# BIOENERGETICS AND GROWTH OF
# STRIPED BASS, *MORONE SAXATILIS*, EMBRYOS AND LARVAE

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## ABSTRACT

Fluctuations in year class size of striped bass are known to be related to development and survival in the early life stages. Bioenergetic aspects of growth and development of striped bass embryos and larvae were determined in the laboratory to discover some of the physiological needs and processes of these stages from fertilization to metamorphosis.

Energy was provided by endogenous (yolk and oil globule) and exogenous (*Artemia* sp.) sources. Initial amounts of yolk and oil varied significantly among eggs from seven different females, and these differences were reflected in different patterns of consumption and growth. Feeding larvae consumed their endogenous oil at rates related to exogenous food intake. Daily food rations of larvae from the onset of feeding to metamorphosis were estimated for field and laboratory conditions. Rations increased with size and age of the larvae. Wild larvae were estimated to have daily rations substantially greater than those of cultured larvae.

Energy outputs were measured in growth and oxygen consumption. Egg size (total dry weight) directly influenced early periods of growth, but later compensatory growth, seen in more rapid growth in larvae from smaller eggs, made up for initial differences. Growth and food consumption were linearly related and, again, different growth characteristics were seen in each batch of fish. Embryos and prefeeding larvae had the highest $Q_{O_2}$, while metabolism on a weight-specific basis increased with tissue dry weight and was best described by a power function.

Gross caloric conversion efficiencies were highest from fertilization to initial feeding. Feeding larvae used their resources at levels under 20% and their conversion efficiencies did not appear to correlate with food concentration.

In an energy budget model, striped bass embryos and larvae given the highest food density consumed yolk energy at constant rates until totally absorbed. Oil globule consumption fluctuated in relation to growth and nonassimilation, rising sharply after first feeding then declining as food intake increased. Metabolism fluctuated according to developmental stage, rising with the onset of active feeding. Nonassimilation steadily increased as larvae relied more on exogenous food.

Striped bass, *Morone saxatilis*, populations have fluctuated historically throughout their ranges, but in recent years they have declined consistently and unexplainably, especially on the west coast of the United States. Present estimates place the population of the San Francisco Bay/Delta estuary at 33% to 40% of its 1960 peak abundance and it is forecasted to decline further (Stevens 1980). Despite availability of considerable information on striped bass (Pfuderer et al. 1975; Rogers and Westin 1975; Horseman and Kernehan 1976; Setzler et al. 1980), factors that control or influence these fluctuations and declines are not known. Field researchers concluded from 20 yr of data collection that year class size directly correlates with survival and growth during the first 60 d of life and this, in turn, is controlled by environmental conditions—

principally the interrelated factors of freshwater flow, water diversion, and food supply (Stevens 1977a, b; Chadwick 1979[2]; Stevens 1980).

To determine the direct causal mechanisms operating between these environmental conditions and early life stage growth and survival, we conducted a series of laboratory experiments over a 6-yr period. Our working hypothesis was that a combination of inherent and environmental factors determined the ability of striped bass embryos and larvae to meet metabolic requirements for successful growth and survival to the pivotal age of 60 d. These factors involve a variety of physiological, morphological, and behavioral functions, and are controlled and/or limited by environmental conditions. Whole organism

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[2]Chadwick, H. K. 1979. Striped bass in California. Prepared for U.S. Environmental Protection Agency, Region II, 27 p.

bioenergetics was selected as our approach because it represents these functions in an integrated and comprehensive fashion.

Bioenergetics of adult fishes has been studied for some time (Ivlev 1939a, b; Winberg 1956; Warren and Davis 1967; Brett and Groves 1979). As interest in fish eggs and larvae grew, knowledge gained from studies of adults was applied toward research on early life stage energetics (Toetz 1966; Laurence 1969, 1971, 1977; Cooney 1973). Most of these publications are concerned with the critical period when larvae begin active feeding and change from endogenous to exogenous energy sources (May 1974b). Other researchers have used bioenergetic studies to assess the effects of pollutants or other environmental conditions on larvae (Laurence 1973; Eldridge et al. 1977).

Our early research on striped bass embryos and larvae has already been reported (Eldridge et al. 1981). Emphasis was on factors associated with food and feeding of larvae and how they related to mortality, point of no return, development, and, to a limited extent, energetics. The research presented here is a detailed analysis of the energy sources, endogenous and exogenous, and their influence on energy outputs in the early life stages of striped bass.

# MATERIALS AND METHODS

## Energy Input Determinations

Component analyses of eggs prior to fertilization were done on eggs from seven different females used for embryo and larval studies and on 34 ripe fish collected at random from natural spawning areas. All eggs came from fish from the Sacramento River, Calif. Three replicates of 25 eggs each were weighed fresh after brief blotting on absorbent filter paper, then dried to constant weights at 60°C and reweighed to yield water contents and total dry weights. Yolks and chorions were dissected from Formalin[3]-preserved eggs with microdissection tools; they then were dried and weighed to the nearest 0.1 μg. These amounts were then subtracted from the total weight to provide oil weights. Total lipid contents were obtained by 2:1 chloroform-methanol extraction in micro-Sohxlet apparatus. Our procedure for caloric determinations of yolk and

oil involved whole egg homogenization followed by centrifugation to separate yolk, oil, and chorion membrane components. Yolk and oil were then aspirated into dishes, oven dried to constant weights at 60°C, and bombed according to standard microbomb calorimetric methods. Estimates of tissue and *Artemia* caloric contents were made from homogenates of whole animals, the larvae being sampled after complete oil globule consumption. All caloric contents are expressed as calories per gram ash-free dry weight.

All measurements of yolk and oil volume and lengths were done with ocular micrometers in dissecting microscopes. All measurements and determinations were performed at least in duplicate and, if possible, in triplicate.

Eggs from seven different females were fertilized artificially according to methods of Bonn et al. (1976). Eggs were incubated in McDonald jars. After hatching, larvae were transferred to hemispherical 8 l acrylic plastic containers held in water tables to stabilize temperature. Initial stocking densities were approximately 150 larvae/container. In three of the seven batches, larvae were reared to the age when feeding begins, 7 d after fertilization (D-7). The remaining four batches were reared to 29 d after fertilization (D-29). During the process we attempted to duplicate natural water quality conditions as much as possible. Temperatures were maintained at 18°C, and oxygen content was at or near saturation throughout the experiments. Photoperiod and light qualities were kept close to natural. Salinities were zero from fertilization to D-4, 1.0‰ from D-5 to D-13, and 3‰ from D-14 to D-29. Each day containers were cleaned and new water and food were added. An endemic small (1-2 μm) green phytoplankter (*Nephroselmus* sp.) was also added in concentrations of $10^2$-$10^3$/ml.

Larvae began feeding consistently on D-7, at which time they were given newly hatched, live *Artemia salina* nauplii (San Francisco Bay Brand). The range of initial food concentrations was selected to include the estimated natural zooplankton densities (0.003 to 0.010/ml (Daniel 1976)) and the concentrations used in other striped bass research. Initial concentrations were 0.00, 0.01, 0.10, 0.50, 1.00, and 5.00 *Artemia*/ml.

To estimate daily exogenous food rations of larvae we used the following formula: daily food ration = (average stomach contents)(hours of active feeding)/digestive time. Detailed studies

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on diel feeding patterns and evacuation rates of larvae in our experimental systems were conducted in the early stages of this study and were presented in Eldridge et al. (1981). Because larvae in all food concentrations consumed their food within 10 h after food was first introduced, we selected 10 h/d for use in the above formula. We found that sampling larval stomachs 1 h after food introduction was most representative of average stomach contents during the active feeding periods. A minimum of 10 larvae was dissected and the stomach contents were quantified for each food ration estimate for each experiment. Evacuation rates of food ingested by larvae which were feeding continuously ranged from 1.5 to 5.5 h with an overall average of 3.3 h. Times of 100% evacuation were combined for different-aged larvae and used in this study (Table 1).

