ENERGY UTILIZATION IN BAY ANCHOVY, *ANCHOA MITCHILLI*, AND BLACK SEA BASS, *CENTROPRISTIS STRIATA STRIATA*, EGGS AND LARVAE[1]

JOHN W. TUCKER, JR.[2]

ABSTRACT

Bay anchovy, *Anchoa mitchilli*, and black sea bass, *Centropristis striata striata*, both produce abundant, small, planktonic eggs and larvae, but these appear to have contrasting nutritional strategies. Developmental changes and energy utilization in eggs, unfed larvae, and fed larvae of the two species suggest that black sea bass are better able to resist fluctuations in food availability (survive and grow at lower prey densities). Black sea bass have more time to find food and develop feeding skills—47 hours between first feeding and yolk exhaustion vs. 8 hours for bay anchovies. Sea bass feed more efficiently than anchovies. Over the first 96 hours after first feeding, capture success averaged 85% for sea bass and 60% for anchovies. Gross growth efficiency of sea bass (13%) was more than twice that of anchovies (5%). Sea bass may also be more resistant to starvation because their yolk lasts longer (180 hours vs. 80 hours after hatching) and because, during starvation, their metabolism is lower and they lose body calories at a lower rate.

An important determinant of survival of larval fishes is their ability to fulfill nutritional requirements after yolk energy is exhausted. The manner in which energy is used by fish eggs and larvae may indicate adaptability of early stages relative to food composition or abundance. Differences in energy utilization among species might result from different feeding strategies or from adaptation to different feeding conditions (Hunter 1980).

The bay anchovy, *Anchoa mitchilli*, a clupeiform planktivore, is a major food item for predaceous fishes along the U.S. Gulf and Atlantic coasts. Adults are pelagic and live in shallow coastal waters from the Gulf of Maine to Yucatan, Mexico (Hildebrand 1963). In North Carolina, spawning by large schools occurs just after sunset in estuaries and coastal waters from late April to early September and peaks during late June to early August (Kuntz 1914; Hildebrand and Cable 1930; pers. obs.). Eggs (which lack oil globules) and larvae are planktonic and occur in estuaries and bays and just offshore. Spawning might occur over a wide temperature range (Dovel 1971), but larval growth is best in the mid to high twenties (Houde 1974). Early juveniles are abundant in brackish water and also enter fresh water.

The black sea bass, *Centropristis striata striata*, a perciform piscivore generally found offshore, supports important commercial and sport fisheries along the U.S. Atlantic coast. It is distributed over the continental shelf and in bays from Cape Cod, MA to Cape Canaveral, FL and occasionally to the Gulf of Maine or Florida Keys (Miller 1959; Musick and Mercer 1977). Adults are demersal, and south of Cape Hatteras they are found on rough bottom over the inner shelf. Spawning takes place over the inner shelf, mostly in spring or summer, depending on latitude (Musick and Mercer 1977). Off North Carolina, peak spawning is from March to early June. Eggs (with a single oil globule) and larvae are planktonic and occur in shelf waters of 15–51 m depth (Kendall 1972). Juveniles are often found in high salinity estuaries and bays but move into deeper water as they grow.

Several aspects of the feeding ecology of bay anchovy larvae have been investigated, but little is known about black sea bass larvae. Houde and Schekter (1981, 1983) compared growth and energetics of bay anchovy; sea bream, *Archosargus rhomboidalis*; and lined sole, *Achirus lineatus*, larvae. No studies of black sea bass larval ecology have been published, but the southern sea bass, *C. striata melana*, has been reared under experimental mariculture conditions in Florida (Hoff 1970; Roberts et al. 1976; Harpster et al. 1977).

This paper presents information on developmental events and energy utilization for bay anchovy and

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[1] Contribution 673, Harbor Branch Oceanographic Institution, Fort Pierce, FL.

[2] Harbor Branch Oceanographic Institution, 5600 Old Dixie Highway, Fort Pierce, FL 34946.

Manuscript accepted November 1988.
Fishery Bulletin, U.S. 78:279–293.

black sea bass from just after fertilization through the eighth day of feeding. Results are used to infer differences in early survival and growth capabilities in nature. Particularly important are differences during the first 96 hours of feeding, which probably arise from adaptations necessary for exploiting different food supplies. Prey densities tend to be lower in the larval black sea bass's habitat (Theilacker and Dorsey 1980).

MATERIALS AND METHODS

The study was conducted with eggs, unfed larvae, and larvae fed for 8 days. The timing of the following developmental events was noted: hatching (H), completion of eye pigmentation (EP), first feeding (FF), yolk exhaustion (EYS), and death of unfed larvae (S). Measurements were made of notochord length (NL), dry weight, % ash, % total carbon, % total nitrogen, % total lipid, energy content, oxygen consumption, feeding efficiency, and feeding rate.

Egg Sources

Bay anchovy eggs usually (40 collections) were obtained 3-5 hours after spawning (before morula stage) by stationary plankton tows in Pivers Island Channel, near Beaufort, NC. For one series of oxygen uptake measurements, eggs and milt were obtained by stripping ripe adult anchovies. Black sea bass eggs were stripped from six females (313–672 g), in which ovulation had been induced by injection of human chorionic gonadotropin, and they were fertilized artificially (Tucker 1984).

Culture Conditions

Physical conditions for rearing experiments approximated those in natural habitats in North Carolina waters during peak spawning. Temperatures were slightly lower than optimal for growth. Bay anchovies were maintained at 24°C and 32‰ with a 14L:10D photoperiod. Black sea bass were maintained at 20°C and 34‰ with a 12L:12D photoperiod. Fluorescent lighting provided 1400 lux at the water surface. Incubation and rearing took place in one to eight (usually six) 10 L black cylindrical fiberglass tanks of filtered seawater. Initial stocking density was 30 or fewer eggs per liter. First-feeding larval density was reduced to fewer than 15/L. Rotifers, *Brachionus plicatilis*, of the same strain investigated by Theilacker and McMaster (1971) were added when larval eye pigmentation was complete, and densities were maintained at about 20/mL. Phytoplankton, *Chlorella* sp. or *Nannochloris* sp., was also added as food for the rotifers. Nutritional quality of starving rotifers diminishes rapidly. Unless well-fed rotifers are added frequently and all of them are eaten quickly, algae must be present in the rearing tanks to maintain their quality. Good rotifer nutrition also ensures that they continue to reproduce, thus maintaining the full size range. Without algae, rotifers not eaten within several hours become empty shells. Without reproduction, a rotifer population tends to consist entirely of large adults.

Measurements and Calculations

The times of eye pigmentation and yolk exhaustion were determined by microscopic examination. Starvation mortality was determined in the 10 L rearing tanks (5 times for each species, 1–3 tanks). In addition, three starvation mortality determinations were made in 2 L dishes using bay anchovy eggs collected on different nights. For each determination, 25 normally developing eggs were placed in each of eight 2 L black glass dishes; dead eggs and larvae were counted and removed periodically, with 100% recovery.

Egg and larval dry weights were determined directly. Daily samples (usually 30 individuals) were taken randomly from the rearing tanks for determination of dry weight. Each group of specimens was rinsed in distilled water and freeze-dried before weighing. Best-fit regression equations were used to predict dry weight at different ages during development. Notochord length of 10–52 specimens was measured at key times during development. Instantaneous, or specific, growth rate was calculated as $g = (\ln W_n - \ln W_0)/T$, in which W_n is the final weight on day n, W_0 is the initial weight on day 0, and T is the interval in days.

