# EARLY LIFE HISTORY OF PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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## ABSTRACT

The early life history of Pacific mackerel, *Scomber japonicus*, is described from laboratory-rearing studies and examination of stomach contents of sea-caught larvae. At 19° C mackerel eggs hatched in 56 hours, larvae were 3.1 mm standard length with a dry weight of 0.04 mg of which 50% was yolk. First feeding occurred 46 hours after hatching; all larvae fed by 60 hours (age 2.5 days). Larvae were then 3.6 mm long with fully pigmented eyes and 10% of the yolk remaining. Starvation was irreversible if larvae were not fed before age 4.5 days. Metamorphosis (15 mm standard length) occurred in 24 days at 16.8° C to 16 days at 22.1° C. Larvae 3-5 days old consumed 87% of their body weight per day and had a mean gross growth efficiency in dry weight of 33%. Oxygen consumption was 6.1 $\mu$l $O_2$ per milligram dry weight per hour at 18° C and 11.4 $\mu$l $O_2$ per milligram dry weight per hour at 22° C. Swimming speeds ranged from 1.3 standard lengths per second for first-feeding larvae to 3.8 standard lengths per second for fish at metamorphosis. Fifty percent of the larvae were able to capture a prey when the width of the prey was 85% of the width of the mouth and 95% were able to do so when the prey was 57% of the width of the mouth. Cannibalism was common in rearing groups; at 8 mm standard length, 50% of the larvae became capable of feeding on other fish larvae and cannibalism ceased when schooling commenced. Chief food items of sea-caught larvae were stages of copepods; maximum food width increased rapidly with larval length and was equivalent to the maximum mouth width. Mean prey width was 38% of mouth width. The larger organisms, constituting half of the prey eaten, accounted for 85-90% of the total volume of food eaten.

The development and distribution of eggs and larvae of the western Pacific population of the Pacific mackerel, *Scomber japonicus*, has been described (Kramer 1960; Kramer and Smith 1970), but little information exists on growth, behavior, and physiology of the larval stages. Incubation times and other data are known for the Japanese population of *S. japonicus* (Watanabe 1970). This paper provides some of the information needed to characterize the early life history of Pacific mackerel, including incubation times, yolk absorption, onset of feeding, vulnerability to starvation, swimming and feeding behavior, food ration, and oxygen consumption.

## METHODS

### Laboratory Experiments and Sea Samples

Eggs were obtained from Pacific mackerel maintained in spawning condition in the laboratory and induced to spawn by hormone injection (Leong 1977). Effects of temperature on incubation time were determined by placing test tubes containing 10 eggs and 25 ml of seawater in a temperature block set to produce a temperature gradient of 11.1°-23.3°±0.2° C (2 SE (standard error)) (Lasker 1964). Hatched eggs were counted at 2-4 h intervals and time from fertilization to 50% hatch estimated. Rate of yolk absorption was determined at 19.4°±0.4° C by measuring the surface areas of the yolk-sac and oil droplet from tracings made with an optical comparator (Wolfson 1965). Six samples, each of 15-25, larvae were taken over the first 72 h after hatching.

To estimate the time of first feeding at 18.9°±0.3° C, groups of larvae without past feeding experience were transferred to a 100 l container containing 150 rotifers/ml (*Brachionus plicatilus*). Four hours later, they were removed and the percentage of larvae that fed and the mean number of rotifers in the gut were calculated. Eight groups of 10-39 larvae were tested at periods from 18 to 114 h after hatching.

A starvation-based mortality curve was estabilished at 19.0°±0.3° C by starting with 1,000 eggs in each of two 200 l containers, and counting and removing dead larvae daily. The age was determined at which starvation became irreversible in first-feeding larvae. Seven hundred and fifty eggs were incubated in each of four 200 l tanks and the resulting larvae were fed for the first time at

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ages 2.5, 3.5, 4.5, and 5.5 d. The percentage survival was determined on the eighth day. Larvae were fed rotifers (50/ml) on the first day of feeding, and rotifers and copepods (*Tisbe* sp.) thereafter.

Vulnerability of newly metamorphosed Pacific mackerel (mean length 16.7 mm SL (standard length)) to starvation was tested at 18.9°±0.2° C by transferring fish from the rearing container to containers without food. One group of fish was starved for 4 d, another for 5 d, and a third was fed *Artemia salina* nauplii. The two starved groups were fed at the end of the starvation period.

Tail beat frequency and amplitude of larval Pacific mackerel (3-5 mm SL) were determined for routine swimming and burst speeds by analysis of cine films taken at 100 frames/s using techniques described by Hunter (1972). Routine swimming speeds of larval mackerel, at 19° C, were measured by counting the number of squares crossed by a larva (3.7-6.6 mm SL) as it swam over a 1 cm grid on the bottom of the rearing tank for 9-153 s; a 3 cm grid was used for larger larvae (7.9-13.1 mm SL) with shorter observation times (3-46 s). The mean of 15-25 visual observations was used as an estimate of speed for the mean length of the larvae in the tank on the day of observation; speeds were adjusted for parallax caused by the difference in depth between the grid and the fish. Speeds of juveniles (>19 mm SL) were measured by timing the fish as they swam a measured distance (35-201 cm) around the perimeter of the rearing tank; in this case mean speeds were for individual fish and observation times ranged from 3 to 26 s.

The size at which Pacific mackerel larvae were capable of ingesting various prey was evaluated by placing them in a 110 l container with the prey and estimating the number that fed by examination of stomach contents. The type of prey, mean prey size, prey density, and duration of feeding respectively were: yolk-sac anchovy larvae, 2.7 mm SL, 8/l, 2 h; *A. salina* nauplii, 0.2 mm wide, 11/l, 4 h; and anchovy eggs, 0.67 mm wide, 10/l, 2 h. The mouth width, prey width, and standard length of the larvae were measured and percentage feeding success was estimated for size classes of larval length and mouth width. The number of fish per size class was >9. Size thresholds for 50% feeding success and 95% success were estimated by probit analysis (Finney 1952) and expressed as a function of mean larval length, or mean prey width/mean mouth width.

The sizes of food items eaten by Pacific mackerel larvae in the sea was determined by examination of the stomachs of 86 larvae taken in routine ichthyoplankton surveys along the California coast. We recorded the length of each larva and the number and maximum width of all identifiable food items (Arthur 1976; Shirota 1970).

Food requirements were estimated by feeding the rotifer *Brachionus plicatilis* to 3-5 d old Pacific mackerel larvae. Seven to eight samples of 9-16 larvae each were taken over each of three 12-h feeding days, the number of rotifers in the guts of each larva were counted, and the counts converted to equivalent dry weight using the conversion factor of 0.16 μg/rotifer (Theilacker and McMaster 1971). Daily changes in larval weight were estimated from mean standard lengths using a length-dry weight conversion given in the results. The rate of gastric evacuation for 4 mm SL larvae was measured. They were allowed to feed for 4 h and then transferred to a tank without food; samples of 13-16 larvae were taken at about hourly intervals until the stomachs were empty. The number of rotifers in stomachs were counted and converted to dry weight, and the rate of gastric evacuation was estimated in terms of dry weight. The daily ration was estimated from the mean stomach contents and the rate of gastric evacuation. Gross growth efficiency was estimated in terms of dry weight from the daily ration and weight gain over 24 h.

