Energy utilization in bay anchovy and black sea bass eggs and larvae contrasting ecological roles

John Wotring Tucker Jr
College of William and Mary - Virginia Institute of Marine Science

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*The College of William and Mary in Virginia*  Ph.D.  1983

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ENERGY UTILIZATION IN BAY ANCHOVY AND BLACK SEA BASS EGGS AND LARVAE

CONTRASTING ECOLOGICAL ROLES

A Dissertation

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

by

John Wotring Tucker, Jr.

1983
APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

DOCTOR OF PHILOSOPHY

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Beaufort Laboratory
I dedicate this dissertation to my brother, Keith.
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ACKNOWLEDGEMENTS

I especially wish to thank John Merriner and Dave Peters for their guidance throughout this research, for our frequent discussions, for their patience, for help in obtaining financial support, and for their reading and criticism of the manuscript. I also thank the other members of my advisory committee, Al Kuo, Jack Musick, and Dick Wetzel, for their advice and reviews of the manuscript.

I wish to express my appreciation to the staff of the Beaufort Laboratory of the Southeast Fisheries Center, National Marine Fisheries Service, where this research was conducted—in particular the following persons: Allyn Powell and Bill Hettler for use of their culture facilities and for much helpful advice; Bud Cross and Don Hoss for their assistance in obtaining support; John DeVane for collaborating on preliminary research; Pete Parker and Doug Willis for helping me obtain sea bass broodstock; Jud Kenworthy and Mike LaCroix for assistance in doing C-H-N analyses; Alex Chester and Dave Colby for statistical assistance and advice.

I thank Brenda Sanders (Duke University Marine Lab) for assistance in doing protein and lipid assays, Ken Webb (Virginia Institute of Marine Science) for use of his C-H-N analyzer, and Dick Wetzel for use of his calorimeter.

I thank the U.S. Coast Guard and the crew of Frying Pan Light Tower for allowing and assisting me to conduct preliminary research on the tower.

And most of all, I thank you, Cyndie.
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ABSTRACT

The objective of this study was a comparison of developmental changes and energy utilization in eggs, unfed larvae, and fed larvae of two marine fish species that both have pelagic early stages, but differ in phylogeny and early life ecology. The bay anchovy (Anchoa mitchilli), a clupeiform, spawns in estuaries and shallow coastal waters. The black sea bass (Centropristis striata striata), a perciform, spawns offshore at 15-50 m depths. Densities of zooplankton eaten by first-feeding fish larvae are normally higher in coastal waters than offshore. An important determinant of survival of larval fishes is their ability to fulfill nutritional requirements after yolk energy is exhausted. Faster-growing larvae are less likely to be preyed upon. The manner in which energy is partitioned may indicate relative plasticity with respect to departures from optimal food composition or abundance. Differences among species might result from different feeding strategies or from adaptation to different feeding conditions.

Energy utilization was assessed by constructing energy budgets \( I = G + M + F\&U \): ingested calories, \( I \), from feeding rates; growth calories, \( G \), from composition and weight; metabolic calories, \( M \), from oxygen uptake; egested and excreted calories, \( F\&U \), by difference.

Three lines of evidence were found that suggest black sea bass are able to resist fluctuations in food availability better (survive and grow at lower densities): (1) Sea bass have more time to find food and develop feeding skills—50 hours between first feeding and yolk exhaustion vs 10 hours for anchovies. (2) Sea bass feed more efficiently and probably pay a lower metabolic price for their food. Over the first five days of feeding, capture success averaged 85% for sea bass and 60% for anchovies. (3) During the first five days, sea bass gross growth efficiency (12%) was twice that of anchovies (6%).

Sea bass may also be more resistant to starvation from complete food deprivation. Their yolk lasts longer. During starvation, their weight-specific metabolism is lower and they lose body calories at a lower rate.

The bay anchovy seems to be adapted to the high food densities, and the black sea bass to the low food densities, that characterize their respective habitats. For sea bass the food supply is more difficult to exploit, and this requires greater efficiency.
ENERGY UTILIZATION IN BAY ANCHOVY AND BLACK SEA BASS EGGS AND LARVAE

CONTRASTING ECOLOGICAL ROLES
Introduction

An important determinant of survival of larval fishes is their ability to fulfill nutritional requirements after yolk energy is exhausted. If a sufficient quantity of appropriate food is not available, mortality may be so high that it affects recruitment to adult stocks (the critical period concept of Hjort 1914, 1926). Larvae surviving at less than optimal food densities grow more slowly and are probably more susceptible to predation and adverse environmental perturbations (e.g., pollution). The manner in which energy is partitioned in fish eggs and larvae may indicate the relative plasticity of early stages with respect to departures from optimal food composition or abundance. Differences among species might result from different feeding strategies or from adaptation to different feeding conditions.

The objective of this study was a comparison of developmental changes and energy utilization in eggs, unfed larvae, and fed larvae of two marine fish species that differ in phylogeny and in early life ecology. The species were bay anchovy (Anchoa mitchilli) and black sea bass (Centropristis striata striata).

The bay anchovy, a coastal clupeiform, is a major food item for other species of commercial and sport importance along the U. S. Gulf and Atlantic coasts (Carr and Adams 1973; Manooch 1973; Christmas et al. 1974). Adults are pelagic and live in estuaries, bays, and shallow coastal waters from the Gulf of Maine to Yucatan, Mexico.
(Hildebrand 1963). In North Carolina, spawning takes place in estuaries and along the coast from late April to early September, with peak spawning from late June to early August (Kuntz 1914; Hildebrand and Cable 1930; pers. obs.). They apparently spawn in large schools just after sunset in estuarine areas such as the lower Newport River, North Carolina (Hildebrand and Cable 1930). The pelagic eggs are swept seaward with the ebb tide and then dispersed. The egg has no oil globule. Hatching occurs in estuaries and bays and just offshore. Although spawning occurs at 9-31°C (Dovel 1971), larval growth is best in the upper part of that range (Houde 1974). Early juveniles are abundant in brackish water.

The black sea bass, a perciform 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, Massachusetts, to Cape Canaveral, Florida, 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 usually found on rough bottom over the inner shelf. Spawning takes place over the inner shelf, mostly in the spring or summer, depending on latitude (Musick and Mercer 1977). Off North Carolina, peak spawning is from March to early June. Eggs and larvae are pelagic and occur in shelf waters of 15-51 m depth (Kendall 1972). Juveniles often are abundant in high salinity estuaries and bays but gradually move into deeper water as they grow larger.

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) compared growth at different prey levels for
bay anchovy, lined sole (*Achirus lineatus*), and sea bream (*Archosargus rhomboidalis*) larvae. They reported that anchovy larvae were capable of relatively high feeding rates after feeding had been established, but during the initial three days required to develop proficiency, anchovies had difficulty feeding at low prey concentrations. Throughout the larval stage, anchovy growth efficiency was the lowest. A possible reason is that, at high feeding rates, much food may pass through the gut so quickly that it is not completely digested (Chitty 1981). 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. 1977).

This paper presents information on significant developmental events and energy utilization for bay anchovy and black sea bass, from just after fertilization through the eighth day of feeding. Experimental results are used to infer differences in early survival and growth capabilities in the sea. Particularly important are differences during the first five days of feeding, which probably result from adaptations necessary for exploiting different food supplies. Densities of zooplankton eaten by first-feeding fish larvae are normally higher in coastal than in offshore waters (Theilacker and Dorsey 1980).
Materials and Methods

Development and examination of energy budgets allowed comparison of survival and growth capabilities from an energetics viewpoint. Experiments were conducted with eggs, unfed larvae, and fed larvae, from just after fertilization until unfed larvae died and until fed larvae had been feeding for 8 d. Culture conditions simulated natural conditions as much as possible, except for (1) higher than natural larval and prey densities, and (2) use of rotifers not encountered in the natural habitats as food. Although the environment was not duplicated in the lab, comparison between the two species is valid.

Comparative assessments were made of the following: developmental events, size and shape changes, composition changes, oxygen consumption, and (in fed larvae) feeding efficiency and rates. The timing of developmental events—hatching (H), completion of eye pigmentation (EP), first feeding, yolk exhaustion (EYS), and death of unfed larvae (S)—was noted. Measures of size and shape were notochord length (NL) and dry weight. Measures of composition included % ash, % total carbon, % total nitrogen, and % total lipid.

Energy utilization was assessed separately for endogenous and exogenous nutrition—i.e., (1) eggs, prefeeding, and starving larvae; (2) feeding larvae. Energy budgets were constructed, based on the equation:

\[ I = G + M + F\&U \]
in which I is ingested calories, G is growth calories, M is metabolic calories, F is egested calories, and U is excreted calories. For eggs and unfed larvae, both I and F are zero and the equation becomes:

$$0 = G + M + U$$

This equation applies to endogenous nutrition. 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. Growth is necessary for survival. Growth calories (G) were estimated from dry weight and proximate analysis data. Ingested calories (I) were estimated from feeding rate data. Metabolic calories (M) were estimated from oxygen uptake data. Egested and excreted calories (F&U) were estimated by difference.

