THE EARLY LIFE HISTORY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

KEVIN M. BAILEY[1]

ABSTRACT

The early life history of Pacific hake, *Merluccius productus*, is described from laboratory and field studies. At ambient temperatures (11°-13°C) egg hatching takes about 100-120 hours; complete absorption of the yolk takes about 150-200 hours. Respiration rates for first feeding larvae at 12°C are 4.8-6.8 μl/mg per hour. Growth rates for at least the first 20 days are slow compared with other larvae in the California Current. First-feeding hake larvae require a daily ingestion of about 0.13 calories.

In this study I present information on the early life history of Pacific hake, *Merluccius productus*, including rates of development, starvation, growth, and metabolism. I have also used samples from Ahlstrom (1959) and others to examine the vertical distribution of eggs and larvae by size class. My objectives in examining these life history processes are to 1) evaluate the hypothesis that the availability of food directly after complete yolk-sac absorption is the critical factor in survival of larval Pacific hake and 2) to determine the relative length of time Pacific hake are in egg and yolk-sac stages and are most vulnerable to invertebrate predators.

The early life history of Pacific hake represents an interesting contrast to other fishes that spawn off the coast of California, including the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*. Compared with these other species the early life history of Pacific hake has been little studied. It is known that hake larvae live below the mixed layer in colder water, and that first-feeding larvae have large mouths, so they can feed on a wide spectrum of food particles (Ciechomski and Weiss 1974; Sumida and Moser 1980). Both the anchovy and mackerel have been subject to intensive investigation as models of the causes of egg and larval mortality. Eggs and larvae of both anchovy and mackerel are found within the warm upper mixed layer (Ahlstrom 1959). Compared with hake larvae, anchovy and mackerel have relatively small mouths at first feeding; thus, the size of ingested food particles is restricted (Hunter 1980). At least for first-feeding anchovy larvae, it has been shown that the availability of food of the proper size and in adequate densities is important to survival (Lasker 1975). The results of the present study, in particular the determination of the food requirements of hake larvae may indicate important differences in the survival strategies of these three fishes.

METHODS

Development and Growth

All laboratory experiments in this study were conducted using eggs collected at Port Susan, Wash. This stock is reproductively isolated from the Pacific hake spawning off the California coast (Utter 1969), but I am assuming that temperature-specific rates of metabolism of larvae hatching from Port Susan eggs are similar to the rates for larvae hatching from eggs spawned in the California Current because 1) egg size is the same, 2) temperature-dependent hatching times are the same (see results this study), and 3) growth to age 2 is the same (Kimura and Millikan 1977).

Eggs were collected with a 500 μm mesh meter net (equipped with a cod end designed to capture live zooplankton) and returned to the laboratory at 5°-10°C. Eggs and larvae were reared in filtered seawater in 1-4 l jars containing 50 ppm each penicillin G potassium and streptomycin sulfate. Egg hatching experiments were done with 3 replicates of 10-20 eggs/l. Percent hatching was checked every 12 h. The eggs used in these experiments were without visible embryos

[1]College of Fisheries, University of Washington, Seattle, WA 98195.

Manuscript accepted January 1982.
FISHERY BULLETIN: VOL. 80, NO. 3, 1982.

and were assumed to be about 12 h old. The time to 50% hatching was determined by interpolation from the linear regression of percent hatching (y) against time (x). Confidence intervals on the 50% hatch time were calculated from the prediction of x from y as:

$$\text{C.L.} = \bar{x} + \frac{b_{yx}(y_i - \bar{y})}{D} \pm H,$$

where $D = b_{yx}^2 - t^2_{(0.05,n-2)} S_b^2$, and

$$H = \frac{t_{(0.05,n-2)}}{D} \sqrt{S_{yx}^2 \left[D\left(1 + \frac{1}{n}\right) + \frac{(y_i - \bar{y})^2}{x^2}\right]}$$

Time to 50% yolk-sac absorption was determined similarly. Survival of yolk-sac larvae appeared to increase substantially under lighting in the cold rooms, which raised temperatures in these experiments to 10.5°C in the 8°C room and to 13.7°C in the 12°C room. The 15°C room was consistently lighted. After hatching at temperature, postyolk-sac larvae were removed, placed in new jars, and observed to determine time to starvation.

Growth was examined by counting daily increments on otoliths. For verification of otolith increments as daily marks, larvae were reared in the laboratory without antibiotics in a 12-h light-dark cycle. Larvae were fed *Artemia salina* nauplii and natural zooplankton strained through a 216 μm mesh net at a concentration of about 1 animal/ml. Field-caught specimens were obtained from several cruises off the California coast in 1977, 1978, and 1979. Both laboratory-reared and field-caught specimens were preserved in 80% ethanol. Larvae were measured (standard length) and otoliths were removed under a dissecting microscope fitted with a polarizing filter. Otoliths were mounted on a glass slide in protex or euparal, and rings on the otoliths were counted at 600-1000× magnification.

