Abstract.—Temporal and spatial variability in growth and mortality rates of bay anchovy, *Anchoa mitchilli*, larvae was analyzed in Chesapeake Bay. Larvae were collected in cruises during June and July 1993, on transects spaced at 18.5-km (10 nmi) intervals over the entire bay. Growth and mortality rates were estimated in lower, mid, and upper bay regions and analyzed in relation to environmental variables, predators (biovolumes of the scyphomedusa *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*), and larval prey (zooplankton abundances). Otolith increment analysis indicated that the mean baywide growth rate of larvae increased significantly from 0.59 mm/d in June to 0.72 mm/d in July. The baywide mortality rate of larvae declined from 0.41 (33.6%/d) in June to 0.23 (20.5%/d) in July. In each month, regional mortality rates were highest in the lower bay. Regionally, mortality ranged from a low of 0.14 (13.1%/d) in the upper bay in July to a high of 0.54 (41.7%/d) in the lower bay in June. Mortality rates declined with increasing larval size. Stage-specific survival was both size-specific and growth-rate dependent as indicated by trends in mortality (M), weight-specific growth (G), and the M/G ratio. Growth rates were positively correlated with temperature and zooplankton abundance. Larval abundances, but not mortality rates, were negatively correlated with gelatinous predator biovolumes. Recruitment potential of bay anchovy was judged to be highest in July in the lower third of Chesapeake Bay. Although lower, production of anchovy prerecruits in June and in other Bay regions was substantial and contributed significantly to prerecruit abundances in 1993.

Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay

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In highly fecund fishes that spawn serially over a protracted season and a broad geographic range, variable patterns of cohort successes and failures may result that not only lead to fluctuating recruitments but that are difficult to detect in the absence of sampling programs that are temporally and spatially intensive. We estimated temporal and regional variability in larval-stage growth and mortality of bay anchovy (*Anchoa mitchilli*), an abundant (Hildebrand and Schroeder, 1928) and highly productive species (Newberger and Houde, 1995; Wang and Houde, 1995) in Chesapeake Bay. In exploratory analyses and simulations, Houde (1996, 1997b) demonstrated that variability in recruitment success of bay anchovy can occur when stage-specific mortality rates vary during early life. Recently, individual-based models of bay anchovy dynamics in Chesapeake Bay have demonstrated how stage-specific mortality and growth processes may operate and how density-dependent regulation could dampen fluctuations in abundance (Wang et al., 1997).

Bay anchovy are an important component of the Chesapeake Bay food web. They are not commercially exploited but are a major prey of harvested species such as bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and striped bass (*Morone saxatilis*) (Hartman and Brandt, 1995) and may represent up to 90% of piscivorous fish diets seasonally (Baird and Ulanowicz, 1989). Spawning by bay anchovy is widespread in the Bay and occurs over a broad range of temperatures and salinities (Dovel, 1971; Houde and Zastrow, 1991). Bay anchovy is a pelagic, serial spawner (Luo and Musick, 1991; Zastrow et al., 1991) that spawns most intensively from May through August in Chesapeake Bay, where it may account for 96–99% of fish egg and 67–88% of larval catches (Olney, 1983). During peak spawning, densities of eggs frequently range from 10 to >1000/m^3 and densities of larvae from 1 to >100/m^3 (Olney, 1983; Dalton, 1987; Dorsey et al., 1996; MacGregor and Houde, 1996; Rilling and Houde, manuscript in review). Within a spawning season, regions of highest egg and larval abundances may shift, as they did from the upper to the lower bay between June and July 1993 (Rilling and Houde, manuscript in review). Such shifts may have important repercussions for bay anchovy production and for production of other fish species and inverte-

brate predators that rely upon bay anchovy as prey.

Because bay anchovy eggs and larvae, and its gelatinous predators, peak in abundance during summer, temporally and spatially variable predation is potentially a significant factor controlling bay anchovy survival and recruitment. Results of mesocosm experiments (Cowan and Houde, 1993) have indicated that up to 20–40% of bay anchovy eggs and larvae in Chesapeake Bay during the peak spawning season may be consumed daily by jellyfish. Purcell et al. (1994) analyzed jellyfish gut contents and estimated that these predators could account for up to 21% of the daily egg mortality and 41% of the larval mortality of bay anchovy in Chesapeake Bay. In site-specific studies, Dorsey et al. (1996) estimated that jellyfish accounted for 0–35%/d of egg mortality, and from 0 to 15%/d of yolksac larval mortality.

Minor variability in daily mortality or growth rates in a 30–50 d period during early life, can generate tenfold or greater differences in recruitment potential of marine fish (Cushing, 1975; Houde, 1987, 1989b). Previous studies in Chesapeake Bay have documented variability in anchovy egg and larval abundances and yolksac larval dynamics at regional scales (Dorsey et al., 1996; MacGregor and Houde, 1996), but this study is the first to provide a comprehensive overview of larval dynamics for the entire Chesapeake Bay. At the outset, we proposed that there are regional and temporal differences or patterns in growth and mortality rates of bay anchovy larvae in Chesapeake Bay. To test this hypothesis, we analyzed otolith microstructure to estimate and compare month-specific (June vs. July), and region-specific (three regions) growth and mortality rates. Increments are deposited daily on sagittal otoliths of bay anchovy, providing a record of age (Fives et al., 1986; Leak and Houde, 1987; Castro and Cowen, 1991; Zastrow et al., 1991). Deposition of otolith increments begins on the third day after hatching and has been documented in laboratory experiments (Leak and Houde, 1987). Here, we discuss how regional or temporal variability in growth and mortality might influence potential for recruitment and production. We
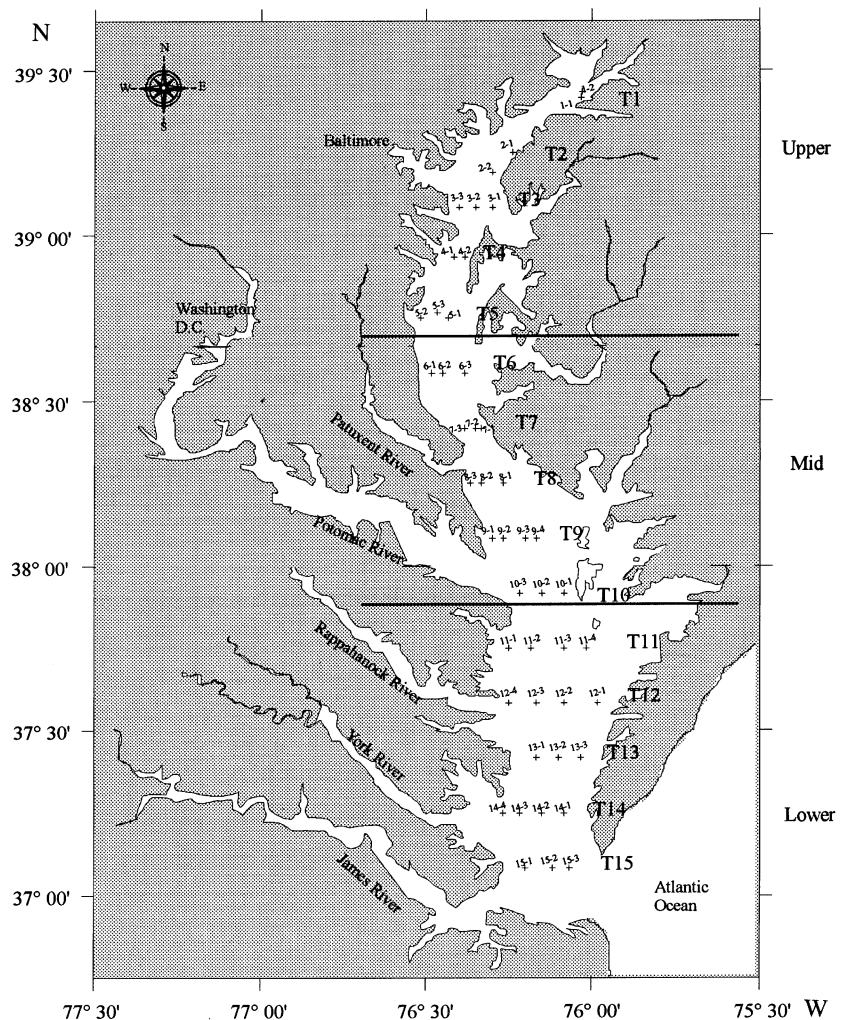