Egg Sources
Both naturally and artificially spawned eggs were used. Anchovy eggs usually (40 collections) were obtained 3-5 h after spawning (before morula stage) by stationary tows of a one-meter, 505 μm mesh plankton net in Pivers Island Channel, near Beaufort, North Carolina. Tows were made during the first half of nights in which high tide had occurred at about 2000 EST (approximate time of peak spawning). Developmental stage versus time was uniform, apparently because nearly all spawning occurred within about one hour, and the time of fertilization was estimated as 2000 EST for all collections. For one oxygen consumption experiment, eggs and milt were obtained by stripping ripe adult anchovies caught near Pivers Island. Sea bass
eggs were stripped from six females that weighed 313-672 g, in which ovulation had been induced by injection of human chorionic gonadotropin (see Appendix II for details), thus the exact time of fertilization was known.

Culture Conditions

Physical conditions for rearing experiments approximated those encountered by larvae in their natural habitats during peak spawning. Anchovies were maintained at 24°C and 32 o/oo with a 14 h photoperiod. Sea bass were maintained at 20°C and 34 o/oo with a 12 h photoperiod. Fluorescent lighting provided about 1400 lux at the water surface. Incubation and rearing took place in ten-liter black cylindrical tanks of filtered sea water, except for anchovy starvation mortality experiments, which were done in two-liter glass dishes with blackened sides.

Because of sampling constraints, biological conditions were less natural, but not likely to cause excessive stress. Initial stocking density was relatively high, 30 or fewer eggs per liter. By the time of first feeding, larval density had been reduced by sampling to fewer than 15 per liter. Tanks designated for feeding were stocked with rotifers at the time larval eye pigmentation was complete. Algae (Chlorella sp. or Nannochloris sp.) were also added, as food for the rotifers to maintain their nutritional quality. A minimum rotifer concentration of 20,000 per liter was maintained, based on the assumption that at this level, prey density would not be a limiting factor. Rotifers were chosen for food because a steady laboratory-cultured supply was available and because their nutritional value is
relatively constant (0.000787 cal/rotifer, Theilacker and McMaster 1971). Wild plankton was rejected as a food source because the supply and quality are so variable that their use would have introduced unacceptable errors in calculation of ingested calories. Rotifers differ from natural prey in certain ways. They may be easier to catch than copepods because they swim more smoothly and do not seem to have as well-developed an escape response. There is no evidence that anchovies or sea bass in nature eat very many rotifers, or that rotifers are more suitable for either.

Measurements and Calculations
Timing of developmental events was determined because they mark the boundaries of growth phases among which energy utilization patterns may differ. At hatching, the chorion, which contains some energy, is discarded and larvae are able to swim weakly. When eye pigmentation is completed, larvae become more active and soon begin to search for food. Time of yolk exhaustion marks the approximate end of the egg's energy supply; after this, exogenous sources of nourishment are required to avoid resorption of body tissue and ultimate starvation mortality. First feeding occurs after vision and digestive system functions are established; this marks the attainment of ability to utilize exogenous sources. Death of unfed larvae is the endpoint for those larvae deprived of food or those unable to find or ingest food. The approximate time of yolk exhaustion was determined by microscopic examination of larval yolksacs. An abundant supply of anchovy eggs allowed a series of three starvation mortality experiments, but sea bass eggs were not available for starvation experiments separate from
rearing experiments. Anchovy starvation mortality was determined with larvae hatched from three batches of eggs collected on different nights. In each experiment, 25 normally-developing eggs were placed in each of eight two-liter, blackened, glass dishes. Dead eggs and larvae were counted and removed periodically. Time to total mortality for unfed sea bass was noted during rearing experiments in the ten-liter tanks.

Changes in size and shape of larvae are related both to growth rates, which vary among developmental stages, and to nutritional status. Samples were taken throughout development for measurement of length and weight. Live notochord lengths of anesthetized larvae held in a dish of water were measured with an ocular micrometer in a dissecting microscope to the nearest 0.01 mm (these were not returned to the tanks). Twelve anchovy length samples and 17 sea bass length samples were taken (10-52 individuals per sample). Weight samples were immediately rinsed with distilled water and freeze-dried. They were stored with dessicant under partial vacuum at \(-10^\circ C\) prior to weighing and were again vacuum-dried just before weighing. Mean weights were calculated to the nearest 0.1 µg. Nearly all weight samples contained 30 individuals. Out of 51 anchovy weight samples, only six contained fewer than 30 individuals and the smallest contained 22. Out of 52 sea bass weight samples, only eight post EYS samples contained fewer than 30 individuals and the smallest contained two.

Regression equations were used to predict dry weight at various ages during development and to provide curves for illustrating trends in the figures. Eleven models were tested for fit. Criteria used for
best fit were maximum coefficient of determination and visual agreement of the curve with data points. The models chosen were not in all cases those traditionally used to describe growth (e.g., exponential). Some traditional models were inappropriate because of the relatively short developmental intervals considered in this study and the major developmental shifts that occur during those first days of life.

Specific growth rate, \( g \), was calculated from predicted weights for each day after EYS. Specific growth rate (Winberg 1956):

\[
g = \frac{(\ln W_n - \ln W_0)}{T}
\]
comes from the first order growth equation:

\[
W_n = W_0 e^{gT}
\]

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 (here \( T = 1 \)).

Condition factor was calculated as mean dry weight divided by mean notochord length. Rapid changes in larval growth rates (as weight and length) cause fluctuations in weight/length\(^3\), the formula used for larger fish, that may lessen its utility for some species (e.g., northern anchovy, \textit{Engraulis mordax}, Zweifel ms, cited by Theilacker 1978).

Measurement of changes in weight and composition permitted an assessment of energy depletion or storage during development. Eggs and larvae were sampled periodically for ashing, elemental analysis, total lipid assays, and bomb calorimetry. The samples were handled as previously described for weight samples. Because of small sample volume and risk of contamination, most samples were ashed in air in a Perkin-Elmer model 240B elemental analyzer at 720°C for 10 min. Some
samples were large enough to provide subsamples to be ashed in a muffle furnace at 500°C for 12 h. Correction factors were calculated from the samples combusted at both temperatures, and all 720°C values were corrected to 500°C levels. Total carbon and nitrogen contents were determined with a Carlo-Erba model 1106 elemental analyzer and some samples were also analyzed with the Perkin-Elmer instrument, for confirmation. Total lipid content of five sea bass samples was estimated by the sulphophosphovanillin technique (Barnes and Blackstock 1973) using a cholesterol standard. Caloric values of 7-10 h old anchovy eggs and 1-4 h old sea bass eggs were determined by combustion in an oxygen microbomb calorimeter calibrated with benzoic acid (6318 cal/g).

Estimates of energy content at particular ages were calculated from protein, lipid, and carbohydrate contents and predicted dry weights. The average energy equivalents for heat of combustion were used for conversion of weight to energy: 5.65 kcal/g protein, 8.66 kcal/g lipid, and 4.10 kcal/g carbohydrate (Brett and Groves 1979). The growth energy budget term G is the difference between body caloric contents at successive ages. Percent protein was estimated as the product of percent nitrogen and 6.025 (Brett and Groves 1979). Because of sample shortages the following assumptions were made: (1) Sea bass carbohydrate content was estimated by subtracting % protein, % total lipid, and % ash from 100%. (2) Anchovy carbohydrate content was assumed to be the same as that estimated for sea bass 7 h eggs, 28 h eggs, 150 h unfed larvae, and 249 h fed larvae. (3) Unfed anchovy % ash was assumed to be the same as for fed 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.

Oxygen uptake for all stages was measured with all-glass capillary differential microrespirometers (Microchemical Specialties Company). Respirometers were calibrated by the potassium ferricyanide-hydrazine sulfate method described by Umbreit et al. (1972). The experimental technique was similar to that described by Grunbaum et al. (1955). The experimental flask and reference flask each held 0.65 ml of air with a suspended, potassium hydroxide saturated, strip of filter paper for absorption of carbon dioxide, and 0.35 ml of 0.2 m membrane filtered sea water (most bacteria were probably removed by the filtration). Salinity and temperature were the same as in rearing tanks, but more closely controlled. Salinity was 32.0 o/oo for anchovies and 34.3 o/oo 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 Gilson respirometer water bath. Fluorescent lighting provided a low light level of about 300 lux. Constant, slight agitation (to promote air-water gas exchange) was provided by the flow of water in the bath. One to six eggs or larvae (number decreasing with age to avoid crowding) were placed in each experimental flask. The respirometers were allowed to equilibrate and the animals to acclimate for 10-60 min, depending on age. The index droplet was stable after 10 min, but time was increased to allow for initially greater activity of older larvae to subside after confinement. Fed larvae had been removed from rearing tanks no less than 1 h after the photoperiod ended, so that measurements did not begin until more than 2 h after feeding. Oxygen
consumption was recorded hourly for periods of 3-9 h (usually 6 h). Because these measurements were made at a low light level on essentially postabsorptive fish whose movement was restricted, they are considered to represent routine metabolism. Regression equations relating oxygen uptake to age were fitted as described for weight data.

Height-specific oxygen uptake \( (Q_{O_2}, \mu l \text{ oxygen consumed/ug/h}) \) was computed to allow comparison independent of size differences. Regression equations of the form \( R = aW^b \) were fitted to data for unfed and fed larvae after EYS. Data used were individual experimental oxygen uptake data \( (R) \) and dry weights predicted for larvae in the experiments \( (W) \).

