

Environmental factors affecting the early life history of bay anchovy *Anchoa mitchilli* in Great South Bay, New York

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ABSTRACT: For bay anchovy *Anchoa mitchilli*, 3 life-history parameters were studied in Great South Bay during late spring and summer of 1987 and 1988: intensity of spawning, larval growth rates, and egg and larval mortality rates. Duration of peak spawning season was highly correlated ($p < 0.01$) with larval food abundance in the field (copepod nauplii + copepodite and adult cyclopoids + copepodite calanoids), but not correlated with salinity or temperature. Cohort mortality rates determined throughout the spawning season were lower in the middle of the peak spawning season (when food availability was maximum) and higher at the beginning and end of the spawning season. Since the duration of the high microzooplankton abundance is so short (4 to 5 wk) and because of the high energy requirements of young bay anchovy, it is proposed that adult bay anchovy spawn during the season of maximum food availability thus enhancing offspring survival. When the effects of the type of habitat were analyzed on a local scale, no difference was found between eelgrass and unvegetated areas in: (1) egg or larval density, (2) larval growth rates, (3) egg and yolk sac larvae mortalities. Mortality rates of older larvae (> 3 d old), however, were higher in eelgrass beds than in unvegetated areas. Since microzooplankton abundances were not different among stations, increased mortality rates in the vegetated areas seem to result from higher levels of predation. This suggests that the hypothesis that vegetated areas are used as preferential zones for spawning and nursing may not be applicable to bay anchovy. When the 3 population parameters studied are considered on a latitudinal basis, it was found that (1) duration of spawning season in Great South Bay is among the shortest reported in the literature, and decreased with increasing latitude; (2) average mortality rates were similar to those reported for populations located at other areas; (3) average larval growth rates tended to be higher in Great South Bay in spite of the lower temperatures during the spawning season. Possible interrelationships among these trends in life-history traits are discussed, and future lines of research on population differentiation are proposed.

INTRODUCTION

With the aim of improving the understanding of the dynamics of recruitment, fishery biologists have studied the early life history of fishes because it is during these stages that the highest abundances and mortality rates occur in natural populations (Rothschild 1986, Houde 1987). It is now clear that environmental factors operating in different time and space scales may strongly affect the early life history of fishes (Bye 1984). On a short time and space scale, for instance, it has been shown that differences in the type of the spawning and nursery habitat may strongly affect larval/juvenile survival of some species. On a larger scale, environmental characteristics varying with latitude

may, for example, constrain the survival of young fishes in different populations (Houde 1989, Conover 1990).

Fish populations living in different habitats exhibit alternative strategies and tactics in their life histories. Among these, variations in timing of the spawning season (Bagenal 1971, Cushing 1975, Sinclair & Tremblay 1984), egg size and yolk content in newly hatched larvae (Blaxter & Hempel 1963, Hempel & Blaxter 1967), and a variety of modes of parental care (Balon 1984) may directly increase the survival of the young. Growth rates of larvae, a life history trait studied intensively only recently (Houde 1987, Miller et al. 1988, Conover 1990, Conover & Present 1990), are very important to young offspring survival because they determine the duration of these young vulnerable life

stages. However, to determine if a life history trait is adaptive under particular environmental circumstances is a difficult task, requiring a detailed knowledge of the environmental variables that affect the expression of the trait (Wootton 1984).

Bay anchovy are suitable material for an investigation on how environmental characteristics operating on different scales may affect the early life history of fishes. Bay anchovy is one of the most abundant species along the US coast (McHugh 1967), it has a wide distribution, from Florida to Maine, (Bigelow & Schroeder 1953, McHugh 1967), and spawns in a variety of coastal environments such as estuaries (Fives et al. 1986), bays (Ferraro 1980, Olney 1983, Houde & Lodval 1984, Monteleone 1988), sounds (Wheatland 1956), and marshes (Weinstein 1979). Bay anchovy eggs and larvae have also been reported to occur in inshore continental shelf waters (Sherman et al. 1984, Voughlitois et al. 1987).

Most of the studies on bay anchovy early life stages have been conducted on populations occurring in the southern portion of their range. Laboratory studies include experiments on feeding habits and efficiency (Detwyler & Houde 1970, Saksena & Houde 1972, Houde 1977, 1978, Houde & Schekter 1978, 1980, 1981, Chitty 1981, Tucker 1989) and descriptions of the ages of first feeding, yolk absorption and point-of-no-return (Kuntz 1913, Houde 1974, Tucker 1989). Throughout the species range, analysis of field data includes descriptions of the egg and larval abundances and the duration of the spawning seasons (Wheatland 1956, Dovel 1967, Olney 1983, Houde & Lodval 1984, Voughlitois et al. 1987, Monteleone 1988) and estimates of larval growth rates for the Biscayne Bay (FL) (Leak & Houde 1987) as well as the Beaufort Bay (NC) populations (Fives et al. 1986). Feeding habits (Houde & Lodval 1984) and egg and larval mortality rates have only been reported for the Biscayne Bay populations (Leak & Houde 1987).

The objective of the present study is to characterize the early life history of bay anchovy in an area near to the northern limit of its distribution: Great South Bay, New York. Three major questions are addressed: (1) What are the environmental characteristics at the onset and during the spawning season of bay anchovy in Great South Bay? (2) What are the larval growth and mortality rates of bay anchovy in different habitats of Great South Bay? (3) Do these population parameters (spawning season, larval growth rates, mortality rates) respond to local environmental conditions or are they characteristics of this species throughout its range? To address the first question, temperature, salinity and larval food availability in the field were determined throughout the season of highest bay anchovy egg and larval abundances in Great South Bay. The second question was answered by comparing larval growth rates and egg and larval mortality rates in the 2 most common types of habitats within the bay: eelgrass beds and unvegetated areas. The third question was addressed by comparing the results obtained in this study with data reported in the literature for populations of this species throughout its range.

METHODS

Study site. The study was done in Great South Bay, on the south shore of Long Island, New York ($40^{\circ}10'N$, $73^{\circ}10'W$). The bay has only one connection (Fire Island Inlet) to the Atlantic Ocean throughout which tidal mixing occurs with open coastal water. The bay has an average depth of 1.5 m, although depths of up to 7 m occur in navigation channels. Dense eelgrass beds (*Zostera marina*) develop along the shoreline (depth < 1 m) especially during spring and summer (Cosper et al. 1987, Dennison et al. 1989), whereas areas deeper than 1 m typically have a sand/mud bottom without vegetation.