I determined energy content of eggs and larvae directly by calorimetry and indirectly by proximate analysis. Eggs and larvae were sampled periodically for ashing, elemental analysis, total lipid assays (black sea bass only), and bomb calorimetry. Ash weights were determined by combustion for 12 hours at 500°C (0.6–2.0 mg subsamples—anchovies: 9 samples, 1 or 2 replicates, 12 determinations; black sea bass: 9 samples, 1 or 2 replicates, 17 determinations). Total carbon and nitrogen contents were determined with a Carlo-Erba[3] model 1106 elemental analyzer (0.5–1.1 mg, usually triplicate, subsam-

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

ples). Total lipid content of five sea bass samples (triplicate subsamples) was estimated by the sulphophosphovanillin technique (Barnes and Blackstock 1973) using a cholesterol standard. Caloric content of 7–10 h old anchovy eggs and 1-4 h old sea bass eggs (5–12 mg subsamples of five samples for each species—anchovies: 1 or 2 replicates, 8 determinations; sea bass: 3 replicates, 15 determinations) was determined by combustion in an oxygen microbomb calorimeter calibrated with benzoic acid.

Caloric content of larvae was estimated using information on the proportions of protein, lipid, carbohydrate, and ash in larvae. Percent protein was calculated as the product of percent nitrogen and 6.025 (Brett and Groves 1979). Because of sample shortages, the following assumptions were made: 1) Black sea bass carbohydrate content was estimated by subtracting % protein, % total lipid, and % ash from 100%. 2) Bay anchovy carbohydrate content was assumed to be the same as that estimated for black sea bass 7 h eggs, 28 h eggs, 150 h unfed larvae, and 249 h fed larvae. 3) Starving anchovy % ash was assumed to be the same as for fed anchovy larvae. 4) Total lipid content for anchovies at four stages was estimated by subtracting % protein, % carbohydrate, and % ash from 100%. The effect of these assumptions on estimated caloric values is minimal because of the small percentages involved; protein is the predominant constituent. The average energy equivalents for heat of combustion were used for conversion of weight to energy: 5,650 cal/g protein, 8,660 cal/g lipid, and 4,100 cal/g carbohydrate (Brett and Groves 1979).

Oxygen uptake was measured with glass capillary differential microrespirometers (Microchemical Specialties Company), calibrated by the potassium ferricyanide-hydrazine sulfate method (Umbreit et al. 1972). The experimental technique was similar to that described by Grunbaum et al. (1955). The experimental and reference flasks each held 0.65 mL of air, a potassium hydroxide saturated filter paper strip for absorption of carbon dioxide, and 0.35 mL of 0.2 μm filtered seawater. Salinity was 32.0‰ for anchovies and 34.3‰ for sea bass. Temperature was maintained at 24.0 ± 0.05°C for anchovies and 20.0 ± 0.05°C for sea bass in a water bath. Fluorescent lighting provided 300 lux. Slight agitation was provided by the flow of water in the bath. One to six eggs or larvae (number decreasing with age) were placed in each experimental flask. The fish were allowed to adjust for 10–60 minutes, depending on age; the index droplet was stable after 10 minutes, but time was increased to allow for initially greater activity of older larvae to subside after confinement. Measurements were made at all times of the day. To ensure that digestion was essentially complete, measurements with fed larvae began more than 2 hours after feeding had ceased. (Digestion time for larger bay anchovy larvae was 1.5 hours; digestion in sea bream up to 100 μg was almost finished by 2.5 hours; Houde and Schekter 1983.) Oxygen consumption was recorded hourly for periods of 3–9 hours (usually 6 hours). The longest that larvae normally would have to go without food is the length of the dark period (10 hours for anchovies and 12 hours for sea bass). Also, when there is light, larvae expect to eat. Therefore, the measurement period for fed larvae was limited to 7 hours. Regression equations relating oxygen uptake to age were fitted. Metabolic energy (energy budget term M) was estimated from oxygen uptake with oxycalorific equivalents 0.00425 cal/μL oxygen for anchovies (24°C) and 0.00431 cal/μL oxygen for sea bass (20°C). Because movement of larvae in the flasks was restricted and feeding larvae normally were much more active (chasing rotifers) than nonfeeding larvae, the resulting total metabolism values were multiplied by the factor two for lighted periods for fed larvae (14 h/d for anchovies and 12 h/d for sea bass). This is the same procedure followed by Houde and Schekter (1983).

Feeding observations were made in the 10 L rearing tanks without handling or otherwise disturbing the larvae. Numbers observed were 160 anchovies, 20 for each day of feeding; 128 sea bass, 5 the day before first feeding, and 10–20 for each day of feeding. Individual larvae were observed for 10 minutes. The number of prestrike flexes, strikes, and successful strikes were recorded and the following ratios were calculated: 1) successful strikes/flexes, 2) successful strikes/total strikes, and 3) strikes/flexes. Successful strikes/total strikes is referred to as capture success. Feeding incidence is the percentage of larvae that captured prey within 10 minutes. Number of rotifers eaten per day was calculated from the mean of observed 10 min feeding rates for each feeding day. Daily ingestion values (energy budget term I) were calculated with the factor 0.000787 cal/rotifer (Theilacker and McMaster 1971). Weight-specific daily ration was calculated using 0.16 μg/rotifer (best available estimate, from Theilacker and McMaster 1971) and predicted larval weights. Energy-specific daily ration was calculated from ingestion estimates and estimates of body energy in calorie per individual. Weight of wild zooplankton provided to first feeding bay anchovies by Houde and Schekter (1983) averaged 0.15 μg/

individual. Detwyler and Houde (1970) found that during the first four feeding days, bay anchovies ate copepod nauplii, copepodites, and adults with daily average widths in the range 50–112 μm. Because they are much easier to catch than copepods, larger rotifers will be eaten. In this study, growth might have been better with a diverse diet, but rotifers were used because their size range is limited and their nutritional quality is relatively well defined.

Energy utilization on a caloric basis was assessed separately for endogenous (eggs, prefeeding and starving larvae) and exogenous (feeding larvae) nutrition. Energy budgets were constructed, based on the equation

$$I = G + M + F\&U$$

in which I is ingestion, G is growth, M is metabolic needs, F is egestion, and U is excretion. For eggs and unfed larvae, both I and F are near zero. Because energy is needed for embryonic growth and metabolism, and some is excreted, the growth term will be negative. The form

$$G = I - M - F\&U$$

may be more appropriate to consider in the context of growth and survival. G in calories was estimated from dry weight and proximate analysis data. I was estimated from feeding rate data. Oxygen uptake data provided M. Egested and excreted calories (F&U) were estimated by difference. With endogenous nutrition, $G = -M - U$, and $U = -G - M$. With exogenous nutrition, $F\&U = I - G - M$. Because F and U were not estimated separately, assimilation ($A = I - F$) is not considered.

