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Effects of Food and Feeding Factors on Laboratory-Reared Striped Bass Larvae

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Abstract

Fluctuations in year-class size of striped bass (*Morone saxatilis*) are believed related to early-life-stage mortality. Factors associated with food and feeding of larvae were studied in the laboratory as they relate to mortality, point of no return, development, and energetics. Mortality of feeding larvae was directly related to density of *Artemia salina* nauplii. Highest mortality coincided with total oil globule absorption. Starved larvae lived an average 31 days after fertilization and did not display a well-defined point of no return. Growth and differentiation directly correlated with food density. Starvation affected the rate of ossification and altered cells and tissues as early as 7 days after hatching. Most of the endogenous energy of newly fertilized eggs is in oil. The rate of oil utilization was inversely related to food density. Daily food rations were estimated after ingestion and digestion rates were determined, and increased with larva size, age, and prey density.

Between 1879 and 1882, 432 juvenile striped bass (*Morone saxatilis*) from the Navesink River, New Jersey, were released into the San Francisco Bay-Delta estuary. The transplant was so successful that, within 10 years, the commercial fishery landed 554 t (Skinner 1962). In less than 100 years, the Pacific range of striped bass has expanded south to 30 km below the United States-Mexico border and north to Barkley Sound, British Columbia (Miller and Lea 1972).

Over the intervening years, sport and commercial catch records have indicated considerable fluctuations in the Pacific striped bass population (Smith and Kato 1979), and present estimates place the population at 33 to 40% of its peak 1960 estimate of 3.0 to 4.5 $\times$ 10^6 fish. Recent field data indicate that mortality during the first 60 days after hatching determines the size of the adult population. Further, abundance of young-of-the-year juveniles is directly related to river outflows and diversion volumes in the Sacramento-San Joaquin River Delta (Chadwick et al. 1977). However, aside from direct export of eggs and larvae out of the estuary via water diversions, the actual causes of mortality remain undetermined. As part of a cooperative research program involving the California Department of Fish and Game, the United States Water and Power Resources Service, and the National Marine Fisheries Service, we have conducted laboratory studies of mortality factors associated with larval food and feeding. Among marine fish larvae, starvation and food and feeding factors are primary causes of mortality (Hunter 1976). This paper summarizes our analyses of food-related mortality and development, and other related features of striped bass larvae.

Methods

Adult striped bass in spawning condition were electrofished in the Sacramento River, injected with human chorionic gonadotropin by methods of Bayless (1972), and transported to the California Department of Fish and Game Central Valleys Hatchery, Elk Grove, California. Mature gametes were stripped from these adults within 26–36 hours. To ensure known percentage of each of nine pairings, eggs from a single female were fertilized with sperm from a single male. Newly fertilized eggs were allowed to water-harden 1.5–2.5 hours. We then transported them to the Tiburon Laboratory where they were incubated in McDonald jars in dechlorinated tap water at 18 C.

Hatching occurred within 48 hours as Rogers et al. (1977) found. Newly hatched larvae were placed in semispherical green acrylic plastic containers filled with 8 liters of water; the containers were placed in water tables. Larva densities differed among studies. In survival studies, two replicate containers with 25 larvae in

each were used. Larvae used for growth and development were stocked at 100 larvae per container at four replicates per food concentration. To approximate natural water quality conditions, salinity was maintained at 1‰ from 6 to 13 days after fertilization and at 3‰ from day 14 until the completion of each experiment. Under average conditions in the San Francisco Bay-Delta estuary, striped bass eggs and prefeeding larvae migrate from upstream waters less than 0.5‰ salinity to approximately those of 1.0‰ within 6 to 7 days after spawning. Larvae then move into shallow nursery areas where average salinities increase 1–3‰ depending on tidal flow and river discharge (Conomos et al. 1979). Water temperatures were maintained at 18.0 ± 0.5 C (±range) and dissolved oxygen was stable at or near saturation.

Larvae were given newly hatched *Artemia salina* nauplii at initial concentrations of 0.00, 0.01, 0.50, 1.0, and 5.0 nauplii/ml; there were two replicate containers per food concentration. These food densities range above and below the estimated field concentration of 0.10 zooplankter/ml (Daniel 1976). Food and water were changed daily in each container.

The "point of no return," the time when starved larvae will not feed even when food is introduced (May 1974), was determined by holding larvae without food (25 larvae per container, two replicates) for 10, 14, 18, 22, 26, and 28 days before nauplii were presented to them. Daily survival and size at the age of 31 days after fertilization were measured.

