ABSTRACT

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| Title of Thesis: | PATTERNS IN DISTRIBUTION, GROWTH, AND TROPHODYNAMICS OF STRIPED BASS EARLY LIFE STAGES IN THE ESTUARINE TRANSITION REGION OF UPPER CHESAPEAKE BAY |
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Variable production of young striped bass *Morone saxatilis* in the estuarine transition region depends on environmental and hydrographic conditions in the estuarine turbidity maximum (ETM) and salt front region of Chesapeake Bay. Spatio-temporal variability in occurrence, growth, and diet of early life stages of striped bass and zooplankton prey were compared in years of average (2007) and poor (2008) production of striped bass juveniles. Stable isotope analyses tracked sources of carbon and nitrogen in larval striped bass diets. The estuarine copepod *Eurytemora affinis* was the most important prey. It and the freshwater cladoceran *Bosmina longirostris* dominated diets of striped bass larvae. *Bosmina* was relatively important in 2007. Larvae grew faster in 2007 than in 2008 and growth was fastest within and up-estuary of the ETM and salt front. Stable isotope analysis indicated that carbon from both marine and terrestrial sources supports production of striped bass larvae.

PATTERNS IN DISTRIBUTION, GROWTH, AND TROPHODYNAMICS OF
STRIPED BASS EARLY LIFE STAGES IN THE ESTUARINE TRANSITION
REGION OF UPPER CHESAPEAKE BAY


By


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Advisory Committee:
Professor Edward D. Houde, Chair
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# Dedication

To my family.

# Acknowledgements

My parents unwittingly fostered my interest in fisheries and marine science. I would like to thank them for not only introducing me to my future career path, but for also supporting me through my undergraduate and graduate research. I am also appreciative of all the friends in Maryland and back home who took helped me balance work and play. Finally, I would like to extend a heartfelt thanks to my husband, Geoff, for following me to Maryland so that I could pursue my degree, cooking me dinner so I could come home to a hot meal, and helping me keep everything in perspective.

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I would like to thank the crew, personnel, and scientists onboard the R/V *Aquarius*, the R/V *Sharp*, and the R/V *Terrapin* for assistance in collecting samples and for making sure I made it safely back to dry land; Ed Martino, Carlos Lozano and Bill Connelly for laboratory and statistical advice; Linton Beaven, Steve Fenske, Erin Voigt, and Jim Seuberling for helping process countless samples. Lisa Kerr and Ryan Woodland provided much needed expertise and advice for stable isotope analysis methodology.

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**Chapter 1: Introduction**

The striped bass *Morone saxatilis* is an anadromous fish that migrates to freshwater or tidal brackish areas to spawn, usually in April and May in the Chesapeake Bay (Dovel 1971). Striped bass spawns large, slightly buoyant eggs in tidal-fresh or oligohaline waters in the Chesapeake Bay and its tributaries (Mansueti 1958; Dovel 1971). Eggs hatch in approximately 2 days (Mansueti 1958; Doroshev 1970). Yolk-sac larvae gain nutrition from yolk and an oil globule and begin active feeding at approximately 5 days post-hatch (Doroshev 1970). Growth and survival of early life stages are the major determinants of recruitment success (Uphoff 1989; Rutherford and Houde 1995; North and Houde 2003).

Striped bass is important within Chesapeake Bay and along the Atlantic coast for its economic value as a commercial and recreational fishery and its ecological value as a predator on fish and invertebrates in estuarine and marine ecosystems. The Chesapeake Bay component of the coast-wide stock historically has produced a large proportion of east coast recruits (90% of the Atlantic Coast recruits: Berggren and Lieberman 1978; 54% of the Rhode Island recruits: Fabrizio 1987). Overfishing of striped bass in the 1970s depleted the adult spawning stock, led to failed recruitments, and caused a collapse of landings, leading to a fishing moratorium in some states and restrictive regulations in others from 1985 – 1989 (Richards and Rago 1999). Reduced fishing mortality and favorable recruitments in 1989 and in the early 1990s aided recovery to historic levels, although strong inter-annual variability in recruitment still occurs, as evidenced by >30-fold variability in the Maryland striped bass juvenile index (http://dnr.maryland.gov/ fisheries /juvindex/).

Coincident with the sharp decline and subsequent recovery of spawning stock

biomass in Chesapeake Bay, there have been many efforts to understand factors affecting

recruitment. Yearly variation in recruitment of striped bass may be caused by large and

variable mortality of larvae. For example, Secor and Houde (1995) estimated a 99.7%

loss of newly hatched striped bass larvae in the Patuxent River, while larvae surviving to

the first-feeding stage suffered an additional 95% loss by 20 days post-hatch. The cohort

production of 8-mm SL striped bass larvae in the Potomac River was positively

correlated with juvenile recruitment indices, indicating that mortality effects prior to 8-

mm SL exercised strong control over recruitment level (Rutherford and Houde 1995).

Furthermore, Ricker spawner-recruit models based solely on upper Bay spawner biomass

could account for only a small percentage of young-of-the-year (YOY) recruitment

variability (3%, North and Houde 2003; 2%, Martino and Houde 2010), implying that

factors contributing to variable survival of larvae exercise strong control over the fate of a

year class.

The estuarine turbidity maximum (ETM) and surrounding region constitute a

prominent feature in many estuaries.  This transition region is characterized by increased

turbidity and suspended sediment due to gravitational circulation and tidal resuspension

(Burchard and Baumert 1998; Sanford et al. 2001). In the upper Chesapeake Bay, the

transition region and its ETM generally occur in close proximity to the salt front (Sanford

et al. 2001; North and Houde 2001). Many fishes, including striped bass, use the ETM

and salt front as a nursery, apparently because the frontal features act to retain larvae by

discouraging down-estuary losses. During a larval release experiment of hatchery-reared

striped bass larvae in the Patuxent River, larvae released downstream of the ETM and salt

front resulted in a complete loss of that release group, while many larvae stocked in or upstream of the salt front were recaptured (Secor et al. 1995). Similar results were obtained in a release experiment of hatchery-produced American shad *Alosa sapidissima* larvae in 2000 (Campfield 2004); larvae were stocked upstream (freshwater) and downstream just below the salt front in the Patuxent River, but recaptures were predominately from the upstream release group.

Additionally, the ETM region has several physical and biological characteristics that could increase egg and larval survival. Retention in the low salinities associated with the ETM region potentially could lower salinity-related mortality. In the Savannah River, survival of striped bass larvae declined with increasing salinity and larvae that hatched from eggs exposed to higher salinities had a smaller length-at-age than larvae hatched from eggs that developed in freshwater (Winger and Lasier 1994). Doroshev (1970) also found that larvae 4-15 days post-hatch had the highest survival in low salinity waters.

The ETM region generally contains high concentrations of zooplankton and may act to enhance larval survival and recruitment by lowering starvation-related mortality. The estuarine calanoid copepod *Eurytemora affinis* and the freshwater cladoceran *Bosmina longirostris* are important prey for striped bass larvae in Chesapeake Bay and its tributaries (Potomac River: Beaven and Mihursky 1980; Choptank River: Uphoff 1989; Patuxent River: Campfield 2004; Campfield and Houde 2011; upper Chesapeake Bay: North and Houde 2006; Martino and Houde 2010), as well as in the Hudson River (Limburg et al. 1997, 1999) and in Lake Marion, South Carolina (Chick and Van Den Avyle 1999). High concentrations of zooplankton, including *E. affinis*, have been associated with the low-salinity zone of the ETM and within the Delta of the San

Francisco Estuary (Kimmerer et al. 1998), and the upper Chesapeake Bay (Boynton et al. 1997; Roman et al. 2001; North and Houde 2001; Martino and Houde 2010). In 1998 and 2003, when striped bass larvae in the upper Chesapeake Bay experienced both a temporal and spatial overlap with these dominant prey species, recruitment levels exceeded levels in years when spatial or temporal mismatches occurred (Martino and Houde 2010).

Increased feeding success of fish larvae in areas such as the ETM where prey is abundant generally leads to higher survival through increased growth rates. Larvae with higher growth rates remain in the vulnerable larval period for shorter periods of time and larger larvae may be less vulnerable to predation (Houde 1989, 2009). Recruitment to the juvenile stage was higher in larval striped bass in the Hudson River when the time at first feeding coincided with a spring bloom in the cladoceran *Bosmina longirostris* (Limburg et al. 1999). Larvae feeding during the bloom likely experienced lower starvation pressures and higher growth, allowing increased survival to the juvenile stage. The individual-based model developed by Cowan et al. (1993) predicted that larvae would experience higher growth and survival rates under circumstances of high prey densities. In Lake Marion, South Carolina, recruitment is largely derived from cohorts of larvae that are advected out of rivers where spawning took place and into the lake area (Bulak et al. 1997) which favors larval survival because of its high prey densities that can support larval production (Chick and Van Den Avyle 1999).

Previous studies have demonstrated that distribution of eggs and larvae of striped bass and white perch in the upper Bay can be explained in part by the location and strength of the ETM and associated salt front (North and Houde 2003, 2006; Martino and Houde 2010). Physics and hydrography in the upper Bay impart inter-annual variability

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to the location and retention strength of the ETM and salt front. The Susquehanna River exercises a major influence on upper Bay physics and hydrography, due to its large freshwater influx that supplies nearly 50% of the annual flow into the Bay (Schubel and Pritchard 1986). Variability in Susquehanna River flow among years can affect location of the ETM: for example, in 1999, a low-flow year, the ETM was weakly developed and located > 15 km up-estuary of its location in 1998, a high-flow year (North and Houde 2001). Moreover, average spring (March-April) freshwater flow is positively and significantly related to striped bass recruitment (North and Houde 2003; Martino and Houde 2010).

Despite the extensive research conducted on striped bass early life stages, causes of recruitment variability still are difficult to ascertain. A model developed by Martino and Houde (2010) related young-of-the-year striped bass recruitment from 1985-2006 to spring freshwater flow and spring temperature, and forecasted recruitments for 2007-2009. The model provided accurate forecasts for both 2007 and 2009, but forecasted recruitment in 2008 was far above that observed. A goal of my thesis is to further investigate factors affecting recruitment of striped bass by evaluating temporal and spatial patterns in early life growth and trophodynamics in 2007, an average recruitment year, and in 2008, a poor recruitment year.

The thesis is presented in four chapters. Chapter 1 is an introduction. Chapters 2 and 3 were written as stand-alone papers to be submitted as manuscripts for future journal publication and, as such, include similar descriptions of surveys and methods. Chapter 4 is an extended summary and conclusions.

Chapter 2 describes patterns in abundance and distribution of early life stages of striped bass and zooplankton prey taxa, and relates variability in growth rates of striped bass larvae to locations with respect to the ETM and salt front features. The analysis was based on samples collected during April and May, 2007 and April-June, 2008. The relative importance of the salt front and ETM as retentive features is discussed and patterns of spatio-temporal overlap of feeding-stage larvae with zooplankton prey are described.

Chapter 3 describes patterns and evaluates factors affecting larval nutrition that may contribute to variable recruitment of striped bass based on analysis of gut contents and a stable isotope analysis to elucidate trophic dynamics and nutrient pathways. Stable isotope analysis of carbon and nitrogen can provide information on the carbon sources supporting nutrition and growth, and on trophic levels of larvae and prey, respectively (DeNiro and Epstein 1981; Minagawa and Wada 1984; Fry and Sherr 1984; Peterson and Fry 1987; Vander Zanden and Rasmussen 2001). In Chapter 3, growth rates of striped bass larvae reported in Chapter 2 were compared to stable isotope values of feeding-stage larvae to determine if variable growth can be explained by nutritional sources. Additionally, stable isotope values of archived, feeding-stage larvae from 1998, a year of average recruitment, and 2003, a year of high recruitment, were included in my stable isotope analysis to evaluate nutrient sources and trophic pathways that may be related to recruitment success.

Chapter 4 is an extensive summary and conclusions of my thesis research.

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**Chapter 2: Spatial and temporal patterns in distribution and growth of striped bass**

***Morone saxatilis* larvae in relation to zooplankton in upper Chesapeake Bay**

## INTRODUCTION

Anadromous fishes such as striped bass *Morone saxatilis* utilize the oligohaline and tidal freshwaters of estuaries to spawn. The early-life dynamics of striped bass are shaped by the environment of these upper estuaries. In Chesapeake Bay and its tributaries, the estuarine turbidity maximum (ETM) region and salt front feature, combined with variable freshwater flow, play an important role in controlling striped bass survival (Secor et al. 1995; North and Houde 2003, 2006; Martino and Houde 2010; Campfield and Houde 2011; Secor et al. *in review*). Zooplankton in the oligohaline-tidal freshwater regions of estuaries also vary in relation to environmental factors and, because they are the primary prey of striped bass larvae (North and Houde 2006; Martino and Houde 2010), their spatio-temporal variability can be a critical factor controlling survival of striped bass early-life stages (Limburg et al. 1999; Chick and Van Den Avyle 1999; Campfield and Houde 2011).

Striped bass adults migrate from the sea to freshwater or tidal brackish areas to spawn, usually in April and May in the Chesapeake Bay (Dovel 1971), which historically has produced the largest proportion of Atlantic coast recruits in most years (Berggren and Lieberman 1978; Fabrizio 1987). Abundance of striped bass age-0 juveniles (100-150 days post-hatch) varies > 30-fold inter-annually (http://dnr.maryland.gov/fisheries /juvindex/). Research has indicated that much of this variability is due to density-independent factors that affect survival of striped bass eggs and larvae. Most eggs and

larvae do not survive. Secor and Houde (1995) estimated a 99.7% loss of newly hatched striped bass yolk-sac larvae in the Patuxent River, while larvae surviving to the first-feeding stage suffered an additional 95% loss by 20 days post-hatch. The cohort production of 8-mm standard length (SL) striped bass larvae in the Potomac River was positively correlated with juvenile recruitment indices, indicating that variable mortality prior to 8-mm SL exercised strong control over recruitment level (Rutherford and Houde 1995). This finding was similar to results from the Choptank River tributary of Chesapeake Bay in which recruitment success was determined before the end of the larval stage (Uphoff 1989). Furthermore, spawner-recruit models including only spawner biomass as the independent variable could only account for a small percentage of variability in abundance of young-of-the-year (YOY) juveniles (3%- -North and Houde 2003; 2%- -Martino and Houde 2010), implying that factors other than egg production contribute to variable survival of larvae and are key to recruitment success.

The estuarine turbidity maximum (ETM) is a feature in many estuaries and is characterized by its increased turbidity and suspended sediment due to gravitational circulation and tidal resuspension (Burchard and Baumert 1998). In the Chesapeake Bay, the ETM generally occurs near the salt front (the intersection of the 1 isohaline with bottom) in the upper reaches of the Bay (Sanford et al. 2001; North and Houde 2001). Larvae of anadromous fishes, including striped bass, the related white perch *Morone americana*, and shads/river herrings *Alosa* spp., use the ETM and surrounding area as a nursery, apparently because the ETM and associated salt front act to retain larvae and zooplankton and discourage down-estuary losses (North and Houde 2001, 2003, 2006; Roman et al. 2001; Martino and Houde 2010; Campfield and Houde 2011).

Physics and hydrography in the upper Bay impart inter-annual variability to the location of the ETM and salt front. A major influence on upper Bay physics is the Susquehanna River which supplies nearly 50% of the annual freshwater flow into the Bay (Schubel and Pritchard 1986). Variability in Susquehanna River flow among years can have a significant effect on the location and character of the ETM (North and Houde 2001). Inter-annual variability in the ETM, the associated salt front, and zooplankton in the estuarine transition region may combine to impart variability in striped bass recruitment.

Retention of larvae within the ETM region may enhance survival by lowering the probability of starvation-related mortality. The freshwater cladoceran *Bosmina longirostris* and the estuarine calaniod copepod *Eurytemora affinis* are common prey items for striped bass larvae in the upper Chesapeake Bay (North and Houde 2006; Martino and Houde 2010), Patuxent River (Campfield and Houde 2011), and Hudson River (Limburg et al. 1999). Within the Delta of the San Francisco Estuary (Kimmerer et al. 1998) and the upper Chesapeake Bay (Boynton et al. 1997; Roman et al. 2001; Martino and Houde 2010), high concentrations of zooplankton, including *E. affinis*, are characteristically associated with the low salinity zone and the ETM.

Increased feeding success of fish larvae in areas such as the ETM where prey is abundant generally leads to higher survival through increased growth rates. Larvae with higher growth rates remain in the vulnerable larval period for shorter periods of time and larger larvae may be less vulnerable to predation (see review in Houde 2009). For cohorts of larval striped bass that experience equal daily mortality rates, cohorts with fastest growth potentially experience order-of-magnitude higher survival (Houde 1989).

Recruitment to the juvenile stage was higher in larval striped bass in the Hudson River when the time at first feeding coincided with a spring bloom in the cladoceran *Bosmina freyi* (Limburg et al. 1999). Larvae feeding during the bloom likely experienced lower starvation pressure and faster growth, allowing increased survival to the juvenile stage. An individual-based model developed by Cowan et al. (1993) predicted that larvae had higher growth and survival rates under circumstances of high prey densities. In Lake Marion, South Carolina, recruitment is largely due to cohorts of larvae that are advected out of rivers where spawning took place into the lake (Bulak et al. 1997), which favors larval survival because the lake has high prey densities (Chick and Van Den Avyle 1999). In 1998 and 2003, striped bass larvae in the upper Chesapeake Bay experienced both a temporal and spatial overlap with high concentrations of *E. affinis* and *B. longirostris* and had much higher recruitment levels than in years when spatial or temporal mismatches occurred (Martino and Houde 2010).

Growth rates of striped bass larvae within the upper Chesapeake Bay (Rutherford and Houde 1995; Rutherford et al. 1997; Martino 2008), Potomac River (Rutherford and Houde 1995; Rutherford et al. 1997), Patuxent River (Secor and Houde 1995), and Hudson River (Limburg et al. 1999) have been reported. Larval growth rates may vary over the course of the spawning season (Campfield 2004), inter-annually (Martino 2008), or in relation to temperature (Rutherford and Houde 1995; Martino 2008).

The objective of this component of my research was to investigate temporal and spatial variability in locations of occurrence and growth rates of striped bass larvae and their zooplankton prey as factors that could affect recruitment of striped bass in the upper Bay in 2007, an average recruitment year, and in 2008, a poor recruitment year. To

accomplish this objective, I investigated 1) the distribution and concentration of known zooplankton prey items, 2) the distribution and abundance of striped bass eggs, yolk-sac larvae, and feeding-stage larvae, and 3) the hatch dates and growth rates of feeding-stage larvae. Additionally, I compared growth rates of striped bass larvae with measures of feeding success (see Chapter 3).

## METHODS

### *Hydrography*

Water temperature data were collected by the Maryland Department of Natural Resources at the Sassafras River-Betterton station (39°22'18.1 N, -76°03'45.0 W; Figure 2-2), which is in close proximity to the spawning and larval nursery areas of striped bass in the upper Chesapeake Bay. Mean daily freshwater flow data (cubic feet per second, cfs) were obtained from the USGS gauge on the Susquehanna River at Conowingo, MD (36°39'28.1 N, 76°10'28.2 W).

### *Research Cruises and Sampling*

Surveys were conducted along a 40-km transect of the upper Chesapeake Bay, extending from just up-bay of the Bay Bridge (latitude 39° 00' N) to the Elk River (latitude 39° 47' N), a region that encompasses the salt front and ETM (Figure 2-1). Depths in this area ranged from 7 to 24 m. Several research vessels and samplers were used to collect ichthyoplankton in the upper Bay (Table 2-1). Surveys on the 44-m RV *Hugh R. Sharp* were conducted in April and May 2007 and 2008. Four "rapid-response" surveys in 2007 and two in 2008 were conducted on the 7.6-m RV *Terrapin*; these surveys followed periods of high freshwater flow to the upper Bay. Additionally in 2008, a single survey was conducted on the 20-m RV *Aquarius* from 4 to 6 June. During all

cruises, CTD deployments were made at 5-10 km intervals in a survey along the Bay channel to obtain depth profiles of salinity, temperature, turbidity, fluorescence, irradiance, and dissolved oxygen. The CTD data were used to define the location of the salt front and ETM and to select sites for zooplankton and ichthyoplankton sampling above, within, and down-estuary of those features.

On the RV *Hugh R. Sharp*, ichthyoplankton and zooplankton were collected in tows of an opening-closing, 1-m$^2$ Tucker Trawl with 280-μm meshes and flow meters. At each station, 4-min deployments were divided into two depth zones (2 min per depth zone), bottom to mid-depth and mid-depth to surface.  A mean of 175.78 (± 4.94 se) m$^3$ of water was filtered at each depth. Samples were preserved in ethanol. In 2008, some ichthyoplankton samples were also collected in a 1/4-m$^2$ mouth-opening, multiple opening closing net environmental sampling system (MOCNESS) equipped with one 333-μm mesh net and four 200-μm mesh nets.  The 333-um mesh net that was towed obliquely over the entire water column provided samples for ichthyoplankton analysis that were preserved in ethanol. The 333-μm mesh net filtered a mean of 110.96 (± 15.65 se) m$^3$.

"Rapid-response" surveys were conducted on the RV *Terrapin* in April and May 2007 and May 2008 to survey hydrographic conditions and ichthyoplankton occurrences with respect to precipitation events (Table 2-1) (Jahn 2010). Paired 60-cm diameter bongo nets with 280-μm meshes and flow meters were deployed in 5-min tows to obliquely sample the water column.  Mean volume filtered per net was 66.95 (± 1.62 se) m$^3$.  Samples from one of the paired-net tows were preserved in ethanol for growth and stable isotope analysis (see Chapter 3).  Samples from the second net were fixed and

preserved in 5% formalin for analysis of striped bass egg production in a related project (Jahn 2010).

The single research cruise on the 20-m RV *Aquarius* in June 2008 was conducted late in the spawning season (Table 2-1) to sample later-stage striped bass larvae. Depth-stratified ichthyoplankton samples were collected in a 1-m$^2$ opening-closing Tucker Trawl with 280-μm meshes and in a 2-m$^2$ opening-closing Tucker Trawl with 707-μm meshes (mean ± se volume filtered per net: 254.21 ± 21.52 m$^3$). The nets were equipped with flow meters. In each deployment, tows were from bottom to mid-depth and from mid-depth to the surface (2 min per depth zone). Samples were preserved in ethanol.

During each cruise, the locations of the ETM and salt front (Table 2-2) were defined by inspection of contour plots of CTD-derived turbidity and salinity (Golden Software, SURFER v7.0). The center of maximum concentration of total suspended solids was designated as the center of the ETM. The salt front was defined as the intersection of the 1 isohaline with the estuary bottom. Based on locations of these features, sampling sites were classified as up-estuary (> 5 km up-estuary of feature), within (within ± 5 km of feature), or down-estuary (> 5 km down-estuary of feature).

***Laboratory Procedures***

*Zooplankton*

Zooplankton from Tucker Trawl and bongo net tows in 2007 and 2008 were analyzed for abundance and distribution. Samples were diluted and zooplankton taxa were enumerated in triplicate, pipette-withdrawn 1-ml aliquots. For statistical analysis, concentrations were calculated as the $\log_{10}$-transformed number per volume filtered

(number per m$^3$); values presented in text are back-calculated geometric means. Additionally, the first 10 individuals viewed under the microscope of dominant organisms were measured on their longest axis using an ocular micrometer.

Student's t-tests were used to test for inter-annual differences in mean concentrations of total zooplankton prey (defined as combined copepod *Eurytemora affinis*, cladoceran *Bosmina longirostris*, and copepod *Acartia tonsa*), and for *E. affinis*, and *B. longirostris*, individually, for samples taken in April and May 2007 and 2008. *Acartia tonsa* was included in total prey because it was common in estuarine waters during late spring and because its similar size to *E. affinis* made it a potentially available prey. Mean concentrations of total zooplankton prey, and of *E. affinis* and *B. longirostris* were analyzed with respect to the ETM and salt front locations in each year in a two-factor analysis of variance with location and season (early: before 15 May; late: after 15 May) as factors, followed by a Tukey-Kramer means comparison test. Values presented in text are back-calculated geometric means.

*Larvae*

Ethanol-preserved striped bass eggs and larvae were sorted from ichthyoplankton samples and identified under a dissecting microscope. Eggs and larvae were enumerated for each sample. Except for the survey in 19-22 April 2008 (Table 2-1), entire samples were examined to remove ichthyoplankton.  High concentrations of zooplankton and ichthyoplankton in the 19-22 April 2008 cruise necessitated subsampling; consecutive 1/8 subsamples were sorted until differences between striped bass numbers in each consecutive subsample were less than 10%.

Volumes of segments of the upper Bay (Cronin 1971) were used to calculate the volume of water ($m^3$) represented by each station that was sampled. The volume represented by each station was defined as the volume encompassed between midpoints of two adjacent stations.  The boundaries for the volume of the furthest up-Bay and down-Bay stations were determined by the mid-point between the most up-estuary or down-estuary station and the adjacent station.  For each station, concentrations of striped bass eggs and larvae, calculated as the number per $m^3$ filtered, for the egg, yolk-sac larva and feeding-stage larva stages were multiplied by the volume of water represented by that station to obtain egg and larval abundances (in total numbers). This approach provided spatially-explicit estimates of total numbers of eggs and larvae with respect to the ETM and salt front features during each cruise. Mean abundances s of eggs and larvae within the volumes represented by each location were analyzed with respect to the ETM and salt front in each year in a two-factor analysis of variance with location and year as factors, followed by a Tukey-Kramer means comparison test. Statistical analysis was conducted on $\log_{10}$ (total abundance (in numbers) + 1) of striped bass eggs and larvae.

Spatial overlap between striped bass feeding-stage larvae and two prey species, *B. longirostris* and *E. affinis*, was measured using the Schoener overlap index (Schoener 1970) for each region with respect to the ETM and salt front for each cruise. Percent overlap was calculated as

$$\text{Percent overlap} = 100[1 - 0.5(\Sigma|p_{ix,t} - p_{jx,t}|)]$$

where $p_{ix,t} = c_{ix,t}/\Sigma c_i$, the proportion of the total concentrations of organism *i* found at region *x* and date *t*, and $p_{jx,t} = c_{jx,t}/\Sigma c_j$, the proportion of the total concentrations of

organism $j$ found at region $x$ and date $t$. High overlap values indicate high spatio-temporal co-occurrence of striped bass larvae and their prey.

Total lengths (TL) of striped bass yolk-sac and feeding-stage larvae were measured with an ocular micrometer. A total of 381 larvae (2007: 115 larvae; 2008: 353 larvae) were then dissected for gut content (Chapter 3) and otolith analysis. For samples with large numbers of larvae, subsamples were analyzed to insure that 3-5 larvae from designated length classes were included. Length classes were designated in 0.5-mm increments for larvae < 8 mm TL and 1-mm increments for larvae > 8 mm TL.

Striped bass larvae deposit daily otolith increments (Jones and Brothers 1987; Secor and Dean 1989; Houde and Morin 1990). Saggital otolith pairs were removed from feeding-stage larvae, mounted on microscope slides and prepared for increment analysis following procedures in Secor et al. (1991). Digital photographs of otoliths were used to enumerate daily growth increments and to measure increment widths. Otolith images were digitized using Image J (http://rsb.info.nih.gov/if/). Each otolith was examined twice for increments. Each increment count was conducted without knowledge of larval length or any prior increment counts. If the two counts differed by < 10%, the second count was accepted as the final count. If counts differed by ≥ 10%, a third count was made. The decision to accept the most recent count was based on the rationale that accuracy in counting increased with experience. If a third count differed by ≥ 10% from either of the previous two counts, the otolith was rejected from further analysis. Of the 468 larvae dissected for age and growth analysis, 87 were rejected. Rejected otoliths were not biased by larval size and similar percentages of otoliths were rejected in 2007 and in 2008.

Age was calculated as the otolith increment count added to a temperature-corrected age of first increment formation from:

$$D = 11.56 - 0.45T$$

where D is the day of first increment deposition and T is temperature in degrees Celsius (Houde and Morin 1990). Hatch dates were calculated as the difference between collection date and age. In my analysis, hatch-date frequencies were not adjusted to account for daily mortality. Thus, they represent the hatch-date distributions of surviving larvae at survey dates. An age-at-length key was constructed for each year based on the mean and standard deviation of ages of otolith-increment-aged larvae within 0.5-mm length classes (<8 mm TL) or 1-mm length classes (≥8 mm TL). Ages of larvae that were not estimated directly from otolith increment counts were estimated from the probability distribution of ages-at-length in each 0.5-mm or 1.0-mm length class (Secor et al. 1994; Jahn 2010).

Individual larva growth rates were estimated by dividing the total length minus mean length-at-hatch by age. Mean length-at-hatch was taken to be 4.0 mm, a length commonly used in growth analyses on striped bass larvae (Rutherford et al. 1997; Limburg et al. 1999; Martino 2008).

## RESULTS

### *Hydrography and ETM/Salt Front Locations*

Mean March-April freshwater flows from the Susquehanna River were similar in 2007 and 2008 (89,159 and 87,048 cfs, respectively; Figure 2-2). Extending the timeframe to include February indicated higher mean flow in 2008 (85,283 cfs), compared to 66,842 cfs in 2007. There were notable differences between the two years

with respect to frequency and magnitude of flow events. In 2007, the upper Bay experienced two peaks in freshwater flow that occurred before research cruises were initiated; the first peak occurred 16-22 March, followed shortly by a peak of similar magnitude from 25-29 March. A third, less pronounced flow event occurred from 16-22 April 2007 (Figure 2-2A). Flow events differed in 2008, with peak events from late winter to early spring. The first peak from 8-12 February 2008 had lower flow rates than the high flows from 6-13 March (Figure 2-2B). There was little variability in freshwater flow after 1 April 2008.