TABLE 1.—Average times (h) required for *Artemia* nauplii to pass through the digestive tracts of continuously feeding striped bass larvae.

| Age (days after fertilization) | Food concentration (*Artemia*/ml) | | | | |
|---|---|---|---|---|---|
| | 0.01 | 0.10 | 0.50 | 1.00 | 5.00 |
| 9-16 | 3.3 | 4.0 | 3.5 | 4.5 | 4.0 |
| 17-24 | 2.5 | 2.8 | 3.5 | 3.5 | 2.3 |
| 25-29 | 2.5 | 2.5 | 3.7 | 4.0 | 3.0 |

## Energy Output Determinations

Growth of embryos and larvae was measured by carefully removing all yolk and oil globules from Formalin-preserved specimens, rinsing the remaining tissues in distilled water, drying at 60°C, and weighing to the nearest 0.1 $\mu$g. Measurements were in duplicate with 3 to 5 speci-

mens per sample. Standard lengths of larvae were measured to the nearest 0.1 mm with an ocular micrometer. Duplicate measurements of 20 larvae each were done. Preserved specimens were measured as soon as possible. The entire set of samples from each experiment required an average of 8 wk to process.

Oxygen consumption was used as a measure of "routine" metabolism (Fry 1971) and was measured with standard manometric techniques using a differential microrespirometer. At least five replicate samples (from 5 to 50 animals/sample depending on age and size) were taken at each test period. Sampling occurred at D-0.5, -1.0, -2.0, -4.0, and on each even day until D-30 (time measured from time of fertilization).

## RESULTS

### Energy Inputs

**Endogenous Sources**

Initial sources of energy for striped bass embryos and early larvae are yolk and oil, the latter contained in a single large globule. The relative composition of these egg components was found to vary considerably between the seven different females used in rearing experiments (Table 2). Oil accounts for most of the variability in dry weight, whereas yolk is more variable in measurements of volume. Caloric contents of these two energy sources were consistent, which indicates that variability of total energy in the egg results from differences in absolute amounts of oil, yolk, or both, rather than differences in the energy content of those materials. Eggs from different females contained widely ranging

TABLE 2.—Dry weights, volumes, and caloric contents of striped bass eggs and egg components at time of fertilization. Three replicates of 25 eggs each were used for dry weights, three replicates of 20 eggs each for volumes, and two replicates of approximately 50 mg (dry weight) were used for caloric content determinations.

| Experiment no. | Mean dry weight (mg) | | | | Mean volume (mm³) | | Caloric content | | | | total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | yolk | | oil | | |
| | yolk | oil | chorion | total | yolk | oil | cal/g | cal/egg | cal/g | cal/egg | cal/egg |
| 1 | 0.114 | 0.150 | 0.022 | 0.286 | 0.67 | 0.21 | 5,687 | 0.648 | 9,223 | 1.383 | 2.031 |
| 2 | 0.089 | 0.137 | 0.023 | 0.249 | 0.65 | 0.20 | 5,720 | 0.509 | 9,360 | 1.282 | 1.791 |
| 3 | 0.131 | 0.089 | 0.028 | 0.248 | 0.57 | 0.13 | 5,622 | 0.736 | 9,133 | 0.813 | 1.549 |
| 4 | 0.106 | 0.251 | 0.016 | 0.373 | 0.52 | 0.21 | 5,641 | 0.596 | 9,869 | 2.477 | 3.073 |
| 5 | 0.118 | 0.189 | 0.014 | 0.321 | 0.20 | 0.17 | 5,635 | 0.665 | 9,627 | 1.819 | 2.484 |
| 6 | 0.089 | 0.128 | 0.014 | 0.231 | 0.38 | 0.18 | 5,635 | 0.502 | 9,738 | 1.247 | 1.749 |
| 7 | 0.083 | 0.115 | 0.012 | 0.210 | 0.62 | 0.14 | 5,625 | 0.467 | 9,655 | 1.110 | 1.577 |
| $\bar{x}$ | 0.104 | 0.151 | 0.018 | 0.274 | 0.516 | 0.177 | 5,652 | 0.589 | 9,515 | 1.447 | 2.036 |
| SE | 0.018 | 0.054 | 0.006 | 0.057 | 0.170 | 0.033 | 37 | 0.100 | 278 | 0.546 | 0.558 |
| Range | 0.089– 0.131 | 0.089– 0.251 | 0.012– 0.028 | 0.210– 0.373 | 0.20– 0.67 | 0.13– 0.21 | 5,641– 5,720 | 0.467– 0.736 | 9,133– 9,869 | 0.813– 2.477 | 1.549– 3.037 |
| C.V. | 17.3 | 35.6 | 33.0 | 20.8 | 33.0 | 18.4 | 0.7 | 16.9 | 2.9 | 37.7 | 27.4 |

amounts of yolk and oil (coefficients of variation 27% and 25% for yolk and oil, respectively) and little (<3%) difference was found in energy contents. The oil globule accounted for an average 55% of the dry weight and 71% of the total energy of the egg. Yolk accounted for 38% of dry weight and 29% of energy. The two sources combined provided an average 2.036 cal/egg.

Yolk contained an average 5,652 cal/g, which agrees with Phillips' (1969) estimate of 5,660 cal/g gross energy for digested protein. Lipid extraction analyses of yolk from three of the seven spawned females showed that only 3.8% of dry weight was lipid material.

Embryos and larvae from the seven different females consumed their yolks linearly (Fig. 1). At hatching an average 58% of the original yolk energies remained, and they were totally utilized between D-6 and D-7, the time when active feeding began. Analyses showed no significant differences in yolk utilization rates but highly significant differences in intercepts ($P \leq 0.01$), further indication of the differences in original yolk reserves.

Initial oil energy contents per egg ranged from 0.8 to 2.5 cal (Table 2) and differed significantly between batches ($P \leq 0.05$). An average 86% of these initial amounts remained at hatching and 71% was present on D-7. Analyses of covariance indicated that the utilization rates from fertilization to feeding (Fig. 2) also were significantly different ($P \leq 0.05$). With the exception of one batch, embryos and larvae consumed their oil energies so that approximately the same amounts of energy remained on D-7.

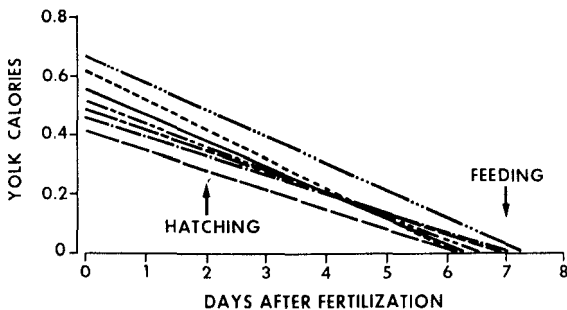The rates at which oil globule calories were utilized and the ages at complete oil energy absorption (D-20 to D-29) appeared related to food concentration (Fig. 3). Starved larvae and those in 0.01 *Artemia*/ml concentrations conserved oil, whereas those fed progressively higher concentrations consumed energy at faster rates. Analyses of covariance showed significant differences in oil consumption among batches within each food concentration. Tests of food concentrations and oil consumption within batches showed all to have highly significant differences ($P \leq 0.01$) in intercepts, and two of the four batches had significant slope differences ($P \leq 0.05$).

### Exogenous Sources

Larvae in all experiments began active feeding 5 d after hatching. Average stomach contents, presented as the average number of ingested *Artemia* and their equivalent calories, are presented in Table 3. These data were further used to calculate daily food rations (Table 4). With some exceptions, larvae increased their exogenous energy intake in direct relation to food availability and age in all food concentrations except 0.01 *Artemia*/ml. Larvae in this low concentration showed no particular trend.

## Energy Outputs

### Growth

Embryonic and prefeeding larval growth, measured in assimilated tissue calories, differed significantly among the seven batches ($P \leq 0.01$).



