ABSTRACT

Title of Thesis: ICHTHYOPLANKTON COMMUNITY STRUCTURE AND FEEDING ECOLOGY IN THE PATUXENT RIVER ESTUARINE TRANSITION ZONE

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Surveys were conducted during spring-early summer of 2000 and 2001 to investigate the spatiotemporal structure of ichthyoplankton assemblages, including hatchery-released American shad *Alosa sapidissima*, and feeding of larval fishes in the Patuxent River, Chesapeake Bay. Ichthyoplankton, zooplankton, and hydrographic data were collected across the Patuxent's estuarine transition zone, including the salt front and Estuarine Turbidity Maximum region. Recaptured American shad larvae cohort mortality (M = 0.20 to 3.01•d^{-1}) and growth (G = -1.28 to 0.87 mm•d^{-1}), low dispersal (±0.4km•d^{-1}), and feeding habits similar to co-occurring species, suggest that the best production will result from larval shad releases upriver of the salt front in early to mid-May. Two ichthyoplankton assemblages were distinguished: 1) riverine – characterized by anadromous species and 2) estuarine – characterized by naked goby *Gobiosoma bosc*.

Temperature, dissolved oxygen, salinity-associated variables (e.g., salt-front location), and the larval prey *Bosmina longirostris* (Cladocera) concentrations were indicators of larval abundance. Abundance, taxonomic diversity, and dietary overlap and potential for competition among larval taxa were highest within and up-estuary of the salt front of the estuarine transition zone.

ICHTHYOPLANKTON COMMUNITY STRUCTURE AND FEEDING ECOLOGY IN THE PATUXENT RIVER ESTUARINE TRANSITION ZONE

by

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Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Master of Science
2004

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ACKNOWLEDGEMENTS

Several organizations and many individuals contributed to support of this study. I thank Maryland Sea Grant for supporting the research (NOAA Award No. NA16RG2207, Maryland Sea Grant R/F-90), S. Minkkinen and B. Richardson of the Maryland Department of Natural Resources Anadromous Fish Restoration Group for collaborating and providing hatchery-produced American shad larvae, and the University of Wisconsin Biological and Biomaterials Preparation, Imaging, and Characterization Laboratory for assisting with epifluorescent microscopy analysis.

I am grateful to the American Fisheries Society Marine Fisheries Section, the Chesapeake Biological Laboratory Graduate Education Committee, and the University of Maryland Graduate School for provision of travel funds to present research results at scientific meetings. Many individuals at the Chesapeake Biological Laboratory provided support in various forms, including B. Pearson, J. Bichy, D. Craige, J. Boynton, E. North, J. Shoji, W. Morrison, E. Martino, and others who assisted in the field and provided advice on statistical analyses. Special thanks to S. Gibson for assisting with processing of zooplankton samples, and J. Olney and D. Bilkovic at the Virginia Institute of Marine Sciences for assisting with larval fish identifications. Thanks to B. Cornwall and other members of the UMCES Research Fleet for advice on sampling and capable assistance in surveys aboard the RV Pisces, RV Orion, and RV Aquarius.

I am grateful to E. Houde for the opportunities and professional support he has provided. Thanks also to my other committee members, W. Boynton and T. Miller, for

their valuable advice and instruction. Thanks to my wife and other family members for their continued support, patience, and perspectives.

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CHAPTER ONE

Evaluating stocking protocols for American shad larvae

ABSTRACT

The decline of American shad (*Alosa sapidissima* (Wilson 1812)) in Chesapeake Bay during the last century has promoted efforts to restore the population. Restoration efforts have emphasized annual releases of hatchery-produced larvae and juveniles in several Bay tributaries. The stocking of shad in the Chesapeake region has shown signs of success. However, optimal times, locations, and environmental conditions for releasing shad larvae were unevaluated. In 2000 and 2001, ichthyoplankton surveys were conducted in the Patuxent River to evaluate larval American shad releases at different times and locations. In 2000, 349,000 shad larvae were released on a single date (8 June) at upriver and downriver sites. In 2001, 364,000 larvae were released in two stocking events, designated as early (10 May) and late (4 June) release dates. Dispersal patterns, vital rates, and other aspects of shad early life history were estimated in an attempt to evaluate and improve protocols for larval shad stocking. Zooplankton densities were estimated and hydrographic variables measured to evaluate environmental conditions associated with survival of released larvae. Few larvae were recaptured. Dispersal rates of stocked larvae were generally low ($\pm$0.4km$\bullet d^{-1}$). Estimated mortality and growth rates were variable. Hydrographic conditions generally were favorable for larval growth and survival in both years, although potentially harmful, episodic events did occur. Feeding habits of larval shad were similar to feeding of co-occurring larvae of other anadromous fishes. Feeding incidences of recaptured shad larvae (92%), prey in guts (5.1-6.5 prey$\bullet$larva^{-1}), and zooplankton densities ($\geq$125 zooplankters$\bullet$liter^{-1}) indicated that shad

larvae were stocked at times and locations favorable for successful foraging. Results indicate that successful stocking of American shad larvae in Chesapeake tributaries is most likely to derive from releases made in early to mid-May rather than earlier or later in the year, and under low-flow conditions during periods of gradually increasing temperatures in tidal freshwater sites upriver from the salt front region.

INTRODUCTION

The American shad (*Alosa sapidissima*) is an anadromous fish historically found along the Atlantic Coast of North America from southern Labrador, Canada to the St. Johns River, Florida (Leim 1924). The species was introduced to rivers on the west coast of the United States in 1871 and established in the Northeast Pacific Ocean. In Chesapeake Bay tributaries, adult spawning runs into freshwater take place from late March to early June. Newly hatched larvae (6-10 mm total length, TL) reside in freshwater rivers, gradually moving downstream as they grow. Transformation to the juvenile stage (25-40 mm TL) is completed 26-45 days after hatching. Young shad spend their first summer in tidal freshwater and brackish regions and migrate seaward out of natal rivers in late fall (Klauda et al. 1991).

In the late 19th century, the Chesapeake Bay supported a large and valuable commercial fishery for American shad. Landings ranged from 6.1-17.4 million pounds (2,767 to 7,893 metric tons) from 1880-1935 (Mansueti and Kolb 1953). However, catches and abundance declined steadily from the late 19th century (Fig. 1.1; CBP 2003) and eventually moratoria were declared on the Chesapeake fishery in both Maryland (1980) and Virginia (1994).

In addition to moratoria, conservation and restoration efforts have included phasing out the coastal ocean gill-net intercept fisheries (ASMFC 1999), reopening of spawning grounds previously blocked by dams (St. Pierre 1996), and stocking hatchery-reared larvae and juveniles in Chesapeake tributaries (Hendricks 1995; Minkkinen et al. 1997). Several dams have been removed from Chesapeake tributaries. Other efforts have been directed at constructing passages at dams allowing adult shad to complete

upstream migrations to historical spawning grounds. In Pennsylvania, Maryland, and Virginia, stocking efforts by state agencies have increased in recent years. For example, the Patuxent River was stocked with 308,000 hatchery-produced American shad larvae in 1995 and was scheduled to receive approximately 2 million stocked larvae in 2000 (Minkkinen et al. 1999). Pennsylvania and Virginia also stock millions of shad larvae each year (Fig. 1.2; CBP 2003). From 1986-1991, Maryland and Pennsylvania stocked the greatest numbers of larvae (3-14 million•yr^{-1}). Virginia began stocking shad larvae in 1989, increased production in the mid-1990s, and in recent years stocked more larvae than all other bay states combined. New York and Delaware began stocking relatively small numbers of larvae (< 1 million) in 2002 and 2003, respectively.

Approximately 30-35 million American shad larvae per year have been stocked in Chesapeake Bay tributaries since 1998. Post-stocking sampling of juveniles has indicated significant survival of stocked larvae (Hendricks 1995). However, increasing larval stocking levels hasn't always led to increased numbers of returning adults (Fig. 1.3; CBP 2003). Recent trends do indicate increases in adult shad returning to the Conowingo Dam at the mouth of the Susquehanna River, but numbers are well below goals set by the Chesapeake Bay Program (CBP 1995).

Based on laboratory tests of environmental factors, Leach and Houde (1999) proposed that the timing of larval release can affect growth and survival potential of stocked American shad larvae. Recent successes in larval mark-release experiments (chemical marks on otoliths) for anadromous fishes indicated that it is possible to make quantifiable supplements to annual recruitments of anadromous fishes through larval stocking (Secor and Houde 1998). Evaluation of stocking protocols could improve

stocking efficacy and the contribution of released fish larvae to young-of-the-year abundance (Hendricks 1995; Leber et al. 1996).

The objective of hatchery release programs for American shad larvae is to restore populations to self-sustaining levels in Chesapeake Bay and to re-establish commercial and recreational fisheries (CBP 1995). The objective of the present study was to determine environmental conditions that promote growth and survival of stocked shad larvae and their potential for recruitment to adult populations. The Patuxent historically supported a healthy shad fishery and has no major dams blocking its spawning areas (Mansueti and Kolb 1953). Excessive nutrient loading and non-point source pollution problems stressed the Patuxent River ecosystem during the 20th century (D'Elia et al. 2003). However, recent efforts to improve water quality in the Patuxent (Boynton 1997) have increased the potential of this tributary for use in restoring anadromous fish populations (CBP 1995).

Previous field and laboratory studies indicated and defined preferred ranges of temperature, salinity, pH, and other environmental variables for young American shad (Crecco and Savoy 1985; Savoy and Crecco 1988; Klauda et al. 1991; Leach and Houde 1999). Based on that knowledge, two objectives were addressed in this study:
1) Determine if stocked American shad larvae survive and grow better under environmental conditions within a favorable range defined in previous experiments (temperature range 15-25°C, salinity < 5.0 psu, pH ≥ 7.0, and dissolved oxygen > 5.0) and 2) Evaluate the potential influence of interspecific competitive interactions in the larval fish community on growth and survival of stocked American shad larvae.

Temporal and spatial variation in larval abundance, dispersal, growth, and survival were evaluated following planned stocking events in the Patuxent River in 2000 and 2001.

METHODS

Larval stocking. American shad larvae are produced at the Manning Fish Hatchery in Cedarville, Maryland. The MD DNR Anadromous Fish Restoration Program collects adult shad during their spring spawning migrations by angling or from the fish lift at the Conowingo Dam on the Susquehanna River. Adult males and females were implanted with a gonadotropin-releasing hormone (GnRHa) and transported by truck to the Manning Hatchery in aerated, 5 psu salt water (Minkkinen et al. 1997). GnRHa doses of 25-50 $\mu g \bullet kg^{-1}$ stimulate maturation, ovulation, and spawning in hatchery tanks (Mylonas et al. 1995). Fertilized eggs were incubated in freshwater in modified McDonald jars and hatched larvae were held and cultured in 1.53-m diameter tanks. Larvae were fed *Artemia* nauplii and a formulated diet (AP100, 100 μm).

Larval shad were marked by immersing them in solutions of oxytetracycline (OTC) at the hatchery to chemically mark developing otoliths. Immersion of larvae in a 200 ppm OTC bath for six hours produced fluorescent marks on individual daily increments of otoliths, thus recording age at marking. Marking otoliths with OTC on multiple dates generated uniquely marked cohorts of larvae that can be identified when recaptured (Hendricks et al. 1991; Houde and Minkkinen 1999). Shad larvae stocked into the Chesapeake Bay system have been successfully marked for several years by applying this method. The technique provides an opportunity to evaluate dispersal, survival, and growth of uniquely marked, stocked cohorts of larval shad. MD DNR

surveys the river for juvenile shad in late summer collecting seined samples, examining otoliths of recaptured shad, and then estimating mortality, growth, and survival of the recaptures stocked during the larval stage (Minkkinen et al. 1999).

When ready for stocking, volumetric sampling at the hatchery provided estimates of larval numbers to facilitate their allocations to each stocking site (or date). Larvae were then transferred to plastic bags of oxygenated water and transported in styrofoam boxes to stocking sites on the Patuxent River (Minkkinen et al. 1997). Bags of larvae were placed in the river for 15-20 minutes to partially acclimate them to ambient temperatures before release.

Several stocking dates and locations in the Patuxent River were utilized in an attempt to identify environmental conditions most favorable for stocked American shad larvae. Hydrographic variables (temperature, salinity, conductivity, dissolved oxygen, pH, and river flow) and the distributions and abundances of larvae and their prey were surveyed. In 2000, 'Upstream' and 'Downstream' stocking sites were compared. An 'Early' vs. 'Late' comparison of stocking dates was evaluated in 2001. In the research plan, one million larvae were designated for each stocking site (or date), which would have provided totals of approximately two million larvae per year. In the experiments, because of low availability, fewer larvae than planned actually were stocked. All hatchery-release larvae were produced by the Maryland Department of Natural Resources.

Year 2000. On 8 June 2000, Maryland DNR stocked approximately 349,000 American shad larvae in the Patuxent River. All larvae were progeny of hatchery-spawning adults collected at Conowingo Dam on the Susquehanna River. Two larval

batches were produced from two different groups of adult female shad. Larvae from the two batches were distinguished by age and multiple tetracycline marks on their otoliths, providing distinct cohorts for each designated stocking site in 2000: 1) an 'upstream' cohort of approximately 209,000 larvae stocked in freshwater at river kilometer (rk) 71 and 2) a 'downstream' cohort of approximately 140,000 larvae stocked in low-salinity waters (0.7 psu) at rk53 (Fig. 1.4). The numbers of larvae stocked were far fewer than the 2 million anticipated in the research plan. Hydrographic variables were measured at each stocking site (Table 1.1).

Year 2001. DNR stocked 364,200 American shad larvae in the Patuxent River on two dates: 1) an 'early' stocking event on 10 May 2001 released approximately 142,700 larvae at rk79 and 2) a 'late' release on 4 June 2001 of approximately 221,500 larvae, also at rk79 (Fig. 1.5). The numbers of larvae stocked once again were well below the 2 million that was anticipated. The early cohort of larvae was derived from 'strip spawning' of Potomac River American shad adults. The late larval cohort was progeny of hatchery-spawning adults collected at Conowingo Dam. Hydrographic variables were measured at the stocking site on each date (Table 1.1).

Stocking mortality. In conjunction with each stocking event, experiments of 24-hr duration were conducted to estimate short-term larval mortality associated with stocking. Experiments were conducted in 76-liter aquaria at the Chesapeake Biological Laboratory (CBL). Larvae from batches that were stocked were transported from the Manning Hatchery to CBL, along with water from the hatchery and from Patuxent River stocking sites (rk71 and rk53 in 2000, rk79 in 2001). One-hundred larvae were placed into each experimental aquarium. Transportation and holding time before stocking in

experimental aquaria was about six hours. Stocking at Patuxent River sites was completed within 2 hours of transporting larvae from the hatchery to the river.

On 8-9 June 2000, there were four experimental aquaria (one tank•treatment^{-1}): 1) the upstream release batch of larvae in hatchery water (control), 2) the upstream release batch in river water from rk71, 3) the downstream release batch of larvae in hatchery water (control), and 4) the downstream release batch in river water from rk53. Water temperatures were 18.5°C in the Manning Hatchery tanks and ranged from 19.5 to 22.0°C in the four experimental aquaria. In 2001, two experimental aquaria – one with hatchery water and one with river water from rk79 – were set up on each stocking date. During the 10-11 May 2001 experiments, water temperatures were 18.0°C in Manning Hatchery tanks and ranged from 19.1 to 21.5°C in experimental aquaria. During the 4-5 June 2001 experiments, water temperatures were 18.9°C in Hatchery tanks and ranged from 17.8 to 19.5°C in experimental aquaria.

Ichthyoplankton surveys. Thirteen ichthyoplankton sampling surveys were conducted on the Patuxent River between 9 May and 5 July 2000. All samples were collected during daylight and each survey was completed in 8-10 hours. Surveys took place weekly before shad larvae were stocked, then for two consecutive days following larval releases, and at 4-day intervals thereafter until 25 days after stocking events. Eleven of the surveys in year 2000 were conducted on the 25-ft RV Pisces. Ichthyoplankton was sampled at 14 sites in the river by towing a 60-cm diameter, paired bongo net with 333-µm meshes. The sites included 10 'regular' stations (Fig. 1.6), at approximately 3.3 river-kilometer intervals, and 4 additional sites that were sampled on some occasions at locations where larvae were judged to most likely occur. Samples

were collected at 3 or more stations above and below each stocking site to estimate daily rates and directions of dispersal.

Station depths in the surveys for years 2000 and 2001 ranged from 2-10 m. Ichthyoplankton tows were oblique from surface to bottom and of 5-min duration. Flow meters in net mouths provided estimates of volumes of water sampled. A mean of 137m^3 of water was filtered in each paired bongo tow (combined paired-net samples). Catches from each net were combined into one sample, preserved in ethanol, brought to the laboratory, and transferred to fresh ethanol within 24 hours before identifying, enumerating, and measuring fish.

In each year, stations were selected above, below, and within the projected shad larvae nursery area. This included the Estuarine Turbidity Maximum (ETM), a region in the Patuxent River subestuary near the salt front, above which larvae may be retained in the nursery area. Physical processes of ETM regions aggregate particles, such as larval fish and their zooplankton prey, and may promote anadromous fish recruitment in estuaries (Boynton et al. 1997). The location of the salt front, defined by conductivity readings of 800-1000µS, was determined in each survey. Stations were sampled downstream of the ETM in an attempt to determine if there were advective losses of shad larvae from the nursery area.

On the last two sampling dates in 2000 (23 June and 5 July), surveys were conducted on the 52-ft RV Orion for juveniles and large shad larvae. A 2-m^2 Tucker trawl with 700-µm meshes and a flowmeter was deployed in these two surveys. Oblique Tucker-trawl tows were of 5-min duration and filtered approximately 575m^3 of water.

During each of the surveys two tows were made at sites where larvae had been stocked. An additional tow was made at stations 1-rk up- and down-estuary of each stocking site.

In 2001, 18 ichthyoplankton surveys were conducted between 24 April and 3 July 2001. Surveys were weekly before stocking, then for two consecutive days following larval releases, and at 4-day intervals thereafter until 25 days after the second stocking event. Fifteen of the surveys were conducted on the RV Pisces. Ichthyoplankton was sampled at 11 sites using the same methods as in 2000. The sites included 10 'regular' stations (Fig. 1.6) and 1 additional station at rk75 that was sampled on some occasions. Two tows were made at both the rk78 and rk71 stations during each survey. These two sites were immediately downstream of the stocking site (rk 79). On three of the 2001 sampling dates (31 May, 27 June, and 3 July) juveniles and large fish larvae were sampled with a 2-m^2 Tucker trawl from either the RV Orion or the 62-ft RV Aquarius at the 10 'regular' stations (Fig. 1.6).

During each survey in both years, zooplankton was collected at the 10 regular stations by pumping 60 liters of water from surface, middle, and bottom depths (20 liters per depth). Pumped water from the three depths was combined and zooplankton filtered onto a 35-µm sieve before preserving in 5% formalin. In the laboratory, zooplankters were identified, enumerated, and measured to evaluate distributions, densities, and sizes of potential prey for shad and other fish larvae.

Hydrographic conditions. A major goal of the study was to determine optimal environmental conditions for survival of stocked shad larvae. Hydrographic parameters (temperature, salinity, dissolved oxygen, conductivity, and pH) were measured during each survey at the 10 regular stations and also at 1 additional downriver station (rk42).

Except for pH, instrument measurements were made of temperature, salinity, conductivity, and dissolved oxygen at surface, mid-water, and near-bottom depths at each station. Water from each depth was pumped into a bucket on deck and meter probes inserted to measure hydrographic variables. Survival and production of young American shad larvae are dependent on pH levels that remain relatively stable and are ≥7.0 (Leach and Houde 1999). The pH was measured at every other station to document levels potentially harmful to shad larvae. Patuxent River flow data were obtained from a U. S. Geological Survey gauge at rk130, near Bowie, Maryland (USGS 2001).

Sample processing. In the laboratory, fish larvae and juveniles were removed from bongo net and Tucker trawl samples, identified, and enumerated under a dissecting microscope. Entire samples were sorted for larval and juvenile alosines (*Alosa* spp., shads and river herring). Other taxa also were identified, counted, and occasionally sub-sampled (1/2 to 1/8 of the whole sample, divided with a plankton splitter) when numbers per taxon were >200. Larvae from each taxon and size class (up to 100 from individual samples) were measured to the nearest 0.1-mm TL with a digital image analysis system.

Patuxent River zooplankton densities (no.•l^{-1}) were determined for several taxonomic categories: *Eurytemora affinis* calanoid copepodites and adults, *Acartia* sp. calanoid copepodites and adults, cyclopoid copepods, harpacticoid copepods, copepod nauplii, barnacle nauplii, invertebrate eggs, rotifers, *Bosmina longirostris* cladocerans, 'other' cladocerans, chironomid insect larvae, and other less common taxa. Zooplankters were counted under a dissecting microscope from 5-ml aliquots of the concentrated river zooplankton samples. For all samples, zooplankters from each represented category were measured with an ocular micrometer.

Dispersal and abundance. Sagittal otoliths of all American shad larvae collected in the ichthyoplankton samples were examined under epifluorescent light (100 watts) at 200x magnification with a Zeiss Axiovert 200 microscope. The emission range of the system was 360-460nm. The presence and pattern of OTC marks on otoliths were recorded to determine larval origin. Larval abundances for each identified cohort were calculated from estimated larval densities (numbers per m^3) at each sampling site. River volumes (m^3) represented by each site were calculated from data in Cox et al. (1980).

Abundances were analyzed with respect to temperature, salinity, and conductivity gradients that were mapped during surveys to determine the distribution of larvae in relation to hydrographic conditions. Directions of dispersal and dispersal rates of recaptured hatchery-origin shad larvae were examined relative to stocking sites, river flow conditions, and other environmental variables. Habitat overlap between American shad larvae and larvae of other species with respect to various environmental conditions was examined using Principal Components Analysis (PCA) of catch-per-unit-effort (CPUE, $no \bullet tow^{-1}$) and hydrographic data to identify associations. PCAs were run on correlation matrices of centered data. Growth and mortality rates of shad larvae were estimated from linear regressions of cohort mean lengths and log-transformed abundances over time. Initial larval abundance estimates for each cohort were adjusted using percent survival results from the 24-hour laboratory experiments.

Foods and feeding. Digestive tracts of all recaptured American shad larvae and larvae of co-occurring taxa ($n_{spp., station} \geq 5$) were analyzed under a dissecting microscope to determine feeding incidences, kinds of prey, prey numbers, prey preferences, and dietary overlap between American shad cohorts and co-occurring species. All prey items

in larval guts were identified, enumerated, and measured with an ocular micrometer. Diets were compared with compositions of potential prey in river zooplankton samples. Prey preferences for larval fish were defined using a linear selection index (Strauss 1979):

$$L = R_{iA} - R_{iR}.$$

R_{iA} is the percent composition of zooplankton prey type i in larval guts, R_{iR} is the percent composition of zooplankton type i in the environment; L can range from -1.0 to +1.0. Positive values of L indicate prey preference and negative values avoidance. The standard error of L was estimated (Strauss 1982) and t-tests conducted to determine if L differed significantly ($p < 0.05$) from 0.

Comparisons of relative diet overlap between larval shad cohorts and other ichthyoplankton taxa were made with Czechanowski's index (Feinsinger et al. 1981):

$$O_{12} = O_{21} = 1 - 0.5 \left(\sum | P_{i1} - P_{i2} | \right).$$

O_{12} is the overlap index value of species/cohort 1 on species/cohort 2, P_{i1} is the proportion of food type i used by species/cohort 1, and P_{i2} is the proportion of food type i used by species/cohort 2. O values may range from 0.0 to 1.0. Values approaching 1.0 indicate strong overlap in diets and those approaching 0.0 indicate no overlap.

Dietary overlap index values were tested for statistical significance by comparing them with null models following procedures in Albrecht and Gotelli (2001). For each species or cohort comparison, utilization data were randomized to create 1000 null assemblages and from these a mean expected dietary overlap value was calculated. The expected model mean and observed dietary overlap index value were compared to the frequency distribution of 1000 null indices calculated from the randomized data sets.

Two-tailed probability values were calculated by tabulating the number of simulated overlaps that were greater or less than the observed overlap.

RESULTS

Larval stocking. Numbers of larvae stocked did not meet specifications in the study plan. The study design called for two million American shad larvae to be stocked in each year of field experiments. These quantities had been estimated to be sufficient to provide enough recaptured larvae to thoroughly evaluate stocking protocols (Houde and Minkkinen 1999). Due to poor weather during adult spawner field collections and problems with larval mortality at the hatchery, MD DNR was unable to provide anticipated numbers of larvae.

Approximately 349,000 American shad larvae were stocked in 2000 and 364,200 in 2001. The ichthyoplankton surveys resulted in a total of 26 recaptures over both years, approximately 10-20% of numbers anticipated had two million larvae been stocked (Houde and Minkkinen 1999). The low numbers stocked and few recaptures compromised rigorous statistical analyses on dispersal, distribution, and vital rate estimates of stocked shad larvae.

Stocking mortality. Survival rates of larvae were variable in the 24-hr laboratory experiments investigating mortality associated with stocking (Table 1.2) but indicated substantial survival potential for the stocked larvae. Survival rate calculations were based on the number of live larvae in each experimental tank after 24 hours. e.g., 33 of 100 larvae in the 8-9 June 2000 river-site water tank were still alive after one day (Table 1.2). In 2000, the 8-9 June experimental results suggested that 33-92% of larvae survived

the stocking process. In the four experimental aquaria, the downstream-stocked larvae had higher survival than the upstream-stocked larvae. Survival rates for upstream and downstream stocked groups were slightly higher in river-site waters than in Manning Hatchery water.

In 2001, the 10-11 May laboratory experimental results suggested that stocking mortality was low (Table 1.2), possibly because water temperatures at the Manning Hatchery and in the river were similar when larvae were stocked (Table 1.1). The 4-5 June experimental results suggested higher mortality associated with stocking, although there were difficulties with stabilization of dissolved oxygen levels during this experiment, which may have contributed to mortality of larvae in the laboratory. Overall, survival rates were good in the 2001 experiments, ranging from 52-92% in hatchery and river-water aquaria, and were higher than those in the year 2000 experiments.

Hydrographic conditions. Year 2000. At the times of larval releases in 2000, river water temperatures were approximately 4 degrees above hatchery temperatures (Table 1.1). The upstream cohort was stocked well above the salt front where conductivity (267 μS) was similar to that in the hatchery (287 μS). The downstream cohort was stocked below the salt front where conductivity (1300 μS) was higher than hatchery-water conductivity. Dissolved oxygen levels at stocking sites were 0.1 to 2.6 $mg \bullet l^{-1}$ higher than those at the hatchery (8.0 $mg \bullet l^{-1}$). The pH levels were: hatchery water, 8.0; upstream river site, 8.2; and downstream river site, 7.4.

River temperatures on 8 June 2000 were ≥ 22.0°C at both stocking sites, which is within the range considered favorable for larval American shad growth and survival. Temperature increased by several degrees in the week following stocking and continued

to increase, reaching 28°C by the end of June and potentially becoming unsuitable for larvae (Fig. 1.7). Precipitation and river flow were below average during spring-early summer 2000 and varied little throughout the sampling period. The salt front shifted 2 km downstream in the week following stocking (Fig. 1.8).

Year 2001. In 2001, river and hatchery water temperatures were similar on both stocking dates (Table 1.1). The two larval releases were made at the same stocking site, which was well above the salt front (Fig. 1.5) where conductivities were 232 μS and 202 μS on 10 May and 4 June, respectively, values slightly lower than hatchery water conductivities (411 μS and 429 μS). On 10 May, dissolved oxygen levels and pH were similar for hatchery water (D.O. = 8.1 $mg \bullet l^{-1}$, pH = 8.0) and river water (D.O. = 8.4 $mg \bullet l^{-1}$, pH = 7.7). Hydrographic conditions also were similar during the 4 June stocking event, when hatchery-water dissolved oxygen (8.2 $mg \bullet l^{-1}$) and pH (8.4) were somewhat higher than river-water values (7.5 $mg \bullet l^{-1}$ and 7.9).

In 2001, river temperatures ranged from 18-24°C in the week following the 10 May stocking event (Fig 1.7). After the release of the 4 June cohort, temperatures increased ~3°C but remained within the range considered favorable for larval shad growth and survival. Shad larvae possibly were stressed by the rapid rise in temperature (+4°C) that occurred in the 11-13 June period, after which temperatures remained above 25°C.

Precipitation and river flow were below the historical average during spring-early summer 2001, but were more variable than in the 2000 sampling period. Several short-duration, high-flow events occurred in the second half of the sampling period during 2001 (Fig. 1.7). A substantial decline in pH occurred in the days after larvae were

stocked on 4 June, following the highest flow event during the 2001 sampling period. Dissolved oxygen levels generally declined each year as the sampling periods progressed, but probably remained above levels considered critical for shad larvae. On 10 May 2001, the early season stocking date, D.O. was > 8.0 $mg \bullet l^{-1}$ at upriver stations near the stocking site, although minimum D.O. values, when averaged over the sampling area, were observed during the 11 May survey. On that date, dissolved oxygen levels were > 5.0 $mg \bullet l^{-1}$ for all sampling sites upriver of river km 64, but were 4 $mg \bullet l^{-1}$ or lower at sites between river km 58 and 56.

Dispersal and abundance. Year 2000. Few American shad larvae were collected in the surveys. In eight surveys conducted within 27 days of larval stocking, all 13 American shad larvae had oxytetracycline (OTC) marks on their otoliths, indicating hatchery origin. All recaptures occurred within 1-7 days after stocking. Twelve of the 13 recaptures (92%) originated from the upstream-stocked larval cohort (Table 1.3). The single larva from the downstream stocking site was recaptured on the day after stocking. Shad larvae stocked at the upstream site dispersed relatively short distances. All recaptured larvae from this cohort were sampled within ±3 km of the stocking site (Fig. 1.8) and mean dispersal rate was +0.3 $km \bullet d^{-1}$ (i.e., transport upriver). The single recapture from the downstream cohort had dispersed 3 km upriver from the stocking site in the one day following stocking (Fig. 1.8).

Five American shad juveniles from the upstream-stocked larval cohort were recaptured during Maryland DNR seine surveys in early August 2000. No juvenile recaptures from the downstream-stocked cohort occurred in the seine surveys, suggesting that upstream stocking promoted survival potential.

Year 2001. Of the 13 American shad larvae collected in 15 surveys within 53 days of the first larval release in 2001, all bore OTC marks indicating hatchery origin. All recaptures from the early-stocked cohort (n =11) were made within 1-7 days of release (Table 1.3). Most larvae (n = 9; 82%) from the early-stocked cohort were captured at a site 3 km down-river of the stocking site (Fig. 1.9). Two early-stocked larvae were collected 8 km down-river of the stocking site. Mean dispersal rate for the early cohort was -0.4 $km \bullet d^{-1}$ (downriver). The two larval recaptures from the late release in 2001 occurred one day after stocking. Their dispersal rate was high (-5.5 $km \bullet d^{-1}$); the two larvae were captured 8 and 11 kilometers down-river of the stocking site (Fig. 1.10).

MD DNR seine surveys recaptured 6 juveniles from the early-stocked larval cohort. Thirty juvenile recaptures from the late-stocked larval cohort occurred in MD DNR seine surveys in 2001.

Co-occurring ichthyoplankton. Several ichthyoplankton taxa co-occurred with larval American shad in the freshwater region of the Patuxent River (Fig. 1.13). A Principal Components Analysis (PCA) revealed two non-discrete ichthyoplankton assemblages: 1) Riverine: characteristic species included young of anadromous and freshwater taxa, predominantly American shad, alewife, other alosines, *Morone* spp., and gizzard shad. This assemblage was diverse and inhabited colder, low-salinity water; and 2) Oligohaline: early-life stages of estuarine-spawned species characterized this low-diversity assemblage that occupied warmer, higher-salinity water. Although two assemblages were distinguished, members of several constituent taxa (moronids, naked goby, and clupeiforms) from each assemblage co-occurred at the salt front.

Growth and mortality. Despite the limited numbers of recaptures, growth and mortality rates of the known-age, stocked American shad larvae were estimated from linear regressions of mean lengths and $\log_e$-transformed abundances over time. In 2000, the estimated instantaneous mortality rate of the upstream-stocked cohort for the 7 days after stocking was $0.22 \cdot d^{-1}$ (= $20\% \cdot d^{-1}$) and the estimated growth rate was 0.46 $mm \cdot d^{-1}$ (Fig. 1.8). The single recaptured larva from the downstream cohort in 2000 at one day after stocking was smaller than the mean length of larvae stocked (G = -1.59 $mm \cdot d^{-1}$) and the apparent instantaneous mortality of the downstream cohort was $2.64 \cdot d^{-1}$ (= $93\% \cdot d^{-1}$). In 2001, the estimated instantaneous mortality of the cohort stocked early in the season was $0.20 \cdot d^{-1}$ (= $18\% \cdot d^{-1}$) (Fig. 1.9). The estimated growth rate for this cohort was faster than for other stocked cohorts (0.87 $mm \cdot d^{-1}$). Larval shad stocked on the later date in 2001 produced only two recaptures, both collected on the day after release. This cohort apparently fared poorly during the larval stage (M = $3.01 \cdot d^{-1}$ (= $95\% \cdot d^{-1}$), G = -1.28 $mm \cdot d^{-1}$; Fig. 1.10), although it was represented by numerous recaptured juveniles in the MD DNR seine surveys.

Foods and feeding. A high feeding incidence was observed in recaptured American shad larvae (92.3%). The overall mean number of prey per gut was 5.9 and mean number of prey per gut did not differ significantly among the four hatchery-release cohorts (Fig. 1.11a). In 2000, the mean prey size ingested was larger for the upstream- than for the single recaptured larva from the downstream-stocked cohort (Fig. 1.11b). All larval shad cohorts ingested copepod nauplii and *Eurytemora affinis* (Fig. 1.11c). In 2000, the single larva from the downstream-stocked cohort had fed primarily on copepod nauplii while the upstream-stocked cohort's diet consisted of similar numbers of copepod

nauplii, *Eurytemora affinis*, and *Bosmina longirostris*. The upstream-stocked larvae in 2000 consumed a greater proportion of *Eurytemora* than other cohorts. In 2001, the eleven recaptured larvae from the early-stocked cohort had consumed mostly copepod nauplii with some *Eurytemora*, *Bosmina*, and invertebrate eggs represented in the diet. The two larvae from the late-stocked cohort had fed exclusively on copepod nauplii and *Eurytemora* copepods.

Only four prey types were observed in guts of the American shad larvae (invertebrate eggs, copepod nauplii, *Bosmina* cladocerans, and *Eurytemora* calanoid copepods) (Fig. 1.11c). In 2000, the total abundance of those potential larval prey in the week following stocking was between 125-250 zooplankters•liter^{-1} (Fig. 1.12a-d). In 2001, the early cohort was stocked during a peak in *Bosmina* production. Zooplankton abundance was between 125-425 zooplankters•liter^{-1} within 1-7 days of this release. The late-stocked cohort in 2001 encountered potential prey abundances of 225-350 zooplankters•liter^{-1} in the week after stocking.

The linear selection index (Strauss 1979, 1982) identified copepod nauplii as a prey source preferred by all of the stocked shad cohorts (Table 1.4a). Although common and important in guts from all cohorts, significant positive selection for *Eurytemora* copepods was only estimated for the upstream-stocked cohort in 2000. Both of the 2001 cohorts showed negative selection for *Bosmina*.

Larval shad cohorts stocked in upriver or downriver locations in 2000 did not have high dietary overlap (Table 1.4b), primarily because only the upstream-recaptured larvae had consumed *Bosmina* (Fig. 1.11c). However, there was significant overlap in diets between the early and late cohorts stocked in 2001. Interestingly, the diets of 2001

cohorts, which had been stocked at an upriver site, were similar to that of the single larva captured downriver in 2000 while diets of recaptured, upriver larvae in 2000 did not significantly overlap diets of the upriver-stocked 2001 larvae (Table 1.4b).

The diets of common riverine larval taxa were analyzed to investigate potential sharing and overlap in utilization of prey resources in the larval nursery area (Fig. 1.14). Excluding small alewife larvae, all taxa and size classes positively selected for *Eurytemora* (Table 1.5a). Most species and size classes did not prefer *Bosmina* and rotifer prey, although *Bosmina* comprised 8-50% of the diet in each larval taxon analyzed. American shad and smaller alewife larvae (both alosine species) positively selected for copepod nauplii. There was high dietary overlap between American shad and the >10-mm length classes of all other taxa (Table 1.5b).

DISCUSSION

Hydrography in tidal fresh and oligohaline waters of Chesapeake Bay tributaries is an expression of the environmental conditions that may either support or be unfavorable to survival of larvae of anadromous fishes. Hydrographic conditions in the Patuxent River were similar in 2000 and 2001, years of below average river flow with water temperatures ranging from 15-29°C during the sampling surveys for American shad larvae. However, individual larval cohorts experienced different trends and patterns in environmental conditions following their respective releases. Crecco and Savoy (1985) concluded that mortality rates of American shad larvae are lower and growth rates higher when flows in the Connecticut River are low and temperatures high during the larval nursery period. In year 2000, when water temperatures were increasing rapidly in

the Patuxent River, larvae from the upstream-stocked cohort were sampled up to 7 days following stocking and grew at a rate typical of that reported for larval alosines. The late-stocked cohort in 2001 also experienced rising temperatures but encountered a period of increased flow, a factor that may have contributed to its apparently high mortality. However, the salt front location did not shift during the high-flow event, suggesting that downstream advection was not the principal cause of that cohort's mortality.

Rapid declines in pH can reduce survival of American shad larvae (Leach and Houde 1999). A decline in pH did occur following the release of the late cohort in 2001 (Figure 1.7), although pH levels observed during the ichthyoplankton surveys remained above 7.5. It is possible that the apparent high mortality experienced by larvae in the late cohort was attributed to the combined influences of declining pH and increased river flow, rather than either hydrographic factor acting alone. Observed dissolved oxygen and pH never reached levels considered potentially harmful for American shad larvae, although pH could have been lower but unobserved immediately after storm events before subsequently recovering to ≥ 7.0 during surveys.

The high mortality experienced by the downstream-stocked cohort in 2000, which was released below the salt front (Figure 1.4), was probably due to advective, down-river loss from the nursery area and not an effect of osmotic stress (Limburg and Ross 1995). Secor et al. (1995) found that larval striped bass stocked below the salt front in the Patuxent River were lost due to advective transport. MD DNR made no juvenile recaptures in its summer seine surveys of the cohort stocked below the salt front, further indicating that these fish were lost to downriver advection.

Studies by North and Houde (2001, 2003) describe the salt front and associated Estuarine Turbidity Maximum (ETM) as hydrographic features that retain larval fish within the tidal freshwater region of the upper Chesapeake Bay estuarine transition zone. Highest concentrations of larval fish and their preferred zooplankton prey are often located near or up-estuary of the salt front (Jassby et al. 1995; Roman et al. 2001; North and Houde 2003). The lower mortality estimates and high feeding success of American shad larvae stocked at upriver sites suggest that the salt front-ETM features contributed to retention of these larvae in favorable environmental conditions that promoted growth and survival.

