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Project Title

NATAL-RIVER TO ESTUARY MIGRATION OF AMERICAN SHAD: ESTIMATING THE VALUE OF ESSENTIAL REARING HABITAT AND IDENTIFYING POTENTIAL POPULATION BOTTLENECKS DURING YEAR-ONE

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I. PROJECT SUMMARY (on-file)

II. COMPLETION REPORT

A. Objective 1: Quantify the contributions to somatic growth from the various dietary resources that support larval and juvenile shad in these systems.

1) *Success*- We were successful in meeting this objective because $\delta^{13}C$ and $\delta^{15}N$ were effective biomarkers for identifying phytoplankton-based and terrestrial matter-based food webs (Hoffman and Bronk, *submitted*), and $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were effective for identifying freshwater-based and estuary-based food webs. The separation between sources of production (phytoplankton-derived matter versus terrestrially-derived matter) was possible because the $\delta^{13}C$ of dissolved inorganic carbon in the river, the carbon source for phytoplankton, was depleted (-9.5 to -19‰), resulting in isotopically light phytoplankton (-30.5 to -40‰, assuming a net fractionation of -21‰) compared to terrestrially-derived matter (-26‰). Thus, in addition to the original project goals, we were able to estimate the amount of tissue derived from either a phytoplankton-based or terrestrial matter-based food web using a stable isotope mixing model (Hoffman, *in press*).

   The stable isotope gradient from marine to fresh water was useful for identifying American shad habitat. Muscle tissue $\delta^{13}C$ and $\delta^{34}S$ were enriched in the lower tidal fresh water compared to the upper tidal fresh water (+7‰ $\delta^{13}C$, +12‰ $\delta^{34}S$), and highly enriched in the York River estuary compared to the upper tidal fresh water of the Mattaponi River (+12‰ $\delta^{13}C$, +17‰ $\delta^{34}S$). We were able to identify multiple habitats within the tidal freshwater nursery habitat because there was a gradient in tissue $\delta^{13}C$ from fish captured in the upper tidal freshwater ($\delta^{13}C$ ca. -32‰) to the salt wedge ($\delta^{13}C$ ca. -25‰) due to the mixing of estuarine-derived, enriched particulate organic matter (POM) with river-borne, depleted POM at the bottom of the food web. Thus, we were not only able to discriminate between American shad that had derived most of their somatic growth from the river or the estuary, but also discriminate between American shad that had grown in various locations within the nursery zone.

2) *Project findings* – Here, we broadly characterize our findings in terms of dietary resources, ontogenetic niche shifts, and habitat use by juvenile American shad of both the tidal freshwater and estuarine habitat.

- The muscle of larval and juvenile American shad in the nursery habitat, based on $\delta^{13}C$ and $\delta^{15}N$ analysis, was derived from a mix of crustacean zooplankton, mostly the calanoid copepod *Eurytemora affinis* and cladocerans *Bosmina spp.*; insect larvae, including the orders Ephemeroptera (mayflies) and Diptera (flies); and gammarid amphipods (Appendix II, Fig. 1). The interpretation of the food web was complicated by the seasonal and spatial variation in the $\delta^{13}C$ and $\delta^{15}N$ composition of the POM at the base of the food web. It was therefore necessary to analyze the data on a sample-by-sample basis to avoid misinterpretation of the data. In general, the $\delta^{13}C$ and $\delta^{15}N$ data indicated a feeding shift in American shad after metamorphosis (40-60 mm TL) that was consistent with a diet that was increasingly based on large macroinvertebrates such as Ephemeropterans, Dipterans and gammarid amphipods.
- The $\delta^{13}C$ and $\delta^{15}N$ analysis of juvenile American shad in the York River estuary was consistent with a diet of estuarine and marine copepods, including *Acartia sp.*, the mysid shrimp *Neomysis Americana* and fish larvae, including Atlantic croaker (*Micropogonias undulatus*), menhaden (*Brevoortia tyrannus*) and Bay anchovy (*Anchoa mitchilli*; Appendix II, Fig. 2).
- We found distinct seasonal variation in the source of American shad production in the Mattaponi River when applying the stable isotope mixing model to the $\delta^{13}C$ data (Appendix II, Fig. 3). In 2003, a high-flow year, the diet of both larvae and juveniles was predominantly (>50%) based on a food-web pathway originating from terrestrially-derived organic matter. In 2004, a typical flow-year, the diet of late-larvae was predominantly based on a food-web pathway originating from phytoplankton. American shad hatched later in the year derived a greater portion of their tissue from phytoplankton those hatched earlier in the year (Appendix II, Fig. 3). Additionally, the production of juveniles in the central and upper tidal freshwater were comprised of a greater proportion of phytoplankton than those down-river. This appeared to be related to the presence of a large retention zone in the central and upper tidal freshwater created by tidal forcing (Hoffman and Bronk, *submitted*).
- American shad captured in the various habitats (upper, central and lower river) in tidal fresh water had distinct $\delta^{13}C$ compositions (Appendix I, Table 1; Appendix II, Fig. 4). This finding implies that the fish are resident in each of these areas. The turnover rate model was modified to estimate the time of residence of juvenile American shad within each habitat that would be most consistent with the observed $\delta^{13}C$ and $\delta^{34}S$ distributions (Hoffman et al., *in prep*). We found that juveniles would have to reside in regions of the Mattaponi River of about 5 to 10 km long for 30-60 days (Appendix I, Table 2).
- The $\delta^{13}C$ composition of estuarine-captured juveniles was related to weight and location, though the relationship explained very little of the variation in the stable isotope composition (Appendix II, Fig. 5). The data likely reflect variable timing of migration to sea and habitat use. Indeed, fish that had a marine isotopic composition ($\delta^{13}C$ ca. -20‰) were captured throughout the York River, implying that they had been at sea for at least two months and recently entered the river. The single-isotope mixing model was used to estimate that the average fraction of somatic growth derived from the estuary habitat of juveniles from the 2000, 2002, 2003 and 2004

year-classes that were captured in the York River estuary was 0.43, 0.63, 0.42 and 0.40, respectively (Appendix II, Fig. 6). The data indicate that juveniles reside and feed within the York River estuary and lower Chesapeake Bay from November to March.

- Turnover modeling supported our interpretation of the data; for both larval and juvenile American shad, field data indicated that growth, and thus, diet, was the major determinant of the isotopic composition of these fish (Appendix II, Fig. 6A, 6B). Additionally, the turnover models indicated that the larvae should have already arrived at equilibrium with the isotopic composition of its diet in the river at the time of first capture, about 15 mm total length (Appendix II, Fig. 6C). This is important because it demonstrates that the data is not biased by the enriched, marine isotopic composition characteristic of American shad during the egg and yolk-sac stages.

3) *New research directions*

- We hypothesize that flow and tides act as important controls for the food-web structure in the Mattaponi River. It may be the case that the dominant food web pathway (allochthonous or autochthonous) influences larval growth and thus recruitment success. Troy Tuckey and J. Hoffman are currently investigating whether there is a spatial and temporal relationship between larval growth rates and the fraction of tissue derived from phytoplankton using the larvae captured in 2004. Aging of larvae by counting daily increments is ongoing.
- The presence of American shad with a marine isotopic composition in the York River estuary indicates that juveniles are entering the system from the lower Chesapeake Bay and coastal regions after spending significant time there. It is not known whether these fish are native to the York River or other coastal tributary. We are currently collaborating with Dr. Simon Thorrold and his PhD student, Ben Walther, both at the Woods Hole Oceanographic Institute, to assign juveniles captured within the York River estuary to their natal tributary using elemental and isotopic analysis of the sagittal otoliths. J. Hoffman plans to analyze the results from the natal tributary assignment to determine if the tissue $\delta^{13}C$ is a useful proxy for identifying juveniles native to the York River system.

B. Objective 2: Determine main areas of habitat use within the respective riverine and estuarine systems during ontogeny

1) *Success*- We were successful in using the historic data set from the VIMS Juvenile Fish and Blue Crab Trawl and VIMS Striped Bass Beach Seine surveys to plot the distribution of American shad within the York River estuary (Hoffman and Olney 2005). The analysis only included data from the York and Mattaponi Rivers due to the sparse collections available from the Pamunkey River, and only included data from those years in which juvenile American shad were caught in both tidal freshwater and brackish waters. Concurrent seine and trawl data were available from 1968 to 2001. In that period, twenty-one years had spatial distribution data that were suitable for describing the downstream limit of the juvenile population.

We were unable to perform a demographic analysis on American shad captured within the York River because the stable isotope data indicated that some juveniles were recent arrivals from the lower Chesapeake Bay or Atlantic coast. Without means to identify the fish as native to the York River system, and recognizing that movements within the estuary were probably not uni-directional, it was clear that any such analysis was too simplistic to describe the age-at-migration or age-structure of these fish.

