth of other temperate fishes have shown that a seasonal cycle is common, which leads us to believe that a seasonal cycle exists for anchovies in the wild. The use of our growth curve for describing the feeding dynamics of northern anchovies of at least 2 yr of age in the California Current is therefore practical until a seasonal growth curve is described for anchovies in the wild.

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