Marine Biology 26, 271-285 (1974)

Effects of Temperature and Delayed Feeding on Growth and Survival of Larvae of Three Species of Subtropical Marine Fishes*

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Abstract

In larvae of the bay anchovy *Anchoa mitchilli* (Valenciennes), the sea bream *Archosargus rhomboidalis* (Linnaeus), and the lined sole *Achirus lineatus* (Linnaeus), growth, survival, and starvation times were investigated at temperatures of 22° to 32°C. The rate at which hours after hatching until starvation decreased in relation to temperature for unfed larvae did not differ significantly among the 3 species, ranging from -5.4 to -6.3 h per degree increase in temperature. The total number of hours until starvation did differ for all 3 species: lined soles survived longest, bay anchovies were intermediate, and sea bream survived the least time. At 28°C, unfed sea bream could survive 90.1 h, bay anchovy 102.3 h, and lined sole 119.8 h. The eyes pigmented at nearly the same time after hatching for sea bream and bay anchovy, but took about 20 h longer at all temperatures for lined sole. Quadratic equations best described the relationship between hours after hatching when the eyes became pigmented and temperature. Eye-pigmentation times became nearly constant for all 3 species at temperatures above 28°C. At 28°C, eyes pigmented about 27 h after hatching for bay anchovy and sea bream but not until 47 h for lined sole. Hours after eye pigmentation when unfed larvae starved was a measure of the effective time that larvae had to commence feeding. Bay anchovies and lined soles were nearly alike in this respect, but sea bream starved at fewer hours after eye pigmentation. Slopes of regressions representing decrease in times to starvation for increasing temperatures ranged from -3.7 to -4.4 h per degree increase in temperature, and were not significantly different among the 3 species. At 28°C, unfed lined soles starved at 70 h after eye pigmentation, bay anchovies starved at 72.5 h, and sea bream at only 62 h. Yolk absorption was most rapid for all species during the first 20 h after hatching, and was faster at higher temperatures. Amounts of yolk remaining at the time eyes became pigmented were less at higher temperatures for bay anchovy and lined sole, but were greater for sea bream, suggesting that sea bream used yolk more efficiently at higher temperatures. Either no yolk or small traces (<0.20%) remained at 24 h after eye pigmentation in all 3 species. Feeding was delayed for periods of 8, 16, 24, 32, 40 and 48 h after eye pigmentation for all species at a series of experimental temperatures from 24° to 32°C. Growth and survival were affected when food was withheld for more than 24 h at 28°C, but survival did not decrease markedly until food was withheld at least 8 h longer. At lower temperatures food could be withheld longer and at higher temperatures for less time. Feeding can be initiated by most larvae for several hours after all visible yolk reserves have been exhausted. All species tested can survive for 24 to 40 h after eye pigmentation at 24° to 28°C without food and still have relatively good growth and survival when food is offered. If the "critical period" is considered relative to time of hatching, lined soles need not find food for 3 to 3.5 days after hatching, but bay anchovy and sea bream must feed within 2.5 days of hatching.

Introduction

Larvae of most marine fishes cannot feed immediately after hatching, but exist on yolk until their eyes and mouthparts become functional. Three species of subtropical marine fish larvae were studied to determine what period of time can expire before they starve or are incapable of establishing themselves as successful feeders: the bay anchovy *Anchoa mitchilli* (Valenciennes): Engraulidae; the sea bream *Archosargus rhomboidalis* (Linnaeus): Sparidae; the lined sole *Achirus lineatus* (Linnaeus): Soleidae. All three are among the most common estuarine fishes in Biscayne Bay, near Miami, Florida (USA). All have pelagic eggs and larvae, although they differ considerably in morphology and behavior. Bay anchovy and lined sole larvae have been investigated in previous culture experiments and results have been reported (Detwyler and Houde, 1970; Houde *et al.*, 1970; Saksena and Houde, 1972; Houde, 1973). Bay anchovies have a geographical range that extends from Cape Cod to Yucatan, including the Gulf of Mexico (Hildebrand,

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1963), and thus are not confined to tropical and subtropical ecosystems. Sea bream and lined soles are more restricted in their distribution. Sea bream have been reported from New Jersey to Rio de Janeiro, including the eastern Gulf of Mexico (Briggs, 1958) and also the West Indies (Randall, 1968), but they are common only from the more tropical parts of the recorded range. Lined soles occur from Florida and the Gulf of Mexico to Uruguay (Briggs, 1958).

Times to starvation for larvae of some temperate-water marine species have been determined, but tropical species are virtually unstudied. The time after hatching during which larvae must establish themselves as active feeders, or risk starvation, has been termed the "critical period" by many fishery scientists. After their yolk supply is exhausted, larval fish must begin feeding within some limited time span. Blaxter and Hempel (1963) found that Atlantic herring *(Clupea harengus)* larvae starved at 11° to 12°C if not offered food within 8.5 to 15 days after hatching. Hempel and Blaxter (1963) also examined the relationship between temperature, yolk-sac absorption and starvation times for herring larvae, noting the decreased time that larvae had available to find suitable food at the higher temperatures. California sardine (*Sardinops caerulea*) larvae probably would starve at 4 days after hatching at 17°C if food were not offered (Lasker, 1965), and northern anchovy (*Engraulis mordax*) required food at 3 days after hatching at 22°C (Lasker *et al.*, 1970). May (1971) reported that grunion (*Leuresthes tenuis*) larvae could survive starvation for up to 2 weeks at 18°C and then begin feeding, but grunion larvae are not typical of most marine species. Wyatt (1972) determined effects of starvation on previously fed plaice (*Pleuronectes platessa*) larvae at 10°C, and found that young larvae could reestablish feeding after 8 days' starvation. Larvae of the mullet *Mugil cephalus*, a tropical species, were first offered food at either 2 or 7 days after hatching at temperatures from 19° to 24°C, but no difference in survival was detected (Kuo *et al.*, 1973). Apparently no similar research has been done on species that typically spawn at temperatures above 22°C. That was the object of this study. It has been suggested that starvation is rapid and irreversible at high temperatures. I tested the idea that tropical marine fish larvae have an abbreviated period of time to establish feeding, using 3 species which are divergent in their systematic status as well as in general morphology.

Other criteria of my research were to examine (1) the relation between time until eye pigmentation and temperature; (2) the relation between percentage yolk remains and time after hatching for the 3 species. Both eye pigmentation and the amount of yolk remaining are indicators of preparedness to feed in most larval fishes. Growth of larvae in relation to temperature also was investigated as another measure of possible effects of delayed feeding.