Metabolic energy represented by oxygen uptake was estimated with the oxycalorific equivalent 0.00463 cal/\( \mu l \) oxygen (Brett and Groves 1979). Total metabolic energy for each interval (energy budget term \( M \)) was estimated as: (regression predicted hourly oxygen uptake for the interval) \( \times \) (number of hours in the interval) \( \times \) (0.00463 cal/\( \mu l \) oxygen). Because feeding larvae were much more active than non-feeding 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 rationale corresponds to that of Houde and Schekter (1983).

Observations of feeding behavior were made to estimate feeding efficiency, incidence, and rate. Observations were made without removing larvae from the rearing tanks or otherwise disturbing them. Numbers of larvae 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 min. The number of flexes preparatory to striking, the number of strikes at a rotifer, and the number of successful strikes were recorded.

Ratios of feeding behavior counts were calculated to provide indices of feeding ability and learning. They were: (1) percentage of successful strikes out of all preparatory flexes (successful strikes/flexes), (2) percentage of successful strikes out of all strikes (successful strikes/total strikes), and (3) percentage of strikes out of all flexes (strikes/flexes). Successful strikes/total strikes is commonly referred to as capture success.

Number of rotifers eaten per day (14 h of feeding by anchovies and 12 h by sea bass) was calculated from observed 10 min feeding rates. Rotifers were of the same strain investigated by Theilacker and McMaster (1971). Daily ingestion values (energy budget term I) were calculated with their factor 0.000787 cal/rotifer.

Daily rations were calculated as percent body weight per day and as percent body calories per day. Weight-specific daily ration was calculated using 0.16 µg/rotifer (Theilacker and McMaster 1971) and predicted larval weights. Caloric daily ration was calculated from caloric ingestion estimates and estimates of body energy in cal/individual.

The energy budget term F&U was estimated by difference. During endogenous nutrition, I and F are zero and \(-G = U + M\) or \(U = -G - M\). During exogenous nutrition, \(F&U = I - G - M\).
Results

Developmental Events

Developmental phases were longer for sea bass than for anchovies. In both species, hatching occurred over a range of several hours. At 24°C, most anchovy eggs hatched (H) at about 28 h after fertilization. At 20°C, most sea bass eggs hatched at about 48 h after fertilization. Anchovy eye pigmentation was complete (EP) at about 60 h; feeding behavior began within a few hours, and successful feeding was first observed at 72 h. Sea bass eye pigmentation was complete at about 110 h; feeding behavior began within a day, and successful feeding was first observed at 133 h. Yolk absorption rate varied among individuals. Yolk was not visible under the microscope (EYS) in anchovies older than 80 h after fertilization. Sea bass reached the same stage at 180 h. This does not preclude the possibility of other, longer lasting, yolk or oil storage depots (e.g., in or around digestive organs) in post yolk sac larvae. Unfed anchovy larvae did not live beyond 150 h. All unfed sea bass larvae that remained in the rearing tanks died by about 245 h.

Size and Shape

Throughout development sea bass were more robust and heavier than anchovies, but actual lengths, and trends in length and weight, were similar. At hatching, larvae were 2.0-2.1 mm NL (Figures 1 and 2).
Figure 1. Live notochord length of unfed and fed bay anchovy larvae: mean plus and minus one standard error. For number of observations, see Measurements and Calculations section.
Figure 2. Live notochord length of unfed and fed black sea bass larvae: mean plus and minus one standard error. For number of observations, see Measurements and Calculations section.
Figure 3. Dry weight of bay anchovy eggs, unfed larvae, and fed larvae.
\[ \mu_g = \frac{1}{0.13897 - 0.0003895 \text{hours}} \]

\[ R^2 = 0.914 \]

\[ \mu_g = 15.84 - 0.05469 \text{hours} \]

\[ R^2 = 0.371 \]

\[ \mu_g = 15.82 - 0.06598 \text{hours} \]

\[ R^2 = 0.825 \]
Figure 4. Dry weight of black sea bass eggs, unfed larvae, and fed larvae.
\( u = \text{eggs} \)
\( \mu g = 32.66 - 0.09646 \text{(hours)} \)
\( R^2 = 0.275 \)

\( u = \text{untreated larvae} \)
\( \mu g = 28.02 e^{-0.004765 \text{(hours)}} \)
\( R^2 = 0.850 \)

\( u = \text{fed larvae} \)
\( \mu g = 5.53 e^{0.007264 \text{(hours)}} \)
\( R^2 = 0.956 \)
Length of unfed larvae reached a maximum between EP and EYS and a minimum between EYS and S. Six days after EYS, fed larvae were 4.1–4.2 mm NL. Sea bass egg weight was about double that of anchovies (Figures 3 and 4). From hatching to total mortality, unfed larvae of both species lost 58% of their weight. Seven days after first feeding, anchovies were 162% of their hatching weight and sea bass 219%. Average specific growth rate (g) for 5 d after EYS was 11.4% per day for anchovies and 17.4% for sea bass. On the eighth day of feeding, g was 20.0% for anchovies and 17.4% for sea bass. The greater robustness of sea bass larvae is reflected in higher condition factors (Figures 5A and 6A). Condition of unfed larvae decreased until death. Anchovy condition factor was low during the first days of feeding and increased more slowly than for sea bass.

Composition
Sea bass eggs and larvae contained about 50% more ash than anchovies (Figures 5B and 6B).

Similar trends in total carbon and total nitrogen content occurred for unfed and fed larvae of both species (Tables 1 and 2, Figures 5C and 6C). Percent carbon decreased slightly at hatching, dropped further until EYS, and then leveled off. Percent nitrogen decreased at hatching, then rose until EYS to constant levels. C/N rose at hatching and then dropped continuously until death of unfed larvae and until 2 d later in fed larvae. Sea bass C/N continued to drop on the eighth feeding day but anchovy C/N rose slightly.

Although data are limited, there was an apparent decrease in total lipid content of sea bass throughout development. Values for the
Figure 5. Changes in condition factor and body composition during growth and starvation of bay anchovies: mean plus and minus one standard error. A. Condition factor, mean dry weight divided by mean notochord length. B. Percent ash. C. Carbon/nitrogen ratio. For number of observations, see Table 1 and Appendix Table 1.
Figure 6. Changes in condition factor and body composition during growth and starvation of black sea bass: mean plus and minus one standard error. A. Condition factor, mean dry weight divided by mean notochord length. B. Percent ash. C. Carbon/nitrogen ratio. For number of observations, see Table 2 and Appendix Table 1.
Table 1. Carbon and nitrogen content of bay anchovy eggs and larvae during growth and starvation.

<table>
<thead>
<tr>
<th>Age (h)</th>
<th>Carbon (%)</th>
<th>Nitrogen (%)</th>
<th>C/N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Eggs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>48.7</td>
<td>11.8</td>
<td>4.12</td>
</tr>
<tr>
<td>7</td>
<td>49.0</td>
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<td>4.16</td>
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<td>48.9</td>
<td>11.6</td>
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<td>9</td>
<td>48.8</td>
<td>11.6</td>
<td>4.21</td>
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<tr>
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<td>4.20</td>
</tr>
<tr>
<td>23</td>
<td>49.6</td>
<td>11.9</td>
<td>4.17</td>
</tr>
<tr>
<td>24</td>
<td>49.5</td>
<td>12.2</td>
<td>4.06</td>
</tr>
<tr>
<td><strong>Unfed Larvae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>31</td>
<td>48.9</td>
<td>11.2</td>
<td>4.38</td>
</tr>
<tr>
<td>36</td>
<td>49.3</td>
<td>11.2</td>
<td>4.40</td>
</tr>
<tr>
<td>83(^a)</td>
<td>44.0</td>
<td>12.0</td>
<td>3.66</td>
</tr>
<tr>
<td>113</td>
<td>42.8</td>
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<td>3.63</td>
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<td>43.1</td>
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</tr>
<tr>
<td>145</td>
<td>43.5</td>
<td>12.2</td>
<td>3.55</td>
</tr>
<tr>
<td>147</td>
<td>42.7</td>
<td>11.8</td>
<td>3.61</td>
</tr>
<tr>
<td><strong>Fed Larvae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>85</td>
<td>43.5</td>
<td>11.7</td>
<td>3.71</td>
</tr>
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<td>100</td>
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<td>42.4</td>
<td>11.9</td>
<td>3.56</td>
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<tr>
<td>247</td>
<td>44.4</td>
<td>12.2</td>
<td>3.65</td>
</tr>
<tr>
<td>252</td>
<td>43.6</td>
<td>11.7</td>
<td>3.71</td>
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</tbody>
</table>

\(^a\) Capable of feeding
Table 2. Carbon and nitrogen content of black sea bass eggs and larvae during growth and starvation.

