

Spatial patterns in diet and distribution of juveniles of four fish species in Delaware Bay marsh creeks: factors influencing fish abundance

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ABSTRACT: Delaware Bay is one of the largest estuaries on the east coast of the United States and provides juvenile habitat for many fish species. We investigated spatial patterns in the diet and distribution of the young-of-the-year of 3 marine transients—the weakfish *Cynoscion regalis*, the spot *Leiostomus xanthurus* and the Atlantic croaker *Micropogonias undulatus*—and the juveniles and adults of 1 estuarine resident, the white perch *Morone americana*, in 5 marsh creeks systems along a salinity gradient running from the poly/mesohaline (12 to 20) lower bay to the meso/oligohaline upper bay (0 to 12). Sampling was conducted monthly from April through November in 1997 and 1998, resulting in over 1700 otter trawl (4.9 m, 6 mm cod-end mesh) samples and 5703 fish stomachs examined, making this one of the largest studies of its kind. We employed a bootstrap technique to generate 95% confidence intervals for proportional consumption of the major prey categories. The diets of the target species differed significantly among the 5 marsh creeks. Mysid consumption was high for all species at the 3 most saline marshes and low at the 2 freshest sites, suggesting either low mysid abundance or availability at the latter sites. Consumption of insect larvae was important only at the freshest site. *L. xanthurus* consumed 80% annelids at the most saline sites, but less than 32% at the other sites. The other important consumer of annelids, *Micropogonias undulatus*, consumed similar quantities of annelids at all sites (32 to 41%). Total stomach fullness was almost always higher at the sites of highest fish abundance. We conclude that the marine transients appear to recruit preferentially to sites of high resource abundance, while *M. americana* is restricted by physico-chemical tolerance during the spring through fall to limited juvenile habitats where it may experience food resource competition.

KEY WORDS: Bootstrap estimation · Delaware Bay · Food habits · Estuary · Juvenile fishes · Marsh creeks · Spatial variation

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INTRODUCTION

The young-of-the-year (YOY) and later juveniles of many fish species use estuaries extensively, presumably benefiting from a combination of high resource availability, low predation pressure and suitable physico-chemical conditions (Nixon & Oviatt 1973, Weinstein 1979, Weinstein et al. 1980, Boesch & Turner 1984, Rountree & Able 1992, Kneib 1997, Able & Fahay 1998, Simenstad et al. 2000). However, estuaries are

dynamic habitats and the attributes that make them beneficial to fishes vary across space and time (Pennock & Sharp 1986, Day et al. 1989, Lankford & Targett 1994). In most estuaries, and drowned river-valley estuaries in particular, physico-chemical conditions vary across the mixing zone, from near oceanic conditions at the mouth of the estuary to near riverine conditions at the head. Sessile fauna that may provide prey for juvenile fishes also vary along the salinity and associated gradients running from the ocean to the head of

the estuary (Gunter 1956, Boesch 1977, O'Neil & Weinstein 1987, Sarre et al. 2000). Similarly, mobile potential prey, competitors and predators vary spatially within estuaries (Gunter 1956, Weinstein et al. 1980), including Delaware Bay (Able et al. 2001). Consequently, fishes encounter a complex mosaic of habitats within an estuary, with varying levels of resources, predators, competitors and physico-chemical suitability (Miller & Dunn 1980, Livingston 1982, Sogard 1994, Greco & Targett 1996, Paperno et al. 2000, Simenstad et al. 2000).

Given this variability, we should expect resource consumption, growth, and survival to also vary, with regions within the estuary contributing different quantities and possibly sizes of 'graduates' at the end of the nursery period. The best nursery habitats are those that produce the greatest number of young fish that will join the adult population and reproduce themselves (Beck et al. 2001, Gillanders et al. 2003). Determining the relative value of estuarine habitats is difficult in open systems, where fishes may move among habitats and where the habitats as well as the fishes' needs may change over time (e.g. with ontogeny during the nursery period, Livingston 1982, Craig & Crowder 2000). Furthermore, it is not clear how the functional attributes of fish nursery habitats interact, so that a habitat that provides enhanced values of one attribute (e.g. feeding success) may offer diminished values of another (e.g. predation refuge) and may not necessarily confer higher fitness (Boesch & Turner 1984, Werner & Hall 1988, Sogard 1992, 1994, Halpin 2000). Finally, some habitats may provide ideal nursery conditions only sporadically (Neill et al. 1994).