Figure 1

Chesapeake Bay. Regions, transects, and station locations for ichthyoplankton samples, zooplankton samples, and CTD casts, 19–22 June and 23–30 July 1993.

compared growth and mortality rates of bay anchovy larvae in relation to abundances of gelatinous predators and zooplankton (larval prey), and in relation to salinity and temperature. Overall, our objective was to determine which region(s) of the Bay and what part of the spawning season contributed most to survival and subsequent production of bay anchovy early-life stages.

Materials and methods

Ichthyoplankton was collected throughout Chesapeake Bay during two baywide cruises, 19–22 June and 23–30 July 1993 (Fig. 1). Forty-six stations were sampled in June and 48 in July. Stations were on 15 transects spaced at 18.5-km (10 nmi) intervals from

the head of the Bay (39°25'N) to near the Bay mouth (37°05'N). Data were analyzed and compared in three regions: upper bay—transects 1–5 (39°25'N–38°45'N); mid bay—transects 6–10 (38°45'N–37°55'N); and lower bay—transects 11–15 (37°55'N–37°05'N).

At each station, ichthyoplankton was collected in one net of an opening-closing, 60-cm bongo sampler with 280-μm meshes and preserved in ethanol. Two tows, of 2-min duration, were made at each station. The first tow was from within 1 m of bottom to the pycnocline, and the second was made from the pycnocline (or middepth when no pycnocline was present) to the surface. Sampling protocols and methods to estimate densities and abundances of organisms are detailed by Rilling and Houde, manuscript in review); only brief descriptions are given here.

Immediately before each tow, a conductivity-temperature-depth (CTD) cast was made from within 1.0 m of bottom to within 1.0 m of the surface to provide depth profiles of temperature, salinity, and dissolved oxygen. To make results comparable to those of Dorsey et al. (1996) and MacGregor and Houde (1996), temperature, salinity, and dissolved oxygen were examined at 3-m depth. Zooplankton from either three or four designated depths was sampled in 10-L Niskin bottles and collected on 35-μm mesh. Gelatinous zooplankters from each ichthyoplankton tow were counted and their biovolumes recorded.

In the laboratory, anchovy larvae were measured to the nearest 0.1 mm standard length (SL). Lengths were corrected for shrinkage during collection and preservation (Theilacker, 1980; Leak, 1986). Small larvae of bay anchovy may be extruded through net meshes (Leak and Houde, 1987). Therefore, we applied a regression method to adjust abundances of <5.5 mm SL larvae collected in the 280-μm net meshes. The regression, which adjusted abundances of larvae upward by factors of 2.3 (at 2.0 mm), 1.9 (at 3.0 mm), 1.6 (at 4.0 mm), and 1.2 (at 5.0 mm larvae), was derived from comparisons of length-specific abundances in paired tows of 53-μm and 280-μm mesh bongo nets made in Chesapeake Bay under conditions similar to those during this survey (MacGregor, 1994; Rilling and Houde, manuscript in review).

Otolith analysis

Otolith microstructure was analyzed to estimate age, growth, and mortality. In the present study, sagittal otoliths from 509 larvae were examined. Otoliths from representative samples of larvae from each region of the Bay were examined for each cruise. Each larva in the otolith analysis was measured to the nearest 0.1 mm SL. Otoliths from larvae of 2.0 to 25.0 mm SL were mounted in "Epon" under a cover

slip, and heated for 24 h at 60°C to harden the epoxy (Secor et al., 1991). Otolith increments were counted on two separate occasions under a compound light microscope at 600 to 1000× magnification by one reader (Rilling). The mean of the two increment counts plus two days was the estimated age.

Growth rates

Growth in length of larvae (mm/d) was estimated from the slopes of the linear regressions of shrinkage-adjusted lengths (SL) on ages from daily otolith-increment analysis:

$$L_t = a + gt,$$

where L_t = standard length (mm) at age t (d);
  t = age (d) = otolith increment count plus two days;
  g = growth rate (mm/d); and
  a = y-intercept, the estimated length (mm) SL at hatch.

Gompertz growth models (Bolz and Burns, 1996) also were fitted to the data for each region and cruise. The fits were no better than those for the linear model and were not considered further in our analysis.

Larval lengths were converted to dry weights (g) from a weight-length relationship:

$$W = 0.1550 \times L^{3.5307},$$

where W = dry weight (g); and
  L = mm SL.

Rates of growth in weight then were estimated from an exponential model, fitted by regressing $\log_e$-transformed dry weights on age:

$$W_t = W_0 e^{Gt},$$

where W_t = dry weight (g) at age t (d);
  W_0 = dry weight (g) at hatch (the y-intercept of the log-linear regression); and
  G = weight-specific growth coefficient (/d).

Coefficients in growth-model regressions were compared among regions and between cruises (months) in analysis of covariance (ANCOVA). The ANCOVAs tested for differences in slopes (growth rates) and y-intercepts in the growth equations. When significant differences were found, a multiple range test (Student-Newman-Keuls) was applied to determine which of the growth rates differed significantly. The

mean baywide growth-in-length and growth-in-weight rates for each cruise were estimated from regressions fitted to pooled length and age data from all stations. Because larvae collected in June were ≤13 mm SL, growth rates of larvae collected in July were estimated from two separate regressions—one for larvae ≤13 mm SL that was directly comparable to the June data and one for larvae >13 mm SL.

Mortality rates

Age-length keys were developed to convert larval length distributions to age distributions from which mortality rates then were estimated. To derive the keys, linear regressions, based upon subsamples of otolith-aged larvae from each cruise and region, were fitted to larval age-on-length relationships. For each regression, the standard error of the estimated regression coefficient was used to calculate a standard normal deviate (z-statistic) from which probabilities of ages of larvae within 1.0-mm length classes were obtained. Six age-length keys were constructed, one for each region and cruise. This maintained the region-specific integrity of size-at-age data, allowing estimation of region-specific mortality rates.

Instantaneous daily mortality rates of larvae were estimated from an exponential model of decline in abundance with respect to age:

$$N_t = N_0 e^{-Mt},$$

where N_t = abundance (number/m^2) at age t (d);
N_0 = estimated initial abundance (y-intercept of regression; number/m^2);
M = instantaneous mortality coefficient (/d); and
t = age (d).