In 2007, water temperature increased steadily from 25 March to 6 April, then declined after the freshwater influx from the second flow peak (Figure 2-2A). Water temperatures subsequently increased, reaching the 12$^{o}$C threshold for striped bass spawning on 24 April 2007 (Figure 2-2A). In 2008, temperature in the upper Bay reached 12$^{o}$C on 12 April, 12 days earlier than in 2007 (Figure 2-2B). Water temperatures fluctuated around a mean of 17.1°C from 21 April to 19 May, before steadily increasing until the end of the spawning season.

Throughout the 2007 sampling season, the salt front was located up-estuary of the ETM (Table 2-2). On 25 April 2007, immediately following the third high-flow event, the salt front was displaced down-estuary and became nearly coincident with the ETM. The locations of the salt front were markedly up-estuary of the ETM in all other cruises, except for 22 May 2007. In 2008, patterns in locations of the salt front and ETM differed (Table 2-2). During two cruises, 17 April and 29 May 2008, the ETM was located up-estuary of the salt front.

The total volume of water representing nursery habitat was smaller in 2007 than in 2008 (4.0 E+08 m$^3$ and 9.2 E+08 m$^3$, respectively) (Table 2-3). Cruise-to-cruise variability in locations of the ETM and salt front affected the total volume of water located up-estuary, within, and down-estuary of these frontal features. Overall, the largest volumes of water were located down-estuary of the salt front and ETM in 2007 and 2008 (Table 2-3). In 2007, 49% of the mean volume was down-estuary of the ETM and 71% was down-estuary of the salt front. In 2008, 72% and 64% of the mean volume was down-estuary of the ETM and salt front, respectively. However, variability in volumes with respect to the ETM was smaller in 2007 than in 2008 (Table 2-3), primarily because of relatively large proportions of water volume up-estuary of the ETM during the first two surveys in 2007.

***Zooplankton Concentration and Distribution***

Mean concentrations of total prey (*E. affinis, B. longirostris, A. tonsa*) did not differ between years (back-transformed geometric means: 983.70 and 1014.12 m$^{-3}$ in 2007 and 2008, respectively). Total prey differed with respect to location and season in 2007. Concentrations within the ETM location in early spring (before 15 May) were higher than concentrations up-estuary of the ETM by almost an order of magnitude (Table 2-4; Figure 2-3A). In 2007, total prey concentrations up-estuary of the salt front in early spring were significantly lower than early spring prey concentrations down-estuary of the salt front and also were lower than up- and down-estuary concentrations in late spring (Table 2-4; Figure 2-3A). In 2008, spatial and temporal trends differed slightly, with total prey concentrations in early spring significantly higher than concentrations

after 15 May (1880.89 and 759.94 m$^{-3}$, respectively). Overall, total prey concentrations were higher down-estuary of the salt front in 2008 than up-estuary of it (Table 2-4; Figure 2-3B).

Concentrations of *Eurytemora affinis*, the most important prey of larval striped bass (see Chapter 3), did not differ between years but there were spatio-temporal trends in its distribution. In early spring 2007, concentrations of *E. affinis* down-estuary of the salt front were ten times higher than concentrations up-estuary of the salt front. Concentrations down-estuary of the salt front declined in late spring (Table 2-4; Figure 2-4A). In 2008, *E. affinis* concentrations were higher in early spring than in late spring (1578.58 and 252.01 m$^{-3}$, respectively) but did not differ significantly with respect to ETM or salt front locations (Table 2-4; Figure 2-4B).

Mean concentration of *Bosmina longirostris*, the second most important prey of striped bass larvae, was an order of magnitude higher in 2007 than 2008 (249.1 and 20.7 m$^{-3}$, respectively). In 2007, *B. longirostris* occurred in highest concentrations up-estuary of the salt front in late spring (Table 2-4; Figure 2-5A). In 2008, concentrations of *B. longirostris* were higher up-estuary than down-estuary of the ETM (20.79 and 2.19 m$^{-3}$, respectively) and were higher in late spring (Table 2-4; Figure 2-5B).

***Striped Bass Abundance and Distribution***

*Eggs*

In 2007, only 5% of the total egg abundances were located down-estuary of the ETM; abundances were considerably higher up-estuary (58%) and within (37%) the ETM (Table 2-5A). The within-ETM (58%) and within-salt front (44%) locations supported

the highest total egg abundances (Table 2-5A) although these locations only represented 25% and 18% of the upper Bay volumes in 2007 (Table 2-3). In 2008, highest total egg abundances were located up-estuary of the salt front and ETM (67% and 69%, respectively). However, on 17 and 29 May, 2008, highest egg abundances were within or down-estuary of the salt front and ETM (Table 2-5A). Statistical tests on mean abundances of striped bass eggs indicated significantly higher mean abundances in 2007 (1.1 E+08) than in 2008 (0.5 E+08) ($p < 0.05$) (Table 2-6; Figure 2-6A,B).

*Yolk-Sac Larvae*

In 2007, abundances of yolk-sac larvae were highest up-estuary of and within the ETM and salt front (> 80%), although most (50.6%) yolk-sac larvae occurred down-estuary of the salt front on 4 May (Table 2-5B). In 2008, total abundances, although variable among cruises, were relatively evenly distributed among locations with respect to the ETM and salt front (Table 2-5B). Despite the significantly higher mean egg abundances in 2007 than in 2008, yolk-sac larvae abundances were slightly, but not significantly, lower in 2007 than in 2008 ( 2.1E+07 in 2007 and 4.2 E+07 in 2008) ($p >$ 0.05; Table 2-6; Figure 2-7A,B). There was substantial cruise-to-cruise variability in abundance of yolk-sac larvae among locations with respect to the salt front or ETM making it difficult to determine if abundance differed significantly among locations (Table 2-5B, 2-6).

*Feeding-Stage Larvae*

In 2007, more than 80% of striped bass feeding-stage larvae occurred up-estuary of the salt front and ETM, with only 1.7% and 4.8% of larvae occurring down-estuary of the ETM and salt front, respectively (Table 2-5C). In contrast, in 2008, the highest numbers of feeding-stage larvae were down-estuary of the salt front and ETM (56% and 57%, respectively) (Table 2-5C). Feeding-stage larvae were > 5 times more abundant in 2007 than in 2008, but the mean abundances of feeding-stage larvae did not differ significantly (2.5 E+07 in 2007; 4.0 E+06 in 2008) ($p > 0.05$; Table 2-6). Although abundances of feeding-stage larvae appeared to vary inter-annually and spatially (Table 2-5C; Figure 2-8), the mean abundances, based on the analysis of log-transformed cruise abundances, did not differ significantly (Table 2-6), a consequence of large cruise-to-cruise variability within locations (Table 2-5C).

***Spatial Overlap of Striped Bass Feeding-Stage Larvae with Prey***

Striped bass feeding-stage larvae overlapped to a high degree with their two primary prey *E. affinis* and *B. longirostris* (Table 2-7). In 2007, highest mean overlap of larvae with both prey organisms occurred within and down-estuary of the ETM feature, but within and up-estuary of the salt front. In general, spatial overlaps between striped bass larvae and the two prey tended to be higher in 2007 than in 2008, although there were exceptions (Table 2-7). The spatial overlap between feeding-stage larvae and *B. longirostris* was particularly high within and down-estuary of the ETM in 2007 (Table 2-7). Spatial overlap between feeding-stage larvae and *E. affinis* was consistently high within the ETM in 2007 and 2008 cruises, with only a single exception, 1 May 2008.

### Age and Growth of Striped Bass Larvae

Larvae that were aged ranged from 5-27 days post-hatch (dph) in 2007 and 3-25 dph in 2008 (Figure 2-9). Mean ages of larvae in collections did not differ significantly between years [2007: $12.1 \pm 0.53$ (se) dph; 2008: $11.3 \pm 0.31$ (se) dph].

Hatch-date distributions of larvae in collections differed between years (Two-sample Kolmogorov-Smirnov test, $D = 0.668$, $p < 0.001$). In 2007, hatch dates of surviving larvae ranged from 25 April to 21 May (Figure 2-10). In 2008, observed hatch dates extended over a longer time period, from 20 April to 3 June (Figure 2-10). In 2008, two peaks were observed- -an early season peak from 29 April to 2 May, as also observed in 2007, and a late season peak from 27 to 30 May 2008.

Individual growth rates of larvae, derived from otolith-aging, were significantly faster in 2007 than in 2008 (Table 2-8; $p = 0.011$. The mean ($\pm$ se) growth rate in 2007 was $0.245 \pm 0.007$ mm d$^{-1}$. In 2008, mean growth rate was $0.223 \pm 0.005$ mm d$^{-1}$ (Figure 2-11A). Location of larvae at time of collection was a significant factor. Larvae collected within or up-estuary of the ETM had higher growth rates (0.038 and 0.041 mm d$^{-1}$ higher, respectively) than larvae collected down-estuary of the ETM (Table 2-8; Figure 2-11B; $p = 0.006$). Similarly, larvae collected down-estuary of the salt front had significantly lower growth rates than larvae within the salt front (Table 2-8; Figure 2-11C; $p = 0.023$). There were no significant year by location interaction effects on growth rates for either the ETM or salt front features.

Individual growth rates of feeding-stage larvae were not related to presence of food in guts at time of collection. Larvae with or without prey in their guts had similar mean growth rates in each year (2007: $0.243 \pm 0.008$ mm d$^{-1}$ food present and $0.249 \pm$

0.013 mm d$^{-1}$ no food. <u>2008</u>: 0.223 ± 0.007 mm d$^{-1}$ food present and 0.218 ± 0.008 mm d$^{-1}$, no food). Additionally, individual growth rates of larvae were unrelated to the number of prey items in guts at the time of capture in either 2007 or 2008 (Figure 2-12).

## DISCUSSION

Spatial and temporal patterns in abundance, distribution, and growth rates of striped bass early life stages in the upper Chesapeake Bay were determined in 2007 and 2008 to help understand processes that control recruitment in striped bass. An objective was to evaluate how the salt front and ETM affected patterns of abundance of striped bass early life stages and zooplankton that serve as their prey. Eggs were approximately two times more abundant in 2007 than in 2008. Although abundances of yolk-sac larvae of striped bass were similar in 2007 and 2008, total abundances of feeding-stage larvae were substantially lower in 2008, a year of exceptionally low YOY recruitment (http://dnr.maryland.gov/fisheries/juvindex/). Concentrations of total zooplankton prey (*Eurytemora affinis*, *Bosmina longirostris*, and *Acartia tonsa*, combined) and of the primary dominant prey *E. affinis* were similar in each year. However, concentrations of the freshwater cladoceran *B. longirostris* were 10 times higher in 2007 than in 2008.

Locations of the salt front and ETM features in Chesapeake Bay can shift and vary under variable freshwater flow and winds (North and Houde 2001). The locations of the salt front and ETM differed considerably in 2007 and 2008. In 2007, the ETM had a relatively stable location down-estuary of the salt front, while in 2008, there was greater separation between the salt front and ETM. Volumes of water with respect to the ETM and salt front differed among surveys, but were highest down-estuary of the salt front and

ETM in both years. In 2008, 72% and 64% of the total sampled volume occurred down-estuary of the ETM and salt front, respectively. In 2007, total abundances of eggs were highest up-estuary and within the ETM (37% and 58%, respectively) and within and down-estuary of the salt front (43% and 35%, respectively). In 2008, highest total egg numbers were located up-estuary of the salt front and ETM (67% and 69%, respectively). In 2007, very few feeding-stage larvae were located down-estuary of the ETM or salt front (2% and 5%, respectively), while in 2008, 57% of feeding-stage larvae were located down-estuary of the ETM and 56% were located down-estuary of the salt front. Statistically, however, the distribution of striped bass eggs and larvae was not clearly associated with the location of the ETM because of the large internal variability within each location. In both years, concentrations of total prey and of *E. affinis* were highest down-estuary of the salt front and ETM early in the season. Later in the season, *B. longirostris*, the second most dominant prey, was more numerous up-estuary of the salt front.

Two patterns in hatch dates of striped bass larvae were observed in 2007 and 2008. The frequency distributions and peaks of early hatch dates were similar in the two years. However, in 2008, a second peak was observed late in the season.

Individual growth rates of striped bass larvae were slightly, but significantly, higher in 2007 than in 2008. Larvae down-estuary of the salt front and ETM grew slower than larvae within or up-estuary in both years, possibly due to lower feeding rates (see Chapter 3). There was no clear relationship between larval growth rates and feeding success measured as the presence/absence or number of prey items in guts at time of capture.

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*Distribution of Striped Bass Eggs and Larvae: Frontal Features and Zooplankton*

I had hypothesized, based on earlier research on the ETM region (e.g., Roman et al. 2001; North and Houde, 2003, 2006; Martino and Houde 2010), that the ETM and its associated salt front acted as a larval retention area, inhibiting down-estuary dispersal of early life stages of striped bass and zooplankton upon which they feed. Recruitment success may be enhanced when larvae are retained within frontal features that support production (Iles and Sinclair 1982; Sinclair and Iles 1985; Sinclair 1988) and the ETM and salt front may serve this role in the upper Chesapeake Bay. Retention of eggs and larvae within salt front and ETM regions is thought to maintain early life stages of striped bass in an environment where salinity is optimal (Winger and Lasier 1994), prey density is high (Boynton et al. 1997; Roman et al. 2001; North and Houde 2001; Martino and Houde 2010), and predation pressure is potentially reduced.

The ETM and salt front features often coincide and can be closely associated, although occasional separation of these features unrelated to tidal dynamics has been observed (Sanford et al. 2001). I observed notable separation (maximum separation: 21 km on 8 May 2007) between the salt front and ETM locations during most of the surveys in 2007 and 2008, indicating that separation may be quite common in upper Chesapeake Bay. Surveys of the upper Bay in May 1996, an extremely wet year with high freshwater flow, indicated that the central region of the ETM was displaced up-estuary as much as 10 km from the salt front (Boynton et al. 1997). In 1998, a moderately wet year, the salt front was generally located near the ETM, although in 1999, a dry year, the salt front was located well up-estuary of the ETM in May (North and Houde 2001). The frequent

occurrence of the ETM at kilometers 35 to 40 in 2007-2008, years of moderate flow, suggests that in the absence of high freshwater flow or wind forcing events, the location of the ETM is largely determined by the bathymetry of the upper Bay (Houde et al. 2009).

The occurrence of high abundances of striped bass eggs up-estuary and within the salt front and ETM in 2007 indicated that these features may provide boundary conditions for spawning by adults or potentially act as a retention feature. In 2007, more than half of the total egg numbers were located within the ETM. However, in 2008, only 7% of eggs occurred within the ETM while 24% were located down-estuary of it. Additionally, 13% of eggs in 2008 were down-estuary of the salt front, where the potential to be washed out of the nursery area is highest. Other research on striped bass eggs in the upper Chesapeake Bay and its tributaries has indicated the importance of both the salt front and the ETM as important features linked to egg distributions. In 1998, North and Houde (2001) found that 75% of striped bass eggs occurred where salinities were < 1 in the upper Bay, while 32.4% of eggs occurred within 10 km of maximum turbidity. In 2001-2003, Martino and Houde (2010) did not find that egg distributions in the upper Bay were associated with the ETM. However, egg concentrations during 2003, the year with highest freshwater flow, were more abundant up-estuary of the ETM than down-estuary. In the Patuxent River, a tributary of the Chesapeake Bay, striped bass eggs generally occurred up-estuary of the salt front (Secor and Houde 1995). Peak densities of eggs in the Potomac River occurred at low salinities (< 600 micromhos cm$^{-2}$, equivalent to < 0.5 salinity) (Rutherford et al. 1997). In the upper Bay in 1988 and 1989, striped bass eggs were in highest abundance near the maximum turbidity zone (i.e., ETM) where

salinities were low (< 1200 micromhos cm$^{-2}$, equivalent to < 1.0 salinity) (Rutherford et al. 1997).

In 2007, a large proportion of striped bass feeding-stage larvae were up-estuary of the salt front and ETM (83% and 85%, respectively). In 2008, the distribution of feeding-stage larvae was very different. Modest numbers of feeding-stage larvae were within the salt front and ETM locations in 2008, but > 55% were down-estuary of those features. The salt front and ETM have been proposed as features that support and retain relatively high concentrations of striped bass larvae. For example, in 1998 surveys, North and Houde (2001) reported that 90.8% of striped bass feeding-stage larvae were collected within 10 km of the ETM, and 46.7% occurred in salinities < 1. In a mark-recapture experiment in the Nanticoke River (Chesapeake Bay), striped bass larvae with chemical marks on their otoliths were released down- and up-estuary of the salt front, but were recaptured only at locations up-estuary of the salt front (Secor et al. *in review*). The higher associations of feeding-stage larvae within the ETM and salt front features in 2007 may have contributed to the higher recruitment in this year. In 2008, the large proportion of feeding-stage larvae down-estuary of both the salt front and ETM may have been lost from the nursery area, contributing to a very low juvenile abundance index that was recorded by Maryland DNR (http://dnr.maryland.gov/ fisheries/ juvindex/).

The distribution of striped bass in other estuarine systems presents a complex picture. Striped bass is an introduced species in the San Francisco Bay Estuary. Although high freshwater flow increases turbidity, a typical ETM is often absent from the complex and deltaic San Francisco Bay Estuary (Kimmerer 2002). However, the location of the intersection of the 2 isohaline (denoted as $X_2$) with the estuary bottom was historically

important in describing striped bass recruitment variability in this system (Jassby et al. 1995). Seaward movement of $X_2$ due to increases in freshwater flow historically was associated with increased recruitment, possibly due to successful transport of larvae to suitable nursery areas by the time of first feeding (Jassby et al. 1995; Kimmerer et al. 2001). Striped bass from northern regions of the range of the Atlantic East Coast stock also appear to have different early life history strategies that are specific to spawning and nursery areas. For example, striped bass spawning in tributaries of the Bay of Fundy and the Gulf of St. Lawrence occurs in the late spring in areas well up-river of the salt intrusion (Rulifson and Dadswell 1995). In these systems, timing of spawning also is important for larval survival due to the magnitude of tides and tidal dynamics. For example, Rulifson and Tull (1999) reported that peak spawning occurred one day prior to the neap tide in the Shubenacadie Estuary, which would minimize down-estuary losses.

I had hypothesized that freshwater flow may be important in determining inter-annual differences in retention and recruitment of striped bass larvae reported in 2007 and 2008. Freshwater flow is an important factor that influences the strength and location of the ETM and salt front. Inter-annual variability in Susquehanna River flow can have a significant effect on the strength (level of turbidity) and location of the ETM. For example, in 1999, low freshwater inputs to the upper Bay resulted in a weakly developed ETM (North and Houde 2001). Based on observed distribution and abundance patterns of striped bass and white perch (*Morone americana*) larvae in high- and low-flow years, North and Houde (2001) hypothesized that decreased level of freshwater flow reduces gravitational circulation within the estuary, weakening the ETM and leading to down-estuary losses of eggs and larvae. The hypothesis further postulated that low freshwater

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flow could reduce zooplankton prey abundances, leading to decreased feeding and growth of striped bass larvae. There is broad support for this hypothesis. Inclusion of freshwater flow in Ricker spawner-recruit models explained an additional 40% of striped bass recruitment variability compared to models that only included spawning-stock biomass (North and Houde 2003; Martino and Houde 2010).

Results of my research, conducted in 2007-2008, years of modest and low recruitment success, respectively, of Chesapeake Bay striped bass, did not support or refute this hypothesis. Freshwater flow volumes differed relatively little in these two years. Additionally, the exceptionally low recruitment outcome in 2008 was unexpected, given the moderate levels of freshwater flow. Hydrographic surveys in 2008 showed lower concentrations of suspended sediments, indicating a weaker ETM than in 2007 (Jahn 2010). The disconnect between freshwater flow volume, early life stages, and YOY recruitment level in 2008 was clearly apparent in predicted versus observed YOY recruitment reported by Martino and Houde (2010) who had constructed a model relating YOY striped bass recruitment from 1985-2006 to spring freshwater flow and spring temperature. Their model had accurately forecasted recruitment for 2007 and 2009, but their forecasted recruitment was far above observed recruitment in 2008. Other measures of freshwater flow, such as the magnitude and frequency of high flow events, may also be important to the hydrography of the upper Bay and consequently the recruitment success of larval striped bass and should be investigated further.

Distribution of striped bass larvae may be influenced not only by the strength and location of frontal features, but also by the distribution of zooplankton prey. Matches of prey with larval production, both temporally (e.g., Cushing 1990) and spatially (e.g.,

Martino and Houde 2010) may be key to survival of feeding-stage striped bass larvae. My research examined spatial and temporal overlap of feeding-stage larvae with different zooplankton prey. Larvae experienced a high degree of spatio-temporal overlap with both *Eurytemora affinis* and *Bosmina longirostris*. Mean overlap of larvae with *Eurytemora* was similar in 2007 and 2008, with highest overlap occurring within the ETM in both years. However, larvae in 2007 also experienced a high degree of overlap with *Bosmina,* especially during the 22 May 2007 survey. There was considerably less overlap of feeding-stage larvae with *Bosmina* in 2008. The availability of *B. longirostris* and its relatively high consumption in 2007 compared to 2008 (see Chapter 3) may have given striped bass larvae a nutritional advantage in 2007.

Peak concentrations of both striped bass and white perch feeding-stage larvae coincided with high concentrations of zooplankton prey in the upper Bay in 1998, when concentrations of *B. longirostris* explained most of the variability in striped bass larval abundances (North and Houde 2003). Additionally, peak concentrations of striped bass and white perch larvae were reported in 1998 when prey concentrations also were high, and North and Houde (2006) suggested that retention within the ETM could result from tracking of prey. Martino and Houde (2010) reported spatio-temporal overlap between zooplankton and striped bass larvae in the upper Bay in years of high freshwater discharge, which also were the years of highest recruitment. In a two-year study in the Nanticoke River, a tributary of Chesapeake Bay, feeding-stage larvae of striped bass occurred up-estuary of the salt front in a region where zooplankton, dominated by *B. longirostris*, were >3 times more abundant than at down-estuary locations (Secor et al. *in review*). A multivariate analysis on abundance of striped bass larvae in the estuarine

transition zone of the Patuxent River, another Chesapeake tributary, found that a significant proportion of the variability in larval abundance was explained by concentrations of zooplankton prey, primarily *E. affinis* and *B. longirostris*, in addition to salt front location (Campfield and Houde 2011).

Spatial overlap of larvae with zooplankton prey is a common theme for fishes in ETM and salt front regions. For example, in the St. Lawrence River Middle Estuary, high abundances of rainbow smelt *Osmerus mordax* larvae occur in the ETM region associated with high zooplankton concentrations (Sirois and Dodson 2000). The ETM in the Chikugo River Estuary in the Ariake Bay, Japan, is an important nursery habitat for Japanese seaperch *Lateolabrax* , *aponicas* (Shoji and Tanaka 2006b). Late larval stage and small juvenile seaperch migrate up-estuary from the Bay and are distributed throughout the Chikugo River sub-estuary (Islam et al. 2006b; Shoji and Tanaka 2006a). Most late-stage larvae are located near the ETM region in the Chikugo River where the dominant zooplankton prey, the copepod *Sinocalanus sinensis,* peaks in abundance (Shoji and Tanaks 2006b). The contingent of early juvenile seaperch located up-estuary and near the ETM, experiences higher protein growth rates and is less likely to starve (Islam et al. 2006a)

### *Larval Hatch Dates, Age, and Growth*

Hatch dates of larvae in my collections ranged from 25 April – 21 May in 2007 and from 20 April – 3 June 3 in 2008. Hatch dates in 2007 are generally similar to those reported from earlier research on upper Bay striped bass larvae. Jahn (2010) estimated spawning dates for upper Bay feeding-stage larvae collected in 2007 and 2008, whose

lengths were converted to ages based on an available age-length key (Kellogg 1996).

Jahn's estimated spawning dates ranged from 25 April – 28 May in 2007 and from 12

April – 28 May in 2008. The earlier spawning and hatch dates in 2008 estimated herein

and by Jahn (2010) could be attributed to earlier occurrence of warmer temperatures in

the upper Bay during early spring 2008. In 2008, the 12°C spawning threshold was

reached 12 days earlier than in 2007. Martino (2008) found a narrower window of hatch

dates in the upper Bay in 2001-2003, with dates ranging from 19 April – 5 May during a

short sampling season that might have missed larvae hatched later in the season.

However, peak hatch dates I observed in 2007 and 2008 were similar to peak hatch dates

in 2001 and 2003 (April 27 and April 30, respectively).  Seltzer-Hamilton et al. (1981)

reported peak larval spawning in mid- to late-April during the 1970s in the Potomac

River tributary. Peak hatch dates from my research and Martino (2008) for spawning in

the upper Bay during the 2001-2008 period were earlier than peak spawning reported in

mid to late May 1988-1989 (Rutherford and Houde 1995).

Hatch-date frequencies of striped bass larvae in 2001-2003 (Martino 2008) and

spawning-date frequencies reported for 2007-2008 (Jahn 2010) did not include a second

peak in hatch dates late in the spawning season as I observed in 2008. In earlier research

on the Potomac River, Rutherford and Houde (1995) did note a second spawning peak in

mid-May of 1989.The distinct second peak of late hatch dates I observed on 5-6 June

2008 could be attributed to inclusion of late sampling dates. Only my study and that of

Rutherford and Houde (1995) included sampling in June. It is possible that peaks in hatch

dates and cohort production of late-spawned larvae could occur in other years.

Growth rates of striped bass larvae in the upper Bay during 2007-2008 were similar to rates reported in the literature.  Growth rates of individual larvae in 2007 and 2008 ranged from 0.06 to 0.48 mm $d^{-1}$, similar to those of larvae from earlier research (Table 2-9). Martino (2008) reported median growth rates of $0.22 - 0.28$ mm $d^{-1}$ for larvae collected in the upper Bay in 2001 and 2003. Growth rates of striped bass larvae and juveniles in the Hudson River ranged from $0.017 - 0.293$ mm $d^{-1}$ in 1994 (Limburg et al. 1999) and from $0.1 - 0.2$ mm $d^{-1}$ in 1973-1976 (Dey 1981). Mean cohort-specific growth rates of striped bass larvae in the Patuxent River were  0.13 mm $d^{-1}$ to 0.42 mm $d^{-1}$ during 1991 (Secor and Houde 1995) and 0.32 and 0.30 mm $d^{-1}$ in 2000 and 2001, respectively (Campfield 2004). Growth rates of striped bass larvae, derived from eggs of Chesapeake Bay adults, in laboratory and field enclosure experiments ranged from 0.29 to 0.36 mm $d^{-1}$ (laboratory) and 0.30 to 0.32 mm $d^{-1}$ (enclosures) (Houde and Lubbers 1986).  Potomac River striped bass larvae grew at rates between $0.11 - 0.53$ mm $d^{-1}$, with growth rates increasing as the spawning season progressed and temperatures increased (Rutherford and Houde 1995). Growth rates of larvae in the San Francisco Estuary ranged from $0.13 - 0.27$ mm $d^{-1}$ (Foss and Miller 2001) and were similar but perhaps a bit slower than those observed for larvae on the Atlantic coast.

The ETM and salt front may act as frontal features that enhance zooplankton production and availability, providing improved conditions for nutrition and growth of striped bass larvae.  In my research, striped bass larvae collected down-estuary of the salt front and ETM had lower growth rates than those within or up-estuary of the features. Similarly, larval rainbow smelt in the St. Lawrence River estuary grew faster within the ETM where prey concentrations were higher than down-estuary of it (Sirois and Dodson

2000). A direct comparison of growth rates and feeding indices from my research (Chapter 3) did not indicate that growth-rate variability in 2007 and 2008 was caused by markedly higher feeding success in the salt front or ETM. Although the salt front and ETM were not characterized by higher total prey densities in these years, *B. longirostris* occurred in much lower concentrations down-estuary of the salt front and was at lower concentrations at all locations in 2008. The lack of relationship between individual growth rates in striped bass larvae and instantaneous measures of feeding success in 2007 and 2008, i.e., feeding incidence and numbers of prey in guts, did not support the argument that retention in frontal features promotes faster growth by elevating feeding success.

Despite the extensive research conducted on striped bass early life stages and factors that affect recruitment, causes of recruitment variability remain elusive. In 2007 and 2008, years of unremarkable environmental conditions and low to average recruitment success for striped bass, distributions of larvae were not simply defined by the ETM or salt front features and associated freshwater flow. The underlying factors or combination of factors that resulted in low recruitment in 2008, but modest recruitment in 2007, are unresolved. However, the large proportion of feeding-stage larvae down-estuary of the salt front and ETM in 2008 may have caused down-estuary loss of larvae, contributing to lower recruitment. There is a considerable body of evidence, including new information in this thesis, that indicates the ETM and salt front features play a role in controlling distribution of striped bass eggs and larvae and the overlap of larvae with their zooplankton prey.