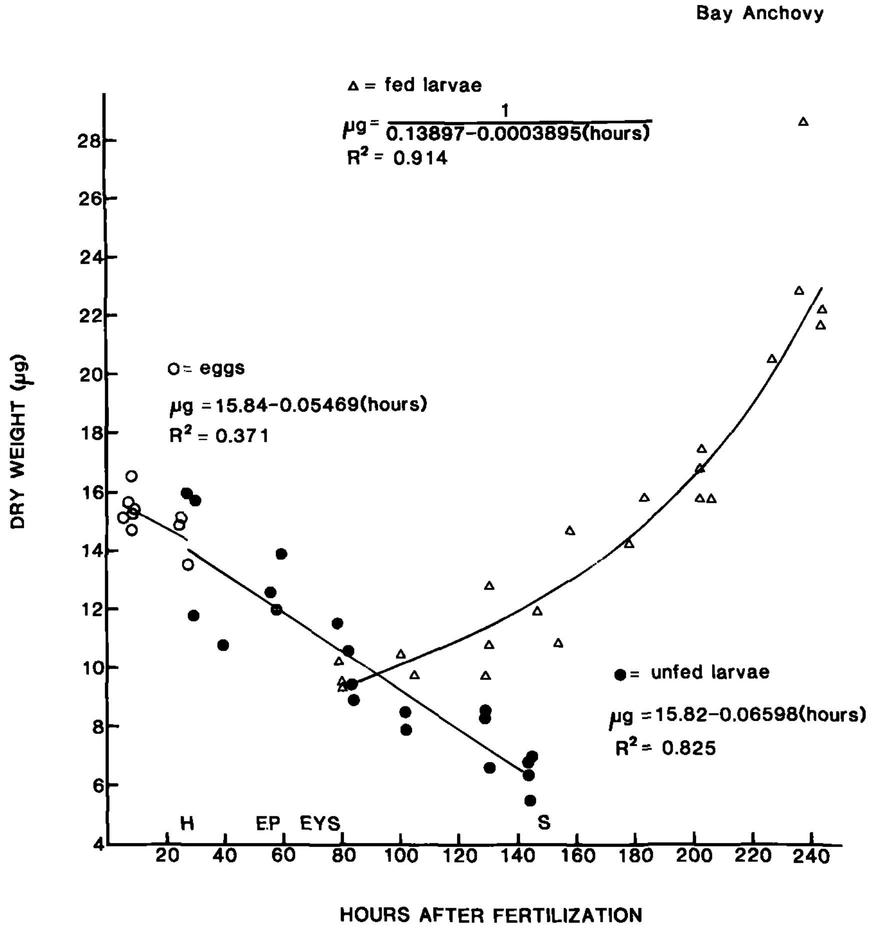


FIGURE 1.—Dry weight of bay anchovy eggs, unfed larvae, and fed larvae.

RESULTS

Developmental Events

Developmental phases were longer for black sea bass at 20°C than for bay anchovies at 24°C (Table 1). Anchovy feeding behavior began within a few hours after EP, and successful feeding was first observed 72 hours after fertilization. Sea bass feeding behavior began several hours after EP, and successful feeding was first observed at 133 hours. Anchovy yolk lasted about 8 hours and sea bass yolk about 47 hours after first feeding. Unfed anchovies in 2 L dishes and 10 L tanks died 5.1 days after hatching (6.2 days after fertilization) and unfed sea bass in 10 L tanks died 8.2 days after hatching (10.2 days after fertilization).

TABLE 1.—Timing of bay anchovy and black sea bass developmental events (hours after fertilization). Starvation = 100% mortality.

	Bay anchovy 24°C	Black sea bass 20°C
Hatching (H)	28	48
Eye pigmentation (EP)	60	110
First-feeding success (FF)	72	133
End of yolk sac (EYS)	80	180
Starvation (S)	150	245

Length and Weight

Throughout development, black sea bass were heavier than bay anchovies of the same age and length, but length at age, and trends in length and weight, were similar. Sea bass egg weight was about twice that of anchovies (32 μg vs. 15 μg; Figs. 1, 2); at hatching, sea bass were heavier (22 μg vs. 14 μg), yet both species were the same length, 2.0–2.1 mm

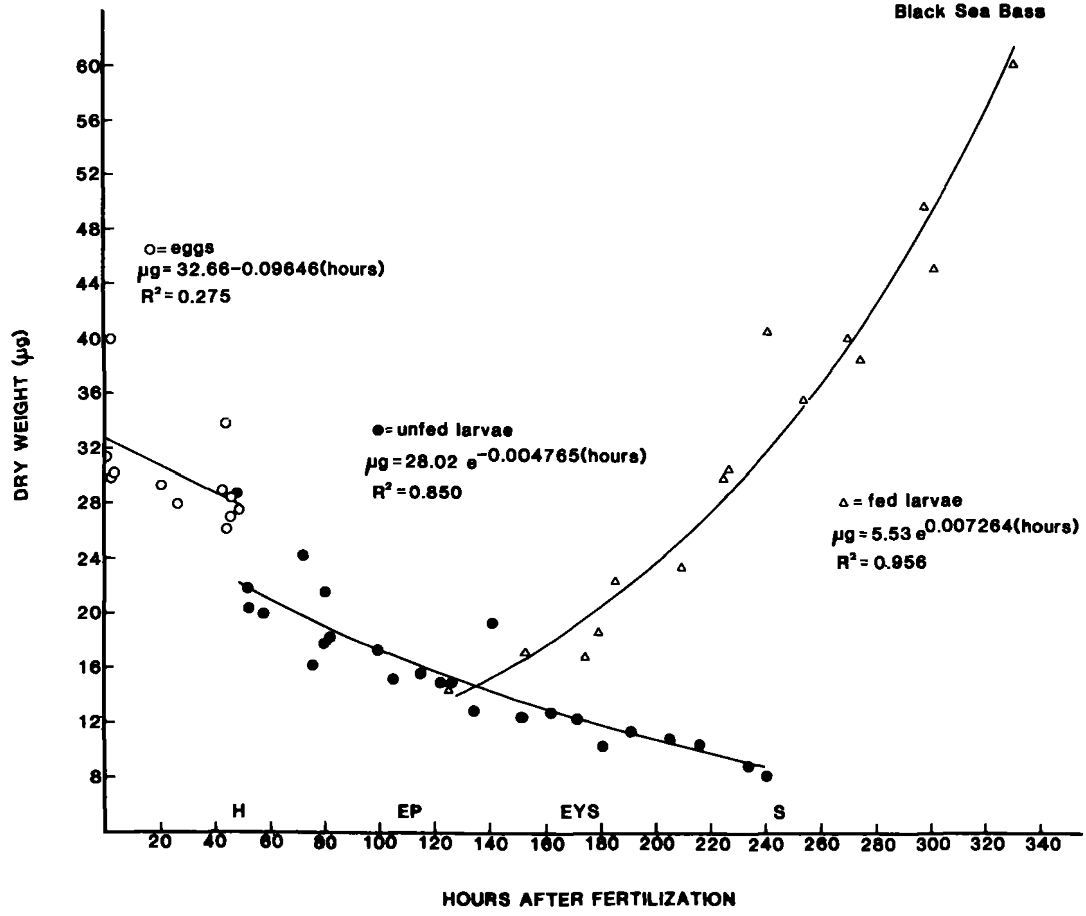


FIGURE 2.—Dry weight of black sea bass eggs, unfed larvae, and fed larvae.