Comparisons of recaptures, growth, and mortality among the four cohorts released into the Patuxent River suggested that American shad larvae should be stocked above the salt front and, if possible, during low-flow conditions when temperatures are relatively constant or gradually increasing and within the range 15-25°C. These recommendations are made with caution because they are based on vital rate estimates derived from very few recaptures. The findings are in agreement with hydrographic conditions suggested as favorable for American shad larvae in the Connecticut River (Crecco and Savoy 1984) and from results of laboratory studies (Leach and Houde 1999). Such conditions are most likely to occur in Chesapeake Bay tributaries during early to mid-May, rather than earlier or later in the year.

Johnson and Dropkin (1995) and Leach and Houde (1999) determined that growth of American shad larvae in laboratory experiments was directly related to prey levels. Field studies in the Connecticut and Hudson Rivers indicated growth and survival of young shad increased when river zooplankton densities were high (Crecco and Savoy

1985; Limburg 1996). Short-term deprivation of food also can have a significant impact on survival and recruitment of shad larvae (Johnson and Dropkin 1995). In the Patuxent River, zooplankton densities and feeding incidences of larval shad cohorts were high, and individual guts contained several prey items. Prey densities of ≥125 zooplankters•l^{-1} occurred consistently throughout the river and were probably sufficient for favorable larval feeding (Houde 1978). There was no evidence that recaptured American shad larvae were experiencing short-term food deprivation following cohort releases. Comparisons of larval shad growth and survival relative to prey levels were not possible because of the small numbers of recaptured larvae and because zooplankton prey were always relatively abundant (>125•l^{-1}) in the Patuxent River following stocking.

Larvae released on 4 June 2001, when compared with the 10 May release, selected larger prey types, possibly as a consequence of increased *Eurytemora* production and abundance in the river. The absence of other large prey types (e.g., chironomid larvae) in guts is noteworthy because these items are consumed by larval American shad (Crecco and Blake 1983). Cyclopoid copepods and chironomids were common in freshwater areas of the Patuxent River, but never highly abundant (<10•l^{-1}) when shad larvae were released.

Copepod nauplii, probably mostly of calanoid copepods, and *Eurytemora* copepods and copepodites were the most important foods of larval American shad in the Patuxent River. The cladoceran *Bosmina* is usually preferred by first-feeding (10-12 mm) and advanced (12-18 mm) American shad larvae in the Connecticut River (Crecco and Blake 1983). Patuxent River shad larvae consumed moderate amounts of *Bosmina* but exhibited negative preference for this cladoceran which was often abundant in the

river (>100•l^{-1}). The contrasting preferences for *Bosmina* between the Connecticut and Patuxent Rivers may be due to differences in *Bosmina* densities in the two systems. *Bosmina* generally is present in above average densities in Chesapeake Bay tributaries compared to other Mid-Atlantic estuaries (Chapter Three). The proportion of *Bosmina* in zooplankton samples from the Connecticuit River (<3%) (Crecco and Blake 1983) was much lower than in the Patuxent River (>30%).

Food habits differed substantially among the four released cohorts (Table 1.4 and Figure 1.11). Upstream- and downstream-stocked cohort diets in 2000 did not overlap significantly. Diets of the early- and late-stocked cohorts in 2001, which were stocked at an upstream site, were similar and resembled diets of the downstream-stocked larvae in 2000. The relatively high proportions of copepod nauplii in shad larvae diets and in the river during the post-stocking period in 2001 led to the diet similarity.

Studies of sympatric alosine larvae in the Connecticut River indicated dietary overlap in larvae of similar sizes (Crecco and Blake 1983). The same pattern was observed in the Patuxent River. Diets of larval American shad and large (>10-mm) length classes of alewife (*A. pseudoharengus*) and moronid species (white perch and striped bass) were most similar. These overlaps may signify competitive interactions that should be considered in developing future release strategies of American shad larvae that take into account spatiotemporal variability in larval occurrences and distributions and minimize potential repressive interactions. White perch larvae in particular can be very abundant and overlap in distribution with larval alosines during late spring-early summer in Chesapeake tributaries (Chapter Two).

The PCA indicated that distributions of released larval American shad and several other taxa overlap (Fig. 1.13). Notable co-occurring species include congeneric anadromous alosines (alewife, *A. pseudoharengus*, and blueback herring, *A. aestivalis*), moronids (striped bass and white perch), and larvae of freshwater taxa (yellow perch, *Perca flavescens*; spottail shiner, *Notropis hudsonius*; and darters, *Etheostoma* spp.). Factor loadings in the PCA illustrated the influences of hydrographic variables on species distributions. Larval distributions were determined primarily by salinity and temperature variables (principal component 1), and secondarily by dissolved oxygen. American shad larvae and co-existing taxa preferred fresh, cooler waters in the upriver section of the estuarine transition zone. Overlapping larval distributions and feeding habits suggest that interactions among American shad and larvae of other taxa are complex and that there is some sharing of nursery resources.

The low numbers of larvae released and subsequent low numbers of recaptures make it difficult to draw strong conclusions regarding American shad stocking protocols. However, survival rate estimates from laboratory experiments conducted in conjunction with larval releases indicated that a high proportion of shad larvae survived procedures associated with the stocking process. Field surveys demonstrated that some stocked shad larvae survived in the river and, if sufficient numbers were released, could be used as environmental probes to estimate how dispersal and vital rates depend on environmental factors and variability. High percentages of recaptured larvae from each of the cohorts were feeding actively at the time of collection. Estimates of growth and survival in these experimental releases indicated that shad larvae stocked at upriver sites in the Patuxent River during May have higher survival potential than those stocked later or at downriver

sites near the salt front. Obtaining estimates of survival potential could be facilitated if higher numbers of larvae were consistently produced by hatchery operations and were available for future field experiments.

Table 1.1. Patuxent River hydrographic conditions and larval shad numbers and ages at each stocking event in 2000 and 2001. Hatchery water temperatures are included for comparison. River flow data are from a U.S. Geological Survey gauge at rk130.

	8 June 2000 UPSTREAM rk 71	**8 June 2000 DOWNSTREAM rk 53**	**10 May 2001 EARLY rk 79**	**4 June 2001 LATE rk 79**
N_{larvae}	209,000	140,000	142,700	221,500
Age (days)	15	13	13	13
Age at marking (days)	9 & 12	3 & 12	3 & 12	9 & 12
Mean length (mm)	14.0	13.1	12.1	14.4
Hatchery water temperature (°C)	18.5	18.5	18.0	18.9
River water temperature (°C)	22.1	22.6	17.9	17.4
Temperature change from Hatchery to river water (°C)	+3.6	+4.1	-0.1	-1.5
Salinity (psu)	0.0	0.7	0.0	0.0
Conductivity (µS)	266.7	1300.0	232.0	202.0
Dissolved oxygen ($mg \cdot l^{-1}$)	10.6	8.1	8.4	7.5
pH	8.2	7.4	7.7	7.9
River flow (cfs)	195	195	159	359
Tidal stage	ebb	low	ebb	ebb

Table 1.2. Percent survival of American shad larvae in 24-hr laboratory experiments (on dates of stocking) to evaluate survival potential of stocked larvae. Patuxent River water was taken from the site of each respective stocking event. Experiments were conducted in 76-liter aquaria at the Chesapeake Biological Laboratory.

Experiment Dates	% Survival in Hatchery Water	% Survival in River Water
June 8-9, 2000 (upstream)	23	33
June 8-9, 2000 (downstream)	78	92
May 10-11, 2001 (early)	90	92
June 4-5, 2001 (late)	52	78

Table 1.3. Numbers of American shad larvae recaptured in the Patuxent River from stocked cohorts in 2000 and 2001.

2000				2001					
Date	Days after stocking	Upstream cohort, 8 June 2000	Downstream cohort, 8 June 2000	Date	Days after stocking	Early cohort, 10 May 2001	Date	Days after stocking	Late cohort, 4 June 2001
9 June	1	5	1	11 May	1	2	5 June	1	2
10 June	2	5	0	12 May	2	4	6 June	2	0
12 June	4	0	0	14 May	4	1	8 June	4	0
15 June	7	2	0	17 May	7	4	11 June	7	0
18 June	10	0	0	21 May	11	0	14 June	10	0
Total recaptures		12	1			11			2

Table 1.4. American shad larvae, Patuxent River. (a) Prey preferences of larval shad by cohort; * indicates significant ($p < 0.05$) Strauss index *L* values; (b) Dietary overlap in larval shad cohorts; * indicates significant ($p < 0.05$) Czechanowski index *O* values.

(a)

	2000		2001	
Cohort Mean length (±SD)	Upstream 14.4 (2.3)	Downstream 11.4	Early 14.0 (2.6)	Late 13.1 (1.5)
Invertebrate egg	-0.01	-0.04	+0.01	-0.30*
Copepod nauplii	+0.13*	+0.50*	+0.46*	+0.65*
Bosmina	-0.07	0.00	-0.32*	-0.30*
Eurytemora	+0.30*	-0.02	+0.07	+0.09

(b)

	Upstream 2000	Downstream 2000	Early 2001	Late 2001
Upstream 2000	-			
Downstream 2000	0.45	-		
Early 2001	0.41	0.75*	-	
Late 2001	0.44	0.99*	0.75*	-

Table 1.5. Patuxent River larval fish feeding analyses. a) Prey preferences, Strauss index *L* values and b) dietary overlap, Czechanowski index *O* values in larval fish taxa and size classes common in the freshwater nursery area of the Patuxent River. * indicates significant ($p < 0.05$) values.

(a)	American shad	alewife <10mm	alewife >10mm	striped bass <10mm	striped bass >10mm	white perch <10mm	white perch >10mm
Eurytemora	+0.20*	+0.05	+0.17*	+0.41*	+0.16*	0.20*	+0.19*
Bosmina	-0.24*	-0.35*	-0.21*	-0.27*	-0.07	-0.19*	+0.10*
Cyclopoids	-0.04	+0.04	+0.01	-0.01	+0.01	+0.05	+0.01
Cop. nauplii	+0.31*	+0.41*	0.00	-0.12*	-0.03	-0.08	-0.08
Rotifers	-0.26*	-0.13*	-0.04	-0.26*	-0.19*	-0.15*	-0.24*
Invert. eggs	-0.06	-0.12*	+0.01	+0.04	+0.10*	+0.15*	+0.01

(b)	American shad	alewife <10mm	alewife >10mm	striped bass <10mm	striped bass >10mm	white perch <10mm	white perch >10mm
American shad	-						
alewife <10mm	0.58	-					
alewife >10mm	0.75*	0.55	-				
striped bass <10mm	0.71	0.44	0.73	-			
striped bass >10mm	0.71*	0.50	0.90*	0.71	-		
white perch <10mm	0.67	0.52	0.87*	0.71	0.93*	-	
white perch >10mm	0.75*	0.45	0.88*	0.79*	0.88*	0.85*	-

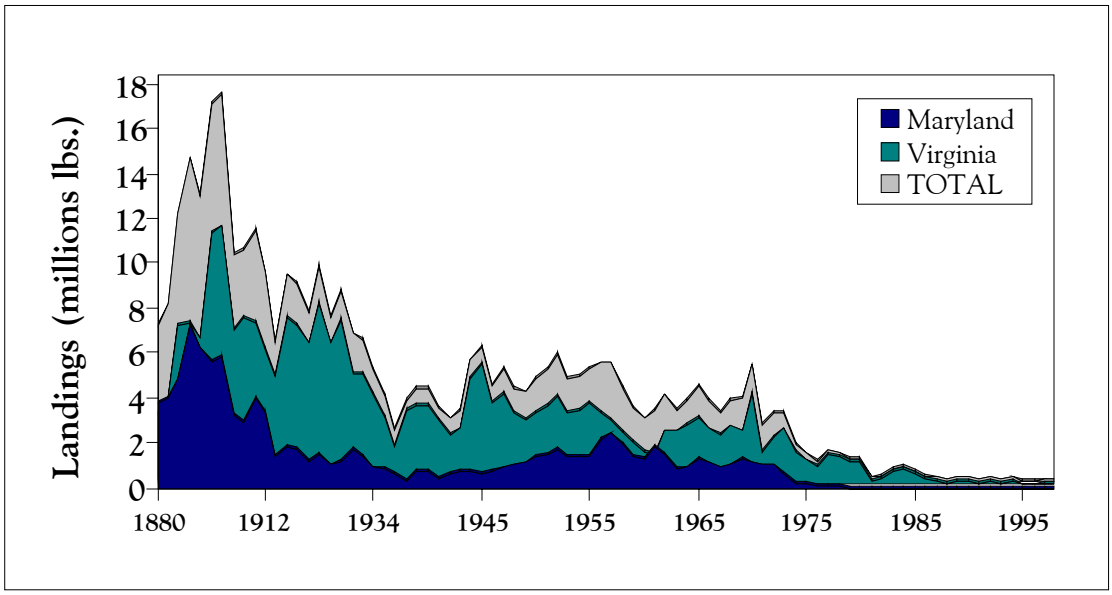


Figure 1.1. American shad landings in Chesapeake Bay (CBP 2003).

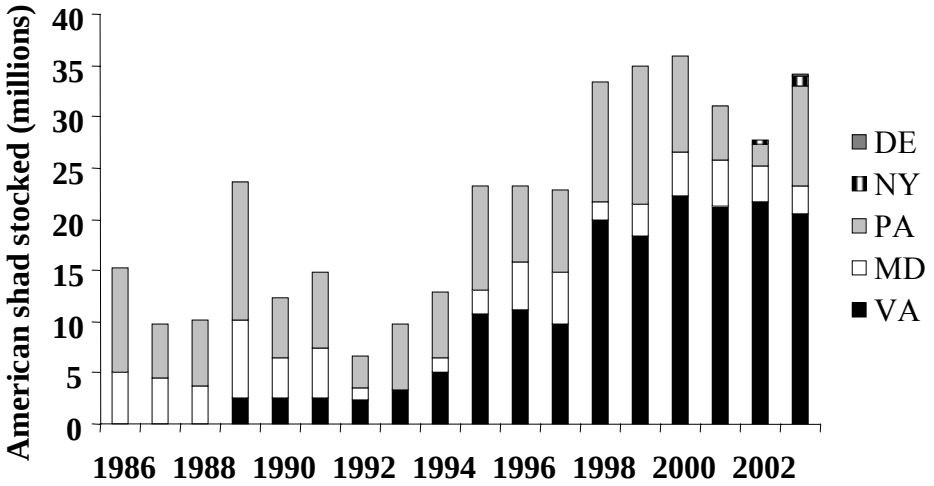


Figure 1.2. Numbers of American shad larvae of hatchery origin stocked into Chesapeake Bay tributaries, 1986-2003 (CBP 2003).

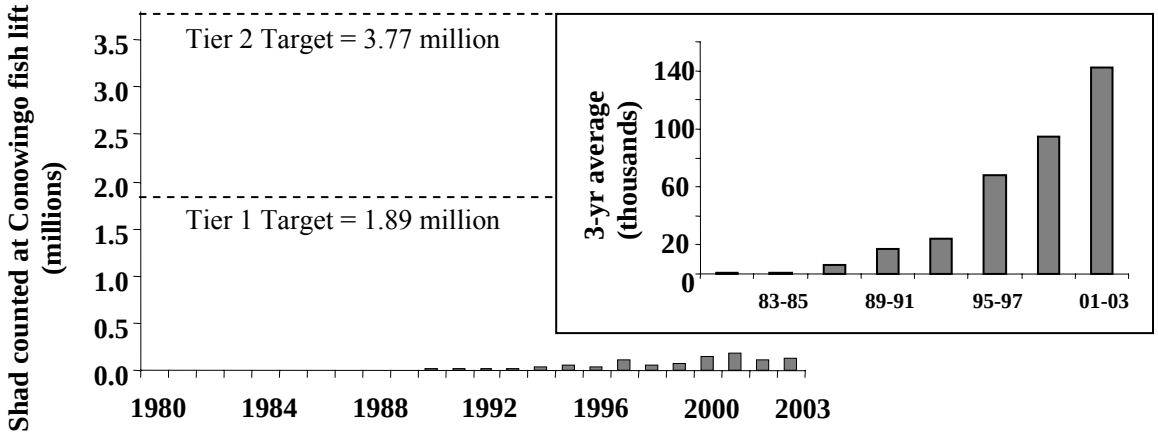


Figure 1.3. Population trends for adult American shad in upper Chesapeake Bay, 1980-2003 and restoration targets (CBP 2003).

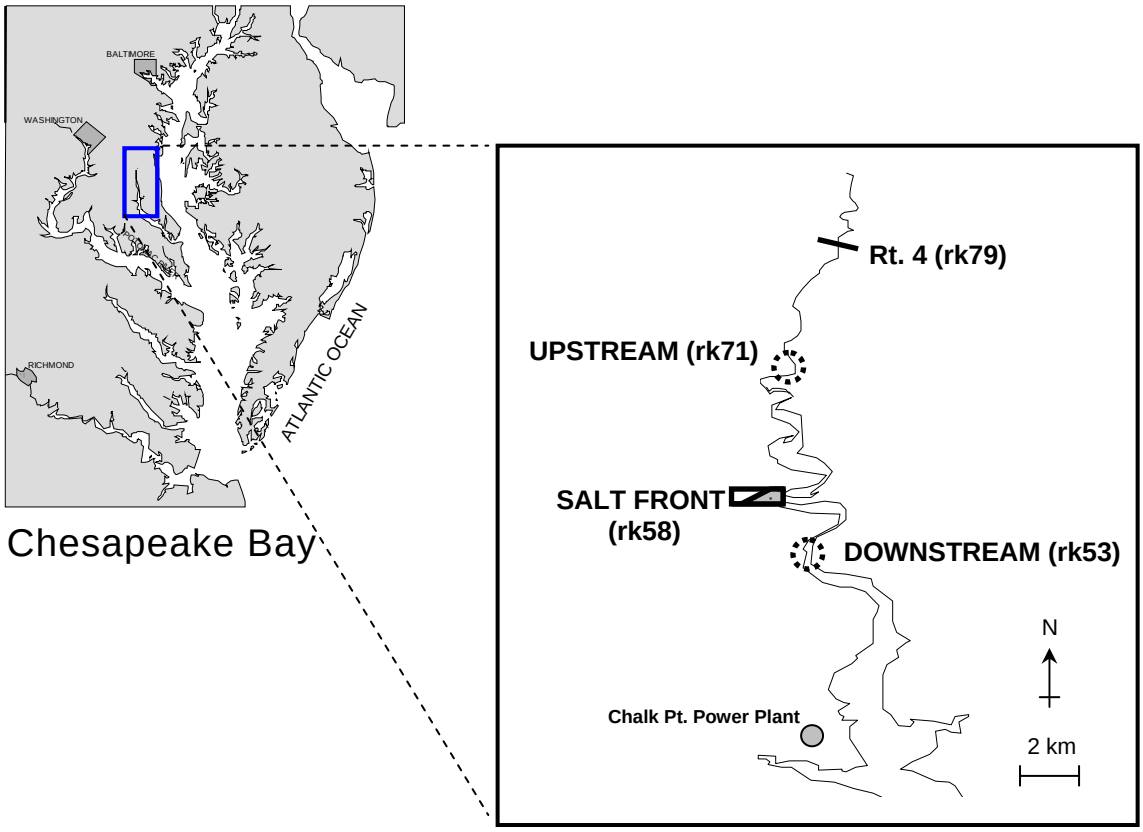


Figure 1.4. Patuxent River study area (right) with 'upstream' and 'downstream' stocking sites and salt front location on 8 June 2000 (rk = river kilometer). Salt front location (in kilometers from river mouth) defined by conductivity readings of 800-1000µS.

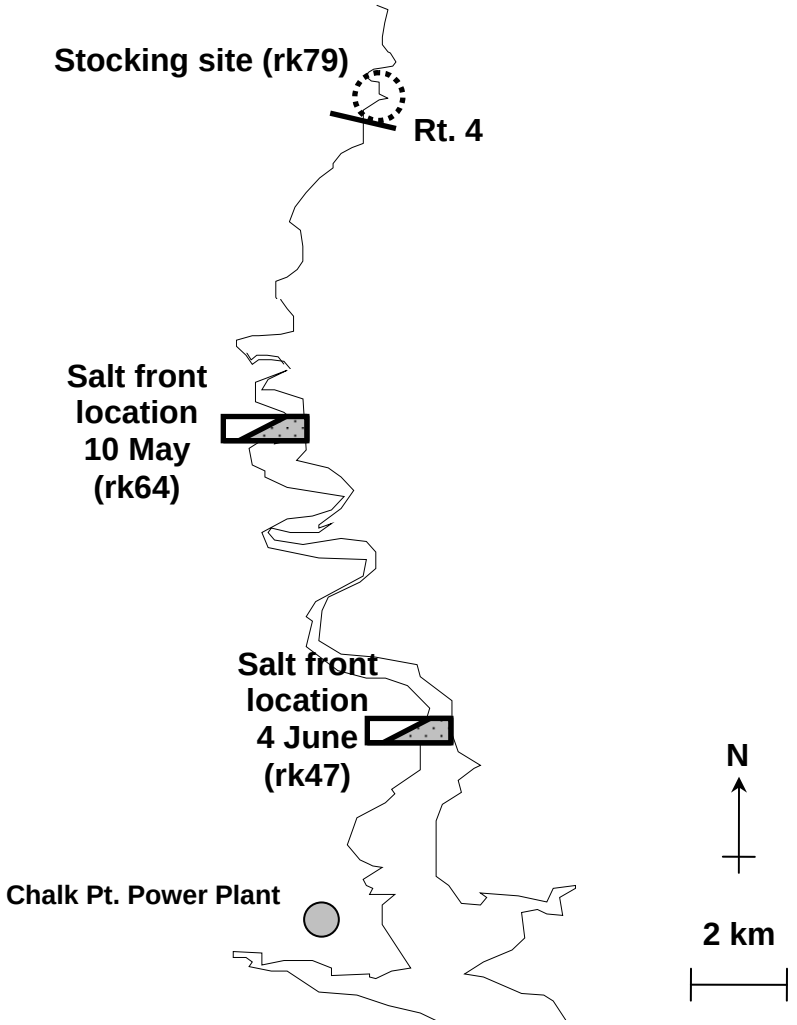


Figure 1.5. Patuxent River: Larval stocking site and salt front locations for both releases (10 May and 4 June) in 2001.

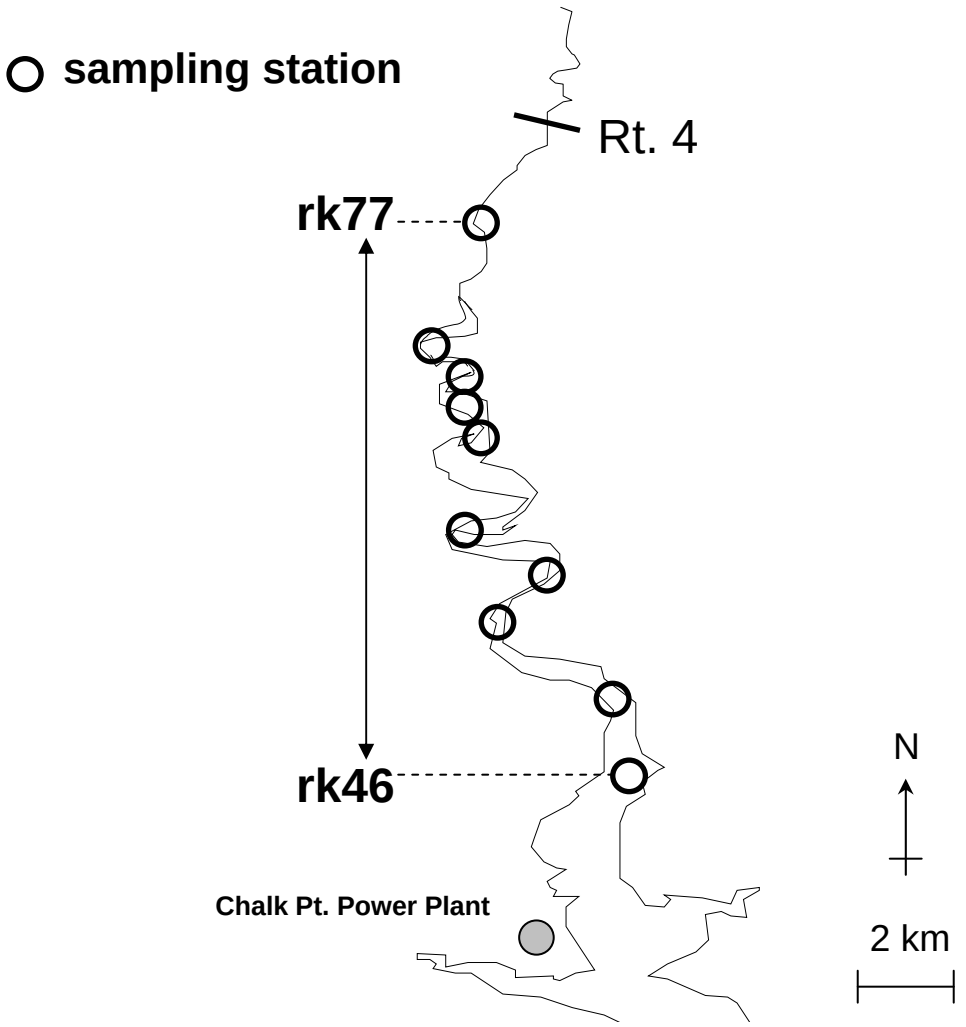


Figure 1.6. Patuxent River study area with regular sampling stations for American shad larvae, years 2000 and 2001.

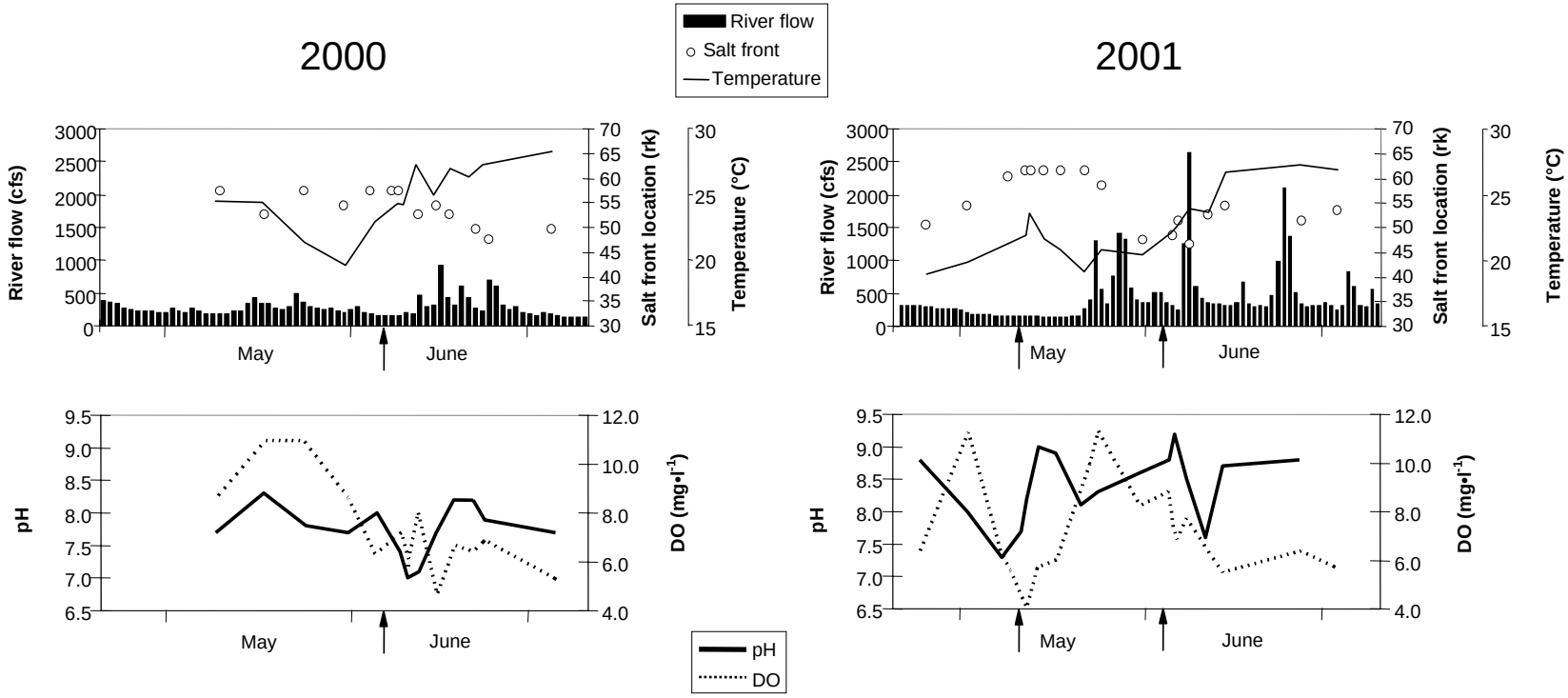


Figure 1.7. Hydrographic conditions for the Patuxent River in 2000 (left) and 2001 (right). Arrows on x-axes indicate stocking dates. Salt front location (in kilometers from river mouth) defined by conductivity readings of 800-1000µS. River flow data were obtained from a U.S. Geological Survey gauge at rk130. Temperature, dissolved oxygen, and pH data are from rk 58, the mid-point of the Patuxent River sampling area.

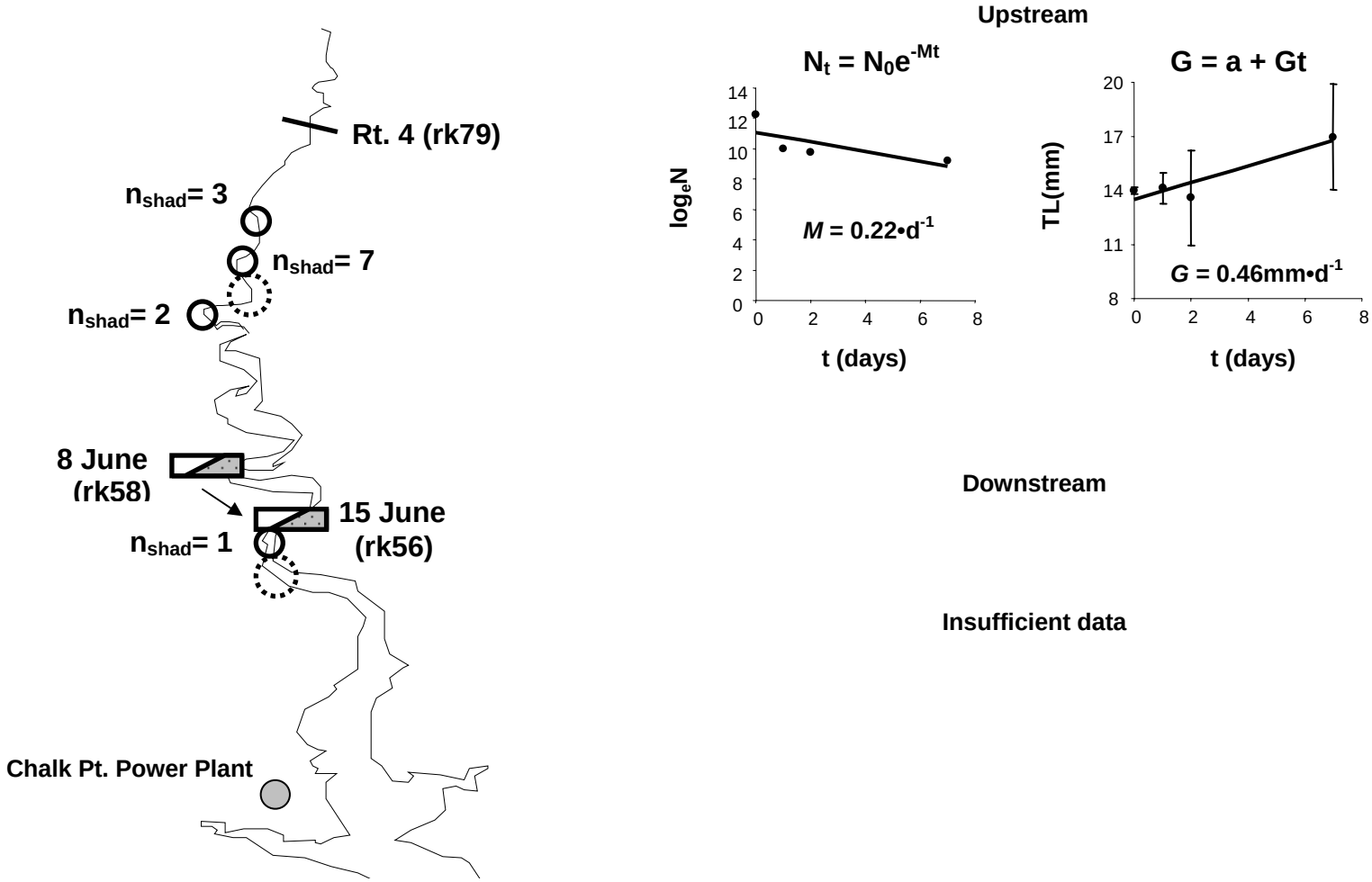


Figure 1.8. American shad larvae, Patuxent River, 2000. Recapture numbers by station for upstream-stocked and downstream-stocked cohorts. Mortality and growth rate estimates are for the upstream cohort. ◌ = stocking site; ▰ = salt front location.

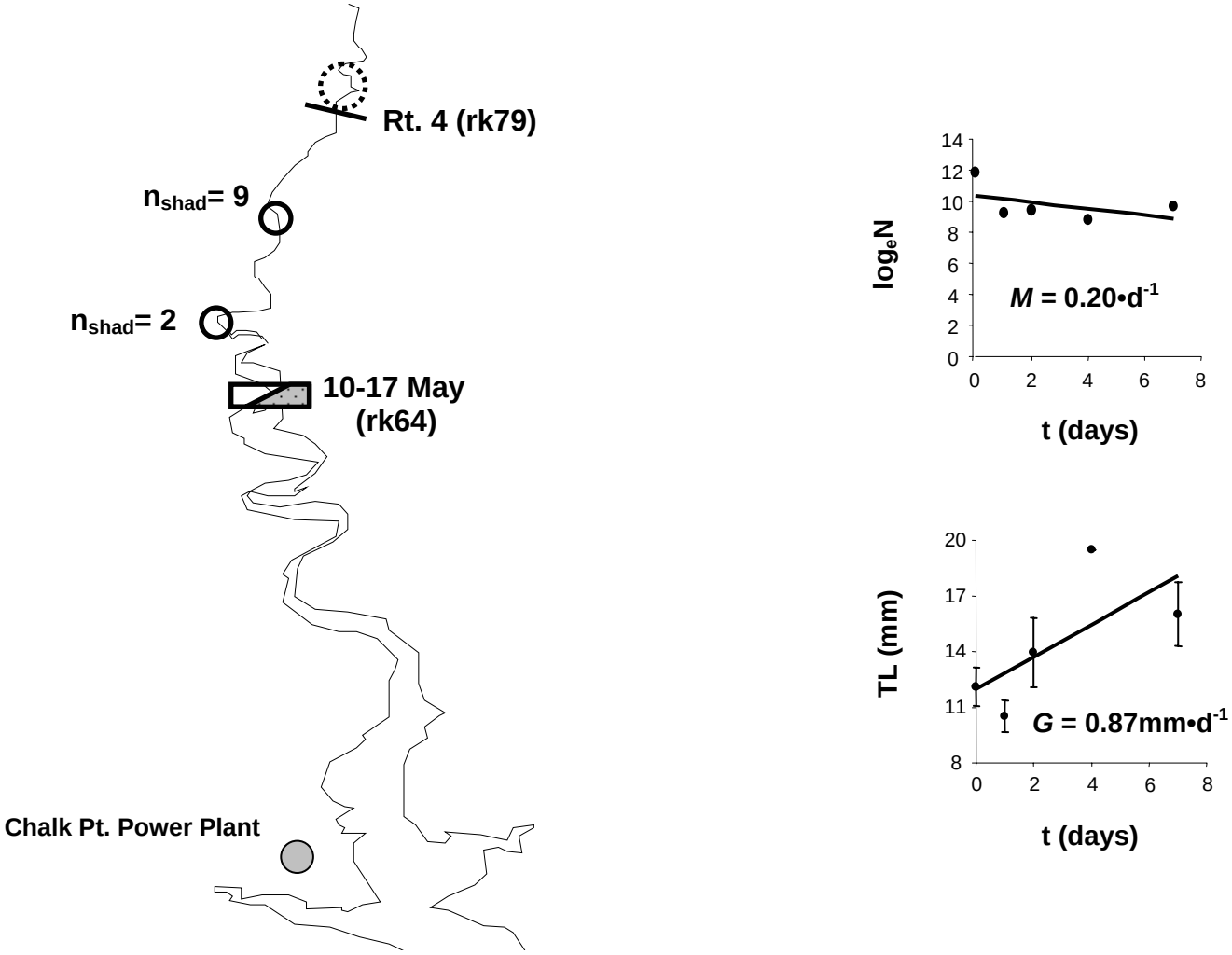


Fig. 1.9. American shad larvae, Patuxent River, 10 May-stocked cohort, 2001. Summary of recapture numbers by sampling station with mortality and growth rate estimates. ◌ = stocking site; ▱ = salt front location.

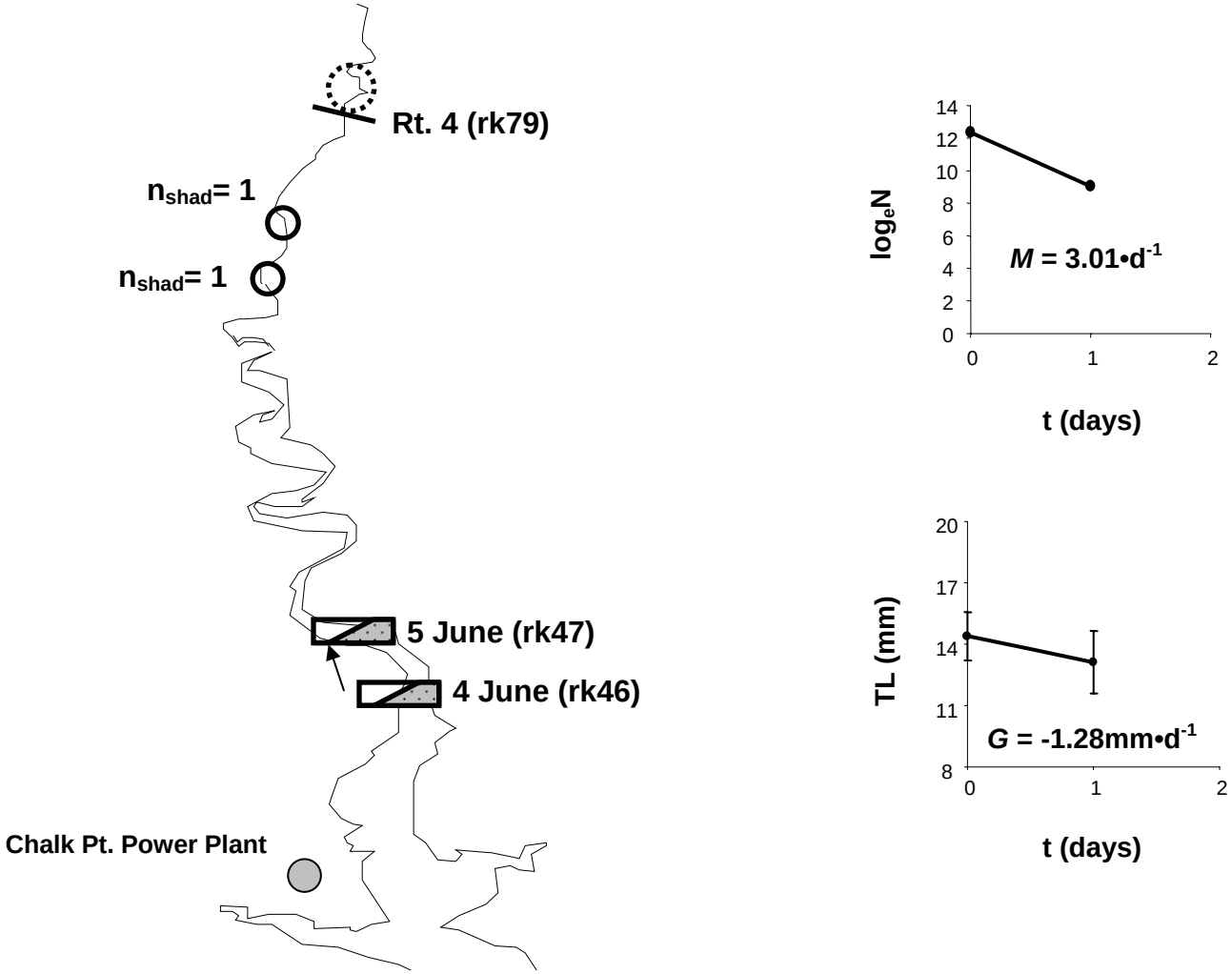


Fig. 1.10. American shad larvae, Patuxent River, 4 June-stocked cohort, 2001. Summary of recapture numbers by sampling station. ◌ = stocking site; ▨ = salt front location.

