

ABSTRACT

Title of Thesis: INTERANNUAL AND REGIONAL PATTERNS OF
ABUNDANCE, GROWTH, AND FEEDING
ECOLOGY OF LARVAL BAY ANCHOVY
(*ANCHOA MITCHILLI*) IN CHESAPEAKE BAY.

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Patterns in abundance, growth, and feeding by larval bay anchovy were examined in Chesapeake Bay from 1995-1999 to evaluate factors that contribute to variable recruitments of this abundant fish. The patterns were examined in relation to environmental factors, including hydrography and distributions of prey (zooplankton) and a probable predator (ctenophore). Larval abundances, sizes, feeding incidences, and growth rates varied annually and regionally. Averaged over five years, mean abundances in July decreased by almost two orders of magnitude from the mouth ($38.1/\text{m}^2$) to the head ($0.6/\text{m}^2$) of the Bay, along a declining salinity gradient. Yearly survey, bay-wide mean abundance varied nearly 10-fold; it was highest in 1998

(42.7/m²) and lowest in 1996 (4.6/m²). Feeding incidence was highest in 1998 (23%) and lowest in 1996 (9%), and varied regionally from 27% in the upper Bay to 13% in the mid Bay. Larvae fed predominantly during daylight. The most common prey ingested were copepod eggs and various life stages of calanoid copepods (primarily *Acartia tonsa*). Growth rates of larvae also differed annually and regionally. Mean growth rate was highest in 1998 (0.81 mm/d) and lowest in 1999 (0.68 mm/d), and varied regionally from 0.83 mm/d in the upper Bay to 0.71 mm/d in the mid Bay. Zooplankton concentration was positively correlated with larval feeding incidence ($r = +0.66$) and growth rate ($r = +0.72$). Larval feeding incidence was strongly correlated ($r = +0.93$) and summer larval abundance significantly correlated ($r = +0.86$) with fall recruitment of young-of-the-year bay anchovy.

INTERANNUAL AND REGIONAL PATTERNS OF ABUNDANCE, GROWTH,
AND FEEDING ECOLOGY OF LARVAL BAY ANCHOVY (*ANCHOA*
MITCHILLI) IN CHESAPEAKE BAY.

by

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DEDICATION

To my grandfather Lt. Col. Charles D. Thibault (“Poppy”):
the best fishing buddy a boy could have

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INTRODUCTION

Variability in survival of larval fish is believed to play an important role in determining subsequent recruitment success (Hjort, 1914; Houde, 1997a). The process is especially important in the Chesapeake Bay, which is an important nursery for many coastal and anadromous fishes (Murdy et al., 1997). Within this complex ecosystem, the abundant bay anchovy (*Anchoa mitchilli*) plays particularly important roles as both a major predator on plankton and a primary source of food for larger piscivores (Houde and Zastrow, 1991). Accordingly, the objective of my research was to analyze and determine the variability in levels of abundance, size distribution, growth, and feeding ecology of larval bay anchovy in Chesapeake Bay.

TIES Project

All samples in my study were collected by the multidisciplinary Trophic Interactions in Estuarine Systems (TIES) project. TIES was a 6-year (1995-2000) project supported by the National Science Foundation's (NSF) Land Margin Ecosystem Research (LMER) Program. The TIES project investigated factors influencing the dynamics and production of the various trophic groups within the Chesapeake Bay ecosystem. Research hypotheses addressed both long-term and large-scale (annual and interannual periods; whole bay) and short-term and smaller-scale (seasonal periods; regions and finer spatial scales) features of production.

Chesapeake Bay

The Chesapeake Bay is the largest estuary in the United States, with a surface area of more than 11,000 km² (Murdy et al., 1997). It drains approximately 175,000 km² from six states, 50% of which is delivered by the Susquehanna River at the head of the bay (Murdy et al., 1997). Despite its large size, the Chesapeake Bay is relatively shallow: ~50% is less than 6 m deep (Murdy et al., 1997). It is a partially mixed estuary with a two-layered flow: freshwater flows seaward on the surface, while saltwater moves up the bay along the bottom (Pritchard, 1956; Goodrich and Blumberg, 1991). Vertical stratification, in conjunction with phytoplankton blooms induced by high allochthonous nutrient input, can cause dissolved oxygen concentrations to decline below 50% saturation below the pycnocline in much of the mesohaline Chesapeake Bay during the summer (Breitburg et al., 1994). Salinities in the Chesapeake Bay range from 32 psu near its mouth to <0.5 psu at the head, and vary both seasonally and annually due to changes in freshwater flow and precipitation (Murdy et al., 1997). The surface water temperature in the bay also fluctuates widely, ranging from 1-4°C in late winter to 28-30°C in late summer (Murdy et al., 1997).

Importance of the Larval Stage

The larval stage of fishes is critical to cohort recruitment success, and also can represent a vital trophic link between planktonic and piscivorous organisms. Survival of larvae and variability in survival rates, often attributed to predation or nutritional causes, can influence the eventual recruitment success of fish year classes. For example, predation may select for higher growth rates and larger larval sizes that could

significantly influence stage-specific survival of cohorts (Meekan and Fortier, 1996; Houde, 1997a), thus controlling potential for recruitment success. Water temperature and prey availability during the larval stage also may have a strong influence on recruitment potential (Houde, 1989; Houde and Zastrow, 1993). Rutherford et al. (1997) showed that larval mortality rates of striped bass (*Morone saxatilis*) in the Potomac River were strongly related to temperature effects, while Secor and Houde (1995) came to a similar conclusion for larval striped bass in the Patuxent River. Limburg et al. (1999) found that both water temperature and zooplankton prey availability during the larval stage significantly influenced white perch (*Morone americana*) recruitment in the Hudson River. Cohort recruitment has also been shown to be enhanced in high-latitude seas if spawning is timed so that larvae develop in concert with plankton stocks when they are at their maximum seasonal abundances (Cushing, 1975; Pope et al., 1994). In a Chesapeake Bay tributary, Rutherford et al. (1997) found significant correlations between larval striped bass growth, mortality, and abundance and subsequent Maryland juvenile recruitment indices, indicating a strong relationship between larval success and recruitment.

Fish larvae sometimes play a key role in the trophic structure of their communities. For example, Young and Davis (1990) found that southern bluefin tuna (*Thunnus maccoyii*) larvae significantly reduced the abundance of the microzooplankton on which they fed. Various studies (Hunter and Kimbrell, 1980; Mills and Forney, 1983) have also shown that fish larvae can be a significant prey source for larger piscivorous fish. van Densen and Vijverberg (1982) presented convincing evidence that adult smelt (*Osmerus eperlanus*) and European perch (*Perca fluviatilis*) growth rates declined as

Daphnia mean sizes decreased due to heavy predation on *Daphnia* by abundant larval fish. However, for abundant, planktivorous species such as bay anchovy, perhaps the most critical link between larvae and higher trophic levels is their role as forage for larger piscivorous predators.

Larval Feeding

Larval foraging behavior and prey selectivity are crucial concepts required to understand the dynamics and consequences of larval feeding. Hjort (1914) put forth the hypothesis of a critical period that exists during early larval development. He believed that during the brief time when larvae consume their yolk reserves and then must begin exogenous feeding, they are most susceptible to starvation mortality. Hjort believed that mortality in the earliest larval stage may exert the greatest influence over future recruitment. Cushing (1972) expanded on this idea by introducing his match-mismatch hypothesis, suggesting that a single period was not as critical as having sufficient overlap in space and time between larval and prey production. In addition, Lasker (1978) proposed his stable ocean hypothesis, which suggested that water column stability directly influenced the patchiness and availability of prey items for recently spawned fish larvae. Although appealing and meritorious, none of these hypotheses has been consistently supported for larval fish in general (Leggett and Deblois, 1994).

An important determinant of larval survival is the time until first feeding. Blaxter and Hempel (1963) introduced the “point-of-no-return” concept, which refers to the duration of time before first feeding when 50% of larvae can survive if provided with food thereafter. This concept implies that prey items are aggregated in patches, and that

the probability of larvae encountering a prey item is important in ensuring that larvae feed before reaching the point-of-no-return. Environmental factors, for example temperature, are also critical in determining how quickly the yolk-sac is absorbed, and thus the time before the point-of-no-return is reached (Miller et al., 1988). Assimilation efficiencies of fish larvae decline with increases in temperature, requiring that larvae of fishes that live in warmer temperatures (28°C) ingest two to four times as much energy as those inhabiting cooler (10°C) ecosystems (Houde and Zastrow, 1993). Houde (1989) argued that subtle changes in average environmental conditions such as temperature could have a greater long-term effect on larval growth and mortality than episodic events, and thus contribute more to variable recruitments.

Fish larvae exhibit size selectivity in their feeding behavior based on the relative sizes of their mouth gapes to prey items (Shirota, 1970; Hunter, 1981). Often, intermediate prey sizes are preferred (Gerking, 1994), allowing larvae to experience large energy gains while still being able to handle the prey items expediently. The existence of prey selection has been demonstrated for larvae of many fish species. Shirota (1970) correlated the gape size of 33 marine and freshwater larval fishes with larval growth rates and available prey sizes. Hunter (1981) and Shirota (1970) found that the size spectrum of ingested prey items increases as larval size increases. Munk (1992) also found strong evidence to this effect in larval herring (*Clupea harengus*). Houde (1997a) suggested that, by progressively including larger, rarer prey items into their diets while still ingesting smaller, less rare items, growing larvae will increase their encounter rates with suitable prey. Houde reasoned, "If larvae exercise strong selection for large prey but neutral or only weak negative selection for smaller prey, the continued inclusion of

smaller prey may assure attainment of a minimum ration as well as increasing or stabilizing G (growth rate) during early life."

Larval Bay Anchovy

The bay anchovy is the most abundant fish species in the Chesapeake Bay (Hildebrand and Schroeder, 1928; Murdy et al., 1997; Jung, 2002), and is a vital link between plankton and piscivores within the complex trophic structure of this estuarine system (Baird and Ulanowicz, 1989; Houde and Zastrow, 1991; Luo and Brandt, 1993; Hagy, 2002). Although not commercially exploited, it may constitute a major portion of the diets of such commercially important piscivores as bluefish (*Pomatomus saltatrix*), striped bass, and weakfish (*Cynoscion regalis*) (Hartman and Brandt, 1995; Buckel and Conover, 1997; Buckel, Fogarty, and Conover, 1999; Buckel et al., 1999).

Bay anchovy in the Chesapeake Bay may live to age 3+ (Wang, 1992; Newberger and Houde, 1995). Individuals become sexually mature 10-12 months after hatching, which corresponds to a fork length of approximately 40-mm (Zastrow et al., 1991). Luo and Musick (1991) reported that bay anchovy hatched in the lower (seaward) part of the Chesapeake Bay early in the spawning season may reach sexual maturity at 80 days of age, and possibly participate in late-season spawning activity during the same year. Bay anchovy is a pelagic serial spawner (Luo and Musick, 1991; Zastrow et al., 1991), producing eggs in Chesapeake Bay primarily between May and September (Dovel, 1971; Olney, 1983; Houde and Zastrow, 1991). Highest spawning activity normally occurs during July (Dalton, 1987). Although spawning occurs throughout the Bay, peak

spawning occurs in the seaward, lower portion (Rilling and Houde, 1999a; Chesapeake Bay LMER Program, 2002).

Larval bay anchovy hatch at 1.8-2.7 mm in length (Fahay, 1983), and are yolk-sac larvae for approximately 24 h (Houde and Zastrow, 1991). In Chesapeake Bay, larvae may occur at temperatures from 15-30°C (Houde and Zastrow, 1991), and can be found over a wide range of salinities from 0.0-31.9 ppt (Dovel, 1971; Olney, 1983). However, they are limited in distribution by dissolved oxygen (DO) concentrations. Although laboratory studies have indicated that some bay anchovy yolk-sac larvae can survive at DO concentrations as low as 1.0 mgL⁻¹ (Chesney and Houde, 1989), 3.0 mgL⁻¹ is generally required for larval survival and growth (Houde and Zastrow, 1991). This could explain the finding of MacGregor and Houde (1996) that “larval bay anchovy were less abundant below the pycnocline than above it” on a single transect surveyed repeatedly across the deep channel of mid-Chesapeake Bay during summer 1987. Rilling and Houde (1999a) in bay-wide surveys found “no significant differences in mean abundances of bay anchovy larvae above or below the pycnocline” in June and July 1993.

Larval bay anchovy abundances and size-frequency distributions can vary considerably on both temporal and regional scales. Olney (1983) found that larval bay anchovy mean concentrations during peak periods in the lower Chesapeake Bay ranged from 1,098-2,403 larvae per 100-m³ from 1971-1973. Regional and local differences in larval abundance also have been documented in the Chesapeake Bay (Dorsey et al., 1996; MacGregor and Houde, 1996; Rilling and Houde, 1999a). In addition, M/G ratios (M = instantaneous daily mortality rate; G = weight-specific growth rate) for bay anchovy larvae, an indicator of stage-specific productivity, were found to fluctuate both regionally

(Rilling and Houde, 1999b) and in an offshore-onshore direction (MacGregor and Houde, 1996), as well as on a monthly basis (Rilling and Houde, 1999b), throughout the Chesapeake Bay.

Larval Bay Anchovy Feeding

Larval bay anchovy is a particulate forager that feeds on a wide variety of prey items ranging from phytoplankton to large zooplankton. In laboratory experiments, Houde (1974) found that larvae at 26°C water temperatures began feeding within 2.5 days of hatching. Arthur (1976) reported that northern anchovy (*Engraulis mordax*) larvae collected from the California Current fed almost exclusively during the day. Young bay anchovy larvae may feed on copepod nauplii, tintinnids, rotifers, algae, and detritus (Detwyler and Houde, 1970; Houde and Lovdal, 1984). In laboratory experiments, Detwyler and Houde (1970) found that older larvae fed on large copepodites and adult copepods. Field studies in Biscayne Bay, Florida revealed that copepods comprised 71% of bay anchovy larval diets by number, followed by mollusc veliger larvae (18%) (Houde and Lovdal, 1984). In a feeding study on European anchovy (*Engraulis encrasicolus*) larvae in the Bay of Biscay, Plounevez and Champalbert (1999) found that composition of the zooplankton community was a significant factor influencing feeding activity, whereas zooplankton abundance was not. Houde and Lovdal (1984) reported a positive correlation between copepod nauplii abundances and mean densities of various fish larvae found in Biscayne Bay, Florida. There were no reports on feeding, food preferences or ontogeny of feeding by larval bay anchovy in Chesapeake Bay.

Objectives

Four objectives were adopted to investigate patterns of abundance, size distribution, growth, and feeding ecology of larval bay anchovy in Chesapeake Bay:

1. Map and compare summer bay anchovy egg and larval abundances and size distributions bay-wide, across three regions of Chesapeake Bay, and above and below the pycnocline from 1995-1999.
2. Estimate and compare feeding and prey selection by bay anchovy larvae over annual, regional, and diel scales.
3. Estimate ages and sizes-at-age, and compare growth rates of bay anchovy larvae over regional, annual, and above-below-pycnocline scales.
4. Determine relationships between biotic (zooplankton concentration, chlorophyll a biomass, and jellyfish biovolume) and abiotic (freshwater inflow, temperature, salinity, and dissolved oxygen) environmental factors with respect to bay anchovy egg abundance and density, and larval anchovy abundance, density, feeding, and population age/size structures, and young-of-year (YOY) recruitment.

METHODS

Ichthyoplankton, zooplankton, and environmental data were collected at stations throughout Chesapeake Bay during the summers of 1995-1999. Larval bay anchovy were identified, enumerated, and measured to develop a database on abundance and size distributions. Bay anchovy eggs, zooplankton, and jellyfish (the ctenophore *Mnemiopsis leidyi*) were identified and enumerated to determine abundances, densities (concentrations), and biovolumes respectively. The sagittal otoliths from selected bay anchovy larvae were analyzed to estimate ages and growth rates and to compare them among years, regions, and depth-layers. The stomachs of 1,485 larvae were dissected and the contents analyzed to investigate larval feeding ecology and prey selectivity. The relationships between bay anchovy egg abundance and density, larval abundance, density, size distribution, feeding, and growth, with respect to biotic and abiotic environmental variables were examined in correlation and multiple regression analyses.

Collections

Ichthyoplankton and environmental data were collected during five summer surveys throughout Chesapeake Bay (Appendices 1-5):

1995: 23-29 July,

1996: 17-22 July,

1997: 11-15 and 22-23 July,

1998: 6-12 August,

1999: 26-30 June.

Only the summer TIES research cruises were included in my analyses because few, or no, larvae were collected in the spring (April-May) and fall (October) cruises. Samples were obtained from the mouth ($36^{\circ} 58' \text{ N}$) to the head ($39^{\circ} 25' \text{ N}$) of the Bay on 10-15 transects (2-6 stations per transect), with each transect separated by 10-20 nautical miles (Figure 1). Forty-four stations were sampled in 1995, 27 in 1996, 39 in 1997, 37 in 1998, and 33 in 1999. Additional samples were obtained at 10 stations along the Bay-channel axis during the 1998 cruise for an above-at-below-pycnocline feeding comparison (Figure 2 and Appendix 6), and at 15 stations (latitude $37^{\circ} 44' \text{ N}$) from 30 July-1 August 2000 for a diel feeding comparison (Figure 2 and Appendix 7). For regional comparisons, the three designated Bay regions were $39^{\circ} 25' \text{ N} - 38^{\circ} 45' \text{ N}$ (upper-Bay), $38^{\circ} 45' \text{ N} - 37^{\circ} 55' \text{ N}$ (mid-Bay), and $37^{\circ} 55' \text{ N} - 36^{\circ} 58' \text{ N}$ (lower-Bay). Interannual comparisons were based on mean values of variables estimated from the bay-wide cruise conducted during summer in each year.

At each station prior to ichthyoplankton sampling, a CTD cast was made to determine the temperature, salinity, dissolved oxygen (DO), and chlorophyll a (indexed by fluorescence) profile of the water column. Measurements of each variable were obtained at 1-m depth intervals (0.5-m depth intervals in 1997) throughout the water column at each station. The average of these values was used to compute the station water-column mean for each variable. Individual station water-column means within each bay region were averaged to compute a mean regional value for each variable (Appendices 8-11). In addition, mean values at 3-m depth are shown for temperature (Appendix 8) and salinity (Appendix 9), mean values at 3-m depth and below the pycnocline are given for DO (Appendix 10), and mean values at 3-m depth and above the

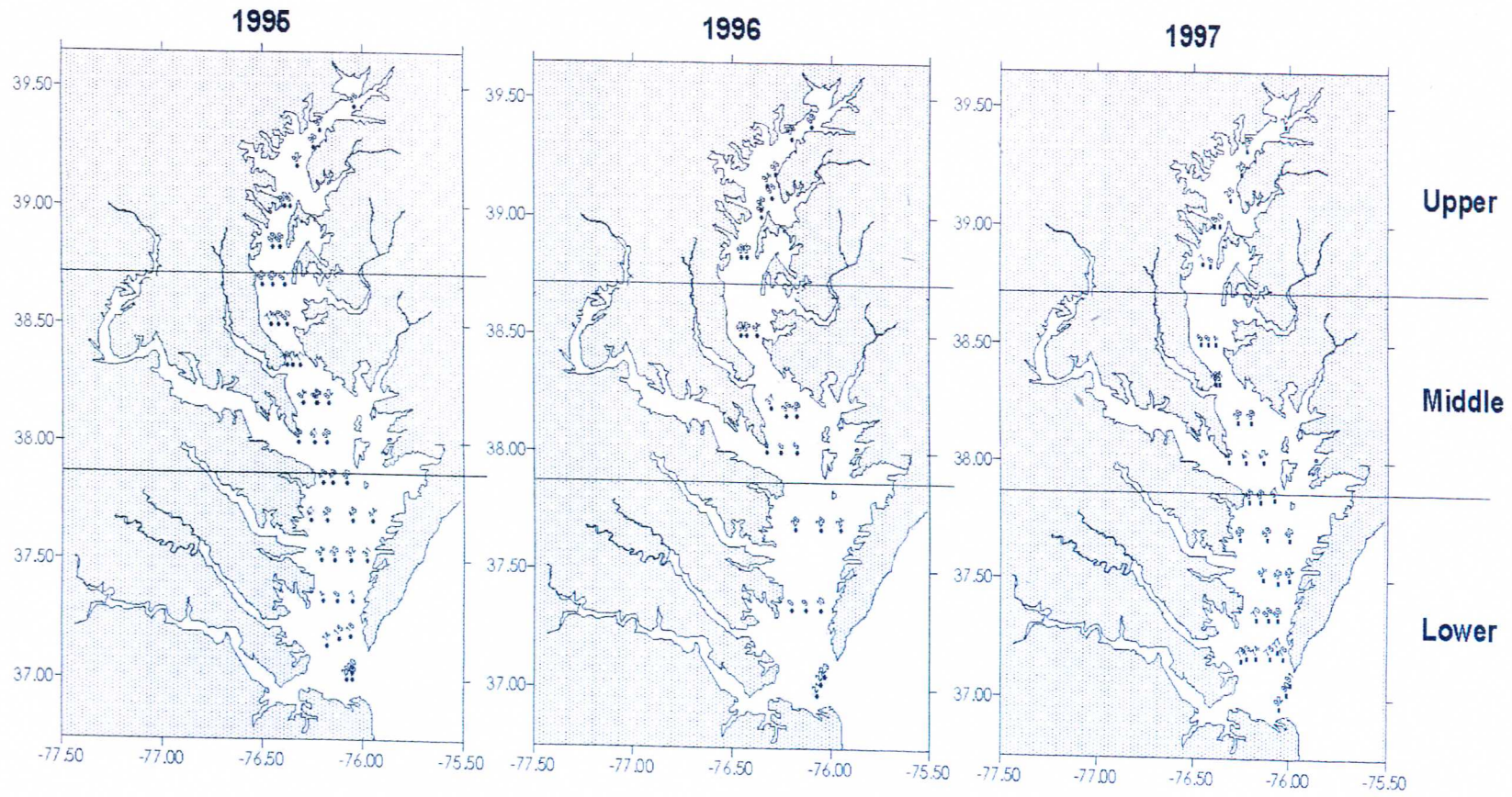


Figure 1. Station numbers, sites, and bay regions (upper, middle, and lower bay) sampled in Chesapeake Bay from 1995-1999. Station locations and sampling information are listed in Appendices 1-5. Latitudes and longitudes are reported as degrees and decimal fractions of degrees.

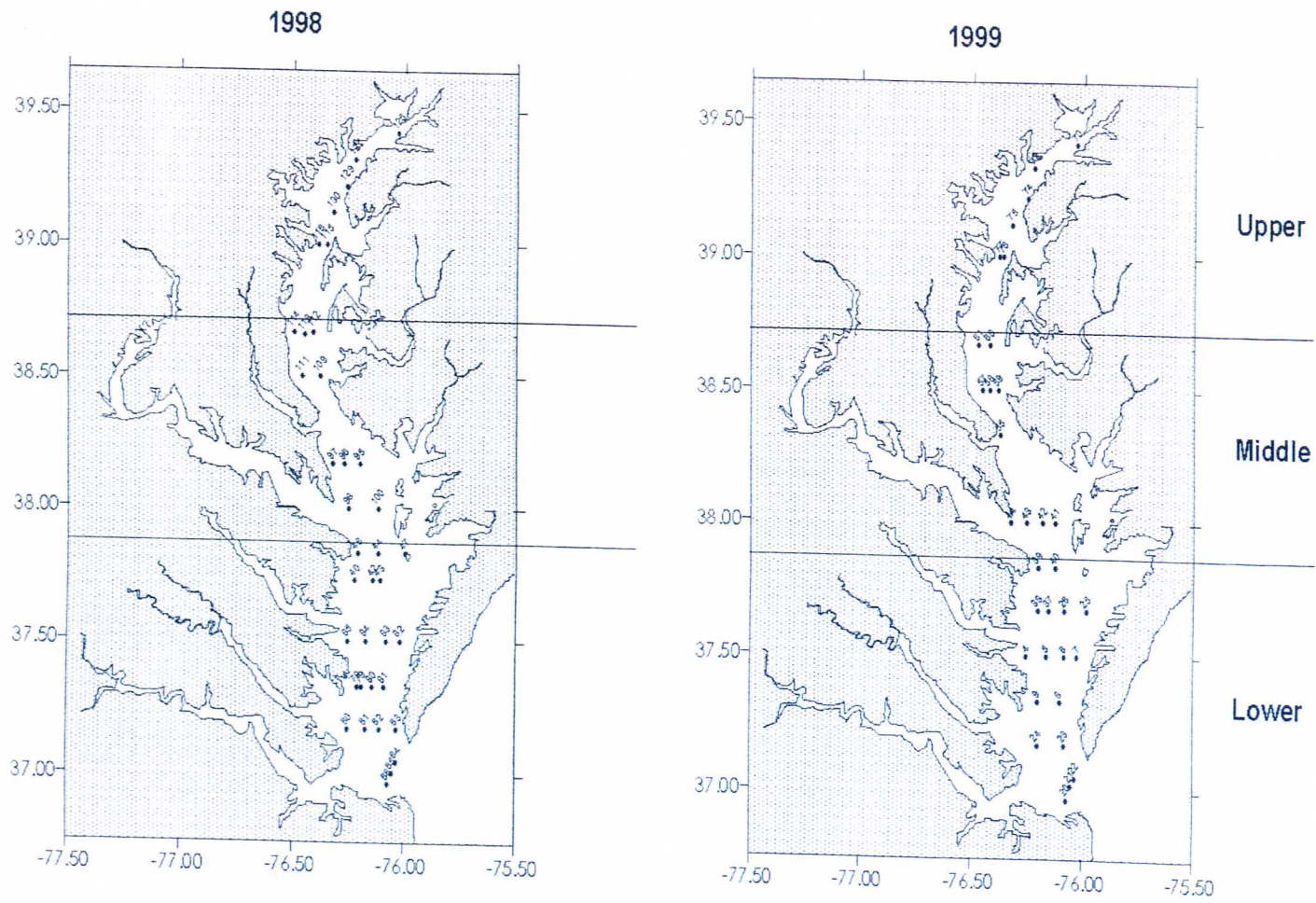


Figure 1 (cont'd)

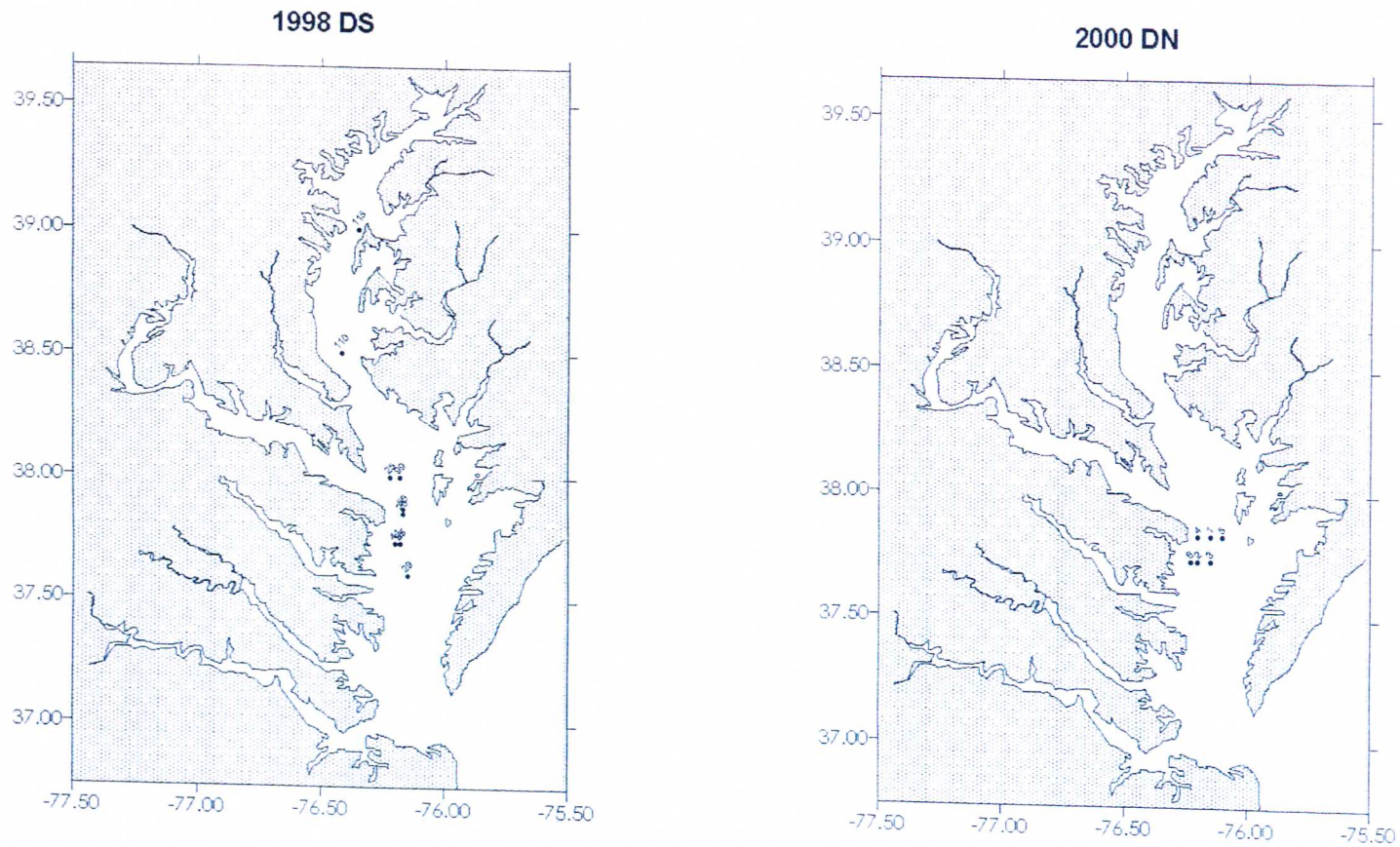


Figure 2. Station numbers and sites sampled in Chesapeake Bay for the 1998 depth-stratified (1998 DS) and 2000 day/night (2000 DN) larval bay anchovy feeding analyses. For the 2000 DN map, numbers on map correspond to the following stations: 1 = 85, 93, 114; 2 = 86, 100, 108; 3 = 87, 101, 107; 4 = 92, 113; 5 = 94, 115; 6 = 99, 109. Station information is listed in Appendices 6 and 7. Latitudes and longitudes are reported as degrees and decimal fractions of degrees.

pycnocline are tabulated for fluorescence (Appendix 11). Analysis of variance (ANOVA) followed by a Tukey's multiple range test was used to determine potential significant differences in each variable between regions.

At 1-2 stations (closest to the channel) per transect, zooplankton samples were collected in 10-liter Niskin bottles attached to the CTD rosette. These samples were obtained at three depths: near-bottom, mid-depth, and near-surface. Once on deck, zooplankton samples were filtered on a 35- μm sieve and preserved in 5% formalin for future laboratory analysis. No zooplankton samples were collected from Niskin bottles in 1995.

Ichthyoplankton and gelatinous zooplankton were 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 minutes at a vessel speed of 1-2 knots. A temperature-depth recorder and flow meters were placed in the nets during each tow to determine temperature, depth, and volume of water filtered by each net. The mean water volume filtered by each net was 118 m^3 (SE = 3.06). The Tucker-trawl samples were preserved in ethanol, which was replaced with fresh ethanol within 48 hours to ensure proper preservation of the samples for future laboratory analysis. Ctenophores from the Tucker-trawl samples were counted and measured on the deck of the research vessel immediately after collection. The biovolumes of all ctenophores collected were measured in a graduated cylinder.

Larvae Identification, Measurements, and Length-frequency Distributions

Fish eggs and larvae were removed and identified from 405 Tucker-trawl samples: 86 samples from 1995 collections, 48 from 1996, 76 from 1997, 102 from 1998 (72 usual samples plus 30 for above-at-below-pycnocline feeding analysis), 63 from 1999, and 30 from 2000 (day/night samples). The identified larvae were the basis for estimation of larval bay anchovy abundances and size distributions. The samples also provided individuals for stomach and otolith (aging) analyses.

Samples with many bay anchovy eggs or larvae were routinely aliquoted using a Folsom plankton splitter. A randomly chosen subsample was then examined to remove all eggs and larvae. If there were fewer than 100 bay anchovy eggs or larvae, then all of the eggs or larvae (or both, if neither met the minimum criteria of 100 individuals found) from subsequent subsamples were removed until either the criteria were met or the total sample had been completely sorted. Regardless of the number of aliquots, all bay anchovy larvae >16 mm were removed from samples because of their relative scarcity.

Bay anchovy larvae removed from each sample were subsequently measured to the nearest 0.1 mm total length (TL) using image analysis software. Theilacker (1980) and Leak (1986) found that anchovy larvae experienced size-dependent shrinkage during capture, handling, and preservation, with smaller larvae experiencing greater relative shrinkage than larger larvae. The lengths of all measured larvae were adjusted according to the following formula (Theilacker, 1980):

$$\log_e L = \log_e X + 0.289 * e^{-0.434 * X * 10^{-0.68}}$$

where L = adjusted larval length (mm);

X = measured larval length (mm);

T = mean net-tow duration and handling time (10 minutes).

As T increases, expected shrinkage increases. For samples with many larvae, the greater of 50 larvae or 20% of the total larvae in the sample were measured. Measured larvae <25.5 mm were separated into 1-mm size classes. For large samples, the total number of larvae in each size class was estimated by dividing the number of measured larvae in each size class in the subsample by the proportion of the subsampled larvae that the size class represented.

Annual bay-wide, regional, and above-below-pycnocline (both regionally and bay-wide for each year) mean larval lengths were estimated from the weighted mean (according to larval abundance) length at each station -- bay-wide, regionally, as well as above and below the pycnocline regionally and bay-wide for each year. Total regional and above-below-pycnocline mean larval lengths were estimated from the weighted mean of the mean regional and above-below-pycnocline lengths for each year. ANOVA followed by a Tukey's multiple range test was used to test for regional and above-below-pycnocline differences in mean length within each sampled year. Annual bay-wide and regional length-frequency distributions were developed from the relative frequency of larvae in each size class across the bay-wide and regional scales. A Kolmogorov-Smirnov goodness-of-fit test (Sokal and Rohlf, 1969) was used to test for differences in the length-frequency distributions between regions in each year. In addition, a visual analysis was performed to determine potential multimodality in the length-frequency distributions.

Egg and Larval Abundance

MacGregor and Houde (1996) found that up to 2.5 times more bay anchovy larvae in small length classes occurred in 53- μm tows than in paired 60-cm, 280- μm Bongo-net tows, due to the extrusion of smaller larvae through meshes of the 280- μm net. The abundance ratio of 53:280- μm catches was >1 for larvae <5.5 mm, based on MacGregor and Houde's (1996) predictive equation:

$$R = 2.958 - 0.342 * L$$

where R = ratio of 53:280- μm larval abundances;

L = larval standard length (mm).

Larval abundances of each 1-mm size class <5.5 mm were multiplied by R to correct for extrusion. Although larval length was measured as total length, the difference between larval bay anchovy standard and total lengths at sizes <5.5 mm is less than the measurement error accepted by this study.

Bay anchovy larvae <25.5 mm that were collected in the Tucker-trawl samples were used to estimate larval abundances. Egg and larval abundances for each sample were calculated according to the following equation:

$$A = (N * D) / V$$

where A = abundance (number of eggs or larvae under 1 m^2);

N = number of eggs or larvae collected per net tow;

D = tow-depth range (m);

V = volume (m^3) of water filtered by tow (determined from the flowmeter).

The total water-column abundance at each station was estimated from:

$$A_{\text{station}} = A_{\text{tow 1}} + A_{\text{tow 2}}$$

where $A_{\text{tow 1}}$ = abundance in tow above the pycnocline;

$A_{\text{tow 2}}$ = abundance in tow below the pycnocline.

Weighted mean water-column densities of eggs and larvae were estimated from:

$$D_{\text{station}} = \frac{(D_{\text{above}} * d_{\text{above}}) + (D_{\text{below}} * d_{\text{below}})}{(d_{\text{above}} + d_{\text{below}})}$$

where $D = N/V$ = density of eggs or larvae (m^{-3}) in a sample;

d = depth range (m) represented by sample.

Annual mean abundance and density was defined as the grand mean of all station abundances or densities within each year. Regional mean abundance and density was defined as the mean of all station abundances or densities within each region. Above-below-pycnocline mean abundances and densities were defined as the means of all above- or below-pycnocline abundances or densities in each region or year. Total regional and above-below-pycnocline mean abundance and density was defined as the mean of the mean regional and above-below-pycnocline abundances or densities for each year.

Before statistical testing, abundance and density estimates were \log_e -transformed, which satisfied the assumption of homogeneity of variances in most instances. The quantity 0.1 was added to all abundances and densities prior to \log_e -transformation to account for zero abundance or density values in the data set. ANOVA followed by a Tukey's multiple range test was applied to test for significant differences among years, regions, and depths.

Zooplankton

Zooplankton was analyzed from 149 Niskin-bottle samples: 21 from 1996, 42 from 1997, 39 from 1998, and 47 from 1999. No 10-L Niskin-bottle samples were collected in 1995. Taxa that were identified are listed in Table 1.

Prior to analysis, each 10-L Niskin-bottle zooplankton sample was filtered onto a 35- μm sieve and then normalized to 200 ml, then halved to 100 ml. Four series of five, 5-ml aliquots (20 5-ml aliquots total) were extracted for enumeration using a calibrated Hensen-Stimpel pipette. Aliquots were examined until either 300 organisms were counted or at least 25% of the normalized sample (50 ml) was sorted, whichever resulted in the enumeration of the greatest number of organisms. Zooplankton counts were multiplied by $200/x$, where x = total sorted volume (ml), then divided by 10 to convert to density (L^{-1}).

For zooplankton density analyses, organisms were categorized as total zooplankton, copepods (adults, copepodites, and nauplii), and copepod nauplii. The mean water-column density at each station was estimated as the weighted mean density of the three depth samples (above, at, and below the pycnocline):

$$D_{\text{station}} = \frac{(D_{\text{above}} * d_{\text{above}}) + (D_{\text{at}} * d_{\text{at}}) + (D_{\text{below}} * d_{\text{below}})}{(d_{\text{above}} + d_{\text{at}} + d_{\text{below}})}$$

where D = density of zooplankton (L^{-1});

d = depth range (m) represented by sample.

Annual mean zooplankton density was defined as the mean of all station densities within each year. Regional mean density was defined as the mean of all station densities within each region. Above-below-pycnocline mean density was defined as the mean of

Table 1. List of zooplankton taxa identified from 10-L Niskin-bottle samples taken from stations along the north-south axis of Chesapeake Bay during the summer TIES cruises from 1995-1999.

Tintinnids
Hydromedusae
Planula
Ctenophore Larvae
Trematodes
Nemerteans
Rotifers
Nematodes
Trochophores
Bivalve Veligers
Gastropod Veligers
Polychaetes: larvae, juveniles
Insecta Larvae
Cumaceans
Decapod Zoeae
Isopods
Ostracods
Mysids
Cladocerans
Barnacles: nauplii, cypris
Calanoid Copepods: *Acartia tonsa*, *Eurytemora sp.*, *Centropages sp.*, others
Cyclopoid Copepods: *Oithona sp.*, others
Harpacticoid Copepods
Chaetognaths
Bryozoans: phoronid larvae, others
Ascidians: eggs, larvae
Ophiuroidean Juveniles
Echinoderm Plutei
Salps
Larvaceans
Hemichordates
Invertebrate Eggs

all above- or below-pycnocline densities in each region or year. Before statistical testing, zooplankton density estimates were \log_e -transformed, which satisfied the assumption of homogeneity of variances in most instances. ANOVA followed by a Tukey's multiple range test was used to test for significant differences between years, regions, and depths.

For anchovy feeding preference analyses, zooplankton was divided into four categories: 1) copepod adults and copepodites, 2) copepod nauplii, 3) invertebrate eggs (comprising copepod eggs and unidentified invertebrate eggs), and 4) other (comprising the remaining zooplankton taxa). Taxa were aggregated to facilitate statistical comparisons with the limited number of prey taxa found in larval bay anchovy stomachs.

Age and Growth Analysis

The sagittal otoliths from 329 bay anchovy larvae were examined to determine ages and growth rates. A representative sample (~25) of larvae <25.5 mm were examined from each bay region in each year. Age was determined by counting daily growth increments (rings) that emanate from the center of the otolith (Pannella, 1971; Fives et al., 1986; Leak and Houde, 1987; Zastrow et al., 1991). Bay anchovy larvae begin to deposit daily growth rings 2 days after hatching (Leak and Houde, 1987). Therefore, age (in days) was estimated by adding 2 to the total number of otolith increments.

Selected larvae were measured to the nearest 0.1 mm TL using an image analysis system. 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 hours. Otolith preparation and analysis methods are those recommended by Secor et al. (1991). Otoliths

were examined under a compound light microscope at 400-1000x using Optimas analytical imaging software (Media Cybernetics, 1999). The increments on each otolith were counted at two different times, with the final age determination being the average of the two counts. A third count was conducted if the difference between the two age determinations was >20% of the lowest estimated age. When the average of the otolith counts resulted in a 0.5-day age class designation, the final age was randomly rounded to the nearest higher or lower 1-day age class.

Although a linear growth model fit the length-at-age data rather well for larvae <30 days of age, a Gompertz growth model explained more of the variability in the data for larvae at the lowest and highest ages. The Gompertz model has been used successfully to parameterize growth of clupeid larvae by Gaughan et al. (2001), Bolz and Burns (1996), and Zweifel and Lasker (1976), as well as for larval northern anchovy (*Engraulis mordax*) by Hunter (1976) and Sakagawa and Kimura (1976). Gompertz growth models were fit to the length-at-age data on regional and annual scales:

$$L_t = a * e^{-b * e^{c * t}}$$

where L_t = total length (mm) at age t ;

t = age (d) = otolith increment count + 2;

a = asymptotic larval length (mm);

b = constant determining growth rate at $t = 0$;

c = growth coefficient.

The parameters a , b , and c are constants that were determined through iteration.

Predicted age-specific growth rates were calculated for each daily age class from age 3 (post-hatch) to 30 days both bay-wide and regionally for each year. These growth rates

were estimated by taking the first derivative (slope) of the growth curve at each daily age class.

For statistical comparison, growth rates (mm/d) were estimated from the slopes of the linear regressions of total lengths (TL) on ages according to the following equation:

$$L_t = a + gt$$

where L_t = total length (mm) at age t ;

t = age (d);

g = growth rate (mm/d) and;

a = regression intercept; an estimate of TL (mm) at hatch.

Bolz and Burns (1996), who used a Gompertz model to describe larval Atlantic herring (*Clupea harengus*) growth, similarly fit a linear model to their size-at-age data before conducting statistical tests for slope (growth rate) differences. Only larvae <30 days of age were included in the linear regressions, because the few older larvae (1-6 per year) tended to cause a disproportionate negative effect on the slopes of the linear length-at-age regressions. Re (1996) found that growth of larval *Engraulis encrasicolus* in the Mira estuary in southwestern Portugal “was adequately described, up to an age of about 30 days, using linear regression analysis.” Analysis of covariance (ANCOVA) followed by a Student-Newman-Keuls multiple range test was applied to the growth data to detect significant differences in growth rates of <30-day-old larvae among years, regions, and bay-wide depths (i.e. above or below the pycnocline) within each year.

Larval Feeding

After measurement to the nearest 0.1 mm TL, larvae were randomly selected from the Tucker-trawl samples for stomach-content analyses. Larvae were selected from five size classes: 1.5-4.4 mm, 4.5-7.4 mm, 7.5-10.4 mm, 10.5-13.4 mm, and 13.5-16.4 mm. The stomachs of 1,485 larvae were analyzed: 205 from 1995, 113 from 1996, 224 from 1997, 300 from 1998, and 281 from 1999. Also included were 156 larvae from 1998 above-at-below-pycnocline samples and 206 larvae from 2000 day/night samples. To the extent possible, larvae from each year's collections were selected according to the following sampling plan: 1) 10 larvae from each size class above and below the pycnocline (50 above and 50 below the pycnocline), 2) from each bay region (100 per region), and 3) from each cruise (300 per cruise). For the specially-collected year 1998 above-at-below-pycnocline samples, approximately 10 larvae from each size class above, at, and below the pycnocline were analyzed (50 above, 50 at, and 50 below the pycnocline). For the specially-collected year 2000 day/night samples, a representative subsample from each size class comprised the ~100 larvae analyzed from both day and night samples (100 day and 100 night) to determine if there were differences in diurnal feeding behavior.

Larvae for stomach analysis were examined under a dissecting microscope. The contents of the entire alimentary canal were manually removed using sharpened pins as dissecting tools. Prey were identified to the lowest taxonomic level possible, then measured using a calibrated, ocular micrometer. Ingested prey items are listed in Table 2. Invertebrate eggs that were found in guts containing an adult copepod were not

Table 2. List of prey items identified from larval bay anchovy stomach analyses during the 1995-2000 feeding study in Chesapeake Bay. Copepods in various life-stages (e. g., adult, copepodite, and nauplius) were consumed by bay anchovy larvae.

Calanoid Copepods:

Acartia tonsa
Eurytemora affinis
Labidocera aestiva
Paracalanus parvus
Pseudodiaptomus coronatus
Temora longicornis
Unidentified

Cyclopoid Copepods

Harpacticoid Copepods

Copepod Eggs

Cladocerans:

Bosmina longirostris

Ostracods

Amphipods

Barnacle Nauplii

Unidentified Planula

Polychaete Juveniles

Rotifers

Tintinnids

Diatoms

Unidentified Invertebrate Eggs

Unidentified Particles

counted. Also, the lengths of partly-digested pieces of prey were extrapolated based on identifiable characteristics to estimate the total length of the ingested prey item.

Feeding incidence (FI), defined as the proportion of larvae with at least one prey item in their gut, was calculated for individual size classes and for all larvae for four categories: regional, annual, above and below the pycnocline, and diel. Statistical comparisons were made by applying Chi-square tests of independence, testing the null hypothesis that FI was uniform within each of the four categories. The mean number of prey per gut (PPG) in feeding larvae also was calculated for individual size classes and for total larvae on an annual, regional, above and below the pycnocline, and diel basis. Total regional and above-below-pycnocline FI and PPG comparisons for the entire larval data set were made using the pooled feeding data. ANOVA followed by a Tukey's multiple range test was used to determine differences within the annual, regional, above and below the pycnocline, and diel categories. For the individual size class FI and PPG data, there were too few feeding larvae in each size class to conduct either Chi-square tests or ANOVA on the regional and above-below-pycnocline levels within each year. Therefore, I pooled the regional and above-below-pycnocline FI and PPG data for all years before conducting statistical tests on those categories.