Development was monitored by removing eggs at 12-hour intervals during incubation, by sampling larvae daily from hatching to day 7 (time measured from fertilization), and by sampling feeding larvae on alternate days until the end of the experiments. Morphometric measurements were made with an ocular micrometer. Dry weights of assimilated tissues, yolk, and chorions were obtained by careful dissection of eggs and larvae, drying for 24 hours at 60 C, and measurement on a microbalance. Oil weights were estimated by subtraction of the weighed body components from total weights. A developmental series was differentially stained for cartilage and bone development with Alcian blue and Alizarin to monitor ossification. Another developmental series was fixed in Bouin's solution, stained with hematoxylin and eosin, and sectioned in 7-μm longitudinal and cross sections.

Bioenergetic studies followed procedures of Eldridge, et al. (1977). Feeding rates were determined by introducing food to larvae held without food for 24 hours, and by removing and examining larvae at 2-hour intervals. Digestion rates were determined by feeding dyed nauplii to larvae for 1.5 hours, replacing uneaten dyed nauplii with unmarked ones (so that larvae could continue feeding), and examining anesthetized larvae every half hour. The dyeing procedure consisted of allowing nauplii to feed on dense cultures of *Nephroselmis* sp. until the intestinal tract was pigmented dark green. In this way, we measured the time required for dyed foods to pass through the digestive tracts of actively feeding larvae.

Results

Mortality

Estimation of mortality during the embryonic and prefeeding larval stages was difficult because spawning success varied greatly. In three spawning seasons, only five of nine spawnings were sufficiently successful to allow us to rear striped bass to metamorphosis. In the four unsuccessful spawnings, nearly 100% mortality occurred, most taking place 12–18 hours after fertilization. In contrast, embryos and larvae in the successful spawnings had high (>80%) survival up to the time of feeding.

For this reason, quantitative emphasis was given to mortality during the larval feeding stage, from 7 to 31 days after fertilization. Survival was directly related to food concentration (Fig. 1). The average daily instantaneous mortality (Y) was inversely correlated ($r = 0.85$) with food concentration (X), and was best described by the equation $Y = 1/(41.90 + 27.56X)$:

Nauplii per milliliter	Instantaneous daily mortality
0.00	0.12
0.01	0.051
0.10	0.027
0.50	0.013
1.00	0.008
5.00	0.006

The overall survival pattern of larvae at all food densities was similar. The small decrease in sur-

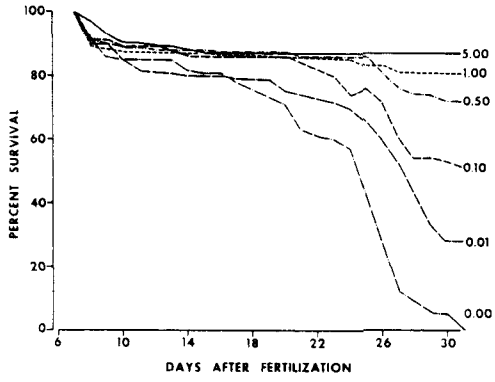

FIGURE 1.—*Survival of striped bass larvae feeding on six different food concentrations of* Artemia salina *(0.00–5.00 nauplii per milliliter).*

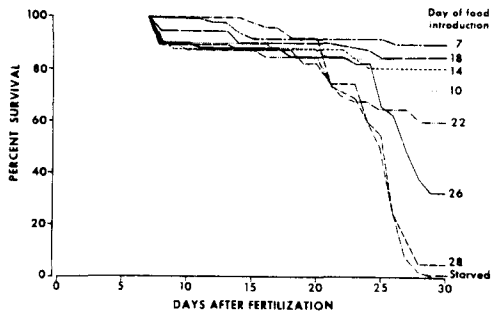

FIGURE 2.—*Survival of striped bass larvae given initial food at progressively later ages (7–28 days after fertilization).*

vival after food introduction is presumably an adjustment to feeding. Increased mortality rates occurred at all food concentrations after day 18, except among larvae at the highest food density (5.0 nauplii/ml), coinciding with the total absorption of the oil globule. Starved larvae demonstrated remarkable resistance to food deprivation by living for 31 days after fertilization.