<table>
<thead>
<tr>
<th>Age (h)</th>
<th>Carbon (%)</th>
<th>Nitrogen (%)</th>
<th>C/N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Eggs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>44.6</td>
<td>10.5</td>
<td>4.24</td>
</tr>
<tr>
<td>1</td>
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<td>11.0</td>
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</tr>
<tr>
<td>3</td>
<td>46.8</td>
<td>10.7</td>
<td>4.36</td>
</tr>
<tr>
<td>3</td>
<td>45.8</td>
<td>10.6</td>
<td>4.33</td>
</tr>
<tr>
<td>4</td>
<td>46.3</td>
<td>10.7</td>
<td>4.31</td>
</tr>
<tr>
<td>43</td>
<td>47.4</td>
<td>11.4</td>
<td>4.15</td>
</tr>
<tr>
<td>44</td>
<td>48.5</td>
<td>11.9</td>
<td>4.07</td>
</tr>
<tr>
<td>47</td>
<td>47.2</td>
<td>11.7</td>
<td>4.04</td>
</tr>
<tr>
<td></td>
<td>Unfed Larvae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>101</td>
<td>45.7</td>
<td>11.0</td>
<td>4.14</td>
</tr>
<tr>
<td>172&lt;sup&gt;a&lt;/sup&gt;</td>
<td>43.9</td>
<td>11.8</td>
<td>3.73</td>
</tr>
<tr>
<td>182</td>
<td>45.8</td>
<td>12.2</td>
<td>3.75</td>
</tr>
<tr>
<td>217</td>
<td>43.9</td>
<td>11.7</td>
<td>3.75</td>
</tr>
<tr>
<td></td>
<td>Fed Larvae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>180</td>
<td>44.2</td>
<td>11.7</td>
<td>3.79</td>
</tr>
<tr>
<td>186</td>
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<td>11.7</td>
<td>3.84</td>
</tr>
<tr>
<td>226</td>
<td>41.8</td>
<td>11.1</td>
<td>3.78</td>
</tr>
<tr>
<td>242</td>
<td>44.0</td>
<td>11.6</td>
<td>3.79</td>
</tr>
<tr>
<td>298</td>
<td>43.0</td>
<td>11.7</td>
<td>3.68</td>
</tr>
</tbody>
</table>

<sup>a</sup> Capable of feeding
Table 3. Caloric content of bay anchovy and black sea bass eggs. Ash percentages used were 6.1% for anchovy and 9.0% for sea bass.

<table>
<thead>
<tr>
<th>Bay Anchovy</th>
<th>Calories per gram</th>
<th>Black Sea Bass</th>
<th>Calories per gram</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (h)</td>
<td></td>
<td>Age (h)</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>5560</td>
<td>1</td>
<td>5621</td>
</tr>
<tr>
<td>8</td>
<td>5372</td>
<td>1</td>
<td>5258</td>
</tr>
<tr>
<td>10</td>
<td>5366</td>
<td>3</td>
<td>5088</td>
</tr>
<tr>
<td>10</td>
<td>5582</td>
<td>3</td>
<td>5456</td>
</tr>
<tr>
<td>10</td>
<td>5506</td>
<td>4</td>
<td>5154</td>
</tr>
<tr>
<td><strong>Mean ± standard deviation</strong></td>
<td></td>
<td><strong>Mean ± standard deviation</strong></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>5477±103</td>
<td>2</td>
<td>5315±220</td>
</tr>
<tr>
<td><strong>Mean (ash-free)</strong></td>
<td></td>
<td><strong>Mean (ash-free)</strong></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>5833</td>
<td>2</td>
<td>5841</td>
</tr>
</tbody>
</table>
five determinations 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%.

Bomb calorimetry energy values of anchovy eggs were higher than for sea bass, but on an ash-free basis, energy content was similar (Table 3).

Oxygen Consumption
The relationship between age and oxygen consumption was complex, depending on species, developmental phase, and nutritional status (Figures 7 and 8). In anchovies, uptake rose until EYS, and continued to rise in fed larvae, but decreased after EYS in unfed larvae. In sea bass, uptake rose until hatching, stayed about the same until first feeding capability, then rose in fed larvae and decreased in unfed larvae. Weight exponents (b) of sea bass were more than double those of anchovies, and within each species, b of starving larvae was more than double that of fed larvae (Table 4).

Feeding Behavior
Sea bass capture success was consistently higher than that of anchovies (Figure 9A). Anchovy capture success increased from 54% on day 1 to 77% on day 8. Sea bass capture success was 70% on day 1, and during days 2-8, remained relatively constant at 86-94%.

Sea bass feeding incidence was higher than that of anchovies during the first four days of feeding (Figure 9B). Anchovy feeding incidence increased from 40% on day 1 to 100% on day 8. Sea bass feeding incidence varied at 85-97% during the first five days and then remained at 100% for days 6-8.
Figure 7. Hourly oxygen consumption by bay anchovy eggs, unfed larvae, and fed larvae.
OXYGEN CONSUMPTION (μl/INDIVIDUAL/h)

Δ = fed larvae
\[ \text{μl oxygen} = 0.06917 + 0.0004744 \text{ (hours)} \]
\[ R^2 = 0.540 \]

* = unfed larvae
< 70 hours:
\[ \text{μl oxygen} = 0.06494 + 0.0005220 \text{ (hours)} \]
\[ R^2 = 0.419 \]

> 70 hours:
\[ \text{μl oxygen} = 0.1681 - 0.0008936 \text{ (hours)} \]
\[ R^2 = 0.795 \]
Figure 8. Hourly oxygen consumption by black sea bass eggs, unfed larvae, and fed larvae.
OXYGEN CONSUMPTION (μl/INDIVIDUAL/h)

- fed larvae
  \[ \mu_l \text{ oxygen} = 0.03563 \times 0.009425 \text{(hours)} \]
  \[ R^2 = 0.835 \]

- unfed larvae
  < 115 hours:
  \[ \mu_l \text{ oxygen} = 0.3621 - 0.005913 \text{(hours)} + 0.0000327 \text{(hours)}^3 \]
  \[ R^2 = 0.522 \]
  > 115 hours:
  \[ \mu_l \text{ oxygen} = 0.2116 - 0.0007323 \text{(hours)} \]
  \[ R^2 = 0.778 \]

- eggs
  \[ \mu_l \text{ oxygen} = 0.009934 + 0.002072 \text{(hours)} \]
  \[ R^2 = 0.884 \]

HOURS AFTER FERTILIZATION

EYS

HOUS AFTER FERTILIZATION
Table 4. Regression statistics for weight-specific oxygen consumption 
\((R = aW^b)\) of bay anchovy and black sea bass larvae. Data are 
from experimental uptake rates and predicted weights.

<table>
<thead>
<tr>
<th></th>
<th>a</th>
<th>b</th>
<th>n</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starving anchovies</td>
<td>0.00244</td>
<td>1.5395</td>
<td>15</td>
<td>0.705</td>
</tr>
<tr>
<td>Fed anchovies</td>
<td>0.02531</td>
<td>0.6544</td>
<td>58</td>
<td>0.255</td>
</tr>
<tr>
<td>Starving sea bass</td>
<td>0.0000069</td>
<td>3.8316</td>
<td>6</td>
<td>0.945</td>
</tr>
<tr>
<td>Fed sea bass</td>
<td>0.00281</td>
<td>1.3679</td>
<td>16</td>
<td>0.753</td>
</tr>
</tbody>
</table>
Figure 9. Feeding behavior of black sea bass and bay anchovy larvae: mean plus and minus one standard error. Capture success is the proportion of strikes at rotifers that were successful. Feeding incidence is the percentage of larvae that ingested at least one rotifer during ten minute observation intervals. For number of observations, see Appendix Tables 2 and 3.
Figure 10. Feeding rates of black sea bass and bay anchovy larvae: mean plus and minus one standard error. For number of observations, see Appendix Tables 2 and 3.
Table 5. Daily rations of bay anchovy and black sea bass feeding on *Brachionus plicatilis*. Values are ratios of ingested weight/body weight and ingested calories/body calories, expressed as percent, for each full day of feeding (2-8).

<table>
<thead>
<tr>
<th>Day of feeding</th>
<th>Bay Anchovy</th>
<th>Black Sea Bass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Weight</td>
<td>Calories</td>
</tr>
<tr>
<td>2</td>
<td>120</td>
<td>111</td>
</tr>
<tr>
<td>3</td>
<td>153</td>
<td>140</td>
</tr>
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<td>4</td>
<td>150</td>
<td>138</td>
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<tr>
<td>5</td>
<td>172</td>
<td>157</td>
</tr>
<tr>
<td>6</td>
<td>143</td>
<td>129</td>
</tr>
<tr>
<td>7</td>
<td>145</td>
<td>130</td>
</tr>
<tr>
<td>8</td>
<td>134</td>
<td>119</td>
</tr>
<tr>
<td>Mean</td>
<td>145</td>
<td>132</td>
</tr>
</tbody>
</table>
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 feeding, 29 on day 2, and 44 on day 8 (day 2-8 mean = 32). In sea bass, mean number of flexes per hour was 48 at first feeding, 74 on day 2, and 59 on day 8 (day 2-8 mean = 63). Anchovy strikes/flexes was 79% at first feeding, 40% on day 2, and 62% on day 8 (day 2-8 mean = 52%). Sea bass strikes/flexes was 38% at first feeding, 26% on day 2, and 67% on day 8 (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
Anchovy feeding rates were considerably lower than those of sea bass (Figure 10). Consumption of rotifers by anchovies rose from 4/h during the first observed hour, to 17/h on day 2, dropped to 12/h on day 4, and then rose to 35/h on day 8.

Daily rations (% body basis) calculated by weight or calories show different trends in the two species (Table 5). Anchovy daily ration peaked on the fifth day and then decreased. Sea bass daily ration reached a low point on the fifth day and then increased.

