

DIEL AND SITE-SPECIFIC FEEDING OF YOUNG STRIPED BASS IN A
HETEROGENEOUS NURSERY HABITAT

A Thesis

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
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ABSTRACT

The Chesapeake Bay spawning stock of striped bass, *Morone saxatilis*, is considered one of the largest sources of juvenile production along the Atlantic coast and exhibits a high degree of interannual recruitment variability. Year class strength is judged by near-shore seine surveys that cover major tributaries of Chesapeake Bay and survey results are incorporated into annual stock assessments. In these surveys, the contribution of the Rappahannock River (Virginia) to total production is significant. In this system, abundance of juveniles is highest at a single seine site, suggesting that juvenile production may be related to habitat heterogeneity and food availability. To evaluate this possibility, we describe daily variability in prey consumption, prey composition, and prey selection of juvenile striped bass at the productive site (RK 89) and habitat-specific patterns in feeding along an estuarine gradient that included the productive site. I examined diets of juvenile striped bass collected in five 24-h seine surveys at RK 89 in 1983 and conducted seine hauls at four stations (RK 89, RK 81, RK 71 and RK 60) in 2004. During 24-hr sampling, more fish were caught at 1800 hours and 2100 hours than at other times. In 2004, significantly more fish were caught at RK 89 than at RK 60. Fish were significantly less full at 0300, 0600 and 0000 hours than at all other times. Prey with the highest Index of Relative Importance values were dipteran larvae, calanoid copepods and polychaetes, ranking 1-3 respectively in both years. Peak mean density of *Bosmina*, other cladocerans, calanoid copepods, and dipteran larvae occurred at RK 89. However, fish were fuller at RK 60 than at RK 89. YOY striped bass showed some indications of selective feeding. As young striped bass grow in the Rappahannock River, they gradually disperse from natal areas into heterogeneous nursery habitats downriver. This ontogeny is reflected in diets as smaller fishes upriver fed on many individuals of smaller plankton prey (especially calanoid copepods) and were less full than cohorts downriver that consumed fewer individuals of larger benthic prey (especially polychaetes).

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Introduction

Striped bass, *Morone saxatilis*, is a popular recreational and valuable commercial fish in Chesapeake Bay (Richards and Rago 1999). Adults occur along the East Coast from the St. Lawrence River to the St. Johns, Florida, and seasonally use Chesapeake Bay for feeding and spawning (Setzler-Hamilton 1981; Grant and Olney 1991; Bilkovic et al. 2002; Walter and Austin 2003). Larvae and young (up to approximately age 2) remain principally in the estuary for feeding and growth (Nichols and Miller 1967). Although the contribution of these cohorts to the Atlantic coastal stock varies with the recruitment success of each year class (Dorazio et al. 1994), the Chesapeake Bay spawning stock is considered to be one of the largest sources of juvenile production for the species (Merriman 1941; Kohlenstein 1981). Striped bass in Chesapeake Bay exhibit a high degree of interannual recruitment variability (Austin et al. 2005; Bilkovic et al. 2002). Catches of juveniles are usually highest in near-shore collections (Shuster 1959; Boynton et al. 1977) and relative year class strength (abundance of age-0 fish) is judged by shallow-water seine surveys that cover major tributaries of Chesapeake Bay in Virginia and Maryland. Survey results are incorporated into annual stock assessments by the Atlantic States Marine Fisheries Commission (Goodyear 1985; Rago et al. 1995; ASMFC 2005).

Complex interactions of physical and biological factors regulate striped bass growth and survival in the first years of life (Ulanowicz and Polgar 1980; Setzler et al. 1980). Although unable to tolerate drops in temperature below 12° C (Kernehan et al. 1981; Uphoff 1989), striped bass are similar to other estuarine species in their ability to survive in highly variable conditions. Optimal environmental conditions are water temperatures below 25°C and dissolved oxygen (D.O.) above 2-3 mg/L (Coutant et al. 1984). Growth rates for young-of-the-year (YOY) striped bass are highest at temperatures of 24-26°C (Coutant et al. 1984) and higher at a salinity of 7 ppt than at 0.5 or 15 ppt (Secor et al. 2000).

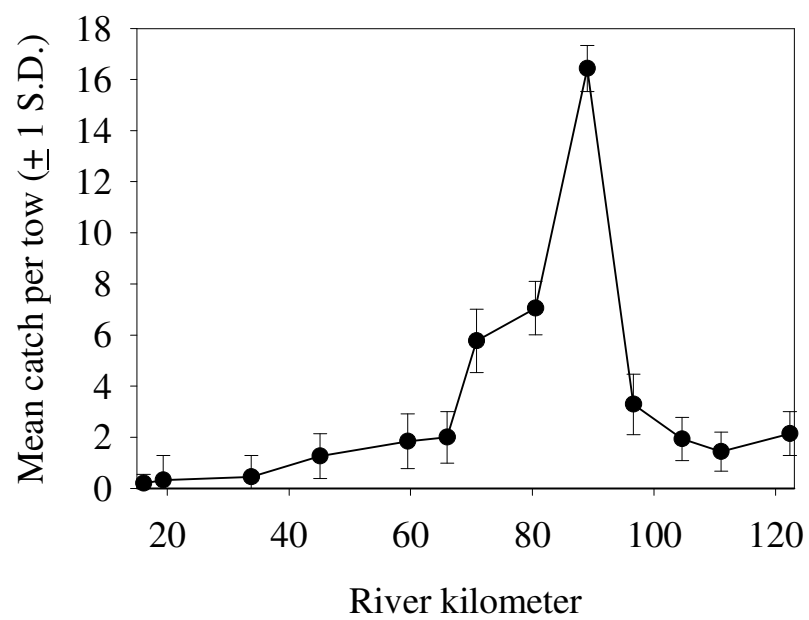
Growth and mortality rates of striped bass vary with age and these dynamics affect the success of a year class (Setzler et al. 1980; Houde 1997). Mortality at the egg and larval stages usually exceeds growth. By the juvenile stage, cohort growth rate (G) can exceed mortality (M) (Houde 1997). The timing of this shift, i.e. when $(M/G) < 1$, is strongly correlated with year class success (Rutherford and Houde 1995). High growth rates result from salubrious environmental conditions and high food availability, and contribute to lower mortality due to predation (Cushing 1975; Leggett and Dublois 1994; Houde 1997).

Diets of YOY and juvenile striped bass vary over different habitats, salinities, time and fish size (Heubach et al. 1963; Markle and Grant 1970; Boynton et al. 1977). Insect larvae and pupae, amphipods, mysids, cladocerans, copepods, benthic polychaetes and fish are consumed by juvenile striped bass in the Potomac and James rivers (Markle and Grant 1970; Boynton et al. 1981; Hartman and Brandt 1995; Ruddershausen and Loesch 2000). Striped bass may exhibit a feeding shift to larger

prey items with an increase in length (Harper et al. 1968; Cooper et al. 1998). However, Boynton et al. (1981) noted no major differences in food habits in fish between 25 and 100mm, and characterized juvenile striped bass as “flexible, non-selective feeders.” At salinities of 0-5 ppt, guts of fish collected near shore were significantly fuller than those captured offshore (Boynton et al. 1977).