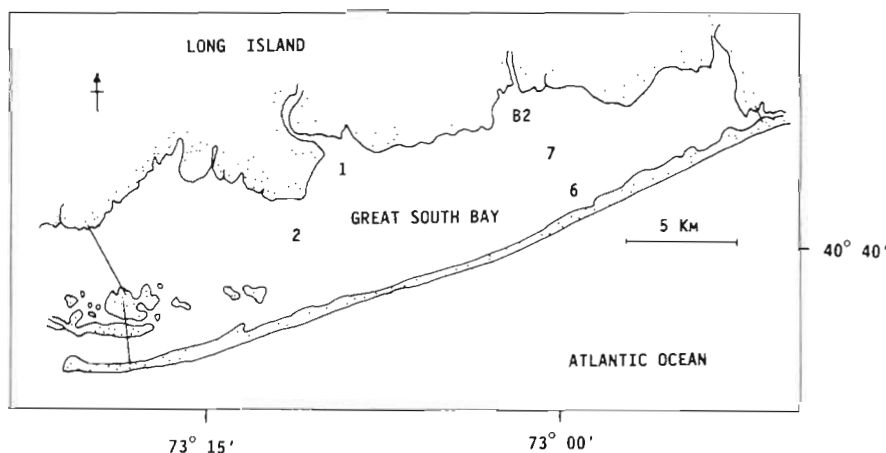


Fig. 1. Great South Bay and the stations sampled during 1987 and 1988. Stns 2, 6 and 7 were the same for both years. Stn 1 was sampled in 1987 only and Stn B2 in 1988 only. Stns B2, 1 and 6 were located on eelgrass areas and Stns 2 and 7 over unvegetated areas

Field work. Series of 7 and 12 cruises were carried out in 1987 and 1988, respectively, during late spring and summer seasons. Four stations were monitored each year (Fig. 1). Three stations were the same in both years (Stns 2, 6, 7), Stn 1 was sampled in 1987 only and Stn B2 during 1988 only. Two stations were located in shallow areas (depth < 1 m) over seagrass beds (1987: Stns 6 and 1; 1988: Stns 6 and B2) while the remaining 2 stations (Stns 2 and 7, both years) were in deeper, non-seagrass areas (depth > 1.5 m). Sampling hours were the same during both years (11:00 to 17:00 h local time).

Surface temperature and salinity were recorded at all stations. In 1988, water samples were taken with a 5 gal (~20 l) bucket from which microzooplankton were collected by filtering seawater (2 l) through a 41 µm mesh sieve. Particles retained in the sieve were preserved in 120 ml jars filled with 4 % formalin for later identification and enumeration. Fish eggs and larvae were collected at all stations in both years with a zooplankton net (303 µm mesh, 0.7 m diameter) equipped with a flowmeter to quantify the volume of water sampled. All plankton tows were made at a speed of 2 knots, in a circular track with the net towed just below the water surface, and for 3 to 18 min. When eelgrass leaves occurred in any sample, they were rinsed in a bucket filled with seawater and the water was filtered through a 303 µm mesh sieve to collect any ichthyoplankton remaining. Ichthyoplankton samples were preserved and stored in 90 % ethanol.

Laboratory work. Microzooplankton: Two 5 ml subsamples were extracted from the 120 ml concentrate containing the microzooplankton samples. Average concentrations from the 2 microzooplankton subsamples were expressed as number individuals per liter seawater. All items considered in the microzooplankton identification and quantification ranged between 50 to 500 µm body length. Seven items were identified in the 1988 microzooplankton samples: copepod nauplii, copepodites and adult cyclopoid copepods, calanoid copepodites, tintinnids, polychaete larvae, and veligers. All these items, except polychaete larvae, have been reported to occur in bay anchovy gut contents (Houde & Lodval 1984).

Larval growth rates. Growth rates reported in this study correspond to average growth rates for all cohorts present at each station during the peak season of larval abundance in each year (third week of June to third week of July). To estimate growth rates, bay anchovy larvae from 2 to 15 mm were picked from each sample collected at each station on each date. Picked larvae were measured for standard length (SL) to the nearest 0.05 mm. Sagittal otoliths were extracted and mounted on a microscope slide in immersion oil for age determination. Otolith diameters were measured along their longest axis and daily increments were counted

with the aid of a computer enhanced video image of the otolith (Optical Pattern Recognition System, BIOSONICS, Inc.). As a check of repeatability, otolith increments were counted at least twice on different dates. Since the deposition of the first increment occurs during the second day after hatching in bay anchovy (Leak & Houde 1987), the age of the larvae was calculated by adding 1 d to the number of increments counted. Standard lengths were corrected for shrinkage due to sampling and preservation according to the algorithms proposed for northern anchovy *Engraulis mordax* by Theilacker (1980). Growth rates were estimated from the slope of the linear regression between corrected SL and larval age.

Abundance corrections: To estimate possible extrusion from the 303 µm net, the catch ratios of 333 µm and 35 µm mesh nets published by Leak & Houde (1987) were utilized as correction factors. This assumes that no larvae can be extruded from the 35 µm mesh net and that only bay anchovy larvae equal to or less than 4.2 mm SL may have been extruded from the 333 µm mesh net.

Cohort mortality rates: Mortality rates were calculated in all stations for all cohorts whose individuals first occurred in the egg stage and which were subsequently collected as larvae on at least 2 later dates. To identify the larvae corresponding to a given cohort, all the larvae were sized and, utilizing the age-length relationships (growth equations, see Table 1), their dates of spawning were back-calculated from the date of sampling. The mortality rates were estimated from an exponential model of decline:

$$N_t = N_0 e^{-Zt} \quad (1)$$

where N_t = number of larvae (standardized by volume sampled) at the age class t ; N_0 = initial number of eggs in the cohort; t = age class in days (maximum age class considered: 15 d old larvae); Z = instantaneous mortality coefficient (mortality rate) (Leak & Houde 1987).

Seasonal average mortality rates. Average mortality rates were calculated for all cohorts present during the peak season of larval abundance utilizing the Converted Length-frequency method described by Essig & Cole (1986). The method consists of averaging throughout the whole season the number of larvae present in each size class. Then, from the age-size regressions described above (growth equations), the average age of each size class is calculated. The resulting seasonal age-frequency distribution is then split into 2 parts to calculate independent estimates of the average mortality rates for (1) individuals from egg stage to 2 d old larvae, i.e. individuals not subject to starvation; yolk stage completed at 1.7 d after hatching (Houde 1978); (2) for 3 d old to 15 d old larvae (exogenous feeding individuals only); (3) for all individuals from the egg stage to larvae 15 d old.