2) *Project Findings*

- We found strong evidence that juvenile American shad remain on the nursery grounds (Mattaponi and Pamunkey rivers) until November and then exit the system to the York River and lower Chesapeake Bay through the winter months. In the twenty-one years analyzed, juvenile American shad caught from July to October were exclusively distributed in tidal freshwater; the farthest downstream that American shad were captured was river km 48, which is the general location of the salt wedge of the York River estuary (Appendix II, Figure 8). The farthest downstream that American shad were caught in November spanned both tidal fresh and brackish water. In December, the downstream limit varied, ranging from the upper to the lower York River (km 0-47). In January and February, the American shad that were caught the furthest downstream were concentrated downriver, with the largest proportions close to the river mouth (km 0). In March, the farthest downstream limit was distributed throughout the York River, from river km 0-47.

  The seine survey samples the entire river system monthly through August and failed to catch any juvenile American shad in the brackish York River during the summer in the twenty-one years examined. All juveniles found in brackish water were captured by the trawl survey, which does not use gear that targets pelagic juveniles. The trawl catch data, therefore, probably represent migration behavior for a very large number of juveniles, and it is impossible at this time to prove or disprove the hypothesis that a small number of juveniles entered the York River in the summer or early fall and escaped detection.

- The stable isotope turnover analysis was consistent with the long-term data set. American shad captured in the upper York River in early January, on average, would have had to enter the brackish York River no later than early December (Appendix I, Table 1). Similar results were obtained using $\delta^{13}C$ and $\delta^{34}S$, simulating movement into the lower York River (Appendix I, Table 2). Many juveniles had an isotopic composition similar to the estuary ($\delta^{13}C$ = -20 to -26‰; Appendix 2, Fig. 5); it is therefore likely that these fish spend weeks to months in the York River estuary during the winter before migrating to coastal habitats.

3) *New research directions* – In order to determine the age at migration and demographic structure of the migratory juveniles, J. Hoffman will be analyzing the Sr:Ca along the axis of the saggital otoliths. This method has been shown to be successful for estimating the age-at-migration for juvenile American shad. First, the fish will be screened for natal tributary using the elemental and isotopic composition of the sagittae (see above). Afterwards, an otolith from each York River fish will be analyzed for Sr:Ca and the age-at-capture estimated by counting daily rings on the otolith.

C. Objective 3: Identify potential population bottlenecks, both temporally (life-history stage) and spatially (habitat)

1) *Success*- The data collected was sufficient to develop mechanistic hypotheses regarding the role of physical forces within the river (flow, tides), spatial differences in habitat, and recruitment of American shad. The data we collected over three different years of varying flow (Appendix II, Fig. 9) and juvenile recruitment (Appendix II, Fig. 10) was sufficient to provide some initial support to these hypotheses, however future research will be necessary to examine these relationships in detail. The demographic analysis of the juvenile population, in particular the comparison between fish located on the nursery grounds and those captured in the York River estuary, remains an important component to the development and testing of any hypothesis regarding the role of habitat in juvenile life history. The new research directions currently being pursed toward identification of juveniles captured within the estuary will be critical to completing the demographic analysis.

2) *Project Findings*

    - This work, along with a recent demographic analysis of juvenile American shad from the Pamunkey River (Hoffman and Olney 2005), support the hypothesis that recruitment success varies temporally, both inter- and intra-annually, within the nursery habitat. River flow is a commonly cited variable that is related to this temporal variation, and it is currently believed that very high flows lead to poor recruitment while high flows augment recruitment. Our data are consistent with this perspective; the highest flow year (2003) had the highest recruitment and the lowest flow year (2002) had the lowest recruitment.

      The data were sufficient to offer a new hypothesis on the connection between river flow and recruitment success. We found that under high flows (2003), a large amount of terrestrially-derived organic matter is delivered to the nursery zone (Hoffman and Bronk, *submitted*). This led to an increase in zooplankton abundance (Appendix II, Figure 11), particularly the copepod *Eurytemora affinis* – an important food item in the diet of larval American shad - which were able to assimilate the terrestrial matter, indicated by the low fraction of tissue derived from phytoplankton (Appendix II, Figure 11). In contrast, flows in 2004 were lower, the phytoplankton bloomed earlier (indicated by higher fraction of tissue derived from phytoplankton), but abundance of *Eurytemora* was lower than in 2003. The high abundance of prey for American shad is probably a factor in the high recruitment observed in 2003. **It is important to note that the recruitment of American shad is therefore linked to the watershed; terrestrially matter appears to support higher in-river production than the river could support on only autochthonous matter.** Thus, preserving the connection between the riparian forests and marshes and the river channel should be part of a conservation strategy for American shad (Hoffman, *in press*).

    - The hypothesis that growth and mortality of young-of-year American shad varies spatially within the nursery habitat is supported by numerous data sets obtained during this research. A test of this hypothesis – the growth rate analysis of larval American shad captured in 2004 – is ongoing.

1. The source and abundance of particulate organic matter varies along the Mattaponi River nursery zone. This is related to the tidal forces in the Mattaponi River, which create a large retention zone in the central and upper tidal freshwater. This region appears to concentrate the amount of phytoplankton in the particulate matter, particularly in July and August during the summer phytoplankton bloom (Hoffman and Bronk, *submitted*). Phytoplankton is likely higher quality food for zooplankton and macroinvertebrates than terrestrially-derived detritus and therefore may be linked to food web dynamics.
2. The central tidal freshwater has the highest zooplankton abundance in the river (Appendix II, Figure 11), particularly during the spring when larvae are at risk of starvation. In 2004, the peak recorded abundance was 45 L^{-1} (river km 87 on 4 May 2004), which is about 10% of peak densities of zooplankton found in the Chesapeake Bay estuary turbidity maximum. In a previous analysis of the long-term data generated from VIMS Juvenile Alosa Index survey, this same region was shown to have the greatest abundance of juvenile American shad.
3. There is a temperature gradient along the Mattaponi River. The nursery habitat for American shad is about 2-4° cooler in the upper tidal freshwater compared to the lower tidal freshwater habitat (Appendix II, Figure 9). Warmer water in the lower river should support faster growth.
4. The stable isotope turnover model indicated that fish remained in small habitats within the river (5-10 km) for a month or longer, which is a sufficient period for habitat differences to influence the population demographics given the rapid mortality and growth rates of young-of-year American shad.

The combined evidence suggests that the central tidal freshwater region (river km 80 to 100) of the Mattaponi River is likely the most important region for recruitment of American shad. Protecting the integrity of this habitat should remain an important goal for stock conservation efforts.

- **The York River estuary is an important habitat for migratory American shad.** The dominant food items were marine calanoids, Atlantic croaker larvae, and the mysid shrimp, *Neomsysis americana*. The timing of Atlantic croaker spawning and the subsequent advection of larvae into the Chesapeake Bay may be an ecologically relevant factor for American shad feeding in the lower Chesapeake Bay. Very little is currently known about the abundance and distribution of mysid shrimp in the Chesapeake Bay, despite their important role as a prey item for many fish species.

3) *New research directions* – This objective primarily integrated various aspects of the proposal. New research directions related to it are listed in conjunction with the first two research objectives.

III. ACCOMPLISHMENTS AND BENEFITS REPORT

A. ACCOMPLISHMENTS

1) Effects

The results of the research project were important to scientists from the Virginia Institute of Marine Science (VIMS) when drafting the requested biological assessment of the proposed King William Reservoir. The stable isotope-based analysis of habitat was important in influencing VIMS scientific opinion regarding the spatial scope of American shad habitat use. In particular, VIMS scientists expressed concern that the localized impacts of the reservoir should be considered based on the results from this project (VIMS letter to Virginia Marine Resource Commission [VMRC] Commissioner William A. Pruitt, 12 March 2003). Additionally, temporal patterns in the occurrence of American shad larvae in the Mattaponi River obtained during this research project were important in influencing scientific opinions regarding the biological impact of the proposed pumping hiatus (VIMS letter to VMRC Commissioner William A. Pruitt, 25 June 2004). The effect of the VIMS biological opinion was to raise the concern of VMRC regarding the impact of the reservoir on the population of American shad in the Mattaponi River. Ultimately, this resulted in increased mitigation efforts by the City of Newport News.

This research project has also expanded our scientific knowledge regarding the relationship between terrestrial and riverine ecosystems in the production of anadromous fishes. Further, the project generated the first estimates of the biologically meaningful temporal and spatial scales of habitat use by larval and juvenile American shad. The effect of these findings has been to encourage scientific interest in obtaining similar data on American shad from other coastal tributaries.

2) Publications

Hoffman, J.C., D.A. Bronk and J.E. Olney. *In prep*. The use of stable isotopes to quantify habitat-specific residence times: an example using juvenile American shad.