Materials and Methods

Egg Collections

Fertilized eggs of all species were collected in 1-m diameter plankton nets suspended from the dock at the Rosenstiel School of Marine and Atmospheric Science (RSMAS). *Anchoa mitchilli* eggs were collected during all seasons. Eggs of *Archosargus rhomboidalis* were available from late September until May, and those of *Achirus lineatus* from May through September. Plankton collections were examined in the laboratory, and living eggs at similar developmental stages were sorted from other plankton by pipettes before being transferred to culture tanks.

Rearing Conditions

Rearing systems were 35-l all-glass aquaria, supplied with filtered seawater that was gently aerated through airstones. The systems were static, except that 10% of the tank volume was replaced each day with freshly drawn seawater from the laboratory system. A total of 170 eggs was stocked in each tank to give a stocking density of about 5 eggs/l, and 5 eggs were preserved to be measured. Experiments were of 7 days duration; preliminary experiments had convinced us that larvae surviving that period of time would likely survive until metamorphosis. Five larvae were preserved in 5% buffered formalin on each of the first 4 days of the experiment, and 3 larvae on the succeeding 2 days to give a total of 26 preserved specimens (15.3% of the original number of eggs that were stocked). All survivors were preserved on the last day. Larvae were preserved to compile a record of growth under the various experimental conditions and to examine the relation of yolk absorption to time after hatching.

Temperatures were controlled to $\pm$ 0.5C° by immersion heaters. Experimental temperatures ranged from 22° to 32°C for bay anchovy and sea bream, but from 24° to 32°C for lined sole. Acclimation of developing embryos from ambient to experimental temperatures never exceeded 1C°/h.

Rearing tanks were lighted continuously by two, 20 W fluorescent "cool white" lamps suspended 20 cm above the water surface. Light levels ranged from 2500 to 2800 lux.

Salinity ranged from 31 to 35°/oo. Amounts of tapwater of 500 cm^3 or less sometimes were added to tanks to insure that salinity did not exceed 35°/oo.

Feeding

Larvae were fed on zooplankton that was collected from the RSMAS dock in 1/2 m, 35μ-mesh plankton nets. By appropriately grading the plankton through 280, 110 and 35μ meshes (Detwyler and Houde, 1970) a fraction consisting almost entirely of copepod nauplii and copepodites was retained by

the 35μ mesh. These ranged from 50 to 100μ in breadth, and were fed to the larvae. Most of these nauplii and copepodites probably were *Oithona nana*, *Acartia tonsa* and *Paracalanus parvus*, since these are the most abundant copepods in Biscayne Bay (Reeve, 1970). Food was maintained at levels of 1000 to 1500 organisms/l. For bay anchovy, the level was maintained nearer to 1500 than for the other two species because bay anchovy apparently have a higher food demand than some other species of larvae (Saksena and Houde, 1972). Food levels were estimated by counting the number of organisms drawn from the tank in 50 ml aliquots and then expanding the count to numbers per liter. Estimates were made 2 to 4 times daily and levels were adjusted by addition of food several times a day. Phytoplankton blooms of *Chlorella* sp. and *Anacystis* sp. were added to and maintained in the rearing tanks. These phytoplankters do not provide nutrition to fish larvae. In previous rearing attempts, larvae in tanks with those phytoplankters starved just as rapidly as they did in tanks with neither zooplankton nor phytoplankton present. The phytoplankton will improve survival and growth of larvae in small rearing systems, and is routinely used in the culture of many marine organisms as a water conditioner (Harada, 1970; Houde, 1973). The blooms apparently reduce levels of nitrogen metabolites that are produced both by the larvae and the zooplankton food (Siddall, in press).

Experimental Design

Experiments were designed so that larvae were first offered food at designated times after the eyes became pigmented. At each experimental temperature, larvae were first fed at one of the following times: 0, 8, 16, 24, 32, 40, or 48 h after eye pigmentation (Table 1). When results were not clear and when time allowed, replicates were run for certain experiments. The feeding schedule was followed for bay anchovy at 24°, 28°, 30° and 32°C; for sea bream at 22°, 26° and 30°C;

Table 1. *Anchoa mitchilli*, *Archosargus rhomboidalis*, *Achirus lineatus*. Summary of data on larvae reared at different temperatures and fed at different hours after eye pigmentation. All experiments began with 170 eggs, and same number of larvae were preserved each day from all experimental units. Experiments were of 7 days duration

Temperature (°C)	Hours when first fed after eye pigmentation	Number of survivors	Growth (mm)					
			Mean standard length of survivors		Mean body depth of survivors		Mean daily increments	
			$\bar{x}$	$S_{\bar{x}}$	$\bar{x}$	$S_{\bar{x}}$	Standard length	Body depth
			Anchoa mitchilli					
22	Not fed	0	-	-	-	-	-	-
22	Not fed	0	-	-	-	-	-	-
24	0	37	5.45	0.12071	0.48	0.00794	+0.483	+0.042
24	8	38	5.75	0.15729	0.46	0.01114	+0.477	+0.036
24	16	62	5.38	0.10934	0.48	0.00721	+0.470	+0.046
24	24	47	4.70	0.13640	0.44	0.01095	+0.400	+0.032
24	32	41	5.19	0.09332	0.47	0.00728	+0.480	+0.033
24	40	42	4.58	0.19330	0.44	0.00748	+0.365	+0.032
24	48	1	4.40	-	0.40	-	+0.270	+0.026
24	Not fed	0	-	-	-	-	-	-
26	Not fed	0	-	-	-	-	-	-
28	0	45	6.48	0.20864	0.51	0.01300	+0.593	+0.047
28	8	49	7.09	0.10051	0.57	0.01253	+0.685	+0.057
28	16	30	6.73	0.23699	0.57	0.01572	+0.700	-
28	24	4	5.99	0.35228	0.56	0.01709	+0.468	+0.045
28	24	20	6.08	0.18983	0.54	0.01393	+0.547	+0.051
28	32	42	6.31	0.15052	0.51	0.00922	+0.513	+0.044