FIGURE 1.—The consumption of yolk calories by seven different batches of striped bass embryos and larvae cultured under identical conditions.
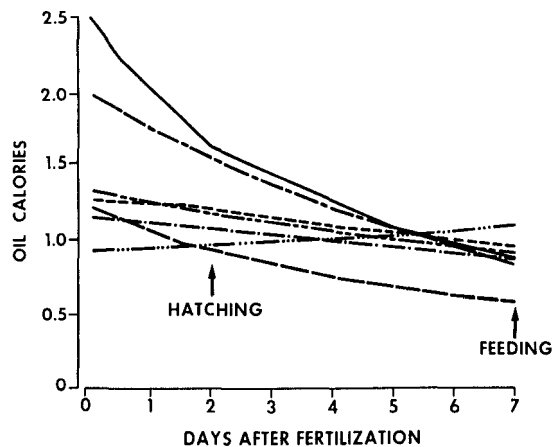


FIGURE 2.—The consumption of oil globule calories by seven different batches of striped bass embryos and prefeeding larvae.
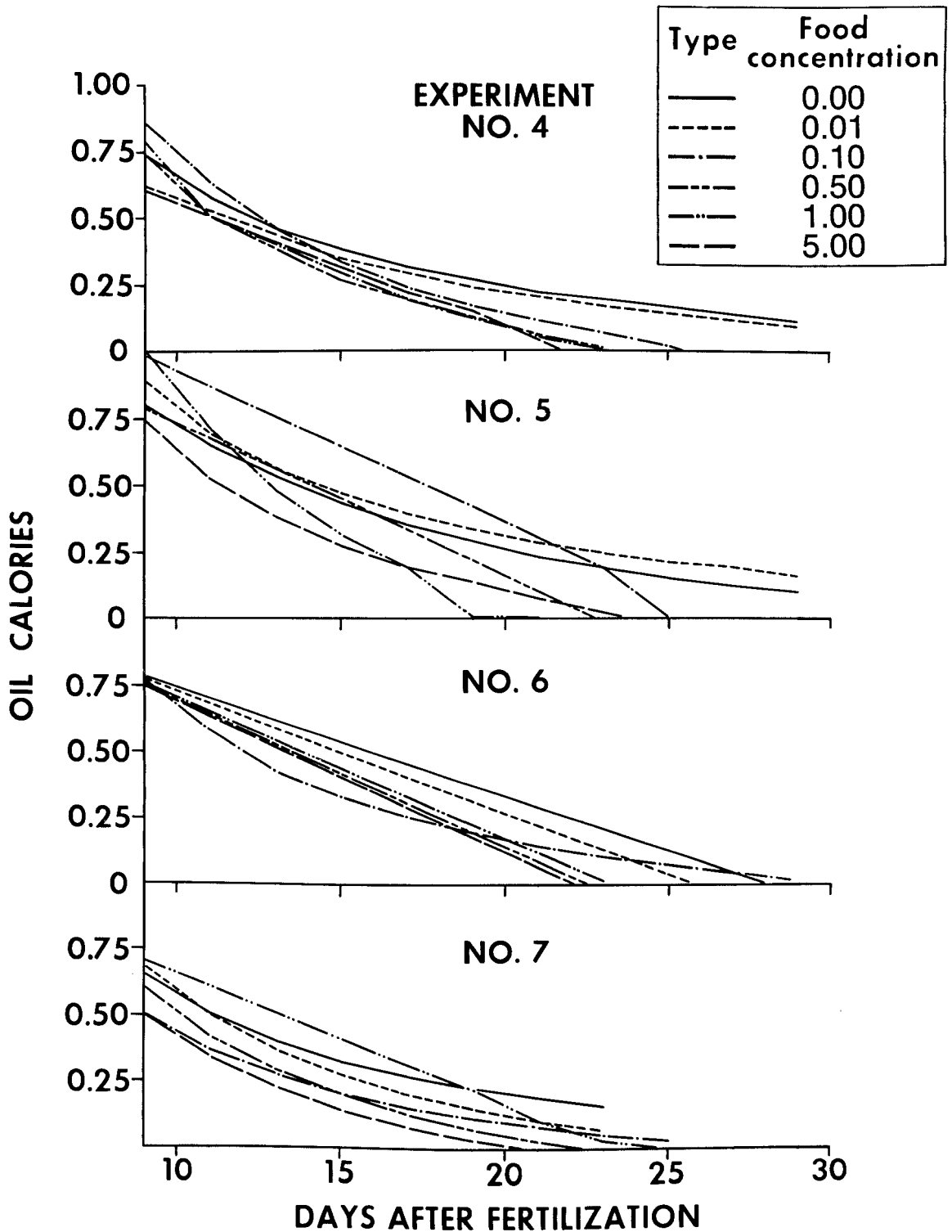
FIGURE 3.—The consumption of oil globule calories by striped bass larvae from four different batches (experiments 4-7) fed six different food concentrations (0.00 to 5.00 *Artemia*/ml).

TABLE 3.—Average stomach contents and their corresponding caloric equivalents of striped bass larvae feeding at different food concentrations from 9 to 29 d after fertilization. Presented as number of food organisms/number of calories per larva.

| Age (days after fertilization) | Food concentrations (no. *Artemia*/ml) | | | | |
|---|---|---|---|---|---|
| | 0.01 | 0.10 | 0.50 | 1.00 | 5.00 |
| 9 | 0.05/0.001 | 0.15/0.001 | 5.40/0.052 | 4.30/0.041 | 7.60/0.073 |
| 11 | 0/0 | 0.85/0.008 | 7.50/0.072 | 11.70/0.112 | 2.80/0.027 |
| 13 | 1.50/0.014 | 3.30/0.032 | 9.20/0.088 | 18.40/0.177 | 9.890/0.094 |
| 15 | 0.05/0.001 | 4.10/0.039 | 23.10/0.222 | 24.00/0.231 | 10.20/0.098 |
| 17 | 0.15/0.001 | 8.40/0.081 | 27.10/0.260 | 39.40/0.39 | 18.60/0.179 |
| 19 | 0/0 | 12.50/0.120 | 29.50/0.283 | 33.30/0.320 | 24.60/0.236 |
| 21 | 0.15/0.001 | 13.00/0.125 | 26.10/0.251 | 40.00/0.384 | 33.70/0.324 |
| 23 | 4.16/0.040 | 14.20/0.136 | 47.40/0.456 | 35.90/0.345 | 53.00/0.509 |
| 25 | 1.10/0.001 | 57.20/0.550 | 17.00/0.163 | 83.10/0.799 | 59.40/0.571 |
| 27 | 0.25/0.002 | 470/0.045 | 65.40/0.628 | 60.20/0.579 | 72.40/0.696 |

TABLE 4.—Estimated daily food ration (number of *Artemia* consumed by one larva in 24 h/equivalent calories consumed in 24 h) of striped bass larvae at different ages feeding at different food densities.

| Age (days after fertilization) | Prey densities (*Artemia*/ml) | | | | |
|---|---|---|---|---|---|
| | 0.01 | 0.10 | 0.50 | 1.00 | 5.00 |
| 9 | 0.2/0.001 | 0.4/0.004 | 15.4/0.148 | 9.6/0.092 | 19.0/0.183 |
| 11 | 0/0 | 2.1/0.020 | 21.4/0.206 | 26.0/0.250 | 7.0/0.067 |
| 13 | 4.6/0.044 | 8.3/0.079 | 26.3/0.253 | 40.9/0.393 | 24.5/0.235 |
| 15 | 0.2/0.001 | 10.3/0.099 | 66.0/0.634 | 53.3/0.513 | 25.5/0.245 |
| 17 | 0.6/0.006 | 30.5/0.294 | 77.4/0.744 | 112.6/1.082 | 82.7/0.794 |
| 19 | 0/0 | 45.5/0.437 | 84.3/0.810 | 95.1/0.914 | 109.3/1.051 |
| 21 | 0.6/0.006 | 47.3/0.454 | 74.6/0.717 | 114.3/1.098 | 149.8/1.439 |
| 23 | 16.6/0.160 | 51.6/0.496 | 135.4/1.301 | 102.6/0.986 | 235.6/2.264 |
| 25 | 1.0/0.010 | 18.8/0.181 | 176.8/1.699 | 150.5/1.446 | 241.3/2.319 |
| 29 | 11.6/0.111 | 58.8/0.565 | 194.3/1.867 | 288.8/2.775 | 410.0/3.940 |

Greater differences were seen in the intercepts than rates, and this, in turn, seemed related to the initial egg sizes (total dry weights). Descriptive equations for assimilated tissue calories of the different experiments are in Table 5. Daily growth coefficients (Laurence 1974) to hatching and to first feeding correlated well with initial egg size. The rate of growth from fertilization to hatching age (avg. $G_W = 1.872$) was three times that to feeding age (avg. $G_W = 0.647$).