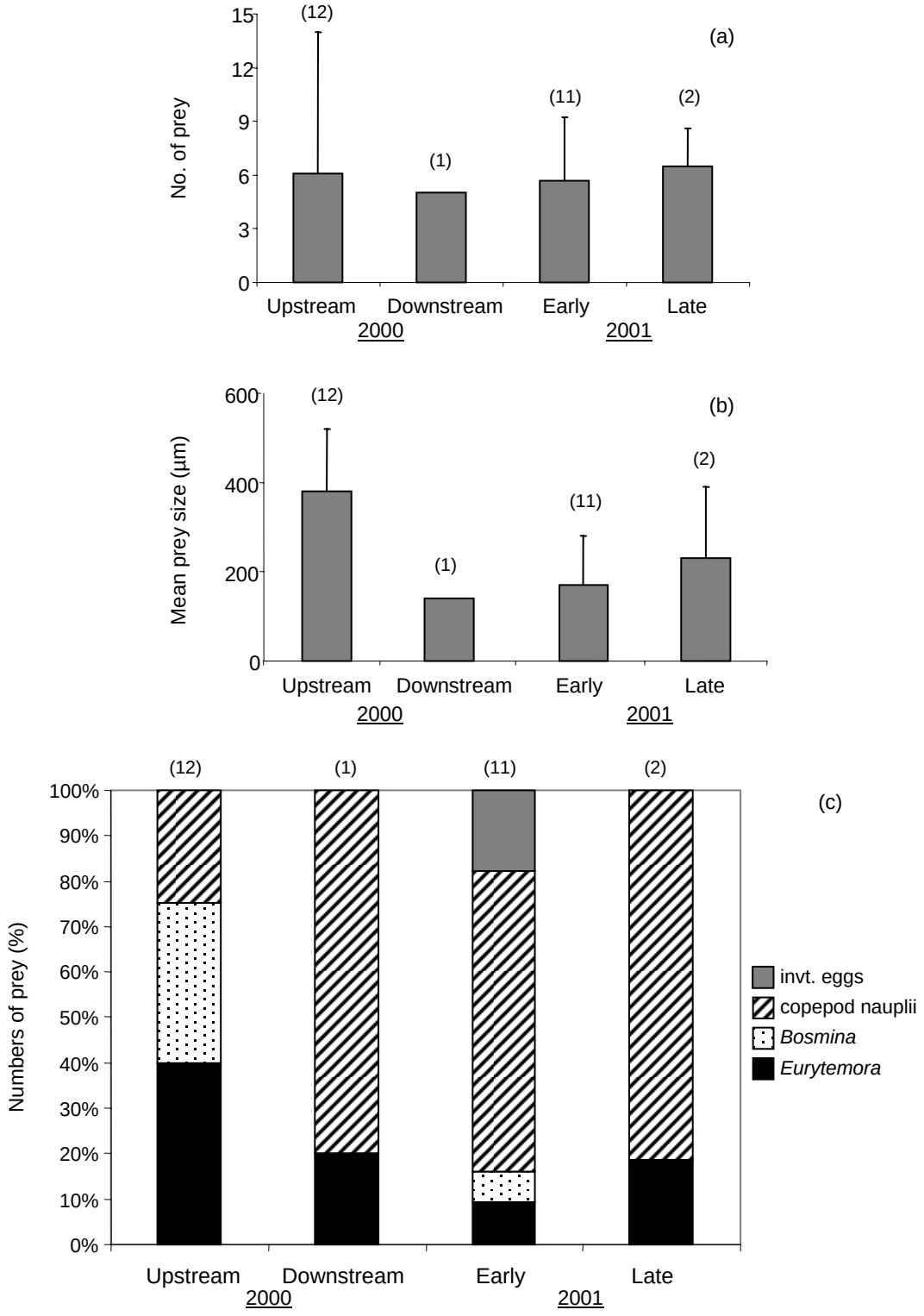


Figure 1.11. Patuxent River, American shad larvae. Mean number of prey (a) and mean prey size (b) per larva for each cohort; lines above bars represent 1 standard deviation of the mean; (c) percentage by number of prey types in larval guts from each cohort. Numbers in parentheses represent number of larvae in the analyses.

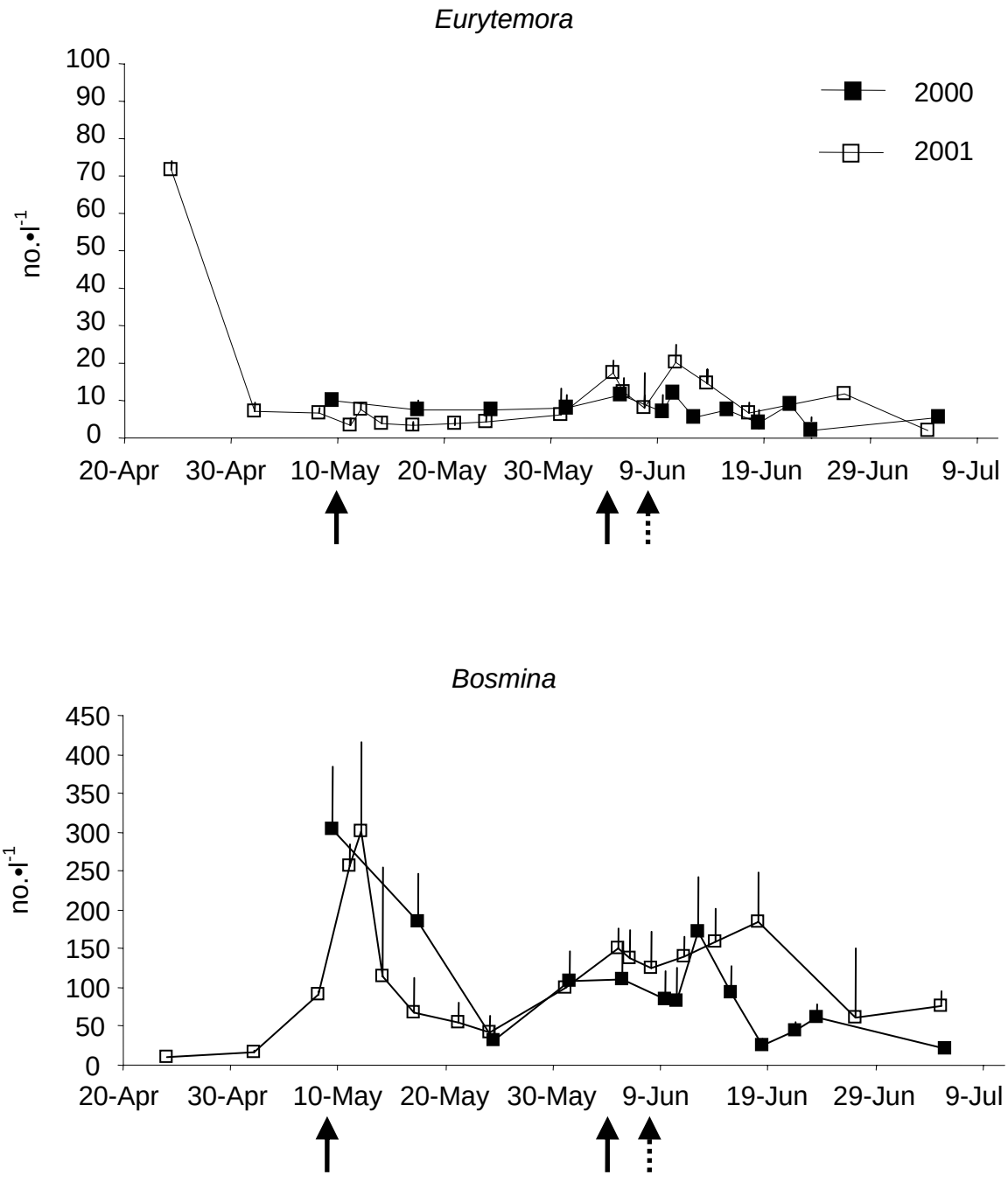


Fig. 1.12a. Temporal changes in *Eurytemora* calanoid copepods/copepodites (above) and *Bosmina* cladoceran (below) densities in the Patuxent River in 2000 and 2001. Vertical bars represent 1 standard error of the mean. Dashed arrow is the stocking date in 2000; solid arrows are stocking dates in 2001. Note different scales on y-axes.

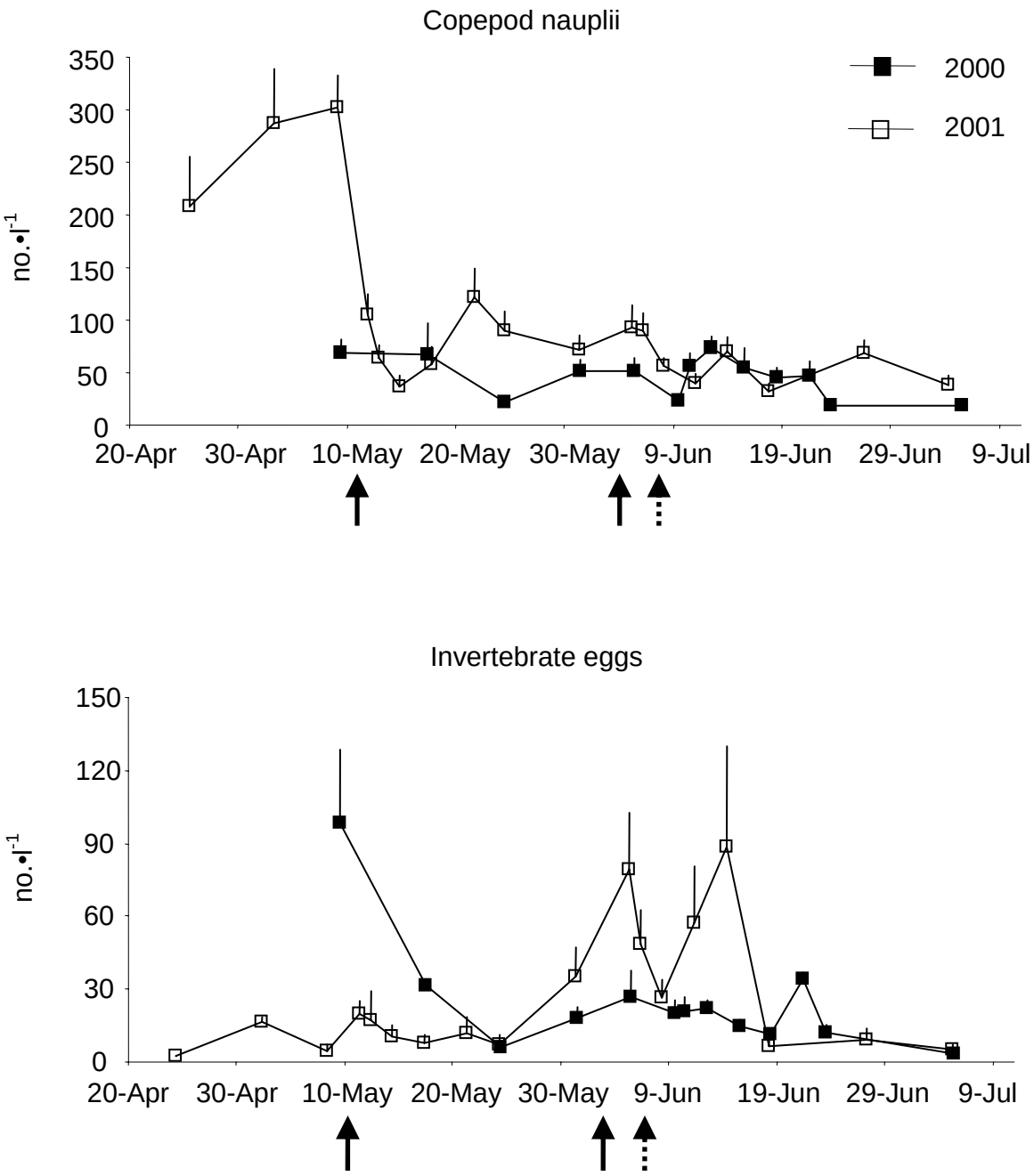
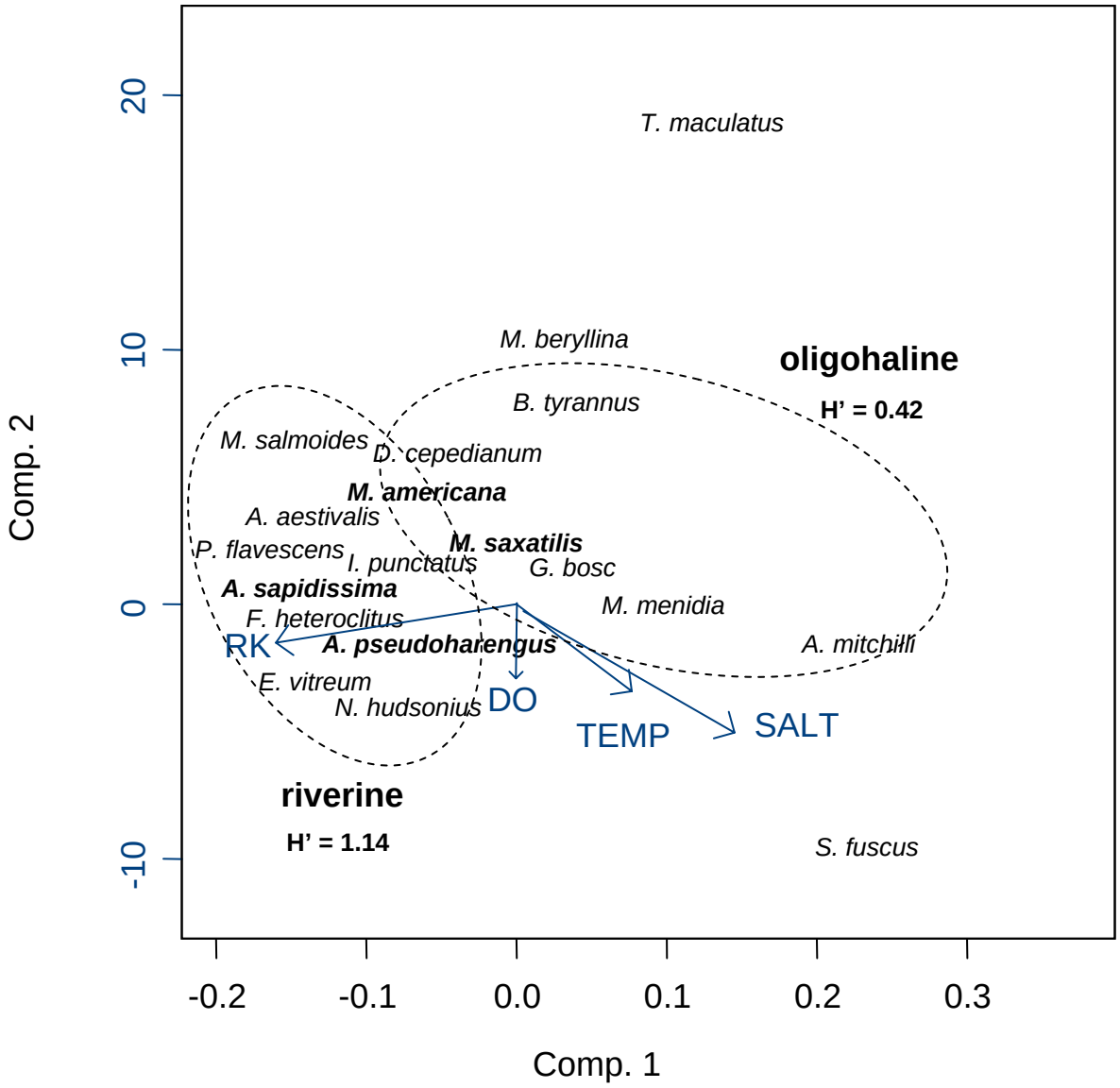


Fig. 1.12b. Temporal changes in copepod nauplii (above) and invertebrate egg (below) densities in the Patuxent River in 2000 and 2001. Vertical bars represent 1 standard error of the mean. The dashed arrow is the stocking date in 2000; solid arrows are stocking dates in 2001. Note different scales on y-axes.



Component	1	2	3	4	5
Variance	33.9	20.7	0.13	0.11	0.07
Loadings	-0.70	-0.40	0.63	2.38	-0.54

Figure 1.13. Principal Components Analysis. Plot of combined data for 2000 and 2001 ichthyoplankton species in the first two principal components and loadings and variances explained by each component. H' = Shannon-Wiener diversity index value (H'_{max} = 2.00). Species in this plot but not noted in text are: *M. salmoides* = largemouth bass; *P. flavescens* = yellow perch; *I. punctatus* = channel catfish; *F. heteroclitus* = mummichog; *E. vitreum* = glassy darter; *N. hudsonius* = spottail shiner; *B. tyrannus* = Atlantic menhaden; *A. mitchilli* = bay anchovy; *M. menidia* = Atlantic silverside; *M. beryllina* = tidewater silverside; *G. bosc* = naked goby; *S. fuscus* = northern pipefish.

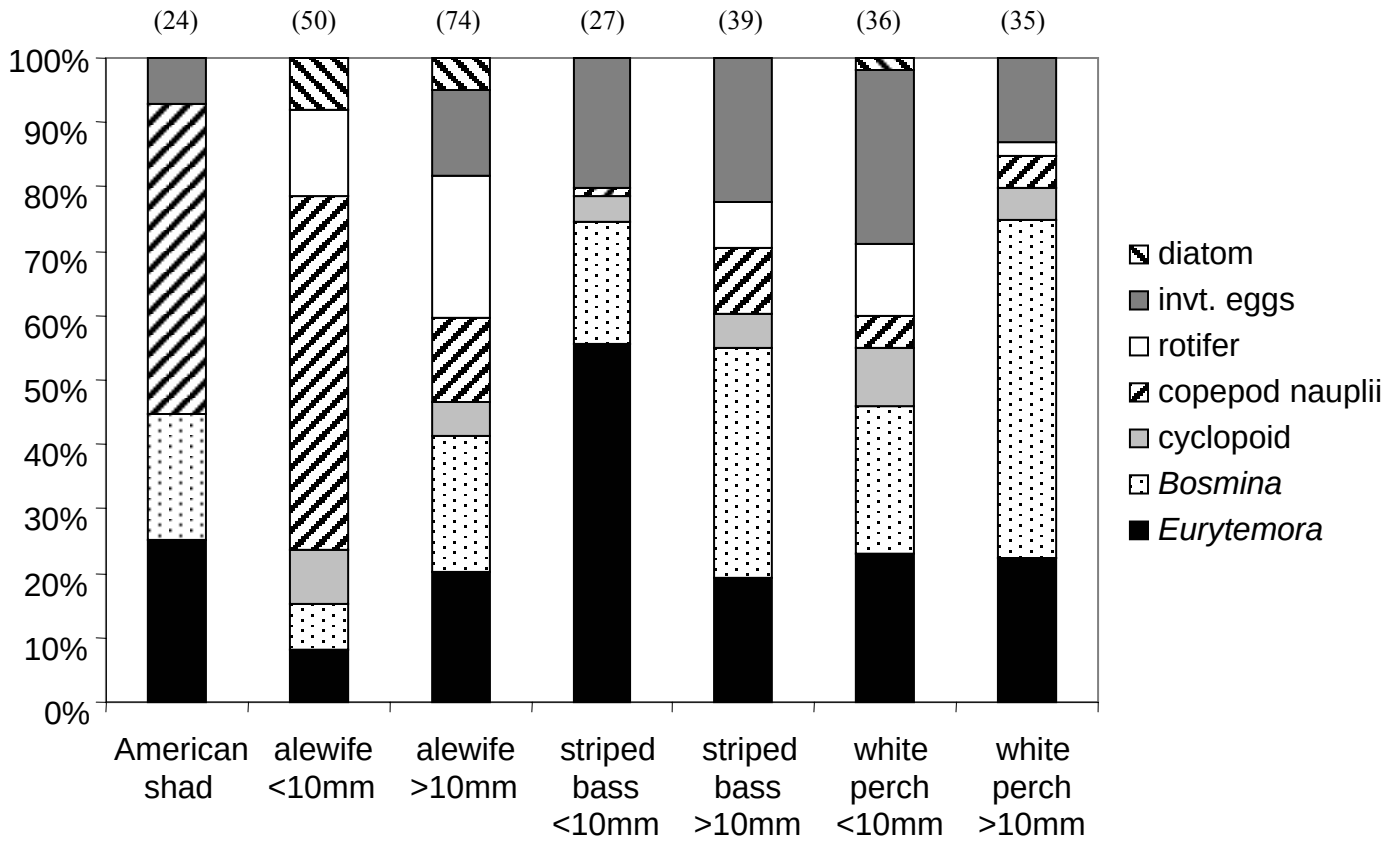


Figure 1.14. Percentage by number of prey types in the guts of common larval fishes, by taxa and size classes, in the freshwater nursery area of the Patuxent River. Combined diet analysis for larvae sampled in 2000 and 2001. Numbers of larvae analyzed in each taxon or size category in parentheses.

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CHAPTER TWO

Ichthyoplankton assemblages in the Patuxent River estuarine transition zone

ABSTRACT

The spatiotemporal structure of ichthyoplankton assemblages and larval growth rates were investigated in the Patuxent River, a tidal subestuary on the western shore of Chesapeake Bay. Comprehensive surveys during spring-early summer of 2000 and 2001 collected larval and juvenile fish, zooplankton, and a suite of data on hydrographic variables across the estuarine transition zone. Larvae of 28 fish species occurred in samples. Taxonomic diversity and richness were greatest in up-estuary regions. Alewife (*Alosa pseudoharengus*) and moronid species (*Morone saxatilis* and *M. americana*) larvae characterized samples from freshwater sites. The down-estuary oligohaline region was characterized by larvae of estuarine-spawned taxa (primarily naked goby, *Gobiosoma bosc*). Multivariate analyses distinguished riverine and estuarine ichthyoplankton assemblages and identified temperature, salinity-associated variables (e.g., salt-front location), dissolved oxygen, and *Bosmina* cladoceran prey concentrations as indicators of larval abundance. Estimated larval growth rates ($mm \bullet d^{-1}$) were similar to ($G_{A.\ pseudoharengus} = 0.39$, $G_{M.\ americana} = 0.20$, $G_{G.\ bosc} = 0.14$) or higher than ($G_{M.\ saxatilis} = 0.30$) those reported in previous studies, indicating that the Patuxent River estuarine transition zone is a favorable nursery area. Ichthyoplankton taxa were often most abundant within and up-estuary of the salt front. Hydrography and ontogenetic migrations contributed to spatiotemporal heterogeneity in distribution patterns of young fish in the Patuxent River and may ultimately control ichthyoplankton aggregations in the salt-front and estuarine transition region.

INTRODUCTION

During spring months several fish species migrate to tidal tributaries in Chesapeake Bay and spawn in similar habitats and under similar environmental conditions. Temperature is the primary cue for spawning. Temperature ranges for spawning overlap broadly for several anadromous alosines (shads and river herring) and moronids (striped bass *Morone saxatilis*, white perch *M. americana*) in Chesapeake Bay tributaries (Table 2.1, data from Funderburk et al. 1991). Naked goby (*Gobiosoma bosc*) spawns farther down-estuary in low-salinity water when temperatures range from 20-28°C. Its larvae, which can be abundant in late spring-summer (Shenker et al. 1983), migrate up-estuary during development and may share nursery resources with anadromous larvae. Bay anchovy (*Anchoa mitchilli*) spawns throughout the Bay and its tributaries at temperatures of 13-30°C, with young often occurring in oligohaline regions of the Patuxent River and other subestuaries during late spring-early summer (Loos and Perry 1991). Overlap in adult spawning periods and areas may lead to overlap in distributions and interactions among developing early-life stages of these abundant species in freshwater or low-salinity regions of Chesapeake Bay tributaries.

There is little knowledge of how larvae partition resources in nursery habitats. Larval distributions and associations are determined by adult spawning periods, hydrographic gradients, biological processes affecting survival (foraging, predation), and ontogenetic migrations (Sabatés 1990; Witting et al. 1999; Miller 2002; Sanvicente-Anorve et al. 2002). My research provides descriptions and evaluates relationships between environmental conditions and ichthyoplankton distributions and assemblages in

the estuarine transition zone of the Patuxent River, a western-shore tributary of Chesapeake Bay.

Two hypotheses were evaluated: 1) Hydrographic gradients define spatio-temporal distributions and assemblages of ichthyoplankton in the Patuxent River estuarine transition zone and 2) Concentrations and length distributions of ichthyoplankton taxa differ significantly above and below the salt front. The salt front is the zone where low-density freshwater moving down-estuary meets higher density, saltier water. Previous studies in the upper region of mainstem Chesapeake Bay reported increased concentrations of zooplankton and larval moronids near the salt front and associated turbidity maximum zone (North and Houde 2001; Roman et al. 2001). Larvae and juveniles of some estuarine-spawning species can be abundant in oligohaline regions (Shenker et al. 1983; Rilling and Houde 1999a; Kimura et al. 2000) and may be attracted to or concentrated in the frontal zone because zooplankton prey is abundant there.

Larval growth rates of Patuxent River fish larvae were estimated to compare seasonal and inter-annual variability in growth of cohorts. Environmental variables were evaluated relative to larval taxa concentrations during spring-early summer. The environmental variables also were included in a multivariate analysis to characterize ichthyoplankton assemblages in the Patuxent River estuarine transition zone.

METHODS

Ichthyoplankton surveys. Thirty ichthyoplankton sampling surveys were conducted on the Patuxent River in 2000 (13 surveys) and 2001 (17 surveys). Surveys took place at 3-7 day intervals between 24 April and 5 July (Table 2.2a).

Ichthyoplankton was sampled at 10 stations in the estuarine transition zone (Table 2.2b and Fig. 1.6). Sites were located at 2-7 river-kilometer intervals; depths at stations ranged from 2-10 meters. All samples were collected during daylight and each survey was completed in 8-10 hours.

Twenty-five of the surveys were conducted on the 25-ft RV Pisces. Samples were collected in a 60-cm diameter, paired bongo net with 333-μm meshes. Tows were oblique from surface to bottom and of 5-min duration. Flow meters in net mouths recorded the volumes of water sampled. A mean volume of 137m^3 of water was filtered in each paired bongo tow (combined paired-net samples). In the latter half of the sampling period in each year, collections of juveniles and large larvae were made in a 2-m^2 Tucker-trawl with 700-μm meshes. Two Tucker-trawl surveys were conducted in 2000 (23 June and 5 July) and three in 2001 (31 May, 27 June, and 3 July) from the 52-ft RV Orion (2000) or the 62-ft RV Aquarius (2001). Oblique, near-bottom to surface, Tucker-trawl tows were of 5-min duration and each filtered a mean volume of 575m^3.

Plankton catches were preserved in ethanol, brought to the laboratory, and transferred to fresh ethanol within 24 hours. Fish larvae and juveniles were identified, enumerated, and measured in the laboratory.

Sampling stations were located above, below, and within the projected larval nursery area of anadromous taxa. This area included the estuarine transition zone, and contained the Estuarine Turbidity Maximum (ETM), a feature in the estuary near the salt front, which is an important nursery area for larval and juvenile fish (Boynton et al. 1997; North and Houde 2001; Winkler et al. 2003). Physical processes in ETM regions aggregate particles such as larval fish and their zooplankton prey and may promote

anadromous fish recruitment in estuaries (Boynton et al. 1997; North and Houde 2003). The location of the salt front, defined by conductivity readings of 800-1000μS, was determined in each survey. Bottom salinities coinciding with the salt front ranged from 0.4-0.5 psu. The salt front location was defined because there is evidence that larvae of anadromous species below the ETM and salt front may be flushed out of suitable nursery areas, and advected down-estuary where they cannot contribute to recruitment (Secor et al. 1995).

Jassby et al. (1995) distinguished the 2-psu isohaline location, referred to as X_2, as a habitat indicator for some planktonic populations in the San Francisco Bay estuary. The ETM and peak abundances of ichthyoplankton and zooplankton of some species were typically found in the vicinity of X_2 (Jassby et al. 1995). In the Patuxent River, ichthyoplankton distributions and concentrations were evaluated with respect to the salt front and the intersection of the 2-psu isohaline with the bottom. Larval length distributions also were analyzed with respect to these features to evaluate how estuarine hydrography may influence ontogenetic migrations.

During each survey in both years, zooplankton (potential prey for fish larvae) was collected at 10 stations by pumping 60 liters of water from surface, middle, and bottom depths (20 liters per depth). Pumped water from the three depths was combined and zooplankton filtered onto a 35-μm sieve before preserving in 5% formalin. Zooplankton samples were brought to the laboratory for identification, enumeration, and measurement.

Hydrographic conditions. Environmental variables (temperature, salinity, dissolved oxygen, conductivity, and pH) were measured during surveys at each station. Instrument measurements of temperature, salinity, conductivity, and dissolved oxygen

were made at surface, mid-water, and near-bottom depths. Water from each depth was pumped into a bucket on deck and meter probes inserted to measure hydrographic variables. Surface pH was measured at every-other station. River-flow data were obtained from a U. S. Geological Survey gauge stationed at rk130, near Bowie, Maryland (USGS 2001).

Sample processing. In the laboratory, fish larvae and juveniles were removed from bongo net and Tucker-trawl samples, identified, and enumerated under a dissecting microscope. Samples were occasionally sub-sampled (1/2 to 1/8 of the whole sample, divided with a plankton splitter) when numbers per taxon were >200. Total lengths of larvae and juveniles (up to 100 per sample) from each taxon and size class were measured to the nearest 0.1-mm with a digital-image analysis system.

Patuxent River zooplankton densities (no.•l^{-1}) were estimated for several taxonomic categories: The calanoid copepods *Eurytemora affinis* copepodites and adults and *Acartia* sp. calanoid copepodites and adults; cyclopoid copepods, harpacticoid copepods, copepod nauplii, barnacle nauplii, invertebrate eggs, rotifers; the cladoceran *Bosmina longirostris*, 'other' cladocerans, chironomid insect larvae, and other less common taxa. Zooplankters were identified and enumerated under a dissecting microscope from 5-ml aliquots of the zooplankton samples that had been concentrated to 25-500ml. For each pumped sample, zooplankters from represented taxa and categories were measured under the microscope with an ocular micrometer.

Abundances, distributions, and assemblages. Larval abundances were calculated from estimated larval densities (numbers per m^3) at each sampling site and river volumes (m^3) represented by each site (Cox et al. 1980). Abundances were

analyzed with respect to hydrographic gradients mapped during surveys to determine the distribution of larvae in relation to environmental conditions. Species richness (*S*, the number of species) and Shannon-Wiener diversity index values (*H'*, incorporating the number of species and their relative abundances) were calculated to compare ichthyoplankton faunal composition among regions in the river.

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \ .$$

p_i is the proportion of species *i* relative to the total number of species. Habitat use and overlap among ichthyoplankton taxa with respect to hydrographic conditions were examined using Principal Components Analysis (PCA) of catch-per-unit-effort (CPUE, no•tow^{-1}) and hydrographic data to identify associations (Miller 2002). PCAs were run on correlation matrices of centered data.

Ichthyoplankton concentrations were compared with respect to freshwater, salt front, and oligohaline regions. Zooplankton densities and hydrographic variables were included in multivariate analyses to distinguish factors that potentially were indicators of larval fish concentrations. In statistical analyses, the normality assumption was met for most taxa by $\log_{10}(x+1)$-transformations of larval fish and zooplankton densities. Initially, larval concentrations were regressed individually on ten independent variables (temperature, salinity, conductivity, dissolved oxygen, pH, river flow, salt front location, copepod nauplii density, calanoid copepod density, and *Bosmina* cladoceran density) in both linear (X) and quadratic (X^2) models. Multiple regressions of larval concentrations then were developed by evaluating combinations of independent variables. A stepwise procedure (forward-backward) was applied to identify variables for inclusion in the best

regressions of concentrations for selected larval taxa. The probability threshold for including or removing variables from models was 0.10. Quality of model fit was assessed using Akaike's Information Criteria (AIC). The model with the smallest AIC value was retained when comparing regressions within each larval taxon.

Growth rates. Larval growth rates of four common species were estimated (alewife, *A. pseudoharengus*; striped bass, *M. saxatilis*; white perch, *M. americana*; and naked goby, *G. bosc*) by modal progression analysis (McGurk 1987; Gulland 1988). For each species, length-frequency distributions were derived by pooling samples across regions for each survey. Under the assumption that length-frequencies were mixtures of normal distributions (cohorts), maximum likelihood techniques were applied to distinguish cohorts and estimate cohort modal lengths (Haddon 2001). Modal length was equated to mean length within each normal distribution of cohort lengths. Linear regressions of larval cohort modal lengths over time were fit and the regression slopes were estimates of growth rates (see example in Fig. 2.10). Cohorts that occurred in fewer than three surveys were excluded from analysis.

RESULTS

Hydrographic conditions. The 31-kilometer segment sampled in the Patuxent River included oligohaline and freshwater regions of the estuarine transition zone. Gradients in measured hydrographic variables were observed across the survey area (Figs. 2.1 and 2.2). Temperatures declined from downriver stations to the upper reaches of the subestuary, most notably at rk78 where water temperatures averaged 2-4°C cooler than at all other stations. During surveys, mean salinity in the sampled river segment was

< 5.0 psu, although salinities at down-estuary stations occasionally approached 10.0 psu. A gradient in dissolved oxygen also was observed, with cooler and lower salinity up-estuary waters being more oxygenated.

Year 2000 An unusual cooling episode occurred in late May, but in general temperatures were > 20°C during the year 2000 survey period and approached 30°C in early July (Fig. 1.7). Precipitation and river flow were below the historical average and were relatively constant during spring-early summer of 2000. The salt front location remained near river kilometer 56 in May before shifting 5 km down-estuary in mid-June, coinciding with small increases in precipitation and river flow. Dissolved oxygen levels were high during the cooling event in May, then decreased to 5.0-7.0 $mg \bullet l^{-1}$ as temperatures increased in June. The pH levels were in the range 7.0-8.5 in all surveys and usually were > 7.5.

Year 2001 Hydrographic conditions were more variable during the 2001 sampling period (Fig. 1.7). Temperatures in late April were < 20°C, fluctuated in early May, and then gradually increased to > 25°C by early summer. The salt front moved 10 km up-estuary in a period of reduced precipitation and river flow during early May. The front then shifted 12 km down-estuary, coincident with several higher flow events in late May and early June. The mean salt front location differed by 2 km between years (rk 54 in 2000, rk 56 in 2001). Dissolved oxygen and pH levels were more variable during the 2001 sampling period than in 2000. Dissolved oxygen was lower in general in 2001 and declined to 4.0 $mg \bullet l^{-1}$ at down-estuary stations during a short-term warming event in early May 2001, although D.O. was generally > 6.0 $mg \bullet l^{-1}$ during the survey period. In the 2001 survey period, pH levels were always above 7.0 and usually > 7.5.

Precipitation and river flow were below the historical average during spring-early summer 2001, and were more variable than during the 2000 sampling period (Fig. 1.7). Several short-duration, high flow events occurred in the second half of the sampling period in 2001 (23-28 May, 9 June, and 23-25 June). These storm-associated events affected time series of the river temperature trend by stabilizing temperatures for several days, thus interrupting the gradual warming trend typically observed at this time of year in Chesapeake tributaries.

Species composition and diversity. In the two years of sampling, a total of 379 tows collected 198,161 larval and juvenile fishes representing 28 taxa (Tables 2.3 and 2.4). Twenty taxa occurred in both years. Species richness for the entire survey area was similar between years ($n_{spp., 2000} = 24$, $n_{spp., 2001} = 23$) and was highest in freshwater when comparing regions within the river. Diversity was higher in the freshwater and salt-front regions (H' = 0.72-0.86) than down-estuary in the oligohaline region (H' = 0.25-0.50).

Year 2000

In 2000, catch-per-unit-effort (CPUE, no.•tow^{-1}) was highest in the oligohaline region (625.1) because *G. bosc* larvae dominated catches there (Table 2.3). CPUE was similar at the salt front (278.9) and in freshwater (212.2). Catches in freshwater had the most variable CPUE ($CV_{FW} = 315\%$); the least variability occurred at the salt front (154%); and variability in the oligohaline region was intermediate (185%). Larval white perch, alewife, and gizzard shad (*Dorosoma cepedianum*) occurred most frequently in freshwater tows. Naked goby, white perch, and striped bass larvae occurred most frequently in salt front and oligohaline regions.

Year 2001

The largest catches of larvae were at the salt front (CPUE = 842.1) in 2001 (Table 2.4). CPUE was lowest in the oligohaline region (189.6) and intermediate in freshwater (538.8). As in 2000, trends in ichthyoplankton taxa occurrences were driven by naked goby and white perch larvae. These two species comprised >80% of the regional catches. Coefficients of variation in CPUE were similar across regions (CV_{FW} = 223%, CV_{SF} = 254%, CV_{OH} = 217%). Ninety-eight percent of freshwater catches were comprised of 3 larval taxa (white perch, alewife, and striped bass). Naked goby was the dominant species in salt front and oligohaline regions.

Several larval taxa (spottail shiner, *Notropis hudsonius*; darters, *Etheostoma* spp.; suckers, *Erimyzon* spp.; yellow perch, *Perca flavescens*) occurred more frequently down-estuary in 2001 than in 2000. Larval yellow perch CPUE in freshwater was 15-fold higher in 2001. Gizzard shad larvae were more common in freshwater in 2000 when CPUE was 4 times higher than in 2001. In 2001, CPUE of larval white perch in freshwater was more than double that in 2000. Striped bass larvae CPUE was more than an order-of-magnitude higher in the freshwater region and 4 times higher at the salt front in 2001 than in 2000.

Naked goby larvae were more common in freshwater in 2000 although CPUE was highest in the oligohaline region. In 2001, larval naked goby CPUE was highest at the salt front. Larval silversides (*Menidia* spp.) occurred more frequently in up-estuary regions and were more abundant throughout the estuarine transition zone in 2001. Sciaenid larvae occurred in salt front and oligohaline regions in 2000 but were nearly absent in 2001.