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Table 1, continued

Temperature (°C)	Hours when first fed after eye pigmentation	Number of survivors	Growth (mm) Mean standard length of survivors $\bar{x}$	$S_{\bar{x}}$	Mean body depth of survivors $\bar{x}$	$S_{\bar{x}}$	Mean daily increments Standard length	Body depth
28	32	0	-	-	-	-	-	-
28	40	0	-	-	-	-	-	-
28	Not fed	0	-	-	-	-	-	-
30	0	5	5.05	0.56691	0.45	0.03202	+0.377	+0.032
30	8	19	7.59	0.08738	0.63	0.01077	+0.795	+0.062
30	16	0	-	-	-	-	-	-
30	24	1	5.28	-	0.46	-	+0.440	+0.042
30	32	0	-	-	-	-	-	-
30	40	0	-	-	-	-	-	-
30	Not fed	0	-	-	-	-	-	-
31	Not fed	0	-	-	-	-	-	-
32	0	9	8.16	0.17233	0.68	0.02102	+0.879	+0.068
32	8	2	5.50	0.70000	0.53	0.13000	+0.385	+0.038
32	16	20	6.79	0.14283	0.50	0.01183	+0.630	+0.041
32	24	0	-	-	-	-	-	-
32	Not fed	0	-	-	-	-	-	-
			Archosargus rhomboidalis					
22	0	98	2.40	0.03312	0.45	0.00762	+0.046	+0.010
22	0	2	1.84	0.01000	0.33	0.00000	-0.056	-0.014
22	8	82	2.67	0.08202	0.54	0.01114	+0.020	+0.024
22	8	4	2.12	0.18166	0.38	0.01849	-0.042	-0.010
22	16	27	2.34	0.04572	0.49	0.01300	+0.033	+0.011
22	16	12	2.40	0.08879	0.49	0.03342	-0.001	+0.003
22	24	20	2.76	0.08348	0.56	0.01942	+0.104	+0.030
22	24	43	2.40	0.05667	0.45	0.01104	+0.016	+0.004
22	32	49	2.32	0.05246	0.46	0.01187	+0.004	+0.008
22	32	45	2.20	0.04064	0.45	0.00990	+0.008	+0.003
22	40	112	2.53	0.02718	0.50	0.00707	+0.060	+0.005
22	40	8	2.77	0.07308	0.47	0.01049	+0.076	+0.003
22	48	0	-	-	-	-	-	-
22	48	0	-	-	-	-	-	-
22	Not fed	0	-	-	-	-	-	-
24	Not fed	0	-	-	-	-	-	-
26	0	73	3.34	0.06482	0.72	0.01808	+0.225	+0.057
26	8	86	3.25	0.06010	0.66	0.01466	+0.223	+0.050
26	16	74	3.43	0.05851	0.70	0.01631	+0.190	+0.048

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Table 1, continued

Temperature (°C)	Hours when first fed after eye pigmentation	Number of survivors	Growth (mm) Mean standard length of survivors $\bar{x}$	$S_{\bar{x}}$	Mean body depth of survivors $\bar{x}$	$S_{\bar{x}}$	Mean daily increments Standard length	Body depth
26	24	7	3.08	0.22924	0.56	0.04672	+0.120	+0.016
26	24	18	3.31	0.09606	0.61	0.0°251	+0.164	+0.028
26	32	0	-	-	-	-	-	-
26	32	33	3.30	0.08447	0.59	0.01921	+0.167	+0.031
26	40	0	-	-	-	-	-	-
26	40	95	2.89	0.02718	0.60	0.00693	+0.112	+0.029
26	48	0	-	-	-	-	-	-
26	Not fed	0	-	-	-	-	-	-
28	Not fed	0	-	-	-	-	-	-
30	0	47	3.60	0.06656	0.84	0.02280	+0.224	+0.069
30	8	87	4.11	0.05778	1.02	0.02047	+0.294	+0.097
30	16	40	3.98	0.07706	0.94	0.03226	+0.288	+0.081
30	24	68	3.56	0.04444	0.77	0.01631	+0.240	+0.063
30	24	11	3.48	0.16359	0.69	0.06122	+0.174	+0.039
30	32	20	3.30	0.10545	0.66	0.02787	+0.160	+0.036
30	32	48	3.60	0.06662	0.70	0.02081	+0.186	+0.040
30	40	0	-	-	-	-	-	-
30	40	0	-	-	-	-	-	-
30	Not fed	0	-	-	-	-	-	-
32	8	0	-	-	-	-	-	-
32	Not fed	0	-	-	-	-	-	-
			Achirus lineatus					
24	0	41	2.66	0.02274	0.65	0.01345	+0.129	+0.043
24	8	77	2.57	0.01284	0.58	0.00843	+P.108	+0.030
24	16	59	2.56	0.02780	0.61	0.01100	+0.096	+0.041
24	24	53	2.39	0.01992	0.51	0.00825	+0.104	+0.029
24	32	46	2.43	0.02149	0.50	0.00975	+0.092	+0.022
24	40	1	One specimen lost — no measurements made					
24	48	5	2.40	0.06399	0.52	0.02419	+0.081	+0.022
24	Not fed	0	-	-	-	-	-	-
26	Not fed	0	-	-	-	-	-	-
28	0	73	2.77	0.02445	0.86	0.01709	+0.158	+0.076
28	8	114	3.19	0.01887	1.18	0.01122	+0.208	+0.118
28	16	33	2.59	0.04777	0.71	0.02691	+0.101	+0.042
28	24	39	2.79	0.05084	0.83	0.02421	+0.143	+0.066

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Table 1, continued

Temperature (°C)	Hours when first fed after eye pigmentation	Number of survivors	Growth (mm)					
			Mean standard length of survivors		Mean body depth of survivors		Mean daily increments	
			$\bar{x}$	$S_{\bar{x}}$	$\bar{x}$	$S_{\bar{x}}$	Standard length	Body depth
28	32	0	-	-	-	-	-	-
28	40	12	2.78	0.05190	0.80	0.01892	+0.126	+0.053
28	48	4	2.42	0.06702	0.61	0.01732	+0.063	+0.020
28	Not fed	0	-	-	-	-	-	-
30	Not fed	0	-	-	-	-	-	-
32	0	0	-	-	-	-	-	-
32	8	21	3.18	0.07171	1.14	0.04532	+0.205	+0.109
32	16	0	-	-	-	-	-	-
32	24	0	-	-	-	-	-	-
32	32	0	-	-	-	-	-	-
32	Not fed	0	-	-	-	-	-	-

and for lined sole at 24°, 28°, and 32°C. Size of larvae and the number of survivors at 7 days after hatching were the criteria used to judge effects of delaying feeding. In addition to the feeding experiments, several experiments in which there was no feeding were conducted at a series of temperatures (Table 1). These experiments provided data to estimate the hours until starvation for larvae in relation to hatching time and time of eye pigmentation. For each species at each temperature, experimental treatments were assigned randomly with respect to the order in which they were run to avoid the possibility that any changes might be occurring in rearing conditions that might be reflected in results. A set of experiments for any one temperature sometimes took several months to complete. To avoid any possible effects of rearing tank position in the culture room, experimental treatments were assigned randomly to culture units that were available.