Larval dry weights (preserved in 80% ethanol for otolith investigations and in 3% Formalin[2] for respiration investigations) were determined on a Cahn 25 Electrobalance after rinsing the larvae in distilled water and subsequently drying them for 24 h at 60°C. Weight loss due to preservation was determined by comparing weights of subsamples of fresh-frozen larvae and preserved larvae, all hatching from the same cohort of eggs. Shrinkage in length was determined by measuring anaesthetized larvae before preservation and then again after 2-3 wk of preservation in 80% ethanol or 3% Formalin. Shrinkage due to preservation delay and death in a wet cod end during or after a plankton tow was simulated by anaesthetizing and measuring larvae, and then placing them on seawater-wetted paper towels for specific time periods. Larvae were then preserved in Formalin. These preservation effects were tested only on first-feeding larvae.

Growth, egg development, and yolk-sac absorption data were fitted with a Gompertz curve using a least-squares nonlinear curve fitting program (SPSS). The Gompertz growth function was selected because it is a flexible nonlinear function commonly used in studies of larval fish (Zweifel and Lasker 1976).

Metabolic Rates

Respiration rates of larvae were measured using a micro-Winkler technique (Carritt and Carpenter 1966). Experiments were conducted in 30 ml glass stoppered jars, at densities of 2-3 larvae/jar, in dim light for 11-14 h. Larvae in filtered seawater were acclimated to temperatures for 12 h. After the experiments were completed and oxygen fixed, jars were kept for 2-10 d at 8°C in the dark before titrating. Experiments were designed to include 3-5 replicates per temperature; however, when bubbles formed during the experiment (a constant problem at 15°) samples were discarded.

Vertical Distribution

Samples from vertical series of tows taken in 1954 and 1955 were reported by Ahlstrom (1959). I sorted and measured these samples to examine size-related vertical distribution. Pacific hake larvae from an additional three vertical series taken in 1969 were sorted and measured. Since there were no apparent day-night differences, all hauls, day and night, were combined. Nonstandardized data consisting of raw numbers per haul, uncorrected for volume of water filtered, were used since more detailed information did not exist for many hauls. Data on numbers of larvae caught per haul were classified into the depth interval where most of the tow took place.

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

RESULTS

Development Times

Egg hatching time shows a marked response to temperature (Fig. 1). Time for 50% hatching of eggs collected at Port Susan ranges from 3.5 d at 15°C to 4.5 d at 12°C (coastal temperature range at 50 m depth is 11°-14°C) and 6.5 d at 8°C (the approximate temperature at Port Susan). Also shown in Figure 1 are the mean hatching times of eggs collected off California that were reported by Zweifel and Lasker (1976).

The time from hatching to complete absorption of the yolk sac is also temperature dependent (Fig. 2). The time for 50% of the sample larvae to completely utilize their yolks is 9.7 d at 10°C, 6.4 d at 12°C, and 4.2 d at 15°C. I was not able to rear larvae to yolk-sac absorption at 8°C. At 8°C, 8-12 d old larvae still had considerable yolk supplies and no functional mouth. A well-developed mouth normally formed after 4 d at 12°C and after 3 d at 15°C.

Both the mean and the maximum length of time to starvation after complete utilization of the yolk decreased with increasing temperature (Table 1). A nonparametric analysis of variance (Kruskal-Wallis; Conover 1971) indicates that temperature has a significant effect on the time to starvation ($P<0.01$). The variance in the mean time to death was large in these experiments due to death occurring not only from starvation, but from other causes such as being trapped in the surface film. These early nonstarvation deaths were excluded from the analysis.

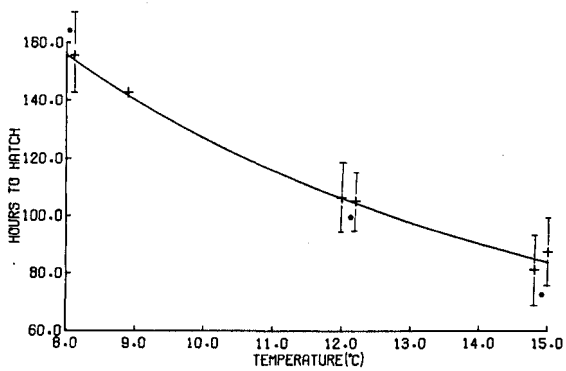

FIGURE 1.—Effect of temperature on time to 50% eggs hatching for Pacific hake, and 95% confidence intervals. Small solid circles are hatching times from Zweifel and Lasker (1976). Data was fitted to a Gompertz curve: $Y = 484.00 * \exp(-2.89 * (1 - \exp(-0.0623 * X)))$.