Metabolic requirements of Pacific mackerel larvae were estimated using a Warburg respirometer and standard manometric techniques (Umbreit et al. 1964) to measure oxygen consumption. One or more Pacific mackerel larvae were added to an 18 ml Warburg flask filled with 4.4-8.7 ml of filtered seawater (salinity 33.58-33.93‰). Larvae >0.06 mg dry weight were tested individually. Twenty-one tests were made at 18.0°C of larvae or groups of larvae ranging in length from 3.7 to 17.9 mm SL (0.038-12.74 mg) and 14 at 22.0° C, of larvae 3.2-10.5 mm SL (0.025-2.86 mg). Flasks were shaken at 102 times/min for 5 out of every 30 min; readings were taken after the first 2 h and continued for 150-360 min. At the end of a test, larvae in each flask were measured, rinsed in distilled water, oven dried to a constant weight, and weighed. Mean weight was obtained for fish tested in groups. All runs were made under normal room illumination, about 700 lx. $\text{Log}_{10}$ oxygen consumption in microliters $O_2$ per hour was regressed on $\log_{10}$ body weight for the 18.0° and 22.0° C experiments. As the slopes were close to unity, oxygen consumption was expressed in microli-

ters per milligram per hour. Metabolic requirements were compared with daily ration by converting oxygen consumption and daily ration to calories (1 $\mu$l $O_2$ = 0.005 cal: one *Brachionus plicatilis* = 0.00085 cal, Theilacker and McMaster 1971).

## Culture of Larvae

Seven groups of Pacific mackerel were reared to metamorphosis to determine growth rates and effects of temperature on growth. The rearing containers were black fiber glass, cylindrical tanks (122 cm in diameter × 36 cm deep). Culture volume increased during the rearing period from 200 to 400 l because of the addition of seawater containing food and algae. Tank temperature was controlled by a regulated water bath, and groups were reared at temperatures ranging from 16.8° to 22.1° C. Illumination at the water surface during the 12-h day was about 2,000 lx. Tanks were started with 3,000 eggs/group. Initially, larvae were fed laboratory-cultured *Brachionus plicatilis*. At age 5 d, laboratory-cultured copepodids and adult copepods (*Tisbe* sp.) were added; 200,000 copepods were added daily until metamorphosis. Initially 30 or more rotifers/ml were added for the first few days of feeding; thereafter the density of rotifers was allowed to decline. On a diet of rotifers alone, growth slowed after larvae reached 5 mm SL and few larvae survived longer than 15 d. Newly metamorphosed juveniles were fed live and frozen adult *A. salina* and minced squid (*Loligo opalescens*) and northern anchovy. From 1 to 6 l of algal culture, *Tetraselmis* sp. (300,000-500,000 cells/ml), were added daily to provide food for rotifers and copepods. Samples of 10 or more larvae were taken on alternate days for length measurements. Some samples were washed in distilled water, dried, and subsequently weighed to obtain a relation between length and dry weight.

# RESULTS

## Hatching, Onset of Feeding and Starvation

Eggs of Pacific mackerel are transparent spheres, ranging in diameter from 1.06 to 1.14 mm (Kramer 1960). Incubation times ranged from 33 h at 23° C to 117 h at 14° C (Figure 1); eggs did not hatch below 14° C. The curve for hatching time as a function of temperature for the western Pacific population (data from Watanabe 1970) appears to be the same as the one for the eastern Pacific population.

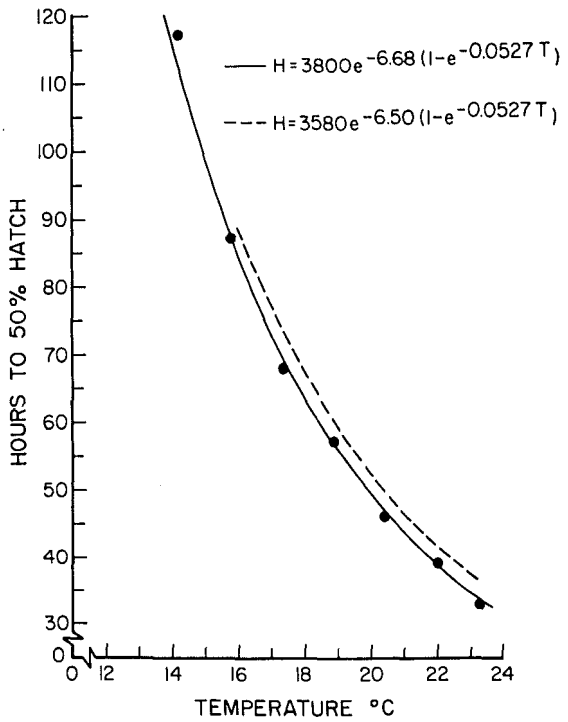


FIGURE 1.—Incubation time (fertilization to 50% hatch) of *Scomber japonicus* eggs. Solid line is for present data, points are estimated time to 50% hatch of eggs in five test tubes per temperature, dashed line is for data of Watanabe (1970). The general equation was developed by Zweifel and Lasker (1976) and fit to the 50% values.

At hatching, larvae averaged 3.1 mm SL (Figure 2B) and weighed 0.040 mg dry weight, of which 50% was yolk. At 19° C, first feeding occurred 46 h after hatching; by 60 h after hatching, all larvae had ingested one or more rotifers in 4 h (Figure 2D). Thus the 50% threshold for onset of feeding at 19° C occurred at about 50 h (2 d) after hatching. At this time larvae were 3.6 mm SL, the eyes were fully pigmented and 10% of the yolk remained, principally the remnants of the oil droplet (Figure 2A, B). Over the threshold for the onset of feeding, the mean number of rotifers in Pacific mackerel stomachs increased from 2 at 46 h to 14 at 68 h (Figure 2E). The larvae in each group had no previous feeding exposure, hence the increase in feeding activity with time could not be attributed to experience.