Measurements and Analyses

Eggs and larvae preserved during experiments were measured using an ocular micrometer. Egg diameters were determined. Standard length (SL), body depth (BD), and both yolk-sac length and yolk-sac height were measured on larvae. Standard lengths and body depths were used to determine growth of larvae. Mean daily growth increments were calculated from the relation:

$$\frac{24}{j} \sum_{1}^{j} \frac{L_b - L_a}{T_b - T_a},$$

where T_b = total elapsed hours since hatching at the time larvae were preserved; T_a = elapsed hours from hatching at the last preservation prior to that at T_b; L_b = mean standard length or body depth of larvae at time T_b; L_a = mean standard length or body depth of larvae at time T_a; j = number of intervals between preservations of larvae during the experiment.

Yolk volumes were calculated from the yolk-sac lengths and heights of preserved larvae. Yolk sacs usually resemble prolate spheroids, and their volume could be estimated by Blaxter and Hempel's (1963) technique from the formula:

$$V = \pi/6 \; LH^2,$$

where L = yolk-sac length; H = yolk-sac height. Occasionally, the yolk sac was spherical and volume then was estimated from the familiar formula for the volume of a sphere: $V = 4/3 \; \pi r^3$.

Survival was determined from the number of larvae alive at the end of experiments, and was expressed as a percentage of the 170 eggs that were stocked. Actual survival rates would have been higher than observed rates because some larvae were preserved on each day of the experiments.

Starvation times at the experimental temperatures were estimated by regression-analysis techniques and analysis of covariance. The hours after hatching when mortality of unfed larvae was complete were regressed on experimental temperatures. This relationship was compared among species by covariance analysis. The hours after eye pigmentation when mortality of all unfed larvae was complete at a series of experimental temperatures

also were analyzed by the regression analysis, covariance technique.

Polynomial regressions were fitted by the least-squares method to estimate the hours between the time of hatching and when eyes became pigmented over the range of experimental temperatures for each species. Polynomials also were used to fit the data of percent yolk remains regressed on hours after hatching for each species at each experimental temperature. Polynomials, rather than exponential models, were used in both cases because they gave better fits to the data.

Results

Starvation of Unfed Larvae in Relation to Hatching Time

The number of hours that elapsed from hatching until all larvae starved was determined for unfed larvae at temperatures ranging from 22° to 32°C. Slopes of the linear regressions (Fig. 1; Table 2), representing the decrease in survival time per

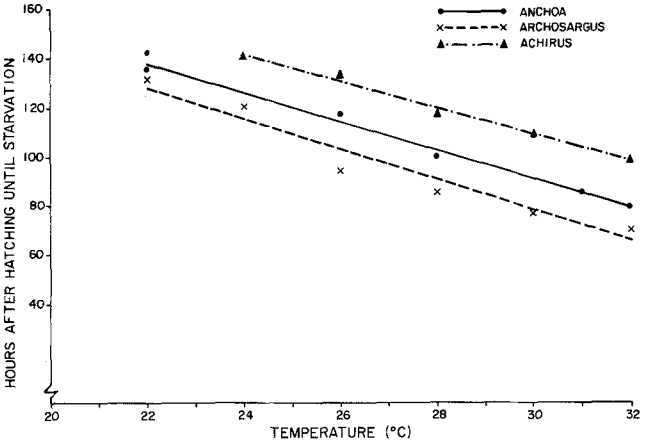

Fig. 1. *Anchoa mitchilli, Archosargus rhomboidalis, Achirus lineatus.* Relationship between hours after hatching until starvation of all unfed larvae and rearing temperatures

Table 2. *Achirus lineatus, Anchoa mitchilli, Archosargus rhomboidalis.* Relationship between temperature and times to starvation after hatching, times to starvation after eye pigmentation, and times between hatching and eye pigmentation for larvae

Relationship	*Achirus lineatus*	*Anchoa mitchilli*	*Archosargus rhomboidalis*
Hours after hatching until starvation *(Y)* regressed on temperature *(X)*	$Y = 271.700 - 5.425X$	$Y = 266.689 - 5.870X$	$Y = 267.042 - 6.318X$
$S_{Y \cdot X}$	2.2042	3.5044	6.3217
0.95 CL on $\hat{b}$	$- 5.425 \pm 1.109$	$- 5.870 \pm 0.902$	$- 6.318 \pm 2.098$
Hours after eye pigmentation until starvation *(Y)* regressed on temperature *(X)*	$Y = 173.600 - 3.700X$	$Y = 179.477 - 3.816X$	$Y = 186.256 - 4.443X$
$S_{Y \cdot X}$	4.2387	1.8241	4.9390
0.95 CL on $\hat{b}$	$- 3.700 \pm 2.130$	$- 3.816 \pm 0.470$	$- 4.443 \pm 1.639$
Hours from hatching until eye pigmentation *(Y)* regressed on temperature *(X)*	$Y = 365.03 - 21.07X + 0.35X^2$	$Y = 191.48 - 10.85X + 0.18X^2$	$Y = 262.03 - 15.70X + 0.26X^2$
$S_{Y \cdot X}$	1.2872	2.2101	2.1774

CL: Carapace length.

Table 3. *Achirus lineatus, Anchoa mitchilli, Archosargus rhomboidalis.* Summary of data on times until eyes become pigmented, times to total starvation, and relationship of yolk volumes to eye pigmentation time and time of starvation. Data are for larvae reared at various temperatures. Values are derived from fitted least-square regressions for the various relationships

Species	Temperature (°C)	Hours from hatching until eye pigmentation	Hours from hatching until total starvation	Hours from eye pigmentation until total starvation	Percent yolk remains at eye pigmentation time	Percent yolk remains at 24 h after eye pigmentation
Achirus lineatus	24	59.3	141.5	84.8	1.84	Trace (<0.10)
	28	47.2	119.8	70.0	~0.75	0.0
	32	46.2	98.1	55.2	0.0	0.0
Anchoa mitchilli	22	38.8	137.5	95.5	3.25	-
	24	33.5	125.8	87.9	2.52	0.0
	28	27.1	102.3	72.6	1.80	0.0
	32	26.4	78.8	57.4	~0.50	0.0
Archosargus rhomboidalis	22	42.4	128.0	88.5	1.62	Trace (<0.10)
	24	34.9	115.4	79.6	-	-
	26	29.5	102.8	70.7	4.84	Trace (<0.20)
	28	26.2	90.1	61.9	-	-
	30	24.9	77.5	53.0	3.81	Trace (<0.10)

degree increase in temperature, ranged from -5.4 to -6.3 h per degree, and did not differ significantly among the three species. The absolute time after hatching to starvation did differ significantly among all three species ($P < 0.01$). At all temperatures, starvation times were shortest for sea bream, intermediate for bay anchovy, and longest for lined sole (Table 3; Fig. 1). At 28°C, a temperature at which all three species are known to spawn, estimated starvation times (hours after hatching) are: sea bream, 90.1 h; bay anchovy, 102.3 h; lined sole, 119.8 h. Since these are the times at which 100% starvation mortality would occur, some individuals succumb many hours prior to these estimated times.