Hoffman, J.C., D.A. Bronk and J.E. Olney. *In prep*. Evidence for terrestrial subsidies to zooplankton and macroinvertebrate production in a coastal plain tributary based on stable isotope analysis.

Hoffman, J.C. and J.E. Olney. *In prep*. Production of young-of-year American shad in the York River based on C, N and S stable isotope composition.

Hoffman, J.C. and D.A. Bronk. *Submitted*. Inter-annual variability in stable carbon and nitrogen isotope biogeochemistry of the Mattaponi River, Virginia. *Limnology and Oceaonography*.

Hoffman, J.C. and K.A. Delano. *Submitted*. Effect of alcohol preservation on stable isotope composition of fish muscle. *Marine Ecology Progress Series*.

Olney, J.C., D.M. Bilkovic, C. Hershner, L. Varnell, H. Wang, and R. Mann. *Submitted*. Six Fish and 600,000 Thirsty Folks - A Fishing Moratorium on American Shad Thwarts a Controversial Municipal Reservoir Project in Virginia, USA. Proceedings of the Fourth World Fisheries Congress.

Hoffman, J.C. *In Press*. Do American shad grow on trees? Linking forests with the life history of a marine fish. *Fisheries*.

Hoffman, J.C. and J.E. Olney. 2005. Cohort-specific growth and mortality of juvenile American shad in the Pamunkey River, Virginia. *Transactions of the American Fisheries Society*, 134(1):1-18.

3) New technologies or techniques

In the course of this research, we have developed a modeling technique whereby stable isotope data may be used to estimate the residence time of a fish within a certain habitat. Although stable isotopes have been used to estimate the residence time of anadromous fish within freshwater, to our knowledge this is the first time a technique has been developed to estimate residence times in relatively small-scale habitats (5-10 river km) within the nursery zone. The model simply requires three data: 1) the distribution of the stable isotope composition of the fish in its previous habitat, 2) the distribution of the stable isotope composition of the fish in its current habitat, and 3) either a known weight-specific growth rate or stable isotope turnover rate. This technique has been presented and received recognition at a regional scientific conference (Annual Meeting of the American Fisheries Society Southern Division). We are currently preparing a scientific manuscript in which the technique is applied to juvenile American shad from the Mattaponi River.

4) Presentations

a. Contributed Presentations

Hoffman, J.C., D.A. Bronk and J.E. Olney. 2005. Do American shad grow on trees? Terrestrial subsidies to the production of larval American shad in a coastal plain tributary. 29th Annual Larval Fish Conference, Barcelona, Spain, July 11-14

Hoffman, J.C. and D.A. Bronk. 2005. Inter-annual variability in the stable carbon and nitrogen isotope biogeochemistry of the Mattaponi River, VA. Atlantic Estuarine Research Society Annual Spring Meeting, Solomons, MD, March 11-12.

Hoffman, J.C. and J.E. Olney. 2005. Do American shad grow on trees? Annual Meeting of the Southern Division of the American Fisheries Society, Virginia Beach, VA, February 11-13. *Received an Honorable Mention.*

Hoffman, J.C., D.A. Bronk and J.E. Olney. 2004. Value of riverine and estuarine habitats for American shad in the York River, Virginia. 134th Annual Meeting of the American Fisheries Society, Madison, WI, August 22-26

Olney, J.C., D.M. Bilkovic, C. Hershner, L. Varnell, H. Wang, and R. Mann. 2004. Six Fish and 600,000 Thirsty Folks - A Fishing Moratorium on American Shad Thwarts a Controversial Municipal Reservoir Project in Virginia, USA. 4th World Fisheries Congress, Vancouver, BC, Canada, May 2-6

Hoffman, J.C., D.A. Bronk and J.E. Olney. 2004. Ecological value of riverine and estuarine habitats for American shad in the York River, Virginia. Atlantic Estuarine Research Society Annual Spring Meeting, Salisbury, MD, March 25-27. *Received an Honorable Mention*.

Hoffman, J.C., D.A. Bronk and J.E. Olney. Determining essential habitat for American shad (*Alosa sapidissima*) in the York River, VA using stable isotope analysis. 27th Annual Larval Fish Conference, Santa Cruz, CA, August 20-23

Hoffman, J.C.. 2003. Development of a new technique to quantify essential fish habitat using stable isotope analysis: a preliminary assessment. XVII Annual Meeting of the Tidewater Chapter of the American Fisheries Society, Beaufort, North Carolina, Jan. 15-17

b. Poster Presentations

Hoffman, J.C., D.A. Bronk and J.E. Olney. 2005. Characterizing movement of young-of-year American shad within the nursery zone using stable isotopes. Annual Meeting of the Southern Division of the American Fisheries Society, Virginia Beach, VA, February 11-13. *Received 2nd place.*

Hoffman, J.C., D.A. Bronk and J.E. Olney. 2003. Determining essential habitat for juvenile American shad in the York River, VA using stable isotope analysis. 17th Biennial Conference of the Estuarine Research Federation, Seattle, WA, September 14-18.

5) Student involvement/training

The grant was used to fund a major component of J. Hoffman's (co-PI) dissertation, which addresses the early life-history and stable isotope ecology of American shad in the York River. J. Hoffman was responsible for obtaining field data, processing samples for stable isotope analysis, analyzing gut contents, aging larval and juvenile American shad, obtaining and analyzing historic collection data from the various surveys, and developing the two models associated with the stable isotope analyses. J. Hoffman is in the Fisheries Department in the School of Marine Science, The College of William and Mary, and is co-advised by Dr. J.E. Olney. He will complete his PhD and expects to graduate in May 2006 with the dissertation "Natal-river to estuary migration of American shad: Estimating the value of essential rearing habitat in riverine and estuarine systems".

Additionally, the project has involved Troy Tuckey, a PhD student advised by J.E. Olney. T. Tuckey has assisted with the processing of larval American shad otoliths and subsequent aging. T. Tuckey is also in the Fisheries Department in the School of Marine Science, The College of William and Mary. He is currently developing his dissertation and will likely complete his PhD in 2008.

6) Interactions

This research project lead to significant interactions with VIMS scientists, the City of Newport News, various consultants hired by the City of Newport News (including fisheries scientists from federal government labs and state universities) , and VMRC regarding the proposed King William Reservoir.

7) Personnel news

J. Hoffman has received numerous awards for presentations and writings on research funded by this grant. They are listed below.

- Student Essay Award, American Fisheries Society—2005
- Student Paper Award, Honorable Mention, Annual Meeting of the Southern Division of the American Fisheries Society—2005
- Student Poster Award, 2nd Place, Annual Meeting of the Southern Division of the American Fisheries Society—2005
- Student Paper Award, Honorable Mention, Atlantic Estuarine Research Society Annual Spring Meeting—2004

B. BENEFITS

There have been both direct social benefits and indirect economic benefits gained from this research project. Qualitatively, the major social benefit is improved marine resource management of American shad in the Mattaponi River in regards to the operation of the King William Reservoir. Currently, the Mattaponi River is believed to support the largest run of American shad of any of Virginia’s coastal tributaries. As a direct result of the biological opinion provided by VIMS, the City of Newport News altered their proposed operation plan to include a pumping hiatus to protect American shad eggs and larvae and added fish screens to the intake pipes to reduce the probability of entraining fish. The indirect economic benefit of the improved management will be the eventual restoration of the American shad fishery. The American shad fishery, once re-opened, could potentially be worth tens of millions of dollars from the combined economic activity related to the commercial and recreational fisheries. Currently, the Pennsylvania Fish and Boat Commission values the restored run of American shad on the Susquehanna River at $30 million annually.

APPENDIX I. TABLES

Table 1. Characteristics of juvenile American shad from the Mattaponi River (km 74-109) and upper York River (km 19-52), including mean total length - TL, mean weight -W, mean $\delta^{13}C$ (SD) and mean residence time to arrive at isotopic equilibrium with the adjacent downstream habitat - t_{equil} (SD). Data are from the 2002 year-class. The habitat-specific mean $\delta^{13}C$ was estimated for each Mattaponi River habitat by weighting $\delta^{13}C$ using the habitat-specific catch composition because juveniles were randomly sub-sampled by capture date and length-class within those habitats.

Habitat	TL (mm)	W (g)	$\delta^{13}C$	t_{equil} (d)
km 104-109	48.5	1.41	-31.3 (0.6)	35.3 (3.6)
km 95-100	52.2	1.78	-30.4 (0.6)	59.0 (4.5)
km 74-87	54.7	2.06	-26.9 (0.5)	41.4 (1.7)
km 19-52	102.2	8.05	-22.7 (1.8)	-

Table 2. Mean, minimum and maximum residence time to arrive at isotopic equilibrium (t_{equil} (d)) with the adjacent downstream habitat estimated from either $\delta^{13}C$ or $\delta^{34}S$. Mattaponi River data are from select juveniles analyzed from four different habitats in June 2002 (n=10 fish per habitat for $\delta^{13}C$ and $\delta^{34}S$), whereas York River data are from juveniles captured at km 13 in January 2003 (n=10).