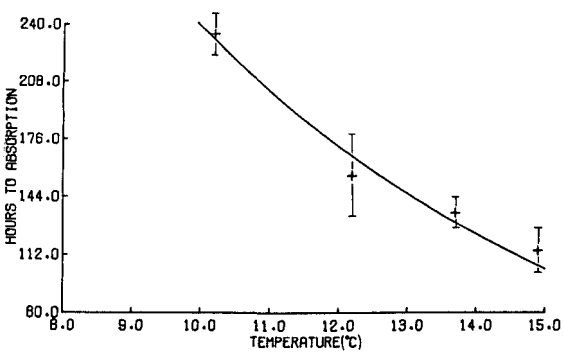

FIGURE 2.—Effects of temperature on 50% time to complete yolk-sac absorption for Pacific hake larvae and 95% confidence intervals. Data was fitted to a Gompertz curve: $Y = 1{,}269.52 * \exp(-108.82 * (1 - \exp(-0.0016 * X)))$.

TABLE 1.—Starvation experiments.

Temperature (°C)	Mean time to starvation (h)	Standard deviation	100% starvation (h)	No. of larvae
8	251.0	65.6	318	3
12	200.2	29.1	235	4
15	150.0	17.8	168	5

Growth Rates

Larvae were reared in the laboratory beyond the yolk-sac stage (±1 d) to verify otolith increments as daily marks. Increments begin to be added 1-2 d before complete yolk-sac absorption, perhaps coinciding with the onset of feeding; after yolk absorption, 1 ring is apparently added each day (Fig. 3). Rings on these otoliths were much fainter than those of field-caught specimens, possibly due to poor feeding, lighting, or other rearing conditions in the lab. Postyolk-sac larvae grown in the laboratory survived up to 10

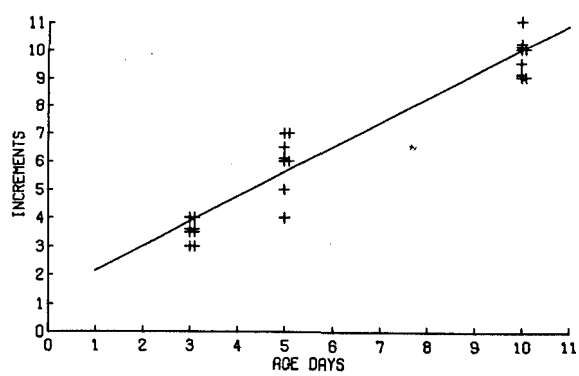

FIGURE 3.—The daily addition of increments by laboratory-reared postyolk-sac Pacific hake larvae.

d beyond the expected starvation date, but I was not able to maintain larvae much older than this.

The growth of field-caught larvae collected off California and stored in 80% ethanol was determined by otolith aging. Readings to 30 increments appear to clearly represent daily deposition of increments. However, after roughly 30 increments, dark bands appearing on the otoliths were separated by several inner rings and it was difficult to distinguish which were daily increments. R. Methot (Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif.) who read many of these otoliths from large larvae, felt that the larger bands were the daily marks. For the large otoliths I read, I followed this assumption.

The growth of Pacific hake larvae in length (not corrected for preservation effects) was fitted with a Gompertz curve (Fig. 4); however, a straight line provides a better fit for larvae <20 d old (Fig. 4, insert). Pacific hake larvae grow slowly in length for at least the first 30 d of posthatching life and then grow rapidly.

Growth in weight was examined by determining a length-weight relationship for larvae (Fig. 5a) and then combining this information with the age-length relationship described above (Fig. 5b). The weights used were from larvae preserved in 80% ethanol and uncorrected for pres-

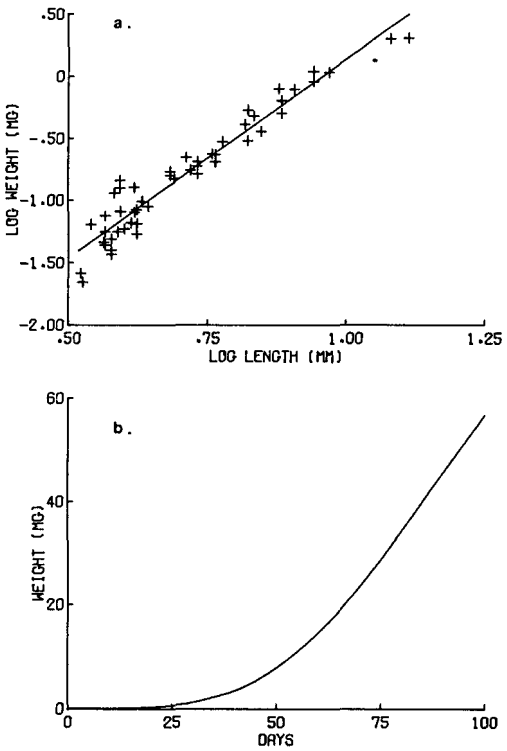

FIGURE 5.—Growth in weight of Pacific hake larvae. a. length-weight relationship of larvae off California (dry weights are from larvae preserved in ethanol), b. age-weight relationship.