Ingested prey types were classified into four categories to facilitate comparison of larval anchovy prey selection and preference. The categories were 1) copepod adults and copepodites, 2) copepod nauplii, 3) invertebrate eggs, and 4) other (comprising the remaining zooplankton taxa). Chi-square tests of independence were conducted to determine if larval prey selection varied with larval size, region, above-below-pycnocline, or year. In order to meet the minimum relative-frequency assumptions of the

Chi-square tests (e.g., absolute expected values cannot be <1, and not more than 20% of the absolute expected values may be <5), I was only able to statistically compare ingested prey types annually and between the annually-pooled regional and above-below-pycnocline data for the total larval data set. For the same reason, variability in prey selection between the five larval size classes could only be tested using the pooled data from all sampled years. Although not tested statistically, regional and above and below the pycnocline ingested prey frequencies are reported for each year.

Prey preference was determined using an index of relative prey preference (Chesson, 1978). This index was used to describe feeding preference of larval bay anchovy and other fish species in Biscayne Bay, Florida (Houde and Lovdal, 1984) and larval blue whiting (*Micromesistius poutassou*) along Porcupine Bank, west of Ireland (Hillgruber and Kloppmann, 1999). The numerical Chesson prey-preference index value α for each prey type i , which can range from 0 to 1, was calculated as:

$$\alpha_i = (r_i/p_i) / \left(\sum_1^m r_i/p_i \right)$$

where r_i = proportion of prey type i in the diet;

p_i = proportion of prey type i in the environment;

m = number of prey types.

Index values higher or lower than $1/m$ indicate preference for or against a prey type respectively, while a value equal to $1/m$ indicates no preference. Index values were calculated for each of the four prey categories (copepod copepodites and adults, copepod nauplii, invertebrate eggs, and other) bay-wide and regionally for each year. Statistical comparisons of α index values (Chesson, 1983) could not be conducted due to the small sample sizes and high proportion of index values at or near 0 or 1.

Size selection in larval feeding was analyzed using several methods. Mean prey length was calculated for each larval size class 1) bay-wide annually, and 2) regionally from the pooled data for all years for each region. ANOVA followed by Tukey's multiple range tests were used to test for significant differences in mean prey length among larval size classes within years and regions. The relationships between larval length and both prey length and relative prey length (prey length/larval length) also were examined in regression analyses.

Prior to analyses, prey length was \log_e -transformed and relative prey length was square root-transformed, which normalized the data and homogenized residual variances in most instances. An arcsine transformation was tested on the relative prey length data, but it neither normalized the data nor homogenized residual variances. The exponential model of the relationship between larval length and prey length provided a better fit than did the power model in which larval length also was \log_e -transformed. ANCOVA followed by Student-Newman-Keuls multiple range tests were applied to determine if there were significant differences in prey size selection among years and regions within each year.

Correlation and Multiple Regression Analyses

Correlation and step-wise multiple regression analyses were conducted to determine relationships between bay anchovy egg abundance and density, larval abundance, density, mean length, FI, PPG, and growth rate, with biotic variables, e.g. zooplankton, copepod, and copepod nauplii densities, chlorophyll a biomass (indexed by fluorescence), gelatinous predator (*M. leidy*) biovolume, and with abiotic environmental

variables, e.g. freshwater inflow, temperature, salinity, and DO. Bay anchovy egg abundance and density, larval abundance and density, *M. leidyi* biovolume, and zooplankton, copepod, and copepod nauplii densities were \log_e -transformed prior to inclusion in the correlation and multiple regression analyses. Regional mean values from each available year for each parameter (n = 11 to 15) were compared in the pair-wise correlation analyses. Pairs of variables were considered to be significantly correlated at the $\alpha=0.05$ level. Additionally, pair-wise correlation analyses were conducted using the annual, bay-wide means (n = 5) of biotic and environmental data, including mean March-May freshwater inflow into Chesapeake Bay (USGS, 2002), and the \log_e -transformed abundances of young-of-year (YOY) bay anchovy collected in October 1995-1999 (Jung, 2002) to determine the possible associations of these variables with bay anchovy recruitment in Chesapeake Bay.

Step-wise, multiple regression analyses were performed individually on six dependent variables: bay anchovy egg abundance, total larval bay anchovy abundance, mean larval length, FI, PPG, and larval growth rate. Independent variables included: bay anchovy egg, bay anchovy larval, zooplankton, copepod, and copepod nauplii densities, *M. leidyi* biovolume, fluorescence, temperature, salinity, DO, and the remaining potential dependent variables that were not designated as a dependent variable in each multiple regression. Bay anchovy egg and larval densities were not used in multiple regression analyses involving larval and egg abundances, respectively, because they were obviously highly correlated. Regional mean values from each available year for each variable (n = 11 to 15) were used in the analyses.

Prior to inclusion in multiple regression analyses, potential independent variables were examined in pair-wise correlation analyses. Pairs of independent variables were considered to be significantly correlated at the $\alpha=0.05$ level. If two or more variables were significantly correlated, then separate multiple regressions were run, each including only one of the correlated independent variables along with the remaining non-correlated variables.

The multiple regression analyses were run using JMP Version 4 statistical software (SAS Institute Inc., 2000). Regressors (independent variables) that had the highest probability of improving the fit of the model were sequentially added to the model (forward selection), until Mallows' C_p value (an alternate measure of total squared error) first approached the number of independent variables in the regression (Mallows 1973). Mallows (1973) suggests that this provides the optimal balance between minimizing the number of regressors and maximizing the R^2 value for the multiple regression equation. The resulting multiple regression equation was used to identify the combination of predictor variables that most influenced the value of the dependent variable. The best fit multiple regression equation for each of the six dependent variables was reported only if it was significant at the $\alpha=0.05$ level.

RESULTS

Hydrography

Environmental variables including water temperature, salinity, dissolved oxygen (DO), and chlorophyll a (indexed by fluorescence) varied throughout Chesapeake Bay in each year of the study, as well as regionally, and across depth-layers during the surveys. MWC temperatures were similar among regions in 1995-1997, but were lower in the lower-bay than in the upper- and middle-bay regions in 1998 and 1999 (ANOVA $P < 0.05$) (Figure 3, Appendix 8). The highest regional MWC temperature was recorded in the upper bay during the 1995 survey (28.7 °C), while the lowest was observed in the lower bay in 1999 (22.6 °C) (Appendix 8).

Salinity increased significantly from the upper bay to the lower bay in each year (ANOVA $P < 0.05$) (Figure 4, Appendix 9). The lowest regional MWC salinity was in the upper bay in 1996 (5.7 ppt), and the highest was in the lower bay in 1999 (22.3 ppt) (Appendix 9).

Regional mean below-pycnocline DO levels were significantly higher in the lower and mid bay than in the upper-bay region in 1996 and 1999 (ANOVA $P < 0.05$), while they were similar throughout all bay regions in 1997 (Figure 5, Appendix 10). Lower-bay mean below-pycnocline DO levels in 1995 and 1998 were significantly higher than mid-bay concentrations (ANOVA $P < 0.05$). The highest regional mean below-pycnocline DO concentration was in the lower bay in 1996 (8.2 mg/L), while the lowest was in the upper bay in 1997 (3.2 mg/L). Although regional mean DO levels below the pycnocline were never less than 3.2 mg/L (Appendix 10), DO dropped below 2.0 mg/L at depths

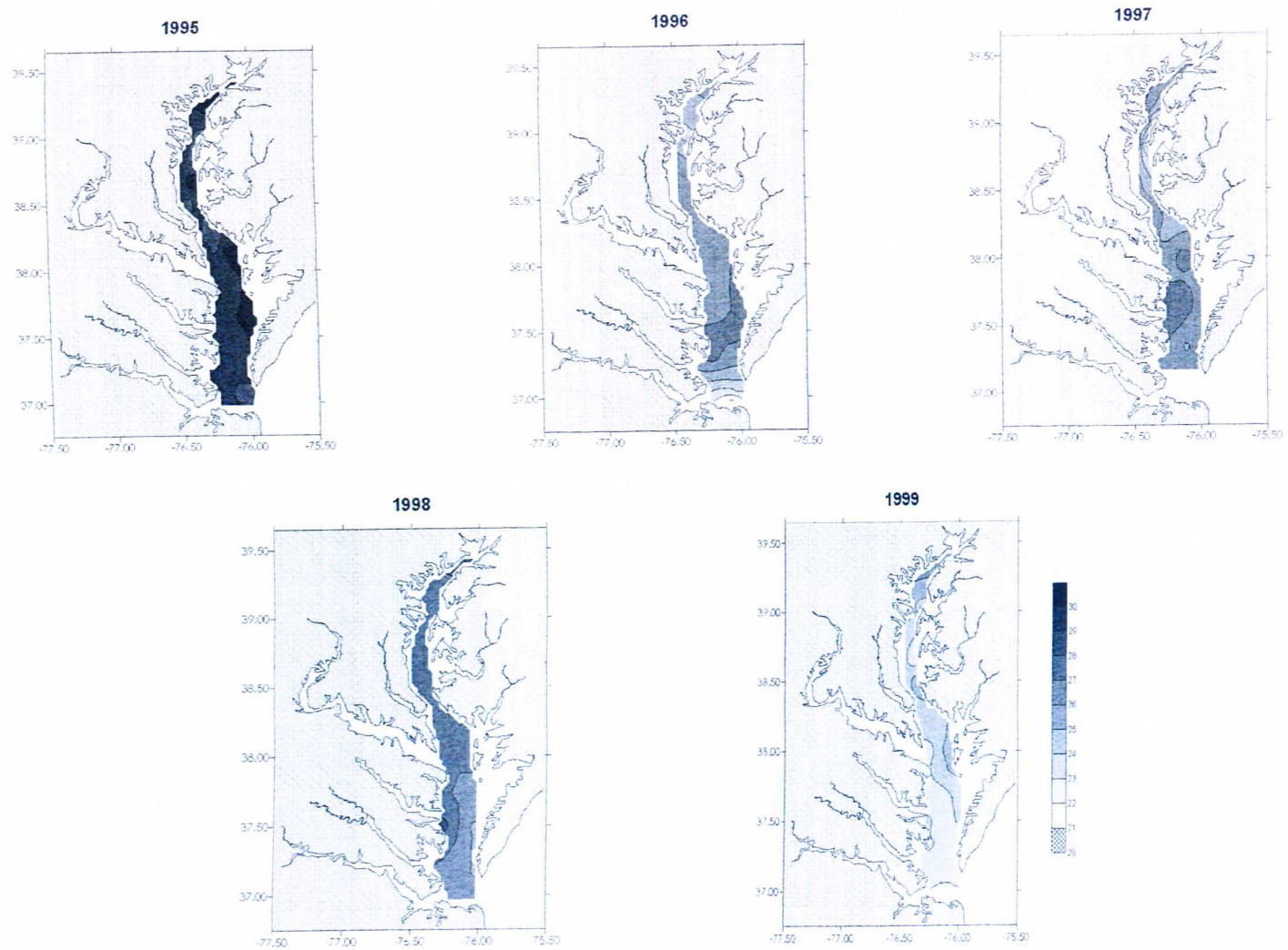


Figure 3. Mean water-column temperature ($^{\circ}\text{C}$) during Chesapeake Bay summer TIES surveys from 1995-1999.

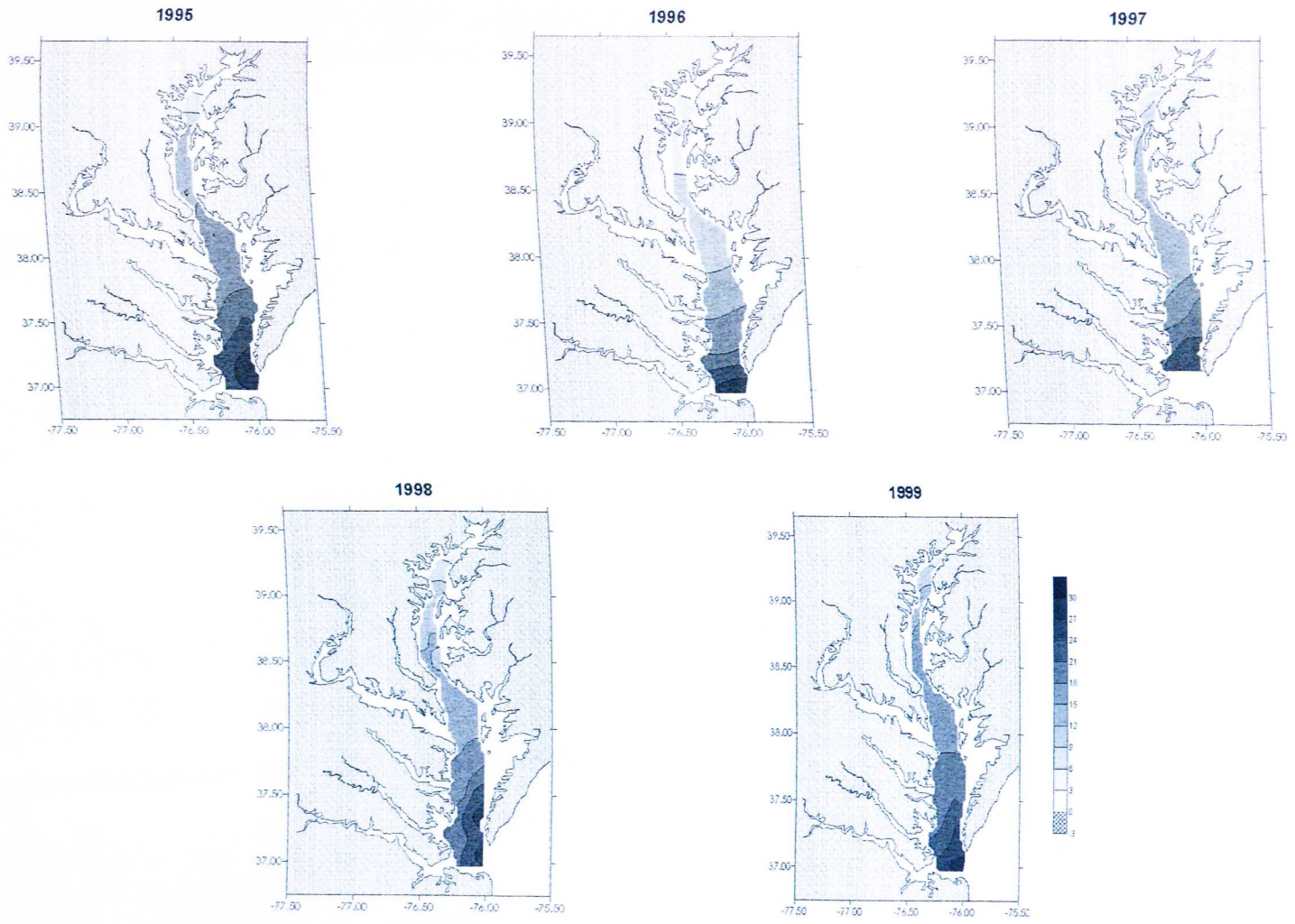


Figure 4. Mean water-column salinity (ppt) during Chesapeake Bay summer TIES surveys from 1995-1999.

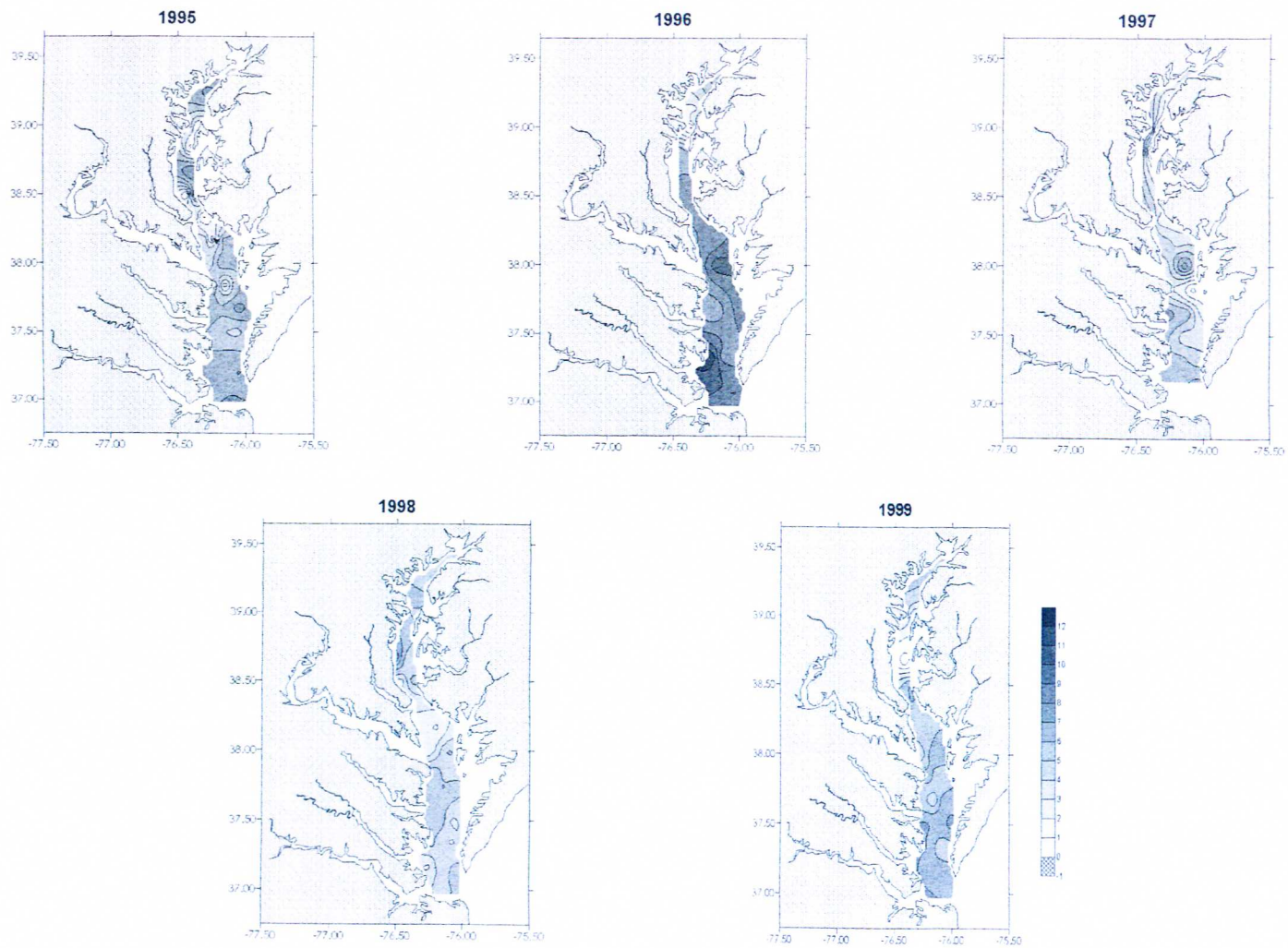


Figure 5. Mean below-pycnocline dissolved oxygen concentration (mg/L) during Chesapeake Bay summer TIES surveys from 1995-1999.

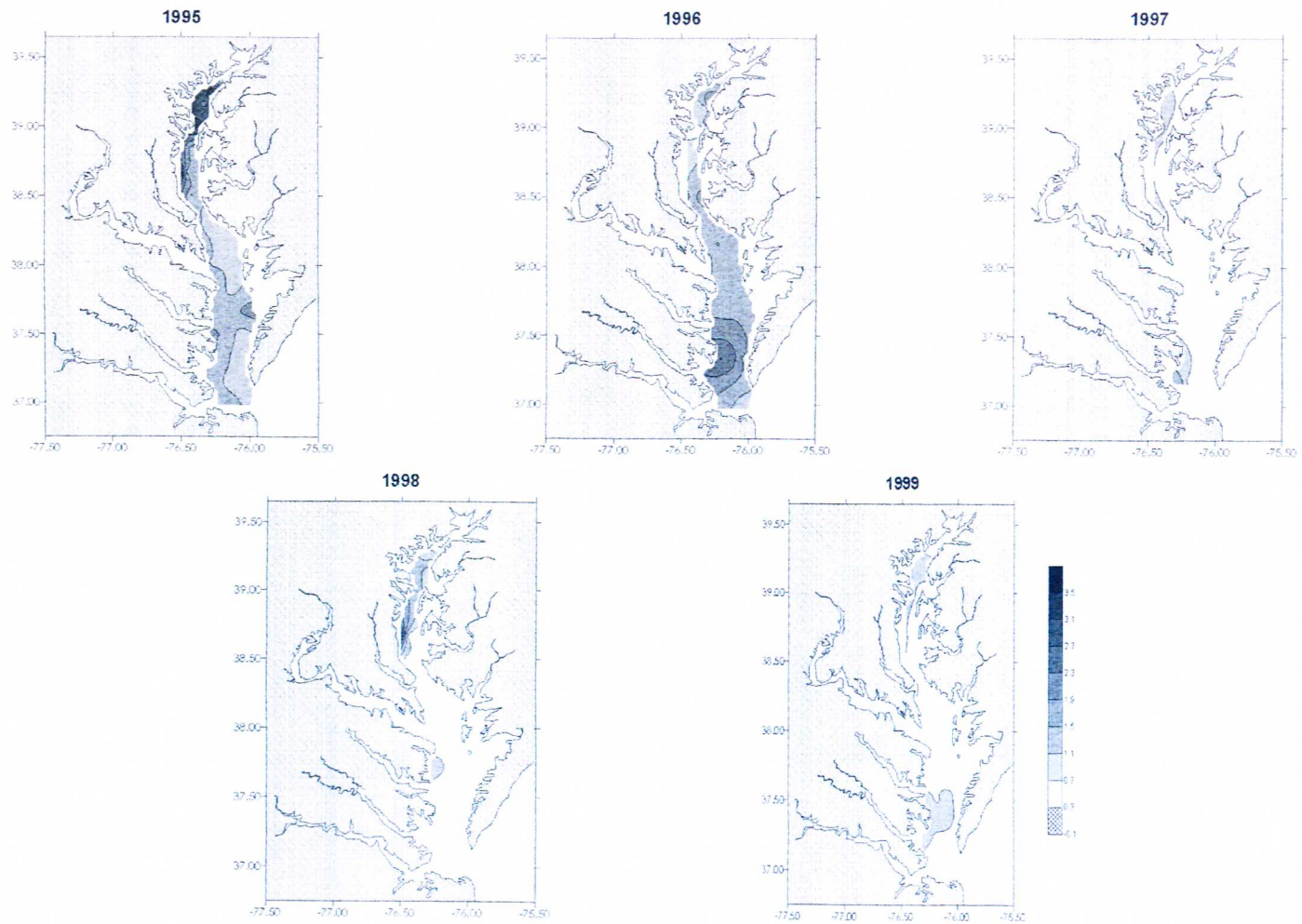


Figure 6. Mean water-column fluorescence (relative fluorescence units), an indicator of chlorophyll a biomass, during Chesapeake Bay summer TIES surveys from 1995-1999.

>13 m (except for 2 lower bay stations in 1998 and 3 lower bay stations in 1999), and approached 0 mg/L at station depths >15 m.

Regional MWC fluorescence levels were significantly higher in the upper bay than in the lower bay in 1995 and 1998, but were similar among regions in 1996, 1997, and 1999 (ANOVA $P < 0.05$) (Figure 6, Appendix 11). The highest regional mean fluorescence was observed in the upper bay in 1995 (2.0 relative fluorescence units, rfu), while the lowest was observed in the lower bay in 1998 (0.5 rfu) (Appendix 11).

Zooplankton Distribution and Densities

The distributions and mean densities of total zooplankton (see Table 1), copepods, and copepod nauplii along the Bay's axis were examined in Chesapeake Bay from 1996-1999 to determine their possible influence on larval bay anchovy distributions, abundances, and feeding ecology. The relative densities and distributions of total zooplankton (Figure 7), copepods (Figure 8), and copepod nauplii (Figure 9) were similar in each of the four years. However, bay-wide mean zooplankton density in July 1997 (171.6 L^{-1}) was more than twice that of June 1999 (83.2 L^{-1}) and more than three times that of July 1996 (49.8 L^{-1}) (ANOVA $P < 0.05$) (Table 3). Bay-wide mean copepod and copepod nauplii densities were significantly higher in 1997 and 1998 than in 1999 and probably 1995 (ANOVA $P < 0.05$) (Table 3). The highest bay-wide mean copepod density was observed in 1997 (101.5 L^{-1}), while the lowest occurred in 1996 (29.9 L^{-1}). Similarly, the highest copepod nauplii density was estimated in 1997 (80.9 L^{-1}), and the lowest in 1996 (23.1 L^{-1}). The most common taxon in the collections was the nauplius stage of the copepod *Acartia tonsa*.

Table 3. Yearly survey and regional mean densities (L^{-1}) of total zooplankton (Table 1), total copepods, and copepod nauplii for summer TIES surveys in Chesapeake Bay from 1996-1999. There is no SE for the upper bay region in 1996, as only one sample for summer collections was available. For within-year regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$).

Zooplankton					Copepods				
Bay Region	Year				Bay Region	Year			
	1996	1997	1998	1999		1996	1997	1998	1999
Upper	58.5	143.7	143.9	152.9 ^a	Upper	24.9	64.7	58.5	67.9 ^a
SE		58.6	42.9	40.0	SE		20.7	17.8	18.6
Mid	44.3	208.9	85.8	38.9 ^b	Mid	30.6	128.1	56.3	6.3 ^b
SE	10.7	44.0	32.4	8.9	SE	5.9	23.9	25.6	3.7
Lower	53.2	159.8	118.7	43.9 ^b	Lower	30.5	114.2	78.1	10.0 ^b
SE	12.8	53.2	14.1	6.5	SE	16.0	51.1	14.7	2.4
Bay-wide					Bay-wide				
Mean	49.8 ^a	171.6 ^b	116.3 ^{ab}	83.2 ^a	Mean	29.9 ^{ab}	101.5 ^b	65.2 ^b	30.6 ^a
SE	7.1	29.0	17.4	20.1	SE	7.0	18.5	10.7	10.0

Nauplii				
Bay Region	Year			
	1996	1997	1998	1999
Upper	23.0	49.9	39.9	51.4 ^a
SE		16.6	11.4	13.9
Mid	22.7	105.1	52.6	5.5 ^b
SE	4.1	17.6	25.1	3.4
Lower	23.6	89.5	58.6	8.3 ^{ab}
SE	14.6	36.9	13.2	2.1
Bay-wide				
Mean	23.1 ^{ab}	80.9 ^b	50.9 ^b	23.6 ^a
SE	6.2	14.1	9.4	7.5

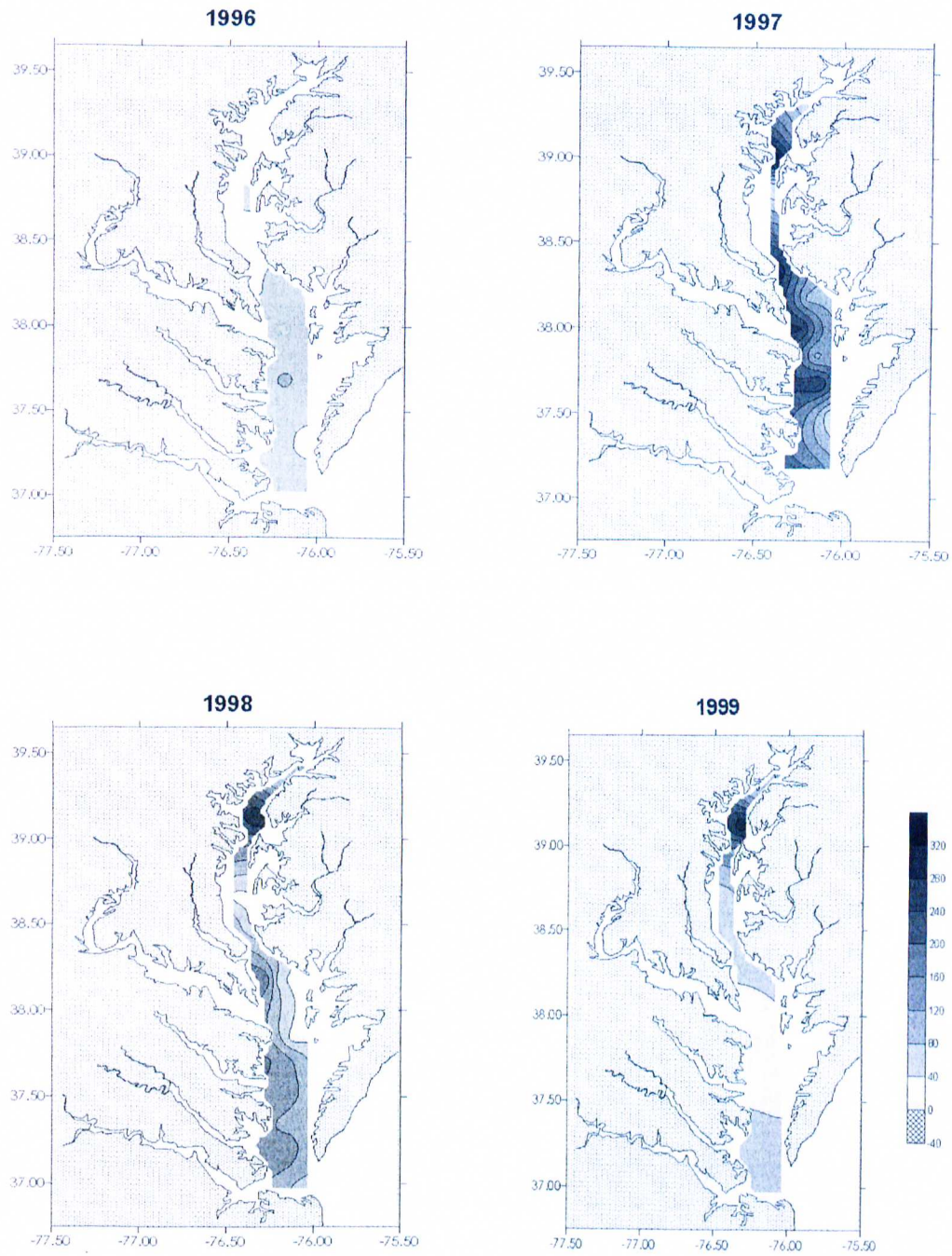


Figure 7. Zooplankton (Table 1) distributions and mean densities (L^{-1}) in Chesapeake Bay summer TIES surveys from 1996-1999. Samples were collected in 10-L Niskin bottles from stations centered on the Bay's north-south axis.

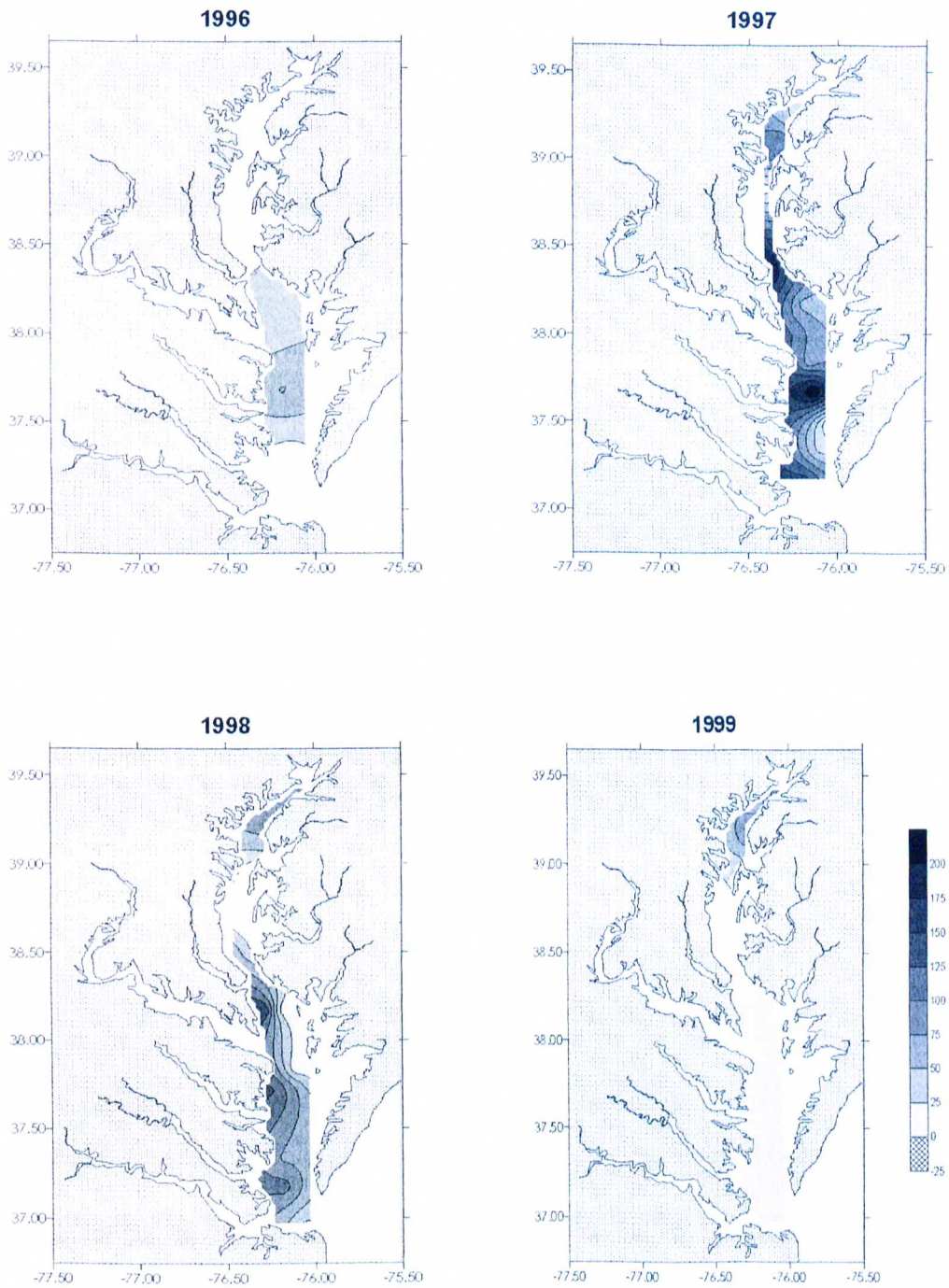


Figure 8. Copepod distributions and mean densities (L^{-1}) in Chesapeake Bay summer TIES surveys from 1996-1999. Samples were collected in 10-L Niskin bottles from stations centered on the Bay's north-south axis.

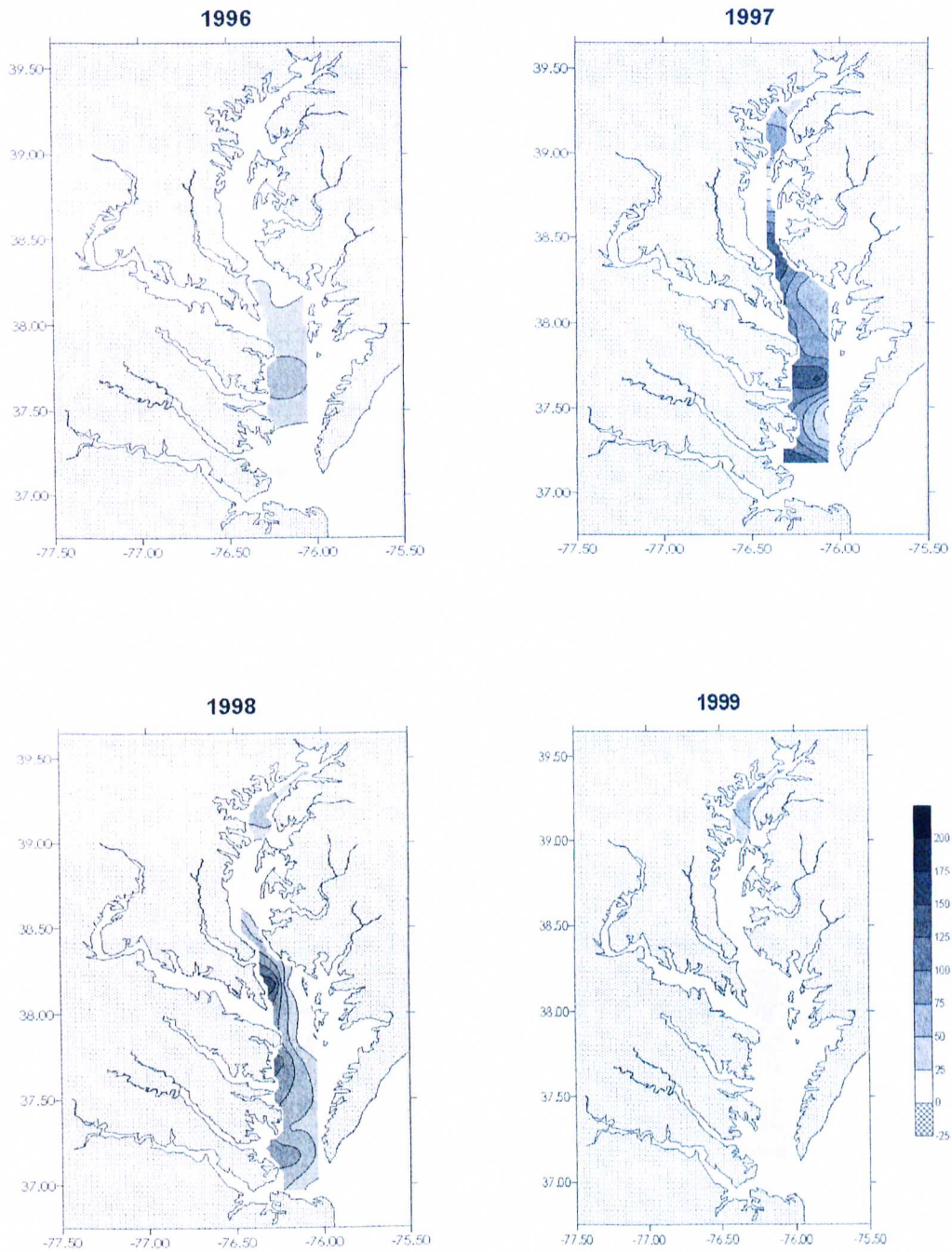


Figure 9. Copepod nauplii distributions and mean densities (L^{-1}) in Chesapeake Bay summer TIES surveys from 1996-1999. Samples were collected in 10-L Niskin bottles from stations centered on the Bay's north-south axis.

The regional mean densities of total zooplankton, copepods, and copepod nauplii were generally similar within years within each taxonomic group. However, in 1999, the upper-bay mean densities of zooplankton (152.9 L^{-1}) and copepods (67.9 L^{-1}) were each significantly higher than those found in the mid ($38.9 \text{ zooplankton/L}$, 6.3 copepods/L) and lower ($43.9 \text{ zooplankton/L}$, 10.0 copepods/L) bay (ANOVA $P < 0.05$) (Table 3). For nauplii during the 1999 season, the mean density in the upper bay (51.4 L^{-1}) was significantly higher than that found in the mid bay (5.5 L^{-1}) (ANOVA $P < 0.05$), and probably higher than the mean nauplii density in the lower bay (8.3 L^{-1}) (Table 3). The highest regional mean densities of zooplankton, copepods, and copepod nauplii all occurred in the mid bay during 1997 ($208.9 \text{ zooplankton/L}$, 128.1 copepods/L , $105.1 \text{ copepod nauplii/L}$), while the lowest densities all occurred in the mid bay during 1999 ($38.9 \text{ zooplankton/L}$, 6.3 copepods/L , $5.5 \text{ copepod nauplii/L}$) (Table 3).

Mean densities of total zooplankton, copepods, and copepod nauplii were higher above than below the pycnocline in each year. However, these differences were only significant for copepods in 1997 (Above = 141.3 L^{-1} ; Below = 74.3 L^{-1}), and copepod nauplii in 1997 (Above = 124.7 L^{-1} ; Below = 51.7 L^{-1}) and 1998 (Above = 63.0 L^{-1} ; Below = 34.7 L^{-1}) (t-test $P < 0.05$) (Table 4).

Concentration differences were examined for other, less abundant zooplankton taxa that were utilized to a lesser extent as prey by larval bay anchovy in Chesapeake Bay. The annual survey and regional densities of cladocerans and rotifers were relatively low, and tintinnids were only collected in the lower bay in 1999 (0.4 L^{-1}). Bay-wide mean cladoceran density was highest in 1998 (mean = 5.96 L^{-1} SE = 4.44) and lowest in 1996 (mean = 0.10 L^{-1} SE = 0.09), while bay-wide mean rotifer density was highest in

Table 4. Above- and below-pycnocline mean densities (L^{-1}) of total zooplankton (Table 1), total copepods, and copepod nauplii for summer TIES surveys in Chesapeake Bay from 1996-1999. For within-year depth comparisons, different superscripts indicate significant differences (t-test $P < 0.05$). Above = above pycnocline; Below = below pycnocline.

Zooplankton

Depth	Year			
	1996	1997	1998	1999
Above	78.6	198.0	142.7	95.1
SE	23.9	31.4	32.6	24.4
Below	35.1	154.9	93.2	67.6
SE	11.3	37.6	21.0	18.4

Copepods

Depth	Year			
	1996	1997	1998	1999
Above	50.9	141.3 ^a	73.3	36.0
SE	22.0	26.7	11.7	11.9
Below	18.0	74.3 ^b	55.5	26.1
SE	5.4	20.2	14.9	8.9

Nauplii

Depth	Year			
	1996	1997	1998	1999
Above	47.3	124.7 ^a	63.0 ^a	31.3
SE	20.6	23.4	10.5	10.1
Below	8.9	51.7 ^b	34.7 ^b	17.0
SE	2.7	14.0	11.1	5.8

1999 (mean = 5.33 L⁻¹ SE = 3.00) and lowest in 1997 (mean = 0.07 L⁻¹ SE = 0.04).

Pooled mean regional cladoceran density was highest in the upper bay (mean = 4.28 L⁻¹ SE = 2.25) and lowest in the lower bay (mean = 0.48 L⁻¹ SE = 0.38), while rotifer density was highest in the lower bay (mean = 5.08 L⁻¹ SE = 2.16) and lowest in the mid bay (mean = 1.15 L⁻¹ SE = 0.63).

Gelatinous Predator (ctenophore) Biovolumes and Distributions

The biovolumes and distributions of *M. leidy*, a predator on bay anchovy eggs and larvae, varied among annual surveys, regionally, and above vs below the pycnocline during the summer TIES surveys. Ctenophore biovolume was highest in the 1996 survey (572.8 ml/m²), a value 3.7 times higher than the lowest observed in 1995 (153.9 ml/m²). Biovolume in 1996 was significantly higher than in 1995 and 1998 (ANOVA P<0.05), and marginally higher than in 1997 and 1999 (Table 5).

Regional ctenophore biovolumes differed among years during the summer TIES surveys (ANOVA P<0.05) (Figure 10). The highest biovolume was estimated in the mid-bay region in 1998 (852.9 ml/m²), while the lowest occurred in the mid bay in 1995 (23.2 ml/m²). Ctenophore biovolume was significantly higher in the lower bay (317.7 ml/m²) than in the mid bay (23.2 ml/m²) in 1995, and was significantly higher in the mid bay (852.9 ml/m²) than in the upper (474.3 ml/m²) and lower (66.2 ml/m²) bay in 1998 (ANOVA P<0.05) (Table 5).

The mean bay-wide ctenophore biovolume was 2-3 times higher above than below the pycnocline in each year (ANOVA P<0.05) (Table 6). Highest bay-wide mean biovolume was above the pycnocline in 1996 (290.4 ml/m²), while the lowest was below

Table 5. Yearly survey and regional mean *Mnemiopsis leidyi* biovolumes (ml/m²) for summer TIES surveys in Chesapeake Bay from 1995-1999. For within-year regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (ANOVA P<0.05).

Bay Region	Year				
	1995	1996	1997	1998	1999
Upper	91.1 ^{ab}	765.0	286.9	474.3 ^a	469.3
SE	21.8	213.2	59.1	244.5	128.1
Mid	23.2 ^a	482.4	145.1	852.9 ^b	366.3
SE	5.8	87.9	36.4	194.0	130.4
Lower	317.7 ^b	470.9	538.3	66.2 ^a	319.8
SE	103.9	105.5	153.9	31.0	116.5
Bay-wide					
Mean	153.9 ^a	572.8 ^b	355.7 ^{ab}	378.1 ^a	370.2 ^{ab}
SE	44.7	85.5	77.4	95.2	71.6

Table 6. Yearly survey and regional above- and below-pycnocline mean *Mnemiopsis leidyi* biovolumes (ml/m²) in Chesapeake Bay during TIES summer surveys from 1995-1999. For within-year depth comparisons for each region and bay-wide, different superscripts indicate significant differences (t-test P<0.05). Above = above pycnocline; Below = below pycnocline.

