

Abstract—Surveys were conducted to evaluate and compare assemblage structure and trophodynamics of ichthyoplankton, and their variability, in an estuarine transition zone. Environmental gradients in the salt-front region of the Patuxent River subestuary, Chesapeake Bay, were hypothesized to define spatiotemporal distributions and assemblages of ichthyoplankton. Larval fishes, zooplankton, and hydrographic data were collected during spring through early summer 2000 and 2001. Larvae of 28 fish species were collected and species richness was similar each year. Total larval abundance was highest in the oligohaline region down-estuary of the salt front in 2000, but highest at the salt front in 2001. Larvae of anadromous fishes were most abundant at or up-estuary of the salt front in both years. Two ichthyoplankton assemblages were distinguished: 1) riverine—characterized predominantly by anadromous species (Moronidae and Alosinae); and 2) estuarine—characterized predominantly by naked goby (*Gobiosoma bosc*) (Gobiidae). Temperature, dissolved oxygen, salinity-associated variables (e.g., salt-front location), and concentrations of larval prey, specifically the calanoid copepod *Eurytemora affinis* and the cladoceran *Bosmina longirostris*, were important indicators of larval fish abundance. In the tidal freshwater region up-estuary of the salt front, there was substantial diet overlap between congeneric striped bass (*Morone saxatilis*) and white perch (*M. americana*) larvae, and also larvae of alewife (*Alosa pseudoharengus*) (overlap = 0.71–0.93). Larval abundance, taxonomic diversity, and dietary overlap were highest within and up-estuary of the salt front, which serves to both structure the ichthyoplankton community and control trophic relationships in the estuarine transition zone.

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Ichthyoplankton community structure and comparative trophodynamics in an estuarine transition zone

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Anadromous and estuarine fishes migrate in the spring months to oligohaline and freshwater regions of tidal tributaries in Chesapeake Bay to spawn, potentially leading to overlapping distributions and diets of their larvae. Spawning seasonality overlaps broadly for anadromous alosines (shads and herrings [*Alosa* spp.]) and moronids (striped bass [*Morone saxatilis*], white perch [*M. americana*]). Estuarine species such as naked goby (*Gobiosoma bosc*) and bay anchovy (*Anchoa mitchilli*) also spawn during late spring and early summer in tidal tributaries, and their larvae occur in oligohaline regions, often near the salt front (Shenker et al., 1983; Loos and Perry, 1991).

There is limited information on foraging by larval fishes in Chesapeake Bay and the influences hydrographic features may have on foraging. Successful larval foraging improves with ontogeny as swimming ability and mouth gape increase, leading to shifts in types and sizes of zooplankton prey selected (Shirota, 1970; Arthur, 1976; Pepin and Penney, 1997). With some exceptions, larvae of closely related estuarine fishes in Chesapeake Bay often have similar diets (Setzler-Hamilton et al.¹) that could result in resource competition within larval

fish assemblages. Feeding habits of alewife (*Alosa pseudoharengus*) larvae in freshwater lakes (Norden, 1968), in laboratory experiments (Miller et al., 1990), and of congeneric larval alosines (American shad [*A. sapidissima*] and blueback herring [*A. aestivalis*]) in estuaries have been described (Crecco and Blake, 1983). Laboratory experiments on prey selection by naked goby larvae (Harding, 1999) and feeding by naked goby larvae in the Patuxent River (Breitbart, 1991) also are described. Foods and feeding by striped bass and white perch larvae have been reported (Setzler et al., 1981; Limburg et al., 1997; Chick and Van den Avyle, 1999; Shoji et al., 2005; Martino and Houde, 2010).

We refer to the frontal region where fresh and oligohaline waters merge as the estuarine transition zone, a region potentially important in controlling occurrences and feeding by fish larvae. This frontal region often contains an estuarine turbidity maximum (ETM) and is an important nursery area for young fish (North and Houde, 2001, 2003; Winkler et al., 2003; Shoji and Tanaka, 2006; Boynton et al.²). Previous research

¹ Setzler-Hamilton, E. M., P. W. Jones, G. E. Drewry, F. D. Martin, K. L. Ripple, M. Beaven, and J. A. Mihursky. 1982. A comparison of larval feeding habits among striped bass, white perch and Clupeidae in the Potomac Estuary. Rep. Md. Univ. Chesapeake Biol. Lab., no. 81–87, p. 1–127.

² Boynton, W. R., W. Boicourt, S. Brant, J. Hagy, L. Harding, E. D. Houde, D. V. Holliday, M. Jech, W. M. Kemp, C. Lascara, S. D. Leach, A. P. Madden, M. R. Roman, L. P. Sanford, and E. M. Smith. 1997. Interactions between physics and biology in the estuarine turbidity maximum (ETM) of Chesapeake Bay, USA. ICES Council Meeting Documents 1997/S:11. (www.ices.dk/products/cmdocsindex.asp).

in the mainstem of Chesapeake Bay has shown above-mean concentrations of zooplankton and larvae of anadromous striped bass and white perch near the salt front and associated ETM, where physical processes act to trap and concentrate plankton (North and Houde, 2001; Roman et al., 2001). Here, we identify ichthyoplankton assemblages and analyze the feeding ecology of larval fishes in the Patuxent River subestuary. We tested two hypotheses: 1) environmental gradients define spatiotemporal distributions and assemblages of ichthyoplankton in the estuarine transition zone; and 2) the salt front plays a key role in controlling assemblage structure and trophic interactions of larval fish communities.

In analyzing trophic relationships of fish larvae co-occurring in the estuarine transition zone, we addressed the following questions:

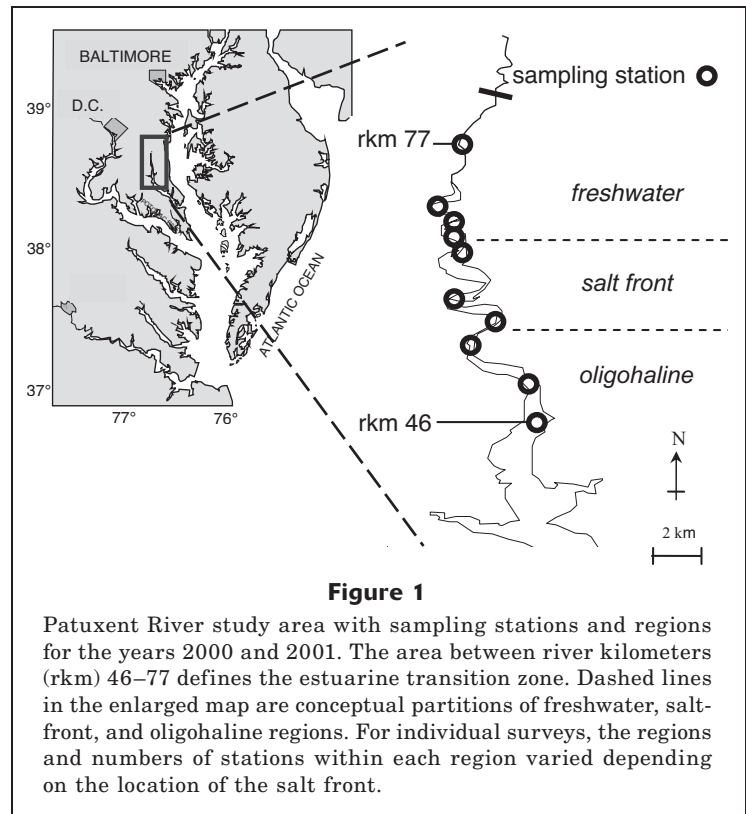
- Are diets controlled by the types of zooplankton prey available?
- Is there significant dietary overlap among co-occurring larval fishes?
- Do the salt front and estuarine transition zone control diets?
- Does selection of prey types and sizes shift during ontogeny?

Materials and methods

Study area and sampling procedures

Ichthyoplankton surveys on the tidal Patuxent River were conducted at 3–7 day intervals between 24 April and 5 July (13 surveys in 2000 and 17 surveys in 2001) to identify larval assemblages and shifts in seasonal abundances. Sampling was conducted from late spring to early summer to coincide with the peak seasonal spawning and larval production periods of anadromous and estuarine fishes. Samples were taken at 10 designated stations along the channel in the estuarine transition zone (Fig. 1). Stations were located at 2–7 river-kilometer intervals where depths ranged from 2 to 10 m. Surveys were conducted during daylight and were of 8–10 hours duration.

Sampling stations were located up-estuary, within, and down-estuary of the salt front in the estuarine transition zone (Fig. 1). The location of the salt front, defined by conductivities of 800–1000 μS (approximate salinities 0.4–0.5), was determined in each survey. Ichthyoplankton distributions, concentrations, and sizes were evaluated with respect to the salt front and site of intersection of the 2.0 isohaline with the bottom (referred to as X_2 by Jassby et al., 1995). Most surveys were conducted from an 8-m boat (11 surveys in 2000; 14 in 2001). Ichthyoplankton was sampled by towing a 60-cm diameter, paired bongo net with 333- μm meshes at 1 m/s in 5-min oblique tows from



the surface to the bottom. Flow meters in net mouths measured volumes of water sampled for use in calculating larval concentrations (no./m³). The mean volume filtered in each tow (combined paired-net samples) was 137 m³ (± 9 m³ standard deviation [SD]). In the final weeks of the survey during each year, juveniles and large larvae were sampled from a 16-m (2000) or a 19-m vessel (2001) with a 2-m² mouth-opening Tucker-trawl with 700- μm meshes (23 June and 5 July 2000, and 31 May, 27 June, and 3 July 2001). Oblique tows were of 5-min duration from near-bottom to surface at approximately 1 m/s and filtered a mean volume of 575 m³ (± 71 m³ SD). Ichthyoplankton samples were preserved in ethanol.

Zooplankton (potential prey for fish larvae) was collected at each station by pumping 20 liters of water from surface, middle, and bottom depths (60 liters total). Water from the three depths was combined and filtered onto a 35- μm sieve to concentrate zooplankton before preserving samples in 5% formalin. In the laboratory, zooplankters were identified, enumerated, and measured.

At each station, measurements of temperature, salinity, conductivity, and dissolved oxygen were made at surface, mid-water, and near-bottom for analysis of ichthyoplankton occurrence and abundance. Surface pH was measured at alternate stations. River-flow data were obtained from a U.S. Geological Survey gauge at river kilometer 130, near Bowie, Maryland (USGS, <http://waterdata.usgs.gov>, accessed April 2010).