Statistical analysis. To determine differences in the mean of environmental parameters (i.e. temperature, salinity, food availability) among stations within each year, analysis of variance (ANOVA; Sokal & Rohlf 1981) was utilized. If there were no differences in parameter means among stations, a mean *t*-test was applied to test for differences of means between years. Logarithmic transformations of the data were utilized when the means were correlated with the variance. Nonparametric statistical tests (Spearman's Rho; Conover 1971) were used to determine independence between paired variables (i.e. correlations between egg/larval abundances per date vs food availability per date). Analysis of covariance (Multiple Slopes *t*-test; Zar 1984) were utilized to determine differences in estimated growth or mortality rates among stations and between years.

RESULTS

Hydrography

During the sampling seasons of both years the water temperature tended to follow a similar seasonal cycle (Fig. 2A). Temperatures at the beginning of the sam-

pling season 1988 (mid June) were higher than those measured at the same date in 1987. Average temperatures during the peak of the spawning season (late June to late July) also differed between years (ANOVA, $p < 0.01$) being lower in 1987 (mean: 22.4°C, SD: 2.7) than in 1988 (mean: 24.4°C, SD: 2.4). A trend of increasing salinity from mid-May until late August (Fig. 2B) was also observed during both years. During the peak period of spawning for bay anchovy, salinity ranged from 26.25 to 27.50 ‰.

Microzooplankton community

Copepod nauplii (Fig. 3A) were the most abundant item among the microzooplankton community throughout the season except on one date in late July when tintinnids (Fig. 3B) became more abundant. Veligers and polychaete larvae together comprised less than 1 % of the total number of individuals counted from all items combined throughout the season. Because of these low abundances, low frequency of occurrence and because of their low energetic value as food for larval bay anchovy (Houde & Lodval 1984), veligers, polychaete larvae and tintinnids were not further considered as major food items for larval bay anchovy.

The major larval food items considered, copepod nauplii (Fig. 3A), cyclopoid copepods (copepodite and adult stages, Fig. 3C), and calanoid copepodites (Fig. 3D), followed a well defined pattern of abundance: concentrations were low early in the season, peaked in mid-July and decreased in late August. Average copepod nauplii densities for the peak of the spawning season (June 23 to July 23) did not differ among stations nor did the average total densities of major larval food items combined among stations (ANOVA, $p < 0.05$).

Egg abundance, timing and duration of the spawning season

In 1987, bay anchovy eggs were first collected on May 20. Mean egg densities for all stations was 0.15 eggs m^{-3} (SD: 0.07) and remained low until mid-June when egg densities exceeded 50 eggs m^{-3} (Fig. 4A). In 1988 the sampling period started later (June 16) and eggs were abundant (> 50 eggs m^{-3}) at all stations (Fig. 4B). Two lines of evidence suggest that spawning had just commenced: (1) only eggs were collected on the first sampling date; (2) the back-calculated dates of spawning for larvae collected on the second sampling date of 1988 (June 23) indicated that no cohort was spawned before June 16. In both years, average egg densities > 50 eggs m^{-3} occurred for only about 4 wk

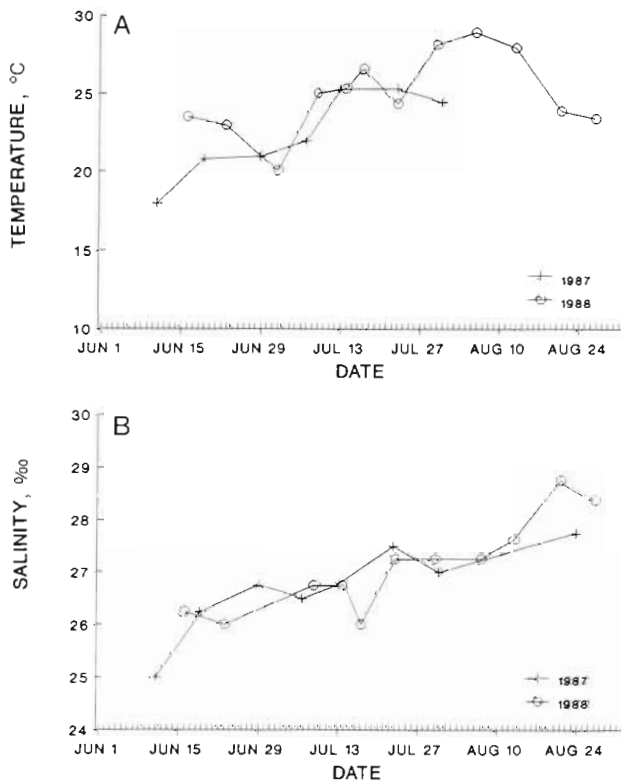


Fig. 2. Average (a) seawater temperature and (b) salinity from 4 stations in Great South Bay, during the 1987 and 1988 bay anchovy spawning periods