Table 2-1. Summary of survey cruises conducted in the upper Chesapeake Bay in 2007 and 2008.

| Cruise | Dates | Research Vessel | Gear | Mesh (µm) | Number of Samples |
|---|---|---|---|---|---|
| BMRR0701 | 25 April 2007 | Terrapin | 60-cm Paired Bongo | 280 | 11 |
| BMRR0702 | 4 May 2007 | Terrapin | 60-cm Paired Bongo | 280 | 9 |
| BM0703 | 11 May 2007 | Hugh R. Sharp | 1 m$^2$ Tucker Trawl | 280 | 44 |
| BMRR0703 | 22 May 2007 | Terrapin | 60-cm Paired Bongo | 280 | 11 |
| BMRR0704 | 29 May 2008 | Terrapin | 60-cm Paired Bongo | 280 | 10 |
| BM0802 | 19-22 April 2008 | Hugh R. Sharp | 1m$^2$ Tucker Trawl | 280 | 48 |
| | | | ¼ m$^2$ MOCNESS | 333 | 36 |
| BMRR0801 | 1 May 2008 | Terrapin | 60-cm Paired Bongo | 280 | 10 |
| BM0803 | 16-20 May 2008 | Hugh R. Sharp | 1 m$^2$ Tucker Trawl | 280 | 54 |
| | | | ¼ m$^2$ MOCNESS | 333 | 42 |
| BMRR0802 | 30 May 2008 | Terrapin | 60-cmPaired Bongo | 280 | 10 |
| MEN0706 | 4-6 June 2008 | Aquarius | 1 m$^2$ Tucker Trawl | 280 | 14 |
| | | | 2 m$^2$ Tucker Trawl | 707 | 16 |

Table 2-2. Locations of the salt front and ETM in distance (km) down-estuary from the
Elk River confluence with Chesapeake Bay in 2007 and 2008. Locations were designated
from visual inspection of contoured CTD data. The CTD on 5 June 2008 did not obtain
measures of total suspended solids and the ETM location could not be defined.

| Date | ETM (km) | Salt Front (km) |
| --- | --- | --- |
| 25 April 2007 | 38 | 35 |
| 4 May 2007 | 35 | 25 |
| 8 May 2007 | 36 | 15 |
| 22 May 2007 | 26 | 24 |
| 30 May 2007 | 37 | 18 |
| | | |
| 17 April 2008 | 25 | 28 |
| 1 May 2008 | 30 | 15 |
| 17 May 2008 | 20 | 20 |
| 29 May 2008 | 18 | 27 |
| 5 June 2008 | | 28 |

Table 2-3. Volumes (m$^3$) of segments of the upper Chesapeake Bay for surveys in 2007 and 2008 with respect to location of the ETM and salt front. Percent of the total volume of each cruise represented by each location is given in parentheses.

| | ETM Location | | | Salt Front Location | | |
|---|---|---|---|---|---|---|
| **2007** | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary |
| 25 April | 1.0E+08 (38) | 9.8E+07 (36) | 7.1E+07 (26) | 5.9E+07 (22) | 7.2E+07 (26) | 1.4E+08 (52) |
| 4 May | 9.6E+07 (27) | 1.2E+08 (34) | 1.4E+08 (40) | 5.7E+07 (16) | 7.4E+07 (21) | 2.3E+08 (63) |
| 11 May | 1.8E+08 (23) | 1.4E+08 (18) | 4.6E+08 (59) | 2.6E+07 (3) | 1.1E+08 (15) | 6.4E+08 (82) |
| 22 May | 7.0E+07 (21) | 7.4E+07 (22) | 1.9E+08 (57) | 7.0E+07 (21) | 3.8E+07 (11) | 2.3E+08 (68) |
| 30 May | 1.4E+08 (55) | 1.2E+08 (45) | - | 1.3E+07 (5) | 5.7E+07 (22) | 1.9E+08 (73) |
| Mean | 1.2E+08 (27) | 1.1E+08 (25) | 2.2E+08 (49) | 0.5E+08 (11) | 0.7E+08 (18) | 2.9E+08 (71) |
| | | | | | | |
| **2008** | | | | | | |
| 17 April | 2.5E+08 (20) | 6.3E+07 (5) | 9.2E+08 (75) | 1.6E+08 (13) | 1.6E+08 (13) | 9.2E+08 (74) |
| 1 May | 7.0E+07 (27) | 6.7E+07 (26) | 1.2E+08 (47) | 1.3E+07 (5) | 5.7E+07 (22) | 1.9E+08 (73) |
| 17 May | 2.3E+08 (12) | 3.1E+08 (16) | 1.4E+09 (73) | 3.1E+08 (16) | 3.0E+08 (15) | 1.4E+09 (69) |
| 29 May | 1.3E+07 (5) | 3.0E+07 (12) | 2.2E+08 (83) | 4.3E+07 (17) | 9.5E+07 (37) | 1.2E+08 (47) |
| 5 June | - | - | - | 2.5E+08 (28) | 2.6E+08 (29) | 3.7E+08 (43) |
| **Mean** | 1.4E+08 (15) | 1.2E+08 (13) | 6.8E+08 (72) | 1.5E+08 (17) | 1.7E+08 (19) | 5.9E+08 (64) |

Table 2-4. Results from analysis of variance and Tukey-Kramer tests on mean concentrations of zooplankton ($\log_{10}(\text{no} \cdot \text{m}^{-3} + 1)$) in 2007 and 2008. The category "all prey items" includes *Eurytemora affinis*, *Bosmina longirostris*, and *Acartia tonsa*. For seasons, early (**e**) designates samples collected before 15 May, while late (**l**) designates samples collected after 15 May. Locations are denoted as up-estuary (**u**; >5 km up-estuary of feature), within (**w**; ±5 km of feature), or down-estuary (**d**; >5 km down-estuary of feature).

| Parameter | Factor | 2007 | | 2008 | |
|---|---|---|---|---|---|
| | | p | Tukey-Kramer | p | Tukey-Kramer |
| All Prey Items | ETM Location | 0.18 | | 0.25 | |
| | Season | 0.50 | | 0.02 | e > l |
| | ETM Location * Season | 0.05 | w-e > u-e | 0.40 | |
| All Prey Items | Salt Front Location | 0.18 | | 0.001 | d > w |
| | Season | 0.04 | | 0.92 | |
| | Salt Front Location * Season | 0.04 | u-l;d-e;d-l > u-e | 0.68 | |
| E. affinis | ETM Location | 0.15 | | 0.42 | |
| | Season | 0.01 | e > l | 0.00 | e > l |
| | ETM Location * Season | 0.11 | | 0.51 | |
| E. affinis | Salt Front Location | 0.11 | | 0.08 | |
| | Season | 0.26 | | 0.05 | e > l |
| | Salt Front Location * Season | 0.04 | d-e > d-l;u-e | 0.64 | |
| B. longirostris | ETM Location | 0.42 | | 0.01 | u > d |
| | Season | 0.37 | | 0.02 | l > e |
| | ETM Location * Season | 0.37 | | 0.36 | |
| B. longirostris | Salt Front Location | 0.01 | | 0.01 | w > d |
| | Season | 0.02 | l>e | 0.67 | |
| | Salt Front Location * Season | 0.01 | u-l > d-e;d-l;u-e | 0.66 | |

Table 2-5. Total abundances of (A) striped bass eggs, (B) yolk-sac larvae, and (C) feeding-stage larvae in locations up-estuary, within, and down-estuary of the ETM and salt front in 2007 and 2008. Percentages of eggs, yolk-sac larvae, and feeding-stage larvae within each location for each survey are given in parentheses. Mean and standard error for each location is given for each year.

23. Eggs

| | ETM Location | | | Salt Front Location | | | Total |
|---|---|---|---|---|---|---|---|
| **2007** | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary | |
| 25 April | 2.7E+08 (18.4%) | 1.1E+09 (77.7%) | 5.7E+07 (3.9%) | 1.0E+08 (7.0%) | 6.8E+08 (47.0%) | 6.7E+08 (45.9%) | 1.5E+09 |
| 4 May | 1.7E+08 (38.0%) | 2.4E+08 (54.5%) | 3.3E+07 (7.5%) | 1.3E+07 (2.9%) | 3.0E+08 (69.0%) | 1.2E+08 (28.1%) | 4.4E+08 |
| 11 May | 5.5E+08 (90.6%) | 4.5E+07 (7.4%) | 1.2E+07 (2.0%) | 4.5E+08 (74.4%) | 5.2E+07 (8.5%) | 1.0E+08 (17.0%) | 6.1E+08 |
| 22 May | 5.4E+07 (19.8%) | 2.2E+08 (78.8%) | 3.9E+06 (1.4%) | 5.4E+07 (19.8%) | 1.6E+08 (56.8%) | 6.4E+07 (23.4%) | 2.7E+08 |
| 30 May | 1.9E+07 (100%) | 0.0E+00 (0.0%) | - | 3.0E+06 (15.9%) | 3.0E+06 (16.2%) | 1.3E+07 (67.9%) | 1.9E+07 |
| Sum | 1.1E+09 (38%) | 1.6E+09 (58%) | 0.1E+09 (4%) | 0.6E+09(22%) | 1.2E+09 (43%) | 1.0E+09 (35%) | |
| Mean (SE) | 2.1E+08 (4.3E+07) | 3.3E+08 (9.2E+07) | 2.6E+07 (4.8E+06) | 1.2E+08 (3.7E+07) | 2.4E+08 (5.5E+07) | 1.9E+08 (5.4E+07) | |
| | | | | | | | |
| **2008** | | | | | | | |
| 17 April | 5.8E+08 (80.5%) | 1.9E+07 (2.7%) | 1.2E+08 (16.8%) | 5.5E+08 (76.8%) | 8.9E+07 (12.4%) | 7.8E+07 (10.8%) | 7.2E+08 |
| 1 May | 1.1E+07 (100%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 9.4E+06 (85.7%) | 1.6E+06 (14.4%) | 0.0E+00 (0.0%) | 1.1E+07 |
| 17 May | 5.1E+06 (4.0%) | 4.1E+07 (32.1%) | 8.2E+07 (64.0%) | 1.7E+07 (13.2%) | 7.3E+07 (57.1%) | 3.8E+07 (29.7%) | 1.3E+08 |
| 29 May | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 2.7E+06 (100%) | 0.0E+00 (0.0%) | 2.7E+06 (100%) | 0.0E+00 (0.0%) | 2.7E+06 |
| 5 June | - | - | - | 1.2E+07 (56.1%) | 8.9E+06 (41.4%) | 5.2E+05 (2.5%) | 2.1E+07 |
| Sum | 6.0E+08 (69%) | 0.6E+08 (7%) | 2.1E+08 (24%) | 5.9E+08 (67%) | 1.8E+08 (20%) | 1.2E+08 (13%) | |
| Mean (SE) | 1.5E+08 (7.2E+07) | 1.5E+07 (4.9E+06) | 5.1E+07 (1.5E+07) | 1.2E+08 (4.9E+07) | 3.5E+07 (8.5E+06) | 2.3E+07 (6.9E+06) | |

Table 2-5, continued.

B. Yolk-Sac Larvae

| | ETM Location | | | Salt Front Location | | | Total |
|---|---|---|---|---|---|---|---|
| **2007** | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary | |
| 25 April | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 |
| 4 May | 1.1E+07 (44.7%) | 1.3E+07 (51%) | 1.1E+06 (4.3%) | 8.2E+05 (3.2%) | 1.2E+07(46.3%) | 1.3E+07 (50.6%) | 2.6E+07 |
| 11 May | 3.0E+07 (98.2%) | 4.3E+05 (1.4%) | 1.2E+05 (0.4%) | 2.8E+07 (88.9%) | 2.3E+06 (7.5%) | 1.1E+06 (3.6%) | 3.1E+07 |
| 22 May | 1.1E+07 (28.2%) | 2.7E+07 (67.0%) | 1.9E+06 (4.8%) | 1.1E+07 (28.2%) | 2.4E+07 (60.6%) | 4.5E+06 (11.2%) | 4.0E+07 |
| 30 May | 4.4E+06 (100%) | 0.0E+00 (0.0%) | - | 2.4E+06 (54.3%) | 2.0E+06 (45.7%) | 0.0E+00 (0.0%) | 4.4E+06 |
| Sum | 5.8E+07 (57%) | 4.0E+07 (40%) | 3.2E+06 (3%) | 4.2E+07 (42%) | 4.1E+07 (40%) | 1.9E+07 (18%) | |
| Mean (SE) | 1.2E+07 (2.3E+06) | 8.1E+06 (2.4E+06) | 7.9E+05 (1.8E+05) | 8.4E+06 (2.3E+06) | 8.1E+06 (2.0E+06) | 3.7E+06 (1.1E+06) | |
| | | | | | | | |
| **2008** | | | | | | | |
| 17 April | 4.8E+07 (35.6%) | 3.9E+07 (29.1%) | 4.8E+07 (35.3%) | 3.5E+07 (26.1%) | 3.3E+07 (24.6%) | 6.6E+07 (49.3%) | 1.3E+08 |
| 1 May | 1.9E+07 (95.5%) | 8.8E+05 (4.46%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 1.9E+07 (95.5%) | 8.8E+05 (4.5%) | 2.0E+07 |
| 17 May | 0.0E+00 (0.0%) | 1.2E+06 (21.0%) | 4.6E+06 (79.0%) | 3.1E+05 (5.3%) | 2.0E+06 (33.5%) | 3.6E+06 (61.1%) | 5.9E+06 |
| 29 May | 0.0E+00 (0.0%) | 3.9E+05 (4.0%) | 9.3E+06 (96.0%) | 3.9E+05 (4.0%) | 7.4E+06 (76.8%) | 1.9E+06 (19.18%) | 9.7E+06 |
| 5 June | - | - | - | 7.8E+05 (58.3%) | 5.6E+05 (41.4%) | 4.0E+03 (0.3%) | 1.3E+06 |
| Sum | 6.7E+07 (39%) | 4.2E+07 (25%) | 6.1E+07 (36%) | 3.7E+07 (22%) | 6.2E+07 (36%) | 7.3E+07 (43%) | |
| Mean (SE) | 1.7E+07 (5.7E+06) | 1.0E+07 (4.8E+06) | 1.5E+07 (5.4E+06) | 7.3E+06 (3.1E+06) | 1.2E+07 (2.7E+06) | 1.5E+07 (5.8E+06) | |

Table 2-5, continued.

## C. Feeding-Stage Larvae

| | ETM Location | | | Salt Front Location | | | Total |
|---|---|---|---|---|---|---|---|
| **2007** | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary | |
| 25 April | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 |
| 4 May | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 |
| 11 May | 3.3E+07 (100%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 3.3E+07 (99.0%) | 3.5E+05 (1.0%) | 0.0E+00 (0.0%) | 3.3E+07 |
| 22 May | 7.1E+07 (79.3%) | 1.6E+07 (18.3%) | 2.2E+06 (2.4%) | 7.1E+07 (79.3%) | 1.3E+07 (14.4%) | 5.7E+06 (6.4%) | 9.0E+07 |
| 30 May | 2.9E+06 (100%) | 0.0E+00 (0.0%) | - | 5.9E+05 (20.6%) | 2.0E+06 (69.6%) | 2.8E+05 (9.8%) | 2.9E+06 |
| Sum | 11.0E+07 (85%) | 1.6E+07 (13%) | 0.2E+07 (2%) | 10.0E+07 (83%) | 1.5E+07 (12%) | 0.6E+07 (5%) | |
| Mean (SE) | 2.1E+07 (6.2E+06) | 3.3E+06 (1.5E+06) | 5.4E+05 (2.2E+05) | 2.1E+07 (6.3E+06) | 3.0E+06 (1.1E+06) | 1.2E+06 (5.1E+05) | |
| | | | | | | | |
| **2008** | | | | | | | |
| 17 April | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 (0.0%) | 0.0E+00 |
| 1 May | 3.1E+06 (85.0%) | 5.5E+05 (15.0%) | 0.0E+00 (0.0%) | 1.7E+05 (4.73%) | 2.9E+06 (80.3%) | 5.5E+05 (80.3%) | 3.7E+06 |
| 17 May | 1.0E+06 (7.5%) | 2.3E+06 (16.7%) | 1.0E+07 (75.7%) | 1.5E+06 (10.8%) | 2.3E+06 (16.7%) | 1.0E+07 (72.5%) | 1.4E+07 |
| 29 May | 1.2E+06 (77.6%) | 0.0E+00 (0.0%) | 3.4E+05 (22.4%) | 1.2E+06 (77.6%) | 3.4E+05 (22.4%) | 0.0E+00 (0.0%) | 1.5E+06 |
| 5 June | - | - | - | 6.5E+04 (46.6%) | 7.5E+04 (53.4%) | 7.4E+01 (0.1%) | 1.4E+05 |
| Sum | 5.3E+06 (28%) | 2.8E+06 (15%) | 11.0E+06 (57%) | 2.9E+06 (15%) | 5.6E+06 (30%) | 11.0E+06 (56%) | |
| Mean (SE) | 1.3E+06 (3.2E+05) | 7.1E+05 (2.7E+05) | 2.7E+06 (1.3E+06) | 5.8E+05 (1.4E+05) | 1.1E+06 (2.8E+05) | 2.1E+06 (8.8E+05) | |

Table 2-6. Results from analysis of variance and Tukey-Kramer tests on abundances of striped bass early life stages ($\log_{10}$(total no + 1)) as a function of year and location with respect to the ETM or salt front. Locations are denoted as up-estuary (**u**; >5 km up-estuary of feature), within (**w**; ±5 km of feature), or down-estuary (**d**; >5 km down-estuary of feature).

| Parameter | Factor | p | Tukey-Kramer |
|---|---|---|---|
| Eggs | ETM Location | 0.58 | |
| | Year | 0.17 | |
| | ETM Location*Year | 0.66 | |
| | | | |
| Eggs | Salt Front Location | 0.39 | |
| | Year | 0.02 | 2007 > 2008 |
| | Salt Front Location*Year | 0.34 | |
| | | | |
| Yolk-Sac Larvae | ETM Location | 0.89 | |
| | Year | 0.58 | |
| | ETM Location*Year | 0.37 | |
| | | | |
| Yolk-Sac Larvae | Salt Front Location | 0.62 | |
| | Year | 0.32 | |
| | Salt Front Location*Year | 0.56 | |
| | | | |
| Feeding-Stage Larvae | ETM Location | 0.26 | |
| | Year | 0.36 | |
| | ETM Location*Year | 0.87 | |
| | | | |
| Feeding-Stage Larvae | Salt Front Location | 0.46 | |
| | Year | 0.66 | |
| | Salt Front Location*Year | 0.98 | |

Table 2-7. Percent overlap between striped bass feeding-stage larvae and and (A) *Bosmina longirostris* or (B) *Eurytemora affinis* for locations with respect to the ETM and salt front in 2007 and 2008.  Schoener (1970) index values.

23. *Bosmina longirostris*

| | ETM Location | | | Salt Front Location | | |
|---|---|---|---|---|---|---|
| | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary |
| 11 May 2007 | 56.36 | 90.03 | 93.83 | 80.63 | 75.72 | 83.86 |
| 22 May 2007 | 96.27 | 97.03 | 93.29 | 96.27 | 97.69 | 92.63 |
| 30 May 2007 | 77.63 | 93.77 | - | 96.45 | 92.99 | 81.96 |
| Mean | 76.65 | 93.61 | 93.56 | 91.12 | 88.80 | 86.15 |
| | | | | | | |
| 1 May 2008 | 73.82 | 73.43 | 100.00 | - | 73.82 | 73.43 |
| 17 May 2008 | 84.77 | 91.11 | 82.09 | 78.70 | 96.31 | 82.95 |
| 29 May 2008 | 80.11 | 87.63 | 66.59 | 67.74 | 71.33 | 95.25 |
| 5 June 2008 | - | - | - | 68.54 | 77.10 | 90.36 |
| Mean | 79.57 | 84.06 | 82.89 | 71.66 | 79.64 | 85.50 |

B. *Eurytemora affinis*

| | ETM Location | | | Salt Front Location | | |
|---|---|---|---|---|---|---|
| | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary |
| 11 May 2007 | 57.07 | 92.16 | 75.82 | 76.16 | 80.91 | 67.98 |
| 22 May 2007 | 95.32 | 99.06 | 94.34 | 95.32 | 99.38 | 94.02 |
| 30 May 2007 | 75.27 | 88.88 | - | 96.22 | 89.32 | 78.60 |
| Mean | 75.89 | 93.37 | 85.08 | 89.23 | 89.87 | 80.20 |
| | | | | | | |
| 1 May 2008 | 75.25 | 84.29 | 85.32 | - | 75.25 | 69.62 |
| 17 May 2008 | 93.36 | 95.68 | 87.23 | 91.10 | 96.22 | 88.96 |
| 29 May 2008 | 83.11 | 93.71 | 52.74 | 76.82 | 67.55 | 85.20 |
| 5 June 2008 | - | - | - | 80.43 | 76.85 | 84.38 |
| Mean | 83.91 | 91.23 | 75.10 | 82.78 | 79.00 | 82.04 |

Table 2-8. Results from analysis of variance and Tukey-Kramer tests on mean individual growth rates (mm d$^{-1}$) of upper Chesapeake Bay striped bass larvae in 2007 and 2008. Locations are denoted as up-estuary (**u**; >5 km up-estuary of feature), within (**w**; ±5 km of feature), or down-estuary (**d**; >5 km down-estuary of feature).

| Factor | SS | df | MS | F | P | Tukey-Kramer |
|---|---|---|---|---|---|---|
| Year | 0.036 | 1 | 0.036 | 6.61 | 0.0106 | 2007 > 2008 |
| ETM Location | 0.057 | 2 | 0.029 | 5.25 | 0.0057 | w; u > d |
| Year * ETM Location | 0.007 | 2 | 0.004 | 0.67 | 0.5101 | |
| | | | | | | |
| Year | 0.036 | 1 | 0.036 | 6.56 | 0.011 | 2007 > 2008 |
| Salt Front Location | 0.042 | 2 | 0.021 | 3.8 | 0.023 | w > d |
| Year * Salt Front Location | 0.008 | 2 | 0.004 | 0.74 | 0.476 | |

Table 2-9. Larval striped bass growth rates (mm d$^{-1}$) reported in literature.

| Growth Rates (mm d$^{-1}$) | Location | Source |
| --- | --- | --- |
| **0.06-0.48** | **Upper Chesapeake Bay** | **current study** |
| 0.19 | Upper Chesapeake Bay | Rutherford et al. 1997 |
| 0.21-0.32 | Upper Chesapeake Bay | Rutherford and Houde 1995 |
| 2001: 0.22; 2003: 0.28 | Upper Chesapeake Bay | Martino 2010 |
| 0.18-0.26 | Potomac River | Rutherford et al. 1997 |
| 0.11-0.53 | Potomac River | Rutherford and Houde 1995 |
| 0.15-0.22 | Patuxent River | Secor and Houde 1995 |
| 0.017-0.293 | Hudson River | Limburg et al. 1999 |
| 0.10-0.20 | Hudson River | Dey 1981 |
| 0.13-0.27 | San Francisco Estuary | Foss and Miller 2001 |
| 0.29-0.36 | Laboratory Study | Houde and Lubbers 1986 |
| 0.30-0.32 | Enclosure Study | Houde and Lubbers 1986 |
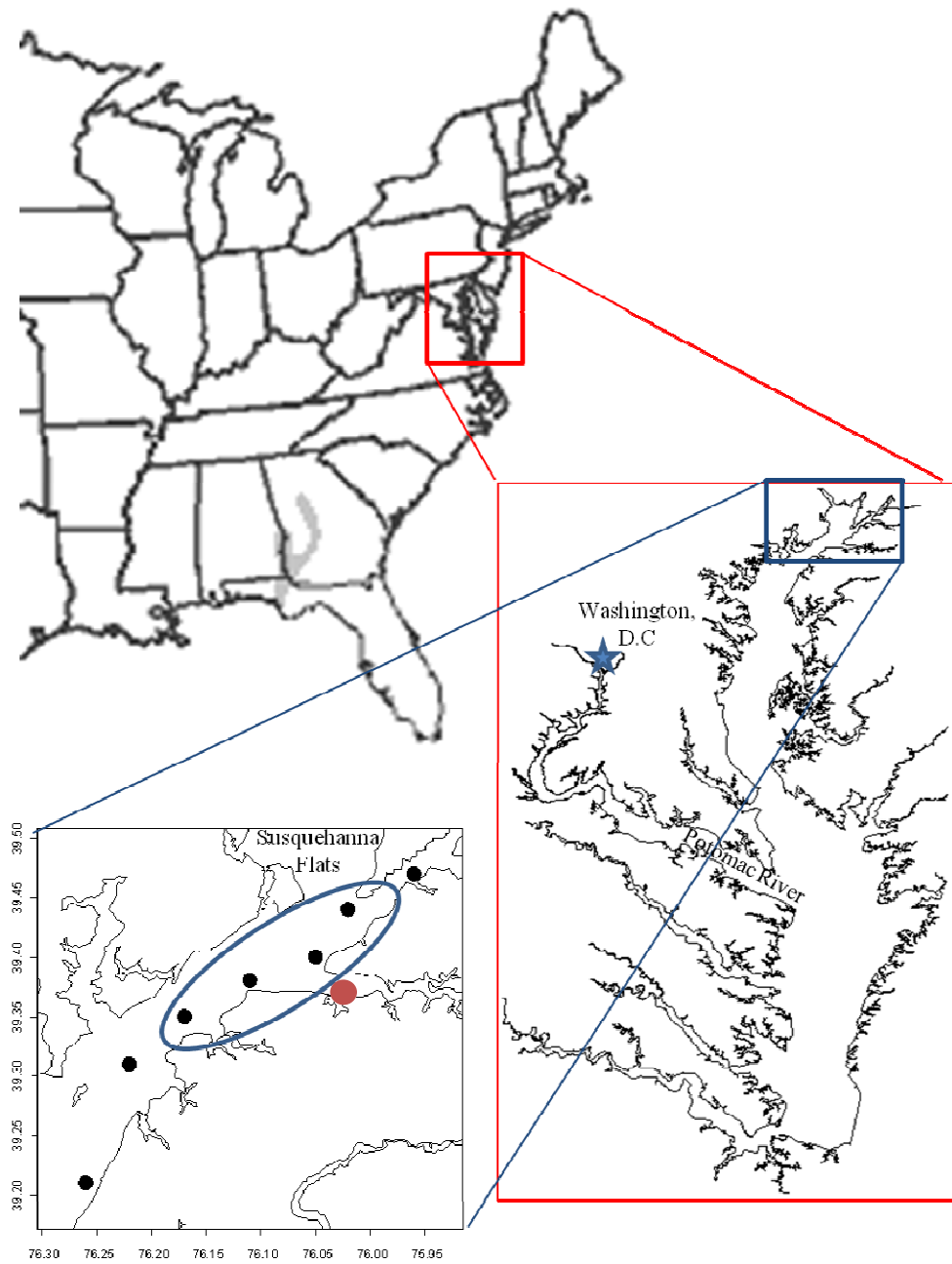
Figure 2-1. Locations of sampling stations in 2007 and 2008 ( ⬤ ). Water temperature

measurements were obtained from a Maryland Department of Natural Resources

monitoring station on the Sassafras River, Betterton, MD ( 🔴 ). Locations of the salt

front and ETM usually fall within the bounds of the blue oval.
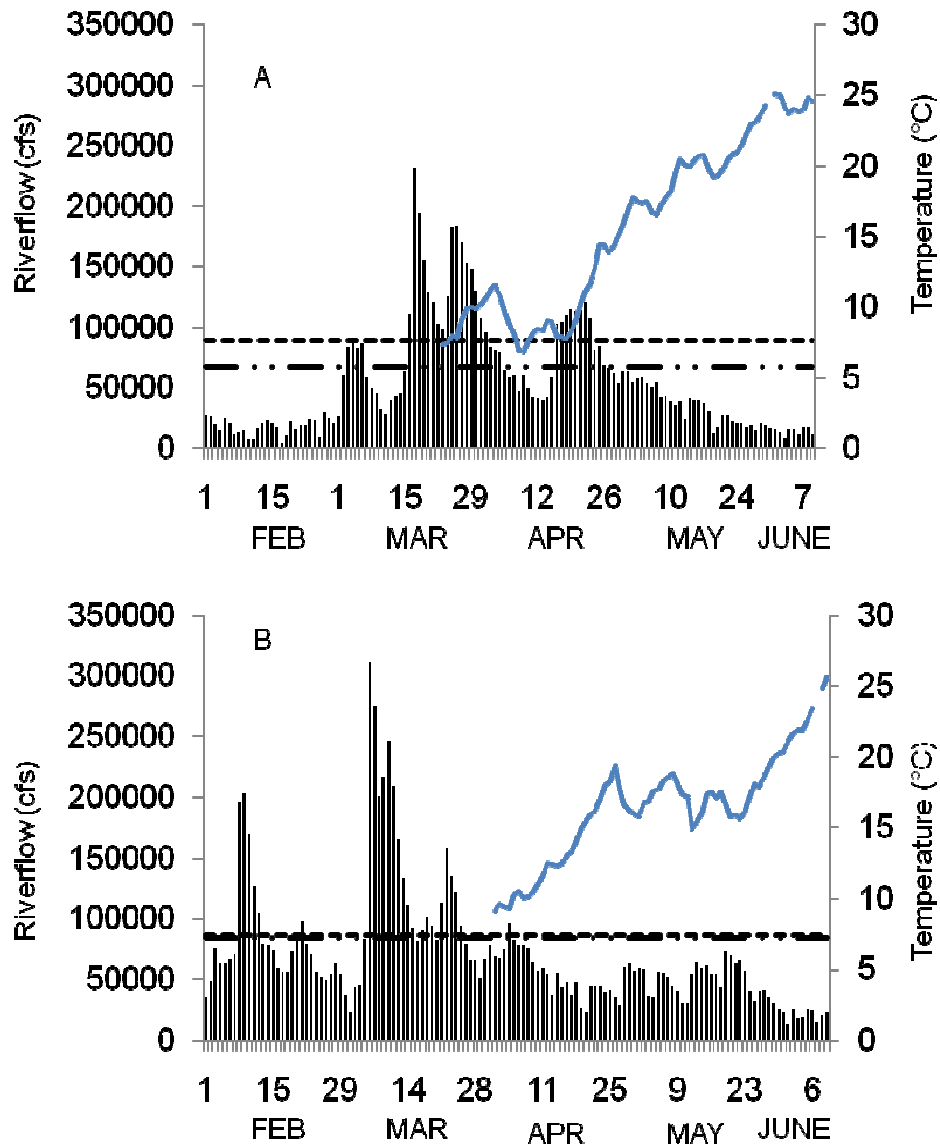
Figure 2-2. Hydrographic conditions in the upper Chesapeake Bay in (A) 2007 and (B) 2008. Mean daily river flow (cubic feet per second, cfs) (black bars) and mean winter-spring river flow for February-April (— · —) and March-April (- - - -) were obtained from a U.S. Geological Survey gauge at Conowingo, MD on the Susquehanna River. Temperature (——) data from the Maryland Department of Natural Resources monitoring station at Betterton, near the mouth of the Sassafrass River.
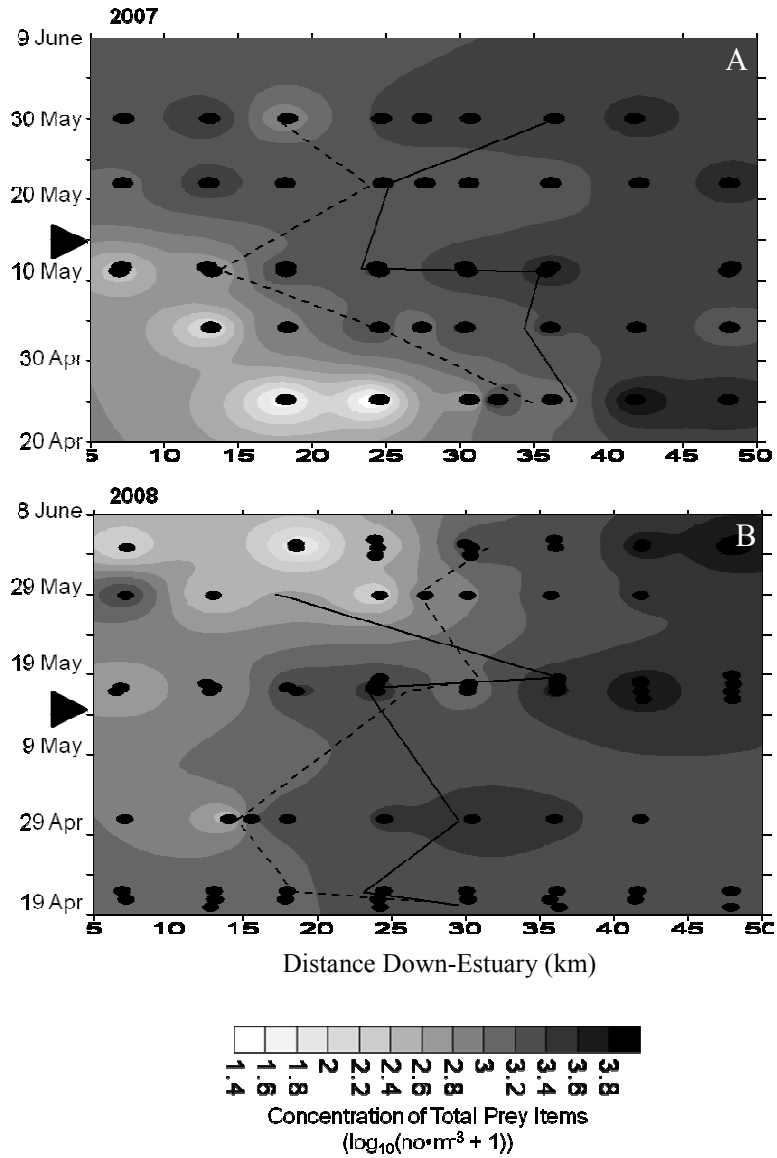
Figure 2-3. Concentration ($\log_{10}(\text{no} \cdot \text{m}^{-3} + 1)$) of total prey items (combined *Eurytemora affinis*, *Bosmina longirostris*, and *Acartia tonsa*) in the upper Bay over time as a function of distance down-estuary (km) in (A) 2007 and (B) 2008. Locations of the salt front (– – –) and ETM (——) are indicated. Black dots represent sampling locations and dates. May 15, the date separating early and late spring, is indicated (▶).