Processing of samples

In the laboratory, fish larvae and juveniles were identified to species and enumerated. Total lengths (up to 100 individuals of each species per sample) were measured to the nearest 0.1 mm. Zooplankton concentrations (no./L) were estimated for several taxonomic categories, including copepodites and adults of the calanoid copepods *Eurytemora affinis* and *Acartia* sp., cyclopoid copepods, copepod nauplii, invertebrate eggs, rotifers, and the cladoceran *Bosmina longirostris*. Lengths of zooplankters were measured under microscope to the nearest 0.1 mm with an ocular micrometer.

Ichthyoplankton distributions, abundances, and assemblages

Larval concentrations (no./m³) at each sampling site were calculated from numbers per tow and measured tow volumes. Total larval abundances in river segments representative of each sampling site were estimated by expanding larval concentrations at sites to abundances in documented river-segment volumes (Cox et al.³). Abundances were analyzed with respect to hydrographic gradients. Species richness and Shannon-Wiener diversity (H') (Magurran, 1988) were calculated to compare ichthyoplankton assemblages among river regions. Habitat use and spatial overlap were examined in principal components analysis (PCA) of catch per unit of effort (CPUE, no. of larvae/tow) and hydrographic data to identify and describe associations (Miller, 2002).

Ichthyoplankton concentrations were analyzed for stations grouped into three designated regions within the estuary: freshwater, salt front, and oligohaline. Freshwater stations had no detectable salinity. Salt front stations had salinities of 0.2–1.0 and oligohaline stations had salinities >1.0. In each survey, a region typically included 3–4 stations (Fig. 1). Zooplankton and hydrographic variables were included in multivariate analyses to evaluate these factors with respect to larval concentrations of alewife, striped bass, white perch, and naked goby. In statistical analysis, the normality assumption generally was met by applying $\log_{10}(x+1)$ transformations to larval fish and zooplankton concentrations. Multiple regressions with larval concentration as the dependent variable were run on combinations of independent variables in a stepwise procedure (forward-backward) to select variables for inclusion as descriptors of larval concentration. Independent variables considered were temperature, salinity, conductivity, dissolved oxygen, pH, river flow, salt front location, and the concentrations of copepod nauplii, calanoid copepods, and *Bosmina*. The probability threshold for including or removing variables was 0.10. The quality of model fits was assessed by using Akaike's information criterion

(AIC). The model with lowest AIC value was retained for each larval taxon (Kleinbaum et al., 1998).

Diet composition

Digestive tracts of larval alewife, striped bass, white perch, and naked goby from the three designated regions were analyzed to determine feeding incidence, kinds of prey, prey numbers, prey sizes, prey selection, and dietary overlap. Larvae were grouped into 1-mm (naked goby) or 2-mm (other taxa) length intervals for diet analyses. In prey selection and dietary overlap comparisons, larvae were analyzed in broader length classes (<10 mm or >10 mm total length [TL]), except for naked goby which was analyzed as a single class (5–12 mm TL). All prey in larval guts were identified, enumerated, and measured with an ocular micrometer. Maximum lengths or widths of each prey taxon were recorded from each larval gut.

Diets of 633 larvae were analyzed (135 alewife; 165 striped bass; 200 white perch; 133 naked goby). Diets and zooplankton concentrations were evaluated from sampling sites throughout the estuarine transition zone (Fig. 1), and from the salt front and intersection of the 2.0 isohaline with bottom. Trophic niche breadth (S), a measure of variability in sizes of prey in the larval diet (Pearre, 1986) was defined as the standard deviation of mean logarithmic (\log_e) prey size. An ontogenetic index (O_L) (Fuiman et al., 1998) was calculated to characterize and compare feeding with respect to developmental state of larvae. Mean prey size and niche breadth estimates were regressed on larval length and ontogenetic state to examine patterns in the sizes of prey consumed.

Selection of prey types and sizes in larval diets was evaluated by applying Strauss's (1979) prey selection index:

$$L = r_i - p_i, \quad (1)$$

where r_i = the proportion of zooplankton prey type i in larval guts;

p_i = its proportion in the environment; and

L can range from -1.0 to $+1.0$.

Positive values indicate prey preference and negative values avoidance. The standard error of L was estimated (Strauss, 1982) and t -tests were conducted to determine whether L differed significantly ($P < 0.05$) from 0.

The importance of prey types and sizes in larval diets was evaluated with a relative importance index (George and Hadley, 1979). For each fish species, the importance (A) of prey type a , for length class i was computed with the following equation:

$$A_{i,a} = \% \text{ frequency of occurrence} \\ + \% \text{ total number} + \% \text{ total weight};$$

$$R_{i,a} = 100 \left(A_{i,a} / \sum_{a=1}^k A_{i,a} \right). \quad (2)$$

³ Cox, A. M., P. A. Waltz, and P. G. Robertson. 1980. Patuxent River Program. Bathymetric investigation of the Patuxent River system, p. 11–83. Maryland Department of Natural Resources, Water Resources Administration, Annapolis, MD.

$R_{i,a}$ (relative importance) is a measure of the importance of prey type a relative to other prey types. $R_{i,a}$ can range from 0 to 100, and high values indicate greater importance. Zooplankton length-weight relationships (Heinle, 1969) were used to estimate weights of prey in larval guts.

To evaluate possible competition, diet overlaps between larval taxa and length classes were evaluated from gut contents with Czechanowski's index: $O_{12}=O_{21}=1-0.5(\sum|P_{i1}-P_{i2}|)$ (Feinsinger et al., 1981). O_{12} is the overlap index value of species-length class 1 on species-length class 2, P_{i1} is the proportion of food type i eaten by species-length class 1, and P_{i2} is the proportion of food type i eaten by species-length class 2. Index values may range from 0.0 to 1.0. Values approaching 1.0 indicate strong overlap. Index values were tested for statistical significance by comparing them with null models following procedures of Albrecht and Gotelli (2001) and Gotelli and Entsminger (2003).

Results

Hydrographic conditions

There were strong gradients in hydrographic variables along the 31-rkm estuarine transition zone of the Patuxent River (Fig. 2). Highest temperatures were down-estuary. Salinities ranged from 0.0 to 10.0 and were highest down-estuary. Dissolved oxygen (DO) tended to be higher in the cooler and fresher up-estuary waters.

In 2000, precipitation and river flow were below the historical average and relatively constant. And, except for an unusual cooling episode in late May, river temperatures generally were $>20^{\circ}\text{C}$ during surveys and approached 29°C in early July (Fig. 3). In May, the salt-front location was stationary near river kilometer (rkm) 56 before shifting 5 rkm down-estuary in mid-June, coincident with small increases in precipitation and river flow. DO levels were >8.0 mg/L in May, but declined to approximately 6.0 mg/L as temperatures increased in June.

In 2001, hydrographic conditions were more variable (Fig. 3). Precipitation and river flow were below historical averages and more variable than in year 2000. River temperatures were $<20^{\circ}\text{C}$ in late April, fluctuated in early May, and gradually increased to $>25^{\circ}\text{C}$ by early summer. The salt front shifted 10 rkm up-estuary in early May, coincident with low precipitation and river flow, before moving 12 rkm down-estuary after high-flow events in late May–early June 2001.

The mean salt front locations were at rkm 56 in 2001 and rkm 54 in 2000. DO and pH levels were more variable in 2001. Although DO at mid-depth declined to 4.0 mg/L at down-estuary stations in early May 2001, DO generally ranged from 5 to 10 mg/L during the two years. The pH ranged from 7.0 to >9.0 and was consistently >7.0 in both years; on average, pH was slightly higher in 2001.

Species composition, diversity, and abundance of ichthyoplankton

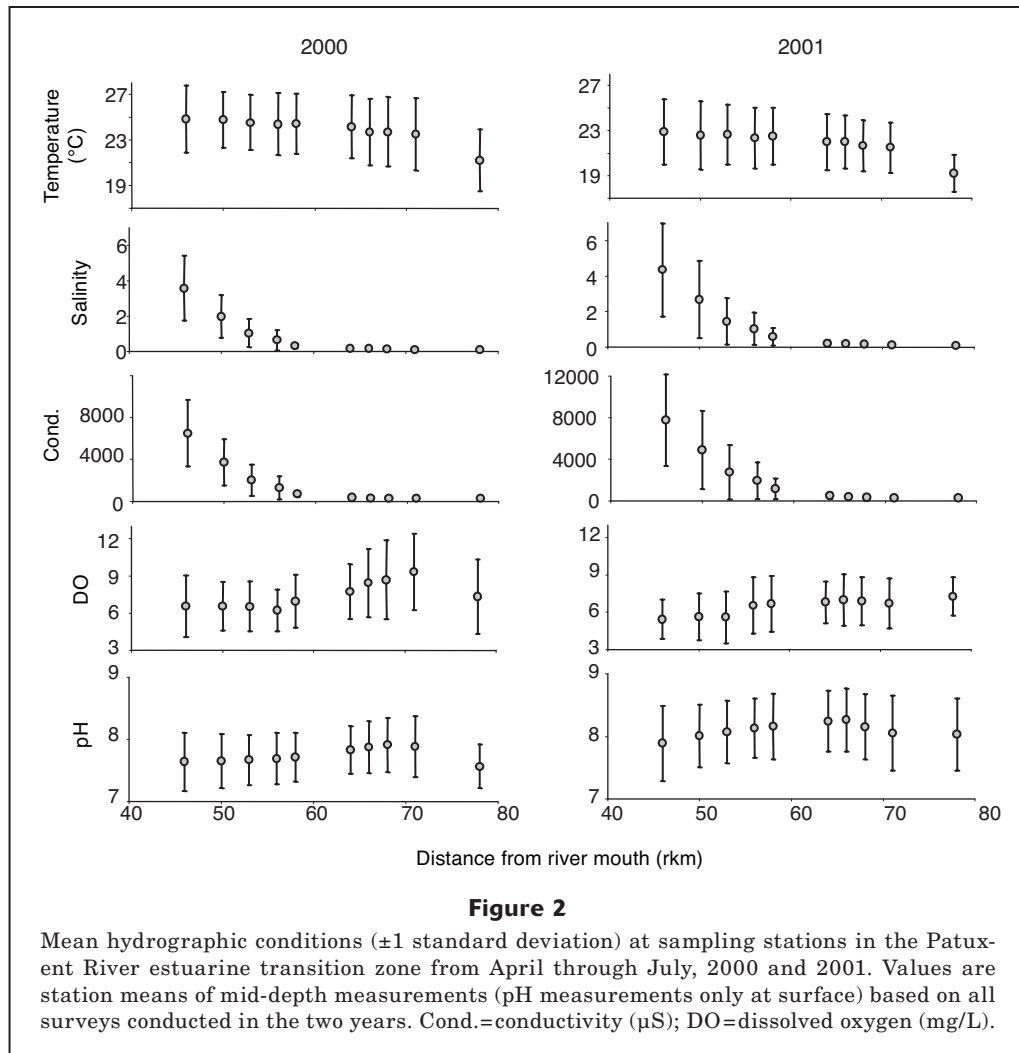
In the two survey years, a total of 198,161 fish larvae were collected, representing 28 taxa (Appendix Tables 1 and 2). Twenty of the taxa occurred in both years. Species richness over the entire survey area was similar between years ($n_{\text{spp.}, 2000}=24$, $n_{\text{spp.}, 2001}=23$). Species diversity was higher in the freshwater and salt-front regions ($H'=0.72-0.86$) than in down-estuary oligohaline waters ($H'=0.25-0.50$). Larval white perch, alewife, gizzard shad (*Dorosoma cepedianum*), and striped bass were the most abundant taxa in freshwater. Naked goby, white perch, and striped bass larvae were the most abundant taxa in salt front and oligohaline regions.