Upper Bay						Mid Bay					
Depth	Year					Depth	Year				
	1995	1996	1997	1998	1999		1995	1996	1997	1998	1999
Above	58.8 ^a	371.5 ^a	186.8	215.6 ^a	248.4 ^a	Above	19.0 ^a	277.4	93.8	497.5 ^a	240.9 ^a
SE	16.3	134.6	48.9	101.0	66.2	SE	5.4	40.9	20.8	168.6	92.0
Below	0 ^b	16.1 ^b	87.7	49.2 ^b	0 ^b	Below	10.4 ^b	206.6	184.4	0.6 ^b	19.8 ^b
SE	0	16.1	35.0	49.2	0	SE	5.7	80.3	90.9	0.4	18.0

Lower Bay						Bay-wide					
Depth	Year					Depth	Year				
	1995	1996	1997	1998	1999		1995	1996	1997	1998	1999
Above	144.7	222.1	211.9 ^a	50.2	159.2	Above	77.5 ^a	290.4 ^a	167.4 ^a	211.3 ^a	205.5 ^a
SE	36.4	63.6	95.8	29.1	68.2	SE	16.8	50.9	45.9	60.3	44.0
Below	60.4	218.5	17.2 ^b	172.9	194.4	Below	27.1 ^b	147.1 ^b	87.4 ^b	96.3 ^b	94.4 ^b
SE	18.6	50.3	10.9	81.5	52.4	SE	8.4	35.8	32.9	42.7	28.9

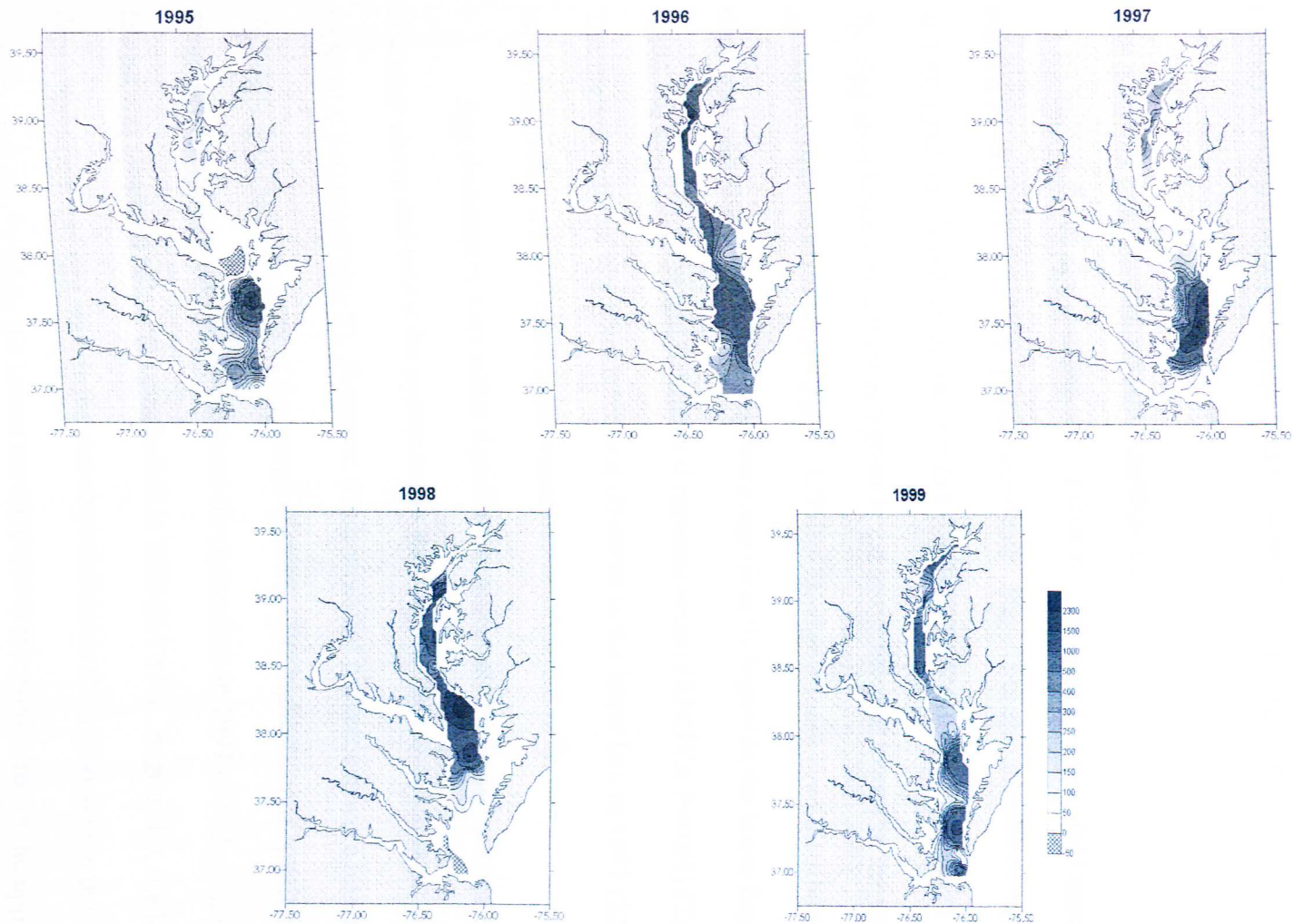


Figure 10. Mean water-column *Mnemiopsis leidyi* biovolume (ml/m^2) in Chesapeake Bay summer TIES surveys from 1995-1999.

the pycnocline in 1995 (27.1 ml/m²). Regionally, ctenophore biovolumes were either significantly higher above than below the pycnocline in each bay region in each year (ANOVA P<0.05) or were similar in the two depth zones (Table 6).

Bay Anchovy Egg Abundances and Distributions

Bay anchovy egg abundances and distributions varied several-fold annually, regionally, and with respect to pycnocline depth. Bay-wide egg abundance was highest in 1997 (262.3 m⁻²) and lowest in 1996 (18.0 m⁻²) (ANOVA P<0.05) (Figure 11, Table 7). Egg abundance generally was highest in the lower bay and lowest in the upper bay in all years except 1999 (Figures 12 and 13, Table 7) when a more even distribution was observed. Abundances and densities were significantly higher in the lower bay than upper bay in 1995-1998 and for the total regional means (ANOVA P<0.05) (Table 7). The highest regional egg abundance was observed in the lower bay in 1997 (339.3 m⁻²), while the lowest was observed in the upper bay in 1996 (0.6 m⁻²).

Egg abundances were either significantly higher above the pycnocline or equally abundant above and below the pycnocline in each region and bay-wide in all years (ANOVA P<0.05) (Table 8). However, depth-stratified differences were less apparent in the upper-bay region in each of the sampling years. The highest depth-specific, bay-wide mean egg abundance was observed above the pycnocline in 1997 (207.2 m⁻²), while the lowest was observed below the pycnocline in 1996 (8.7 m⁻²). Regionally, the highest depth-specific mean egg abundance was observed above the pycnocline in the lower bay in 1997 (266.6 m⁻²), while the lowest occurred above the pycnocline in the upper bay in 1996 (0.08 m⁻²).

Table 7. Yearly survey and regional mean bay anchovy egg abundances (m^{-2}) and densities (m^{-3}) from summer TIES surveys in Chesapeake Bay from 1995-1999. For within-year and total regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$).

Egg Abundance (m^{-2})

Bay Region	Year					Total
	1995	1996	1997	1998	1999	
Upper	1.9 ^a	0.6 ^a	7.9 ^a	20.5 ^a	166.2	39.4 ^a
SE	1.0	0.4	4.6	12.5	70.0	31.9
Mid	69.4 ^b	14.6 ^b	316.4 ^b	26.1 ^{ab}	208.6	127.0 ^{ab}
SE	21.8	4.2	102.1	7.3	47.9	58.6
Lower	79.9 ^b	38.7 ^b	339.3 ^b	255.6 ^b	154.0	173.5 ^b
SE	37.4	17.0	87.2	92.4	28.0	55.5
Bay-wide						
Mean	56.0 ^a	18.0 ^a	262.3 ^b	139.6 ^{ab}	171.3 ^b	129.4
SE	16.5	6.5	55.7	49.7	25.0	43.2

Egg Density (m^{-3})

Bay Region	Year					Total
	1995	1996	1997	1998	1999	
Upper	0.2 ^a	0.05 ^a	0.7 ^a	2.1 ^a	15.9	3.8 ^a
SE	0.1	0.03	0.4	1.3	6.2	3.0
Mid	5.9 ^b	1.4 ^b	30.1 ^b	2.5 ^{ab}	25.5	13.1 ^{ab}
SE	1.6	0.4	7.2	0.7	5.6	6.1
Lower	8.6 ^b	3.9 ^b	41.9 ^b	27.6 ^b	18.7	20.1 ^b
SE	4.1	1.9	10.5	10.3	3.3	6.8
Bay-wide						
Mean	5.4 ^{ab}	1.8 ^a	29.5 ^{cd}	15.0 ^{bc}	19.7 ^d	14.3
SE	1.7	0.7	5.9	5.5	2.7	5.0

Table 8. Yearly survey and regional above- and below-pycnocline mean bay anchovy egg abundances (m^{-2}) from summer TIES surveys in Chesapeake Bay from 1995-1999. For within-year and total depth comparisons for each region and bay-wide, different superscripts indicate significant differences (t-test $P < 0.05$). Above = above pycnocline; Below = below pycnocline.

Upper Bay							Mid Bay						
Depth	Year					Total	Depth	Year					Total
	1995	1996	1997	1998	1999			1995	1996	1997	1998	1999	
Above	1.1	0.08	5.3	13.2	146.2	33.2	Above	59.2 ^a	6.5	252.7 ^a	18.8	162.3 ^a	99.9
SE	0.6	0.06	3.2	8.7	68.1	28.4	SE	21.0	1.8	95.2	6.7	42.8	47.0
Below	0.8	0.5	2.6	7.3	20.0	6.2	Below	10.2 ^b	8.1	63.7 ^b	7.3	44.4 ^b	26.8
SE	0.5	0.3	1.8	4.3	8.0	3.7	SE	4.3	2.5	17.5	2.3	15.3	11.6

Lower Bay							Bay-wide						
Depth	Year					Total	Depth	Year					Total
	1995	1996	1997	1998	1999			1995	1996	1997	1998	1999	
Above	65.8	21.2	266.6 ^a	179.4	129.2 ^a	132.4	Above	46.8 ^a	9.2	207.2 ^a	97.8	142.1 ^a	100.6
SE	36.3	7.7	72.7	62.0	21.3	43.0	SE	15.8	3.1	47.9	33.6	22.3	34.9
Below	14.1	17.5	72.7 ^b	76.2	24.8 ^b	41.1	Below	9.2 ^b	8.7	55.1 ^b	41.7	29.2 ^b	28.8
SE	9.7	11.2	19.3	34.0	12.9	13.7	SE	3.9	3.9	11.4	17.8	7.7	9.1

Table 9. Yearly survey and regional above- and below-pycnocline mean bay anchovy egg densities (m^{-3}) from summer TIES surveys in Chesapeake Bay from 1995-1999. For within-year and total depth comparisons for each region and bay-wide, different superscripts indicate significant differences (t-test $P < 0.05$). Above = above pycnocline; Below = below pycnocline.

Upper Bay							Mid Bay						
Depth	Year					Total	Depth	Year					Total
	1995	1996	1997	1998	1999			1995	1996	1997	1998	1999	
Above	0.2	0.01	0.7	2.1	19.0	4.4	Above	9.0 ^a	1.2	37.9	2.8	24.6	15.1
SE	0.1	0.01	0.4	1.4	7.4	8.2	SE	2.6	0.3	11.0	0.9	5.7	7.1
Below	0.2	0.09	0.6	2.1	9.8	2.6	Below	2.1 ^b	1.7	17.8	2.0	22.8	9.3
SE	0.1	0.06	0.5	1.2	5.0	1.8	SE	0.7	0.5	5.3	0.6	6.0	4.6

Lower Bay							Bay-wide						
Depth	Year					Total	Depth	Year					Total
	1995	1996	1997	1998	1999			1995	1996	1997	1998	1999	
Above	13.8	3.7	50.9	32.4	22.8 ^a	24.7	Above	8.5 ^a	1.6	36.2	17.5	22.3 ^a	17.2
SE	7.3	1.2	12.8	11.6	3.7	8.1	SE	2.9	0.5	7.6	6.2	2.9	5.9
Below	2.7	5.1	29.6	22.1	9.0 ^b	13.7	Below	1.8 ^b	2.3	19.8	12.1	13.1 ^b	9.8
SE	1.6	3.8	9.5	10.7	4.2	5.2	SE	0.7	1.3	5.1	5.6	3.0	3.4

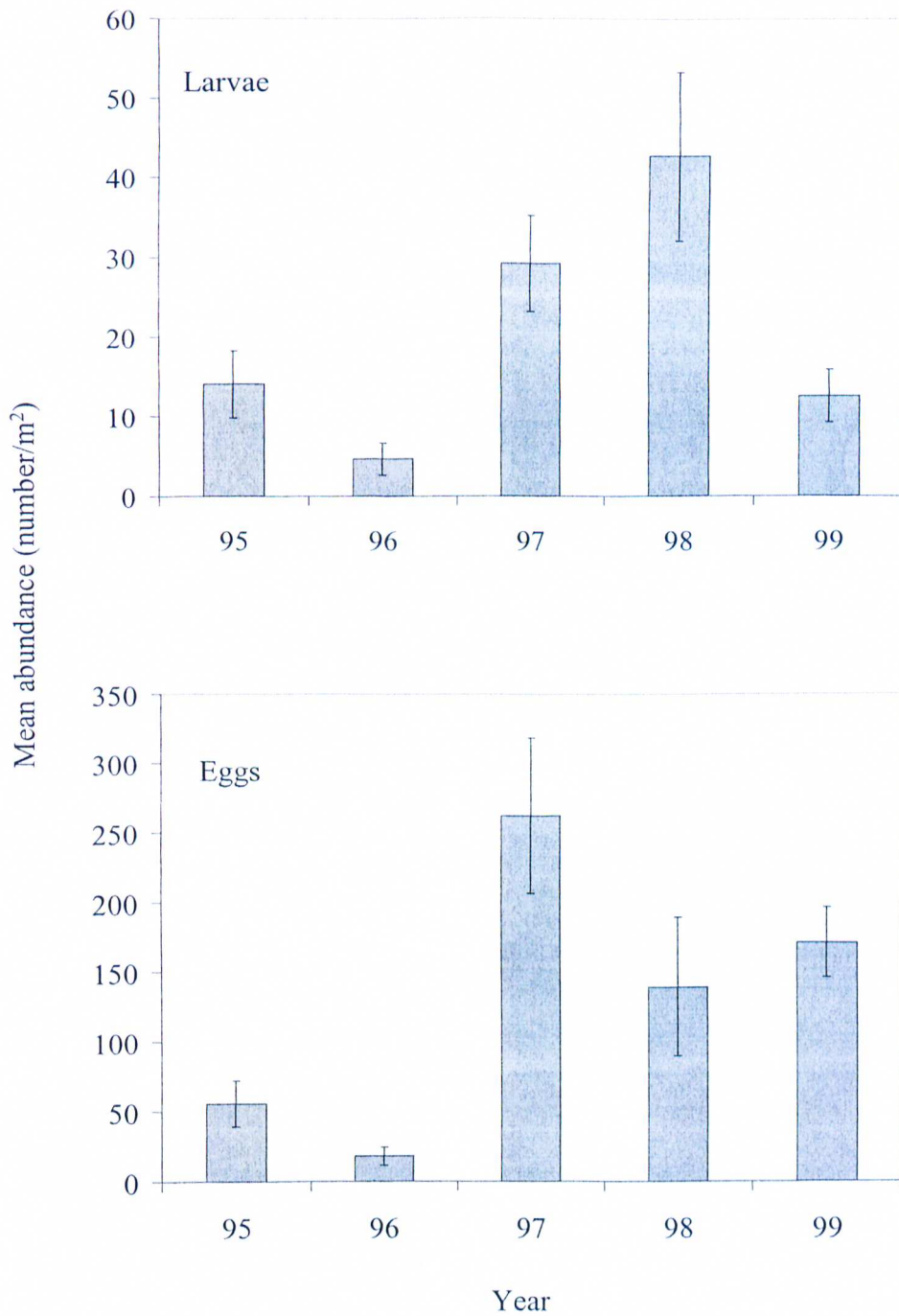


Figure 11. Bay-wide mean bay anchovy larval and egg abundances (m^{-2}) for TIES summer surveys in Chesapeake Bay from 1995-1999. Error bars represent ± 1 SE.

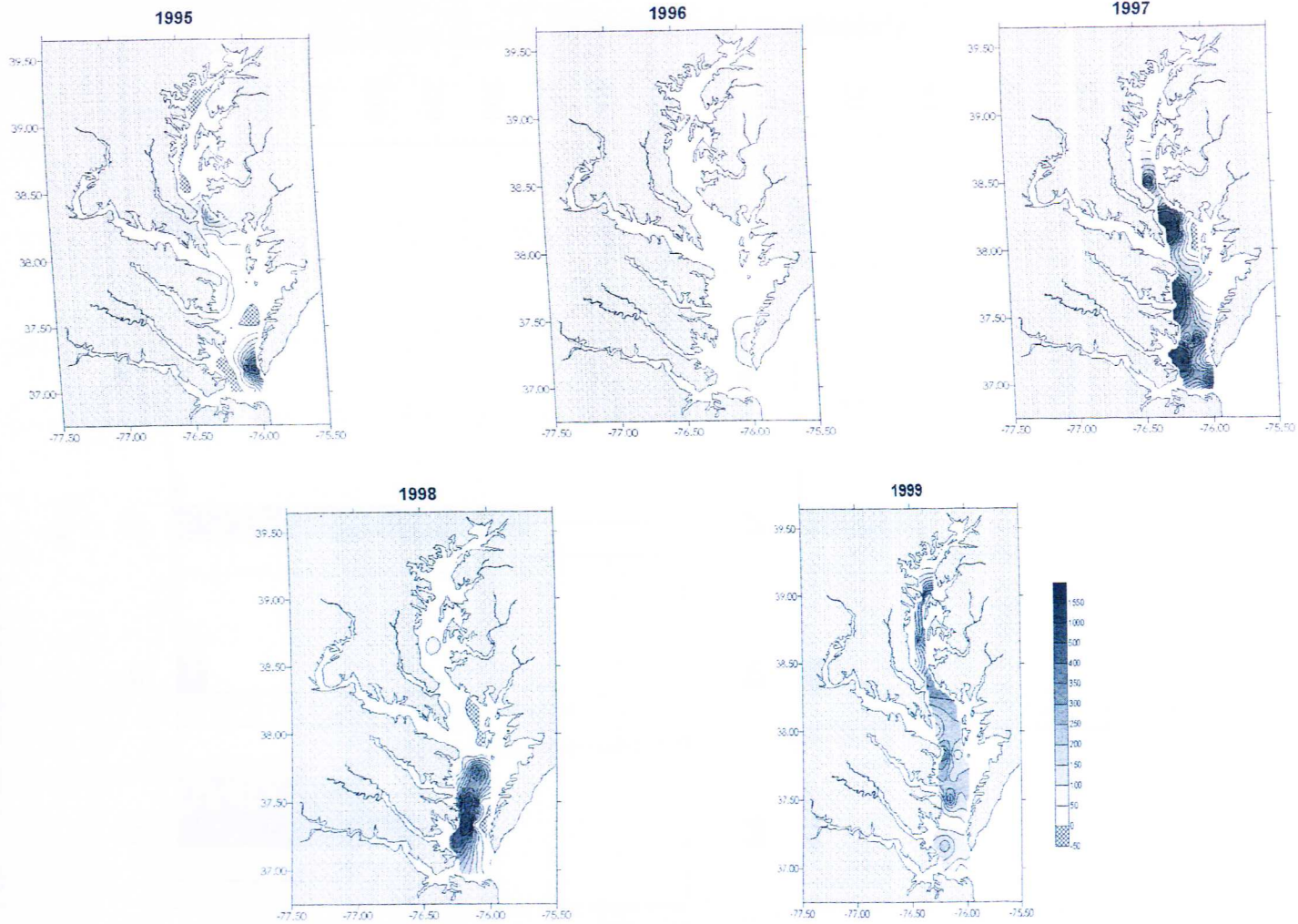


Figure 12. Mean water-column bay anchovy egg abundance (m^{-2}) from summer TIES surveys in Chesapeake Bay from 1995-1999.

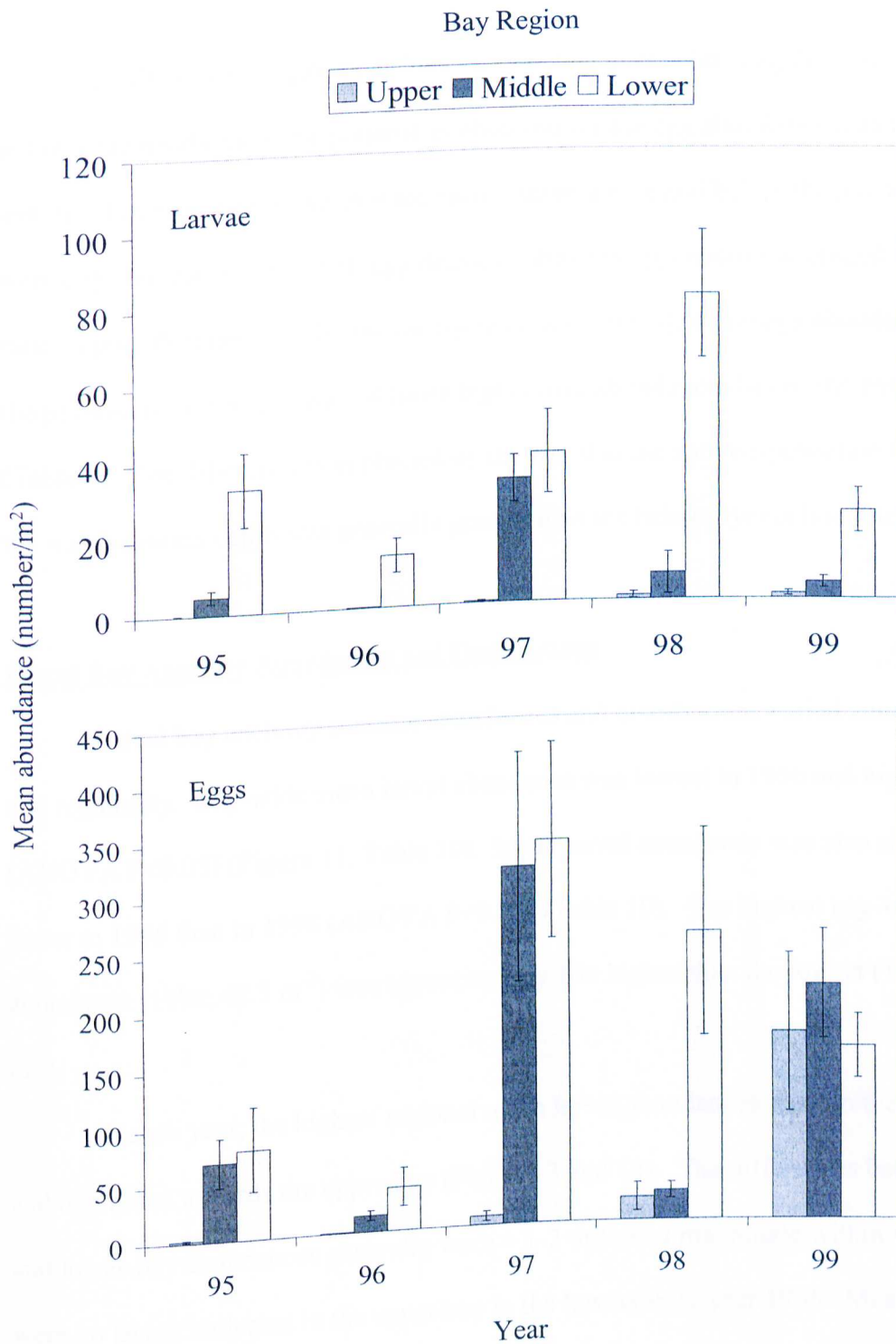


Figure 13. Regional mean bay anchovy larval and egg abundances (m⁻²) for TIES summer surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. Error bars represent +/- 1 SE.

Yearly survey, regional, and above vs below pycnocline egg densities (number per m³) had nearly the same patterns as observed for the egg abundance data (Tables 7 and 9). However, egg densities were more similar above and below the pycnocline than were egg abundances. Overall, egg densities above the pycnocline averaged nearly 2 times higher than densities below the pycnocline (Table 9), while egg abundances above the pycnocline averaged nearly 4 times higher than abundances below the pycnocline (Table 8). The difference is explained by the fact that the above-pycnocline fraction of the water-column depth was generally greater than the below-pycnocline fraction.

Larval Bay Anchovy Abundances and Distributions

Larval bay anchovy summer abundances and distributions varied among years and regionally. Bay-wide mean larval abundance was lowest in 1996 and highest in 1998 (ANOVA $P < 0.05$) (Figure 11, Table 10). Mean larval abundance was also significantly lower in 1995 than in 1998 (ANOVA $P < 0.05$) (Table 10). The highest bay-wide mean abundance (1998; 42.7 m⁻²) was approximately 10x higher than the lowest (1996; 4.6 m⁻²).

In each year, the highest regional mean larval abundances were in the lower bay and decreased towards the upper bay (Figure 13 and 14). The differences between upper- and lower-bay abundances generally were > 1-2 orders of magnitude within years. There were no larvae collected in the upper bay in the low-salinity year 1996. Mean abundances of larvae in the lower bay were significantly higher than mean abundances in both the mid- and upper-bay regions in all years except 1997 (ANOVA $P < 0.05$) when the

Table 10. Yearly survey and regional mean larval bay anchovy abundances (m^{-2}) and densities (m^{-3}) from summer TIES surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. For within-year and total regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$).

Larval Abundance (number/ m^2)

Bay Region	Year					Total
	1995	1996	1997	1998	1999	
Upper	0.09 ^a	0 ^a	0.4 ^a	1.1 ^a	1.3 ^a	0.6 ^a
SE	0.04	0	0.2	0.9	0.6	0.3
Mid	4.9 ^b	0.2 ^a	32.8 ^b	6.9 ^a	4.3 ^a	9.8 ^b
SE	1.6	0.07	6.2	5.6	1.5	5.8
Lower	32.8 ^c	13.7 ^b	39.7 ^b	81.0 ^b	23.3 ^b	38.1 ^b
SE	9.7	4.5	11.0	16.9	5.9	11.6
Bay-wide						
Mean	14.0 ^{ab}	4.6 ^a	29.2 ^c	42.7 ^{bc}	12.5 ^{bc}	20.6
SE	4.2	2.0	6.0	10.7	3.3	6.8

Larval Density (number/ m^3)

Bay Region	Year					Total
	1995	1996	1997	1998	1999	
Upper	0.009 ^a	0 ^a	0.03 ^a	0.1 ^a	0.2 ^a	0.07 ^a
SE	0.003	0	0.01	0.09	0.1	0.04
Mid	0.5 ^b	0.01 ^a	3.6 ^b	0.7 ^a	0.5 ^a	1.1 ^b
SE	0.2	0.006	0.7	0.6	0.2	0.6
Lower	3.2 ^c	1.4 ^b	4.9 ^b	8.1 ^b	3.0 ^b	4.1 ^c
SE	0.8	0.5	1.6	1.7	0.7	1.1
Bay-wide						
Mean	1.4 ^{ab}	0.5 ^a	3.5 ^c	4.3 ^{bc}	1.6 ^{bc}	2.2
SE	0.4	0.2	0.8	1.1	0.4	0.7

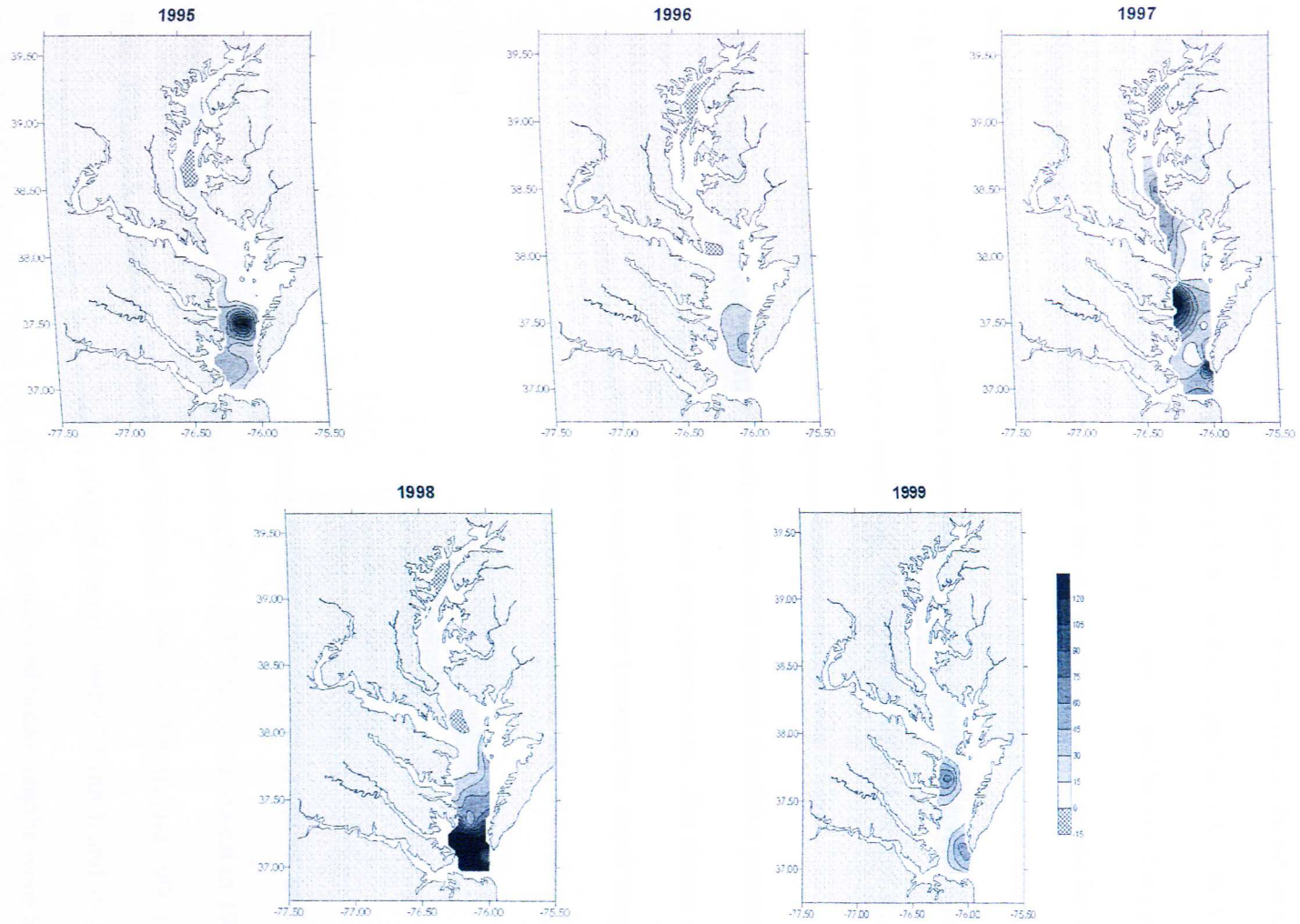


Figure 14. Mean water-column larval abundance (m^{-2}) for TIES summer surveys in Chesapeake Bay from 1995-1999.

abundances were similar in the lower and mid bays (Table 10). Mean abundances in the mid bay were significantly higher than those in the upper bay in 1995 and 1997 (ANOVA $P < 0.05$) (Table 10). For combined-years regional larval data, mean abundances decreased from 38.1 m^{-2} in the lower bay to 0.6 m^{-2} in the upper bay (ANOVA $P < 0.05$).

Mean larval abundances were generally similar above and below the pycnocline. Although no significant differences in mean larval abundances were found between the two depth layers, either within regions or bay-wide within years (t-test $P > 0.05$) (Table 11), the observed abundances usually were slightly higher above the pycnocline. For the total above- and below-pycnocline comparison, the mean above-pycnocline abundance was 12.8 m^{-2} , while the mean below-pycnocline abundance was 7.8 m^{-2} .

Considering larval densities, yearly cruise and regional densities generally followed the same patterns observed in the larval abundance data. The above- and below-pycnocline densities generally were more similar because the depth range above the pycnocline usually was greater than the depth range below the pycnocline (Tables 10 and 12).

Length Comparisons

Mean lengths of larval bay anchovy differed among years, regions, and depth layers. Bay-wide mean length was highest in 1996 (13.7 mm) and lowest in 1997 (5.3 mm) (Figure 15, Table 13). Mean larval lengths in 1995 (10.3 mm) and 1996 (13.7 mm) were significantly longer than those in 1997 (5.3 mm), 1998 (7.1 mm), and 1999 (5.4 mm) (ANOVA $P < 0.05$) (Table 13). Regionally, observed mean lengths were longest in the upper bay and shortest in the mid bay in 1995, 1997, and 1999, although the

Table 11. Yearly survey and regional above- and below-pycnocline mean larval bay anchovy abundances (m^{-2}) for TIES summer surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. There were no significant differences found between depths within regions or years (t-test $P > 0.05$). Above = above pycnocline; Below = below pycnocline.

Upper Bay

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	0.08	0	0.3	0.9	0.8	0.4
SE	0.03	0	0.1	0.8	0.4	0.2
Below	0.01	0	0.06	0.2	0.5	0.1
SE	0.007	0	0.03	0.07	0.3	0.09

Mid Bay

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	3.4	0.05	12.2	1.5	2.7	4.0
SE	1.2	0.02	3.7	0.7	1.2	2.1
Below	1.5	0.1	20.6	5.5	1.6	5.9
SE	0.8	0.06	5.5	5.1	0.9	3.8

Lower Bay

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	14.8	10.5	21.3	59.8	17.6	24.8
SE	4.5	3.6	9.6	14.8	5.6	8.9
Below	17.9	3.2	18.4	21.2	5.8	13.3
SE	5.6	1.0	7.2	4.6	1.5	3.7

Bay-wide

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	6.8	3.5	14.0	30.5	9.2	12.8
SE	1.9	1.5	4.8	8.8	3.0	4.7
Below	7.2	1.1	15.2	12.2	3.3	7.8
SE	2.4	0.5	4.0	3.1	0.8	2.6

Table 12. Yearly survey and regional above- and below-pycnocline mean larval bay anchovy densities (m^{-3}) for TIES summer surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. For within-year and total depth comparisons for each region and bay-wide, different superscripts indicate significant differences (t-test $P < 0.05$). Above = above pycnocline; Below = below pycnocline.

Upper Bay

Pycnocline Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	0.01	0	0.05	0.2	0.2	0.08
SE	0.006	0	0.02	0.1	0.1	0.04
Below	0.003	0	0.01	0.05	0.2	0.06
SE	0.002	0	0.004	0.02	0.1	0.05

Mid Bay

Pycnocline Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	0.6	0.01	1.9 ^a	0.2	0.4	0.6
SE	0.2	0.004	0.4	0.1	0.1	0.3
Below	0.3	0.02	6.0 ^b	1.3	0.8	1.7
SE	0.1	0.01	1.7	1.3	0.3	1.1

Lower Bay

Pycnocline Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	3.0	1.9	3.7	10.0	2.9	4.3
SE	0.8	0.6	1.6	2.3	0.9	1.5
Below	3.5	0.8	5.9	5.3	3.5	3.8
SE	1.0	0.4	2.4	1.3	1.2	0.9

Bay-wide

Pycnocline Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	1.4	0.6	2.4	5.1	1.5	2.2
SE	0.4	0.3	0.8	1.4	0.5	0.8
Below	1.4	0.3	4.7	3.1	1.9	2.3
SE	0.4	0.1	1.3	0.8	0.6	0.8

Table 13. Yearly survey and regional mean larval bay anchovy total lengths (mm) for TIES summer surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. For within-year and total regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$).

Bay Region	Year					Total
	1995	1996	1997	1998	1999	
Upper	15.7 ^{ab}	-	13.2	10.3 ^{ab}	8.4	10.0
SE	14.8	-	7.3	4.3	2.0	7.4
Mid	6.3 ^a	10.1	4.5	14.3 ^b	4.0	6.0
SE	1.7	5.8	0.7	1.5	1.1	1.8
Lower	10.9 ^b	13.8	5.8	6.7 ^a	5.5	7.6
SE	0.6	0.6	0.5	0.3	0.3	0.9
Bay-wide						
Mean	10.3 ^c	13.7 ^c	5.3 ^a	7.1 ^b	5.4 ^{ab}	7.1
SE	0.5	1.3	0.4	0.3	0.7	1.1

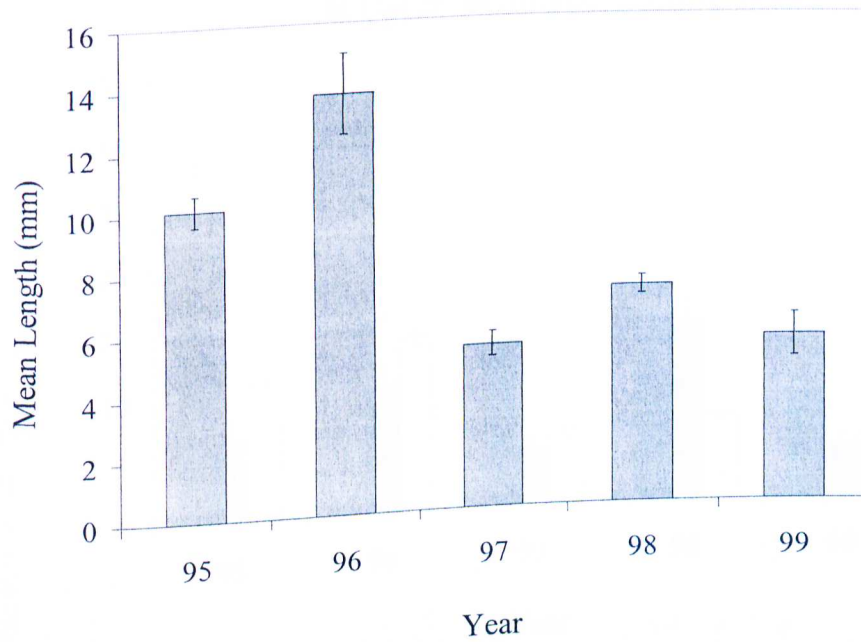


Figure 15. Bay-wide mean total lengths (mm) of larval bay anchovy during summer TIES surveys in Chesapeake Bay from 1995-1999. Error bars represent +/- 1 SE.

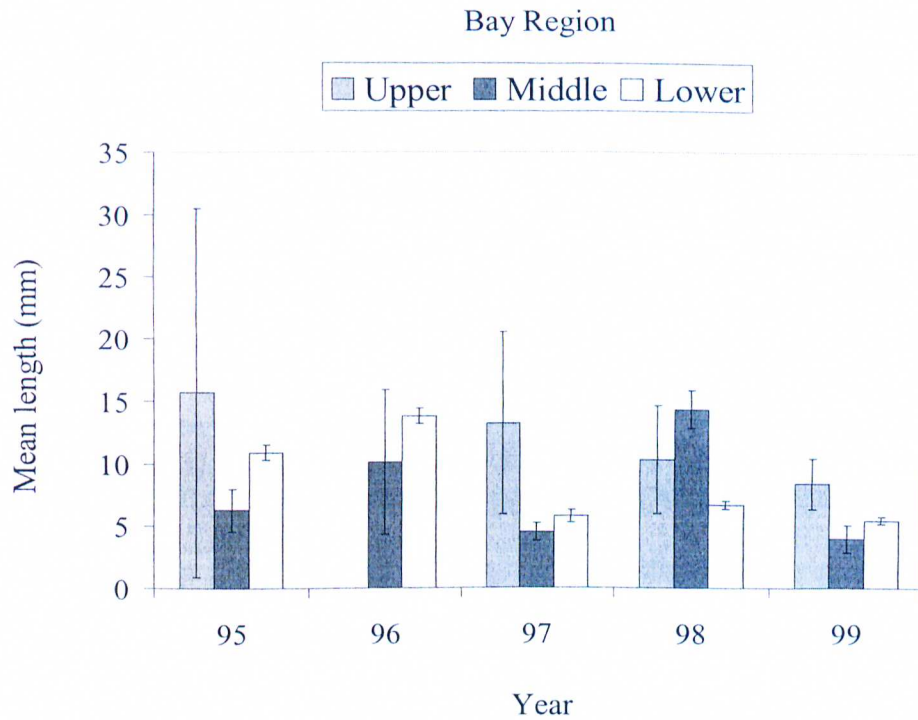


Figure 16. Regional mean total lengths (mm) of larval bay anchovy from summer TIES surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. Error bars represent +/- 1 SE.

differences were not significant (ANOVA $P > 0.05$) (Figure 16, Table 13). In contrast, in 1998 the largest larvae were in the mid bay (mean = 14.3 mm). There were no larvae in the upper bay samples in 1996, but the mid-bay larval mean length (10.1 mm) was still less than that of the lower bay (13.8 mm). For the combined-years regional lengths, larvae were largest in the upper bay (mean = 10.0 mm), and smaller in the mid- and lower-bay regions (means = 6.0 and 7.6 mm, respectively) (Table 13). However, none of the observed differences in mean length between regions differed significantly (ANOVA $P > 0.05$).

Mean bay-wide larval length was longer for below-pycnocline larvae in 1998 and 1999 (ANOVA $P < 0.05$), but did not differ significantly between the depth layers in 1995-1997 (Table 14). In 1998, mean larval length was significantly longer above, rather than below, the pycnocline in the upper-bay region, but mean length was significantly shorter above the pycnocline in the lower bay in that year (ANOVA $P < 0.05$). For combined-years, there were no differences in bay-wide mean lengths above and below the pycnocline (Table 14).

Relative length frequencies (LFs) varied annually (Figure 17) and regionally (Figures 18-22) in each year. In 1995 the mid-bay LF distribution differed from that of the upper- and lower-bay regions (Kolmogorov-Smirnov test $P < 0.05$) (Figure 18). There was no significant difference between the LF distributions of the mid and lower bay in 1996 (Kolmogorov-Smirnov test $P > 0.05$) (Figure 19). In 1997 and 1999, all three bay regions had different LF distributions (Kolmogorov-Smirnov test $P < 0.05$) (Figures 20 and 22). In 1998, the lower bay LF distribution was significantly different from LFs in the upper and mid bay (Kolmogorov-Smirnov test $P < 0.05$) (Figure 21).

Table 14. Yearly survey and regional above- and below-pycnocline mean larval bay anchovy total lengths (mm) for TIES summer surveys in Chesapeake Bay from 1995-1999. No larvae were collected in the upper-bay samples in 1996. For within-year and total depth comparisons for each region and bay-wide, different superscripts indicate significant differences (t-test $P < 0.05$). Above = above pycnocline; Below = below pycnocline.

Upper Bay

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	16.7	-	12.8	11.1 ^b	7.4	10.1
SE	3.3	-	1.7	0.7	1.1	1.1
Below	9.3	-	15.3	6.7 ^a	9.3	9.1
SE	8.1	-	4.1	1.7	1.5	1.9

Mid Bay

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	6.4	13.9	4.5	13.3	4.2	5.5
SE	0.8	3.4	0.5	0.9	0.3	1.9
Below	6.2	9.0	4.4	14.5	3.9	6.4
SE	1.3	2.4	0.4	0.5	0.4	1.6

Lower Bay

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	10.5	14.0	6.1	6.0 ^a	5.1	7.1
SE	1.0	0.7	0.6	0.3	0.4	1.1
Below	11.3	13.0	5.6	8.4 ^b	6.5	8.5
SE	0.9	1.2	0.7	0.6	0.6	1.5

Bay-wide

Depth	Year					Total
	1995	1996	1997	1998	1999	
Above	9.8	14.0	5.7	6.1 ^a	5.1 ^a	6.7
SE	0.7	0.5	0.4	0.3	0.3	1.0
Below	10.9	12.8	5.1	9.1 ^b	6.2 ^b	7.7
SE	0.7	1.0	0.4	0.5	0.5	1.3

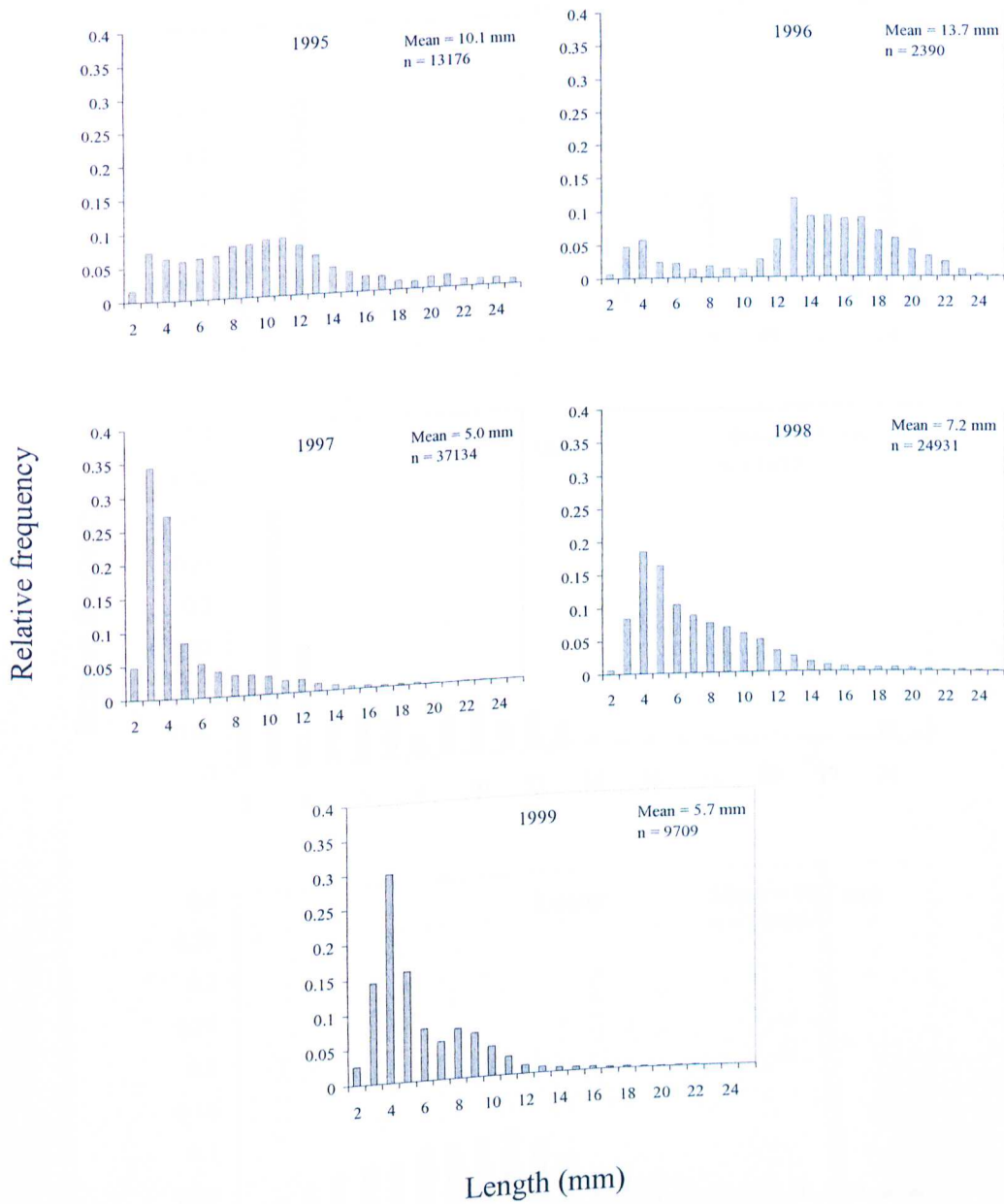


Figure 17. Yearly survey bay-wide relative length-frequencies of larval bay anchovy in Chesapeake Bay from 1995-1999. n represents the number of larvae collected in each year from which the length-frequency distributions were developed.