Standard lengths at hatching (3.9±0.6 mm), and especially at first feeding (5.8±0.3 mm) (Table 5), also correlated well with initial egg size. Smaller standard deviation of D-7 larvae

than of newly hatched larvae (coefficients of variation 5% vs. 15%) suggests larval lengths converged with age.

Growth characteristics of feeding larvae were unique to each batch within each food concentration as was found in earlier stages. Examples are given in Figures 4 and 5 which present growth in tissue calories and standard lengths of larvae fed the high food ration (5.0 *Artemia*/ml).

Within each batch, growth was linearly related to food concentration (Fig. 6). Differences in overall growth are again apparent. Experiment 7 larvae grew fastest.

Larval length-weight relations were exponen-

TABLE 5.—Best descriptive equations ($y$ = tissue calories, $x$ = days after fertilization), initial egg dry weights, standard length, and growth coefficients of striped bass embryos and prefeeding larvae.

| Experiment | Initial egg size ($\mu$g) | Best fit growth equation (tissue cal) | Standard errors of estimate | Standard lengths (mm) | | Daily instantaneous growth coefficients[1] | |
|---|---|---|---|---|---|---|---|
| | | | | at hatching | at feeding | to hatching | to feeding |
| 1 | 286 | $y = 0.159359 (x^{0.576582})$ | 0.0480 | 4.7 | 5.5 | 1.966 | 0.624 |
| 2 | 249 | $y = 0.107496 (x^{0.847936})$ | 0.0653 | 4.0 | 5.6 | 1.844 | 0.630 |
| 3 | 248 | $y = 0.133695 (x^{0.860384})$ | 0.0446 | 4.7 | 5.7 | 1.733 | 0.694 |
| 4 | 373 | $y = 0.139619 (x^{0.732174})$ | 0.0537 | 3.2 | 6.1 | 2.172 | 0.715 |
| 5 | 321 | $y = 0.190165 (x^{0.767811})$ | 0.0537 | 3.2 | 6.1 | 2.172 | 0.715 |
| 6 | 231 | $y = 0.090892 (x^{0.828653})$ | 0.0187 | 3.6 | 5.9 | 1.763 | 0.633 |
| 7 | 210 | $y = 0.115968 (x^{0.892893})$ | 0.0763 | 3.7 | 5.4 | 1.733 | 0.580 |

[1]Daily instantaneous growth coefficients = log$_e$ W/days after fertilization where $W$ = dissected tissue dry weight in micrograms.
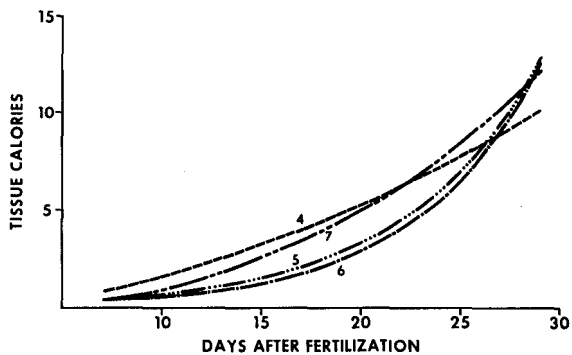
FIGURE 4.—Growth of four batches of feeding striped bass larvae measured in calories of assimilated tissue from first feeding (D-7) to D-29.
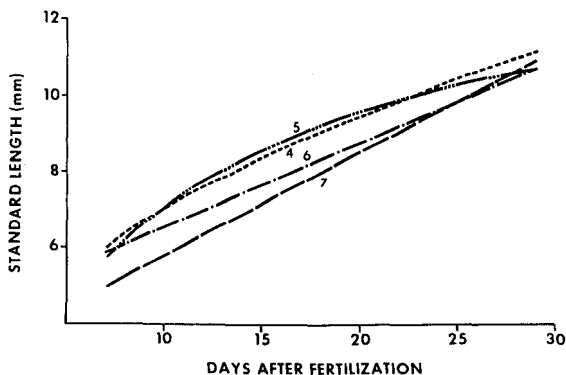


FIGURE 5.—Growth of four batches of feeding striped bass larvae measured in standard lengths from first feeding (D-7) to D-29.
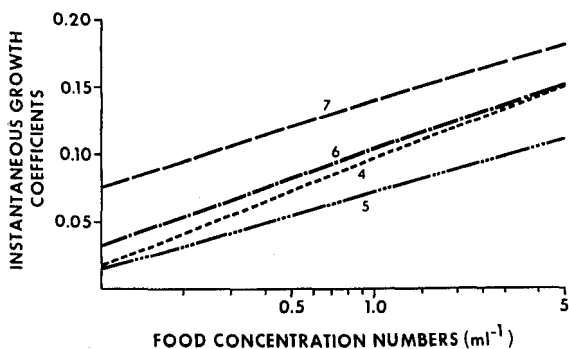


FIGURE 6.—Instantaneous growth coefficients of four batches of feeding striped bass larvae that fed on six different food concentrations (0.00 to 5.00 *Artemia*/ml).

tial for all fish groups (Fig. 7). Experiment 7 larvae were the heaviest per unit length and did not attain the lengths that other larvae did. All larvae put on weight rapidly after reaching a standard length of about 8 mm.

## Oxygen Consumption

Metabolic rates of embryos and larvae are presented in Figure 8. Embryos and prefeeding larvae had the highest $Q_{O_2}$'s. After feeding began oxygen consumption stabilized and remained constant for the duration of the experimental period. On a weight-specific basis oxygen consumption increased with tissue dry weight and was best described by a power function (Fig. 8), although the relationship appears almost linear.

## Utilization Efficiency

Gross caloric conversion efficiencies were highest from fertilization to initial feeding, followed closely by efficiencies during the embryonic period (Table 6). Only in larvae from the highest food concentration did conversion efficiencies remain at elevated levels. Larvae feeding at the other food concentrations used their resources at levels under 20%, and their conversion efficiencies did not appear to correlate with food concentration. Starved larvae had the lowest efficiency and demonstrated negligible growth after D-7.