Point of No Return

Larvae did not display a well-defined point in time when they were not able to successfully ingest and utilize food. Over 70% of the larvae given food on and before 18 days after fertilization survived (Fig. 2). Larvae deprived of food for longer periods appeared to undergo an adjustment when weaker larvae died. Mortality then stabilized, but at progressively lower levels. We observed that survival seemed to depend on the larva's ability to capture prey, which was a function of prey density and remaining strength. Size of larvae on day 31 was inversely related to their age at first food introduction (Table 1). As in mortality, larvae deprived of food from age 18 days or less grew to approximately similar lengths. Comparative weights reflected starvation times more clearly than lengths.

Development

Growth, as measured by tissue dry weight, was linear for embryos and larvae up to the time of feeding (Fig. 3). Newly hatched larvae averaged 3.4 mm standard length (SL) and length increased hyperbolically to 6.0 mm by day 7 when they began feeding (Fig. 4).

Growth rates of larvae correlated with food concentrations (Fig. 4). Below 0.10 nauplii/ml (the estimated concentration of zooplankton in the delta), larvae decreased in size and growth rates were negative. Food concentrations higher than 0.10 nauplii/ml resulted in increased growth rates, the highest being at food concentrations of 5.0 nauplii/ml.

Rates, rather than sequences, of larval differentiation were markedly affected by food density. Our differential staining technique distinguished cartilage from endochondral bone that preforms in cartilage. When larvae began to feed 7 days after fertilization, they exhibited extensive cartilage in the branchiocranium.

TABLE 1.—*Mean sizes ± SD of striped bass larvae on day 31 following delayed first feeding.*

	Age at food introduction (days from fertilization)					
	7	10	14	18	22	26
Standard length (mm)	10.8 ± 0.5	11.4 ± 0.5	10.4 ± 0.8	9.0 ± 1.2	7.4 ± 0.8	6.1 ± 0.3
Dry weight (μg)	7.12 ± 0.10	5.83 ± 0.18	3.43 ± 0.40	1.54 ± 0.70	0.36 ± 0.17	0.14 ± 0.02

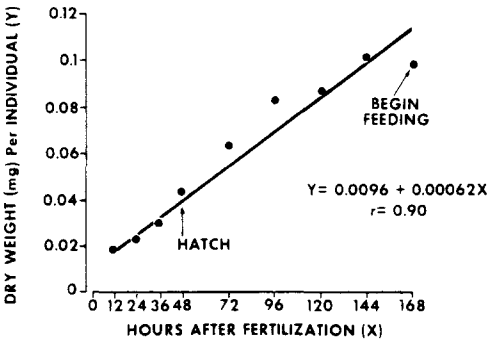

FIGURE 3.—*Dry weight of dissected tissue of striped bass embryos and prefeeding larvae.*

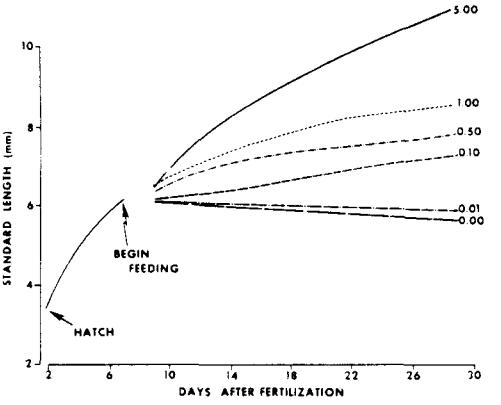

FIGURE 4.—*Standard lengths of striped bass larvae feeding on six concentrations of* Artemia salina *(0.00–5.00 nauplii per milliliter).*

The upper and lower jaw bones, cleithrum, branchiostegals, and bases of the pectoral fins (coracoid and scapula) were well formed in cartilage. In the absence of food and at the lowest food concentration (0.01 nauplii/ml), no change in the amount of cartilage or ossification was seen for 31 days, when the remaining larvae died. In larvae fed 5.0 nauplii/ml, ossified bones were found as early as day 9. The rate of ossification was slower with each decrease in food concentration. In all cases, ossification began in the cleithrum, premaxillary, maxillary, and dentary bones.

Examination of sectioned larvae revealed differences in cells and tissues between fed and starved larvae beginning as early as day 9. Most obvious were the deterioration and disintegration of cells in tissues associated with the digestive tracts of starved larvae (Fig. 5). Tissue conditions of starved larvae closely paralleled those reported for jack mackerel, *Trachurus symmetricus*, and northern anchovy, *Engraulis mordax* (O'Connell 1976; Theilacker 1978).