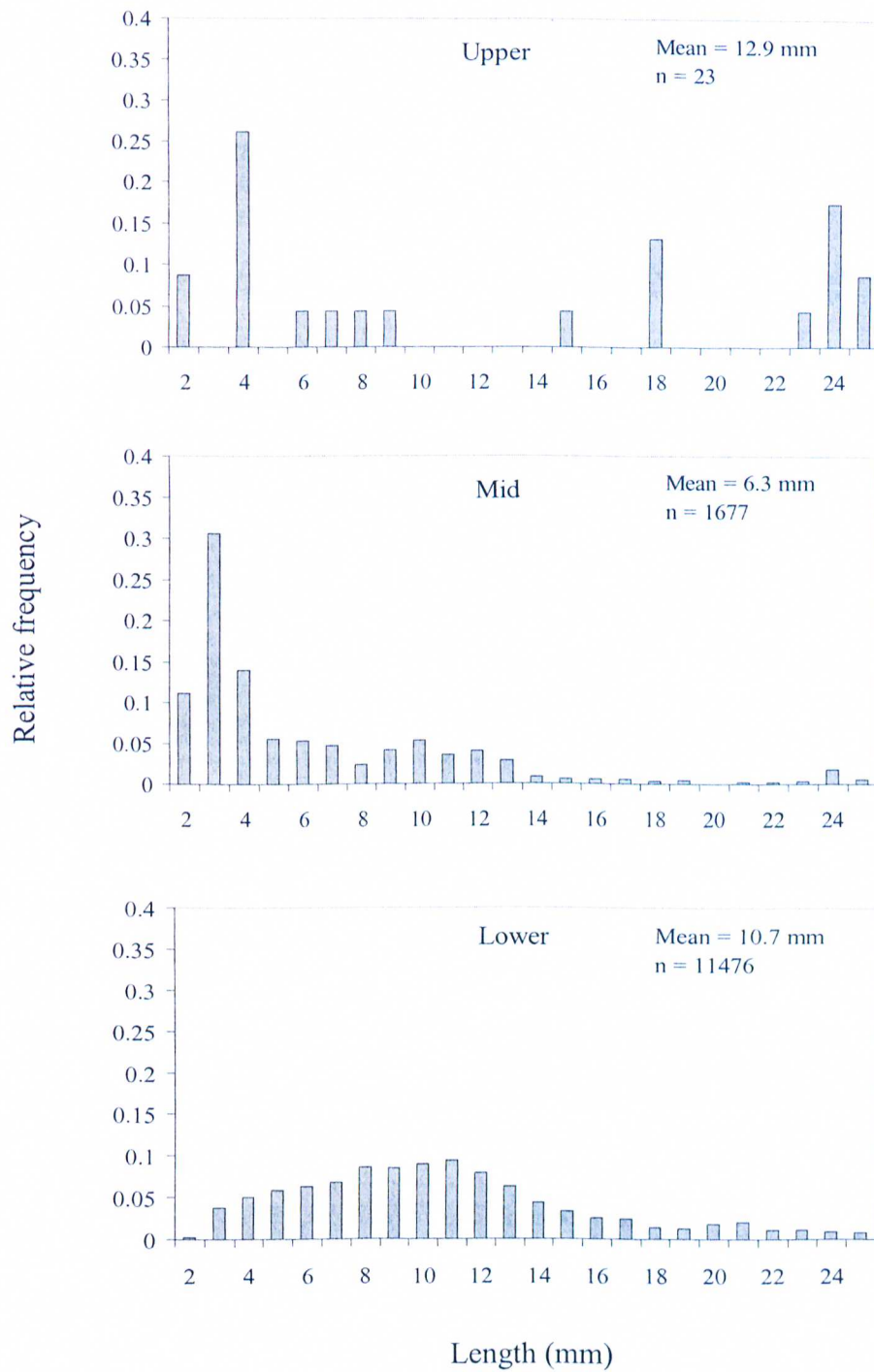


Figure 18. 1995 regional (upper, mid, and lower bay) relative length-frequencies of larval bay anchovy in Chesapeake Bay. n represents the number of larvae collected in each region from which the length-frequency distributions were developed.

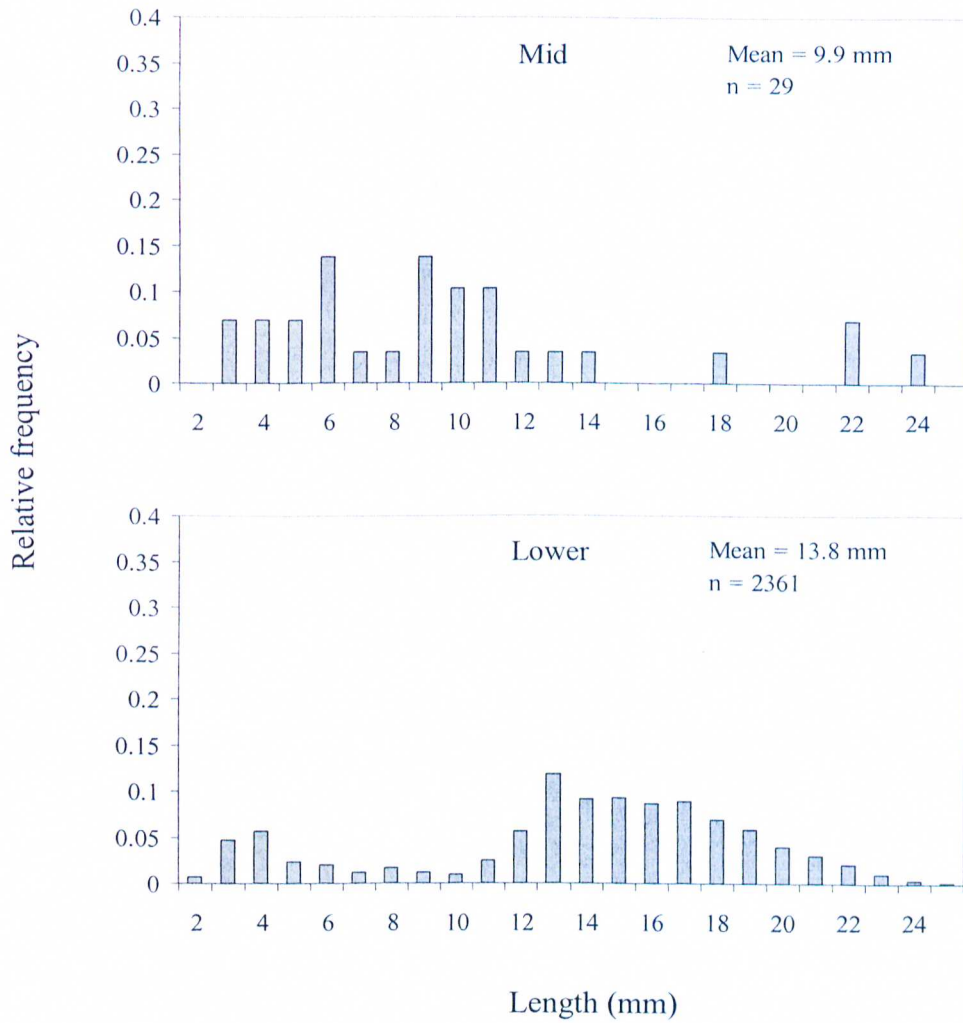


Figure 19. 1996 regional (mid and lower bay) relative length-frequencies of larval bay anchovy in Chesapeake Bay. No larvae were collected in the upper-bay samples. n represents the number of larvae collected in each region from which the length-frequency distributions were developed.

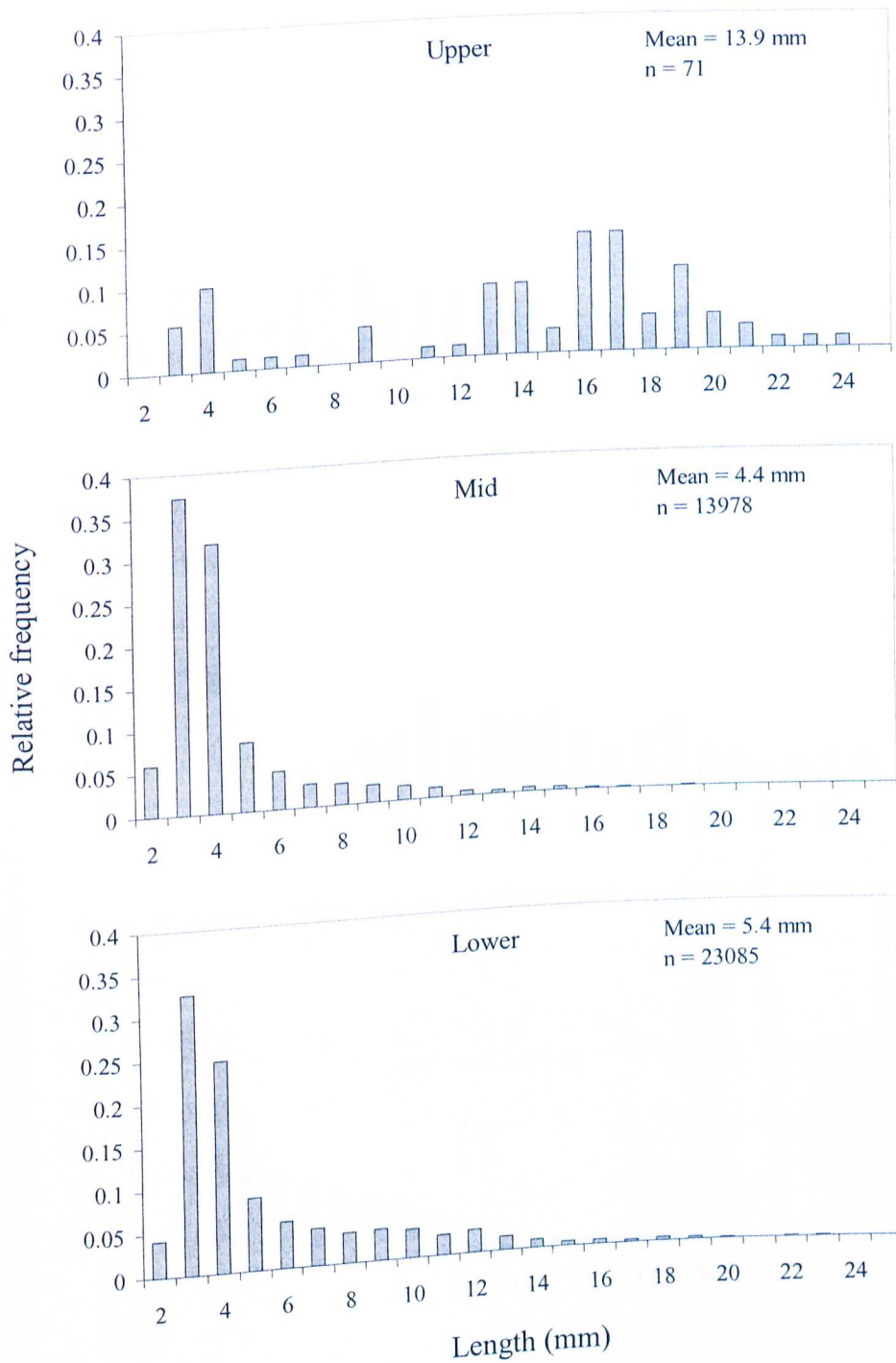


Figure 20. 1997 regional (upper, mid, and lower bay) relative length-frequencies of larval bay anchovy in Chesapeake Bay. n represents the number of larvae collected in each region from which the length-frequency distributions were developed.

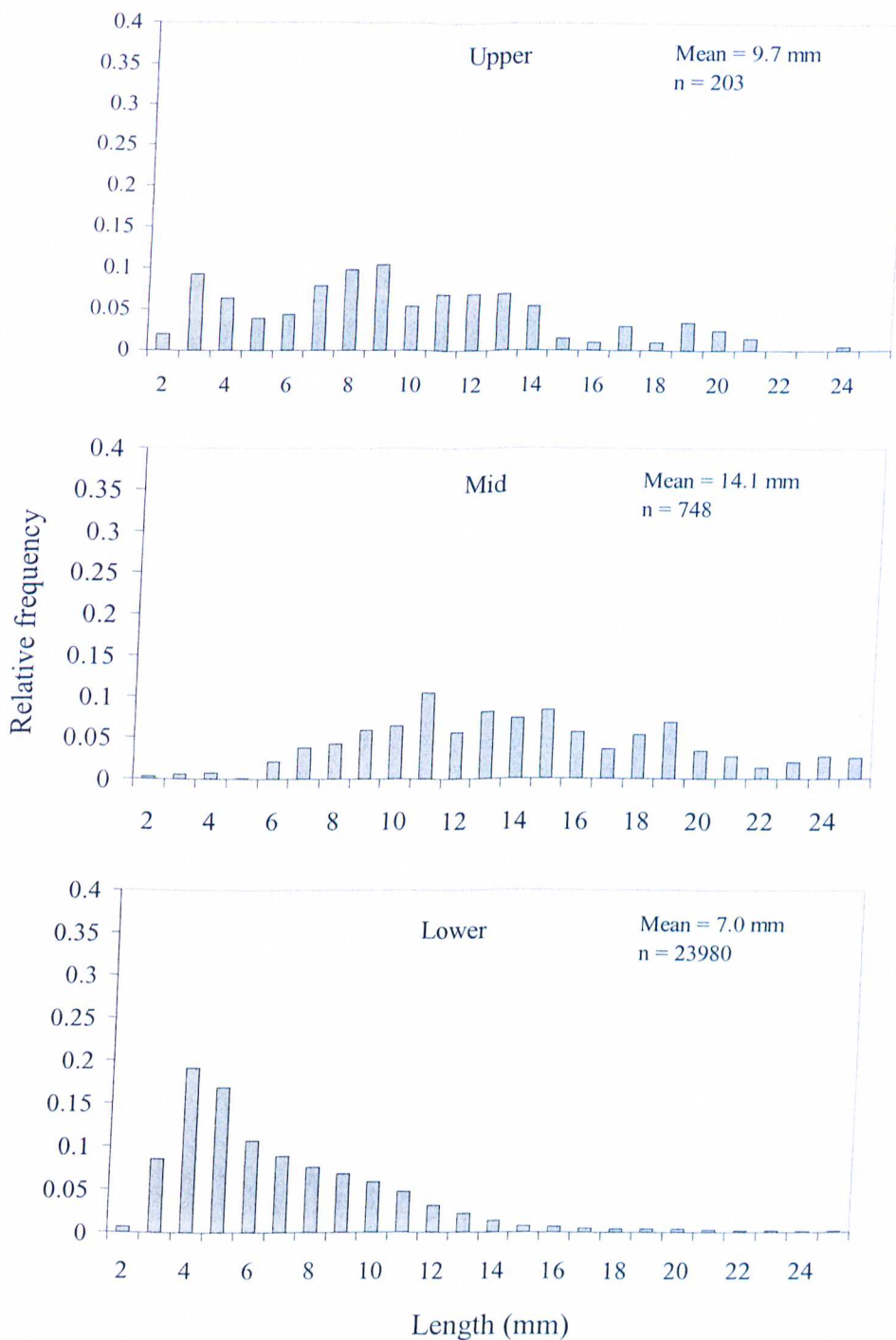


Figure 21. 1998 regional (upper, mid, and lower bay) relative length-frequencies of larval bay anchovy in Chesapeake Bay. n represents the number of larvae collected in each region from which the length-frequency distributions were developed.

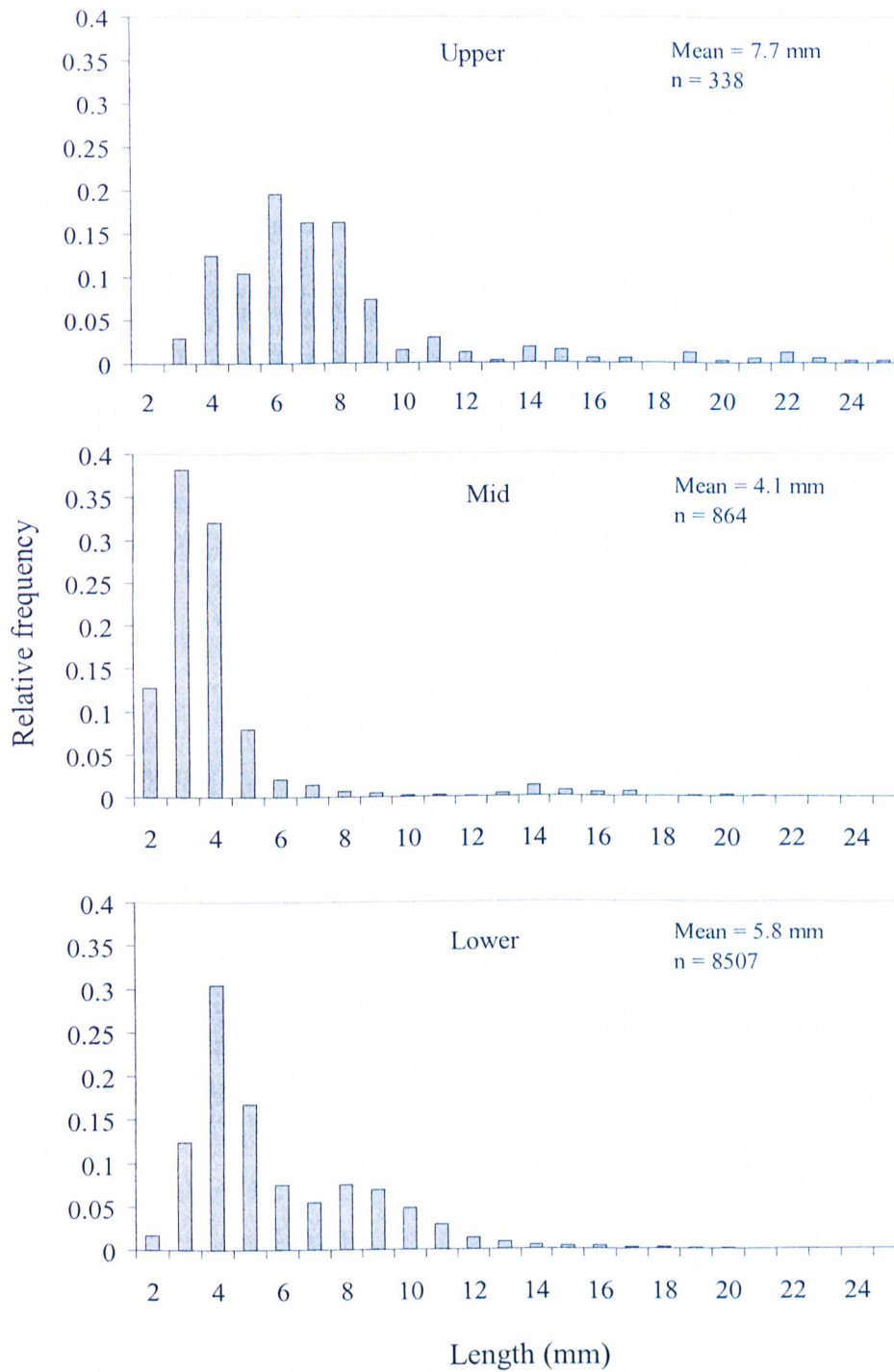


Figure 22. 1999 regional (upper, mid, and lower bay) relative length-frequencies of larval bay anchovy in Chesapeake Bay. n represents the number of larvae collected in each region from which the length-frequency distributions were developed.

LF distributions were not always unimodal. The bay-wide LF distribution in 1995 had three modes: the primary mode at 11 mm, a secondary mode at 3 mm, and a tertiary mode at 21 mm (Figure 17). The bay-wide LF distribution in 1996 was bimodal, with modes at 13 mm and 4 mm (Figure 17). However, the bay-wide LF distributions for 1997-1999 were all unimodal, with the small modal lengths ranging from 3 to 4 mm (Figure 17).

Regional LF distributions in the upper bay tended to be multimodal for each year. LFs were bimodal for the mid- and lower-bay regions in 1995 and 1996 (Figures 18-22). The mid- and lower-bay LF distributions in 1997-1999 were generally unimodal, with modal lengths between 3 and 4 mm (Figures 20-22). However, the mid bay in 1998 had four apparent modes: a primary mode at 11 mm, a secondary mode at 15 mm, a tertiary mode at 19 mm, and a quaternary mode at 24 mm (Figure 21).

Growth

Bay-wide and regional length-at-age data for larval bay anchovy were fit to a Gompertz growth model for each year and region (Figures 23-29). The pooled-years, bay-wide, and regional growth rates at age (days) were estimated from the Gompertz models for larvae 3-30 days of age (Tables 15 and 16). Maximum larval growth rates (mm/d) occurred from 8-12 days post-hatch during all years. The pooled-years bay-wide growth rate for < 30-day-old larvae was 0.75 mm/day based on the linear model fit to the data (Figure 23, Table 17). Individual year's bay-wide growth rates ranged from 0.68 mm/day in 1999 to 0.81 mm/day in 1998 (Table 17). Growth rates in 1995 and 1998 were significantly higher than in 1999 (ANCOVA $P < 0.05$).

Table 15. Bay-wide growth rates (mm/day) at age (days) for larval bay anchovy derived from data fit to the Gompertz model. Chesapeake Bay, 1995-1999.

Age (days)	Year					Pooled Mean
	1995	1996	1997	1998	1999	
3	0.64	0.64	0.69	0.62	0.68	0.66
4	0.73	0.69	0.75	0.68	0.75	0.73
5	0.82	0.73	0.80	0.73	0.81	0.78
6	0.89	0.77	0.85	0.78	0.86	0.83
7	0.94	0.80	0.88	0.82	0.89	0.87
8	0.98	0.82	0.90	0.85	0.91	0.89
9	1.00	0.83	0.91	0.87	0.91	0.91
10	1.01	0.84	0.91	0.89	0.90	0.91
11	1.00	0.84	0.91	0.90	0.88	0.90
12	0.99	0.84	0.89	0.90	0.85	0.89
13	0.96	0.83	0.87	0.90	0.82	0.87
14	0.92	0.82	0.84	0.89	0.78	0.84
15	0.88	0.80	0.81	0.87	0.73	0.81
16	0.84	0.78	0.78	0.86	0.69	0.78
17	0.79	0.75	0.74	0.83	0.64	0.74
18	0.74	0.72	0.70	0.81	0.59	0.70
19	0.69	0.70	0.66	0.78	0.55	0.66
20	0.63	0.67	0.62	0.75	0.50	0.62
21	0.59	0.63	0.58	0.72	0.46	0.58
22	0.54	0.60	0.54	0.68	0.42	0.54
23	0.49	0.57	0.51	0.65	0.38	0.50
24	0.45	0.54	0.47	0.62	0.35	0.46
25	0.41	0.51	0.44	0.58	0.31	0.43
26	0.37	0.48	0.40	0.55	0.28	0.39
27	0.34	0.45	0.37	0.52	0.26	0.36
28	0.31	0.42	0.34	0.49	0.23	0.33
29	0.28	0.40	0.31	0.46	0.21	0.30
30	0.25	0.37	0.29	0.43	0.19	0.28

Table 16. Regional (upper, mid, and lower bay) growth rates (mm/day) at age (days) for larval bay anchovy derived from data fit to the Gompertz model. Chesapeake Bay, 1995-1999. No larvae were collected in the upper bay in 1996.

Age (days)	Year														
	1995			1996		1997			1998			1999			
	Upper	Mid	Lower	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	
3	0.45	0.64	0.65	0.70	0.57	0.70	0.75	0.53	0.63	0.60	0.64	0.70	0.56	0.50	
4	0.68	0.73	0.74	0.75	0.61	0.76	0.83	0.56	0.70	0.65	0.71	0.77	0.59	0.53	
5	0.92	0.81	0.81	0.79	0.65	0.81	0.91	0.60	0.76	0.69	0.77	0.82	0.62	0.57	
6	1.12	0.87	0.87	0.83	0.69	0.86	0.96	0.63	0.81	0.73	0.82	0.87	0.64	0.59	
7	1.27	0.92	0.92	0.85	0.72	0.90	0.99	0.66	0.85	0.76	0.86	0.91	0.66	0.62	
8	1.35	0.96	0.95	0.87	0.75	0.93	1.00	0.68	0.88	0.79	0.90	0.94	0.67	0.64	
9	1.36	0.99	0.97	0.88	0.77	0.95	1.00	0.70	0.90	0.81	0.93	0.97	0.67	0.66	
10	1.32	1.00	0.98	0.88	0.78	0.96	0.98	0.71	0.90	0.83	0.95	0.98	0.66	0.68	
11	1.23	1.00	0.98	0.87	0.80	0.96	0.95	0.73	0.89	0.84	0.96	0.98	0.65	0.69	
12	1.12	0.99	0.97	0.86	0.80	0.95	0.91	0.73	0.88	0.85	0.96	0.98	0.64	0.70	
13	1.00	0.97	0.95	0.84	0.80	0.94	0.86	0.74	0.86	0.85	0.96	0.97	0.62	0.71	
14	0.88	0.94	0.92	0.82	0.80	0.92	0.80	0.73	0.83	0.85	0.95	0.95	0.60	0.71	
15	0.76	0.90	0.88	0.80	0.79	0.90	0.75	0.73	0.79	0.84	0.93	0.93	0.58	0.71	
16	0.64	0.86	0.84	0.77	0.78	0.87	0.69	0.72	0.76	0.84	0.91	0.90	0.55	0.71	
17	0.54	0.82	0.80	0.73	0.77	0.84	0.63	0.71	0.72	0.82	0.88	0.87	0.52	0.70	
18	0.46	0.77	0.76	0.70	0.76	0.81	0.58	0.70	0.67	0.81	0.85	0.84	0.50	0.69	
19	0.38	0.72	0.71	0.67	0.74	0.77	0.53	0.69	0.63	0.79	0.82	0.80	0.47	0.68	
20	0.31	0.68	0.66	0.63	0.72	0.73	0.48	0.67	0.59	0.77	0.79	0.76	0.44	0.67	

Table 16 (cont'd)

Age (days)	Year														
	1995			1996		1997			1998			1999			
	Upper	Mid	Lower	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	Upper	Mid	Lower	
21	0.26	0.63	0.62	0.60	0.69	0.70	0.43	0.65	0.55	0.75	0.75	0.73	0.41	0.65	
22	0.21	0.58	0.57	0.56	0.67	0.66	0.39	0.63	0.51	0.73	0.72	0.69	0.38	0.64	
23	0.17	0.54	0.53	0.53	0.65	0.62	0.35	0.61	0.47	0.70	0.68	0.65	0.36	0.62	
24	0.14	0.49	0.49	0.49	0.62	0.58	0.31	0.59	0.43	0.68	0.65	0.61	0.33	0.60	
25	0.12	0.45	0.45	0.46	0.60	0.55	0.28	0.57	0.40	0.65	0.61	0.57	0.31	0.58	
26	0.10	0.42	0.41	0.43	0.57	0.51	0.25	0.55	0.36	0.63	0.57	0.54	0.29	0.56	
27	0.08	0.38	0.38	0.40	0.54	0.48	0.22	0.52	0.33	0.60	0.54	0.50	0.27	0.54	
28	0.06	0.35	0.34	0.37	0.52	0.45	0.19	0.50	0.30	0.57	0.51	0.47	0.24	0.52	
29	0.05	0.32	0.31	0.35	0.49	0.42	0.17	0.48	0.28	0.55	0.47	0.44	0.23	0.50	
30	0.04	0.29	0.29	0.32	0.47	0.39	0.15	0.46	0.25	0.52	0.44	0.40	0.21	0.48	

Table 17. Yearly survey and regional daily growth rates (mm/day) of larval bay anchovy in Chesapeake Bay from 1995-1999. Growth rates were estimated from the linear regression of length on age of larvae <30 days of age. No larvae were collected in the upper bay in 1996. For within-year and pooled regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (ANCOVA $P < 0.05$).

		Growth Rate (mm/day)					
		Year					
Bay Region	1995	1996	1997	1998	1999	Pooled	
Upper	0.74	-	0.83 ^a	0.77 ^b	0.82 ^a	0.83 ^a	
SE	0.13	-	0.03	0.03	0.05	0.02	
Mid	0.77	0.83	0.80 ^{ab}	0.76 ^b	0.55 ^b	0.71 ^b	
SE	0.04	0.09	0.05	0.03	0.03	0.03	
Lower	0.80	0.73	0.70 ^b	0.86 ^a	0.68 ^a	0.75 ^b	
SE	0.06	0.04	0.04	0.03	0.05	0.02	
Bay-wide							
Mean	0.78 ^a	0.74 ^{ab}	0.76 ^{ab}	0.81 ^a	0.68 ^b	0.75	
SE	0.03	0.04	0.03	0.02	0.04	0.01	

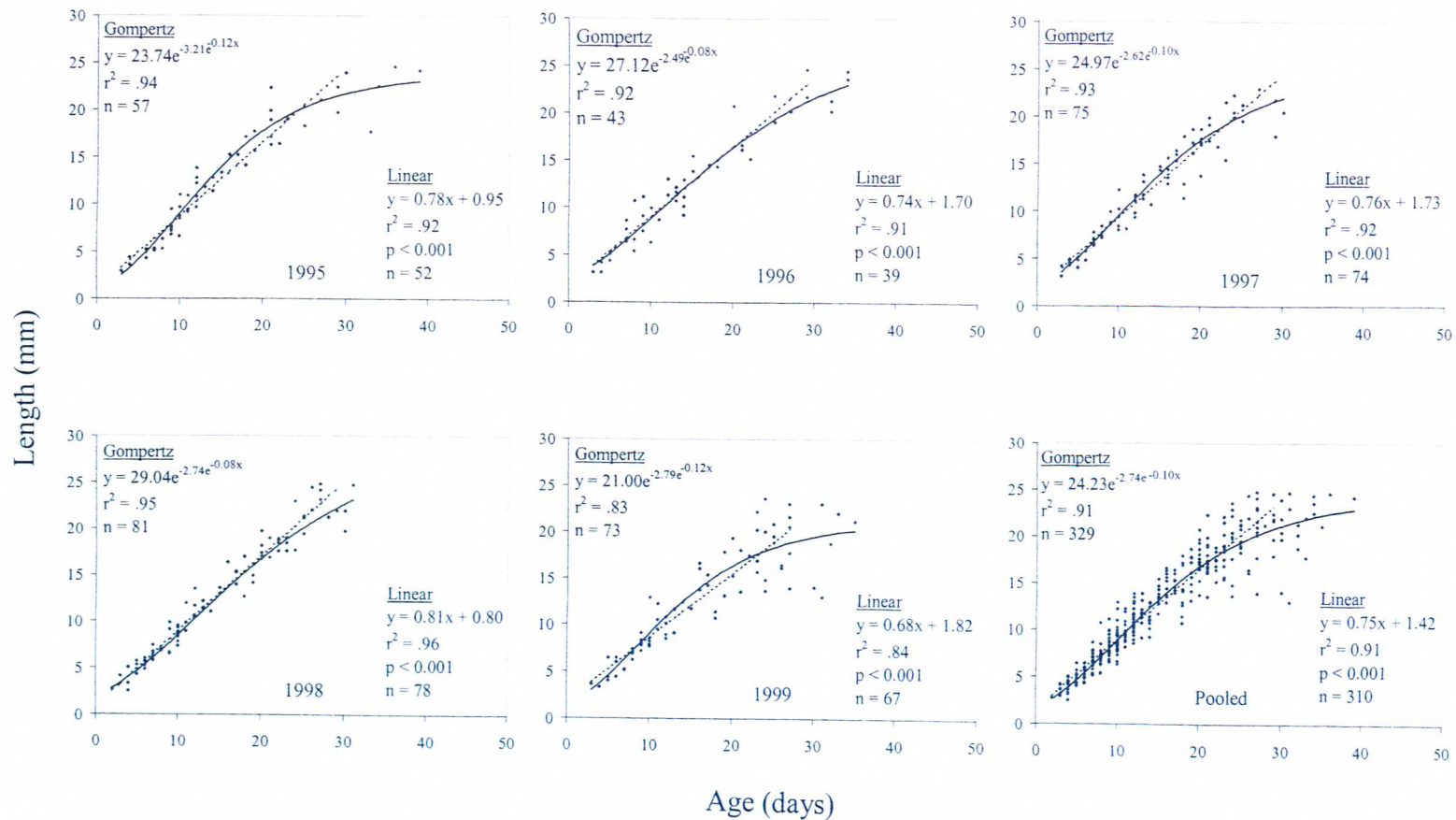


Figure 23. Bay-wide Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy from summer TIES surveys in Chesapeake Bay from 1995-1999. Y = larval total length (mm), x = larval age (days).

Gompertz model is represented by solid line; linear model is represented by dashed line.

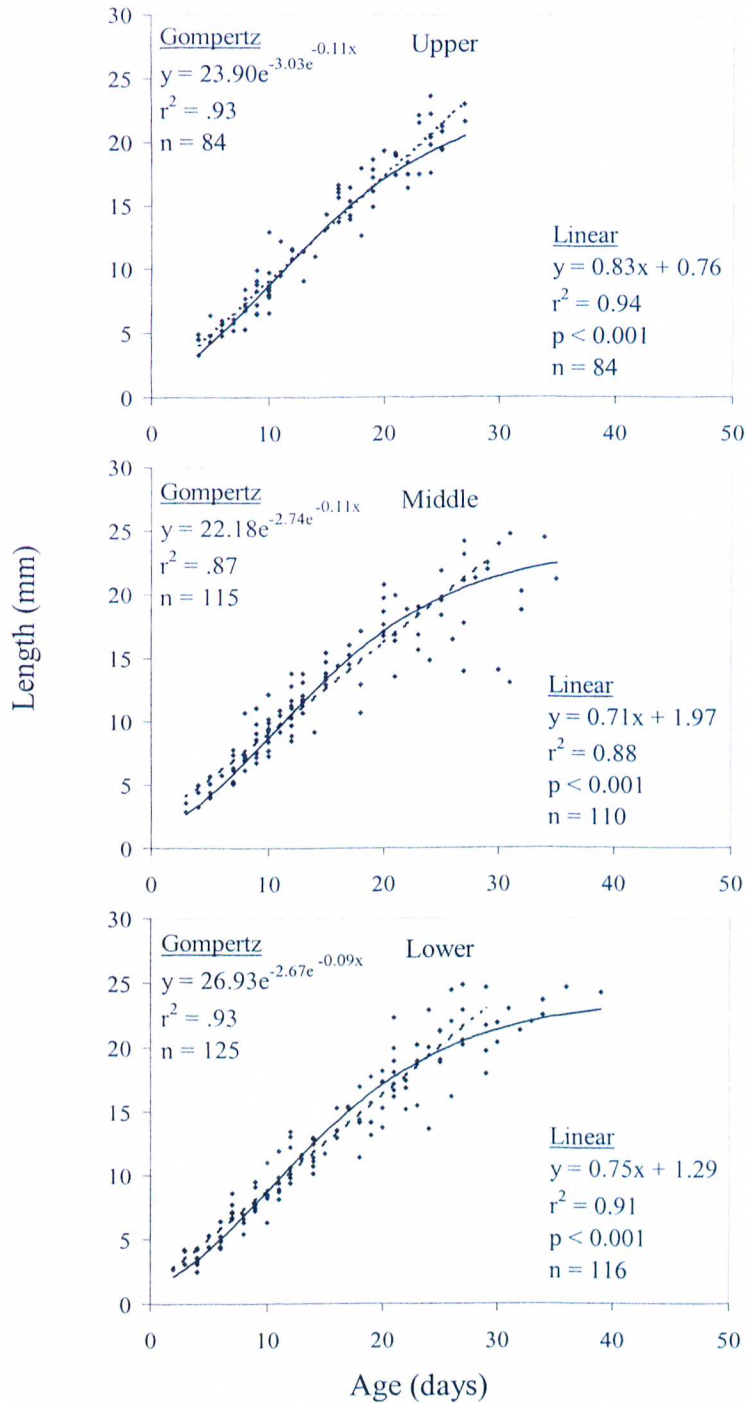


Figure 24. Pooled (all years data) regional (upper, middle, and lower bay) Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy from summer TIES surveys in Chesapeake Bay from 1995-1999. Y = larval total length (mm), x = larval age (days). Gompertz models are represented by solid lines; linear models are represented by dashed lines.

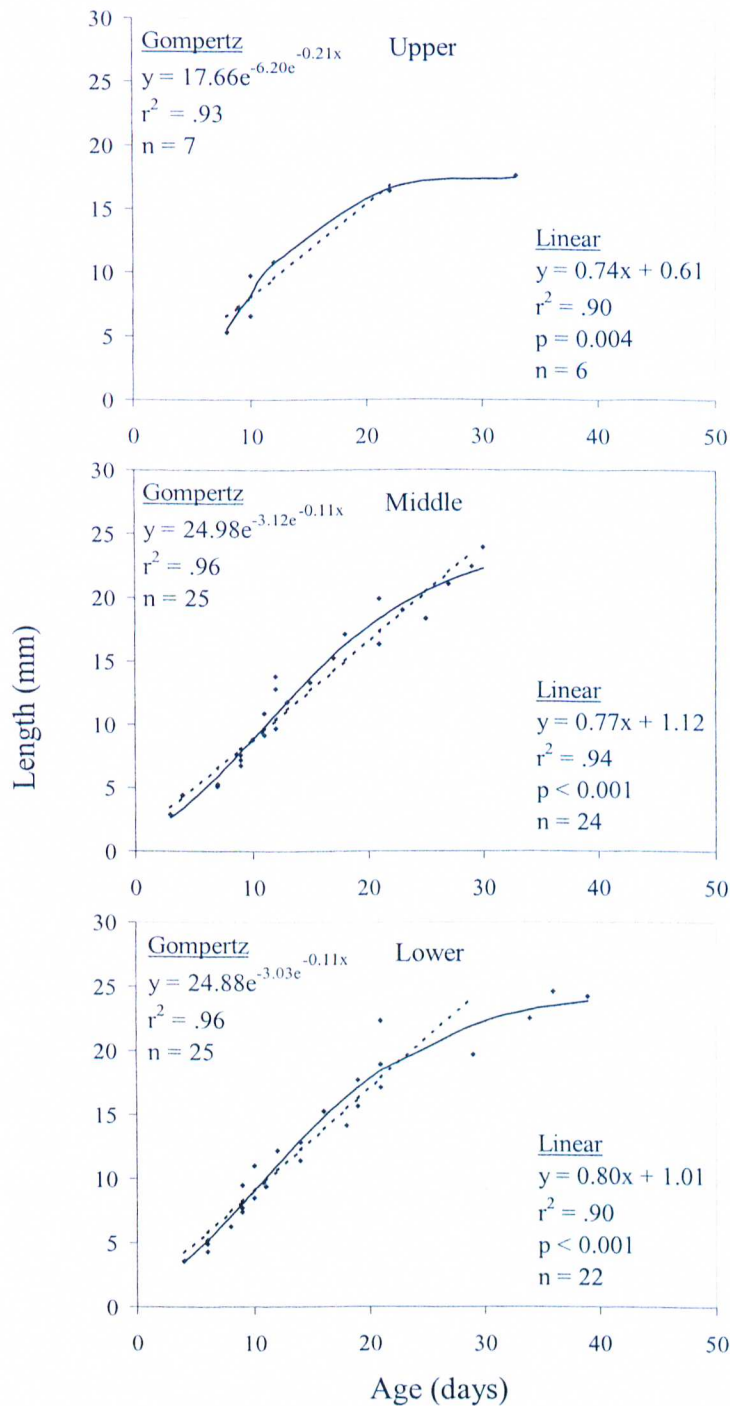


Figure 25. 1995 regional (upper, middle, and lower bay) Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy in Chesapeake Bay. Y = larval total length (mm), x = larval age (days). Gompertz models are represented by solid lines; linear models are represented by dashed lines.

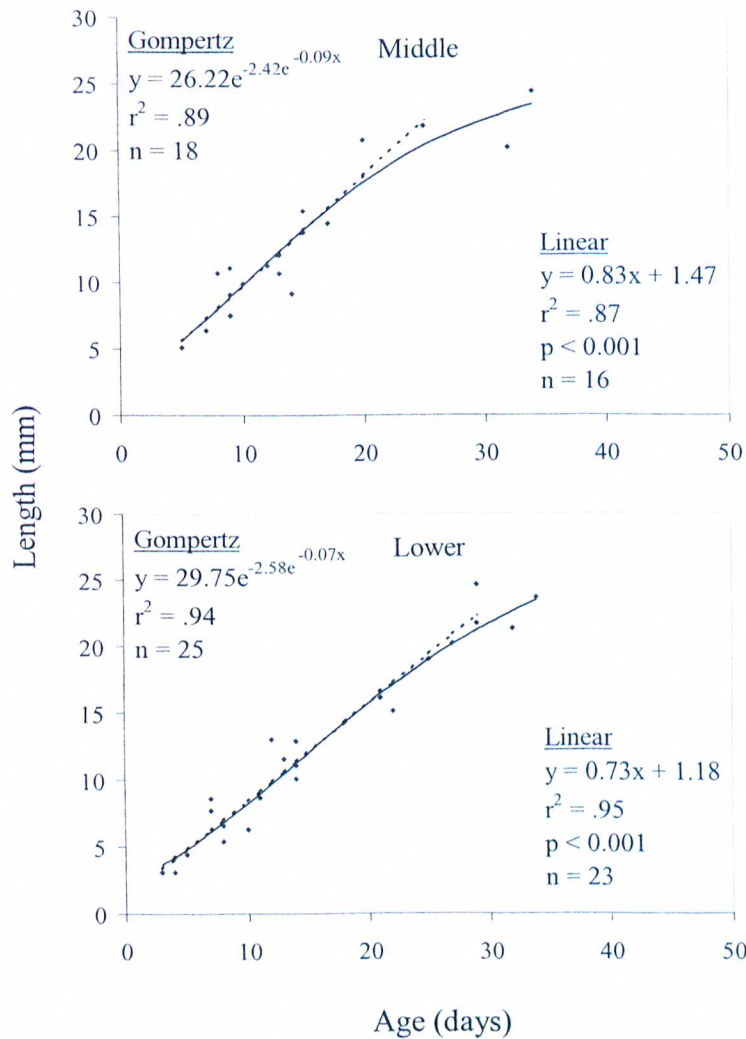


Figure 26. 1996 regional (middle and lower bay) Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy in Chesapeake Bay. No larvae were collected in the upper bay in this year. Y = larval total length (mm), x = larval age (days). Gompertz models are represented by solid lines; linear models are represented by dashed lines.

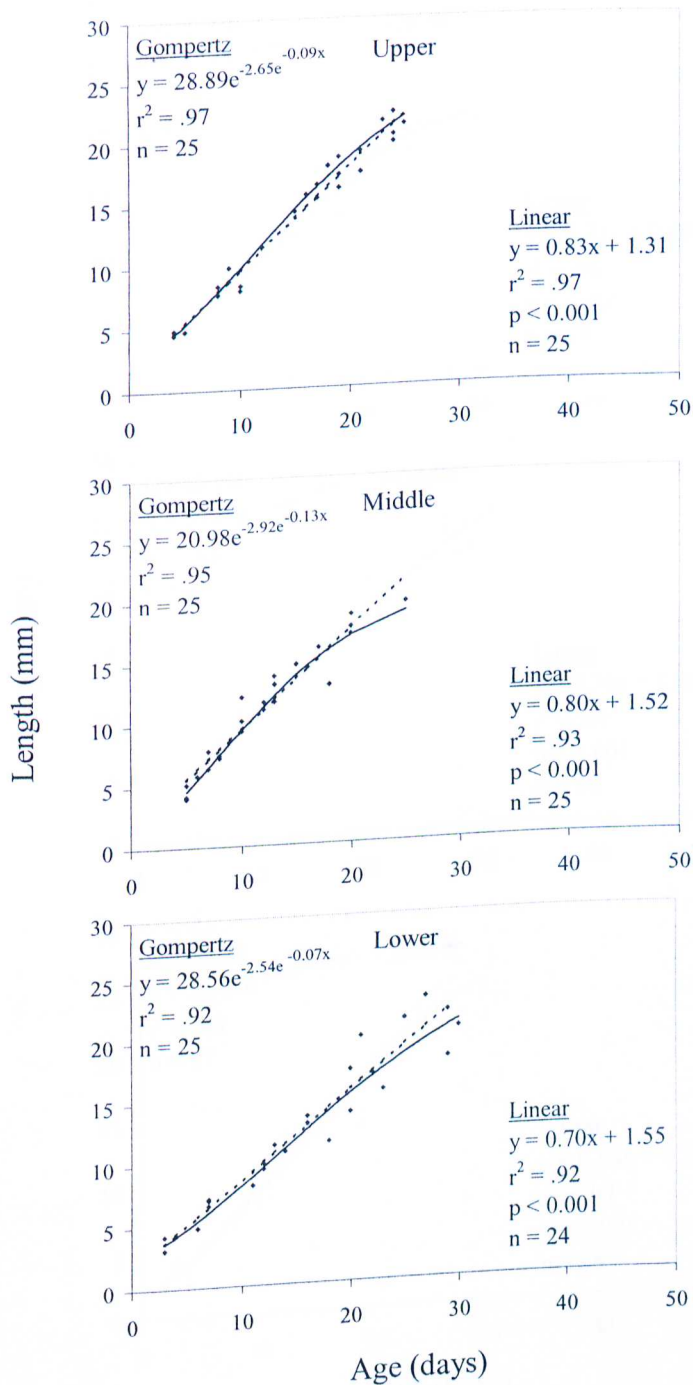


Figure 27. 1997 regional (upper, middle, and lower bay) Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy in Chesapeake Bay. Y = larval total length (mm), x = larval age (days). Gompertz models are represented by solid lines; linear models are represented by dashed lines.