NL. Six days after EYS, fed larvae of both species were 4.1–4.2 mm NL (sea bass 58 μg, anchovies 19 μg). After 168 hours past first feeding, sea bass weighed 49 μg and anchovies 22 μg. Length of unfed larvae reached a maximum between EP and EYS (anchovies, 3.4 mm; sea bass, 3.2 mm) and a minimum between EYS and S (anchovies, 3.0 mm; sea bass, 2.9 mm).

Body Composition

Similar trends in total carbon and total nitrogen content occurred for unfed and fed larvae of both species (Table 2). Percent nitrogen was relatively constant. Percent carbon and C/N decreased between hatching and yolk exhaustion, and then were relatively constant. Although data are limited, there was an apparent decrease in total lipid content of black sea bass throughout development. Values for the five samples were 1 h eggs, 14.5%; 4 h eggs, 15.6%; 217 h unfed larvae, 12.9%; 186 h fed larvae, 12.1%; 298 h fed larvae, 10.4%. Sea bass eggs and larvae contained about 50% more ash than anchovies (Table 3). Bomb calorimetry energy values were similar. Mean values in calories per gram for eggs were anchovies, 5,477 (SD 103, n = 5), ash-free 5,833; sea bass, 5,315 (SD 220, n = 5), ash-free 5,841. Representative calculations of caloric content for energy budgets are shown in Table 4.

Oxygen Consumption

The relationship between age and oxygen consumption depended on species, developmental phase, and nutritional status (Figs. 3, 4). In bay anchovies, oxygen uptake increased continuously. In black sea bass, uptake rose until hatching, dropped, then rose again. Uptake decreased for unfed larvae.

Feeding Behavior

Black sea bass capture success was consistently higher than that of bay anchovies (Fig. 5). Anchovy capture success increased from 54% on feeding day 1 to 77% on feeding day 8. Sea bass capture success was 70% on feeding day 1, and during feeding days 2–8 remained relatively constant at 86–94%.

Sea bass feeding incidence was higher than that of anchovies during the first four feeding days (Fig. 5). Anchovy feeding incidence gradually increased from 40% on feeding day 1 to 100% on feeding day 8. Sea bass feeding incidence varied at 85–97% during the first five feeding days and then remained at 100% for feeding days 6–8.

Sea bass larvae had a higher flexing rate but lower strike per flex rate than anchovies. In anchovies, mean number of flexes per hour was 9 at first feed-

TABLE 2.—Carbon and nitrogen content of bay anchovy and black sea bass eggs and larvae during growth and starvation.

Age (h)	Feeding day	n	% Carbon $\bar{x}$	% Carbon SD	% Nitrogen $\bar{x}$	% Nitrogen SD	C/N
Bay anchovy							
Eggs							
8		5	48.9	(0.2)	11.7	(0.1)	4.18
24		2	49.6	(0.1)	12.0	(0.2)	4.12
Unfed larvae							
34		2	49.1	(0.3)	11.2	(0)	4.39
98	2	2	43.4	(0.8)	11.9	(0.1)	3.64
145	4	3	43.1	(0.4)	12.0	(0.2)	3.59
Fed larvae							
92	1	2	43.4	(0.1)	11.6	(0.1)	3.72
146	4	1	44.5		12.2		3.63
202	6	1	42.4		11.9		3.56
248	8	3	43.8	(0.6)	12.0	(0.3)	3.65
Black sea bass							
Eggs							
2		5	46.2	(1.1)	10.7	(0.2)	4.32
45		3	47.7	(0.7)	11.7	(0.2)	4.09
Unfed larvae							
101		1	45.7		11.0		4.14
177	2	2	44.8	(1.3)	12.0	(0.3)	3.74
217	4	1	43.9		11.7		3.75
Fed larvae							
183	3	2	44.6	(0.5)	11.7	(0)	3.82
234	5	2	42.9	(1.6)	11.4	(0.4)	3.78
298	7	1	43.0		11.7		3.68

TABLE 3.—Ash content of various stages of bay anchovy and black sea bass.

Age (h)	n	Ash (%)	SD (%)
Bay anchovy			
Eggs			
[1]9	5	7.0	0.7
12	4	6.1	0.6
Fed larvae			
85	1	8.7	
146	1	9.0	
248	3	10.1	2.0
Black sea bass			
Eggs			
[1]2	4	9.5	0.7
13	4	9.0	1.9
Unfed larvae			
101	1	11.6	
172	1	13.9	
217	1	14.6	
Fed larvae			
186	1	13.2	
298	1	17.7	

[1] Values from calorimetry for comparison only, not used in energy budget calculations.

ing, 29 on feeding day 2, and 44 on feeding day 8 (feeding day 2-8 mean = 32). In sea bass, mean number of flexes per hour was 48 at first feeding, 74 on feeding day 2, and 59 on feeding day 8 (feeding day 2-8 mean = 63). Anchovy strikes/flexes was 79% at first feeding, 40% on feeding day 2, and 62% on feeding day 8 (feeding day 2-8 mean = 52%). Sea bass strikes/flexes was 38% at first feeding,

TABLE 4.—Calculation of energy content of bay anchovy and black sea bass eggs and larvae. See Table 1 regarding acronyms.

	Bay anchovy					Black sea bass				
	Protein (%)	Lipid[1] (%)	Carboh.[2] (%)	Ash (%)	Energy[3] cal/g	Protein (%)	Lipid (%)	Carboh.[1] (%)	Ash (%)	Energy[3] cal/g
Eggs										
Early	70.5	12.5	10.9	6.1	5,512	64.5	15.0	11.5	9.0	5,415
Late	73.5	12.3	8.1	6.1	5,550	70.5	15.0	5.5	9.0	5,508
Unfed larvae										
Hatchling	67.5	12.3	13.3	6.9	5,424	66.3	15.0	8.4	10.3	5,389
EYS	72.0	9.9	9.5	8.6	5,315	71.7	13.2	1.1	14.0	5,239
Starvation	72.0	15.2	3.8	[4]9.0	5,540	71.7	12.9	0.4	15.0	5,184
Fed larvae										
First feeding	71.8	9.1	10.5	8.6	5,275	67.4	13.3	7.1	12.2	5,251
7 d after FF	71.8	14.6	3.5	10.1	5,465	69.6	10.4	2.1	17.9	4,919

[1] Estimated as the difference between 100% and the other components.
[2] Assumed to be the same as for sea bass at the same age.
[3] Including ash.
[4] Assumed to be the same as for fed larvae at the same age.