Regional patterns in mean CPUE differed between years and were driven by larvae of two species, naked goby and white perch. In 2000, mean combined-species CPUE increased directionally from freshwater to oligohaline regions (Table 2.3). In 2001, mean CPUE was highest in the salt-front region, intermediate in freshwater, and lowest in oligohaline regions (Table 2.4). When comparing years, mean CPUE was higher in freshwater and salt-front regions in 2001 than in 2000, but lower in the oligohaline region.

Distributions and assemblages. Alosines (*Alosa* spp.) underwent a down-estuary ontogenetic migration (Fig. 2.3). Yolk-sac larvae were collected ≥10 kilometers above the salt front. Alosine post-yolk-sac larvae, primarily alewife, occurred in the freshwater region. Young-of-the-year (YOY) alosine juveniles were collected farther down-estuary, near the salt front, in late-season Tucker-trawl tows. Gizzard shad larvae (not included in Fig 2.3) were common throughout the sampling area.

White perch exhibited a ubiquitous distribution that overlapped with alewife and congeneric striped bass. All early-life stages of white perch were present throughout the estuarine transition zone in early-season collections (Fig. 2.3). However, distributions of length classes differed later in the season when larger white perch larvae occurred near and just up-estuary of the 2-psu isohaline while smaller larvae were found only in freshwater. Striped bass yolk-sac larvae occurred most frequently above the salt front in freshwater and were not common in samples after mid-June. Striped bass post-yolk-sac larvae and juveniles (<75mm) were distributed within and up-estuary of the salt front-ETM region (Fig. 2.3).

Larvae and YOY individuals of estuarine- and coastal-spawning fishes became more common later in the sampling period during each year. Naked goby larvae arrived in the oligohaline region between 2-24 May and underwent an up-estuary ontogenetic migration, with large larvae (>10mm) occurring frequently in salt front and freshwater regions in June and July (Fig. 2.3). The distributions of bay anchovy (*Anchoa mitchilli*) larvae and juveniles and Atlantic menhaden (*Brevoortia tyrannus*) juveniles also expanded into the sampling area during the survey periods, as these YOY clupeoid fishes dominated late season Tucker-trawl collections (Fig. 2.3).

In the Patuxent subestuary, ontogenetic migrations contributed to overlap in distributions of several young fishes at the salt front in spring-early summer. White perch, striped bass, and naked goby were the most common species, with high numbers of bay anchovy arriving in this region later in the season. A principal components analysis revealed two non-discrete ichthyoplankton assemblages in the estuarine transition zone in 2000 and 2001 (Figs. 2.4 and 2.5):

1) Riverine: characteristic species included young of anadromous and freshwater taxa, predominantly *Morone* spp., alewife, other alosines, and gizzard shad. Yolk-sac larvae were common in this diverse assemblage, which inhabited colder, more highly oxygenated water.

2) Oligohaline: early-life stages of estuarine-spawned species characterized this low-diversity assemblage. Increasing water temperatures associated with greater spawning activity may account for marked increases in larval naked goby concentration in this assemblage as the survey periods progressed. In late June, juvenile Atlantic menhaden and bay anchovy joined the assemblage as temperatures reached 24°C.

Assemblage structure and species associations were similar between years. Although two assemblages were distinguished, members of several constituent taxa (moronids, naked goby, and clupeiformes) from each assemblage co-occurred at the salt front. This was most notable in late spring-early summer when small juveniles and larger length classes of larvae became prevalent in the 0-3 psu region of the estuarine transition zone (Fig. 2.3).

Larval abundance and growth. The relative abundances of anadromous and estuarine ichthyoplankton taxa changed directionally across the estuarine transition zone (Fig. 2.6). Several ichthyoplankton taxa distributions overlapped at the salt front. Concentrations of common taxa were compared among salt front, freshwater, and oligohaline regions (Fig. 2.7). Larval alewife concentration was always higher up-estuary of the salt front. In both years, larval white perch concentration was higher at the salt front than down-estuary. Its concentration down-estuary of the salt front was lower than at or up-estuary of the salt front in 2001. Larval striped bass concentration was higher in 2001, most notably within and up-estuary of the salt front region, but there were no significant differences among regions or years due to the variability in concentrations. Naked goby larvae concentration was highest below the salt front in 2000 but at the salt front in 2001.

Larvae of anadromous fishes were most abundant early in the sampling periods, most notably in surveys conducted between 24 April and 15 June (Fig. 2.8). White perch abundance was an order of magnitude higher than striped bass in the earliest collections during both years and generally was higher than striped bass abundance throughout each sampling period. Temporal patterns in alewife, striped bass, and white perch abundances

were similar in both years, and these three taxa dominated freshwater catches until mid-June. The earliest collections of naked goby (an estuarine species) were made on 24 May 2000 and 2 May 2001 (Fig. 2.9). Larval naked goby abundance peaked during the second week of June in both years, when temperatures in the oligohaline region reached 25°C. Catches of menhaden juveniles were not made until June in each year. Bay anchovy larvae increased in catches from late May to July, when surveys were terminated.

The descriptive analyses and PCA indicated that hydrographic factors were important in determining ichthyoplankton distributions and concentrations in the estuarine transition zone. Multiple regression analyses were conducted to determine whether hydrographic and zooplankton prey variables described a significant amount of variability in larval concentrations. Results are summarized in Table 2.5.

Temperature, dissolved oxygen, salt front location, and concentrations of *Bosmina* cladoceran prey were significant in the models for alewife larvae. Modeled parameter estimates suggested that alewife in 2000 was most abundant up-estuary of the salt front where dissolved oxygen levels and cladoceran concentrations were highest. In 2001, the multiple regression model indicated larval alewife concentration was highest up-estuary of the salt front in cooler temperatures.

Prey concentrations also described a significant amount of variability in larval moronid concentrations. Salinity and *Bosmina* and calanoid copepod densities were significant in the 2000 striped bass model (Table 2.5). In 2001, prey concentrations, salt front location, dissolved oxygen, and temperature were positively related to striped bass abundance, with highest larval concentrations near the salt front where prey densities also were high. A complex model with several significant variables best described white

perch larvae concentrations in 2000 (Table 2.5). Copepod nauplii density was the only non-significant variable. In 2000, concentrations of white perch were highest in more saline waters near the salt front that had elevated prey concentrations (*Bosmina* and calanoid copepods). The 2001 model differed markedly. Parameter estimates in 2001 suggested white perch larvae were most abundant in cooler, low-salinity habitat, regardless of prey concentrations.

The 2000 larval naked goby model was unique because the copepod nauplii variable was significant (Table 2.5). Parameter estimates suggested larval concentrations were highest in waters with lower oxygen levels, low *Bosmina* densities, and high copepod nauplii densities. In 2001, temperature and salt-front location described a significant amount of variability in naked goby larvae concentrations, and parameter estimates indicated that concentrations were highest in waters with higher temperatures within the salt front-ETM region. The 2001 outcome reflects the increase in larval goby concentrations from early- to late-season surveys that is coincident with increasing temperatures and migration of its larvae up-estuary.

In larval growth analyses, cohorts were specified from individual normal distributions in multi-modal plots of length frequency data (Fig. 2.10). Nine alewife cohorts were identified with sufficient numbers to estimate growth rates: cohorts I-IV in 2000 and cohorts V-IX in 2001 (Table 2.6). Estimated growth rates for larval alewife cohorts in 2000 ranged from 0.36 to 0.41 $mm \bullet d^{-1}$. Cohort-specific growth rate estimates for larval alewife in 2001 ranged from 0.36-0.47 $mm \bullet d^{-1}$. Variation in cohort growth rates was low in each year, but somewhat higher in 2001 (CV = 10.6%) than in 2000 (CV

= 5.8%). Mean growth rate estimates for alewife larvae did not differ between years (p = 0.37).

Two striped bass larval cohorts with sufficient occurrences to estimate growth rates were identified in 2000 and four were identified in 2001 (Table 2.6). In 2000, the earlier cohort had a higher growth rate than the later cohort. The pattern of lower estimated growth rates for later cohorts also was observed in 2001. Mean larval growth rate estimates for striped bass were similar between years (p = 0.75). Variation in cohort growth rates in 2000 (CV = 20.2%) may have been greater than in 2001 (CV = 13.1%).

The modal analysis of length frequencies identified 11 cohorts of larval white perch suitable for growth analysis, more than for any other taxa. In 2000, larval cohort growth rate estimates were lower early in the season (Table 2.6). The opposite trend was observed in 2001. Variability in larval white perch cohort growth rates was higher in 2001 (CV_{2000} = 19.2%, CV_{2001} = 41.0%). The mean cohort-specific larval growth rate of white perch appeared to be higher in 2001 (0.24 mm•d^{-1}), but because of the high, among-cohort variability, growth rates did not differ significantly between years (p = 0.12).

Estimated growth rates of three naked goby larvae cohorts (Table 2.6) were similar in 2000 (G = 0.12 to 0.14 mm•d^{-1}). Three cohorts in 2001 had estimated growth rates averaging 0.15 mm•d^{-1} (Table 2.6) and were more variable (CV_{2001} = 17.6%) than in 2000 (CV_{2000} = 8.7%). Mean cohort growth rates for naked goby larvae did not differ significantly between years (p = 0.39).

DISCUSSION

Hydrographic gradients and species distributions. Hydrographic conditions in the Patuxent River during the April-July period were similar in 2000 and 2001, which were both years of below-average river flow. Flow was more variable in 2001 in response to several storm events. Time-series observations of river flow explain changes in salt front location and isohaline distributions between surveys and years. High-flow events resulted in down-estuary shifts of these features, most notably in late May–early June of 2001, and also caused shifts in the distributions of larval taxa.

A relatively rich faunistic composition of larvae was found in the freshwater region in both years, as numerically dominant alosine and moronid larvae co-occurred with larvae of several freshwater species. Dominant taxa in the Patuxent River salt-front region varied between years, although taxonomic diversity was moderately high and similar to that of the freshwater region. White perch was the most abundant larval taxon at the salt front in 2000, but naked goby was numerically dominant in 2001. In contrast, naked goby larvae were most abundant in the low-diversity oligohaline region in 2000. Differences could have been a result of variable physical-biological interactions at the salt front or variable, spatially-explicit mortality that differed between years. Naked goby and its distribution patterns strongly influenced spatial trends in total ichthyoplankton abundance because it is abundant and its CPUE was highest in oligohaline and salt front regions in 2000 and 2001, respectively. The dominance of naked goby in catches throughout the estuarine transition zone during 2000 and 2001 was consistent with observations by Shenker et al. (1983). *G. bosc* was the dominant taxon in their ichthyoplankton collections across a similar sampling area in the Patuxent River during

spring-early summer 1977. Variances associated with total catches (i.e., relative abundances) of fish larvae differed between 2000 and 2001. The coefficient of variation in CPUE was similar for the three designated regions in 2001 but was roughly two times higher in the freshwater region during 2000 than in the salt front or oligohaline regions.

Gobies and anchovies are often the numerically dominant taxa in estuarine and coastal ichthyoplankton communities worldwide (Houde and Alpern Lovdal 1984; McGowen 1993; Newton 1996; Witting et al. 1999; Sanvicente-Anorve et al. 2002; Somarkis et al. 2002). Their dominance tends to be most conspicuous in the low-salinity region, contributing to low diversity-index values that are typical of oligohaline larval nursery areas in many estuarine systems (Neira and Potter 1992; Newton 1996).

Distributions of alewife, striped bass, and white perch post-yolk-sac larvae consistently overlapped in both years. However, alewife early-life stages were restricted to the freshwater region while moronids had a broader distribution and also occurred in the oligohaline region. These anadromous taxa consistently overlapped in distribution with larvae of the ubiquitous gizzard shad. This clupeid species was most abundant in year 2000 collections in the freshwater region but also was common in the salt-front region of the estuary. With regard to moronid and alosine larvae, observations in the Patuxent estuary were similar to those elsewhere in Chesapeake Bay where the moronids were common in salinities of 0-3 psu (North and Houde 2001) while the centers of alosine distributions were further up-estuary (Setzler et al. 1981; Bilkovic et al. 2002).

In both years, larval alewife concentrations were highest several kilometers up-estuary of the salt front. Concentrations of striped bass larvae were similar among regions in 2000 but had a more distinctive spatial pattern in 2001, when their highest

concentration occurred in the freshwater region. The apparent difference may be partly due to the earlier start of surveys in April, 2001 when sampling potentially covered a broader temporal range of striped bass spawning activity in freshwater. White perch concentrations were highest within and up-estuary of the salt front and ETM features in both years. In the Potomac River, Setzler-Hamilton et al. (1982) observed the highest concentration of clupeid (alosines) larvae up-estuary of the highest larval moronid concentrations. They also reported peak concentrations of clupeid and moronid larvae in the 1st two weeks of May. Their result differs from results in the Patuxent River, when peak concentrations of alewife and moronid larvae occurred from the 1st week of May to the 1st week of June in 2000 and in late April in 2001. In 2000 and 2001, larvae of estuarine-spawning taxa (e.g., menhaden, bay anchovy, naked goby) exhibited a gradient of decreasing concentrations in an up-estuary direction. However, these species often were relatively abundant in the frontal zone.

Ontogenetic migrations or shifts in distribution during early-life history explained the distributions of length classes in anadromous species and estuarine- and coastal-spawned taxa. Small length classes (<10mm) of naked goby larvae, which originated from spawning down-estuary in oligohaline and mesohaline regions (Shenker et al. 1983), first arrived in the Patuxent River estuarine transition zone from 2-24 May. The seasonal increase in larval goby mean lengths, the increase in variability of lengths, and the up-estuary movement of larvae to lower salinities as the sampling period progressed each year were similar to observations from Patuxent River ichthyoplankton surveys in the late 1970s (Shenker et al. 1983). The earliest collections of *G. bosc* in the Shenker et al. study occurred on 5 May at river-kilometer 44, while dates of first occurrence in the

present study were 24 May 2000 (rk 46-58) and 2 May 2001 (rk 46-53). Dates of observed maximum concentrations of naked goby larvae differed between studies. Peak concentrations occurred in late June in the Potomac River (1974-1976) (Setzler et al. 1981) and in the Patuxent River (23 June 1977) (Shenker et al. 1983). Peak concentrations occurred earlier in the Patuxent in the present study (10 June 2000 and 11 June 2001). However, mean concentrations throughout the respective sampling areas were similar between the Shenker et al. and present study (N_{1977} = 18.3•m^{-3}, $N_{2000\text{-}2001}$ = 25.8•m^{-3}).

Bay anchovy and Atlantic menhaden YOY (late-stage larvae and small juveniles) became common in 2000 and 2001 samples after the 2nd week of June. Their initial appearances and concentrations in samples may have been biased by gear selection. A large proportion of samples containing these two species occurred in the 2-m^2 Tucker-trawl collections made toward the end of sampling periods in each year. The 2-m^2 Tucker-trawl almost certainly was more effective than the 60-cm diameter bongo tows in capturing juvenile fish. However, the low numbers of larval-stage anchovies collected in the bongo-net surveys earlier in the year supports the finding of Kimura et al. (2000) that up-estuary dispersal of young *A. mitchilli* occurs in the late larvae-early juvenile stage. Collections of large larvae and juveniles of bay anchovy in the oligohaline and salt-front regions of the Patuxent River in 2000 and 2001 also were consistent with data from the Patuxent in 1987 (Loos and Perry 1991) and the Hudson River where large larvae and juveniles were found up-estuary of areas where small larvae were collected (Schultz et al. 2000). Loos and Perry (1991) suggested that up-estuary transport is facilitated by baroclinic circulation and its effects on small larvae that occur near bottom. Schultz et al.

(2003) concluded that larger, post-flexion bay anchovy larvae vertically migrate to promote up-estuary transport.

In the Patuxent River, Atlantic menhaden and bay anchovy YOY became more common in oligohaline and freshwater regions as the survey periods progressed. Directed transport and ontogenetic migration into these regions may be an adaptation that improves foraging and survival potential of young fish that find favorable conditions in the estuarine transition zone. Bay anchovy early life stages in the mainstem Chesapeake Bay experienced lower mortality rates and higher growth rates in the oligohaline region than in mesohaline or polyhaline regions (Rilling and Houde 1999b).

As larval fish develop and transform to the juvenile stage, they occupy habitats with hydrographic conditions that often differ from those near spawning grounds. This situation was evident in the Patuxent River estuarine transition zone as feeding-stage larvae and YOY from anadromous and estuarine taxa converged in the low-salinity region around the salt front. The timing and location of adult spawning and ontogenetic migrations contribute to aggregation and coexistence (Tzeng and Wang 1993), but estuarine physics also play an important role. Fronts can act as barriers that maintain discrete larval assemblages (Iles and Sinclair 1982; Grioche and Kuobbi 1997) and may also serve as retention features where peaks in ichthyoplankton abundance are observed (Anderson and Gardner 1986; Kiorboe et al. 1988; Thorrold and McKinnon 1995; Grothues and Cowen 1999; Munk et al. 1999).

The salt-front structure in the tidal Patuxent River may contribute to the observed coexistence and maximum concentrations of anadromous and estuarine ichthyoplankton in this region. Moronid larvae also were very abundant up-estuary of the front. Thorrold

and McKinnon (1995) observed a similar spatial organization in larval carangid abundance in a Great Barrier Reef lagoon. They suggested that larval survival and recruitment potential were higher up-estuary of the frontal zone because highest copepod densities, and therefore more favorable feeding conditions, occurred in lower salinity waters. In the Patuxent River, densities of *Eurytemora* copepods, often the preferred prey of fish larvae (Chapter Three), were highest either up-estuary or near the salt front.

Previous studies in Chesapeake Bay and its tributaries indicated that moronid larvae below the salt front and ETM may be advected down-estuary and lost from the nursery area (Secor et al. 1995; Secor and Houde 1996; North and Houde 2003). My collections in the Patuxent River corroborate these findings. Striped bass and white perch yolk-sac larvae were virtually absent down-estuary of the 2-psu isohaline and total concentrations of moronid larvae also declined down-estuary of the 2-psu isohaline. The declines and absence of moronid larvae below the salt front do not conclusively demonstrate advective loss of larvae. However, Secor et al. (1995) released marked hatchery-source striped bass larvae in the Patuxent River and reported recaptures from all groups except those released below the salt front, providing strong circumstantial evidence that the salt front serves as a retention feature. In the American shad evaluation component of my study (Chapter 1), only a single larva was recaptured from the hatchery-produced cohort released below the salt front, and no juvenile recaptures of this cohort were made by summer seine surveys conducted by Maryland DNR.

The 0-3 psu region of Chesapeake tributaries typically includes the salt front and often-associated ETM (North and Houde 2001, 2003; Sanford et al. 2001). As larvae develop and acquire improved swimming capabilities, they appear to converge at the salt

front-ETM, possibly in response to, or by tracking, increased zooplankton prey concentrations associated with these features (Roman et al. 2001; North and Houde submitted). But, competition for prey resources and predator-prey interactions within this aggregation also may increase in early summer as YOY of estuarine- and coastal-spawned species arrive and co-occur in the salt front-ETM regions. Evaluating the net benefits to juvenile fishes that occupy salt front-ETM regions in Chesapeake Bay is an important direction for future research.

Ontogenetic migrations of anadromous and estuarine fish early life stages may be facilitated by two potential mechanisms: 1) selective tidal stream transport (STST) – the vertical migrations of larvae and juveniles utilizing tides for transport to favorable nursery areas – or 2) maintenance in residual bottom currents that advect larval fish up-estuary. Evidence for vertical migration in moronid larvae is conflicting. Previous research in Chesapeake Bay indicated that vertical distributions of striped bass and white perch larvae varied by developmental stage, in response to varying prey concentrations, or by maintaining position in bottom waters (Boynton et al. 1997; North and Houde 2001). However, Bennett (1998) and Bennett et al. (2002) observed striped bass larvae using tidally-timed vertical migration in the San Francisco Bay estuary. Contrasting transport mechanisms promoting larval retention in the salt front-ETM region were observed in the St. Lawrence River estuary. Larval rainbow smelt (*Osmerus mordax*) used STST to move up-estuary towards the ETM (Laprise and Dodson 1989) while tomcod (*Microgadus tomcod*) larvae were retained in nursery areas by remaining in residual deep-water circulation (Laprise and Dodson 1990). The oblique tows in my study did not permit evaluation of larval vertical distributions during different tidal

phases in the Patuxent River. However, frequent occurrences of small, pre-metamorphosis stage larvae of estuarine and anadromous species in the salt-front region of the Patuxent River suggest that physical transport mechanisms are important in promoting their aggregation or retention.

Larval growth. Estimated growth rates for the larval taxa that were analyzed by progression of modes in length-frequency distributions did not differ significantly between years (Table 2.6). A broader range of growth rates was observed for larval alewife in 2001 than in 2000, primarily due to higher growth rates for cohorts later in the season in 2001. In contrast, lower cohort growth rates were observed later in the season for striped bass larvae in both years and for white perch larvae in 2001. Temperatures were well above (>25°C) the optimum for larval growth of striped bass and white perch (15-20°C) after the 2nd week of June in both years and may have negatively impacted growth in late-season moronid cohorts. The highest growth rate for a cohort of naked goby larvae was estimated for the earliest 2001 cohort.

Estimated growth rates of alewife larvae in the Patuxent River (G = 0.36-0.47 mm•d^{-1}) were similar to those of alosine larvae in other studies, e.g., American shad (*Alosa sapidissima*) (G = 0.20-0.62) (Crecco and Savoy 1985; Leach and Houde 1999). The ranges of larval striped bass cohort growth rates estimated from otolith analysis by Rutherford and Houde (1995) in the Potomac River (0.11-0.53 mm•d^{-1}) and Upper Chesapeake Bay (0.18-0.36 mm•d^{-1}) overlapped the range that was estimated for Patuxent River larval striped bass (G = 0.25-0.36 mm•d^{-1}) in 2000 and 2001. The mean growth rate estimate for Patuxent striped bass larval cohorts (G = 0.30 mm•d^{-1}) in 2000 and 2001 was higher than the estimate by Secor et al. (1993) in 1991 (G = 0.17 mm•d^{-1}).

The 2000-2001 estimate also is higher than estimates for striped bass larvae in the Nanticoke River (G = 0.24 mm•d^{-1}) in 1992-1993 (Kellogg et al. 1996), in the Hudson River (G = 0.23 mm•d^{-1}) (Limburg et al. 1999), or in the Potomac River (0.24 mm•d^{-1}) and upper Chesapeake Bay (G = 0.26 mm•d^{-1}) (Rutherford and Houde 1995). Estimates of larval white perch growth rates in the Patuxent River (G = 0.20 mm•d^{-1}) were similar to those based on otolith analyses of Hudson River larvae (G = 0.22 mm•d^{-1}) (Limburg et al. 1999).

Using length-frequency data from Shenker et al. (1983), I estimated mean growth rate of Patuxent River naked goby larvae for the year 1977 to be 0.12 mm•d^{-1}. This rate was equal to the minimum growth rate estimated for a naked goby larval cohort in the 2000 and 2001 surveys. Growth rate estimates of naked goby larvae in laboratory experiments were generally higher than rates in the Patuxent River, ranging from 0.15-0.30 mm•d^{-1} (E. D. Houde, unpublished laboratory data, Chesapeake Biological Laboratory, personal communication).

Assemblage structure. Two ichthyoplankton assemblages, one of riverine and one of estuarine origin, were distinguished using multivariate (PCA) analyses of samples collected in the Patuxent River estuarine transition zone. The distributions of larval taxa from these assemblages reflected the influence of salinity and, secondarily, temperature and dissolved oxygen, on ichthyoplankton community structure. Ichthyoplankton taxa varied in their fidelity to environmental indicators. Salinity or salt front location described a significant amount of the variability in multiple regression models of larval concentration for all taxa that were analyzed.

The salt front was a good indicator of larval concentrations in all models, excepting striped bass in 2000 and white perch in 2001. Temperature was an important variable in all 2001 models, with higher concentrations of striped bass, white perch and naked goby larvae occurring at warmer temperatures and higher concentrations of alewife at low temperatures. Dissolved oxygen was significant in models for naked goby, white perch, and alewife larvae concentrations in 2000 and striped bass in 2001. Parameter estimates suggested that concentrations of anadromous taxa were highest at elevated dissolved oxygen levels while naked goby concentrations were higher in less-oxygenated water. Concentrations of the cladoceran *Bosmina longirostris* and calanoid copepods, which serve as prey for fish larvae, were significant in multiple regressions of larval concentrations for anadromous taxa but not for naked goby. Concentrations of anadromous larval taxa were highest where *Bosmina* and calanoid copepod densities were high. Goby larvae did exhibit an affinity for higher densities of copepod nauplii, which tended to occur below the salt front.

Prey density variables were always significant in Year 2000 models but were less important in 2001, except for striped bass. In research on coastal ichthyoplankton communities, maximum larval concentrations were often found in areas of elevated zooplankton densities, although hydrographic factors generally were more important in estimating larval taxa concentrations (Sabatés 1990; Smith et al. 1999). Limburg et al. (1999) reported that larval moronids co-occurring with blooms of zooplankton in the Hudson River had higher recruitment potential but suggested that temperature may be of equal or greater importance in Chesapeake Bay.

Temperature and salinity often are the most important variables controlling distributions of ichthyoplankton. For example, Somarkis et al. (2002) found that temperature and salinity explained a significant amount of variability in larval taxa distributions and abundances in coastal waters of the Aegean Sea. In near-shore waters of the St. Lucia estuary, South Africa, temperature was the most important variable in models of larval fish concentrations (Harris et al. 1999). Salinity was the most important hydrographic variable explaining ichthyoplankton abundances and distributions at the mouth of the Tanshui River estuary, Taiwan (Tzeng and Wang 1993). In contrast, a comparison of three South African estuaries indicated that turbidity was the best indicator of larval fish concentrations, with temperature and salinity being of secondary importance (Harris and Cyrus 2000).

In the Patuxent River estuarine transition zone and low-salinity regions of other estuaries (Tzeng and Wang 1992; Rakocinski et al. 1996), relationships between environmental variables and fish early-life history stages were more complex. Salinity and salinity-associated factors (e.g., salt-front location) were often most important, but temperature and dissolved oxygen also had significant effects on larval fish distributions and abundances. In the Patuxent River, concentrations of particular zooplankton prey taxa also were important explanatory variables. Each of these factors potentially is linked to precipitation and river flow, which intuitively may have a stronger influence on ecological interactions within an estuary than in coastal or shelf systems.

This is the first comprehensive ichthyoplankton community study in the Patuxent River estuary. Ichthyoplankton assemblages in the Patuxent were defined along hydrographic gradients. Several taxa could not be assigned unambiguously to a single

assemblage. There was a gradient in species composition across the estuarine transition zone rather than clearly-defined associations. Riverine and oligohaline assemblages overlapped in both years. However, ordination analysis revealed tighter grouping for each assemblage in 2001 than in 2000. In 2001, river flow was higher, temperatures were approximately 2°C lower, and the upriver-downriver gradient in dissolved oxygen was less developed. These inter-annual differences in hydrographic factors may have contributed to the less defined aggregations and assemblage structure in 2000 relative to 2001.

An assemblage transition zone occurred in the salt-front region of the Patuxent River where distributions of constituent taxa from riverine and estuarine assemblages overlapped. This type of distribution differs from ichthyoplankton community structure often observed on continental shelves, where taxa of defined coastal and oceanic assemblages do not usually coexist (Richardson et al. 1980; Young et al. 1986). Other estuarine studies also have reported gradients in larval fish assemblages and seasonal changes in taxonomic dominance (Rakocinski et al. 1996; Witting et al. 1999) due to broad distributions of constituent taxa from identified assemblages with respect to salinity and temperature levels. In the Patuxent River estuary, patterns in ichthyoplankton taxa arrivals, occurrences, distributions, and peak abundances indicated a predictable seasonal progression in ichthyoplankton assemblage structure.

Table 2.1. Spawning temperatures for anadromous and estuarine fishes in Chesapeake Bay (Funderburk et al. 1991).

Species	Spawning temperature range (°C)
alewife (*Alosa pseudoharengus*)	10-22
American shad (*Alosa sapidissima*)	12-21
striped bass (*Morone saxatilis*)	11-24
white perch (*Morone americana*)	10-20
naked goby (*Gobiosoma bosc*)	20-28
bay anchovy (*Anchoa mitchilli*)	13-30

Table 2.2. Survey descriptions (a) and sampling station locations (b) for Patuxent River ichthyoplankton surveys in 2000 and 2001.

(a)

		Survey dates	
Research Vessel	**Ichthyoplankton sampler**	**2000**	**2001**
Pisces	60-cm diameter, paired bongo net, 333-µm meshes	9, 17, 24, and 31 May; 5, 9, 10, 12, 15, 18, and 21 June	24 April; 2, 8, 11, 12, 14, 17, 21, and 24 May; 5, 6, 8, 11, and 14 June
Orion or *Aquarius*	2-m^2 Tucker-trawl, 700-µm meshes	23 June; 5 July	31 May; 27 June; 3 July

(b)

River kilometer	**Latitude**	**Longitude**
78	38°48.00’	76°42.09’
71	38°45.22’	76°41.98’
68	38°44.40’	76°41.07’
66	38°43.80’	76°41.75’
64	38°42.73’	76°42.10’
58	38°40.29’	76°41.88’
56	38°39.35’	76°41.05’
53	38°38.49’	76°41.55’
50	38°36.91’	76°40.30’
46	38°35.33’	76°40.44’

Table 2.3. Year 2000. Larval fish species composition, frequency of occurrence (Freq = proportion of tows positive), CPUE (no.•tow^{-1}), and SE of CPUE by region in the Patuxent River estuarine transition zone in spring-early summer 2000. The 'Salt front' region includes stations ±3-km from the salt front location (see Fig. 1.4). H' = Shannon-Wiener diversity index values (H'$_{max}$ = 2.0).

	Freshwater			Salt front			Oligohaline		
Species	Freq	CPUE	SE	Freq	CPUE	SE	Freq	CPUE	SE
Anguilla rostrata	0.01	0.01	0.01	-	-	-	-	-	-
Anchoa mitchilli	0.01	0.01	0.01	0.19	0.31	0.15	0.35	0.73	0.26
Alosa aestivalis	0.14	0.52	0.20	-	-	-	-	-	-
Alosa mediocris	0.07	0.09	0.04	0.03	0.03	0.03	-	-	-
Alosa sapidissima	0.10	0.13	0.05	0.03	0.03	0.03	-	-	-
Alosa pseudoharengus	0.73	28.84	10.46	0.13	0.13	0.06	-	-	-
Dorosoma cepedianum	0.59	14.39	4.82	0.34	1.25	0.50	0.12	0.27	0.16
Notropis hudsonius	0.04	0.06	0.03	-	-	-	-	-	-
Etheostoma spp.	0.10	0.11	0.04	-	-	-	-	-	-
Fundulus heteroclitus	0.07	0.08	0.04	-	-	-	-	-	-
Fundulus majalis	0.01	0.01	0.01	-	-	-	-	-	-
Erimyzon spp.	0.06	0.06	0.03	0.03	0.03	0.03	-	-	-
Ictalurus punctatus	0.01	0.01	0.01	0.03	0.03	0.03	-	-	-
Menidia beryllina	0.13	0.17	0.06	0.03	0.03	0.03	0.12	0.12	0.06
Menidia menidia	-	-	-	0.16	0.19	0.08	0.31	1.23	0.77
Syngnathus fuscus	-	-	-	-	-	-	0.04	0.04	0.04
Lepomis gibbosus	0.01	0.01	0.01	-	-	-	-	-	-
Perca flavescens	0.03	0.06	0.04	-	-	-	-	-	-
Morone americana	0.80	160.59	74.80	0.97	167.11	64.09	0.73	27.27	8.05
Morone saxatilis	0.31	5.61	2.28	0.53	11.14	4.12	0.38	3.21	1.46
Pomoxis annularis	0.24	0.45	0.13	0.06	0.09	0.07	-	-	-
Sciaenidae spp.	-	-	-	0.03	0.16	0.16	0.08	0.27	0.23
Gobiosoma bosc	0.14	1.00	0.46	0.81	98.30	42.99	0.92	591.90	227.69
Trinectes maculatus	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	

Table 2.4. Year 2001. Larval fish species composition, frequency of occurrence (Freq = proportion of tows positive), CPUE (no.•tow^{-1}), and SE of CPUE by region in the Patuxent River estuarine transition zone in spring-early summer 2001. The 'Salt front' region includes stations ±3-km from the salt front location (see Fig. 1.4). H' = Shannon-Wiener diversity index values (H'$_{max}$ = 2.0).

	Freshwater			Salt front			Oligohaline		
Species	Freq	CPUE	SE	Freq	CPUE	SE	Freq	CPUE	SE
Anchoa mitchilli	-	-	-	0.14	0.34	0.22	0.13	1.31	0.97
Alosa aestivalis	0.16	0.85	0.19	-	-	-	-	-	-
Alosa mediocris	0.03	0.03	0.02	-	-	-	-	-	-
Alosa sapidissima	0.11	0.13	0.05	-	-	-	-	-	-
Alosa pseudoharengus	0.81	25.10	9.13	0.34	0.76	0.30	-	-	-
Dorosoma cepedianum	0.36	2.99	1.31	0.38	2.10	0.83	0.05	0.18	0.16
Notropis hudsonius	0.15	0.62	0.34	0.03	0.03	0.03	-	-	-
Etheostoma spp.	0.28	0.96	0.23	0.10	0.10	0.06	-	-	-
Fundulus heteroclitus	0.18	0.20	0.05	-	-	-	-	-	-
Erimyzon spp.	0.42	4.11	1.28	0.10	0.14	0.08	0.03	0.03	0.03
Menidia beryllina	0.14	0.39	0.23	0.31	0.45	0.14	0.31	1.49	0.54
Menidia menidia	0.11	0.13	0.04	0.28	1.17	0.61	0.59	4.87	1.41
Membras martinica	-	-	-	0.07	0.07	0.05	-	-	-
Syngnathus fuscus	-	-	-	-	-	-	0.05	0.05	0.04
Opsanus tau	-	-	-	-	-	-	0.05	0.05	0.04
Perca flavescens	0.07	0.92	0.59	0.07	0.07	0.05	-	-	-
Morone americana	0.83	429.34	128.28	1.00	194.07	39.55	0.49	8.05	2.49
Morone saxatilis	0.40	72.72	37.88	0.66	45.17	22.62	0.54	4.44	1.93
Micropterus salmoides	0.01	0.01	0.01	-	-	-	-	-	-
Pomoxis annularis	0.17	0.27	0.09	0.03	0.03	0.03	-	-	-
Sciaenidae spp.	0.01	0.03	0.03	-	-	-	-	-	-
Gobiosoma bosc	0.01	0.01	0.01	0.72	597.62	405.02	0.92	169.10	65.64
Trinectes maculatus	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	

Table 2.5. Multiple regression models evaluating relationships between concentrations (no.•m^{-3}) of common larval taxa (alewife, striped bass, white perch, and naked goby) and abiotic and biotic factors in 2000 and 2001. Organism concentrations were $\log_{10}(x+1)$-transformed. Independent variables were entered into models 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 Criteria (AIC) indicate quality of model fit. The salt front location was modeled as a dichotomous variable (0 when station located at or up-estuary of the salt front, 1 when below). $N_{2000} = 11$; $N_{2001} = 14$.

	Independent Variables							Model Fit			
Dependent Variables	Salinity	Temperature	Dissolved oxygen	Salt front location	*Bosmina* cladocera	Calanoid copepods	Copepod nauplii	AIC	R^2	df	p
A. pseudoharengus											
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
M. saxatilis											
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
M. americana											
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
G. bosc											
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

Table 2.6. Cohort-specific growth rate estimates ($mm \cdot d^{-1}$) and standard errors (in parentheses) based on length-frequency analyses for larval alewife, striped bass, white perch, and naked goby in 2000 and 2001. Cohorts listed chronologically.

2000		2001	
Cohort	G (SE)	Cohort	G (SE)
	A. pseudoharengus (alewife)		
I	0.41 (0.02)	V	0.39 (0.05)
II	0.36 (0.01)	VI	0.38 (0.03)
III	0.39 (0.02)	VII	0.36 (0.05)
IV	0.37 (0.02)	VIII	0.47 (0.03)
		IX	0.42 (0.01)
Mean = 0.38, CV = 5.8%		**Mean = 0.40, CV = 10.6%**	
	***t* = -0.97, p = 0.37**		
	M. saxatilis (striped bass)		
I	0.36 (0.02)	III	0.34 (0.04)
II	0.27 (0.04)	IV	0.31 (0.03)
		V	0.25 (0.03)
		VI	0.28 (0.02)
Mean = 0.32, CV = 20.2%		**Mean = 0.30, CV = 13.1%**	
	***t* = 0.41, p = 0.75**		
	M. americana (white perch)		
I	0.13 (0.02)	VI	0.32 (0.02)
II	0.13 (0.02)	VII	0.36 (0.01)
III	0.18 (0.02)	VIII	0.29 (0.02)
IV	0.20 0.02)	IX	0.18 (0.01)
V	0.17 (0.02)	X	0.16 (0.02)
		XI	0.12 (0.03)
Mean = 0.16, CV = 19.2%		**Mean = 0.24, CV = 41.0%**	
	***t* = -1.81, p = 0.12**		
	G. bosc (naked goby)		
I	0.14 (0.02)	IV	0.18 (0.01)
II	0.14 (0.01)	V	0.13 (0.02)
III	0.12 (0.01)	VI	0.14 (0.06)
Mean = 0.13, CV = 8.7%		**Mean = 0.15, CV = 17.6%**	
	***t* = -1.00, p = 0.39**		

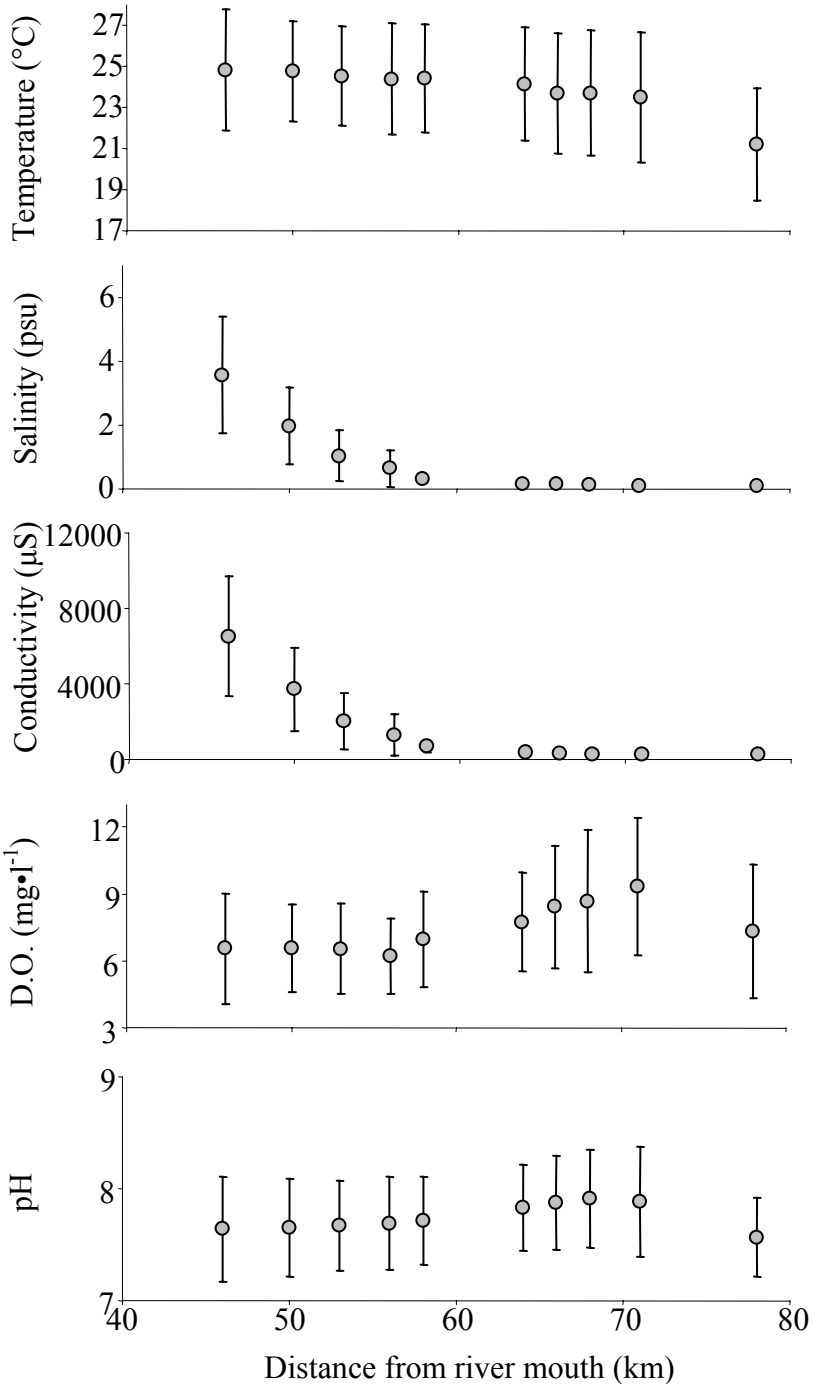


Figure 2.1. Year 2000. Hydrographic conditions across sampling stations in the Patuxent River estuarine transition zone from April-July, 2000. Values are station means (±1 standard deviation) of mid-depth measurements (pH measurements only at surface).

