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Spatial ecology and growth in early life stages of bay anchovy *Anchoa mitchilli* in Chesapeake Bay (USA)

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ABSTRACT: The bay anchovy *Anchoa mitchilli* is the most abundant fish in Chesapeake Bay (USA) and is a vital link between plankton and piscivores within the trophic structure of this large estuarine ecosystem. Baywide distributions and abundances of bay anchovy eggs and larvae, and larval growth, were analyzed in a 5 yr program to evaluate temporal and spatial variability based on research surveys in the 1995–1999 spawning seasons. Effects of environmental variability and abundance of zooplankton that serve as prey for larval bay anchovy were analyzed. In the years of these surveys, 97.6% of eggs and 98.8% of larvae occurred in the polyhaline lower bay. Median egg and larval abundances differed more than 10-fold for surveys conducted in the 5 yr and were highest in the lower bay. Within years, median larval abundance (ind. m^{-2}) in the lower bay was generally 1–2 orders of magnitude higher than upper-bay abundance. Salinity, temperature, and dissolved oxygen explained 12% of the spatial and temporal variability in egg abundances and accounted for 27% of the variability in larval abundances. The mean, baywide growth rate for larvae over the 5 yr period was 0.75 ± 0.01 mm d^{-1}, and was best explained by zooplankton concentration and feeding incidence. Among years, mean growth rates ranged from 0.68 (in 1999) to 0.81 (in 1998) mm d^{-1} and were fastest in the upper bay. We identified environmental factors, especially salinity, that contributed to broadscale variability in egg and larval production.

KEY WORDS: Larval bay anchovy · Abundance · Growth · Spatiotemporal variation · Chesapeake Bay

1. INTRODUCTION

Bay anchovy *Anchoa mitchilli* (Engraulidae) is distributed broadly along the coast of the Northwest Atlantic Ocean from Maine, USA, to Mexico (Able & Fahay 1998, 2010) and is the most abundant fish species in Chesapeake Bay (Hildebrand & Schroeder 1928, Murdy et al. 1997, Jung & Houde 2003). The bay anchovy (hereafter BA) is a vital link between plankton and piscivores within the complex trophic structure of this estuarine system (Baird & Ulanowicz 1989, Houde & Zastrow 1991, Luo & Brandt 1993, Jung & Houde 2003, Ihde et al. 2015). Although not exploited by fisheries, BA is a major component of the diets of economically important piscivores, including bluefish *Pomatomus saltatrix*, striped bass *Morone saxatilis*, and weakfish *Cynoscion regalis* (Hartman & Brandt 1995, Ihde et al. 2015). Defining and quantifying the role of important forage taxa such as BA within the Chesapeake Bay ecosystem provides knowledge to support developing ecosystem-based fisheries management (Kemp et al. 2005, Houde 2011, Ihde et al. 2015).

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BA is a pelagic, serial spawner (Luo & Musick 1991, Zastrow et al. 1991) that spawns in Chesapeake Bay primarily between May and September (Dovel 1971, Olney 1983, Houde & Zastrow 1991, Rilling & Houde 1999a), with highest spawning activity occurring in July (Dalton 1987). Intense spawning activity occurs in mid-June when water temperatures reach 25°C and remains elevated through mid-August (Houde & Zastrow 1991). Eggs of BA incubate for ≤24 h, and larvae at hatching are 1.8–2.7 mm in length (Houde & Zastrow 1991, Able & Fahay 2010). In Chesapeake Bay, larvae occur at temperatures ranging from 15 to 30°C (Houde & Zastrow 1991) and over a wide range of salinities, from 0 to 31.9 (Dovel 1971, Olney 1983). Although BA spawning and larval ecology have been researched in Chesapeake Bay, primarily at small temporal and spatial scales (Loos & Perry 1991, Dorsey et al. 1996, MacGregor & Houde 1996, North & Houde 2004), inter-annual and baywide spatial variability in occurrence and distribution of BA early life stages have not been described. Prior to the analysis presented here, only Rilling & Houde (1999a) had conducted a baywide analysis of BA eggs and larvae, which was restricted to a 2 mo period in a single year. North & Houde (2004) evaluated factors controlling the small-scale distribution and abundance of BA eggs and larvae at 2 sites in mid-Chesapeake Bay, finding that wind-forced circulation patterns, below-pycnocline dissolved oxygen concentrations, and diel changes in vertical distribution of larvae and their copepod prey acted to control dispersal of BA early life stages.

Small pelagic fishes, including anchovies and sardines, undergo large interannual fluctuations in abundance that are often attributed to recruitment variability governed by oceanographic and environmental variability (Hjort 1914, Schwartzlose & Alheit 1999, Checkley et al. 2009). For unfished species, including BA, environmental factors and predation acting on eggs and larvae are believed to be the dominant causes of recruitment variability (Jung & Houde 2004a,b). This may be especially true for species such as BA that are essentially annual fishes (Newberger & Houde 1995). Environmental factors influence metabolism, distributions, habitat preferences, and feeding ecology, all of which affect vital rates (e.g. growth and survival) of early life stages of fishes (Houde 2008, Peck et al. 2012), leading to variable survival and recruitment (Houde 2008). In a 2 mo analysis and comparison in 1993, environmental factors were found to affect abundance, growth, and survival of BA eggs and larvae in Chesapeake Bay (Rilling & Houde 1999a,b), but no analysis of among-year temporal and spatial variability, and implications for recruitment, was conducted. Research reported here evaluates variability and potential mechanisms driving the baywide abundance and distribution of BA eggs and larvae, and of larval growth, through an analysis of environmental variability in 1995–1999 over the extensive spatial and environmental gradients in Chesapeake Bay.

We addressed 3 main objectives: (1) analyze differences in abundances and distributions of BA eggs and larvae in the 5 survey years, (2) analyze factors affecting spatial differences among bay regions in egg and larval abundances, and (3) estimate larval growth rates and their spatio-temporal patterns of variability during early development.

2. MATERIALS AND METHODS

2.1. Features of the study area

Chesapeake Bay is the largest estuary in the USA, with a surface area of more than 11 500 km^2 that drains a catchment of ~175 000 km^2; 50% of the bay's freshwater is delivered by the Susquehanna River at the head of the bay (Murdy et al. 1997, Kemp et al. 2005). Despite its large size, Chesapeake Bay is shallow, with a mean depth of 6.5 m and ~50% of its area less than 6 m deep. It is a partially mixed estuary (Pritchard 1956, Goodrich & Blumberg 1991). Vertical stratification, in conjunction with phytoplankton blooms induced by high allochthonous nutrient inputs of land origin, can cause dissolved oxygen concentrations to decline to low, sometimes hypoxic, levels in sub-pycnocline waters of the mesohaline zone during summer (Breitburg et al. 1994, Kemp et al. 2005). Salinities in brackish regions range from 0.5 to 32.0, and vary both seasonally and annually due to changes in freshwater discharge and precipitation (Kemp et al. 2005). The surface water temperature in the bay also ranges widely, from 1–4°C in late winter to 28–30°C in mid-summer.

2.2. Trophic Interactions in Estuarine Systems (TIES) program

The TIES program (1995–1999) investigated factors influencing the dynamics and production of trophic groups within the Chesapeake Bay ecosystem. The program was designed and conducted to address research objectives focused on both long-term and large-scale (i.e. annual and inter-annual periods,

whole bay) and short-term and smaller-scale (i.e. seasonal periods, bay regions, and finer spatial scales) features of biological production. Three research cruises were conducted each year; sampling for ichthyoplankton and fishes in TIES has been described and summarized (Auth 2003, Jung & Houde 2003, 2004b). For research described herein, only the summer TIES research cruises (June–August period) were included in our analyses (Table 1) because those cruises were conducted during peak BA spawning in Chesapeake Bay (Zastrow et al. 1991). Few larvae or eggs of BA occurred during the spring (April–May) and fall (October) TIES cruises.

Table 1. Survey years, dates, and number of visited sampling sites, vertical CTD casts, zooplankton and egg and larval ichthyoplankton samples, and larval bay anchovy otoliths analyzed for growth

Year	Dates	No. of stations	CTD	Zoo-plankton	Eggs and larvae	Otoliths analyzed
1995	23–29 July	44	44	–	86	57
1996	17–22 July	27	27	21	48	43
1997	11–15, 22–23 July	39	39	42	76	75
1998	6–12 August	37	37	39	102	81
1999	26–30 June	33	33	47	93	73

2.3. Ichthyoplankton collection

Ichthyoplankton was analyzed from the 5 baywide TIES summer cruises conducted aboard the RV 'Cape Henlopen' (University of Delaware) from 1995–1999. In each cruise, BA eggs and larvae were collected in 8 d surveys. Samples were obtained from the mouth to the head of the bay on 10–16 cross-bay transects (2–6 stations per transect), with each transect separated by 18–36 km (Fig. 1). Additional stations were sampled in the narrow confines of the upper bay.

Ichthyoplankton was collected using a 1 m^2 mouth-opening Tucker trawl with two 280 µm mesh nets. One net was fished from the pycnocline to the surface; the other from within 1 m of bottom to the pycnocline (or mid-depth when no pycnocline was present). The nets were opened and closed with a messenger, and each net was fished for 2 min at a vessel speed of 1–2 knots. A temperature and depth recorder was attached to the net frame, and flow meters were fixed in nets during each tow to record temperature, depth, and volume of water filtered by each net. The mean water volume filtered by each net tow was 118 m^3 (SE = 3.06 m^3). Samples were preserved immediately in ethanol.

For regional analysis, stations were aggregated into 3 contiguous regions along the main axis of the bay (Fig. 1). The regions are defined by salinity levels that were designated in previous research on Chesapeake Bay (Boynton & Kemp 1985, Jung & Houde 2003) and which correspond coarsely to salinities as defined by Feyrer et al. (2015): oligohaline, upper bay (km 0–40, salinity 1–12), mesohaline, middle bay (km 40–190, salinity 6–19), and polyhaline, lower bay (km 190–300, salinity 9–28).

2.4. Environmental data

At each station prior to ichthyoplankton sampling, a CTD cast was made to determine the temperature (°C), salinity, dissolved oxygen (DO; mg l^{-1}), and chlorophyll *a* (chl *a*; mg l^{-1}, indexed by fluorescence) profile of the water column. CTD casts were made from the surface to near-bottom for station depths ranging from 4 to 33 m. Measurements of each variable were obtained at 1 m depth intervals (0.5 m depth intervals in 1997) throughout the water column

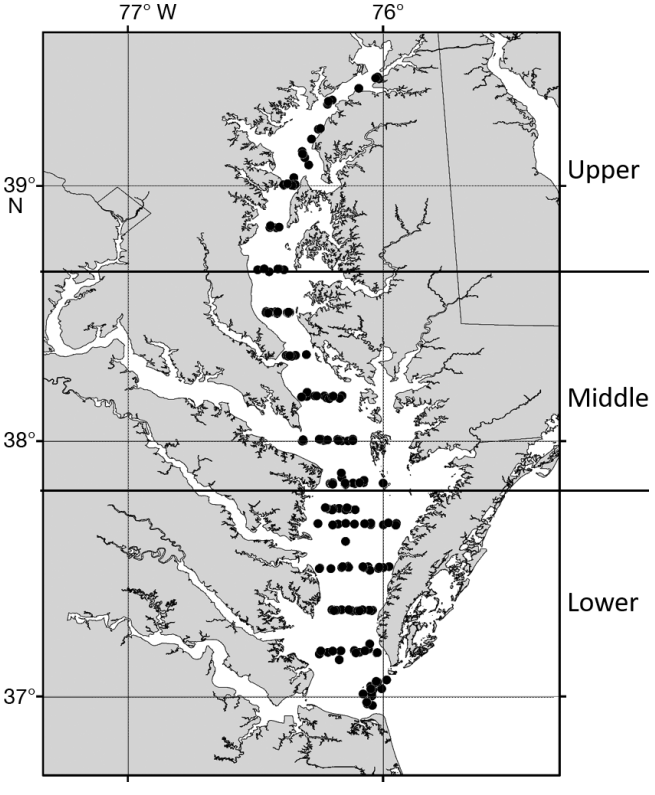

Fig. 1. Ichthyoplankton, zooplankton, and environmental data were collected during summer surveys (June/July/August) in each year from 1995–1999 at stations on across-bay transects distributed from the mouth to the head of Chesapeake Bay, USA

at each station. The average of these values was used to compute a station mean water-column metric for each variable during each cruise. Additionally, for each variable, individual station metrics within each bay region were averaged to compute regional means (Table 1).