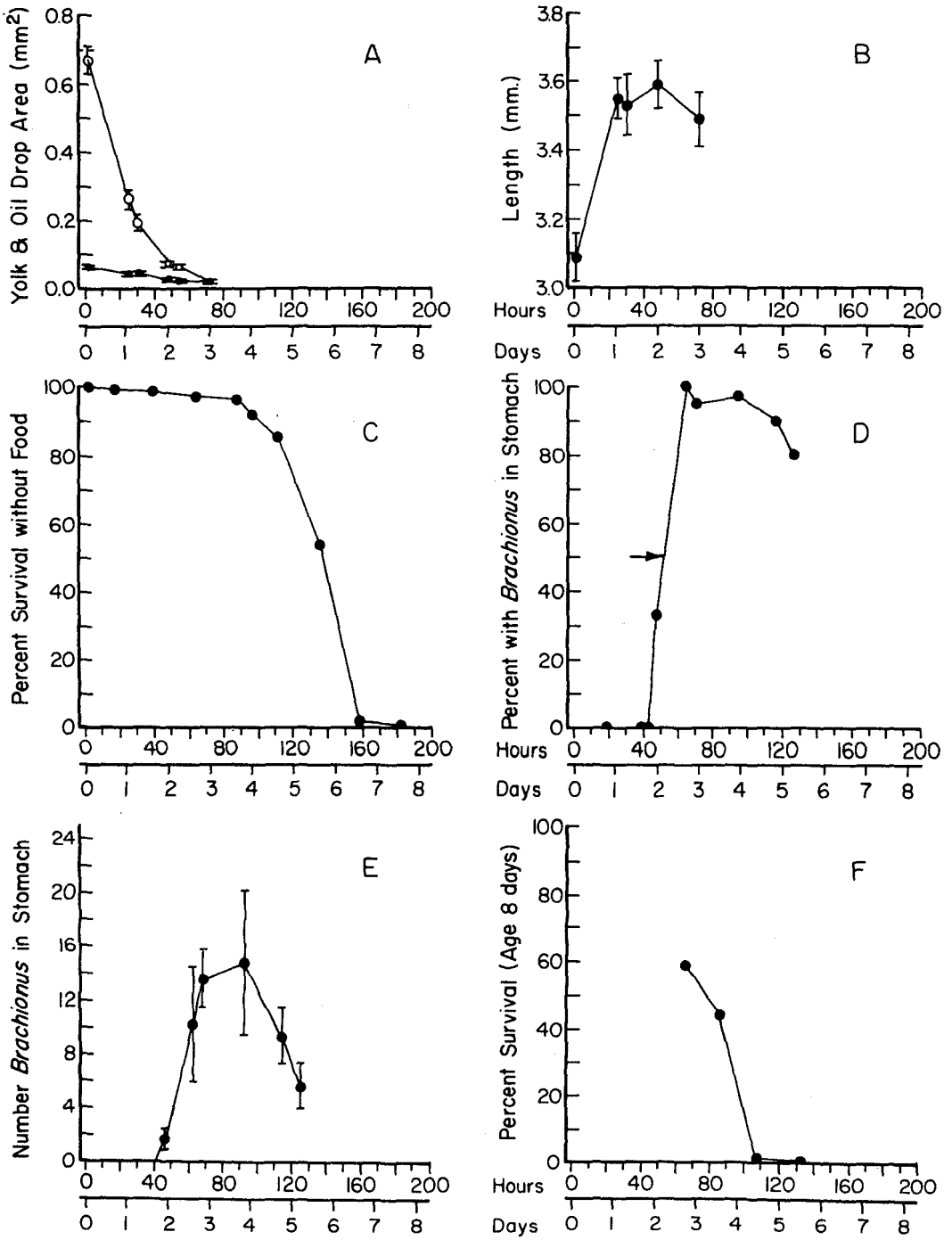


FIGURE 2.—Yolk absorption, onset of feeding, starvation, and point of irreversible starvation in Pacific mackerel larvae at 19° C: A. Rate of yolk absorption—open circles mean area of yolk-sac, solid circles mean area of oil droplet (mm²). B. Mean length of larvae from hatching through yolk-absorption. C. Percent survival of larvae without food. D. Percent of larvae tested at various times after hatching that had ingested one or more *Brachionus plicatilis* in a 4-h test period—arrow indicates the 50% threshold for the onset of first feeding. E. Mean number of *B. plicatilis* per positive stomach of larvae tested at various times after hatching. F. Percentage survival at age 8 d for larvae fed for the first time at age 2.5, 3.5, 4.5, and 5.5 d—percentages are plotted at the time food was first added. Bars in A, B, and E represent ±2 SE of mean.

If larvae were not fed, most died between ages 4 and 7 d and none survived longer than 7 d (Figure 2C). Highest survival (on the eighth day after hatching) occurred when food was added for the first time at age 2.5 d; survival was somewhat lower if food was added at 3.5 d and negligible if added at 4.5 d (Figure 2F). Thus at 19° C starvation appeared irreversible if food was not provided before 4.5 d.

Pacific mackerel larvae, unlike herring or anchovy (Blaxter and Hempel 1963; Lasker et al. 1970), did not cease swimming or feeding at the time of irreversible starvation. At age 5 d, the incidence of larvae with rotifers in their stomachs was relatively high (80%) (Figure 2D), but the average number of rotifers per positive stomach was much less than in larvae fed first at age 2 or 3 d (Figure 2E). Thus at age 5 d, most larvae were still able to feed, but owing to their weakened condition, none were able to capture enough prey to survive.

Vulnerability of larvae to starvation persisted through metamorphosis. All juvenile Pacific mackerel appeared emaciated and swam slowly by the fourth day of starvation. Mortality of 10% occurred in the group starved 4 d; 50% mortality occurred in those fish starved 5 d. All juveniles surviving 4 and 5 d of starvation recovered when food was added; no mortality occurred in the controls. Thus, newly metamorphosed Pacific mackerel were able to withstand 1 or 2 d more of starvation than first-feeding larvae, but they were better able to recover from food deprivation.

## Growth

Growth in length of Pacific mackerel larvae was slow and almost linear over the first 10-15 d until larvae reached about 6-7 mm SL; there followed a rapid acceleration through metamorphosis. We did not fit equations to these data because none of the standard growth equations gave a good fit to the entire growth curve. The effect of temperature on growth was not distinguishable over the initial growth period, but became obvious during the period of rapid growth (Figure 3, Table 1). To provide an index of the effect of temperature on growth, we expressed the duration of the larvae period (hatching to metamorphosis, 15 mm) as a function of temperature (inset in Figure 3). The $Q_{10}$ was 3.0 when calculated from the equation in Figure 3 for the temperature range of our observations (16.8°-22.1° C).

The length-weight relation for Pacific mackerel larvae and juveniles is shown in Figure 4. The form of this equation was developed by James Zweifel and used by Hunter (1976) to express the length-weight relation for northern anchovy larvae. The curvilinear nature of the length-weight relation, still evident in the log-log plot (Figure 4), indicates that if a linear regression of $\log_{10}$ weight

TABLE 1.—Growth data (millimeters SL) for seven groups of *Scomber japonicus* larvae reared at different mean temperatures from hatching through metamorphosis.