TABLE 6.—Mean gross caloric conversion efficiencies (in percent) for striped bass embryos, prefeeding larvae, and larvae feeding at different prey concentrations.

| To hatching | To initial feeding | Food concentrations (*Artemia*/ml) to 29 d after fertilization | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | 0.00 | 0.01 | 0.10 | 0.50 | 1.00 | 5.00 |
| 37.7 | 43.8 | 15.0 | 19.0 | 13.9 | 17.3 | 18.7 | 31.9 |

# DISCUSSION

## Energy Inputs

Striped bass eggs were found to be high in energy content and to vary considerably in size. Undoubtedly the high proportion of lipids (found mostly in the oil globule) makes the striped bass egg one of the most energy-rich of fish eggs. At 7,808 cal/g striped bass eggs exceed the caloric values of eggs from freshwater, anadromous, and marine fishes which normally range from 5,386 to 6,238 cal/g (Hayes 1949; Smith 1957,

Experiment 4   $Y=0.00170543e^{(0.680339X)}$
$r=0.97$

Experiment 5   $Y=0.00600652e^{(0.533521X)}$
$r=0.96$

Experiment 6   $Y=0.00236324e^{(0.652494X)}$
$r=0.93$

Experiment 7   $Y=0.00121027e^{(0.796209X)}$
$r=0.89$

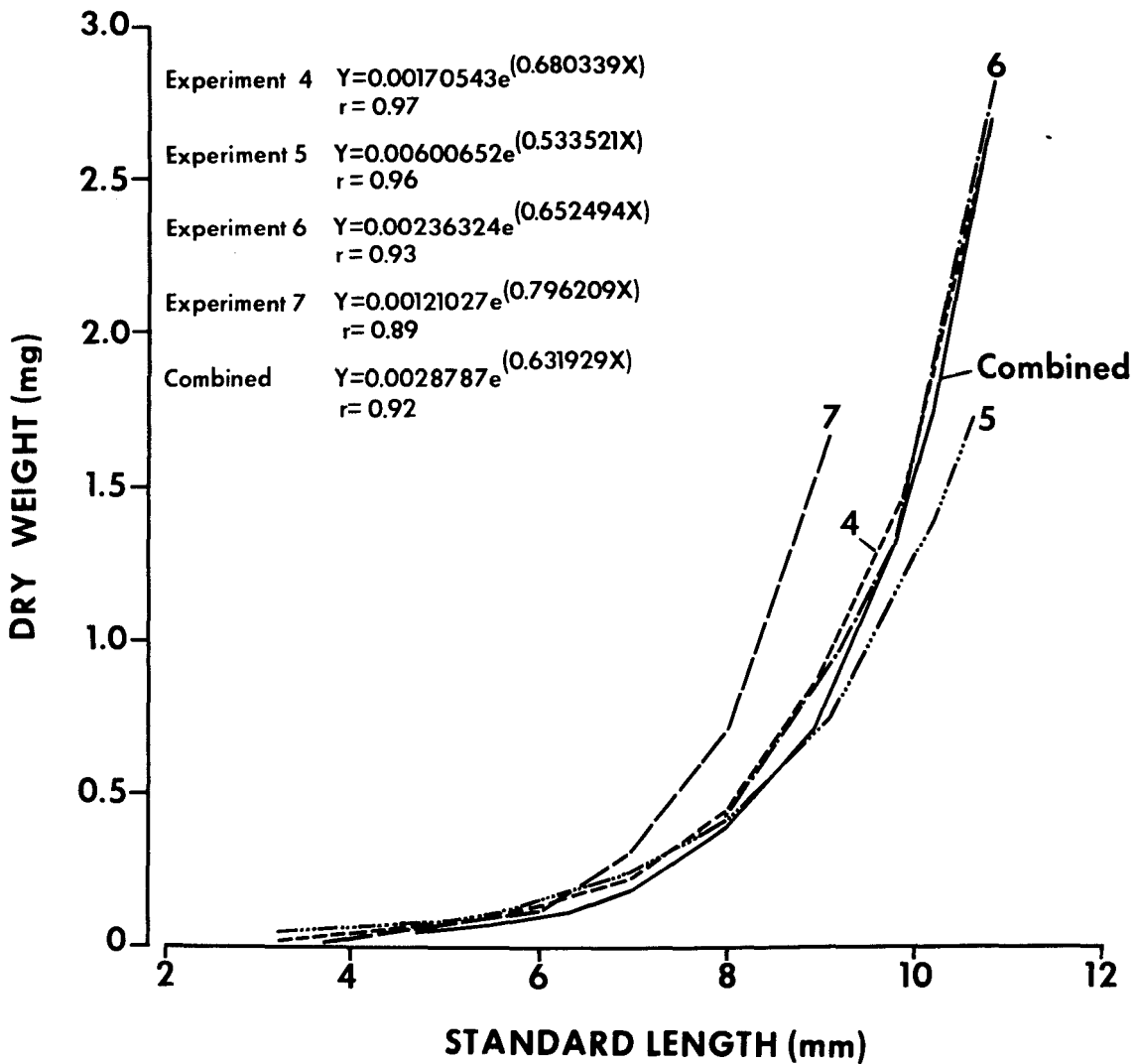Combined        $Y=0.0028787e^{(0.631929X)}$
$r=0.92$

FIGURE 7.—Assimilated tissue dry weights and corresponding standard lengths of four batches of striped bass larvae.

1958; Flüchter and Pandian 1968; Blaxter 1969). Egg size variability was not unexpected as eggs are reported to vary within and among a variety of fish species (*Clupea harengus*, Blaxter and Hempel 1963; *Sardinops caerulea*, Lasker 1962; *Trachurius symmetricus*, Ware 1975; Theilacker 1980[4]).

It appears from studies of embryos and larvae with large oil globules that the energy from the oil is important to larval growth and survival, and the influence of this energy source is present for long periods. In this study and that of Rogers and Westin (1981), striped bass larvae retained their oil energy reserves for extended periods, especially when starved. This is not common in fishes although similar retention of the oil globule was noted in *Bairdiella icistia* (May 1974a) and *Leuresthes tenuis* (May 1971; Ehrlich and Muszuski in press). The oil globule also seemed to help striped bass larvae avoid or prolong the typical point-of-no-return, the time of irreversible starvation (Eldridge et al. 1981). In a review of larval fish physiology, Theilacker (1980) concluded that in addition to egg size and activity, egg lipid level relates most to larval resilience.

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[4]Theilacker, G. H. 1980. A review of pelagic larval fish behavior and physiology. Presented at Institute del Mar del Peeru (IMARPE) Workshop, April 21-May 5, 1980.

$$y = 0.0276310 \, x^{0.721444}$$
$$r = 0.97$$
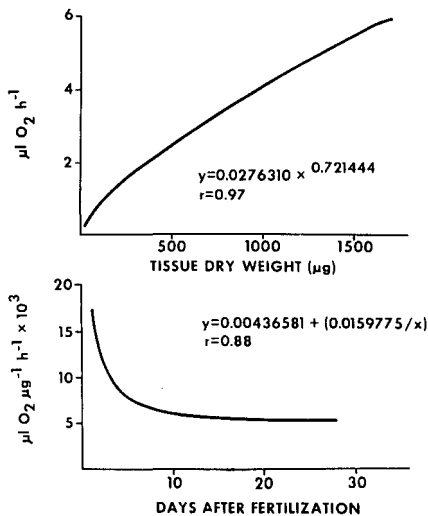
$$y = 0.00436581 + (0.0159775/x)$$
$$r = 0.88$$

FIGURE 8.—Oxygen consumption of striped bass embryos and larvae plotted against assimilated tissue dry weight (above) and age (below).

In an attempt to compare our laboratory derived estimates of daily food ration with those from wild striped bass larvae we obtained stomach content data of 1,468 field-caught larvae (sized to 11.9 mm SL) spawned from 1971 to 1973. The summarized data of Table 7 show wild larvae were smaller (4.0 to 4.9 mm) than laboratory larvae (6.1 mm) at the time of first feeding. This is possibly due to differences in preservation methods. When wild larvae attained sizes of 7.0 to 7.9 mm, over 75% were feeding. This agrees with our laboratory observation that over 80% of the 2-wk-old and older larvae (>7.0 mm SL) fed actively in food concentrations of 0.50 Artemia/ml and greater. The overall average of feeding incidence for wild larvae was 70.5%. Wild larvae also displayed preference for cladocerans, Cyclops sp. and Eurytemora sp., which, together, accounted for 89% of all food consumed. Other studies of striped bass from east coast nursery areas showed that the largest part of the larval diet consisted of small crustacea and microplankton (Meshaw 1969; Humphries and Cumming 1972).