In both years, ichthyoplankton abundance was dominated by larvae of naked goby and white perch, which together comprised 94% and 89% of the catches, respectively, in 2000 and 2001. In 2000, catch per unit of effort (CPUE, no. of larvae/tow) was highest in the oligohaline region (625.1) where naked goby larvae dominated (Appendix Table 1). CPUEs were lower and similar in the salt front (278.9) and in freshwater (212.2). The coefficient of variation (CV) in CPUE, an indicator of spatial heterogeneity, indicated that catches were most variable in freshwater ($\text{CV}_{\text{FW}}=315\%$) and least variable at the salt front (154%). In 2001, CPUE was highest at the salt front (842.1) (Appendix Table 2) and lowest in the oligohaline region (189.6), primarily because larvae of naked goby were concentrated at the salt front in 2001. Relative variability in CPUE was similar across the freshwater, salt-front, and oligohaline regions in 2001 (CV range 217–254%).

Larvae of several freshwater fishes (spottail shiner [*Notropis hudsonius*]; darters [*Etheostoma* spp.]; suckers [*Erimyzon* spp.]; yellow perch [*Perca flavescens*]) were far more abundant in 2001 than in 2000 (Appendix Tables 1 and 2). For example, the concentration of yellow perch larvae was 15 times higher in 2001. In contrast, larvae of gizzard shad, a freshwater species, were 4 times more abundant in 2000 than in 2001.

Additionally, in the freshwater region in 2001, concentrations of white perch larvae were >2 times higher and concentrations of striped bass larvae were >10 times higher than in 2000 (Fig. 4). Larvae of anadromous striped bass also were relatively abundant at the salt front in 2001 than in 2000. Larvae of naked goby, an estuarine species, although of comparable abundance in the two years, were concentrated in the oligohaline region in 2000, but at the salt front in 2001 (Appendix Tables 1 and 2, Fig. 4). The regional difference in goby abundance between years may be related to differences in the timing of production of these larvae in the two years (Fig. 5). Goby larvae occurred first on 2 May in 2001 and had time to disperse into the salt front region during June. In 2000, goby larvae did not occur until 24 May and then were mostly collected in the oligohaline region, downriver from the salt front.

Differing regional patterns in overall larval abundance between years were largely attributable to the



two most abundant species, naked goby and white perch. In 2000, their mean combined-species CPUE increased directionally from freshwater to oligohaline regions (Appendix Table 1). In contrast, in 2001 their combined mean CPUE was highest at the salt front, intermediate in freshwater, and lowest in the oligohaline region (Appendix Table 2).

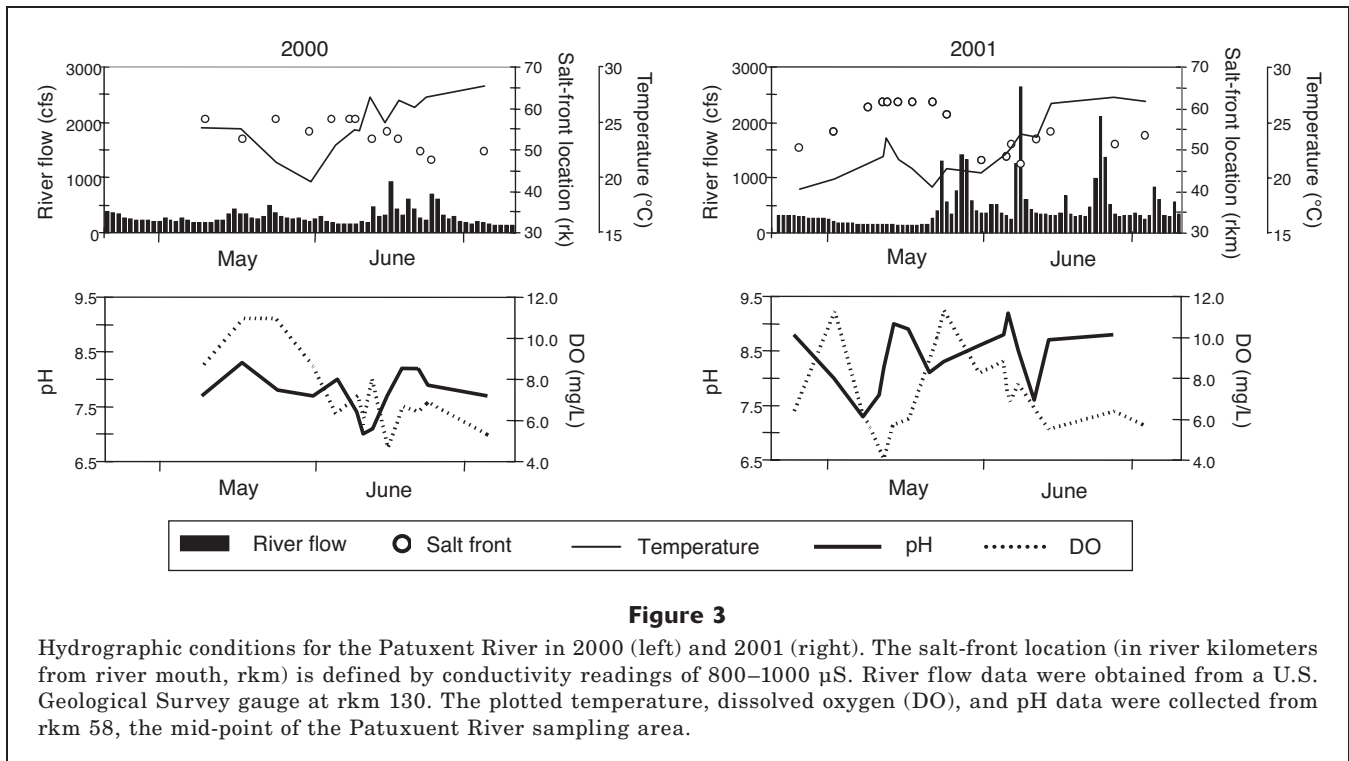
Occurrences and abundances of larvae of anadromous species differed with respect to location of the salt front. Yolk-sac larvae of striped bass occurred most frequently up-estuary of the salt front in tidal freshwater, whereas most feeding-stage larvae and small juveniles (<75 mm) were found either within or up-estuary of the salt front. White perch larvae were broadly distributed throughout the estuarine transition zone, overlapping with alosines (mostly alewife) and congeneric striped bass.

Larvae of alewife were consistently most abundant up-estuary of the salt front (Fig. 4). In 2001, larval white perch were clearly more abundant in freshwater than at the salt front or down-estuary, but in 2000 they were equally abundant at the salt front and in

freshwater. Larval striped bass concentrations did not differ significantly among the three regions ($P > 0.08$) or between 2000 and 2001 ($P > 0.07$), although their numbers tended to be relatively high at the salt front and in freshwater in 2001 (Fig. 4).

Temporal patterns in abundances of alewife, striped bass, and white perch were broadly similar in both years. Abundance of white perch larvae was an order of magnitude higher than striped bass in the earliest seasonal collections in each year and generally was higher than that of striped bass throughout the survey periods (Fig. 5). Although larval naked goby were present earlier in the season during 2001, their abundance peaked in the second week of June in both years (Fig. 5), when temperatures in the oligohaline region reached 25°C.

In each year, catches of larvae and small juveniles of the estuarine- and coastal-spawning species became increasingly common later in the sampling period. Small juveniles of menhaden and bay anchovy dominated the late-season (June and July) collections in Tucker trawls. Naked goby larvae occurred first in the oligohaline



region in May and were dispersed up-estuary where large individuals (>10 mm) occurred in the salt-front and freshwater regions in June and July.

Assemblage analysis

A principal components analysis (PCA) defined riverine and oligohaline ichthyoplankton assemblages in the estuarine transition zone (Fig. 6). The first two principal components explained 60% and 59% of the variance in assemblage structure in years 2000 and 2001, respectively:

- 1 Riverine assemblage—comprised anadromous and freshwater taxa, predominantly white perch, striped bass, alewife and other alosines, and gizzard shad. Yolk-sac larvae were common in this assemblage, which tended to occur in fresher, cooler, more oxygenated water.
- 2 Oligohaline assemblage—estuarine-spawning species, such as naked goby, characterized this low-diversity assemblage. In late June, when water temperature reached 25 °C, juvenile Atlantic menhaden and bay anchovy joined this assemblage.

Overall, assemblage structure and species associations were similar for the two years. Oligohaline and riverine assemblages were defined each year, but several constituent taxa (moronids, naked goby, alosines, and gizzard shad) from each assemblage were found at the salt front. Overlap between the two assemblages occurred at the lower end of the salinity vector in each year's PCA

(Fig. 6), coinciding with salinities of 0.2–1.0 that typically contain the salt-front feature.

Zooplankton distribution and abundance

Highest concentrations of combined zooplankton taxa occurred near and up-estuary of the salt front. Mean concentration was significantly higher in 2001 ($t=-4.59$, $P<0.01$), primarily because rotifers peaked at 4000/L. In 2000, when rotifers were less abundant, the seasonal trend in zooplankton abundance was driven by the cladoceran *Bosmina longirostris*.