| Age | 22.1° C[1] | | | 20.4° C | | | 19.6° C | | | 19.5° C | | | 19.2° C | | | 18.9° C | | | 16.8° C | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (days) | *n* | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD | *n* | $\bar{x}$ | SD |
| 1 | | | | | | | | | | 10 | 3.1 | 0.24 | | | | | | | 31 | 3.5 | 0.12 |
| 2 | 14 | 3.3 | 0.21 | 16 | 3.8 | 0.06 | 16 | 3.7 | 0.10 | 15 | 3.9 | 0.09 | 15 | 3.8 | 0.06 | | | | | | |
| 3 | 14 | 3.5 | 0.30 | | | | | | | | | | | | | | | | | | |
| 4 | 10 | 3.6 | 0.22 | 18 | 3.8 | 0.26 | 33 | 4.2 | 0.23 | 10 | 4.0 | 0.17 | 15 | 4.0 | 0.20 | 10 | 3.7 | 0.20 | | | |
| 5 | | | | | | | | | | | | | | | | | | | | | |
| 6 | 10 | 3.9 | 0.21 | 15 | 4.2 | 0.41 | 15 | 4.8 | 0.44 | 13 | 4.2 | 0.14 | 15 | 4.4 | 0.37 | 10 | 4.1 | 0.39 | 15 | 4.3 | 0.42 |
| 7 | | | | | | | | | | 27 | 4.5 | 0.40 | | | | | | | | | |
| 8 | 12 | 4.5 | 0.55 | 15 | 5.7 | 0.77 | 15 | 6.0 | 0.39 | 25 | 4.7 | 0.56 | 15 | 5.0 | 0.40 | | | | 15 | 5.1 | 0.43 |
| 9 | | | | | | | | | | | | | 5 | 5.9 | 0.13 | | | | | | |
| 10 | 12 | 6.0 | 1.13 | 15 | 6.3 | 0.91 | 15 | 6.6 | 0.70 | 15 | 4.8 | 0.43 | 19 | 5.6 | 0.77 | 11 | 5.2 | 0.45 | | | |
| 11 | | | | | | | | | | | | | | | | | | | 15 | 6.5 | 0.70 |
| 12 | 22 | 8.4 | 1.88 | 16 | 8.2 | 1.31 | 15 | 6.5 | 0.75 | 11 | 5.9 | 1.08 | 25 | 6.4 | 0.68 | 12 | 6.1 | 0.60 | 15 | 7.0 | 0.50 |
| 13 | | | | | | | | | | | | | | | | | | | | | |
| 14 | 10 | 8.9 | 1.46 | 10 | 11.5 | 1.54 | 15 | 8.4 | 1.12 | 30 | 6.4 | 1.09 | 15 | 6.6 | 0.80 | | | | 17 | 7.7 | 1.40 |
| 15 | | | | | | | | | | | | | | | | | | | 11 | 8.1 | 1.08 |
| 16 | 10 | 14.9 | 1.45 | 15 | 14.1 | 2.01 | 15 | 8.9 | 1.76 | 16 | 8.5 | 2.21 | 15 | 7.1 | 0.81 | 13 | 7.6 | 1.50 | | | |
| 17 | | | | | | | | | | 10 | 10.0 | 2.71 | | | | 12 | 9.0 | 1.33 | 15 | 10.3 | 2.11 |
| 18 | | | | 15 | 17.8 | 1.70 | 15 | 10.3 | 2.48 | | | | 15 | 10.3 | 3.21 | 13 | 9.4 | 1.61 | 17 | 10.8 | 2.84 |
| 19 | 15 | 24.1 | 5.81 | | | | | | | | | | | | | | | | | | |
| 20 | | | | | | | 15 | 12.5 | 3.18 | 17 | 17.7 | 4.21 | 15 | 11.7 | 2.88 | | | | 9 | 11.5 | 2.81 |
| 22 | | | | | | | 15 | 17.5 | 4.51 | | | | 15 | 14.6 | 4.62 | | | | | | |
| 23 | | | | | | | | | | | | | | | | 15 | 13.7 | 1.26 | | | |
| 24 | | | | | | | 24 | 20.4 | 5.10 | | | | 16 | 18.5 | 5.38 | 10 | 19.8 | 2.36 | | | |
| 25 | | | | | | | | | | | | | | | | | | | 17 | 17.1 | 5.07 |

[1]Juvenile growth (age, *n*, $\bar{x}$, and (SD)): 26 d, 13, 34.4 mm (4.37); 29 d, 9, 43.9 mm (3.60); 39 d, 5, 55.0 mm (8.74); and 47 d, 9, 67.3 mm (10.30).

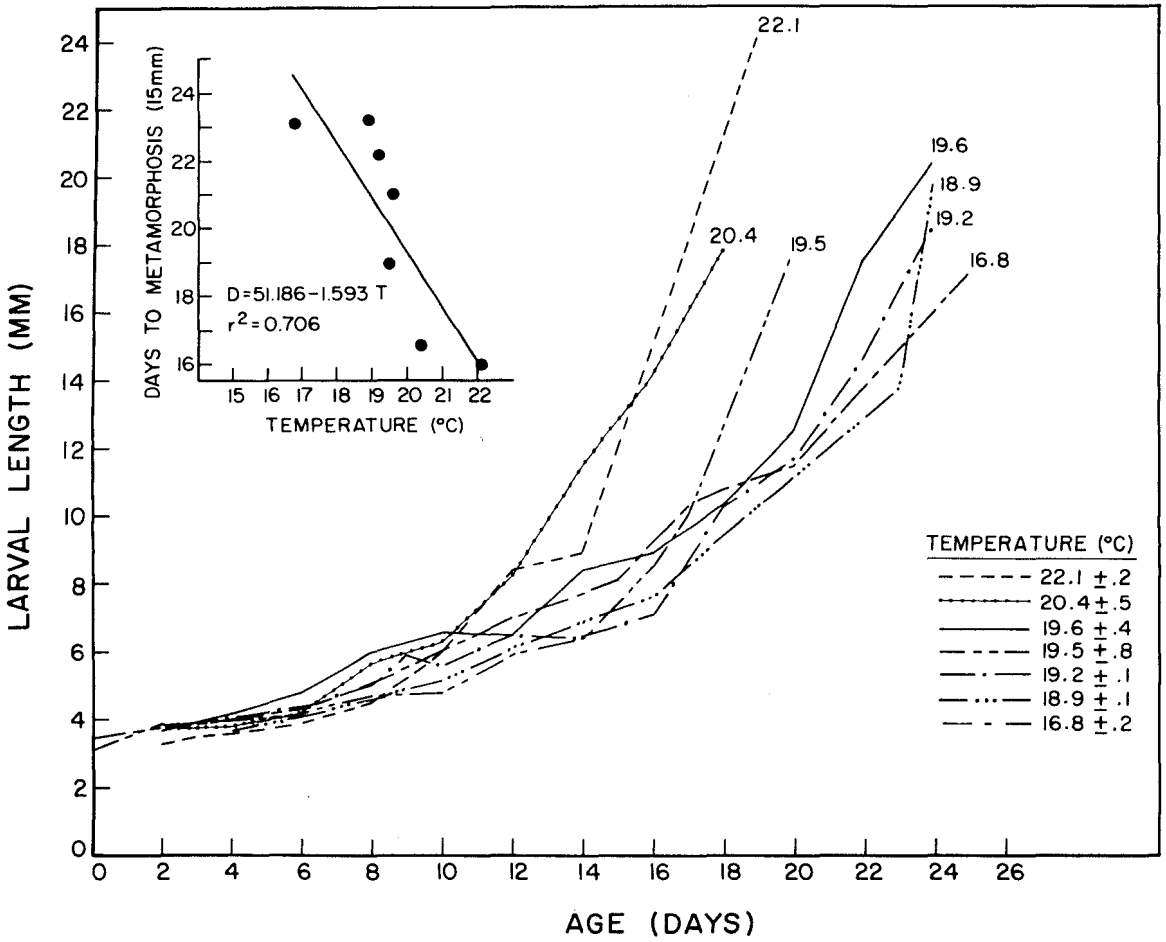


FIGURE 3.—Growth of seven groups of Pacific mackerel larvae reared in the laboratory from hatching (age 0 d) through metamorphosis (15 mm SL). Lines connect means given in Table 1; rearing temperatures (±2 SE) given on right side of figure and at end of lines. Inset at top: elapsed time (days) from hatching to metamorphosis (15 mm), as a function of rearing temperature.

on $\log_{10}$ length were used, it would produce inaccurate estimates.

## Swimming Behavior

At typical cruising speeds, larval Pacific mackerel (3-5 mm SL) have a high tail beat frequency of about 30 beats/s and a low tail beat amplitude of 0.16 standard length. At slow speeds, tail beat frequency remained relatively constant but the amplitude of the tail beat changed. At higher speeds, both amplitude and frequency changed but the relative increase in amplitude was much greater than that of frequency (Table 2). Thus larval Pacific mackerel, unlike the adults (Hunter and Zweifel 1971), predominantly modulate tail beat amplitude to effect changes in speed.