The data were fitted to the log-linear form of the model after log$_e$-transformation of the abundance data.

Region-specific mortality coefficients were estimated and compared within each cruise by analysis of covariance (ANCOVA). Mean baywide mortality rates for each cruise (month) were estimated by pooling abundance-at-age data from all stations and then compared in ANCOVA. When significant, ANCOVAs were followed by a multiple comparison test (Student-Newman-Keuls) to determine which mortality estimates differed significantly. Two separate mortality rates were estimated for larvae collected in July—one for larvae ≤13 mm SL (<18-day-old larvae) that was directly comparable to the June data that included only larvae of those ages, and one for larvae >13 mm SL (≥18-day-old larvae). Length-specific mortality rates also were estimated, by regress-

ing log$_e$-transformed abundances of larvae on 1-mm length classes.

M/G ratio and stage-specific survivorship

Stage-specific survival can be estimated from the M/G ratio, where M is the instantaneous mortality rate, and G is the weight-specific growth coefficient. The M/G ratios were compared between cruises and among the three designated regions of Chesapeake Bay. The ratio M/G is an indicator of stage-specific survivorship and production potential of larval cohorts (Houde, 1996, 1997a, 1997b). The ratio, sometimes termed the "physiological mortality rate," expresses a population's mortality per unit of individual growth (Beyer, 1989).

Stage-specific survival of bay anchovy larval cohorts was estimated as

$$S = [W_s / W_0]^{-(M/G)},$$

where S = stage-specific survival = N_s/N_0;
N_s = number of survivors at the end of a stage;
N_0 = number alive at the beginning of a stage;
W_s = dry weight of a 12-mm-SL bay anchovy larva (1000 mg);
W_0 = dry weight of a 3-mm-SL bay anchovy larva (10 g). [Note: This weight is more accurate than weight estimated for a 3-mm larva from the weight-length relationship, which overestimated weights of the smallest larvae]; and
M/G = ratio of instantaneous mortality coefficient (M) and weight-specific growth coefficient (G).

Survival to 12 mm SL, the largest length class fully represented in collections in each of the months, was calculated for each region by multiplying stage-specific survival rate (S) by estimated abundance of the smallest fully represented length class (i.e. N_0 at 3 mm SL). Stage-specific survival rates also were estimated for egg to 3-day larva, 3-day to 10-day larva, and 10-day to 18-day larva. Age-specific production at a station was obtained by multiplying estimated larval density (number/m^3) by the volume represented by the station. Regional productions were obtained by summation of larval abundances for all stations in each region.

Correlations and predictions

Multiple regression analyses were applied to determine if bay anchovy larval growth and mortality

rates could be related to biological or environmental factors. The four independent variables considered for inclusion were gelatinous predator biovolume (mL/m^2), zooplankton density (number/L), temperature, and salinity. Mean regional estimates of independent variables were entered into the regression model. Prior to multiple regression analysis, simple correlation analyses were run to determine which independent variables might be colinear and unsuitable for inclusion in the multiple regression model (SAS Institute, 1990). Pairs of independent variables with a correlation coefficient >0.70 were considered highly correlated and thus excluded from the multiple regression analysis.

Zooplankton analyses

In the laboratory, zooplankton organisms were identified by using a dissecting microscope. Zooplankton that were potential prey of larval anchovy were enumerated, i.e. copepods, barnacle nauplii, gastropod veligers, bivalve veligers, cladocerans, rotifers, tintinnids, polychaete larvae, and chaetognaths. Copepods were categorized as adults, copepodites, and nauplii. Densities of zooplankters were calculated as

$$D = N/V,$$

where D = density of organisms (number per liter);
$\quad\quad N$ = number of organisms in a 10-L Niskin-bottle sample; and
$\quad\quad V$ = sample volume (10 liters).

Densities were weighted according to the depth range represented by each sample to obtain a weighted mean density in the entire water column:

$$\overline{D} = \frac{\sum_{i=1}^{k} D \times m}{\sum_{i=1}^{k} m},$$

where m = depth ranges represented by each Niskin-bottle sample; and
$\quad\quad k$ = number of Niskin-bottle samples taken on a CTD cast (3 or 4).

Results

Hydrography

Mean temperatures, salinities, and oxygen levels at 3-m depth in Chesapeake Bay differed significantly between June and July 1993 (*t*-test, *P*<0.0001). In each month, there was a well established pycnocline. Baywide mean temperature increased from 25.3°C in June to 26.6°C in July. Mean salinity baywide increased from 10.1 psu in June to 15.9 psu in July (Table 1) and increased in both months between the upper and lower regions of the Bay (ANOVA, *P*<0.001). Mean dissolved oxygen levels decreased from 7.8 mg/L in June to 6.3 mg/L in July. In June, 3-m DO levels ranged from 4.1 to 12.6 mg/L ; in July they were lower, 4.6 to 8.4 mg/L. Hypoxic and near-anoxic conditions (≤2.0 mg O$_2$/L) were most prevalent in the deep channel of the mid bay region, especially in July.

Growth

Baywide, mean growth rate of anchovy larvae increased from 0.59 mm/d in June to 0.72 mm/d in July (ANCOVA, *P*<0.001) (Fig. 2). When the analysis included only larvae ≤13 mm SL, an even higher baywide growth rate was estimated in July (0.78 mm/d) than in June (0.59 mm/d) (ANCOVA, *P*<0.001). Estimated lengths at 15 days after hatching were 11.65 mm SL in June and 13.72 mm SL in July.

Growth rates did not differ significantly among regions in June or July (ANCOVA, *P*>0.05) (Fig. 3). The regional estimates of growth-in-length rates ranged from 0.53 mm/d in the lower bay during June to 0.78 mm/d in the upper bay in July. Although not significantly different, the highest regional growth rates for each month were in the upper bay. The
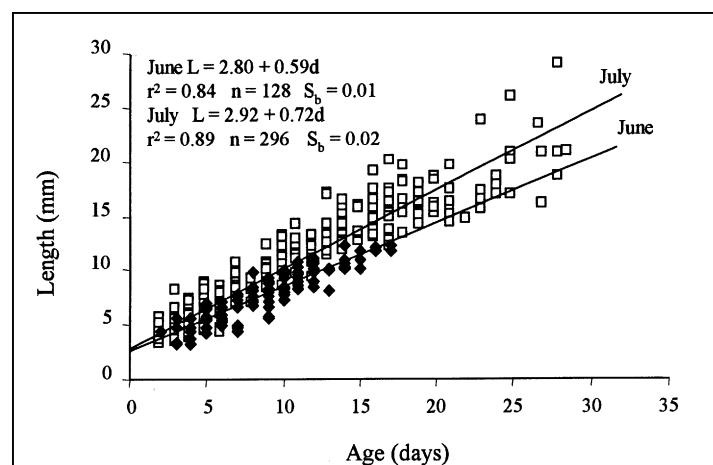

Figure 2

Baywide linear growth models for bay anchovy larvae in Chesapeake Bay, June and July 1993. L = standard length (mm), d = age in days, estimated from otolith-increment analysis. ◆ = June, □ = July.