2.5. Zooplankton collection

At 1–2 stations (closest to the bay channel, <15 m deep) on each transect, zooplankton was collected in 10 l Niskin bottles attached to the CTD rosette. Use of Niskin bottles is a reliable method to sample mesozooplankton in Chesapeake Bay (Roman et al. 2001, Elliott et al. 2013).

Niskin-bottle samples were taken at 3 depths to sample zooplankton above, at, and below the pycnocline. Zooplankton samples were filtered on a 35 µm sieve and preserved in 5% buffered formalin.

A total of 149 zooplankton samples were analyzed from the 1996–1999 collections. No zooplankton was collected in 1995. Prior to analysis, zooplankton samples were standardized to a 200 ml volume. Four series of 5 aliquots of 5 ml (n = 20 aliquots total) were extracted for enumeration using a calibrated Hensen-Stempel pipette. Aliquots were examined until either 300 organisms were counted or at least 25% of the standardized sample (50 ml) was sorted, whichever resulted in enumeration of the greatest number of organisms. Zooplankton counts were converted to estimated concentrations (l^{-1}) at each sampled site.

For zooplankton analyses, organisms were categorized as total zooplankton, copepods (aggregate of adults, copepodites, and nauplii), and copepod nauplii (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m651p125_supp.pdf). These 3 groups represent the main prey categories for BA during early ontogenesis (Houde & Alpern-Lovdal 1984, Auth 2003). The mean water-column concentration at each site was estimated as the weighted mean concentration of the 3 depths sampled by the Niskin bottles. The annual median zooplankton concentrations include all station concentrations in each year's survey.

2.6. Bay anchovy eggs and larvae

BA eggs and larvae were identified from 405 Tucker-trawl samples in 1995–1999 (Table 1). In the laboratory, samples were fully examined or subsampled using a Folsom plankton splitter when eggs and larvae were abundant. For subsampled cases, a randomly chosen subsample was examined to identify and count eggs and larvae. If there were fewer than 100 BA eggs or larvae in the subsample, then all of the eggs or larvae (or both, if neither met the minimum criteria of 100 individuals) from subsequent subsamples were removed until either 100 eggs and larvae had been removed or the total sample had been completely sorted. BA larvae removed from each sample were measured to the nearest 0.1 mm total length (TL) using image analysis software. Following Theilacker (1980) and Leak (1986), who found that anchovy larvae experienced size-dependent shrinkage during capture, handling, and ethanol preservation, the lengths of all measured larvae were adjusted according to Theilacker's (1980) adjustment formula:

$$\log_e TL_{adj} = \log_e X + 0.289 \times e^{-0.434 \times X \times T^{-0.68}} \quad (1)$$

where TL_{adj} = adjusted larval total length (mm); X = measured larval total length (mm); and T = mean net-tow duration and handling time (10 min).

2.7. Egg and larval abundance

MacGregor & Houde (1996) found that up to 2.5 times more BA larvae in small length classes were retained by a 53 µm net compared to a 280 µm net in tows of a paired Bongo-net sampler. Therefore, to account for extrusion of smaller larvae through the 280 µm mesh of our Tucker trawl, we adjusted catches based on the equation of MacGregor & Houde's (1996), which we applied to larvae <5.5 mm TL, the size at which 53:280 µm catches are expected to be equal:

$$R = 2.958 - 0.342 \times L \quad (2)$$

where R = ratio of 53:280 µm larval catch abundances; and L = larval standard length (SL, mm), where SL = 0.97 × TL.

Larval abundances of each 1 mm length class <5.5 mm TL were multiplied by R to adjust for extrusion. The minor difference between TL (our measurement) and SL (= 0.97 TL) had a negligible effect on the abundance adjustment for larvae <5.5 mm.

BA larvae ≤25.5 mm TL were included in estimates of larval abundance. Egg and larval abundances for each sample were estimated as:

$$A = (N \times D_1) / V \quad (3)$$

where A = abundance (number of eggs or larvae under 1 m^2); N = number of eggs or larvae collected per net tow; D_1 = tow-depth range (m); and V = volume (m^3) of water filtered by tow (determined from the flowmeter).

The total water-column abundance (number under 1 m^2) at each sampled site was estimated as the sum of the abundances from the depth ranges sampled by the 2 Tucker-trawl nets in each tow.

2.8. Abundance data analysis

Preliminary assessment showed that residuals of the BA data were not normally distributed using standard analysis of variance (ANOVA). Accordingly, differences in egg and larval abundances among the 3 Chesapeake Bay regions were described with the median and 2.5th and 97.5th percentiles, and the significance of the regional differences was tested with non-parametric Kruskal-Wallis tests (i.e. ANOVA on ranks).

Effects and significance of environmental variables on abundance of BA larvae and eggs were evaluated with a generalized additive model (GAM; Wood 2017) that allowed fitting non-parametric response curves. In addition to the effect of environmental variability (i.e. salinity, temperature, DO; Table 2), we also tested the stability of the links found in a supplementary analysis (Figs. S1 & S2 and Tables S4 & S5 in Supplement 2 at www.int-res.com/articles/suppl/m651p125_supp.pdf), by including an interaction with a categorical variable 'year' to all smooth terms of the final model. The best GAMs were identified through a forward selection procedure (using Akaike's information criterion corrected for small sample size [AICc]; Burnham & Anderson 2002) in the modeling process and ecological meaningfulness (e.g. smoothness and shape of the curve, pre-existing literature) as selection criteria. To account for non-normality in abundance distributions, a Gamma error distribution with log link was applied and, to avoid overfitting, the number of knots in the smooth terms (i.e. parameter degrees of freedom) was set to 4. Due to some missing values in the zooplankton data, zooplankton abundance was not included in the same model with the environmental variables, but was included as a second step, plotting the residuals of BA egg and larval abundances from the best environmental model on zooplankton concentrations. The residuals from the best environmental models for the BA eggs and larvae were analyzed with a spatial GAM (tensor product of latitude and longitude as predictor; Gaspard et al. 2019) to assess the presence of spatial autocorrelation that could have induced a model misspecification (Wood 2017).

2.9. Feeding and stomach analyses

In related research, larval BA stomach contents and feeding relationships were analyzed (Auth 2003, T. Auth unpubl. data; see Tables S2 & S3 in Supplement 1). For the analysis reported here, feeding incidence (FI) is defined as the proportion of the examined larvae with at least 1 prey in the gut. Feeding incidence and prey per gut (PPG) were derived from Auth (2003) and T. Auth (unpubl. data) and are applied herein as response variables in our analysis of larval growth rates.

Table 2. (A) Dependent and (B) independent variables included in the statistical analyses of bay anchovy (BA) egg and larval abundances. TIES: Trophic Interactions in Estuarine Systems project

Variable	Explanation	Abbreviation
(A) Dependent variables		
Egg abundance	Mean BA egg abundances (m^{-2}) in summer TIES surveys in 1995–1999	Eggs
Larval abundance	Mean larval BA abundances (m^{-2}) in 1995–1999. No larvae occurred in upper bay samples in 1996	Larvae
Growth rate	Mean annual growth rate of BA larvae (mm d^{-1})	G
(B) Independent variables		
Zooplankton concentration	Concentration of zooplankton in samples (l^{-1})	Zooplankton
Copepod concentration	Concentration of copepods in samples (l^{-1})	Copepods
Nauplii concentration	Concentration of copepod nauplii in samples (l^{-1})	Nauplii
Temperature	Mean water-column temperature (°C)	Temperature
Oxygen	Mean dissolved oxygen (mg l^{-1})	DO
Salinity	Mean water-column salinity	Salinity
Fluorescence	Mean water-column fluorescence (relative fluorescence units) representing chlorophyll *a* biomass	Chl *a*
Feeding index	Proportion of BA larvae with at least 1 prey item in the gut	FI
Prey per gut	Mean number of prey items in the gut of BA larvae	PPG

For our analysis, prey were identified to the lowest possible taxonomic level. Invertebrate eggs in larval BA guts containing an adult copepod were not enumerated because of potential confounding with eggs attached or carried by female copepods. Feeding incidence was calculated for individual length classes and for all larvae in the designated regional and annual categories. The mean number of prey per gut in feeding larvae was calculated for larvae on an annual and regional basis. FI and PPG were analyzed as factors to explain BA larvae growth rate.

2.10. Age and growth analysis

The sagittal otoliths from 329 BA larvae were examined (Table 1) to determine ages and growth rates. A representative sample (~25) of larvae <25.5 mm was examined from each of the 3 bay regions in each year. Age was determined from counts of daily growth increments in otoliths (Rilling & Houde 1999a). BA larvae begin to deposit daily growth rings 2 d after hatching (Leak & Houde 1987). Therefore, age (in days) was estimated by adding 2 to the number of otolith increments.

Sagittal otoliths were extracted and mounted under a dissecting microscope in SPUR resin on a glass slide and heated in an oven at 60°C for 8–12 h. Otolith preparation and analysis methods followed Secor et al. (1991) and Rilling & Houde (1999a). Otoliths were examined under a compound light microscope at 400–1000× using Optimas analytical imaging software (Media Cybernetics 1999). The increments on each otolith were counted at 2 different times, with the final age determination being the average of the 2 counts. A third count was conducted if the difference between the 2 age determinations was >20% of the lowest estimated age. When the average of the otolith counts resulted in a 0.5 d age class designation, the final age was randomly rounded to the nearest higher or lower 1 d age class.

In our initial analysis, a linear growth model was fitted to the length-at-age data for larvae <30 d of age. We also fitted a Gompertz model to our data for larvae from 2 to 40 d of age. The Gompertz model has been used frequently to parameterize and estimate growth of clupeoid larvae and provides a useful approach for estimating growth rates within larval length or age classes when rates are changing with development (e.g. Sakagawa & Kimura 1976, Zweifel & Lasker 1976, Bolz & Burns 1996, Gaughan et al. 2001). The Gompertz growth model was fit to our BA length-at-age data:

$$L_t = a \times \exp\left(-\exp^{-kG\left(\frac{t-X_0}{b}\right)}\right) \quad (4)$$

where L_t = total length (mm) at age t; a = age (d) = otolith increment count + 2; b = asymptotic larval total length (mm); and X_0 = inflection point of the curve; the age at which absolute growth rate begins to decline.