Energetics

The endogenous energy sources of striped bass embryos and larvae consist of yolk and oil, the latter in the form of a single large globule (Fig. 6). These egg constituents, as well as total weights, varied considerably among females (Table 2). Eggs initially weighed 285 μg with a coefficient of variation of 19% (100·SD/mean). The average energy available to the beginning embryo was 2.068 calories. Although the oil contributed 55% of the egg weight, it supplied 72% of the total egg energy at 9,441 cal/g. Proteinaceous yolk (5.404 cal/g) was 38% of egg weight, but accounted for only 28% of total energy.

Larvae used their yolk reserves first (Eldridge$_2$ et al. 1977). Total yolk absorption coincided with the onset of feeding on day 7. The efficiency of energy conversion to this point of development was 56.2%. To hatching it was 53.9%. The rate of utilization of the remaining oil was inversely related to the amount of food available; starved larvae retained their oil globule for the longest period while fed larvae channeled oil energy into feeding and development (Fig. 7).

Estimates of exogenous energy utilization, expressed as daily food ration, required information on food intake and digestion rates. In our experimental conditions, larvae fed most actively the first 10 hours after food introduction (Fig. 7). Limited feeding occurred at night. Day-12 larvae were the most active nocturnal feeders. Prey densities related most directly to feeding rates in the oldest larvae. Larvae in low food densities consistently fed at the lowest rates, while larvae in higher densities varied more. Larvae with the most food available (5.0 nauplii/ml) fed at lower rates at ages 12 and 21 days, but were seen to extend their feeding well into the night.

The time required for a unit of food to pass through the digestive tract of a larva under experimental conditions of continuous feeding ranged from 1.5 to 5.5 hours (Table 3). Times varied considerably and patterns were not

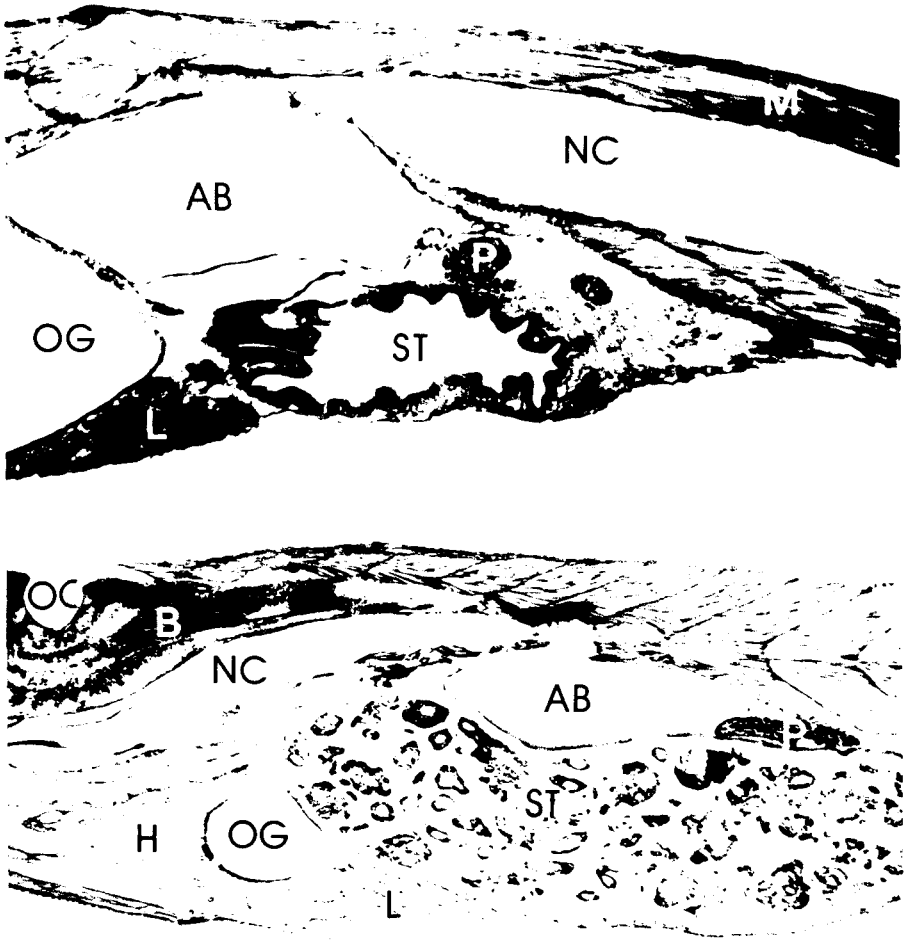

FIGURE 5.—*Longitudinal sections through midsections of 21-day-old starved (above) and fed (below) striped bass larvae. AB = air bladder; B = brain; H = heart; L = liver; M = muscle; NC = notochord; OC = otic capsule; OG = oil globule; P = pancreas; ST = stomach.*