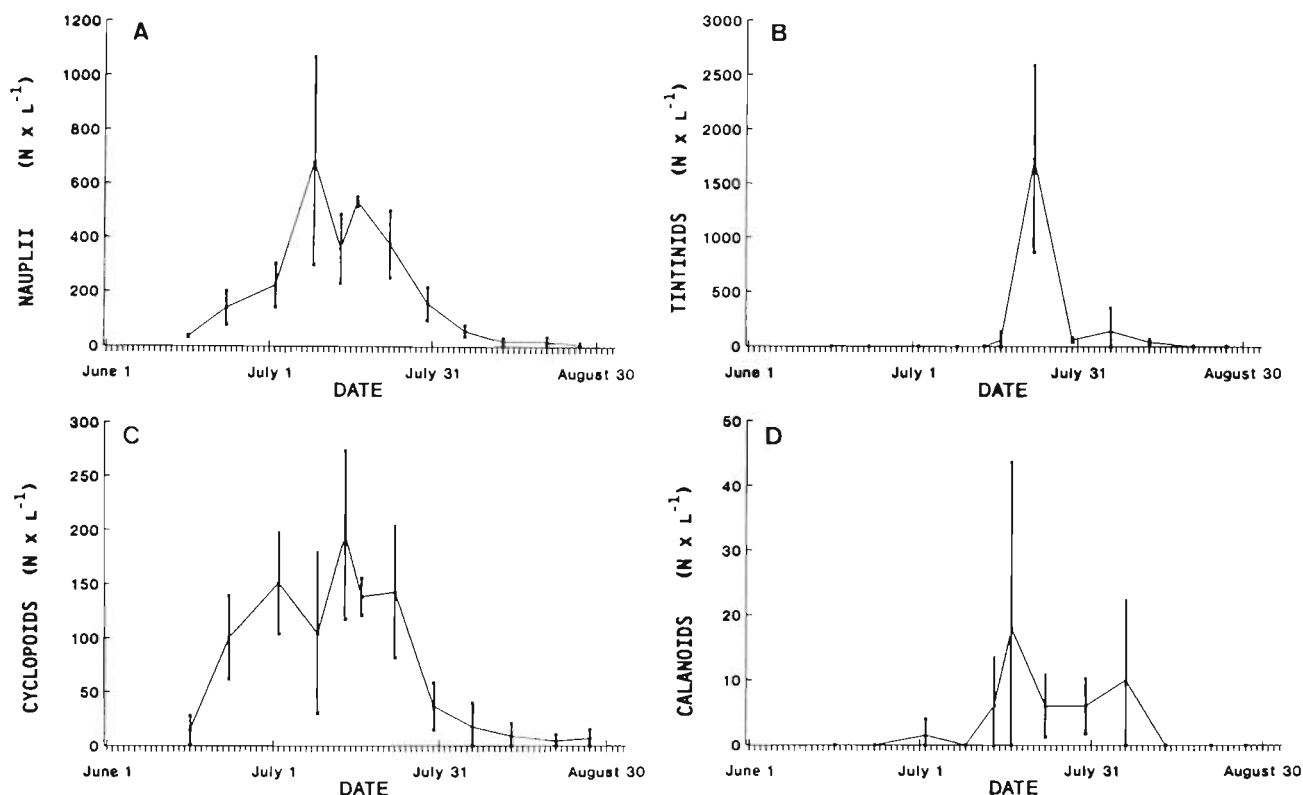


Fig. 3. Average microzooplankton abundances from 4 stations in Great South Bay during the bay anchovy spawning period of 1988. (A) Calanoid nauplii, (B) tintinnids, (C) cyclopoids (copepodites and adults) and (D) calanoid copepodites

(peak of the spawning season), from the third week of June to the third week of July. By the last week of July, egg densities decreased to less than 10 eggs m^{-3} and during August, average densities never exceeded 2 eggs m^{-3} in either year.

During the peak of the spawning season in 1987 and 1988, there were no differences in average egg densities among stations (ANOVA, $p > 0.05$). Throughout the sampling period in both years, there was no apparent relationship between average egg densities and temperature or salinity per date (Spearman Rank Test, $p > 0.05$). In 1987, the average temperature at the onset of the peak spawning period was 20.8°C while in 1988 it was 23.5°C . A high correlation (Spearman Rank Test, $p < 0.01$) throughout the 1988 sampling period was found, however, between the average number of eggs per date and larval food density (nauplii + cyclopoid and calanoid copepodites + adult cyclopoids) (Fig. 5).

Larval densities

Larvae were first collected on June 19 during the 1987 sampling season and on June 23 in 1988. Mean larval densities larger than $25 \times 100 \text{ m}^{-3}$ occurred from the first to the last week of July in 1987 and, from the third week

of June to the third week of July in 1988 (Fig. 6A, B). Maximum larval density per station occurred in both years during the third week of July [1987: $4199 \times 100 \text{ m}^{-3}$ (Stn 6); 1988: $8393 \times 100 \text{ m}^{-3}$ (Stn 1)]. There were no differences in mean larval density among stations in either year [$\log(n+1)$ transformed data, ANOVA, $p > 0.05$]. Mean larval densities throughout the season of peak spawning were higher in 1988 than in 1987 at all stations except Stn 6, where they were lower [$\log(n+1)$ transformed data, t -test, $p < 0.01$]. Mean larval density for all stations combined through the season of peak spawning in 1988 (mean: $1250 \times 100 \text{ m}^{-3}$, SD: 1137) was twice as high as in 1987 (mean: $598 \times 100 \text{ m}^{-3}$, SD: 634).

There were no apparent relationships between temperature or salinity by date and larval densities throughout both sampling seasons (Spearman Rank Test, $p > 0.05$). However, there was a high correlation between average larval density by date and larval food density in 1988 (Spearman Rank Test, $p < 0.001$) (Fig. 7).

Larval growth rates

Linear regressions were calculated to describe the size-at-age relationship for 2 to 15 d old larvae (Table 1).

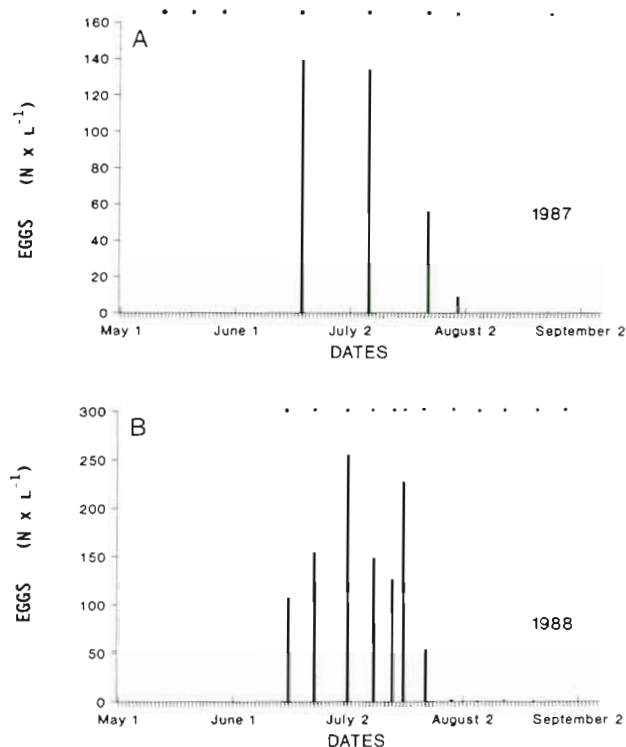


Fig. 4. *Anchoa mitchilli*. Average egg abundances collected from 4 stations in Great South Bay during the bay anchovy spawning seasons (A) 1987, (B) 1988. Points on top of the figure indicate the sampling dates in each year