The parameters a and b were estimated through least squares iteration. Age-specific growth rates were calculated, based on the Gompertz model, for individuals in each post-hatch daily age class from age 3 to 40 d, both baywide and regionally for each year. The age-specific growth rates were estimated by taking the first derivative of the Gompertz growth curve for each daily age. To explore stage-specific regional and temporal differences in larval growth rates, BA larvae were aggregated into the age groups 2–5, 6–15, and 16–30 d, and the Gompertz model growth rates were derived and compared among years and regions.

The slopes of simple linear regressions of length-on-age for larvae <30 d of age, when growth rates were nearly linear, were compared:

$$L_t = L_0 + G \times t \quad (5)$$

where L_t = total length (mm) at age t; t = age (d); G = growth rate (mm d^{-1}); and L_0 = length at hatch (mm).

Analysis of covariance (ANCOVA) followed by a Student-Newman-Keuls multiple range test was applied to the linear-model growth data to detect and evaluate significant differences in growth rates of <30 d old larvae among years and among regions within each year.

3. RESULTS

3.1. Environmental and zooplankton variability

Water temperature, salinity, DO, and chl *a* varied among bay regions and throughout Chesapeake Bay during the survey periods in each year (Fig. 2). Regional median water-column (MWC) temperature varied between 22.6 and 29.0°C (lower bay in 1999 and upper bay in 1995, respectively). As expected, regional median salinities were lowest in the oligohaline upper bay (7.0–12.4) and increased towards the polyhaline lower bay (16.5–22.4; Fig. 2). Lowest and highest MWC DO were measured in 1999 in the upper bay and 1996 in the lower bay (4.4 and 9.4 mg l^{-1}, respectively). The lowest and highest median chl *a* were registered in the lower bay: 0.43 and 1.91 mg l^{-1} (1998 and 1996, respectively).

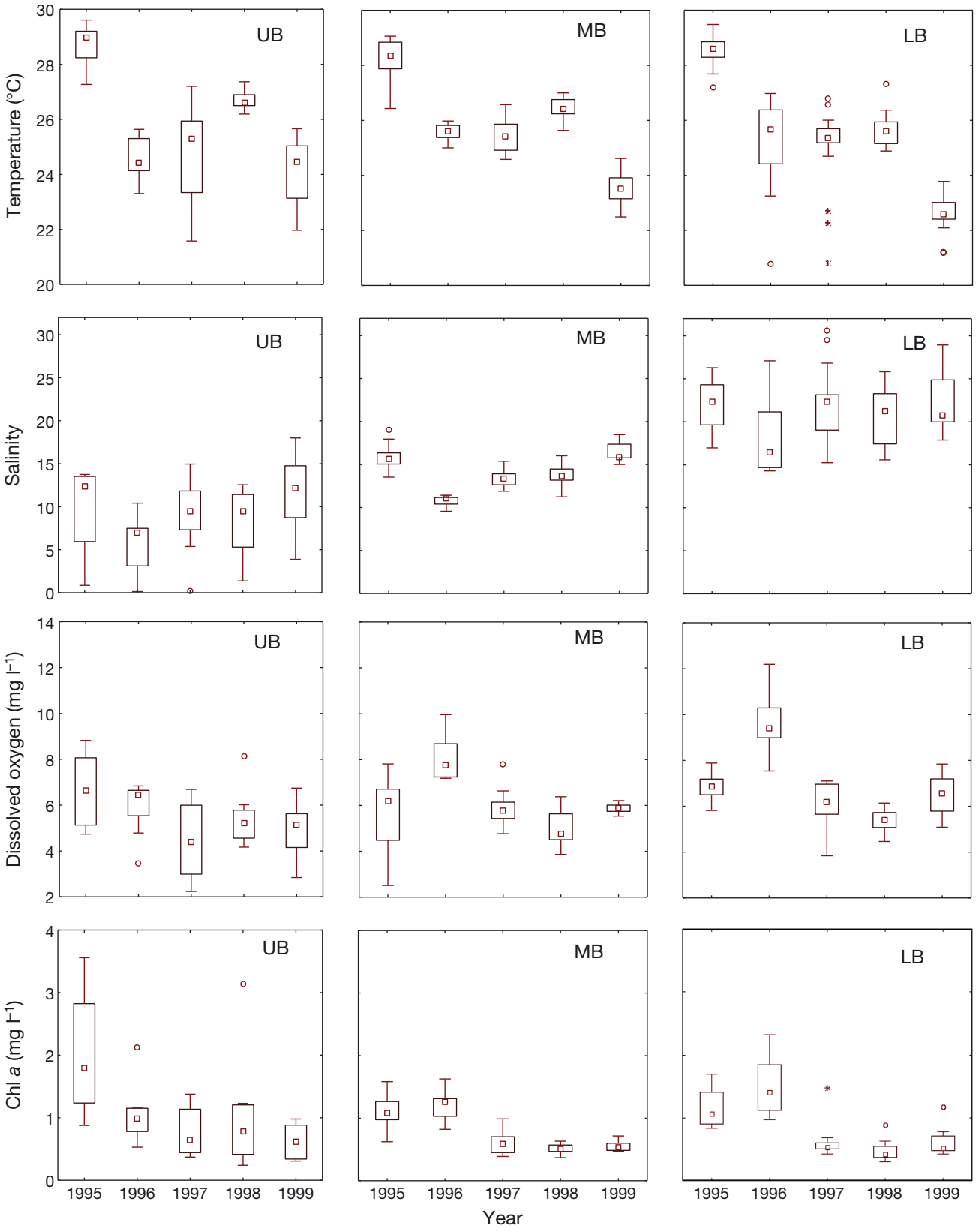

Fig. 2. Median temperature, salinity, dissolved oxygen, and chl *a* values in 3 bay regions: upper bay (UB), middle bay (MB), and lower bay (LB) in 1995–1999. The ends of the boxes define the 25th and 75th percentiles, a square inside the box defines the median, error bars define the non-outlier range, and dots represent outliers and extreme values

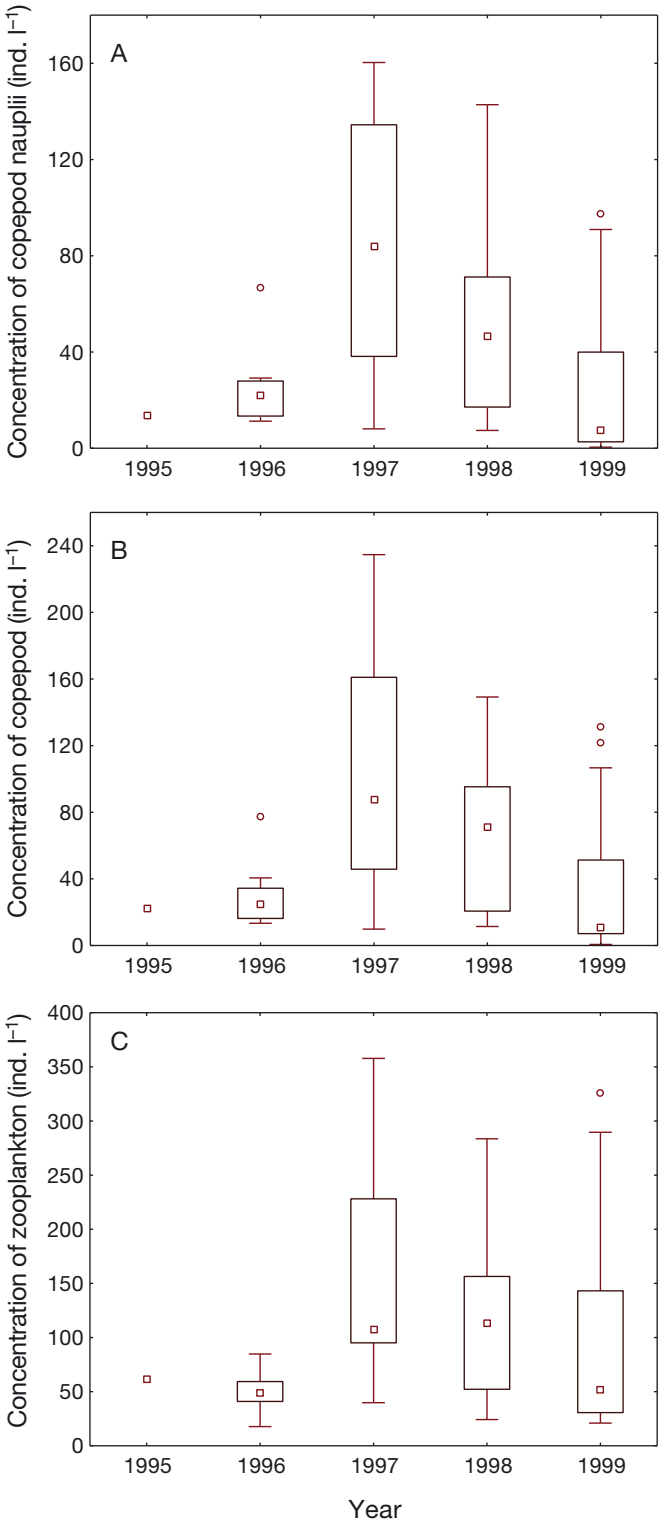

Fig. 3. Median baywide water-column (A) copepod nauplii, (B) copepod, and (C) zooplankton concentrations in Chesapeake Bay in 1996–1999. The ends of the boxes define the 25th and 75th percentiles, a square in the box defines the median, error bars define the non-outlier range, and dots represent outliers and extreme values. Note different scales on *y*-axes

Baywide median zooplankton concentrations differed (Fig. 3). In 1997 and 1998, concentrations were more than twice those of 1996 and 1999. Baywide median copepod and copepod nauplii concentrations were higher in 1997 and 1998 than in 1999. The highest observed copepod nauplii concentration occurred in 1997, and the lowest in 1999. For combined zooplankton taxa, there was regional variability among years in concentrations of zooplankton (Table S1 in Supplement 1). The highest regional concentrations of zooplankton, copepods, and copepod nauplii all occurred in the middle bay during 1997, while the lowest concentrations also occurred in the middle bay during 1999.

3.2. Eggs and larvae

Egg abundance and distribution varied among years and regions (Table 3, Figs. 4 & 5). Baywide median egg abundance differed more than 10-fold, and was highest in 1997 (125.3 m^{-2}) and lowest in 1996 (7.1 m^{-2}). Eggs generally were most abundant in the lower bay and less abundant in the upper bay in all years except 1999, when a more even distribution was observed. Egg abundance was significantly different among regions, with highest abundance in the lower bay and lowest abundance in the upper bay in 1995–1999 (Kruskal-Wallis chi-squared = 37.12, df = 2, F = 23.9, $p < 0.0001$; Table 3, Fig. 4). The highest regional median egg abundance occurred in the lower bay in 1997, while the lowest occurred in the upper bay in 1996.