readily apparent. When data are combined, digestion generally appeared to be shorter at the middle ages in all food concentrations. Larger larvae feeding in the two higher food densities had progressively lower digestion times.

From the above feeding and digestion rates we calculated daily food rations according to the formula: $FR = NH/D$, where FR = daily food ration, N = average number of nauplii in stomachs, H = hours of active feeding, and D = digestion time. The results were also expressed in calories and equivalent numbers of zooplankters (Table 4). The latter figures were calculated from relative compositions of different food items (unpublished data, California Department of Fish and Game) in guts of wild larvae and their caloric values (Cummins 1967; Laurence 1974). Daily rations increased with larva size and age, and prey density. In the two high food densities, the ration actually decreased between the 21- and 33-day larvae. This was most likely a result of limited food supply for the older larvae because they were

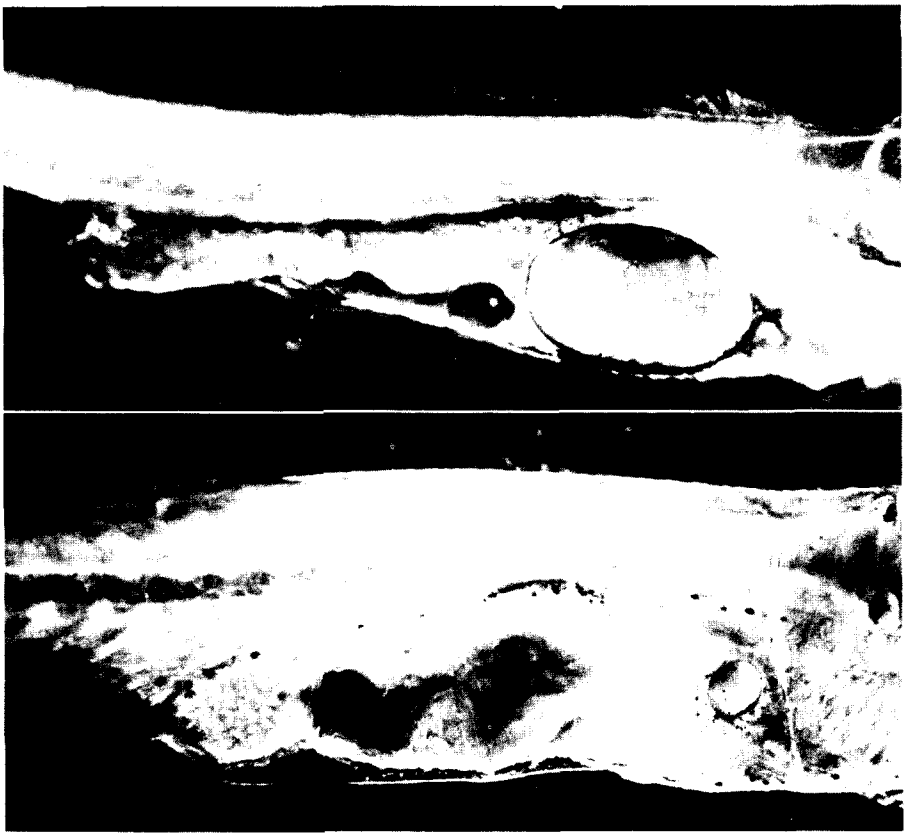

FIGURE 6.—*Photomicrographs of live striped bass larvae 19 days after fertilization. Note different sizes of oil globules in starved (above) and fed (below) larvae.*

more efficient feeders and grazed the finite food supply more quickly.

Discussion

Major findings of our research are in general agreement with comparable studies (Daniel 1976; Lal et al. 1977; Miller 1977; Rogers and Westin 1977; Rogers et al. 1977; Rogers 1978).