Cruising speeds of Pacific mackerel increased markedly over the larval period from 0.46 cm/s (1.3 standard body lengths/s) for first-feeding larvae (3.6 mm SL) to 5.6 cm/s (3.8 standard body lengths/s) for fish at metamorphosis (Figure 5). This differs from the pattern in adult fishes where speed relative to size decreases with an increase in fish size (Webb 1975).

## Feeding Behavior

Upon sighting a prey (rotifer or copepod), a Pacific mackerel larva advanced toward the prey,

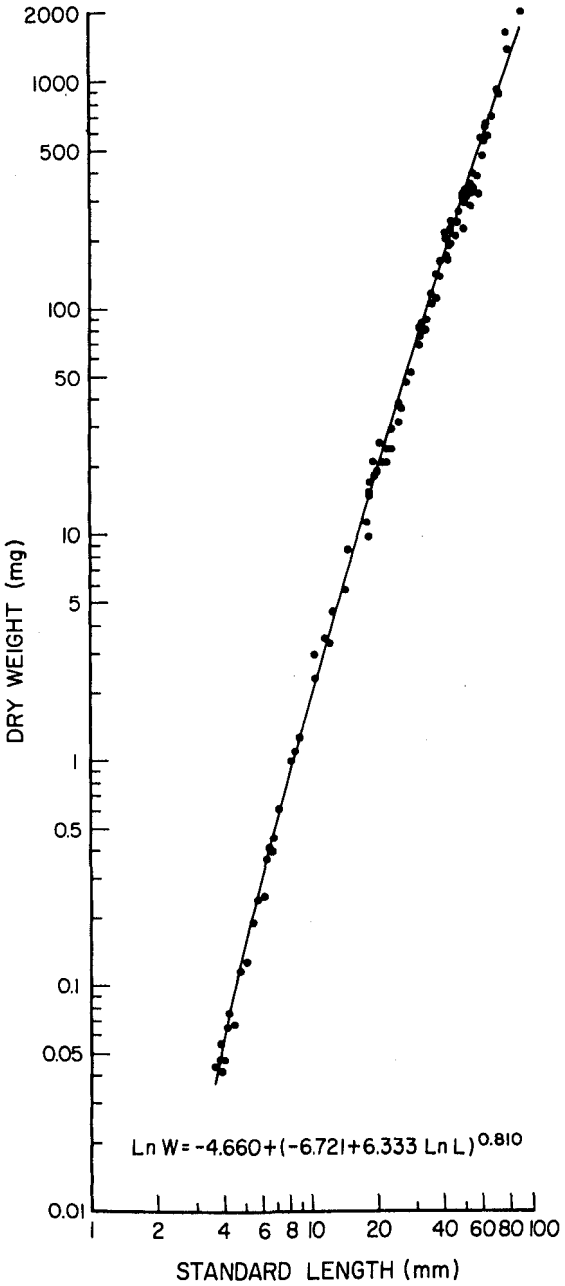


FIGURE 4.—Relation between dry weight (W) of larval and juvenile Pacific mackerel in milligrams and standard length (L) in millimeters. Points are observed values for individuals >18 mm and for larvae <18 mm; points are means for groups of 15 larvae.

stopped, drew back the tail, and held it in a slightly recurved, high amplitude position while the rest of the body remained relatively straight.

TABLE 2.—Tail beat frequency and amplitude and speed of 3-5 mm larval Pacific mackerel ($\bar{x}$ = 4.23±0.09 mm SL) expressed as a function of standard length.

| N | Swimming speed (SL/s) Class interval | Mean | Tail beat Frequency (beats/s) | Tail beat Amplitude/SL |
|---|---|---|---|---|
| 18 | 0.01- 1.0 | 0.58 | 33.2 | 0.12 |
| 30 | 1.01- 2.0 | 1.48 | 30.2 | 0.16 |
| 9 | 2.01- 3.0 | 2.48 | 30.2 | 0.17 |
| 3 | 3.1 - 5.0 | 4.00 | 37.5 | 0.18 |
| 3 | 10.1 -15.0 | 12.18 | 39.4 | 0.29 |
| 1 | — | 37.04 | 38.9 | 0.33 |

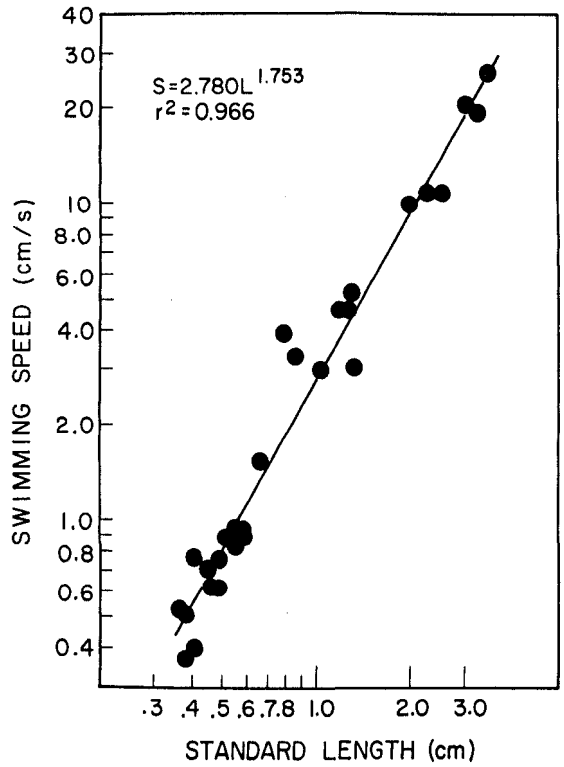


FIGURE 5.—Relation between swimming speed and standard length of Pacific mackerel larvae ($log_{10}$ scales) at 19° C. Each point <2.0 cm is the mean of 15-25 observations. For ≥2.0 cm, individual fish were measured.

Feeding involved driving the tail posteriorly and opening the mouth. Larvae often attacked the same prey two or more times if the previous strike was unsuccessful, and repositioned for subsequent strikes by moving backward. Handling times were negligible because the prey was engulfed instantaneously. Older Pacific mackerel larvae developed a set of motor patterns for feeding on fish larvae; larvae were seized from the side and carried crosswise in the mouth. Larger prey were repeatedly released and grasped until they ceased

struggling, then released and ingested, usually head first. Handling times increased with prey size.

The length at which 50% of Pacific mackerel larvae were capable of capturing and ingesting anchovy yolk-sac larvae ($LD_{50}$, Finney 1952) was 8.1 mm SL (95% confidence interval, 7.2-9.5 mm) (Figure 6). Sibling cannibalism began when the mean length of the group was about 8 mm SL. At this size, the mean length of six cannibals was 10.8 mm SL (range 9.9-12.0 mm) and that of their prey was 6.2 mm SL (range 5.9-6.5 mm). Cannibalism in rearing containers ended as Pacific mackerel approached metamorphosis (15 mm SL) and schooling began. Rearing at higher temperatures increased the growth rate and thereby decreased the period over which sibling cannibalism occurred. Consequently, survival at metamorphosis was higher in groups reared at 20°-22° C (5-6%) than it was at 19° C or lower temperatures (1-2%).