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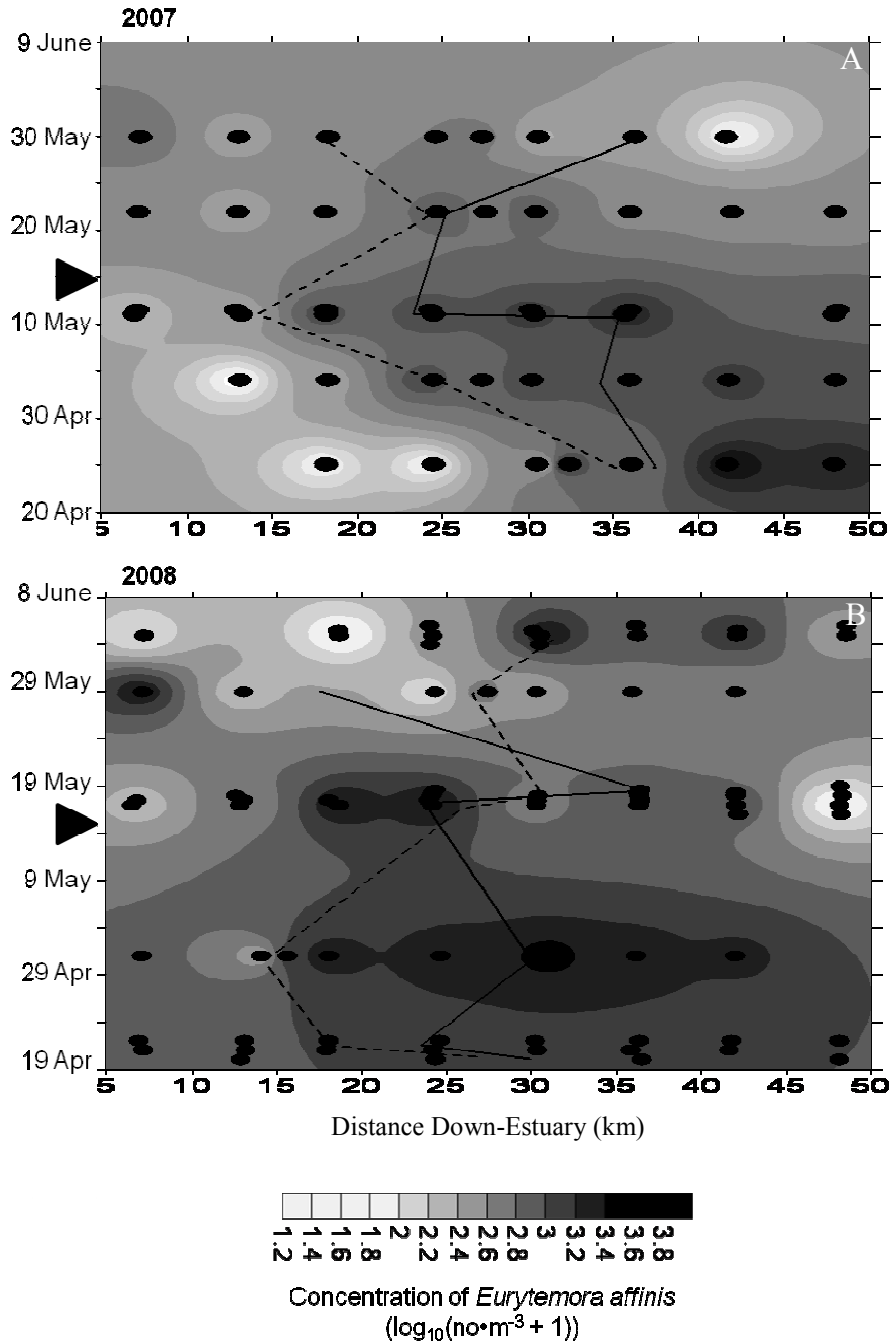
Figure 2-4. Concentration ($\log_{10}(\text{no} \cdot \text{m}^{-3} + 1)$) of *Eurytemora affinis* in the upper Bay over time as a function of distance down-estuary (km) in (A) 2007 and (B) 2008. Locations of the salt front (– – –) and ETM (——) are indicated. Black dots represent sampling locations and dates. May 15, the date separating early and late spring, is indicated (▶).
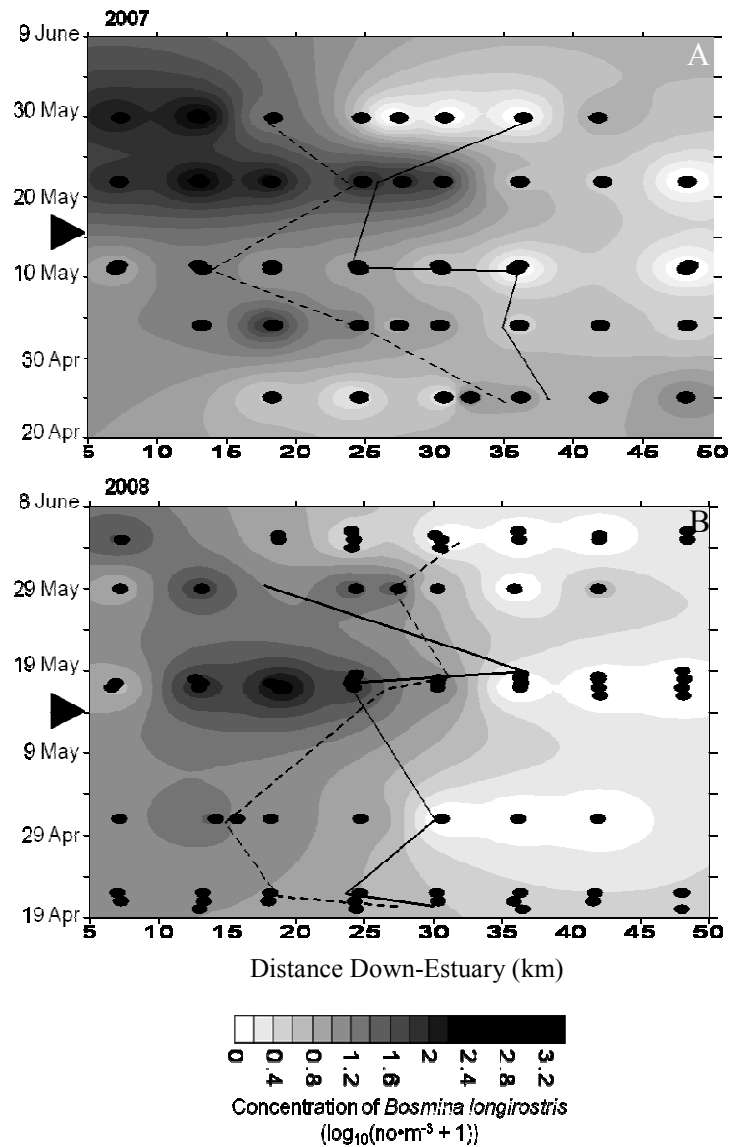
Figure 2-5. Concentration ($\log_{10}(\text{no}\bullet\text{m}^{-3} + 1)$) of *Bosmina longirostris* in the upper Bay over time as a function of distance down-estuary (km) in (A) 2007 and (B) 2008. Locations of the salt front (– – –) and ETM (——) are indicated. Black dots represent sampling locations and dates. May 15, the date separating early and late spring, is indicated ( ▶ ).
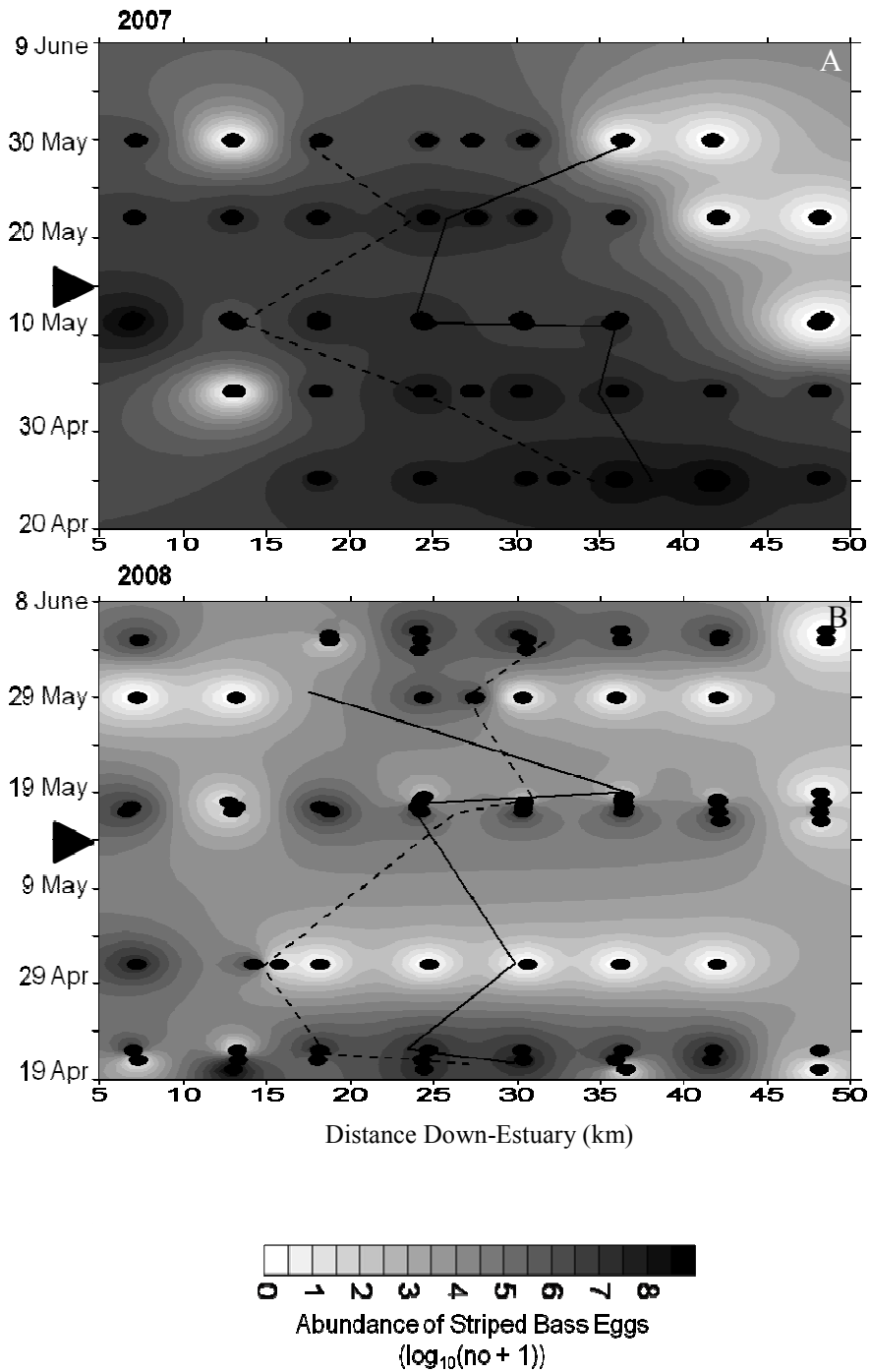
Figure 2-6. Abundance ($\log_{10}$(no + 1)) of striped bass eggs in the upper Bay over time as a function of distance down-estuary (km) in (A) 2007 and (B) 2008. Locations of the salt front (– – –) and ETM (———) are indicated. Black dots represent sampling locations and dates. May 15, which separates early and late spring, is indicated (▶).
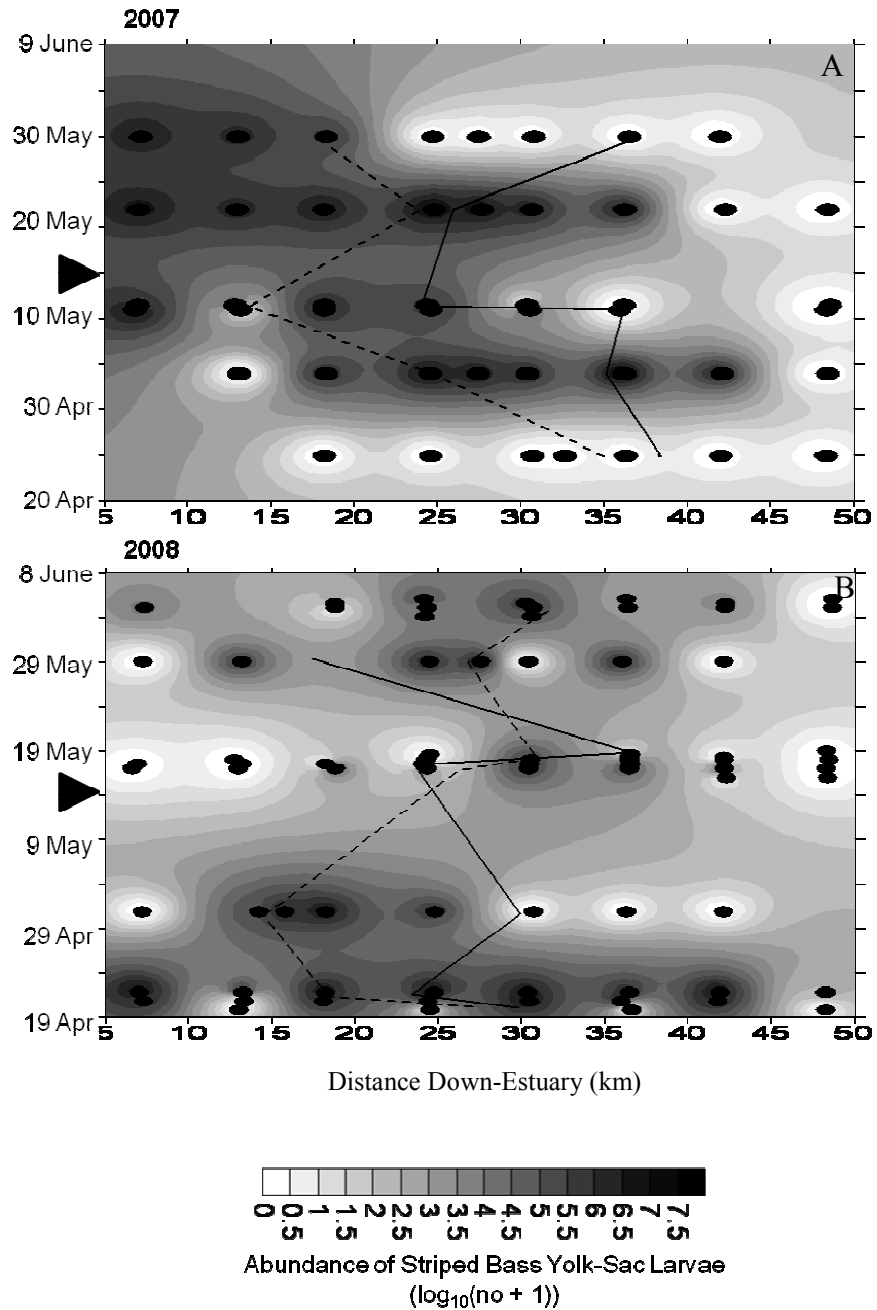
Figure 2-7. Abundance ($\log_{10}$(no + 1)) of striped bass yolk-sac larvae in the upper Bay

over time as a function of distance down-estuary (km) in (A) 2007 and (B) 2008.

Locations of the salt front (– – –) and ETM (——) are indicated. Black dots represent

sampling locations and dates. May 15, which separates early and late spring, is indicated

(▶).

Figure 2-8. Abundance ($\log_{10}(no + 1)$) of striped bass feeding-stage larvae in the upper

Bay over time as a function of distance down-estuary (km) in (A) 2007 and (B) 2008.

Locations of the salt front (– – –) and ETM (———) are indicated. Black dots represent

sampling locations and dates. May 15, which separates early and late spring, is indicated

(▶).
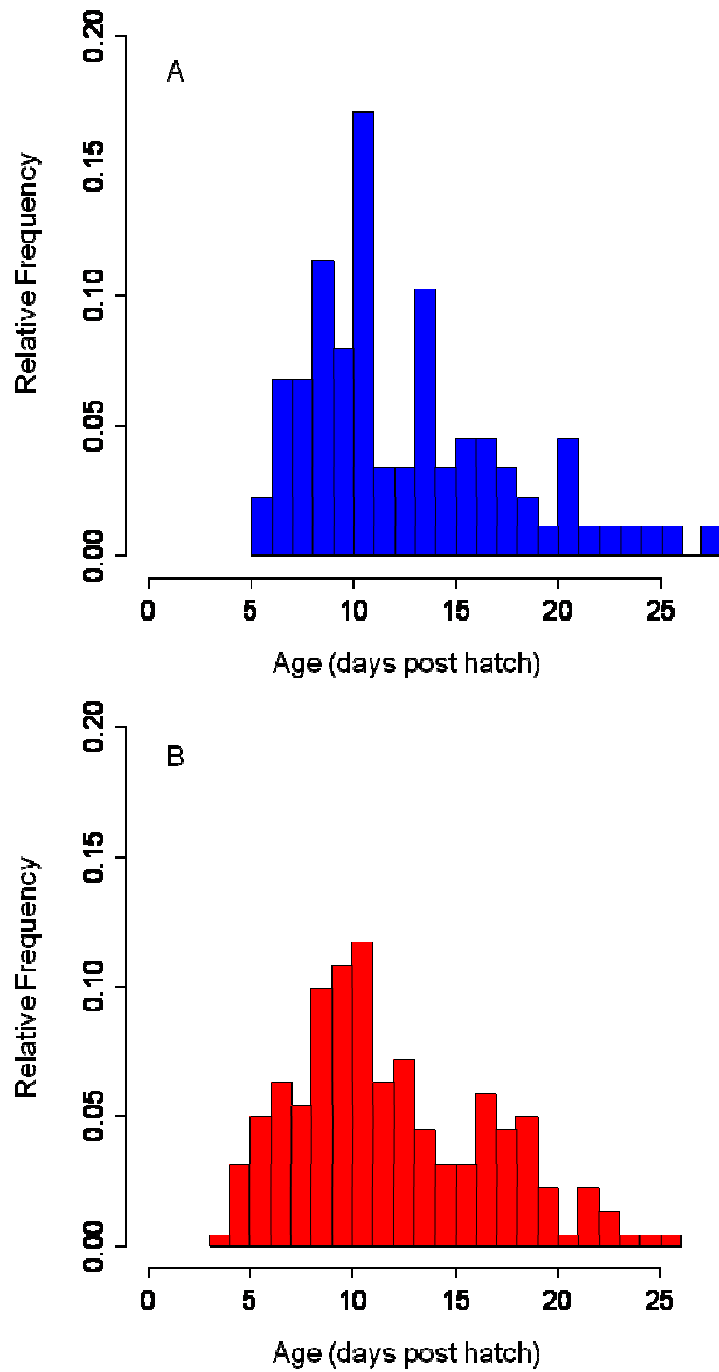
Figure 2-9. Relative age-frequency distributions of striped bass feeding-stage larvae in
(A) 2007 and (B) 2008.
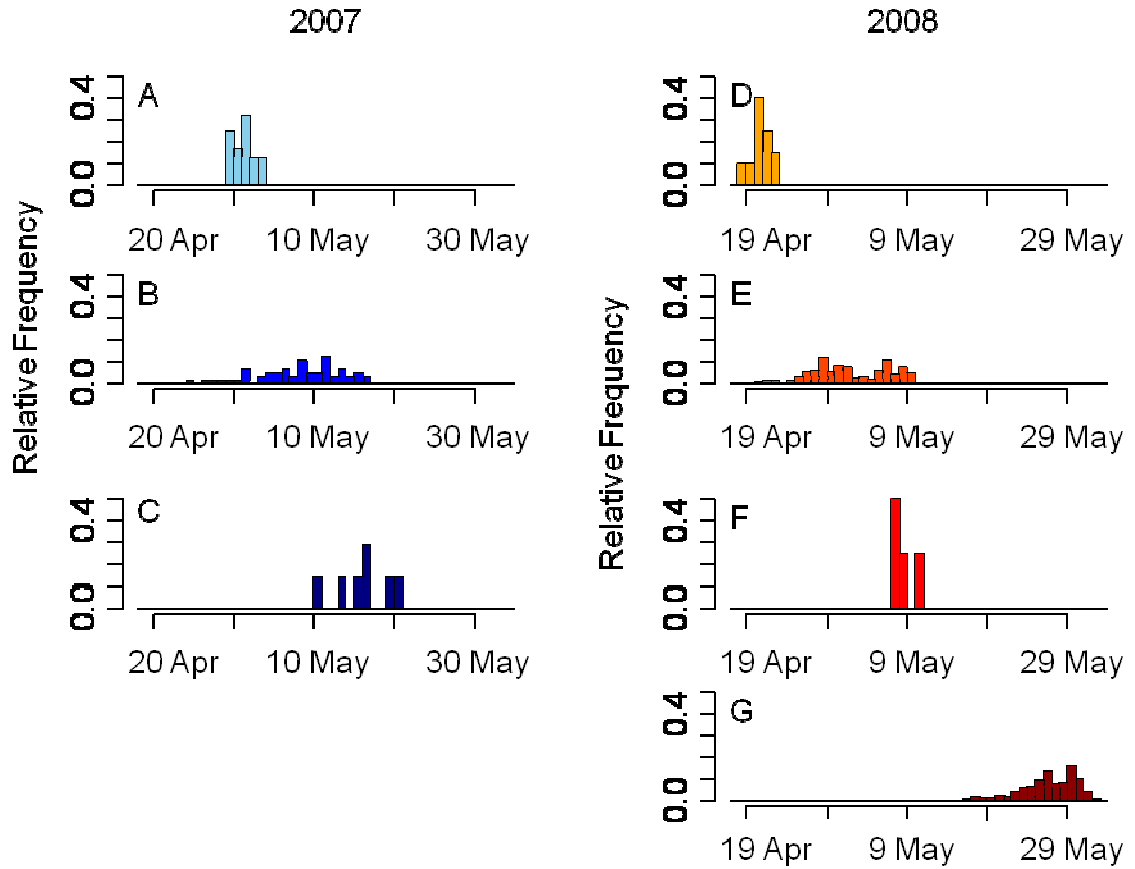
Figure 2-10. Relative hatch-date frequencies of striped bass larvae sampled on (A) 11 May 2007, (B) 22 May 2007, (C) 30 May 2007, (D) 1 May 2008, (E) 16-20 May 2008, (F) 29 May 2008, and (G) 5-6 June 2008.
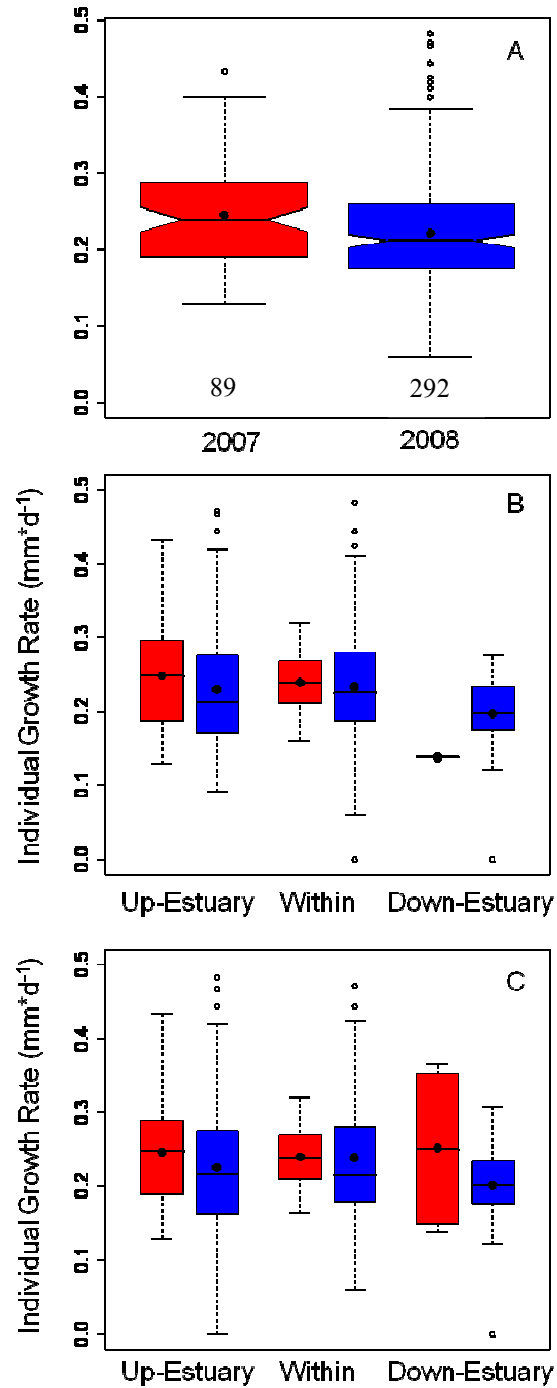
Figure 2-11. Individual growth rates (mm day$^{-1}$) of striped bass larvae (A) in 2007 and 2008, (B) with respect to the ETM in 2007 (red) and 2008 (blue), and (C) with respect to the salt front in 2007 (red) and 2008 (blue). Median (—) and mean (●) values indicated. The numbers of larvae successfully aged are given in plot A.
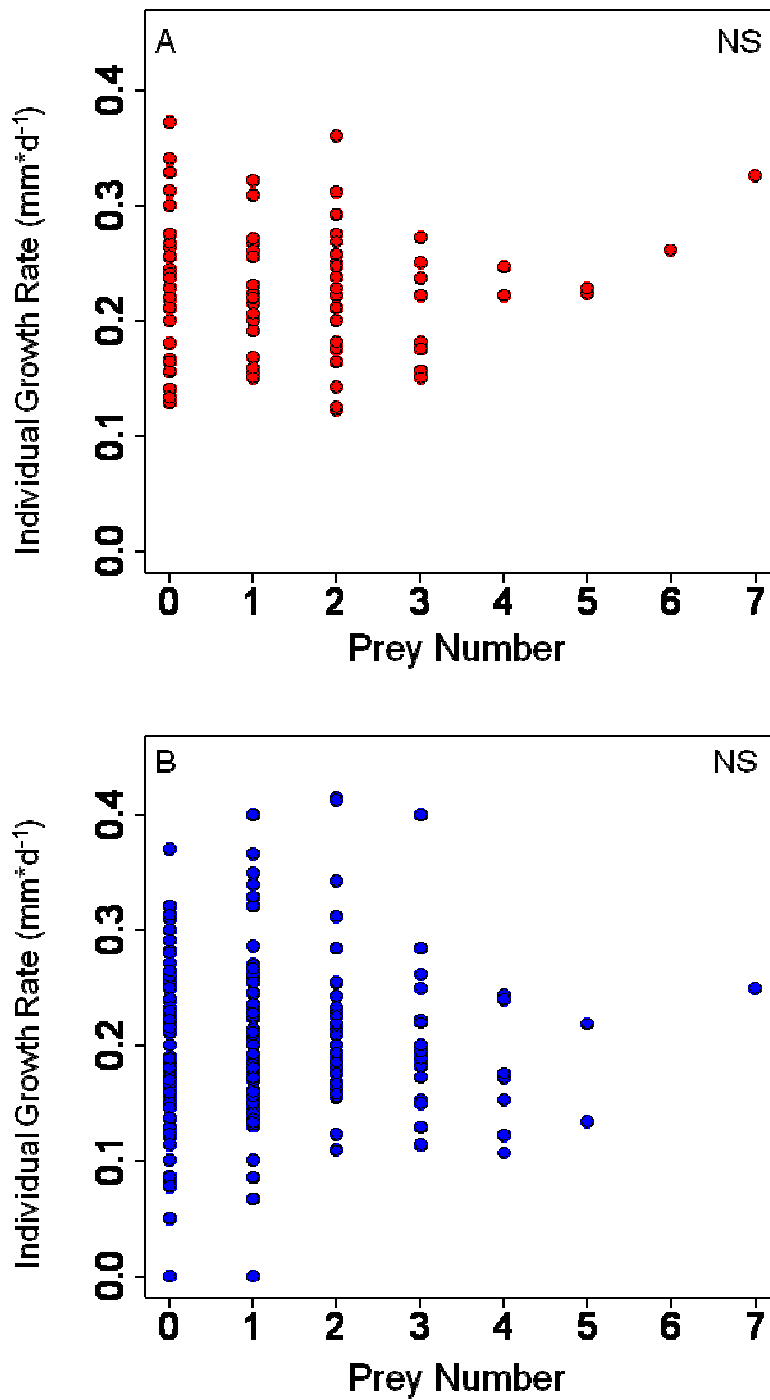
Figure 2-12. Relationship between number of prey in larval guts and individual growth rate (mm day^{-1}) for striped bass larvae collected in (A) 2007 and (B) 2008.