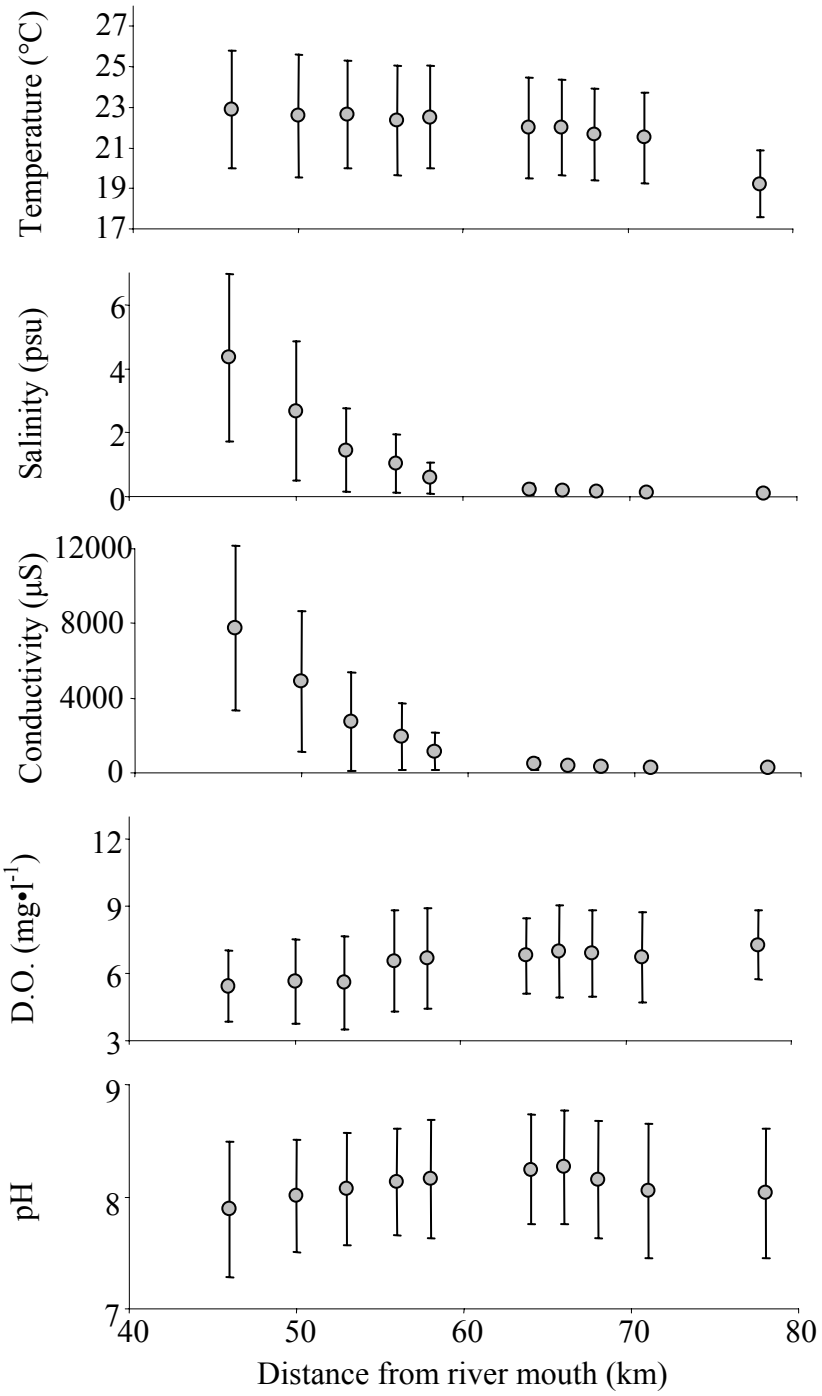
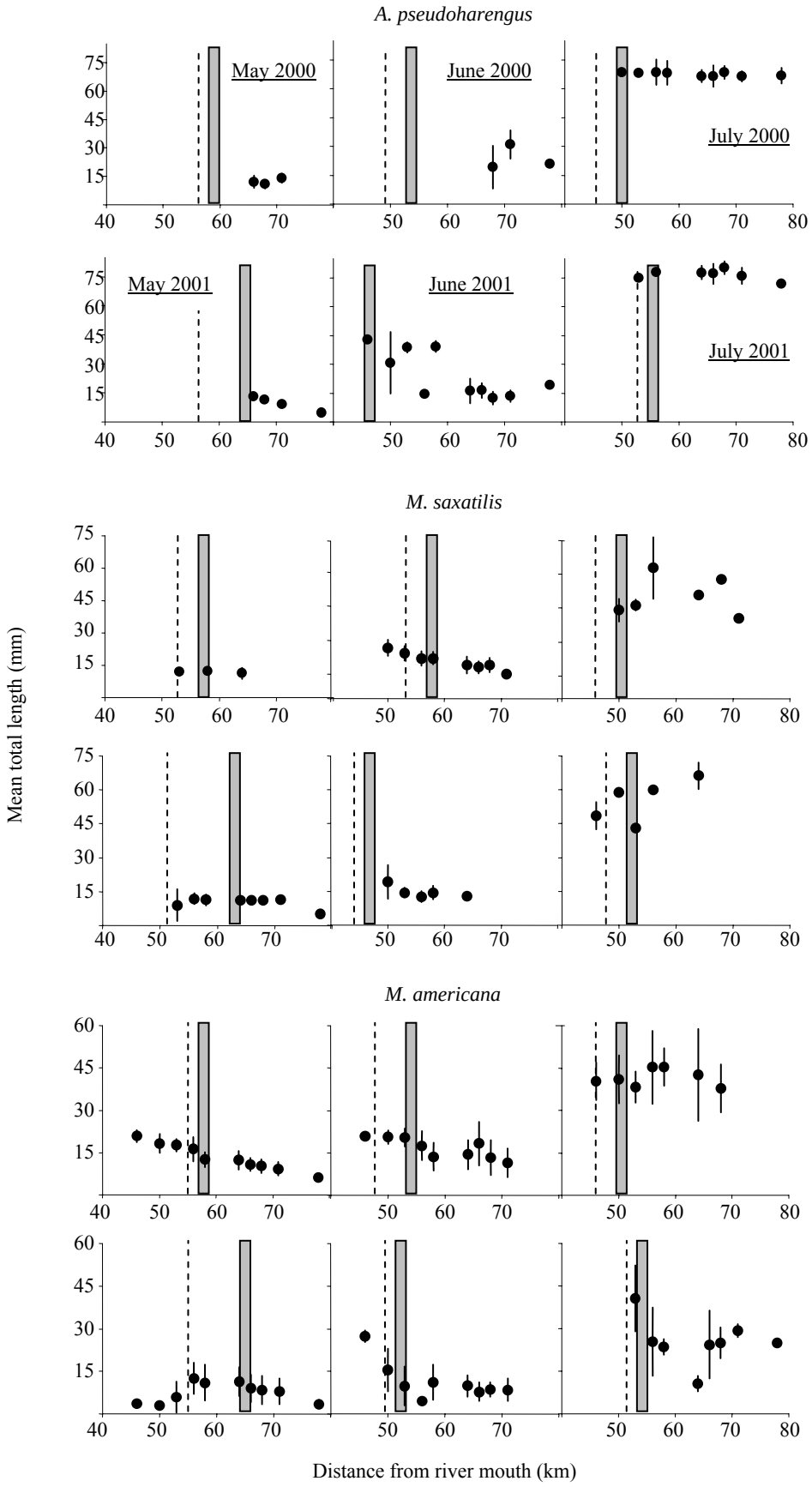
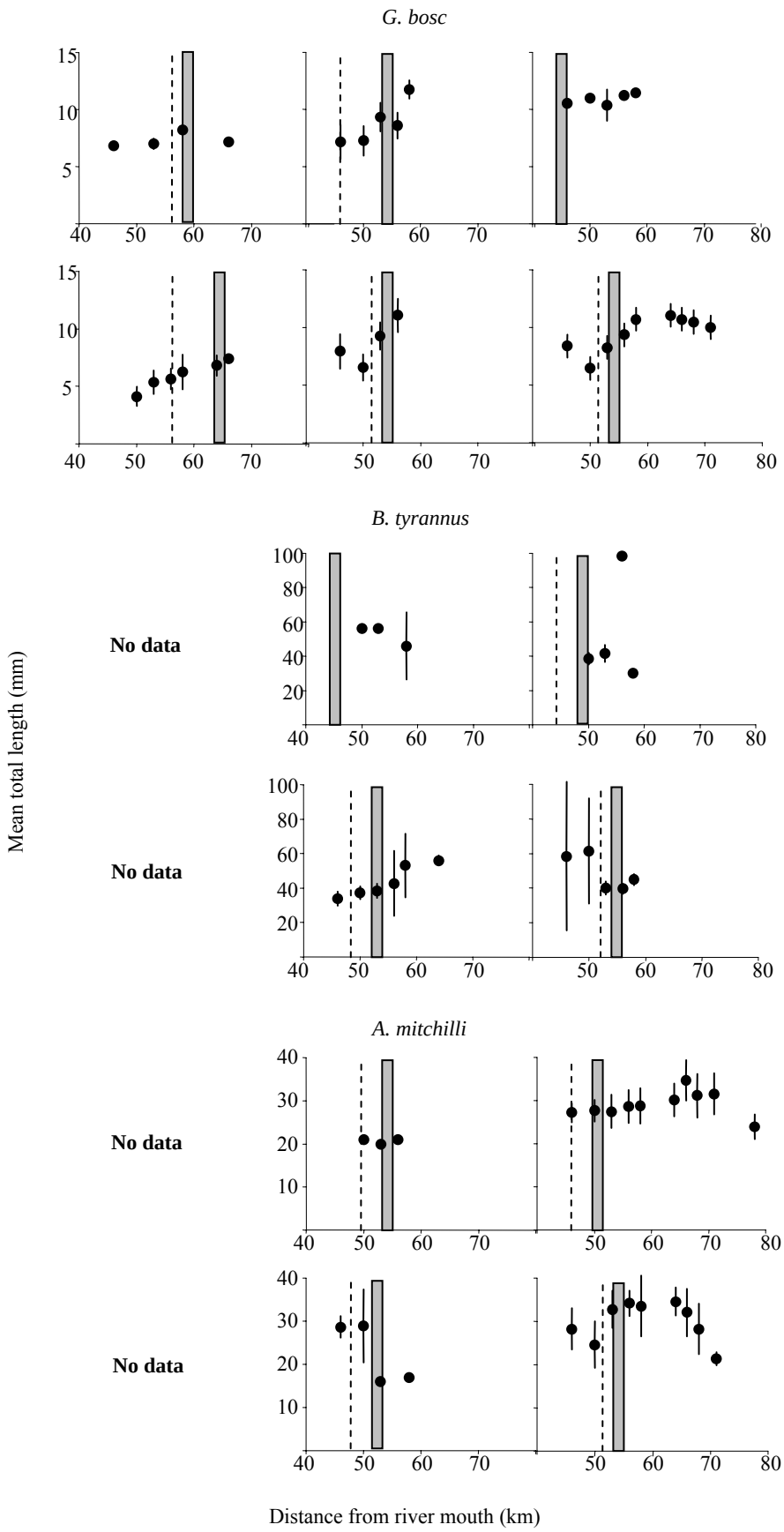
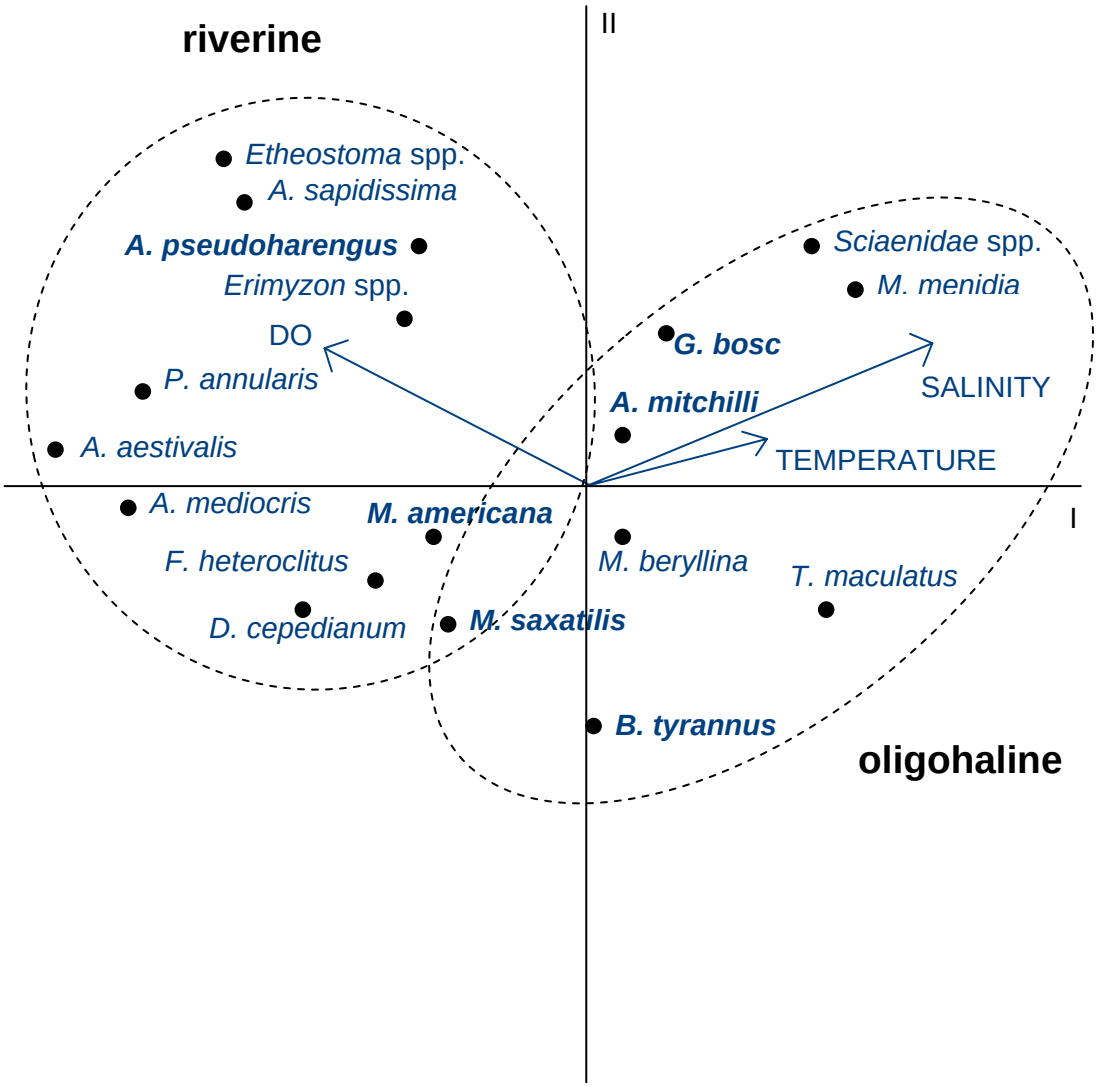


Figure 2.2. Year 2001. Hydrographic conditions across sampling stations in the Patuxent River estuarine transition zone from April-July, 2001. Values are station means (±1 standard deviation) of mid-depth measurements (pH measurements only at surface).

Figure 2.3. Spatiotemporal changes in lengths of *Alosa pseudoharengus* (alewife), *Morone saxatilis* (striped bass), *M. americana* (white perch), *Gobiosoma bosc* (naked goby), *Brevoortia tyrannus* (Atlantic menhaden), and *Anchoa mitchilli* (bay anchovy) in the Patuxent River estuarine transition zone. Mean lengths from May, June, and July sampling dates in 2000 (plots in top panels) and 2001 (plots in bottom panels) show ontogenetic migrations of young fish during spring-early summer. Black bars indicate ±1 SD of the mean length for each station within individual surveys. Grey vertical bars = salt front location; dashed vertical lines = 2psu isohaline.

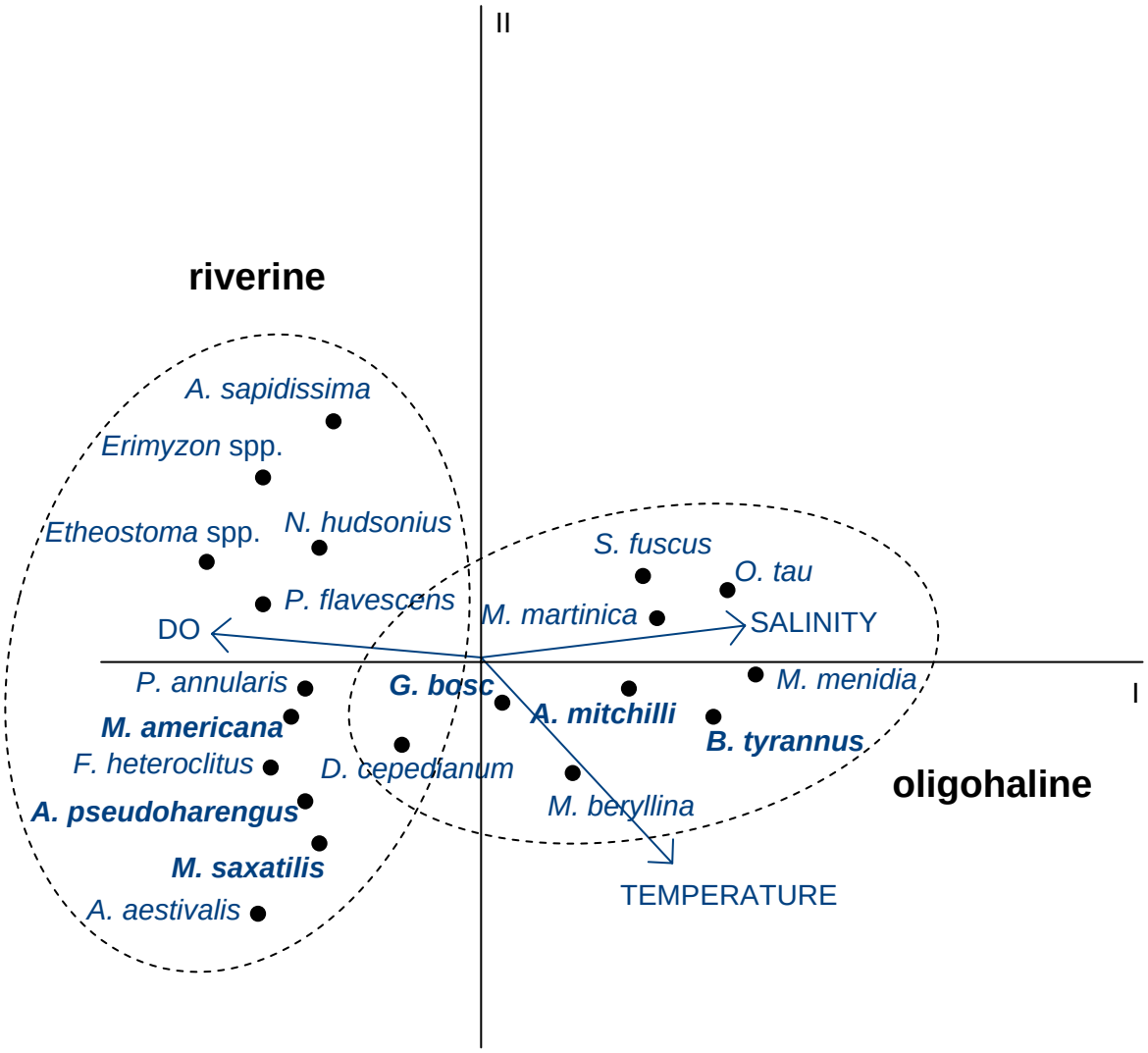

A. pseudoharengus
May 2000
June 2000
July 2000
May 2001
June 2001
July 2001
M. saxatilis
M. americana
Mean total length (mm)
Distance from river mouth (km)


G. bosc
B. tyrannus
A. mitchilli
No data
No data
No data
No data
Mean total length (mm)
Distance from river mouth (km)



Component	1	2	3	4	5
Variance	0.39	0.21	0.13	0.09	0.06
Loadings	-1.65	0.86	0.91	-1.95	2.18

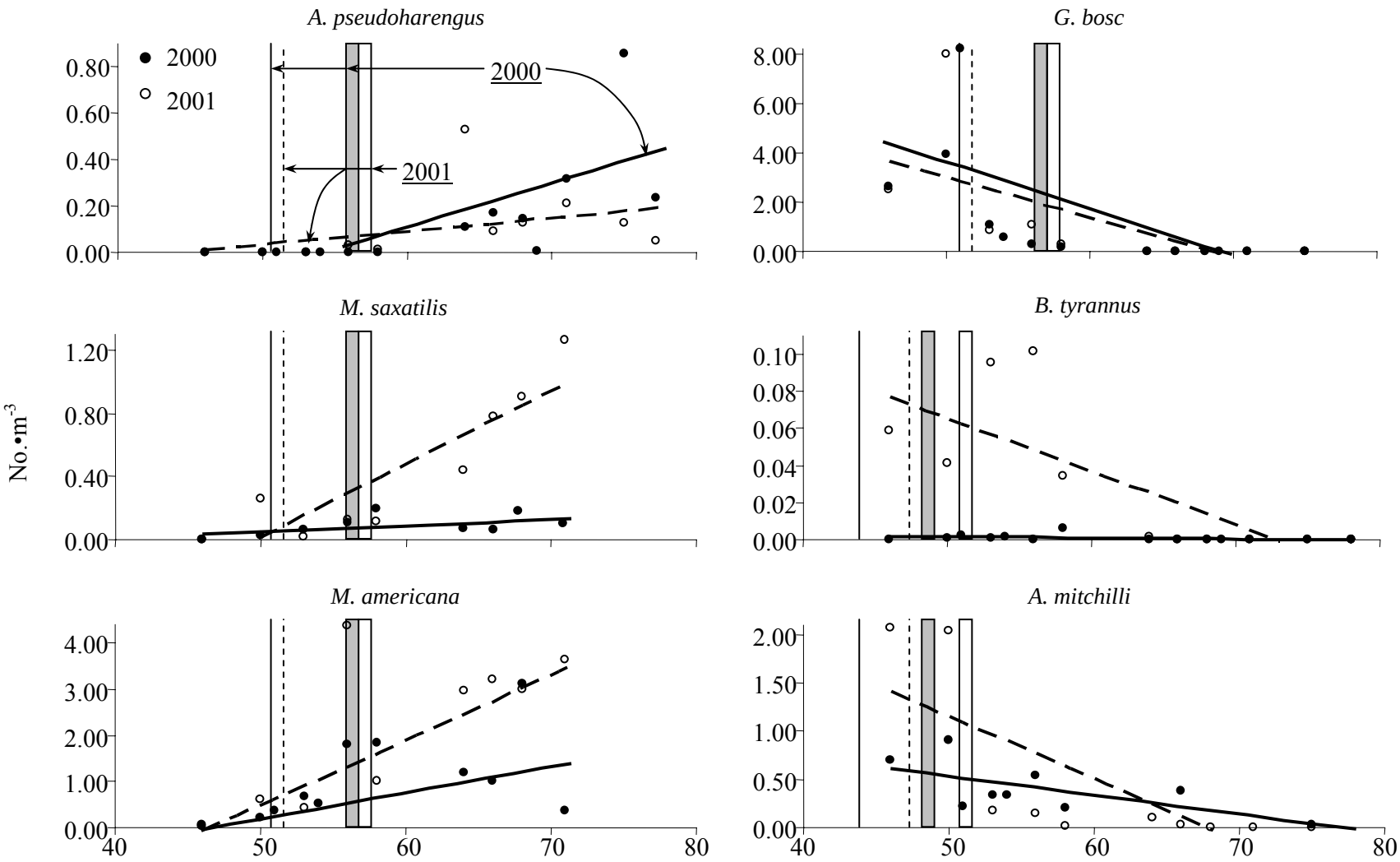
Figure 2.4. Year 2000. Principal Components Analysis. Plot of ichthyoplankton species in the first two principal components and loadings and variances explained by each component.



Component	1	2	3	4	5
Variance	0.43	0.16	0.11	0.09	0.07
Loadings	-0.13	-1.33	0.15	1.20	0.11

Figure 2.5. Year 2001. Principal Components Analysis. Plot of ichthyoplankton species in the first two principal components and loadings and variances explained by each component.

Figure 2.6. Spatial patterns in mean ichthyoplankton concentration (no.•m^{-3}) across the Patuxent River estuarine transition zone. Vertical bars = salt front locations; vertical lines = 2psu isohalines. *A. mitchilli* and *B. tyrannus* data are from Tucker-trawl surveys only. Note the different y-axis scales for each species.


A. pseudoharengus
2000
2001
2000
2001
G. bosc
M. saxatilis
B. tyrannus
M. americana
A. mitchilli
No.•m-3
Distance from river mouth (km)

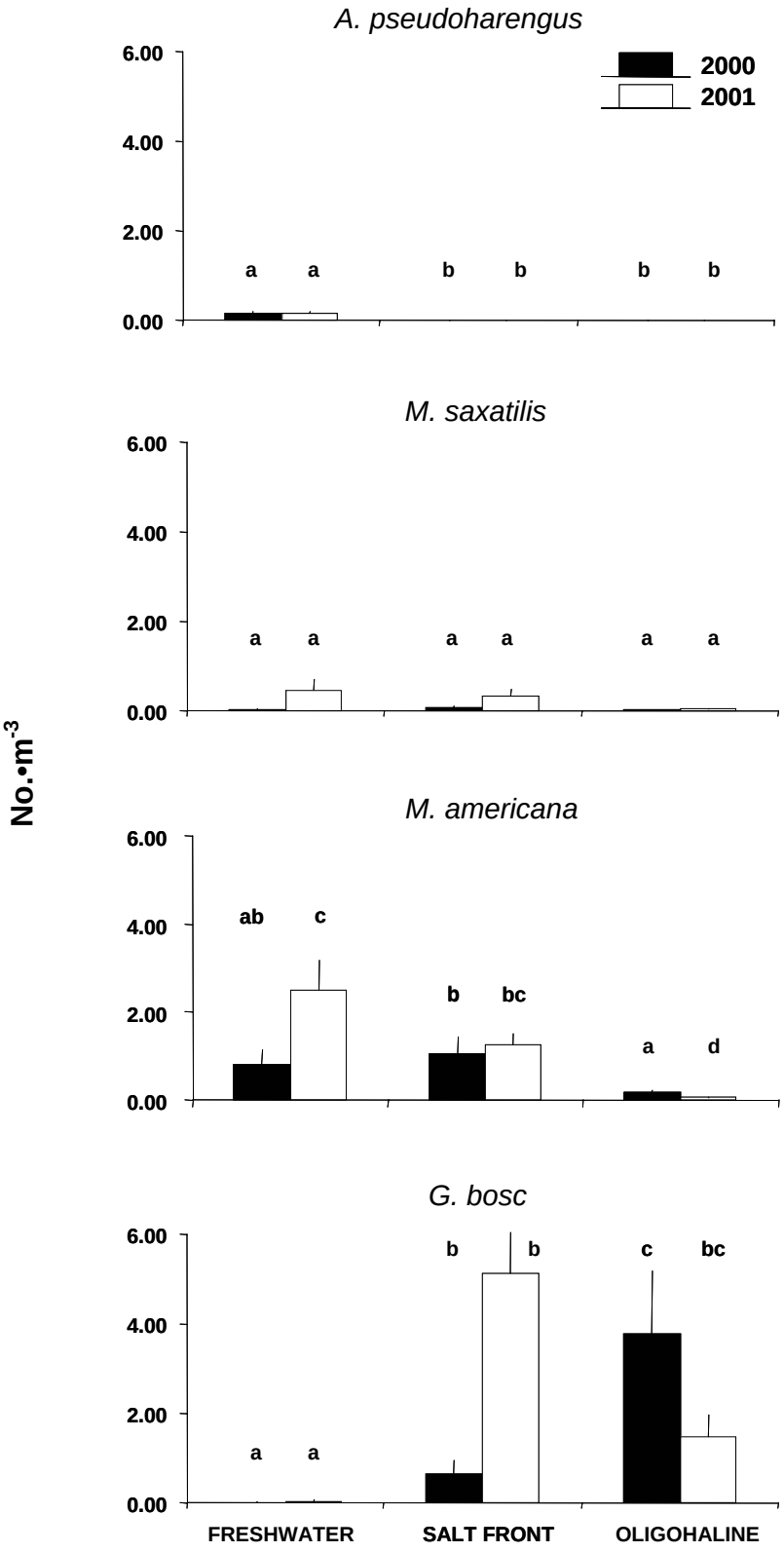


Figure 2.7. Larval concentration (no.•m^{-3}) comparisons by region. Student *t*-tests with unequal variances were applied. Significant differences are indicated by different letters ($p < 0.05$). Vertical lines represent standard errors of the mean.

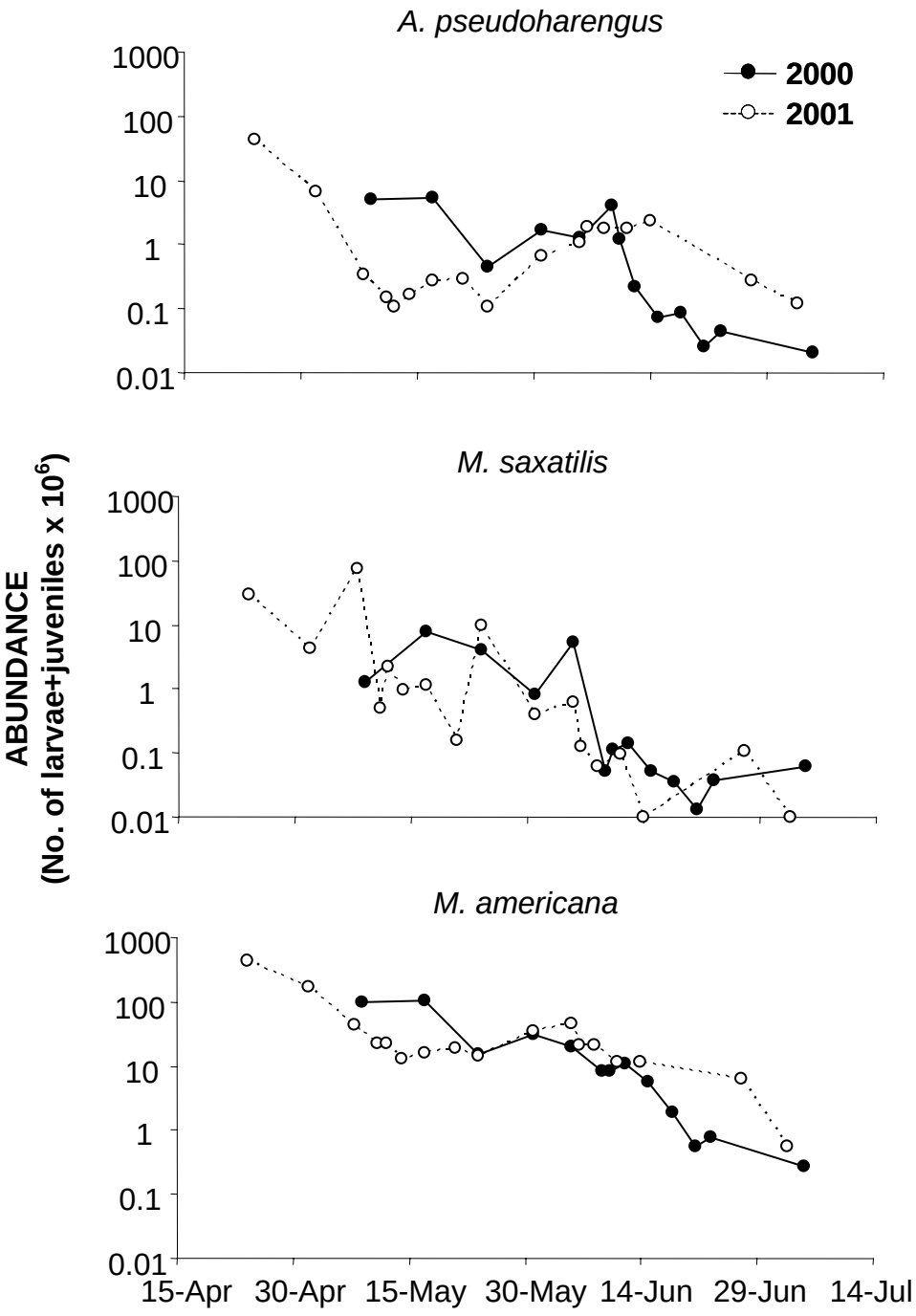


Figure 2.8. Temporal patterns in abundance (log-scale) of anadromous ichthyoplankton taxa in the Patuxent River, 2000-2001. Abundance values = $\sum$ ([no.•m^{-3} at station *i*] x [station *i* volume, m^3]).

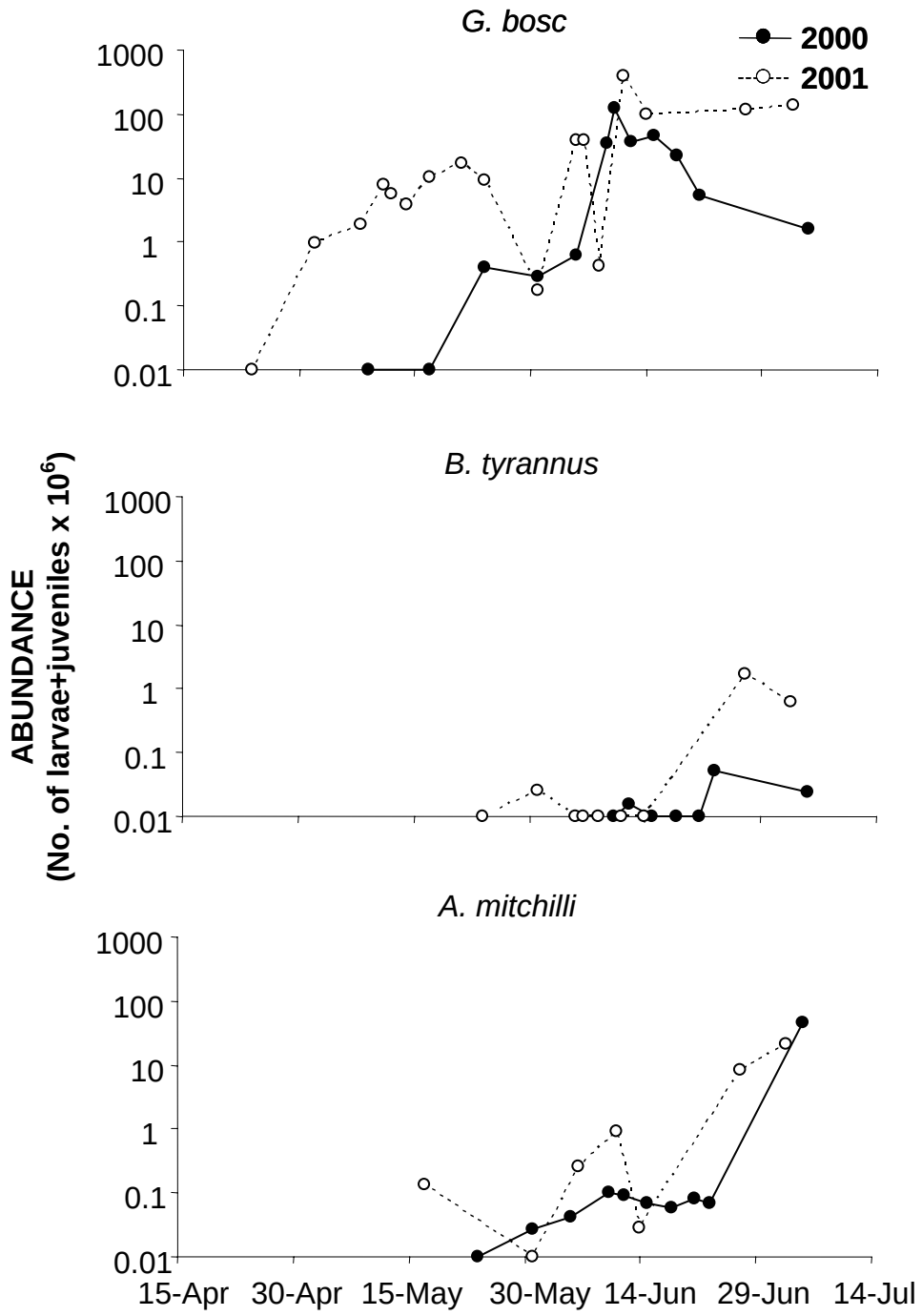


Figure 2.9. Temporal patterns in abundance (log-scale) of estuarine ichthyoplankton taxa in the Patuxent River, 2000-2001. Abundance values = $\sum$ ([no.•m^{-3} at station *i*] x [station *i* volume, m^3]).