Near metamorphosis, Pacific mackerel were able to eat relatively large fish larvae. Three Pacific mackerel, 15.4-16.0 mm SL, placed in a rearing tank with northern anchovy larvae (12.0-20.6 mm SL) captured and began to ingest larvae of 11.7-13.5 mm SL, within 6 min. Thus, as Pacific mackerel larvae grew from 8 mm SL to metamorphosis, the size of anchovy larvae, they were able to eat increased from about 3 to 13 mm SL. This increase in prey size was not closely related to mouth size of the Pacific mackerel because the mouth can be greatly expanded when ingesting a larval fish. Mouth size probably was inversely related to handling time as in the case for adult fishes (Kislalioglu and Gibson 1976).

When prey are engulfed rather than seized, mouth size may give a good indication of the size of prey a larvae is capable of ingesting. The relation between mouth width and length in Pacific mackerel larvae was slightly curvilinear, and mouth width increased from 0.216 mm for first-feeding larvae (3.6 mm SL) to 0.987 mm at metamorphosis (15 mm SL) (Figure 7).

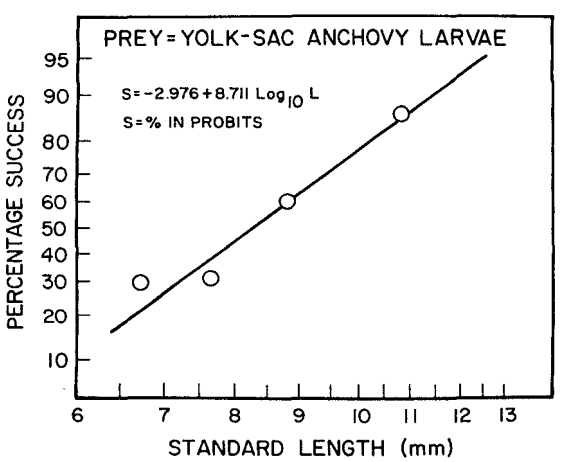


FIGURE 6.—Percentage of Pacific mackerel larvae (probit scale) that captured one or more yolk-sac anchovy larvae in relation to standard length of the mackerel ($log_{10}$ scale). The length class was variable. Larvae were ranked by length and classes set at 10 observation intervals. The $LD_{50}$ was 8.1 mm (95% confidence interval 7.2-9.5 mm).

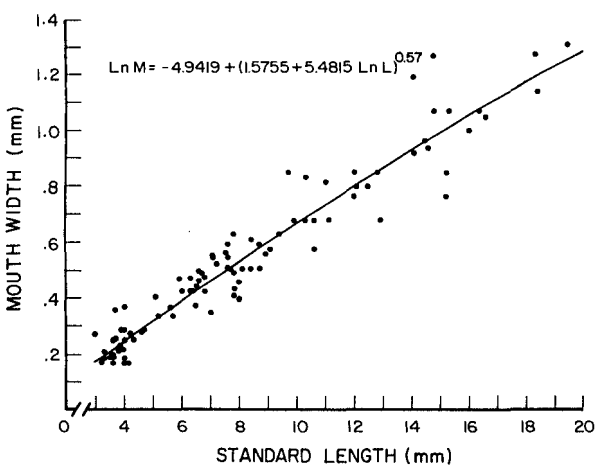


FIGURE 7.—Mouth width as a function of standard length of Pacific mackerel larvae. Points represent single larva.

The threshold, in terms of length for feeding on *A. salina* nauplii, was distinctly different from that for feeding on anchovy eggs. The 50% threshold for nauplii was 4.5 mm SL (95% confidence interval, 4.1-4.8 mm) and that for eggs was 12.2 mm SL (11.3-13.1 mm). This could be expected because anchovy eggs are nearly three times as large as *A. salina* nauplii. On the other hand, when feeding success was expressed as a function of the ratio, mean prey width/mean mouth width, the percentage feeding success of Pacific mackerel fed *A. salina* was similar to that of larvae fed eggs (Figure 8). At first feeding, relative prey size (prey width/mouth width) was near unity for larvae fed either *A. salina* or eggs, indicating the width of the mouth established the upper size limit of prey. Since the 50% threshold for relative prey size for the combined data given in Figure 8 was 0.85 (95% confidence interval,

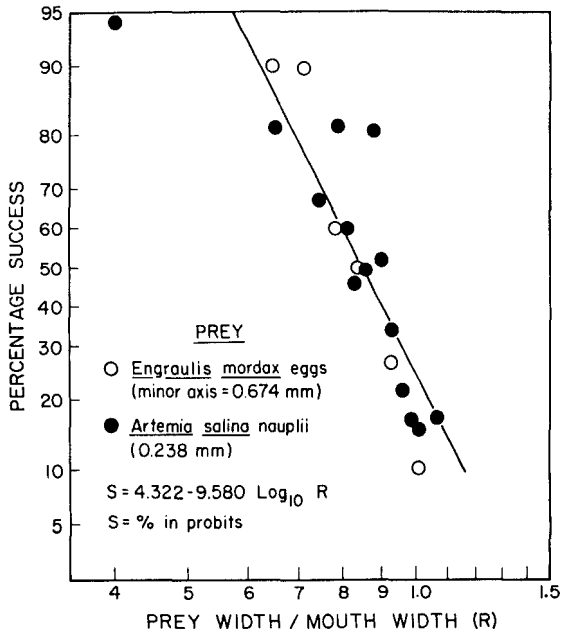


FIGURE 8.—Relation between average feeding success (probit scale) and average relative prey size (prey width/mouth width), for larval groups fed *Artemia salina* nauplii (closed circles) and northern anchovy eggs (open circles). Each point is the percentage success of fish within a mouth width/prey size class, where $n>9$. Line is the regression of percentage success probit on $\log_{10}$ of the prey-width to mouth-width ratio, for *A. salina* nauplii and anchovy egg data combined. The $LD_{50}$ for the combined data was 0.85 (95% confidence interval 0.79-0.91).

0.79-0.91) and the 95% threshhold was 0.57 (0.47-0.70), nearly all Pacific mackerel larvae (95%) were able to ingest a prey when it was 57% of the width of the mouth and 50% were able to do so when it was 85% of the mouth width.

Nearly all prey eaten by Pacific mackerel larvae in the sea fell within the range of sizes predicted from the laboratory work; few prey exceeded the width of the mouth (Figure 9). Fifty-nine percent of all identifiable food items in the stomachs of sea-caught larvae were stages of copepods; other items included cladocerans, oikopleurans, gastropods, invertebrate eggs, diatoms, fecal pellets, and one fish larvae.

Although laboratory data indicated that 50% of Pacific mackerel larvae were able to ingest prey having a width of 85% of the mouth width, the mean diameter of prey eaten in the sea was 38±2% (2 SE) of the mouth width. Thus, a substantial number of prey eaten by larvae in the sea was much smaller than the maximum size of prey they were capable of ingesting. This may reflect a shortage of larger prey in the sea. Larger prey probably are important nutritionally. If one assumes the prey given in Figure 8 to be spherical, then 50% of the prey items accounted for about 85-90% of the total volume of food, depending on larval size. Conversely, the small prey items that contributed 50% by number, contributed only 10-15% of the total volume of prey eaten. This calculation underestimates the volume of the larger prey because they are more elongate or less spherical than smaller ones. Nevertheless, it indicates that prey less than the mean size eaten contributed relatively little nutritionally to the diet of Pacific mackerel larvae, and that the relatively large, but more rare, prey probably made the major contribution to growth.