Eye Pigmentation

The times after hatching when eyes became pigmented were determined for each species over a range of temperatures (Fig. 2). Bay anchovy and sea bream larvae had nearly identical times until eye pigmentation over the temperature range that was tested, but lined soles took longer. Fitted polynomial regressions showed that quadratic equations adequately described the relationship for all three species (Table 2; Fig. 2). These regressions were used to predict hours from hatching until eye pigmentation for each species within the range of experimental temperatures (Table 3). Time from hatching until eye pigmentation represents the time that larvae presumably can gain nutrition only from their yolk reserves and not from exogenous sources. Lined soles spend about 20 h longer than anchovies or sea bream in this phase of larval life (Table 3). For the three species, relatively little decrease occurred in the time from hatching until the eyes were pigmented at temperatures above 28°C (Fig. 2), suggesting that the time after hatching when an exogenous food source becomes necessary is nearly constant for each of the species at temperatures of 28°C and higher. This implies that larvae may be nearer to starvation when their eyes become functional at temperatures above 28°C than at lower temperatures, because the rate of yolk absorption would continue to increase at higher temperatures with no corresponding decrease in the time after hatching when larvae could begin searching for food.

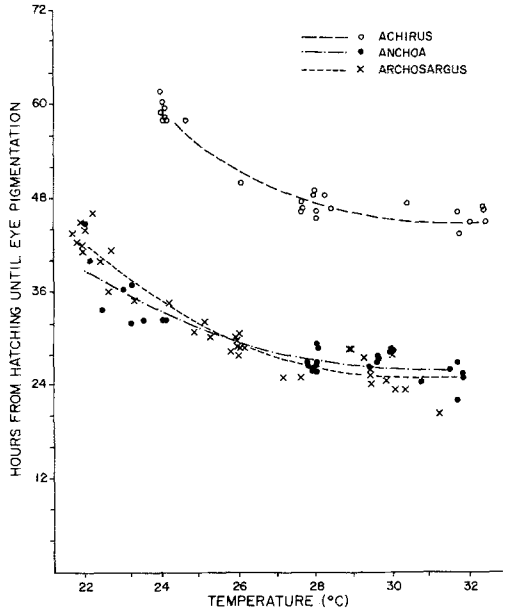

Fig. 2. *Anchoa mitchilli, Archosargus rhomboidalis, Achirus lineatus*. Relationship between hours after hatching when eyes become pigmented and rearing temperatures of larvae

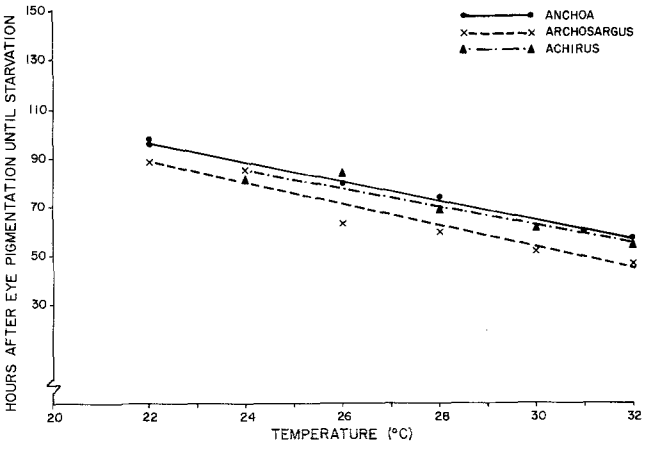

Fig. 3. *Anchoa mitchilli, Archosargus rhomboidalis, Achirus lineatus*. Relationship between hours after eye pigmentation until starvation of all unfed larvae and rearing temperatures

Starvation of Unfed Larvae in Relation to Time of Eye Pigmentation

The times after eye pigmentation when all unfed larvae starved also were regressed on temperature (Fig. 3), and were more alike among species than were the regressions of times after hatching until starvation on temperature (Fig. 1). Slopes of the linear regressions representing the decrease in time to starvation per degree increase in temperature ranged from -3.7 to -4.4 h per degree, and did not differ significantly among species. Tests of adjusted means detected no differences in the absolute time after eye pigmentation until starvation between lined soles and bay anchovies, but both of these species differed significantly ($P < 0.01$) from sea bream, which starved in less time than the other two species. Comparative data based on the regressions are given in Table 3. Starvation time in relation to the time when eyes become pigmented is a measure of the "effective time" until starvation, because only after eye pigment has developed do larvae search for food. Although unfed lined sole larvae starved at a longer time after hatching than the other species, their "effective starvation time" was nearly the same as for bay anchovies and not much different from sea bream because the eyes took considerably longer to pigment in lined soles than in the other species (Table 3).

Yolk Absorption

Yolk was absorbed rapidly during the first 20 h after hatching, but more slowly later, for all species within the experimental temperature range (Fig. 4). As expected, yolk was absorbed more rapidly at high temperatures than at lower temperatures. Traces of yolk (< 0.10%) remained for more than 85 h after hatching in lined soles and for more than 105 h after hatching in sea bream, but the last traces were gone before 50 h after hatching in bay anchovies. The rate of yolk absorption during the first 20 h after hatching was greatest in lined sole and least in sea bream, but lined soles absorbed yolk more slowly than sea bream during subsequent hours. In most cases, polynomial regressions gave acceptable fits to the data (Table 4) for times that extended to 40 h after hatching.

Yolk volumes differed among eggs of the three species. Sea bream eggs had a yolk volume of 0.34 mm^3, lined soles 0.22 mm^3, and bay anchovy 0.15 mm^3. Sea bream eggs and larvae are larger than those of the other two species, but no measure of the ratio of yolk weight to weight of newly hatched larvae is available for these species. Efficiency of yolk utilization and its relation to growth and survival of newly hatched larvae also have not been determined.