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**Chapter 3: Feeding, Sources of Nutrition, and Isotopic Composition of Early Life**

**Stages of Striped Bass (*Morone saxatilis*)**

**INTRODUCTION**

The anadromous striped bass (*Morone saxatilis*) spawns in the transition area between salt and fresh waters in Chesapeake Bay, where its larvae feed on zooplankton, including both marine and freshwater taxa (Martino and Houde 2010). Striped bass is abundant in the Bay, but experiences > 30-fold inter-annual variability in young-of-the-year recruitment success (http://dnr.maryland.gov/ fisheries/juvindex/). Historically, feeding success and trophodynamics have been hypothesized to be factors controlling survival of fish larvae (Hjort 1914; Cushing 1990), either by starvation or through variability in growth and larval stage duration (Anderson 1988; Houde 2009). In Chesapeake Bay, recruitment variability in striped bass has been associated with variability in nutritional-, physical-, and climate-related factors that act to control survival of early life stages (Uphoff 1989; Secor et al. 1995; Rutherford et al. 1997; North and Houde 2001, 2006; Martino and Houde 2010).

For striped bass, the nursery area and its properties are particularly important in controlling recruitment potential. Adult striped bass migrate to the freshwater or brackish reaches of the Chesapeake Bay in April and May to spawn (Dovel 1971). Semi-buoyant striped bass eggs and yolk-sac larvae are often retained in the region of the estuarine turbidity maximum (ETM) (North and Houde 2003, 2006; Martino and Houde 2010). The ETM is a common feature of many coastal plain estuaries that often is located near the salt front (the intersection of the 1 isohaline with the estuary floor) and is

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characterized by high turbidity and suspended sediment due to gravitational circulation and tidal resuspension (Roman et al. 2001; Sanford et al. 2001). The ETM and salt front regions are prime nursery habitats for striped bass larval stages because of elevated concentrations of zooplankton prey (Kimmerer et al. 1998; Boynton et al. 1997; Roman et al. 2001; Martino and Houde 2010), optimal salinity range (Winger and Lasier 1994; Doroshev 1970), and potentially reduced predation from visual predators.

The estuarine calaniod copepod *Eurytemora affinis* and the freshwater cladoceran *Bosmina longirostris* are common prey of striped bass larvae in the upper Chesapeake Bay (North and Houde 2006; Martino and Houde 2010), Patuxent River (Campfield and Houde 2011), and Hudson River (Limburg et al. 1997, 1999). Spatial and temporal differences in the abundance and distribution of *E. affinis* and *B. longirostris* could affect larval diet and nutrition. Peak concentrations of *E. affinis* generally occur in April, while a *B. longirostris* bloom begins in late April and early May and continues until early June (Kimmel and Roman 2004; Martino and Houde 2010; see Chapter 2 of this thesis). *Eurytemora affinis* occurs in high concentrations at the ETM and salt front of the upper Chesapeake Bay (Roman et al. 2001). In other estuaries such as the San Francisco Estuary it also occurs in low salinities (Kimmerer et al. 1998), but it can occur in more saline waters (Devreker et al. 2008). Peak concentrations of *B. longirostris* occur up-estuary of the salt front and ETM (North and Houde 2003; Martino and Houde 2010; see Chapter 2 of this thesis).

An important objective in understanding trophodynamics in ETM regions of estuaries is to determine the relative importance of marine and terrestrial carbon in the support of primary and secondary consumers, i.e., zooplankton and fish larvae,

respectively. Research on high-turbidity estuaries has produced contrasting results regarding the importance of marine or terrestrial support of production. For example, in the maximum turbidity zone of the Gironde Estuary, France, a high zooplankton biomass is present despite low concentrations of phytoplankton, suggesting that contributions of terrestrial particulate organic matter delivered to the MTZ (= ETM) are important to support nutrition of lower trophic levels in the absence of *in situ* carbon production (David et al. 2006). In contrast, in the St. Lawrence River ETM, an inverse relationship between chlorophyll and zooplankton biomass suggests that phytoplankton produced *in situ* or advected to the ETM zone from upstream locations was depleted from consumption by zooplankton (Winkler et al. 2003). In the upper Chesapeake Bay, primary production was found to be low within the ETM (Houde et al. 2009). The importance of different carbon sources in the upper region of estuaries may vary spatially and inter-annually, primarily due to variability in levels of freshwater inputs. In the ETM of the San Francisco Bay Estuary, low freshwater flow was associated with low levels of chlorophyll and bacteria, while high freshwater flow was associated with the opposite (Hollibaugh and Wong 1999). Additionally, these authors reported that phytoplankton was more important to primary consumers up-estuary of the ETM than in the ETM where detrital organic matter was more important.

Stable isotope analysis of carbon and nitrogen, based on the fractionation between heavy ($^{13}$C and $^{15}$N) and light ($^{12}$C and $^{14}$N) isotopes, can be effectively used in ecological research to investigate nutritional sources and processes (Peterson and Fry 1987). Carbon isotope values fractionate little between a consumer and its prey (DeNiro and Epstein 1981; Fry and Sherr 1984; Minagawa and Wada 1984; Herzka and Holt 2000; Post 2002)

and can therefore be useful indicators of the source of carbon in diets. For example, it has been demonstrated that pelagic carbon sources have more negative $\delta^{13}$C values than benthic carbon sources, which is valuable in settlement research on transforming reef fish larvae that are transitioning from a pelagic to a benthic diet (Herzka and Holt 2000; Tanaka et al. 2008). Regional evaluation of $\delta^{13}$C in organisms can also be used to differentiate between marine and terrestrial nutritional sources because $\delta^{13}$C of terrestrial carbon is considerably more negative than marine carbon (Peterson and Fry 1987; Wainright et al. 1996; Boynton et al. 1997). Nitrogen isotopes serve as an indicator of trophic level because predators become enriched in $^{15}$N, with each increase in trophic level contributing a 3 – 5‰ increase in $\delta^{15}$N (Peterson and Fry 1987; Vander Zanden and Rasmussen 2001; Post 2002).

In my research, a comparative analysis of prey from stomach analysis and carbon and nitrogen stable isotopes of organisms in the ETM region was conducted to address questions of food sources and trophic pathways that support striped bass early life stages. If terrestrial carbon is important to primary and secondary consumers, i.e., zooplankton and striped bass larvae, variability in its availability and consumption could contribute to inter-annual and spatial variability in growth and survival of the larvae. Temporal-spatial differences in nitrogen stable isotope signatures of striped bass larvae may reveal differences in availability of types of dominant prey resources to larvae.

A combined carbon and nitrogen isotope analysis can supplement traditional gut contents analysis. Gut contents analysis provides an assessment of the number and types of prey taxa present in guts at capture, and serves as an indicator of successful feeding. Larvae that feed successfully are likely to have higher growth rates and possibly higher

recruitment potential (Hjort 1914; Anderson 1988; Houde 1989, 2009; Cushing 1990).

However, gut contents analysis is a snapshot of recent feeding and does not account for

long-term trends in fish diet; it may under-represent important, easily-digested prey

items, while over-estimating the importance of prey items with longer digestion times

(Hyslop 1980). In stable isotope analysis, all digested material is incorporated into the

tissue of the predator, allowing application of isotope mixing models to determine the

relative importance of different prey (Phillips and Gregg 2001).

The goal of my thesis research was to evaluate feeding and explain nutritional

sources and trophic pathways that support growth of striped bass larvae. I conducted a

gut contents analysis to determine spatial and inter-annual variability in feeding by

striped bass feeding-stage larvae from the upper Chesapeake Bay in 2007 and 2008. I

then analyzed $\delta^{13}C$ and $\delta^{15}N$ of striped bass yolk-sac and feeding-stage larvae and

zooplankton prey. I also quantified C:N as a proxy for lipid content to determine if there

might be  differences in nutritional condition of striped bass larvae and their prey in 2007

and 2008. Finally, I compared stable isotope values of feeding-stage larvae from 2007

and 2008, years of near-average and poor recruitment, respectively, with stable isotope

values of archived larvae collected in 1998 and 2003, years of relatively high and high

recruitment, respectively, to evaluate possible differences in nutrition that may have

contributed to recruitment variability.

## METHODS

### *Research Cruises and Sampling*

Surveys were conducted along a 40-km transect in the upper Chesapeake Bay, extending from just up-bay of the Bay Bridge to the Elk River, a region that encompasses the salt front and ETM (Figure 3-1). Depths in this area ranged from 7 to 24 m. Several research vessels and samplers were used to collect ichthyoplankton (Table 3-1). Surveys on the 44-m RV *Hugh R. Sharp* were conducted in April and May of 2007 and 2008. Four surveys in 2007 and two in 2008 were conducted on the 7.6-m RV *Terrapin*; these "rapid-response" surveys followed periods of high freshwater flow to the upper Bay. In 2008, a single survey was conducted on the 20-m RV *Aquarius* from 4 – 6 June. During all cruises, CTD deployments were made at 5-10 km intervals along the Bay channel to obtain depth profiles of salinity, temperature, turbidity, fluorescence, irradiance, and dissolved oxygen. The CTD data were examined to define the location of the ETM and salt front and to select stations for zooplankton and ichthyoplankton sampling that were up-estuary, within, and down-estuary of these features.

Striped bass larvae that had been collected in the upper Bay study region in 1998 and 2003 were available to supplement my stable isotope analyses. Archived larvae and data from the 1998 and 2003 cruises had been used in previous research on larval striped bass distribution, feeding, and growth rates (North and Houde 2001, 2003, 2006; Martino 2008; Martino and Houde 2010).

On RV *Hugh R. Sharp* cruises, ichthyoplankton and zooplankton were collected in tows of an opening-closing, 1-m$^2$ Tucker Trawl with 280-μm meshes and flow meters (Table 3-1). At each station, 4-min deployments were divided into two depth zones (2 min per depth zone), bottom to mid-depth and mid-depth to surface. A mean of 175.78 (± 4.94 se) m$^3$ of water was filtered at each depth. Samples were preserved in ethanol. In

2008, some ichthyoplankton samples also were collected in a 1/4-m$^2$ mouth-opening, multiple opening closing net and environmental sampling system (MOCNESS) equipped with one 333-μm mesh net and four 200-μm mesh nets.  The 333-um mesh net that was towed obliquely over the entire water column provided samples for ichthyoplankton analysis that were preserved in ethanol. The 333-μm mesh MOCNESS net filtered a mean of 110.96 (± 15.65 se) m$^3$.

"Rapid-response" surveys were conducted on the RV *Terrapin* in April and May 2007 and May 2008 to survey hydrographic conditions and ichthyoplankton occurrences with respect to precipitation events (Table 3-1) (Jahn 2010). Paired 60-cm diameter bongo nets with 280-μm meshes and flow meters were deployed in 5-min oblique tows to sample the water column.  Mean volume filtered per net was 66.95 (± 1.62 se) m$^3$. Samples from one of the paired-net tows were preserved in ethanol for stable isotope analysis on zooplankton and striped bass larvae.  Samples from the second net were fixed and preserved in 5% formalin for analysis of striped bass eggs and spawning in a related project (Jahn 2010).

The single research cruise on the 20-m RV *Aquarius* was conducted late in the spawning season in 2008 (Table 3-1) to attempt to sample later-stage striped bass larvae. Depth-stratified ichthyoplankton samples were collected in two gears: a 1-m$^2$ opening-closing Tucker Trawl with 280-μm meshes and a 2-m$^2$ opening-closing Tucker Trawl with 707-μm meshes (mean ± se volume filtered per net: 254.21 ± 21.52 m$^3$). Nets were equipped with flow meters. In each deployment, tows were from bottom to mid-depth and from mid-depth to the surface (2 min per depth zone). Samples were preserved in ethanol.

For each cruise, the locations of the ETM and salt front were defined by inspection of contour-plotted depth profiles of turbidity and salinity (Golden Software, SURFER v7.0) in the upper Bay. The site of maximum concentration of total suspended solids was designated as the center of the ETM. The salt front was defined as the intersection of the 1 isohaline with the estuary bottom. Based on locations of these features, sampling sites were classified as up-estuary (> 5 km up-estuary of feature), within (within ± 5 km of feature), or down-estuary (> 5 km down-estuary of feature).

### Laboratory Procedures

*Striped Bass Larvae*

Striped bass larvae were removed from ichthyoplankton samples. Total lengths (TL) of yolk-sac and feeding-stage larvae were measured under a stereomicroscope with an ocular micrometer. Samples or subsamples of feeding-stage larvae were dissected for gut contents analysis. For samples with large numbers of larvae, subsamples were taken to insure that 3-5 larvae from available length classes were included; length classes were designated in 0.5-mm increments for larvae < 8 mm TL and 1-mm increments for larvae > 8 mm TL. A total of 564 larvae from surveys in 2007 and 2008 were dissected for gut contents analysis.

The entire digestive tract was removed for analysis. All prey items were identified to the lowest taxonomic level feasible and, when intact, were measured under a microscope with an ocular micrometer. Gut contents analysis was quantified using three metrics: 1) feeding incidence ($F_i$, the proportion of larvae with food in their guts), 2) the number of prey items in guts (referred to as feeding success), and 3) percent prey

composition ($C_i$, as the number of prey type $i$ divided by the total number of prey items present). Strauss' Index (L), a measure of prey selection, was calculated as:

$$L = r_i - P_i$$

where $r_i$ and $P_i$ are the proportions by number of prey type $i$ in the diet and in the environment, respectively (Strauss 1979). $P_i$ was calculated from estimates of zooplankton concentrations (see Chapter 2). Values of L can range from -1 to +1, with negative values indicating prey avoidance and positive values indicating selection for a prey item. Student's t-tests, as recommended by Strauss (1979, 1982), were applied to determine if avoidance or selection was significant.

*Stable Isotopes: Sample Preparation, Zooplankton*

Individuals of the copepod *E. affinis* and the cladoceran *B. longirostris* (known to be key prey for larval striped bass) were obtained from the Tucker Trawl and bongo net samples. For the stable isotope analysis, samples of ~200 *E. affinis* and ~700 *B. longirostris* were rinsed onto ashed (400$^{\circ}$F for 1 hour) GF/F filters and freeze-dried in a Labconco Freezone2.5 freeze-drier for a minimum of 24 h. Due to presence of inorganic carbon in the exoskeletons of zooplankton (Carabel et al. 2006), a subset of samples of both species was acidified prior to analysis for carbon stable isotope values by rinsing each sample with 1M HCl, followed by rinsing with deionized water, and then freeze-drying for 24 h. Dried samples were weighed and encapsulated in tin capsules.

*Stable Isotopes: Sample Preparation, Striped Bass Larvae*

Ethanol-preserved yolk-sac and feeding-stage larvae were measured for total length under a microscope with an ocular micrometer prior to additional body measurements and dissection for gut contents (this chapter) and otolith-based aging analysis (Chapter 2). Striped bass feeding-stage larvae from archived 1998 and 2003 samples were included in my stable isotope analysis to expand the analyses and compare larval stable isotope signatures during favorable (2003), moderate (1998, 2007) and poor (2008) recruitment years. Gut tracts were removed from all striped bass larvae to insure that only prey assimilated into larval tissue was included in the larval stable isotope signature. Stable isotope analysis of striped bass eggs was not conducted due to the poor condition of eggs after collection. Isotope signatures of newly-hatched yolk-sac larvae were presumed to be similar to eggs.

Prepared larvae were rinsed, dried for 24 h in a Labconco Freezone2.5 freeze-drier, weighed, and encapsulated in tin capsules. To achieve a minimum weight of 0.1 mg, it was necessary to pool from 2-4 larvae of similar size for stable isotope analysis as necessary. Additionally, when larvae were pooled an effort was made to include larvae with similar types and number of prey in their guts.

*Stable Isotope and C:N Analyses*

All stable isotope samples were submitted to the University of California Davis Stable Isotope Facility where they were analyzed on a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope-ratio mass spectrometer. Isotope values are expressed in the δ notation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X = $\delta^{13}$C or $\delta^{15}$N and R = ratio of the heavy isotope ($\delta^{13}$C or $\delta^{15}$N) to the light

isotope ($\delta^{12}$C or $\delta^{14}$N). Standards were Pee Dee limestone and atmospheric nitrogen gas

for carbon and nitrogen analyses, respectively (Peterson and Fry 1987).

The effect of the acidification of zooplankton on nitrogen isotope values is

debated (Bunn et al. 1995; Pinnegar and Polunin 1999). To determine if samples for $\delta^{15}$N

must be analyzed separately from those for $\delta^{13}$C, a preliminary analysis of un-acidified

nitrogen samples was compared to acidified samples. As expected, in this comparison

acid-rinsed samples had significantly lower $\delta^{13}$C values than samples rinsed only with

deionized water. *Bosmina longirostris* $\delta^{15}$N values did not differ between preparation

methods (Students t-test), but acid-rinsed samples of *E. affinis* had slightly, but

significantly, lower $\delta^{15}$N values compared to non-acid-rinsed samples (11.64‰ and

11.71‰, respectively).  Because of these differences, $\delta^{13}$C values of acid-rinsed samples

and $\delta^{15}$N values of non-acid-rinsed samples were used in all statistical analyses.

Amounts of carbon and nitrogen in zooplankton and striped bass larvae were

obtained during the stable isotope mass spectroscopy analysis and were converted to

molar C:N ratios. C:N ratios, which serve as a proxy for lipid concentrations

(McConnaughey and McRoy 1979; Sweeting et al. 2006; Post et al. 2007), were

compared among years and locations for striped bass larvae and their prey to test for

possible differences in nutritional condition.  All taxa analyzed had high C:N ratios,

necessitating a correction for lipid content.  I used the recent equation of Post et al.

(2007) to make this correction, which provided a good fit to my lipid data:

$$\delta^{13}C' = \delta^{13}C - 3.32 + 0.99 * C{:}N$$

Lipid corrections resulted in enrichment of $\delta^{13}$C for zooplankton and striped bass larvae.

*Statistical analysis*

Possible inter-annual and location differences in prey incidence were evaluated in a multiple comparisons test for proportions (Zar 1999). Anticipating a probable relationship between striped bass larval size and prey number (Martino 2008), larvae for gut content analysis were separated into three length classes: < 6 mm, 6 – 8 mm, and > 8 mm TL. Analysis of variance (ANOVA) was used to test for inter-annual differences in mean $\log_{10}$-transformed number of prey per larval gut using length category and year as factors. Within each year, ANOVA was run to evaluate possible location differences in mean $\log_{10}$-transformed number of prey per larval gut, with location designated as ETM or salt front and length category as factors. A chi-square test of independence was applied to determine if there were inter-annual or location differences in the proportion of designated prey taxa (*Eurytemora affinis*, *Bosmina longirostris*, and other) consumed.

Stable isotope values were normally distributed in 2007, but not in 2008. However, parametric testing of stable isotope values was conducted because of precedent set by previous studies and because of the robust nature of analysis of variance. Student's t-tests were run to determine if there were between-year differences in mean stable isotope values of zooplankton and yolk-sac larvae and in lipid content of zooplankton and larvae. Within each year, analysis of variance (ANOVA) was applied to test for differences in mean values of stable isotopes and lipid levels with respect to locations of the salt front and ETM, followed by a Tukey's HSD test.

When there was a significant regression relationship between stable isotope values and lengths of feeding-stage larvae, analysis of covariance was run, with length as

covariate,  to determine if there were inter-annual and location (separately for each year) differences in stable isotope values, while accounting for potential effects of ontogeny and growth. In cases where there was no relationship between stable isotope value and larval length, a Student's t-test and ANOVA were used to determine inter-annual and location differences, respectively, in isotope values.

A Student's t-test was applied to determine if mean stable isotope values differed due to the presence/absence of prey in larval guts in each year. A Spearman's rank correlation test was applied to determine if stable isotope values were correlated with 1) the number of prey per larval gut, 2) the percent composition by number of *E. affinis* and *B. longirostris* in larval guts, and 3) growth rates of larvae (Chapter 2).

To investigate for a possible relationship between juvenile index values for YOY striped bass and $\delta^{15}N$ and $\delta^{13}C$ stable isotope values of feeding-stage larvae in 1998, 2003, 2007, and 2008, a regression analysis was conducted. The geometric means of the juvenile index values of abundance for YOY striped bass in September in the upper Chesapeake Bay were obtained from the Maryland Department of Natural Resources (http://dnr.maryland.gov/ fisheries/ juvindex/).

### RESULTS

*Diet: gut contents analysis*

The incidence of prey in guts of feeding-stage striped bass larvae was similar in 2007 and 2008, with 62.6% and 63.5% containing prey, respectively.  There were no significant differences in feeding incidence among locations with respect to the ETM in either year.  In 2007, no feeding-stage larvae were collected down-estuary of the ETM and highest prey incidence occurred within the ETM (68%) and salt front (66%) (Figure

3-2). In 2008, the lowest prey incidence (45%) occurred at locations up-estuary of the ETM (Figure 3-2). Location with respect to the salt front significantly affected prey incidence in both years. In 2007, prey incidence was similar up-estuary and within the salt front but was significantly lower down-estuary of the salt front. In 2008, prey incidence was significantly lower ($p < 0.05$) within the salt front than up-estuary of the salt front (Figure 3-2).

The level (success) of feeding increased as a function of larval length in 2007 and 2008. Mean prey per gut increased from < 0.5 prey to > 2 prey as larvae grew from approximately 4 to 10 mm (Figure 3-3). Results from the two-way ANOVA indicated that the mean number or prey per gut did not differ inter-annually (Table 3-2A). In 2007, the level of feeding did not differ by location with respect to the salt front or ETM (Table 3-2B). In 2008, the level of feeding did not differ by location with respect to the ETM, but larvae up-estuary of the salt front had significantly higher feeding success than larvae within the salt front (Table 3-2B). There were no significant interactions between larval size and capture location with respect to feeding success.

The estuarine copepod *Eurytemora affinis* and the freshwater cladoceran *Bosmina longirostris* were dominant prey for striped bass larvae. Other prey, including *Acartia* sp., detritus, unattached copepod eggs, and unidentifiable material, comprised relatively small percentages of the larval diet. *Eurytemora affinis* was a major diet constituent, comprising at least 50% of larval diets in both years and in all locations with respect to the salt-front or ETM (Figure 3-4). Results of a Chi-square analysis indicated that percent composition varied inter-annually ($X^2 = 86.54$, p<0.001). The difference was mainly attributed to shifting importance of *B. longirostris* in larval diets. In 2007, *B.*

*longirostris* comprised 32% of prey consumed, but in 2008 only 5% of the larval diet was *B. longirostris* (Figure 3-4A). Percent composition also varied spatially with respect to the ETM and salt front locations in both years (2007: ETM: $X^2 = 6.65$, *p*=0.04; Salt Front: $X^2 = 6.10$, *p*=0.05; 2008: ETM: $X^2 = 30.05$, *p*<0.001; Salt Front: $X^2 = 17.09$, *p*=0.002). In 2007, larvae up-estuary of the salt front and ETM had the highest reliance on *B. longirostris* (35%), compared to only 19% within the ETM or salt front (Figures 3-4B,C). In 2008, larvae within the ETM contained the largest percentage of *B. longirostris* (Figure 3-4D). Larvae up-estuary from the salt front in 2008 had a slightly higher percentage *B. longirostris* in the diet than larvae within the salt front (Figure 3-4E).

The importance of *E. affinis* and *B. longirostris* in diets of striped bass larvae, based on percent composition by number, was clear but Strauss' selectivity index did not indicate a consistent propensity for selection or avoidance of these prey across locations in either year. In 2007, *E. affinis* was positively selected throughout the study region (Table 3-3). However, in 2008, larvae did not positively select *E. affinis* up-estuary of the ETM or within the salt front (Table 3-3). In 2007, there was negative preference for *B. longirostris* by striped bass larvae throughout the study region (Table 3-3) despite its rather common occurrence in diets. In 2008, larvae neither selected nor avoided *B. longirostris* (Table 3-3).

***Stable isotope analysis of zooplankton and striped bass larvae***

*Zooplankton*

The estuarine copepod *Eurytemora affinis* and the freshwater cladoceran *Bosmina longirostris* had distinctive stable isotope compositions. Mean values of $\delta^{13}C$ and $\delta^{15}N$ were depleted in *B. longirostris* relative to *E. affinis* (Figure 3-5).

*Eurytemora affinis*

There were no between-year differences in $\delta^{13}C$ values, but between-year differences in $\delta^{15}N$ were significant (Table 3-4). *Eurytemora affinis* was enriched in $\delta^{15}N$ in 2007 relative to 2008 (Table 3-4; Figure 3-5). There was spatial variation in $\delta^{13}C$ values of *E. affinis* in each year. In 2007, $\delta^{13}C$ in *E. affinis* up-estuary of the ETM was significantly depleted compared to *E. affinis* within and down-estuary of the ETM (Table 3-5; Figure 3-6A). With respect to the salt front, *E. affinis* down-estuary was significantly enriched in $^{13}C$ by 3.76‰ in 2007 (Table 3-5; Figure 3-6B). In 2008, *E. affinis* did not differ in $\delta^{13}C$ with respect to the ETM location (Figure 3-7A). In 2008, *E. affinis* $\delta^{13}C$ values were similar up-estuary and within the salt front but $\delta^{13}C$ was enriched in *E. affinis* down-estuary of the salt front, although to a lesser extent than in 2007 (Table 3-5; Figure 3-7B).

Spatial variability in $\delta^{15}N$ of *E. affinis* also was detected. In both years, *E. affinis* up-estuary of the salt front and ETM had the highest observed values of $\delta^{15}N$ (Table 3-6; Figures 3-6, 3-7). The result was significant for *E. affinis* collected up-estuary of the salt front in 2007, where it was enriched by > 2‰ over *E. affinis* within or down-estuary of the salt front. In 2008, *E. affinis* collected up-estuary and within the ETM had similar values of $\delta^{15}N$ but this isotope value was significantly elevated in $\delta^{15}N$ compared to *E. affinis* down-estuary (Table 3-6; Figure 3-7A).

*Bosmina longirostris*

There were significant inter-annual differences in isotopic composition of *Bosmina longirostris*. In 2007, mean $\delta^{13}$C and $\delta^{15}$N values were significantly enriched relative to values in 2008 by 1.29‰ and 1.62‰, respectively (Table 3-4; Figure 3-5).

Spatially, *B. longirostris* was not present in sufficient numbers down-estuary of the salt front or ETM in either year to yield sufficient material for stable isotope analysis. *Bosmina* collected up-estuary and within the salt front and ETM had very similar isotope values, especially in $\delta^{13}$C. The small sample sizes for *Bosmina* collected within and up-estuary of the features in both years precluded statistical analysis of stable isotope values (Tables 3-5, 3-6; Figures 3-6, 3-7).

*Striped Bass Yolk-Sac Larvae*

Striped bass yolk-sac larvae had the most elevated $\delta^{13}$C and $\delta^{15}$N values of the zooplankton and striped bass life stages analyzed, indicating they were expressing a maternal signature. Adult striped bass feed in a more marine environment (high $\delta^{13}$C) and at a high trophic level (high $\delta^{15}$N). Striped bass yolk-sac larvae had slightly, but significantly, higher $\delta^{13}$C values in 2008 than in 2007 (Table 3-4, Figure 3-5). Yolk-sac larvae had similar and not significantly different values of $\delta^{15}$N in each year. Spatially, $\delta^{13}$C values of yolk-sac larvae did not differ by location in 2007 or 2008 (Table 3-5; Figures 3-6, 3-7). There was an apparent trend of decreasing $\delta^{15}$N values with distance down-estuary of the salt front and ETM in both years, although the apparent trend was not significant (Table 3-6; Figures 3-6, 3-7).

*Striped Bass Feeding-Stage Larvae*

Stable isotope values of feeding-stage larvae varied with respect to length, indicating that larvae undergo a shift from the maternal stable isotope signature observed in yolk-sac larvae to that characteristic of zooplanktivores. Larvae experienced a gradual, and variable among individuals, shift from an enriched, marine carbon signature to a depleted estuarine or terrestrial carbon signature with increasing length ($p < 0.001$; $r^2_{adj}$ = 0.30) (Figure 3-8A). Analysis of covariance, conducted to evaluate between-year differences in the relationship between $\delta^{13}C$ and length, indicated that slopes of the relationship between $\delta^{13}C$ and length did not differ in 2007 and 2008. However, the intercept of the regression in 2008 was significantly lower than that in 2007 ($p < 0.05$) (Figure 3-8B). Additionally, the mean $\delta^{13}C$ value of feeding-stage larvae was slightly lower in 2008 than in 2007 (Table 3-4).