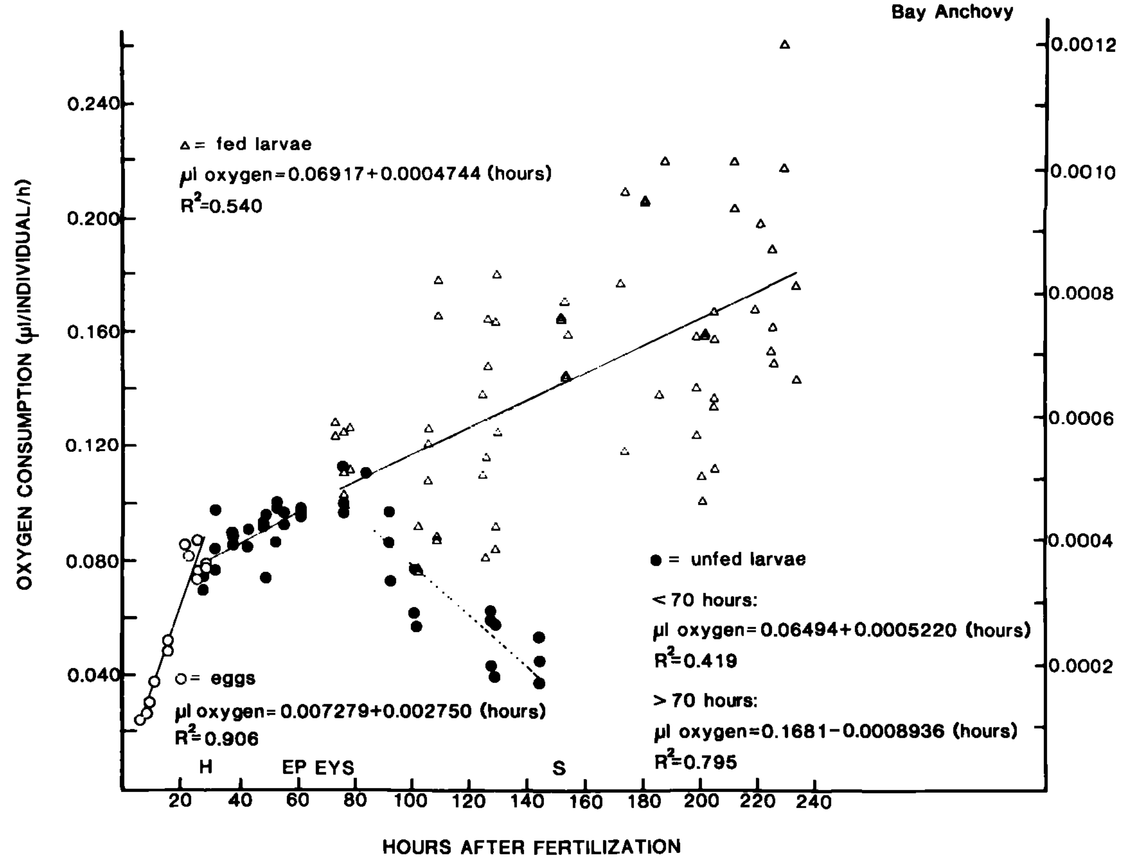
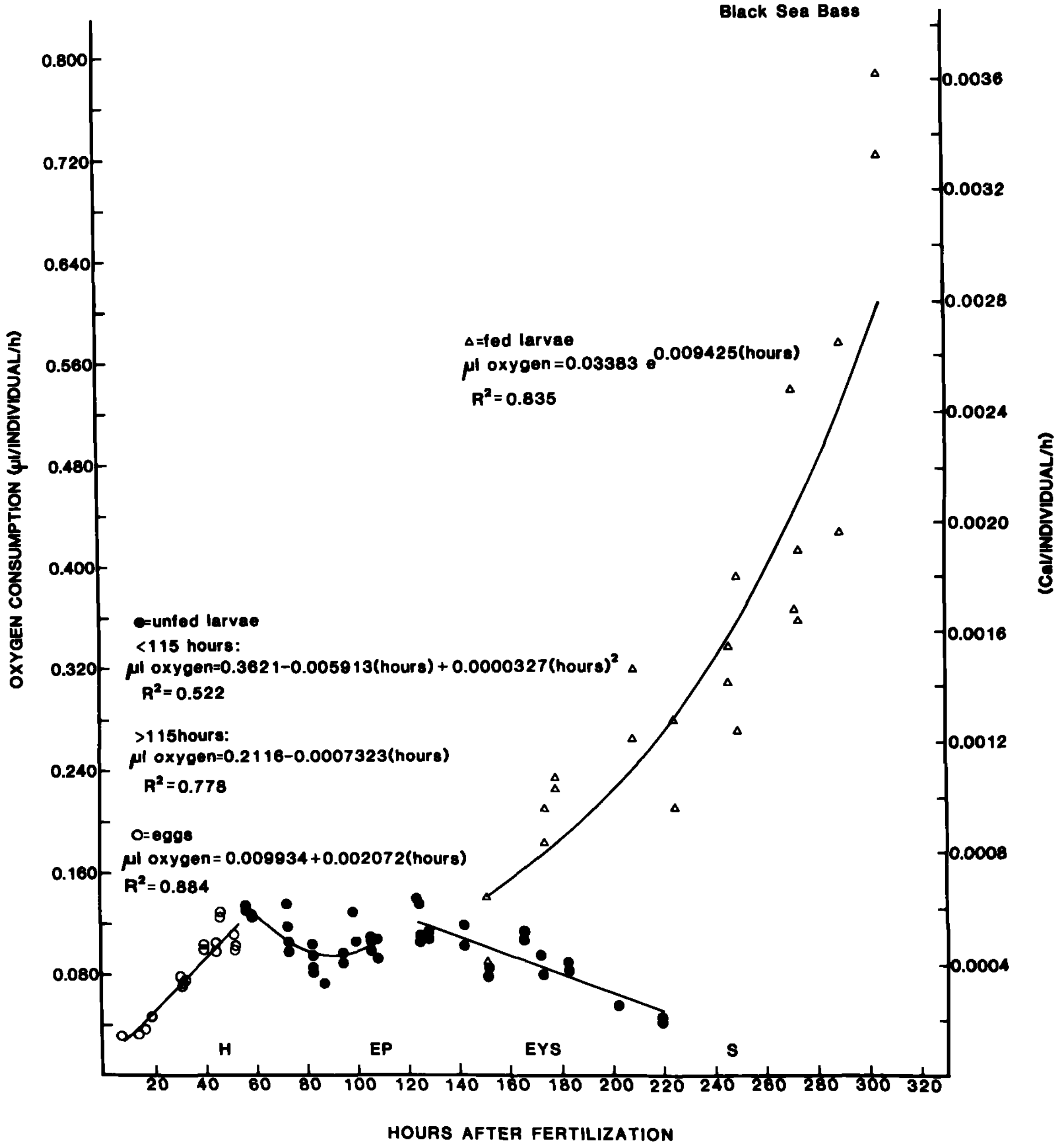


FIGURE 3.—Hourly oxygen consumption by bay anchovy eggs, unfed larvae, and fed larvae.

26% on feeding day 2, and 67% on feeding day 8 (feeding day 2–8 mean = 39%). During the first week of feeding, sea bass inspected more rotifers per unit time than anchovies did, but struck at a lower proportion of them. By the end of the week, these differences had diminished. Although observations were made at all times of the day, no trend with time of day was detected.