Using these data we calculated daily caloric rations, according to the previously described formula, for each size category of wild larvae (Table 7). Caloric equivalences for the different food types were obtained from the literature (Richman 1958; Cummins 1967; Clutter and Theilacker 1971; Laurence 1976; Sitts 1978). In-

TABLE 7.—Average feeding incidences, stomach contents by food item, equivalent caloric values, and calculated daily caloric rations of 1,468 striped bass larvae collected in the San Francisco Bay/Delta estuary during 1971-73. The last column presents laboratory-derived average caloric rations for larvae of comparable sizes.

| Larval size (mm SL) | % with food in stomachs | Neo-mysis | Coro-phium | Clado-cerans | Cyclops | Diap-tomus | Eury-temora | Acartia | Harpac-ticoids | Misc. copepods | Total caloric equi-valent | Estimated daily ration (cal) | Laboratory derived average ration (cal) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3.0-3.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | — |
| 4.0-4.9 | 16.1 | 0 | 0.01 | 0.29 | 0.18 | 0 | 0.24 | 0.01 | 0.03 | 0.01 | 0.107 | 0.646 | — |
| 5.0-5.9 | 32.6 | 0.02 | 0.09 | 0.82 | 0.60 | 0 | 0.28 | 0.01 | 0.01 | 0.01 | 0.299 | 1.801 | |
| 6.0-6.9 | 57.5 | 0 | 0.10 | 0.80 | 0.81 | 0.01 | 0.38 | 0.01 | 0.01 | 0.01 | 0.317 | 1.910 | 0.183 |
| 7.0-7.9 | 76.7 | 0.02 | 0.11 | 0.82 | 1.00 | 0.01 | 0.49 | 0.01 | 0.02 | 0.01 | 0.357 | 2.152 | 0.151 |
| 8.0-8.9 | 80.9 | 0.04 | 0.14 | 0.97 | 1.22 | 0.01 | 0.63 | 0.01 | 0.02 | 0.01 | 0.436 | 2.627 | 0.520 |
| 9.0-9.9 | 84.7 | 0.09 | 0.18 | 1.08 | 1.25 | 0.01 | 0.68 | 0.01 | 0.03 | 0.02 | 0.496 | 2.989 | 1.245 |
| 10.0-10.9 | 85.3 | 0.16 | 0.22 | 1.31 | 1.27 | 0.04 | 0.82 | 0.01 | 0.01 | 0.02 | 0.599 | 3.609 | 2.607 |
| 11.0-11.9 | 82.9 | 0.19 | 0.28 | 1.51 | 1.37 | 0.02 | 0.92 | 0.01 | 0.02 | 0.01 | 0.689 | 4.151 | N/A |

formation on natural feeding duration was taken from Miller,[5] which showed that wild larvae feed 24 h a day but feed more intensely during crepuscular periods. Evacuation rate was set at 5 h, a compromise between our estimate of 3.3 h for larvae fed *Artemia* at 18°C and the estimate of 11 to 12 h made by McHugh and Heidinger (1977) for larvae given *Artemia* and held at 25°C. Daily caloric rations for wild larvae range from 0.646 cal for smaller larvae to 4.151 cal for 11.0 to 11.9 mm SL larvae. These rations are higher than those of laboratory larvae. Except for the largest cultured larvae, rations were usually one-half the field larvae rations. Thus within equivalent size categories wild larvae appear to have daily rations substantially greater than those of cultured larvae. Other estimates of daily rations of striped bass larvae range widely. Miller (footnote 5) concluded that field-caught larvae (6.8 to 9.2 mm SL) consumed rations equivalent to 0.159 cal for rotifers or up to 2.958 cal for cladocerans. Doroshev (1970) estimated daily intake of laboratory-reared larvae to be 9.704 to 29.112 cal, consisting of *Cyclops* nauplii or small copepods. Our average calculated daily estimates for the different food concentrations for the 29-d experimental period fall within Miller's estimates of wild larvae (Table 8).

TABLE 8.—Mean daily caloric rations of striped bass larvae given five different food densities from D-7 to D-29.

| Food density (Artemia/ml) | Mean overall daily caloric ration (calories/larva per d) |
|---|---|
| 0.01 | 0.035 |
| 0.10 | 0.439 |
| 0.50 | 0.802 |
| 1.00 | 0.823 |
| 5.00 | 1.313 |

## Energy Outputs

Our results suggest that there is compensatory growth in embryos and larvae that offsets initial egg size differences. The size ranges are not as broad in newly hatched larvae and larvae at first feeding (D-7) (seen in Table 5) as they are in the eggs. Likewise, initial egg size corresponds better to the size ranking of larvae at hatching age than it does to larvae at feeding age. The mean instantaneous growth coefficient during the 2-d embryonic period was 1.872 with a coefficient of

variation (C.V.) of 8.5% (Table 5). From hatching to first feeding it was 0.647 with a decreased C.V. of 7.0%, an indication of narrowing diversity. Further compensatory growth was seen in tissue weights and standard lengths of feeding larvae (Figs. 4, 5), and convergence of sizes was seen in all food concentrations above 0.10 *Artemia*/ml. Weights were similar on D-25 and lengths on D-27. In the two higher food concentrations, sizes converged by D-17. Compensatory growth was documented years ago in salmon fry (Hayes and Armstrong 1942), so this is not necessarily unique to striped bass. Theilacker (in press) more recently found that growth rates of jack mackerel larvae varied with egg size.

Growth of feeding striped bass larvae was clearly tied to exogenous food consumption as seen in Figure 6. This relation is well established in other larval fishes (O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; May 1974a; Houde 1977; Taniguchi in press).

Growth rates of our larvae, especially those in the higher food concentrations, are similar to findings with other populations of striped bass (Rogers et al. 1977). The most comparable study (Daniel 1976) included continuous introduction of *Artemia* for 10 d in concentrations of 0.004 to 0.030 nauplii/ml. Twenty-five days after hatching larvae grew to an average standard length of 8.5 mm. Fish used in the present study were longer than Daniel's in the two higher food concentrations and smaller in the three lower concentrations. As in our study, Daniel's larvae also grew directly in relation to food density. Tissue weights of Daniel's fish fed the 0.008 and greater *Artemia*/ml concentrations approximated those of our fish fed concentrations of 0.005 and above. Our larvae that fed at 5.0, however, were all heavier than Daniel's larvae. Lal et al. (1977) also cultured California striped bass larvae but in varying salinities. Larvae of comparable age feeding on *Artemia* (densities unreported) were similar to our larvae from the 0.50 nauplii/ml. Larvae from our higher densities were larger.

Oxygen consumption measurements varied directly with size, age, and temperature. Because temperature was held constant in all tests, age and size were the most influential factors affecting oxygen consumption, and these factors produced distinctive patterns. The high metabolic rates ($Q_{O_2}$'s) demonstrated by embryos and newly hatched larvae were probably the results of the activity accompanying hatching and of the high metabolic needs associated with rapid tis-

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[5]Miller, P. E., Jr. 1978. Food habit study of striped bass post yolk-sac larvae. The Johns Hopkins University, Chesapeake Bay Institute, Spec. Rep. 68, Ref. 78-8.

sue growth and differentiation. These needs remained high into the period of feeding transformation and then leveled off to nearly constant rates after D-10. Similar patterns have been seen in other fishes (Smith 1957; Blaxter 1969). The relation of oxygen consumption to weight is usually described in a log-log transformation with a slope approximating 0.8 (Winberg 1956). Our slope of 0.72 shows that our equation describes the weight-metabolism relation up to the final size encountered. Laurence (1977) found winter flounder metabolism profoundly changed after metamorphosis resulting in a curvilinear pattern described best by a third degree polynomial equation. It is likely that striped bass would show similar tendencies when measured further along in development.