While juvenile fishes should choose habitats that maximize growth, predation may force fishes into habitats where growth is reduced (Sogard 1992, 1994). Werner & Gilliam (1984) suggested that when rapid-growth habitats are rendered risky by predation, fishes should choose habitats that minimize the ratio of predation risk to growth rate. This appears to be true for several freshwater (Cerri & Fraser 1983, Werner et al. 1983, Power 1984, Werner & Hall 1988) and marine (Schmitt & Holbrook 1985, Dahlgren & Eggleston 2000) fish species. When predation is high, this behavior, while still optimizing fitness, may result in the concentration of juvenile fishes in refuge habitats, resulting in inter- and intra-specific competition and reduced growth (Mittelbach 1988, Walters & Juanes 1993).

Measuring fish abundance and relative foraging success across several sites allows inferential conclusions about the forces structuring how fishes assort themselves among available sites (Gilliam & Fraser 1987). If fishes are abundant and achieve high relative foraging success, it suggests that high resource abundance is responsible. Conversely, finding high abundance in

areas of low relative foraging success suggests either favorable physico-chemical conditions or low predation pressure. Additionally, knowledge of the specific prey types consumed at different sites can lead to a more complete understanding of how habitat selection operates. For example, fishes have been shown to grow faster when consuming a preferred prey compared to an equal quantity of an alternate prey (Lankford & Targett 1997).

Delaware Bay is a drowned river-valley estuary that provides juvenile habitats for many marine transient and resident fishes (Able et al. 2000, 2001). Salinity, temperature, substrate and biota vary spatially within the bay (Pennock & Sharp 1986, Able et al. 2001, Grothues & Able 2003). In this study, we investigated the abundance and spatial variability in diets and total prey consumed of juvenile fishes in marsh creeks along the long axis of the bay and tested the null hypothesis that the juveniles of 3 transient species of fishes, *Cynoscion regalis* (weakfish), *Leiostomus xanthurus* (spot), and *Micropogonias undulatus* (Atlantic croaker) and the juveniles and young adults of 1 resident, *Morone americana* (white perch), are distributed randomly with respect to stomach fullness. We considered 2 alternatives: (1) fishes are more abundant where feeding success is high, or (2) fishes are less abundant where feeding success is high. Alternative 2 would suggest that factors other than resource availability, including physico-chemical conditions and predation levels, control juvenile habitat selection.

MATERIALS AND METHODS

Sampling sites. We sampled the fish assemblage along the New Jersey coast of Delaware Bay (Fig. 1, Table 1) monthly, from April to November, at 4 salt marsh sites in 1997 and 5 sites in 1998. The most northerly site (Mill Creek) was only sampled in 1998. These sites ranged from the poly/mesohaline lower bay (mean salinity 12 to 20) to the oligo/mesohaline upper bay (0 to 12) and have been described in detail in Able et al. (2000, 2001). Of the sampling sites, 3 were undergoing or had undergone restoration as part of the Public Service Enterprise Group's Estuary Enhancement Program during (or prior to) this study (Weinstein et al. 1997). The 2 sites closest to the ocean, Dennis Township and Moores Beach, are close to each other and have similar physico-chemical conditions and fish faunas (Able et al. 2000). Data from these 2 sites were pooled and treated as a single site, which we refer to as Dennis/Moores. For some analyses, we also pooled data from the 3 most northerly sites, and refer to these collectively as the upper bay sites.

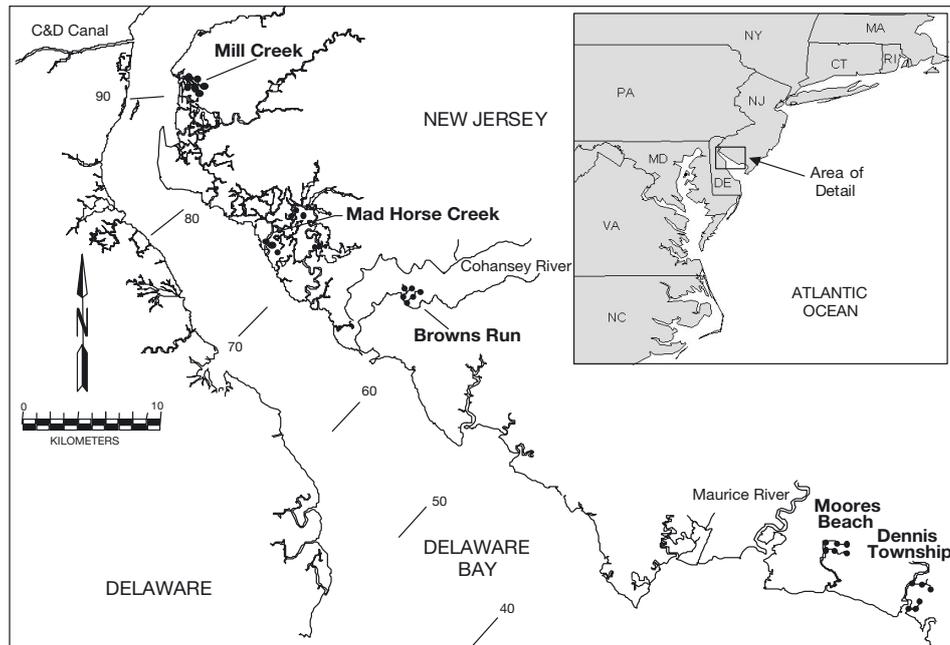


Fig. 1. Marsh creek sampling sites in Delaware Bay in 1997 and 1998. Trawling stations within sites are indicated (●)