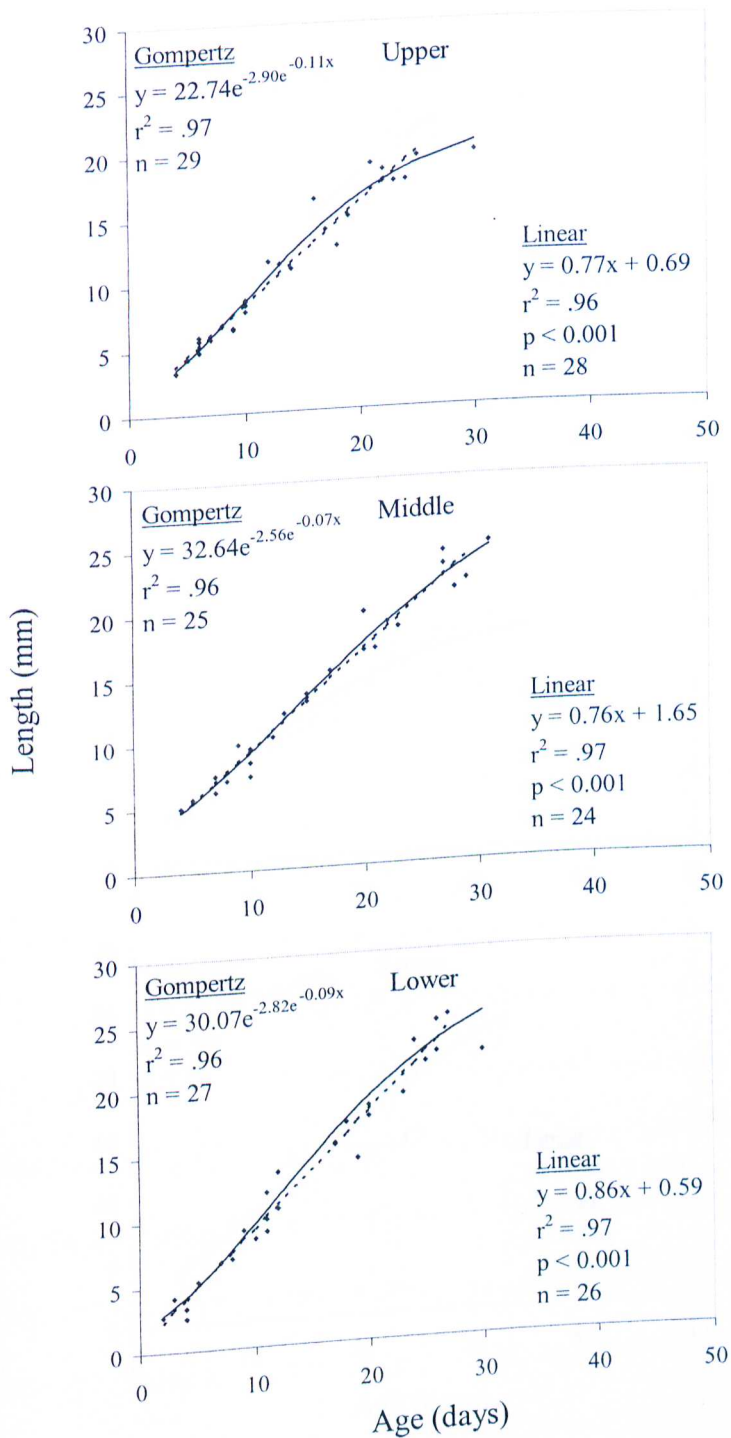


Figure 28. 1998 regional (upper, middle, and lower bay) Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy in Chesapeake Bay. Y = larval total length (mm), x = larval age (days). Gompertz models are represented by solid lines; linear models are represented by dashed lines.

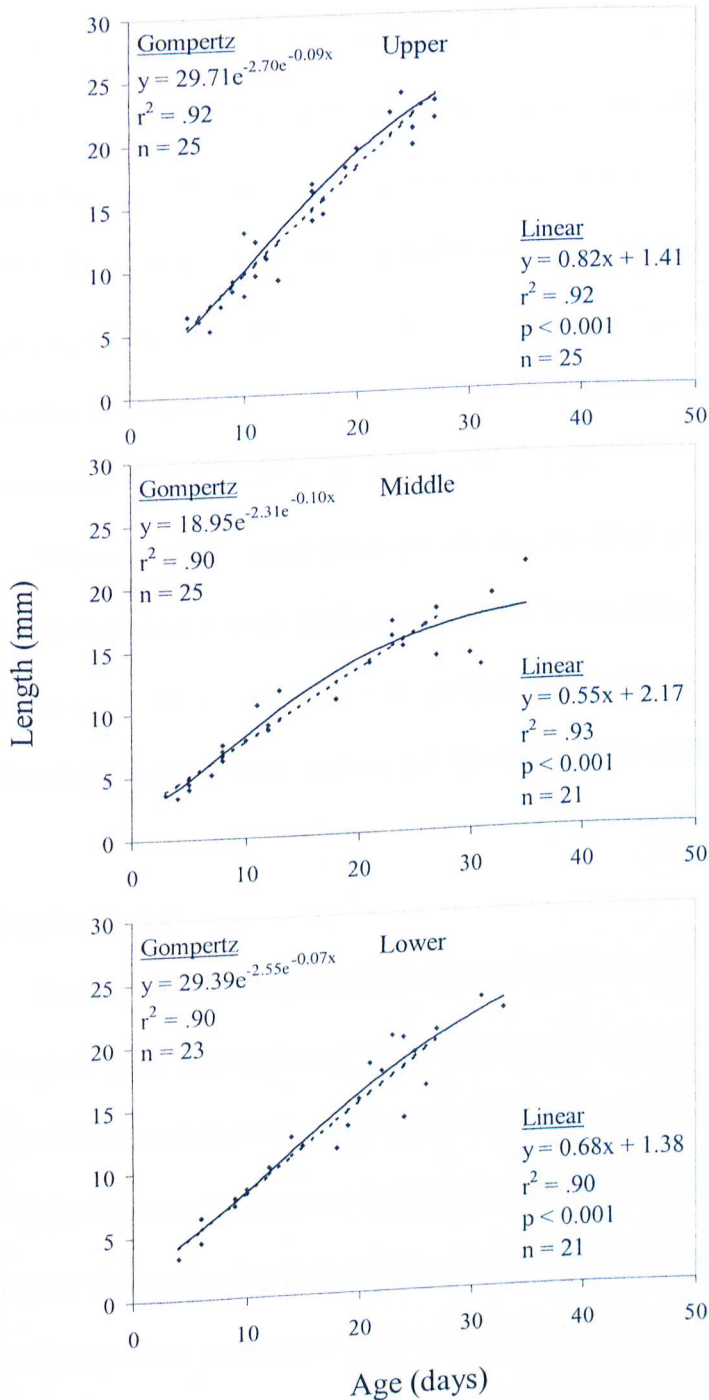


Figure 29. 1999 regional (upper, middle, and lower bay) Gompertz and linear (for larvae <30 days of age) growth models for larval bay anchovy in Chesapeake Bay. Y = larval total length (mm), x = larval age (days). Gompertz models are represented by solid lines; linear models are represented by dashed lines.

The pooled-years growth rate in the upper bay (0.83 mm/day) was significantly higher than growth rates in the mid (0.71 mm/day) and lower (0.75 mm/day) bay (Figure 24, Table 17). Regional growth rates within years were higher in the upper bay than in the lower bay in 1997 and 1999, but were highest in the lower bay in 1998 (ANCOVA $P < 0.05$). There were no significant differences between the regional growth rates estimated in 1995 and 1996 (ANCOVA $P > 0.05$). The highest regional growth rate (0.86 mm/day) was estimated for the lower bay in 1998, while the lowest rate (0.55 mm/day) was estimated for the mid-bay region in 1999 (Table 17).

The estimated pooled-years growth rate of larvae collected above the pycnocline (0.77 mm/day) was slightly higher than that of larvae collected below the pycnocline (0.73 mm/day). However, there were no significant differences in growth rates of larvae in either depth layer within years or for the pooled data (ANCOVA $P > 0.05$) (Table 18).

Feeding Incidence

Feeding incidence (FI), the proportion of examined larvae with at least one prey item in their guts, varied among yearly surveys and regionally, but did not differ in larvae collected above or below the pycnocline. Highest regional FI tended to be in the upper bay, while the lowest FI was most often observed in larvae from the mid-bay region. FI was higher during the day than at night, and generally increased with larval size. Also, ingested prey items were more often in the hindguts rather than the foreguts of larvae.

Bay-wide FI was low, ranging from 0.09 in 1996 to 0.23 in 1998 (Figure 30, Table 19). FI in 1996 was significantly lower than in 1998 and 1999, while FI in 1998 was higher than in both 1996 and 1997 (χ^2 -test $P < 0.05$). Pooled over the five years,

Table 18. Yearly survey bay-wide above- and below-pycnocline daily growth rates (mm/day) of larval bay anchovy in Chesapeake Bay from 1995-1999. Growth rates were estimated from the linear regression of length on age for larvae <30 days of age. There were no significant differences between depths zones within years or for the pooled data (ANCOVA $P>0.05$).

Pycnocline Depth	Growth Rate (mm/day)					Pooled
	1995	1996	1997	1998	1999	
Above	0.81	0.74	0.80	0.83	0.66	0.77
SE	0.05	0.05	0.03	0.03	0.05	0.02
Below	0.76	0.74	0.72	0.78	0.69	0.73
SE	0.05	0.06	0.04	0.03	0.05	0.02

regional FI was significantly higher in the upper bay (0.27) than in the mid (0.13) or lower (0.17) bay (χ^2 -test $P < 0.05$). Regional FI was highest in the upper bay in 1995, 1997, and 1999, but not in 1998. There were no bay anchovy larvae collected in upper-bay samples in 1996. Mid-bay FI was lowest in all years except 1997 (Table 19). The highest regional FI was estimated for the upper bay in 1995 (0.43), while the lowest was estimated for the mid bay in 1996 (0.06).

Bay-wide, the above- and below-pycnocline FI did not differ significantly in any year or for the 5-year pooled data set (χ^2 -test $P > 0.05$) (Table 20). In a separate bay-wide survey during summer 1998 (Figure 2), FI was significantly higher above the pycnocline (0.26) than at the pycnocline (0.08) (χ^2 -test $P < 0.05$), while below-pycnocline FI was intermediate (Table 20). There was no significant difference in FI above or below the pycnocline within regions in any year (χ^2 -test $P > 0.05$).

TIES Tucker trawl collections were made during daylight, usually between 0900 and 2100 hrs. In a separate diel survey conducted from 30 July - 1 August 2000, larval FI was nine times higher during the day (0.27) than at night (0.03) (χ^2 -test $P < 0.0001$). In fact, the only food items found in the night samples were carapaces of large copepods in the hindguts of larvae collected soon after dusk, suggesting that these food items may have been consumed during the day, but were not fully digested or expelled when the larvae were captured.

The larval gut location in which prey items were found also was examined using the pooled data from all larvae with prey in their guts. Only 8% of prey items were located in the foreguts of larval bay anchovy, whereas 92% were in the hindguts (χ^2 -test $P < 0.0001$).

Table 19. Yearly survey and regional larval bay anchovy feeding incidences in Chesapeake Bay from 1995-1999. No larvae were collected in the upper bay in 1996. For within-year and pooled regional comparisons and between-year bay-wide comparisons, different superscripts indicate significant differences (Chi-square $P < 0.05$).

Bay Region	Year					Pooled
	1995	1996	1997	1998	1999	
Upper	0.43 ^a	-	0.25 ^a	0.22 ^{ab}	0.31 ^a	0.27 ^a
Mid	0.10 ^b	0.06	0.21 ^a	0.12 ^a	0.10 ^b	0.13 ^b
Lower	0.20 ^{ab}	0.09	0.09 ^b	0.30 ^b	0.13 ^b	0.17 ^b
Bay-wide	0.16 ^{abc}	0.09 ^a	0.16 ^{ab}	0.23 ^c	0.17 ^{bc}	0.17

Table 20. Bay-wide above- and below-pycnocline larval bay anchovy feeding incidences in Chesapeake Bay from 1995-1999. Feeding incidences were determined for above and below the pycnocline only, except for a separate bay-wide survey conducted at ten stations in 1998 (98DS), which also included samples taken at the pycnocline (Figure 2). There were no significant differences between depth zones within years or for the pooled data set (Chi-square $P>0.05$). For within-98DS depth comparisons, different superscripts indicate significant differences (Chi-square $P<0.05$). Above = above pycnocline; At = at pycnocline; Below = below pycnocline.

Depth	Year					Pooled	98DS
	1995	1996	1997	1998	1999		
Above	0.16	0.08	0.18	0.25	0.17	0.19	0.26 ^a
At							0.08 ^b
Below	0.17	0.04	0.12	0.21	0.18	0.16	0.14 ^{ab}

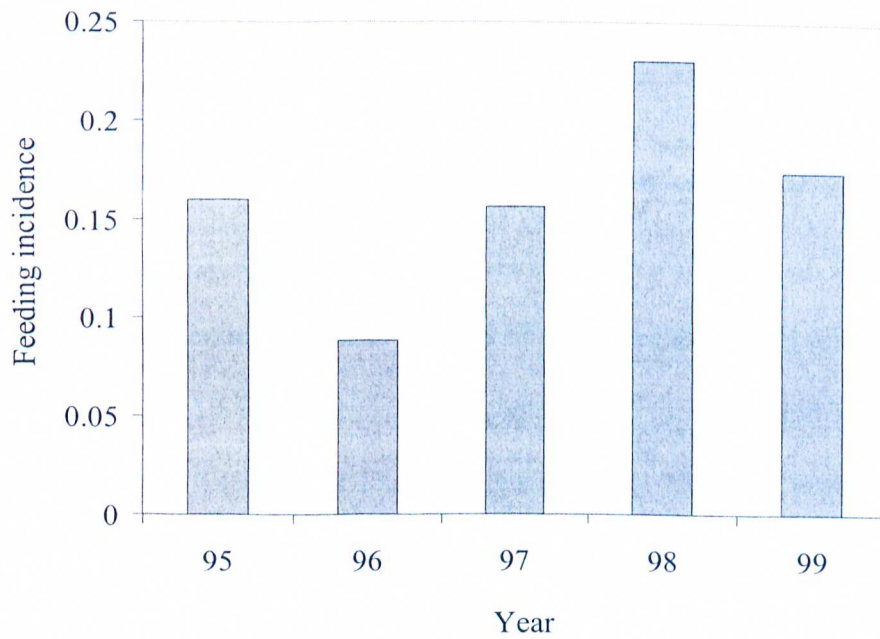


Figure 30. Yearly survey bay-wide feeding incidences of larval bay anchovy in Chesapeake Bay from 1995-1999.

For pooled data from the five years, FI clearly increased as larval size increased (Figure 31), from a low of 0.09 for 2.5-4.4 mm larvae to a high of 0.23 for 13.5-16.4 mm larvae (Table 21). This relationship was not as readily apparent when individual year's data were analyzed. However, in the two years where significant differences did occur (1998 and 1999), the largest size-class had higher FI than the smallest (χ^2 -test $P < 0.05$) (Table 21). For within larval size-class yearly survey comparisons, FI for 2.5-4.4 mm larvae was significantly higher in 1998 (0.17) than in 1999 (0.04) (χ^2 -test $P < 0.05$). Also, FI for large, 13.5-16.4 mm larvae was higher in 1998 (0.37) than in 1996 (0.05), 1997 (0.13), and 1999 (0.19). FI of 13.5-16.4 mm larvae in 1996 was lower than either 1995 (0.26) or 1998 (χ^2 -test $P < 0.05$). The intermediate larval size classes had similar FIs between years (χ^2 -test $P > 0.05$) (Table 21).

For the pooled 1995-1999 data, regional FI was highest in the upper bay and lowest in the mid-bay region for all larval size classes except 4.5-7.4 mm larvae, for which FI was lowest in the lower bay (Table 22). Much like the pooled years comparisons, the pooled FIs of the larger size classes were generally higher than the FIs of smaller size classes on a pooled regional basis (χ^2 -test $P < 0.05$) (Table 22).

There were no significant differences in pooled FI between above- and below-pycnocline larvae for any of the larval size classes (χ^2 -test $P > 0.05$) (Table 23). In addition, the FIs of the larger size classes were generally higher than the FIs of the smaller size classes for pooled above- and below-pycnocline larvae (χ^2 -test $P < 0.05$) (Table 23).

Table 21. Yearly survey and pooled feeding incidences for five size classes of larval bay anchovy in Chesapeake Bay from 1995-1999. For within-year and pooled larval size class comparisons, different letter superscripts indicate significant differences (Chi-square $P < 0.05$). For within larval size class yearly survey comparisons, different numeric superscripts indicate significant differences (Chi-square $P < 0.05$). No larvae in the 2.5-4.4 and 4.5-7.4 mm size classes were found with prey in their guts in 1996.

Size Class	Year					Pooled
	1995	1996	1997	1998	1999	
2.5-4.4 mm	¹² 0.16	¹² 0	¹² 0.07	¹ 0.17 ^a	² 0.04 ^a	0.09 ^a
4.5-7.4 mm	0.13	0	0.21	0.11 ^a	0.23 ^b	0.16 ^b
7.5-10.4 mm	0.15	0.17	0.16	0.20 ^a	0.21 ^b	0.18 ^{bc}
10.5-13.4 mm	0.12	0.19	0.21	0.21 ^a	0.19 ^b	0.19 ^{bc}
13.5-16.4 mm	²³ 0.26	¹ 0.05	¹² 0.13	³ 0.37 ^b	¹² 0.19 ^b	0.23 ^c

Table 22. Pooled regional feeding incidences for five size classes of larval bay anchovy in Chesapeake Bay from 1995-1999. For within-region larval size class comparisons, different letter superscripts indicate significant differences (Chi-square $P < 0.05$). For within larval size class regional comparisons, different numeric superscripts indicate significant differences (Chi-square $P < 0.05$). No larvae in the 2.5-4.4 mm size class were found with prey in their guts in any upper-bay samples.

Size Class	Bay Region		
	Upper	Mid	Lower
2.5-4.4 mm	0 ^a	0.06 ^a	0.12 ^{ab}
4.5-7.4 mm	¹ 0.26 ^b	¹² 0.16 ^b	² 0.10 ^a
7.5-10.4 mm	¹ 0.27 ^b	² 0.13 ^{ab}	¹² 0.19 ^{cb}
10.5-13.4 mm	¹ 0.33 ^b	² 0.16 ^b	² 0.16 ^{ab}
13.5-16.4 mm	¹ 0.32 ^b	² 0.13 ^{ab}	¹ 0.29 ^c

Table 23. Pooled above- and below-pycnocline feeding incidences for five size classes of larval bay anchovy in Chesapeake Bay from 1995-1999. For within-depth larval size class comparisons, different superscripts indicate significant differences (Chi-square $P < 0.05$). There were no significant differences between depth zones within larval size classes (Chi-square $P > 0.05$).

Size Class	Depth	
	Above Pycnocline	Below Pycnocline
2.5-4.4 mm	0.07 ^a	0.11 ^a
4.5-7.4 mm	0.18 ^b	0.13 ^{ab}
7.5-10.4 mm	0.17 ^b	0.20 ^{ab}
10.5-13.4 mm	0.23 ^b	0.16 ^{ab}
13.5-16.4 mm	0.26 ^b	0.21 ^b

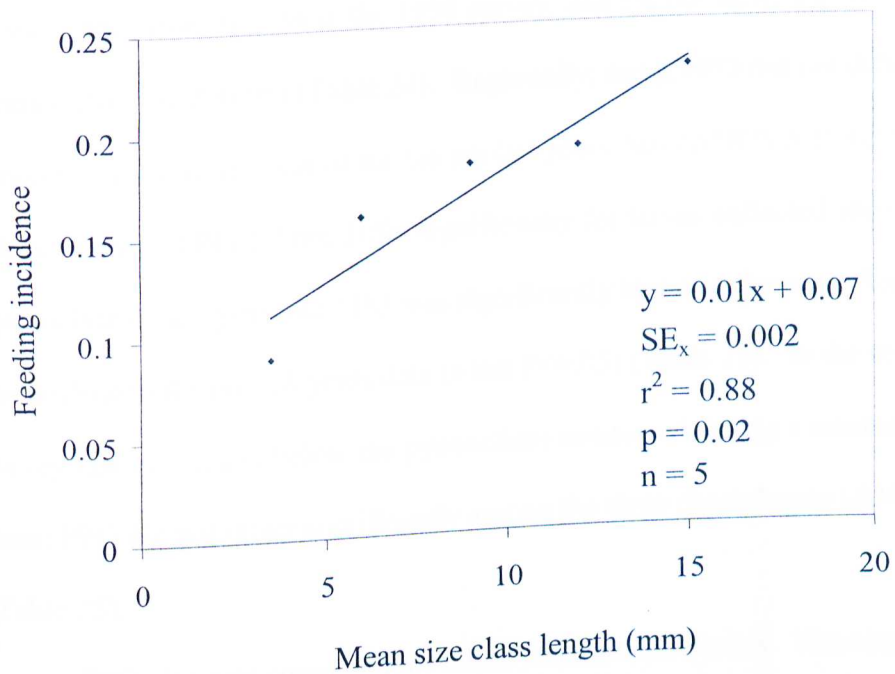


Figure 31. Linear regression of pooled-data feeding incidence vs. mean length of bay anchovy larvae in each of five larval size classes in Chesapeake Bay from 1995-1999.

Numbers of Prey

The bay-wide mean number of prey items per larval gut (PPG) ranged from 1.22 in the 1999 survey to 1.54 in the 1998 survey, and did not differ significantly among years (ANOVA $P>0.05$) (Table 24). Regionally, mean PPG did not differ significantly among regions in any year or for the pooled-years data (ANOVA $P>0.05$) (Table 24). In addition, mean PPG did not differ significantly for larvae collected above and below the pycnocline in any year, but PPG was significantly higher in larvae collected above the pycnocline in the pooled-years data (t-test $P<0.05$) (Table 25). In the separate 3-depth survey (above, at, and below the pycnocline) conducted during a summer 1998 cruise, mean PPG did not differ significantly among the three depth layers (ANOVA $P>0.05$) (Table 25).

PPG also was compared for the five larval size classes. The observed pooled mean PPG was highest for 2.5-4.4 mm larvae (1.69), lowest for 4.5-7.4 mm larvae (1.26), then increased for each length class up to 13.5-16.4 mm (Table 26). There were no significant differences in pooled mean PPG among larval size classes (ANOVA $P>0.05$). There also were no significant differences in mean PPG by length class among or within regions, or within larval length classes for either yearly cruise or regional comparisons (ANOVA $P>0.05$) (Tables 26 and 27). It is possible that mean PPG was higher for larvae collected above compared to larvae collected below the pycnocline for each larval length class, although the consistently higher PPG for above-pycnocline larvae was only significant for 7.4-10.4 mm larvae (t-test $P<0.05$) (Table 28). There were no significant

Table 24. Yearly survey and regional mean numbers of prey per gut for larval bay anchovy in Chesapeake Bay from 1995-1999. No larvae were collected in the upper bay in 1996. There were no significant differences among regions within years or within the pooled data, or among years bay-wide (ANOVA $P > 0.05$).

Bay Region	Year					Pooled
	1995	1996	1997	1998	1999	
Upper	1.33	-	1.40	1.50	1.11	1.3
SE	0.33	-	0.24	0.22	0.08	0.1
Mid	1.10	1.00	1.38	1.30	1.11	1.3
SE	0.10	0	0.19	0.15	0.11	0.1
Lower	1.60	1.56	1.00	1.60	1.54	1.5
SE	0.18	0.34	0	0.19	0.24	0.1
Bay-wide	1.42	1.50	1.29	1.54	1.22	1.4
SE	0.12	0.31	0.12	0.13	0.08	0.1

Table 25. Bay-wide above- and below-pycnocline mean numbers of prey per gut for larval bay anchovy in Chesapeake Bay from 1995-1999. Mean prey per gut was determined for larvae collected above and below the pycnocline only, except for a separate bay-wide survey conducted at ten stations in 1998 (98DS) (Figure 2), which also included samples collected at the pycnocline. There were no significant differences between depth layers within years (t-test $P>0.05$) or for the 98DS depth comparisons (ANOVA $P>0.05$). For depth comparisons within the pooled-years data, different superscripts indicate significant differences (ANOVA $P<0.05$). Above = above pycnocline; At = at pycnocline; Below = below pycnocline.

Depth	Year					Pooled	98DS
	1995	1996	1997	1998	1999		
Above	1.50	1.50	1.45	1.74	1.32	1.5 ^a	1.15
SE	0.20	0.29	0.18	0.20	0.15	0.1	0.10
At							1.25
SE							0.25
Below	1.35	1.50	1.00	1.27	1.15	1.2 ^b	1.71
SE	0.14	0.50	0	0.14	0.09	0.1	0.47

Table 26. Yearly survey and pooled mean prey per gut for five size classes of larval bay anchovy in Chesapeake Bay from 1995-1999. There were no significant differences for within-year or pooled-years larval length-class comparisons, or for yearly survey larval length-class comparisons (ANOVA $P>0.05$).

Size Class	Year					Pooled
	1995	1996	1997	1998	1999	
2.5-4.4 mm	2.00	-	1.00	1.67	2.00	1.69
SE	0.55	-	0	0.49	1.00	0.27
4.5-7.4 mm	1.50	-	1.50	1.00	1.13	1.26
SE	0.22	-	0.30	0	0.09	0.10
7.5-10.4 mm	1.50	1.25	1.00	1.57	1.00	1.28
SE	0.34	0.25	0	0.20	0	0.09
10.5-13.4 mm	1.00	1.80	1.22	1.80	1.22	1.47
SE	0	0.58	0.22	0.42	0.22	0.17
13.5-16.4 mm	1.18	1.00	1.50	1.71	1.50	1.52
SE	0.12	0	0.34	0.22	0.27	0.12

Table 27. Pooled regional mean prey per gut for five length classes of larval bay anchovy in Chesapeake Bay from 1995-1999. There were no significant differences for within-region larval length-class comparisons, or for within larval length-class regional comparisons (ANOVA $P>0.05$).

Size Class	Bay Region		
	Upper	Mid	Lower
2.5-4.4 mm	-	1.00	1.92
SE	-	0	0.34
4.5-7.4 mm	1.13	1.33	1.36
SE	0.09	0.26	0.15
7.5-10.4 mm	1.14	1.20	1.35
SE	0.10	0.13	0.15
10.5-13.4 mm	1.38	1.15	1.67
SE	0.21	0.15	0.37
13.5-16.4 mm	1.56	1.42	1.53
SE	0.34	0.19	0.17

Table 28. Pooled above- and below-pycnocline mean prey per gut for five length classes of larval bay anchovy in Chesapeake Bay from 1995-1999. There were no significant differences for within-depth-layer larval length-class comparisons (ANOVA $P>0.05$). For between-depth-layer comparisons within larval length-classes, different superscripts indicate significant differences (t-test $P<0.05$).

Size Class	Depth	
	Above Pycnocline	Below Pycnocline
2.5-4.4 mm	2.33	1.30
SE	0.56	0.21
4.5-7.4 mm	1.32	1.19
SE	0.15	0.10
7.5-10.4 mm	1.45 ^a	1.08 ^b
SE	0.14	0.08
10.5-13.4 mm	1.62	1.17
SE	0.26	0.17
13.5-16.4 mm	1.55	1.40
SE	0.16	0.17

differences in mean PPG among length classes within the above- or below-pycnocline layers (ANOVA $P > 0.05$) (Table 28).

Kinds of Prey: Frequency and Preference

Copepod eggs, nauplii, copepodites, and adult copepods were the primary prey items ingested by larval bay anchovy in Chesapeake Bay from 1995-1999, comprising 72% of the identifiable food items (Figure 32). The calanoid copepod *Acartia tonsa* was the dominant species eaten, and is the most abundant copepod species in the Bay. Diatoms numerically accounted for 7% of the total diet, rotifers 6%, tintinnids 4%, and cladocerans 4%. Nine unidentified planula larvae comprised a small fraction of the larval diet, but were found only in the guts of four <4.4 mm bay anchovy larvae, all of which were collected at two stations in the lower bay in 1995.

Relative prey frequencies were examined for the pooled prey data and bay-wide for each year (Figure 32). Prey frequencies for four prey categories (copepod copepodites and adults, copepod nauplii, invertebrate eggs, and other prey) differed in 1995 from all other years (χ^2 -test $P < 0.05$). The prey frequencies in 1996 were similar to those in 1999, but were significantly different in the other years (χ^2 -test $P < 0.05$). Relative prey frequencies for the four prey categories were similar in 1997, 1998, and 1999 (χ^2 -test $P > 0.05$).

Pooled-years regional (Figure 33) and above-below-pycnocline (Figure 34) prey frequencies also were analyzed. Prey frequency distributions were similar for the pooled-years regional data (χ^2 -test $P > 0.05$). However, there was a significant difference between the pooled above- and below-pycnocline prey frequency distributions (χ^2 -test $P = 0.01$).

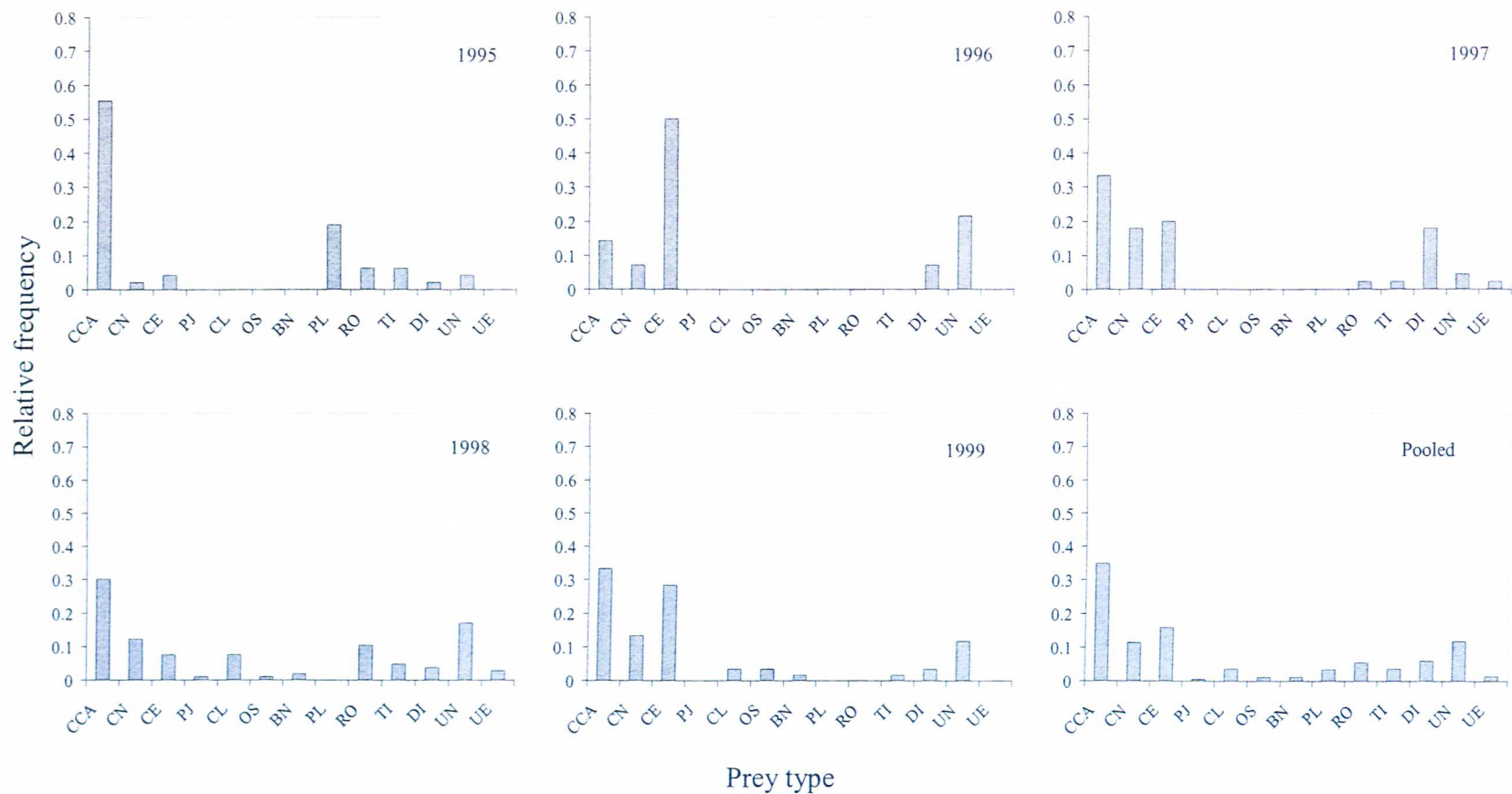


Figure 32. Bay-wide yearly survey and pooled relative frequencies of prey items ingested by larval bay anchovy in Chesapeake Bay from 1995-1999. CCA = copepod copepodites/adults, CN = copepod nauplii, CE = copepod eggs, PJ = polychaete juveniles, CL = cladocerans, OS = ostracods, BN = barnacle nauplii, PL = unidentified planula larvae, RO = rotifers, TI = tintinnids, DI = diatoms, UN = unidentified food items, and UE = unidentified invertebrate eggs.

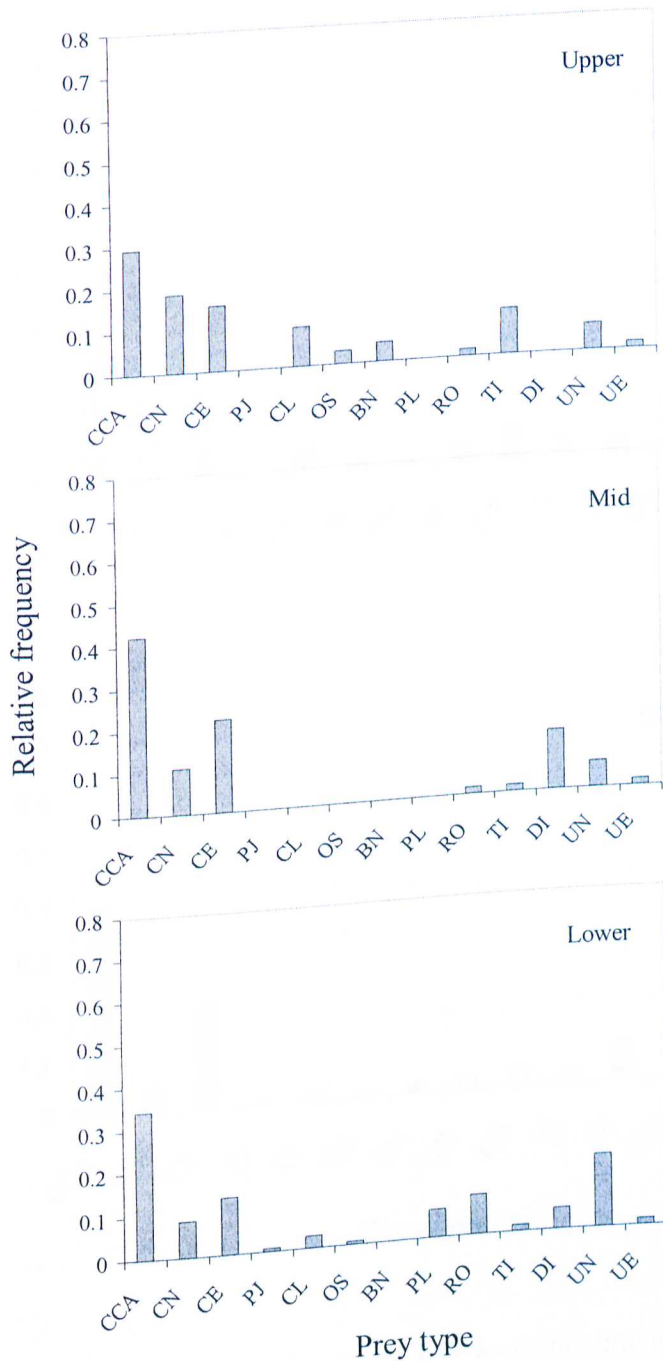


Figure 33. Pooled-years regional (upper, mid, and lower bay) relative frequencies of prey items ingested by larval bay anchovy in Chesapeake Bay from 1995-1999. CCA = copepod copepodites/adults, CN = copepod nauplii, CE = copepod eggs, PJ = polychaete juveniles, CL = cladocerans, OS = ostracods, BN = barnacle nauplii, PL = unidentified planula larvae, RO = rotifers, TI = tintinnids, DI = diatoms, UN = unidentified food items, and UE = unidentified invertebrate eggs.

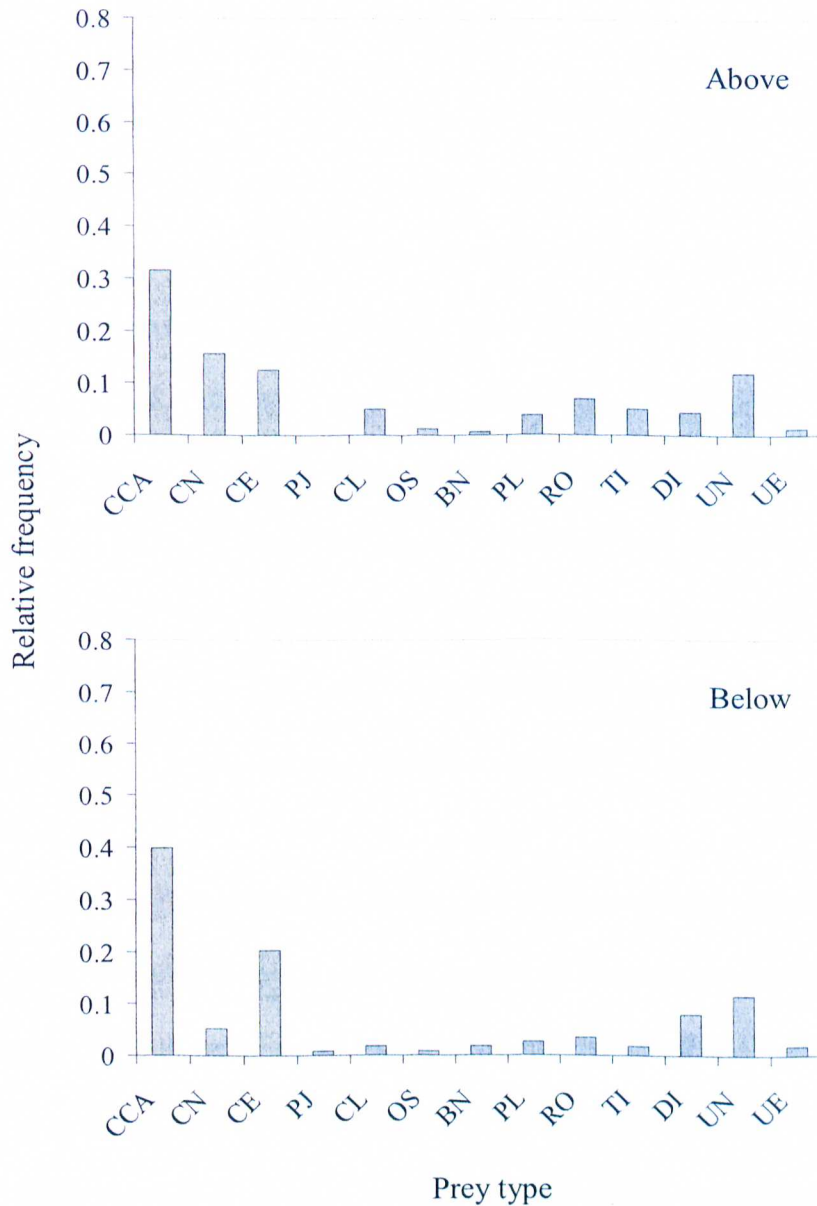


Figure 34. Pooled-years above- and below-pycnocline relative frequencies of prey items ingested by larval bay anchovy in Chesapeake Bay from 1995-1999. CCA = copepod copepodites/adults, CN = copepod nauplii, CE = copepod eggs, PJ = polychaete juveniles, CL = cladocerans, OS = ostracods, BN = barnacle nauplii, PL = unidentified planula larvae, RO = rotifers, TI = tintinnids, DI = diatoms, UN = unidentified food items, and UE = unidentified invertebrate eggs.

Below-pycnocline larvae had fed more often on adult and copepodite stages of copepods and their eggs than had above-pycnocline larvae, which more frequently consumed copepod nauplii and smaller zooplankton taxa than did the below-pycnocline larvae. The pooled prey frequency distributions for each of the five larval length classes all differed significantly as well (χ^2 -test $P < 0.05$), as larger larvae switched to ingesting larger prey (e.g., copepod adults and copepodites) (Figure 35). The regional and above-below-pycnocline prey frequency distributions of bay anchovy larvae for each year (1995-1999) also were examined (Figures 36 and 37), but could not be tested statistically because they did not meet the minimum relative-frequency assumptions of the χ^2 -test. There were no apparent regional or above-below-pycnocline patterns since larval size seemed to determine prey type and size ingested more than the location or depth occupied by larval bay anchovy.

Annual and regional relative prey preference index values for 1) copepod copepodites and adults, 2) copepod nauplii, 3) invertebrate eggs (predominantly copepod eggs), and 4) all other zooplankton taxa were calculated as Chesson's α (1978) index for relative prey preference (Figure 38, Table 29). Larval bay anchovy showed a negative preference for both copepod nauplii and non-copepod zooplankton in regional and among yearly surveys analyses. Copepod copepodites and adults were preferred prey in 1997, 1998, and 1999, but were selected against in 1996. Copepod copepodites and adults also generally were preferred in each region, except for the mid and lower bay in 1996, the upper bay in 1997, and the lower bay in 1999. Larval bay anchovy exhibited a strong preference for invertebrate eggs in 1996-1998, but a slight negative preference for that

Table 29. Yearly survey and regional relative prey preference index values (Chesson's alpha) for copepod adults and copepodites, copepod nauplii, invertebrate eggs, and all other zooplankton taxa (other) in relation to larval bay anchovy feeding in Chesapeake Bay from 1996-1999. No larvae were collected in the upper bay in 1996. Zooplankton samples were not collected in 1995. Index values are Chesson's (1978) alpha. Index values <0.25 indicate preference against a prey type, values equal to 0.25 indicate no preference for a prey type, and values >0.25 indicate preference for a prey type.

Copepod copepodites/adults					Copepod nauplii				
Bay Region	Year				Bay Region	Year			
	1996	1997	1998	1999		1996	1997	1998	1999
Upper	-	0	0.54	0.59	Upper	-	0.005	0.21	0.10
Mid	0	0.42	0.47	0.84	Mid	0	0.06	0.005	0
Lower	0.002	0.85	0.34	0.19	Lower	0.0003	0.05	0.04	0.01
Bay-wide	0.002	0.26	0.35	0.69	Bay-wide	0.0003	0.03	0.04	0.08

Invertebrate eggs					Other				
Bay Region	Year				Bay Region	Year			
	1996	1997	1998	1999		1996	1997	1998	1999
Upper	-	0.99	0	0.07	Upper	-	0.008	0.24	0.24
Mid	1	0.40	0.52	0.14	Mid	0	0.12	0.009	0.02
Lower	0.997	0	0.41	0.80	Lower	0.0003	0.10	0.21	0.001
Bay-wide	0.997	0.63	0.50	0.15	Bay-wide	0.0003	0.08	0.11	0.07

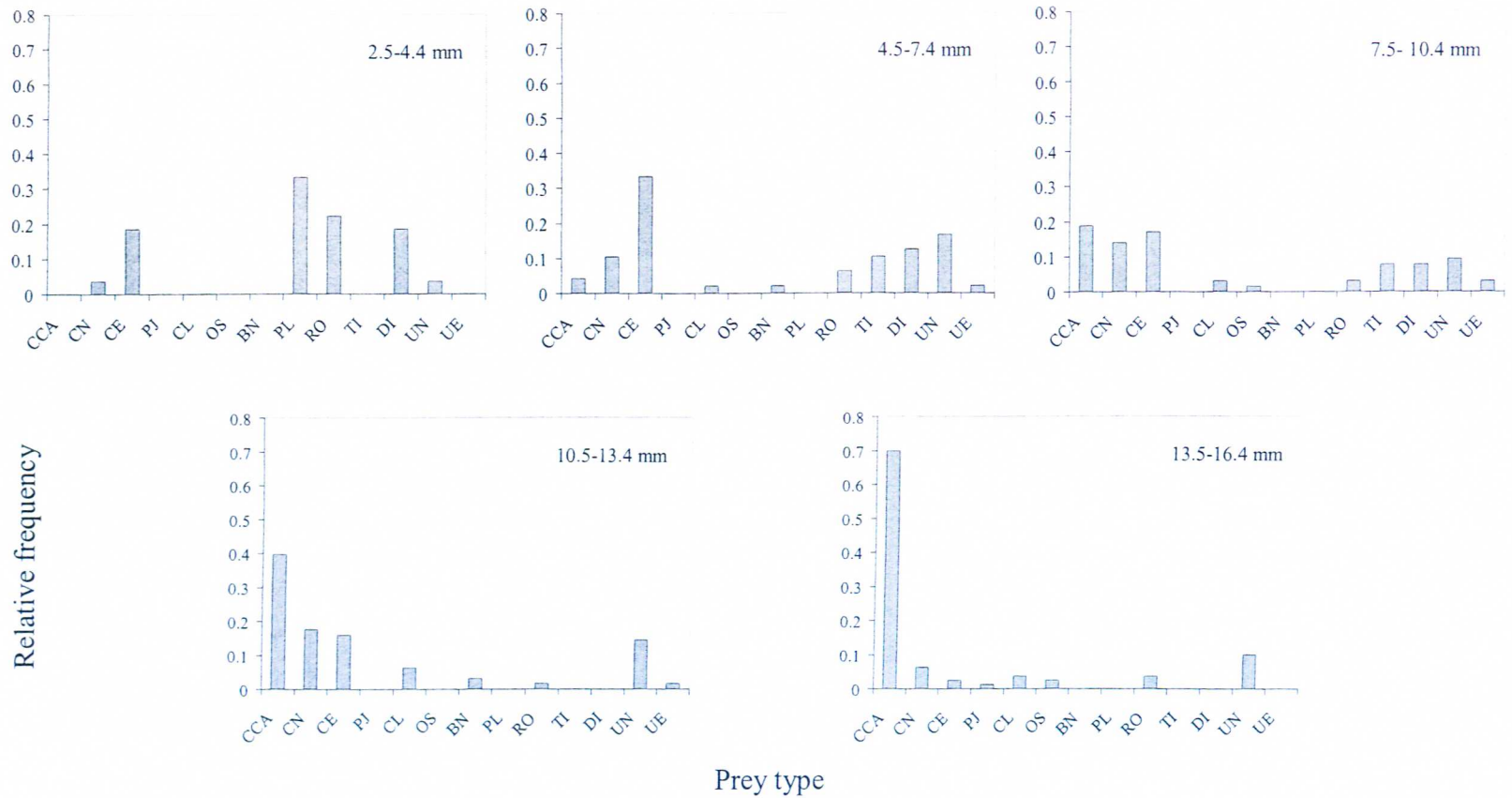


Figure 35. Bay-wide pooled relative frequencies of prey items ingested by five length classes of larval bay anchovy in Chesapeake Bay from 1995-1999. CCA = copepod copepodites/adults, CN = copepod nauplii, CE = copepod eggs, PJ = polychaete juveniles, CL = cladocerans, OS = ostracods, BN = barnacle nauplii, PL = unidentified planula larvae, RO = rotifers, TI = tintinnids, DI = diatoms, UN = unidentified food items, and UE = unidentified invertebrate eggs.