Zooplankters that are potential prey for larval fish differed in their spatiotemporal patterns of distribution and abundance. Naupliar stages of copepods, mostly *Eurytemora affinis* or *Acartia tonsa*, were common throughout the sampling area, but were often most abundant near and down-estuary of the salt front. Mean nauplii concentration was higher in 2001 ($t=6.01$, $P<0.01$). The cladoceran *B. longirostris* was most abundant in the freshwater region (Fig. 7) and was uncommon at stations where salinity was >2. Its mean concentration did not differ significantly between years ($t=-0.68$, $P=0.50$).

Adult stages of the two abundant calanoid copepods, *Acartia tonsa* and *Eurytemora affinis*, had different distributions. *Acartia* occurred down-estuary of the salt front and abundance was similar in each year. *Eurytemora* were present throughout the estuarine transition zone, but usually were most abundant in the salt-front region, especially in 2001 (Fig. 7). The mean *Eurytemora* and *Acartia* concentrations did not differ

significantly between years (*Eurytemora*, $t=-1.35$, $P=0.18$; *Acartia*, $t=0.71$, $P=0.48$).

Cyclopoid copepods (primarily *Oithona* spp.) were more abundant ($P<0.01$) in 2000 than in 2001. Cyclopoid abundance was highest near or up-estuary of the salt front. In 2001, rotifers were the most abundant zooplankters and occurred in highest concentrations within or up-estuary of the salt front. Rotifer mean concentration was 12 times higher in 2001 than in 2000 ($P<0.01$).

Environmental factors and larval abundances

The descriptive analyses and PCA indicated that hydrographic factors and larval prey controlled ichthyoplankton distributions in the two years. Multiple regression models identified some environmental factors that explained variability in ichthyoplankton abundance (Table 1).

The model results indicated that alewife larvae were most abundant up-estuary of the salt front, where DO levels and *Bosmina* concentrations were highest (year 2000) and where temperatures were relatively cool (year 2001). For alewife, temperature, dissolved oxygen (DO), salt front location, and concentration of *Bosmina* were significant descriptors of larvae abundance.

For larval striped bass, concentrations of potential prey explained a significant proportion of variability in larvae abundance. In year 2000, salinity and concentrations of *Bosmina* and calanoid copepods were significant factors (Table 1). In 2001, potential prey, salt front location, DO, and temperature were positively related to striped bass abundance, which was highest near the salt front and coincident with high prey densities.

For white perch larvae, levels of salinity, DO, and temperature were positively related to white perch abundance in 2000, and highest concentrations were near the salt front, coincident with high prey concentrations (Table 1). The white perch regression model differed markedly in 2001 when only temperature and salinity explained a significant portion of variability in white perch larvae abundance.

For larvae of naked goby, concentration of copepod nauplii was a significant factor explaining goby abundance in year 2000 (Table 1) when concentrations were highest in oligohaline waters below the salt front that had relatively low DO levels, low *Bosmina* densities, and high copepod nauplii densities. In 2001, concentration of goby larvae was not significantly related to any prey-density variable, but larvae were most abundant in the relatively warm water within the salt-front region.

Diets and prey

Feeding incidence in the four taxa of fish larvae that we examined ranged from 72% to 97%. Feeding incidence

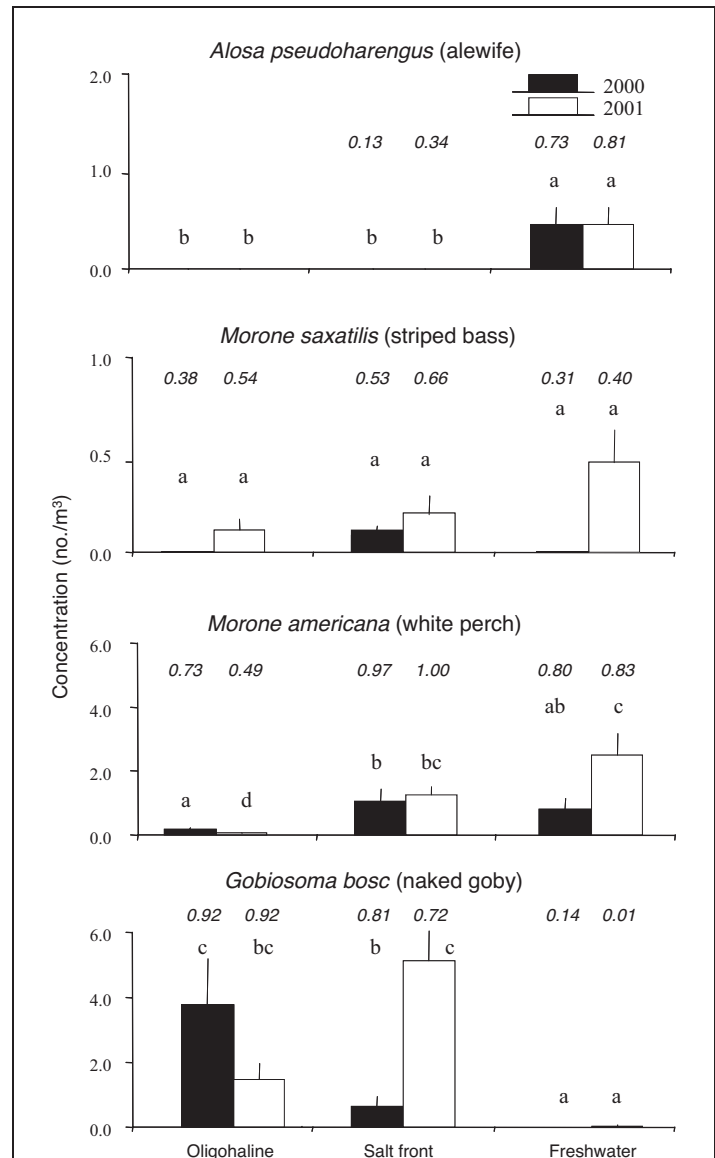
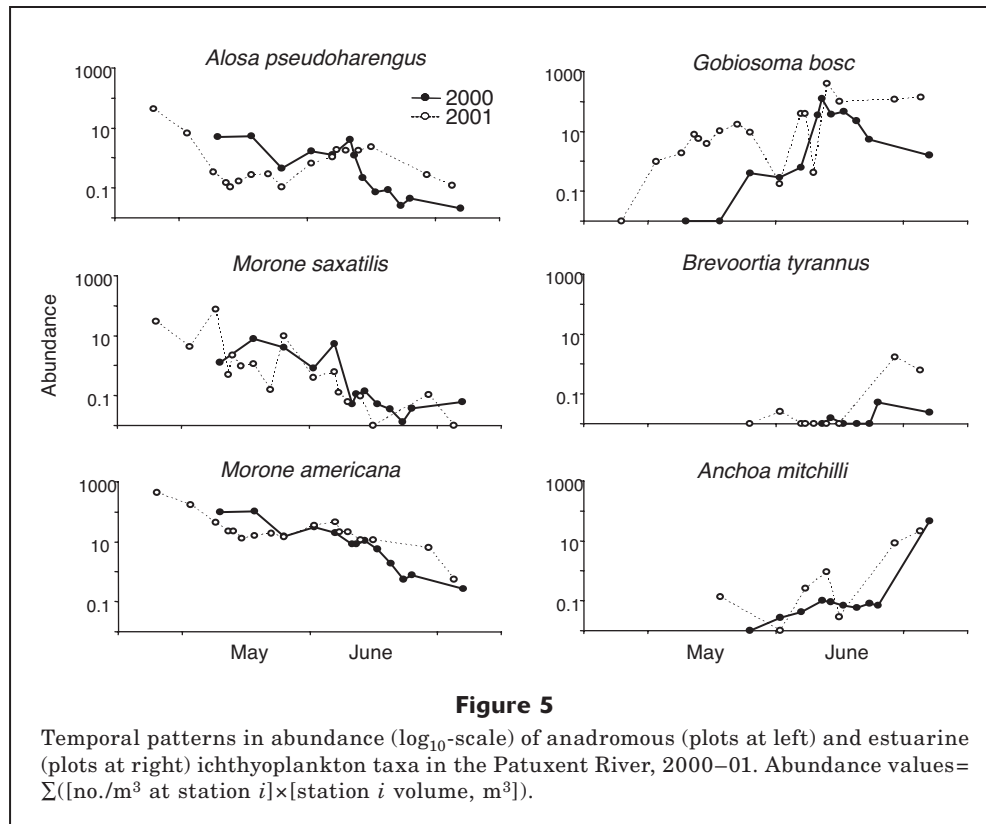


Figure 4

Larval concentrations (no./m³) by region. Student *t*-tests with unequal variances were applied. Significant differences are indicated by different letters ($P<0.05$). Vertical lines are standard errors of the mean. Note differences in scale of *y* axes. Values in italics are frequencies of positive tows.

did not differ significantly among the freshwater, salt-front, and oligohaline regions.

The diet of larval alewife was diverse (Fig. 8), differed between years, and shifted with ontogeny and growth. Copepod nauplii and rotifers represented >50% of diets in ≤ 11 mm alewife larvae. Invertebrate eggs and larger prey (i.e., *Eurytemora* and *Bosmina*) were more common in >11 mm alewife larvae. *Bosmina* and cyclopoid copepods were more frequent in alewife diets in 2000, whereas rotifers and *Eurytemora* were more common in 2001.



Striped bass larvae primarily consumed relatively large zooplankters (*Eurytemora*, *Acartia*, and *Bosmina*; Fig. 8), with no obvious ontogenetic shift in prey size. Calanoid copepodites and adults were the dominant prey of striped bass larvae down-estuary of the salt front. In the salt-front and freshwater regions, *Bosmina* was common prey of 11–19 mm larvae. *Acartia* was eaten by >11-mm striped bass only in year 2000 and only in the oligohaline region.

Diets of small white perch larvae were relatively diverse, but larger larvae fed predominantly on *Bosmina* and the calanoid copepods *Eurytemora* and *Acartia* (Fig. 8). The calanoid copepods were dominant prey down-estuary of the salt front. As for striped bass, *Acartia* was eaten by white perch only in 2000.

Naked goby larvae had the least diverse diet. In the oligohaline region, they fed almost exclusively on copepod nauplii and calanoid copepods, including *Acartia*, in both years (Fig. 8). In the salt front region, the diet of goby larvae was more diverse.