There was no relationship between $\delta^{15}N$ in feeding-stage larvae and total length (Figure 3-9) for lengths included in the analysis. The mean value of $\delta^{15}N$ for feeding-stage larvae in 2007 was 1.99‰ enriched over the mean value in 2008 ($p < 0.001$) (Table 3-4; Fig 3-5).

In 2007 and 2008, there were no statistical differences in the mean $\delta^{13}C$ values of feeding-stage larvae among locations analyzed in the upper Bay (Table 3-5; Figures 3-6, 3-7). There were significant location differences in mean $\delta^{15}N$ values. In both years, feeding-stage larvae up-estuary of the ETM and salt front were enriched in $\delta^{15}N$ over larvae located within and down-estuary of the features (Table 3-6; Figures 3-6, 3-7).

*Diet: Comparison of stable isotope and gut-contents analyses*

In 2007, striped bass larvae with prey in their guts at time of capture had $\delta^{13}$C values significantly more depleted (t=2.31, $p < 0.05$) than larvae without prey (-22.34 ± 0.10‰ se and -21.62 ± 0.29‰ se, respectively; Figure 3-10A). In 2008, the relative values were similar for larvae with and without prey in their guts and the means did not differ significantly (Figure 3-10B). The mean $\delta^{15}$N values did not differ significantly for larvae with or without prey in their guts in either year (Figure 3-11A,B).

There were weak indications of relationships between larval stable isotope signatures and the number of prey items in guts, although results were inconsistent for years and locations. In 2007, there was no significant correlation between either $\delta^{13}$C or $\delta^{15}$N values and number of prey in guts (Table 3-7A). In 2008, values of both isotopes decreased with increasing number of prey in guts (Table 3-7A). With respect to locations, in both 2007 and 2008 there were no significant correlations between $\delta^{13}$C values and the number of prey in guts (Table 3-7B), but there were two significant ($p < 0.01$) correlations between prey number and $\delta^{15}$N with respect to location (Table 3-7B).

The percent composition by number of the two most common prey, *E. affinis* and *B. longirostris*, in larval striped bass guts was not significantly related to mean $\delta^{13}$C or $\delta^{15}$N values of striped bass larvae.

*Relationship between stable isotope levels and striped bass larval growth rate*

In 2007, there was no relationship between $\delta^{13}$C or $\delta^{15}$N values of feeding-stage striped bass larvae and larval growth rate, regardless of the location where the larvae were collected (Table 3-8A,B). In 2008, there were overall significant negative

relationships between both stable isotopes and larval growth rate (Table 3-8A). In 2008, all growth rate and stable isotope correlations with respect to the salt front were negative and three were significant (Table 3-8B). In contrast, growth rates of larvae within the ETM in 2008 were positively correlated with $\delta^{15}$N levels (Table 3-8B).

### *Lipid levels of zooplankton and larvae*

Lipid content of *E. affinis*, inferred from C:N ratios measured during mass spectroscopy, were modestly but significantly (t = 2.129, *p* < 0.05) higher in 2008 (3.94 ± 0.02 se) than in 2007 (3.88 ± 0.02 se).  In each year, lipid content of *E. affinis* was similar among locations with respect to the salt front and the ETM (Table 3-9). Lipid content of *B. longirostris* did not differ between years or among locations in the upper Bay (Table 3-9).

Mean lipid contents (C:N) of yolk-sac larvae, imparted from maternal contributions, were similar in 2007 (5.77 ± 0.08 se) and 2008 (5.93 ± 0.24 se). Lipid content of yolk-sac larvae did not differ by location with respect to the ETM or salt front in either year (Table 3-9).

There were no significant inter-annual differences in lipid content of feeding-stage larvae. The C:N ratios for 2007 and 2008 were 5.47 ± 0.05 se and 5.55 ± 0.08 se, respectively. There was significant spatial variation in C:N ratios of feeding-stage larvae in 2007 when larvae up-estuary of the ETM and salt front had lower C:N ratios (lipid levels) than larvae within the features (*p* < 0.001; Table 3-9). In 2008, location was not a significant factor with respect to larval C:N.

*Stable isotope analysis of historic samples*

Feeding-stage larvae in 2007 had a distinctive isotopic signature, with significantly higher $\delta^{15}N$ values (ANOVA, $p = 0.05$) than observed for larvae in 1998, 2003, and 2008 (Figure 3-12). Feeding-stage larvae in 2008, the year of lowest YOY recruitment, had mean $\delta^{15}N$ values similar to larvae from 1998 and 2003, years of moderate and high YOY recruitment, respectively. Moreover, although $\delta^{13}C$ values of larvae in 2007 were intermediate, they were significantly higher (ANOVA, $p < 0.05$) than mean $\delta^{13}C$ of larvae in 1998. Larvae in 2007 and 2003, the years with highest recruitment, had the highest $\delta^{13}C$ values, indicating a stronger input of marine carbon in their diets.

A comparison of September YOY juvenile-index recruitment levels (from Maryland Department of Natural Resources seine surveys) for the upper Bay and larval-stage stable isotope values indicated no significant correlation between mean $\delta^{13}C$ or $\delta^{15}N$ isotope values and YOY recruitment (Figure 3-13).

## DISCUSSION

Nutritional sources and trophic pathways in striped bass larvae were evaluated in upper Chesapeake Bay by analyzing stable isotope signatures of zooplankton and larvae, as well as larval gut contents. The copepod *Eurytemora affinis* and the cladoceran *Bosmina longirostris* were dominant prey. *Eurytemora* was eaten by larvae throughout the upper Bay region while *Bosmina* became increasingly important within and up-estuary of the salt front. The gut contents analysis did not detect inter-annual variability in prey incidence (fraction of larvae with one or more prey in the gut) in 2007 and 2008,

but there was spatial variability in prey incidence with respect to the salt front and ETM. A second measure, feeding success, defined as the number of prey per gut, varied primarily with respect to size of larvae but did not differ inter-annually.

The analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes in zooplankton and striped bass larvae detected inter-annual and spatial variability in the isotope signatures, in addition to ontogenetic variability during the transition from yolk-sac to feeding-stage larvae in striped bass. Most notably, $\delta^{15}N$ values of zooplankton and feeding-stage larvae were significantly elevated in 2007, especially up-estuary of the salt front and ETM. Gut contents analysis and stable isotope analysis each provided important insights into larval trophodynamics. A retrospective analysis of stable isotope values in archived striped bass larvae from surveys in 1998 and 2003, combined with the analysis conducted on larvae hatched in 2007 and 2008, did not show significant concordance between stable isotope signatures and level of success of striped bass recruitment in upper Chesapeake Bay. Inclusion of larvae from additional years may provide insight into potential correlations between isotope values and recruitment.

### *Diet analysis: Gut contents*

Prey incidence and feeding success of striped bass larvae were similar in 2007 and 2008. Mean number of prey per gut increased with larval length. The increased number of prey in guts of larger striped bass larvae was not unexpected and was observed in previous research on striped bass (Martino 2008). In 2007 and 2008, only minor differences in prey incidence and feeding success were observed in larvae with respect to the ETM or salt front.

The prey composition of striped bass larvae in the upper Chesapeake Bay in 2007 was similar to that of < 10 mm TL larvae in the freshwater nursery area of the Patuxent River tributary in 2000 and 2001 (Campfield 2004; Campfield and Houde 2011).  In both studies, *E. affinis* was the most important prey but *B. longirostris* also was important.  In my upper Bay research in 2007, 56% of the diet items in 2007 were *E. affinis* while 32% were *B. longirostris.* In the Patuxent River study, approximately 50% of the diet items were *E. affinis*, while *B. longirostris* contributed 20%. Campfield (2004) also recorded inter-annual and spatial variability in prey composition similar to results in my research. He reported that *B. longirostris* contributed more to larval striped bass diets in 2000 than in 2001. In the upper Bay, Martino and Houde (2010) also noted differences in the importance of *B. longirostris* in larval striped bass diets in 2001 and 2003.  In 2001, a year of average recruitment, *B. longirostris* was present in < 22% of larval guts, while in 2003, a year of high recruitment, *B. longirostris* incidence increased to 50%.  In the upper Bay during 1998 and 1999, North and Houde (2006) reported that *E. affinis* contributed from 85.4% to 93.5% of items in larval diets, with only minor percentages of *B. longirostris*. Uphoff (1989) found that copepods and cladocerans, not identified to species but probably represented by *E. affinis* and *B. longirostris*, were dominant in striped bass larval guts in the Choptank River tributary.  In fact, Uphoff's five-year study found that cladocerans were the dominant prey in the Choptank.

In the upper Bay, the evidence suggests that higher proportions of *B. longirostris* occur in larval diets in years of above average recruitment of striped bass.  While *E. affinis* is clearly the most important prey under most circumstances, the addition of *B. longirostris* to the diet may be advantageous in supporting growth and survival of larvae,

especially up-estuary of the salt front and ETM where *B. longirostris* is most abundant. Although *B. longirostris* was not shown to be a preferred prey in my study, based on a prey selectivity analysis (Strauss 1979, 1982), it appears that, when *E. affinis* is at low abundance, larvae rely more on *B. longirostris* to provide nutritional support. In some circumstances, striped bass larvae do positively select *B. longirostris*. For example, in freshwater Lake Marion, South Carolina, larvae selected *B. longirostris* (Chick and Van Den Avyle 1999). Beaven and Mihursky (1980) reported that larvae in the Potomac River tributary of Chesapeake Bay positively selected *B. longirostris*, in addition to copepods. And, recruitment to the juvenile stage was higher for striped bass in the Hudson River when larval-stage first feeding coincided with a spring bloom of *B. freyi* (Limburg et al. 1999). *Bosmina longirostris* may be especially important for striped bass larvae hatched late in the spawning season. Concentrations of *E. affinis* often begin to decline in April, while concentrations of *B. longirostris* peak later in the upper Bay (Martino and Houde 2010; Chapter 2 of this thesis) and also in Bay tributaries (Campfield and Houde 2011). Limburg et al. (1997 and references therein) suggested that larvae may benefit from feeding on *B. longirostris* based on optimal foraging theory, presuming that cladocerans are easier to capture than copepods, and thus reduce energetic cost of feeding.

### *Gut contents and stable isotope analyses*

A drawback to gut contents analysis in determining contributions of prey toward nutritional support in fishes is bias in evaluating diet components with different digestion times. A second drawback is that gut contents analysis only describes the most recent feeding. Stable isotope analysis partly addresses these shortcomings, since the stable

isotope composition of consumed prey is incorporated into predator tissues with known changes from the isotopic signature of the prey. At the least, stable isotope analysis complements traditional gut contents analysis by providing additional dimensions to understanding sources of nutrition.

My observation of declines in $\delta^{13}$C and $\delta^{15}$N levels in feeding-stage striped bass larvae relative to levels in yolk-sac larvae resulted from the transition from maternally derived signatures in yolk-sac larvae to signatures of feeding-stage larvae that are consuming estuarine zooplankton. Estuarine zooplankton typically have lower $\delta^{13}$C and $\delta^{15}$N values than yolk-sac larvae of striped bass, which expressed $\delta^{13}$C and $\delta^{15}$N signatures resembling those of a high-level predator, i.e., their mothers. Pepin and Dower (2007) recorded similar results for larvae of several marine fishes that exhibited decreasing $\delta^{13}$C values with increasing larval length and weight. They concluded that the decrease represents a shift away from the maternal carbon signature.

There was no detectable relationship between stable isotope values and percent composition by number of either *Bosmina* or *Eurytemora* prey in guts of striped bass larvae. The lack of relationship could partly be attributed to the masking effect of remaining maternal signature in young larvae. The time required for a fish to fully assimilate the isotopic signature of prey items is determined by growth rates (Hoffman et al. 2007). Young-of-the-year American shad, which had instantaneous growth coefficients of 0.05-0.20 d$^{-1}$, required 7-30 days to assimilate and express a stable isotope signature fully indicative of their prey (Hoffman et al. 2007). However, a direct comparison of stable isotope compositions of predator and prey is not the optimal analytical approach. Rather, a mixing model approach would be better to describe the

relative contribution of sources to the stable isotope composition of larval fish for comparison with larval diets.

In a stable isotope analysis where $n$ stable isotopes are analyzed, a system of equations can be solved for $n+1$ sources (prey). Additionally, the IsoError software (http://www.epa.gov /wed/ pages/ models.htm) allows for error estimates of sources (prey) and mixtures (consumers) to be included in a two or three source mixing model providing percent contribution of possible prey items (Phillips and Gregg 2001). I attempted to apply a mixing model approach using *E. affinis, B. longirostris*, and yolk-sac larvae as the three "prey" sources that affect the stable isotope composition of feeding-stage larvae. Yolk-sac larvae were assumed to express the maternal signature which would be present at the beginning of the feeding stage. Source values were corrected for trophic enrichment by assuming $\Delta^{13}C$ and $\Delta^{15}N$ values of 0.05‰ and 3.40‰ per trophic level, respectively (DeNiro and Epstein 1981; Fry and Sherr 1984; Minagawa and Wada 1984; Peterson and Fry 1987; Herzka and Holt 2000; Vander Zanden and Rasmussen 2001; Post 2002). *Bosmina longirostris* was assumed to be one trophic level below feeding-stage striped bass larvae due to its herbivorous diet (Kerner et al. 2004). Because knowledge is insufficient regarding trophic level differences between *E. affinis* or striped bass yolk-sac larvae and feeding-stage larvae, several possible trophic level corrections were investigated. My attempted trophic level corrections resulted in source $\delta^{15}N$ values well below those observed in feeding-stage larvae. Consequently, a mixing model solution was undefined (Phillips and Gregg 2003). It is clear that stable isotope signatures of feeding-stage striped bass larvae are intermediate between zooplanktivores and piscivores, a reflection of their combined

dietary and maternal influences, respectively. Mixing models applied to later-stage larvae of striped bass may prove to be more informative because larvae will have fully assimilated an isotope signature representative of their food sources.

### *Stable isotope preparation and methodology*

Stable isotope methodology lacks consensus, especially regarding sample preservation, lipid extraction, and sample acidification to remove inorganic material. The use of frozen tissue is generally recommended for stable isotope analysis, because samples preserved in formalin or ethanol may have enriched/depleted carbon/nitrogen values (Carabel et al. 2006, 2009; Hoffman et al. 2007). Ethanol-preserved fish can be approximately 0.4‰ and 0.2‰ higher in $\delta^{13}$C and $\delta^{15}$N values, respectively, compared to frozen samples (Hoffman, unpublished data). Ethanol-preserved zooplankton have $\delta^{13}$C and $\delta^{15}$N values that reportedly are higher by 0.4‰ and 0.6‰, respectively, than frozen zooplankton (Feuchtmayer and Grey 2003). My ethanol-preserved samples of zooplankton and striped bass larvae possibly were enriched in $\delta^{13}$C and $\delta^{15}$N. However, since all samples in my analyses were ethanol-preserved and treated similarly, any bias presumably would be consistent, allowing valid comparisons between years and among locations. Nevertheless, care should be taken when comparing results from my study with others in which different preservation methods were used. In such comparisons, trends in isotope values, not mean values, should be compared.

The method used to account for lipids, which lead to decreased $\delta^{13}$C values, is debated. Mass balance equations, using C:N ratios, are frequently used rather than lipid extraction. Several methods have been suggested for lipid correction (McConnaughey

and McRoy 1979; Kiljunen et al. 2006; Sweeting et al. 2006; Post et al. 2007) with no consensus on which is preferred.  I applied the equation given in Post et al. (2007) because other equations have been shown to be faulty, e.g., the McConnaughey and McRoy (1979) equation, or because the equation did not apply to all trophic levels e.g., Kiljunen et al. (2006). Since all lipid correction methods were developed for frozen samples, correction for lipids in ethanol-preserved samples may differ and should be investigated further.  It should be noted that different preservation methods had no effect on the reported C:N ratios of marine primary producers or invertebrates from different trophic levels (Carabel et al. 2009).

Another source of debate is effects on $\delta^{13}C$ and $\delta^{15}N$ values of acid-washing to remove inorganic carbon. It is widely agreed that since the exoskeleton of zooplankton is rarely incorporated into the tissue of its predators, the exoskeleton should be removed or dissolved through acid-washing. My analysis indicated that acid-washing depleted $\delta^{15}N$ values of *E. affinis*, relative to non-acid-washed samples, a result differing from Bunn et al. (1995), who found that acid-washing enriched $\delta^{15}N$ signatures of penaeid shrimp. However, there is agreement that when acid-washing is conducted, stable isotope analysis of carbon and nitrogen should be conducted separately, which was the case in my research.

There have been several research projects in the upper Chesapeake Bay in recent years from which archived samples of striped bass larvae were available for stable isotope analysis. However, for these samples to be useful, it is imperative that long-term storage in ethanol did not affect relative levels of carbon and nitrogen isotopes. Long-term storage of marine invertebrates in ethanol had no significant effect on mean $\delta^{13}C$ or

$\delta^{15}N$ values (Carabel et al. 2009). In my comparative analysis, I assumed there was no selective loss over time of light or heavy isotopes that would bias results. Consequently, results of my analysis on archived larval striped bass should be interpreted cautiously until storage-time effects on preserved fish tissue have been evaluated.

### *Trophic pathways*

A comparison of my stable isotope values of *B. longirostris* from the upper Chesapeake Bay with *Bosmina* in the Mattaponi River, a tributary in the lower Chesapeake Bay (Hoffman et al. 2007), indicated that values of $\delta^{13}C$ (Table 3-10) were similar. However, Chesapeake Bay *Bosmina* have mean $\delta^{13}C$ values that are depleted compared to those from the St. Lawrence River estuarine transition zone (Table 3-10) (Barnard et al. 2006; Winkler et al. 2007). It is possible that *Bosmina* in the tidally energetic St. Lawrence are more dependent on marine, rather than terrestrial, sources of carbon for nutrition than are *Bosmina* in the Chesapeake.

Values of $\delta^{13}C$ in *E. affinis* from the Mattaponi River (Hoffman et al. 2007) were similar to those in upper Chesapeake Bay (Table 3-10). Comparing ecosystems, values of $\delta^{15}N$ at the low end of the range I recorded in *E. affinis* from upper Chesapeake Bay are similar to $\delta^{15}N$ in *E. affinis* from other systems, including the Parker River (Hughes et al. 2000) and St. Lawrence River (Barnard et al. 2006; Winkler et al. 2007). However, the *Eurytemora* in my research had a much broader range of $\delta^{15}N$ values, spanning values indicative of nearly two trophic levels ($\Delta^{15}N = 6.74$‰).

*Eurytemora affinis* differed in its stable isotope values from *Bosmina longirostris* primarily in its higher mean $\delta^{15}N$ value. This difference is consistent with results for

*Eurytemora* and *Bosmina* in the York River Estuary of Virginia (Hoffman et al. 2008). The enriched values of $\delta^{15}N$ of *E. affinis* compared to *B. longirostris* are likely due to diet breadth. *Eurytemora* is known to consume detritus, particle-attached bacteria, and microzooplankton in addition to phytoplankton (Heinle et al. 1977; Berk et al. 1977; Boak and Goulder 1983; Kleppel 1993; David et al. 2006). While phytoplankton is a higher quality food source for copepods than detritus and may be preferred over detritus-derived, terrestrial plant material or microzooplankton, phytoplankton often is present in low concentrations in ETM regions and must be supplemented to support zooplankton nutrition (Heinle et al. 1977; Sobczak et al. 2002; David et al. 2006).

Inter-annual differences in $\delta^{13}C$ and $\delta^{15}N$ were detected in zooplankton and striped bass larvae from the upper Chesapeake Bay. In general, $\delta^{13}C$ values were slightly higher in 2007 than in 2008, suggesting a potentially greater influence of marine carbon on the plankton foodweb in 2007. These results suggest that the influence of terrestrial carbon on trophic pathways and trophodynamics was less important in 2007, the year of average recruitment, than in 2008, when recruitment was poor. If true, these results contrast with results from young-of-year American shad in the Mattaponi River, a Virginia tributary of the Chesapeake Bay. Shad recruitment was higher when high freshwater flow increased the reliance by shad on terrestrial organic matter, which resulted in depleted $\delta^{13}C$ values (Hoffman et al. 2007).

The values of $\delta^{15}N$ were higher in zooplankton and feeding-stage striped bass larvae in 2007 than in 2008, with the exception of yolk-sac larvae, which were similar in each year. The higher $\delta^{15}N$ values of feeding-stage larvae in 2007 apparently are related to feeding on zooplankton which also had higher $\delta^{15}N$ in 2007. However, it is more

difficult to explain the inter-annual difference in $\delta^{15}N$ values of zooplankton. The higher $\delta^{15}N$ value of *E. affinis* in 2007 may have been related to shifts in diet associated with amounts of freshwater flow, which were slightly higher in 2007. In research on the Patuxent and Choptank tributaries of Chesapeake Bay, carbon from microzooplankton was more readily available to copepods (*E. affinis* and *Acartia* spp.) during an average flow year, while microzooplankton and phytoplankton were equally available during a year with below-average freshwater flow (Reaugh et al. 2007). A diet dominated or enhanced by microzooplankton could lead to increased $\delta^{15}N$ values in *Eurytemora*.

Despite inter-annual differences in $\delta^{13}C$ and $\delta^{15}N$, spatial variability in stable isotope values was similar in 2007 and 2008. The $\delta^{13}C$ values of *E. affinis* were most depleted up-estuary of the salt front and ETM, becoming more enriched within and down-estuary of these features, which is indicative of a marine carbon contribution. These results are similar to those for seston and zooplankton in the ETM region during 1996, when $\delta^{13}C$ values were indicative of a decreasing presence of terrestrial carbon influence down-estuary (Boynton et al. 1997). Spatial trends in $\delta^{13}C$ of estuarine organisms are reported for other estuarine and marine systems. In the Gironde River estuary, France, the overall $\delta^{13}C$ values in adults of nine abundant fishes tended to be enriched in $\delta^{13}C$ with distance down-estuary (Pasquaud et al. 2008). Depleted $\delta^{13}C$ values in numerous taxa from freshwater regions relative to more oligohaline regions also was documented in a subtropical lagoon in southern Brazil (Garcia et al. 2007) and in a Mediterranean coastal lagoon (Vizzini et al. 2005).

Spatially, nitrogen isotope signatures of zooplankton and striped bass larvae in my research followed a pattern where higher $\delta^{15}N$ values occurred up-estuary. These results

resembled results on juvenile striped bass from the Delaware River, in which $\delta^{15}N$ values increased upriver from the oligohaline region (Wainright et al. 1996). Hagy (2002), based on stable isotope analysis, noted that mesozooplankton in the upper Chesapeake Bay fed at a higher trophic level than mesozooplankton in mid- or down-Bay locations. Spatial variability in zooplankton that I observed for $\delta^{15}N$ could be due, in part, to a higher level of omnivory in locations up-estuary of the ETM and salt front.

***Striped bass larvae growth rates, stable isotopes and nutritional sources***

In 2007, there was no detectable relationship between stable isotope values of $\delta^{13}C$ or $\delta^{15}N$ and individual growth rates of feeding-stage larvae. However, in 2008, larvae up-estuary of the salt front had faster growth rates that were inversely correlated with $\delta^{13}C$ values. This result suggests the potential importance of allochthonous carbon from freshwater or terrestrial sources in supporting larval growth and survival, at least in some years.

No firm conclusions could be drawn from the analysis of the spatial relationship between $\delta^{15}N$ values and growth rates of feeding-stage larvae. In 2008, larvae within the ETM had $\delta^{15}N$ levels positively related to growth rates while larvae within the salt front had a negative relationship. There were no statistically significant relationships between larval growth rates and $\delta^{15}N$ in 2007.

***Recruitment potential and stable isotope composition***

My analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotope values for striped bass feeding-stage larvae in 2007 and 2008, years of average and poor recruitment, respectively, compared

to larvae from archived collections in 1998 and 2003, years of moderate and high YOY recruitment, respectively, did not explain how sources of nutritional support might affect striped bass recruitment. There were no significant correlations between YOY recruitment level, as measured by the Maryland DNR juvenile seining index, and stable isotope values. Indeed, except for 2007 when $\delta^{15}$N values were exceptionally high, there was only modest variability in mean values of stable isotopes of feeding-stage larvae among the four years. The results suggest that strong recruitment years cannot be attributed to primarily autochthonous or allochthonous carbon sources that support larval nutrition; rather, a mixture of the two sources is utilized in all years. However, this conclusion is based on only four years of data. Inclusion of additional years of recruitment and isotope data may elucidate potential correlations between carbon sources and recruitment.

Table 3-1. Summary of research cruises and sampling surveys conducted in the upper

Chesapeake Bay, 2007 and 2008.

| Cruise | Dates | Research Vessel | Gear | Mesh (µm) | Number of Samples |
|--------|-------|-----------------|------|-----------|-------------------|
| BMRR0701 | 25 April 2007 | Terrapin | 60-cm Paired Bongo | 280 | 11 |
| BMRR0702 | 4 May 2007 | Terrapin | 60-cm Paired Bongo | 280 | 9 |
| BM0703 | 11 May 2007 | Hugh R. Sharp | 1 m$^2$ Tucker Trawl | 280 | 44 |
| BMRR0703 | 22 May 2007 | Terrapin | 60-cm Paired Bongo | 280 | 11 |
| BMRR0704 | 29 May 2008 | Terrapin | 60-cm Paired Bongo | 280 | 10 |
| BM0802 | 19-22 April 2008 | Hugh R. Sharp | 1 m$^2$ Tucker Trawl | 280 | 48 |
|  |  |  | ¼ m$^2$ MOCNESS | 333 | 36 |
| BMRR0801 | 1 May 2008 | Terrapin | 60-cm Paired Bongo | 280 | 10 |
| BM0803 | 16-20 May 2008 | Hugh R. Sharp | 1 m$^2$ Tucker Trawl | 280 | 54 |
|  |  |  | ¼ m$^2$ MOCNESS | 333 | 42 |
| BMRR0802 | 30 May 2008 | Terrapin | 60-cm Paired Bongo | 280 | 10 |
| MEN0706 | 4-6 June 2008 | Aquarius | 1 m$^2$ Tucker Trawl | 280 | 14 |
|  |  |  | 2 m$^2$ Tucker Trawl | 707 | 16 |

Table 3-2. Results from two-way ANOVA determining the effect of larval size and (A) year or larval size and (B) location on the $\log_{10}$-tranformed number of prey in larval guts. Three size categories were analyzed: < 6mm (a), 6 – 8 mm (b) and >8 mm (c). Locations are denoted as up-estuary (**u**; >5 km up-estuary of feature), within (**w**; ±5 km of feature), or down-estuary (**d**; >5 km down-estuary of feature).