In each year, larval abundance was highest in the lower bay and decreased directionally towards the upper bay (Table 3, Fig. 4). Within years, the difference between upper and lower bay abundances generally was more than 1–2 orders of magnitude. In the lowest-salinity year 1996, no BA larvae occurred in collections in the upper bay. Median abundance

Table 3. Spatial variability of bay anchovy egg and larval abundances in 3 regions of Chesapeake Bay: median values (number m^{-2}) and 2.5 and 97.5 % quantiles for both variables across Chesapeake bay regions

Variable	Region	Median (2.5; 97.5 percentiles)	n
Eggs	Upper	0.9 (0.1; 533)	43
	Middle	50.9 (15; 1074)	54
	Low	64.8 (15; 1434)	74
Larvae	Upper	0.1 (0; 7)	43
	Middle	1.9 (0; 64)	54
	Low	21.7 (10; 222)	74

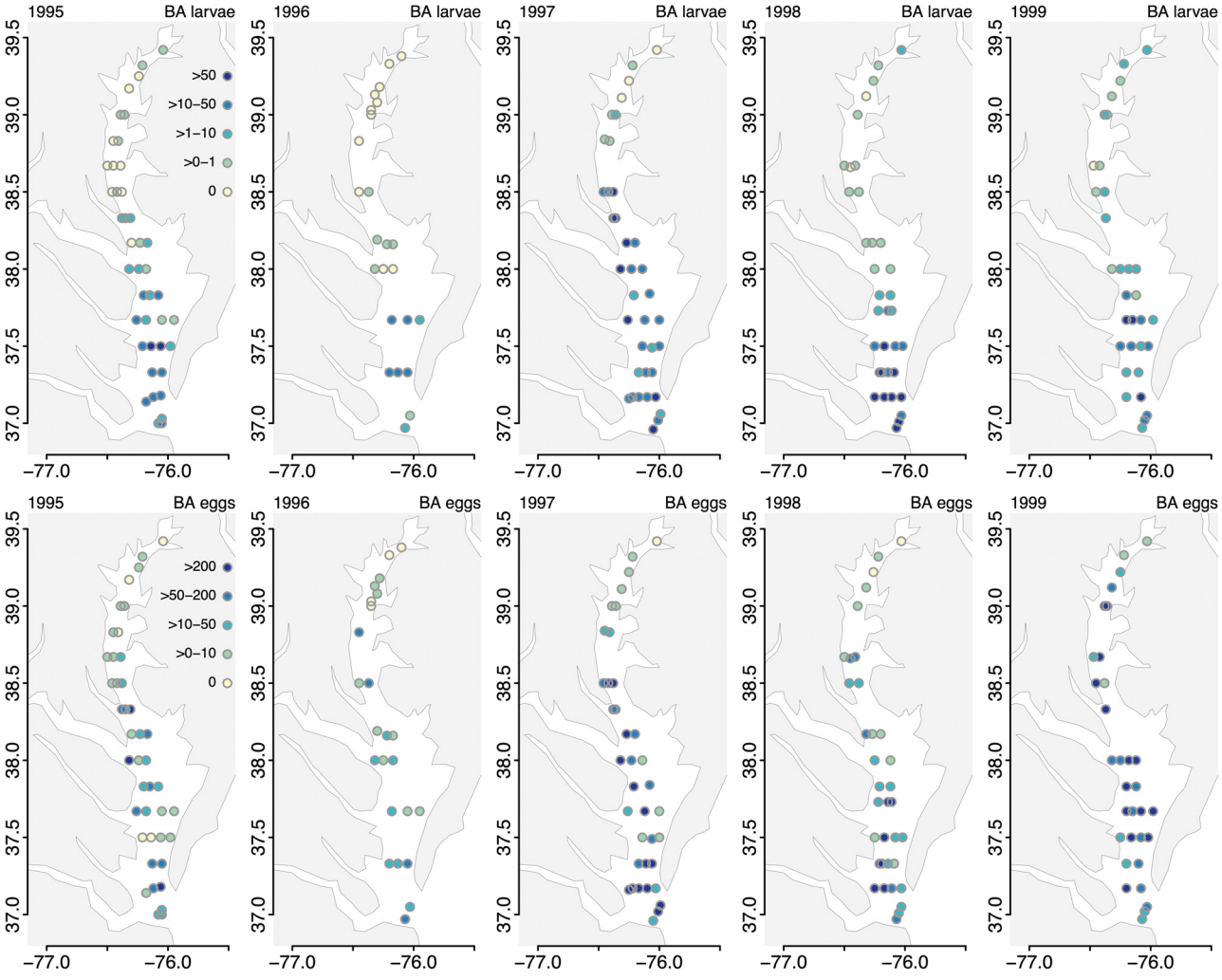

Fig. 4. Spatial distribution of water-column bay anchovy (BA) egg and larvae abundances (number m^{-2}) in the samples collected from Chesapeake Bay in 1995–1999

of larvae in the lower bay was significantly higher than in both the middle and upper bay regions (Table 3, Figs. 4 & 5) in all years except 1997, when abundances were similar in the lower and middle bays. Abundances of larvae were higher in the middle bay than in the upper bay in 1995 and 1997. For the pooled 5 years, regional, median abundance of BA larvae declined directionally from 21.7 m^{-2} in the lower bay to 0.1 m^{-2} in the upper bay (Kruskal-Wallis chi-squared = 94.55, df = 2, F = 99.8, $p < 0.0001$).

The forward selection GAM indicated that both egg and larval abundances correlated best, in decreasing order of significance, with salinity, DO, and temperature (Table 4, Fig. 6). The variability explained by each of these variables, and for the final model, was higher for larvae than eggs. Residuals in the final GAM model for BA larvae indicated no spatial patterns (R^2 = 0.00078, p = 0.80), and there was an insignificant spatial pattern in the residuals for the model fitted to eggs (i.e. latitude × longitude interaction; R^2 = 0.03, p = 0.052; Table 4), indicating no spatial autocorrelation in BA egg distribution patterns. Abundance of BA eggs and larvae increased until salinity reached 20, after which abundances decreased. For DO, the highest egg and larval abundances occurred near 6 mg l^{-1}. The modeled outcomes for temperature differed for eggs and larvae. For eggs, there was a broad but variable peak level of abundance in the 22–26°C range while larval abundance peaked slightly at 26–27°C.

Adding an interaction with year to each term in the final GAMs (see Tables S4 & S5 in Supplement 2) indicated that the salinity effect was most consistent across cruises with respect to both BA eggs and larvae abundances. The temperature effect was least stable, which can be explained by the fact that the

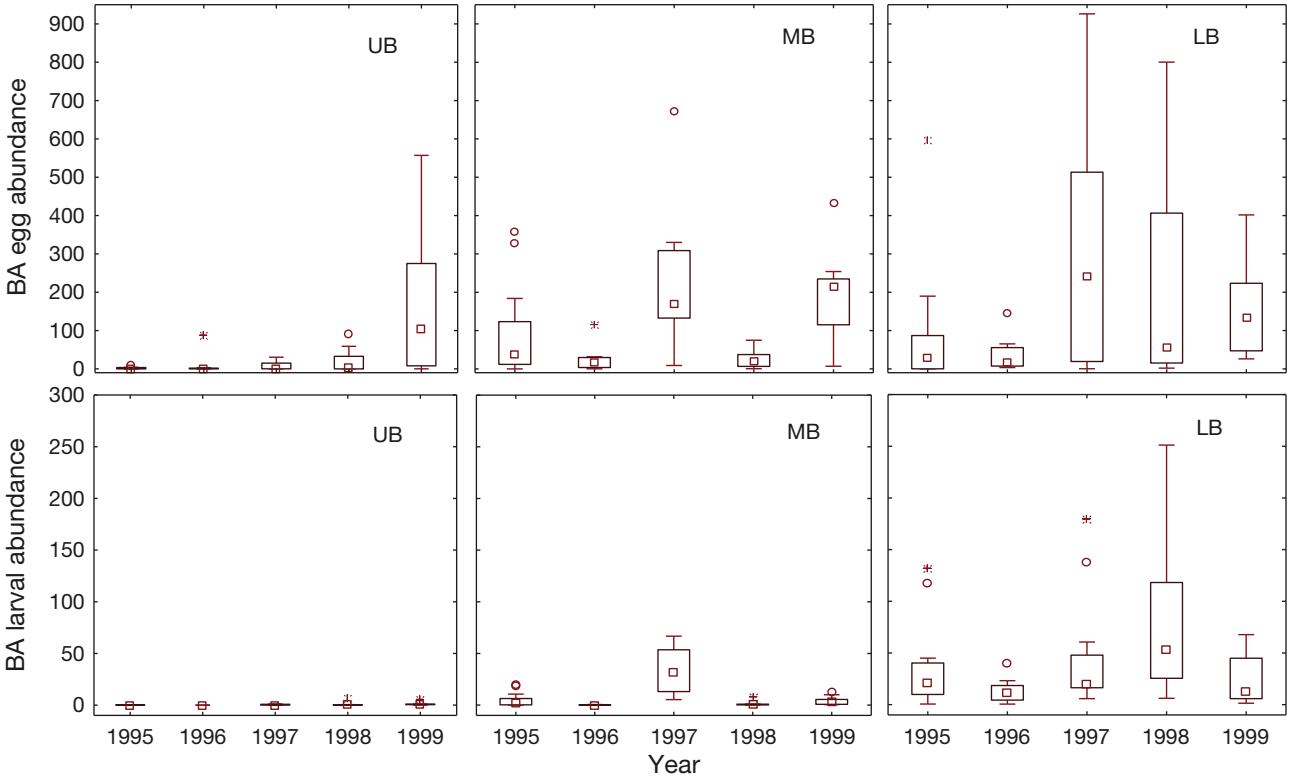

Fig. 5. Median regional water-column bay anchovy (BA) egg and larval abundances (number m^{-2}) in Chesapeake Bay from 1995–1999: upper bay (UB), middle bay (MB), and lower bay (LB). The ends of the boxes define the 25th and 75th percentiles, a square inside the box defines the median, error bars define the non-outlier range, and dots represent outliers and extreme values

temperature ranges in each year did not always overlap.

The residual pattern in egg abundance (but not larval abundance) indicated that egg abundance was higher than expected closer to the western shore after accounting for the correlations with salinity, DO, and temperature (Fig. 7). Residual variability in the BA egg abundance was correlated with abundance of total copepods (n = 55, $R^2_{adj.}$ = 0.115, p = 0.045) after accounting for the correlations with environmental variables (Fig. 8). Residual variability in larval abundance did not correlate significantly with copepod abundance, but the residuals did suggest a positive, albeit non-significant, relationship ($R^2_{adj.}$ = 0.04, p = 0.06; Fig. 8).

Table 4. Forward selection of generalized additive model (GAM) gamma error distribution with log-link function statistics for significant response variables and their combination for bay anchovy (BA) (A) eggs and (B) larvae. AICc: Akaike's information criterion corrected for small sample size; $R^2_{adj.}$: adjusted proportion of variance explained. Results of GAM (Residuals ~ te [Latitude (Lat), Longitude (Long)]) product represents a spatial autocorrelation test for BA eggs and larvae (te: tensor product smooth function). DO: dissolved oxygen

(A) Forward selection modeling of the abundance of BA eggs
Step 1: Salinity, $R^2_{adj.}$ = 0.07, AICc = 1794
Step 2: + DO, $R^2_{adj.}$ = 0.11, AICc = 1785
Step 3: + Temperature, $R^2_{adj.}$ = 0.12, AICc = 1768
GAM (Residuals ~ te [Lat, Long]; spatial autocorrelation test):
$R^2_{adj.}$ = 0.03, p = 0.052 (no significant spatial pattern in the residuals)

(B) Forward selection modeling of the abundance of BA larvae
Step 1: Salinity, $R^2_{adj.}$ = 0.172, AICc = 1236
Step 2: + DO, $R^2_{adj.}$ = 0.235, AICc = 1211
Step 3: + Temperature, $R^2_{adj.}$ = 0.266, AICc = 1197
GAM (Residuals ~ te [Lat, Long]; spatial autocorrelation test):
$R^2_{adj.}$ = 0.0078, p = 0.8 (not significant)

3.3. Growth rate

Growth rate of BA larvae was positively related to feeding incidence (n = 14, F = 6.2, R^2 = 0.625, p < 0.01) and zooplankton concentration (n = 11, F = 8.1, R^2 = 0.845, p < 0.01), indicating a strong response of larval growth to prey availability.