Energy Budgets
Sea bass lost weight and calories more slowly than anchovies during starvation but gained weight and calories faster when fed (Tables 6
Table 6. Energy budget for bay anchovy eggs and larvae. See text for methods.

<table>
<thead>
<tr>
<th>Age (h)</th>
<th>Weight (ug)</th>
<th>Weight Change (ug)</th>
<th>Protein (%)</th>
<th>Lipid (%)</th>
<th>Carbo. (%)</th>
<th>Ash (%)</th>
<th>Body Calories</th>
<th>Growth Calories</th>
<th>Food Calories</th>
<th>Metabolic Calories</th>
<th>Metabolic Excreted Calories</th>
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</thead>
<tbody>
<tr>
<td>7</td>
<td>15.4</td>
<td>-0.3</td>
<td>70.5</td>
<td>12.5</td>
<td>10.9</td>
<td>6.1</td>
<td>0.085</td>
<td>-0.002</td>
<td>0</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>14</td>
<td>15.1</td>
<td>-0.8</td>
<td>72.0</td>
<td>11.9</td>
<td>10.0</td>
<td>6.1</td>
<td>0.083</td>
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</tr>
<tr>
<td>hatch</td>
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<td>73.5</td>
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<tr>
<td>33</td>
<td>13.6</td>
<td>-1.6</td>
<td>67.5</td>
<td>12.3</td>
<td>13.3</td>
<td>6.9</td>
<td>0.074</td>
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<td>0.002</td>
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<td>10.5</td>
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<td>72.0</td>
<td>11.6</td>
<td>7.6</td>
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Table 7. Energy budget for black sea bass eggs and larvae. See text for methods.

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<th>Weight Change (ug)</th>
<th>Protein (%)</th>
<th>Lipid (%)</th>
<th>Carbo. (%)</th>
<th>Ash (%)</th>
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<th>Growth Calories</th>
<th>Food Calories</th>
<th>Metabolic Calories</th>
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Figure 11. Energy partitioning in fed bay anchovy and black sea bass larvae. \( I = \) ingested calories; \( G + M = \) sum of growth and metabolic calories; \( G = \) calories added to or lost from body.
CALORIES PER DAY

Bay Anchovy

G + M

G

DAYS AFTER FERTILIZATION

2 4 6 8 10 12

CALORIES PER DAY

Black Sea Bass

G + M

G

DAYS AFTER FERTILIZATION

2 4 6 8 10 12
Table 8. Percent of ingested calories used for growth (gross growth efficiency), metabolism, and both (coefficient of utilization) in bay anchovy and black sea bass larvae.

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<th></th>
<th>Black Sea Bass</th>
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<td>G/I (%)</td>
<td>M/I (%)</td>
<td>(G+M)/I (%)</td>
<td>Weight (µg)</td>
<td>G/I (%)</td>
<td>M/I (%)</td>
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<td>36</td>
<td></td>
<td>13</td>
<td>29</td>
<td>42</td>
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</table>
and 7, Figure 11). Unfed anchovies died 5 d after hatching and sea bass in 8 d. From hatching to death, unfed anchovies lost 55% of their calories; sea bass lost 60% of theirs. During the first seven full days of feeding, anchovies increased in weight by 156% and in calories by 165%; sea bass increased in weight by 240% and in calories by 217%. Total calories ingested were 0.718 by anchovies and 1.203 by sea bass.

Food Conversion Efficiency and Metabolic Component
Food conversion efficiency (K\textsubscript{1}, gross growth efficiency, G/I) and metabolic component (M/I) changed with age, and trends differed between species (Table 8). In anchovies K\textsubscript{1} rose; in sea bass K\textsubscript{1} rose and then decreased. In anchovies M/I decreased; in sea bass M/I increased and then decreased. Overall coefficient of utilization, (G+M)/I, was 36% for anchovies and 42% for sea bass.

Five Day Energy Budget
A striking difference in early growth capability is revealed by restricting the energy budget to the first five days of feeding (Figure 12). Sea bass ingested about 60% more calories than anchovies. The metabolic components and egested and excreted components were similar in both species. However, sea bass gross growth efficiency was twice that of anchovies.
Figure 12. Energy budgets for bay anchovy and black sea bass larvae for the first five days of feeding. I = ingested calories; G = percent of ingested energy used for growth; M = percent used for metabolism; F&U = percent egested and excreted.
Discussion

Length of the interval between first feeding and yolk exhaustion is a significant factor in survival ability of fish larvae, because it is the period of transition from endogenous to exogenous feeding. Larvae with shorter periods have less time to improve feeding ability to the point that they can grow well with only external food sources. Anchovies first feed only 8 h before their yolk is exhausted, and they do not have positive growth until after EYS. Like Pacific sardines (Lasker 1962), bay anchovies may be particularly vulnerable to food shortages at first feeding. Houde (1974) concluded that at 24°C, bay anchovy larvae must be fed within 32.5 h after EYS to avoid high mortality, and within 40.5 h to avoid complete mortality. In contrast (the present study shows that) sea bass have two full days of 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 three days after EYS.

Although growth in length was similar, sea bass grew faster than anchovies in weight and calories. Sea bass specific growth rate was constant, but anchovy specific growth rate started lower than sea bass's and rose higher. This is an indication that anchovies may have a problem with early growth. Anchovy and sea bass growth rates ranged from 11% to 20% per day. These are reasonable for early larvae, but probably would have decreased with age or decreasing
temperature and increased with better food. Moksness (1982) calculated a $g$ of 4.1% for capelin (*Mallophus villosus*) reared at 6-20°C in an outdoor basin for 3-127 days after hatching (age effect). Laurence (1975) calculated specific growth rates for winter flounder (*Pseudopleuronectes americanus*) from yolk exhaustion to metamorphosis (7-11 wk) of 5.8% at 5°C and 10.1% at 8°C (age and temperature effects). Houde and Schekter (1981) calculated a $g$ of 34% for bay anchovies reared at 26°C with 1000 wild zooplankton prey per liter (food effect). Their larvae were 2 days older than mine but had a more varied and probably more nutritious diet consisting mostly of copepod nauplii. However, their food density was much higher than natural.

Physiology may be affected by body size. Sea bass eggs weighed twice as much as anchovy eggs. Starving sea bass weighed 50% more than starving anchovies. After 8 days of feeding, sea bass weighed three times as much as anchovies.

The greater ash content of sea bass is probably related to their greater size and consequent need for more structural material (Figures 5B and 6B).

The C/N ratio patterns are similar—a rise at hatching resulting from loss of the chorion, which has a low C/N ratio; decrease after hatching resulting from greater depletion of lipid relative to protein; C/N slow to rise in fed larvae probably because protein is accumulated faster than lipid. These trends are similar in other species (May 1971; Ehrlich 1974a, 1974b). As Ehrlich (1974a, 1974b) suggested, fast growth (i.e., protein deposition) is probably more important to early larvae than energy storage (i.e., lipid
deposition). Only later in development can the fish afford the luxury of storing lipids at the expense of reducing growth.

Egg and larval caloric values derived from proximate analyses compare well with those from bomb calorimetry and with published values for other species. Derived values for eggs were 5512 cal/g for anchovies and 5415 cal/g for sea bass (less than a 2% difference from microbomb values, Table 3). Energy content of northern anchovy eggs is 5450 cal/g (Hunter and Leong 1981). Derived values for fed larvae 9 d after hatching were: anchovies, 5465 cal/g, 6079 cal/g ash-free; sea bass, 5003 cal/g, 5984 cal/g ash-free. These values are within the ranges for postlarvae of four marine fish species: 4904-6001 cal/g, 5694-6418 cal/g ash-free (Thayer et al. 1973). Extreme ash-free values were 5771-6088 cal/g for anchovies and 5950-6099 cal/g for sea bass.

Patterns of oxygen consumption were generally similar in the two species (Figures 7 and 8). One difference was a decrease in sea bass oxygen uptake during the two days after hatching, with no similar decrease for anchovies. The decrease for sea bass probably resulted from lowered activity prior to the development of vision. The interval between hatching and EP was much shorter for anchovies (a little over 1 d vs 2.5 d), probably too short a time for activity to decrease much or too short to detect a decrease before larvae could see and became more active. A posthatching peak in oxygen uptake was noted in Atlantic herring by Holliday et al. (1964). Lasker and Theilacker (1962) found that uptake in Pacific sardines (Sardinops caerulea) increased just after hatching, but was variable, depending on activity. On the eighth day of feeding (oldest fish in Figures 7
and 8), sea bass consume oxygen at three times the rate of anchovies. This results partly because, at that stage, sea bass have two and a half times as much respiring tissue, and partly because sea bass are more active ($Q_{O_2}$ of sea bass is $0.012 \ \mu l \ O_2/ g/h$ vs $0.009$ for anchovies).

The large differences in weight exponents ($b$) between species and between unfed and fed larvae may be attributable to interactions between activity level and weight (Table 4). The fed sea bass exponent was higher than that of anchovies, probably because sea bass activity accelerated faster with age (from feeding observations). For each species, the unfed exponent was higher than the fed exponent, probably because during starvation, activity decreased rapidly but rate of weight loss decelerated. Departure from the theoretical $b = 0.86$ (Brett and Groves 1979) is not particularly surprising. Hoss and Peters (1976) emphasized that fish size and developmental stage may have large effects on the value of the weight exponent, and that these effects are not often considered or recognized.