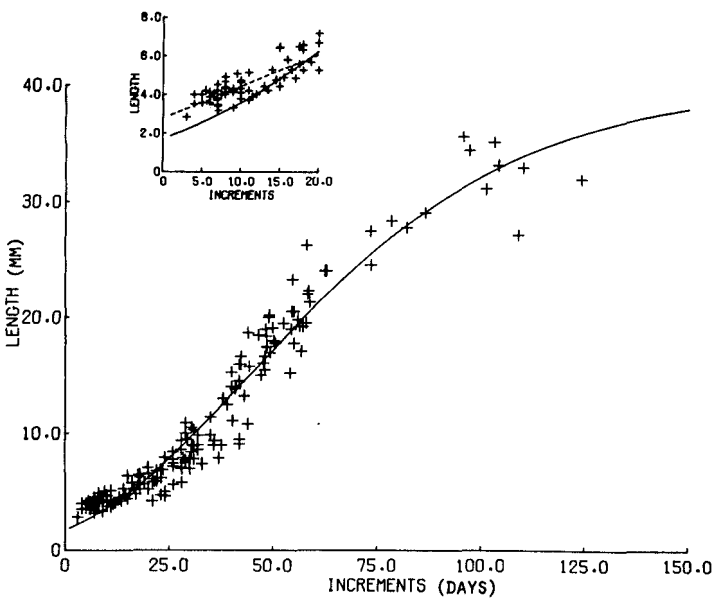

FIGURE 4.—The growth of larvae caught off southern California determined from otolith increments. A Gompertz curve was fit to the data, $Y = 1.72 * \exp(3.15 * (1 - \exp(-0.02624 * X)))$. Insert: daily growth for the first 20 d was fit better with a straight line: $Y = 2.75 + 0.16X$.

ervation effects. Increase in weight also appears to be slow for at least the first 30 d of posthatching life.

Weight loss of first-feeding larvae due to preservation in 80% ethanol was 57.8%, probably due mostly to loss of lipids and soluble proteins; weight loss in 3% Formalin was 24.1% (Table 2).

Shrinkage in length of first-feeding larvae preserved in Formalin was 8.9%; shrinkage of larvae preserved in ethanol was 3.6% (Table 3). Shrinkage due to delay in preservation was examined. Larvae in the 9-min delayed group decreased 17% in length, while those in the 29-min group decreased 40% in length. Most larvae, and especially larger larvae, probably do not die during the tow, and I have observed that in Puget Sound most larvae are alive after capture with a jar-type cod end. However, after a typical CalCOFI tow it probably takes an average of 5-10 min to remove and wash the cod end before preserving the larvae. I estimate that in routine sampling surveys small Pacific hake larvae probably shrink 9-20% in length due to handling. Shrinkage of large larvae was not tested and is probably different.

TABLE 2.—Weight loss due to preservation, determined by comparing fresh-frozen larvae to preserved larvae. Dry weights in milligrams.

	Live	80% ethanol	3% Formalin
Mean dry-weight (mg)	0.083	0.035	0.063
Standard deviation	0.007	0.004	0.006
No. of larvae	5	5	5
% of live weight	100.0	42.2	75.9

TABLE 3.—Shrinkage in standard length of first-feeding larvae due to preservative and related to delay in time of preservation, determined by comparing standard lengths of live larvae with preserved larvae. Three larvae per treatment; lengths are in millimeters.

	Ethanol	Formalin			
Preservative:	80%	3%	3%	3%	3%
Minutes delay	0	0	9	16	29
Mean live length	4.44	4.63	4.52	4.46	4.52
Mean fixed length	4.28	4.22	3.73	3.70	2.71
% length loss	3.6	8.9	17.5	17.0	40.1

Metabolic Rates

Respiration rates for Pacific hake larvae increase as a function of temperature and size (Fig. 6; Table 4). The experimental temperatures represent the range encountered by hake larvae within the spawning region. At 12°C, the mean temperature larvae experience off California,