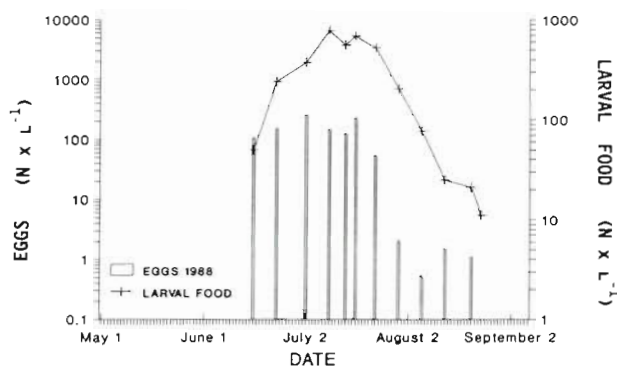


Fig. 5. *Anchoa mitchilli*. Average larval food abundance (copepod nauplii + calanoid and cyclopoid copepodites + adult cyclopoids) and bay anchovy egg abundances at the 4 stations sampled in Great South Bay during the 1988 sampling season

Larval growth rates were not significantly different at all stations in both years (ANCOVA, $p > 0.05$). Average growth rates for all larvae in Great South Bay (from common regression, Fig. 8) were not different between years ($G_{1987} = 0.58 \text{ mm d}^{-1}$; $G_{1988} = 0.56 \text{ mm d}^{-1}$) (Slope t -test, $p > 0.05$). There were no apparent relationships between larval growth rates by station and seasonal average temperature by station in either year, nor

between larval growth rates by station and average larval abundances by station (ANCOVA, $p > 0.05$).

To determine if the growth rates were negatively affected by the low food concentrations found in the field at the beginning and end of the spawning season, the dates of spawning of all larvae aged in 1988 were back-calculated and independent growth rates were estimated for larvae spawned at the peak of the spawning season (July 1 to 16) and for larvae spawned at the beginning and end of the same season (before July 1 and after July 16). The average growth rate estimated for larvae spawned in the middle of the spawning season ($G_p = 0.529 \text{ mm d}^{-1}$, $R^2 = 0.88$) was not different (Slope t -test, $p > 0.05$) from the growth rate of larvae spawned off the peak spawning season ($G_{op} = 0.556 \text{ mm d}^{-1}$, $R^2 = 0.95$).

Cohort mortality rates

Cohort mortality rates were calculated only for the 1988 spawning season because of the low sampling frequency in 1987. Five cohorts were followed from

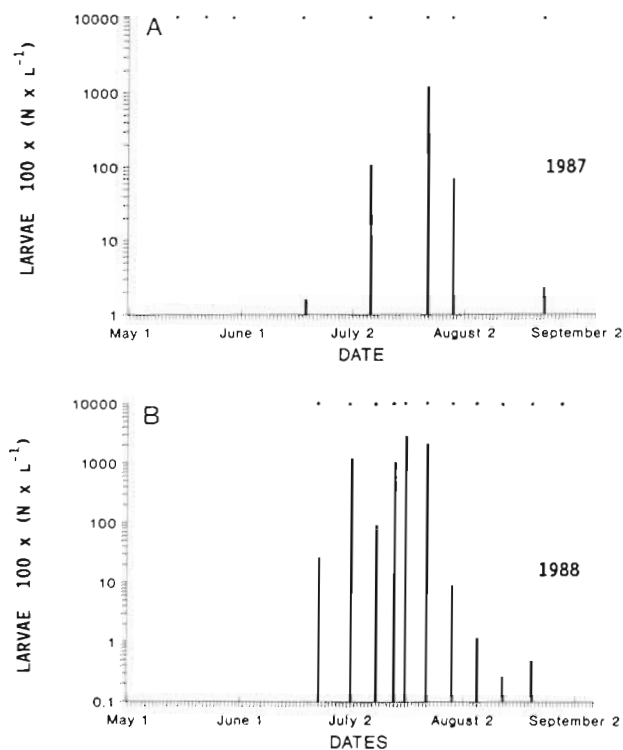


Fig. 6. *Anchoa mitchilli*. Average larval density (from 4 stations sampled) in Great South Bay during the bay anchovy spawning season (A) 1987, (B) 1988. Points on top of the figures indicate the sampling dates in each year. Larval densities are expressed as number of larvae in 100 m^3 in both years

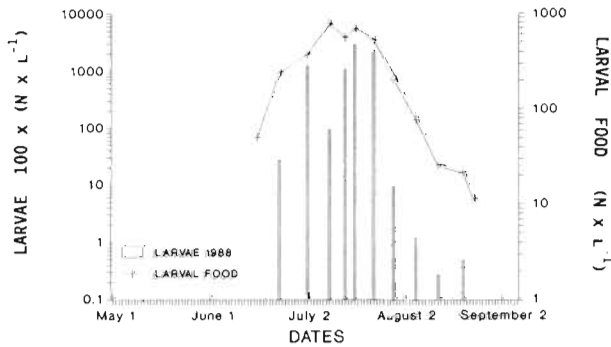


Fig. 7 *Anchoa mitchilli*. Average larval food abundance (copepod nauplii + calanoid and cyclopoid copepodites + adult cyclopoids) and bay anchovy larval density at the 4 stations sampled in Great South Bay during the 1988 sampling season

the egg stage. These 5 cohorts corresponded to eggs spawned on June 23 and July 2, 9, 14 and 17. The cohort mortality rates calculated for those 5 cohorts varied between $Z_c = -0.32 \text{ d}^{-1}$ and $Z_c = -0.89 \text{ d}^{-1}$ (Table 2). There were no cohorts in which the mortality coefficients were positive, which would be indicative of immigration to the sampling area. Mortality

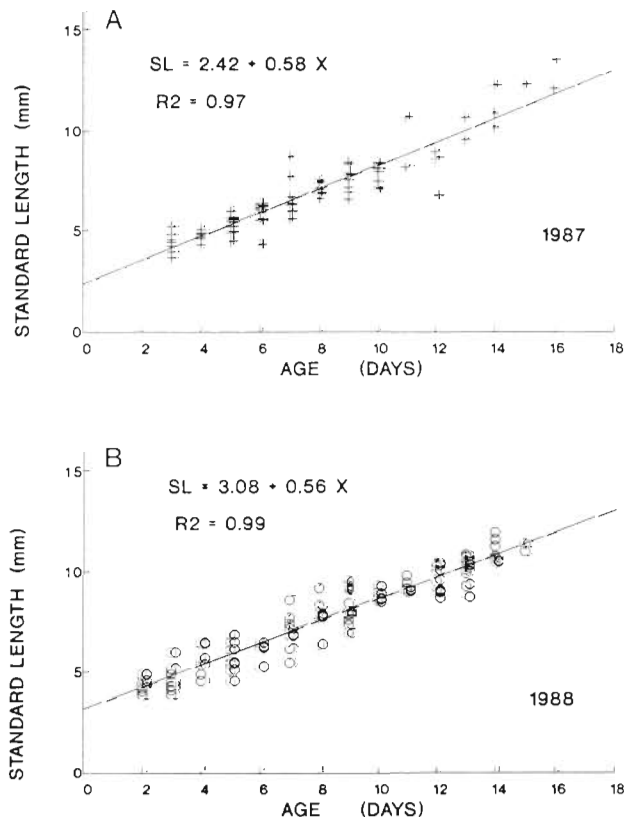


Fig. 8. *Anchoa mitchilli*. Common regressions (calculated from the growth equations for larvae collected at 4 different stations in Great South Bay) describing growth-in-length of larval bay anchovy in (A) 1987 and (B) 1988