In Virginia, the contribution of the Rappahannock River to total striped bass juvenile production usually exceeds that of the York River and occasionally exceeds abundance in the James River (Austin et al. 2005). Abundance of juveniles on the Rappahannock River is highest at a single seine site (river kilometer 89 or RK 89) in a transect of 15 seine stations extending along a 100-km reach. Historical catches at RK 89 were 2- to 7-fold higher than adjacent sites in 1986-2005 (Figure 1), suggesting that juvenile production may be related to habitat heterogeneity and food availability. To evaluate this possibility, we designed a study to describe daily variability in prey consumption, prey composition, and prey selection of juvenile striped bass at the productive site (RK 89) and habitat-specific patterns in feeding along an estuarine gradient that included the productive site.

Figure 1. Geometric mean catch per tow for Virginia Institute of Marine Science juvenile striped bass seine survey stations on Rappahannock River, VA. Mean values from 1986-2005.

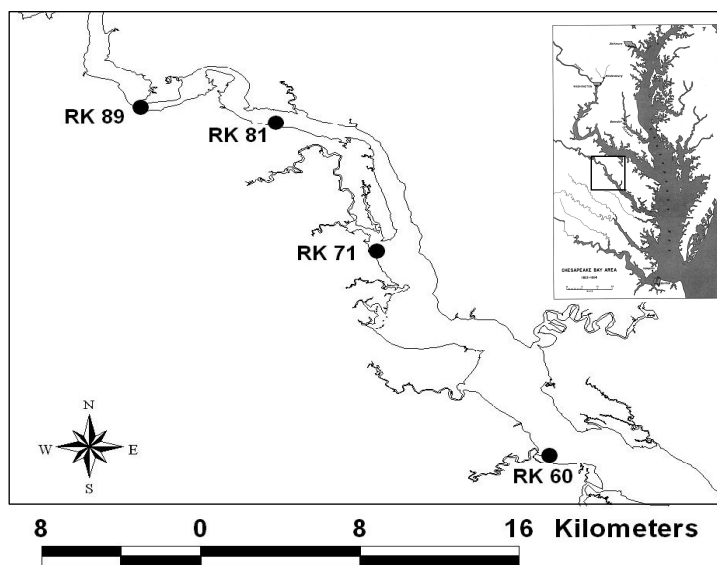


Methods

Study Locations

Sampling occurred along a 29-km reach of the Rappahannock River (Virginia) in 2003 and 2004 at four locations that included the site of high juvenile catch rates (Figure 2). All stations were below the head of tide with an average tidal range of 0.5 meters. Salinity historically varied longitudinally from approximately 5 ppt at RK 60, to 0 ppt at RK 89 (Austin et al. 2005). These salinity data and previous suspended sediment mapping (Nichols and Poor 1967) indicate that some sampling locations (RK 71, 81 and 89) were within the zone of estuarine turbidity maximum, ETM. High suspended sediments (Nichols and Poor 1967) and zooplankton concentration (Roman et al. 2001) have been documented along the bottom at or above the salt wedge (1.0 isohaline) in the ETM. All seine collections were made at depths of approximately 1 m. Stations at river kilometers 60, 71 and 81 had wide shoals (1.0 m average depth) extending more than thirty meters towards the channel. The shoal at station RK 89 was narrow, extending approximately eleven meters towards the channel. Shoreline sediments at RK 60 and RK 71 were sand to mud with increasing depth, while sediments at RK 81 and RK 89 were sand dominated. No submerged vegetation was present at any station. Private piers that extended to the channel were located approximately 40 yards downstream of RK 81 and 25 yards downstream of RK 89.

Figure 2. Map of the sampling station for 2003-- river kilometer (RK) 89, and stations for 2004-- river kilometers 60, 71, 81 and 89 of the Rappahannock River, Virginia. Inset of Chesapeake Bay.



Field and Laboratory Analyses

To describe feeding behavior, we examined diets of juvenile striped bass collected in five 24-h seine surveys (one haul every three hours for a total of eight samples) with a 30.5 m bagless seine at the productive site (RK 89) (Figure 2). Surveys occurred at approximately two-week intervals from the end of June through August of 2003. To evaluate habitat-specific patterns, we conducted seine hauls in 2004 at four stations (RK 89, RK 81, RK 71 and RK 60), sampling at maximum ebb current. To expedite synoptic sampling, seining occurred in early to late afternoon utilizing two boat crews. Each station was sampled once in rapid succession following the up-river progression of afternoon ebb tide. One sampling crew started seining at the lower-most station (RK 60) and the other crew started later at RK 81. This method was repeated five times at two-week intervals during the period of late June through August. One additional seine haul was added if a minimum number of 10 striped bass was not caught in the first haul.

Plankton samples were obtained using a hand-towed epi-benthic sled. The sled was a half-ellipse shaped metal frame mounted on runners and fitted with a plankton net (300 μ m mesh, mouth opening 30.5 cm x 36.8 cm x 91.4 cm) and a flowmeter to estimate volume filtered over a 20-meter tow distance. Two sled samples were taken at three-hour time intervals (2003 study) and at each location (2004 study). Samples were also taken with a hand-towed neuston net. These samples are not discussed but results of neuston and benthic tows are given in the Appendices. Cod end contents were preserved with 10% buffered Formalin. At each

time period or location, water temperature, salinity, pH and dissolved oxygen were recorded using a Hydrolab[®].

All juvenile striped bass were measured to the nearest millimeter. Those specimens 30-90 mm fork length (FL), were preserved in 10% buffered Formalin. Fish below this range were not fully recruited to the gear and growth rate studies in the Rappahannock showed that fish above this size may be age-one (Kline 1990). Randomly selected individuals within one standard deviation (SD) above and below the modal fish length per survey (per sampling date) were included for gut content examination in 2003. Up to twenty fish were analyzed per time block per day. All fish within the size range were analyzed in 2004 because fewer specimens were captured.

Fish stomachs were removed in the lab, transferred into 70% ethanol, and dissected. Stomach contents were identified to the lowest possible taxon, sorted, enumerated, dried at 50° C for 72 hrs and weighed to the nearest 0.01 mg. The dry fish weight, including the emptied stomach, was measured. Weight estimates per individual prey item were made by pooling individuals to determine an average weight per individual. When the total weight of a prey taxon from a single gut equaled less than 0.2 mg, the pooled weight estimates were used for subsequent analysis rather than direct measured weight. Aliquots (usually 1/32 or 1/64) of whole plankton samples were examined under a stereomicroscope. Only those taxa that appeared in stomachs were enumerated. Counts were expanded by aliquot size and tow volume to determine density (number/m³).

Statistical Analysis

Stomach fullness was indexed as the ratio of stomach content dry weight to body dry weight multiplied by 100 for each individual (Index of Relative Fullness, IRF; Hyslop 1980). One-way ANOVA was performed on 2003 fullness data (transformed to the power 0.25) by time interval with multiple comparisons Tukey tests. Transformation of 2004 fullness data did not satisfy the assumption of homogeneity of variances. Therefore, a Kruskal-Wallis test was performed by location followed by multiple comparison Dunn's tests. In these analyses, we used predicted tidal stage data (Tides and Currents 2.0) since no current measurements were available.

An Index of Relative Importance (IRI) was estimated for each prey type per time period in 2003 and per location in 2004 (Pinkas et. al. 1971). The formula is $IRI = (\%N + \%W) * \%F$, where N is number of prey type A encountered in all guts, W is total weight of prey type A in all guts, and F is frequency of occurrence, or number of stomachs containing prey type A. The formula is modified by Cortes (1997) as $\%IRI = (IRI_A / \sum(IRI_{A1-A\infty})) * 100$. A modified $\%IRI$ value was calculated for each prey type and time (or location) combination to serve as a comparable value for other studies.