Figure 3

Linear growth models for bay anchovy larvae in upper, mid, and lower Chesapeake Bay regions, June and July 1993. L = standard length (mm), d = age in days, estimated from otolith-increment analysis.
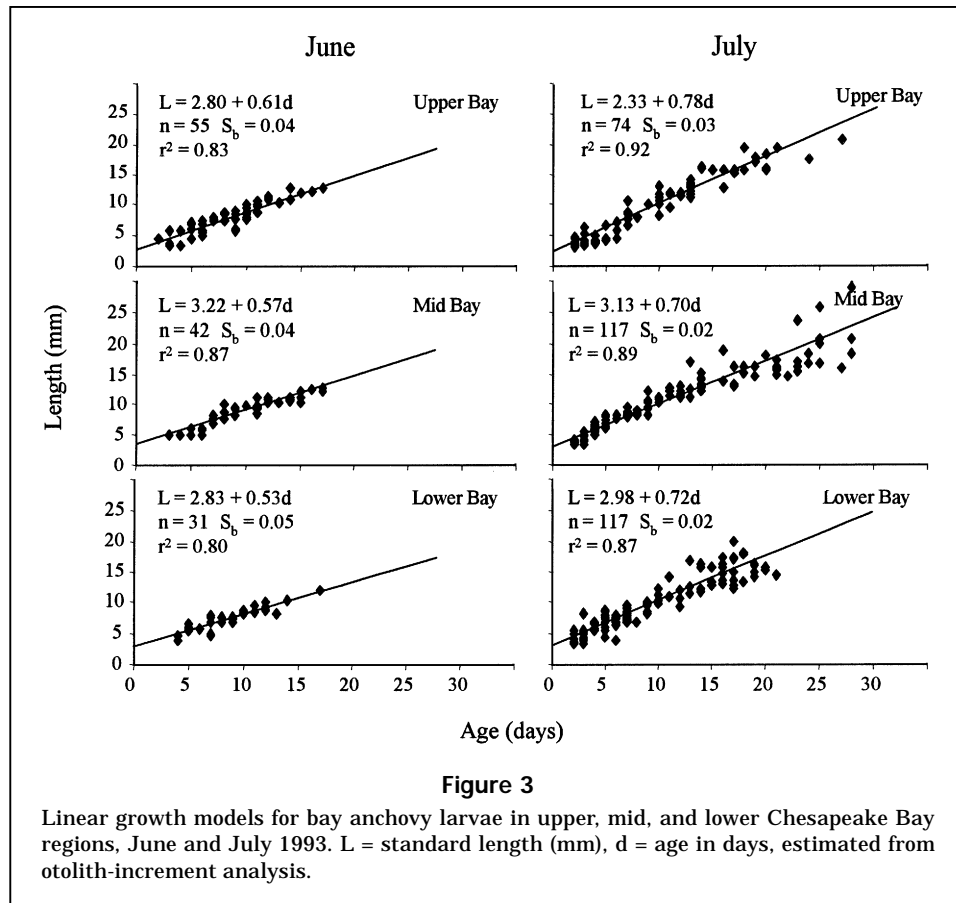
y-intercepts of the linear regressions ranged from 2.33 mm to 3.22 mm and did not differ significantly among regions or between June and July (ANCOVA, $P>0.05$).

Growth in weight was rapid for surviving larvae. Baywide, estimated weight-specific growth rates G (/d) for larvae ≤13 mm SL (Table 1) increased from 0.26 in June (29.7%/d) to 0.35 in July (41.9%/d) (ANCOVA, $P<0.05$). For the ≤13 mm larvae, the highest regional G was 0.40 in the upper bay in July (49.2%/d), and the lowest G was 0.25 in the mid bay in June (28.4%/d). In July, an estimated baywide G for larvae >13 mm SL was only 0.11 (11.6%/d), a rate much lower than that of smaller larvae.

Mortality

Larvae experienced high mortality rates. Baywide instantaneous mortality coefficients M (/d) for larvae in all age classes declined significantly from 0.41 (33.6%/d) in June to 0.23 (20.5%/d) in July (ANCOVA, $P<0.0001$) (Fig. 4). When the data analysis included only larvae <18-days old (the oldest age represented in June) estimated July M = 0.22 (19.7%/d), a rate still significantly lower than the June rate (ANCOVA, $P<0.001$).

Larval mortality rates differed significantly among regions in June and July (ANCOVA, $P<0.0001$). Highest mortality rates in each month were in the lower bay. Regional daily rates ranged from 0.14 (13.1%/d) to 0.54 (41.7%/d) (Fig. 5). In June, the mid bay mortality rate was significantly lower than upper and lower bay rates. In July, when all regional mortality rates differed significantly, the lower bay had the highest mortality rate and the upper bay had the lowest rate (Student-Neumann-Keuls test).

Length-specific mortality rates (/mm) declined dramatically as larval length increased (Fig. 6). In June, the length-specific mortality rates ranged from 0.45/mm for 2–5 mm SL larvae to 0.07/mm for 10–13 mm SL larvae. In July, the rates were lower, ranging from 0.33/mm for 2–5 mm SL larvae to 0.05/mm for 10–13 mm SL larvae. The highest regional length-specific rate, 0.64/mm, occurred in the mid bay during July for the 2–5 mm SL class.

M/G ratio, production, and survival

The baywide *M/G* ratio declined from 1.59 in June to 0.67 in July (Fig. 7), indicating a nearly 70-fold higher survival and biomass production of cohorts

Table 1

Summarized data, Chesapeake Bay cruises, 19–22 June and 23–30 July 1993. Data include anchovy weight-specific growth rates (/d), mean biovolumes (mL/m^2) of gelatinous predators *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, mean densities (organisms/L) of zooplankton (ZOOP), mean regional temperatures (T) and salinities (S) at 3-m depth. Identical superscripts indicate no significant difference (*P*>0.05, Tukey's multiple range test) among regions or between months. SE = standard error.

Region	T (°C)	S (psu)	ZOOP (/L)	Vol. of *M. leidyi* (mL/m^2)	Vol. of *C. quinquecirrha* (mL/m^2)	Weight-specific growth rate *G* (/d)
June						
Upper bay	25.4^a	5.8^a	326.8^a	41.4^a	0.0^a	0.28^a
SE			116.7	22.1	—	0.01
Mid bay	25.3^a	9.7^b	23.1^b	999.5^b	0.0^a	0.25^a
SE			7.2	211.3	—	0.01
Lower bay	25.3^a	14.7c	68.6^b	516.8^a	0.0^a	0.25^a
SE			21.7	134.4	—	0.02
July						
Upper bay	26.8^a	8.9^a	442.5^a	229.6^a	30.7^a	0.40^a
SE			91.3	65.2	12.1	0.02
Mid bay	26.8^a	12.6^b	162.5^b	204.5^a	36.4^a	0.37^a
SE			35.5	44.7	7.9	0.03
Lower bay	26.2^a	26.2c	277.2^a	12.1^b	22.0^a	0.28^a
SE			40.0	7.2	11.8	0.02
Baywide						
June	25.3^a	10.1^a	138.5^a	560.7^a	0.0^a	0.26^a
SE			43.9	104.2	—	0.01
July	26.6^b	15.9^b	289.0^b	139.1^b	29.5^b	0.35^b
SE			27.4	6.1		

in the 3–12 mm SL size range during July. The increase in growth and decline in mortality rates between June and July accounted for the drops in *M/G* ratio. On average, larval cohorts lost biomass in June (*M/G*>1.0), but gained biomass in July (*M/G*<1.0). In June, cohorts at 12 mm SL supported only 6.6% of the biomass present at 3 mm SL, whereas, in July, cohorts at 12 mm SL supported 457.1% of their 3-mm-SL biomass. Each regional *M/G* ratio also declined between June and July.