Prey utilization, preference, and importance

Mean prey size increased with larval length and ontogenetic state in alewife, white perch, and naked goby, but not in striped bass (Table 2). Functional relationships between prey ingestion and either larval size or ontogenetic state differed among taxa. Niche breadth (standard deviation of mean logarithmic prey size) increased significantly in naked goby with respect to

larval length or ontogenetic state, but not in the other species.

Larval prey preference and importance differed among the three regions of the estuarine transition zone and were generated primarily by prey availability and larval sizes. In general, *Eurytemora* was a preferred and important prey, especially for the moronid larvae and for large alewife larvae (>10 mm) (Table 3A). *Bosmina* was an important prey across taxa and larval sizes, but was only preferred by large white perch larvae and large striped bass larvae in the salt-front region. Rotifers and cyclopoid copepods were eaten, but were neither positively selected nor important prey for larvae of the four species. In the oligohaline region, *Acartia* was positively selected by naked goby and large (>10-mm) white perch larvae. Copepod nauplii were positively selected and important prey for small (<10-mm) alewife and naked goby larvae but were generally neither selected nor important for white perch and striped bass.

Overall, diets of large (>10-mm) larvae strongly overlapped among taxa ($O=0.88-0.90$). Diet overlaps among larval taxa and sizes were strongest in the freshwater region (Table 3B). However, the diet of small alewife in freshwater did not overlap significantly with diets of other taxa or size classes. At the salt front, the only significant overlap in diets of larval fish was between naked goby and small white perch (Table 3B). In the oligohaline region, diet overlap was

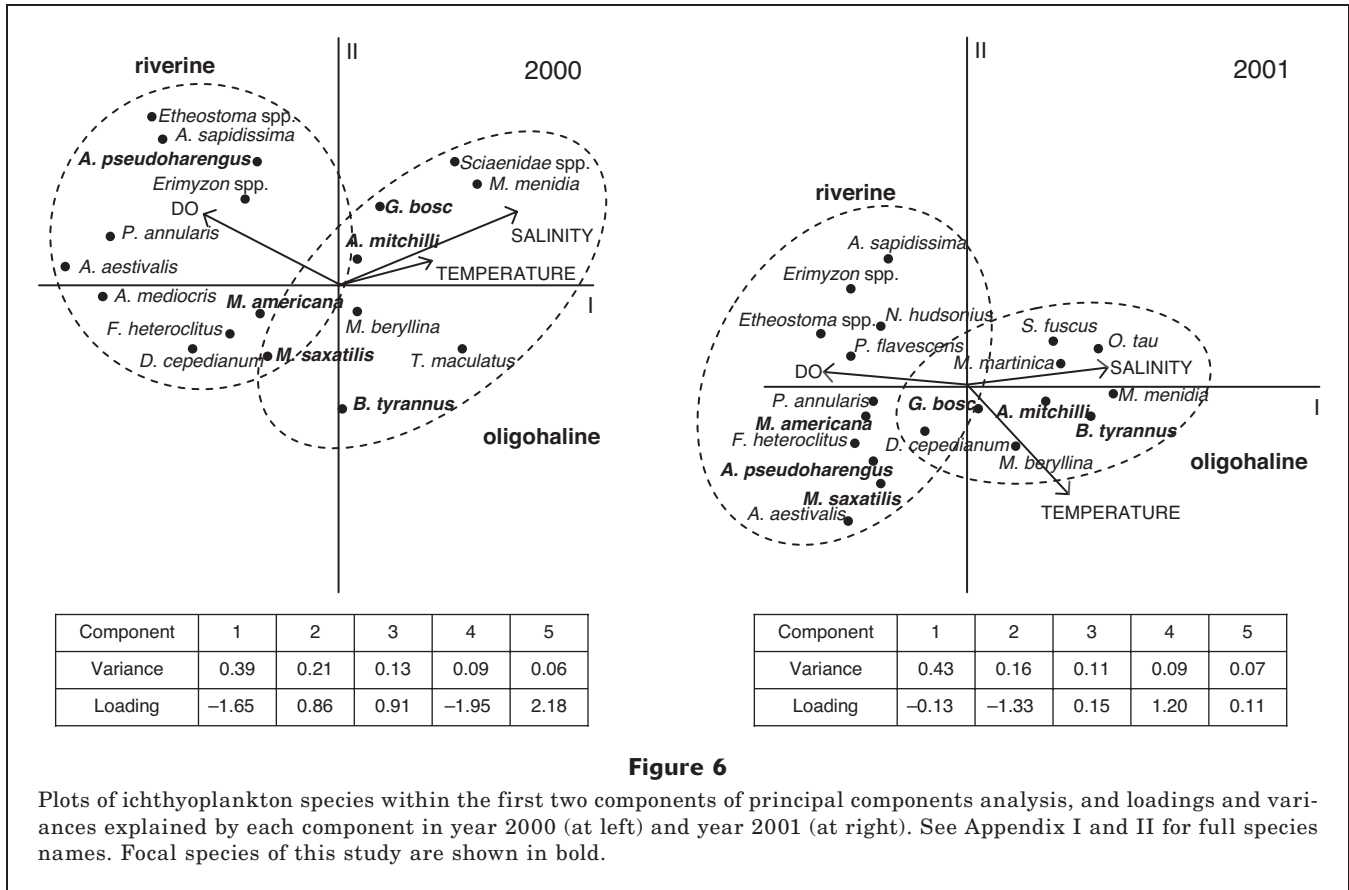


Figure 6

Plots of ichthyoplankton species within the first two components of principal components analysis, and loadings and variances explained by each component in year 2000 (at left) and year 2001 (at right). See Appendix I and II for full species names. Focal species of this study are shown in bold.

significant among large (>10-mm) white perch and striped bass larvae.

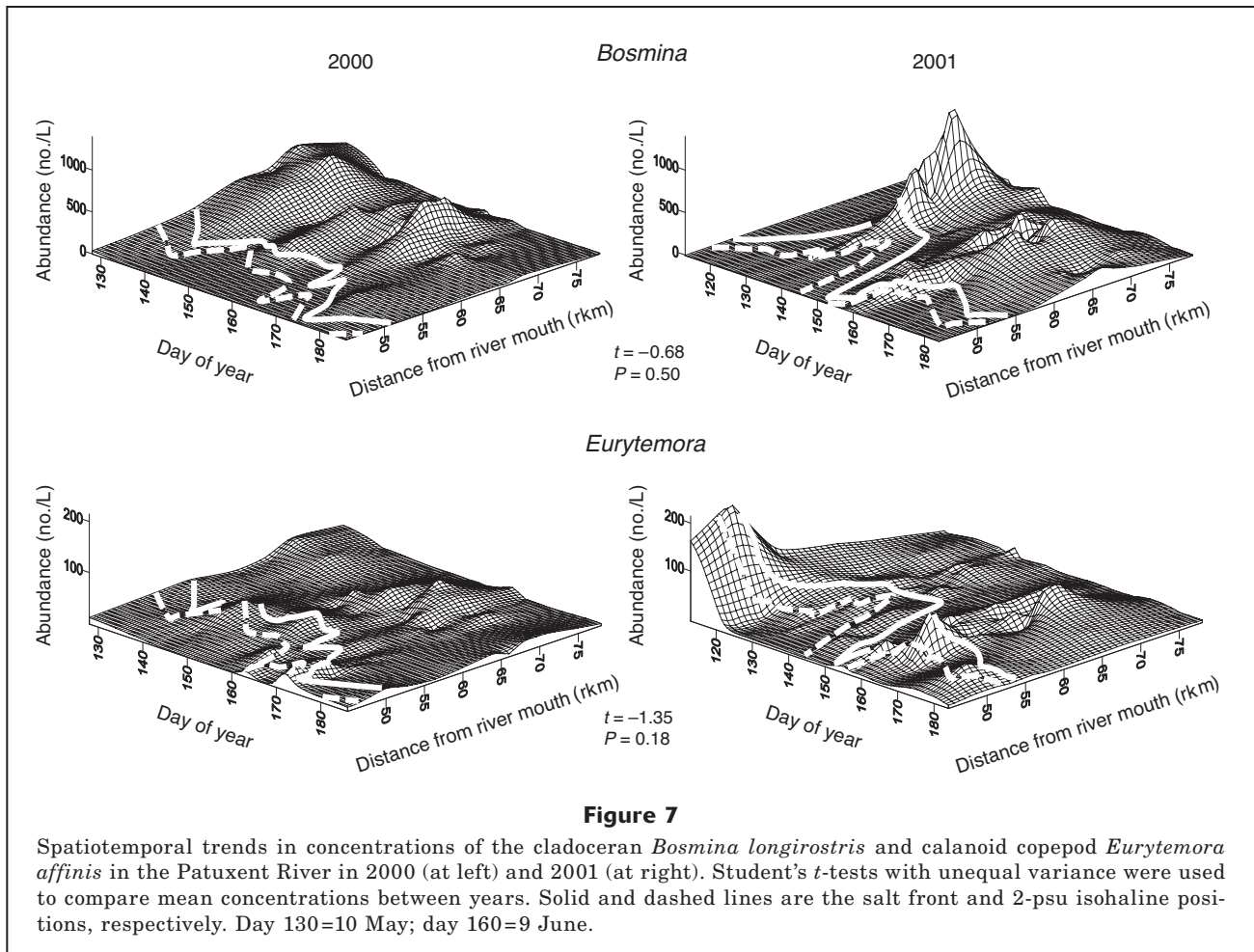
Discussion

Estuarine transition zones in coastal plain estuaries are regions of strong hydrographic gradients that control distributions of ichthyoplankton and zooplankton and, potentially, their trophic interactions. We propose that the larval assemblage structure, zooplankton distributions, and trophodynamics observed in the Patuxent River provide insight into the role of salt front-ETM features and dynamics in other temperate estuaries that receive variable freshwater inputs and which support fishes with diverse life histories (estuarine-dependent, anadromous, and freshwater resident). We documented interannual variability of the ichthyoplankton assemblages in the estuarine transition zone of the Patuxent River in 2000 and 2001. Two larval assemblages, riverine and estuarine, were identified in each year. In 2000, abundance of ichthyoplankton was highest in the oligohaline region immediately below the salt front, but in 2001 highest abundance was at the salt front. Our two hypotheses were supported: 1) environmental gradients defined distributions and assemblages of larvae, and 2) the salt front was a factor controlling assemblage structure and trophic interactions.