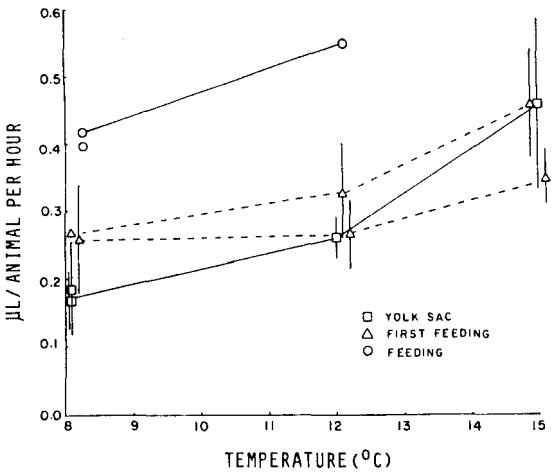

FIGURE 6.—The effect of temperature on mean respiration rates (µl/animal per h) of Pacific hake larvae of different stages. Vertical bars are ±1 standard deviation.

respiration rates for first-feeding larvae are 4.8-6.8 µl/mg-dry wt per h. These respiration rates were determined in 30 ml bottles, which did appear to slightly impair the swimming activity of larvae. Consequently, these rates are considered to be within the range between routine and active metabolism. The dry weights reported in Table 4 are of Formalin-preserved larvae, uncorrected for weight loss due to preservation. With the correction, weight specific rates would be 25% lower.

Vertical Distribution

Ahlstrom (1959) noted that Pacific hake eggs (and also most unsized hake larvae) were aggregated near the base of the mixed layer. From my analysis, most small larvae <8 mm were caught in the 50-100 m depth interval (Fig. 7), which corresponds to Ahlstrom's observations. Larger larvae were caught deeper; however, large larvae near the surface may be more able to avoid capture. An analysis by Lenarz (1973) indicates that larger larvae are probably able to avoid plankton nets in daytime. Large larvae, >12 mm, appear to be close to the surface later in the year (May-June), and have been caught at depths of only 25-50 m in nighttime plankton tows (A. Alvariño[3]). From my own observation in June

[3]A. Alvariño, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1979.

TABLE 4.—Summary of respiration experiments. Dry weights are of Formalin preserved larvae, uncorrected for weight loss due to preservation.

Temperature (°C)	Experiment	Mean length (mm)	Mean weight (mg)	Replicates	Larvae/jar	µl/animal per h	SD	µl/mg-dry wt per h
8	a. yolk sac	—	—	3	3	0.170	0.044	4.47
	b. yolk sac	3.49	0.038	3	5	0.185	0.072	4.87
	c. 1st feeding	3.81	0.049	2	2	0.271	—	5.53
	d. 1st feeding	3.97	0.055	4	3	0.260	0.083	4.73
	e. feeding	3.95	0.068	3	1	0.402	0.244	5.91
	f. feeding	3.97	0.070	2	1	0.426	—	6.09
12	a. yolk sac	—	—	—	—	—	—	—
	b. yolk sac	3.49	0.038	4	3	0.261	0.027	6.87
	c. 1st feeding	3.81	0.049	3	2	0.332	0.066	6.78
	d. 1st feeding	3.97	0.055	3	3	0.265	0.052	4.82
	e. feeding	—	—	—	—	—	—	—
	f. feeding	3.97	0.070	2	2	0.549	—	7.84
15	a. yolk sac	—	—	—	—	—	—	—
	b. yolk sac	3.49	0.038	4	3	0.460	0.126	12.11
	c. 1st feeding	3.81	0.049	3	3	0.467	0.080	9.53
	d. 1st feeding	3.97	0.055	4	3	0.345	0.041	6.27
	e. feeding	—	—	—	—	—	—	—
	f. feeding	—	—	—	—	—	—	—

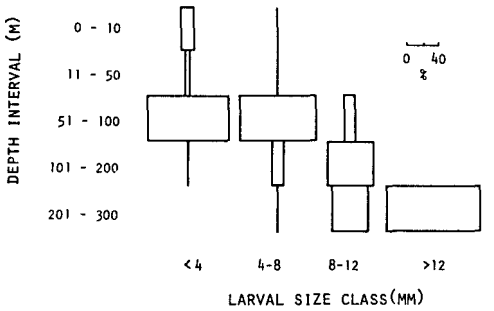

FIGURE 7.—The vertical distribution of Pacific hake larvae off the California coast shown as the percent of larvae within each depth interval by size class. Sample numbers are 1174, LT 4 mm; 1051, 4-8 mm; 19, 8-12 mm; 5, GT 12 mm; total sample of 2,249 larvae.

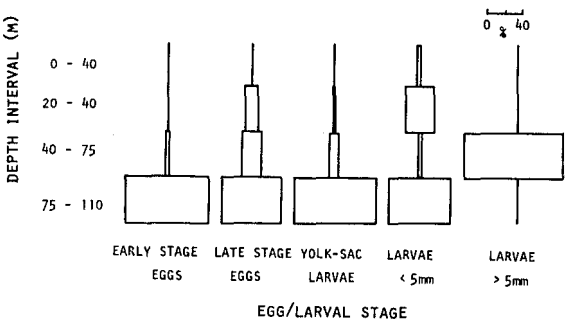

FIGURE 8.—The vertical distribution of Pacific hake eggs and larvae at Port Susan, Wash., shown as the percent of eggs or larvae within each depth interval by developmental stage or size class. Sample numbers: early stage eggs, 2,845; late stage eggs, 1,147; yolk-sac larvae, 409; larvae LT 5 mm, 31; larvae GT 5 mm, 12; total sample of 4,444.