Simulation start		km 104	km 96-102	km 85-89	km 74-78
Simulation end		km 96-102	km 85-89	km 74-78	km 13
$\delta^{13}C$	Mean	32	31	29	52
	Minimum	21	24	13	36
	Maximum	39	36	42	63
$\delta^{34}S$	Mean	27	36	23	49
	Minimum	18	29	13	33
	Maximum	35	43	28	66

APPENDIX II. FIGURES

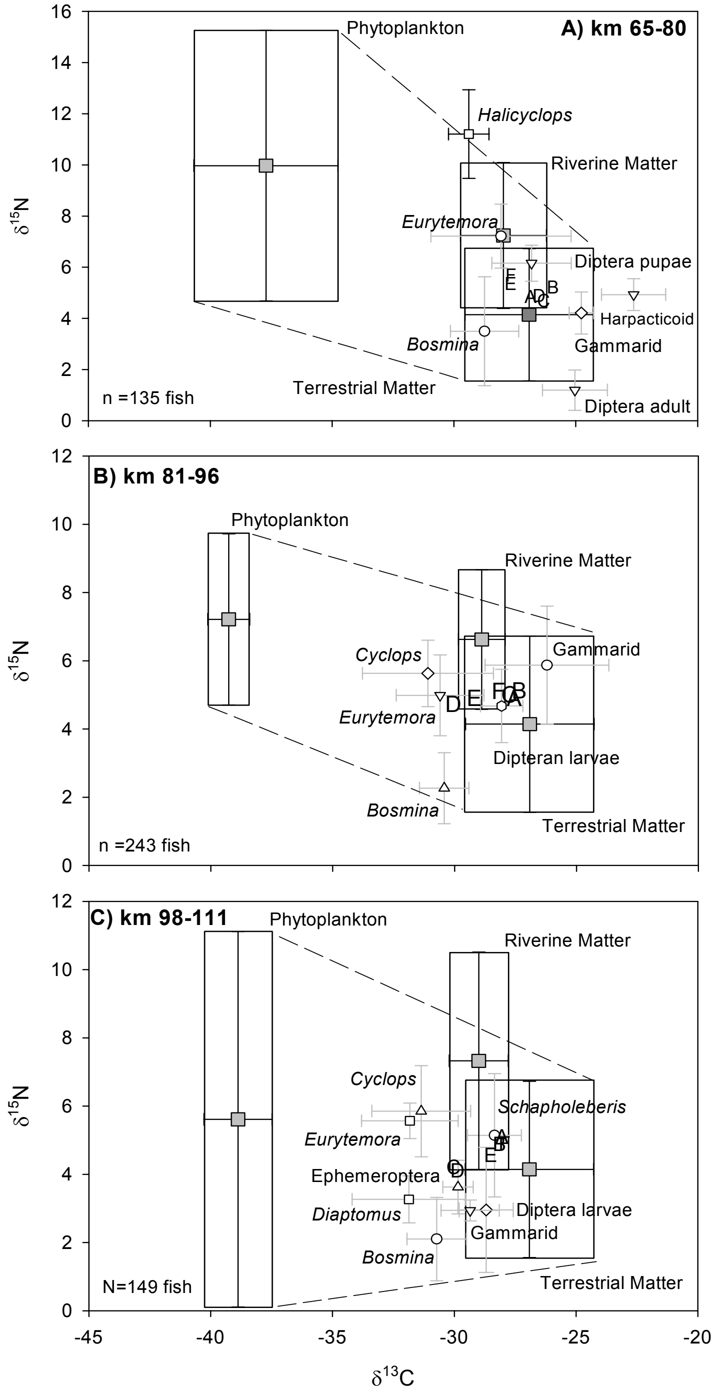

Figure 1. Food web relationships for the tidal fresh water of the Mattaponi River, Virginia. Averages (± SD) estimated from May-August 2003. Phytoplankton δ^{13}C was estimated from DIC δ^{13}C ($\delta^{13}C_{phyto} = \delta^{13}C_{DIC} - 21‰$) and δ^{15}N was estimated from the two end-member mixing model using *Eurytemora affinis* as a representative grazer. Terrestrial matter δ^{13}C and δ^{15}N was measured under high flow conditions. Zooplankton and macroinvertebrates were adjusted for one trophic level enrichment (-0.4‰ δ^{13}C, -3.4‰ δ^{15}N), American shad for two trophic levels (-0.8‰ δ^{13}C, -6.8‰ δ^{15}N). Various size classes are shown for American shad (A: 15-20 mm; B: 20-25 mm TL; C: 25-30 mm TL; D: 30-40 mm TL, E: 40-60 mm TL; F: 60-80 mm TL).

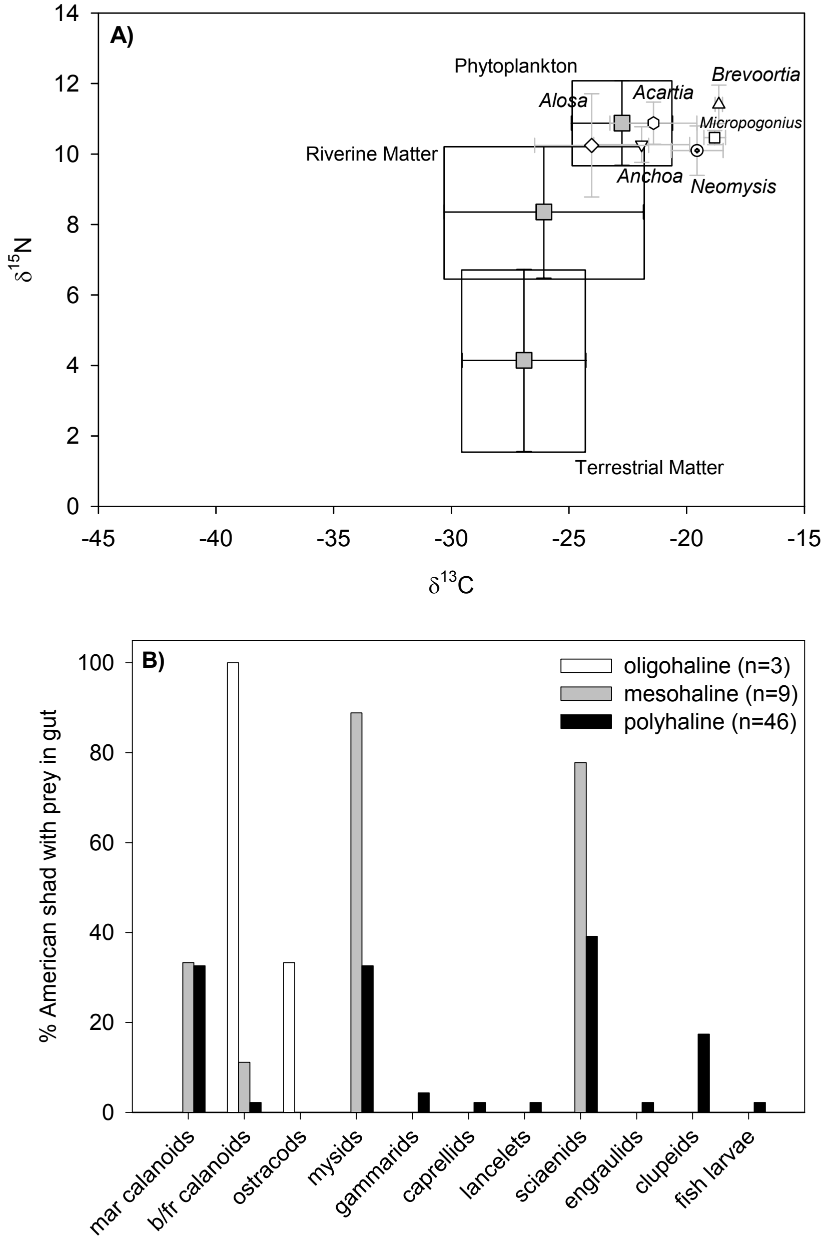

Figure 2. Food web relationships for the polyhaline portion of the York River, Virginia based on stable isotope analysis (A) and gut content analysis (B). Average δ^{13}C and δ^{15}N (± SD) estimated from November 2003 – March 2004 for *Acartia spp.*, *Neomysis americana*, larval *Anchoa mitchilli* (bay anchovy), larval *Brevoortia tyrannus* (menhaden) and larval *Micropogonius undulatus* (Atlantic croaker). Averages for juvenile *Alosa sapidissima* (American shad) were estimated from March 2004 (n=10; > 80 mm TL). Phytoplankton δ^{13}C was estimated from DIC δ^{13}C ($\delta^{13}C_{phyto} = \delta^{13}C_{DIC} - 21‰$) and δ^{15}N was estimated from the two end-member mixing model using *Acartia spp.* as a representative grazer. *Acartia spp.*, *Neomysis americana* and *Brevoortia tyrannus* were adjusted for one trophic level enrichment (-0.5‰ δ^{13}C, -3.4‰ δ^{15}N); *Alosa sapidissima*, *Anchoa mitchilli* and *Micropogonius undulatus* were adjusted for two trophic levels (-1.0‰ δ^{13}C, -6.8‰ δ^{15}N). Gut content analysis (B) was performed on all juveniles captured in the York River from November 2002 to March 2003.