Predicted abundance of larval daily cohorts at 12 mm SL, based upon the *M/G* ratios and estimated regional abundance-at-age data, was highest in the upper bay in June but shifted to the mid and lower bay in July (Table 2). Stage-specific mortality rates, estimated from declines in abundances, were highest for the youngest stages, and declined with increasing age (Table 3). In this analysis, abundances were estimated for cohorts at 18 days after hatching, when regional mean lengths ranged from 12.4 to 16.4 mm SL. Despite highest regional mortality, daily cohorts from the lower bay in July produced the most 18-day-old larvae (1.5 × 10^8). The daily production of 18-day-old larvae in the lower bay was 3.4–4.6 times higher than in other regions in July, and from 7 to 50 times higher than in other regions in June.

Cumulative mortalities from egg to 18-day old larval stage were lowest in the mid bay in June but lowest in the upper bay in July. Interestingly, those regions had experienced the greatest egg to 3-day-old larval mortalities, which then were followed by low mortality in older larvae (Table 3).

Predators and prey

There was a significant between-cruises difference in mean combined biovolumes of two common gelatinous predators of bay anchovy eggs and larvae, the ctenophore *Mnemiopsis leidyi*, and the scyphomedusa *Chrysaora quinquecirrha*, (*t*-test, *P*<0.001) (Table 1). Mean biovolumes of the ctenophore shifted regionally and declined by a factor of four in July. The scyphomedusan did not occur in June and had a mean biovolume of 29.5 mL/m^2 in July, and there was no indication of regional differences (ANOVA *P*>0.05) (Table 1).
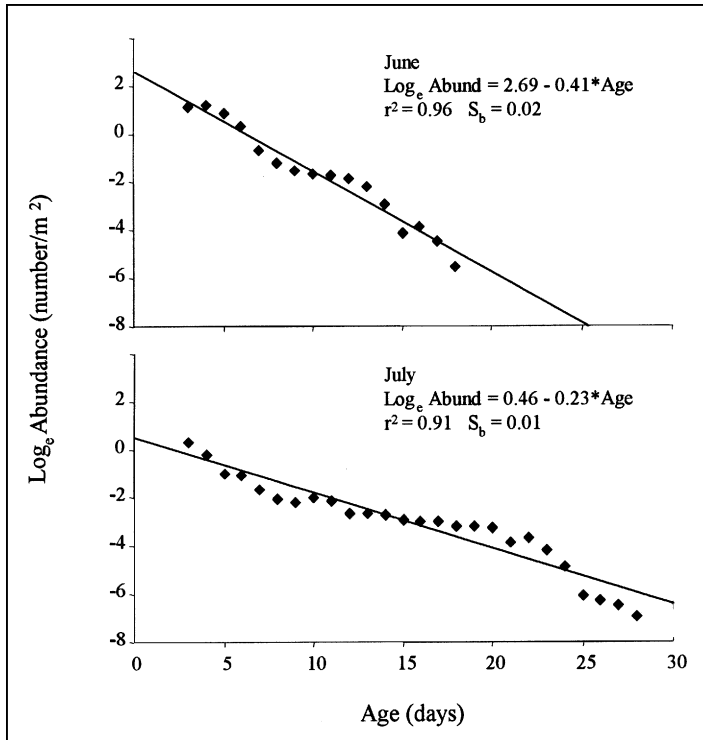
Figure 4

Age-specific survival curves for bay anchovy larvae in Chesapeake Bay, June and July 1993. The age-specific abundance estimates for each day class were derived from age-length keys.

Table 2

Predicted cohort survivorships of bay anchovy larvae in the upper, mid, and lower Chesapeake Bay in June and July 1993. N_0 = estimated number of smallest fully represented length class of larvae (3 mm SL). M/G = ratio of instantaneous mortality rate (/d) to weight- specific growth rate (/d), survival rate $(S) = [W_s/W_0]^{-(M/G)}$ where W_s = dry weight of a 12-mm-SL larva (1000 μg), W_0 = dry weight of a 3-mm-SL larva (10 mg), and apparent survivorship at 12 mm = $S \times N_0$.

Region	N_0 (3-mm-SL larvae)	M/G	Survival rate	Apparent survivorship at 12 mm SL
June				
Upper bay	2.59×10^{10}	1.72	0.0004	1.04×10^7
Mid bay	2.49×10^8	0.87	0.0180	4.48×10^6
Lower bay	7.28×10^9	2.17	0.00005	3.64×10^5
July				
Upper bay	5.95×10^8	0.35	0.200	1.19×10^8
Mid bay	2.08×10^{10}	0.62	0.058	1.21×10^9
Lower bay	11.72×10^{10}	1.19	0.004	4.69×10^8

Baywide, the mean density of zooplankton that are potential prey of anchovy larvae doubled between June and July (t-test, $P<0.05$) (Table 1). Mean density of zooplankton was highest in the upper bay in June (ANOVA, $P<0.05$) and was higher in the upper and lower bay than in the mid bay in July (ANOVA, $P<0.05$). Nauplii of the copepod *Acartia tonsa* were the single most abundant zooplankter collected. Tintinnids, rotifers, and the cyclopoid copepod *Oithona* sp. also were common. Mean density of copepod nauplii, a major prey of bay anchovy larvae, increased from 36.9/L in June to 110.5/L in July (t-test, $P<0.05$).

Correlations

At the regional level, few correlations were judged to be significant at the α = 0.05 level between biological and environmental variables (Table 4). The low degrees of freedom (n=6) and corresponding low power made it difficult to reject null hypotheses. Several coefficients were high enough to suggest possible correlations. Anchovy larval abundances were positively correlated with egg abundances (r=+0.96, $P<0.01$) and negatively correlated with gelatinous predator biovolumes (r=–0.87, $P<0.05$) (Fig. 8A). Larval growth rate was positively correlated with temperature (r=+0.94, $P<0.01$) (Fig. 8B) and possibly related to zooplankton density (r=+0.72, $P<0.11$). Although not significant at α = 0.05, anchovy egg abundances and zooplankton densities both may have been negatively correlated with gelatinous predator biovolumes (r =–0.76, P=0.08).

Predicting larval growth and mortality

Regional variability in anchovy larval growth-in-length rate for the combined June and July cruises was explained reasonably well by a two-variable regression model that included temperature and zooplankton density (r^2=0.93):

$$g = 0.32 + 0.05X_1 + 0.004X_2,$$

where g = larval growth rate (mm/d);
X_1 = $\log_e$ zooplankton density (organisms/L); and
X_2 = temperature (°C).