Greatest mortality of striped bass larvae occurs when the endogenous energy source (yolk and oil) is exhausted. Differences in the ages of larvae when mortality rates were highest are

TABLE 2.—*Dry weights and caloric contents of six unfertilized striped bass eggs.*

	Dry weight (μg)				Caloric content (cal)		
Egg	Yolk	Oil	Chorion	Total	Yolk	Oil	Total
1	0.089	0.128	0.014	0.231	0.481	1.208	1.689
2	0.131	0.089	0.028	0.248	0.708	0.840	1.548
3	0.089	0.137	0.023	0.249	0.481	1.293	1.774
4	0.114	0.150	0.022	0.286	0.616	1.416	2.032
5	0.118	0.189	0.014	0.321	0.638	1.784	2.422
6	0.106	0.251	0.016	0.373	0.573	2.370	2.943
Mean ± SD	0.108 ± 0.017	0.157 ± 0.056	0.019 ± 0.006	0.285 ± 0.054	0.583 ± 0.090	1.485 ± 0.530	2.068 ± 0.528

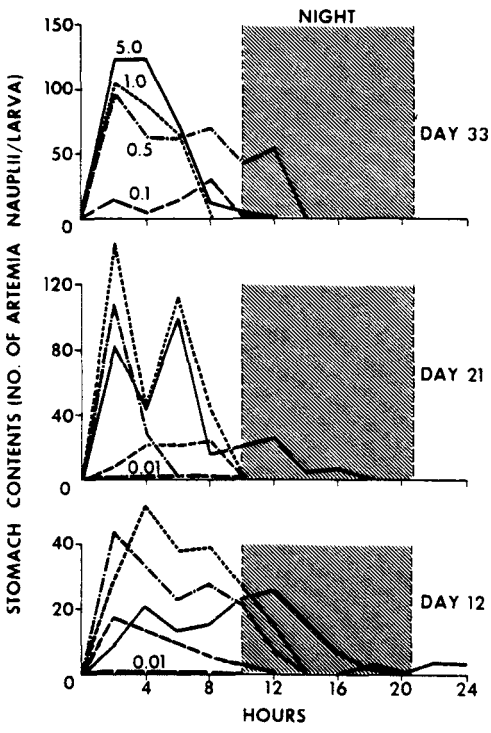

FIGURE 7.—*Twenty-four-hour feeding rates of striped bass larvae of three ages fed five concentrations of* Artemia salina *(0.01–5.00 nauplii per milliliter). Larvae fed 0.01 nauplii per milliliter had died by day 33.*

TABLE 3.—*Digestion rates (hours/larva) of striped bass larvae fed different concentrations of dyed* Artemia salina *nauplii. Hours to 50 and 100% signify time required for either half or all of sampled larvae to completely evacuate dyed nauplii.*

Prey concentrations (nauplii/ml)	Larva age (days from fertilization)	Larva standard length (mm)	Evacuation	
			Hours to 50%	Hours to 100%
		Experiment 1		
0.01	11	5.7	3.0	3.0
	20	5.6	1.5	2.5
0.10	11	6.0	3.5	4.5
	20	6.3	2.0	3.0
	33	9.3	2.0	2.0
0.50	11	6.7	3.5	4.0
	20	7.3	3.5	5.0
	33	8.0	4.5	4.5
1.00	11	6.7	2.5	3.5
	20	7.5	3.5	4.5
	33	8.2	5.0	5.0
5.00	11	7.0	2.0	2.5
	20	9.6	2.0	2.5
	33	10.8	2.5	3.0
		Experiment 2		
0.01	9	6.1	3.5	3.5
	20	5.9	1.5	1.5
	28	6.1	2.5	2.5
0.10	9	6.3	3.0	3.5
	20	6.7	2.0	2.5
	28	6.7	3.0	3.0
0.50	9	6.3	3.0	3.0
	20	7.6	1.5	2.0
	28	7.6	2.5	3.0
1.00	9	6.4	4.0	5.5
	20	8.1	1.0	2.5
	28	9.4	3.0	3.0
5.00	9	6.4	4.0	5.5
	20	9.9	1.0	2.0
	28	10.6	2.5	3.0

attributable to differences in times of total yolk and oil absorption.

Larva survival is related to food availability. This relationship was supported by other studies (Daniel 1976; Miller 1977) despite different prey concentrations and experimental conditions.