Anchovy oxygen uptake was similar to that found by Houde and Schekter (1983), who measured uptake by eggs and larvae at $26^\circ C$ by another method, with an oxygen electrode. They reported mean uptake by eggs and yolksac larvae of $0.030 \ \mu l/h$ and $0.066 \ \mu l/h$, and predicted a rate of $0.168 \ \mu l/h$ for $20.9 \ \mu g$ dry weight feeding larvae (compare with $0.180 \ \mu l/h$ in the present study).

Sea bass are more active and efficient feeders and spend more time feeding. Judging from capture success (Figure 9A), sea bass were more capable than anchovies from first feeding through the eighth feeding day. At first feeding, anchovies weighed about $10 \ \mu g$ and sea bass
about 15 µg; sea bass were 2.5 d older and apparently were better developed than anchovies. Anchovies in this study had about the same first-feeding capture success (54%) as Houde and Schekter's (1980) anchovies (49%) and sea bream (53%). Capture success of 20 µg anchovies in the present study (70%) was intermediate between Houde and Schekter's anchovies (60%) and sea bream (61%) and their lined sole (81%). Sea bass first feeding capture success (70%) was about the same as that of lined sole, and at 50 µg body weight, capture success was 90% for both species (higher than anchovies, 72%, and sea bream, 68%). Northern anchovy larvae feeding on 10,000-60,000 Brachionus per liter at 17-18°C (Hunter 1972) were less successful than bay anchovies in the present study, but still consumed more rotifers per hour. Northern anchovy capture success ranged from 11% at first feeding to 60% on day 8. Bay anchovy larvae, which feed less efficiently and are closer to starvation than black sea bass larvae, probably require a compensatory mechanism for good survival—perhaps environmental (i.e., better food supply).

Bay anchovy feeding rates were lower than those of black sea bass and northern anchovies. On the eighth day, rate of rotifer consumption was 13/h for bay anchovies and 35/h for black sea bass. For northern anchovies, a striking rate of about 50/h (Hunter 1974) multiplied by 60% capture success (Hunter 1972) gives a feeding rate of 30 rotifers/h on day 8. Northern anchovies were able to eat more rotifers than bay anchovies because they struck more often.

The low point for sea bass daily ration on day 5, just before the age of death for unfed larvae, may have resulted from a metabolic or digestive shift concurrent with EYS, from the presence of
inefficiently feeding larvae that were close to starvation, or from diminishing acceptability of rotifers.

Although, because of different experimental conditions, direct comparisons cannot be made, daily rations for bay anchovies and black sea bass were intermediate among published estimates from rearing experiments using high larval and food densities. Theilacker and Dorsey (1980), in a review article, reported weight-specific daily rations of 70-300% for larvae fed 1000 or more prey per liter. Houde and Schekter (1983) reported very high calorie-specific daily rations of 202-379% for 10-100 pg bay anchovies fed 1000 copepod nauplii per liter at 26°C. Their larvae also had unusually high growth rates. Lined sole daily rations also were rather high, 165-297% (with 1000 nauplii per liter). Sea bream daily rations were about average, 121-234% (with 500 nauplii per liter). Another species that has a high daily ration is winter flounder; Laurence (1977) estimated weight-specific rations as high as 300% a day. Barahona-Fernandes and Conan (1981) reported feeding rates for 10-75 d old European seabass (Dicentrarchus labrax) fed Artemia nauplii at 19°C; recalculation of their data yields weight-specific daily rations of 30-80%. Apparently, daily rations for larvae of many species are higher than those of the the adults because of the necessity for fast early growth.

Sea bass conserved weight and calories better than anchovies during starvation, and also grew better when fed (Tables 6 and 7, Figure 11). 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 day of feeding, fed anchovies
lost more weight and calories than unfed anchovies. During the first
day of feeding, fed sea bass lost about the same weight and calories
as unfed sea bass. This implies that anchovies at first lost more
energy to feeding activity than they gained from their food while sea
bass broke even.

In starving larvae of both species, metabolic calories exceeded
those supplied from the body and yolk during and just after yolk
depletion (negative values in column F&U, Tables 6 and 7). This could
be a result of measurement error, but another possibility is that
larvae obtained extra energy by ingesting microorganisms or other
small organic particles, or by absorbing nutrients (Davenport and

Gross growth efficiencies of 10% for anchovies and 13% for sea
bass (Table 8) were at the lower end of the known range for early
larvae. Published $K_1$ values for larvae fed 1000 or more prey per
liter are 11-41% (Houde and Schekter 1983, Theilacker and Dorsey
1980). Houde and Schekter (1983) reported that in bay anchovies
reared at 26°C with 1000 nauplii per liter as food, gross growth
efficiency decreased from 21% at 10 µg, to 12% at 20 µg and 11% at 50
µg. In the present study, anchovy $K_1$ increased between 10 and 20 µg.
The decrease in sea bass gross growth efficiency after day 5 may be
related to decreasing suitability of rotifers as food for sea bass
(see Appendix II). After the first few days of feeding, larval growth
of both species probably would have been enhanced by the addition of
larger, more nutritious prey (Hunter 1980). The effect on growth may
have been greater for sea bass, which have larger mouths and probably can handle larger prey. As a larva grows larger, 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, decreasing growth efficiency after the fifth day, and constant specific growth rate (anchovy growth rate increased). If benefit:cost (food energy:energy expended in feeding) drops close to one, the principle of fast early growth is violated and the larva becomes easy prey.

The overall M/I values of 26% for anchovies and 29% for sea bass are a little lower than Brett and Groves' (1979) average of 44% for typical, young, well-fed, fast-growing carnivorous fish; however, M/I is typically low for larvae. Houde and Schekter (1983) estimated M/I for bay anchovies as 13% at 10 μg and 8% at 20 μg. M/I for the perciform sea bream was 31% at 10 μg and 16% at 20 μg; for the pleuronectiform lined sole, 19% at 10 μg and 14% at 20 μg. One explanation for Houde and Schekter's lower M/I for anchovies is that their larval ingestion rates were about twice those in the present study. 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. If this value is adjusted for activity, as done for all of the above species, by a factor of 1.5 (12 h light per day), it becomes 27%, which is close to my estimates for anchovies and sea bass.

The coefficient of utilization, which is metabolizable energy expressed as a fraction of ingested energy, (G + M)/I, was slightly
higher in sea bass (42%) than in anchovies (36%). Houde and Schekter (1983) estimated (G + M)/I for bay anchovies as 34% at 10 μg and 20% at 20 μg. (G + M)/I for sea bream was 68% at 10 μg and 37% at 20 μg; for lined sole, 37% at 10 μg and 27% at 20 μg. The overall value for bay anchovies in the present study, 36%, was somewhat higher than theirs. However, in this study, G/(G + M) was 31% and M/(G + M) was 69%, as compared to averages of 62% and 38% for 10-20 μg larvae in Houde and Schekter’s study. Apparently, under very good feeding conditions, bay anchovy larvae are capable of exceptional growth rates. Sea bass in the present study had overall (G + M)/I of 42%, similar to that of sea bream. Sea bass G/(G + M) was 33% and M/(G + M) was 67%. Sea bream (10-50 μg) averages were 59% and 41%; lined sole (10-50 μg) averages were 49% and 51% (Houde and Schekter 1983). Except for Houde and Schekter’s anchovies and sea bream, the estimates given above are similar to those of Brett and Groves (1979) for typical, young, fast-growing, well-fed, carnivorous fish: G/(G + M) = 40%, M/(G + M) = 60%. The two perciforms utilized more of their food than the clupeiform or pleuronectiform larvae. Houde and Schekter's larvae (fed copepods) used more of their metabolizable energy for growth than did sea bass or anchovies fed rotifers.

The coefficient of utilization for young fish has been estimated at 65-75% by Ware (1975). The lower estimates of 36% and 42% in the present work emphasize the possible variation to be found with larvae, which may be more sensitive to the wide range of feeding conditions to which they are exposed in the laboratory and in nature. These conditions are more difficult to evaluate for larvae and early juveniles, which pass through rapid and sometimes extreme
developmental changes.

Ingested energy unaccounted for by growth and metabolism, 64% 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 older fish, but similar to values for larvae of the three species studied by Houde and Schekter (1983). However, Houde and Schekter's mean F&U/I for 10-20 μg anchovies was somewhat higher, about 76%, possibly because of overeating and resultant partial digestion.

A gross growth efficiency twice that of anchovies would enable sea bass to grow just as fast with less food (Figure 12). The difference in efficiency is probably related to the fact that food is harder to find for a sea bass larva over the continental shelf than for an anchovy larva in an estuary. 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 larval feeding ecology of these species, especially when they should encounter patches of food organisms of similar nutritional density. For good survival and growth, bay anchovy larvae may need to feed in denser prey patches to compensate for their low feeding and growth efficiencies. Sea bass and other more efficient species would require lower prey densities.
Conclusions

Three lines of evidence suggest that black sea bass are able to resist fluctuations in food availability better (survive and grow at lower prey densities) than bay anchovies: (1) Sea bass have more time to find food and develop feeding skills. (2) Sea bass feed more efficiently and probably pay a lower metabolic price for their food. (3) During the first five days of feeding, sea bass gross growth efficiency is twice that of anchovies.