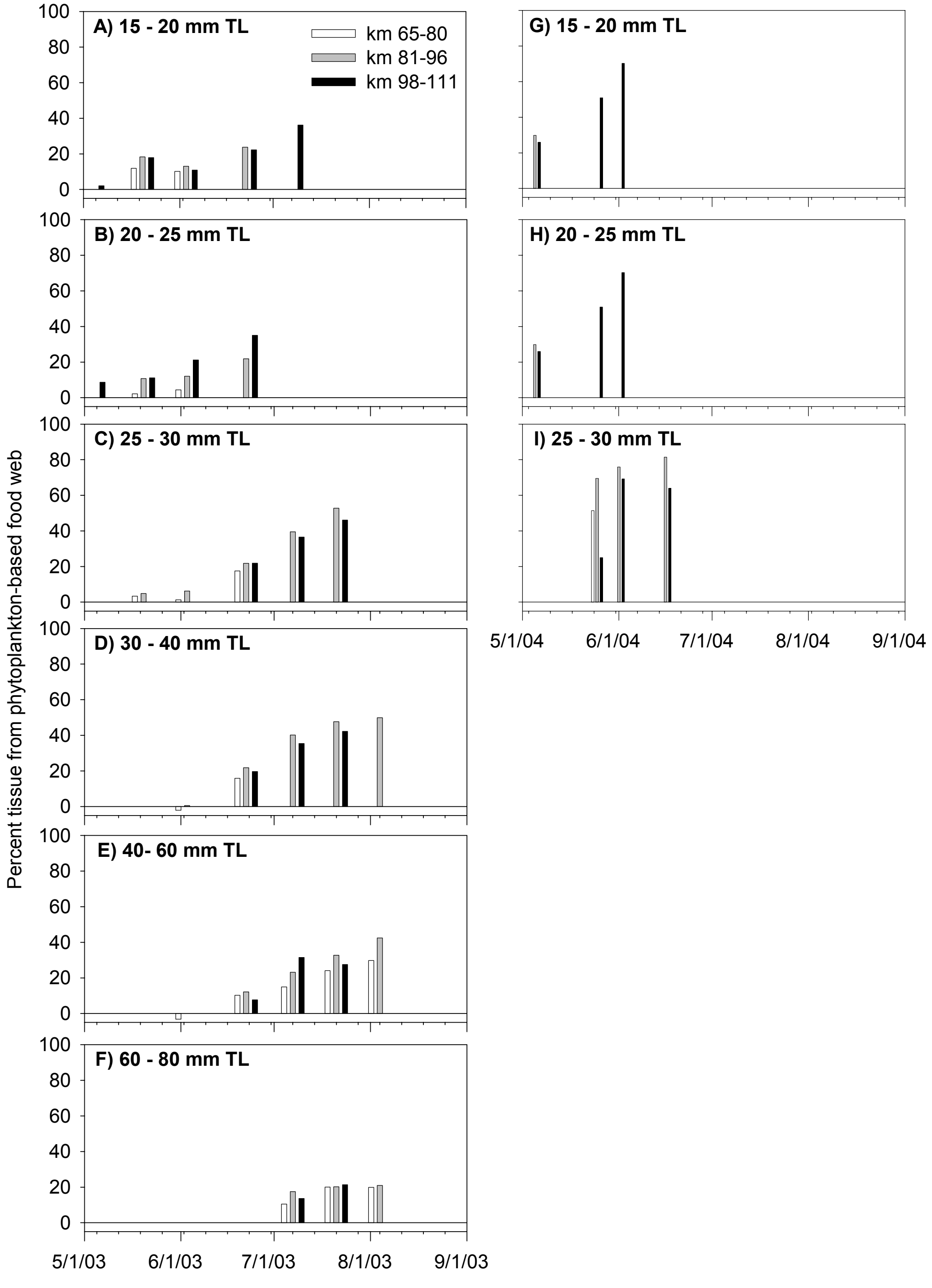

Figure 3. Seasonal and temporal variation in the percent of American shad tissue derived from a phytoplankton based food web (versus terrestrial matter-based food web) in 2003 and 2004. Panels corresponding to various size-classes.

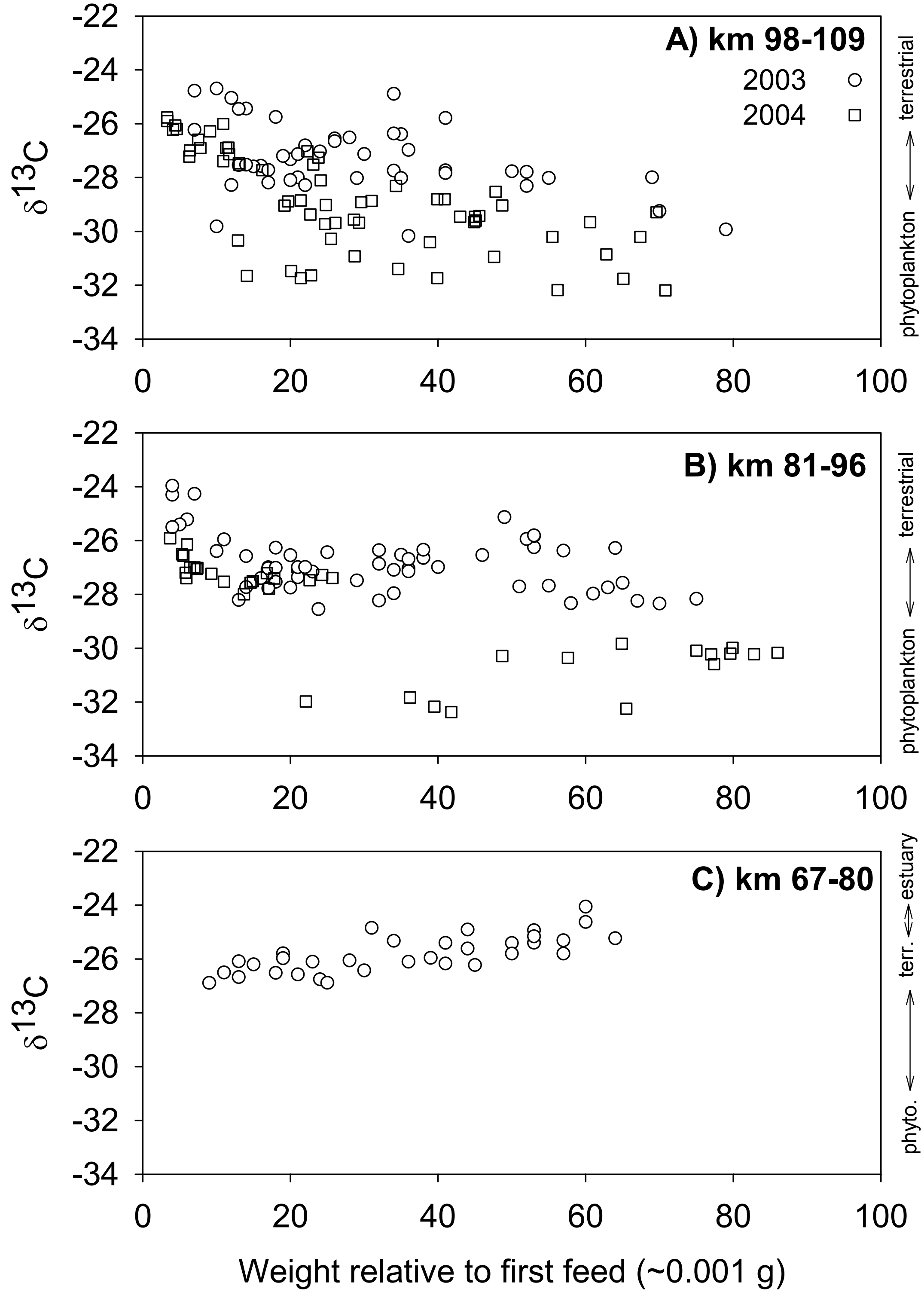

Figure 4. Change in tissue $\delta^{13}C$ of larval American shad relative to weight-specific growth for 2003 (circle) and 2004 (squares).