1979, large larvae were also caught in midwater trawls near the surface in nighttime.

In contrast to eggs and larvae off the California coast, which are found at midwater, Pacific hake eggs and larvae in Puget Sound are located near the bottom of the water column. This is shown in Figure 8 for animals sampled at Port Susan (maximum depth, 110 m). This trend was also observed for animals collected at Dabob Bay (maximum depth, 175 m); the majority of eggs and larvae were found in the bottom 25 m of the water column. The difference in vertical distribution between eggs off California and eggs in Puget Sound may be explained as follows. The water at a reference level of 100 m is less saline (29.3‰) and less dense (1.0228) in Puget Sound than water off the California coast (33.6‰ 1.0258). Off California, eggs are spawned at 200-500 m depth, are relatively buoyant compared with the surrounding water, and rise upward to a level of equal buoyancy. Eggs in Puget Sound are spawned near bottom (Thorne 1977). Assuming that they are about the same density as the California eggs, these eggs are relatively less buoyant in the less dense water of Puget Sound, and therefore remain near the bottom.

DISCUSSION

Compared with eggs and larvae of other fishes in the California Current system, rates of development, growth, and metabolism of Pacific hake eggs and larvae are slow. These factors may be indicative of survival tactics (Hunter 1980), and differences could reflect the relative importance of certain environmental conditions, such as food abundance and predation pressure, in larval sur-

vival. Hunter (1980) contrasted several types of life history tactics for larvae of marine fishes. He indicated that in relatively cold water, where metabolic costs are low, a tactic of slow growth, feeding on large prey, and passive hunting may be common. This does appear to be the strategy of Pacific hake larvae. This tactic is quite different from that of high metabolism, fast growth, and active hunting demonstrated by other larvae, such as Pacific mackerel and to a lesser extent northern anchovy. Larvae of Pacific hake are located in colder water than larvae of Pacific mackerel and northern anchovy (Ahlstrom 1959) and compared with these other species the growth of Pacific hake larvae is slow (Fig. 9). Metabolic rates are difficult to compare because of different experimental techniques, but as a lower limit (due to the restrictive container size), 3-5 d old Pacific mackerel larvae require about 0.411 μl-O_2/animal per h at 19°C (Hunter and Kimbrell 1980). This compares with 0.265 μl-O_2/animal per h for first-feeding Pacific hake larvae at 12°C from this study.

I have calculated the energetic requirements of a first-feeding Pacific hake larva based on the routine metabolic rate at 12°C (the ambient temperature off the California coast) and growth in weight for larvae caught in the field, after correcting for preservation effects (Table 5). These values were converted to calories assuming values of 1 μl-O_2 = 0.005 cal and 1 mg-dry weight of

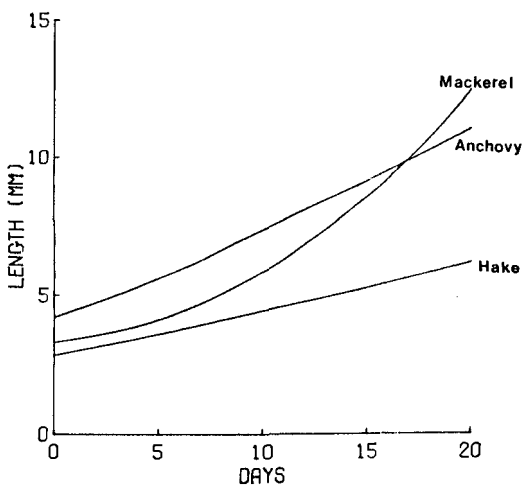

FIGURE 9.—Comparative growth of field-caught Pacific hake larvae (at 11°-14°C; this study), field-caught anchovy larvae (13°-16°C; Methot and Kramer 1979), and laboratory-reared Pacific mackerel larvae (19°-20°C; Hunter and Kimbrell 1980).

TABLE 5.—Caloric requirement of first-feeding Pacific hake larvae from growth and metabolism.

Respiration rate at 12°C = 0.30 μl/animal per h.