A.

| Factor | SS | df | MS | F | P | Tukey |
|---|---|---|---|---|---|---|
| Size Category | 2.78 | 2 | 1.39 | 25.73 | <0.001 | a < b < c |
| Year | 0.04 | 1 | 0.04 | 0.67 | 0.41 | |
| Size Category*Year | 0.27 | 2 | 0.14 | 2.54 | 0.08 | |

B.

| Year | Factor | SS | df | MS | F | P | Tukey |
|---|---|---|---|---|---|---|---|
| 2007 | | | | | | | |
| | Size Category | 1.83 | 2 | 0.92 | 14.33 | <0.001 | a < b < c |
| | ETM Location | 0.04 | 2 | 0.02 | 0.29 | 0.75 | |
| | Size Category* ETM Location | 0.003 | 2 | 0.001 | 0.02 | 0.98 | |
| | Size Category | 1.83 | 2 | 0.92 | 14.93 | <0.001 | a < b < c |
| | Salt Front Location | 0.28 | 2 | 0.14 | 2.25 | 0.11 | |
| | Size Category* Salt Front Location | 0.37 | 4 | 0.09 | 1.51 | 0.20 | |
| 2008 | | | | | | | |
| | Size Category | 0.86 | 2 | 0.43 | 8.38 | <0.001 | a < b < c |
| | ETM Location | 0.21 | 2 | 0.11 | 2.05 | 0.13 | |
| | Size Category* ETM Location | 0.17 | 4 | 0.04 | 0.81 | 0.52 | |
| | Size Category | 0.82 | 2 | 0.41 | 8.50 | <0.001 | a < b,c |
| | Salt Front Location | 0.64 | 2 | 0.32 | 6.65 | 0.001 | u > i |
| | Size Category* Salt Front Location | 0.05 | 4 | 0.01 | 0.28 | 0.89 | |

Table 3-3. Feeding selectivity of striped bass larvae. Strauss' selectivity index for 2007 and 2008 with respect to the ETM and the salt front. Values can range from -1 to +1. Negative and positive values indicate prey avoidance and selection, respectively. Asterisks indicate different levels of significance.

|  | With Respect to ETM | | | With Respect to Salt Front | | |
|---|---|---|---|---|---|---|
|  | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary |
| **2007** | | | | | | |
| *E. affinis* | +0.33*** | +0.29*** | - | +0.33*** | +0.28*** | +0.37‡ |
| *B. longirostris* | -0.28*** | -0.25*** | - | -0.28*** | -0.25*** | -0.25‡ |
| **2008** | | | | | | |
| *E. affinis* | -0.29** | +0.05 | +0.07 | +0.03 | -0.21* | +0.08 |
| *B. longirostris* | +0.06 | +0.19 | +0.01 | +0.12 | +0.05 | +0.01 |

\* $p<0.05$
\*\* $p < 0.01$
\*\*\* $p < 0.001$
‡ insufficient data for t-test

Table 3-4. Mean ± standard errors for C and N stable isotope values of zooplankton and striped bass larvae in upper Chesapeake Bay in 2007 and 2008. Symbols denote levels of significance.

| | 2007 | | 2008 | |
| --- | --- | --- | --- | --- |
| | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{13}C$ | $\delta^{15}N$ |
| *B. longirostris* | -26.30±0.22‰* | 10.66±0.42‰* | -27.59±0.27‰* | 9.04±0.20‰* |
| *E. affinis* | -25.52±0.49‰ | 12.09±0.33‰* | -25.71±0.36‰ | 11.28±0.21‰* |
| Yolk-Sac Larvae | -19.89±0.11‰* | 18.14±0.17‰ | -19.57±0.11‰* | 17.84±0.39‰ |
| Feeding-Stage Larvae | -22.10±0.12‰[†] | 17.13±0.13‰[‡] | -22.37±0.25‰[†] | 15.14±0.28‰[‡] |

[*]   Student's t-test, $p < 0.05$
[†]    ANCOVA, $p < 0.05$
[‡]    ANCOVA, $p < 0.001$

Table 3-5. Mean ± standard error $\delta^{13}$C values for zooplankton and striped bass larvae from different locations in the upper Chesapeake Bay, designated with respect to the ETM and salt front in 2007 and 2008. Superscripts denote significant (ANOVA, $p <$ 0.05) differences in isotope values between locations. Up-estuary and within-feature samples of *B. longirostris* were the same with respect to the ETM and salt front.

| Year | Feature | Species/Stage | Up-Estuary | Within | Down-Estuary |
|------|---------|---------------|------------|--------|--------------|
| 2007 | ETM | *B. longirostris* | -26.29±0.31‰ | -26.32‰ | - |
| | | *E. affinis* | -27.22±0.30‰[a] | -24.67±0.68‰[b] | -23.32±1.13‰[b] |
| | | Yolk-Sac Larvae | -19.94±0.13‰ | -19.65±0.15‰ | -19.62‰ |
| | | Feeding-Stage Larvae | -22.22±0.13‰ | -21.61±0.23‰ | - |
| | Salt Front | *B. longirostris* | -26.29±0.31‰ | -26.32‰ | - |
| | | *E. affinis* | -27.84±0.44‰[a] | -26.33±0.43‰[a] | -23.79±0.65‰[b] |
| | | Yolk-Sac Larvae | -19.91±0.14‰ | -19.96±0.28‰ | -19.61±0.01‰ |
| | | Feeding-Stage Larvae | -22.19±0.13‰ | -21.83±0.26‰ | -21.84±0.99‰ |
| | | | | | |
| 2008 | ETM | *B. longirostris* | -27.32‰ | -27.86‰ | - |
| | | *E. affinis* | -26.13±0.55‰ | -25.85±0.45‰ | -24.77±0.80‰ |
| | | Yolk-Sac Larvae | - | -19.45‰ | -19.33±0.20‰ |
| | | Feeding-Stage Larvae | -21.02±0.27‰ | -20.87±0.21‰ | -20.45±0.17‰ |
| | Salt Front | *B. longirostris* | -27.32‰ | -27.86‰ | - |
| | | *E. affinis* | -26.63±0.49‰[a] | -26.16±0.52‰[a] | -24.18±0.39‰[b] |
| | | Yolk-Sac Larvae | -19.70±0.10‰ | -19.59±0.13‰ | -19.22±0.60‰ |
| | | Feeding-Stage Larvae | -20.94±0.19‰ | -20.71±0.27‰ | -20.59±0.23‰ |

Table 3-6. Mean ± standard error $\delta^{15}$N values for zooplankton and striped bass larvae from different locations in the upper Chesapeake Bay, designated with respect to the ETM and salt front in 2007 and 2008. Superscripts denote significant (ANOVA, $p < 0.05$) differences in isotope values between locations. Up-estuary and within-feature samples of *B. longirostris* were the same with respect to the ETM and salt front.

| Year | Feature | Species/Stage | Up-Estuary | Within | Down-Estuary |
|------|---------|---------------|-----------|--------|--------------|
| 2007 | ETM | *B. longirostris* | 10.65±0.60‰ | 10.69‰ | - |
| | | *E. affinis* | 12.63±0.68‰ | 11.76±0.08‰ | 11.54±0.26‰ |
| | | Yolk-Sac Larvae | 18.21±0.19‰ | 18.08±0.40‰ | 17.10‰ |
| | | Feeding-Stage Larvae | 17.38±0.14‰[a] | 16.11±0.25‰[b] | - |
| | Salt Front | *B. longirostris* | 10.65±0.60‰ | 10.69‰ | - |
| | | *E. affinis* | 13.72±1.20‰[a] | 11.55±0.19‰[b] | 11.65±0.14‰[b] |
| | | Yolk-Sac Larvae | 18.23±0.21‰ | 17.87±0.16‰ | 17.94±0.84‰ |
| | | Feeding-Stage Larvae | 17.58±0.13‰[a] | 15.96±0.26‰[b] | 15.08±0.36‰[b] |
| 2008 | ETM | *B. longirostris* | 9.23‰ | 8.84‰ | - |
| | | *E. affinis* | 12.10±0.22‰[a] | 11.68±0.47‰[a] | 10.48±0.04‰[b] |
| | | Yolk-Sac Larvae | - | 18.13 | 17.61±0.71‰ |
| | | Feeding-Stage Larvae | 17.59±0.27‰[a] | 16.78±0.21‰[ab] | 15.56±0.40‰[b] |
| | Salt Front | *B. longirostris* | 9.23‰ | 8.84‰ | - |
| | | *E. affinis* | 11.39±0.41‰ | 11.80±0.34‰ | 10.63±0.14‰ |
| | | Yolk-Sac Larvae | 18.19±0.17‰ | 17.70±0.60‰ | 17.55±2.01‰ |
| | | Feeding-Stage Larvae | 15.34±0.39‰[a] | 15.61±0.49‰[ab] | 13.52±0.60‰[b] |

Table 3-7. Correlation coefficients for the relationship between stable isotope values and the number of prey in larval guts (A) in 2007 and 2008 and (B) with respect to the ETM and salt front. Significant correlations are indicated (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

A.

| Year | $\delta^{13}C$ | $\delta^{15}N$ |
|------|------|------|
| 2007 | -0.08 | -0.08 |
| 2008 | -0.25* | -0.27* |

B.

| Year | Feature | $\delta^{13}C$ | | | $\delta^{15}N$ | | |
|------|---------|------------|--------|-------------|------------|--------|-------------|
| | | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary |
| 2007 | ETM | -0.09 | -0.39 | - | -0.14 | 0.25 | - |
| | Salt Front | -0.14 | 0.04 | 0.26 | -0.30** | 0.31 | -0.77 |
| 2008 | ETM | -0.003 | -0.06 | 0.04 | -0.03 | -0.70** | -0.18 |
| | Salt Front | -0.28 | -0.32 | 0.18 | -0.32 | -0.34 | -0.06 |

Table 3-8. Correlation coefficients for the relationship between stable isotope values and growth rates of feeding-stage striped bass larvae (A) in 2007 and 2008 and (B) with respect to the ETM and salt front. Significant correlations are indicated (*$p < 0.05$;**$p < 0.01$;***$p < 0.001$).

A.

| Year | $\delta^{13}C$ | $\delta^{15}N$ |
|------|------|------|
| 2007 | -0.08 | -0.09 |
| 2008 | -0.44*** | -0.32* |

B.

| | | $\delta^{13}C$ | | | $\delta^{15}N$ | | |
|------|---------|---------|--------|---------|---------|--------|---------|
| Year | Feature | Up-Estuary | Within | Down-Estuary | Up-Estuary | Within | Down-Estuary |
| 2007 | ETM | -0.14 | 0.02 | - | -0.12 | -0.31 | - |
| | Salt Front | -0.19 | 0.24 | - | -0.03 | -0.04 | - |
| 2008 | ETM | -0.21 | 0.19 | 0.22 | 0.12 | 0.67* | 0.08 |
| | Salt Front | -0.38* | -0.53** | -0.47 | -0.29 | -0.62** | -0.25 |

Table 3-9. Mean ± standard errors for C:N ratios, which serve as a proxy for lipid content in *Eurytemora affinis, Bosmina longirostris,* striped bass yolk-sac larvae, and striped bass feeding-stage larvae in 2007 and 2008 relative to the ETM and the salt front. C:N results of *B. longirostris* with respect to the salt front were the same as for *B. longirostris* with respect to the ETM and are not included in the table. Insufficient numbers of *B. longirostris* were present down-estuary of the salt front and ETM for analysis in both 2007 and 2008. Superscripts designate significant differences (Tukey HSD, $p < 0.05$).

| | Year | ETM Up-Estuary | ETM Within | ETM Down-Estuary | Salt Front Up-Estuary | Salt Front Within | Salt Front Down-Estuary |
|---|---|---|---|---|---|---|---|
| *E. affinis* | 2007 | 3.88 ± .03 | 3.85 ± .03 | 3.91 ± .06 | 3.93 ± .03 | 3.84 ± .05 | 3.88 ± .03 |
| | 2008 | 3.99 ± .04 | 3.93 ± .03 | 3.91 ± .03 | 3.96 ± .03 | 3.96 ± .04 | 3.90 ± .04 |
| *B. longirostris* | 2007 | 4.35 ± 0.23 | 4.15 | - | | | |
| | 2008 | 4.10 | 4.09 | - | | | |
| Yolk-Sac Larvae | 2007 | 5.75 ± .09 | 5.74 ± .26 | 6.24 | 5.72 ± .09 | 5.71 ± .18 | 6.25 ± .002 |
| | 2008 | - | 5.52 | 5.22 ± .29 | 6.23 ± .33 | 5.92 ± .36 | 5.34 ± .88 |
| Feeding-Stage Larvae | 2007 | 5.38 ± .05[a] | 5.81 ± .12[b] | - | 5.36 ± .05[a] | 5.82 ± .12[b] | 5.52 ± .49[ab] |
| | 2008 | 5.51 ± .11 | 5.40 ± .09 | 5.78 ± .19 | 5.62 ± .10 | 5.34 ± .18 | 5.72 ± .18 |

Table 3-10. $\delta^{13}$C and $\delta^{15}$N values of zooplankton and striped bass larvae from this study (2007 and 2008 only; bold text) compared to published results.

| | $\Delta^{13}$C | $\delta^{15}$N | Location | Reference |
|---|---|---|---|---|
| *B. longirostris* | -20.9 to -20.1‰ | 8.2 to 8.8‰ | St. Lawrence River ETZ | Barnard et al. 2006 |
| *B. longirostris* | -20.5±0.1‰ | - | St. Lawrence River ETZ | Winkler et al. 2007 |
| ***B. longirostris*** | **-27.9 to –26.0‰** | **8.8 to 11.7‰** | **upper Chesapeake Bay** | **this study** |
| *B. freyi* | -29.9 ± 0.8‰ | - | Mattaponi River, VA | Hoffman et al. 2007 |
| *E.affinis* | -29.2±1.5‰ | - | Mattaponi River, VA | Hoffman et al. 2007 |
| *E.affinis* | -21.8 to -20.3‰ | 9.2 to 12.5‰ | St. Lawrence River ETZ | Barnard et al. 2006 |
| *E. affinis* nauplii | -21.0±1.03‰ | - | St. Lawrence River ETZ | Winkler et al. 2007 |
| *E. affinis* adults | -21.3±0.2‰ | - | St. Lawrence River ETZ | Winkler et al. 2007 |
| *E. affinis* | - | 8.6‰ | Parker River, MA | Hughes et al. 2000 |
| ***E. affinis*** | **-29.0 to -20.1‰** | **9.9 to 16.7‰** | **upper Chesapeake Bay** | **this study** |
| **Yolk-sac larvae** | **-21.1 to -18.6‰** | **15.4 to 20.0‰** | **upper Chesapeake Bay** | **this study** |
| **Feeding-stage larvae** | **-25.7 to -18.9‰** | **9.9 to 19.5‰** | **upper Chesapeake Bay** | **this study** |
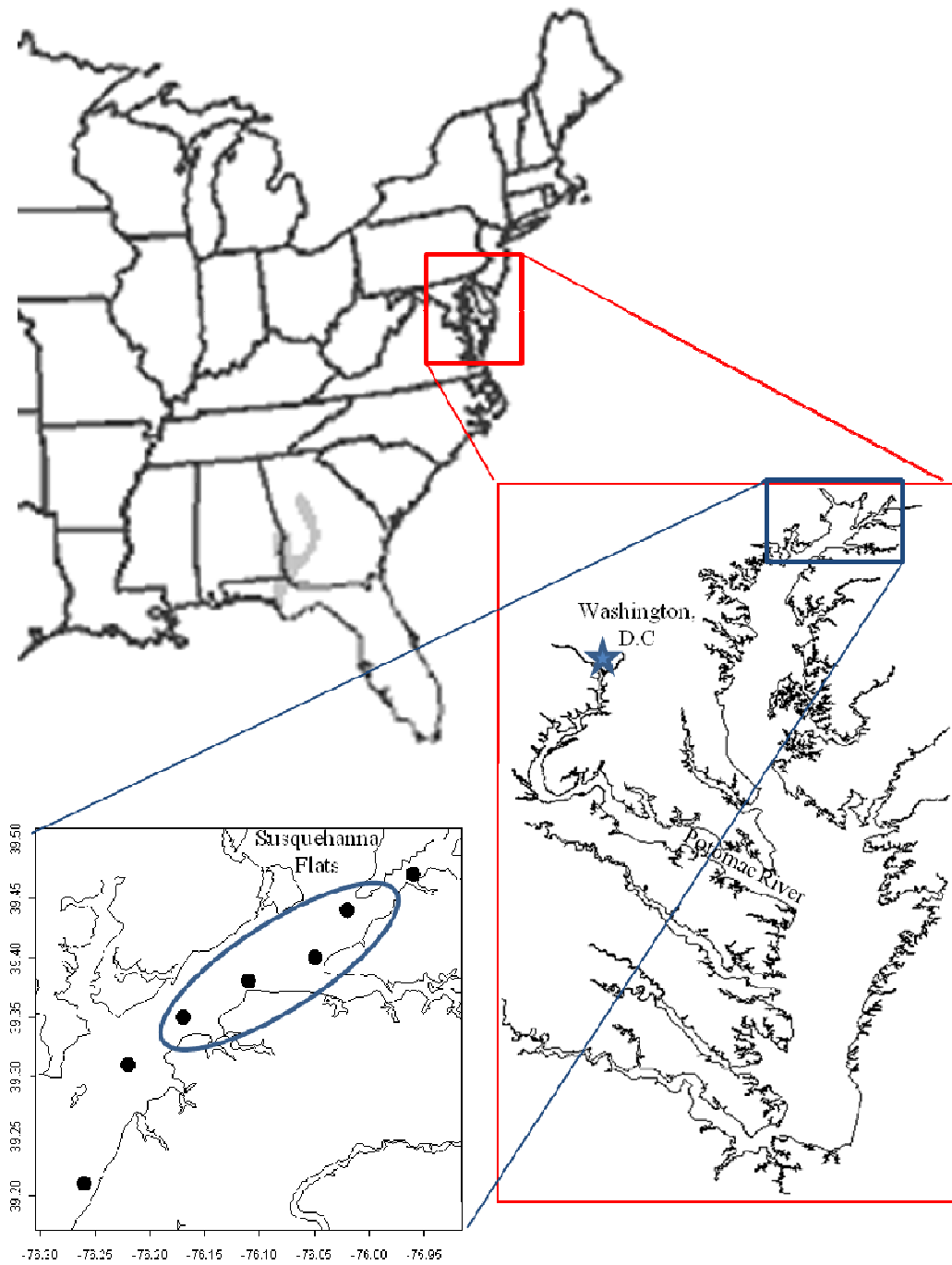
Figure 3-1. Locations of sampling stations, 2007 and 2008 ( ● ), in the channel of upper Chesapeake Bay, USA.  Locations of the salt front and ETM usually fall within the bounds of the blue oval.
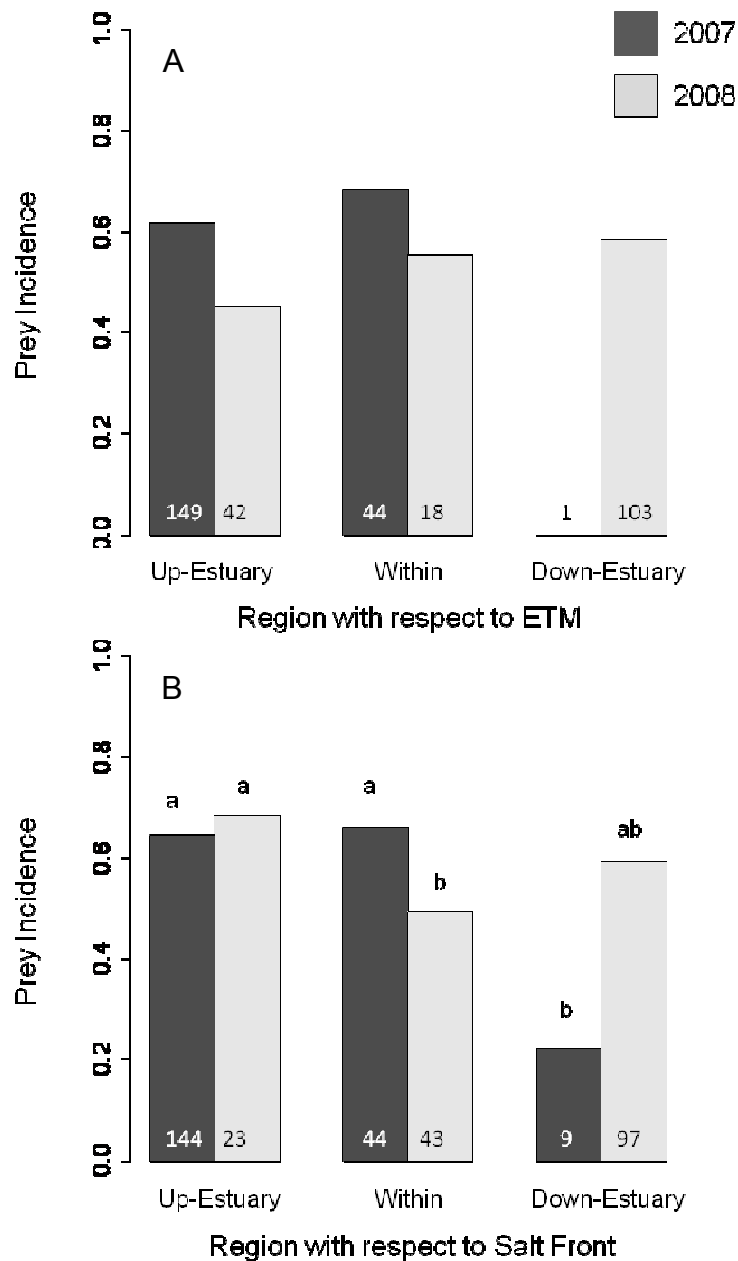
Figure 3-2. Prey incidence for striped bass feeding-stage larvae in 2007 (dark gray bars) and 2008 (light gray bars) with respect to (A) the ETM and (B) the salt front. Numbers within bars represent the number of larvae dissected for each location-year. Letters above bars represent significant differences from a multiple comparison test (Zar 1999).
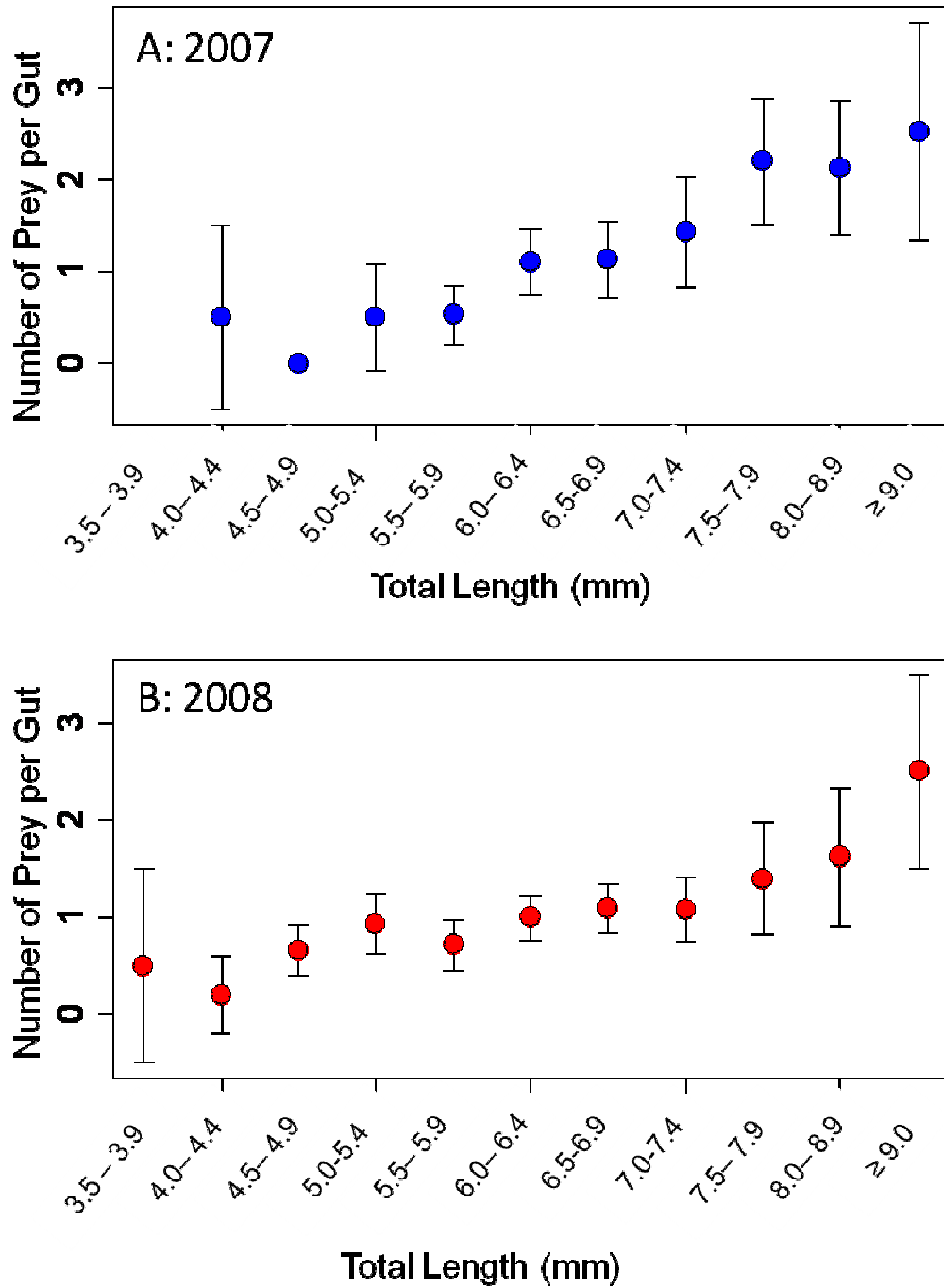
Figure 3-3. Number of prey in larval striped bass guts (mean ± se) for size classes in (A) 2007 and (B) 2008.

Figure 3-4. Percent composition by number of two dominant diet constituents,

*Eurytemora affinis* and *Bosmina longirostris*, and other prey (e.g. detritus, unidentified

material) in relation to year (A); location with respect to the ETM in 2007 (B) and 2008

(D); and location with respect to the salt front in 2007 (C) and 2008 (E).