Larval assemblages and environmental factors

Moronid and alosine larvae occurred in fresh to oligohaline waters of the Patuxent River subestuary. Although moronids are commonly found in salinities of 0–3 (North and Houde, 2001), the distribution centers of alosine larvae occur in freshwater further up-estuary (Setzler et al., 1981; Bilkovic et al., 2002). In addition to interannual differences in overall distributions, ontogenetic migrations or shifts are common, resulting in species distributions that are most discrete during the earliest larval stages and greater overlaps in taxa distributions during ontogeny. For example, larvae of alewife at all stages were confined to the freshwater region, and small naked goby larvae were confined to the oligohaline region. However, during ontogeny naked goby larvae dispersed up-estuary and its late-stage larvae were found with alewife in freshwater.

A salt front and estuarine turbidity maximum (ETM) often characterize coastal plain estuaries. In Chesapeake Bay, they typically occur in the 0–3 salinity region of the mainstem Bay and its tributaries (North and Houde, 2001, 2003; Sanford et al., 2001). As larval fishes develop, they may converge at the salt front-ETM through passive transport and retention related to hydrographic and circulation features. Convergence also could be facilitated by active tracking by larvae of elevated zooplankton prey concentrations, especially



the copepod *Eurytemora affinis*, in the salt-front–ETM feature (Roman et al., 2001; North and Houde, 2006). Interannual differences in the timing and level of freshwater runoff control spatiotemporal variability in the salt front–ETM feature, and the occurrences, abundances, and distributions of striped bass larvae and their zooplankton prey (Martino and Houde, in press). The potential importance of the salt front as a retention feature has been recognized in previous research in Chesapeake Bay and its tributaries in which striped bass eggs or larvae, if advected below the salt front and ETM, apparently were lost to down-estuary dispersal (Secor et al., 1995; North and Houde, 2003; North et al., 2005; Secor and Houde⁴). Our survey results support these findings and, additionally, we have documented distributions and overlaps of larval taxa and zooplankton prey in this estuarine transition zone.

Larvae of striped bass and white perch were abundant above the salt front and in close proximity to

it. Their yolk-sac larvae were virtually absent down-estuary of the 2.0 isohaline and abundance levels of all moronid larval stages declined to near-zero levels down-estuary of the 2.0 isohaline. Declines and absences do not conclusively demonstrate failed retention or advective loss. However, Secor et al. (1995) released millions of marked, hatchery-source striped bass larvae in the Patuxent River and recaptured larvae from all release groups except those released below the salt front, providing strong circumstantial evidence that the front serves as a retention feature.

We documented patterns in ichthyoplankton taxa occurrences, distributions, and peak abundances in the estuarine transition zone that indicate a predictable seasonal progression in assemblage structure and distribution. A PCA identified riverine and estuarine ichthyoplankton assemblages. The two assemblages were characterized best by their occurrences with respect to salinity and, secondarily, to temperature and dissolved oxygen. Some taxa could not be assigned unambiguously to either the riverine or estuarine assemblage because of extensive overlap of taxa in the transition zone. This ambiguity differs from reported ichthyoplankton assemblage structures often observed

⁴ Secor, D. H., and E. D. Houde. 1996. Episodic water quality events and striped bass recruitment: larval mark-recapture experiments in the Nanticoke River. Final Report to Maryland Department of Natural Resources, 271 p. Center for Environmental Science, Univ. Maryland, Solomons, MD.

Table 1

Multiple regression models evaluating relationships between concentrations (no./m³) of common larval taxa (alewife [*Alosa pseudoharengus*], striped bass [*Morone saxatilis*], white perch [*Morone americana*], and naked goby [*Gobiosoma bosc*]) and abiotic and biotic variables in 2000 and 2001. Organism concentrations were log₁₀(x+1)-transformed. Independent variables were entered into models by using stepwise procedures. Parameter estimates and standard errors (in parentheses) are reported for independent variables that described a significant amount of variability in larval concentrations (*=*P*<0.10, **=*P*<0.05, ***=*P*<0.01). Akaike's information criterion (AIC) indicates quality of model fit. The salt-front location was modeled as a dichotomous variable (0 when the station located at or up-estuary of the salt front, 1 when below the salt front). *n*_{surveys, 2000} = 11; *n*_{surveys, 2001} = 14. *r*² = coefficient of determination.

Dependent variables	Independent variables							Model fit			
	Salinity	Temperature	Dissolved oxygen	Salt-front location	<i>Bosmina</i> cladocera	Calanoid copepods	Copepod nauplii	AIC	<i>r</i> ²	df _{model}	<i>P</i>
<i>Alosa pseudoharengus</i>											
2000			0.01 (0.01) *	-7.96 (3.20) **	1.17 (0.23) ***			4.76	0.88	3	<0.001
2001		-0.01 (0.01) *		-7.88 (1.16) ***				3.45	0.81	2	<0.001
<i>Morone saxatilis</i>											
2000	3.39 (0.62) ***				2.31 (0.43) ***	2.67 (1.39) *		15.15	0.86	3	0.002
2001		0.01 (0.01) *	0.03 (0.01) **	26.46 (4.14) ***	0.83 (0.23) ***	2.50 (0.59) ***		7.41	0.90	5	<0.001
<i>Morone americana</i>											
2000	1.28 (0.17) ***	0.01 (0.01) *	0.02 (0.01) **	11.62 (1.63) ***	1.62 (0.16) ***	2.40 (0.33) ***		0.61	0.99	6	<0.001
2001	-0.25 (0.03) ***	0.01 (0.01) *						2.22	0.84	2	<0.001
<i>Gobiosoma bosc</i>											
2000			-0.02 (0.01) **	6.65 (3.21) *	-1.12 (0.27) ***		0.90 (0.42) *	4.01	0.93	4	0.002
2001		0.01 (0.01) ***		8.64 (1.58) ***				7.45	0.76	2	<0.001

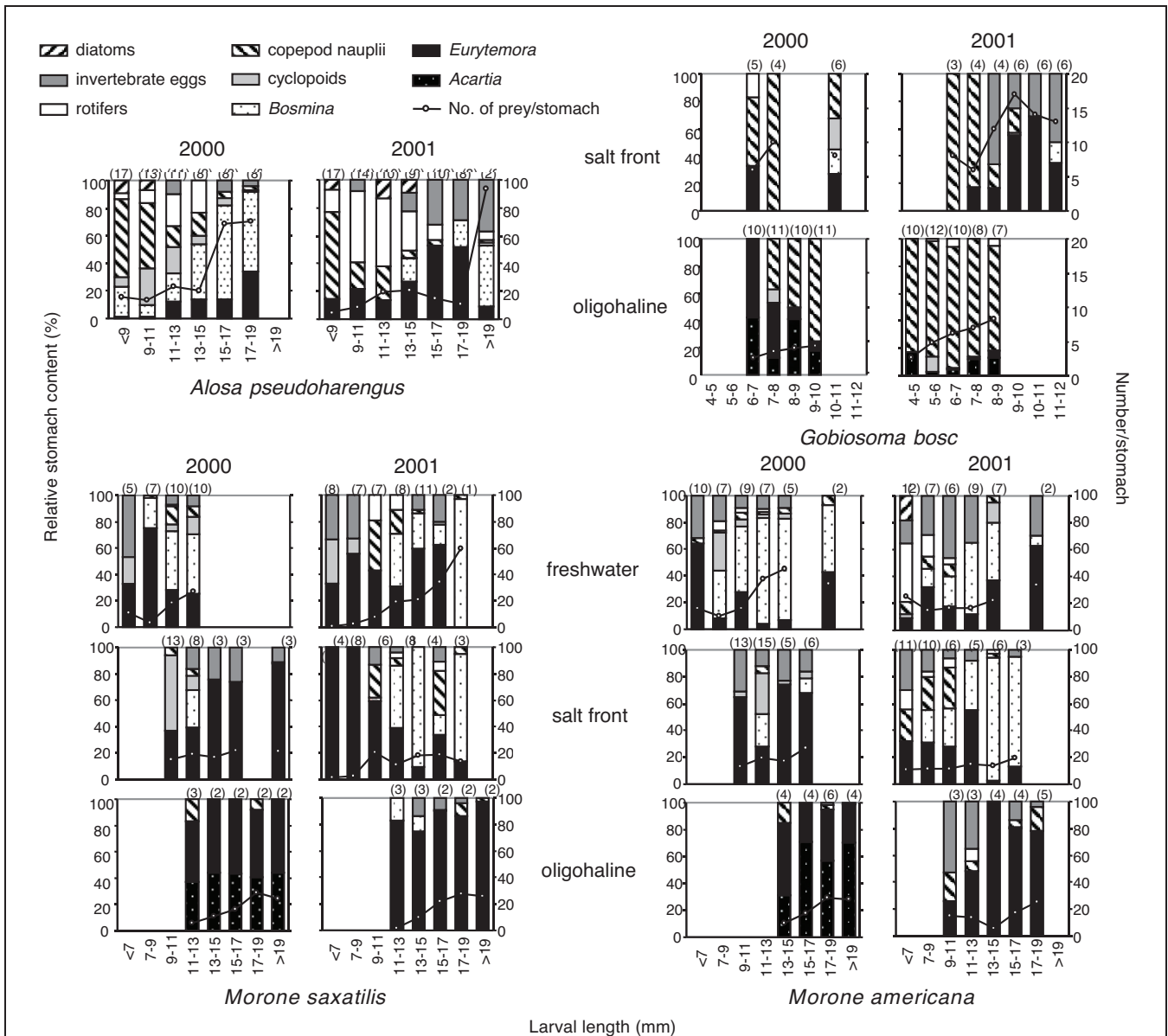


Figure 8

Relative stomach content (% by numbers; bars) and total stomach content (number of prey per stomach; lines) for 2-mm length classes of alewife (*Alosa pseudoharengus*) larvae (all sampled larvae were from freshwater stations), for 2-mm length classes of striped bass (*Morone saxatilis*) and white perch (*Morone americana*) larvae from freshwater, salt-front, and oligohaline stations, and for 1-mm length classes of naked goby (*Gobiosoma bosc*) larvae from salt-front and oligohaline stations. The number of larvae analyzed is shown in parentheses.

on continental shelves, where taxa in coastal and oceanic assemblages frequently have quite distinct distributions (Richardson et al., 1980; Young et al., 1986; Munk et al., 2004). In estuaries, gradients in larval and juvenile fish assemblages, often with overlaps, and seasonal shifts in taxonomic dominance are typically explained by salinity and temperature regimes (Rakocinski et al., 1996; Witting et al., 1999; Martino and Able, 2003) and this appears to be the case in the Patuxent River.