Table 1. *Anchoa mitchilli*. Growth-in-length linear regressions (growth equations) for bay anchovy larvae at every station in Great South Bay during the peak of the 1987 and 1988 spawning seasons. R^2 : coefficient of determination of the regression; N: number of larvae considered in the regressions

Year	Stn	Growth equation	R^2	N	SE growth coeff.
1987	1 ^a	$SL = 2.198 + 0.562 \text{ AGE}$	0.93	27	0.030
	2	$SL = 2.686 + 0.538 \text{ AGE}$	0.91	16	0.046
	6 ^a	$SL = 2.568 + 0.594 \text{ AGE}$	0.79	23	0.066
	7	$SL = 2.909 + 0.523 \text{ AGE}$	0.83	21	0.054
1988	B2 ^a	$SL = 3.653 + 0.554 \text{ AGE}$	0.95	22	0.029
	2	$SL = 3.141 + 0.550 \text{ AGE}$	0.93	25	0.032
	6 ^a	$SL = 2.518 + 0.578 \text{ AGE}$	0.94	30	0.026
	7	$SL = 3.123 + 0.554 \text{ AGE}$	0.91	29	0.033

^a Eelgrass station

rates were different among cohorts (ANCOVA, $p < 0.05$). A negative relationship, although marginally nonsignificant ($0.05 < p < 0.10$), was found between the mean cohort mortality rates (from pooled regressions) and the larval food densities averaged across cohort spawning date and the 2 subsequent dates of sampling (Fig. 9).

Average seasonal mortality rates

For egg and yolk-sac larvae (Table 3a), no differences in average seasonal mortality rates (converted length frequency method) among stations were detected in either year (ANCOVA, $p > 0.05$). In 1987 the percentage of mortality varied from 69 to 98.2% d^{-1} and, in 1988 from 78.9 to 90.6% d^{-1} . Seasonal mortality rates for larvae 3 to 15 d old (Table 3b) were

Table 2. *Anchoa mitchilli*. Mortality rates (Z) calculated for cohorts spawned on 5 dates in 1988. Ranges correspond to the cohort mortality rates calculated for larvae at the different stations. Pooled mortality coefficient $Z(p)$, standard error of the coefficient and percentage of daily mortality were calculated from the pooled regression from all cohorts spawned in the same date

Cohort (date spawn.)	Z (range)	No. stations	$Z(p)$	SE of coeff.	Percent. daily mort.
Jun 23, 1988	0.56–0.65	4	0.603	0.053	45.2
Jul 2, 1988	0.48–0.89	4	0.615	0.128	45.9
Jul 9, 1988	0.32–0.66	4	0.493	0.113	38.9
Jul 14, 1988	0.51–0.61	4	0.502	0.094	39.4
Jul 17, 1988	0.72–0.79	2	0.758	0.164	53.1

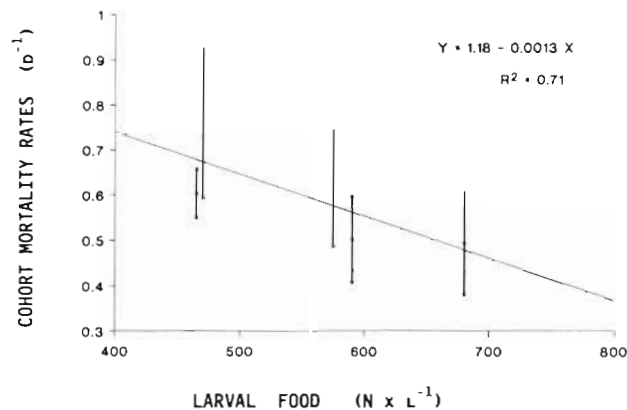


Fig. 9. *Anchoa mitchilli*. Individual cohort mortality rates (d^{-1}) of bay anchovy and average food concentrations encountered by each cohort during the peak of the spawning season in 1988. Average food concentrations were calculated from 3 different dates in which the cohorts were sampled

lower than for egg and yolk-sac larvae and were different among stations in both years (ANCOVA, $p < 0.05$). Seasonal mortality rates of old larvae (common regression of paired stations) in eelgrass stations were higher (1987: $Z_e = 0.383 d^{-1}$; 1988: $Z_e = 0.421 d^{-1}$) than at stations in unvegetated areas (1987: $Z_u = 0.183 d^{-1}$; 1988: $Z_u = 0.269 d^{-1}$) in both years (Slope t -test, $p < 0.01$).

The seasonal average mortality rates (from converted length-frequency method) for eggs and larvae combined, however, were not different among stations during either year (ANCOVA, $p > 0.05$; Table 4). The percent of daily mortality for eggs and all larvae combined ranged between 31.42 and 40.61 % d^{-1} in 1987, and between 30.54 and 42.59 % d^{-1} in 1988. The aver-

age mortality rates for all Great South Bay egg and larvae (common regression for all stations) were not different between years (1988: $Z_{88} = 0.46 d^{-1}$; 1987: $Z_{87} = 0.42 d^{-1}$) (Slope t -test, $p > 0.05$). Corresponding percentage of daily mortalities were 34.62 % d^{-1} in 1987 and 37.01 % d^{-1} in 1988.

DISCUSSION

Local scale

Habitat characteristics have been considered a factor affecting survival of early life stages of fishes in a variety of coastal environments. Because of their higher densities in vegetated areas, it has been proposed that some fish and invertebrate species preferentially select these habitats for spawning and as nurseries. Whether this is true for bay anchovy is not known; however, the fact that another clupeid (*Clupea harengus*) is dependent on vegetated habitats for spawning (Jones et al. 1978), and that bay anchovy is a common component of the ichthyofauna in these areas (Olney & Boehlert 1988, Shima & Cowen 1989), suggests that a relationship might exist. Among the hypotheses proposed to explain the preferential use of areas with submerged vegetation, those dealing with the increased protection against predators (Stoner 1983, Wilson et al. 1987, McIvor & Odum 1988) or with increased food availability (Carr & Adams 1973, Adams 1976, Stoner 1983) have received the most attention.