Sea bass may also be more resistant to starvation from complete food deprivation. Their yolk lasts longer. During starvation, their weight-specific metabolism is lower and they lose body calories at a lower rate.

Bay anchovy and black sea bass larvae are similar to those of closely related species. In an extensive review article, Hunter (1980) described contrasting ecological roles for two types of marine fish larvae. The "engrauliform" type of larva has a small mouth and eats large numbers of small food organisms. It feeds from a sinuous posture, is not persistent in attacking, and has low feeding capacity and maneuverability. It has lower growth and metabolic rates. The larval bay anchovy fits into this category. Hunter's "scombriform" type of larva has a large mouth and eats small numbers of large food organisms. It feeds from a more rigid posture, is persistent in attacking, and has higher feeding capacity and maneuverability. It
has higher growth and metabolic rates. The larval black sea bass fits fairly well into this category. Generalizations on feeding ability along phylogenetic lines based on the present study are unwarranted, because the habitats differ as well as relationships. However, the present study provides evidence for behavioral adaptation to environmental conditions for larvae of the two species—the bay anchovy apparently needing a denser food supply than black sea bass.

Two opposing extrinsic determinants of larval survival, food availability and predation pressure, have been much discussed. The consensus is that most larvae in the sea are probably eaten before they can grow up. Growth rate and susceptible size range determine the length of time that larvae are vulnerable to each group of predators. If, during a particular growth phase (size range), larvae are confronted with high predation pressure, those most likely to survive are the ones that can evade predators the best, but also, and perhaps equally important, grow out of the vulnerable phase the fastest. The bay anchovy larva has low growth efficiency, but its food (in estuaries and coastal waters) is relatively abundant. The black sea bass larva grows more efficiently. It has to, because its food (offshore) is not very abundant. Anchovy larvae may also face greater predation pressure (e.g., estuarine plankton samples taken during the summer in North Carolina often contain large numbers of anchovy eggs and larvae and large numbers of chaetognaths, which prey on anchovies, pers. obs.). The bay anchovy larva seems to be adapted to the high food conditions, and the black sea bass larva to the low food conditions, that characterize their respective habitats.
The energetics approach permits comparison of species' adaptations to their feeding environments. Black sea bass are capable of good survival and growth at low prey densities. High prey density may improve growth, but is not essential and might be superfluous. Fluctuations in food supply may be less important to larval sea bass. Factors such as reduction of the spawning population by overfishing may be more important than larval mortality in regulating population size. To survive and grow well, bay anchovies are obligated to feed in high densities of prey. They would not do well in the sea bass's habitat. Fluctuations in density of zooplankton prey in estuaries might strongly influence survival and recruitment to anchovy populations. Because many of man's environment-degrading activities are concentrated in estuaries, the bay anchovy is in a particularly vulnerable position. Although not commercially important, the bay anchovy, because of its abundance and importance as a forage fish, is very important ecologically. It is possible that environmental degradation could reduce population sizes in some areas, perhaps affecting other species higher in the food web.
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APPENDIX I

Tables
Appendix Table 1. Ash content of various stages of bay anchovy and black sea bass. Values given under ash % are: percent ± one standard deviation (number of samples). Ash values from calorimetry are for comparison only and were not used in energy budget calculations.

<table>
<thead>
<tr>
<th>Age (h)</th>
<th>Stage</th>
<th>Unfed ash %</th>
<th>Fed ash %</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>Eggs</td>
<td>7.0±0.7(5)(^a)</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Eggs</td>
<td>6.1±0.6(4)(^b)</td>
<td></td>
</tr>
<tr>
<td>85</td>
<td>EYS</td>
<td>8.7 (1)(^d)</td>
<td></td>
</tr>
<tr>
<td>146</td>
<td>Larvae</td>
<td>9.0 (1)(^d)</td>
<td></td>
</tr>
<tr>
<td>248</td>
<td>Larvae</td>
<td>10.1±2.0(3)(^d)</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Age (h)</th>
<th>Stage</th>
<th>Unfed ash %</th>
<th>Fed ash %</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Eggs</td>
<td>9.5±0.7(4)(^a)</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Eggs</td>
<td>9.0±1.9(4)(^c)</td>
<td></td>
</tr>
<tr>
<td>101</td>
<td>YS</td>
<td>11.6 (1)(^e)</td>
<td></td>
</tr>
<tr>
<td>172</td>
<td>EYS</td>
<td>13.9 (1)(^e)</td>
<td></td>
</tr>
<tr>
<td>186</td>
<td>EYS</td>
<td>13.2 (1)(^d)</td>
<td></td>
</tr>
<tr>
<td>217</td>
<td>Starv.</td>
<td>14.6 (1)(^d)</td>
<td></td>
</tr>
<tr>
<td>298</td>
<td>Larvae</td>
<td>17.7 (1)(^d)</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) From calorimetry
\(^b\) 2 combusted at 500\(^\circ\)C; 2 at 720\(^\circ\)C and corrected
\(^c\) 3 combusted at 500\(^\circ\)C; 1 at 720\(^\circ\)C and corrected
\(^d\) Combusted at 720\(^\circ\)C and corrected
\(^e\) Combusted at 500\(^\circ\)C
Appendix Table 2. Rotifer consumption by bay anchovy larvae. Data are summarized by age (in days after first feeding) for each of three experiments in 1981. Means and standard errors are in rotifers consumed per individual per hour.

| Day of feeding | Experiment Am 81-3 | | | Experiment Am 81-5 | | | Experiment Am 81-6 | | |
|-------------|-----------------|-------|-------|-----------------|-------|-------|-----------------|-------|
| Age (h)    | Mean | SE | No. of tanks | Mean | SE | No. of tanks | Age (h) | Mean | SE | No. of tanks | Mean | SE | No. of tanks | Mean | SE | No. of tanks |
| 1<sup>a</sup> | 72 | 6.0 | 2.7 | 5 | 5 | 67 | 0 | 5 | 5 | 85 | 3.6 | 1.5 | 5 | 5 | 119 | 8.4 | 3.6 | 5 | 5 |
| 2        | 90 | 6.8 | 2.1 | 5 | 15 | 72 | 1.2 | 1.2 | 5 | 5 | 140 | 3.6 | 1.5 | 5 | 5 | 165 | 12.0 | 3.3 | 5 | 5 |
| 3        | 114 | 6.8 | 1.0 | 5 | 15 | 184 | 3.4 | 2.4 | 5 | 5 | 215 | 10.8 | 2.2 | 5 | 5 | 214 | 12.0 | 4.2 | 5 | 5 |
| 4        | 137 | 7.6 | 1.7 | 5 | 15 | 208 | 12.6 | 1.8 | 5 | 10 | 240 | 15.6 | 2.2 | 5 | 10 | 238 | 13.2 | 2.9 | 5 | 5 |
| 5        | 161 | 9.2 | 1.0 | 5 | 15 | 239 | 10.8 | 2.2 | 5 | 5 | 240 | 15.6 | 2.2 | 5 | 10 | 238 | 13.2 | 2.9 | 5 | 5 |
| 6        | 180 | 13.8 | 2.9 | 5 | 10 | 208 | 12.6 | 1.8 | 5 | 10 | 240 | 15.6 | 2.2 | 5 | 10 | 238 | 13.2 | 2.9 | 5 | 5 |
| 7        | 208 | 12.6 | 1.8 | 5 | 10 | 239 | 10.8 | 2.2 | 5 | 5 | 240 | 15.6 | 2.2 | 5 | 10 | 238 | 13.2 | 2.9 | 5 | 5 |
| 8        | 239 | 10.8 | 2.2 | 5 | 5 | 240 | 15.6 | 2.2 | 5 | 10 | 238 | 13.2 | 2.9 | 5 | 5 | 238 | 13.2 | 2.9 | 5 | 5 |

<sup>a</sup> Feeding rates were recorded in a fourth experiment (Am 81-22) at age 70 h: Mean 0, 5 tanks, 5 larvae.
### Appendix Table 3. Rotifer consumption by black sea bass larvae.

Data are summarized by age (in days after first feeding for each of two experiments in 1981 and 1982). Means and standard errors are in rotifers consumed per individual per hour.

<table>
<thead>
<tr>
<th>Day of feeding</th>
<th>Experiment Cs 81-1</th>
<th>Experiment Cs 82-2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Age (h)</td>
<td>Mean</td>
</tr>
<tr>
<td>0</td>
<td>118</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>144</td>
<td>11.4</td>
</tr>
<tr>
<td>2</td>
<td>162</td>
<td>16.4</td>
</tr>
<tr>
<td>3</td>
<td>187</td>
<td>11.6</td>
</tr>
<tr>
<td>4</td>
<td>212</td>
<td>12.4</td>
</tr>
<tr>
<td>5</td>
<td>236</td>
<td>16.8</td>
</tr>
<tr>
<td>6</td>
<td>260</td>
<td>19.8</td>
</tr>
<tr>
<td>7</td>
<td>283</td>
<td>25.2</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX II

Hormone-induced ovulation of black sea bass and rearing of larvae
Black sea bass (*Centropristis striata striata*) support important commercial and sport fisheries along the U.S. Atlantic coast. Adults are distributed over the continental shelf and in bays from Cape Cod, Massachusetts, to Cape Canaveral, Florida, and occasionally to the Florida Keys (Miller 1959; Musick and Mercer 1977). Spawning takes place over the inner shelf, mostly in the spring or summer, depending on latitude. Juveniles often occur in high salinity estuaries and move into deeper water as they grow larger. Black sea bass and southern sea bass (*C. striata melana*) may have mariculture potential. Southern sea bass have been reared in Florida under experimental mariculture conditions by Hoff (1970) for 7 d after fertilization and by Roberts et al. (1977) for 26 d.