At all sites, we established 6 trawling stations in representative marsh creeks within the sites. These creek stations were located along a gradient from deeper subtidal locations to shallow subtidal or intertidal locations. The deepest stations were in creeks that were over 50 m across and as deep as 4 m at high tide and emptied directly into the bay. The shallower stations were in smaller creeks that were 5 to 10 m across and about 1.5 to 3 m deep at high tide and generally emptied into the larger creeks.

Field collections. Fishes were collected by 4.9 m otter trawl (6 mm cod-end mesh) from April through November in 1997 and 1998. Trawling began about 2 h prior to daylight high tides and finished about 2 h after high tide, usually within 3 d of a spring tide. Each tow was made against the tidal current at an engine speed of 2500 rpm and lasted 2 min. We made 4 replicate

tows at each station, resulting in 24 tows site⁻¹ mo⁻¹. All fishes were counted and a subsample of up to 20 individuals from each tow was measured to the nearest mm (fork length [FL] for fishes with forked tails, total length [TL] for all others). All fishes kept for food-habits analysis were either preserved in buffered 10% formalin (fishes <140 mm) or injected with buffered 10% formalin and frozen (≥140 mm). Each month, at each site, preserved fishes were separated into 4 tide-stage/creek-size samples: flood tide/large creek, flood tide/small creek, ebb tide/small creek, ebb tide/large creek.

In the laboratory, fishes kept for food-habits analysis were separated by species and measured to the nearest 0.5 mm. They were then pooled into 10 mm size classes up to 139 mm, 30 mm size classes from 140 to 199 mm, and 100 mm size classes starting at 200 mm.

Table 1. *Cynoscion regalis*, *Leiostomus xanthurus*, *Morone americana* and *Micropogonias undulatus*. Sampling sites, salinity and number of stomachs examined during April to November sampling, 1997 and 1998. Salinity values are minimum monthly mean, grand mean, and maximum monthly mean during the sampling period

Site	Years sampled	Salinity			No. of stomachs examined				
		Min.	Mean	Max.	<i>C. regalis</i>	<i>L. xanthurus</i>	<i>M. americana</i>	<i>M. undulatus</i>	Total
Dennis/Moores	1997, 1998	11.0	17.9	21.6	380	719	97	1561	2757
Browns Run	1997, 1998	2.0	7.1	13.0	53	197	562	50	862
Mad Horse Creek	1997, 1998	0.7	9.4	14.0	303	243	450	112	1108
Mill Creek	1998	0	2.8	6.7	86	0	611	279	976
Total					822	1159	1720	2002	5703

Table 2. Names, categories and descriptions of aggregated prey categories used in trophic analyses

Category	Description
Annelids	All polychaetes and oligochaetes
Crustaceans	All crustaceans excluding copepods, decapod zoeae, mysids, ostracods and other small planktonic crustaceans
Fishes	All fishes and fish remains including eggs and larvae
Insects	All larval and adults insects (almost exclusively dipteran larvae)
Meiobenthos	Harpacticoid copepods, ostracods, nematodes
Mollusks	All bivalve mollusks including clam siphons
Mysids	All mysid shrimps (almost exclusively <i>Neomysis americana</i>)
Zooplankton	Calanoid copepods, decapod zoeae, cumaceans

In all the analyses and figures that follow, we will refer to a size class by using the lower length boundary of that size class. The stomach contents of up to 12 individuals (O'Neil & Weinstein 1987) per size class, species, site, month, and tidal-stage/creek-size were removed and placed together in a sample vial filled with a solution of Rose Bengal and 95% ethyl alcohol. For each of these samples the weight of each prey category was determined according to the sieve fractionation method of Carr & Adams (1972). Small *Micropogonias undulatus* that first recruited to the sites in September through November were not included in any analyses. *Morone americana* were separated into 2 size classes prior to diet composition analysis: 50 to 139 mm and 140 to 299 mm.

Prey categories. All prey items were identified to the lowest practical taxonomic level. For most data analyses we grouped prey into 8 general categories (Table 2). These categories were chosen to highlight different feeding modes of the predator species and are not taxonomically exact. For example, mysids, crustaceans and zooplankton are separate categories, although mysids can be considered zooplankton and both are crustaceans. Unidentified crustaceans and crustacean parts were assigned to the crustacean category, so that the crustacean category includes unidentified mysids, meiobenthos and zooplankton. Unidentified prey items were eliminated from the calculation of gravimetric prey proportions but were included in the calculation of total fullness (see next subsection).