## Ration, Growth Efficiency and Metabolism

Pacific mackerel larvae (age 3-5 d) fed actively throughout the day; the gut was filled within the first hour of feeding and it remained full throughout the remainder of the 12-h feeding day, despite a high rate of gastric evacuation. Evacuated *Brachionus plicatilis* were well digested; only the lorica remained after digestion. Our measurements of evacuation rates indicated that about half the gut contents was evacuated in 2 h (Figure 10). Growth of larvae used for ration estimates was about the same as that for other groups reared at 19° C (Figure 3). To grow at this rate in the laboratory, Pacific mackerel larvae (age 3-5 d) consumed an average of about 87% of their dry body weight per day, or about 165-538 rotifers/day (Table 3). This estimate of ration was based on the dry weight of the mean number of rotifers in stomachs, adjusted for the rate of evacuation (Stauffer 1973). The mean gross growth efficiency in dry weight was 33%, which falls within the range of estimates for fish larvae and young fishes (Pandian 1967; Stepien 1976).

Our respiration experiments indicated that Pacific mackerel larvae at 18.0° C consumed 6.1±1.4 (2 SE) $\mu$l $O_2$/mg per h ($n$ = 24) and at 22.0° C they consumed 11.4±3.0 $\mu$l $O_2$/mg per h ($n$ = 14). By interpolation, the rate at 19° C, the temperature of the ration experiments, is estimated as 7.4 $\mu$l $O_2$/mg per h. This metabolic expenditure, converted to calories per day (footnote 6, Table 3) was, on the average, about 18% of the mean daily ration for larvae given in the table. This is probably an underestimate of their metabolic requirement because the activity of larvae confined in

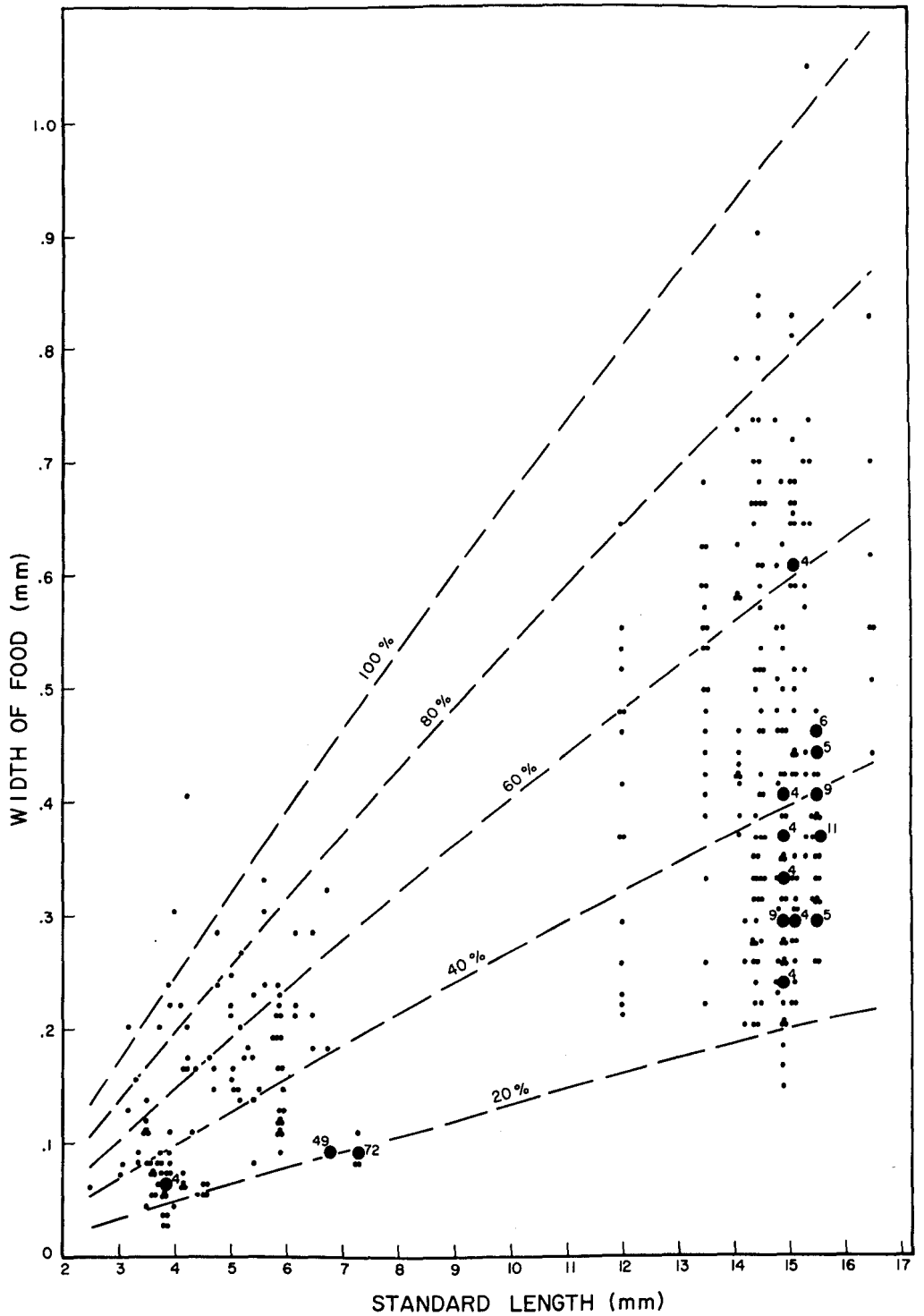


FIGURE 9.—Width of foods eaten in the sea by Pacific mackerel larvae of various standard lengths. Each small point is the width of a single prey; larger points represent multiple points for prey of the same size and number observations. Dashed lines indicate the prey width equal to 20-80% of the mouth width, or equal to the mouth width (100%), for Pacific mackerel larvae of 3-16 mm (calculated from data given in Figure 7).

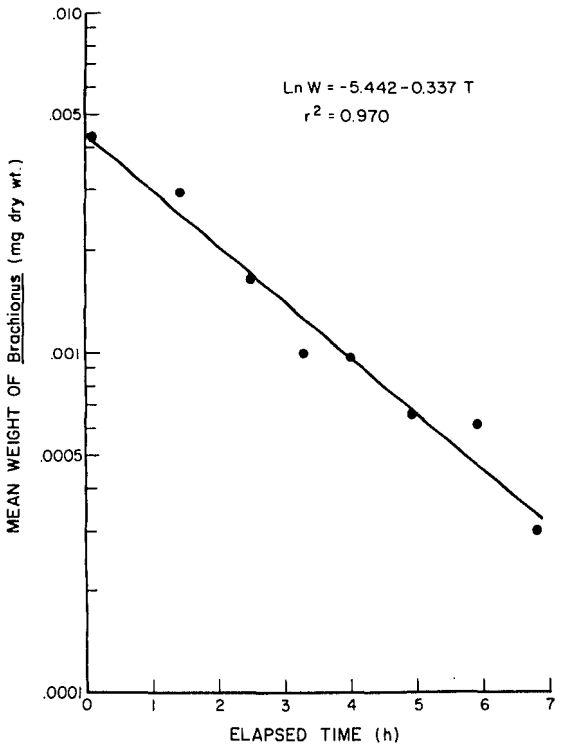


FIGURE 10.—Rate of gastric evacuation of 4.01±0.03 mm SL Pacific mackerel larvae fed *Brachionus plicatilis*. Each point represents the mean dry weight of *B. plicatilis* in guts of 13-16 larvae. Dry weight estimated by counting numbers of *B. plicatilis* in stomachs and multiplying by the mean dry weight of one *B. plicatilis* (0.16μg) (Theilacker and McMaster 1971).