One-way MANOVA was applied to the $\%IRI$ data to test for differences between fish size classes, tide stages and time intervals for the most important prey items of the 2003 data, and between fish size classes and locations for the 2004 data. To facilitate inter-annual comparison, $\%IRI$ values for *Bosmina freyi* (hereafter referred to as *Bosmina*), and fish scales were tested both years. Since data were not normally distributed, the $\%IRI$ data were transformed to the power of 0.35, which produced the most normal distribution and was a better fit than the recommended

arcsin squareroot transform (Zar 1999). Correspondence analysis was used to evaluate patterns in the %IRI and %W data for important prey items and locations. ANOVAs were performed to test differences in fish length by time interval and location.

Selectivity indices were not calculated because relative prey availability in the environment could not be determined for all taxa. To qualitatively evaluate prey selection, proportions of a prey type in the environment and its proportion found in guts were plotted for four important prey types by sampling date and river kilometer for the 2004 study.

Results

We collected 2107 juvenile striped bass (2003, n= 1685; 2004, n= 422).

Surface water temperatures in 2003 were 24.3 to 33.3° C, dissolved oxygen values were 5.8-8.5 mg/l, and pH values were 7.1-8.3 (Table 1). In 2004 water temperatures were 24.5 to 31.3° C, dissolved oxygen values were 3.4-9.4 mg/l and pH values were not available. Salinities by location were RK 60: 1.4-3.5ppt, RK 71: 0.1-0.4ppt, RK 81: 0.1-1.0ppt, and RK 89: 0-0.1ppt.

Lengths of fish in seine hauls were 36-74 mm FL and increased over the sampling period (Table 1). In 2003, fish were significantly larger at 0000 and 0300 hours than at 1200 hours ($p = 0.009$, $df = 7$; Table 2). In 2004, fish were significantly larger at river RK 60 than at RK 71 ($p = 0.009$, $df = 3$; Table 2). Fish length was not related to tidal stage ($p = 0.121$). During 24-hr sampling, more fish were caught at 1800 hours and 2100 hours than at other times (1800, n=364; 2100, n=359; 0000, n=244; 0300, n=139; 0600, n=123; 0900, n=169; 1200, n=125; 1500, n=162). In 2004, significantly more fish were caught at RK 89 (n=234) than at RK 60 (n=32; $p = 0.041$, $df = 3$).

Fish analyzed for gut contents totaled 619 in 2003 and 352 in 2004. Fish with empty stomachs totaled 29 and 12, respectively. Fish with the highest numbers of prey in their guts were generally between 43 and 60 mm, with numbers of prey per individual dropping sharply at larger sizes (Figure 3).

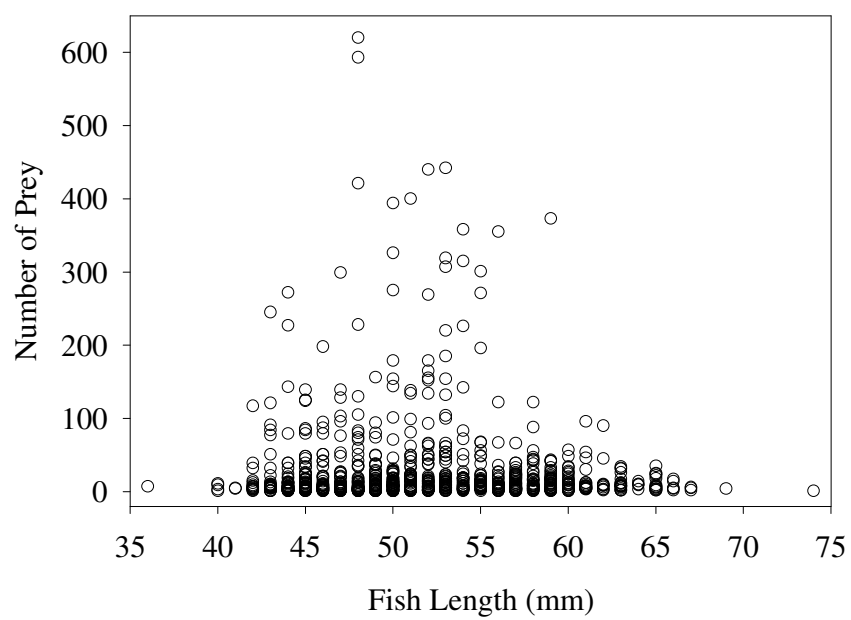
Table 1. Summary of collections fish size and environmental data. Environmental values are daily averages. 2003 values are from RK 89 and 2004 values are averaged across all stations.

Date	Temp. (°C)	D.O. (mg/L)	Salinity (ppt)	pH	Total Fish	Modal fish length (mm)	Fish length range (mm)
6/26/2003	25.8	7.5	0.0	7.1	378	45	(42 - 48)
7/10/2003	29.1	8.5	0.1	7.8	484	48	(43 - 53)
7/24/2003	29.1	8.1	0.1	8.3	511	54	(49 - 59)
8/14/2003	29.3	8.2	0.0	8.0	223	57	(49 - 67)
8/21/2003	29.7	7.8	0.1	8.3	89	59	(51 - 67)
6/28/2004	28.6	8.3	1.1	-	180	48	(36 - 55)
7/12/2004	30.6	7.9	1.0	-	111	52	(40 - 63)
7/26/2004	25.9	7.2	0.5	-	69	59	(48 - 65)
8/9/2004	30.0	7.2	0.4	-	32	57	(46 - 65)
8/24/2004	29.3	5.8	0.6	-	30	56	(53 - 74)

Table 2. Results of statistical tests performed for fish abundance, length, and fullness, %IRI and each of its components. All tests by time are from 2003 and all tests by location are from 2004. *Significance at the $p = 0.05$ level. Parametric multiple comparisons used post-hoc Tukey test; non-parametric used Dunn's test. Size classes are A: 42-50 mm, B: 51-59 mm, and C: 60-69 mm.

Data type	Statistical test	Factors	df	P-value	Multiple Comparison
Fish Abundance					
	ANOVA	time	7	0.31	
	Kruskal-Wallis	location	3	0.041*	RK 60< RK 89
Fish Length					
	ANOVA	time	7	0.009*	1200< 0000, 0300
	ANOVA	location	3	0.009*	RK 71< RK 60
	ANOVA	tidal stage	3	0.121	
Fish Fullness					
	ANOVA	time	7	<0.001*	0300, 0600, 0000< 0900, 1800, 1200, 1500, 2100
	Kruskal-Wallis	location	3	<0.001*	RK 81,89< 60; 89< 71,81
	ANOVA	tidal stage	3	0.495	
Index of Relative Importance (%IRI)					
	MANOVA	time	7	0.052*	calanoid copepods- not distinct dipteran larvae- 0000< 0900 scales- 1500, 1200< 0300, 0600; 1500< 0300
	MANOVA	location	3	0.001*	calanoid copepods- RK 60,71,81< 89 dipteran larvae- RK 60< 71,81,89 dipteran pupae- RK 60< 71,81
	MANOVA	size class (2003)	2	0.003*	calanoid copepods- class C< class A dipteran pupae- class A< class B, class C
	MANOVA	size class (2004)	2	0.75	
	MANOVA	tidal stage	3	0.771	

Figure 3. Number of prey per fish by fish length (n = 906 fish).



Diel changes in gut fullness were significant with significantly less full at 0300, 0600 and 0000 hours than at all other times ($p < 0.001$, $df = 7$; Table 2). The 2003 transformed fullness data were fitted to a sine-cosine curve to test the hypothesis that fullness followed a diel pattern. The sine-cosine regression was as follows: $IRF = 0.64 - 0.08\cos(t) - 0.12\sin(t) - 0.05\sin(2t)$ (Figure 4a). Fish were most full between 1200 and 2100 hours and least full at 0300 and 0600 hrs ($p < 0.05$; t -values for the parameters were 62.9, -5.5, -8.5, and -3.4, respectively). Tidal stage, however, did not affect average fish fullness in 2003 (ANOVA, $p < 0.05$).