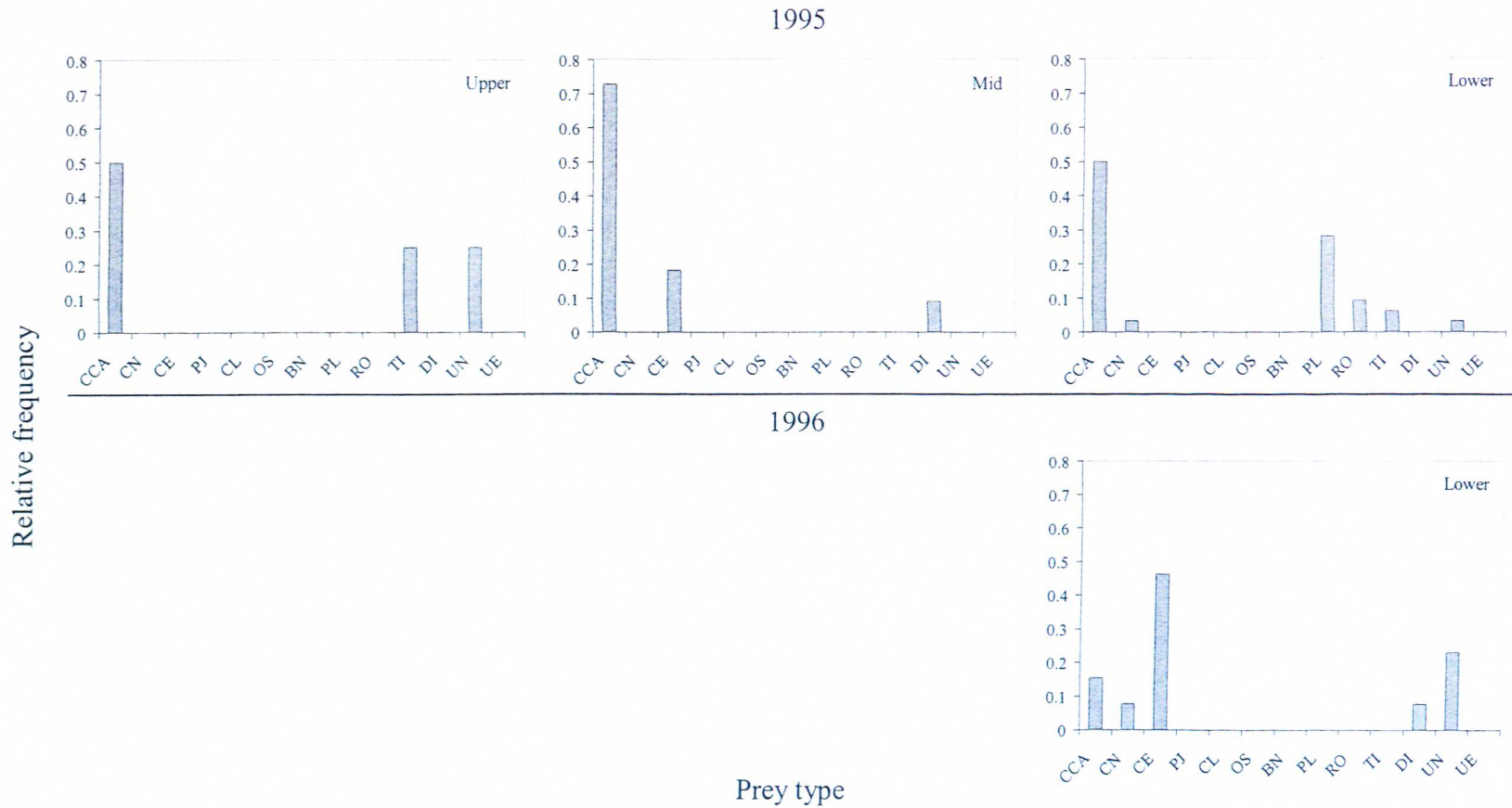


Figure 36. Regional (upper, mid, and lower bay) relative frequencies of prey items ingested by larval bay anchovy in Chesapeake Bay from 1995-1999. In 1996, no larvae were collected in the upper bay, and only one copepod egg was found in one larval gut in the mid bay. CCA = copepod copepodites/adults, CN = copepod nauplii, CE = copepod eggs, PJ = polychaete juveniles, CL = cladocerans, OS = ostracods, BN = barnacle nauplii, PL = unidentified planula larvae, RO = rotifers, TI = tintinnids, DI = diatoms, UN = unidentified food items, and UE = unidentified invertebrate eggs.

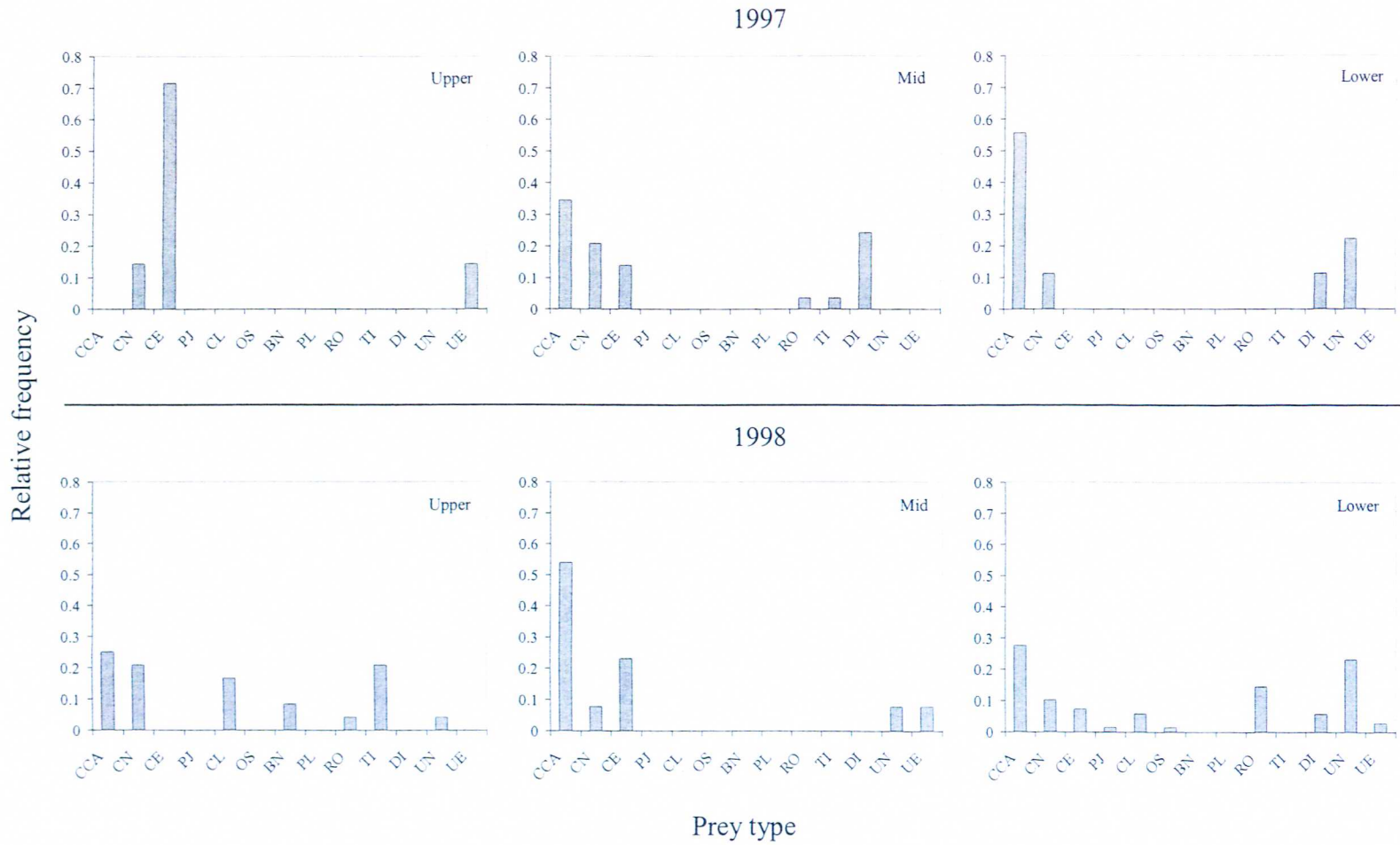


Figure 36 (cont'd)

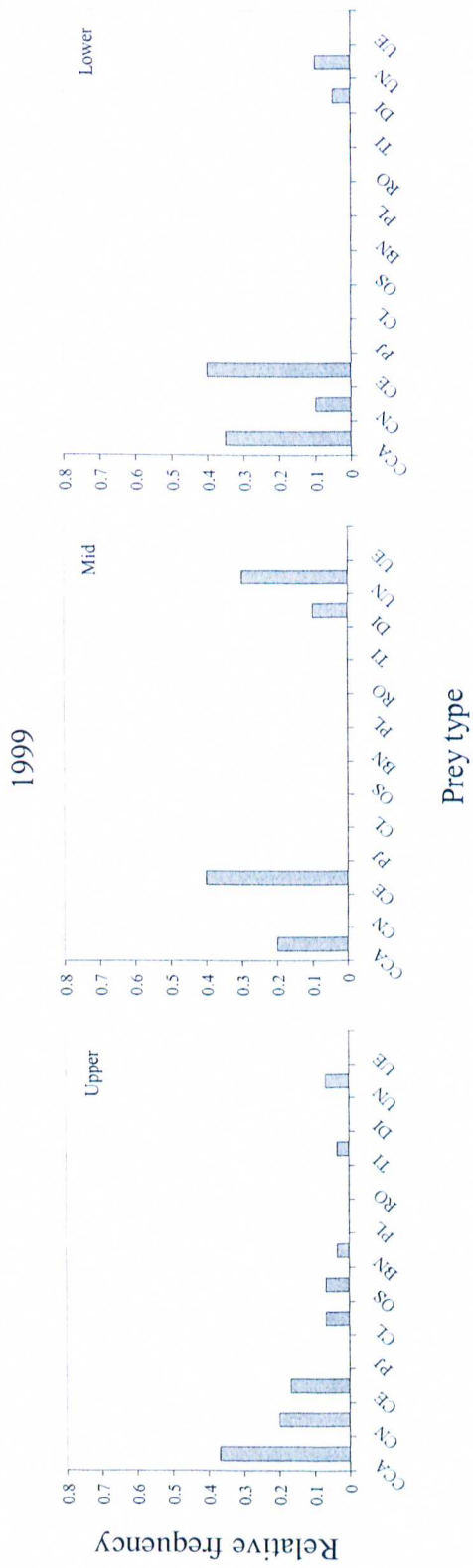


Figure 36 (cont'd)

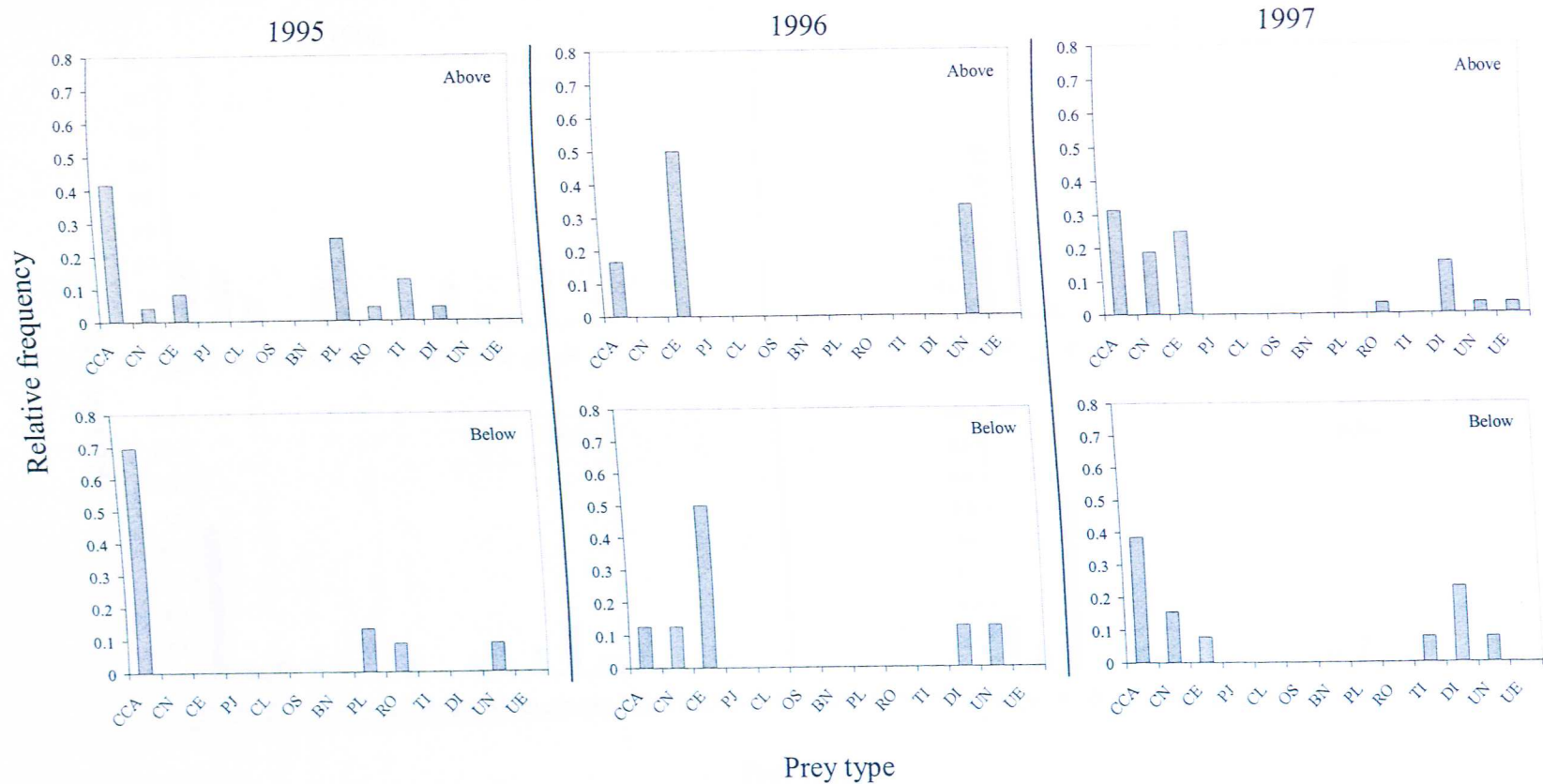
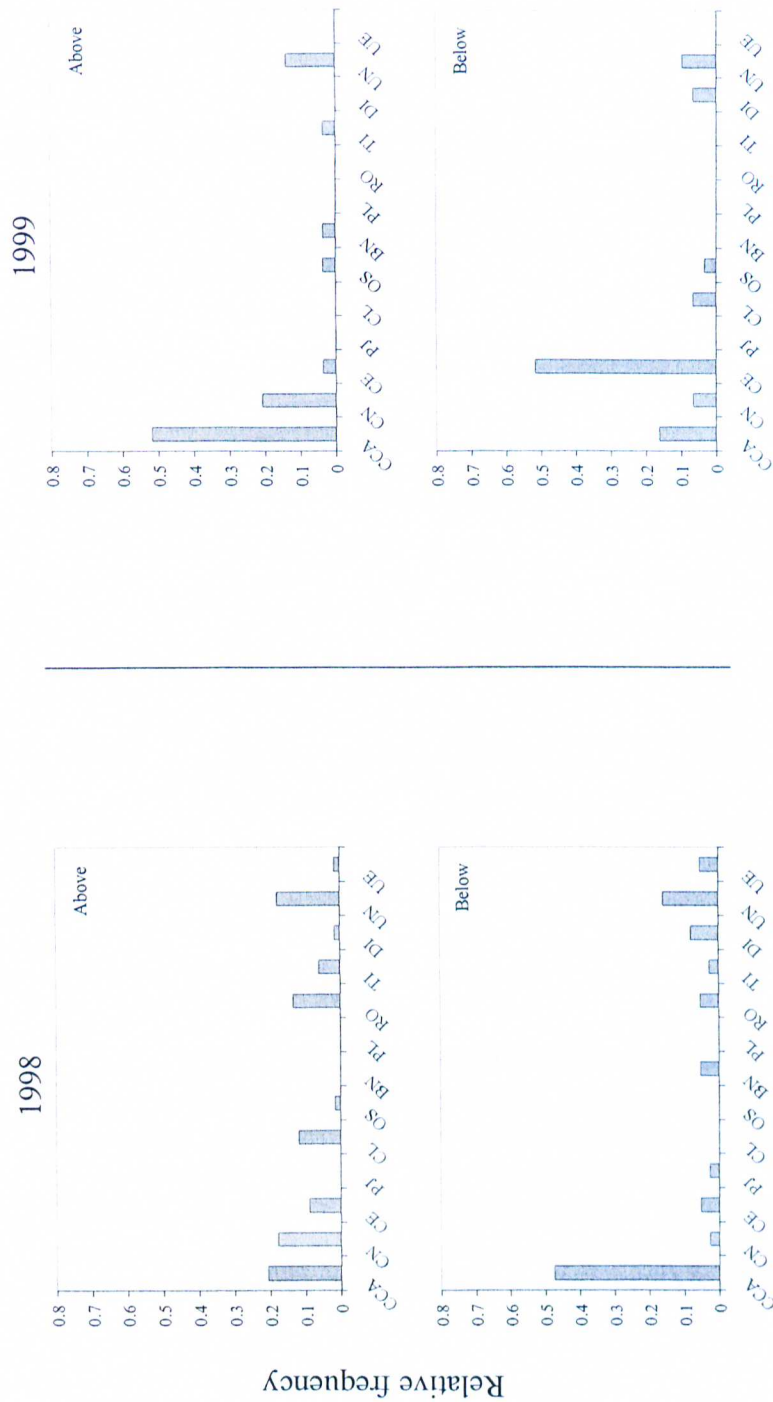


Figure 37. Bay-wide above-/below-pycnocline relative frequencies of prey items ingested by larval bay anchovy in Chesapeake Bay from 1995-1999. CCA = copepod copepodites/adults, CN = copepod nauplii, CE = copepod eggs, PJ = polychaete juveniles, CL = cladocerans, OS = ostracods, BN = barnacle nauplii, PL = unidentified planula larvae, RO = rotifers, TI = tintinnids, DI = diatoms, UN = unidentified food items, and UE = unidentified invertebrate eggs.



Prey type

Figure 37 (cont'd)

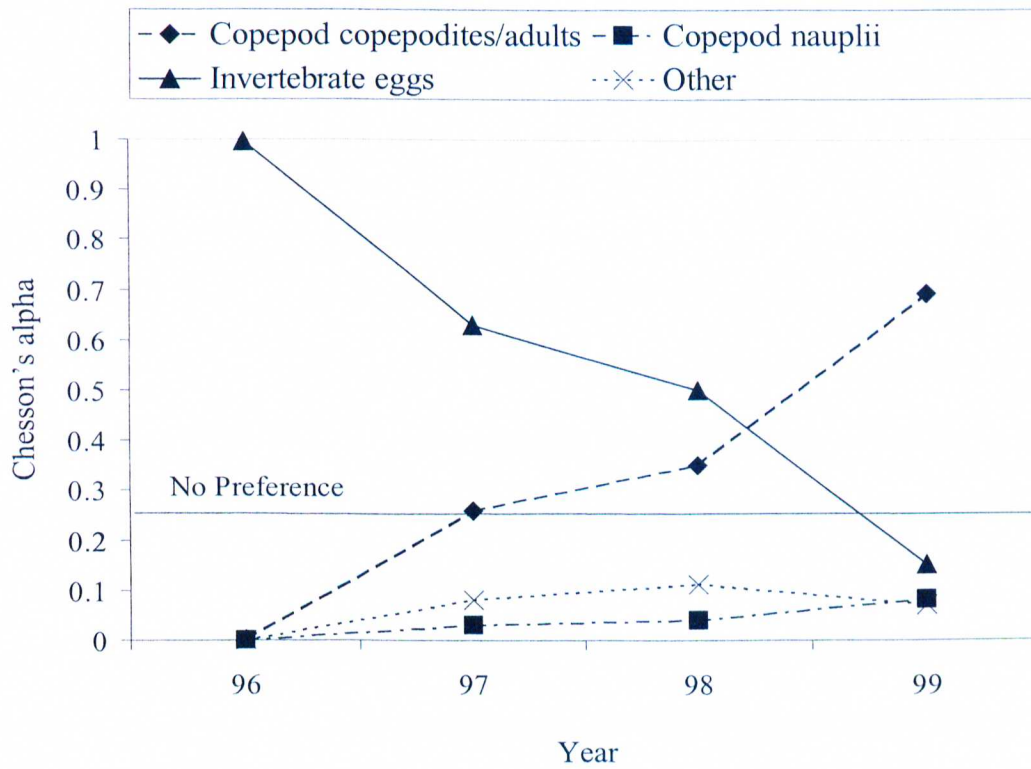


Figure 38. Yearly survey relative prey preference index values for copepod adults and copepodites, copepod nauplii, invertebrate eggs, and all other zooplankton taxa (other) for larval bay anchovy in Chesapeake Bay from 1996-1999. Zooplankton samples were not collected in 1995. Index values are Chesson's (1978) α for relative prey preference. Index values <0.25 indicate preference against a prey type, values equal to 0.25 indicate no preference for a prey type, and values >0.25 indicate preference for a prey type.

prey category in the upper and mid bay in 1999. Invertebrate eggs were highly preferred food in most regions and years, except for the lower bay in 1997, the upper bay in 1998, and the upper and mid bay in 1999. The extraordinarily high α index values for invertebrate eggs in 1996 resulted because eggs were rare in the zooplankton samples, yet a predominant prey in larval guts in that year.

Prey Size and Larval Length Comparisons

Ingested prey length increased exponentially with larval size, but the rates of increase generally did not differ among yearly surveys or regionally. Although the mean prey size increased with larval length, big larvae continued to ingest smaller prey items. Relative prey length (prey length/larval length) increased at a gradual exponential rate, but generally did not differ annually or regionally.

Mean prey length for the pooled-years collections increased exponentially in larvae from the smallest (2.5-4.4 mm) to the largest (13.5-16.4 mm) length classes. The pooled-data mean prey length increased from 0.07 mm for 2.5-4.4 mm larvae to 0.73 mm for 13.5-16.4 mm larvae, and differed significantly between each length class except for 2.5-4.4 mm and 4.5-7.4 mm larvae (ANOVA $P < 0.05$) (Table 30). Mean length of ingested prey also increased from the smallest to the largest larval length classes in each year except for 1996 (ANOVA $P < 0.05$) (Table 30). For among-years comparisons within larval length classes, there were no significant differences among years for the 2.5-4.4 mm, 4.5-7.4 mm, and 13.5-16.4 mm larvae (ANOVA $P > 0.05$). Ingested mean prey

lengths did differ among years for the 1995 and 1997 larvae in the 7.5-10.4 mm and 10.5-13.4 mm classes (ANOVA $P < 0.05$) (Table 30).

Pooled-years regional mean prey lengths also increased significantly from the smallest to the largest larval length classes in each bay region (ANOVA $P < 0.05$) (Table 31). For comparisons within larval length classes among regions, there were no significant differences between regions for the 2.5-4.4 mm, 7.5-10.4 mm, and 10.5-13.4 mm larvae (ANOVA $P > 0.05$). However, mean prey length for 4.5-7.4 mm larvae was smaller in the mid bay (0.07 mm) than in the lower bay (0.14 mm), and mean prey length for 13.5-16.4 mm larvae was larger in the mid bay (0.91 mm) than in the lower bay (0.66 mm) (ANOVA $P < 0.05$).

The relationships between prey and larval lengths were described well by exponential regressions, indicating a constant rate of increase in prey size added in the larval diet through ontogeny. Regressions were fit to the pooled-years and annual bay-wide prey and larval length data (Figure 39). Mean prey length calculated from the pooled data was 0.361 mm. There were significant, positive slopes for \log_e prey length regressed on larval length for each year except 1996. Slope coefficients ranged from 0.18 in 1998 to 0.26 in 1995 ($P < 0.001$). The slope of the regression line in 1995 was significantly higher than that in 1998 (ANCOVA $P < 0.05$), but there were no other significant differences observed between remaining years (ANCOVA $P > 0.05$) (Figure 39). Regional regressions of \log_e prey length on larval length also were fit for the years 1995-1999 (Figure 40). Slopes of the relationships were generally similar among regions. The only significant difference between regional slopes was found in 1998, in

Table 30. Yearly survey and pooled-years bay-wide mean prey lengths (mm) for five length classes of larval bay anchovy in Chesapeake Bay from 1995-1999. No larvae were collected in the upper bay in 1996. For within-year and within pooled-years larval length-class comparisons, different letter superscripts indicate significant differences (ANOVA $P < 0.05$). For within larval length-class yearly survey comparisons, different numeric superscripts indicate significant differences (ANOVA $P < 0.05$). OP = observed pooled mean prey length; PP = predicted pooled mean prey length for 3.5, 6.0, 9.0, 12.0, and 15.0 mm larvae from regression equation of \log_e prey length (y) on larval length (x) for pooled data: $y = 0.21x - 3.77$ (Figure 39).

Size Class	Year					OP	PP
	1995	1996	1997	1998	1999		
2.5-4.4 mm	0.04 ^a	-	0.09 ^a	0.09 ^a	0.07 ^a	0.07 ^a	0.05
SE	0.002	-	0.01	0.02	0.01	0.007	
4.5-7.4 mm	0.15 ^a	-	0.08 ^a	0.10 ^{ab}	0.10 ^a	0.10 ^a	0.08
SE	0.05	-	0.01	0.02	0.01	0.01	
7.5-10.4 mm	¹ 0.33 ^b	¹² 0.19	² 0.09 ^a	¹² 0.17 ^{ab}	¹² 0.20 ^a	0.20 ^b	0.15
SE	0.06	0.06	0.03	0.03	0.05	0.02	
10.5-13.4 mm	³ 0.73 ^{bc}	¹ 0.15	²³ 0.60 ^b	¹² 0.29 ^b	²³ 0.51 ^b	0.40 ^c	0.29
SE	0.11	0.05	0.12	0.05	0.09	0.04	
13.5-16.4 mm	0.97 ^c	0.15	0.81 ^b	0.61 ^c	0.83 ^b	0.73 ^d	0.54
SE	0.08	0	0.08	0.07	0.10	0.05	

Table 31. Pooled-years regional mean prey lengths (mm) for five length classes of larval bay anchovy in Chesapeake Bay from 1995-1999. No larvae in the 2.5-4.4 mm length class collected in the upper bay had prey items in their guts. For within-region larval length-class comparisons, different letter superscripts indicate significant differences (ANOVA $P < 0.05$). For within larval length-class regional comparisons, different numeric superscripts indicate significant differences (ANOVA $P < 0.05$).

Size Class	Bay Region		
	Upper	Mid	Lower
2.5-4.4 mm	-	0.08 ^{ab}	0.07 ^a
SE	-	0.02	0.008
4.5-7.4 mm	¹² 0.10 ^a	¹ 0.07 ^a	² 0.14 ^{ab}
SE	0.01	0.01	0.03
7.5-10.4 mm	0.20 ^b	0.18 ^b	0.21 ^b
SE	0.04	0.05	0.04
10.5-13.4 mm	0.46 ^c	0.36 ^c	0.37 ^b
SE	0.06	0.07	0.07
13.5-16.4 mm	¹² 0.77 ^c	² 0.91 ^d	¹ 0.66 ^c
SE	0.09	0.07	0.06

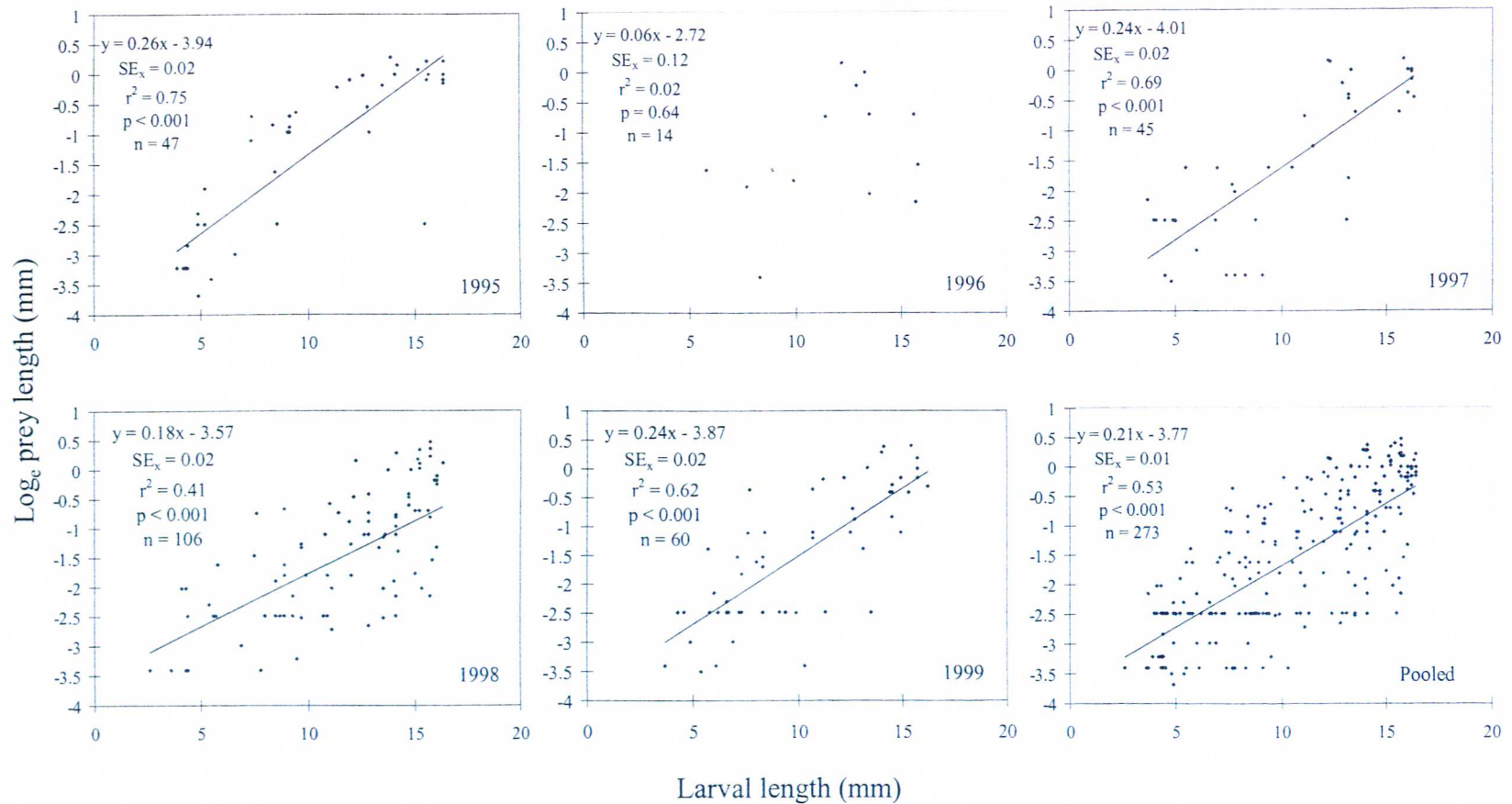


Figure 39. Bay-wide pooled and yearly survey regression equations of \log_e prey length (mm) on larval length (mm) for larval bay anchovy in Chesapeake Bay from 1995-1999. The regression fit was not significant in 1996. $y = \log_e$ prey length (mm), $x =$ larval length (mm).

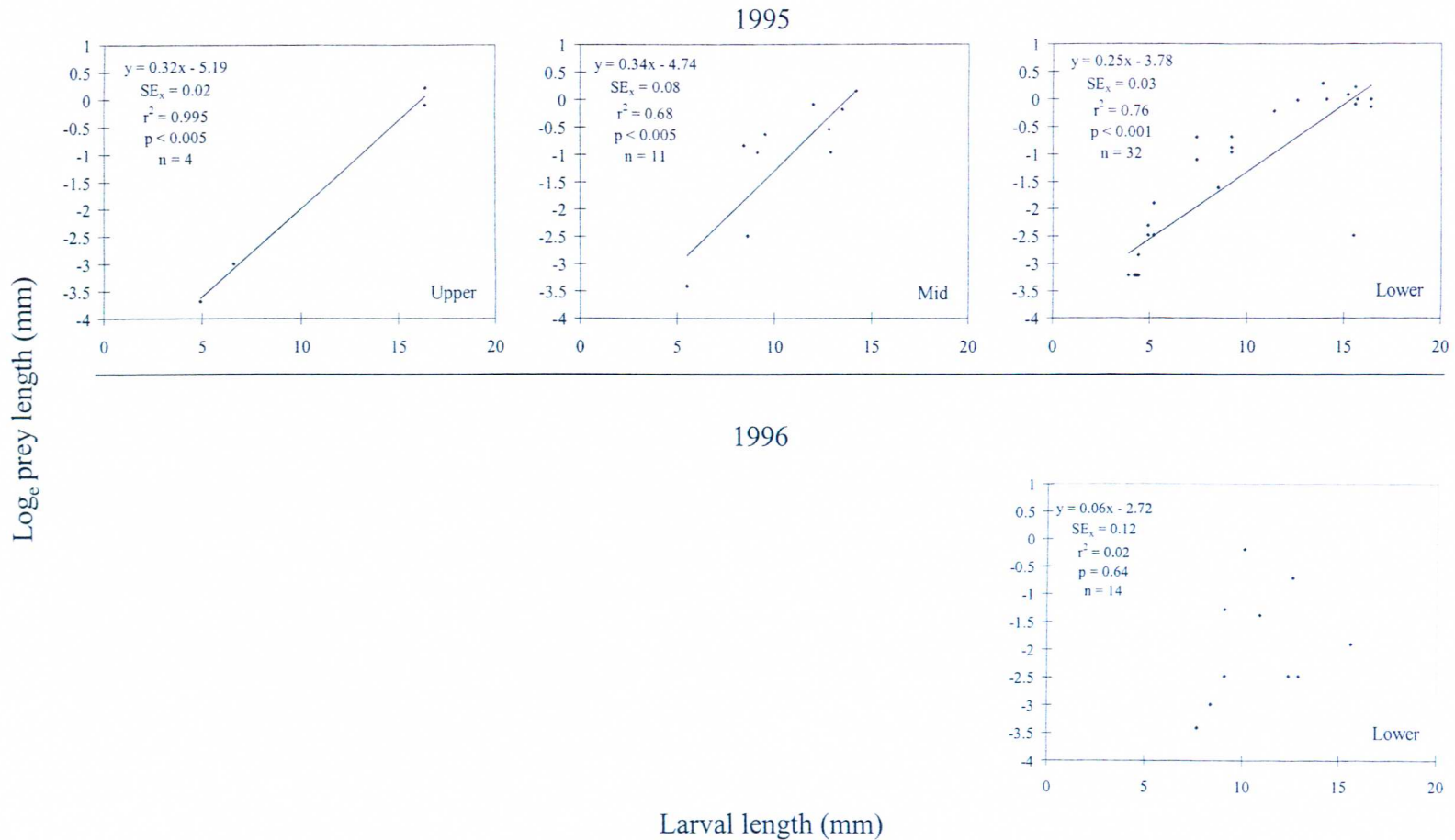


Figure 40. Regional (upper, mid, and lower bay) regressions of \log_e prey length (mm) on larval length (mm) for larval bay anchovy in Chesapeake Bay from 1995-1999. In 1996, no larvae were collected in the upper bay, and only one larva was found with a single copepod egg in its gut in the mid bay. The regression fit was not significant for the lower bay in 1996. $y = \log_e$ prey length (mm), $x =$ larval length (mm).

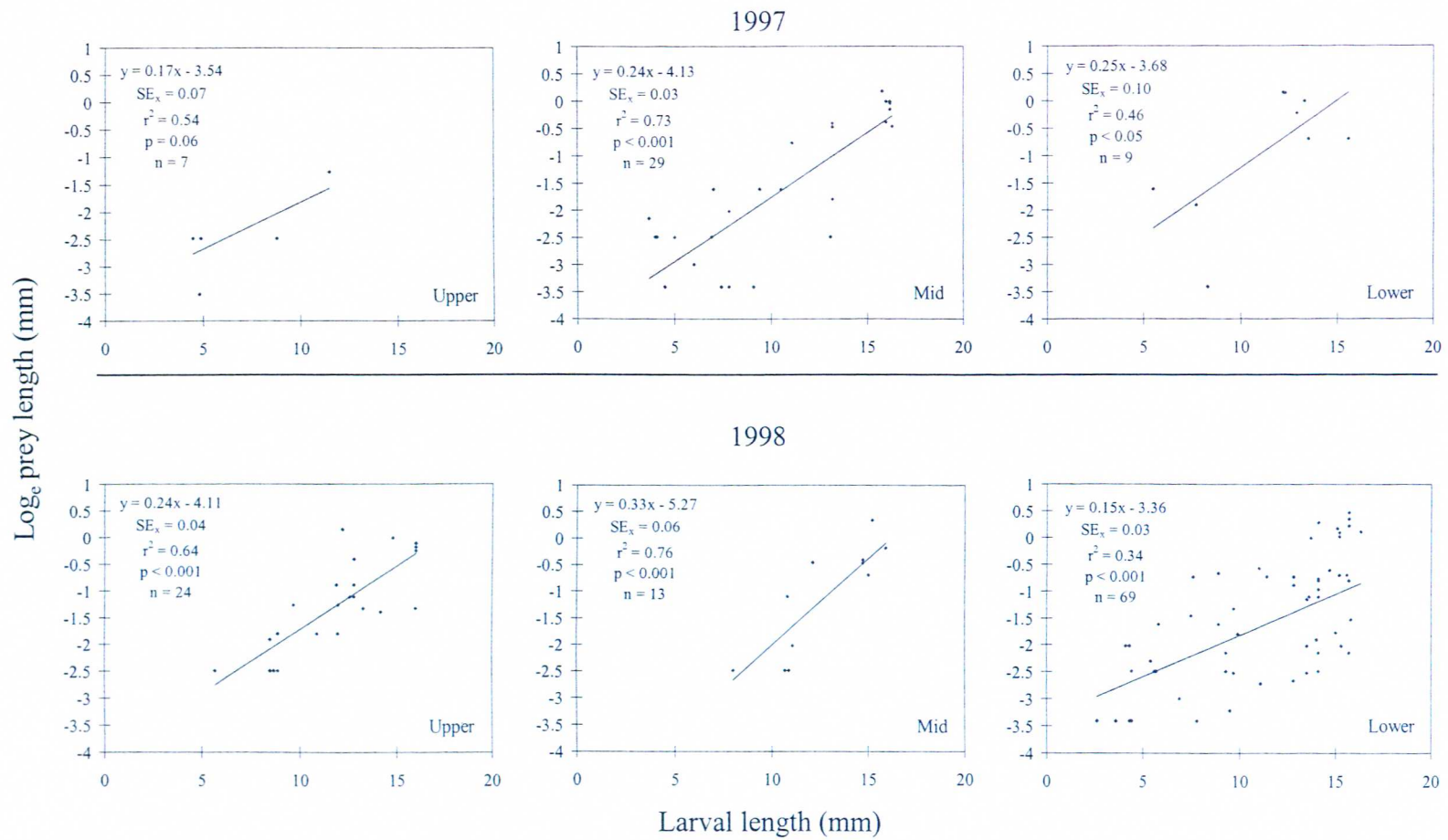
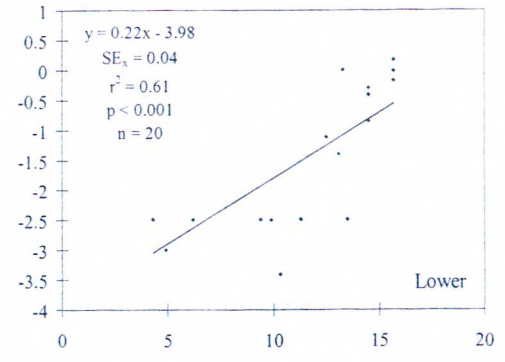
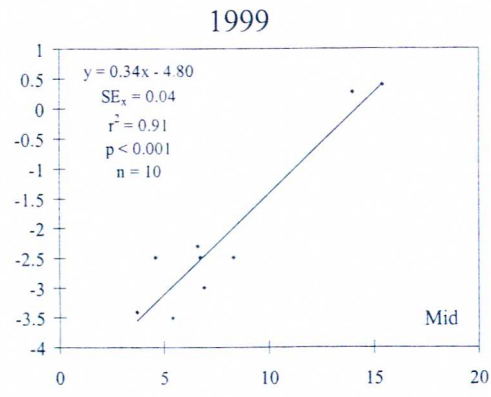
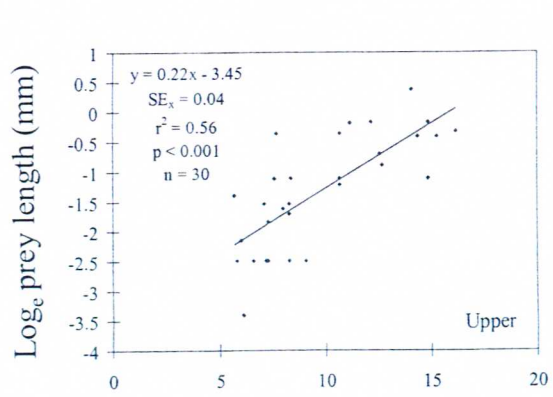


Figure 40 (cont'd)



Larval length (mm)

Figure 40 (cont'd)

which the slope of the mid-bay regression (0.33) was higher than that of the lower-bay (0.15) (ANCOVA $P < 0.05$).

The square root of relative prey length (prey length/larval length) also was regressed on larval length. The mean relative prey length of the pooled-years data was 0.03. The square root of relative prey length increased significantly ($P < 0.005$) as larvae grew in each year except 1996 (Figure 41), indicating a significant, though small and gradual, increase in the relative size of prey items added to the larval diet as larval length increased. The slope of the regression line for the pooled data was 0.008. The slope of the 1995 regression (0.012) was greater than that of 1998 (0.006) (ANCOVA $P < 0.05$). Slopes for all other years were similar (ANCOVA $P > 0.05$) (Figure 41).

When regional square root relative prey lengths were regressed on larval length for the years 1995-1999 (Figure 42), significant and positive slopes ($P < 0.05$) were found in all cases, except for the lower bay in 1996 and 1997, and in the upper bay in 1997 ($P > 0.05$). In 1998, the slope of the mid-bay regression (0.019) was greater than that of the lower-bay (0.004), while in 1999, the slope of the mid-bay regression (0.021) was greater than that of the upper- (0.010) and lower-bay (0.009) (ANCOVA $P < 0.05$) (Figure 42). There were no other significant differences between regional slopes within years.

Correlations

There were 22 pairs of regional biotic and abiotic variables that were significantly correlated at the $\alpha = 0.05$ level (Table 32). YOY abundance in October was positively correlated with larval FI ($r = 0.93$ $P = 0.02$). Not surprisingly, bay anchovy larval

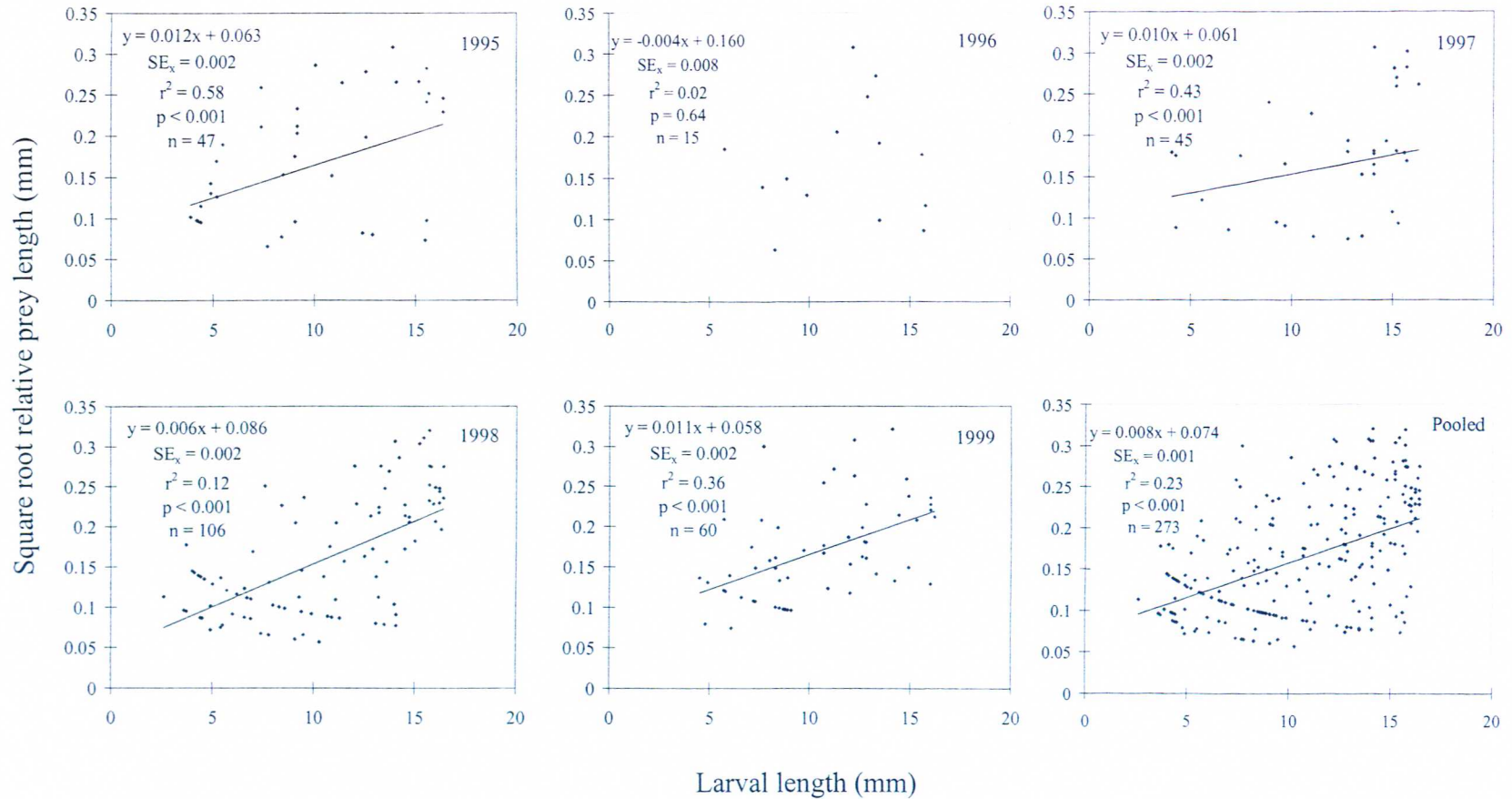


Figure 41. Bay-wide pooled-years and yearly survey regressions of square-root relative prey length (mm) on larval length (mm) for larval bay anchovy in Chesapeake Bay from 1995-1999. The regression fit was not significant in 1996. y = square-root [prey length (mm)/larval length (mm)], x = larval length (mm).