Warburg flasks was probably less than that of free-swimming larvae. These respiration measurements do establish a lower limit to food ration, because the ration would have to exceed the metabolic requirement just to meet maintenance costs.

## DISCUSSION

The characteristics of the embryonic period (duration of incubation and yolk-sac periods, extent of yolk reserves, size at first feeding, and ability to withstand starvation) were similar to other temperate fishes with small pelagic eggs (Lasker et al. 1970; Zweifel and Lasker 1976) and did not differ greatly from some subtropical species (Houde 1974). Small differences in these characteristics may be of importance (Houde 1974) but growth, metabolism, feeding, and swimming behavior are of more value in characterizing the early life history of Pacific mackerel.

Pacific mackerel larvae grew rapidly, completing metamorphosis (15 mm SL) in 2-3 wk. Fast growth appears to be characteristic of scombroid larvae and is even more rapid in tropical scombroids: *Auxis thazard* grew to 64 mm SL in 17 d (Harada, Murata, and Furutani 1973) and *A. tapeinosoma* grew to 49 mm SL in 18 d (Harada, Murata, and Miyashita 1973). Fast growth requires a large food ration; we found that Pacific mackerel larvae consumed about 87% of their dry

TABLE 3.—Estimate of ration, metabolism, and growth efficiency of 3-5 d old Pacific mackerel larvae fed *Brachionus plicatilis*.

| | | | Experimental conditions | | | | |
|---|---|---|---|---|---|---|---|
| | | | Larval weight[1] | | | Mean weight in stomachs[2] | |
| Larval age (d) | Temperature (°C) | Larval SL±2 SE (mm) | On day of ration estimation (μg) | Gain 1 d after estimation (μg) | Food density (no./ml) | No. of samples[3] | $\bar{x}$±2 SE (μg) |
| 3 | 18.7 | 3.66±0.03 | 37.8 | 5.2 | 157 | 7 | 4.8±0.8 |
| 4 | 19.0 | 3.76±0.02 | 43.0 | 14.0 | 47 | 8 | 6.9±1.0 |
| 5 | 19.4 | 4.38±0.08 | 84.6 | 37.5 | 198 | 7 | 15.6±4.5 |
| $\bar{x}$ | 19.0 | 3.93 | 55.1 | 18.9 | 134 | | 9.1 |

| | Ration, metabolism, and growth efficiencies | | | | | |
|---|---|---|---|---|---|---|
| | Ration[4] | | | | | |
| Larval age (d) | μg/d | Percent body weight/d | [5]cal/d | Metabolic rate[6] (cal/d) | Weight gain[7] (cal) | Gross growth efficiency[8] (percentage) |
| 3 | 26.5 | 70 | 0.141 | 0.0338 | 0.026 | 20 |
| 4 | 38.1 | 89 | 0.203 | 0.0384 | 0.070 | 37 |
| 5 | 86.2 | 102 | 0.460 | 0.0756 | 0.188 | 44 |
| $\bar{x}$ | 50.3 | 87 | 0.268 | 0.0493 | 0.094 | 33 |

[1]Calculated from mean larval length using relation given in Figure 4.
[2]Mean counts of *B. plicatilis* in stomach converted to weight using one *B. plicatilis* = 0.16 μg (Theilacker and McMaster 1971).
[3]Each sample consisted of 13-16 larvae; sampling began after first hour of feeding.
[4]Ration = $(r \times k \times t) + r$, where $r$ is mean stomach contents, $k$ is rate of gastric evacuation (0.377), and $t$ is duration of feeding period (12 h). (From G. Stauffer, unpubl. manuscr., Southwest Fisheries Center, La Jolla, Calif.)
[5]Caloric value of *B. plicatilis* = 5,335 cal/g (Theilacker and McMaster 1971).
[6]Maintenance requirement from: 7.45 μl $O_2$/mg per h; 1 μl $O_2$ = 0.005 cal; time = 24 h; and dry weight of larvae on day ration estimated.
[7]Caloric value of weight gained assumed to equal 5,000 cal/g.
[8]Gross efficiency (dry weight) = weight gain/ration.

weight per day and weight increased from 0.034 mg to 7.5 mg over the larval period. To capture sufficient numbers of prey to support such rapid growth requires that the size of the prey and the size of the mouth increase rapidly. Our analysis of sea-caught Pacific mackerel larvae showed that the maximum size of prey did increase rapidly, more or less, in proportion to mouth size. The mean and minimum size of prey eaten by Pacific mackerel changed more slowly but the smaller prey, those less than the average size, may constitute <15% of the volume of food eaten. A similar pattern of rapidly increasing prey size with length also has been documented for *Scomber japonicus* larvae by Shirota (1970) and Yokota et al. (1961).

A dependency on larger prey and fast growth requires faster swimming to increase the volume of water searched for prey because abundance declines with increased prey size (Sheldon et al. 1972). The swimming behavior of Pacific mackerel larvae appeared consistent with this argument. Cruising speeds increased rapidly with length, roughly to the 1.8 power, and speeds of the larger larvae were at the upper end of the range, typical of larval fishes (3 SL/s) (Blaxter 1969). Higher speeds require a greater metabolic expenditure. The rate of oxygen consumption for Pacific mackerel (6-11 $\mu$l $O_2$/mg per h) was above that for other marine fish larvae (Blaxter 1969) indicating a higher-than-average metabolic expenditure despite the fact that the rates probably do not reflect the entire cost of high speed swimming.

Piscivorous feeding was an important behavioral trait in the early life history of Pacific mackerel because larvae were no longer limited to prey sizes equal to or less than the size of an open mouth. In piscivorous feeding, prey were seized, manipulated and the mouth greatly expanded during ingestion, permitting consumption of much larger diameter foods. In our samples of sea-caught larvae, only one stomach contained a larval fish, but the actual incidence may be higher because larvae are digested rapidly. Cannibalism, a correlate of piscivorous feeding, was common in laboratory groups after the larvae reached 8 mm SL. This also has been observed from stomach contents of the Atlantic mackerel, *S. scombrus* (Lett 1978). Cannibalism appears to be a common feature of scombroid life history; Mayo (1973) remarked that *Euthynnus alletteratus*, *Scomberomorus cavalla*, *S. regalis*, and *Auxis* sp. became cannibalistic at about 5 mm SL. He also noted that cannibalism ceased as the fish became juveniles which agrees with our observation that cannibalism ended as Pacific mackerel approached metamorphosis and began to school. The extent that cannibalism affected the form of our laboratory growth curves is unknown. Although cannibalism was high in all groups, survival was higher in groups reared at high temperatures because of the faster growth rate, which meant faster transit through cannibalistic sizes.

In summary, traits that characterize the early life history of Pacific mackerel are the interrelated characteristics of fast growth, fast swimming, high metabolism, a dependence on increasingly larger prey, and cannibalism. The high food requirements of the larvae, and the fact that in the sea they feed upon many prey substantially smaller than they are capable of eating, indicates that growth or survival in the sea might be limited by the availability of larger prey.

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