Results of this study, however, suggest that (1) the eelgrass areas of Great South Bay are not being selected as preferential zones of spawning or nurseries, because the average eggs and larval densities in these

Table 3. *Anchoa mitchilli*. Average seasonal mortality rates calculated bay anchovy in Great South Bay. (a) Egg and yolk-sac period only; (b) larval period after yolk-sac stage (exogenous-feeding larvae)

Spawning season 1987				Spawning season 1988			
Stn	Mortality rate (Z)	SE of coeff.	Daily mort. (%)	Stn	Mortality rate (Z)	SE of coeff.	Daily mort. (%)
(a) Egg/yolk-sac period							
1 ^a	-2.452	3.370	91.4	B2 ^a	-2.200	0.758	88.9
2	-3.989	1.734	98.2	2	-2.366	2.322	90.6
6 ^a	-1.193	1.766	69.7	6 ^a	-2.235	2.440	89.3
7	-3.019	2.001	95.1	7	-1.558	1.183	78.9
(b) Larval period							
1 ^a	-0.425	0.034	34.6	B2 ^a	-0.481	0.029	38.2
2	-0.199	0.058	18.1	2	-0.240	0.019	21.3
6 ^a	-0.334	0.074	28.4	6 ^a	-0.362	0.019	30.4
7	-0.177	0.046	16.2	7	-0.397	0.036	32.8

^a Eelgrass station

Table 4. *Anchoa mitchilli*. Average mortality rates (Converted Length-frequency method; Essig & Cole 1986) of bay anchovy from the egg through the larval stage in different stations within Great South Bay during the peak of the 1987 and 1988 spawning seasons. *N*: number remaining; *t*: time

Year	Stn	Mortality equation	R ²	SE of coeff.	Daily mort. (%)
1987	1 ^a	$N(t) = 122.31 \exp(-0.395 t)$	0.58	0.094	32.6
	2	$N(t) = 38.08 \exp(-0.521 t)$	0.49	0.166	40.6
	6 ^a	$N(t) = 462.24 \exp(-0.389 t)$	0.72	0.069	32.2
	7	$N(t) = 47.05 \exp(-0.377 t)$	0.54	0.097	31.4
1988	B2 ^a	$N(t) = 1044.04 \exp(-0.555 t)$	0.92	0.043	42.5
	2	$N(t) = 101.51 \exp(-0.413 t)$	0.66	0.079	33.8
	6 ^a	$N(t) = 155.89 \exp(-0.364 t)$	0.73	0.057	30.5
	7	$N(t) = 697.56 \exp(-0.509 t)$	0.88	0.049	39.8

^a Eelgrass station

areas were not different from other habitats, (2) for egg and yolk-sac larvae, vegetated areas do not provide refuge against predators, because the mortality rates for these stages were as high in eelgrass habitats as in unvegetated areas (Table 3a) and, (3) for older larvae these areas are zones where increased larval mortality rates may occur (Table 3b). Lower food available in eelgrass beds does not seem to account for these higher mortality rates in older larvae because larval food concentrations were found to be similar among stations. Lethal damage caused by mechanical action of the eelgrass leaves on the larvae or increased number of predators in these areas remain as possible explanations.

In lower Chesapeake Bay, Olney & Boehlert (1988) attributed the strong decreases in larval bay anchovy abundances during daytime to increased levels of predation in the seagrass beds. Lubbers et al. (1990), in the same bay, found higher abundances of piscivorous fishes in submerged plant areas than on unvegetated zones. In Great South Bay, potential predators on bay anchovy may include Atlantic silverside *Menidia menidia*, mummichog *Fundulus heteroclitus*, bluefish *Pomatomus saltatrix*, summer flounder *Paralichthys dentatus*, striped bass *Morone saxatilis*, ctenophores *Mnemiopsis leydyi* and the adult bay anchovies, as cannibalism was reported to occur by other anchovy species (Hunter & Kimbrell 1980, Hunter & Dorr 1982, Brownell 1985). All these potential predators have been reported both to feed on young bay anchovies (Poole 1964, Schaefer 1970, Richards 1976, Friedland et al. 1988, Monteleone 1988) and to occur in Great South Bay during the bay anchovy spawning season. Although it is still not well known whether these potential predators preferentially utilize the vegetated areas for feeding, 2 predators (mummichog and adult bay anchovy) were more abundant in eelgrass than in sand bottom areas of Great South Bay (Briggs & O'Connor 1971).

Geographical scale

The bay anchovy spawning season in Great South Bay is among the shortest reported in the literature for this species and comparable only to that reported for Long Island Sound (Wheatland 1956). A pattern of shorter duration of spawning season with increasing latitude is evident for populations spawning along the Northwest Atlantic Coast (Table 5). Proximal causes may include latitudinal changes in temperature, salinity, or photoperiod (Bye 1990). The evolutionary consequences of this latitudinal pattern may be very important in determining different life histories throughout the species range. For instance, populations located in the north, where the reproductive season is very short, may evolve alternative reproductive tactics to counteract the shortness of their spawning season. These reproductive tactics may include physiological, morphological or ethological changes to increase the adult reproductive output or to enhance their offspring survival.

The correlation between the egg or larval densities and the microzooplankton abundance (Figs. 5 & 7) suggests that larval food availability determines the intensity and timing of the peak spawning period of bay anchovy in Great South Bay. There are several reasons why the peak spawning period of bay anchovy should co-occur with a period of high larval food availability. First, time constraint: the small amount of yolk reserves in recently hatched bay anchovy larvae, sufficient to sustain larvae for only 1.7 d after hatching (Houde 1978), and extremely short time required to get to the point of irreversible starvation (point-of-no-return) (1.4 d after yolk depletion), suggest that young larvae must find food very soon after hatching in order to survive. Second, larval size constraint: the small size of bay anchovy at hatching (1.8 to 2.7 mm; Fahay 1983) makes their mobility and capability of finding food very reduced. To facilitate encountering food, larvae must

Table 5. *Anchoa mitchilli*. Duration of bay anchovy spawning seasons and peak periods of spawning along the Northwest Atlantic coast of the USA. Duration of the peak spawning periods (mo) are approximated