Fish fullness was significantly different by location ($p < 0.001$, $df = 3$; Table 2). Fish at RK 60 were fuller than fish at RK 81 and RK 89, and fish at RK 71 and RK 81 were fuller than those at RK 89. The 2004 transformed fullness data were assessed for fit to a linear regression as the data appeared to follow a linear pattern between locations. The linear model for 2004 was $IRF = -0.014x + 0.846$ (Figure 4b). The model shows a significant negative linear relationship (t values = 25.9 and -6.2, respectively).

A cumulative prey curve of 2003 data approached an asymptote of about 22 prey taxa at a sample size (>500 individuals) that exceeded the number of fish captured in any tow (Figure 5). Twenty-four total prey types were identified in both studies; mysids and juvenile mummichogs (*Fundulus* sp.) were found in guts only in 2004 (Table 3). Most frequently occurring prey included calanoid copepods (Order Calanoida) and the fly larvae (Order Diptera). Fish scales were analyzed as prey in this study because of their frequency in fish guts and because it could not be determined if they were intentionally eaten.

Figure 4a-b. a. Regression (diamond) of sine-cosine model against Index of Relative Fullness values for all fish (2003). b. Regression (diamond) of negative linear model against Index of Relative Fullness values for all fish (2004).

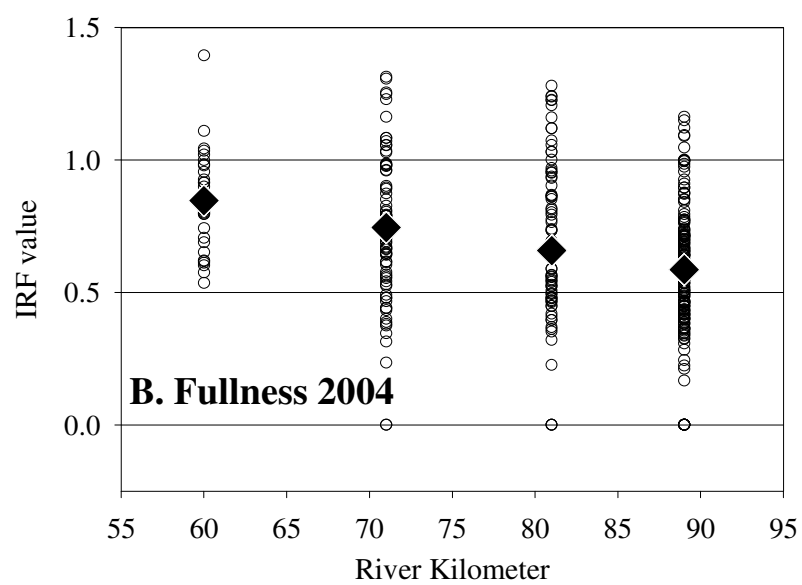
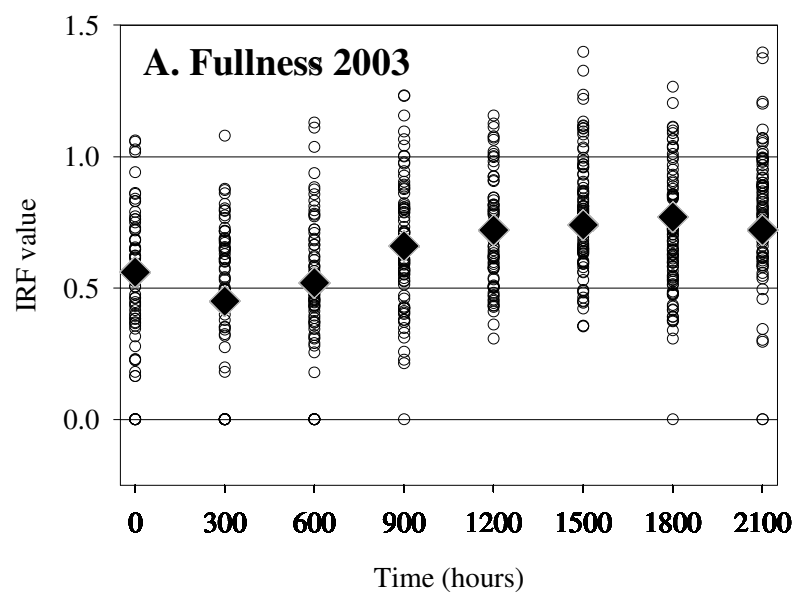


Figure 5. Cumulative prey curve for all analyzed fish in 2003.

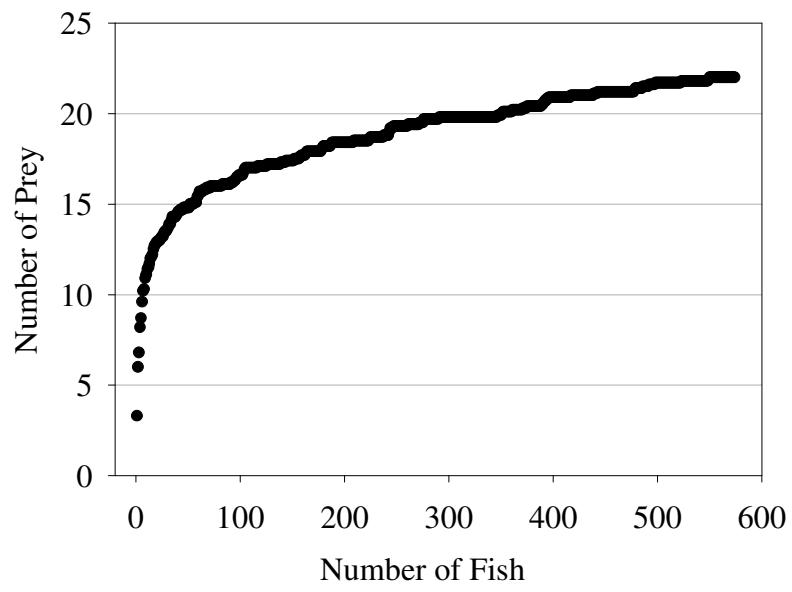


Table 3. List of prey eaten by striped bass in 2003 and 2004. Molluscs, *Neomysis americana* and juvenile *Fundulus* sp. seen only in 2004.

Phylum	Taxon	Common Name	
Nematoda	unknown	oligochaetes	
Annelida	family Spionidae	polychaetes	
Arthropoda	class Arachnida	mites	
	subclass Ostracoda	ostracods	
	order Cladocera, <i>Bosmina freyii</i>	bosmina	
	order Cladocera, family Daphnidae, <i>Diaphanosoma brachyurum</i> , <i>Leptodora kindtii</i>	other cladocerans	
	order Calanoida, <i>Eurytemora affinis</i>	calanoid copepods	
	family Cyclopoidae	cyclopoid copepods	
	order Harpacticoida	harpacticoid copepods	
	subclass Branchiura, genus <i>Argulus</i>	fish lice	
	family Ergasilidae	parasitic copepods	
	family Palaemonidae, <i>Neomysis americana</i>	shrimps	
	order Cumacea	cumaceans	
	family Anthuridae	isopods	
	suborder Gammaridea	amphipods	
	order Decapoda	mud crabs	
	genus <i>Chironomus</i> , genus <i>Chaoborus</i>	dipteran larvae	
	genus <i>Chironomus</i>	dipteran pupae	
	class Insecta, order Hemiptera	other insects	
	Mollusca	class Bivalvia, class Gastropoda	molluscs
	Chordata	unknown	fish eggs
		family Ichthaluridae	fish larvae
genus <i>Fundulus</i>		fish juveniles	
	unknown	fish scales	

In both years, %IRI values of dipteran larvae, calanoid copepods and polychaetes were highest, ranking 1-3 respectively (Table 4). These taxa were followed in importance by fish scales and dipteran pupae in 2003, and by *Bosmina* and dipteran pupae in 2004. The five most important prey items made up 77.2% and 92.3% of the total IRI in each year, respectively (Table 3).