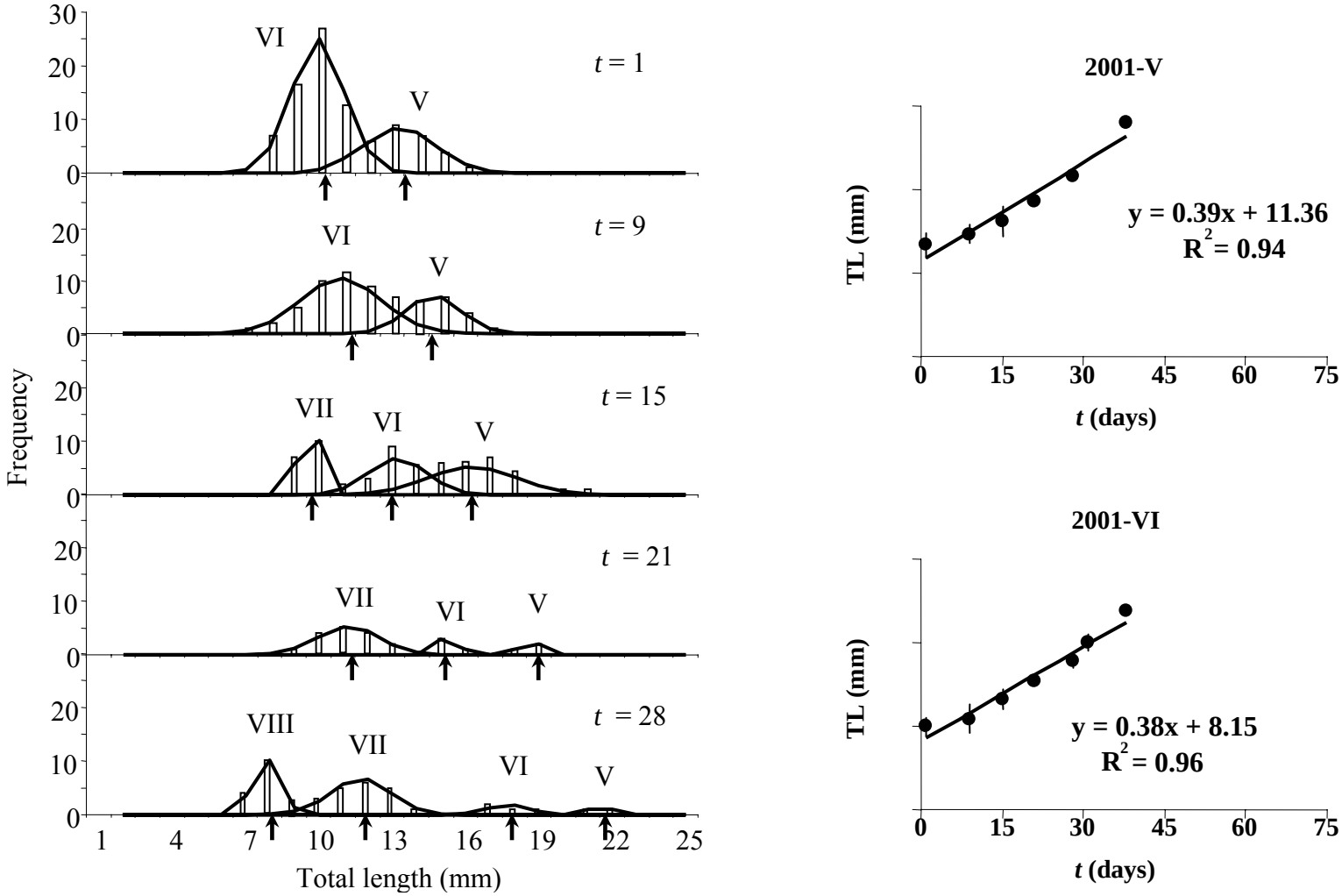


Figure 2.10. Length-frequency distributions of alewife larvae collected from 24 April-21 May 2001 in the Patuxent River. Cohorts were identified in a modal analysis (Haddon 2001). Roman numerals indicate individual cohorts (see Table 2.6). Arrows are cohort modal lengths used in estimating larval growth rates.

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CHAPTER THREE

Feeding ecology of larval fishes in the Patuxent River estuarine transition zone

ABSTRACT

Feeding habits of co-occurring larvae of fish species were investigated in the oligohaline and freshwater regions of the Patuxent River, Chesapeake Bay. Regional and size-dependent diet composition was described for alewife (*Alosa pseudoharengus*), striped bass (*Morone saxatilis*), white perch (*M. americana*), and naked goby (*Gobiosoma bosc*) larvae (first-feeding to pre-juvenile stages) collected in ichthyoplankton surveys during 2000 and 2001. Diet compositions were evaluated with respect to densities of potential zooplankton prey in the environment. Prey preferences of first-feeding larvae differed among larval taxa. The calanoid copepod *Eurytemora affinis* was the most important and preferred food of striped bass larvae. Copepod nauplii were the preferred and most important prey of small alewife and naked goby larvae, while both *E. affinis* and the cladoceran *Bosmina longirostris* were important and preferred prey of larger white perch larvae (>10mm) in up-estuary regions. Diets of striped bass and white perch were most similar (overlap analysis) in freshwater (O = 0.71-0.93). Moronid diets overlapped with the diet of large (>10 mm) alewife larvae in the freshwater region. The diets of naked goby larvae and small (<10 mm) white perch larvae overlapped in the salt front region. Naked goby was the only species to exhibit a positive relationship between trophic niche breadth (increasing standard deviation of the mean logarithmic prey size) and larval length. Mean prey size increased significantly during larval ontogeny in alewife, white perch, and naked goby, but not in striped bass. Ontogenetic shifts in larval feeding were observed for each species. As a consequence, large zooplankton prey

comprised >50% of the diets in large larval length classes. Feeding habits were complex and indicate that dietary overlap among larvae and the potential for competition were highest within and upriver from the salt front-Estuarine Turbidity Maximum region of the estuarine transition zone.

INTRODUCTION

Information on food habits and foraging is valuable to understand how trophic relationships may act or contribute to control levels of recruitment in fishes. Larvae of most species prey on zooplankton. Larval feeding abilities and mouth gape size change during ontogeny and determine the type and size of prey selected (Shirota 1970; Arthur 1976; Schael et al. 1991). As larvae grow and develop, their feeding success may be affected by the presence and availability of suitable prey in the environment. Previous analyses of larval feeding in a broad range of species have described ontogenetic shifts in preferred prey types, with first-feeding larvae selecting smaller prey (diatoms, rotifers, and copepod nauplii) and more developed larvae feeding on calanoid copepods and other large zooplankters (Last 1980; Hunter 1981). These patterns can lead to variable degrees of dietary overlap within larval fish assemblages. Closely related species often have similar diets (Setzler-Hamilton et al. 1982), although this is not always the case (Govoni et al. 1983).

Contrasting trends in trophic niche breadth (defined as the standard deviation of the mean logarithmic prey size) among larval taxa have been observed during larval fish ontogeny. A constant niche breadth was reported by Pearre (1986) for several species and by Munk (1992; 1997) for Atlantic herring (*Clupea harengus*) and cod (*Gadus morhua*) larvae. Increasing or decreasing niche breadths were observed in multi-species comparisons of larvae from the Northwest Atlantic (Pepin and Penney 1997) and Indian Ocean (Young and Davis 1990).

Larvae of anadromous and estuarine-spawning fish species coexist in the estuarine transition zone (ETZ) of Chesapeake Bay tributaries (Chapter Two). The ETZ

is the region in an estuary where fresh and oligohaline waters meet. It contains an estuarine turbidity maximum and is an important nursery area for young fish.

Spatiotemporal overlap of taxa distributions and length classes creates potential for overlap in larval foraging. In this study, the feeding ecology of abundant ichthyoplankton taxa in the Patuxent River was investigated to characterize potential overlaps and interactions among coexisting larvae of fish species. Gut contents were analyzed from larvae captured during ichthyoplankton surveys in 2000 and 2001 in the freshwater and oligohaline regions of the Patuxent River. A suite of diet indices was used to determine the importance of prey types and sizes in the larval diets of four common species and to evaluate potential ontogenetic shifts in feeding habits. The selected taxa included larvae of three anadromous species (alewife *Alosa pseudoharengus* (Clupeidae), striped bass *Morone saxatilis*, and white perch *M. americana* (Moronidae)) and one estuarine-spawned species, the naked goby *Gobiosoma bosc* (Gobiidae). Larval diets were compared between years and regions, and analyzed with respect to zooplankton in the river to describe larval feeding and trophic ecology in the estuarine transition zone of the Patuxent River.

Only limited information and data were available from previous estuarine research on alewife and naked goby larvae diets. Feeding habits of alewife larvae in lakes (Norden 1968), in laboratory experiments (Miller et al. 1990), and of larvae of congeneric species (American shad, *Alosa sapidissima*, and blueback herring, *A. aestivalis*) in estuaries (Crecco and Blake 1983) have been reported. However, no information was found on larval alewife foraging in coastal ecosystems. Laboratory experiments of prey selection in first-feeding naked goby larvae (Harding 1999) and

feeding of demersal, settlement-stage larvae in the Patuxent River (Breitburg 1991) have been described. My study evaluated foraging by pelagic, first-feeding to settlement-stages of naked goby larvae. Striped bass and white perch larval feeding have been described previously (Margulies 1989; Tsai 1991; Limburg et al. 1997) but only rarely in a multi-species comparison context (Setzler-Hamilton et al. 1982) or in relation to prominent hydrographic features (Shoji et al. submitted). Knowledge of feeding by larval fishes in the estuarine transition zone also is useful when considering potential interspecific interactions that hatchery-source larvae (e.g., American shad) may face in programs directed towards restoration of anadromous fish populations (see Chapter One).

The objective of my analysis was to characterize feeding habits of larvae of common species that coexist in the estuarine transition zone of the Patuxent River. Three hypotheses were evaluated: 1) Diets of fish larvae are determined by composition of zooplankton prey available in the environment; 2) Larval selection of prey types and sizes shifts during ontogeny; 3) High dietary overlap occurs between larvae of different species that are of similar size or ontogenetic state. Diet composition, number of prey in larval guts, trophic niche breadth, and indices of prey selection, relative importance, and dietary overlap were used to describe feeding habits of larvae and interactions among larval taxa.

METHODS

Larval fish collections. Larvae were collected during 30 ichthyoplankton sampling surveys conducted on the Patuxent River in 2000 (13 surveys) and 2001 (17 surveys). Surveys took place at 3-7 day intervals between 24 April and 5 July. Samples

were collected during daylight from the 25-ft RV Pisces and each survey was completed in 8-10 hours. Ichthyoplankton was sampled at 10 stations (Fig. 1.6) in the estuarine transition zone towing a 60-cm diameter, paired bongo net with 333-μm meshes. Sites were located at approximately 3.3 river-kilometer intervals. Station depths ranged from 2-10 meters. Tows were oblique from surface to bottom and of 5-min duration. Catches from each net were combined into one sample, preserved in ethanol, returned to the laboratory, and transferred to fresh ethanol within 24 hours.

Sample processing. Larvae were identified and total lengths measured to the nearest 0.1-mm with a digital-image analysis system. Digestive tracts of common larval taxa were analyzed under a dissecting microscope to determine feeding incidences, kinds of prey, prey numbers, prey sizes, prey preferences, and dietary overlap between co-occurring species. Larval abundances and size distributions of species differed among regions of the sampling area (Chapter Two). Diets were analyzed for larvae of alewife, striped bass, white perch, and naked goby. Gut contents of alewife, striped bass, and white perch larvae of all represented lengths from freshwater samples were analyzed because these taxa were frequently collected in the freshwater portion of the river. Diets were examined for larvae of both moronid species and naked goby that were common in the salt front and oligohaline regions. Gut contents of large goby larvae and all represented length classes of striped bass and white perch larvae from the salt front region were analyzed. Large moronid larvae and small naked goby larvae occurred most frequently in down-estuary stations and were selected for diet analyses in this region.

Larvae were grouped into 2-mm length intervals for stomach-content analyses, except for naked goby which was analyzed in 1-mm length classes. In prey selection and

dietary overlap analyses, larvae were separated into broader length classes (<10mm or >10mm) except for naked goby, which was grouped into a single length class (5-12mm). No 4-6mm naked goby larvae were analyzed in 2000, because newly-hatched larvae presumably occurred closer to spawning sites that were down-estuary of the sampling area in 2000. All prey items in larval guts were identified, enumerated, and measured with an ocular micrometer. If available, maximum lengths or widths (whichever was greater) of 1-20 items per prey taxon were measured within each larval gut. Larval diet compositions were compared to compositions of potential prey in river zooplankton samples.

Larvae for diet analysis were selected from surveys at 1-week intervals in both years. The number of larvae analyzed and percentage with empty stomachs are described in Figure 3.1. Gut samples from a total of 633 larvae were evaluated ($N_{A.\ pseudoharengus}$ = 135; $N_{M.\ saxatilis}$ = 165; $N_{M.\ americana}$ = 200; $N_{G.\ bosc}$ = 133). Larval diets were evaluated from sites along the upriver-downriver extent of the estuarine transition zone, which included freshwater, salt front, and oligohaline regions. This zone contained the Estuarine Turbidity Maximum (ETM), a region in the estuary, near the salt front, which is an important nursery area for larval fish (Boynton et al. 1997; North and Houde 2001, 2003; Winkler et al. 2003). Physical processes in ETM regions aggregate particles, potentially including larval fish and their zooplankton prey, and may promote anadromous fish recruitment in estuaries (Boynton et al. 1997). The location of the salt front, defined by conductivity readings of 800-1000µS, was determined in each survey.

Jassby et al. (1995) distinguished the 2-psu isohaline position, referred to as X_2, as a habitat indicator for planktonic populations in the San Francisco Bay estuary. The

ETM and peak abundances of ichthyoplankton and zooplankton were typically found in the vicinity of X_2 (Jassby et al. 1995). In the Patuxent River, larval fish are often most abundant near or up-estuary of the 2-psu isohaline (Chapter Two). Zooplankton densities and larval diets were evaluated with respect to the salt front and the intersection of the 2-psu isohaline with the bottom. Larval guts from a broad range of length classes also were analyzed with respect to these features to evaluate how estuarine hydrography influences ontogenetic shifts in diet.

Hydrographic conditions. Hydrographic parameters (temperature, salinity, dissolved oxygen, conductivity, and pH) were measured during surveys at each station (Fig. 1.7). Instrument measurements were made of temperature, salinity, conductivity, and dissolved oxygen at surface, mid-water, and near-bottom depths. Water from each depth was pumped into a bucket on deck and meter probes inserted to measure hydrographic variables. Surface pH was measured at every-other station. Patuxent River flow data were obtained from a U. S. Geological Survey gauge at rk130, near Bowie, Maryland (USGS 2001).

Zooplankton abundance. During each survey, zooplankton was collected at 10 stations by pumping 20 liters of water from surface, middle, and bottom depths (60 liters total). Pumped water from the three depths was combined and zooplankton filtered onto a 35-μm screen before preserving in 5% formalin. In the laboratory, zooplankters were identified, enumerated, and measured to evaluate distributions, densities, and sizes of potential prey for fish larvae.

Patuxent River zooplankton densities (no.•l^{-1}) were estimated for several taxonomic categories: *Eurytemora affinis* calanoid copepods and copepodites; *Acartia*

tonsa calanoid copepods and copepodites; cyclopoid copepods; harpacticoid copepods; copepod nauplii; barnacle nauplii; invertebrate eggs; rotifers; *Bosmina longirostris* cladocerans; 'other' cladocerans; chironomid insect larvae; and other less common taxa. Zooplankton was identified and enumerated under a dissecting microscope from 5-ml aliquots of the river zooplankton samples that had been concentrated to 25-500ml.

Analysis. The trophic niche breadth (S) of larvae was defined as the standard deviation of mean logarithmic ($\log_e$) prey size and therefore is a measure of variability in sizes of prey included in the diet. Niche breadth and the relationship of prey size to larval length were estimated following the methods of Pearre (1986). Fuiman's Ontogenetic Index (Fuiman et al. 1998) also was incorporated in analyses to determine the ontogenetic states of larvae in between-species feeding comparisons. The mean and standard deviation of the log-transformed distribution of prey lengths were estimated for each larval length interval. Length intervals were selected to produce the maximum number of predator length classes containing 5 or more prey length values. The standard deviation of log-transformed prey size in each predator length interval described the niche breadth of larvae (Pearre 1986). Mean prey size and niche breadth estimates were regressed on larval length and ontogenetic state (described below) to characterize possible ontogenetic patterns in utilization of different prey sizes.

The selection of prey types and sizes in larval diets was evaluated with Strauss' prey selection index (1979):

$$L = r_i - p_i.$$

r_i is the percent composition of zooplankton prey type i in larval guts, p_i is the percent composition of zooplankton type i in the environment; the range of L is -1.0 to +1.0.

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

The importance of prey types and sizes in larval diets was evaluated with George and Hadley's (1979) relative importance index. For prey type a,

Ai_a = % frequency of occurrence + % total number + % total weight;

$$Ri_a = 100(Ai_a/\sum_{a=1}^{k} Ai_a).$$

The range of Ri_a is 0-100, with higher index values indicating greater importance. Prey length-weight relationships were incorporated from Heinle (1969) to estimate total weights of prey in larval guts.

Comparisons of relative diet overlap between larval taxa and length classes were made with Czechanowski's index (Feinsinger et al. 1981):

$$O_{12} = O_{21} = 1 - 0.5 (\sum | P_{i1} - P_{i2} |).$$

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 used by species/length class 1, and P_{i2} is the proportion of food type i used by species/length class 2. O values may range from 0.0 to 1.0. Values approaching 1.0 indicate strong overlap in diets and those approaching 0.0 indicate no overlap.

Dietary overlap index values (O) calculated from gut content data were tested for statistical significance by comparing them with null models following procedures described by Albrecht and Gotelli (2001). For each species and/or length class comparison, observed dietary overlap index values were compared to frequency distributions of 1000 null indices calculated from randomized prey resource utilization

data sets. Two-tailed probability values were calculated by tabulating the number of simulated overlaps that were greater or less than the observed overlap.

RESULTS

Hydrographic conditions. The 31-kilometer sampling region in the Patuxent River included oligohaline and freshwater habitats of the estuarine transition zone. Gradients in hydrographic variables were observed across the survey area (Figs. 2.1 and 2.2). Temperatures were highest at down-estuary stations and lower at up-estuary locations, most notably at rk78 where water temperatures were 2-4°C cooler than at all other stations. Mean values of station salinities ranged from 0.0-4.0 psu, although salinities at the most down-estuary stations occasionally approached 10.0 psu. A gradient in dissolved oxygen also was observed, with colder, fresher, up-estuary waters being more oxygenated.

Year 2000 Excluding an unusual cooling episode that occurred in late May, temperatures generally were >20°C during the 2000 survey period and approached 30°C in early July (Fig. 1.7). Precipitation and river flow were below the historical average and were relatively constant during spring-early summer of 2000. The salt front location remained near river kilometer 56 in May before shifting 5 km down-estuary in mid-June, coincident with slight increases in precipitation and river flow. Dissolved oxygen levels were high during the cooling event in late May, then declined to 5.0-8.0 $mg \bullet l^{-1}$ as temperatures increased in June. The pH was consistently in the 7.0-8.5 range during all surveys.

Year 2001 Hydrographic conditions were more variable during the 2001 sampling period (Fig. 1.7). Temperatures were <20°C in late April, fluctuated in early May, and then gradually increased to >25°C by early summer. The salt front moved 10 km up-estuary in a period of reduced precipitation and river flow during early May. The front then shifted 12 km down-estuary, responding to several higher-flow events in late May and early June. The mean salt front location differed by 2 km between years (rk 54 in 2000, rk 56 in 2001). Dissolved oxygen and pH levels were more variable during the 2001 sampling period. Dissolved oxygen declined to 4.0 $mg \bullet l^{-1}$ at down-estuary stations during a short-term warming event in early May, but was generally 6-10 $mg \bullet l^{-1}$ during the survey period. Levels of pH were consistently > 7.0 during spring-early summer 2001. Precipitation and river flow were below the historical average during spring-early summer 2001 but were more variable than in the 2000 sampling period. In 2001, several short-duration, high-flow events occurred in the second half of the sampling period. These storm events tended to stabilize river temperatures for several days, interrupting the gradual warming trend typically observed.

Zooplankton distribution and abundance. Spatiotemporal patterns in zooplankton distribution and abundance varied among taxa and years in the Patuxent River. Copepod nauplii, probably of calanoid copepods, were common throughout the sampling area but often were at highest concentrations near and below the salt front (Fig. 3.2). Mean nauplii concentrations were higher in 2001 ($t = 6.01$, $p < 0.01$) with highest concentrations occurring early (24 April to 24 May (days 113-144)) in each year. Maximum densities of 264 and 618 $nauplii \bullet l^{-1}$ were observed in 2000 and 2001, respectively, and occurred in the salt front-ETM region.

The cladoceran *Bosmina longirostris* was most abundant in freshwater and rarely occurred in samples below the 2-psu isohaline (Fig. 3.2). Consistent spatiotemporal trends in its abundance and distribution were observed. A peak in concentration occurred in mid-May of each year, with a maximum abundance of >1000•l^{-1} on 12 May 2001 (day 132). Another peak in concentration was observed during the 2nd week of June in both years. Mean concentrations did not differ significantly between years.

Two calanoid copepod taxa were common in Patuxent River zooplankton samples. *Acartia tonsa* was only collected down-estuary of the salt front and exhibited similar and consistent trends in abundance in each year (Fig. 3.3). A peak in its concentrations (45.3-55.3•l^{-1}) occurred during early May (days 120-135). A secondary peak in concentrations (27.0-28.0•l^{-1}) was observed in the 11-15 June period (days 162-166). Overall, mean *Acartia* concentrations did not differ significantly between years.

Eurytemora affinis occurred throughout the Patuxent River estuarine transition zone, although its highest concentrations were often observed in the salt front-ETM region (Fig. 3.3). Maximum concentrations occurred early in each year's sampling period, with 215 *Eurytemora*•l^{-1} in the salt front region on 24 April 2001 (day 114). The observed mean *Eurytemora* concentration throughout the sampling area in 2001 (14.69•l^{-1}) was slightly higher than in 2000 (11.89•l^{-1}) but these mean levels did not differ significantly (t = -1.35, p = 0.18).

Cyclopoid copepod (primarily *Oithona* spp.) mean concentration was significantly and notably higher in 2000 ($p < 0.01$) than in 2001 when densities remained below 10•l^{-1} throughout the sampling area (Fig. 3.4). Cyclopoid abundance was highest near or up-estuary of the salt front. A maximum concentration of 168 cyclopoids•l^{-1}

occurred early in the 2000 sampling period. The cyclopoid copepod group was the only zooplankter group that was more abundant in 2000 than in 2001.

In 2001, the most abundant zooplankters included in the surveys were rotifers (Fig. 3.4). Rotifers occurred in highest concentrations in or up-estuary of the salt front-ETM region and peaked at concentrations of >4000•l^{-1} from 2-14 May 2001 (days 122-134). Mean concentration of rotifers was considerably higher in 2001 than in 2000 ($p <$ 0.01).

Mean total zooplankton concentration was significantly higher in 2001 ($t = -4.59$, $p < 0.01$), although the difference was primarily due to rotifer concentrations that peaked at 4000•l^{-1} during the 2nd week of May 2001 (Fig. 3.5). In contrast, rotifer abundance was relatively low in 2000 and trends in total zooplankton distribution and abundance were driven by *Bosmina*. Maximum concentrations of the combined zooplankton taxa occurred near and up-estuary of the salt front.

Diet composition and prey numbers in guts. Overall, feeding incidence was high (72-97%). The highest percentages of empty stomachs occurred in larvae from freshwater, although there were no statistically significant differences in feeding incidence among regions (Fig. 3.1). Small larvae usually had a higher percentage of empty stomachs. The percentages of empty guts in small length classes were significantly lower than in large length classes for alewife and white perch larvae in freshwater in 2001 and for striped bass larvae in the salt front region in 2000. In between-year comparisons, incidence of feeding was significantly higher for large alewife and white perch larvae in the freshwater region in 2001, although the percentage of large alewife and white perch larvae with prey was >85% in both years.

Larval alewife had the most diverse diets. This was the only larval taxon to consistently feed on large centric diatoms, although diatoms were a minor component of its diet (Fig. 3.6). An ontogenetic shift in larval alewife diet was observed. Copepod nauplii and rotifers comprised >50% of diets in ≤11mm larvae. Invertebrate eggs and larger prey items (i.e., *Eurytemora* and *Bosmina*) were more common in diets of larger alewife larvae. Higher proportions of *Bosmina* and cyclopoid copepods were consumed by alewife larvae in 2000, while in 2001 rotifers and *Eurytemora* were more common in their diets.

Most prey items consumed by striped bass larvae were larger zooplankters (*Eurytemora*, *Acartia*, and *Bosmina*; Fig. 3.7). The diversity of prey items was higher in freshwater and salt front regions than in the oligohaline region. Calanoid copepodites and adults were the dominant prey in striped bass larval diets down-estuary from the salt front. In 2001, copepod nauplii occurred in diets more commonly and *Bosmina* was common in 11-19mm striped bass larvae. *Acartia* was only found in stomachs of >11mm larvae in the oligohaline region in 2000. No ontogenetic shift in prey size was apparent in striped bass larvae because large prey items were common in all length classes in all regions. Striped bass larvae were more likely to consume *Eurytemora* copepods than were white perch larvae at first-feeding (Figs. 3.7 and 3.8).

Eurytemora and *Bosmina* occurred regularly in larval white perch diets from the freshwater region in both years (Fig. 3.8). Rotifers and copepod nauplii were more common in 2001, most notably in small white perch larvae. *Bosmina*, copepod nauplii, and rotifers also were more common in diets at the salt front in 2001. Calanoid copepods were the dominant prey in white perch larval diets below the salt front. As in striped

bass, *Acartia* was observed in white perch larval stomachs only in 2000. An ontogenetic diet shift was observed in white perch larvae. A broad range of prey items was eaten by small length classes while larger larvae fed predominantly on *Bosmina* and calanoid copepods.

Naked goby larvae had the least diverse diets. In the oligohaline region, goby larvae fed almost exclusively on copepod nauplii and calanoid copepods (Fig. 3.9). *Acartia* was common in all length classes of larvae collected below the salt front. In 2001, copepod nauplii comprised >80% of diets of larvae from this region. In the salt front region, greater numbers of large naked goby larvae were available for analysis and their diets were more diverse. A shift in naked goby feeding habits occurred with ontogeny. Copepod nauplii and calanoid copepods were dominant in diets of the smaller larvae, which were mostly collected below the salt front. The largest goby larvae also had consumed invertebrate eggs (predominantly copepod eggs), *Bosmina*, and cyclopoid copepods.

The number of prey in larval guts generally increased with ontogeny and larval size but there were exceptions. For example, some intermediate length classes (e.g., 7-9mm striped bass larvae in year 2000 freshwater samples; Fig. 3.7) had consumed relatively few, but often larger prey items. Most of the between-year comparisons of mean numbers of prey in guts within length classes did not indicate significant differences (Student's *t*-tests, $p < 0.05$). However, large larval alewife 15-19mm, contained more prey in 2000 than in 2001 (Fig. 3.6). There also were significant between-year differences in prey numbers ingested by intermediate length classes of

white perch larvae in freshwater, where guts of 11-15mm larvae contained fewer prey in 2001 than in 2000.

Prey size and trophic niche breadth. The functional relationships of size- and stage-dependent prey ingestion varied among taxa (Figs. 3.10-3.13). Mean prey size increased significantly with larval length and ontogenetic state in alewife, white perch, and naked goby but there was no significant relationship for striped bass larvae (Fig. 3.11). Niche breadth (the standard deviation of the mean logarithmic prey size), which represents the relative variability in prey size, may have increased marginally with larval striped bass length ($p = 0.08$) but the relationship was not significant.

Alewife larvae consumed larger prey with growth and ontogeny (Fig. 3.10). There was no significant increase in niche breadth with larval alewife length or ontogenetic state, although prey size was highly variable in some large alewife larvae length classes.

The mean size of prey ingested was relatively constant during larval striped bass growth and ontogeny (Fig. 3.11). Trophic niche breadth may have increased slightly with increasing larval length and ontogenetic state, but the relationships were not statistically significant.

Mean prey size increased rapidly with respect to white perch larval length ($R^2 = 0.49$, $p < 0.01$) and ontogenetic state ($R^2 = 0.45$, $p < 0.01$) (Fig. 3.12). The rate of increase in prey size was faster than in other taxa. The relationship between niche breadth and predator length in larval white perch appeared to differ from the other species. Observed variability in prey size apparently decreased with increasing larval perch length, although the rate of decrease was not statistically significant ($p = 0.27$).

In naked goby, moderate but significant ($p = 0.05$) increases in prey size occurred with increasing larval length and ontogenetic state (Fig. 3.13). There also were significant increases in niche breadth ($p < 0.01$) as larval goby length and ontogenetic state increased.

At equal lengths (e.g., 10mm), alewife larvae were least developed and naked goby larvae were more advanced than the other species examined (Fig. 3.14). The ontogenetic states of larvae of the moronid species changed at the same rate with increasing larval length and were intermediate in comparison to alewife or naked goby larvae. In interspecific comparisons of prey preference, importance, and overlap indices, alewife larvae >10mm should be compared to <10mm moronid and naked goby larvae to facilitate comparisons of larvae at similar developmental stages.

Prey importance, prey preference, and dietary overlap. Values of the Strauss prey selection, relative importance, and Czechanowski dietary overlap indices were calculated (Tables 3.1-3.3) for four common larval taxa. Two length classes of each species were analyzed: 1) small larvae (<10mm) to compare foraging habits among 1st feeding stages and 2) large larvae (>10mm) to evaluate potential ontogenetic shifts in feeding habits. For interspecific comparisons, naked goby larvae were aggregated into a single length category because the range of larval lengths was relatively small (4-12mm) compared to other taxa examined (4-24mm).

Freshwater Region

In the freshwater region of the Patuxent River, small alewife larvae showed strong positive selection for copepod nauplii and did not prefer invertebrate eggs, rotifers, or *Bosmina* (Table 3.1a). Copepod nauplii were the most important prey type for small

alewife larvae. Large alewife larvae preferred *Eurytemora* but showed no preference for *Bosmina*, although *Bosmina* was the most important prey. Striped bass larvae in both length groups selected *Eurytemora* and did not prefer rotifers. Small striped bass larvae did not prefer *Bosmina* while large striped bass larvae showed weak preference for invertebrate eggs. *Eurytemora* was the most important prey for small striped bass and white perch larvae, while both *Eurytemora* and *Bosmina* were important in the diets of large moronid larvae. Small white perch larvae selected against rotifers and *Bosmina* but positively selected *Eurytemora* and invertebrate eggs. *Eurytemora* and *Bosmina* were preferred by large white perch while rotifers were avoided. The relative importance of, and preferences for, invertebrate eggs should be interpreted with caution. The eggs may have been copepod eggs that were dislodged from egg sacs when larvae ate adult female *Eurytemora*.

There was significant dietary overlap between several larval taxa and length classes in the freshwater region (Table 3.1b). Diets of large larvae of the four taxa had strong overlap (O = 0.88-0.90). The diet of large alewife larvae also overlapped with small white perch larvae. Small alewife larvae did not show significant dietary overlap with any taxon or size of larvae. Small striped bass and large white perch larval diets were similar. The diet of large striped bass larvae overlapped with diets of large and small larvae of white perch. Overlap in the diets of small and large white perch larvae in the freshwater region was significant. The diets of small and large striped bass larvae were not as similar.

Salt Front Region

At the salt front, food preferences and potential for overlap in diets were evaluated for naked goby larvae and small and large length classes of the two moronid species (Table 3.2). *Eurytemora* was preferred and rotifers were avoided by all larval taxa and length classes. Naked goby larvae also selected against *Bosmina* and cyclopoids. Both length classes of striped bass larvae avoided copepod nauplii but had contrasting affinities for *Bosmina*. Large white perch larvae also showed negative selection for copepod nauplii and preference for *Bosmina*. Small white perch larvae avoided cyclopoid copepods. *Eurytemora* was important in the diets of each larval taxon and length class (Table 3.2). *Bosmina* was of secondary importance in the large moronid larval diets, which was similar to observations in the freshwater region. Copepod nauplii were the second most important item in the diet of naked goby larvae at the salt front. There was little significant overlap in diets of larval taxa at the salt front (Table 3.2b). The single significant overlap was for naked goby and small white perch larvae. Moderate but not statistically significant dietary overlap ($O > 0.60$) occurred between naked goby and large moronid larvae, and between small and large white perch larvae.

Oligohaline Region

Naked goby and the large length classes of moronid larvae were analyzed in the down-estuary, oligohaline portion of the Patuxent's estuarine transition zone (Table 3.3). Larvae in this region generally showed preference for the calanoid copepods *Acartia* and *Eurytemora*. Copepod nauplii were preferred by goby larvae but avoided by the large larvae of the two moronid species. Rotifers were consistently selected against by all larvae. Copepod nauplii were the most important component in the diet of naked goby

larvae. Both copepod species were important in larval moronid diets. In the oligohaline region, *Eurytemora* was favored and most important for striped bass larvae while *Acartia* was most important for larval white perch. There was little overlap in diets of naked goby and moronid larvae but high overlap in large white perch and large striped bass larvae from the oligohaline region (Table 3.3b).

DISCUSSION

There was evidence that prey types in larval diets were determined by the composition of the zooplankton community. Not surprisingly, this finding has been documented in several larval feeding studies (Last 1978b; Limburg et al. 1997; Hillgruber and Kloppmann 1999). Variability in abundances of zooplankters was most notable for copepod nauplii, cyclopoid copepods, and rotifers, all of which differed substantially in abundance between years. In the case of cyclopoids, they were on average 16 times more abundant in 2000 than in 2001. Copepod nauplii and rotifers were 2 and 12 times more abundant in 2001. The differences in abundances between years and in spatio-temporal distributions affected diets of larval fishes. For example, cyclopoid copepods were virtually absent from larval fish diets in 2001 when cyclopoids were uncommon in the Patuxent River. Copepod nauplii, most of which probably were *Eurytemora affinis* or *Acartia tonsa*, were consumed more frequently and in greater numbers by larval moronids and naked goby in 2001. And, rotifers were more common in larval diets of the four species of fish in 2001.

The mean concentrations of *Bosmina* and calanoid copepod prey species in the Patuxent River did not differ between 2000 and 2001. However, the proportions of these

zooplankton groups in larval guts did differ between years. Alewife and white perch in freshwater had eaten higher proportions of *Bosmina* in 2000, while larval striped bass in the salt front region consumed more *Bosmina* in 2001. *Acartia* was common in moronid guts only in 2000. The mean salt front location was similar between years. However, the more variable temporal trends in river flow and temperature in 2001 may have led to differences in the timing, intensity, and spatial distribution of calanoid copepod and *Bosmina* blooms compared to 2000. These differences could have affected spatio-temporal overlap in distributions and peak densities of these prey types and fish larvae.

Gradients in water mass properties across hydrographic fronts can create areas of higher zooplankton abundance and more favorable foraging habitat for fish larvae (Munk 1997; Hillgruber and Kloppmann 1999; North and Houde 2003). In the Patuxent River, densities of larger prey items (e.g., *Bosmina* and *Eurytemora*) were highest near and up-estuary of the salt front-ETM. Feeding incidences (72-97%) and mean numbers of prey per gut (typically 5-50 plankters) for the four species of fish were very high in these areas.

Feeding incidence. The greater percentage of empty stomachs in larvae from the freshwater region may be partly attributed to the higher numbers of small-size anadromous fish larvae sampled there. Small, early-stage larvae are more likely to have few or no prey in their guts (Hunter 1981). In numerous marine fish taxa, larvae at the onset of exogenous feeding experience low feeding success (0-10%), most notably in clupeiform species (Rosenthal and Hempel 1970; Hunter 1972; Arthur 1976; Checkley 1982). During growth and ontogeny, feeding incidence typically increases to ≥90%. There are exceptions to these trends. For example, larvae of flatfishes (20-60%) (Blaxter

and Staines 1971; Last 1978a) and tunas (30-55%) (Young and Davis 1990) are highly successful first-feeders. Differences in feeding incidence between taxa are often related to mouth gape (Shirota 1970; Hunter 1981; Schael et al. 1991). Early-stage tuna and flatfish larvae, which have high feeding incidence, have a wider mouth gape and can utilize a broader size range of available prey, whereas engraulids (a clupeiform) possess a relatively small mouth gape and are able to feed only on a limited range of smaller prey.

In the Patuxent Estuary, elevated abundances of zooplankton near the salt front-ETM may account for the high feeding incidences of larvae in this region, since prey densities (500 to >4000•l^{-1}) were frequently well above thresholds determined to be sufficient for successful larval growth and survival (Houde 1978). Research in the St. Lawrence River Estuary indicated highest feeding incidence (58%) in rainbow smelt larvae (<25mm) within the ETM region while incidence was 24% below the ETM (Dauvin and Dodson 1990).

Feeding success of moronid larvae in the Patuxent River was relatively high overall but within the range reported previously. For example, feeding incidence in larval white perch ≤10mm was highly variable in upper Chesapeake Bay (16-96%) (Shoji et al. submitted). Setzler-Hamilton et al. (1982) observed feeding incidences in white perch larvae of 64-96% in the Potomac Estuary for larvae of sizes similar to those in my study. They also analyzed striped bass and clupeid (probably *Alosa* spp.) larvae and reported incidences of 38-97% and 56-95%, respectively. These feeding incidences were similar to ranges observed in the Patuxent Estuary in 2000 and 2001. Feeding success in the Setzler-Hamilton et al. (1982) study and in my study was high compared to other larval feeding investigations. This outcome is probably due to inclusion of large length

classes of larvae and the relatively high concentrations of suitable prey in Chesapeake Bay tributaries.

Chick and van den Avyle (1999) analyzed larval striped bass feeding incidence at different zooplankton prey levels (1-100•l^{-1}) and argued that foraging success is influenced by spatio-temporal variability in prey. Comparing their results to feeding success of striped bass larvae in the Patuxent River indicates that distributions and concentrations of prey (50-1000•l^{-1}) in the Patuxent were favorable for striped bass feeding, growth, and survival, and supported the high observed feeding incidence.

Feeding incidence of naked goby larvae was higher in the salt front region of the Patuxent River than in oligohaline habitat. However, goby larvae were larger near the salt front than down-estuary. Overall feeding success of naked goby in 2000 and 2001 was high compared to values reported by Harding (1999) for early-stage larvae (18-47%) and by Breitburg (1991) for larger larvae (12-68%) that were similar in size range to those in my study (4-14mm).

Diet composition. Numbers of prey per gut typically increase with larval size (Detwyler and Houde 1970). This was generally true of the four larval taxa examined in the Patuxent River, although some length classes fed on high numbers of small prey (rotifers, diatoms, copepod nauplii), interrupting this trend (e.g., 11-15mm alewife larvae in 2001). The significantly higher numbers of prey per gut observed in 2000 for 15-19mm alewife and 11-15mm white perch larvae in freshwater were due to higher consumption of *Bosmina* cladocerans. *Bosmina* mean densities did not differ between 2000 and 2001 but short-term blooms in the freshwater region - e.g., 13-20 May 2000 (days 133-140) - may explain the between-year differences in larval feeding.

Diet composition of alewife larvae was similar to that found in previous studies of alewife and other alosine larvae (Norden 1968; Crecco and Blake 1983). A large range of prey types was identified in the Patuxent River. First-feeding alewife larvae consumed mostly small prey items (rotifers, diatoms, copepod nauplii). Larger prey became more common in larger alewife larvae. A diverse diet and increasing utilization of cladocerans and copepods with ontogeny also was reported for alewife larvae in Lake Michigan (Norden 1968). The inclusion of diatoms at first-feeding is common in clupeid larvae (Hunter 1981; Govoni et al. 1983).