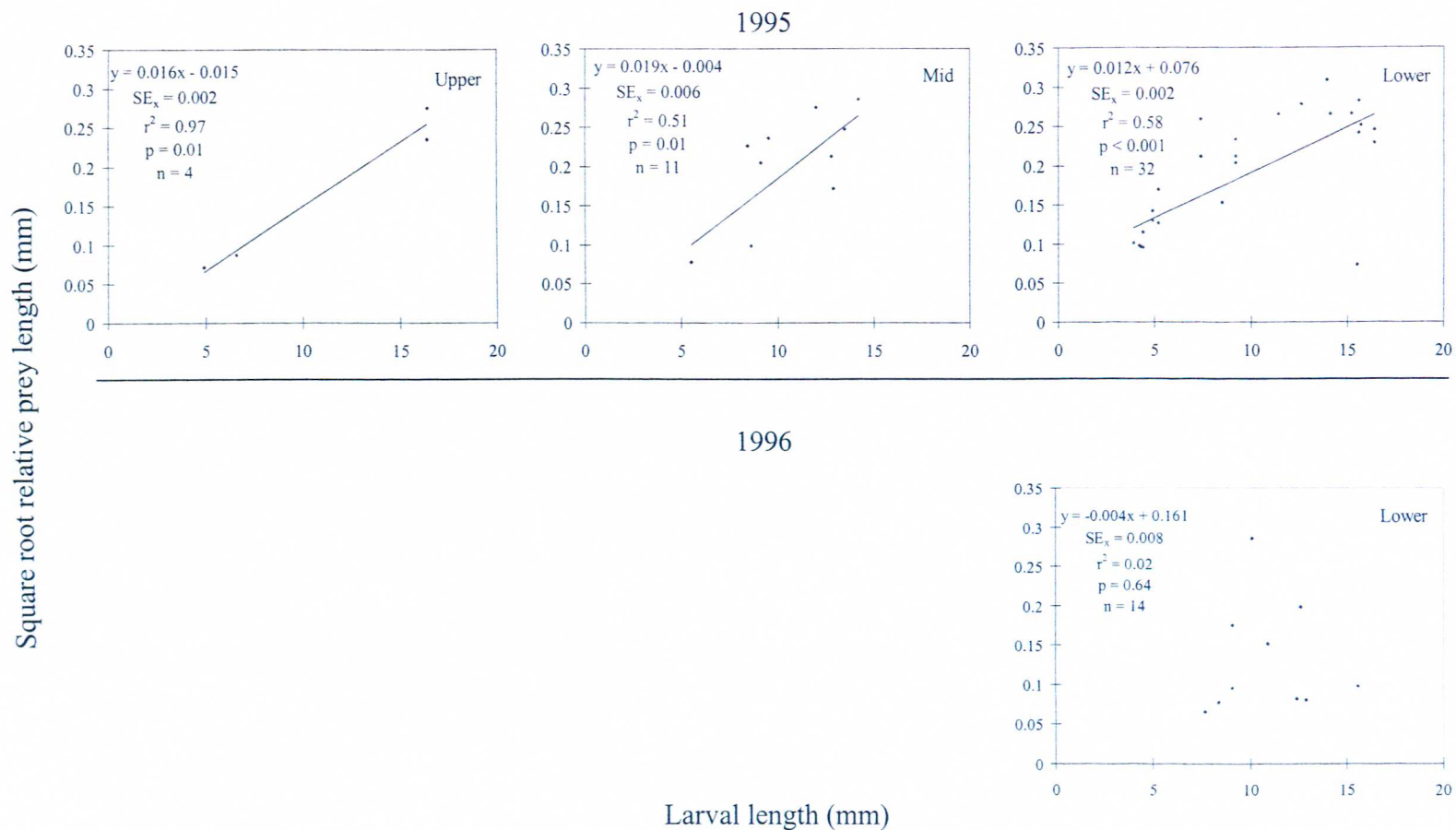


Figure 42. Regional (upper, mid, and lower bay) regressions of square-root relative prey length (mm) on larval length (mm) for larval bay anchovy in Chesapeake Bay from 1995-1999. In 1996, no larvae were collected in the upper bay, and only one larva was found with a single copepod egg in its gut in the mid bay. The regression fits were not significant for the lower bay in 1996, and for the upper and lower bay in 1997. y = square-root [prey length (mm)/larval length (mm)], x = larval length (mm).

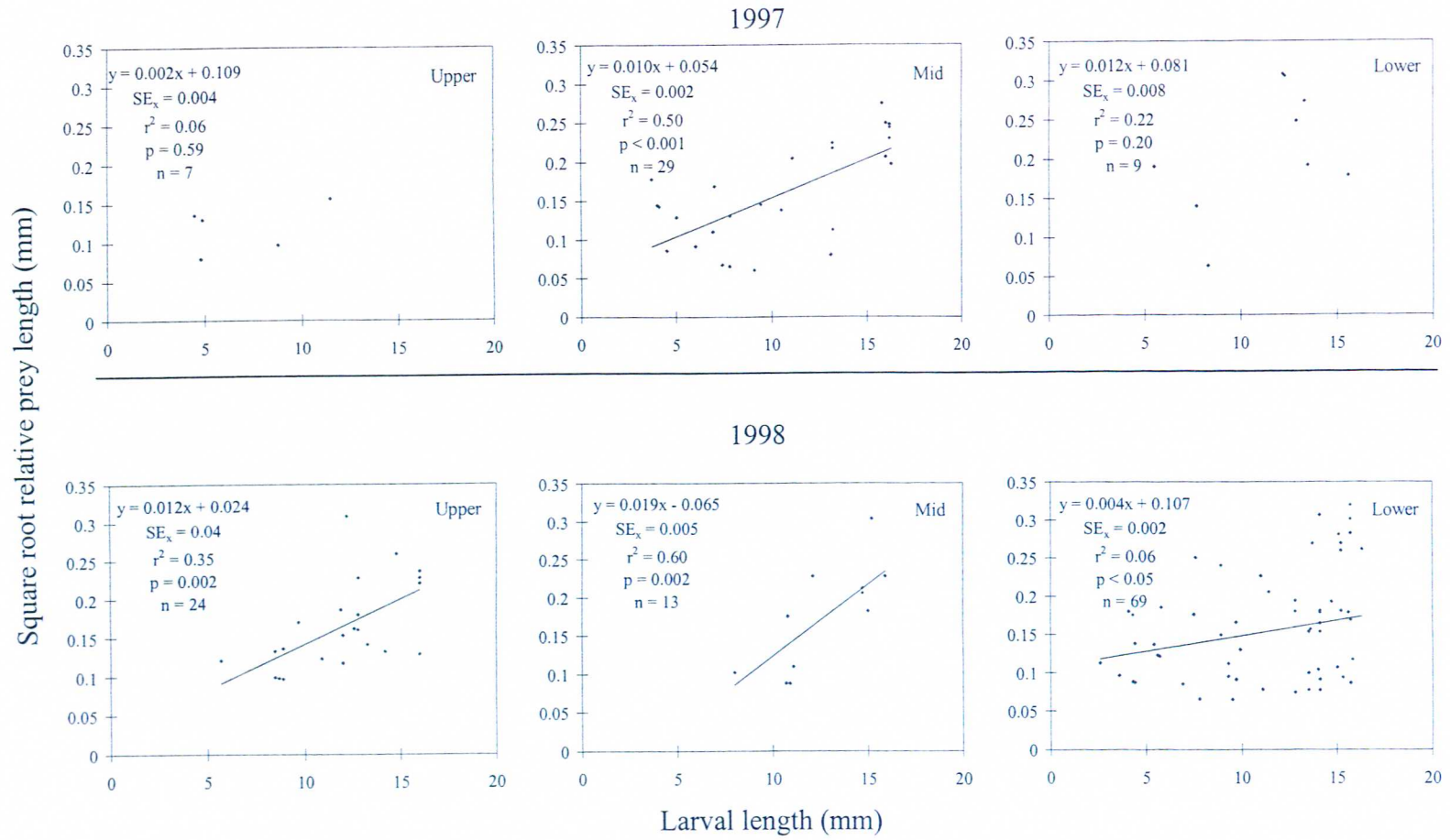


Figure 42 (cont'd)

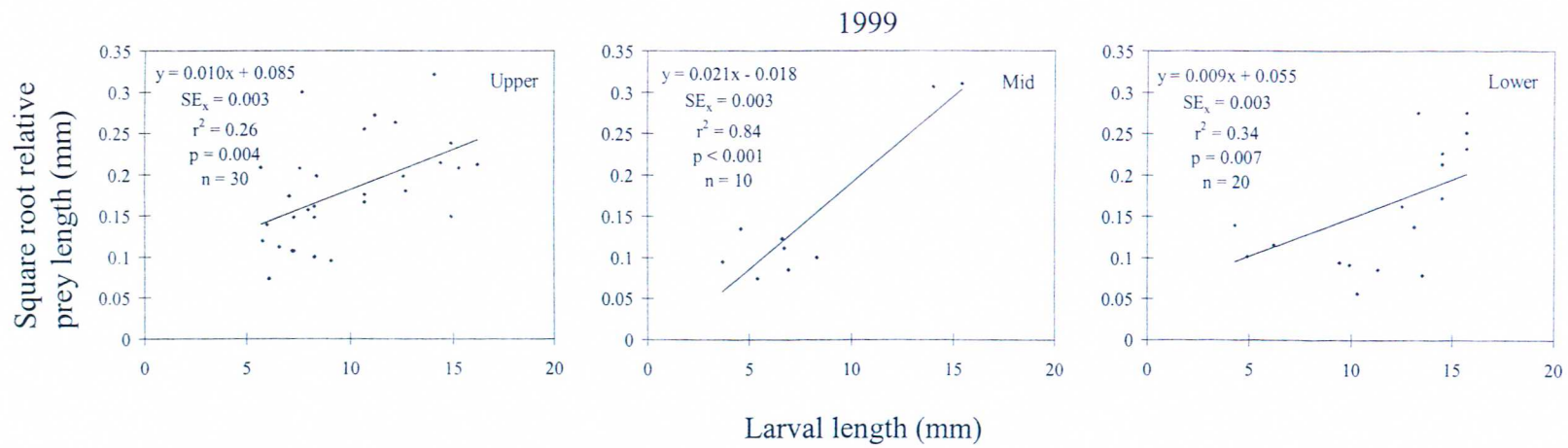


Figure 42 (cont'd)

abundance was strongly and positively correlated with bay anchovy larval density ($r = 0.94$ $P < 0.0001$). Larval abundance and larval density were strongly correlated with bay anchovy egg abundance ($r = 0.79$ and $r = 0.76$, respectively $P < 0.001$), and bay anchovy egg density ($r = 0.79$ and $r = 0.77$, respectively $P < 0.001$). Larval abundance and larval density were negatively correlated with larval length ($r = -0.53$ and $r = -0.55$, respectively $P = 0.05$). In addition, larval abundance and larval density were positively correlated with salinity ($r = 0.87$ and $r = 0.86$, respectively $P < 0.0001$), because most larvae were located in the seaward, more saline region of the bay where peak spawning occurred.

Egg abundance was positively correlated with egg density ($r = 0.99$ $P < 0.0001$). Egg abundance and egg density were positively correlated with salinity ($r = 0.72$ and $r = 0.72$, respectively $P < 0.01$), and were negatively correlated with larval length ($r = -0.83$ and $r = -0.86$, respectively $P < 0.001$) and the measure of fluorescence that indexed chlorophyll a biomass ($r = -0.61$ and $r = -0.62$, respectively $P < 0.05$). Chlorophyll a biomass also was positively correlated with both temperature ($r = 0.59$ $P = 0.02$) and larval length ($r = 0.60$ $P = 0.02$).

Larval growth rate was positively correlated with copepod density ($r = 0.72$ $P = 0.01$). Zooplankton concentration was positively correlated with larval bay anchovy FI ($r = 0.66$ $P = 0.03$), and negatively correlated with below-pycnocline DO ($r = -0.67$ $P = 0.02$). However, mean water-column DO and DO at 3-m depth did not exhibit significant negative correlations with zooplankton concentration ($r = -0.55$ $P = 0.06$ and $r = -0.31$ $P = 0.32$, respectively).

Table 32. Simple correlation coefficients for the regional means ($n = 11-15$) of fourteen variables and the annual means ($n = 5$) of eleven variables (in relation to YOY abundance and freshwater inflow) measured during summer TIES surveys in Chesapeake Bay from 1995-1999. The parameters include: \log_e larval bay anchovy abundance (m^{-2}), \log_e larval bay anchovy density (m^{-3}), \log_e bay anchovy egg abundance (m^{-2}), \log_e bay anchovy egg density (m^{-3}), larval length (mm), linear growth rate (G) (mm/day), feeding incidence (FI), and prey per gut (PPG), \log_e ctenophore biovolume (ml/m^3), \log_e zooplankton density (m^{-3}), mean March-May freshwater inflow (FWI) into Chesapeake Bay ($\times 10^3$ ft³/s), based on estimates by the USGS (2002), mean water-column temperature ($^{\circ}C$), salinity (ppt), chlorophyll a biomass (indexed by fluorescence), and below-pycnocline dissolved oxygen (DO) (mg/L). \log_e mean bay-wide bay anchovy young-of-year (YOY) abundance (m^{-2}) was based on October of 1995-1999 estimates by Jung (2002). Larval growth rate (G) was compared to copepod density and not total zooplankton density. * = $P < 0.05$, ** = $P < 0.01$.

	Larval Abundance	Larval Density	Egg Abundance	Egg Density	Larval Length	G	FI	PPG
Larval Abundance		0.94**	0.79**	0.79**	-0.53*	-0.11	-0.31	0.35
Larval Density			0.76**	0.77**	-0.55*	-0.06	-0.16	0.36
Egg Abundance				0.99**	-0.83**	-0.35	-0.47	-0.18
Egg Density					-0.86**	-0.40	-0.40	-0.16
Larval Length						0.30	0.33	0.26
G							0.38	0.22
FI								0.33
YOY Abundance	0.86	0.80	0.69	0.66	-0.81	0.21	0.93*	-0.13

Table 32 (cont'd)

	Ctenophore Biovolume	Zooplankton Density	Temp.	Salinity	Fluor.	DO	FWI
Larval Abundance	-0.17	0.23	-0.11	0.87**	-0.50	0.07	0.19
Larval Density	-0.22	0.21	-0.15	0.86**	-0.40	0.17	-0.04
Egg Abundance	-0.12	0.05	-0.41	0.72**	-0.61*	0.09	-0.22
Egg Density	-0.10	0.07	-0.44	0.72**	-0.62*	0.07	-0.28
Larval Length	0.23	-0.03	0.46	-0.44	0.60*	0.12	0.20
G	-0.21	0.72*	0.35	-0.29	0.05	-0.25	0.47
FI	-0.32	0.66*	0.30	-0.36	0.26	-0.35	0.22
PPG	-0.07	0.06	0.11	0.23	0.09	0.20	0.73
Jelly Biovolume		-0.31	-0.46	-0.18	-0.19	0.18	0.12
Zooplankton Density			0.43	-0.12	-0.38	-0.67*	-0.18
Temperature				-0.10	0.59*	-0.04	-0.10
Salinity					-0.27	0.34	-0.50
Fluorescence						0.48	-0.22
YOY Abundance	-0.46	0.67					0.32

Multiple Regressions

Four multiple regression equations were developed to describe the relationships between bay anchovy larval abundance, egg abundance, larval length, and feeding incidence with several independent variables (Table 33). Egg abundance, temperature, and larval prey per gut explained 88% of the variability in larval abundance (Regression 1, Table 33). All three independent variables had positive coefficients, indicating that larval abundance increased with increases in egg abundance, temperature, and larval prey per gut. Modeled values of larval abundance differed from each year's observed values by a minimum of 24% in 1999 to a maximum of 92% in 1996 (Figure 43).

Salinity (a regional effect) and chlorophyll a biomass (fluorescence) explained 70% of the variability in bay anchovy egg abundance (Regression 2, Table 33). The positive coefficient for salinity is indicative of the high spawning activity in the high-salinity waters of the lower bay, while the negative coefficient for chlorophyll a biomass could indicate lower spawning activity by bay anchovy in regions of high chlorophyll a biomass. Modeled egg abundances differed from observed abundances from 10% in 1996 to 41% in 1998 (Figure 44).

Ctenophore biovolume and egg density explained 81% of the variability in mean larval length (Regression 3, Table 33). The negative coefficient for egg density appears to be related to the higher concentration of larger larvae near the head of the bay where bay anchovy spawning activity is reduced. The positive coefficient for ctenophore biovolume is not easily explained or understood, but could be in part a result of selective predation by ctenophores on smaller, less mobile bay anchovy larvae. Modeled values of

larval length differed from each year's observed values by a minimum of 4% in 1996 to a maximum of 38% in 1997 (Figure 45).

Zooplankton density, larval density, and ctenophore biovolume explained 72% of the variability in larval feeding incidence (Regression 4, Table 33). Increases in zooplankton density were associated with increases in larval feeding incidence, while larval density and ctenophore biovolume appeared to negatively influence larval feeding incidence. Modeled values of larval feeding incidence differed from each year's observed values by a minimum of 3% in 1996 to a maximum of 37% in 1998 (Figure 46). There was no significant multiple regression that explained a significant amount of variability in larval growth rate or prey per gut.

Table 33. Multiple regression equations that best describe the relationships of 1) larval bay anchovy abundance (m^{-2}), 2) bay anchovy egg abundance (m^{-2}), 3) larval length (mm), 4) larval growth rate (mm/day), and 5) feeding incidence with a suite of independent variables. SPRC = standardized partial regression coefficients.

Regression Equation	Dependent Variable	Independent Variables	SPRC	Multiple R ²	P value
(1) $Y = -19.69 + 1.23X_1 + 4.91X_2 + 0.43X_3$	Larval abundance (m^{-2})	Egg abundance (X_1), Larval prey per gut (X_2), Temperature (X_3)	$X_1 = 7.69$ $X_2 = 4.55$ $X_3 = 2.69$	0.88	$p < 0.0001$
(2) $Y = 1.28 + 0.23X_4 - 2.11X_5$	Egg abundance (m^{-2})	Salinity (X_4), Fluorescence (X_5)	$X_4 = 3.83$ $X_5 = -2.74$	0.70	$p = 0.0007$
(3) $Y = 5.81 - 2.20X_6 + 1.03X_7$	Larval length (mm)	Egg density (X_6), Ctenophore biovolume (X_7)	$X_6 = -6.47$ $X_7 = 1.94$	0.81	$p < 0.0001$
(4) $Y = 0.30 + 0.08X_8 - 0.09X_9 + 0.03X_{10}$	Larval feeding incidence	Zooplankton density (X_8), Ctenophore biovolume (X_9), Larval density (X_{10})	$X_8 = 2.67$ $X_9 = -2.64$ $X_{10} = -1.50$	0.72	$p = 0.02$

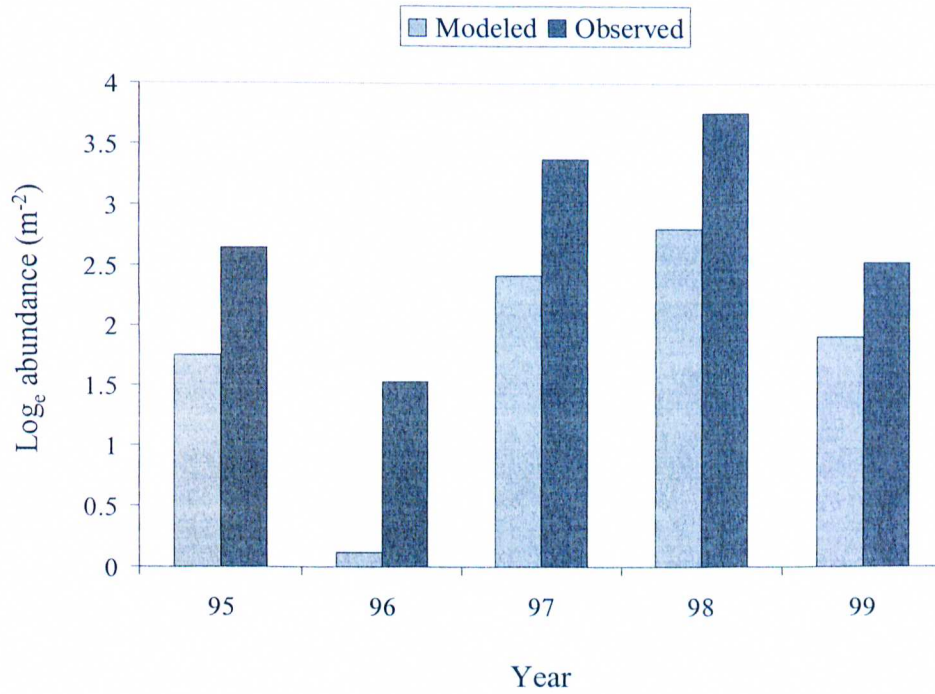


Figure 43. Observed vs modeled \log_e larval bay anchovy abundances (m^{-2}) (multiple regression equation 1, Table 33) from summer TIES surveys in Chesapeake Bay from 1995-1999.

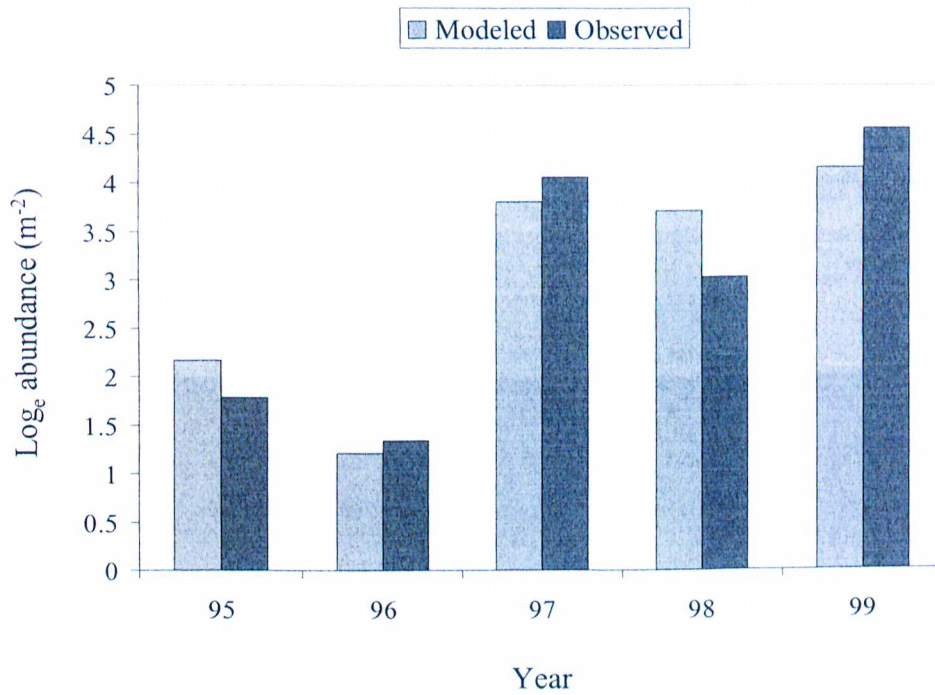


Figure 44. Observed vs modeled \log_e bay anchovy egg abundances (m^{-2}) (multiple regression equation 2, Table 33) from summer TIES surveys in Chesapeake Bay from 1995-1999.

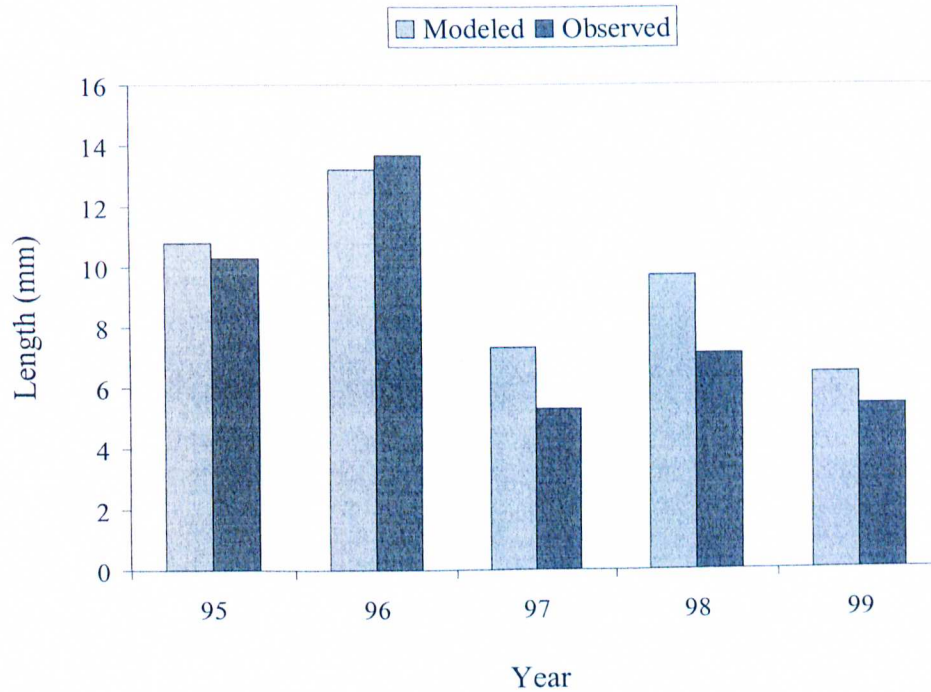


Figure 45. Observed vs modeled larval bay anchovy lengths (mm) (multiple regression equation 3, Table 33) from summer TIES surveys in Chesapeake Bay from 1995-1999.

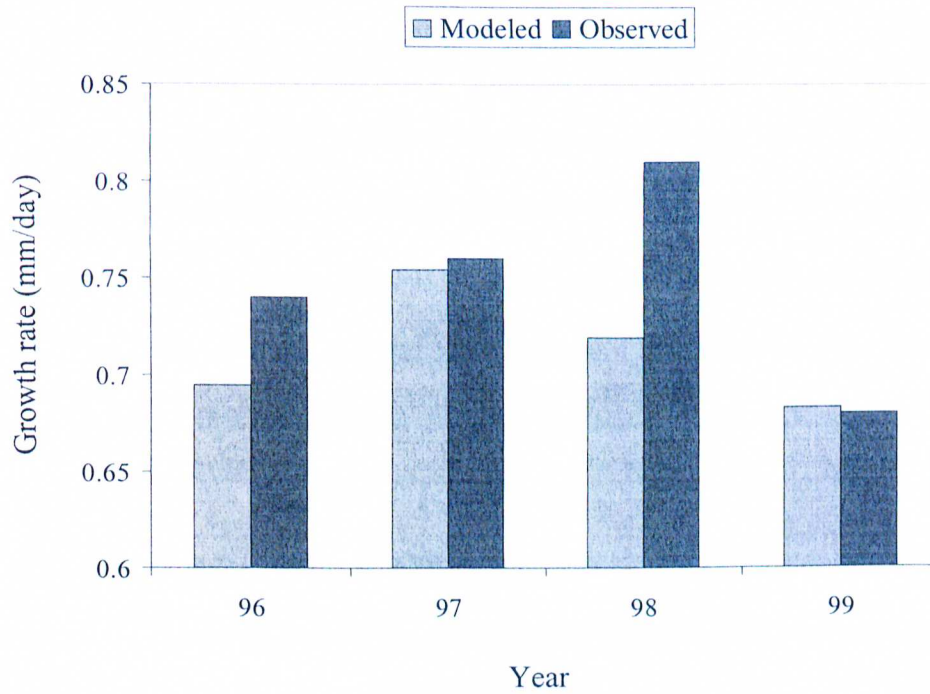


Figure 46. Observed vs modeled larval bay anchovy growth rates (mm/day) (multiple regression equation 4, Table 33) from summer TIES surveys in Chesapeake Bay from 1995-1999.

DISCUSSION

Abundances and Distributions

A knowledge of the patterns of abundance and distribution of bay anchovy eggs and larvae in Chesapeake Bay is critical to understand spawning habits of adults, and the habitat use, environmental requirements, and survival of larvae that could determine future recruitment. Processes affecting the condition and survival of larval-stage fish can control the future recruitment of a year class (Houde, 1987). Such control may be especially important for bay anchovy, which is essentially an annual species in Chesapeake Bay whose population is primarily comprised of YOY and age 1 individuals (Newberger and Houde, 1995). Newberger and Houde (1995) believed that “interannual changes in (bay anchovy) abundance, when they do occur, do so as a consequence of recruitment fluctuations.” Jung's (2002) analysis and stock-recruitment modeling of bay anchovy dynamics confirms the importance of pre-juvenile abundance, distribution, and survival in the establishment of YOY abundance levels in October of each year.

Year-to-year bay anchovy egg and larval abundances varied 15 and 9 fold, respectively, during this five-year study. Some of this variation may be attributed to differential cruise timing between sampled years. Olney (1983) reported that bay anchovy egg and larval densities in the lower Chesapeake Bay varied 4 and 2 fold, respectively, from 1971-1973, while Re (1996) reported greater variations in *Engraulis encrasicolus* egg (24 fold) and larval (35 fold) densities in the Mira estuary in southwestern Portugal from 1985-1992. Among-year variability in larval abundance during this study, although shy of being significantly correlated at the $\alpha=0.05$ level ($r =$

0.86 $P = 0.06$), was closely concordant with October YOY bay anchovy abundances in Chesapeake Bay from 1995-1999, further supporting the hypothesized link between larval abundance and recruitment. Wang (1999) reached a similar conclusion based on modeled bay anchovy bioenergetics and recruitment dynamics in Chesapeake Bay. In addition, Kideys et al. (1999) found that the lowest abundances of *E. encrasicolus* eggs and larvae recorded in the Black Sea from 1957-1996 coincided with the lowest catches of adults from those year classes.

Spawning by bay anchovy occurred throughout the bay, but the highest spawning activity was concentrated in the lower, most seaward bay region. In all sampled years, egg and larval abundances decreased from the mouth to the head of the bay along a declining salinity gradient. In 1996, no larvae were collected in the upper-bay samples, and few were collected in the mid bay. However, YOY bay anchovy in mid-water trawl collections from the July 1996 cruise were estimated to represent abundances of >30 mm individuals equal to 4.2×10^8 in the upper bay and 2.8×10^9 in the mid bay (Jung, 2002), indicating that spawning may have occurred in these bay regions earlier in the year or, alternatively, that YOY fish had migrated to these regions. Bay anchovy mean egg and larval abundances were 12-65 and 74-365 times higher, respectively, in the lower bay than in the upper bay in the four-year period, 1995-1998. This pattern of regional differences in egg and larval abundance also was observed by Rilling and Houde (1999a) in July 1993. The regional differences in my study were not as apparent in 1999, when sampling was conducted during late June rather than July. It is notable that the more uniform regional patterns of egg and larval abundances observed in June 1999 were similar to those observed by Rilling and Houde (1999a) in their June 1993 survey.

The importance of the lower bay region to bay anchovy egg and larval production is even more apparent if the volume differences between the three regions are considered. The volume of the lower bay ($26.6 \times 10^9 \text{ m}^3$) is approximately 1.5 times that of the mid bay ($16.8 \times 10^9 \text{ m}^3$) and more than three times that of the upper bay ($8.7 \times 10^9 \text{ m}^3$) (Cronin, 1971; Rilling and Houde, 1999a). Using the mean regional estimated densities for eggs and larvae from 1995-1999, estimated bay anchovy egg and larval regional abundances increased on average from 3.29×10^{10} to 5.35×10^{11} and from 6.06×10^8 to 1.09×10^{11} , respectively, from the upper to the lower bay. Mean regional abundance of bay anchovy eggs in the lower bay was 2.5 times higher than in the mid bay and 16 times higher than in the upper bay. The mean regional abundance of bay anchovy larvae in the lower bay was 6 times higher than in the mid bay and 180 times higher than in the upper bay.

Although comparable in distribution to previous studies, the regional mean abundances of bay anchovy eggs and larvae observed in this study were approximately one order of magnitude lower than those reported for the lower bay by Olney (1983), the mid and lower bay by Dorsey et al. (1996), the mid bay by MacGregor and Houde (1996), and bay-wide by Rilling and Houde (1999a). This may indicate a decline in bay anchovy stock size in Chesapeake Bay in the last decade of the 20th century that could have important ecological consequences for both higher and lower trophic levels. Based on abundance indices developed from fishery-independent surveys conducted by the Virginia Institute of Marine Science (VIMS) in the mainstem and tributaries of the mid and lower bay, Houde and Wood (2002) reported that the bay anchovy population in Chesapeake Bay had decreased steadily from highs in the mid 1980s to a 20-year low in

1996. However, abundances began to increase in the late 1990s, and may be leveling off or increasing slowly into 2001 (Houde and Wood, 2002). Data from TIES mid-water trawl surveys in October indicated a steady increase in bay anchovy recruitment and fall abundance in the 1995-2000 period (Jung, 2002).

Many factors were correlated with egg and larval abundances. Some correlations are easily explained. For example, egg and larval abundances both were positively correlated with each other and salinity. These correlations primarily are an indicator of the concentrated spawning by bay anchovy in the high salinity lower bay and inevitable geographic overlap between eggs and larvae resulting from the short ≤ 24 -hour hatching time of eggs.

Perhaps surprisingly, chlorophyll a biomass was negatively correlated with egg abundance, indicating that adult bay anchovy did not spawn preferentially on a spatial or temporal scale that overlaps with areas of high phytoplankton abundance. MacGregor and Houde (1996) found that highest densities of bay anchovy eggs were in an offshore area where chlorophyll a concentrations were average or lower than those nearshore in mid Chesapeake Bay where bay anchovy spawning activity was lower. The negative correlation also is indicative of a regional effect resulting from chlorophyll a concentrations generally being higher in the upper and mid bay (Appendix 11), while egg abundances followed the opposite pattern (Table 7).

In multiple regression analyses, number of prey per larval gut and mean water-column temperature were positively related to larval abundance. This could indicate that larvae are more effective feeders in areas of high temperature, if these temperatures increase their predation capacity and assimilation efficiencies. Dorsey et al. (1996),

Rilling and Houde (1999a), and Fulling and Peterson (1999) all reported significant positive correlations between zooplankton densities and larval bay anchovy abundances. Peebles (2002) found that bay anchovy egg abundance in the Manatee River estuary, Florida was positively related to the concentration of the calanoid copepod *Acartia tonsa* and water temperature, while Peebles et al. (1996) reported that copepod density and water temperature were significantly and positively correlated with densities of preflexion (= small) bay anchovy larvae in Tampa Bay. However, it may be that the regional temperature differences recorded from 1995-1999 in the present study were not sufficiently variable to have a large effect on larval abundance and distribution, as temperature only accounted for 10% of the total variability accounted for by the multiple regression equation describing larval abundance (Table 33, Regression 1). I agree with Rilling and Houde (1999a), who stated that “it is likely that many factors act together to promote suitability of the lower Bay as a spawning and nursery area for bay anchovy, despite its broad tolerance of environmental conditions and its ability to spawn and produce viable larvae over a wide range of conditions (Houde and Zastrow, 1991).”

Larval Feeding

Feeding success of larval fishes is critical in maintaining high growth rates and, potentially, the capacity to avoid predation, which can directly influence future recruitment success (Houde, 1987; Miller, 1994; Re, 1996; Plounevez and Champalbert, 1999; Hillgruber and Kloppmann, 2000; Gonzalez-Quiros and Anadon, 2001). In the present study, feeding incidence of larval bay anchovy was strongly and positively correlated with October YOY abundance of bay anchovy ($r = 0.93$ $P = 0.02$), evidence

supporting the contention that recruitment of bay anchovy in Chesapeake Bay is determined at least in part by larval-stage processes, in this case feeding success.

Larval bay anchovy was found to feed almost exclusively during the day. This diel behavior is common in clupeiform larvae especially and larval fish in general that rely on visual acuity to locate and attack living prey (Arthur, 1976; Last, 1980; Batty, 1987; Re, 1996; Conway et al., 1998). However, Hillgruber and Kloppmann (1999) found that a high proportion of blue whiting (*Micromesistius poutassou*, family Gadidae) larvae on Porcupine Bank west of Ireland continued to feed throughout the night. In the present study, most guts of larval bay anchovy were empty at night and only carapaces of a few copepods were found in the hindguts of larvae collected soon after dusk, which probably represented undigested food from daylight feeding.

Larval bay anchovy feeding incidence (FI) in Chesapeake Bay was low, and varied by year and regionally. Larval bay anchovy FI for all sizes combined varied among years from 0.09-0.23, and averaged 0.17 over the five-year study. Although FIs observed in the present study were lower than those reported for laboratory-reared bay anchovy larvae by Detwyler and Houde (1970) (0.61) and for the clupeid *Clupea harengus* reported by Heath et al. (1989) (~0.33) and Cohen and Lough (1983) (0.43-0.50), they were comparable to FIs reported for other larval engraulids: 0.02 (Berner, 1959) and 0.10 (Arthur, 1976) for larval *E. mordax*, 0.14 for larval *E. japonica* (Matsushita et al., 1988), 0.22 for larval *E. ringens* (de Mendiola, 1974), 0.30 for larval *E. anchoita* (Ciechomski, 1967), and 0.49 for larval *E. encrasicolus* (Conway et al., 1998). The relatively low FI found in this study and other field studies may be a consequence of gut-content egestion during collection (Cohen and Lough, 1983). The

observed variability in FI between years and regions may have resulted from differences in zooplankton density, which was positively correlated with larval bay anchovy FI. This explanation is supported by numerous studies that have also found that prey concentrations can affect feeding success in larval fish (Anderson, 1994; Fortier et al., 1995; Conway et al., 1998).

FI may be positively related to larval size. In the present study, FI of larval bay anchovy generally increased with larval size, a pattern that was consistent over years, regions, and above and below the pycnocline. Matsushita et al. (1988) reported a steady increase in the rate of feeding (FI) of *E. japonica* larvae from 5.0 to 20.0 mm, while Munk and Kiorboe (1984) reported increased FI in laboratory-reared *C. harengus* larvae from 5 to 11 days post-hatch. FI may increase in larger larvae because of increased feeding efficiency (percent of attacks that lead to ingestion) during ontogeny. Several laboratory studies have shown that feeding efficiency of larval herring *C. harengus* increases as a function of age (Rosenthal, 1969; Blaxter and Staines, 1971; Munk and Kiorboe, 1985).

However, there also is evidence that larval FI may initially increase with larval size in engraulids, then decrease at intermediate sizes, before increasing again in larger larvae. For example, Arthur (1976) and Conway et al. (1998) reported increases in larval FI of *E. mordax* and *E. encrasicolus* with size up to approximately 4.5 mm, then a decreased FI between approximately 4.5-7.5 mm, before a subsequent increase at larger larval sizes. In another example, Berner (1959) observed an initial increase in FI for larval *E. mordax* from 3.0-5.0 mm, then a steady decrease in FI from 5.1-13.0 mm. And, Ciechomski (1967) found that FI for larval *E. anchoita* decreased from 5.1-9.0 mm,

before increasing at longer larval lengths, while de Mendiola (1974) observed a steady decline in FI of larval *E. ringens* between 5.1 and 15.0 mm, before an increase in longer larvae. If a fraction of 'intermediate-size' larvae were declining in nutritional condition and were on the verge of starving, then their FI would decline. In my study, there was no apparent decrease in FI of bay anchovy in the 4.4-7.5 mm larval size class, although FI did not increase significantly until larvae were ≥ 7.5 -13.4 mm.

The mean number of prey items per larval bay anchovy gut (PPG) was low and relatively invariable. Mean PPG ranged from 1.00-1.60 regionally, and averaged 1.4 over the 5-year study. The maximum number of prey items in an individual larval gut was 7, ingested by a 12.8-mm larva. Mean PPG in this study was marginally less than that reported for engraulid larvae by other studies: for example, 2-5 PPG (Detwyler and Houde, 1970) for larval bay anchovy in the laboratory, 1-3 PPG (Duka, 1969) and 1-4 PPG (Conway et al., 1998) for larval *E. encrasicolus*, and 1.7-2.6 PPG for larval *E. anchoita* (Vinas and Ramirez, 1996). Cohen and Lough (1983) identified several factors that could influence the PPG of fish larvae, including "differences in larval size, prey size, plankton supply, gut clearance time (temperature-dependent) and loss of gut content during capture."

Mean PPG in the present study did not differ significantly among larval size classes. Conway et al. (1998) also observed no significant differences in PPG among sizes for larval *E. encrasicolus*, nor did Noskov et al. (1979) for larval *C. harengus*. In contrast, in comparing different size classes of larval *C. harengus*, Hentschel (1950) did observe an increase in PPG for larvae of 7-45 mm, while Bowers and Williamson (1951), perhaps surprisingly, observed a decrease for 6->15 mm herring larvae. Gonzalez-Quiros

and Anadon (2001) found that PPG decreased with larval *M. poutassou* size, while Hillgruber and Kloppmann (2000) reported that PPG in *M. poutassou* increased up to 5.5 mm then decreased in larvae >6 mm in length. However, Hillgruber and Kloppmann (1999) claimed that prey per gut “provide(s) only an indication for larval feeding conditions and (is) potentially misleading when larvae are feeding on different taxonomic groups of differing sizes.” In the present study, larval bay anchovy added larger prey to their diet as they grew, so that a relatively constant PPG among size classes does not imply lower caloric intake for larger larvae.

Larval engraulids, and larval fish in general, feed primarily on various life stages of copepods (de Mendiola, 1974; Arthur, 1976; Last 1980; Conway et al., 1998). Smaller prey, for example tintinnids, were found to be important prey of small larval bay anchovy (Houde and Lovdal, 1984; Re, 1996). Copepod eggs, nauplii, copepodites, and adult copepods were the primary prey ingested by larval bay anchovy in Chesapeake Bay from 1995-1999, comprising 72% of the identifiable food items. It is common for larval clupeiforms to consume various life-stages of the most abundant copepod species found in the water column (Gosheva and Slonova, 1976; Noskov et al., 1979; Last, 1980; Cohen and Lough, 1983). This was the case in the present study, where the calanoid copepod *Acartia tonsa* was the dominant species consumed, and the most abundant copepod species in the Bay.

Larval size appeared to be the primary factor influencing larval bay anchovy prey selection among years, regions, and above and below the pycnocline in Chesapeake Bay. As larval size increased, larvae shifted from selecting smaller prey species and copepod stages to larger ones. Copepod eggs, nauplii, rotifers, tintinnids, and diatoms dominated

the diets of 2.5-7.4 mm larvae, while 7.5-10.4 mm larvae added a greater percentage of copepod nauplii, copepodites, and adult copepods to their diet. Copepodites and adult copepods comprised 47% of the identified prey items in 10.5-13.4 mm larvae, which increased to 78% for 13.5-16.4 mm larvae. Increases in prey size with larval size have been reported in many feeding studies on clupeiform larvae and on fish larvae in general (Detwyler and Houde, 1970; Arthur, 1976; Hunter, 1981; Houde and Lovdal, 1984). Bay anchovy larvae in Chesapeake Bay continued to eat the smaller, more plentiful food items as they grew, possibly insuring their ability to maintain growth and metabolism while adding larger, more nutritionally profitable prey (Arthur, 1976; Houde and Lovdal, 1984; Houde, 1997a).

The relative size of larval prey items (prey size/larval size) can be used as a scalar of predator-prey interactions (Werner and Hall, 1974; Werner, 1977; Crowder, 1985). According to Miller et al. (1988), "Both small and large prey may be of lower utility (sensu Werner, 1977) than those of intermediate sizes." In both experimental and field studies, Munk (1992) found that larval *C. harengus* attack success on prey items decreased linearly from near 100% at a relative prey length (RPL) of 0.005 to near 0% at a RPL of 0.08. He determined that a RPL range of 0.025-0.030 was optimal for attack success in all larval size classes calibrated for differential prey concentrations (Munk, 1992).

In the present study, mean RPL for bay anchovy larvae was 0.03, and increased slightly with larval size (RPL = .017 for 2.5-4.4 mm larvae, RPL = .017 for 4.5-7.4 mm larvae, RPL = .023 for 7.5-10.4 mm larvae, RPL = .033 for 10.5-13.4 mm larvae, RPL = .048 for 13.5-16.4 mm larvae). This indicates that, although bay anchovy larvae may be

feeding on prey near a potentially optimal RPL, there is generally a significant, though gradual, increase in the size of prey items added to the diet of larval bay anchovy in Chesapeake Bay relative to larval size during ontogeny. This is evidence supporting Brooks and Dodson's (1965) 'efficiency of size' hypothesis, which proposes that available prey increases as larval size increases, due to the ability of larvae to incorporate both those prey items available to smaller larvae and increasingly larger prey items relative to their own body size as they grow. However, Munk's (1992) findings of "uniformity of relative prey size spectra...implies that, *a priori*, the available biomass of food (as proportion of predator biomass) will not increase (as larval size increases)."

Larval bay anchovy in Chesapeake Bay generally exhibited positive feeding preference for invertebrate eggs (predominately copepod eggs) and copepod copepodites/adults, and a negative preference for copepod nauplii and other prey taxa. However, copepod nauplii were the dominant potential prey of bay anchovy larvae in zooplankton samples and were the primary food item consumed by 7.5-13.4 mm larvae. Houde and Lovdal (1984) found that larval bay anchovy in Biscayne Bay, Florida preferred copepodites and adult copepods, but showed no preference for copepod nauplii which were the most consumed prey. In a literature review of larval *C. harengus* feeding ecology, Blaxter (1965) reported that copepod adults were preferred prey, while nauplii were rarely ingested by herring larvae despite comprising approximately 50% of the plankton in the environment. Hillgruber and Kloppmann (1999) reported that larval blue whiting on Porcupine Bank showed a strong preference for copepod eggs, while Conway et al. (1998) found that *E. encrasicolus* larvae consumed free-spawned copepod eggs in proportion to their density in the water column.