Eye Pigmentation and Yolk Absorption

The hours after hatching at which eyes would become pigmented (Fig. 2; Table 2) were substituted into the polynomial regressions (Table 4) to predict percentage yolk remaining at the time of eye pigmentation (Table 3) for each experimental temperature. In the two cases where there were no

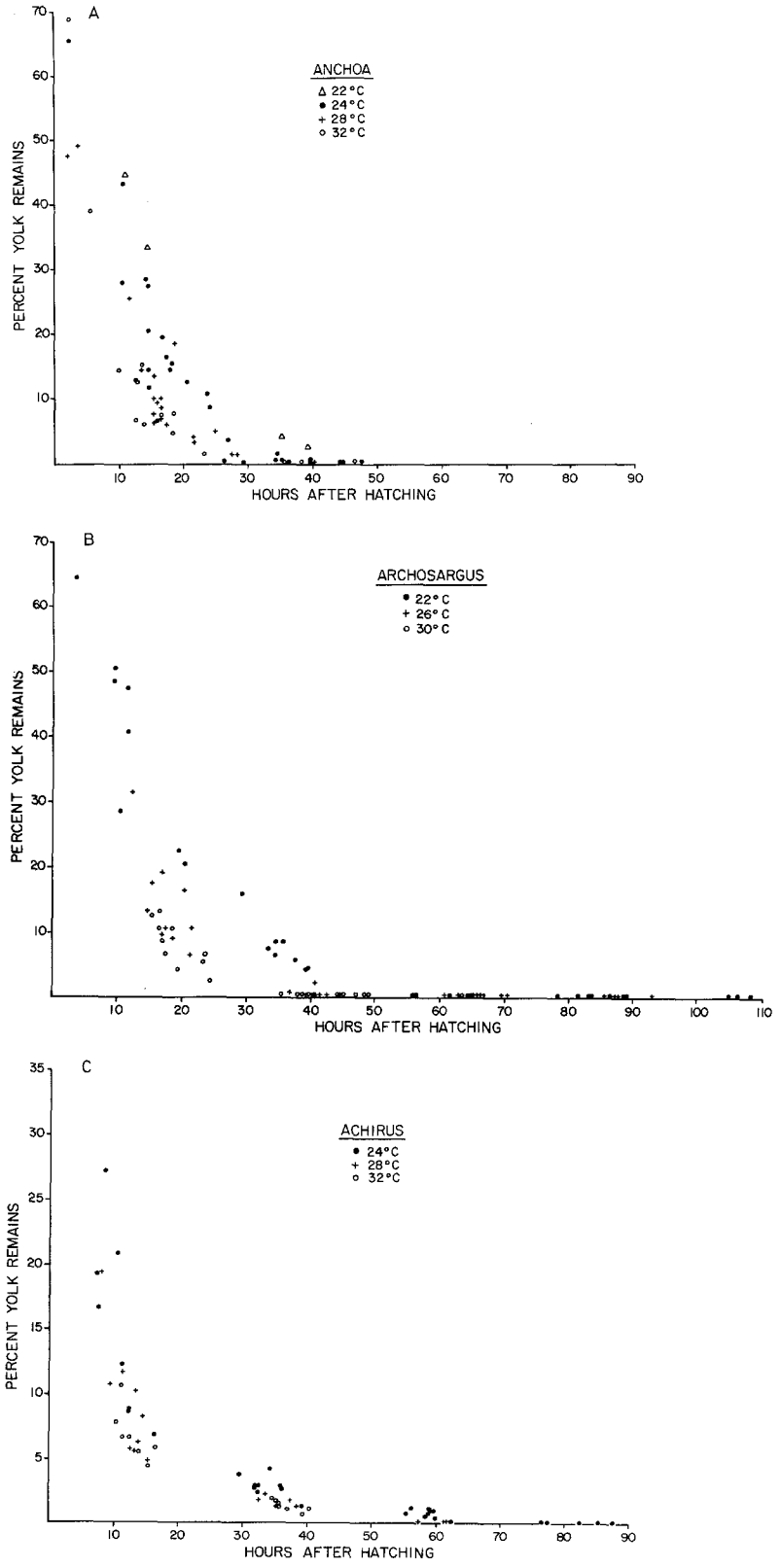

Fig. 4. Relationship between percent of yolk remaining and hours after hatching for larvae of (A) *Anchoa mitchilli*, (B) *Archosargus rhomboidalis*, (C) *Achirus lineatus*, cultured at various temperatures

Table 4. *Anchoa mitchilli, Archosargus rhomboidalis, Achirus lineatus.* Polynomial regressions relating percent yolk remains *(Y)* to hours after hatching *(X)* for larvae of bay anchovies, sea bream, and lined sole. Data plotted in Fig. 4

Species	Temperature (°C)	Equation	$S_{Y \cdot X}$
Anchoa mitchilli	22	$Y = 85.6630 - 4.41472X + 0.05904X^2$	1.32776
	24	$Y = 78.0254 - 6.02725X + 0.17160X^2 - 0.00176X^3$	5.43969
	28	$Y = 61.7139 - 5.27068X + 0.15520X^2 - 0.00156X^3$	4.13618
	32	No polynomials out to 4th degree provided a good fit to data	
Archosargus rhomboidalis	22	$Y = 68.4864 - 2.60670X + 0.02428X^2$	4.44647
	26	$Y = 37.7239 - 1.59697X + 0.01635X^2$	3.77051
	30	$Y = 32.1751 - 1.68216X + 0.02181X^2$	1.73078
Achirus lineatus	24	$Y = 29.8870 - 1.66222X + 0.03132X^2 - 0.00019X^3$	3.01568
	28	No polynomials out to 4th degree provided a good fit to data	
	32	$Y = 19.1894 - 1.40390X + 0.03894X^2 - 0.00038X^3$	1.13949

satisfactory fits to the data on yolk remains (Table 4), the predictions were made by eye from Fig. 4A and C. Less than 5% of the yolk remained when eyes became pigmented in all species at all test temperatures, but two different trends were observed (Table 3). For both bay anchovies and lined soles, yolk remaining at time of eye pigmentation decreased as temperature increased, suggesting that the necessity for food would be more critical at that time at the higher temperatures. Sea bream, however, had more yolk remaining when their eyes became pigmented at higher temperatures than 22°C, suggesting that efficiency of yolk utilization was better at 26°C and that the need for food at time of eye pigmentation might not be as critical as for the other two species at that temperature. At 24 h after eye pigmentation, none of these species had more than a trace of yolk remaining at any of the temperatures (Table 3).

Feeding Delay and Effects on Growth and Survival

The three species were able to begin feeding and survive until the experiments ended when feeding was delayed for many hours after the eyes became pigmented (Table 1). Fewer hours without feeding could be tolerated at the higher temperatures, but in the case of sea bream (Table 1) many fed successfully and survived at 30°C when feeding was delayed as long as 32 h after eye pigmentation (a.e.p.). All the species could survive if food was withheld for 32 h a.e.p. or more at temperatures of 28°C or lower. Feeding, therefore, can be initiated, with only minor effects on both growth and survival, for several hours after all visible yolk reserves have been exhausted, since no yolk or only the smallest traces were present at 24 h a.e.p. (Table 3).