There were significant differences in %IRI values for calanoid copepods, dipteran larvae and fish scales between time intervals ($p = 0.052$, $df = 7$; Table 2). Dipteran larvae had significantly higher values at 0900 hrs than at 0000 hrs (Table 2). Scales had significantly higher values at 0300 than at 1500 hrs and values at 0600 hrs were higher than at 1200 and 1500 hrs.

There were highly significant differences in %IRI values by fish size class ($p = 0.003$, $df = 2$; Table 2). The calanoid copepod prey category was significantly more important to smaller fish (42-50mm, class A) than to large fish (60-69mm, class C). Dipteran pupae were significantly more important to classes B and C than to class A. Results of MANOVA tests for differences in %IRI and its components by tidal stage in 2003 were not significant.

Values of %IRI for dipteran larvae and pupae varied significantly by location ($p = 0.001$, $df = 3$; Table 2). Calanoid copepod %IRI values were significantly higher at RK 89 than at kilometers 60, 71, and 81. Dipteran larvae values were significantly higher at kilometers 71, 81 and 89 than at RK 60. Dipteran pupae %IRI values were significantly higher at kilometers 71 and 81 than at RK 60 (Table 2). Fish in 2004 showed no significant differences in %IRI (or any of its components) by size class.

Table 4. Index of relative importance (%IRI) values for prey items making up at least 1% IRI in each year of the study. Percent frequency of occurrence (%F) of prey, and percent of prey by number (%N) and weight (%W) are given. Values separated by comma are 2003 and 2004 data, respectively. Total frequency (Freq.), number and weight (Wt.) each are combined for both years. NA = not applicable, cop. = copepods, mat. = material.

Prey	%IRI	%F	%N	%W	Freq.	Number	Wt. (mg)
Dipteran larvae	34.8, 39.0	71.4, 81.8	13.8, 16.3	17.0, 16.2	699	3961	180.5
Calanoid cop.	13.6, 34.6	36.8, 44.7	21.6, 48.9	1.8, 3.8	369	8482	27.7
Polychaetes	11.8, 6.7	24.7, 15.0	1.0, 0.5	29.2, 29.9	197	223	318.5
Scales	10.1, 1.0	32.5, 15.9	10.9, 3.1	8.8, 1.3	246	2166	65.1
Dipteran pupae	6.9, 4.6	41.7, 29.7	5.2, 3.7	5.2, 9.2	347	1260	72.0
Unknown mat.	6.2, 0.3	30.7, 7.4	0.0, 0.0	12.8, 2.5	206	NA	97.2
Bosmina	5.6, 6.3	13.6, 20.0	23.7, 20.1	2.2, 1.4	148	6030	20.6
Cladocerans	4.4, 1.1	34.6, 19.4	7.5, 3.7	0.6, 0.2	270	1651	4.6
Cyclopoid cop.	1.9, 0.0	15.1, 1.2	6.8, 0.1	1.3, 0.0	93	1169	9.0
Other copepods	1.7, 0.0	13.9, 0.9	7.0, 0.0	0.9, 0.0	85	1199	6.0
Amphipods	1.3, 0.5	11.2, 9.1	0.5, 0.5	6.6, 3.5	97	138	58.8
Insects	1.0, 2.9	9.0, 17.1	0.5, 0.7	6.3, 11.1	111	142	87.2
Shrimp	0.0, 1.0	0.0, 10.9	0.0, 1.1	0.0, 5.3	37	111	21.2

Correspondence analyses (CA) performed with six important prey items by location and %IRI values depicted a gradient of stations and food types along the axis of the first component and a separation in ordination space between the productive station (RK 89) and the most down-river station (RK 60) (Figure 6). Calanoid copepods and polychaetes were associated with stations RK 89 and RK 60, respectively. Dipteran pupae, larvae and *Bosmina* were clustered closely with RK 71 and RK 81. Fish scales occupied an intermediate position but were not closely aligned to RK 89. This pattern was maintained when CA was performed on %W (results are not shown) except that scales occupy a position closer to RK 89.

Peak mean density of *Bosmina* ($7890/m^3$), other cladocerans ($1076/m^3$), calanoid copepods ($617/m^3$), and dipteran larvae ($154/m^3$) occurred at RK 89 (Figure 7). Cruise-specific patterns varied but in general, mean density of *Bosmina*, other cladocerans and dipteran larvae generally declined downriver from RK 89 to RK 60. Calanoid copepods were occasionally more abundant at the downriver station. Polychaetes, scales and dipteran pupae were not present in sled samples.

Proportions (%N) of four prey taxa in plankton samples did not correspond to their proportions in gut contents for 2004 (Figure 8). In general, cladocerans were more abundant in the plankton than in gut contents, while calanoid copepods and dipteran larvae were more abundant in gut contents than in the plankton. Calanoid copepods comprised a higher proportion of gut contents at RK 89 than their proportion of the plankton. Similarly, proportions of consumed dipteran larvae were higher than proportions in sled samples at RK 71 and 89 (Figure 8i, k, l).

Figure 6. Correspondence analysis by location and %IRI for important prey items in 2004.

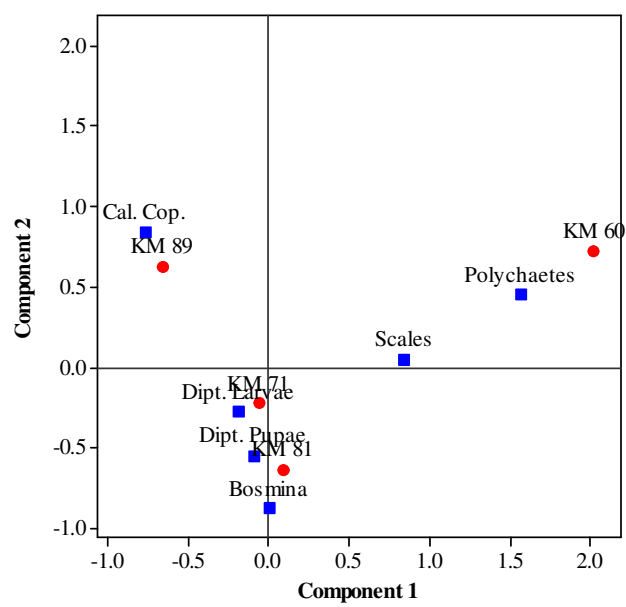


Figure 7. Absolute prey abundances of A. *Bosmina*, B. cladocerans, C. calanoid copepods, and D. dipteran larvae. Values are averages of two epi-benthic plankton tows.