Feeding preference for invertebrate eggs might be positively biased if there is increased digestion time for eggs relative to other prey items (Conway et al., 1994). However, since anchovy larvae have narrow, straight alimentary canals and fast gut-passage times of between 30 minutes and 3 hours (Re, 1996; Conway et al., 1998), prey items in their guts presumably fairly represent the spectrum of food recently ingested. There are several explanations that may account for the dominance of copepod eggs in larval guts relative to their concentration in the water column. Many copepod species, such as the abundant *Acartia tonsa*, are serial spawners that contribute to most free-spawned copepod eggs in the water column (Roman et al., 2001). Eggs could have been freed from ingested gravid copepods after they were eaten, and remained in larval guts after the copepod had been digested and its carapace expelled. Also, some copepod species, such as *Eurytemora affinis*, which was found in larval guts, carry their eggs in external sacs (Roman et al., 2001) that may have been dislodged during ingestion of a copepod by larvae. In 1996 bay-wide and 1997 upper bay, 75% and 86% respectively of the ingested prey items in larval bay anchovy guts were invertebrate (copepod) eggs, although virtually no free-spawned eggs were found in the associated zooplankton samples. This led to the unusually high positive preferences for invertebrate eggs that are reported for the entire bay in 1996 and the upper bay in 1997 (Chesson's $\alpha = 0.99$). The elevated Chesson's α value for invertebrate eggs in 1996 resulted in lower α values for other taxa (i. e., copepodites and adult copepods), and gave the impression of a decline in larval preference for invertebrate eggs and an increase in preference for copepodites and adult copepods from 1996-1999 (Figure 38).

Larval Growth

Relatively fast growth in the larval stage can reduce starvation potential, minimize the duration time when size-selective predation occurs, and may enhance recruitment (Houde, 1987; Bailey et al., 1996; Meekan and Fortier, 1996). In this study, larval growth rate of bay anchovy was not correlated with fall YOY abundance ($r = 0.21$ $P = 0.73$). Simulation models generally have concluded that increases in both the means and variances of larval growth rate result in increased potential for larval survival and recruitment of marine fish (Pepin, 1989; Rice et al., 1993; Cowan et al., 1996). Allain et al. (2002) found evidence for growth-selective survival of Bay of Biscay anchovy (*E. encrasicolus*) between the larval and juvenile stages. In the present study, variability in growth rate was evident during the bay anchovy larval stage, but it did not have a clear relationship to future recruitment of a cohort (Houde, 1996; Houde, 1997b).

Although differences in growth rates observed in the present study were modest, their effect on stage-specific survivorship might have been substantial. Larval bay anchovy could have reached the average length of metamorphosis (30 mm) in approximately 34 days post-hatch in 1998, the year of highest mean growth rate (0.81 mm/day), while they would have required 40.5 days to reach that length in 1999, the year of lowest mean growth rate (0.68 mm/day). Using Rilling and Houde's (1999b) estimate for Chesapeake Bay-wide larval mortality rate of bay anchovy in July (0.23 d^{-1}), the difference in growth rate of 0.13 mm/day between 1998 and 1999 could have generated an ~4.5-fold difference in survivorship to metamorphosis between the two years.

Bay anchovy growth in the larval stage was nicely fit by a Gompertz growth model. An examination of the residuals of size-at-age for each 1-mm larval length class

from the pooled data revealed no apparent estimation bias (either over or under) in growth rate for any larval length class. Age-specific growth rates were highest for larvae at approximately 10 days of age, when they ranged from 0.84 mm/day in 1996 to 1.01 mm/day in 1995. Growth rate steadily declined at older ages, reaching values at 30 days of age between 0.19 mm/day in 1999 and 0.43 mm/day in 1998. The relatively low modeled growth rates of older age classes of larvae are partly a consequence of the asymptotic nature of the Gompertz model. Another contributing factor could have been aging error due to inaccurate counts of the number of growth increments along the cloudy, outer edge of otoliths from the largest larvae. It is probable that growth rate declines in older larvae as they undergo metamorphosis into the juvenile stage. In a synthesis of published growth data from earlier research, Houde (1997b) reported that larval bay anchovy growth rate decreased from 0.57 mm/day for first-feeding larvae to 0.24 mm/day for late-stage larvae. The Gompertz model is reported to be a good descriptor of growth in fish larvae because it accounts for variable, age-specific growth and has been used successfully in several studies to parameterize the growth of clupeid and engraulid larvae (Hunter, 1976; Bolz and Burns, 1996; Gaughan et al., 2001).

Growth rates of bay anchovy derived from linear regressions of length on age of the <30-day old larvae varied among yearly surveys and regionally in Chesapeake Bay. Bay-wide growth rates ranged from 0.68 mm/day in 1999 to 0.81 mm/day in 1998, with a mean of 0.75 mm/day over the 5-year study. The growth rates in this study were comparable, or perhaps a bit higher, than those reported for larval bay anchovy in previous studies in the laboratory and in estuaries along the east coast of North America (Table 34). Moreover, the growth rates in this study are very similar to those reported by

Table 34. Growth rates reported for larval bay anchovy from various studies in the laboratory and in estuaries along the east coast of North America.

Location	Growth Rate (mm/day)	Source
Laboratory experiments	0.37-0.59	Houde and Schekter (1981)
Patuxent River, MD (tributary of Chesapeake Bay)	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	Leak and Houde (1987)
Chesapeake Bay, MD (Mesocosms in Patuxent River, a mid-bay tributary)	0.39-0.61	Cowan and Houde (1990)
Great South Bay, NY	0.52-0.59	Castro and Cowen (1991)
Chesapeake Bay, MD/VA (Bay-wide in June)	0.53-0.61	Rilling and Houde (1999b)
Chesapeake Bay, MD/VA (Bay-wide in July)	0.70-0.78	Rilling and Houde (1999b)
Hudson River Estuary, NY	0.39-0.88	Jordan et al. (2000)
Chesapeake Bay, MD (Mid bay)	0.38-0.43	O'Brien (2002)
Chesapeake Bay, MD (Mid-bay biopatch)	0.52-0.54	O'Brien (2002)
Chesapeake Bay, MD/VA (Bay-wide from 1995-1999)	0.68-0.81	Present study (2003)

Rilling and Houde (1999b) for their July 1993 data (0.70-0.78 mm/day), which is the only other bay-wide study conducted throughout Chesapeake Bay. However, Rilling and Houde (1999b) reported lower growth rates (0.53-0.61 mm/day) for larval bay anchovy in Chesapeake Bay in June. Interannual variability in growth rate of larval bay anchovy in the Hudson River estuary was reported by Jordan et al. (2000) for 1995 (median = 0.48 mm/day) and 1996 (median = 0.55 mm/day).

An important factor affecting larval growth rate was the density of prey items in the environment. Copepod and copepod nauplii densities were both strongly and positively correlated with larval bay anchovy growth rate ($r = +0.72$ $P = 0.01$ and $+0.69$ $P = 0.02$, respectively). Regional relative prey densities in each year closely mirrored regional larval growth rates. The highest recorded regional zooplankton density (208.9 L^{-1}) was observed in the mid bay in 1996 and coincided with one of the highest regional larval bay anchovy growth rates (0.83 mm/day), while the lowest regional zooplankton density (38.9 L^{-1}) and lowest larval growth rate (0.55 mm/day) both occurred in the mid bay in 1999. Many field and laboratory studies have reported a similar positive relationship between larval fish growth rates and prey abundance (Gotceitas et al., 1996; Oozeki and Zenitani, 1996; Cass-Calay, 1997;). Rilling and Houde (1999b) also reported that larval bay anchovy growth in Chesapeake Bay was positively related to zooplankton density, while Gaughan et al. (2001) reached the same conclusion for larval sardine *S. sagax* off the coast of southern Australia.

In laboratory experiments, Saksena and Houde (1972) reported that larval bay anchovy growth rate increased from 0.48 to 0.54 mm/day as prey concentration increased five-fold from 621 to 3323 L^{-1} , and Houde (1978) reported increases in larval bay

anchovy growth from 0.32 to 0.63 mm/day as laboratory prey concentrations increased from 27 to 4731 L⁻¹. Some field and laboratory studies on larval clupeids have not found growth to be limited by prey availability (Owens et al., 1990; McGurk et al., 1993). However, this result may only apply to larvae exposed to prey concentrations higher than a minimal level required for larval growth (Gaughan et al., 2001). Cowan and Houde (1990) obtained reasonably high growth rates (0.39-0.63 mm/day) for larval bay anchovy in mesocosm experiments in a tributary of Chesapeake Bay at prey concentrations as low as 50 L⁻¹, and did not find a significant relationship between prey concentration and larval growth for prey densities ranging from 50 to 5000 L⁻¹. Based on the results of laboratory experiments, Houde (1978) suggested that a prey concentration of 107 L⁻¹ was required for 10% of larval bay anchovy to survive to metamorphosis. Types, sizes, and concentrations of prey all are likely to contribute to growth-rate variability in larval anchovy. Larval bay anchovy growth in Chesapeake Bay probably varies much like that observed by Castro and Cowen (1991) in Great South Bay, New York, where growth was related to, but not dependent on, food concentration alone.

While zooplankton concentration may have enhanced larval bay anchovy growth through increased feeding success, density-dependent competition among anchovy larvae may have led to reduced feeding and growth rates in regions of high larval abundance. Larval density, in the multiple regression analysis, was negatively related to larval feeding incidence. Although not significant, larval abundance was negatively correlated with both larval growth rate and feeding incidence ($r = -0.11$ $P = 0.70$ and $r = -0.31$ $P = 0.29$, respectively). Density-dependent processes have been argued to regulate larval growth-rate variability in several simulation models (Jones, 1973; Jones and Hall, 1974;

Ware, 1975; Shepard and Cushing, 1980). Matsushita et al. (1988) found a clear decrease in the rate of feeding of field-collected larval Japanese anchovy (*E. japonica*) with increasing larval density. Cowan and Houde (1990) observed that larval bay anchovy growth rate declined from 0.64 to 0.41 mm/day as stocking density of eggs increased from 10 to $>1000 \text{ m}^{-3}$ in a mesocosm experiment in mid-Chesapeake Bay. Wang et al. (1997) suggested that "density-dependence via food limitation may be operating in the bay anchovy population in the mid-(Chesapeake) Bay," although their model outputs indicated that density dependence mostly influences YOY growth rather than growth of larval stages. However, Wang et al. (1997) also argue that "the effect of density-dependent growth...may slide between early life stages by acting differentially upon a life stage that exceeds a threshold in any given year, due either to environmental variability or population size, or both."

In the present study, highest bay anchovy larval densities were consistently in the lower bay where peak spawning occurred, while growth rates were generally higher in the upper bay. The observed regional differences in larval densities and growth rates may be evidence for density-dependent growth in larval bay anchovy in Chesapeake Bay. If so, an up-bay transport mechanism could benefit the recruiting bay anchovy population by alleviating the density-dependent condition in the lower bay through transport of a fraction of the larval population to productive habitats in the upper bay where fewer larvae were hatched. There is evidence that such up-bay transport occurs, although it may not be effective until late-larval or early-juvenile stages (Loos and Perry, 1991; Kimura et al., 2000).

Although there are indications that density dependence may affect larval and YOY bay anchovy feeding and growth, Hagy (2002) found that mesozooplankton production in Chesapeake Bay during the summer was not fully utilized by predators, primarily bay anchovy and ctenophores, in the mid and lower bay. Predator-prey interactions between bay anchovy, ctenophores, and sea nettles (a scyphomedusa) could be partially responsible for the underexploitation of zooplankton production in the mid and lower bay (Hagy, 2002). Hagy also hypothesizes that zooplankton could have "occupied the lower water column to the extent permitted by hypoxia (Roman et al., 1993), perhaps to avoid predation by bay anchovy, a visual predator (Luo et al., 1996)." However, I found that zooplankton abundance was the same or higher above, rather than below the pycnocline, and that larval bay anchovy abundance, feeding, and growth did not differ significantly between the two depth layers.

Hypoxic conditions could affect the survival and growth of bay anchovy larvae. Such conditions in the bottom layer of stratified estuaries such as Chesapeake Bay are common during the summer months (Taft et al., 1980; Breitburg et al., 1999; Keister et al., 2000), and have been shown to cause decreases in survival of many organisms, including bay anchovy larvae (Chesney and Houde, 1989; Breitburg, 1994) and copepods (Roman et al., 1993). Low dissolved oxygen can affect many aspects of predator-prey interactions because behaviors and physiological processes are influenced by it (Breitburg et al., 1999). Such effects include alteration of predator-prey encounter rates (Roman et al., 1993; Breitburg, 1994; Keister, 1996), foraging location (Rahel and Nutzman, 1994), prey capture rates (Breitburg et al., 1994), and predator avoidance behaviors (Breitburg et al., 1997). In the present study, below-pycnocline dissolved

oxygen (BPDO) concentrations were negatively correlated with zooplankton density ($r = -0.67$ $P = 0.02$) but not with larval bay anchovy growth rate ($r = -0.25$ $P = 0.39$). Based on these results, it is likely that larval bay anchovy feeding and subsequent growth either were unaffected, or slightly enhanced, in areas of low mean BPDO, which were associated with high zooplankton concentrations. Jung (2002) also found a negative correlation between YOY recruits of bay anchovy in October and mean BPDO for lower Chesapeake Bay in July-August from 1995-2000, suggesting that high plankton productivity, low mean DO, and above-average larval anchovy production are conditions that lead to high recruitments of bay anchovy in Chesapeake Bay.

SUMMARY

1. Ichthyoplankton, zooplankton, and environmental data were collected at stations throughout Chesapeake Bay during the summers of 1995-1999. Larval bay anchovy were identified, enumerated, and measured to develop a database on abundance and size distributions. Bay anchovy eggs, zooplankton, and jellyfish (the ctenophore *Mnemiopsis leidyi*) were identified and enumerated to determine abundances, densities (concentrations), and biovolumes, respectively. The sagittal otoliths from selected bay anchovy larvae were analyzed to estimate ages and growth rates and to compare them among years, regions, and depth-layers. The stomachs of 1,485 larvae were dissected and the contents analyzed to investigate larval feeding ecology and prey selectivity. The relationships between bay anchovy egg abundance and density, larval abundance, density, size distribution, feeding, and growth, with respect to biotic and abiotic environmental variables were examined in correlation and multiple regression analyses.
2. Abundances and distributions of bay anchovy eggs and larvae varied among years and regionally in Chesapeake Bay. Bay-wide mean egg abundance was highest in 1997 (262.3 m^{-2}) and lowest in 1996 (18.0 m^{-2}). Bay-wide larval abundance was highest in 1998 (42.7 m^{-2}) and lowest in 1996 (4.6 m^{-2}). Larval abundance was positively correlated with bay anchovy egg abundance, and both were negatively correlated with mean larval length. Egg abundance was negatively correlated with chlorophyll a biomass. Temperature and larval prey per gut were positively related to larval abundance in a multiple regression analysis. Egg and larval abundances were

highest in the lower bay (most seaward) and declined up-estuary along a declining salinity gradient, indicating that the lower bay is the region of highest spawning activity.

3. Mean lengths of larval bay anchovy differed among years, regions, and depth zones. Mean length was longest in 1996 (13.7 mm) and least in 1997 (5.3 mm). Regionally, mean lengths were generally longest in the upper bay and shortest in the mid bay. Mean larval length was longer below than above the pycnocline in 1998 and 1999, but was similar between depth layers in 1995-1997.
4. Total zooplankton, copepod adults/copepodites, and copepod nauplii densities were strongly and positively correlated with each other in a regional analysis. There were no obvious trends or patterns in annual and regional densities. Zooplankton densities above the pycnocline were the same or higher than below the pycnocline in each survey year.
5. Biovolumes and distributions of the ctenophore *Mnemiopsis leidyi*, a known predator of bay anchovy eggs and larvae, varied annually and regionally, but with no obvious trend or pattern. However, bay-wide mean ctenophore biovolume was 2-3 times higher above than below the pycnocline in all sampled years.
6. Growth of bay anchovy larvae was described well by a Gompertz model. Maximum stage-specific larval growth occurred at approximately 10 days of age. Linear regression was used to directly compare growth rates of larvae <30 days of age. Larval growth rates varied among years and regionally, but were similar for larvae collected above or below the pycnocline. Mean growth rate was highest in 1998

(0.81 mm/day) and lowest in 1999 (0.68 mm/day). Regional growth rates were generally highest in the upper bay and lowest in the mid bay.

7. Larval feeding incidence (the proportion of larvae with food in the gut) varied annually and regionally. Bay-wide feeding incidence was low and ranged from 0.09 in 1996 to 0.23 in 1998. Highest regional feeding incidence tended to be in the upper bay, while the lowest was most often in the mid bay. Feeding incidence was nine times higher during the day (0.27) than at night (0.03), and generally increased with larval size. Feeding incidence was positively correlated with zooplankton density. In a multiple regression analysis, larval bay anchovy density was negatively related to feeding incidence, which is evidence for possible density dependence in the larval stage.
8. Mean number of prey per gut was low, ranging from 1.22 in 1999 to 1.54 in 1998. Prey per gut did not differ annually, regionally, with respect to pycnocline depth, or between larval size classes.
9. The copepodite and adult stages of the calanoid copepod *Acartia tonsa* were the dominant prey items in larval bay anchovy guts. Copepod copepodites/adults and copepod eggs were preferred prey items based on a preference analysis (Chesson's α), while copepod nauplii and other zooplankton taxa (e.g. cladocerans, rotifers, barnacle nauplii etc.) were negatively selected by larval bay anchovy. Copepod copepodites/adults comprised 40% of the ingested prey, other zooplankton taxa comprised 28%, invertebrate eggs comprised 19%, and copepod nauplii comprised 13%.

10. Lengths of ingested prey ranged from 0.025 to 1.60 mm, and increased exponentially with larval size. These rates of increase generally were similar among years and regions. Although mean prey size increased with larval length, larger larvae continued to ingest smaller prey. Relative prey length (prey length/larval length) ranged from 0.003 to 0.103, and mean values generally did not differ among years or regions. Mean relative prey length (RPL) for bay anchovy larvae was 0.03, and increased slowly with larval size (RPL = .017 for 2.5-4.4 mm larvae, RPL = .017 for 4.5-7.4 mm larvae, RPL = .023 for 7.5-10.4 mm larvae, RPL = .033 for 10.5-13.4 mm larvae, RPL = .048 for 13.5-16.4 mm larvae), implying that the size-range of suitable prey increases with larval size.
11. Abundance of recruited young-of-the-year bay anchovy in October was positively correlated with both larval feeding incidence and larval abundance during the summer surveys. This evidence supports the hypothesis that larval-stage processes influence recruitment of bay anchovy in Chesapeake Bay.
12. Zooplankton density was positively correlated with larval feeding incidence and larval growth rate, indicating a probable link between zooplankton density and recruitment potential of bay anchovy.

Appendix 1. 1995 cruise. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling, CTD = physical factor sampling), and Tucker trawl tow depths (m). Although the bottom 1-m of each tow depth was not sampled, the density of bay anchovy eggs and larvae in that depth layer was assumed to equal the average density in the part of each tow depth that was sampled. Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
4	7/23	0935	37.33	-76.2	TT, CTD	9	0-5, 5-9
6	7/23	1200	37.33	-76.13	TT, CTD	13	0-6, 6-13
7	7/23	1258	37.33	-76.05	TT, CTD	10	0-4, 4-10
14	7/23	2208	37.14	-76.18	TT, CTD	9	0-4, 4-9
15	7/23	2259	37.17	-76.12	TT, CTD	8	0-4, 4-8
16	7/23	2350	37.18	-76.06	TT, CTD	9	0-5, 5-9
28	7/24	1410	37	-76.08	TT, CTD	8	0-4, 4-8
29	7/24	1620	37	-76.05	TT, CTD	9	0-4, 4-9
30	7/24	1705	37.03	-76.05	TT, CTD	5	0-3, 3-5
31	7/24	1955	37.5	-75.98	TT, CTD	8	0-5, 5-8
32	7/24	2058	37.5	-76.06	TT, CTD	14	0-5, 5-14
33	7/24	2208	37.5	-76.14	TT, CTD	10	0-6, 6-10
34	7/24	2305	37.5	-76.21	TT, CTD	8	0-4, 4-8
44	7/25	1130	37.67	-75.95	TT, CTD	7	0-4, 4-7
45	7/25	1300	37.67	-76.05	TT, CTD	11	0-5, 5-11
46	7/25	1415	37.67	-76.18	TT, CTD	11	0-5, 5-11
47	7/25	1510	37.67	-76.26	TT, CTD	11	0-5, 5-11
48	7/25	1705	37.83	-76.2	TT, CTD	11	0-4, 4-11
49	7/25	1900	37.83	-76.15	TT, CTD	19	0-7, 7-19
50	7/25	2000	37.83	-76.08	TT, CTD	9	0-5, 5-9
56	7/26	0330	38	-76.32	TT, CTD	11	0-5, 5-11
57	7/26	0423	38	-76.24	TT, CTD	10	0-6, 6-10
58	7/26	0505	38	-76.18	TT, CTD	7	0-4, 4-7
62	7/26	0935	38.17	-76.17	TT, CTD	7	0-3, 3-7
63	7/26	1050	38.17	-76.23	TT, CTD	12	0-9, 9-12
64	7/26	1130	38.17	-76.3	TT, CTD	12	0-8, 8-12
65	7/27	1247	38.17	-76.23	TT, CTD	30	0-15, 15-30
71	7/27	0115	38.33	-76.31	TT, CTD	20	0-10, 10-20
72	7/27	0200	38.33	-76.35	TT, CTD	11.5	0-7, 7-11.5
73	7/27	0238	38.33	-76.38	TT, CTD	9	0-6, 6-9
74	7/27	0410	38.5	-76.46	TT, CTD	10	0-4, 4-10
79	7/27	1000	38.5	-76.42	TT, CTD	28	0-11, 11-28

Appendix 1 (cont'd)

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
80	7/27	1045	38.5	-76.38	TT, CTD	8	0-4, 4-8
81	7/27	1245	38.67	-76.39	TT, CTD	8	0-4, 4-8
82	7/27	1330	38.67	-76.45	TT, CTD	10	0-5, 5-10
83	7/27	1430	38.67	-76.5	TT, CTD	8	0-5, 5-8
88	7/27	2214	38.83	-76.41	TT, CTD	16.5	0-10, 10-16.5
89	7/27	2355	38.83	-76.45	TT, CTD	8	0-4, 4-8
90	7/28	0223	39	-76.39	TT, CTD	8	0-4, 4-8
91	7/28	0300	39	-76.36	TT, CTD	15	0-10, 10-15
92	7/28	0423	39.17	-76.32	TT, CTD	5	0-2.5, 2.5-5
96	7/28	0909	39.42	-76.04	TT, CTD	6	0-3, 3-6
97	7/28	1225	39.32	-76.21	TT, CTD	10	0-5, 5-10
98	7/28	1500	39.25	-76.24	TT, CTD	6	0-3, 3-6

Appendix 2. 1996 cruise. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling, CTD = physical factor sampling, Niskin = 10-L Niskin bottle zooplankton sampling), and Tucker trawl tow depths (m). Although the bottom 1-m of each tow depth was not sampled, the density of bay anchovy eggs and larvae in that depth layer was assumed to equal the average density in the part of each tow depth that was sampled. Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
5	7/17	1157	38	-76.17	TT, CTD	8.5	0-4, 4-8.5
6	7/17	1244	38	-76.25	TT, CTD, Niskin	12	0-6, 6-12
7	7/17	1410	38	-76.32	TT, CTD	13	0-8, 8-13
8	7/17	1810	37.33	-76.2	TT, CTD	8	0-4, 4-8
9	7/17	1935	37.33	-76.13	TT, CTD, Niskin	12	0-6, 6-12
10	7/17	2150	37.33	-76.05	TT, CTD, Niskin	9	0-6, 6-9
21	7/18	1215	36.97	-76.07	TT, CTD	12	0-6, 6-12
22	7/18	1300	37.02	-76.05	Niskin	14.7	
23	7/18	1402	37.05	-76.03	TT, CTD	9	0-5, 5-9
24	7/18	1750	37.67	-75.95	TT, CTD	8	0-4, 4-8
25	7/18	1844	37.67	-76.05	TT, CTD	11	0-6, 6-11
26	7/18	2117	37.67	-76.18	TT, CTD, Niskin	12	0-6, 6-12
37	7/19	1427	38.19	-76.3	TT, CTD, Niskin	12	0-6, 6-12
38	7/19	1520	38.16	-76.22	TT, CTD, Niskin	12	0-6, 6-12
39	7/19	1605	38.16	-76.17	TT, CTD	9	0-4.5, 4.5-9
52	7/20	1205	38.5	-76.45	TT, CTD	11	0-5.5, 5.5-11
53	7/20	1406	38.5	-76.42	Niskin	19	
54	7/20	1523	38.5	-76.37	TT, CTD	8	0-5, 5-8
55	7/20	1731	38.83	-76.42	Niskin	18	
56	7/20	2007	38.83	-76.45	TT, CTD	9	0-4.5, 4.5-9
89	7/22	1205	39.38	-76.1	TT, CTD	13	0-6, 6-13
90	7/22	1300	39.33	-76.2	TT, CTD	12	0-6, 6-12
93	7/22	1542	39.18	-76.28	TT, CTD	12	0-6, 6-12
94	7/22	1638	39.13	-76.32	TT, CTD	12	0-6, 6-12
95	7/22	1741	39.08	-76.3	TT, CTD	9	0-6, 6-9
96	7/22	1845	39.03	-76.35	TT, CTD	13	0-9, 9-13
97	7/22	2005	39	-76.35	TT, CTD	19	0-11, 11-19

Appendix 3. 1997 cruise. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling, CTD = physical factor sampling, Niskin = 10-L Niskin bottle zooplankton sampling), and Tucker trawl tow depths (m). Although the bottom 1-m of each tow depth was not sampled, the density of bay anchovy eggs and larvae in that depth layer was assumed to equal the average density in the part of each tow depth that was sampled. Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
4	7/11	1113	38.5	-76.38	TT, CTD, Niskin	7	0-4, 4-7
5	7/11	1255	38.5	-76.46	TT, CTD	9	0-5, 5-9
6	7/11	1430	38.5	-76.42	TT, CTD	11	0-6, 6-11
7	7/11	1722	38.84	-76.45	TT, CTD	9	0-5, 5-9
8	7/11	1818	38.83	-76.41	TT, CTD, Niskin	19	0-11, 11-19
9	7/11	1948	39	-76.39	TT, CTD, Niskin	7	0-4, 4-7
10	7/11	2037	39	-76.36	TT, CTD	17	0-9, 9-17
21	7/12	1030	39.42	-76.02	TT, CTD	11	0-6, 6-11
23	7/12	1257	39.32	-76.22	TT, CTD, Niskin	11	0-5, 5-11
25	7/12	1459	39.22	-76.25	TT, CTD, Niskin	9	0-5, 5-9
26	7/12	1629	39.11	-76.31	TT, CTD, Niskin	6	0-5, 5-6
36	7/13	1254	38.33	-76.38	TT, CTD	7	0-4, 4-7
37	7/13	1344	38.33	-76.36	TT, CTD, Niskin	8	0-4, 4-8
38	7/13	1510	38.17	-76.27	TT, CTD	14	0-9, 9-14
39	7/13	1550	38.17	-76.2	TT, CTD, Niskin	8	0-6, 6-8
40	7/13	1724	38	-76.32	TT, CTD	12	0-9, 9-12
41	7/13	1815	38	-76.23	TT, CTD, Niskin	10	0-6, 6-10
42	7/13	1924	38	-76.14	TT, CTD	5	0-3, 3-5
52	7/14	1029	37.5	-76	TT, CTD	8	0-6, 6-8
53	7/14	1200	37.49	-76.06	TT, CTD, Niskin	10	0-6, 6-10
54	7/14	1305	37.5	-76.14	TT, CTD	8	0-6, 6-8
55	7/14	1600	37.83	-76.21	TT, CTD	10	0-6, 6-10
56	7/14	1646	37.83	-76.15	Niskin	20	
57	7/14	1816	37.84	-76.08	TT, CTD	9	0-5, 5-9
58	7/14	2005	37.67	-76.26	TT, CTD	7	0-6, 6-7
59	7/14	2113	37.67	-76.12	TT, CTD, Niskin	9	0-6, 6-9
60	7/14	2204	37.67	-76	TT, CTD	13	0-6
68	7/15	0840	37.33	-76.11	TT, CTD, Niskin	11	0-6, 6-11
69	7/15	0957	37.33	-76.06	TT, CTD	12	0-7, 7-12
70	7/15	1043	37.33	-76.17	TT, CTD	9	0-6, 6-9
72	7/15	1251	37.16	-76.25	TT, CTD	8	0-4, 4-8
73	7/15	1332	37.17	-76.22	TT, CTD	10	0-6, 6-10
74	7/15	1415	37.17	-76.17	TT, CTD, Niskin	8	0-6, 6-8
75	7/15	1516	37.17	-76.1	TT, CTD	6	0-4, 4-6
76	7/15	1615	37.17	-76.03	TT, CTD	7	0-4, 4-7
77	7/20	1300	37.2	-76.06	TT	8	0-5, 5-8
90	7/22	2354	37.02	-76.01	TT, CTD	6	0-3.5, 3.5-6
91	7/23	0049	37.06	-75.99	TT, CTD	7	0-4, 4-7
92	7/23	1958	36.96	-76.05	TT, CTD	14	0-7, 7-14

Appendix 4. 1998 cruise. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling, CTD = physical factor sampling, Niskin = 10-L Niskin bottle zooplankton sampling), and Tucker trawl tow depths (m). Although the bottom 1-m of each tow depth was not sampled, the density of bay anchovy eggs and larvae in that depth layer was assumed to equal the average density in the part of each tow depth that was sampled. Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
40	8/6	1045	37.73	-76.22	TT, CTD, Niskin	11	0-7, 7-11
42	8/6	1346	37.73	-76.14	TT, CTD	10	0-7, 7-10
43	8/6	1445	37.73	-76.11	TT, CTD, Niskin	8.5	0-5, 5-8.5
44	8/6	1600	37.83	-76.12	TT, CTD, Niskin	12	0-6, 6-12
46	8/6	1910	37.83	-76.21	TT, CTD	12	0-6, 6-12
47	8/6	2043	37.83	-76	TT	10	0-6, 6-10
60	8/8	1427	37.17	-76.25	TT, CTD	11	0-8, 8-11
61	8/8	1509	37.17	-76.17	TT, CTD, Niskin	10.5	0-7, 7-10.5
62	8/8	1548	37.17	-76.11	TT, CTD	7.5	0-4, 4-7.5
63	8/8	1633	37.17	-76.03	TT, CTD	7	0-4, 4-7
64	8/8	1731	37.05	-76.03	TT, CTD	9	0-5, 5-9
65	8/8	1815	37.01	-76.05	TT, CTD	13	0-10, 10-13
66	8/8	1845	36.97	-76.07	TT, CTD, Niskin	13	0-7, 7-13
78	8/9	1407	37.33	-76.21	TT, CTD	9	0-5, 5-9
79	8/9	1440	37.33	-76.19	TT, CTD, Niskin	9	0-6, 6-9
80	8/9	1526	37.33	-76.14	TT, CTD	11	0-6, 6-11
81	8/9	1600	37.33	-76.09	TT, CTD	17	0-10, 10-17
82	8/9	1752	37.5	-76.02	TT, CTD	9	0-5, 5-9
83	8/9	1842	37.5	-76.08	TT, CTD, Niskin	13	0-5, 5-13
84	8/9	2002	37.5	-76.17	TT, CTD	9	0-4, 4-9
85	8/9	2040	37.5	-76.25	TT, CTD	8	0-4, 4-8
95	8/10	1326	38.17	-76.2	TT, CTD, Niskin	10	0-8, 8-10
96	8/10	1421	38.17	-76.27	TT, CTD, Niskin	10	0-7, 7-10
97	8/10	1557	38.17	-76.32	TT, CTD	10.5	0-8, 8-10.5
98	8/10	1642	38	-76.25	TT, CTD	10	0-6, 6-10
100	8/10	1858	38	-76.12	TT, CTD	9.5	0-5, 5-9.5
109	8/11	1005	38.5	-76.38	TT, CTD, Niskin	8	0-5, 5-8
111	8/11	1242	38.5	-76.46	TT, CTD, Niskin	9	0-7, 7-9
112	8/11	1439	38.67	-76.41	TT, CTD	11	0-7, 7-11
113	8/11	1520	38.66	-76.45	TT, CTD, Niskin	9	0-6, 6-9
114	8/11	1607	38.67	-76.5	TT, CTD	9	0-6, 6-9
115	8/11	1820	39	-76.35	Niskin		
116	8/11	1932	39	-76.39	TT, CTD	8	0-5, 5-8
125	8/12	0703	39.42	-76.03	TT, CTD, Niskin	10	0-6, 6-10
127	8/12	0914	39.32	-76.22	TT, CTD, Niskin	12	0-9, 9-12
129	8/12	1024	39.22	-76.26	TT, CTD	6	0-4, 4-6
130	8/12	1118	39.12	-76.32	TT, CTD, Niskin	8	0-6, 6-8

Appendix 5. 1999 cruise. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling, CTD = physical factor sampling, Niskin = 10-L Niskin bottle zooplankton sampling), and Tucker trawl tow depths (m). Although the bottom 1-m of each tow depth was not sampled, the density of bay anchovy eggs and larvae in that depth layer was assumed to equal the average density in the part of each tow depth that was sampled. Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
4	6/26	1425	37.5	-76.25	TT, CTD	4.5	0-3, 3-4.5
5	6/26	1510	37.5	-76.16	TT, CTD	8	0-5, 5-8
6	6/26	1549	37.5	-76.08	TT, CTD, Niskin	10	0-5, 5-10
7	6/26	1630	37.5	-76.02	TT, CTD	8	0-5, 5-8
8	6/26	1801	37.33	-76.1	TT, CTD	15	0-10, 10-15
9	6/26	1856	37.33	-76.2	TT, CTD, Niskin	5	0-3, 3-5
20	6/27	1114	36.97	-76.07	TT, CTD, Niskin	7	0-6, 6-7
21	6/27	1217	37.02	-76.05	TT, CTD	11	0-8, 8-11
22	6/27	1300	37.05	-76.03	TT, CTD	6	0-5, 5-6
23	6/27	1413	37.17	-76.08	TT, CTD	6	0-5, 5-6
24	6/27	1502	37.17	-76.2	TT, CTD, Niskin	10	0-7, 7-10
25	6/27	1828	37.67	-75.98	TT, CTD	8	0-5, 5-8
26	6/27	1923	37.67	-76.08	TT, CTD	8	0-7, 7-8
37	6/28	1154	37.67	-76.15	TT, CTD, Niskin	12.5	0-10, 10-12.5
38	6/28	1245	37.67	-76.2	TT, CTD	9	0-5.5, 5.5-9
39	6/28	1404	37.83	-76.2	TT, CTD, Niskin	9.5	0-8.5, 8.5-9.5
40	6/28	1450	37.83	-76.12	TT, CTD, Niskin	7.5	0-6.5, 6.5-7.5
41	6/28	1559	38	-76.12	TT, CTD	8	0-6, 6-8
42	6/28	1633	38	-76.18	TT, CTD	8	0-6, 6-8
43	6/28	1707	38	-76.25	TT, CTD, Niskin	7	0-6.5, 6.5-7
44	6/28	1746	38	-76.32	TT, CTD	9.5	0-8, 8-9.5
55	6/29	1216	38.33	-76.37	TT, CTD, Niskin	7.5	0-5, 5-7.5
57	6/29	1422	38.5	-76.45	TT, CTD	9	0-5, 5-9
58	6/29	1450	38.5	-76.42	Niskin	7	
59	6/29	1535	38.5	-76.38	TT, CTD	6	4.5-6
60	6/29	1655	38.67	-76.42	TT, CTD	24	0-13, 13-24
61	6/29	1730	38.67	-76.47	TT, CTD, Niskin	8.5	0-5, 5-8.5
70	6/30	0715	39.42	-76.03	TT, CTD, Niskin	10	0-8, 8-10
72	6/30	0910	39.33	-76.22	TT, CTD, Niskin	9	0-5, 5-9
74	6/30	1000	39.22	-76.25	TT, CTD, Niskin	9	0-7, 7-9
75	6/30	1052	39.12	-76.32	TT, CTD, Niskin	6	0-4.5, 4.5-6
76	6/30	1137	39	-76.36	TT, CTD, Niskin	15	0-11.5, 11.5-15
77	6/30	1210	39	-76.38	TT, CTD	5.5	0-3.5, 3.5-5.5

Appendix 6. Year 1998 depth-stratified stations used to conduct an above, at, and below pycnocline feeding analysis on bay anchovy larvae. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling), and Tucker trawl tow depths (m). Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
25	8/5	1140	38	-76.22	TT	23	0-14, 14-20, 20-23
26	8/5	1345	37.85	-76.17	TT	44	0-14, 14-16.5, 16.5-18
27	8/5	1533	37.73	-76.18	TT	20	0-13, 9-14, 13-15
29	8/5	1904	37.6	-76.15	TT	13	0-3.5, 3.5-8.5, 8.5-13
41	8/6	1222	37.73	-76.2	TT	27	0-15.5, 15.5-21, 15.5-25
55	8/7	1159	37.73	-76.18	TT	28	0-11.5, 11.5-16.5, 16.5-28
56	8/7	1345	37.87	-76.17	TT	40	0-10, 10-14.5, 14.5-18
99	8/10	1753	38	-76.18	TT	14	0-7, 7-10, 10-14
110	8/10	1059	38.5	-76.42	TT	21	0-7, 7-12, 12-18
115	8/11	1820	39	-76.35	TT	20	0-7.5, 7.5-10.5, 10.5-15

Appendix 7. Year 2000 day/night samples for diel feeding comparison by bay anchovy larvae. List of station dates, times, locations, depths (m), operations conducted (TT = Tucker trawl ichthyoplankton sampling), and Tucker trawl tow depths (m). Latitudes (N) and longitudes (W) are reported as degrees and decimal fractions of degrees.

Station	Date	Time	Latitude	Longitude	Operation	Station Depth	TT Tow Depths
85	7/30	1151	37.83	-76.15	TT	19	0-5, 5-19
93	7/31	0155	37.83	-76.15	TT	19	0-6.5, 6.5-19
114	8/1	1242	37.83	-76.15	TT	18	0-8.5, 8.5-18
86	7/30	1339	37.73	-76.2	TT	22	0-5.5, 5.5-22
100	7/31	1200	37.73	-76.2	TT	22	0-5.5, 5.5-22
108	8/1	0509	37.73	-76.2	TT	25	0-9, 9-25
87	7/30	1446	37.73	-76.15	TT	13	0-7, 7-13
101	7/31	1300	37.73	-76.15	TT	12	0-5.5, 5.5-12
107	8/1	0110	37.73	-76.15	TT	15	0-6.5, 6.5-15
92	7/30	2333	37.83	-76.2	TT	13	0-8.5, 8.5-13
113	8/1	1040	37.83	-76.2	TT	11	0-5.5, 5.5-11
94	7/31	0218	37.83	-76.1	TT	10.5	0-4.5, 4.5-10.5
115	8/1	1438	37.83	-76.1	TT	8	0-5.5, 5.5-8
99	7/31	1047	37.73	-76.23	TT	6	0-3.5, 3.5-6
109	8/1	0600	37.73	-76.23	TT	6	0-3.5, 3.5-6

Appendix 8. Regional mean water temperature (°C) during the summer TIES cruises in Chesapeake Bay from 1995-1999. Cruise dates include: July 23-28, 1995; July 17-22, 1996; July 11-23, 1997; August 6-12, 1998; and June 26-30, 1999. MWC Temp = mean water-column temperature; 3-m Temp = temperature at 3-m depth. For within-year regional comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$). SE = standard error. N = number of

Cruise	Region	N	MWC Temp	3-m Temp
1995	Upper	11	28.7	29.2
1 SE			0.2	0.1
1995	Mid	16	28.2	29.2
1 SE			0.2	0.1
1995	Lower	17	28.5	29.1
1 SE			0.1	0.2
1996	Upper	8	24.6	25.0
1 SE			0.3	0.1
1996	Mid	8	25.6	25.8
1 SE			0.1	0.1
1996	Lower	8	25.1	25.9
1 SE			0.7	0.5
1997	Upper	8	24.7	26.1
1 SE			0.7	0.2
1997	Mid	12	25.4	26.1
1 SE			0.2	0.1
1997	Lower	17	25.0	25.7
1 SE			0.4	0.4
1998	Upper	8	26.7 ^a	27.0 ^a
1 SE			0.1	0.1
1998	Mid	9	26.5 ^a	27.0 ^a
1 SE			0.1	0.1
1998	Lower	18	25.6 ^b	26.2 ^b
1 SE			0.1	0.2
1999	Upper	8	24.1 ^a	24.9 ^a
1 SE			0.5	0.2
1999	Mid	9	23.5 ^a	24.4 ^{ab}
1 SE			0.2	0.1
1999	Lower	15	22.6 ^b	23.8 ^b
1 SE			0.2	0.2

Appendix 9. Regional mean salinity (ppt) during the summer TIES cruises in Chesapeake Bay from 1995-1999. Cruise dates include: July 23-28, 1995; July 17-22, 1996; July 11-23, 1997; August 6-12, 1998; and June 26-30, 1999. MWC Salin = mean water-column salinity; 3-m Salin = salinity at 3-m depth. For within-year regional comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$). SE = standard error. N = number of stations.

Cruise	Region	N	MWC Salin	3-m Salin
1995	Upper	11	9.9 ^c	9.4 ^c
1 SE			1.3	1.3
1995	Mid	16	15.8 ^b	14.5 ^b
1 SE			0.3	0.2
1995	Lower	17	21.9 ^a	20.6 ^a
1 SE			0.7	0.7
1996	Upper	8	5.7 ^c	4.2 ^c
1 SE			1.3	1.0
1996	Mid	8	10.8 ^b	10.4 ^b
1 SE			0.2	0.2
1996	Lower	8	18.3 ^a	17.2 ^a
1 SE			1.8	1.5
1997	Upper	8	9.1 ^c	7.0 ^c
1 SE			1.6	1.3
1997	Mid	12	13.4 ^b	12.6 ^b
1 SE			0.3	0.2
1997	Lower	17	22.1 ^a	20.3 ^a
1 SE			1.0	1.2
1998	Upper	8	8.3 ^c	7.7 ^c
1 SE			1.4	1.3
1998	Mid	9	13.7 ^b	12.9 ^b
1 SE			0.4	0.4
1998	Lower	18	20.7 ^a	19.4 ^a
1 SE			0.8	0.7
1999	Upper	8	11.6 ^c	10.6 ^c
1 SE			1.6	1.4
1999	Mid	9	16.5 ^b	15.5 ^b
1 SE			0.4	0.3
1999	Lower	15	22.3 ^a	20.0 ^a
1 SE			0.9	0.8

Appendix 10. Regional mean dissolved oxygen (DO) (mg/L) during the summer TIES cruises in Chesapeake Bay from 1995-1999. Cruise dates include: July 23-28, 1995; July 17-22, 1996; July 11-23, 1997; August 6-12, 1998; and June 26-30, 1999. MWC DO = mean water-column DO; 3-m DO = DO at 3-m depth; BP DO = DO below the pycnocline. For within-year regional comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$). SE = standard error. N = number of stations.

Cruise	Region	N	MWC DO	3-m DO	BP DO
1995	Upper	11	6.7 ^{ab}	7.5	5.5 ^{ab}
1 SE			0.4	0.5	0.7
1995	Mid	16	5.7 ^b	7.6	3.9 ^b
1 SE			0.4	0.2	0.6
1995	Lower	17	6.9 ^a	7.4	6.2 ^a
1 SE			0.1	0.1	0.2
1996	Upper	8	5.9 ^c	7.2 ^b	4.4 ^b
1 SE			0.4	0.3	0.8
1996	Mid	8	8.1 ^b	8.6 ^b	7.5 ^a
1 SE			0.4	0.5	0.4
1996	Lower	8	9.6 ^a	10.8 ^a	8.2 ^a
1 SE			0.5	0.6	0.5
1997	Upper	8	4.5 ^b	6.7 ^b	3.2
1 SE			0.6	0.5	0.9
1997	Mid	12	5.9 ^a	7.5 ^{ab}	4.1
1 SE			0.2	0.1	0.6
1997	Lower	17	6.2 ^a	7.6 ^a	4.9
1 SE			0.2	0.1	0.3
1998	Upper	8	5.4	5.8	5.1 ^a
1 SE			0.4	0.5	0.5
1998	Mid	9	5.0	5.9	3.6 ^b
1 SE			0.3	0.2	0.6
1998	Lower	18	5.4	5.9	4.8 ^a
1 SE			0.1	0.1	0.2
1999	Upper	8	4.9 ^b	5.5 ^b	3.5 ^b
1 SE			0.5	0.4	0.8
1999	Mid	9	5.9 ^{ab}	6.0 ^{ab}	5.6 ^a
1 SE			0.1	0.1	0.3
1999	Lower	15	6.5 ^a	6.7 ^a	6.4 ^a
1 SE			0.2	0.3	0.3

Appendix 11. Regional mean fluorescence (relative fluorescence units), representing chlorophyll a biomass, during the summer TIES cruises in Chesapeake Bay from 1995-1999. Cruise dates include: July 23-28, 1995; July 17-22, 1996; July 11-23, 1997; August 6-12, 1998; and June 26-30, 1999. MWC F = mean water-column F; 3-m F = F at 3-m depth; AP F = F above the pycnocline. For within-year regional comparisons, different superscripts indicate significant differences (ANOVA $P < 0.05$). SE = standard error. N = number of stations.

Cruise	Region	N	MWC F	3-m F	AP F
1995	Upper	11	2.0 ^a	2.4 ^a	2.3 ^a
1 SE			0.3	0.4	0.3
1995	Mid	16	1.1 ^b	1.4 ^b	1.3 ^b
1 SE			0.1	0.1	0.1
1995	Lower	17	1.2 ^b	1.2 ^b	1.2 ^b
1 SE			0.1	0.1	0.1
1996	Upper	8	1.1	1.5	1.3
1 SE			0.2	0.4	0.3
1996	Mid	8	1.2	1.5	1.4
1 SE			0.1	0.1	0.1
1996	Lower	8	1.5	1.7	1.6
1 SE			0.2	0.2	0.2
1997	Upper	8	0.7	1.0	0.9
1 SE			0.1	0.1	0.1
1997	Mid	12	0.6	0.7	0.7
1 SE			0.1	0.1	0.1
1997	Lower	17	0.6	0.7	0.7
1 SE			0.1	0.1	0.1
1998	Upper	8	1.0 ^a	1.3 ^a	1.2 ^a
1 SE			0.3	0.5	0.4
1998	Mid	9	0.5 ^{ab}	0.6 ^{ab}	0.6 ^{ab}
1 SE			0.03	0.03	0.03
1998	Lower	18	0.5 ^b	0.5 ^b	0.5 ^b
1 SE			0.03	0.04	0.04
1999	Upper	8	0.6	0.8 ^a	0.7 ^a
1 SE			0.1	0.1	0.1
1999	Mid	9	0.6	0.6 ^b	0.6 ^{ab}
1 SE			0.03	0.05	0.04
1999	Lower	15	0.6	0.4 ^b	0.4 ^b
1 SE			0.1	0.02	0.02

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