Larval growth rates increased with increasing temperatures and zooplankton densities. Temperature accounted for more of the variability in growth rate than did zooplankton density. Observed and model-
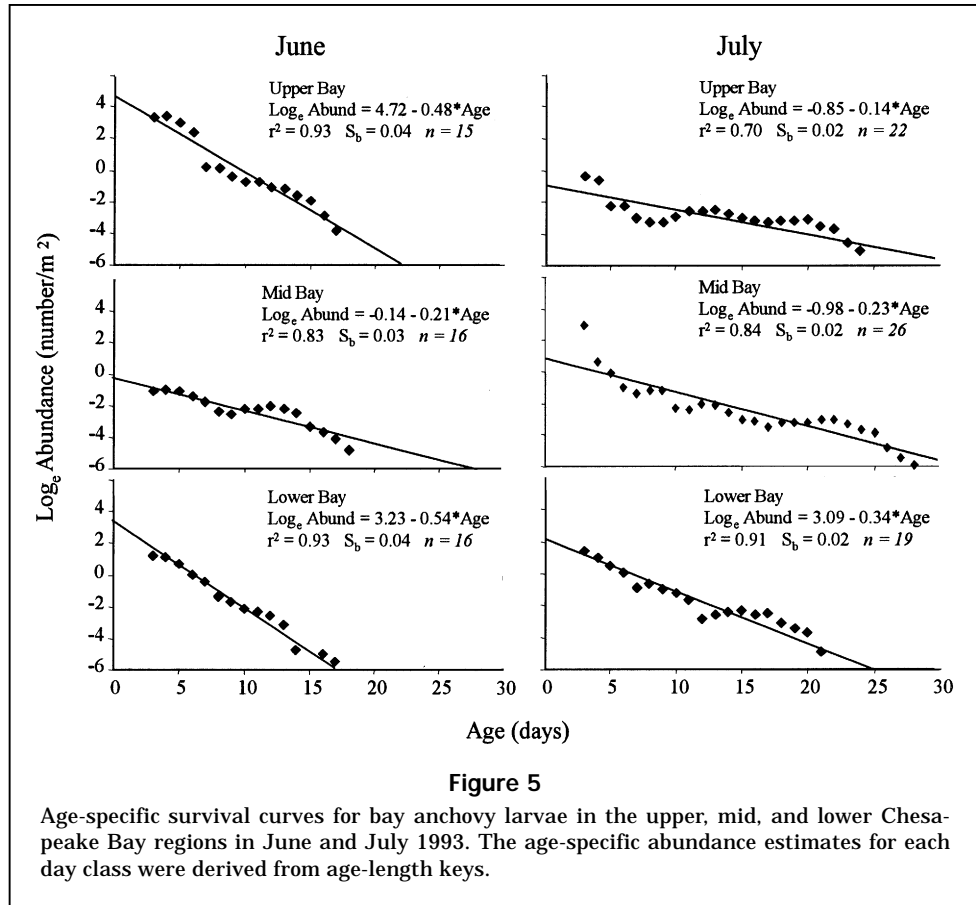
Figure 5

Age-specific survival curves for bay anchovy larvae in the upper, mid, and lower Chesapeake Bay regions in June and July 1993. The age-specific abundance estimates for each day class were derived from age-length keys.

Table 3

Estimated abundances, stage-specific mortality rates, and daily cohort production of bay anchovy larvae in the upper, mid, and lower Chesapeake Bay in June and July 1993, based upon declines in total numbers of larvae between stages. Stage A = estimated daily production of anchovy eggs by region. Stage B = estimated number of the smallest fully represented age class of larvae (3-d-old larvae). Stage C = estimated number of 10-day-old larvae. Stage D = estimated number of oldest represented age class of larvae (18-d-old larvae). Apparent loss rates for each stage, and cumulative mortalities also are given.

Region	Stage A (egg production)	Stage B (3-d old larvae)	Apparent loss rate A → B (M/d)	Stage C (10-d old larvae)	Apparent loss rate B → C (M/d)	Stage D (18-d old larvae)	Apparent loss rate C → D (M/d)	Cumulative mortality B → D	Apparent survival
June									
Upper	8.87×10^{11}	2.59×10^{10}	1.18	4.42×10^8	0.58	2.16×10^7	0.38	7.09	0.0008
Mid	10.44×10^{11}	2.49×10^8	2.78	1.06×10^8	0.12	6.52×10^6	0.35	3.64	0.0263
Lower	23.28×10^{11}	7.28×10^9	1.92	1.42×10^8	0.56	2.45×10^6	0.51	8.00	0.0003
July									
Upper	3.21×10^{11}	5.95×10^8	2.09	4.14×10^7	0.38	3.26×10^7	0.03	2.90	0.055
Mid	1.53×10^{12}	2.08×10^{10}	1.43	1.33×10^8	0.72	4.39×10^7	0.14	6.16	0.002
Lower	6.58×10^{12}	11.72×10^{10}	1.34	9.29×10^8	0.69	1.50×10^8	0.22	6.66	0.001

predicted values of mean regional larval growth rates differed by no more than 6%. No satisfactory multiple regression model could be fit for larval mortality.

Discussion

Cohorts of bay anchovy larvae in Chesapeake Bay do not experience uniform growth and mortality.

Growth rates were temporally variable, and mortality rates were both spatially and temporally variable. It was clear that variability in these rates could significantly alter production and recruitment potentials. Baywide, larval growth rates were higher in July than in June. The larval growth rates that we report are higher and more variable than rates reported previously for bay anchovy in the laboratory

and in most field studies (Table 5). Gallagher et al. (1983) did report equivalent and higher growth rates (0.59–0.93 mm/d) in the Patuxent River tributary of Chesapeake Bay.

Temporal and spatial variability in anchovy larval growth rates was related to both zooplankton density and temperature. The mean baywide growth rate of larvae increased from 0.59 mm/d in June to 0.72 mm/d in July, corresponding to increases in mean water temperatures and mean copepod nauplii densities. The increase in larval growth rate between months corresponded to a coincident 1.3°C increase in mean temperature at 3-m depth and to a major increase in zooplankton abundance. On the basis of laboratory experiments, Houde (1978) predicted minimal prey concentration for 10% survival of bay anchovy larvae at 26°C to be 107 copepod nau-
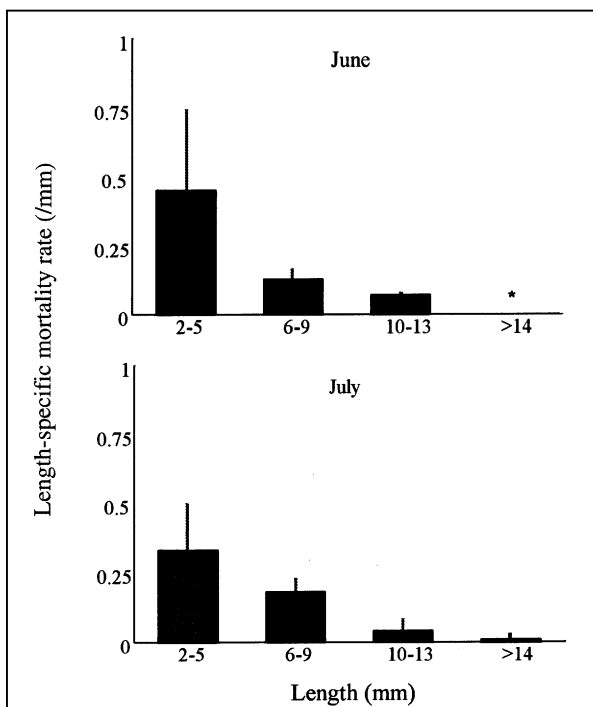

Figure 6

Baywide mean length-specific mortality rates (/mm) of bay anchovy larvae in four length classes during June and July 1993. Error bars are ≈1 SE. * = no data.
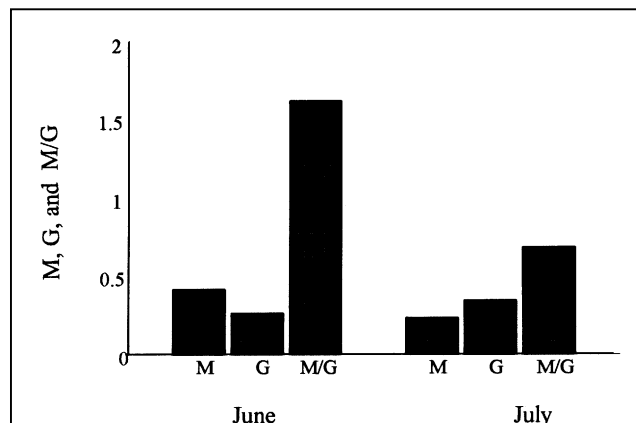

Figure 7

Baywide daily instantaneous mortality rate (M), weight-specific growth rate (G), and M/G ratios for bay anchovy larvae in Chesapeake Bay, June and July 1993.