Feeding Rate and Daily Ration

Black sea bass feeding rates were considerably higher than those of bay anchovies (Fig. 6). Daily consumption of rotifers by anchovies increased from 4/h during the first feeding day to 13/h on feeding day 8. Sea bass rotifer consumption rose from 11/h on feeding day 1 to 17/h on feeding day 2, dropped



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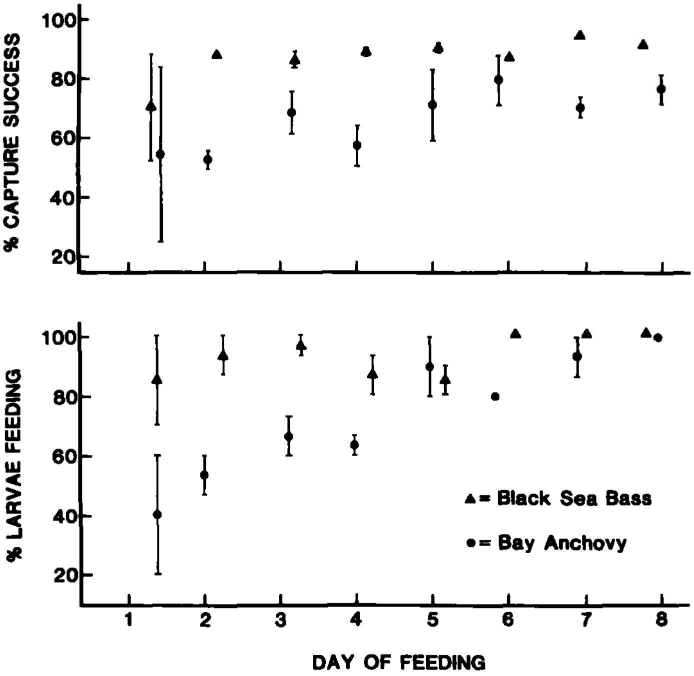

FIGURE 5.—Feeding behavior of bay anchovy and black sea bass larvae (mean ± SE when $n > 1$).

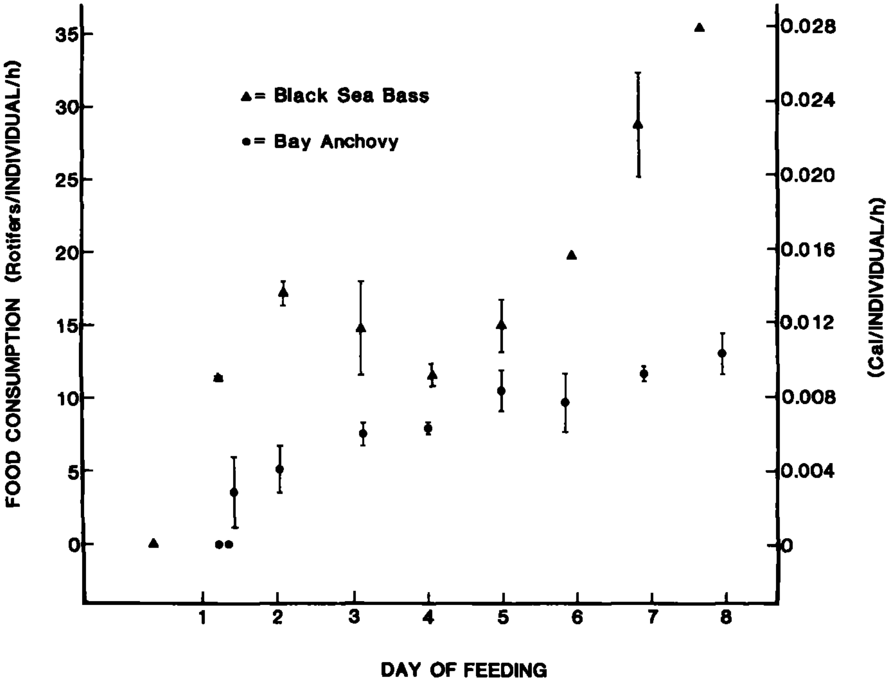

FIGURE 6.—Feeding rates of bay anchovy and black sea bass larvae (mean ± SE when $n > 1$).

to 12/h on feeding day 4, and then rose to 35/h on feeding day 8.

Average daily ration was slightly higher for anchovies than for sea bass. For the 168 hours after first feeding, anchovy daily ration averaged 138% by weight and 126% by calories, compared to 126% by weight and 122% by calories for sea bass.

Energy Budgets

Total energy ingested during the 168 h period was 0.665 cal by bay anchovies and 1.191 cal by black sea bass (Tables 5, 6). Gross growth efficiency (K_1, G/I) and metabolic component (M/I) changed with age of larvae. Anchovy G/I increased from −18% to 15% (overall 9%), while sea bass G/I rose from 9% to 19% then dropped to 12% (overall 14%). Percent of ingested energy used for metabolism by anchovies (M/I) decreased from 44% to 21% (overall 24%), while sea bass M/I increased from 16% to 37% then dropped to 30% (overall 28%). Overall F&U/I was 67% for anchovies and 58% for sea bass.

Four-Day Energy Budgets

A striking difference in early growth capability is revealed by restricting the energy budget to the first 96 hours after first feeding. Black sea bass ingested 1.8 times as much energy as bay anchovies, 0.543 vs. 0.299 cal. Egested and excreted components (F&U/I = 63% and 68%) were similar. Sea bass metabolic component was slightly lower (M/I = 24% vs. 27%) and gross growth efficiency was higher than that of anchovies (G/I = 13% vs. 5%).

DISCUSSION

Length of the interval between first feeding and yolk exhaustion is an important factor affecting survivability of fish larvae because it is the period of transition from endogenous to exogenous feeding. Bay anchovies first feed only 8 hours before their yolk is exhausted, and they do not have positive growth until after EYS. Like Pacific sardines, *Sardinops caerulea* (Lasker 1962), bay anchovies may be particularly vulnerable to food shortages at first feeding. In contrast, black sea bass have 2 days of

TABLE 5.—Energy budget for bay anchovy eggs and larvae during growth and starvation. In the first column, developmental events are indicated in parentheses. G, M, and F&U as percentages of I are given in parentheses.

				G =	I −	M −	F&U
Age (h)	Weight (µg)	Weight change (µg)	Body calories	Growth calories	Food calories	Metabolic calories	Egested and excreted calories
Eggs							
7	15.4		0.085				
28(H)	14.3	−1.1	0.079	−0.006	0	0.003	0.003
Unfed larvae							
33	13.6		0.074		0	0.002	
60(EP)	11.9	−1.7	0.064	−0.010	0	0.010	0
72	11.1	−0.8	0.059	−0.005	0	0.005	0
80(EYS)							
96	9.5	−1.6	0.051	−0.008	0	0.009	−0.001
120	7.9	−1.6	0.043	−0.008	0	0.007	0.001
144	6.3	−1.6	0.035	−0.008	0	0.005	0.003
150(S)	5.9	−0.4	0.033	−0.002	0	0.001	0.001
Fed larvae							
72(FF)	11.1		0.059				
80(EYS)							
96	9.8	−1.3	0.052	−0.007(−18%)	0.039	0.017(44%)	0.029(74%)
120	10.8	1.0	0.058	0.006 (8%)	0.071	0.020(28%)	0.045(64%)
144	12.1	1.3	0.065	0.007 (8%)	0.085	0.021(25%)	0.057(67%)
168	13.6	1.5	0.073	0.008 (8%)	0.104	0.023(22%)	0.073(70%)
192	15.6	2.0	0.084	0.011 (10%)	0.111	0.025(22%)	0.075(68%)
216	18.2	2.6	0.099	0.015 (13%)	0.119	0.027(22%)	0.077(65%)
240	22.0	3.8	0.120	0.021 (15%)	0.136	0.028(21%)	0.087(64%)

Age: from fertilization.
Weight: measured.
Weight change: from column 2.
Body calories = (weight) (estimated caloric content).
G = Growth calories = change in body calories.
I = Food calories = (average feeding rate) (feeding time) (0.000787 cal/rotifer).
M = Metabolic calories (measured µL O_2/h) (0.00425 cal/µL O_2) (38 hours).
F&U = Egested and excreted calories = I − M − G.

feeding and positive growth before their yolk is exhausted. (Neither species had an advantage in survival time after yolk exhaustion; unfed larvae of both species died within 3 days after EYS.) Starving sea bass weighed 50% more than starving anchovies. Time from hatching to starvation for unfed bay anchovies in both 2 L dishes and 10 L tanks was 122 hours (Table 1). Houde (1974) reported this period to be 126 hours in 35 L aquaria.