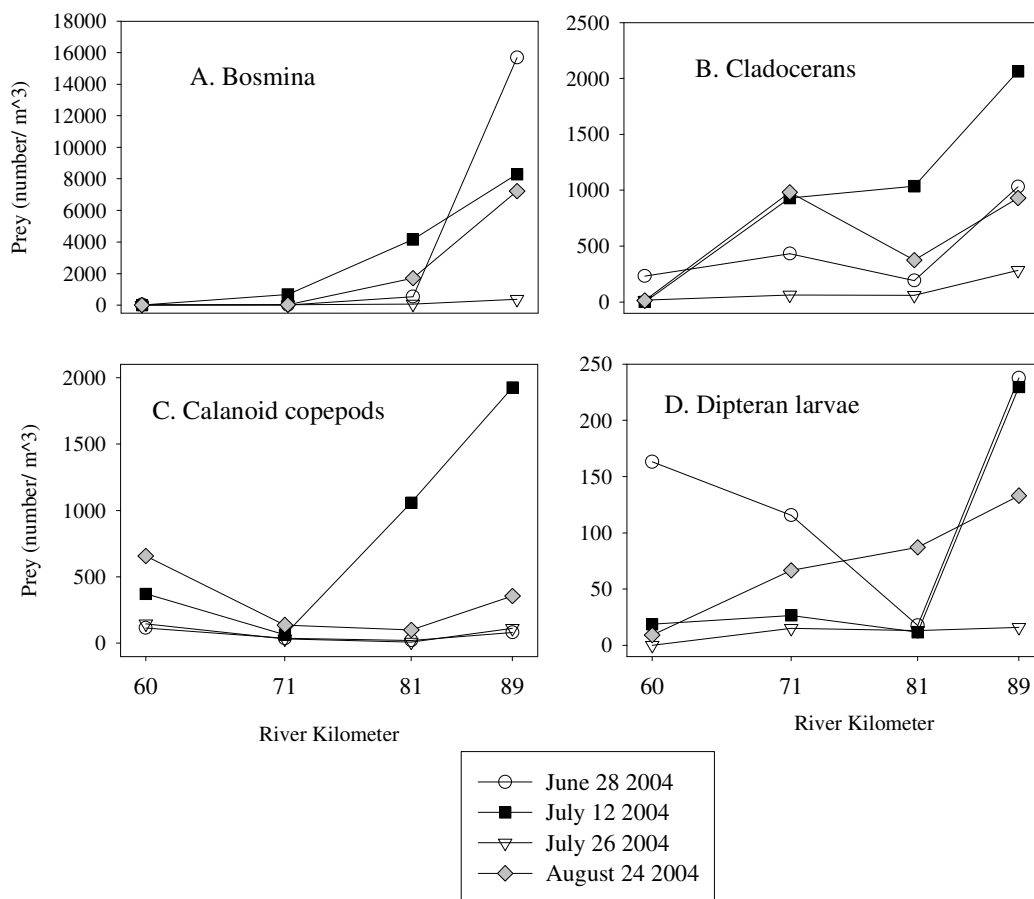
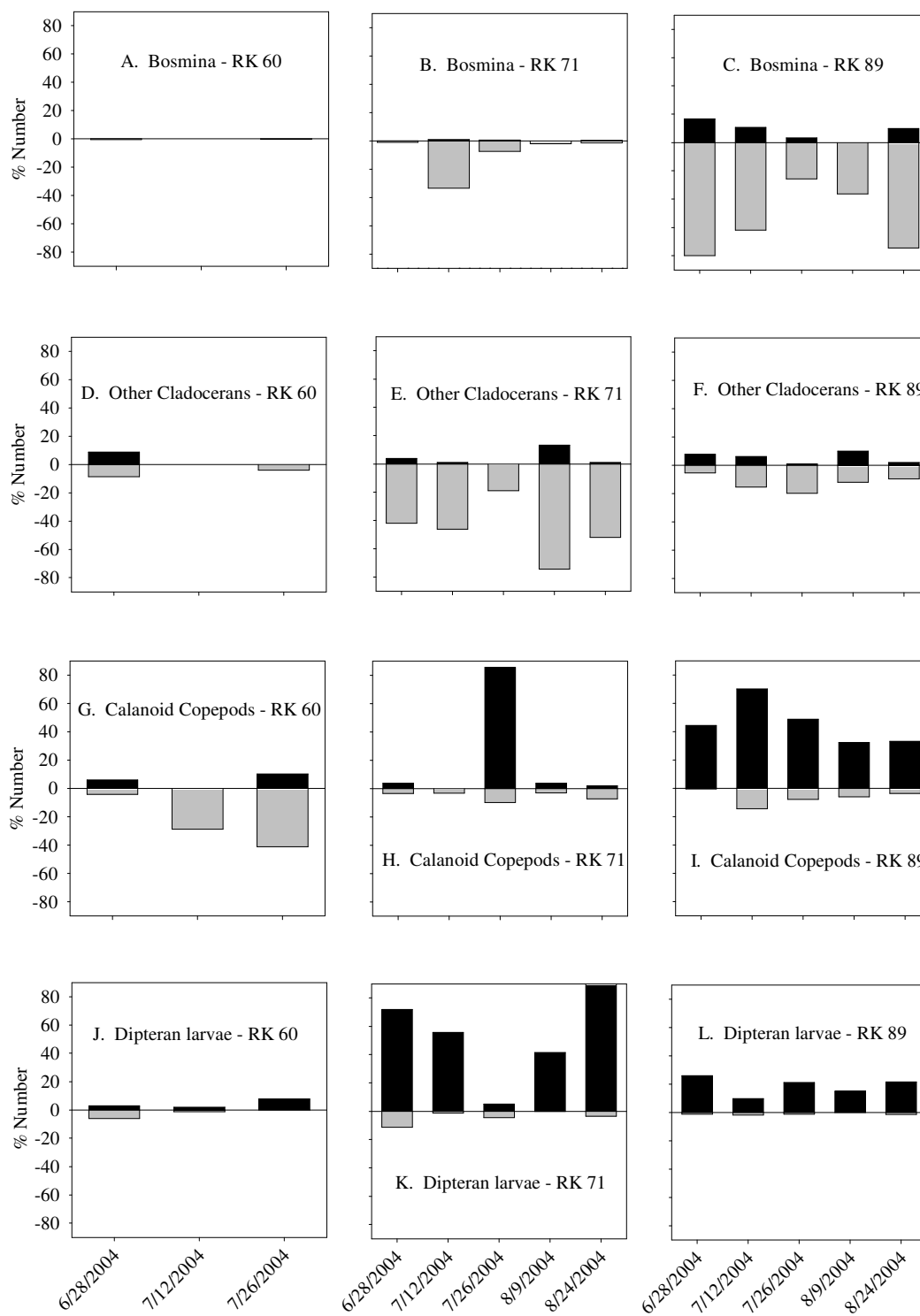


Figure 8. Proportion (% number) of prey type in epi-benthic sled samples (grey bars) and in gut contents (black bars) at three locations. RK 50 excluded due to its similarity to RK 44. Dipteran larvae were likely underestimated in epi-benthic samples.



Discussion

As young striped bass grow in the Rappahannock River, they gradually disperse from upriver natal areas into heterogeneous nursery habitats downriver. In our sample, mean fish length increased over time of sampling and mean length was largest at the most downriver location. This ontogeny is reflected in diets as smaller fishes upriver fed on many individuals of smaller plankton prey (especially calanoid copepods) and were less full than cohorts downriver that consumed fewer individuals of larger benthic prey (especially polychaetes). Along the sampled transect, diets of juveniles captured at stations that were between the upriver and downriver sites were also distinct, attesting to the diverse feeding habits and habitats of juveniles produced in the system. Similar ontogenetic and spatial patterns have been reported in other systems. A shift to larger prey with increases in fish length was reported for YOY striped bass by Harper et al. (1968) and Cooper et al. (1998). Spatial feeding variability in heterogeneous prey environments is also reported by Cooper et al. (1998) and Chick and Van Den Avyle (1999).