		Length (mm)	Weight (mg)	Corrected weight (mg)[1]
Growth:	day 4	3.412	0.0440	0.0694
	day 5	3.577	0.0512	0.0808

Weight gain = 0.011 mg/d = 0.0550 calories[2]
Respiration = 7.20 μl/d = 0.0360 calories[3]
0.0910 calories

Daily ration = Metabolism + Growth + Nonassimilated + Egestion
Daily ration × 0.7 = Metabolism + Growth
Daily ration = 0.130 calories

[1]Corrected for preservation effects.
[2]5.003 cal/mg-dry wt tissue (Laurence 1977).
[3]0.005 cal/μl-O_2 (Laurence 1977).

larval fish tissue = 5.003 cal (Laurence 1977). The average first-feeding hake larva thus requires 0.091 cal/d to maintain and grow. This value is likely to be an underestimate of the caloric requirement due to an undetermined amount of energy needed to attack, capture, and digest prey animals. Estimates of assimilation coefficients range from 0.8 (Healy 1972; Dagg 1976) to 0.5 (Vlymen 1977). Assuming an assimilation coefficient of 0.7, as suggested by Ware (1975) and Laurence (1977), Pacific hake larvae would need to ingest 0.130 cal/d to satisfy metabolic and growth costs. Although this seems to be a reasonable estimate, significant errors may arise from the factors used for length-weight conversion, preservation effects, and from the assumed assimilation coefficient. I would suggest a more thorough examination of these factors in future experiments.

Using Sumida and Moser's (1980) report on the stomach contents of 3-4 mm Pacific hake larvae (Table 6), I calculated an estimate of daily ration that can be compared with the above estimate. Several approximations are necessary in this calculation, including 1) a feeding period of 12 h, 2) a digestion time, which I assume to be 5 h—ranges for other species are 3-8 h for herring (Werner and Blaxter 1980) and 2-4 h for Pacific mackerel (Hunter and Kimbrell 1980), and 3) a value of 5.2519 cal/mg-dry wt for copepods (Laurence 1976). The daily ration can then be calculated as: Daily ration = Stomach content weight × Feeding period/Digestion time (Feigenbaum 1979; Laurence 1977). For small Pacific hake larvae the daily ration thus calculated is 0.129 cal, which compares very closely with the previous estimate.

Hunter and Kimbrell (1980) calculated that 3-5 d old Pacific mackerel larvae require 0.143 cal/d to maintain and grow, based on the weight

TABLE 6.—Average daily ration of 3-4 mm Pacific hake larvae (data from Sumida and Moser 1980, table 1). Number prey/stomach includes those with empty guts.

Prey organism	Total length (mm)[1]	Prosome length (mm)[2]	Dry weight (mg)[3]	No. prey/ stomach	Dry weight/ stomach (mg)
Adults					
Clausocalanus	1.15	0.70	0.006	0.38	0.00228
Paracalanus	1.0	0.57	0.004	0.29	0.00116
Calocalanus	1.0	0.57	0.004	0.08	0.00032
Oithona	0.95	0.52	0.003	0.03	0.00009
Calanoid unid.	1.04	0.60	0.004	0.09	0.00036
Disintegrated	1.04	0.60	0.004	0.08	0.00032
Copepodites					
Calanus sp.	1.50	1.00	0.050	0.02	0.00100
Oithona			0.002	0.03	0.00006
Calanoid			0.002	1.09	0.00218
Cyclopoid			0.002	0.03	0.00006
Disintegrated			0.002	0.21	0.00042
Nauplii			0.001	2.00	0.00200
Eggs			0.0005	1.06	0.00056
					0.01025

Calories per stomach = 0.01025 mg × 5.2519 cal/mg-dry wt[4] = 0.05383 cal.

$$\text{Daily ration} = \frac{\text{Calories in stomach} \times \text{Feeding period}}{\text{Digestion time}} \quad \text{(Feigenbaum 1979; Laurence 1977)}$$

$$= \frac{0.0538 \times 12}{5} = 0.129 \text{ cal/d.}$$

[1]From Brodskii 1967; Fulton 1968.
[2]From Total length = 1.16 × prosome length + 0.34; Fulton 1968.
[3]From Vidal 1978; Feigenbaum 1979.
[4]5.2519 cal/mg-dry weight conversion for copepods (Laurence 1976).

gain of laboratory-reared larvae and metabolic rates at 19°C. As they note this must be a lower limit. Assuming the same assimilation coefficient that I used for hake, 0.7, mackerel would need to ingest 0.204 cal/d to satisfy this ration requirement. First-feeding hake larvae have very large mouths compared with either mackerel or anchovy (Fig. 10), so they may feed on a wide size range of planktonic animals (including adult copepods); hake larvae could satisfy daily rations by capturing 25 nauplii or 15 small copepodites or 6 small calanoid adults or 1 *Calanus* adult. In contrast, both first-feeding mackerel and anchovy require a smaller size range of food particles (Hunter 1980). At least for anchovy, their survival depends on finding patches of small food organisms, such as the dinoflagellate, *Gymnodinium* (Lasker 1975). To satisfy its ration requirement a first-feeding Pacific mackerel larva would have to capture 4,000 *Gymnodinium* cells, 240 rotifers, or 39 copepod nauplii. It seems evident that they require high density patches of prey for successful feeding, whereas hake larvae may not require such dense patches of food for successful first-feeding.