Area	Total season	Peak months	Duration peak (mo)	Source
Biscayne Bay (FL)	Feb–Nov ^a	Apr–Oct ^b	7	^a Leak & Houde (1987) ^b Houde & Lodval (1984)
Beaufort Bay (NC)	Apr–Sep	–	–	Hildebrand & Cable (1930)
Chesapeake Bay	May–Sep ^c	May–Aug ^d	4	^c Doval (1967) ^d Olney (1983)
Barneget Bay (NJ)	Apr–Aug	Jun–Jul	2	Voughlitois et al. (1987)
Great South Bay (NY)	May–Aug	Jun–Jul	1–1.5	Monteleone (1988) This study
Long Island Sound	May–Aug	Jun–Jul	1–1.5	Wheatland (1956)

occur in areas of high food abundance. Third, efficiency constraints: the low efficiency in energy utilization of larval bay anchovy (Tucker 1989) suggests that their food requirements are very high during the larval period. Laboratory experiments have shown that minimum food concentrations of 25 to 60 nauplii l^{-1} are required for bay anchovy larvae to achieve between 1 to 5% of survival at 16 d (Houde 1978). In Great South Bay, concentrations above these thresholds are found only during the summer from late June to late July, the peak of the spawning season. The correlation between food availability and individual cohort mortality rates (although marginally not significant, $0.10 > p > 0.05$; Fig. 9) supports the contention that food may be tightly linked to larval survival in Great South Bay.

The larval growth rates determined for bay anchovy in Great South Bay are in the upper limit reported for this species in other areas. Larval growth rates, calculated from data corrected for shrinkage according to the algorithms proposed by Leak (1986), range from 0.43 to 0.56 $mm\ d^{-1}$ in Biscayne Bay (Leak & Houde 1987). For Beaufort Bay larvae, Fives et al. (1986) calculated larval growth rates of 0.25 $mm\ d^{-1}$ for 1 to 12 d larvae and 0.31 $mm\ d^{-1}$ for 13 to 24 d old larvae (average for 1 to 49 d old larvae: 0.49 $mm\ d^{-1}$). In Great South Bay mean growth rates (corrected for larval shrinkage after Theilacker 1980) were 0.58 and 0.56 $mm\ d^{-1}$ in 1987 and 1988 (when corrected for shrinkage after Leak 1986, they were 0.71 and 0.66 $mm\ d^{-1}$ respectively). Temperature and food availability are usually referred to as major positive factors regulating larval growth (Houde 1989). Temperature alone, however, does not explain the higher larval growth rates in Great South Bay because when compared at the same temperature (22 to 24°C) they grew faster than Biscayne Bay larvae (0.43 $mm\ d^{-1}$). Growth rates as high as those in Great South Bay occurred only at the highest temperatures (29.0 to 30.7°C) in Biscayne Bay (Leak & Houde 1987). Food availability also does not explain

the differences in growth rates because high microzooplankton concentrations have also been reported for Florida (Houde & Lodval 1984).

The advantages associated with rapid attainment of a larger body size (i.e. to avoid predation or to overcome other environmental constraints) may be very important for populations having short breeding seasons. Conover & Present (1990) found that the length of the growing season and growth rates varied with latitude in *Menidia menidia* and proposed that the increased growth rates in northern populations are the result of selection occurring during the winter season on smaller fish. Although the present study does not test this hypothesis on bay anchovy, our results suggest that another environmental constraint, the short season of larval food availability, may act as a selective agent on growth rates. Individuals having low growth rates and spawned at the middle or end of the food season will not be able to complete their larval stage because this stage will last longer than the season itself. Those individuals having higher growth rates will have a greater chance of finishing their larval stage within the food season and their probability of surviving will be increased even more because attaining a large size sooner may result in an extra advantage to avoid predation.

The bay anchovy mortality rates determined in Great South Bay are higher than those reported for larvae of many other fish species (Bannister et al. 1974, Graham & Townsend 1985, Hewitt et al. 1985, Essig & Cole 1986, McGurk 1986, Crecco & Savoy 1987) but are in agreement with those reported for bay anchovy in other areas. Leak & Houde (1987), utilizing data from Murphy & Clutter (1972) to correct for sampler avoidance, have calculated mortality rates for bay anchovy cohorts spawned in 4 different months in Biscayne Bay. Of the 13 cohorts where eggs were included in the calculations, 10 had mortality rates higher than $Z_c = 0.5\ d^{-1}$. Of the 18 individual cohort mortality rates

calculated in Great South Bay (Table 2), 15 fall in the same range ($Z_c > 0.5 \text{ d}^{-1}$). Similarly, the average mortality rates reported for all cohorts spawned during the 4 months studied in Biscayne Bay (FL) ranged from 0.30 to 0.45 d^{-1} (mean: 0.37 d^{-1} , SD: 0.07) and, in Great South Bay the averages from all stations were 0.42 and 0.46 d^{-1} in 1987 and 1988 respectively. In spite of differences in the calculations, results from both studies show that bay anchovy experience high mortality rates during the youngest stages. Starvation and predation are usually considered to be the 2 major causes of mortality during early life stages of fish (Hunter 1984). The very low larval food concentrations in Great South Bay at the beginning and at the end of the spawning season may have resulted in starvation or predation facilitated by poor larval nutrition (Table 2). However, at the middle of the spawning season, food did not appear to be limiting; therefore, most of the mortality in this period (about 40 % d^{-1} ; Table 2) may be attributed to causes other than starvation (i.e. predation). Further studies on the larval health condition (i.e. histologic analysis) at different times during the spawning season should help assigning relative importance to these 2 potential sources of mortality.

Differences in life history traits among the bay anchovy populations may arise from differences in habitat characteristics. The population spawning in Biscayne Bay (Florida), where the larval food supply is relatively constant throughout the year and where the temperatures are higher than in northern latitudes, has a long spawning season and its larvae have lower and variable growth rates. The population spawning in Great South Bay (New York), where the larval food availability is restricted to a very short period during the year and where the temperatures are lower than in southern latitudes, has a short spawning season in which larvae grow at high rates. Whether these differences are the result of local, short-term environmental characteristics that occurred in 1987 and 1988 only, or if they have evolved in the populations in response to long-term environmental constraints, has not been investigated for bay anchovy. However, matching the season of reproduction with the period of maximum potential larval food abundance is a common feature for several fish species (Cushing 1967, Bagenal 1971). Additionally, growth rates may have a genetic basis and that they represent a character on which selection may operate was recently demonstrated by Conover & Present (1990). Whether these 2 adaptive responses occur together in other seasonally breeding fish populations, remains to be explored.

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