Growth of larvae might have been slightly reduced by container size; however, anchovies and sea bass were reared in the same tanks and the comparison should not be affected by container size.

Although growth in length was similar, sea bass gained weight faster than anchovies (Table 7). At hatching, sea bass weighed 1.6 times as much as anchovies. After 7 days of feeding, sea bass weighed 2.2 times as much as anchovies (Figs. 1, 2). At a

TABLE 6.—Energy budget for black sea bass eggs and larvae during growth and starvation. In the first column, developmental events are indicated in parentheses. G, M, and F&U as percentages of I are given in parentheses.

				G	= I	− M	− F&U
Age (h)	Weight (μg)	Weight change (μg)	Body calories	Growth calories	Food calories	Metabolic calories	Egested and excreted calories
Eggs							
2	32.5		0.176				
48(H)	28.0	−4.5	0.154	−0.022	0	0.013	0.009
Unfed larvae							
62	20.8		0.112		0	0.008	
86	18.6	−2.2	0.099	−0.013	0	0.010	0.003
110(EP)	16.6	−2.0	0.088	−0.011	0	0.010	0.001
133	14.9	−1.7	0.078	−0.010	0	0.012	−0.002
157	13.3	−1.6	0.070	−0.008	0	0.011	−0.003
180(EYS)							
181	11.8	−1.5	0.062	−0.008	0	0.009	−0.001
205	10.5	−1.3	0.055	−0.007	0	0.007	0
229	9.4	−1.1	0.049	−0.006	0	0.006	0
245(S)	8.7	−0.7	0.045	−0.004	0	0.003	0.001
Fed larvae							
133(FF)	14.9		0.078				
157	17.3	2.4	0.090	0.012 (9%)	0.138	0.022(16%)	0.104(75%)
180(EYS)							
181	20.6	3.3	0.107	0.017(11%)	0.155	0.028(18%)	0.110(71%)
205	24.5	3.9	0.126	0.019(14%)	0.132	0.035(27%)	0.078(59%)
229	29.2	4.7	0.148	0.022(19%)	0.118	0.043(36%)	0.053(45%)
253	34.7	5.5	0.175	0.027(18%)	0.152	0.056(37%)	0.070(45%)
277	41.4	6.7	0.206	0.031(15%)	0.206	0.069(34%)	0.106(51%)
301	49.2	7.8	0.242	0.036(12%)	0.290	0.086(30%)	0.168(58%)

Age: from fertilization.
Weight: measured.
Weight change: from column 2.
Body calories = (weight) (estimated caloric content).
G = Growth calories = change in body calories.
I = Food calories = (average feeding rate) (feeding time) (0.000787 cal/rotifer).
M = Metabolic calories (measured μL O_2/h) (0.00431 cal/μL O_2) (36 hours).
F&U = Egested and excreted calories = I − M − G.

TABLE 7.—Percent change in weight and energy content of bay anchovy and black sea bass during developmental phases. Instantaneous growth rates are given. FF = First feeding.

	Hatching to starvation			First feeding to starvation			Hatching to 168 h after FF			First feeding to 168 h after FF		
	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)
Bay anchovy												
Weight change	5.1	−58	−17	3.2	−47	−19	8.8	58	5	7.0	98	10
Energy change		−57	−16		−44	−18		58	5		103	10
Black sea bass												
Weight change	8.2	−61	−12	4.7	−42	−11	10.5	120	7	7.0	230	17
Energy change		−63	−12		−42	−12		100	7		210	16

lower temperature (15.5°C), northern anchovies lost 10% of their weight per day during the first 3 days of starvation (Theilacker 1987), versus 17% per day for bay anchovies (Table 5) and 11% per day for black sea bass (Table 6). The greater ash content of sea bass (Table 3) is probably related to their greater size and consequent need for more structural material.

Egg and larval caloric values calculated from proximate analysis data (Table 4) are similar to bomb calorimetry values for anchovy and sea bass eggs and to published values for other species. Calculated values for eggs were 5,512 cal/g for anchovies and 5,415 cal/g for sea bass (less than a 2% difference from measured values, 5,477 and 5,315 cal/g). Energy content of northern anchovy, *Engraulis mordax*, eggs was 5,450 cal/g (Hunter and Leong 1981). Calculated values for larvae fed for 7 days were bay anchovies, 5,465 cal/g, 6,079 cal/g ash-free; black sea bass, 4,919 cal/g, 5,991 cal/g ash-free. These numbers are within the ranges given by Thayer et al. (1973) for postlarvae of four marine fish species: 4,904–6,001 cal/g, 5,694–6,418 cal/g ash-free. Ranges of calculated ash-free values were 5,771–6,088 cal/g for bay anchovies and 5,950–6,099 cal/g for black sea bass. The possible effect of varying lipid and carbohydrate content is small. Houde and Schekter (1983) used a constant value of 5,000 cal/g, and Theilacker (1987) used 5,400 cal/g in constructing energy budgets for larval fish.

Patterns of oxygen consumption were generally similar for the two species (Figs. 3, 4). The decrease for black sea bass during the 0.5 day after hatching probably resulted from reduced activity prior to the development of vision. The interval between hatching and EP was shorter for bay anchovies (1.3 days vs. 2.5 days). Lasker and Theilacker (1962) found that oxygen uptake in Pacific sardines increased just after hatching, but was variable, depending on activity. On the eighth day of feeding, sea bass consumed oxygen at three times the rate of anchovies. At that stage, sea bass had two and a half times as much respiring tissue, and were more active (Q_{O_2} of sea bass was 12 μL O_2/mg/h vs. 9 for anchovies). However, at 20 μg, bay anchovy and black sea bass Q_{O_2} was the same and was intermediate among those of other species (Table 8). Early bay anchovy oxygen uptake was similar to that found by Houde and Schekter (1983), who reported mean uptakes of 0.030 μL/h/egg and

TABLE 8.—Comparison of growth characteristics of well-fed larvae of five species. See Tables 1 and 5 regarding acronyms.