Small and large striped bass larvae fed heavily on calanoid copepods (primarily *Eurytemora affinis*). The cladoceran *Bosmina longirostris* also was a significant component of the diet of striped bass larvae collected in salt-front and freshwater regions. These observations were consistent with results of previous studies in which calanoid copepod and cladoceran prey were the most common items in diets of striped bass larvae (Beaven and Mihursky 1980; Setzler-Hamilton et al. 1982; Limburg et al. 1997).

The diet of white perch larvae was more diverse than that of striped bass. Diets of the smallest white perch larvae consisted of rotifers, copepod nauplii, invertebrate eggs, *Eurytemora* copepodites and adults, and even small numbers of centric diatoms. Larger white perch larvae fed primarily on *Bosmina* and *Eurytemora* and *Acartia* copepodites and adults. Setzler-Hamilton et al. (1982) reported ontogenetic diet shifts in both moronid species from the Potomac River that were similar to those in the Patuxent River. Although both white perch and striped bass larvae fed on *Eurytemora* and *Acartia* calanoid copepods in the Patuxent and Potomac systems, white perch consumed a higher percentage of *Acartia*. This difference might be related to a smaller mouth gape in white

perch larvae in comparison to striped bass larvae. *Acartia* is less robust than *Eurytemora* and may be easier to capture and ingest by the relatively gape-limited larval white perch. Shoji et al. (submitted) found higher proportions of *Eurytemora* in the diets of 3-9mm white perch larvae from the ETM of upper Chesapeake Bay than were reported for the Patuxent and Potomac Rivers. In the Hudson River, *Bosmina* comprised a greater percentage of the diet in white perch larvae <10mm (Limburg et al. 1997) than observed in Chesapeake Bay or its tributaries.

Fewer prey types were found in larval naked goby diets than in alewife or moronid larvae. Copepod nauplii were dominant in larval goby guts, most notably in larvae collected down-estuary of the salt front in 2001. A shift from copepod nauplii to feeding on calanoid copepodites and adults was observed as naked goby larvae grew and developed. Based on laboratory experiments, Harding (1999) described a similar shift from feeding on small prey types (nauplii, bivalve veligers) to copepods during ontogeny of larval naked goby.

Size spectrum and trophic niche breadth. The diet shift toward larger prey in naked goby also was reflected in the size-spectrum analysis. Mean prey size increased significantly with increasing larval goby length. Alewife and white perch larvae from the Patuxent River also consumed prey of larger size with ontogeny. In striped bass, mean prey size did not increase with growth. Its first-feeding larvae have relatively large gapes, and a high proportion of calanoid copepods was eaten by striped bass larvae at first-feeding. Because striped bass larvae began feeding on large prey, there was less scope for consumption of increasing prey sizes during growth. The striped bass results were unusual because sizes of ingested prey typically increase with length in fish larvae

(Arthur 1976; Young and Davis 1990; Economou 1991), although other studies on striped bass also have reported a high proportion of calanoid copepod prey in first-feeding larvae (Beaven and Mihursky 1980; Setzler-Hamilton et al. 1982). Other species with large mouth gapes may have diets similar to striped bass larvae. For example, a relatively constant mean prey size during ontogeny also was documented for larval Argentine hake, *Merluccius merluccius*, because its larvae fed initially on calanoid copepodites and adults (Ciechomski and Weiss 1974). On the other hand, Pacific hake (*Merluccius productus*) larvae, fed upon a wide range of prey from first-feeding to late larval stages. For example, Cass-Calay (2003) reported copepod eggs and nauplii occurring frequently in guts of 3-11mm Pacific hake larvae. Although Sumida and Moser (1980) found copepod eggs and nauplii to be less frequently consumed by Pacific hake larvae, they reported, as did Cass-Calay (2003) that calanoid copepodites and adults were eaten by hake larvae in all length classes.

The trophic niche breadth of striped bass larvae apparently did increase modestly ($p = 0.08$) as larvae grew, suggesting that a wider range of prey types was consumed with larval length. Diet composition results for intermediate length classes of striped bass (9-13mm) supported this relationship, although the largest larvae (≥17mm) confined feeding to large prey sizes (Fig. 3.11). Trophic niche breadths of white perch and alewife larvae did not shift with growth and ontogeny. In Lake Michigan, niche breadth of larval alewife also was constant (Norden 1968). These results contrast with results for congeneric American shad, *Alosa sapidissima*, and blueback herring, *A. aestivalis*, larvae in the Connecticut River that exhibited increasing niche breadth with increasing larval length (Crecco and Blake 1983). In the Patuxent River, there was a strong relationship

between larval length in naked goby and variability in prey size ingested, i.e., an increase in niche breadth (Fig. 3.13; $p < 0.01$). In laboratory experiments, Harding (1999) also described a broader niche breadth with ontogeny in feeding of naked goby larvae.

The varying results among taxa in the Patuxent River are consistent with findings in previous larval fish diet studies that described contrasting ontogeny-niche breadth relationships among a broad range of species. In the case of blue whiting, *Micromesistius poutassou*, larvae from the North Sea, there was a dome-shaped response in niche breadth, driven by the tendency of large larvae to feed exclusively on the largest prey available (i.e., calanoid copepodites) (Gonzalez-Quiros and Anadon 2001). Pepin and Penny (1997) noted an increase in trophic niche breadth in larvae of 6 of 10 species investigated. They found that even congeneric larvae showed substantial variation in the niche breadth-ontogeny functional relationship, similar to my observations of *Morone* spp. larvae in the Patuxent River. The niche breadth-larval length regression slopes (Figs. 3.10-12) were not significant ($p > 0.05$) for the three larval anadromous taxa in my analysis. Constant niche breadths also were described for larval sprat, *Sprattus sprattus*, and Atlantic cod, *Gadus morhua*, in the Bornholm Basin (Baltic Sea) (Voss et al. 2003) and cod larvae in the North Sea (Munk 1997). In the Patuxent River, larvae of the estuarine-spawning naked goby did show a significant increase in niche breadth during ontogeny. In the St. Lawrence Estuary, the feeding niche of rainbow smelt increased with larval length (Dauvin and Dodson 1990). A multi-species comparison of larval tunas in the Indian Ocean revealed both increasing and decreasing trends in niche breadth with respect to ontogeny among larvae of taxa that were studied (Young and Davis 1990).

The insignificant niche-breadth regressions for the three anadromous taxa examined in the Patuxent River indicate that the 'prey-size window' (Pearre 1986) remained constant as larvae grew. Pearre (1986), based on size-spectra considerations, concluded that a constant niche breadth means a constant or declining available prey biomass pool as larvae become larger. However, other measures of larval feeding in the Patuxent did not indicate prey resource limitation in large larvae. Feeding incidence was >85% in large larvae (>10mm) and densities of preferred zooplankton prey in the environment apparently were more than sufficient for successful foraging (Houde 1978).

Hunter (1981) and Houde (1997) argued that increasing prey size and niche breadth with larval ontogeny are indicators of strategies to increase survival potential in larval-stage fishes. For larvae feeding initially on small prey, the addition of large prey to the diet during ontogeny may increase growth rates. In the Patuxent River, larval white perch, alewife, and naked goby foraging habits followed this pattern. Although mean prey size did not increase during striped bass larval development, their ability to select larger prey of high energy content (calanoid copepods) at first-feeding also may have promoted survival potential.

Prey preference, importance, and overlap in diets. In general, fish larvae in the Patuxent River estuarine transition zone preferred calanoid copepod prey. Numerous larval foraging studies have demonstrated the important role copepods play in diets of young fish (Last 1980; Govoni et al. 1983; Houde and Alpern Lovdal 1984). The only exception in the Patuxent study was the small length class of alewife larvae, which apparently selected against calanoid copepods because of its relatively small mouth gape.

Rotifers were consistently not preferred by the four larval taxa and length classes in the Patuxent River.

In the freshwater region of the Patuxent, all larvae of the four species showed no preference for *Oithona* sp., a common cyclopoid copepod. Small alewife larvae positively selected copepod nauplii but not cyclopoid copepodites. This result contrasts with that of Setzler-Hamilton et al. (1982), who found that clupeid larvae in the Potomac preferred cyclopoid copepods. Dietary overlap occurred frequently among larval taxa and length classes in the freshwater region of the Patuxent River. High dietary overlap between white perch length classes suggested that this was the only species examined for which intraspecific competition might occur. This result is in agreement with Pearre's (1986) conclusion that in most cases large and small individuals of the same species seldom compete for prey resources.

Eurytemora was an important component in diets of all species examined at the salt front of the Patuxent River. The Patuxent River larvae had contrasting affinities with respect to consumption of *Bosmina*. Moronid larvae did not positively select *Bosmina* in the Patuxent (although it was important) but *Bosmina* was, at times, a preferred prey of larval striped bass and white perch in the Hudson River (Limburg et al. 1997). The lack of preference for *Bosmina* in the Patuxent probably is due to its high concentrations in this river where its abundances were an order of magnitude higher (100-1000•l^{-1}) than in the Hudson River (1-100•l^{-1}). In the Patuxent and Hudson Rivers, larval moronids fed primarily on the largest prey available. Small prey types were not preferred relative to their abundance in the environment.

Eurytemora was the most important prey type in Shoji et al.'s (submitted) analysis of larval white perch feeding in the upper Chesapeake Bay salt front-ETM region. This copepod also was the most important food for white perch and striped bass larvae in the Patuxent River in 2000 and 2001. Calanoid copepods also were the most important prey items in large naked goby larvae at the salt front of the Patuxent River while copepod nauplii were the most important prey for small naked goby and alewife larvae. The significant dietary overlap between naked goby and first-feeding white perch larvae at the salt front suggests potential competition since these larvae are very abundant there during late spring-early summer.

There was high dietary overlap between large larvae of white perch and striped bass in the oligohaline region. Although copepod nauplii were the principal food source for naked goby larvae, they did share calanoid copepod prey with moronid larvae in the oligohaline region. Here, *Acartia* was preferred by both white perch and goby larvae although *Acartia* was more common in goby diets while *Eurytemora* occurred more frequently in white perch guts. Overlap in diets may be of greater consequence in the salt front-ETM region than in the oligohaline region because the goby and the two moronid species were common there and positively selected *Eurytemora*. Although concentrations of fish larvae are often higher in the ETM region, the potential for feeding competition is uncertain because larval fish populations generally are not believed to be capable of significantly grazing down zooplankton prey resources (Pepin and Penney 2000). It remains possible, however, that foraging interactions may intensify under some conditions in estuarine nursery areas where larvae are highly concentrated during the spawning season of anadromous fishes.

Table 3.1. Freshwater Region. (a) Prey preferences and importance of prey types and (b) dietary overlap in larval fish taxa and size classes common in the freshwater region of the Patuxent River, 2000-2001. Relative importance index Ri_a values in italics. * indicates significant ($p < 0.05$) Strauss selection index L values. Significance of Czechanowski overlap index O values indicated by * = $p < 0.05$ or ** = $p < 0.01$.

(a)	alewife <10mm	alewife >10mm	striped bass <10mm	striped bass >10mm	white perch <10mm	white perch >10mm
Eurytemora	+0.05 *13.03*	+0.17* *14.84*	+0.41* *55.76*	+0.16* *30.73*	0.20* *34.71*	+0.19* *30.33*
Bosmina	-0.35* *18.50*	-0.21* *33.31*	-0.27* *25.50*	-0.07 *29.13*	-0.19* *17.75*	+0.10* *34.27*
Cyclopoids	+0.04 *18.07*	+0.01 *12.02*	-0.01 *2.59*	+0.01 *12.07*	+0.05 *11.20*	+0.01 *9.41*
Copepod nauplii	+0.41* *39.45*	0.00 *17.04*	-0.12* *9.61*	-0.03 *11.30*	-0.08 *10.15*	-0.08 *10.54*
Rotifers	-0.13* *10.96*	-0.04 *18.14*	-0.26* *0.00*	-0.19* *6.72*	-0.15* *11.08*	-0.24* *5.58*
Invertebrate eggs	-0.12* *0.00*	+0.01 *4.64*	+0.04 *6.54*	+0.10* *10.05*	+0.15* *15.11*	+0.01 *9.87*

(b)	alewife <10mm	alewife >10mm	striped bass <10mm	striped bass >10mm	white perch <10mm	white perch >10mm
alewife <10mm	-					
alewife >10mm	0.55	-				
striped bass <10mm	0.44	0.73	-			
striped bass >10mm	0.50	0.90**	0.71	-		
white perch <10mm	0.52	0.87*	0.71	0.93**	-	
white perch >10mm	0.45	0.88*	0.79*	0.88*	0.85*	-

Table 3.2. Salt Front Region. (a) Prey preferences and importance of prey types and (b) dietary overlap in larval fish taxa and size classes common in the salt front region of the Patuxent River, 2000-2001. Relative importance index Ri_a values in italics. * indicates significant ($p < 0.05$) Strauss selection index L values. Significance of Czechanowski overlap index O values indicated by * = $p < 0.05$ or ** = $p < 0.01$.

(a)	naked goby	striped bass <10mm	striped bass >10mm	white perch <10mm	white perch >10mm
Eurytemora	+0.26* *48.25*	+0.87* *100.00*	+0.11* *35.14*	+0.17* *44.71*	+0.12* *34.38*
Bosmina	-0.14* *5.81*	-0.17* *0.00*	+0.13* *26.78*	-0.06 *12.89*	+0.15* *26.63*
Cyclopoids	-0.11* *3.63*	-0.13 *0.00*	-0.04 *13.04*	-0.13* *0.00*	+0.02 *20.40*
Copepod nauplii	+0.03 *28.25*	-0.25* *0.00*	-0.16* *10.02*	0.00 *23.38*	-0.22* *4.46*
Rotifers	-0.25* *1.94*	-0.26* *0.00*	-0.24* *3.52*	-0.15* *11.15*	-0.26* *2.31*
Invertebrate eggs	+0.08 *12.12*	-0.04 *0.00*	+0.07 *11.49*	+0.06 *7.87*	+0.07 *11.82*

(b)	naked goby	striped bass <10mm	striped bass >10mm	white perch <10mm	white perch >10mm
naked goby	-				
striped bass <10mm	0.58	-			
striped bass >10mm	0.71	0.52	-		
white perch <10mm	0.86**	0.46	0.46	-	
white perch >10mm	0.66	0.50	0.51	0.68	-

Table 3.3. Oligohaline Region. (a) Prey preferences and importance of prey types and (b) dietary overlap in larval fish taxa and size classes common in the oligohaline region of the Patuxent River, 2000-2001. Relative importance index Ri_a values in italics. * indicates significant ($p < 0.05$) Strauss selection index L values. Significance of Czechanowski overlap index O values indicated by * = $p < 0.05$ or ** = $p < 0.01$.

(a)	naked goby	striped bass >10mm	white perch >10mm
Acartia	+0.11*	+0.07	+0.10*
	18.40	*31.98*	*38.11*
Eurytemora	+0.07	+0.35*	+0.30*
	16.86	*41.66*	*29.44*
Bosmina	-0.04	+0.02	-0.04
	0.00	*3.20*	*2.13*
Cyclopoids	+0.03	-0.01	-0.01
	14.08	*0.00*	*3.22*
Copepod nauplii	+0.13*	-0.42*	-0.39*
	46.70	*8.72*	*9.99*
Rotifers	-0.19*	-0.21*	-0.19*
	3.96	*0.00*	*0.00*
Invertebrate eggs	-0.02	+0.09	+0.07
	0.00	*14.44*	*17.12*

(b)	naked goby	striped bass >10mm	white perch >10mm
naked goby	-		
striped bass >10mm	0.35	-	
white perch >10mm	0.41	0.81**	-

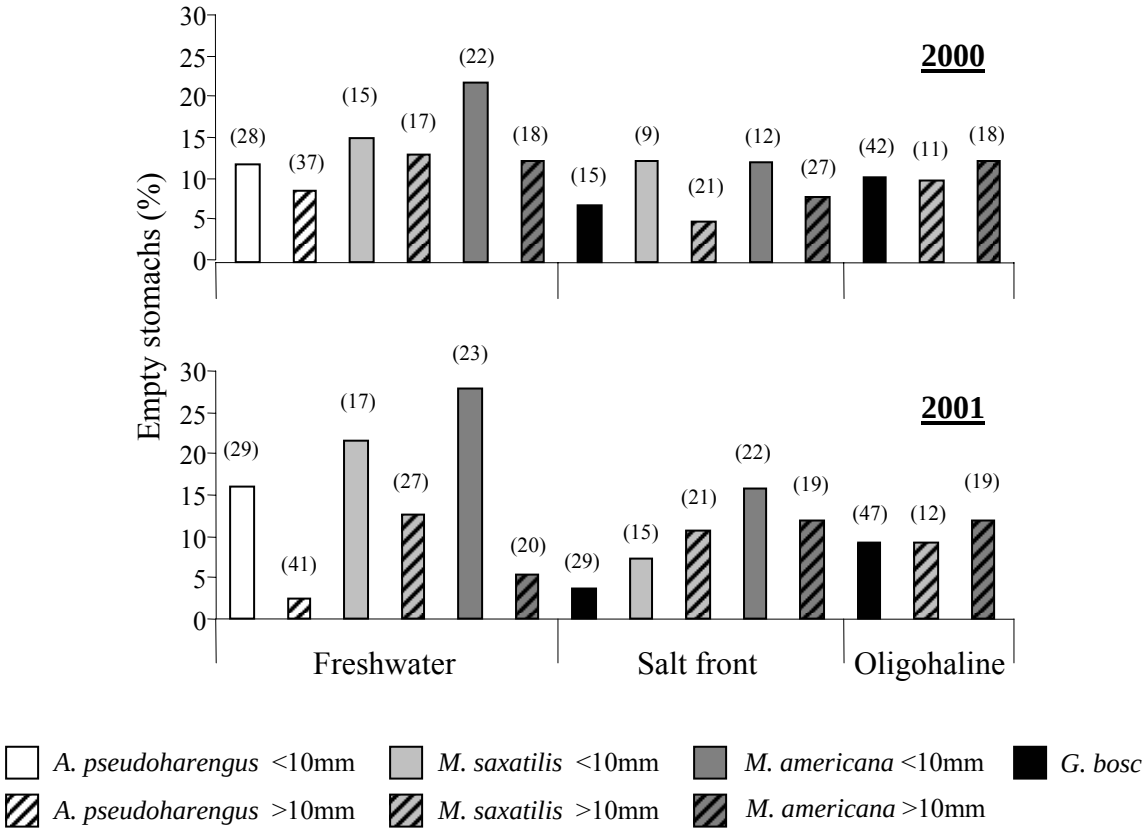

Figure 3.1. Percentage of empty larval stomachs for different taxa, length classes, and regions in the Patuxent River, 2000 and 2001. Total numbers of larvae analyzed from each length class in parentheses.

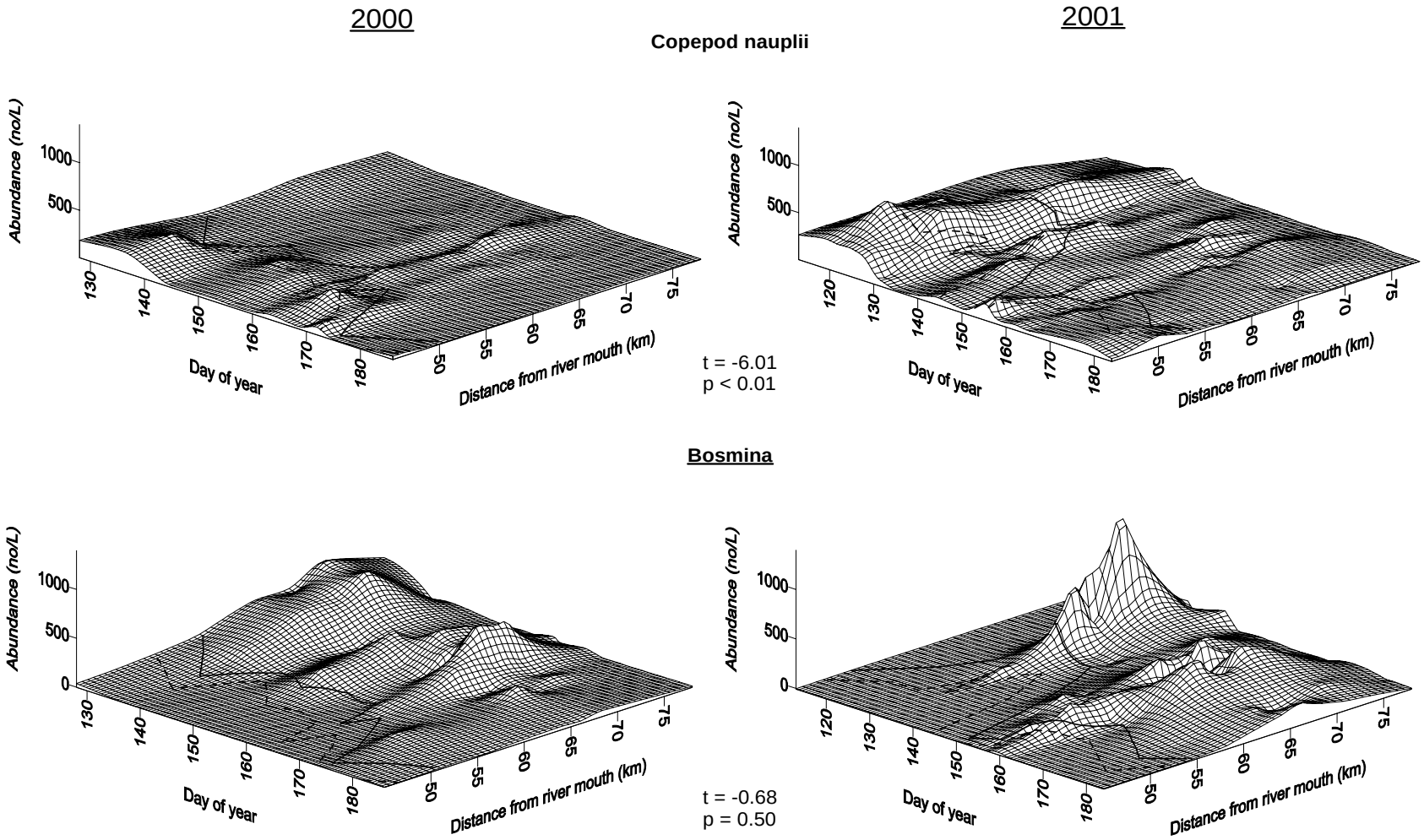

Figure 3.2. Spatiotemporal trends in copepod nauplii (top) and the cladoceran *Bosmina longirostris* (bottom) concentrations in the Patuxent River in 2000 and 2001. Student's *t*-tests with unequal variance were used to compare mean concentrations between years. Solid and dashed lines are the salt front and 2-psu isohaline positions, respectively. Day 130 = 10 May; day 160 = 9 June.

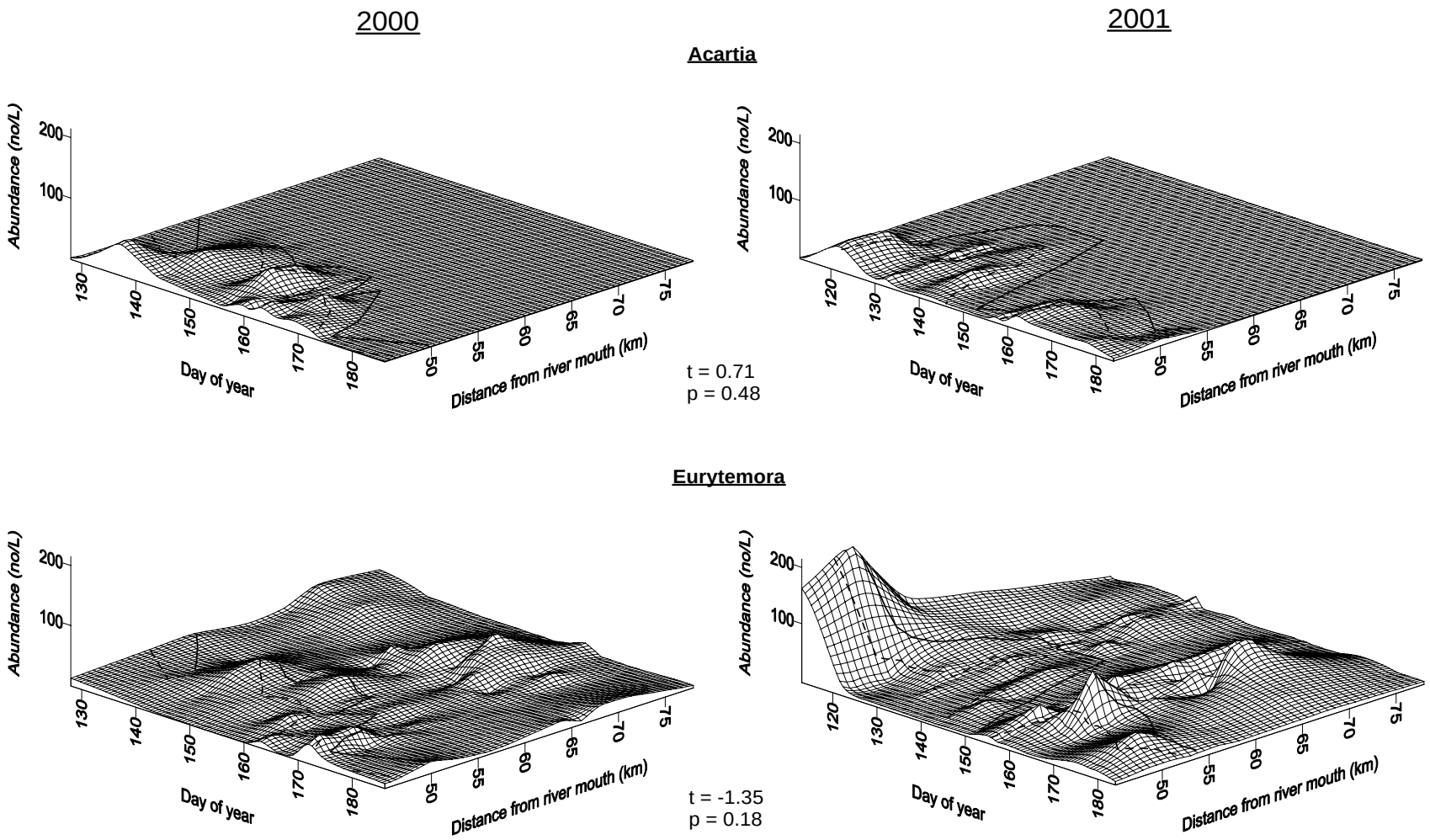

Figure 3.3. Spatiotemporal trends in concentrations of the calanoid copepods *Acartia* sp. (top) and *Eurytemora affinis* (bottom) in the Patuxent River in 2000 and 2001. Student's *t*-tests with unequal variance were used to compare mean concentrations between years. Solid and dashed lines are the salt front and 2-psu isohaline positions, respectively. Day 130 = 10 May; day 160 = 9 June.

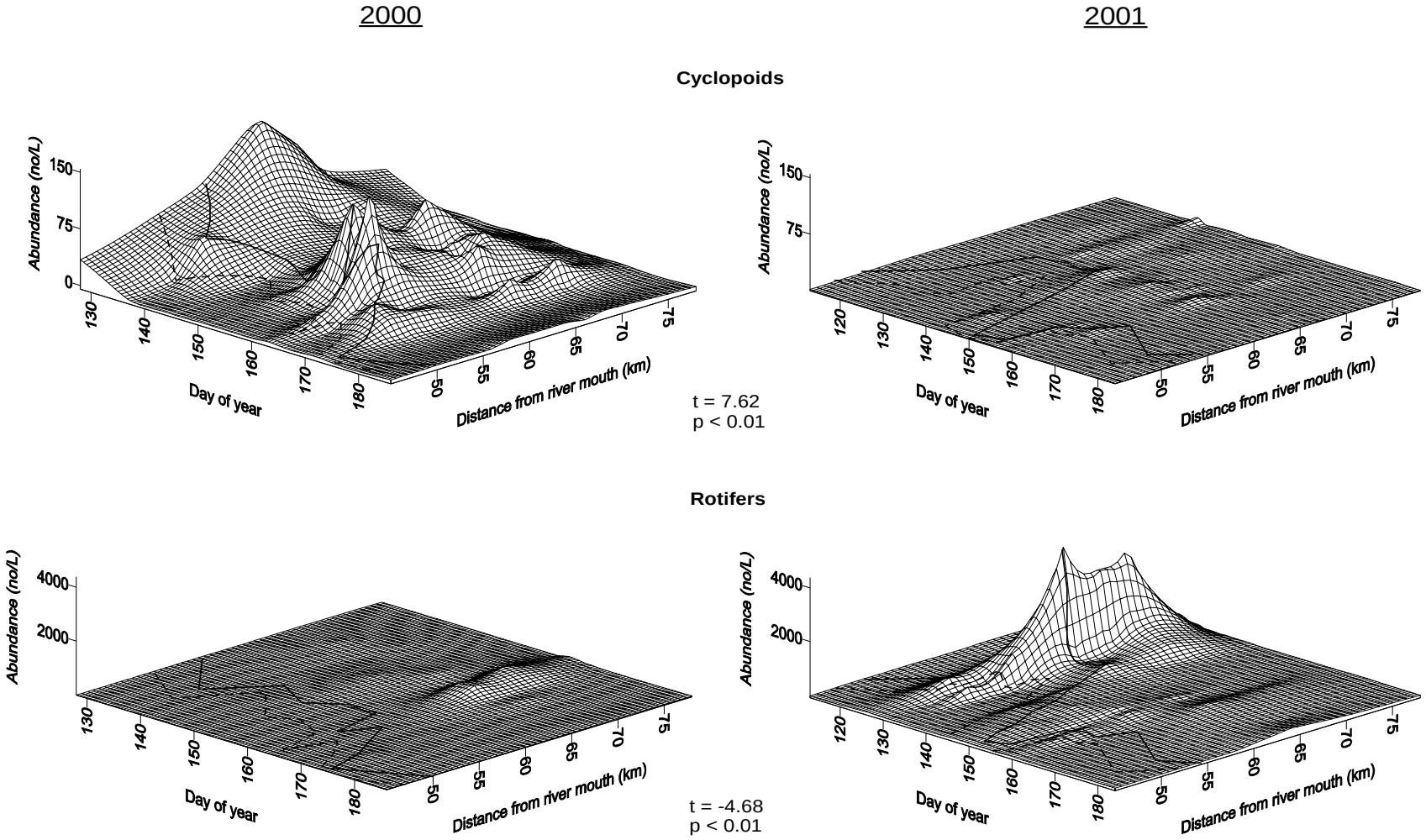

Figure 3.4. Spatiotemporal trends in cyclopoid copepod (top) and rotifer (bottom) concentrations in the Patuxent River in 2000 and 2001. Student's *t*-tests were used to compare mean concentrations between years. Solid and dashed lines are the salt front and 2-psu isohaline positions, respectively. Day 130 = 10 May; day 160 = 9 June. Y-axes scales differ for cyclopoids and rotifers.

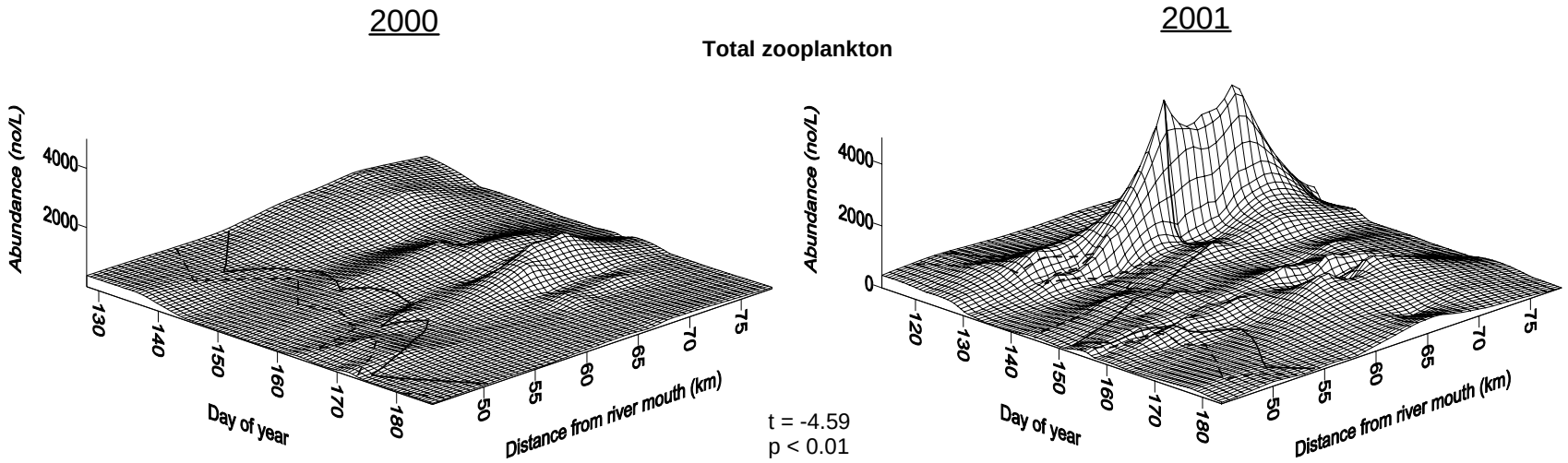

Figure 3.5. Spatiotemporal trends in total zooplankton concentrations in the Patuxent River in 2000 and 2001. Student's *t*-tests with unequal variance were used to compare mean concentrations between years. Solid and dashed lines are the salt front and 2-psu isohaline positions, respectively. Day 130 = 10 May; day 160 = 9 June.

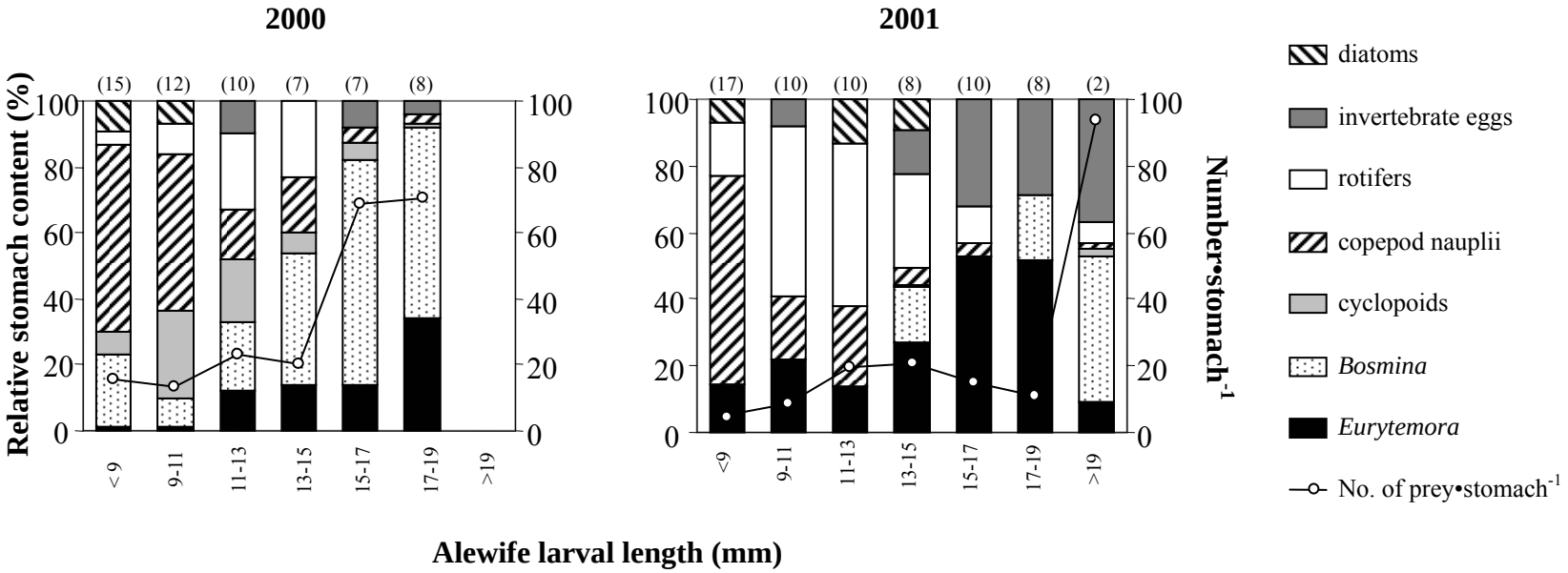

Figure 3.6. Alewife. Relative stomach content (% by numbers) and total stomach content (number per stomach) for 2-mm length classes of alewife larvae (all sampled larvae were from freshwater stations). Numbers of larvae analyzed in parentheses.

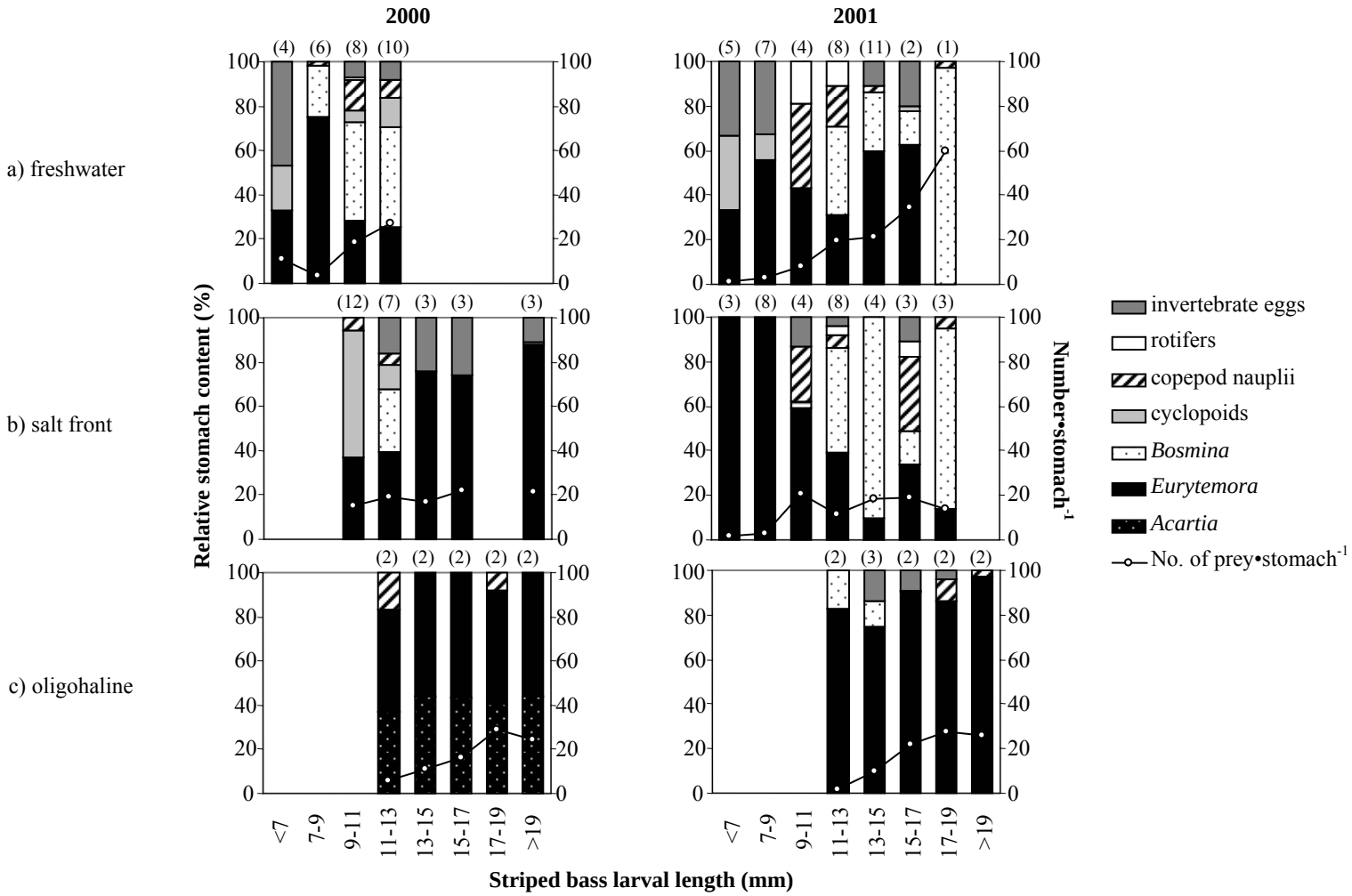

Figure 3.7. Striped bass. Relative stomach content (% by numbers) and total stomach content (number per stomach) for 2-mm length classes of striped bass larvae from a) freshwater, b) salt front, and c) oligohaline stations. Numbers of larvae analyzed in parentheses.