Lengths-at-age for BA larvae from the 3 bay regions, pooled over the 5 years, were broadly similar (Fig. 9). The pooled-years, baywide, and regional growth rates-at-age of

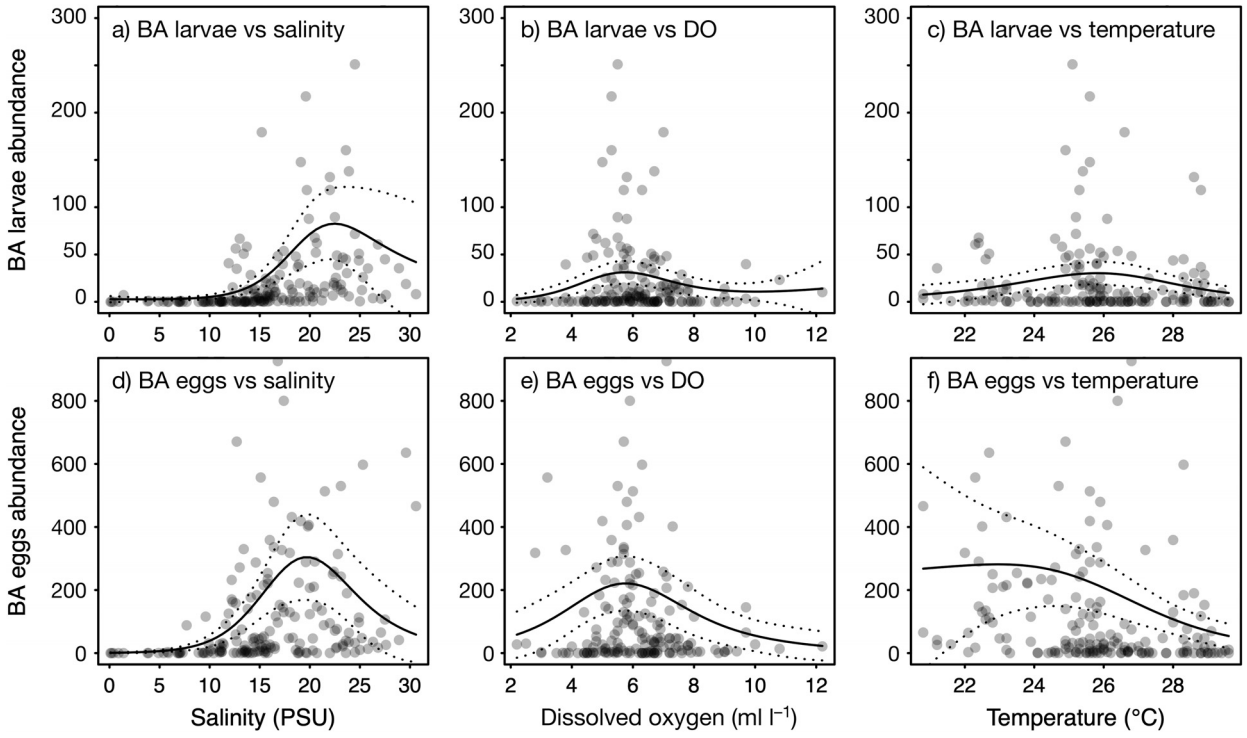

Fig. 6. Non-linear links between bay anchovy (BA) larvae and egg abundances (number m^{-2}) and salinity, dissolved oxygen (DO), and temperature as estimated with forward selection generalized additive models (GAMs) for surveys in 1995–1999. Solid lines represent the predicted values from the GAMs, and dotted lines the approximate 95 % confidence intervals (±2 SE). Note different scales on *y*-axes

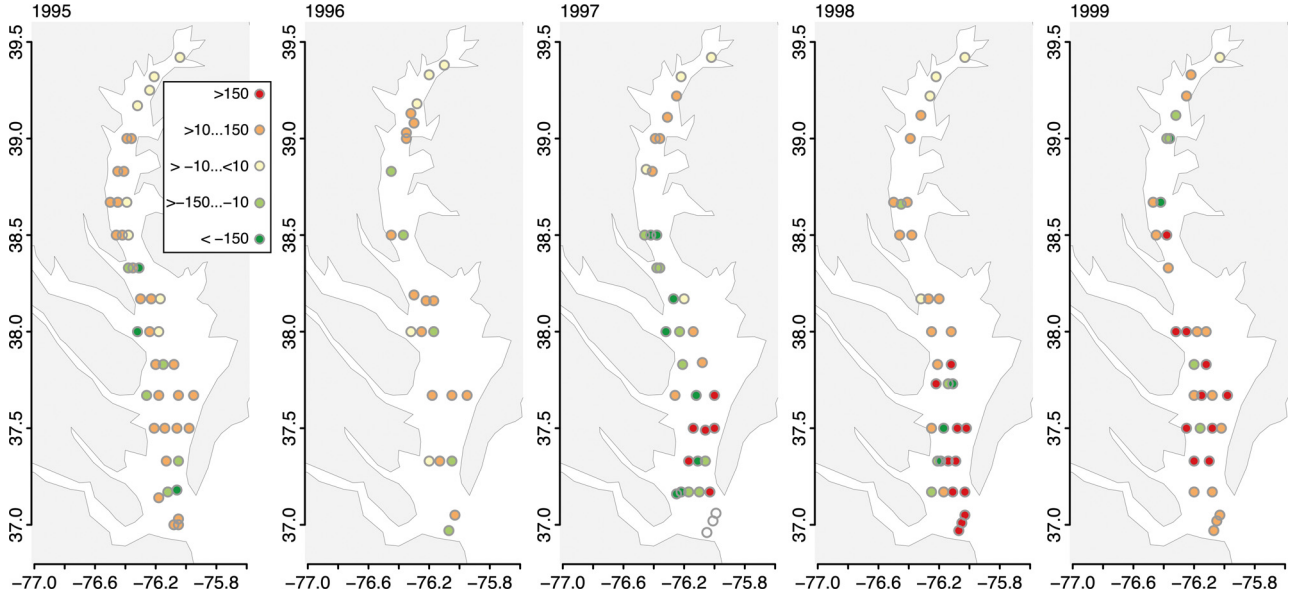

Fig. 7. Spatial pattern detected in the residuals of bay anchovy eggs after accounting for the correlations with salinity, dissolved oxygen, and temperature in the generalized additive models

larvae were estimated from the Gompertz growth models (Tables 5 & 6). The mean growth rate of early-stage larvae at 3–5 d post-hatch was 0.69 mm d^{-1} (Table 6A). The modeled rates were highest for larvae 6–15 d post-hatch (0.86 mm d^{-1}) but declined in older larvae 16–30 d old (0.54 mm d^{-1}; Table 6B,C). Except for the oldest age group, the lowest growth rates, with a few exceptions, were observed in the

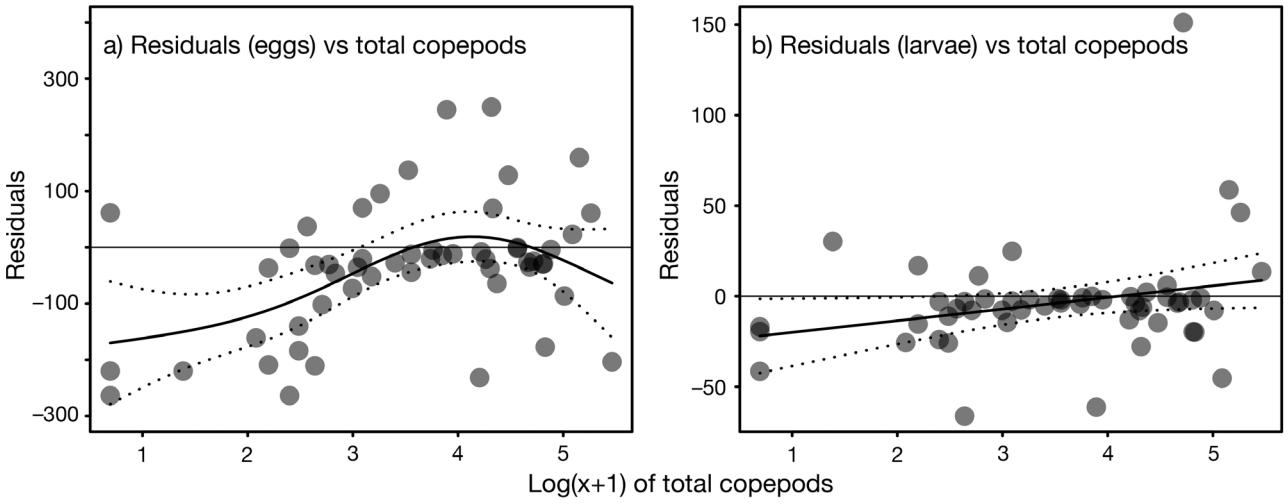

Fig. 8. Relationship between residuals of bay anchovy egg and larvae abundances from the generalized additive model environmental (salinity, dissolved oxygen, temperature) model and total copepod abundance in 1995–1999. Note different scales on *y*-axes

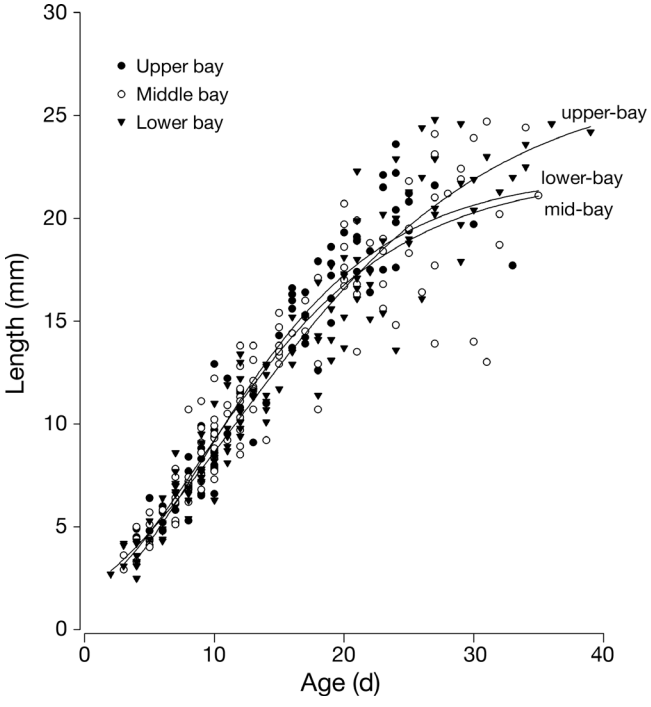

Fig. 9. Regional (upper, middle, and lower bay) length-at-age data from otolith-aging analysis, and fitted Gompertz growth model regressions (see Table 5) for bay anchovy larvae <40 d of age in Chesapeake Bay, 1995–1999

lower bay (Table 6). For pooled years, the fastest larval growth rates occurred in the upper bay. Growth rates were lower and similar in the middle and lower bays.