Peak feeding activity occurs in daylight. We observed the lowest values of the fullness index in darkness (0000-0300) and stomach fullness increased from early morning (0600) to late afternoon (1800). During hours of darkness, prey items were mostly large, including amphipods, larger cladocerans, and dipteran larvae and pupae. Copepods and smaller prey were seen less frequently in guts at those times, perhaps

due to differential digestion times, a pattern consistent with other studies of feeding by young moronids (Voigtlander and Wissing 1974). Heubach et al. (1963) found YOY striped bass digestion times for copepods and amphipods to be between six and eight hours. Light effects upon the vision of fish have also been suggested contributors to the pattern of items found in guts (Voigtlander and Wissing 1974).

Calanoid copepods were significantly more important (by %IRI) to fish 42-50 mm (class A) than to fish 60-69 mm (class C). Although size classes were associated with particular sampling dates, absolute abundances of calanoid copepods in the plankton samples remained similar throughout the sampling season. Thus, the shift in prey importance by fish size class probably reflects real ontogenetic trends in prey selection, rather than a shift in prey availability.

Juvenile striped bass may exhibit selectivity towards certain prey. Calanoid copepods and dipteran larvae were found in disproportionately high numbers in guts. Chick and Van Den Avyle (1999) also reported similar selectivity for adult copepods and insects by larval striped bass in lentic and riverine sampling. Although Nemerson and Able (2003) found young striped bass to be non-selective feeders, the fish in their study represent a larger size range of mostly age one individuals. A shift towards a more generalized feeding behavior may occur with growth.

Prey distributions differed by location and influenced feeding patterns of juvenile striped bass. Densities of *Bosmina*, other cladocerans and dipteran larvae were highest upriver and lowest downriver. These distributions were likely due to the increased salinity at RK 60 relative to other locations, in agreement with observations by Zhao (1991) and Williams and Williams (1998). Mysids and palaemonid shrimp

have been found in higher densities in increased salinity relative to freshwater (Markle and Grant 1970).

High juvenile abundance at RK 89 corresponded with the highest prey densities and may be related to the spatial and temporal dynamics of the estuarine turbidity maximum (ETM). Setzler-Hamilton et al. (1981) and Harding and Mann (2003) also found that higher striped bass larvae and juvenile abundances were correlated with high prey densities. Zooplankton retention above the region of the estuarine turbidity maximum (ETM) has been documented in Chesapeake Bay (Roman et al. 2001). Zooplankton densities, especially *Eurytemora* sp. copepods, can be an order of magnitude higher within the ETM than in nearby collections (Roman et al. 2001). Roman et al. (2001) also found that macrozooplankton was concentrated “near the bottom at the toe of the salt wedge,” but that zooplankton biomass increased in the mid and upper water column during max ebb and flood tides. Tidal currents may promote resuspension of both sediments and zooplankton (Castel and Viega 1990). Similar peak current velocities to those found by Roman et al. (2001) (60 to 80 cm/s) were predicted for our max ebb current collections (51 to 67 cm/s; Tide and Currents 2.0). Nichols and Poor (1967) found the highest suspended sediments in the Rappahannock River were upstream of RK 60 and upstream of the 6ppt isohaline. Study locations RK 71, RK 81 and RK 89 may have been within the zone of the Rappahannock River ETM during 2004, although only salinity data from the shoals were collected to delineate ETM location. Channel salinity and suspended sediment measurements would be required to definitively place the ETM and should be incorporated in future studies of this zone. Nichols and Poor (1967) observed a

lateral “intrusion of relatively salty channel water into bordering shoals” in what he termed the upper estuary (approximately upstream of RK 58). However, higher mid-channel salinities relative to the shoals’ surface (due to estuarine circulation) may indicate that the ETM was farther upstream towards RK 89.

Aggregation of zooplankton in the ETM may be less evident in nearshore shoals than in the channel, since zooplankton were found to be in highest concentration near the bottom. The study by Roman et al. (2001) was conducted in greater depths (ave. 12 m) than our study (ave. 1 m). It is possible that the narrow shelf at RK 89 (approx. 11 m) relative to the other locations (> 30 m) provided for increased proximity to the channel and to higher densities of zooplankton. Other hydrographic or habitat characteristics at RK 89 may contribute to high zooplankton densities and should be further investigated. In addition, competition by other juvenile or smaller fish species may have influenced observed patterns of feeding. White perch, *Morone americana*, shares much of the diet of YOY striped bass (Ruddershausen and Loesch 2000). White perch were especially abundant at RK 60 and relatively low in abundance at RK 89. Future studies should consider multispecies interactions.

The significant variability in juvenile striped bass abundance observed over small spatial scales in the Rappahannock River is likely due to differences in prey availability and salinity. Nemerson and Able (2003) found that high YOY striped bass catches in Delaware Bay were correlated with low salinity and were proximal to potential nursery areas. The striped bass spawning area in the Rappahannock River described by Grant and Olney (1991) encompassed RK 89; high densities of striped

bass eggs were found there. A partial explanation for abundances, therefore, may be proximity to nursery area.

Catches of juvenile striped bass were highest in evening samples and this observation is consistent with previous observations (Boynton et al. 1977). Seine hauls at RK 89 are taken consistently during late morning by the Virginia striped bass seine survey (Austin et al. 2005). Our data suggest that daylight surveys of juvenile abundance conducted by Maryland and Virginia underestimate abundance of young striped bass, especially in years of low recruitment. In these years, sampling during evening hours would likely produce higher abundance indices than daylight sampling. Regardless, stations are sampled in the same order each year by the Virginia survey (Austin et al. 2005) and the daylight index has shown meaningful relationships to stock size (Goodyear 1985) and M/G dynamics (Houde 1997). However, because the Maryland survey does not sample locations in the same order each round (Eric Durell pers. comm.), time of collection may affect abundance indices in that survey.

Appendix A. Numbers of zooplankton per m³ in neuston net samples in June 2003 (values are the average of two repeated tows). Neuston net dimensions: mesh size 300um, 35.6 cm x 17.8 cm x 121.9 cm, General Oceanic Flowmeter, 20 meter tow distance. Neuston sampling procedures same as benthic procedures for 2003.

Time interval	1800	2100	0	300	600	900	1200	1500
Date	6/26/2003	6/26/2003	6/27/2003	6/27/2003	6/27/2003	6/27/2003	6/27/2003	6/27/2003
Calanoid cop.	25.7	2601.5	1035.7	3416.3	65.2	19.2	6.1	80.8
Cyclopod cop.	13.2	1137.5	1366.1	1217.1	16.0	26.0	12.2	0.0
Harpactacoid cop.	0.6	9.5	0.0	0.0	0.0	0.0	0.0	0.0
Cop. Nauplii	12.3	29.3	25.2	39.0	14.5	14.2	0.0	0.0
Unknown cop.	9.5	95.9	58.9	60.4	11.8	19.0	6.1	12.4
Bosmina	46.2	29.3	50.5	147.6	51.8	48.1	24.4	28.0
Other cladocerans	31.6	214.4	320.1	427.1	28.5	24.4	652.4	40.4
Dipteran larvae	56.9	2.4	20.2	72.6	8.2	21.3	448.8	18.7
Ostracods	7.6	58.5	25.2	100.8	6.3	39.5	226.7	15.5
Mite/ spiders	5.1	0.0	8.4	10.7	1.1	6.0	61.3	6.2
Other insects	16.6	6.7	64.0	51.8	7.2	18.3	260.7	46.6
Larval fish	1.2	9.5	0.0	0.0	0.0	0.0	6.1	0.0
Polychaete larvae	2.6	0.0	16.8	45.7	13.2	3.8	0.0	3.1
Gastropods	0.6	0.0	18.5	5.4	0.0	1.3	0.0	3.1

Appendix B. Numbers of zooplankton per m³ in neuston net samples in August 2003 (values are the average of two repeated tows). Neuston net dimensions: mesh size 300um, 35.6 cm x 17.8 cm x 121.9 cm, General Oceanic Flowmeter, 20 meter tow distance. Neuston sampling procedures same as benthic procedures for 2003.