Published reports of artificial spawning of black sea bass date back to Earll (1884) who reported fertilization of eggs from ripe fish freshly caught off South Carolina. Wilson (1889) obtained eggs from ripe fish caught off Massachusetts and described in detail development of embryos and some aspects of early yolk sac larvae. Hettler and Clements (1978) induced ovulation of black sea bass by intramuscular injection of 0.75 IU human chorionic gonadotropin (HCG) per gram body weight, but did not elaborate on the technique. They used the eggs for thermal shock experiments. Hettler and Powell (1981) reported that they had induced ovulation of black sea bass and described general methods that could be used for larval culture of several species. There are no known published records of black sea bass being reared past the yolk sac stage. This note describes a technique that met with consistent success for inducing ovulation in black sea bass females, and presents results from larval rearing experiments of 12-56
d duration. These results were obtained in conjunction with a study of energy utilization in eggs and larvae.

Adult male and female black sea bass were captured in March or April by hook and line or trap fishing in Onslow Bay off North Carolina, at 20-36 m depths, and were taken to the laboratory. They were maintained in 1,000 or 2,000 L tanks at 18.0-19.5°C with a 12 h photoperiod (300-500 lux at the water surface). They were fed chopped squid, clams, and fish. Most males were ripe when captured and remained so in captivity without hormonal treatment. Ripe females occasionally were obtained during preliminary trials, and one spontaneously shed eggs into a holding tank. About 650 eggs were recovered; 5% had been fertilized and developed to hatching. Attempts were made to induce ripening of several females with HCG injections, without first checking oocyte diameters. Only one such attempt was successful (641 g female, Appendix Table II-1).

Consistent success was attained only when a minimum oocyte diameter of 0.4 mm was used as the criterion for choosing female spawners. The following technique was employed. Females were anesthetized with tricaine methanesulfonate (anesthesia was not necessary for injections and was not used during stripping to avoid possible effects on the gametes). Ovarian biopsies were then taken with fire-polished glass capillary tubes (inside diameter 1 mm) used as catheters. Females with 0.4 mm or larger oocytes were chosen for spawning (Appendix Table II-1). Typically, injections of HCG were given on two consecutive days. The first dose was 0.7-1.7 IU per gram body weight and the second dose, 0.6-0.8 IU. Two of the six females required a third injection. The HCG was injected intramuscularly
Appendix Table II-1. Spawning data for black sea bass females.

<table>
<thead>
<tr>
<th>Female wet weight (g)</th>
<th>313</th>
<th>351</th>
<th>466</th>
<th>492</th>
<th>641</th>
<th>672</th>
</tr>
</thead>
<tbody>
<tr>
<td>Final water temperature (°C)</td>
<td>18.0</td>
<td>18.5</td>
<td>18</td>
<td>18</td>
<td>18</td>
<td>19.5</td>
</tr>
<tr>
<td>Mean oocyte diameter prior to first injection (mm)</td>
<td>0.57</td>
<td>0.56</td>
<td>0.64</td>
<td>0.60</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>HCG doses (IU)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>First</td>
<td>500</td>
<td>375</td>
<td>600</td>
<td>550</td>
<td>500</td>
<td>500</td>
</tr>
<tr>
<td>Second</td>
<td>250</td>
<td>200</td>
<td>300</td>
<td>275</td>
<td>500</td>
<td>250</td>
</tr>
<tr>
<td>Third</td>
<td>375</td>
<td></td>
<td>250</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interval(s) between injections (h)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>24</td>
<td>24</td>
<td>25</td>
<td>25</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Time from first injection to ovulation (h)</td>
<td>72</td>
<td>36</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Date of ovulation</td>
<td>Apr 24</td>
<td>Apr 8</td>
<td>Apr 4</td>
<td>Apr 6</td>
<td>Mar 23</td>
<td>Apr 14</td>
</tr>
<tr>
<td>Mean egg dry weight prior to hatching (μg)</td>
<td>27.0</td>
<td>27.5</td>
<td>28.4</td>
<td>28.8</td>
<td>33.8</td>
<td></td>
</tr>
</tbody>
</table>
between the dorsal and pectoral fin with an insulin syringe. Two days after the first injection, the fish were anesthetized and biopsies were again taken to check oocyte development. Mature eggs (about 0.9 mm diameter) were stripped from the females 47-199 h after the first injection. Some of the eggs obtained at 94 and 199 h were overmature and a number were atretic; however, useable quantities of viable eggs were obtained. Apparently, two or three days is enough time for ovulation to occur. Larger females tended to produce larger eggs (Appendix Table II-1).

A wet fertilization method was used. Milt was collected with an insulin syringe (without needle) from ripe males. Eggs were stripped into 100 ml of filtered seawater at 20°C and 34 o/oo salinity. Milt was added to the eggs and swirled for 10 min. Then the eggs were washed with several hundred ml of seawater. Normally-developing, floating, fertilized eggs were immediately removed with a pipette and placed in rearing tanks. Some eggs from each of the six spawns were incubated in a static system of 10 L black cylindrical tanks containing filtered seawater at 20°C and 34 o/oo. The water was treated once, before introduction of the eggs, with a commercial preparation of nitrofurazone and furazolidone. Larvae were reared in the same tanks for 12-20 d with no appreciable mortality. Fluorescent lighting provided 1400 lux at the water surface for 12 h/day. Rotifers (Brachionus plicatilis) were stocked 5 d after fertilization and maintained at a density of 20,000/L. About 200 ml of a dense culture of algae (Chlorella sp. or Nannochloris sp.) were added with the rotifers and replenished every 3-4 d. Under these conditions, hatching occurred 2 d after fertilization, eye pigmentation was
complete on the fifth day, and yolk exhaustion occurred at 7-8 d. (Additional larvae, kept under similar conditions but without food, died within 10 d after fertilization.) Fertilized egg diameters were 0.84-0.98 mm. Hatchling notochord length was 2.0 mm (Fig. 1). Mean dry weight decreased from 21 μg at hatching to a minimum of 12 μg on day 5, and then increased to 45 μg on day 12 (after seven full days of feeding).

Two additional experiments were conducted in static 100 L black cylindrical tanks containing filtered seawater at 19-20°C and 30-35 o/oo. Fluorescent lighting provided 800 lux at the water surface for 12 h/day. Rotifers and algae were stocked as in the 10 L tanks. Beginning on day 10, *Artemia salina* nauplii were also stocked. In these experiments, only length data were collected. One tank (Exp. 1B, Fig. 1) was stocked with 2000 eggs from the same batch of eggs used in the 10 L tanks (Exp. 1A). During the first 12 d, 65 individuals were removed and preserved; on day 19, 100 larvae were preserved; between 24 and 56 d, 22 were preserved (total recovery 9%). The second tank (Exp. 2) was stocked with 1,000 eggs from another batch. During the first 10 d, 86 individuals were removed and preserved; between 14 and 26 d, 37 more were preserved (total recovery 12%).

Growth rates were good until the third week (Fig. 1). After day 15, more than half the larvae were noticeably emaciated, which probably indicates a dietary deficiency. However, two robust juveniles in Exp. 1B survived to day 56 (standard lengths: 10.6, 12.2 mm).
Appendix Figure 1. Growth of black sea bass larvae and juveniles in three 19-20°C experiments. Hatching is indicated by H and yolk exhaustion by E. Notochord lengths were measured before, and standard lengths after flexion. Vertical bars are length ranges. Horizontal bars are three standard errors above and below mean length. Rotifers were fed to larvae in 10 L tanks. Rotifers and Artemia were fed to fish in 100 L tanks.
Body length (mm) vs. days after fertilization.

- Exp. 1A: 10-liter tanks, eggs from 492 g female
- Exp. 1B: 100-liter tank, eggs from 492 g female
- Exp. 2: 100-liter tank, eggs from 466 g female

Key:
- ● Human embryo (HE)
- △ Notochord flexion
- □ Transformation

Days after fertilization range from 0 to 60.
This study has shown that ovulation of black sea bass can be induced routinely, and that larvae can be reared through transformation in the laboratory. During the spawning season, females that have initial oocyte diameters greater than 0.4 mm, that are kept at 18°C and are given injections of HCG (1.0 and 0.7 IU/g) on consecutive days, should ovulate about 2 d after the first injection. Larvae fed only Brachionus will grow well until about day 12. Poor growth of older larvae fed only Brachionus and Artemia probably indicates a requirement for transitional or supplemental food such as copepod nauplii. Possible improvements include extension of spawning time in the laboratory (e.g., by temperature and photoperiod manipulation) and development of a larval feeding regimen that would maximize production of juveniles in a mariculture setting.

References


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