The pooled-years, baywide mean growth rate, based on the linear regression model for all larvae <30 d old, was 0.75 mm d^{-1}. Baywide mean growth rates ranged from 0.68 mm d^{-1} in 1999 to 0.81 mm d^{-1} in 1998 (Table 7). Growth rates in 1995 and 1998 were significantly higher than in 1999 (ANCOVA, $p < 0.05$). For pooled years, growth rate in the upper bay (0.83 mm d^{-1}) was significantly higher than growth rates in the middle (0.71 mm d^{-1}) and lower bay (0.75 mm d^{-1}). Regional growth rates within years were higher in the upper bay than in the lower bay in 1997 and 1999, but were higher in the lower bay in 1998 (ANCOVA, $p < 0.05$). The highest regional growth rate (0.86 mm d^{-1}) was estimated in the lower bay in 1998, while the lowest rate (0.55 mm d^{-1}) was estimated for the middle bay region in 1999 (Table 7).

4. DISCUSSION

4.1. Abundance and distribution

In our multi-year analysis, we detected substantial variability in abundances of BA eggs and larvae and also differences in distributions attributable to environmental factors in Chesapeake Bay. Results indicated that environmental conditions supporting successful spawning and larval production in the lower bay may contribute most importantly to annual recruitment in most years. We found that spawning by BA occurred throughout Chesapeake Bay in the 5 years of our analysis, but that highest spawning was concentrated in the lower bay. In each year, egg and larval abundances decreased from the lower bay region towards the upper bay along a declining salinity gradient. In 1996, the year of lowest salinity,

Table 5. (A) Gompertz and (B) linear growth model statistics for bay anchovy larvae from 3 regions of Chesapeake Bay based on 1995–1999 survey data. All models and parameters were significant at $p < 0.0001$

Region	N	*F*	$R^2_{adj.}$	Model
(A) Gompertz models				
Upper	108	397.7	0.87	G = 22.19 × exp(−exp(−(age − 8.99)/7.98))
Middle	108	401.7	0.87	G = 22.17 × exp(−exp(−(age − 8.85)/8.77))
Lower	113	819.0	0.93	G = 26.87 × exp(−exp(−(age − 11.47)/11.71))
All regions	329	1595.1	0.91	G = 24.22 × exp(−exp(−(age − 9.91)/9.82))
(B) Linear models				
Upper	108	1032.1	0.93	G = 1.03 + 0.80 × age
Middle	108	676.8	0.86	G = 2.22 + 0.69 × age
Lower	113	1253.2	0.92	G = 1.35 + 0.73 × age
All regions	329	2253.7	0.88	G = 2.02 + 0.70 × age

Table 6. Mean daily growth rates (mm d^{-1}) of bay anchovy larvae in 3 length groups. Gompertz-modeled growth rates for larvae (A) 3–5 d, (B) 6–15 d, and (C) 16–30 d old for 5 years and 3 bay regions. No larvae occurred in upper bay collections in 1996

Bay region	1995	1996	1997	1998	1999
(A) 3–5 d					
Upper	0.68	–	0.79	0.70	0.80
Mid	0.73	0.77	0.83	0.67	0.59
Lower	0.73	0.61	0.55	0.71	0.55
(B) 6–15 d					
Upper	1.16	–	0.93	0.85	0.95
Mid	0.95	0.86	0.91	0.82	0.64
Lower	0.94	0.75	0.70	0.92	0.67
(C) 16–30 d					
Upper	0.25	–	0.62	0.50	0.65
Mid	0.55	0.53	0.38	0.70	0.36
Lower	0.53	0.64	0.60	0.68	0.61

no BA larvae occurred in our upper bay samples, and few larvae were collected in the middle bay. However, highest salinity during our survey years was recorded in 1999, but we did not record the highest upper bay egg abundances in that year. This may indicate that other environmental factors, or perhaps variability in spawning stock biomass and its distribution (Jung & Houde 2004b), or adult feeding conditions (Peebles et al. 1996), have a substantial influence on inter-annual patterns of egg abundance.

It is notable that, despite low salinity in the upper bay in 1996 and low larval abundances there (the lowest in the 1995–1999 series), estimates of juvenile BA (>30 mm TL) abundance in the upper bay from midwater trawl collections in July 1996 were substantial (estimate = 4.2×10^8 individuals) compared to the middle bay (estimate = 2.8×10^9 individuals; Jung 2002). These distributions suggest that spawning might have been more intense in the upper bay in weeks prior to our survey or, alternatively and more likely, juvenile BA had dispersed to the upper bay region from the middle and lower bay. In this regard, Kimura et al. (2000), based on otolith chemistry, provided strong evidence that late-stage (>20 mm) BA larvae disperse upbay.

Area-scaled egg and larval abundances, expressed as numbers under 1 m^2, were orders of magnitude higher in the lower bay than in the upper bay in the 4 yr period 1995–1998, but abundances were more evenly distributed in 1999. The calculated total abundances of eggs and larvae in the lower bay relative to the other bay regions are even higher than the scaled abundances because of the greater surface area and volume of the polyhaline lower bay. Total volume of the lower bay is 3 times that of the oligohaline upper bay (26.7×10^9 and 8.7×10^9 m^3, respectively). Calculating total numbers of eggs from our estimated concentrations (number m^{-3}) yields estimated region-wide abundances of 3.3×10^{10}, 1.9×10^{12}, and 7.8×10^{13} in the upper, middle, and lower bays, respec-

Table 7. Survey (years) and regional daily growth rates (mm d^{-1}; ±1 SE) of larval bay anchovy (BA) in Chesapeake Bay in 1995–1999, estimated from the linear regression model. Within-year and pooled regional comparisons and among-year baywide comparisons that have different superscripts indicate significant differences (ANCOVA, Bonferroni post hoc test, $p < 0.05$). No BA larvae occurred in upper bay collections in 1996

Bay region	1995	1996	1997	1998	1999
Upper	0.74 ± 0.13^{a}	–	0.83 ± 0.03^{a}	0.77 ± 0.03^{b}	0.82 ± 0.05^{a}
Mid	0.77 ± 0.04^{a}	0.83 ± 0.09^{a}	0.80 ± 0.05^{ab}	0.76 ± 0.03^{b}	0.55 ± 0.03^{b}
Lower	0.80 ± 0.06^{a}	0.73 ± 0.04^{a}	0.70 ± 0.04^{b}	0.86 ± 0.03^{a}	0.68 ± 0.05^{a}
Baywide mean	0.78 ± 0.03^{a}	0.74 ± 0.04^{ab}	0.76 ± 0.03^{ab}	0.81 ± 0.02^{a}	0.68 ± 0.04^{b}

tively. Corresponding concentrations of larvae in the upper, middle, and lower bays were 6.1×10^8, 1.6×10^{11}, and 1.6×10^{13}, respectively. Eggs and larvae of BA are common throughout Chesapeake Bay, but in the years of our surveys, 97.6% of eggs and 98.8% of larvae occurred in the polyhaline lower bay. Results from our 5 yr analysis indicating that the lower bay had higher BA egg and larval production than other regions is consistent with the result from 2 baywide surveys in June and July 1993 that also reached this conclusion (Rilling & Houde 1999a). Abundances that we calculated for the lower bay region are similar to those reported by Olney (1983).

It is important to note that the regional differences in egg abundance (ind. m^{-2}) we observed in 1995–1998, and which Rilling & Houde (1999a) had also reported for 1993, were not observed in 1999 when our survey was conducted in late June rather than July. In 1999, egg and larval abundances were similar in the 3 bay regions. Mid- and upper-bay salinities in 1999 were the highest we observed for these regions during our 5 surveyed years. It is probable that the relatively uniform distribution of BA eggs throughout the bay in 1999 was related to a more even distribution of adult spawners in this high-salinity year. Despite the relatively high egg abundances (ind. m^{-2}) in the upper bay in 1999, larval abundances were highest in the lower bay, at levels similar to observations in the other years.

The regional patterns in egg and larval abundances that we observed in 1995–1998 differ from distributions reported by Rilling & Houde (1999a) based on their 2 surveys in June and July 1993. In June 1993, Rilling & Houde (1999a) reported highest abundances of BA eggs and larvae in the upper bay, a result similar to our observation for eggs in June 1999, despite salinity levels (mean = 5.9) in 1993 being lower than the mean salinity we observed (11.6) in June 1999. In July 1993, Rilling & Houde (1999a) observed a reduced abundance of eggs in the upper bay relative to June abundances, indicative of lower spawning. In our June 1999 survey, we observed a relatively even spatial distribution of eggs compared to other years when our survey was conducted in July or early August. It may be that the higher salinities observed in June 1999 in the upper and middle bays explain the distribution pattern of BA eggs. However, the results of Rilling & Houde (1999a) for 1993 show that, despite low salinities, high spawning output can occur in the upper and middle bays in some years, which may partly relate to spawning seasonality or other unexplained variability. It also is notable that Rilling & Houde (1999a) reported substantially higher production of eggs and larvae in July than in June, indicating that spawning by BA, which occurs from May through September in Chesapeake Bay, peaks in July and can be twice as high in July as in June.

We found that baywide BA egg and larval abundances (ind. m^{-2}) varied 15- and 9-fold, respectively, among our 5 surveys in 1995–1999, and that hydrological conditions in the Bay explained a substantial fraction of inter-annual variability in egg and larval abundances. Salinity, DO, and temperature contributed to the GAM variability in egg and larval abundances. For these contributing factors, egg and larval abundances increased only in the low to middle levels of their observed ranges. These findings indicate that BA adults generally prefer to spawn at the higher salinities occurring in the lower bay. The strong propensity for egg and larval abundances to be correlated is in part a consequence of a short (≤24 h) hatching time of BA eggs (Zastrow et al. 1991), leading to coincident distributions of eggs and newly hatched larvae.

The association of eggs and larvae with the higher salinities in the lower bay suggests that abundances depend indirectly on salinity differences caused by inter-annual variability in precipitation and runoff in the Chesapeake Bay watershed, and water exchange with the Atlantic Ocean (Kemp et al. 2005). Jung & Houde (2004b) suggested that freshwater runoff occurring months before the BA spawning season and its influence on baywide salinity in Chesapeake Bay play a role in determining adult BA distributions and spawning, thus controlling egg and larval distributions and explaining their higher abundances in the lower bay. North & Houde (2004) analyzed depth distributions of BA larvae in mid-Chesapeake Bay and simulated their dispersal, tentatively concluding that larvae >6 mm length were relatively abundant below the pycnocline where flux was upbay and thus had high probability of upbay dispersal. High freshwater flows and discharge into the bay are not usual during the spawning season of bay anchovy and are not likely to be a substantial factor causing massive downbay dispersal of eggs or larvae. In fact, Kimura et al. (2000) found that >20 mm BA larvae disperse upbay, based on otolith chemistry. Loos & Perry (1991) demonstrated that small BA larvae used selective tidal stream transport to move upriver in the tidal Patuxent River, a tributary of Chesapeake Bay.