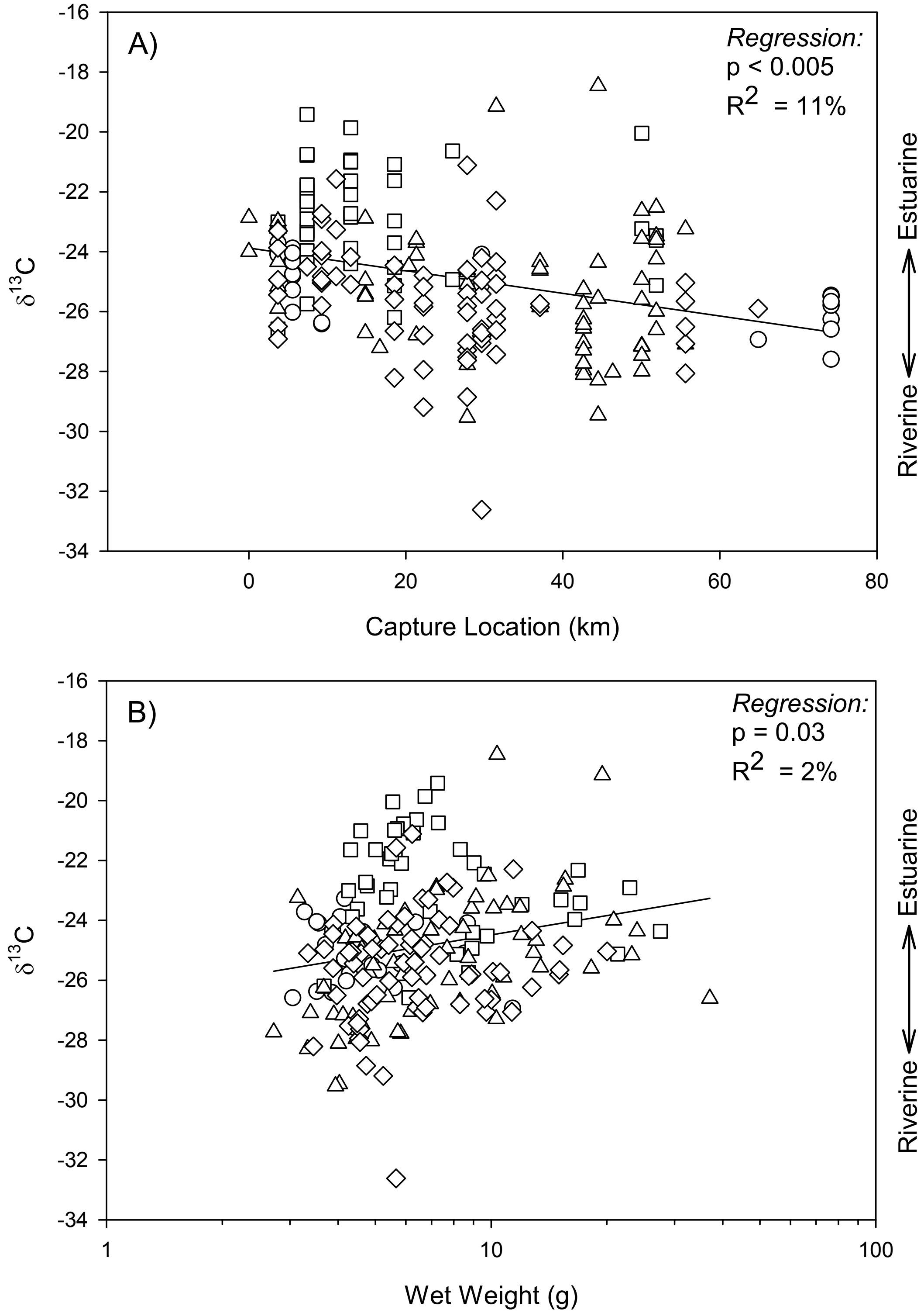

Figure 5. Variation in tissue $\delta^{13}C$ of juvenile American shad captured in the York and Pamunkey Rivers during the winter (Nov. – Mar.) versus capture location (A; mouth of York River is km 0, mouth of Pamunkey River is km 52) and wet weight (B). Juveniles are represented from numerous year-classes: 2000 (circle), 2002 (square), 2003 (triangle) and 2004 (diamond). Total number of fish sampled was 197.

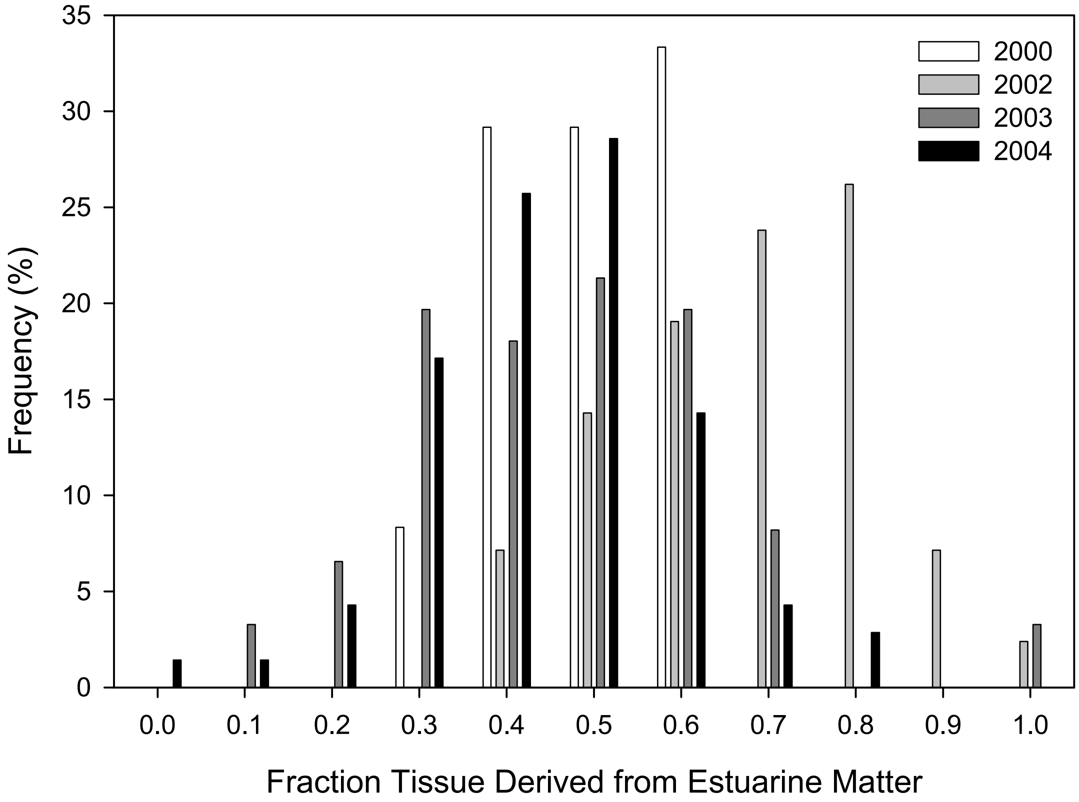

Figure 6. Fraction of tissue derived from estuarine versus riverine habitat based the on two-end member mixing model for juvenile American shad from four different year-classes that were captured in the York River estuary. The respective end-members were -30.4‰ $\delta^{13}C$ (riverine), based on the population mean of juveniles captured in 2002 in the central tidal freshwater, and -18.3‰ (estuarine), based on the average isotopic composition of larval Sciaenids and *Neomsysis americana* captured in the York River estuary.