Figure 3-5. C-N isotope bi-plot of zooplankton (*Eurytemora affinis* and *Bosmina longirostris*) and larval striped bass in 2007 (blue) and 2008 (red). Error bars represent one standard error.
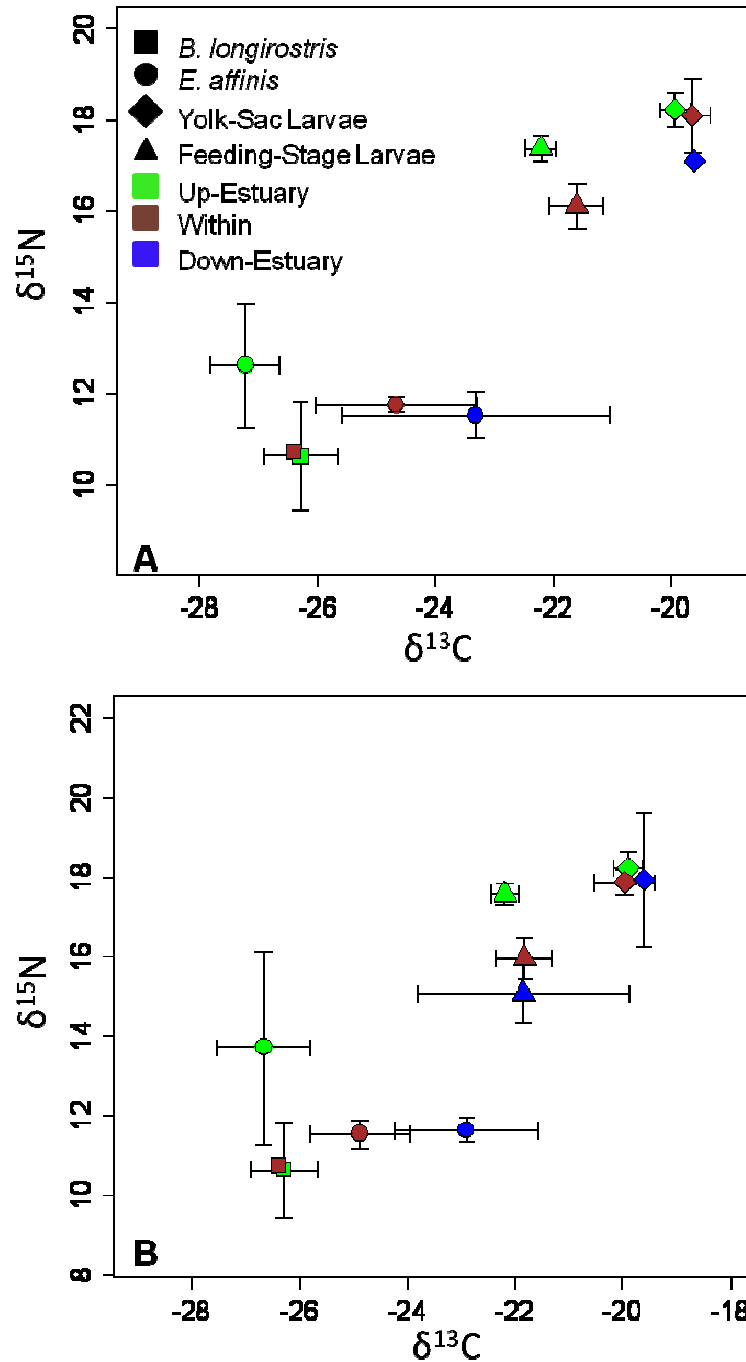
Figure 3-6. 2007. C-N stable isotope bi-plot of zooplankton and larval striped bass collected up-estuary, within, and down-estuary of the (A) ETM and (B) salt front. Error bars represent one standard error.
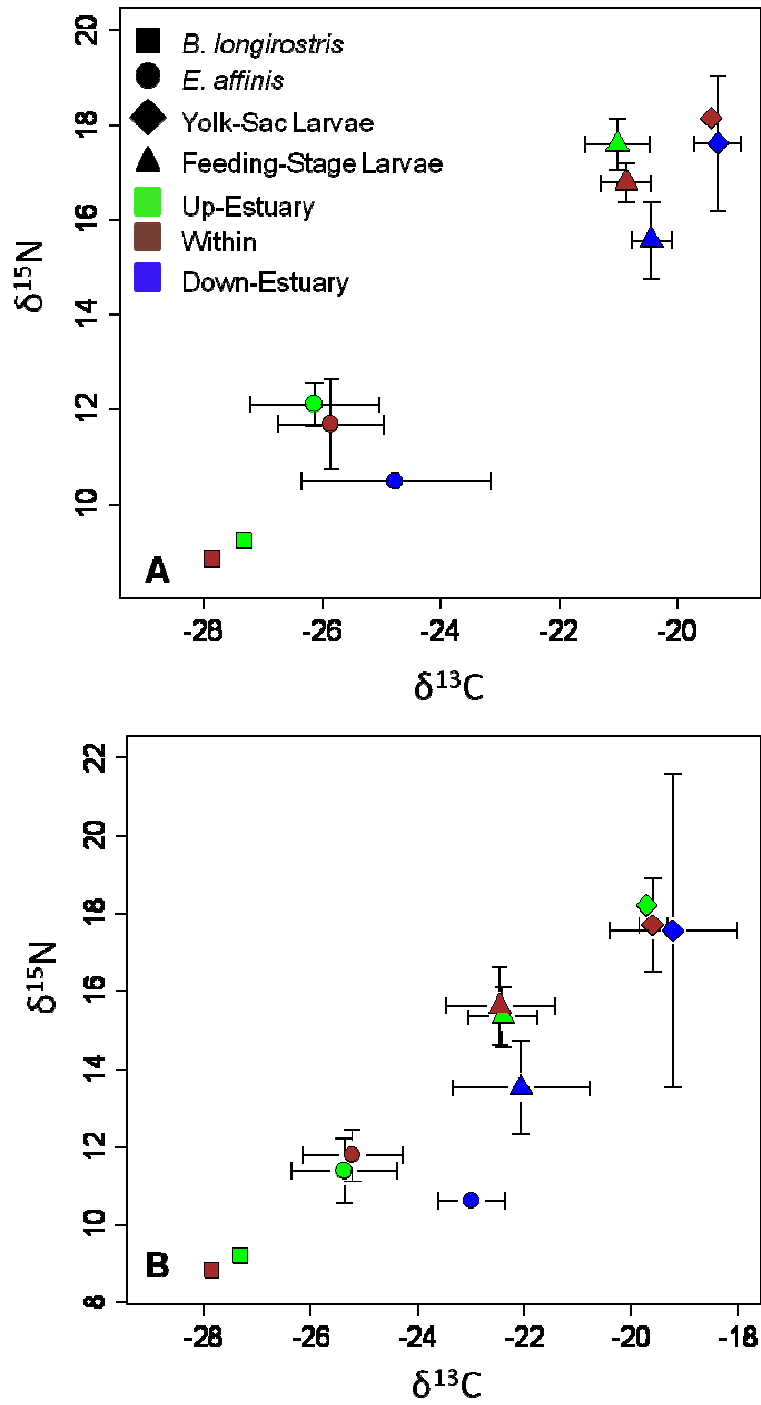
Figure 3-7. 2008. C-N stable isotope bi-plot of zooplankton and larval striped bass collected up-estuary, within, and down-estuary of the (A) ETM and (B) salt front. Error bars represent one standard error.
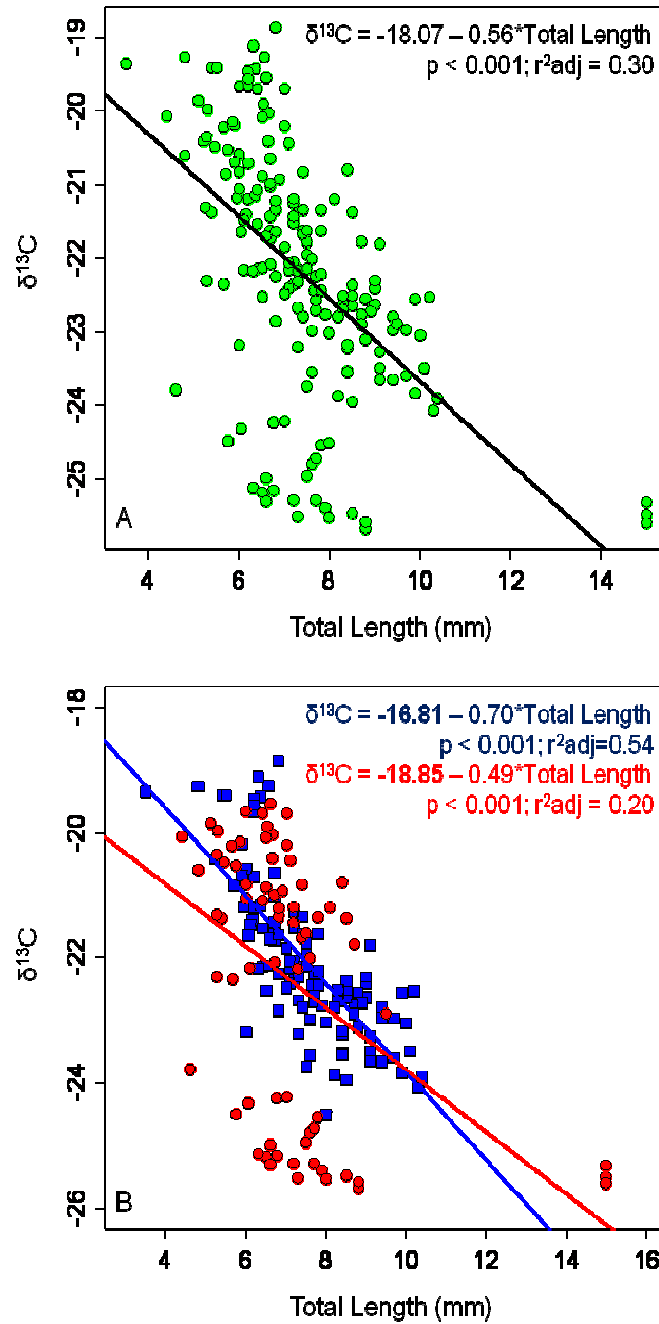
Figure 3-8. Relationship between $\delta^{13}C$ and total length (mm) for feeding-stage, striped bass larvae in (A) combined years and (B) in 2007 (blue) and 2008 (red). Bold values in the regression equation in panel B indicate significant differences.
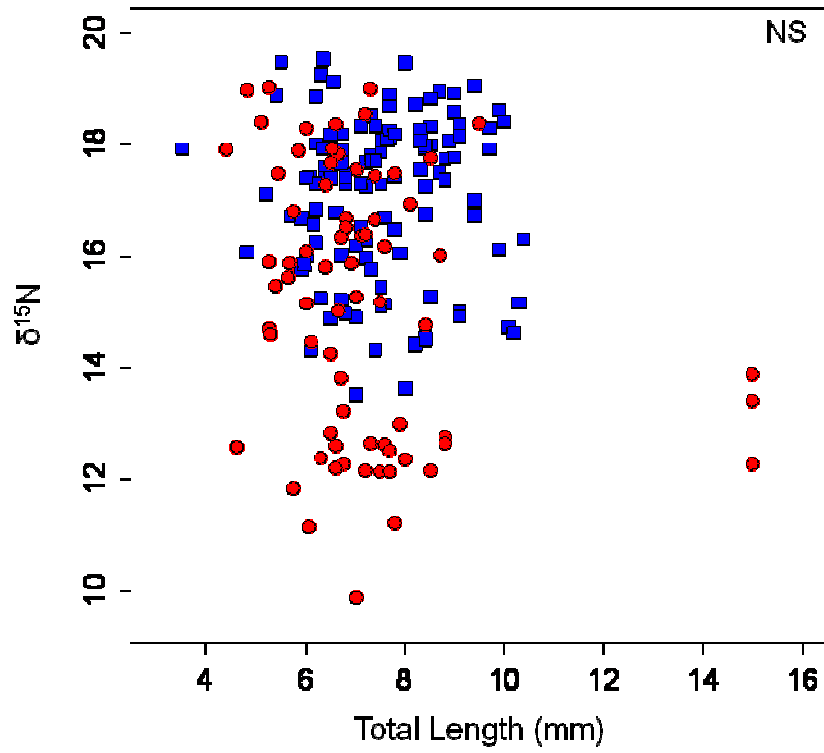
Figure 3-9. Plot of $\delta^{15}N$ on total length (mm) for feeding-stage, striped bass larvae in 2007 (blue) and 2008 (red).
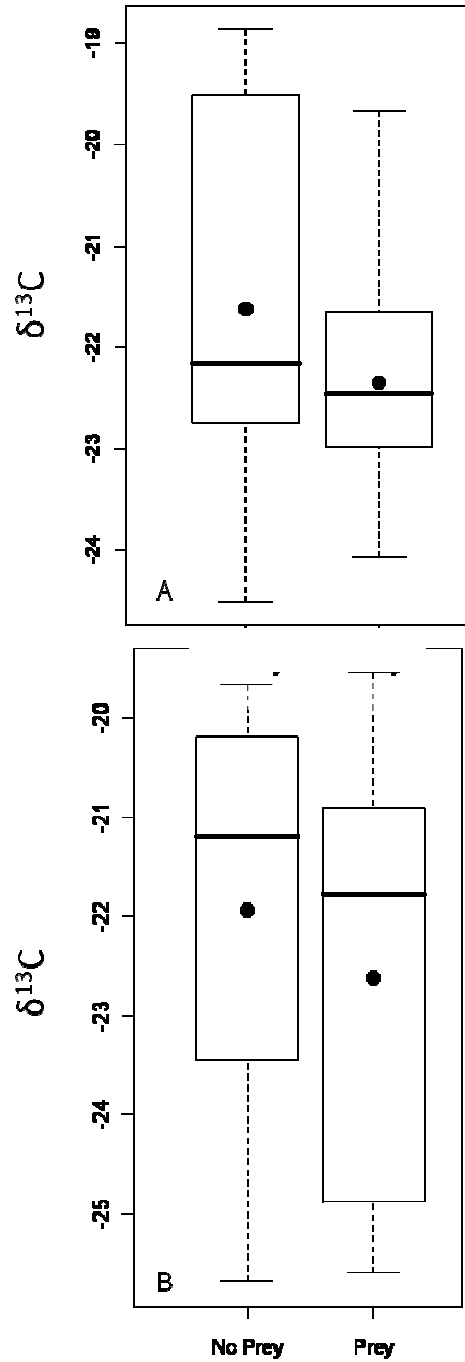
Figure 3-10. $\delta^{13}C$ values in relation to prey incidence (presence or absence of prey in the gut) for striped bass larvae in (A) 2007 and (B) 2008. Median (horizontal bars) and mean (solid circles) isotope values.
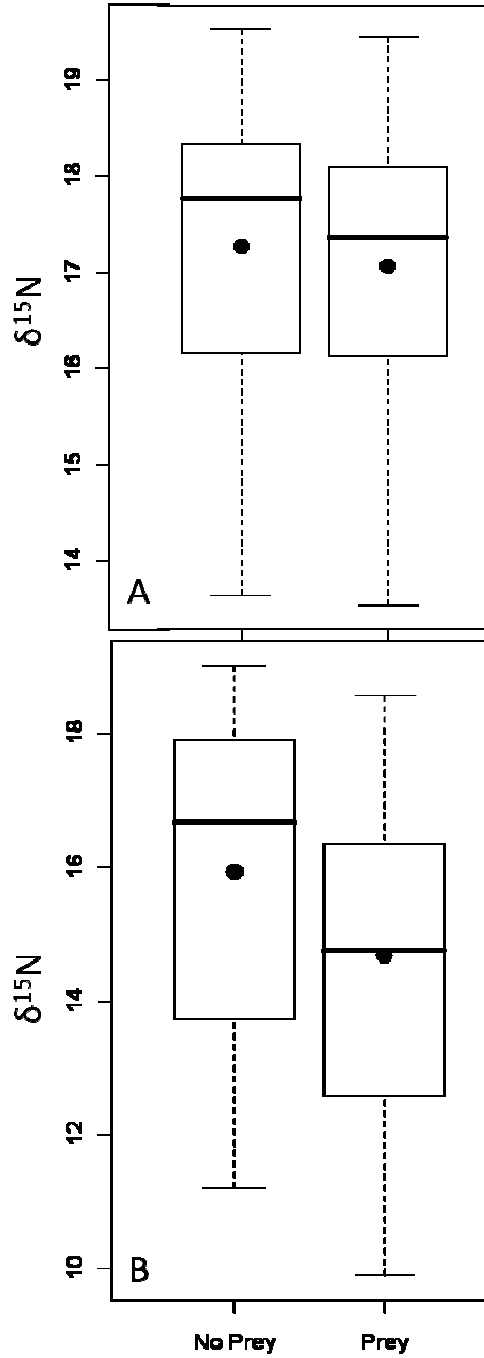
Figure 3-11. $\delta^{15}N$ values in relation to prey incidence (presence or absence of prey in the gut) for striped bass larvae in (A) 2007 and (B) 2008. Median (horizontal bars) and mean (solid circles) isotope values.
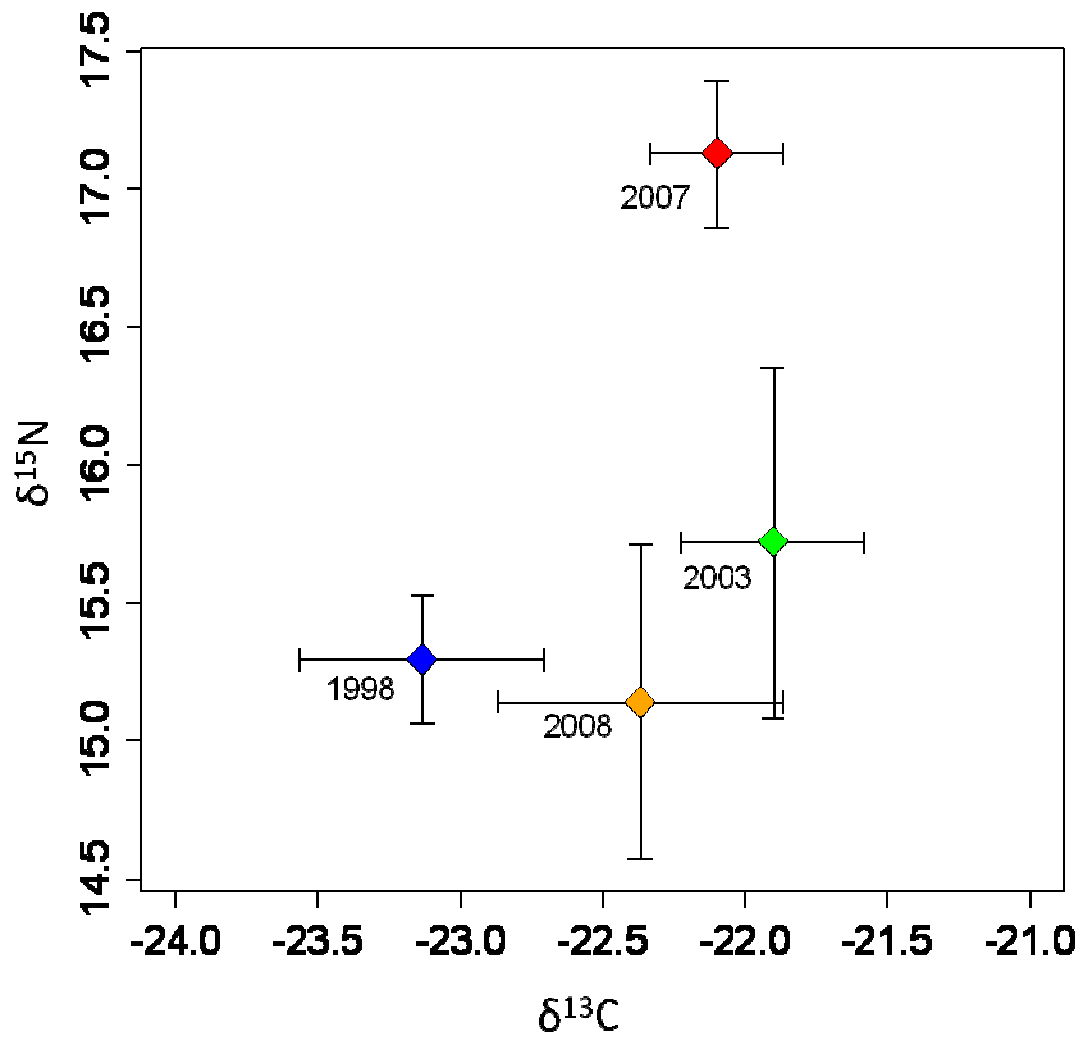
Figure 3-12. C-N bi-plots for stable isotope values of feeding-stage striped bass larvae in 1998, 2003, 2007, and 2008- -years of high (1998 and 2003), moderate (2007), and poor (2008) recruitment.
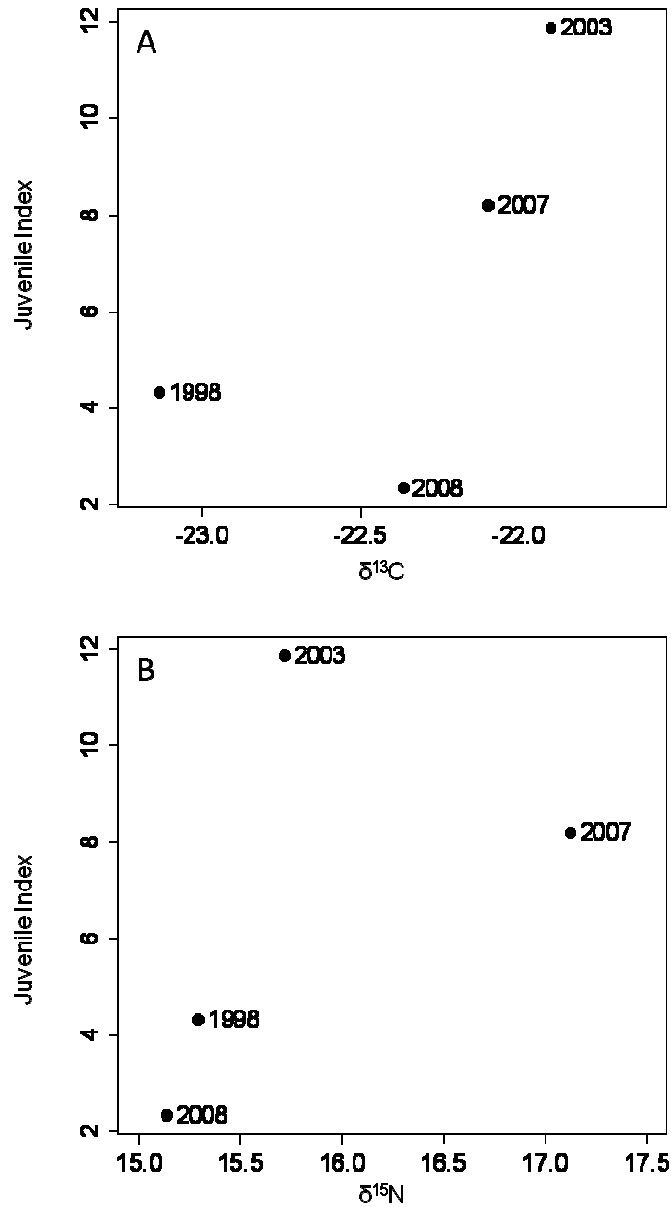
Figure 3-13. Relationship between young-of-the-year striped bass juvenile index (geometric mean) for upper Chesapeake Bay and mean values of (A) $\delta^{13}C$ and (B) $\delta^{15}N$ in larvae collected in 1998, 2003, 2007, and 2008 from the upper Chesapeake Bay. Juvenile index values were obtained from Maryland Department of Natural Resources (http://dnr.maryland.gov/fisheries/juvindex/).

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## Chapter 4: Summary and Conclusions

The region encompassing the estuarine turbidity maximum (ETM) and associated salt front constitutes the major nursery area for striped bass *Morone saxatilis* in Chesapeake Bay. In this research, spatial and temporal patterns in abundance, distribution, growth, feeding, and nutritional sources supporting early life stages of striped bass were investigated based on ichthyoplankton collected during years of average (2007) and poor (2008) recruitment. An objective of the research was to evaluate patterns in early life processes that potentially contribute to recruitment variability.

The thesis is presented in four chapters. Chapter 1 is an introduction that provides a summary of factors affecting larval survival, including a review of research on striped bass early life stages within ETM regions. Chapter 2 is an analysis of spatio-temporal variability in distribution and abundance patterns of zooplankton and striped bass early life stages and an otolith-aging analysis to estimate ages, hatch dates and growth rates of larvae. Chapter 3 investigates feeding, nutrient sources and trophic pathways supporting growth of striped bass larvae. Two approaches- -gut contents analysis and stable isotope analysis–were followed.  Chapter 4 is a summary and conclusions.

Summary:

1. Surveys to collect hydrographic data, ichthyoplankton and zooplankton were conducted along a 40-km transect in the upper Chesapeake Bay in April and May 2007 and in April, May, and June 2008.  The sampling region encompassed the salt front and ETM features. Samples were classified in terms of season (early spring: before 15 May; late spring: after 15 May) and

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location (up-estuary: > 5 km up-estuary of feature; within: ± 5 km of feature; down-estuary: > 5 km down-estuary of feature). Data were analyzed separately with respect to the salt front and ETM since locations of these features often differed.

2. Mean spring-months (March-April) freshwater flow was similar in each year (89,159 cfs in 2007 and 87,048 cfs in 2008), although pulse-flow events in 2007 were greater in magnitude and duration than in 2008. Water temperature increased as the spring season progressed, with variability in temperature associated with freshwater flow events occurring in both years. Water temperature reached the 12°C threshold for striped bass spawning 12 days earlier in 2008 than in 2007. However, temperatures were lower, on average, during the 2008 season than in 2007.

3. Mean concentrations of total prey, which included the copepod *Eurytemora affinis*, the cladoceran *Bosmina longirostris*, and the copepod *Acartia tonsa*, did not differ significantly between years, but spatio-temporal patterns did differ. In early spring 2007, higher concentrations of total prey were within the ETM than up-estuary. Lowest concentrations of total prey were located up-estuary of the salt front in early spring 2007. In 2008, concentrations of total prey were higher early in the spring than later. Spatially, total prey concentrations were lower up-estuary of the salt front in 2008.

4. Concentrations of *Eurytemora affinis* copepodites and adults, the most common prey of striped bass larvae, were similar in 2007 and 2008 (mean = 482.1 and 417.8 m$^{-3}$, respectively). In early spring 2007, concentrations down-

estuary of the salt front were higher than concentrations up-estuary. In 2008, concentrations of *Eurytemora* were higher early in the season and did not differ in location with respect to the salt front or ETM.

5. Mean concentration of *Bosmina longirostris*, the second most common prey, was > 10 times higher in 2007 than in 2008 (mean = 249.1 and 20.7 m$^{-3}$, respectively). In 2007, *Bosmina* was present in highest concentrations up-estuary of the salt front late in the season. In 2008, concentrations of *Bosmina* also were higher later in the spring, while spatially, higher concentrations were located up-estuary of the ETM than down-estuary.

6. Striped bass eggs were more than two times more abundant in 2007 than in 2008. In 2007, abundance was highest in the ETM and salt front. In 2008, abundance was highest up-estuary of the ETM and salt front.

7. Mean abundances of striped bass yolk-sac larvae were slightly, but not significantly, higher in 2008. In 2007, total abundances of yolk-sac larvae were highest up-estuary of and within the ETM and salt front. In 2008, abundances, although variable, tended to be highest within and down-estuary of the salt front, with only 22% of yolk-sac larvae located up-estuary of the salt front.

8. Feeding-stage larvae were more than five times more abundant in 2007 than in 2008. Total numbers of feeding-stage larvae were highest up-estuary of the salt front and ETM in 2007, with only 2% of feeding-stage larvae located down-estuary of the ETM. In 2008, > 55% of larvae were down-estuary of both the salt front and ETM.

9. Hatch-date distributions of larvae in collections differed significantly between years. In 2007, the hatch-date distribution was uni-modal with highest hatch frequency from 29 April to 1 May. In 2008, two peaks in hatch dates occurred: 29 April to 2 May and 27 to 30 May. The recorded inter-annual differences in hatch-date distributions could have resulted from late-season sampling in 2008.

10. Otolith-derived individual growth rates of striped bass feeding-stage larvae were slightly but significantly higher in 2007 than in 2008 (mean = 0.245 ± 0.007 se mm d$^{-1}$ and 0.223 ± 0.005 se mm d$^{-1}$, respectively).  Larvae collected down-estuary of the salt front and ETM experienced slowest growth rates.

11.  Overall prey incidence (the proportion of larvae with prey in gut) was nearly identical for feeding-stage striped bass larvae in 2007 and 2008 (62.6% and 63.5%, respectively). Highest prey incidence occurred within the ETM (68%) or salt front (66%) in 2007, while in 2008, locations within the ETM and up-estuary of the salt front had the highest percentages of larvae containing prey (66% and 69%, respectively).

12. The level (success) of feeding (measured as number of prey per gut) increased as a function of larval length in 2007 and 2008 and did not differ inter-annually. In 2007, the level of feeding did not differ by location with respect to the salt front or ETM. In 2008, larvae up-estuary of the salt front had significantly higher feeding success than larvae within the salt front.

13. The estuarine copepod *Eurytemora affinis* and the freshwater cladoceran *Bosmina longirostris* were important prey in the larval striped bass diet.

*Eurytemora* comprised a large percentage of diet regardless of location and year, while percent composition of *Bosmina* differed between years and spatially. In 2007, 32% of prey consumed was *Bosmina*, while only 5% of larval diet was attributed to *Bosmina* in 2008. In 2007, feeding-stage larvae had the highest percentage of *Bosmina* in the diet at locations up-estuary of the ETM and salt front. In 2008, larvae within the ETM had eaten a larger percentage of *Bosmina* than larvae up- or down-estuary.

14. Strauss' selectivity index indicated that *Eurytemora affinis* was positively selected throughout the study region in 2007 while B*osmina longirostris* was selected against. In 2008, larvae selected against *Eurytemora* up-estuary of the ETM or within the salt front. In 2008, larvae neither preferred nor avoided *Bosmina.*

15. Prey incidence and feeding success at time of collection were not related to growth rates of striped bass larvae in either 2007 or 2008.

16. *Bosmina longirostris* and *Eurytemora affinis* had distinct carbon and nitrogen stable isotope compositions. Mean values of $\delta^{13}$C and $\delta^{15}$N were depleted in *Bosmina* relative to *Eurytemora*, indicating that nutrition of *Bosmina* is more dependent on terrestrial carbon sources and feeds at a lower trophic level.

17. For *Eurytemora affinis*, there were no significant inter-annual differences in $\delta^{13}$C values, but $\delta^{15}$N was enriched in 2007 relative to 2008. In 2007, *Eurytemora* $\delta^{13}$C values increased with distance down-estuary. In 2008, *Eurytemora* down-estuary of the salt front was enriched in $\delta^{13}$C, implying a reliance on marine carbon sources. The $\delta^{15}$N values of *Eurytemora* also varied

spatially. In each year, *Eurytemora* collected up-estuary of the salt front and ETM had the highest values of $\delta^{15}N$. Up-estuary increases in $\delta^{15}N$ suggest a more omnivorous diet for *Eurytemora* located up-estuary of the ETM and salt front.

18. Isotopic composition of *Bosmina longirostris* differed between years. In 2007, mean $\delta^{13}C$ and $\delta^{15}N$ values were significantly enriched by 1.29‰ and 1.62‰, respectively, relative to values in 2008. Spatially, $\delta^{13}C$ and $\delta^{15}N$ of *Bosmina* within and up-estuary of the salt front and ETM were similar.

19. Stable isotope $\delta^{13}C$ and $\delta^{15}N$ values of yolk-sac larvae of striped bass were elevated compared to zooplankton and feeding-stage striped bass larvae. Stable isotope values of yolk-sac larvae, a life stage preceding active feeding, represent the maternal isotope signature. In 2008, yolk-sac larvae had higher $\delta^{13}C$ values than larvae in 2007. There was no inter-annual or spatial difference in mean $\delta^{15}N$ values for yolk-sac larvae.

20. As feeding-stage striped bass larvae increased in size, they experienced a downward shift in $\delta^{13}C$ from a maternally-derived marine signature to a more estuarine signature. In an analysis of covariance, slopes of relationships between $\delta^{13}C$ and larval length were similar in 2007 and 2008, but the intercept was significantly lower in 2008, indicating higher reliance on terrestrially-derived or freshwater carbon sources. There were no spatial differences in the $\delta^{13}C$-larval length relationship in either year.

21. For feeding-stage striped bass larvae there was no relationship between $\delta^{15}N$ values and total length. The mean $\delta^{15}N$ value was enriched by 1.99‰ in 2007

relative to 2008. In each year, feeding-stage mean $\delta^{15}$N values were highest up-estuary of the salt front and ETM, a result similar to spatial variation of $\delta^{15}$N in zooplankton prey.

22. Ratios of C:N of zooplankton taxa and larvae were measured concurrently with stable isotope analysis as a proxy for lipid content. Lipid content of *Eurytemora affinis* was slightly but significantly higher in 2007 than in 2008 but did not vary spatially in either year. There was no inter-annual or spatial variability in lipid content of *Bosmina longirostris* and yolk-sac larvae of striped bass. Notably, in 2007, feeding-stage larvae up-estuary of the salt front and ETM had significantly lower C:N ratios (and lipid content) than larvae within the features.

23. Young-of-the-year (YOY) recruitment index (Maryland Department of Natural Resources; http://dnr.maryland.gov/fisheries /juvindex/) values for striped bass were compared to $\delta^{13}$C and $\delta^{15}$N values of feeding-stage larvae collected in 1998, 2003, 2007, and 2008. There was no significant correlation between level of the YOY recruitment index and mean values of either stable isotope.

Recruitment indices of YOY striped bass in September (Maryland DNR) in the upper Chesapeake Bay were higher in 2007 than in 2008. The Maryland DNR index value in 2008 was almost four times lower than the index value in 2007 and less than half of the 30-year average. In the upper Bay, previous analyses of recruitment and environmental conditions suggested that high recruitment occurred in years of high

freshwater flow. Average spring freshwater flows were similar in 2007 and 2008, indicating that patterns in flow or other environmental factors are important in exercising control over recruitment variability.

In 2007, feeding-stage larvae were more abundant, with highest concentrations located up-estuary of the salt front and ETM, overlapping both spatially and temporally with high concentrations of the freshwater cladoceran *Bosmina longirostris* and the estuarine copepod *Eurytemora affinis*. In this year, concentrations of *Eurytemora* peaked earlier in the spring than *Bosmina* and were in highest concentrations down-estuary of the salt front. However, high concentrations of *Eurytemora* persisted later in the spring in 2007, overlapping the peak in occurrences of striped bass feeding-stage larvae and occurring in relatively high numbers near the salt front and ETM. Both *Eurytemora* and *Bosmina* are important prey, with the bulk of the larval diet composed of *E. affinis*. The relatively high consumption of *Bosmina* by larvae up-estuary of the salt front and ETM in 2007 may have provided important secondary support to larval nutrition and growth.

Stable isotope analysis may also help to explain factors contributing to recruitment variability in 2007 and 2008. Larvae in 2007 had $\delta^{15}N$ levels considerably higher than those in 2008, suggesting an additional trophic link in the food web that supported larval production. However, given the few years of data on stable isotope levels, variability in relative contributions of either terrestrial or marine carbon sources could not be confirmed as an indicator of YOY recruitment level.

Striped bass larvae grew faster in 2007 than in 2008, especially in locations up-estuary and within the salt front and ETM. Faster growth rates may have been supported by enhanced feeding success or related to the different nutritional content of food sources

up-estuary of the salt front and ETM in 2007. Regardless of the source, the increased growth rates may have favored higher recruitment in 2007 by reducing the larval stage duration.

Results presented here are for two years when striped bass experienced average (2007) and low (2008) recruitment success. Patterns in distribution and nutrition of striped bass larvae, based on results in my thesis research and on evidence from earlier research, are likely to differ in response to environmental conditions that prevail in a given year. The roles of the ETM and salt front, and their provision of support to larval retention and nutrition, differ from year-to-year, and are responsive to freshwater flow and other environmental variability. Future research investigating fine-scale spatio-temporal variability in the distribution, growth, and nutritional support of striped bass in the upper Chesapeake Bay during years of differing environmental conditions – especially freshwater flow – will provide additional insights and key information on trophic linkages that are critical for striped bass nutrition and growth.

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