Table 4

Correlation coefficients at the regional level (n=6) for data collected in Chesapeake Bay, June and July 1993. The seven variables include mean regional instantaneous larval mortality rate (M, /d), larval growth rate (g, mm/d), egg and larval abundances (number/m^2), log$_e$-combined gelatinous predator biovolumes (mL/m^2) of *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, zooplankton density (organisms/L), and temperature and salinity at 3-m depth. * = $P<0.05$, ** = $P<0.01$. In each case, n = 6, $r_{.05,4}$ = 0.81.

	M	g	Egg abundance	Larval abundance	Jelly biovolume	Zooplankton density	Temperature (°C)
g	−0.685						
Egg abundance	0.364	0.056					
Larval abundance	0.434	0.165	0.955**				
Jelly biovolume	−0.287	−0.380	−0.765	−0.868*			
Zooplankton density	−0.039	0.721	0.251	0.477	−0.761		
Temperature	−0.771	0.938**	−0.027	0.037	−0.170	0.555	
Salinity	0.111	0.091	0.524	0.521	−0.132	−0.072	0.067

plii/L. In the present study, nauplii densities often exceeded that level in July, but levels were lower and potentially limiting during June, especially in the mid bay (mean=9.7 nauplii/L) and lower bay (mean=17.7 nauplii/L).

During each month, fastest growth rates were estimated for larvae from the upper bay where copepod nauplii were most abundant (means=84.8 nauplii/L in June and 157.5 nauplii/L in July). Lowest growth was estimated during June in the mid and lower bay, where copepod nauplii densities and mean temperatures were lowest. Although temperature alone may exercise an important control over larval growth, (Houde, 1989a; Pepin, 1991), a combination of factors, including prey availability, effects of body size, or growth-rate dependent mortality, may operate to control growth rates and survival potential (Bailey and Houde, 1989; Heath, 1992; Leggett and DeBlois, 1994). In the case of bay anchovy, all of these factors may operate, but temperature and prey level apparently predominate. There also was an effect of body size; growth rate of larvae >13 mm declined. In a synthesis analysis, Houde (1997b) reported that average weight-specific growth coefficients of bay anchovy declined progressively from 0.573 (77.3%/d) in newly hatched larvae to 0.065 (6.7%/d) in near-metamorphosis individuals.

Our baywide instantaneous daily mortality rates decreased from 0.41 in June to 0.23 in July 1993. This decline was co-incident with increasing growth rate, suggesting that cohorts of rapidly growing larvae in July might have been less vulnerable to size-selective or growth-rate dependent predation. From length-specific and age-specific analyses of mortality, it was clear that mortality rates were greatest for the smallest and youngest larvae

Figure 8

Relationship between (**A**) mean regional bay anchovy larval abundance and gelatinous predator biovolumes and (**B**) mean regional bay anchovy larval growth rates and temperature at 3-m depth in Chesapeake Bay, June and July 1993.

(Table 3). Houde (1997b), analyzed the accumulated data on bay anchovy larvae from Chesapeake Bay and demonstrated that mortality rate (M) declined predictably with respect to body weight raised to the −0.318 power. In the present study, mortality from the egg to 3-day-old larval stage was 2 to 7 times higher than mortality from the 3- to 10-day-old larval stage. Interestingly, mean baywide mortality rates for the egg to 3-day-old stage (yolksac and first-feeding larvae) were similar in June and July (82%/d in June, 79%/d in July), but mortality rates for the
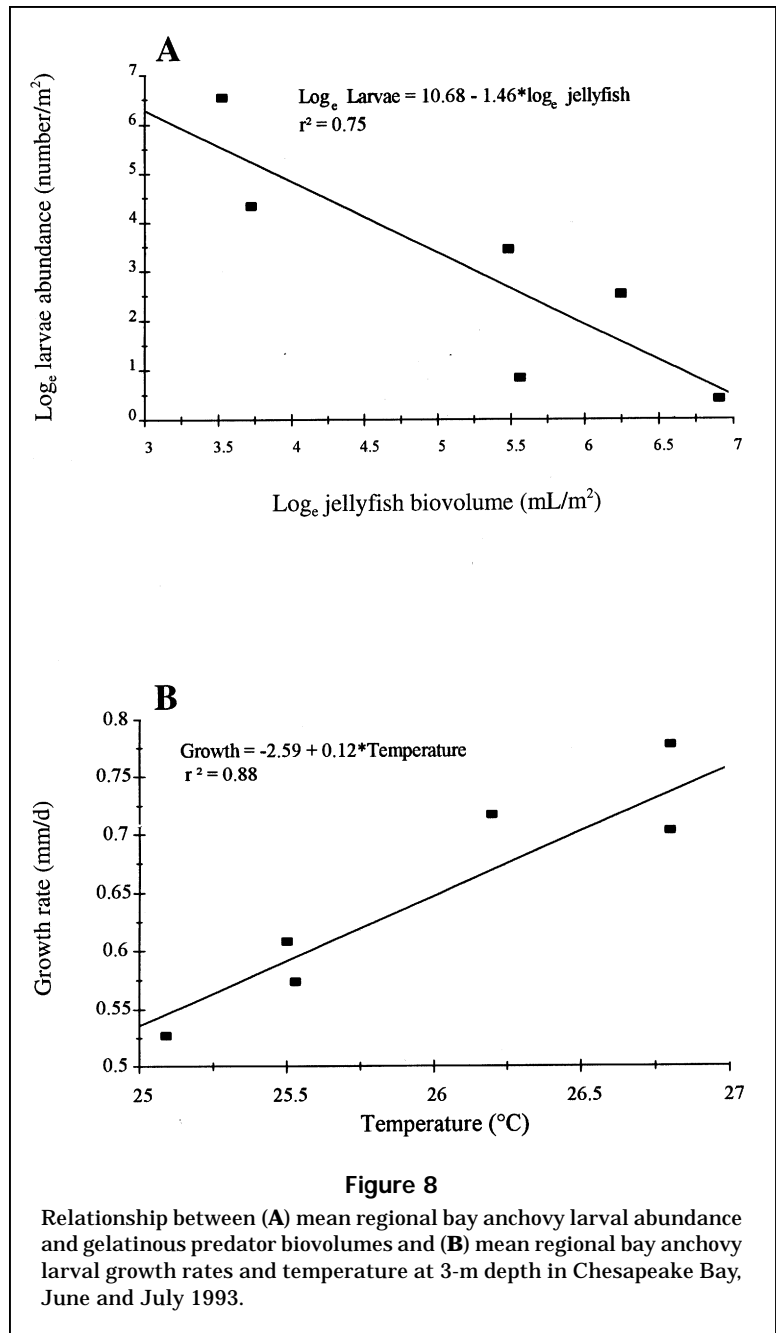
10 to 18-day-old larval stage were considerably lower in July (34%/d in June, 12%/d in July), implying that conditions had become more favorable for feeding-stage larvae in July. Baywide cumulative mortality rates for egg to 18-day-old larvae indicated that <0.1% of a daily cohort survived to 18 days after hatching in June and that ~1.6% survived to 18 days in July.