Anchoa mitchilli

Bay anchovies were tested at 24°, 28°, 30° and 32°C; survival was good at 24° and 28°C (Table 1). At 24°C, survival was not affected by feeding delays as long as 40 h a.e.p. (74 h after hatching: a.h.). Survival averaged more than 25% for 24°C tests when larvae were fed within that time period. At 28°C there apparently were no effects for feeding delays of as much as 32 h a.e.p. (59 h a.h.) although one replicate under those conditions had no survivors. Mean survival at 28°C for feeding delays of 32 h a.e.p. or less was 16%. At 30° and 32°C, feeding delays of more than 16 h a.e.p. (about 42 h a.h.) were not tolerated by larvae. Mean survival was low at all feeding times at 30° and 32°C. Feeding delays of 8 h beyond the times that gave good survival almost always resulted in complete mortality of bay anchovies at all test temperatures.

Growth of anchovies decreased if feeding was delayed more than 32 h a.e.p. at 24°C, 16 h a.e.p. at 28°C, and only 8 to 16 h at 30° or 32°C. The largest larvae and best growth rates occurred at the highest temperatures (Table 1). For the combined 0 and 8 h feeding delays, weighted mean standard lengths of survivors at the end of experiments were 5.60 mm at 24°C, 6.80 mm at 28°C, 7.06 mm at 30°C, and 7.59 mm at 32°C. Mean standard length of newly-hatched larvae that were preserved less than 20 h a.h. was 2.90 mm, based on specimens from 24 experiments.

Archosargus rhomboidalis

Sea bream were tested at 22°, 26° and 30°C; in general survival was good at 26° and 30°C (Table 1). Survival at 22°C was variable, suggesting that this temperature might be approaching the lower lethal limit for the species. Preliminary experiments indicated that the sea bream will not survive for 7 days at 32°C under any feeding regime. There was no indication that delayed feeding at 22°C was the cause of mortality for delays as long as 40 h a.e.p. (82 h a.h.). Survival averaged 25% for 22°C tests where feeding began in that time period. Feeding delays as long as 40 h a.e.p. (69 h a.h.) resulted in good survival at 26°C, but survival became variable when feeding was delayed 24 h or longer a.e.p. Mean survival for feeding delays of 40 h and less was 25% at 26°C. At 30°C, survival was not seriously affected by feeding delays as long as 32 h a.e.p. (57 h a.h.). Mean survival at 30°C for delayed feedings in that time period was 27%. Feeding delays of 48 h a.e.p. at 22° and 26°C, and of 40 h a.e.p. at 30°C resulted in complete mortality.

Growth of sea bream larvae was poor and unpredictable for all experimental units at 22°C (Table 1). At 26°C, growth decreased when feeding was delayed more than 16 h a.e.p., but the effect was not serious until 40 h a.e.p. The best growth occurred at 30°C; no effects caused by delayed feeding were evident until 24 h a.e.p. At 30°C, the biggest larvae were produced when feeding was delayed 16 h a.e.p. or less. For the combined 0 to 16 h feeding delays, weighted mean standard lengths of survivors at the end of experiments were 2.48 mm at 22°C, 3.20 mm at 26°C, and 3.94 mm at 30°C. Mean standard length of newly-hatched larvae less than 20 h a.h. was 2.26 mm, based on specimens from 40 experiments.

Achirus lineatus

Lined sole larvae were tested at 24°, 28° and 32°C; survival was good at 24° and 28°C, but at 32°C there were survivors only in the experiment with feeding delayed 8 h a.e.p. (Table 1). At 32°C, it is frequently difficult to rear larvae of Biscayne Bay fishes. This temperature may be near the upper lethal limit for lined soles, although we have reared them at 32°C in some experiments. At 24°C, survival was not affected by delaying feeding as long as 32 h a.e.p. (91 h a.h.) and survival averaged 32% for experiments with feeding delays within that time period. Survival at 28°C was best when larvae were fed at 0 to 8 h a.e.p. (47 to 55 h a.h.), but remained high for delays as long as 24 h a.e.p. (71 h a.h.). The mean survival at 28°C for feeding delays of 24 h a.e.p. or less was 38%. Unlike bay anchovies and sea bream, some lined sole larvae survived if not fed for many hours after the longest delay that still gave good survival (Table 1). At both 24° and 28°C, a few larvae survived when feeding was delayed as long as 48 h a.e.p. (107 h a.h. at 24°C and 95 h a.h. at 28°C).

Best growth at 24°C occurred when lined sole larvae were fed at 16 h a.e.p. or sooner. At 28°C, effects of delayed feeding on growth were unclear. The best growth at 28°C was recorded for larvae that were first fed at 8 h a.e.p., but no serious inhibitory effects were noted until feeding was delayed for 48 h a.e.p. Larvae from the single experiment at 32°C that had survivors grew well, but no better than larvae from the 8 h a.e.p. experiment at 28°C. For the combined experiments with feeding delays from 0 to 16 h a.e.p., weighted mean standard lengths of survivors at the end of experiments were 2.59 mm at 24°C, 2.96 mm at 28°C, and 3.18 mm at 32°C. Mean standard length of newly-hatched larvae that were preserved less than 20 h a.h. was 1.94 mm, based on specimens from 17 experiments.

Discussion and Conclusions

The question of whether "critical periods" occur at the time of yolk absorption in the larval stages of fishes was raised by Hjort (1914), but remains little understood even today. Marr (1956) reviewed the problem and found no proof that "critical periods" existed for larvae of several species of marine fishes. Farris (1960) also discussed the problem and believed that "critical periods" of high mortality during the larval life did occur for some species, but that the high mortality occurred prior to yolk-sac absorption. Recently, fishery scientists have argued both for and against the "critical period" hypothesis and its implication of food availability as a major factor in the early life mortality of marine fishes. Mikhman (1969) believed that *Clupeonella delicatula* in the Sea of Azov (USSR) underwent high larval mortality when zooplankton densities were less than 250 to 300/1, but neither Duka (1969) nor Dekhnik *et al.* (1970) believed food abundance was a limiting factor for larvae of some Sea of Azov and Black Sea fishes.

Laboratory studies of feeding by larval fishes indicated that high survival rates probably cannot occur at the relatively low food levels normally found in nature (O'Connell and Raymond, 1970; Hunter, 1972; Saksena and Houde, 1972). It has been suggested that, at the time of exogenous feeding, larvae must be carried into patches of rela-

tively dense plankton to avoid mortality due to starvation. Larvae of tropical fishes have relatively little time, compared to fishes from more temperate waters, to find suitable food in the natural environment or to encounter a rich patch of suitable food because of their rapid development. Perhaps the time element is important in determining how successful larvae are in establishing themselves as active feeders. In temperate waters, larvae may be capable of initiating feeding over a period of several days (Blaxter and Hempel, 1963), or can be deprived of food for several days and reestablish feeding (Wyatt, 1972), thus increasing the probability of surviving by encountering a "patch" of suitable food; however, it was believed that tropical species would starve very soon after they became capable of ingesting food if such food were not available in adequate concentration.