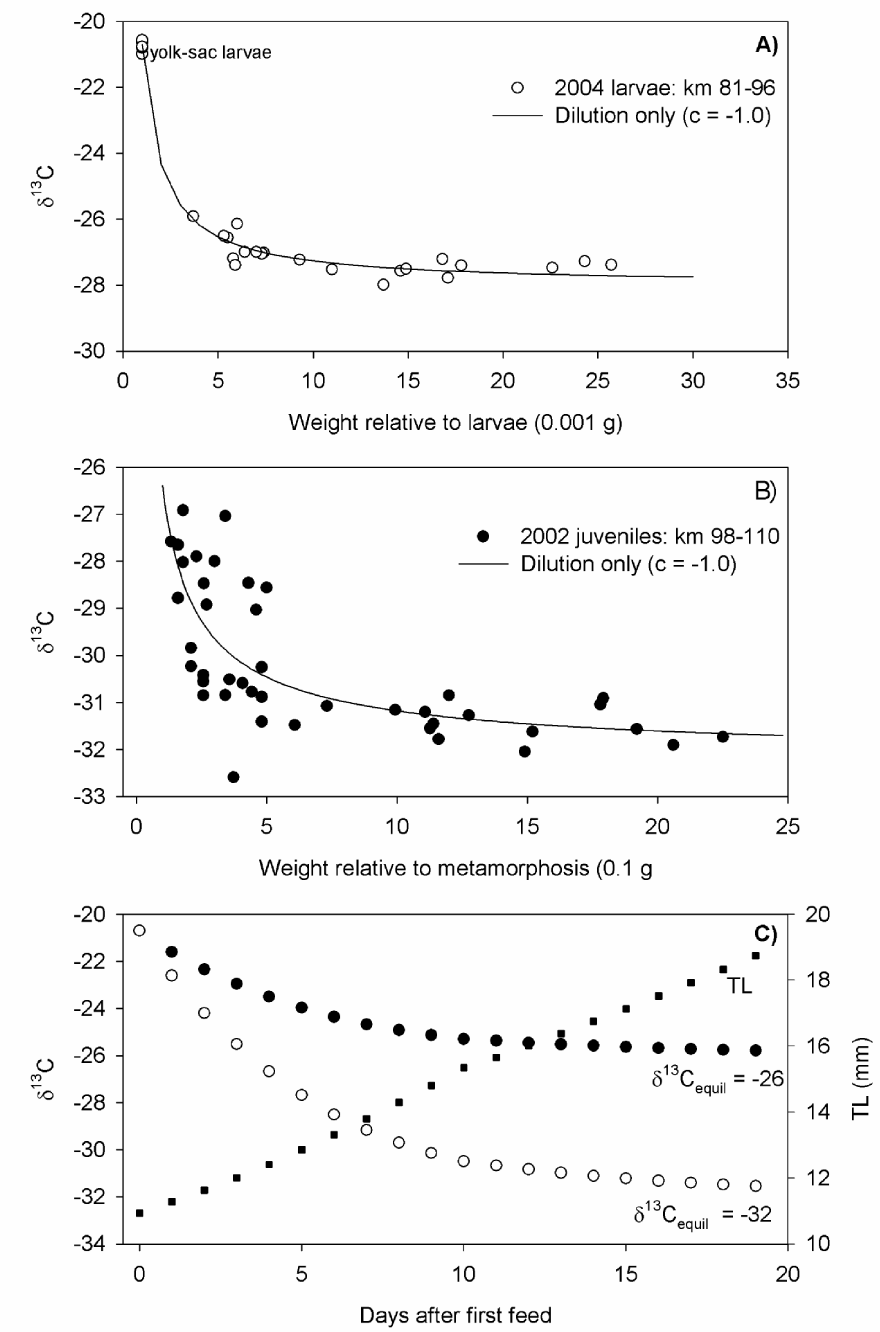

Figure 7. Modeled and simulated turnover of young-of-year American shad in the Mattaponi River, VA. Turnover of larvae (A) and juveniles (B) was fit using a power function ($\delta^{13}C = \delta^{13}C_{equil} + (\delta^{13}C_{init} - \delta^{13}C_{equil}) * W_r^C$, where $W_r = W_f / W_i$ and W is weight for initial [init, i] and final [f], or equilibrium [equil], sampling). When $c = -1.0$, growth dominates turnover. For larvae, $c = -1.1$ (SE = 0.1). For juveniles, $c = 0.7$ (SE = 0.4). Turnover of first-feeding larvae (C) was simulated using an exponential growth function ($\delta^{13}C = \delta^{13}C_{equil} + (\delta^{13}C_{init} - \delta^{13}C_{equil}) * e^{-(k+m)t}$) in which isotope composition is a function of growth (k) and metabolism (m). Larvae were simulated using a previous estimate of the stage-specific G (k) for American shad, assuming $m = 0$ and $\delta^{13}C_{init} = -20.7‰$, the average of five composite samples of yolk-sac stage larvae sampled from the Harrison Lake hatchery.

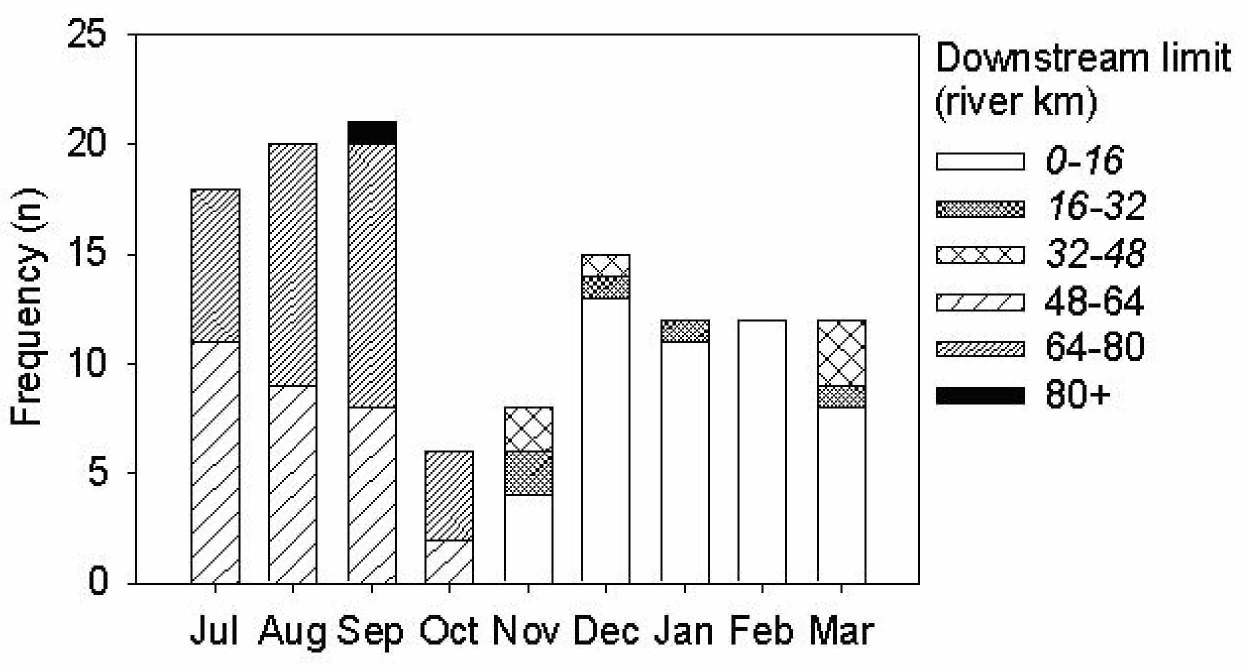

Figure 8. Location of the downriver limit where juvenile American shad were captured in the Mattaponi and York Rivers by month for twenty-one years of catch data during 1968-2001. Italicized notation in the legend indicates regions of brackish water, where river kilometer 0 is the mouth of the York River and river km 52 is the mouth of the Mattaponi River.