Strong gradients in water mass properties, especially temperature and salinity, combined with complex circulation processes at hydrographic fronts can act as hydrodynamic particle traps and provide favorable foraging habitat for fish larvae (Nakata et al., 1995; Munk, 1997; Hillgruber and Kloppmann, 1999; North and Houde, 2003; Islam and Tanaka, 2005). In estuaries, temperature and salinity often are the most important variables delineating ichthyoplankton distributions. As examples, in the St. Lucia estuary, South Africa, tem-

Table 2

Linear regressions evaluating larval total length (TL, mm) and ontogenetic state (O_L) in relation to logarithmic mean prey length (PL, μm) and trophic niche breadth (S) for common larval taxa in the Patuxent River, 2000–01. r^2 =coefficient of determination.

	Model	r^2	P
<i>Alosa pseudoharengus</i> (alewife), $n=135$			
Log _e prey length on larval length	$PL = 1.90 + 0.02TL$	0.17	0.01
Niche breadth on larval length	$S = 0.15 + 0.01TL$	0.06	0.12
Log _e prey length on ontogenetic state	$PL = 1.54 + 0.01O_L$	0.16	0.01
Niche breadth on ontogenetic state	$S = 0.02 + 0.01O_L$	0.06	0.14
<i>Morone saxatilis</i> (striped bass), $n=165$			
Log _e prey length on larval length	$PL = 2.58 - 0.01TL$	0.02	0.43
Niche breadth on larval length	$S = 0.17 + 0.01TL$	0.07	0.08
Log _e prey length on ontogenetic state	$PL = 2.73 - 0.01O_L$	0.02	0.32
Niche breadth on ontogenetic state	$S = 0.01 + 0.01O_L$	0.06	0.11
<i>Morone americana</i> (white perch), $n=200$			
Log _e prey length on larval length	$PL = 1.94 + 0.04TL$	0.49	0.01
Niche breadth on larval length	$S = 0.39 - 0.01TL$	0.03	0.27
Log _e prey length on ontogenetic state	$PL = 1.49 + 0.01O_L$	0.45	0.01
Niche breadth on ontogenetic state	$S = 0.41 - 0.01O_L$	0.01	0.55
<i>Gobiosoma bosc</i> (naked goby), $n=133$			
Log _e prey length on larval length	$PL = 2.07 + 0.03TL$	0.18	0.05
Niche breadth on larval length	$S = 0.13 + 0.05TL$	0.60	0.01
Log _e prey length on ontogenetic state	$PL = 1.82 + 0.01O_L$	0.19	0.05
Niche breadth on ontogenetic state	$S = 0.50 + 0.01O_L$	0.56	0.01

perature was the most important variable explaining larval fish distributions and abundances (Harris et al., 1999) and salinity was most important in the Tanshui River estuary, Taiwan (Tzeng and Wang, 1993). Larval fish distributions and abundances in estuaries tend to be most responsive to salinity-related factors (e.g., salt-front location), which can be strongly linked to precipitation and freshwater flow. In the Patuxent River subestuary, we found that concentrations of particular zooplankton prey, which also are responsive to salinity and temperature conditions, were significant in explaining ichthyoplankton abundances and distributions.

In multiple regression models, the location of the salt front usually was a good indicator of larval concentrations for most taxa included in the models (Table 1). Additionally, concentrations of anadromous fish larvae were highest where densities of the cladoceran *Bosmina longirostris* and calanoid copepods were high. These zooplankters, which are important prey for fish larvae in Chesapeake Bay (Setzler et al., 1981; Shoji et al., 2005; North and Houde, 2006; Martino and Houde, 2010), were significant in explaining concentrations of larvae of anadromous species in the Patuxent River, but not the estuarine naked goby. Goby larvae tended to occur where concentrations of copepod nauplii were high down-estuary of the salt front.

Concentrations of zooplankton that are potential prey were significant explanatory variables in regression models for all ichthyoplankton taxa in 2000, but were less important in 2001. The reasons for the differences

between years are unclear, but may be explained in part by the greater variability and intensity in estuarine physics (river flow, salt front location) in 2001. In the Hudson River, Limburg et al. (1999) reported that cohorts of larval moronids co-occurring temporally and spatially with zooplankton blooms, including *Bosmina*, had higher recruitment potential. In Chesapeake Bay and its tributaries, temperature and freshwater flow may be of equal or greater importance (Rutherford and Houde, 1995; North and Houde 2001), although recent evidence has identified a strong relationship between recruitment success of striped bass and a temporal-spatial match of zooplankton production in the ETM region (Martino and Houde, 2010).

Trophic interactions

Larval diets in the estuarine transition zone were influenced by the composition of the zooplankton community, which differed in 2000 and 2001. On average, the location of the salt front was similar in both years. But, more variable temporal trends in river flow and temperature in 2001 affected the timing, intensity, and spatial distribution of copepod and *Bosmina* production that in turn influenced larval diets. Cyclopoid copepods, which were 16 times more abundant in 2000 than in 2001, were common in larval fish diets only in 2000. Copepod nauplii and rotifers were relatively important in diets of larval moronids and naked goby in 2001 when these small zooplankters were most abundant

Table 3

(A) Prey preferences and importance of prey types and (B) dietary overlap for larval fish taxa and size classes common in the Patuxent River, 2000–01. Relative importance index R_i values are shown in italics. * indicates significant ($P < 0.05$) Strauss's selection index L values. Significance of Czechanowski overlap index O values are indicated by * $P < 0.05$ or ** $P < 0.01$. AP = alewife (*Alosa pseudoharengus*); MS = striped bass (*Morone saxatilis*); MA = white perch (*Morone americana*); GB = naked goby (*Gobiosoma bosc*).

A	Freshwater						Salt front						Oligohaline	
	AP <10 mm	AP >10 mm	MS <10 mm	MS >10 mm	MA <10 mm	MA >10 mm	GB	MS <10 mm	MS >10 mm	MA <10 mm	MA >10 mm	GB	MS >10 mm	MA >10 mm
<i>Acartia</i>														
<i>Eurytemora</i>	+0.05	+0.17*	+0.41*	+0.16*	0.20*	+0.19*	+0.26*	+0.87*	+0.11*	+0.17*	+0.12*	+0.07	+0.07	+0.10*
	<i>13.03</i>	<i>14.84</i>	<i>55.76</i>	<i>30.73</i>	<i>34.71</i>	<i>30.33</i>	<i>48.25</i>	<i>100.00</i>	<i>35.14</i>	<i>44.71</i>	<i>34.38</i>	<i>16.86</i>	<i>41.66</i>	<i>38.11</i>
<i>Bosmina</i>	-0.35*	-0.21*	-0.27*	-0.07	-0.19*	+0.10*	-0.14*	-0.17*	+0.13*	-0.06	+0.15*	-0.04	+0.02	-0.04
	<i>18.50</i>	<i>33.31</i>	<i>25.50</i>	<i>29.13</i>	<i>17.75</i>	<i>34.27</i>	<i>5.81</i>	<i>0.00</i>	<i>26.78</i>	<i>12.89</i>	<i>26.63</i>	<i>0.00</i>	<i>3.20</i>	<i>2.13</i>
Cyclopoids	+0.04	+0.01	-0.01	+0.01	+0.05	+0.01	-0.11*	-0.13	-0.04	-0.13*	+0.02	+0.03	-0.01	-0.01
	<i>18.07</i>	<i>12.02</i>	<i>2.59</i>	<i>12.07</i>	<i>11.20</i>	<i>9.41</i>	<i>3.63</i>	<i>0.00</i>	<i>13.04</i>	<i>0.00</i>	<i>20.40</i>	<i>14.08</i>	<i>0.00</i>	<i>3.22</i>
Copepod nauplii	+0.41*	0.00	-0.12*	-0.03	-0.08	-0.08	+0.03	-0.25*	-0.16*	0.00	-0.22*	+0.13*	-0.42*	-0.39*
	<i>39.45</i>	<i>17.04</i>	<i>9.61</i>	<i>11.30</i>	<i>10.15</i>	<i>10.54</i>	<i>28.25</i>	<i>0.00</i>	<i>10.02</i>	<i>23.38</i>	<i>4.46</i>	<i>46.70</i>	<i>8.72</i>	<i>9.99</i>
Rotifers	-0.13*	-0.04	-0.26*	-0.19*	-0.15*	-0.24*	-0.25*	-0.26*	-0.24*	-0.15*	-0.26*	-0.19*	-0.21*	-0.19*
	<i>10.96</i>	<i>18.14</i>	<i>0.00</i>	<i>6.72</i>	<i>11.08</i>	<i>5.58</i>	<i>1.94</i>	<i>0.00</i>	<i>3.52</i>	<i>11.15</i>	<i>2.31</i>	<i>3.96</i>	<i>0.00</i>	<i>0.00</i>
Invertebrate eggs	-0.12*	+0.01	+0.04	+0.10*	+0.15*	+0.01	+0.08	-0.04	+0.07	+0.06	+0.07	-0.02	+0.09	+0.07
	<i>0.00</i>	<i>4.64</i>	<i>6.54</i>	<i>10.05</i>	<i>15.11</i>	<i>9.87</i>	<i>12.12</i>	<i>0.00</i>	<i>11.49</i>	<i>7.87</i>	<i>11.82</i>	<i>0.00</i>	<i>14.44</i>	<i>17.12</i>
B	AP <10 mm	AP >10 mm	MS <10 mm	MS >10 mm	MA <10 mm	MA >10 mm	GB	MS <10 mm	MS >10 mm	MA <10 mm	MA >10 mm	GB	MS >10 mm	MA >10 mm
AP>10 mm	0.55													
MS<10 mm	0.44	0.73					0.58							
MS>10 mm	0.50	0.90**	0.71				0.71	0.52				0.35		
MA<10 mm	0.52	0.87*	0.71	0.93**			0.86**	0.46	0.46					
MA>10 mm	0.45	0.88*	0.79*	0.88*	0.85*		0.66	0.50	0.51	0.68		0.41	0.81**	

in the plankton. Although mean concentrations of *Bosmina* and calanoid copepods did not differ significantly in 2000 and 2001, their representation in larval diets did differ. For example, larval alewife and white perch in the freshwater region consumed higher proportions of *Bosmina* in 2000, whereas larval striped bass in the salt-front region consumed more *Bosmina* in 2001. The calanoid copepod *Acartia* occurred down-estuary of the salt front in the oligohaline region and was equally abundant during the two years but was common in diets of moronid larvae only in 2000. We could not explain why consumption of *Acartia* differed between the two years but note that moronid larvae in 2001 strongly preferred *Eurytemora* as prey.