Anchoa mitchilli, *Archosargus rhomboidalis* and *Achirus lineatus* were deprived of food in my experiments for periods of time that exceeded the times when visible yolk was absorbed. All of these species were capable of initiating feeding and surviving to the end of the experiments when feeding was delayed for many hours after the eyes became pigmented and the yolk was absorbed. Table 5 summarizes data from Tables 1 to 3 and Fig. 4, showing the survival capability for larvae of the three species. In relation to yolk-absorption time, lined sole larvae seem somewhat more susceptible to starvation than sea bream or bay anchovy. This implication could be misleading, however, because all of the species can begin feeding before the yolk is completely absorbed, when the eyes and mouth become functional. Except for bay anchovies at 32°C, yolk was not completely absorbed in these species until after the eyes had been pigmented for several hours (Table 5). Presently, it is not known what minimum quantity of yolk constitutes a significant source of energy for any of these larvae.

Yolk-absorption times at the high temperatures in my experiments are faster than times recorded for most other marine species. Observed differences in yolk-absorption times among species are quite large, and presumably are important to larvae that are establishing themselves as active feeders. Blaxter and Hempel (1963) reported that larvae of the Atlantic herring *Clupea harengus* took 84 to 168 h after hatching to absorb their yolk at 11° to 12°C, the large variance being accounted for by differing egg sizes. Lasker (1965) found that the California sardine *Sardinops caerulea* absorbed their yolk within 180 h at 14°C. Larvae of the tautog *Tautoga onitis* took from 84 h at

Table 5. *Anchoa mitchilli*, *Archosargus rhomboidalis*, *Achirus lineatus*. Summary of survival capabilities for larvae of bay anchovies, sea bream, and lined soles in relation to eye pigmentation times and yolk absorption times. Data summarize results of Tables 1–3 and Fig. 4

Species	Temperature (°C)	Hours after hatching when yolk is absorbed[a]	Hours after eye pigmentation when		Hours after yolk absorption before which larvae must be fed
			Yolk absorbed[a]	Survival remains good if larvae fed before	
Anchoa mitchilli	24	41.0	7.5	40	32.5
	28	36.6	9.5	32	22.5
	32	27.4	1.0	16	15.0
Archosargus rhomboidalis	22	52.9	10.5	40	29.5
	26	50.0	20.5	40	19.5
	30	40.9	16.0	32	16.0
Achirus lineatus	24	79.8	20.5	32	11.5
	28	59.7	12.5	24	11.5
	32	58.2	12.0	--	--

[a]Less than 0.5% yolk remains.

22°C to 156 h at 16°C to absorb yolk (Laurence, 1973), and larvae of the striped mullet *Mugil cephalus* took 120 h at 22° to 24°C (Kuo *et al.*, 1973). Northern anchovy larvae *(Engraulis mordax)* absorbed their yolk in 36 h at 22°C (Lasker *et al.*, 1970). The species that I studied varied considerably (Table 5). Lined soles took a relatively long time to absorb yolk (58 to 80 h, 32° to 24°C), sea bream an intermediate time (41 to 53 h, 30° to 22°C) and bay anchovy the least time (27 to 41 h, 32° to 24°C). It is tempting to predict times to starvation for different species from data on yolk-absorption times, but there are other factors involved. Despite their fast yolk-absorption time, unfed bay anchovy survived longer than sea bream larvae over the same temperature range (Figs. 1 and 3), and effects on growth and survival of fed larvae of both species were similar for feeding delays of the same time. In fact, bay anchovy larvae may have tolerated feeding delays better than sea bream at any given temperature (Table 5). The quality of yolk and the amount of swimming activity by larvae also are factors that will differ among species and influence starvation times. Studies of efficiency of yolk utilization by marine fish larvae have indicated that great variation occurs among species (Lasker, 1962; Blaxter and Hempel, 1966; Ryland and Nichols, 1967; Laurence, 1973), and will affect starvation times of the various species.

Temperature affects both the time that eyes become pigmented and the rate at which yolk is absorbed. Because lined soles took about 20 h longer for their eyes to become pigmented at all experimental temperatures than did bay anchovies or sea bream, they had less yolk remaining at the time that they acquired eye pigment than the other two species (Table 3). This would explain the necessity of lined soles to begin feeding at somewhat earlier times in relation to eye pigmentation and yolk absorption (Table 5) than bay anchovies or sea bream. At the time of eye pigmentation, lined soles and bay anchovies had relatively more yolk remaining at the lower experimental temperatures than at higher temperatures (Table 3), but sea bream had the largest yolk reserves at an intermediate temperature. Sea bream that developed at intermediate temperatures would seemingly have an advantage over those at higher or lower temperatures in establishing themselves as active feeders. At intermediate temperatures they have both the capability to search for exogenous food sources and a relatively large endogenous food supply to sustain them if food is not abundant or readily available.

At 24° to 28°C, which is within the range of spawning temperatures for the three species that we investigated, the "critical periods" do not differ greatly among the species if the time of first feeding is examined in relation to time of eye pigmentation. To avoid mortality they must be fed within 24 to 40 h a.e.p. To insure that growth during the first week after hatching is not reduced, feeding should begin within 16 to 32 h a.e.p. If the "critical period" is considered relative to time of hatching, lined soles need not find food for 3 to 3.5 days after hatching, but sea bream and bay anchovy larvae must feed within 2.5 days of hatching. At 22°C, Lasker *et al.* (1970) reported good survival of northern anchovy larvae that were fed at times up to 3 days after hatching. The "critical periods" that I found for the three species are shorter than those for more temperate marine fishes, but there is no necessity to provide food immediately after eye pigmentation for any of the species. In nature, all three species could exist for at least 1 day a.e.p. without food. It is still possible that, in nature, these larvae might not be transported to a patch of suitable food within that 1-day period, and that mass starvation could occur at the low food concentrations normally found in subtropical marine ecosystems.

Acknowledgements. Thanks go to N. Chitty and A. Chitty for helping to construct rearing facilities. Assistance in culture operations was provided by A. Cardet, W. Stepien, A.K. Taniguchi, and L. Swanson. Drs. G.C. Laurence and V.P. Saksena criticized drafts of the manuscript during its preparation. Financial support for the research was provided by National Science Foundation, Division of Biological Oceanography, Grant GA 34138.

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Date of final manuscript acceptance: April 22, 1974. Communicated by J. Bunt, Miami