Zooplankton plays a key role in supporting production of fish larvae, including BA. For BA larvae, Dorsey et al. (1996), Rilling & Houde (1999a), and Fulling & Peterson (1999) all reported significant positive correlations between zooplankton concentra-

tions and larval BA abundances. In our analysis, the residuals of BA egg, and possibly larval, abundances were positively correlated with copepod concentrations, suggesting that adult BA spawners sought out areas of high copepod abundance, as postulated by Peebles et al. (1996), and that larval production is higher in these regions. Results from other research in Chesapeake Bay indicated that BA larvae had fed more effectively in areas of low salinity, where prey items were more abundant (Rilling & Houde 1999a, T. Auth unpubl. data). Although they did not report on larval feeding, Castro & Cowen (1991) reported qualitatively (but not statistically significantly) higher mortality rates of BA larvae in Great South Bay, New York, at lower zooplankton prey concentrations during the peak of the spawning season, suggesting that zooplankton prey levels were important for survival, but noted the difficulty in confirming this relationship. Jordan et al. (2000) found that neither temperature nor salinity variations explained differences in growth rates of BA larvae in the Hudson River, and speculated that growth-rate variability there was governed by patchiness of zooplankton. Neither Castro & Cowen (1991) nor Jordan et al. (2000) could demonstrate unequivocally a direct influence of zooplankton concentration on larval BA vital rates.

In our research, the spatial pattern of the residuals in BA egg abundance, after accounting for effects of environmental variables (Fig. 7), showed that higher abundances of eggs in the lower bay occurred closer to the western shore and were lower in the center of the bay and near the eastern shore. The observed pattern may have occurred because spawning adults were most abundant in areas of higher zooplankton concentrations near the western shore. Peebles (2002) found that BA egg abundance in the Manatee River estuary, Florida, was positively related to the concentration of the copepod *Acartia tonsa* and water temperature, which is in agreement with our findings. In Tampa Bay, Florida, Peebles et al. (1996) reported that copepod concentration and water temperature were significantly and positively correlated with concentrations of preflexion (i.e. first-feeding) BA larvae. Results could indicate that, in order to maintain sufficiently high nutrition levels during the serial-spawning period (income breeding), adult BA selected spawning areas with high copepod concentrations to support their high egg production. As Peebles et al. (1996) noted, such areas also would have a high concentration of copepod nauplii, a favored prey of larval BA. Based on our residual plots of BA egg abundance relative to copepod concentration for Chesapeake Bay (Fig. 8), we show that the more intensive spawning and more abundant eggs in the lower bay are related to higher zooplankton concentrations, which would provide better feeding conditions for adult BA. On the other hand, spawning and egg abundance were strongly related to higher salinity levels in the lower bay that also could influence distribution of spawning adults (Jung & Houde 2004b). Moreover, the much larger volume of water in the lower bay compared to the middle and upper bays further emphasizes the importance of the lower bay as reproductive habitat for BA in Chesapeake Bay.

Numerous factors, including predation on early life stages and the level of spawning stock biomass, act together to promote suitability of the lower Chesapeake Bay as a spawning and nursery area for BA (Rilling & Houde 1999a, Jung & Houde 2004b). While BA has a broad tolerance of environmental conditions and the ability to spawn and produce viable larvae over a wide range of conditions (Houde & Zastrow 1991), we found that salinity in Chesapeake Bay is a key variable governing spawning and that larval growth rate is positively related to zooplankton concentration. Rilling & Houde (1999a,b), also found that BA larval abundance was positively associated with zooplankton concentration and salinity, but negatively associated with abundance of gelatinous predators in June 1993. They suggested that predation was a probable controller of BA larval abundance in Chesapeake Bay. Govoni & Olney (1991), Purcell et al. (1994), and Decker et al. (2007) speculated that gelatinous predators, which consume BA eggs and larvae (Cowan & Houde 1993, Purcell et al. 1994), were on average less abundant in the lower Chesapeake Bay compared to other bay regions. Accordingly, predation by gelatinous predators may partly account for the lower abundances of eggs and larvae in the upper bay. Based on the finding by Purcell et al. (1994) of substantial predation on BA eggs and larvae by the scyphomedusa *Chrysaora quinquecirrha* (= *chesapeaki*) and the ctenophore *Mnemiopsis leidyi*, Rilling & Houde (1999a) postulated that jellyfishes, which were most abundant in the middle and upper bay regions in 1993, may have caused the high larval BA mortality they observed in June 1993.

4.2. Growth rate

The pooled mean growth rates of BA larvae for the 3 regions in our 5 yr analysis ranged from 0.71 mm d^{-1} (middle bay) to 0.83 mm d^{-1} (upper bay) and are similar to those reported by Rilling & Houde (1999b) for their July 1993 data (0.70–0.78 mm d^{-1}). However,

our ranges of growth rates are notably higher than those reported by Rilling & Houde (1999b) for June 1993 (0.53–0.61 mm d^{-1}). Variability in growth rates of BA larvae reported in other research is substantial. In the Hudson River estuary, rates of growth of BA larvae were more variable than those we estimated in Chesapeake Bay. For example, Jordan et al. (2000) estimated growth rates ranging from 0.39–0.88 mm d^{-1} in 1995 and 0.41–0.77 mm d^{-1} in 1996, with mean rates lower than those we estimated in Chesapeake Bay. Other research on BA larvae documents the considerable variability in growth rates; for example, 0.59–0.93 mm d^{-1} in the Patuxent River, Maryland (Gallagher et al. 1983), 0.43–0.56 mm d^{-1} in Biscayne Bay, Florida (Leak & Houde 1987), and 0.25–0.51 mm d^{-1} in the Newport River Estuary, North Carolina (Fives et al. 1986).

We found that zooplankton prey abundance significantly influenced larval BA growth rate in Chesapeake Bay for our 5 yr analysis. Positive relationships between larval growth rates and zooplankton concentrations are frequently reported for marine and estuarine fish larvae (e.g. Zenitani et al. 2009, Houde 2016). In laboratory experiments, growth rates of BA larvae were strongly and positively related to prey concentrations (Houde 1978), the rates increasing from 0.38 mm d^{-1} at 50 prey l^{-1} to 0.59 mm d^{-1} at 1000 prey l^{-1} (Houde & Schekter 1981). In Chesapeake Bay, regional relative prey densities in each year of our 5 yr study were concordant with regional BA larvae growth rates. The highest recorded mean regional zooplankton concentration (208.9 l^{-1}) was observed in the middle bay in 1996 and coincided with one of our highest observed regional larval growth rates (0.83 mm d^{-1}), while the lowest mean regional zooplankton concentration (38.9 l^{-1}) and lowest larval growth rate (0.55 mm d^{-1}) both occurred in the middle bay in 1999. Rilling & Houde (1999b) also reported that larval BA growth was positively related to zooplankton density in Chesapeake Bay. They found that fastest growth rates in June and July 1993 occurred in the upper bay, where copepod nauplii were most abundant (mean = 84.8 nauplii l^{-1} in June and 157.5 nauplii l^{-1} in July), while the lowest growth rates were observed in June in the middle and lower bays, where copepod nauplii densities and temperatures were lowest. In general, it is apparent that growth rates of BA larvae from different estuaries or between different years within the same estuary can vary widely and that temperature and prey abundances are important agents governing this variability.

Although regional and inter-annual differences in growth rates of BA observed in our research were modest, the effect of variable growth on stage-specific survivorship and recruitment potential have been demonstrated to be substantial in marine fishes (Arula et al. 2015, Houde 2016). For BA larvae, we estimated that length at metamorphosis (30 mm TL) would have been reached in approximately 35 d post-hatch in 1998, the year of highest mean growth rate (0.81 mm d^{-1}), but would have required 41 d in 1999, the year of lowest mean growth rate (0.68 mm d^{-1}). Relatively fast growth in the larval stage can reduce starvation potential, minimize the time interval when size-selective predation occurs, and may enhance recruitment (Houde 1987, 2016, Bailey et al. 1996, Meekan & Fortier 1996). Using Rilling & Houde's (1999b) July 1993 estimated baywide BA larval mortality rate of 0.23 d^{-1}, our observed difference in growth rate of 0.13 mm d^{-1} between 1998 and 1999 could have generated a >4-fold difference in survival to size at metamorphosis during those 2 years, at least for the cohorts present during our ichthyoplankton surveys. Takasuka et al. (2003, 2007) found that growth-selective predation occurred on larvae of the Japanese anchovy *Engraulis japonicus* in Sagami Bay, Japan, and that larvae with higher growth rates potentially had higher survival rates and potential to recruit. In Chesapeake Bay, Jung & Houde (2004b) reported that the highest recruitment of BA in the 1995–1999 period occurred in 1998, the year when we observed the fastest larval growth (0.81 mm d^{-1}).

The Chesapeake Bay is undergoing continual and accelerated changes in water quality, water-column vertical structure, and productivity (Kemp et al. 2005) during recent decades attributable to human activities and ongoing climate change. Based on climate projections, winter–spring runoff, water column stratification, and hypoxia are all predicted to increase in the 21st century (Howarth et al. 2006, Ni et al. 2019) leading to probable changes in bay productivity (Najjar et al. 2010, Harding et al. 2015, Ni et al. 2019). These changes are likely to result in regional shifts in bay salinities, which we demonstrated affect spawning and early-life ecology of BA. Changes in Chesapeake Bay associated with eutrophication and resulting hypoxia are potential threats to zooplankton production (particularly copepods), a main prey resource for BA larvae and young of other fishes (Kimmel et al. 2012, Roman et al. 2019). The ongoing changes could reduce the reproductive capacity of BA, a concern for fisheries managers who recognize the ecological importance of this forage fish in ongoing efforts to develop ecosystem-based fisheries management for Chesapeake Bay.

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LITERATURE CITED

Able KW, Fahay MP (1998) The first year of life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, NJ

Able KW, Fahay MP (2010) Ecology of estuarine fishes: temperate waters of the western North Atlantic. Johns Hopkins University Press, Baltimore, MD

Arula T, Laur K, Simm M, Ojaveer H (2015) Dual impact of temperature on growth and mortality of marine fish larvae in a shallow estuarine habitat. Estuar Coast Shelf Sci 167:326–335

Auth TD (2003) Interannual and regional patterns of abundance, growth, and feeding ecology of larval bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. MSc thesis, University of Maryland, College Park, MD

Bailey KM, Picquelle SJ, Spring SM (1996) Mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1988–91. Fish Oceanogr 5:124–136

Baird D, Ulanowicz RE (1989) The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol Monogr 59:329–364

Bolz G, Burns BR (1996) Age and growth of larval Atlantic herring, *Clupea harengus*: a comparative study. Fish Bull 94:387–397

Boynton WR, Kemp WM (1985) Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. Mar Ecol Prog Ser 23:45–55

Breitburg DL, Steinberg N, DuBeau S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. Mar Ecol Prog Ser 104:235–246

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY

Castro LR, Cowen RK (1991) Environmental factors affecting the early life history of bay anchovy *Anchoa mitchilli* in Great South Bay, New York. Mar Ecol Prog Ser 76: 235–247

Checkley D, Alheit J, Oozeki Y, Roy C (2009) Climate change and small pelagic fish. Cambridge University Press, New York, NY

Cowan JH Jr, Houde ED (1993) Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Mar Ecol Prog Ser 95:55–65

Dalton P (1987) Ecology of bay anchovy (*Anchoa mitchilli*) eggs and larvae in the mid-Chesapeake Bay. MSc thesis, University of Maryland, College Park, MD