Feeding incidences (72–97%) in larvae and mean numbers of prey per gut (typically 5–50 zooplankters) were high in the salt front-ETM of the Patuxent River. In the estuarine transition zone, the two calanoid copepods *Eurytemora affinis* and *Acartia* sp. were important and generally were positively selected prey. Only small alewife larvae, which have small mouth gape, did not select these relatively large calanoid copepods. The abundant cladoceran *Bosmina* also was important prey of fish larvae, although it usually was not positively selected. Combined contributions of the important, larger prey *Bosmina* and *Eurytemora* to diets of larger larvae were highest within and up-estuary of the salt-front-ETM.

The copepod *Eurytemora affinis* was the most important food of white perch and striped bass larvae in the Patuxent River. It also was the most important prey consumed by these larvae in the salt-front-ETM of upper Chesapeake Bay and was particularly important in high freshwater-flow years (Shoji et al., 2005; Martino and Houde, 2010). This copepod is hypothesized to play a vital role in supporting the nutrition of larval fishes in the salt-front transition regions of Chesapeake Bay (North and Houde, 2006) and its tributaries, a role similar to that proposed for the calanoid copepod *Sinocalanus sinensis* and larval Japanese sea bass *Lateolabrax japonicus* in the transition region of the Chikugo River estuary (Islam and Tanaka, 2005; Shoji and Tanaka, 2007).

Although concentrations of fish larvae are often high, with taxa overlaps in the salt front-ETM region, it is not certain that feeding competition occurs. Larval fish populations generally are not capable of significantly grazing down zooplankton prey resources (Pepin and Penney, 2000). Still, it is possible that foraging interactions are intense where larvae are highly concentrated. In the estuary, diet overlaps among larvae may be of greatest consequence in the salt front-ETM region where larvae of estuarine species such as naked goby and anadromous species such as white perch and striped bass are abundant and have a common preference for *Eurytemora* as prey. Despite differences in the hydrographic conditions and prey available to larvae in the Patuxent River, the abundances of juvenile striped bass, white perch, and alewives in the summers of 2000 and 2001, based on monitoring surveys conducted by

Maryland Department of Natural Resources (<http://www.dnr.state.md.us/fisheries/juvinindex/index.html>, accessed April 2010), were similar, indicating that environmental conditions in these two years were not sufficiently different to generate the high (up to 100-fold) recruitment variability seen in the 25-yr survey time series.

Hydrographic features define assemblages and, in part, control trophic relationships of ichthyoplankton and zooplankton within estuarine transition zones. The larvae of many fish species and abundant zooplankton prey coexist here, within and up-estuary of the salt front and ETM. High dietary overlap is indicative of strong trophic interactions among larval fish taxa. Despite the potential for competition, larvae in this transition region may have a trophodynamic advantage derived from high prey densities and the benefits of hydrodynamic retention. Together, these conditions provide a relatively stable environment that is favorable for larval production and survival in the estuarine transition region.

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Appendix Table 1

Year 2000. Larval fishes: species composition, frequency of occurrence (Freq=proportion of tows positive), no./tow, and standard error (SE) of no./tow by region in the Patuxent River estuarine transition zone from spring through early summer 2000. The salt front region includes stations ± 3 rkm from the salt-front location (see Fig. 1). H' =Shannon-Wiener diversity index values ($H'_{\max}=2.0$).

Species	Freshwater			Salt front			Oligohaline		
	Freq	no./tow	SE	Freq	no./tow	SE	Freq	no./tow	SE
<i>Anguilla rostrata</i> (American eel)	0.01	0.01	0.01	—	—	—	—	—	—
<i>Anchoa mitchilli</i> (bay anchovy)	0.01	0.01	0.01	0.19	0.31	0.15	0.35	0.73	0.26
<i>Alosa aestivalis</i> (blueback herring)	0.14	0.52	0.20	—	—	—	—	—	—
<i>Alosa mediocris</i> (hickory shad)	0.07	0.09	0.04	0.03	0.03	0.03	—	—	—
<i>Alosa sapidissima</i> (American shad)	0.10	0.13	0.05	0.03	0.03	0.03	—	—	—
<i>Alosa pseudoharengus</i> (alewife)	0.73	28.84	10.46	0.13	0.13	0.06	—	—	—
<i>Dorosoma cepedianum</i> (gizzard shad)	0.59	14.39	4.82	0.34	1.25	0.50	0.12	0.27	0.16
<i>Notropis hudsonius</i> (spottail shiner)	0.04	0.06	0.03	—	—	—	—	—	—
<i>Etheostoma</i> spp. (darters)	0.10	0.11	0.04	—	—	—	—	—	—
<i>Fundulus heteroclitus</i> (mummichog)	0.07	0.08	0.04	—	—	—	—	—	—
<i>Fundulus majalis</i> (striped killifish)	0.01	0.01	0.01	—	—	—	—	—	—
<i>Erimyzon</i> spp. (chubsuckers)	0.06	0.06	0.03	0.03	0.03	0.03	—	—	—
<i>Ictalurus punctatus</i> (channel catfish)	0.01	0.01	0.01	0.03	0.03	0.03	—	—	—
<i>Menidia beryllina</i> (inland silverside)	0.13	0.17	0.06	0.03	0.03	0.03	0.12	0.12	0.06
<i>Menidia menidia</i> (Atlantic silverside)	—	—	—	0.16	0.19	0.08	0.31	1.23	0.77
<i>Syngnathus fuscus</i> (Northern pipefish)	—	—	—	—	—	—	0.04	0.04	0.04
<i>Lepomis gibbosus</i> (pumpkinseed)	0.01	0.01	0.01	—	—	—	—	—	—
<i>Perca flavescens</i> (yellow perch)	0.03	0.06	0.04	—	—	—	—	—	—
<i>Morone americana</i> (white perch)	0.80	160.59	74.80	0.97	167.11	64.09	0.73	27.27	8.05
<i>Morone saxatilis</i> (striped bass)	0.31	5.61	2.28	0.53	11.14	4.12	0.38	3.21	1.46
<i>Pomoxis annularis</i> (white crappie)	0.24	0.45	0.13	0.06	0.09	0.07	—	—	—
Sciaenidae spp. (drums)	—	—	—	0.03	0.16	0.16	0.08	0.27	0.23
<i>Gobiosoma bosc</i> (naked goby)	0.14	1.00	0.46	0.81	98.30	42.99	0.92	591.90	227.69
<i>Trinectes maculatus</i> (hogchoker)	0.01	0.01	0.01	0.06	0.06	0.04	0.04	0.04	0.04
Total		212.2			278.9			625.1	
CV (%)		315			154			185	
Number of species		21			15			10	
H'		0.85			0.86			0.25	

Appendix Table 2

Year 2001. Larval fishes: species composition, frequency of occurrence (Freq= proportion of tows positive), no./tow, and standard error (SE) of no./tow by region in the Patuxent River estuarine transition zone from spring through early summer 2001. The salt-front region includes stations ± 3 rkm from the salt-front location (see Fig. 1). H' =Shannon-Wiener diversity index values ($H'_{\max}=2.0$).

Species	Freshwater			Salt front			Oligohaline		
	Freq	no./tow	SE	Freq	no./tow	SE	Freq	no./tow	SE
<i>Anchoa mitchilli</i> (bay anchovy)	—	—	—	0.14	0.34	0.22	0.13	1.31	0.97
<i>Alosa aestivalis</i> (blueback herring)	0.16	0.85	0.19	—	—	—	—	—	—
<i>Alosa mediocris</i> (hickory shad)	0.03	0.03	0.02	—	—	—	—	—	—
<i>Alosa sapidissima</i> (American shad)	0.11	0.13	0.05	—	—	—	—	—	—
<i>Alosa pseudoharengus</i> (alewife)	0.81	25.10	9.13	0.34	0.76	0.30	—	—	—
<i>Dorosoma cepedianum</i> (gizzard shad)	0.36	2.99	1.31	0.38	2.10	0.83	0.05	0.18	0.16
<i>Notropis hudsonius</i> (spottail shiner)	0.15	0.62	0.34	0.03	0.03	0.03	—	—	—
<i>Etheostoma</i> spp. (darters)	0.28	0.96	0.23	0.10	0.10	0.06	—	—	—
<i>Fundulus heteroclitus</i> (mummichog)	0.18	0.20	0.05	—	—	—	—	—	—
<i>Erimyzon</i> spp. (suckers)	0.42	4.11	1.28	0.10	0.14	0.08	0.03	0.03	0.03
<i>Menidia beryllina</i> (inland silverside)	0.14	0.39	0.23	0.31	0.45	0.14	0.31	1.49	0.54
<i>Menidia menidia</i> (Atlantic silverside)	0.11	0.13	0.04	0.28	1.17	0.61	0.59	4.87	1.41
<i>Membras martinica</i> (rough silverside)	—	—	—	0.07	0.07	0.05	—	—	—
<i>Syngnathus fuscus</i> (Northern silverside)	—	—	—	—	—	—	0.05	0.05	0.04
<i>Opsanus tau</i> (oyster toadfish)	—	—	—	—	—	—	0.05	0.05	0.04
<i>Perca flavescens</i> (yellow perch)	0.07	0.92	0.59	0.07	0.07	0.05	—	—	—
<i>Morone americana</i> (white perch)	0.83	429.34	128.28	1.00	194.07	39.55	0.49	8.05	2.49
<i>Morone saxatilis</i> (striped bass)	0.40	72.72	37.88	0.66	45.17	22.62	0.54	4.44	1.93
<i>Micropterus salmoides</i> (largemouth bass)	0.01	0.01	0.01	—	—	—	—	—	—
<i>Pomoxis annularis</i> (white crappie)	0.17	0.27	0.09	0.03	0.03	0.03	—	—	—
<i>Sciaenidae</i> spp. (drums)	0.01	0.03	0.03	—	—	—	—	—	—
<i>Gobiosoma bosc</i> (naked goby)	0.01	0.01	0.01	0.72	597.62	405.02	0.92	169.10	65.64
<i>Trinectes maculatus</i> (hogchoker)	0.01	0.01	0.01	—	—	—	0.03	0.03	0.03
Total		538.8			842.1			189.6	
CV (%)		223			254			217	
Number of species		19			14			11	
H'		0.72			0.78			0.50	