From the results of this study, I infer that the first feeding of Pacific hake larvae is not as important to their survival as it is for Pacific mackerel and also for northern anchovy. This concept is supported by 1) the lower daily ration of hake larvae due to temperature-dependent activity and growth, 2) larger food items in the diet of hake larvae which provide more calories per prey item, 3) the relatively longer starvation time for hake larvae, i.e., they take 6-12 d to starve after complete yolk utilization, whereas anchovy take only about 4 d (Lasker et al. 1970), and 4) the ability of hake larvae to feed while still having yolk reserves (Sumida and Moser 1980). In addition, there is evidence of high energy wax esters in eggs of *Merluccius* (Mori and Saito 1966); thus larvae may have a longer safety period to find food. This concept does not exclude the possibility of a critical starvation period occurring later in larval or postlarval life, when stored energy reserves are exhausted and energetic demands are greater.

Predation may be relatively important as a factor influencing survival of Pacific hake larvae. Egg and yolk-sac stages of marine fish appear to be the stages most vulnerable to predation (Theilacker and Lasker 1974; Hunter 1980). Because of the colder temperatures that Pacific hake eggs and larvae inhabit, and resulting growth and development rates that are slow compared with Pacific mackerel (Hunter and

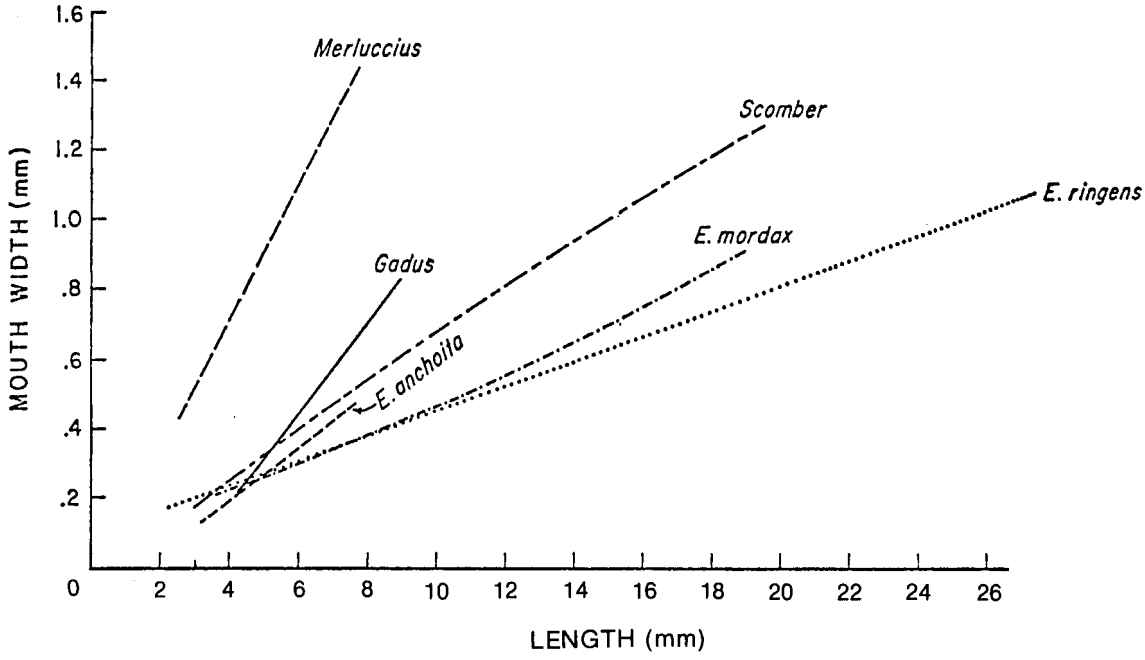

FIGURE 10.—Mouth sizes of larvae of hake, mackerel, anchovy, and cod by length class (Hunter 1980).

Kimbrell 1980) and northern anchovy (Zweifel and Lasker 1976), Pacific hake spend a longer time in vulnerable stages. Consequently, predation pressure on hake eggs and larvae may be high.

ACKNOWLEDGMENTS

I thank W. Wooster, D. Gunderson, M. Tillman, and two reviewers for editing and commenting on the manuscript. I further thank R. Methot for instruction in reading otoliths and J. Yen, J. Hunter, and R. Francis for helpful discussions. G. Moser, E. Ahlstrom, and A. Alvariño provided the vertical series samples, and J. Yen, G. Stauffer, and P. Smith provided opportunities for field sampling. Financial support was given by the Northwest and Alaska Fisheries Center.

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