Reviews (Blaxter 1969; Eldridge et al. 1977) show that efficiencies during the strictly endogenous energy period of embryos and prefeeding larvae ranged from 40% to 70%. Our findings with striped bass tended toward the low side of this range. *Micropterus salmoides* was most similar to striped bass, with efficiencies of 35.2% to hatching and 43.9% to feeding (Laurence 1969). Like those of striped bass, the eggs of *M. salmoides* also possess large oil globules, and their larvae have similar predatory behavior. Gross growth efficiencies of aquatic consumers in general normally fluctuate between 15% and 35% (Welch 1968). Efficiencies of larval and postlarval fishes have also been found to be within this range (Ivlev 1939a; Laurence 1973, 1977). Ivlev (1945) believed postembryonic stages were restricted to efficiencies <35%, and fish normally have decreasing efficiencies with age (Parker and Larkin 1959; Theilacker footnote 4). All our efficiency values support these conclusions. Whether feeding or not, our older larvae had lower conversion efficiencies, probably resulting from increased metabolic demands associated with greater activity.

All organisms must balance input and output energies to successfully survive, grow, and ultimately reproduce. The essential relations between input and output energies and the equation which balances them have been well discussed by several authors (Winberg 1956; Warren and Davis 1967; Warren 1971; Wiegert 1976). This paper presents data that make up the basic parameters of an energy budget. The basic relation of these components can be presented in:

$$Q_I = Q_W + Q_G + Q_M$$

where $Q_I$ = input energies, whether endogenous, exogenous, or a combination of the two

$Q_W$ = waste energy

$Q_G$ = growth energy

$Q_M$ = metabolic energy.

All but $Q_W$ have been studied by us, and the effects of food density and initial egg size have been discussed. In Figure 9 we present a graphic model of the energy budget of striped bass embryos and larvae fed the high ration diet (5.0 *Artemia*/ml). This model approximates that of Laurence (1977) except that we include input energies of yolk and oil, and we present the relations against time as rates (i.e., calories consumed or expended per 24 h period per organism).

When the energy budget is presented in these terms, some distinctive patterns emerge. Yolk provides a constant energy input until it is exhausted on or about D-7. Oil is used rapidly at first, then more slowly until yolk energy is no longer available and the animal initiates feeding. At this time, the larva increases its use of oil
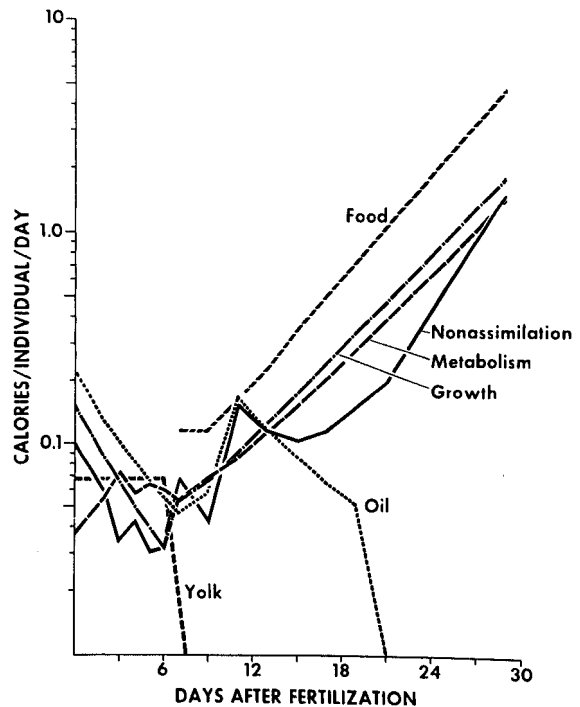


FIGURE 9.—Energy budget of input calories (yolk, oil, and food) and output calories (growth, metabolism, and nonassimilation) presented in calories per individual embryo or larva per day.

until exogenous feeding becomes established, after which it gradually decreases consumption of oil until oil energy is depleted. An initial adjustment to exogenous energy intake is followed by a continuously increasing exogenous input concomitant with decreased reliance on oil energy. Growth showed an interesting pattern that suggested it is closely linked to oil energy prior to feeding and to exogenous food energy after initiation of feeding. Growth rates declined steadily to D-6 and increased abruptly thereafter.

Metabolism increased steadily during incubation and hatching. After the energy consuming hatching process it decreased slightly to the onset of feeding. After D-7, increasing activity associated with feeding resulted in continuously increasing metabolism.

Nonassimilation is the energy remaining after metabolism and growth are subtracted from the total energy input. When energy input is endogenous, nonassimilation comprises poor utilization and/or redeposition of yolk and oil into other tissues. Nonassimilation of exogenous food is mostly due to undigested food. In this model nonassimilation fluctuated with oil input energy and growth to first feeding. It increased during adjustment to feeding and declined when both oil and food calories were available. As *Artemia* became the main energy source nonassimilation increased. Poor digestion in older larvae in the form of nearly intact *Artemia* in the intestines was seen commonly, especially in the high food rations.

The bioenergetics model and its parameters are presently being used to measure various abiotic and biotic stresses, including pollutants. It promises to be a useful method for assessing the effects of these factors.

## ACKNOWLEDGMENTS

## LITERATURE CITED

BLAXTER, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. III, p. 177-252. Acad. Press, N.Y.
BLAXTER, J. H. S., AND G. HEMPEL.
1963. The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Perm. Int. Explor. Mer 28:211-240.
BONN, E. W., W. M. BAILEY, J. D. BAYLESS, K. E. ERICKSON, AND R. E. STEVENS (editors).
1976. Guidelines for striped bass culture. Am. Fish. Soc., Striped Bass Comm. Southern Div. Spec. Rep., 103 p.
BRETT, J. R., AND T. D. D. GROVES.
1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (editors), Fish physiology, Vol. 8, p. 280-352. Acad. Press, N.Y.
CLUTTER, R. I., AND G. H. THEILACKER.
1971. Ecological efficiency of a pelagic mysid shrimp; estimates from growth, energy budget, and mortality studies. Fish. Bull., U.S. 69:93-115.
COONEY, T. D.
1973. Yolk sac stage energetics of the larvae of three Hawaiian fishes. M.S. Thesis, Univ. Hawaii, Honolulu, 57 p.
CUMMINS, K. W.
1967. Calorific equivalents for studies in ecological energetics. 2d ed. Univ. Pittsburgh, Pittsburgh, 52 p.
DANIEL, D. A.
1976. A laboratory study to define the relationship between survival of young striped bass (*Morone saxatilis*) and their food supply. Calif. Dep. Fish Game, Admin. Rep. 76-1, 13 p.
DOROSHEV, S. I.
1970. Biological features of the eggs, larvae and young of the striped bass [*Roccus saxatilis* (Walbaum)] in connection with the problem of its acclimatization in the U.S.S.R. J. Ichthyol. 10:235-248.
EHRLICH, K. F., AND G. MUSZUSKI.
In press. The relationship between temperature-specific yolk utilization and temperature selection of larval grunion. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178.
ELDRIDGE, M. B., T. ECHEVERRIA, AND J. A. WHIPPLE.
1977. Energetics of Pacific herring (*Clupea harengus pallasi*) embryos and larvae exposed to low concentrations of benzene, a monoaromatic component of crude oil. Trans. Am. Fish. Soc. 106:452-461.
ELDRIDGE, M. B., J. A. WHIPPLE, D. ENG, M. J. BOWERS, AND B. M. JARVIS.
1981. Effects of food and feeding factors on laboratory-reared striped bass larvae. Trans. Am. Fish. Soc. 110:111-120.
FLÜCHTER, J., AND T. J. PANDIAN.
1968. Rate and efficiency of yolk utilization in developing eggs of the sole *Solea solea*. Helgol. wiss. Meeresunters. 18:53-60.
FRY, F. E. J.
1971. The effect of environmental factors on the physiology of fish. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 6, p. 1-98. Acad. Press, N.Y.
HAYES, F. R.
1949. The growth, general chemistry, and temperature relations of salmonid eggs. Q. Rev. Biol. 24:281-308.
HORSEMAN, L. O., AND R. J. KERNEHAN.
1976. An indexed bibliography of the striped bass, *Morone saxatilis*, 1670-1976. Ichthyol. Assoc. Bull. 13, 118 p.