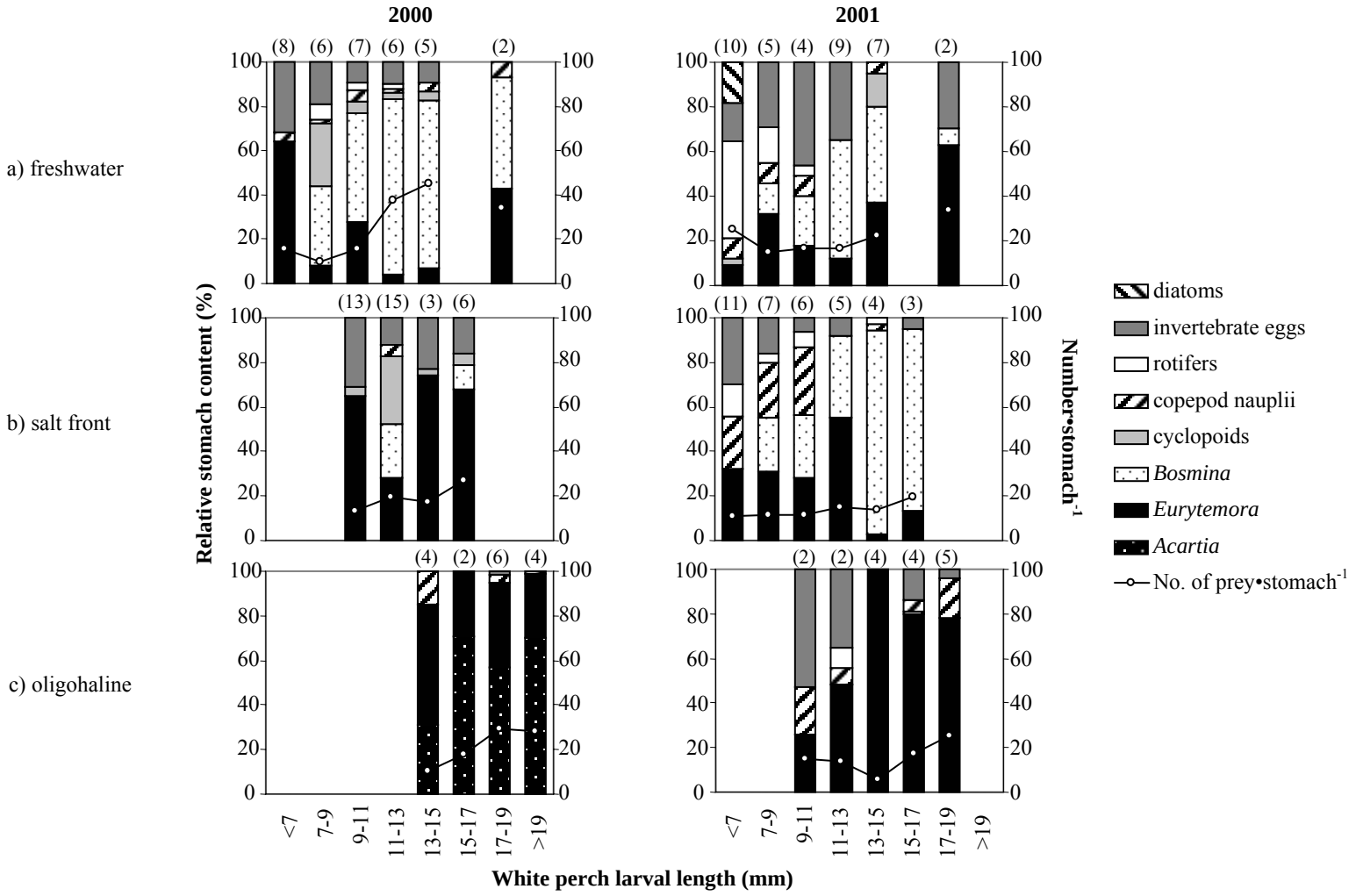

Figure 3.8. White perch. Relative stomach content (% by numbers) and total stomach content (number per stomach) for 2-mm length classes of white perch larvae from a) freshwater, b) salt front, and c) oligohaline stations. Numbers of larvae analyzed in parentheses.

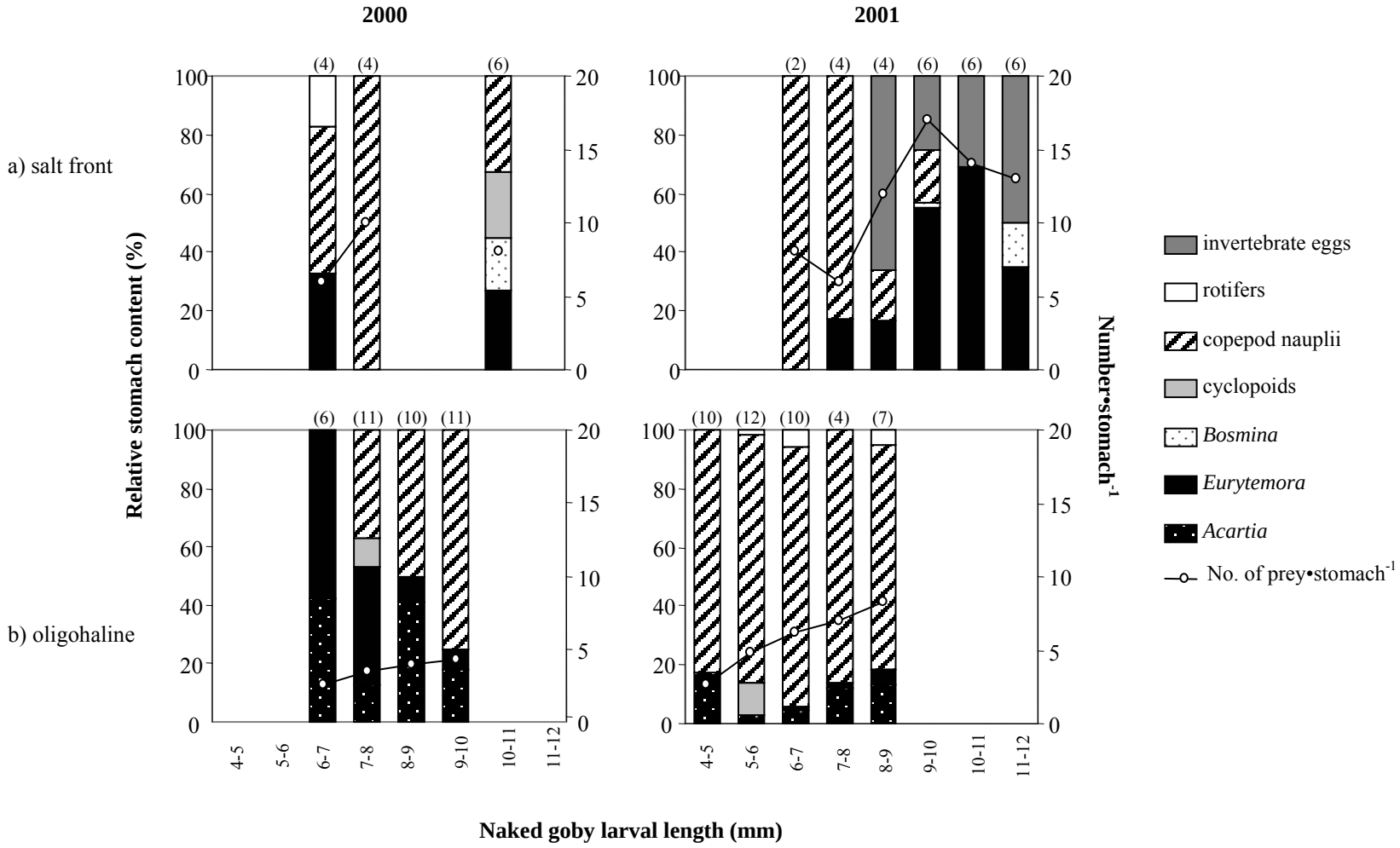

Figure 3.9. Naked goby. Relative stomach content (% by numbers) and total stomach content (number per stomach) for 1-mm length classes of naked goby larvae from a) salt front and b) oligohaline stations. Numbers of larvae analyzed in parentheses.

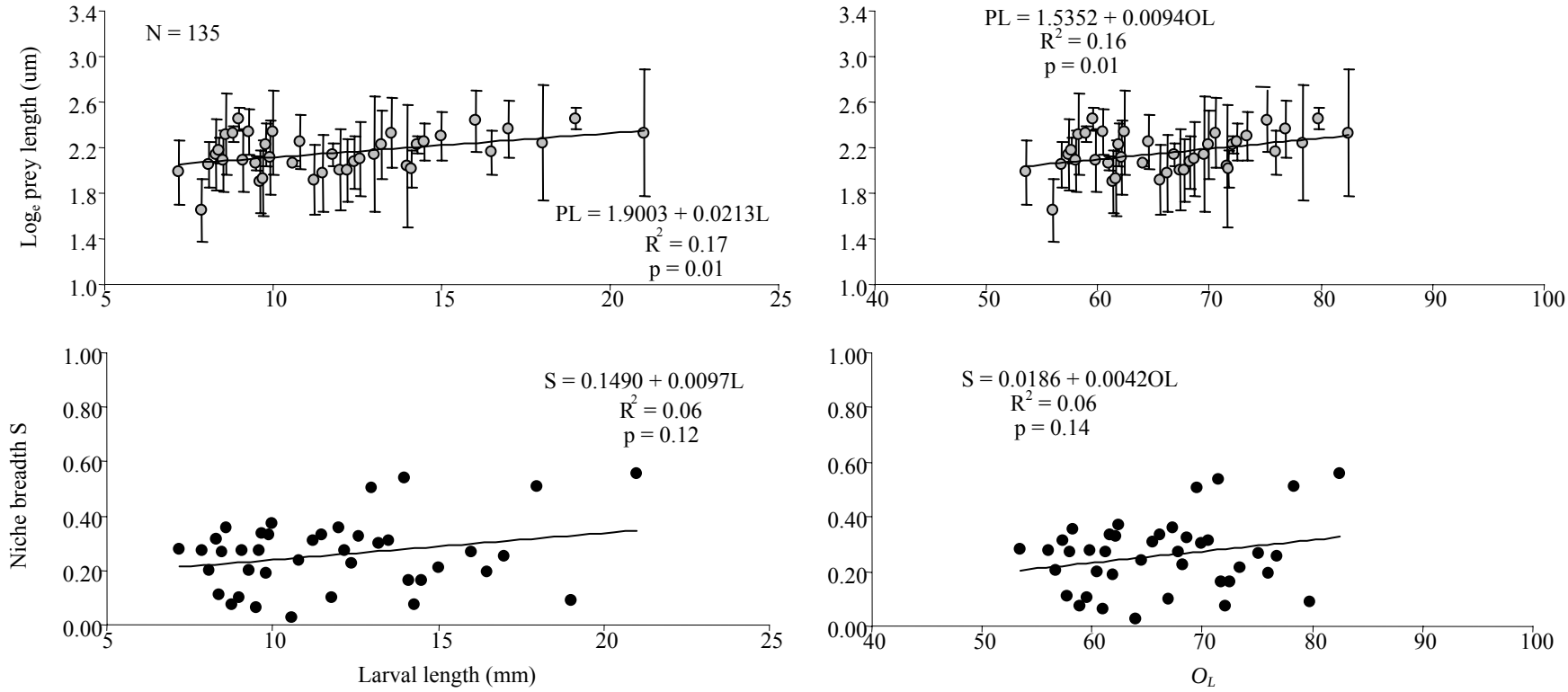

Figure 3.10. Alewife larval length (mm) and ontogenetic state (O_L) in relation to logarithmic mean prey length (µm) (±1 standard deviation) and trophic niche breadth **S** in the Patuxent River, 2000-2001.

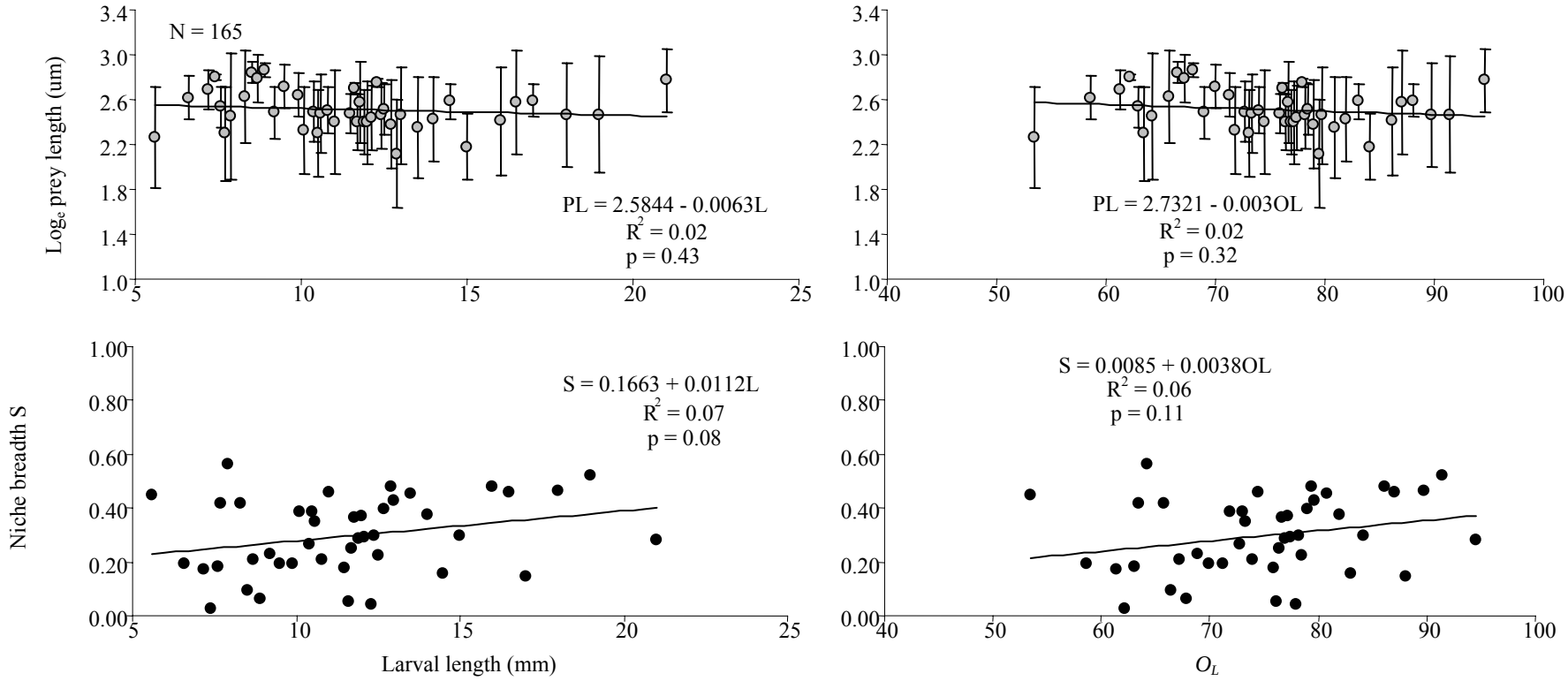

Figure 3.11. Striped bass larval length (mm) and ontogenetic state (O_L) in relation to logarithmic mean prey length (μm) (±1 standard deviation) and trophic niche breadth **S** in the Patuxent River, 2000-2001.

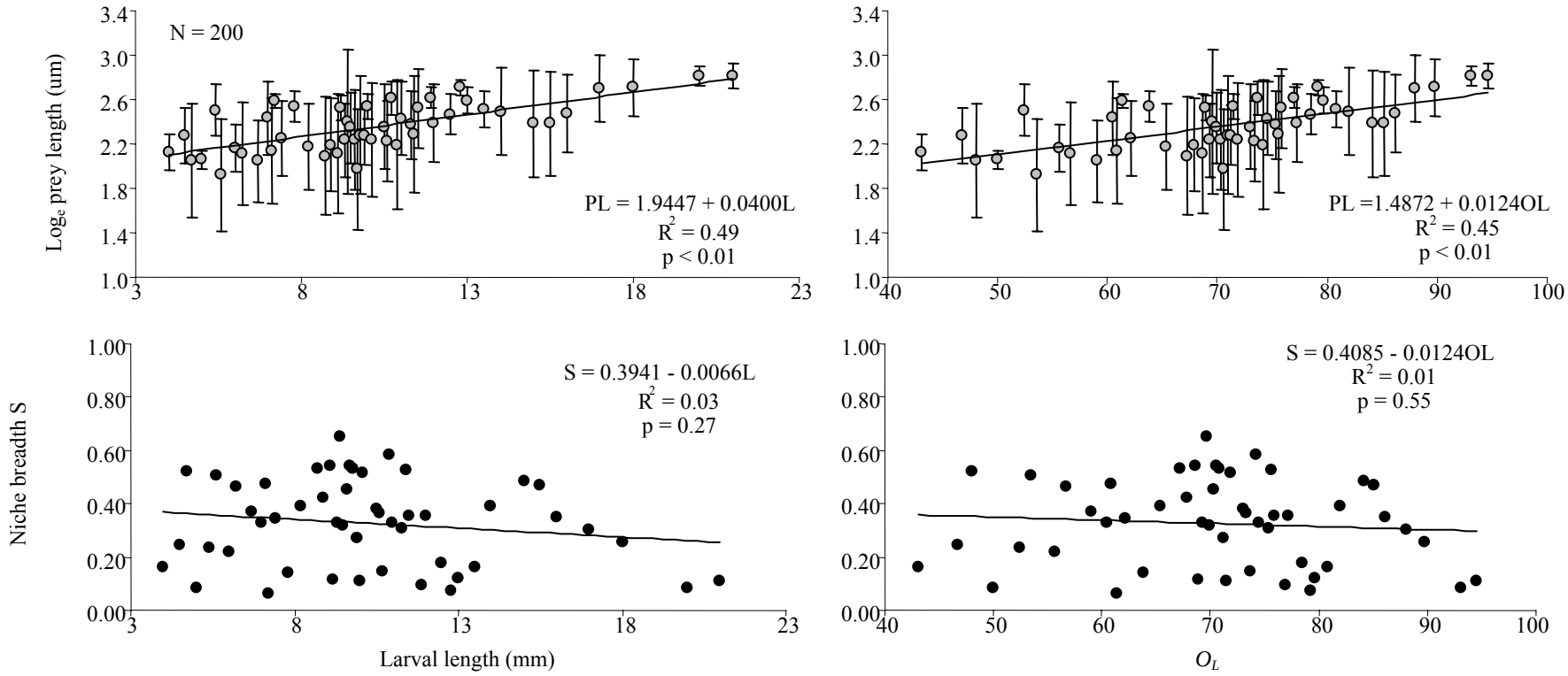

Figure 3.12. White perch larval length (mm) and ontogenetic state (O_L) in relation to logarithmic mean prey length (μm) (±1 standard deviation) and trophic niche breadth **S** in the Patuxent River, 2000-2001.

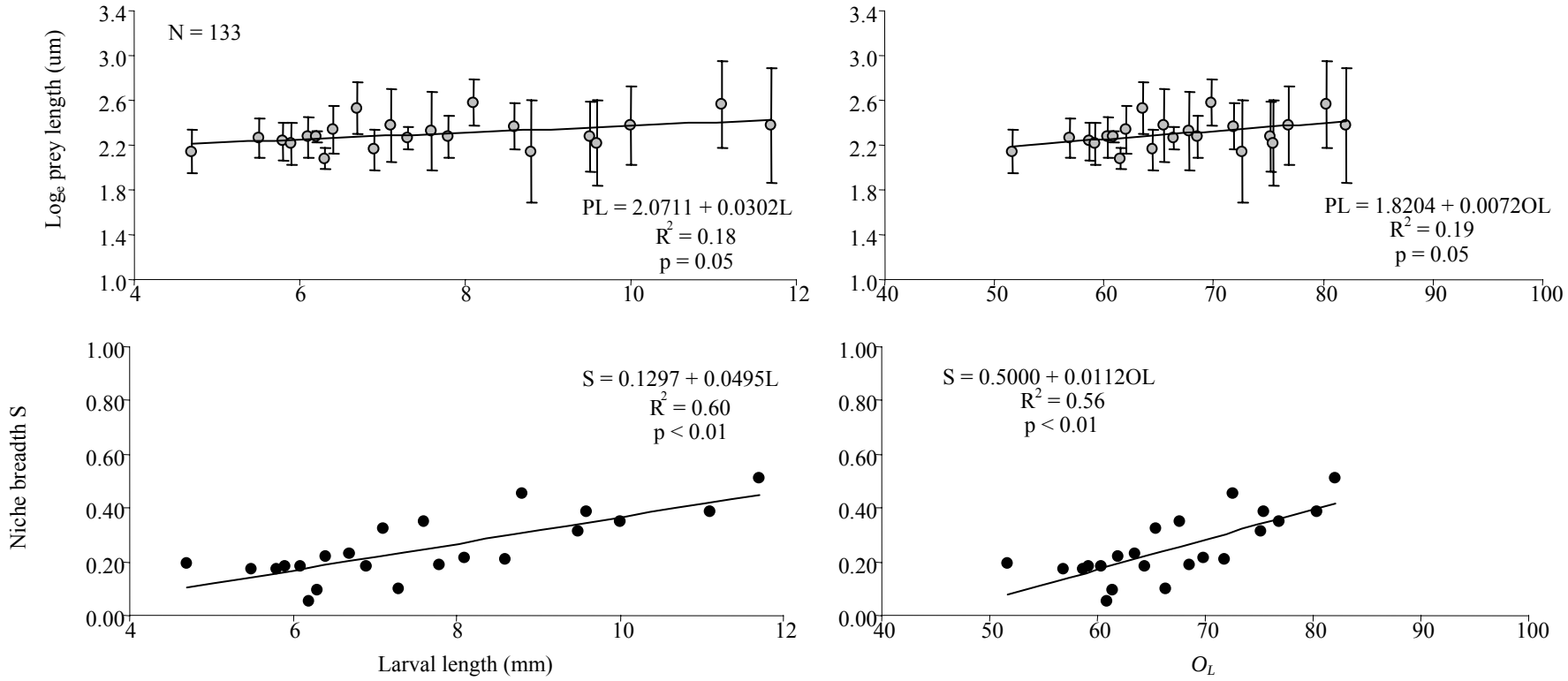

Figure 3.13. Naked goby larval length (mm) and ontogenetic state (O_L) in relation to logarithmic mean prey length (μm) (±1 standard deviation) and trophic niche breadth **S** in the Patuxent River, 2000-2001.

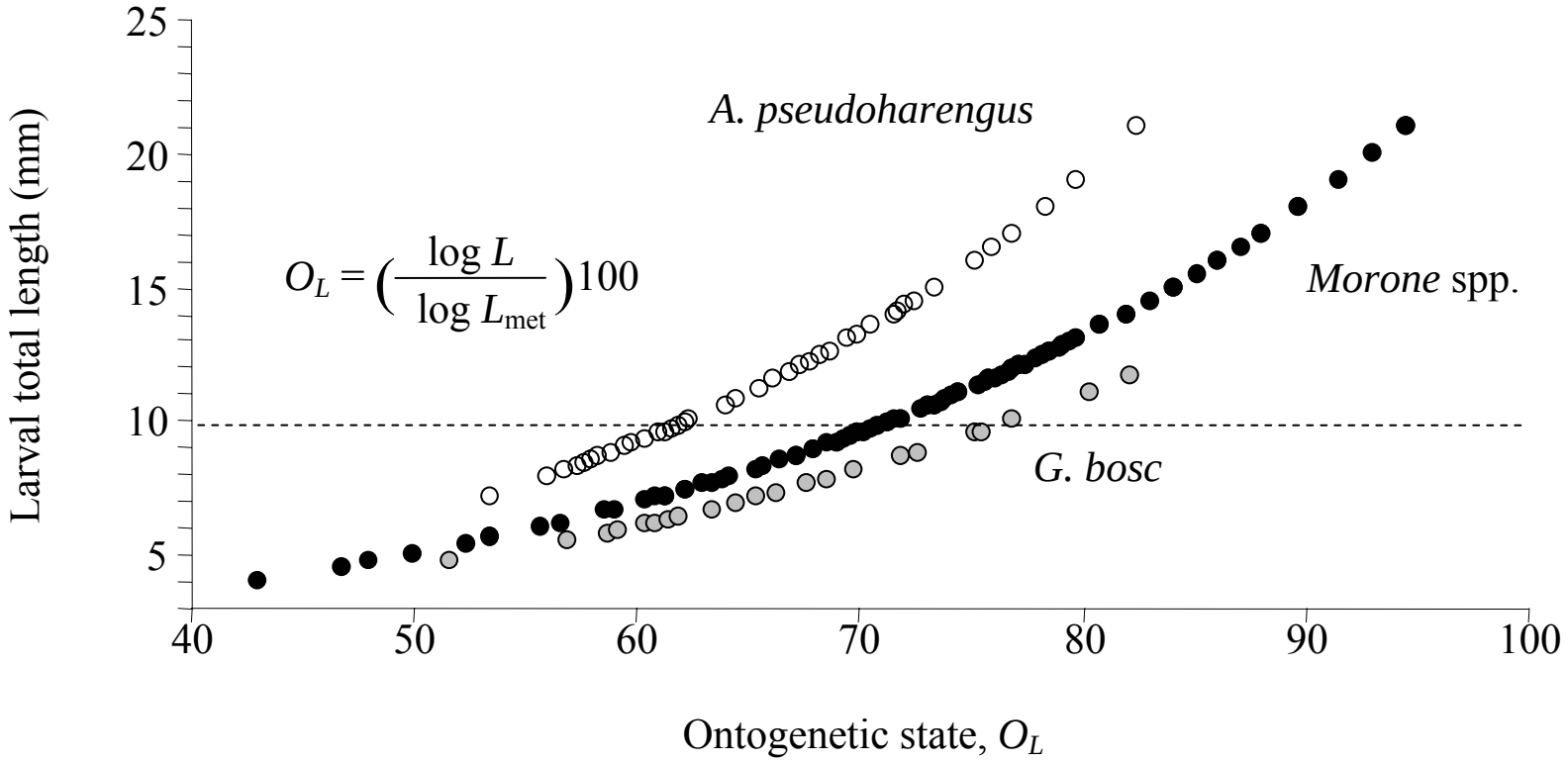

Figure 3.14. Ontogenetic index and larval length of alewife, striped bass, white perch, and naked goby larvae. O_L is the ontogenetic index, a numerical representation of the ontogenetic state (% development) of a larva of length L, where L_{met} is the length at which the species completes metamorphosis. Input values from Able and Fahay (1998): $L_{\text{met, } A.\ pseudoharengus}$ = 35mm, $L_{\text{met, } M.\ saxatilis}$ = 20mm, $L_{\text{met, } M.\ americana}$ = 20mm, and $L_{\text{met, } G.\ bosc}$ = 15mm.

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CHAPTER FOUR

Summary and Conclusions

Estuarine transition zones (ETZs) in Chesapeake Bay and its tributaries serve as important nursery areas for early life stages of anadromous and estuarine fishes. In my research, the spatio-temporal structure of ichthyoplankton assemblages and feeding habits of larvae were investigated in the ETZ of the Patuxent River, a tidal subestuary on the western shore of the Bay. The objective was to evaluate spatio-temporal relationships in occurrence, abundance, and potential for interactions among ichthyoplankton taxa, including hatchery-released American shad larvae.

The thesis is presented in three chapters. Dispersal, growth, and mortality rates were estimated for released shad larvae in an attempt to evaluate and improve stocking protocols for restoration of this species in Chesapeake Bay (Chapter One). Multivariate analyses were applied to describe the ichthyoplankton community, its distribution in the ETZ, associations among taxa, and relationships to environmental and biological factors (Chapter Two). Food habits and indices of feeding success for four species of anadromous and estuarine-spawning larval fishes were described and analyzed with respect to environmental variability and interactions among the species in the ETZ (Chapter Three). Considering larval stocking to restore American shad, results will be useful in determining optimal times and locations to release hatchery-produced larvae to minimize potential repressive interactions and promote survival.

Surveys during spring-early summer of 2000 and 2001 sampled larval and juvenile fish and zooplankton, and collected data on a suite of hydrographic variables across the ETZ. Surveys were conducted prior to and following releases of American

shad larvae at designated sites in the tidal Patuxent River. Sampling stations were located above, below, and within the projected larval nursery area of anadromous taxa. This area included the salt front, and the Estuarine Turbidity Maximum (ETM), a feature near the salt front that may aggregate particles, including larval fish and their zooplankton prey, and is an important nursery area for larval and juvenile fish.

Summary of results:

1. In year 2000, larval American shad (349,000) were stocked into the Patuxent River by the Maryland Department of Natural Resources on 8 June. Two groups of larvae were released: 1) an 'upstream' cohort stocked in freshwater upriver of the salt front-ETM and 2) a 'downstream' cohort stocked in low-salinity waters (~0.7 psu), immediately downriver of the salt front. In 2001, DNR stocked 364,200 American shad larvae in the Patuxent River. Larvae were released on two dates: 1) an 'early' stocking event, 10 May and 2) a 'late' release, 4 June. The stocking site on both dates in 2001 was in freshwater, 15-30 river kilometers upriver of the salt front.
2. In conjunction with each stocking event, 24-hr laboratory experiments were conducted to estimate short-term mortality of American shad larvae that might be associated with stocking. Survival rates were variable (23-92%) but indicated substantial survival potential for the released larvae. Surprisingly, survival rates were always higher in stocking-site river waters than in hatchery waters (controls).
3. The numbers of American shad larvae stocked were far below the 2 million planned for each year. As a consequence, relatively few larvae were recaptured, thus compromising rigorous statistical analyses on dispersal, distribution, and vital rate

estimates of the stocked larvae. Estimates that were obtained indicated low dispersal rates (±0.4km•d^{-1}), and highly variable growth (G = -1.28 to 0.87mm•d^{-1}) and instantaneous mortality rates (M = 0.20 to 3.01•d^{-1}).

4. Comparisons of vital rate estimates for American shad larvae released at different locations in the Patuxent River suggested that the best production of larval shad will result from releases upriver of the salt front-ETM. Results also suggested that hatchery releases of shad larvae in early to mid-May will fare better than releases in early June.

5. Feeding incidences of recaptured shad larvae (92%), prey in guts (5.1-6.5 prey•$larva^{-1}$), and zooplankton densities in the river (≥125 zooplankters•$liter^{-1}$) indicated that shad larvae were stocked at times and locations favorable for successful foraging. Copepod nauplii and *Eurytemora affinis* copepods/copepodites were the most important foods of stocked American shad larvae. Larval shad feeding habits were similar to those of co-occurring larvae of other anadromous fishes, most notably large, >10mm alewife, striped bass, and white perch larvae.

6. Twenty-eight species of ichthyoplankton occurred in samples. Highest taxonomic diversity and richness occurred upriver of the salt front-ETM in the freshwater region.

7. Alosines (*Alosa* spp., shads and river herring) exhibited a downriver ontogenetic shift. Larvae were primarily distributed in the freshwater region but larger larvae and juveniles sometimes occurred downriver near the salt front. A contrasting pattern was observed for naked goby larvae, in which small larvae arrived in the oligohaline region in May and subsequently migrated or were transported upriver to the salt front-ETM region as they grew. White perch larvae were ubiquitously distributed in the

ETZ and had substantial overlap with alewife and congeneric striped bass. The distribution of late-stage striped bass larvae and small juveniles centered around the salt front-ETM region but smaller larvae occurred more frequently in the freshwater region.

8. Two ichthyoplankton assemblages were distinguished in Principal Component Analyses (PCA): 1) a Riverine Assemblage – characterized by larval alosines, including alewife and the stocked American shad, and moronid species (striped bass and white perch), and 2) an Oligohaline Assemblage - characterized by larvae of estuarine-spawned taxa (primarily naked goby). Factor loadings in PCAs suggested that salinity and temperature were the primary hydrographic variables that controlled taxa distributions and distinguished ichthyoplankton assemblages.

9. Highest concentrations of anadromous fish larvae were observed within and up-river of the salt front. For example, mean concentrations of white perch larvae ranged from 0.90-2.60•m^{-3} in freshwater and salt front-regions and were <0.25•m^{-3} in the oligohaline region. Naked goby, the dominant larval taxon of estuarine-spawning species, had highest mean concentration (3.90•m^{-3}) in the oligohaline region in 2000 but was most abundant (5.20•m^{-3}) in the salt front region in 2001.

10. Temperature, dissolved oxygen, salinity-associated variables, and *Bosmina* cladoceran prey concentrations were significant variables in multiple regression models describing larval abundance of alewife, striped bass, white perch and naked goby. A between-years comparison indicated that prey densities and hydrography both were important in explaining variability in larval concentrations in 2000. In 2001, prey-density variables were significant in only one of the models (striped bass)

while temperature was a common variable in models for each of the four dominant species.

11. Estimated mean larval growth rates ($mm \bullet d^{-1}$), based on analysis of cohort modal lengths, were: $G_{alewife} = 0.39$, $G_{striped\ bass} = 0.30$, $G_{white\ perch} = 0.20$, $G_{naked\ goby} = 0.14$. Mean growth rates were similar to those estimated in previous studies, except for striped bass, which was higher. Mean growth rates did not differ between years 2000 and 2001.

12. Regional and size-dependent diet compositions were described for alewife, striped bass, white perch, and naked goby larvae (first-feeding to pre-juvenile stages). Diet compositions were evaluated with respect to densities of potential zooplankton prey and in relation to region of the river where larvae were collected. Diets were compared between years.

13. Spatio-temporal patterns in zooplankton distributions and concentrations varied among taxa and years. The copepod *Eurytemora affinis*, a favored prey of larval fish, occurred throughout the estuarine transition zone, although often in highest concentrations in the salt front-ETM region. The copepod *Acartia tonsa* only occurred downriver of the salt front. Mean *Eurytemora* concentrations (2000: $11.89 \bullet l^{-1}$; 2001: $14.69 \bullet l^{-1}$) were similar between years. Cyclopoid copepod mean concentration was much higher in 2000 ($21.93 \bullet l^{-1}$) than in 2001 ($0.76 \bullet l^{-1}$) when densities were below $10 \bullet l^{-1}$ throughout the sampling area. Cyclopoid abundance was highest near or upriver of the salt front. The cladoceran *Bosmina longirostris* was most abundant above the salt front and its mean concentrations (2000: $92.11 \bullet l^{-1}$; 2001: $104.56 \bullet l^{-1}$) did not differ between years. Rotifers occurred in highest

concentrations in or upriver of the salt front-ETM region and reached concentrations of >4000•l^{-1} in 2001. Mean concentration of rotifers was significantly higher in 2001 (315.93) than in 2000 (43.81). Copepod nauplii were abundant throughout the sampling area, and maximum densities occurred in the salt front-ETM region. Mean nauplii concentrations were higher in 2001 (99.38) than in 2000 (45.04).

14. Feeding incidence (percentage of larvae with prey in gut) of fish larvae was high overall (72-97%). The highest percentages of empty guts occurred in freshwater, although mean feeding incidence did not differ among regions.

15. In the freshwater region, copepod nauplii were the most important prey type for small alewife larvae. Large alewife larvae preferentially selected *Eurytemora* but *Bosmina* was its most important prey. *Eurytemora* was the most important prey for small striped bass and white perch larvae in the freshwater region, while both *Eurytemora* and *Bosmina* were important constituents in diets of large moronid larvae. Striped bass larvae in small (<10mm) and large (>10mm) length classes positively selected *Eurytemora*. Small white perch larvae positively selected *Eurytemora* and invertebrate eggs. *Eurytemora* and *Bosmina* were preferred by large white perch larvae.

16. In the salt front region, *Eurytemora* was preferred and rotifers were negatively selected by all larval taxa and length classes. *Eurytemora* was important in diets of each of the larval taxa in the salt front-ETM region. It was important in small and large larvae of striped bass, white perch, and naked goby, and in the large (>10mm) length class of alewife. *Bosmina* was of secondary importance in the diets of large

moronid larvae in this region, which was similar to observations in the freshwater region.

17. In the oligohaline region, larval taxa (striped bass, white perch, and naked goby) generally showed preference for the calanoid copepods *Acartia* and *Eurytemora*. Copepod nauplii were preferred by goby larvae but negatively selected by the large larvae of both moronid species. Copepod nauplii were the most important component in the diet of naked goby larvae. *Eurytemora* was the most important constituent in diets of striped bass larvae, while *Acartia* was most valuable for larval white perch in the oligohaline region.

18. Diets of larval striped bass and white perch were most similar (overlap analysis) in freshwater (O = 0.71-0.93). The moronid diets overlapped with the diet of large (>10 mm) alewife larvae in the freshwater region. The diets of naked goby larvae and small (<10 mm) white perch larvae overlapped in the salt-front region. Dietary overlap among larvae and potential for competition were judged to be highest within and upriver of the salt front-ETM region.

19. Mean prey size increased significantly during ontogeny for three of the four larval taxa analyzed (excepting striped bass). Naked goby was the only larval taxon with a positive relationship between trophic niche breadth (the standard deviation of the mean logarithmic prey size) and larval length, indicating a broader spectrum of prey sizes in the diet of larger larvae.

Dispersal, growth, and mortality of released American shad larvae, and associations among anadromous and estuarine larval taxa in the ETZ, indicate that successful stocking of American shad larvae in Chesapeake tributaries is most likely to derive from releases made in early to mid-May rather than earlier or later in the year. The best production will result from shad larvae being released during periods of gradually increasing temperatures at tidal freshwater sites upriver of the salt front and estuarine turbidity maximum regions.

Results of my research indicate that two ichthyoplankton assemblages occur during spring-early summer in the Patuxent River ETZ. Overlaps in species distributions and diets were highest within and upriver of the salt front-ETM region. In this region of the estuarine transition zone, interactions among larval taxa potentially have significant competitive effects on feeding and growth of larval fish and on their potential for survival and recruitment.