Striped bass larvae are highly resistant to food deprivation as evidenced by their long survival times when starved and the apparent absence of a "point of no return." Rogers and Westin (1981) had similar results in studies of east coast striped bass. The absence of a point of no return has only been noted in bairdiella, *Bairdiella icistia* (May 1971) and California grunion, *Leuresthes tenuis* (Ehrlich and Muszanski, in press). Miller (1977) concluded the point of no return for striped bass was 10 days after hatching. We believe the rearing conditions in his system were more stressful than in either Rogers (1978) or ours, such that overall survival was probably affected. The biggest contrast was in the smaller rearing containers, higher stocking densities for larvae and food, and the use of fresh water throughout his experiment. In particular, we found a gradual increase of salinity, as is normal for striped bass, to be beneficial.

Development of striped bass larvae, as measured by growth and differentiation, is directly correlated with prey concentration. The growth rates of our larvae fed at the highest concentration compared favorably with those of wild and laboratory-reared striped bass for the same developmental period (Mansueti 1958; Hum-

TABLE 4.—*Daily food rations (expressed in numbers of* Artemia salina *nauplii, equivalent calories, or equivalent wild zooplankters consumed per larva per day) of striped bass larvae fed different concentrations.*

Prey concentration (nauplii/ml)	Larva age (days from fertilization)	Daily food ration		
		Nauplii	Calories	Wild zooplankton
0.01	12	0.3	0.003	0.4
	21	1.9	0.018	2.5
0.10	12	22.8	0.218	29.9
	21	28.7	0.274	37.6
	33	66.0	0.630	86.5
0.50	12	79.5	0.759	104.3
	21	56.4	0.539	74.0
	33	173.3	1.655	227.4
1.00	12	115.6	1.104	151.7
	21	151.0	1.442	198.1
	33	102.7	0.981	134.8
5.00	12	111.2	1.062	145.9
	21	247.0	2.359	324.1
	33	225.2	2.150	295.4

phries and Cumming 1973; Daniel 1976; Lal et al. 1977; Rogers 1978). Larvae feeding at the estimated average field zooplankton density developed at a much slower rate.

Descriptions of the sequence and rate of utilization of the yolk and oil reserves are not consistent in the literature. Yolk and oil were resorbed simultaneously (Mansueti 1958; Doroshov 1970) or the oil persisted after total yolk absorption (Doroshov 1970; Miller 1977; Rogers 1978; this study). In no instance was the oil globule reported to persist for as long as in our study. A full discussion of the role of the oil globule is given by Eldridge, et al. (1977). We postulate that the oil functions as an energy reserve that can be conserved when food is not abundant.

The energy content of oil per unit volume is approximately double that of yolk, which makes it more practical. In the event of food deprivation, the larva can utilize this energy source rather than resorb tissue. During active feeding, oil energy and exogenous food energy both were mobilized to maximize growth. This helps to shorten the duration of the vulnerable larval life stage. This reserve could account for much of the reported resilience and adaptability of striped bass larvae (Doroshov 1970; Davies 1973; Rogers et al. 1977).

Preliminary results from the ossification and histology studies seem to indicate that differentiation in starved larvae is noticeably affected as early as 9 days after fertilization. Detailed descriptions of these processes should provide indicators that could be applied to wild larvae, as was done with northern anchovy and jack mackerel (O'Connell 1976; Theilacker 1978).

In our laboratory studies, the estimated concentration of zooplankton in the San Francisco Bay-Delta estuary (0.1 zooplankter/ml) resulted in larval survival of 51% for the feeding stage but development of the larvae was suppressed, meaning the duration of the larval stage was prolonged. Because the larval period is inherently one of high mortality, extending its duration increases mortality. Growth of our larvae feeding at the high rations approximated that of wild larvae; yet there was up to a 50-fold difference in food densities. This discrepancy may not be as divergent after we compare computed rations of wild larvae with our results, and also consider that our laboratory larvae did not have a constant density throughout a day. Nonetheless, the apparent need of striped bass larvae for food densities greater than 0.1 organism/ml in order to attain normal growth rates leads us to suggest that wild zooplankton densities may be underestimated. Zooplankton estimates are spatially integrated and provide no information on the degree of patchiness. We hypothesize that wild larvae locate patches of zooplankters denser than 0.1 zooplankter/ml, and thereby find food to meet their metabolic requirements. In similar fashion northern anchovies are believed to associate with zooplankton patches (Hunter and Thomas 1974; Lasker 1975).

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