Decker MB, Brown CW, Hood RR, Purcell JE and others (2007) Predicting the distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Mar Ecol Prog Ser 329:99–113

Dorsey S, Houde E, Gamble J (1996) Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay. Fish Bull 94:257–267

Dovel WL (1971) Fish eggs and larvae of the upper Chesapeake Bay. NRI Spec Rep 4. Natural Resources Institute, University of Maryland, College Park, MD

Elliott DT, Pierson JJ, Roman MR (2013) Copepods and hypoxia in Chesapeake Bay: abundance, vertical position and non-predatory mortality. J Plankton Res 35: 1027–1034

Feyrer F, Cloern JE, Brown LR, Fish MA, Hieb KA, Baxter RD (2015) Estuarine fish communities respond to climate variability over both river and ocean basins. Glob Change Biol 21:3608–3619

Fives JM, Warlen SM, Hoss DE (1986) Aging and growth of larval bay anchovy, *Anchoa mitchilli*, from the Newport River estuary, North Carolina. Estuaries 9:362–367

Fulling G, Peterson M (1999) Estimation of small scale patchiness of zooplankton and an associated predator, *Anchoa mitchilli.* Gulf Res Rep 11:151–158

Gallagher R, Hirshfield M, Perry E (1983) Age, growth, and mortality estimates for larval bay anchovy (*Anchoa mitchilli*) in the Patuxent River. Benedict Estuarine Research Laboratory, Benedict, MD

Gaspard G, Kim D, Chun Y (2019) Residual spatial autocorrelation in macroecological and biogeographical modeling: a review. J Ecol Environ 43:19

Gaughan D, Fletcher W, White K (2001) Growth rate of larval *Sardinops sagax* from ecosystems with different levels of productivity. Mar Biol 139:831–837

Goodrich DM, Blumberg AF (1991) The fortnightly mean circulation of Chesapeake Bay. Estuar Coast Shelf Sci 32: 451–462

Govoni JJ, Olney JE (1991) Potential predation on fish eggs by the lobate ctenophore *Mnemiopsis leidyi* within and outside the Chesapeake Bay plume. Fish Bull 89:181–186

Harding LW Jr, Adolf JE, Mallonee ME, Miller WD and others (2015) Climate effects on phytoplankton floral composition in Chesapeake Bay. Estuar Coast Shelf Sci 162:53–68

Hartman KJ, Brandt SB (1995) Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Trans Am Fish Soc 124:520–537

Hildebrand SF, Schroeder WC (1928) Fishes of Chesapeake Bay. Fish Bull 43:367–388

Hjort J (1914) Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. Rapp PV Reùn Cons Int Explor Mer 20:1–228

Houde ED (1978) Critical food concentrations for larvae of three species of subtropical marine fishes. Bull Mar Sci 28:395–411

Houde ED (1987) Fish early life dynamics and recruitment variability. In: Hoyt RD (ed) 10th Annual Larval Fish Conference, Symposium 2. American Fisheries Society, Bethesda, MD, p 17–29

Houde ED (2008) Emerging from Hjort's shadow. J Northwest Atl Fish Sci 41:53–70

Houde ED (2011) Managing the Chesapeake's fisheries: a work in progress. Maryland Sea Grant College, College Park, MD

Houde ED (2016) Recruitment variability. In: Jakobsen T, Fogarty MJ, Megrey BA, Moksness E (eds) Fish repro-

ductive biology: implications for assessment and management. Wiley-Blackwell, Hoboken, NJ, p 98–187

Houde ED, Alpern-Lovdal J (1984) Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuar Coast Shelf Sci 18:403–419

Houde ED, Schekter RC (1981) Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp PV Reùn Cons Int Explor Mer 178:441–453

Houde ED, Zastrow C (1991) Bay anchovy, *Anchoa mitchilli*. In: Funderburk SL, Fordan SJ, Mihursky JA, Riley D (eds) Habitat requirements for Chesapeake Bay living resources, 2nd edn. Living Resources Subcommittee, Chesapeake Bay Program, Annapolis, MD, p 1–14

Howarth RW, Swaney DP, Boyer EW, Marino R, Jaworski N, Goodale C (2006) The influence of climate on average nitrogen export from large watersheds in the Northeastern United States. Biogeochemistry 79:163–186

Ihde TF, Houde ED, Bonzek CF, Franke E (2015) Assessing the Chesapeake Bay forage base: existing data and research priorities. Final Report 15-005. Chesapeake Bay Program Scientific and Technical Advisory Committee, Edgewater, MD

Jordan RC, Gospodarek AM, Schultz ET, Cowen RK, Lwiza K (2000) Spatial and temporal growth rate variation of bay anchovy (*Anchoa mitchilli*) larvae in the mid Hudson River estuary. Estuaries 23:683–689

Jung S (2002) Fish community structure and the spatial and temporal variability in recruitment and biomass production in Chesapeake Bay. PhD dissertation, University of Maryland, College Park, MD

Jung S, Houde ED (2003) Spatial and temporal variabilities of pelagic fish community structure and distribution in Chesapeake Bay, USA. Estuar Coast Shelf Sci 58:335–351

Jung S, Houde ED (2004a) Production of bay anchovy *Anchoa mitchilli* in Chesapeake Bay: application of size-based theory. Mar Ecol Prog Ser 281:217–232

Jung S, Houde ED (2004b) Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. Fish Bull 102:63–77

Kemp WM, Boynton WR, Adolf JE, Boesch DF and others (2005) Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Mar Ecol Prog Ser 303:1–29

Kimmel DG, Boynton WR, Roman MR (2012) Long-term decline in the calanoid copepod *Acartia tonsa* in central Chesapeake Bay, USA: an indirect effect of eutrophication? Estuar Coast Shelf Sci 101:76–85

Kimura R, Secor DH, Houde ED, Piccoli PM (2000) Up-estuary dispersal of young-of-the-year bay anchovy *Anchoa mitchilli* in the Chesapeake Bay: inferences from microprobe analysis of strontium in otoliths. Mar Ecol Prog Ser 208:217–227

Leak JC (1986) The relationship of standard length and otolith diameter in larval bay anchovy, *Anchoa mitchilli* (Val.). A shrinkage estimator. J Exp Mar Biol Ecol 95: 167–172

Leak JC, Houde ED (1987) Cohort growth and survival of bay anchovy *Anchoa mitchilli* larvae in Biscayne Bay, Florida. Mar Ecol Prog Ser 37:109–122

Loos JJ, Perry ES (1991) Larval migration and mortality rates of bay anchovy in the Patuxent River. In: Hoyt RD (ed) Larval fish recruitment and research in the Americas. Tech Rep NMFS 95. National Oceanic and Atmospheric Administration, Washington, DC, p 65–76

Luo J, Brandt SB (1993) Bay anchovy *Anchoa mitchilli* production and consumption in mid-Chesapeake Bay based upon a bioenergetics model and acoustic measurements of fish abundance. Mar Ecol Prog Ser 98:223–236

Luo JG, Musick JA (1991) Reproductive biology of the bay anchovy in Chesapeake Bay. Trans Am Fish Soc 120: 701–710

MacGregor JM, Houde ED (1996) Onshore–offshore pattern and variability in distribution and abundance of bay anchovy *Anchoa mitchilli* eggs and larvae in Chesapeake Bay. Mar Ecol Prog Ser 138:15–25

Meekan MG, Fortier L (1996) Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian Shelf. Mar Ecol Prog Ser 137:25–37

Murdy EO, Birdsong RS, Musick JA (1997) Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, DC

Najjar RG, Pyke CR, Adams MB, Breitburg D and others (2010) Potential climate-change impacts on the Chesapeake Bay. Estuar Coast Shelf Sci 86:1–20

Newberger TA, Houde ED (1995) Population biology of bay anchovy *Anchoa mitchilli* in the mid Chesapeake Bay. Mar Ecol Prog Ser 116:25–37

Ni W, Li M, Ross AC, Najjar RG (2019) Large projected decline in dissolved oxygen in a eutrophic estuary due to climate change. J Geophys Res Oceans 124:8271–8289

North EW, Houde ED (2004) Distribution and transport of bay anchovy (*Anchoa mitchilli*) eggs and larvae in Chesapeake Bay. Estuar Coast Shelf Sci 60:409–429

Olney JE (1983) Eggs and early larvae of the bay anchovy, *Anchoa mitchilli*, and the weakfish, *Cynoscion regalis*, in lower Chesapeake Bay with notes on associated ichthyoplankton. Estuaries 6:20–35

Peck MA, Baumann H, Bernreuther M, Clemmesen C and others (2012) The ecophysiology of *Sprattus sprattus* in the Baltic and North Seas. Prog Oceanogr 103:42–57

Peebles EB (2002) Temporal resolution of biological and physical influences on bay anchovy *Anchoa mitchilli* egg abundance near a river-plume frontal zone. Mar Ecol Prog Ser 237:257–269

Peebles EB, Hall JR, Tolley SG (1996) Egg production by the bay anchovy *Anchoa mitchilli* in relation to adult and larval prey fields. Mar Ecol Prog Ser 131:61–73

Pritchard DW (1956) The dynamic structure of a coastal plain estuary. J Mar Res 15:33–42

Purcell JE, Nemazie DA, Dorsey SE, Houde ED, Gamble JC (1994) Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Mar Ecol Prog Ser 114:47–58

Rilling GC, Houde ED (1999a) Regional and temporal variability in distribution and abundance of bay anchovy (*Anchoa mitchilli*) eggs, larvae, and adult biomass in the Chesapeake Bay. Estuaries 22:1096–1109

Rilling GC, Houde ED (1999b) Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay. Fish Bull 97:555–569

Roman MR, Holliday DV, Sanford LP (2001) Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. Mar Ecol Prog Ser 213:215–227

Roman MR, Brandt SB, Houde ED, Pierson JJ (2019) Interactive effects of hypoxia and temperature on coastal pelagic zooplankton and fish. Front Mar Sci 6:139

Sakagawa GT, Kimura M (1976) Growth of laboratory-reared northern anchovy, *Engraulis mordax*, from southern California. Fish Bull 74:271–279

Schwartzlose R, Alheit J (1999) Worldwide large-scale fluctuations of sardine and anchovy populations. Afr J Mar Sci 21:289–347

Secor DH, Dean JM, Laban EH (1991) Manual for otolith removal and preparation for microstructural examination. Baruch Institute Tech Rep 91-1. University of South Carolina, Columbia, SC

Takasuka A, Aoki I, Mitani I (2003) Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. Mar Ecol Prog Ser 252:223–238

Takasuka A, Aoki I, Oozeki Y (2007) Predator-specific growth-selective predation on larval Japanese anchovy *Engraulis japonicus.* Mar Ecol Prog Ser 350:99–107

Theilacker GH (1980) Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish Bull 78: 685–692

Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC Press, New York, NY

Zastrow CE, Houde ED, Morin LG (1991) Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy *Anchoa mitchilli* in mid-Chesapeake Bay. Mar Ecol Prog Ser 73:161–171

Zenitani H, Kono N, Tsukamoto Y, Masuda R (2009) Effects of temperature, food availability, and body size on daily growth rate of Japanese anchovy *Engraulis japonicus* larvae in Hiuchi-nada. Fish Sci 75:1177–1188

Zweifel JR, Lasker R (1976) Prehatch and posthatch growth of fishes – a general model. Fish Bull 74:609–621

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