HOUDE, E. D.
1977. Food concentration and stocking density effect on survival and growth of laboratory-reared larvae of bay anchovy *Anchoa mitchilli* and lined sole *Achirus lineatus*. Mar. Biol. (Berl.) 43:333-341.

HUMPHRIES, E. T., AND K. B. CUMMING.
1972. Food habits and feeding selectivity of striped bass fingerlings in culture ponds. Proc. 25th Annu. Conf. Southeast. Assoc. Game Fish Comm. 1971:522-536.

IVLEV, V. S.
1939a. The effect of starvation on energy transformation during the growth of fish. Dokl (C.R.) Akad. Nauk SSSR, Nov. Ser. 25:90-92.
1939b. (Energy balance in the carp.) [In Russ., Engl. summ.] Zool. Zh. 18:303-318.
1945. The biological productivity of waters. [In Russ.] Ups. Sourem. Biol. 19:98-120. (Translated by W. E. Ricker, 1966. J. Fish. Res. Board Can. 23:1727-1759.)

LAL, K., R. LASKER, AND A. KULJIS.
1977. Acclimation and rearing of striped bass larvae in sea water. Calif. Fish Game 63:210-218.

LASKER, R.
1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine *Sardinops caerulea* (Girard). J. Fish. Res. Board Can. 19:867-875.

LAURENCE, G. C.
1969. The energy expenditure of largemouth bass larvae, *Micropterus salmoides*, during yolk absorption. Trans. Am. Fish. Soc. 98:398-405.
1971. Feeding and bioenergetics of largemouth bass larvae (*Micropterus salmoides*). Ph.D. Thesis, Cornell Univ., Ithaca, 139 p.
1973. Influence of temperature on energy utilization of embryonic and prolarval tautog, *Tautoga onitis*. J. Fish. Res. Board Can. 30:435-442.
1974. Growth and survival of haddock *(Melanogrammus aeglefinus)* larvae in relation to planktonic prey concentration. J. Fish. Res. Board Can. 31:1415-1419.
1976. Caloric values of some North Atlantic calanoid copepods. Fish. Bull., U.S. 74:218-220.
1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. Fish. Bull., U.S. 75:529-546.

MAY, R. C.
1971. Effects of delayed initial feeding on larvae of the grunion, *Leuresthes tenuis* (Ayres). Fish. Bull., U.S. 69:411-425.
1974a. Effects of temperature and salinity on yolk utilization in *Bairdiella icistia* (Jordan & Gilbert). (Pisces: Sciaenidae). J. Exp. Mar. Biol. Ecol. 16:213-225.
1974b. Larval mortality in marine fishes and the critical period concept. *In* J. H. S. Blaxter (editor), The early life history of fish, p. 3-19. Springer-Verlag, N.Y.

MCHUGH, J. J., AND R. C. HEIDINGER.
1977. Effects of light on feeding and egestion time of striped bass fry. Prog. Fish-Cult. 39:33-34.

MESHAW, J. C., JR.
1969. A study of feeding selectivity of striped bass fry and fingerlings in relation to zooplankton availability. M.S. Thesis, N.C. State Univ., Raleigh, 58 p.

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

PARKER, R. R., AND P. A. LARKIN.
1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16:721-745.

PFUDERER, H. A., S. S. TALMAGE, B. N. COLLIER, W. VAN WINKLE, JR., AND C. P. GOODYEAR.
1975. Striped bass - a selected annotated bibliography. Oak Ridge Natl. Lab., Environ. Sci. Div., Publ. 615, 158 p.

PHILLIPS, A. M., JR.
1969. Nutrition, digestion, and energy utilization. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 1, p. 391-432. Acad. Press, N.Y.

RICHMAN, S.
1958. The transformation of energy by *Daphnia pulex*. Ecol. Monogr. 28:273-291.

ROGERS, B. A., AND T. WESTIN.
1975. A bibliography on the biology of the striped bass, *Morone saxatilis* (Walbaum). Univ. R.I., Mar. Tech. Rep. 37, 134 p.
1981. Laboratory studies on effects of temperature and delayed initial feeding on development of striped bass larvae. Trans. Am. Fish. Soc. 110:100-110.

ROGERS, B. A., D. T. WESTIN, AND S. B. SAILA.
1977. Life stage duration studies on Hudson River striped bass. Univ. R.I., Applied Mar. Res. Group, NOAA Sea Grant, Mar. Tech. Rep. 31, 111 p.

SAKSENA, V. P., AND E. D. HOUDE.
1972. Effect of food level on the growth and survival of laboratory-reared larvae of bay anchovy (*Anchoa mitchilli* Valenciennes) and scaled sardine (*Harengula pensacolae* Goode & Bean). J. Exp. Mar. Biol. Ecol. 8:249-258.

SETZLER, E. M., W. R. BOYNTON, K. V. WOOD, H. H. ZION, L. LUBBERS, N. K. MOUNTFORD, P. FRERE, L. TUCKER, AND J. A. MIHURSKY.
1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). U.S. Dep. Commer., NOAA Tech. Rep. NMFS CIRC-433, 69 p.

SITTS, R. M.
1978. Ecological aspects of estuarine shrimps *Neomysis mercedis, Crangon franciscorum* and *Palaemon macrodactylus*. Ph.D. Thesis, Univ. California, Davis, 88 p.

SMITH, S.
1957. Early development and hatching. *In* M. E. Brown (editor), The physiology of fishes, Vol. 1, p. 323-359. Acad. Press, N.Y.
1958. Yolk utilization in fishes. *In* D. Rudnick (editor), Embryonic nutrition, p. 33-53. Univ. Chicago Press, Chicago.

STEVENS, D. E.
1977a. Striped bass (*Morone saxatilis*) monitoring techniques in the Sacramento-San Joaquin Estuary. *In* W. Van Winkle (editor), Proceedings of the conference on assessing the effects of power-plant-induced mortality on fish populations, Gatlinburg, Tenn., May 3-6, 1977, p. 91-109. Pergamon Press, N.Y.
1977b. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento-San Joaquin Estuary, California. Trans. Am. Fish. Soc. 106:34-42.
1980. Factors affecting the striped bass (*Morone saxatilis*) fisheries of the West Coast. Presented to Fifth Annual Mar. Rec. Fish. Symposium, March 1980, Boston, Mass.

TANIGUCHI, A. K.
In press. Survival and growth of spotted seatrout (*Cy-*

*noscion nebulosus*) larvae in relation to temperature, prey abundance and stocking density. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178.

THEILACKER, G. H.
In press. Effect of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus*, larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178.

TOETZ, D. W.
1966. The change from endogenous to exogenous sources of energy in bluegill sunfish larvae. Invest. Indiana Lakes Streams 7:115-146.

WARE, D. M.
1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32:33-41.

WARREN, C. E.
1971. Biology and water pollution control. W. B. Saunders Co., Phila., 434 p.

WARREN, C. E., AND G. E. DAVIS.
1967. Laboratory studies on the feeding, bioenergetics, and growth of fish. *In* S. D. Gerking (editor), The biological basis for freshwater fish production, p. 175-214. J. Wiley and Sons, N.Y.

WELCH, H. E.
1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49:755-759.

WIEGERT, R. G. (editor).
1976. Ecological energetics. Dowden, Hutchinson, and Ross., Inc., Stroudsburg, Pa., 457 p.

WINBERG, G. G.
1956. (Rate of metabolism and food requirements of fishes.) [In Russ.] Nauch. Tr. Belorussk. Gos. Univ. Imeni V.I. Lenina, Minsk, 253 p. (Fish. Res. Board Can. Transl. Ser. 194, 239 p.)