Predation is a major cause of mortality in the early life of marine fishes (Leggett, 1986; Bailey and Houde, 1989; Leggett and DeBlois, 1994) and may

Table 5
Reported growth and mortality rates of bay anchovy larvae in field studies.

Location	Growth (mm/d)	Mortality (M/d)	Source
Patuxent River, MD	0.59–0.93		Gallagher et al. (1983)
Newport River Estuary, NC	0.25–0.51		Fives et al. (1986)
Biscayne Bay, FL	0.43–0.56	0.30–0.45	Leak and Houde (1987)
Mesocosms in Chesapeake Bay, MD	0.39–0.61	0.08–0.23	Cowan and Houde (1990)
Great South Bay, NY	0.52–0.59	0.32–0.89	Castro and Cowen (1991)
Chesapeake Bay, MD (yolksac larvae)		0.41–4.24	Dorsey et al. (1996)
Chesapeake Bay, MD		0.23–1.20	MacGregor and Houde (1996)
Chesapeake Bay, MD	0.53–0.78	0.14–0.54	This study, range of regional rates

be the major agent of mortality operating on bay anchovy in Chesapeake Bay. The gelatinous zooplankters *M. leidyi* and *C. quinquecirrha,* are known to be important predators on eggs and larvae of bay anchovy (Feigenbaum and Kelly, 1984; Monteleone and Duguay, 1988; Cowan and Houde, 1993; Purcell et al., 1994). In Chesapeake Bay, the peak periods of bay anchovy spawning and gelatinous zooplankton abundance overlap during June and July (Cowan and Houde, 1993; Purcell et al., 1994), facilitating the predator-prey interaction. We found gelatinous predator biovolumes to be significantly higher in June, when only *M. leidyi* was present, than in July when both species occurred. *Chrysaora quinquecirrha*, a potentially more powerful predator on anchovy eggs and larvae than *M. leidyi* (Purcell et al., 1994), occurred only in July, but at low mean biovolumes that were uniform in the three Bay regions. It is worth noting that *C. quinquecirrha* is also a predator on *M. leidyi* (Purcell and Cowan, 1995), resulting in a predator-prey interaction that potentially has a sparing effect on anchovy eggs and larvae (Cowan and Houde, 1992).

The large biovolumes of gelatinous predators probably contributed to the greater mortality rates in June compared with July. However, the six mortality coefficients from the regional estimates were not significantly correlated with gelatinous predator biovolumes (Table 4), despite the strong, negative, linear relationship between anchovy larval abundance and gelatinous predator biovolume (r^2=0.75; Fig. 8A) for the combined June and July regional data. This negative correlation may have been a consequence of predation, but it also could have been generated by lower egg production of anchovy in areas where jellyfish were abundant, as Dorsey et al. (1996) hypothesized in site-specific studies of bay anchovy egg and yolksac larval mortality. Although we cannot conclude unequivocally that gelatinous

predators accounted for high mortality rates, it is likely that they were significant consumers of anchovy larvae.

Abundance data illustrated in survival curves (Figs. 4 and 5) showed several modes, which suggested that cohort-specific mortality might be variable on shorter time scales than we studied and might be changing as a function of ontogeny, age, or size. Other factors also could have biased our mortality estimates or contributed to regional variability in rates, for example, pulses of spawning that produce variable initial abundances of daily cohorts or immigration and emigration of larvae into and out of a region. Because mortality is size-specific, the presence of larger larvae in July could have led to a lower estimate of mortality rate during that period. But, when only larvae of equivalent lengths (i.e. ≤13 mm SL) were analyzed, estimated mortality rates remained nearly twice as high in June (*M*=0.41) as in July (*M*=0.22). If some larvae were being advected up the bay, as Dovel (1971) had hypothesized, this process could have contributed to biased estimates of higher mortality rates in the lower bay.

Despite a high cumulative mortality rate, the lower bay in July had the highest production of larvae surviving to 18 days after hatching for the June–July 1993 period (Table 3). This result is due to high spawning activity and initial concentrations of larvae in the lower bay (Rilling and Houde, manuscript in review), a high growth rate of larvae, and, importantly, the relatively large volume of water in the lower bay, which supported a large contingent of anchovy larvae.

Survival and recruitment potential of anchovy cohorts were responsive to variability in both mortality rates and growth rates that they experienced. The ratio *M/G*, an index of stage-specific mortality, is an important indicator of comparative production and survival potential during early life (Houde, 1996,

1997a). The baywide M/G ratio for bay anchovy larvae declined from 1.59 in June to 0.67 in July. The low M/G ratio in July is a reflection of the coincident decline in larval mortality rate and increase in growth rate that occurred between June and July. The difference in M/G ratios between months implies a 70-fold higher survival potential through the larval stage for July-hatched cohorts.

M/G ratios <1.0, signifying high regional production potential, were observed in the mid bay in June and in the mid and upper bay in July. Larvae in those regions tended to have lowest mortality rates. An abundance of large larvae generally indicates higher survival rates of cohorts, but size-selective mortality or transport (or both) of larvae into a region (Fortier and Leggett, 1982, 1985; Norcross and Shaw, 1984; Boehlert and Mundy, 1988) could have contributed to the relative abundances of large larvae and low M/G ratios. In the Patuxent River subestuary of Chesapeake Bay, progressive increases in larval length upriver were reported by Loos and Perry (1991), who hypothesized (with supporting evidence) that transport of larvae was primarily responsible. Similarly, MacGregor and Houde (1996) reported a gradient in bay anchovy larval size on a cross-Bay transect that was repetitively sampled; smallest larvae were found offshore and largest larvae, inshore. In the present study, selective up-bay transport of larvae could have acted to reduce the M/G ratio in the upper bay between June and July, but we cannot confirm it.

In summary, mortality rates of bay anchovy early-life stages were both temporally and regionally variable at one-month temporal and at 60-km spatial scales in Chesapeake Bay. Growth rates showed strong temporal variation but no significant regional differences. Stage-specific survival, which depended upon both mortality and growth rates, was both size-specific and growth-rate dependent. We found no obvious indication of density-dependent mortality (i.e. no correlations between egg or larval abundances and mortality or growth rates), although recent individual-based modeling suggests that density-dependence in early-life could be an important regulator of bay anchovy recruitments in Chesapeake Bay (Wang et al., 1997). The lower Chesapeake Bay in July was the major source of potential recruits in 1993. Temperature, zooplankton prey, and gelatinous predators all are believed to have contributed to temporal and regional differences in growth and mortality of larvae. Further research is needed to define scales and patterns of processes that control variability in production and recruitment of bay anchovy. This will require coupled biophysical studies and development of models that, up to now, have essentially emphasized only biology.

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