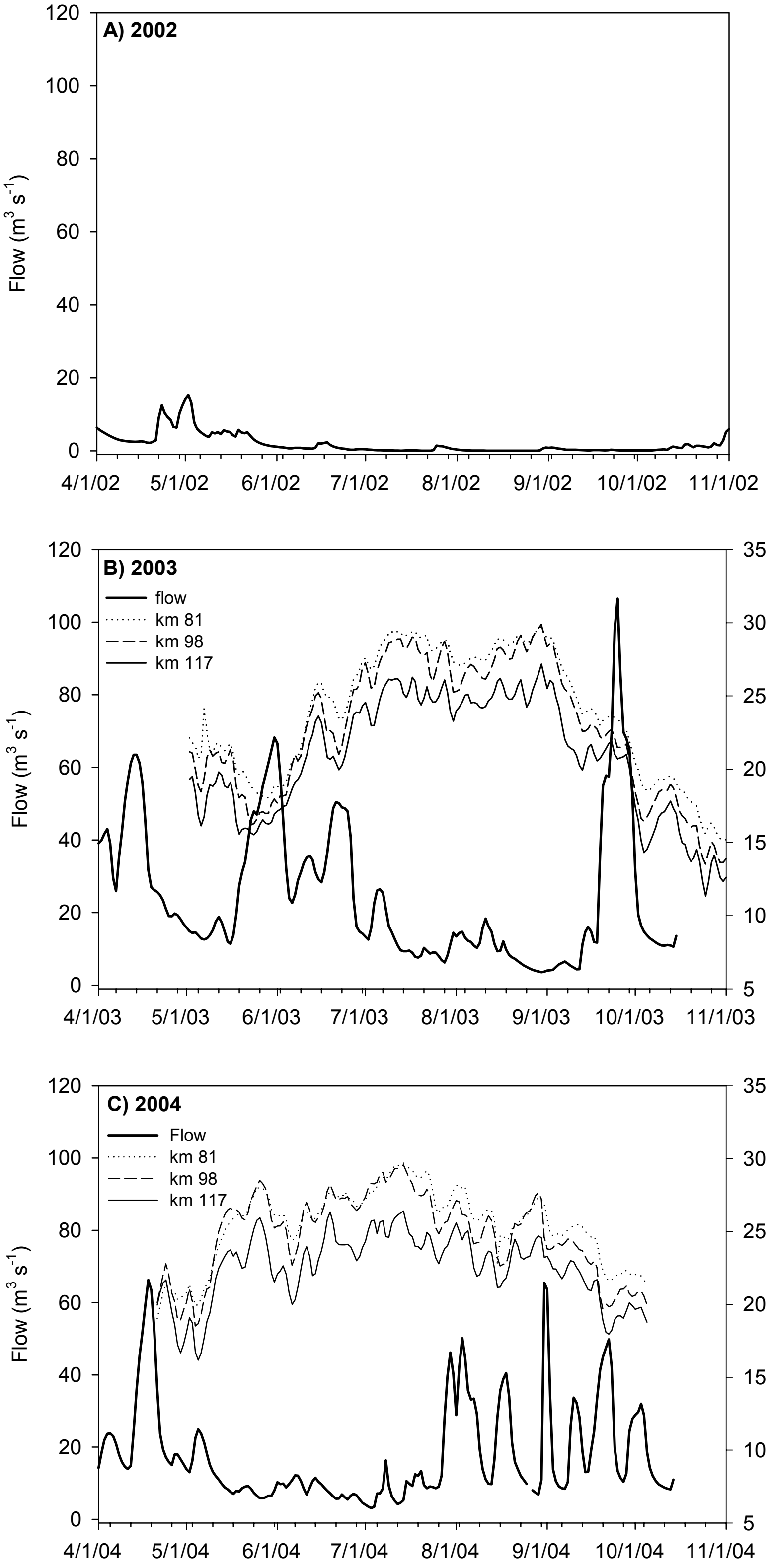

Figure 9. Seasonal variation in river flow and temperature at the lower, central and upper tidal freshwater regions of the Mattaponi River in 2002 (A), 2003 (B) and 2004 (C).

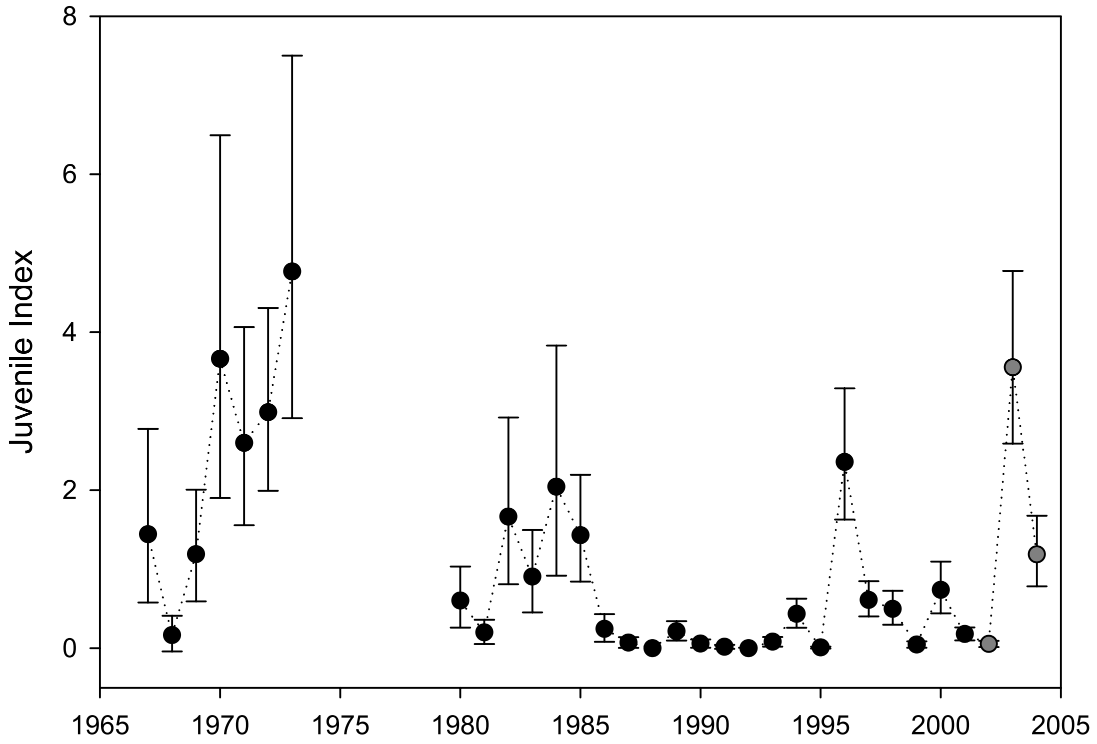

Figure 10. Catch index of juvenile American shad caught by the VIMS Striped Bass Beach Seine survey in the James, York and Rappahannock rivers. Gray color indicates years included in this study.

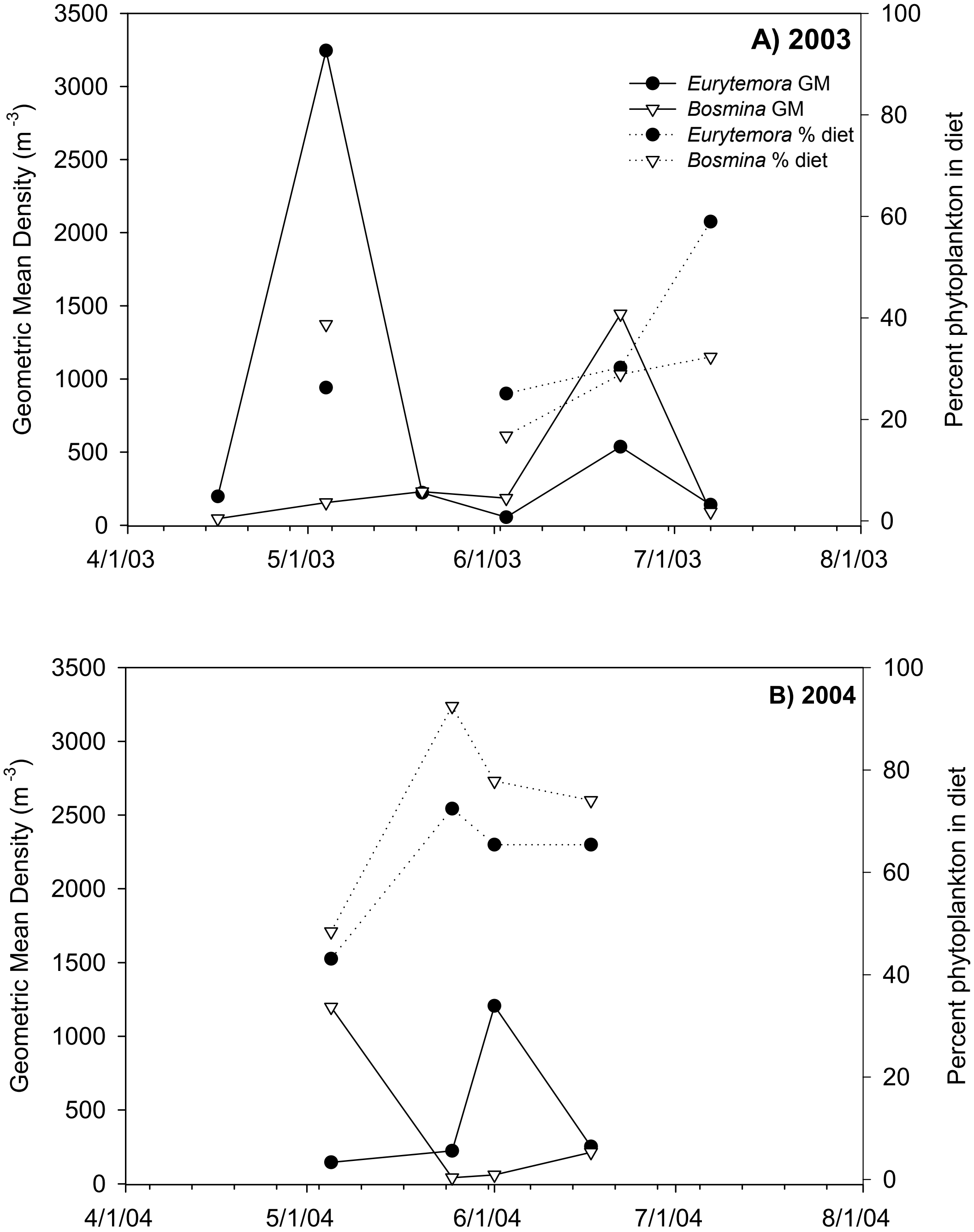

Figure 11. Mattaponi River zooplankton abundance (*Eurytemora affinis*, *Bosmina sp.*) and percent of the zooplankton diet derived from phytoplankton versus terrestrial matter. Abundance is presented as the geometric mean and percent diet was estimated as the arithmetic mean of all the stations for which estimates were available on each date.