Time interval	1800	2100	0	300	600	900	1200	1500
Date	8/14/2003	8/14/2003	8/15/2003	8/15/2003	8/15/2003	8/15/2003	8/15/2003	8/15/2003
Calanoid cop.	6.1	84.8	78.4	142.9	2.9	2.7	3.3	0.5
Cyclopod cop.	4.6	220.6	213.8	360.1	2.9	5.2	1.3	6.8
Harpactacoid cop.	0.0	0.0	0.0	7.4	2.5	0.0	0.0	12.5
Cop. Nauplii	0.0	0.0	55.3	28.5	1.4	0.0	0.0	0.0
Unknown cop.	1.6	25.5	60.0	71.7	0.0	1.4	0.7	0.0
Bosmina	126.5	729.6	3052.3	761.7	179.1	40.7	95.0	155.5
Other cladocerans	3.1	25.5	269.1	64.9	0.0	5.0	0.6	28.3
Dipteran larvae	37.4	33.9	18.4	7.4	0.0	1.4	1.3	140.8
Ostracods	22.5	322.4	141.5	203.5	5.0	4.6	4.7	557.5
Mite/ spiders	1.5	0.0	18.4	13.7	0.0	2.4	0.0	49.9
Other insects	6.0	50.9	0.0	6.8	2.9	4.9	0.0	163.5
Larval fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaete larvae	10.5	0.0	0.0	7.4	7.1	0.0	0.0	1.0
Gastropods	0.0	0.0	0.0	7.4	0.0	0.0	0.0	0.0

Appendix C. Numbers of zooplankton per m³ in benthic net samples in June 2003 (values are the average of two repeated tows).

Time interval	1800	2100	0	300	600	900	1200	1500
Date	6/26/2003	6/26/2003	6/27/2003	6/27/2003	6/27/2003	6/27/2003	6/27/2003	6/27/2003
Calanoid cop.	68.0	2170.2	1908.0	5440.0	89.3	94.5	70.6	1627.5
Cyclopod cop.	5.7	1582.3	2091.9	2368.0	34.3	6.6	21.1	12.2
Harpactacoid cop.	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Cop. Nauplii	0.0	29.0	20.2	0.0	4.6	0.0	0.0	0.0
Unknown cop.	0.0	2.1	20.8	0.0	3.0	3.7	1.3	114.2
Bosmina	58.3	211.2	244.4	1056.0	228.2	325.4	249.5	1554.8
Other cladocerans	19.6	92.3	204.1	480.0	19.4	24.1	46.9	51.8
Amphipod	0.0	2.3	0.3	1.0	0.0	0.0	0.0	0.0
Dipteran larvae	11.9	30.0	20.2	96.0	23.6	5.7	6.2	13.8
Ostracods	20.5	68.0	50.7	0.0	15.4	13.9	20.5	20.6
Mite/ spiders	0.0	0.0	0.0	0.0	1.6	1.6	0.0	0.0
Other insect	0.8	1.4	21.8	2.0	1.6	1.6	6.0	6.9
Larval fish	1.1	0.0	20.2	32.0	0.0	0.0	2.7	0.0
Polychaetes	0.0	0.0	10.4	0.0	26.1	8.5	4.9	19.0

Appendix D. Numbers of zooplankton per m³ in benthic net samples in August 2003 (values are the average of two repeated tows).

Time interval	1800	2100	0	300	600	900	1200	1500
Date	8/14/2003	8/14/2003	8/15/2003	8/15/2003	8/15/2003	8/15/2003	8/15/2003	8/15/2003
Calanoid cop.	350.7	798.4	2091.8	1420.8	136.2	341.5	778.4	171.3
Cyclopod cop.	1052.1	2301.7	4706.6	6314.1	236.1	306.1	128.0	831.8
Harpactacoid cop.	0.0	0.0	0.0	265.6	254.2	0.0	0.0	0.0
Cop. Nauplii	1663.4	3474.2	7321.4	3465.8	3286.4	1683.7	1777.1	5258.1
Unknown cop.	130.3	2097.9	4706.6	1427.5	608.3	94.2	645.2	1124.9
Bosmina	68432.6	46528.8	98315.6	42910.3	41607.0	18745.3	20857.3	27195.6
Other cladocerans	0.0	1291.2	5229.6	3113.9	1153.0	141.3	732.3	1688.5
Amphipod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dipteran larvae	260.7	203.8	523.0	2038.2	254.2	106.0	261.2	317.8
Ostracods	701.4	203.8	1045.9	1248.3	136.2	47.1	0.0	415.9
Mite/ spiders	0.0	0.0	0.0	0.0	0.0	47.1	0.0	0.0
Other insect	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Larval fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polychaetes	0.0	0.0	0.0	0.0	0.0	0.0	87.1	0.0

Appendix E. Numbers of zooplankton per m³ in neuston net and standard deviations at four sampling locations. Neuston net dimensions: mesh size 300um, 35.6 cm x 17.8 cm x 121.9 cm, General Oceanic Flowmeter. Neuston sampling procedures same as benthic procedures for 2004 except tow distance increased to 30 meters for neuston samples. Values shown derived from average of values from 5 sampling days. Cop. = copepods, ave = average, stdev = standard deviation.

River kilometer	60	60	71	71	81	81	89	89
Value	ave	stdev	ave	stdev	ave	stdev	ave	stdev
Calanoid cop.	0.5	0.5	0.1	0.3	5.2	5.2	13.8	24.2
Cyclopod cop.	0.1	0.3	0.5	0.7	7.3	13.7	5.9	4.0
Harpactacoid cop.	0.7	1.1	6.0	5.8	0.4	0.6	0.0	0.0
Cop. Nauplii	0.3	0.4	0.0	0.0	0.0	0.0	0.2	0.5
Unknown cop.	0.2	0.4	0.0	0.0	0.2	0.4	0.5	1.1
Bosmina	0.3	0.6	0.3	0.6	19.1	16.4	31.7	33.4
Other cladococerans	2.1	2.2	55.1	111.3	38.6	54.1	83.0	116.8
Dipteran larvae	0.5	0.8	10.6	17.0	3.1	3.6	6.0	5.0
Ostracods	29.4	33.6	37.7	63.6	7.9	3.1	26.1	16.2
Decapod zoea	3.1	6.9	3.9	5.5	0.0	0.0	0.0	0.0
Mite/ spiders	0.5	1.2	3.4	5.2	1.8	1.3	3.5	2.4
Other insects	1.8	1.6	27.3	53.3	5.0	4.4	14.5	10.2
Larval fish	0.8	0.6	0.8	1.2	0.0	0.0	0.0	0.0
Polychaetes	6.3	4.3	6.2	1.3	6.2	4.5	10.6	7.6
Gastropods	1.9	2.3	2.6	2.9	1.2	0.8	1.1	1.8

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