	Northern anchovy[1] 16°C	Bay anchovy[2] 26°C	Bay anchovy[3] 24°C	Black sea bass[3] 20°C	Sea bream[2] 26°C	Lined sole[2] 28°C
Age at FF (d after H)	3.0	~1.5	1.8	3.5	~1.5	~2.0
Capture success at FF (%)	[4]11	49	54	70	53	69
Capture success 20 μg (%)	[4]39	60	74	87	61	81
Daily ration (weight) 17–22 μg (%)	81	281	138	166	198	252
I component 17–22 μg (cal/d)	0.06	0.332	0.136	0.155	0.234	0.297
Oxygen uptake 20 μg (μL O_2/ind/h)	0.134	0.144	0.178	0.179	0.218	0.240
Q_{O_2} 20 μg (μL O_2/mg/h)	6.7	7.2	8.9	8.9	10.9	12.0
M component 17–22 μg (cal/d)	0.010	0.025	0.028	0.028	0.037	0.041
M/I 17–22 μg (%)	17	8	21	18	16	14
Inst. Grth. (wt or cal) 17–22 μg (%)	19	34	19	17	40	32
G component 17–22 μg (cal/d)	0.020	0.041	0.021	0.017	0.050	0.038
G/I = K_1 17–22 μg (%)	33	12	15	11	21	13
(G + M)/I = CU 17–22 μg (%)	50	20	36	29	37	27

[1] Theilacker 1987 (except capture success).
[2] Houde 1974; Houde and Schekter 1980; Houde and Schekter 1983.
[3] Present study.
[4] Hunter 1972.

0.066 μL/h/yolk-sac larva, at 26°C, two degrees higher.

Sea bass were more active, were more efficient feeders, and spent more time feeding than anchovies (Fig. 5). Sea bass also were more capable predators from first feeding through the eighth feeding day. At first feeding, sea bass were 2.5 days older and were better developed than anchovies. Bay anchovies in this study had about the same capture success (Table 8) as bay anchovies and sea bream studied by Houde and Schekter (1980). Black sea bass capture success was similar to that of lined sole. Northern anchovy larvae feeding on 10–60 *Brachionus*/mL at 17°–18°C (Hunter 1972) were less successful than bay anchovies in the present study, but they struck more often and therefore consumed more rotifers per hour. Northern anchovy capture success was relatively low, ranging from 11% at first feeding to 60% on feeding day 8. For 20 μg larvae, a rate of about 50 strikes/h (Hunter and Thomas 1974) multiplied by 39% capture success gives a feeding rate of 20 rotifers/h vs. 13/h for bay anchovies and 16/h for black sea bass.

Daily rations for bay anchovies and black sea bass were intermediate among published estimates from rearing studies using high larval and food densities (Table 8). Theilacker and Dorsey (1980), in a review article, reported weight-specific daily rations of 70–300% for larvae fed one or more prey mer mL. Houde and Schekter (1983) reported high weight or calorie-specific daily rations of 202–379% for 10–100 μg bay anchovies fed 1 copepod nauplius/mL at 26°C.

During the first 3 days of starvation, weight and calorie loss were similar for both species; however, sea bass conserved weight and calories better during the late stages of starvation (Tables 5, 6, 7). Sea bass also gained weight and calories faster when fed (Table 7). Conservation probably resulted partly from a rearing temperature four degrees lower and partly from physiological differences. Better growth probably resulted from a combination of more efficient feeding, higher ingestion rate, lower temperature, and different physiology. During the first 24 hours after EP, fed anchovies lost more weight and calories than unfed anchovies (−0.015 vs. −0.008 cal). During the first 24 hours after EP, fed sea bass lost about the same weight and calories as unfed sea bass (−0.011 vs. −0.010 cal). This implies that anchovies at first lost more energy to feeding activity than they gained from their food, while sea bass broke even.

Overall gross growth efficiencies (G/I) of 9% for anchovies and 14% for sea bass were at the lower end of the known range for early larvae. Published G/I values for larvae fed one or more prey per mL are 11–46% (Theilacker and Dorsey 1980; Houde and Schekter 1983; Theilacker 1987). The decrease in sea bass gross growth efficiency after 4 days of feeding (229 hours, Table 6) may be related to decreasing suitability of rotifers as food for sea bass (Tucker 1984). After the first few days of feeding, larval growth of both species probably would have been enhanced by the addition of larger prey (Hunter 1980). The effect of small prey on growth may have been greater for sea bass, which have larger mouths and probably can handle larger prey. As a larva grows, the benefit:cost ratio for feeding on constant energy food particles tends to decrease (Theilacker and Dorsey 1980). This principle appears to apply to sea bass, as suggested by reduced feeding after the first two days and decreasing growth efficiency after the fourth day. If, in nature, benefit:cost (food energy:expended energy) drops close to one, the rule of fast early growth is violated and the larva is vulnerable to a given type of predator for a longer time.

Overall M/I values of 24% for anchovies and 28% for sea bass were lower than Brett and Groves' (1979) average of 44% for typical, young, well-fed, fast-growing carnivorous fish; however, M/I is likely to be lower in larvae. One explanation for Houde and Schekter's (1983) lower M/I for anchovies (Table 8) is the high ingestion rate. Hunter and Kimbrell (1980) estimated that 3–5 d old Pacific mackerel, *Scomber japonicus*, use about 18% of ingested calories for metabolism at 19°C.

Overall coefficient of utilization (CU), which is metabolizable energy expressed as a fraction of ingested energy, (G + M)/I, was slightly lower in anchovies (33%) than in sea bass (42%). The coefficient of utilization for young fish has been estimated at 73% (G = 29%, M = 44%) by Brett and Groves (1979) and 65–75% by Ware (1975). Ingested energy unaccounted for by growth and metabolism, 67% for anchovies and 58% for sea bass, was assumed to have been egested or excreted, F&U/I. These values are higher than Brett and Groves' (1979) mean of 27% for young fish, but similar to values for other larvae. Larvae are not as efficient at using their food energy as larger fish but do not need as much of it for activity and maintenance.

The energetics approach can be used to compare adaptations to feeding environments. Although rotifers are not normally eaten in large quantities by anchovies or sea bass in nature, the results of this study are probably indicative of normal feeding ecology, especially if larvae encounter patches of food organisms of similar nutritional value. The bay anchovy larva has low feeding and growth efficiencies, but its food (in estuaries and coastal waters) is relatively abundant. To compensate for low efficiency, it is obligated to feed in high densities of prey. Fluctuations in density of zooplankton prey in estuaries might strongly influence survival and recruitment to anchovy populations. The black sea bass larva feeds and grows more efficiently. It has to because its food (offshore) is not very abundant. The bay anchovy larva seems to be adapted to the high prey densities, and the black sea bass larva to the low prey densities, that characterize their respective habitats (Theilacker and Dorsey 1980). The results of this study parallel those of Houde and Schekter (1983).

ACKNOWLEDGMENTS

I thank John Merriner, Dave Peters, Allyn Powell, Bill Hettler, Alex Chester, Dave Colby, Bud Cross, John DeVane, Don Hoss, Jud Kenworthy, Al Kuo, Mike LaCroix, Curtis Lewis, Jack Musick, Pete Parker, Brenda Sanders, Ken Webb, Dick Wetzel, Doug Willis, the U.S. Coast Guard, and anonymous referees for technical and editorial assistance. The study was supported by and conducted at the Beaufort Laboratory of the Southeast Fisheries Center, National Marine Fisheries Service, during 1978–82. It is part of a dissertation submitted to the College of William and Mary in partial fulfillment of the requirements for the Ph.D. degree.

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