Data analysis. We evaluated fish abundance for each species by comparing the mean number of individuals caught per 2 min tow, averaging across each

set of 4 replicate tows and then again across month and region to get an estimate of catch per unit effort (CPUE). All standard errors of mean CPUEs are based on this method. For clarity, we pooled the upper bay sites prior to comparing abundances among regions.

We compared fish diets by expressing the weight of each prey category consumed as a proportion of total prey weight consumed, and modified the bootstrap resampling procedure of Tirasin & Jørgensen (1999) to generate approximate 95% confidence intervals (CIs) for proportional consumption by category. Because our samples contained the pooled stomach contents of 1 to 12 individual fish, we adjusted the likelihood that an individual sample would be resampled during a bootstrap iteration using an increasing, asymptotic function of the number of fish within each sample (Tirasin & Jørgensen 1999). We used 2 approaches to develop the shape of the weighting function. First, we plotted the number of different, non-aggregated prey taxa found in samples of 1 to 12 stomachs. Second, we plotted the reciprocal of the coefficient of variation of the mean total stomach contents weight fish⁻¹ derived from samples of 1 to 12 stomachs. Finally, we fitted a step function by hand to the resultant curves that determined the likelihood that a given sample's data was resampled (Fig. 2).

The bootstrap procedure we employed to determine CIs for proportional consumption for each species at 1 site can be summarized as follows: (1) produce a raw data matrix where rows are samples and columns are prey categories and the elements are the weight of each prey category consumed in the sample divided by the number of stomachs within the sample; (2) replicate each sample (row) *w* times using the weighting function; (3) draw a bootstrap sample

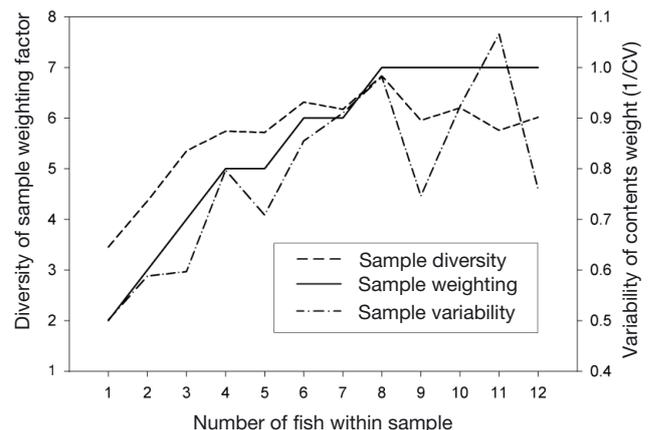


Fig. 2. Prey taxa diversity, total contents weight variability and sample weighting for samples of 1 to 12 fish. See 'Materials and methods, Data analysis' for details

from the data matrix with replacement, restricting the resampling by size class such that the bootstrap sample for each size class is drawn only from the original samples in that size class and the total number of resamples equals the original number of samples within a size class; (4) calculate proportional consumption for each prey category and size class for the bootstrap sample; (5) calculate the frequency of occurrence of each size class at all sites combined; (6) calculate weighted mean proportional consumption across all size classes combined using the above frequencies as the weights; (7) repeat 5000 times, rank the resultant 5000 pseudo-proportions (sequentially by each prey category) and choose the appropriate percentile pseudo-proportions to establish the desired CIs. For standard 95% CIs, Step 7 would entail choosing the 2.5 and 97.5 percentile bootstrap proportions. We used the bias-correction method of Manly (1997) to adjust the percentiles chosen to represent the 95% CIs, based on the difference between the point estimate and the mean of the bootstrap distribution. When comparing diet proportions, we considered those whose 95% CIs overlapped as statistically similar, and those that did not as statistically different.

We used a modified version of the index of relative fullness (IRF) recommended by Herbold (1985) to assess the total quantity of prey found in each sample. This index seeks to remove possible bias introduced when the fullness of individuals of different sizes are compared by using regression analysis to predict a maximum fullness for each fish and then presenting the actual fullness of each fish as a percentage of this maximum. The IRF value for each sample is the actual fullness for the sample divided by the regression-predicted maximum fullness for the sample. We eliminated detritus, sand, sediments and all other non-digestible items prior to conducting any fullness analyses, but included unidentified prey. We used Wilcoxon 2-sample rank-sum tests to test for significant differences in fullness among sites.

While 3 of the sites were undergoing or had undergone restoration during (or prior to) this study, our work in the sites to date has indicated that juvenile fishes use the restored sites, with respect to abundance, growth and food habits, in a manner similar to the nearby reference sites (Able et al. 2000, 2001, Nemerson 2001, Grothues & Able 2003). Similarly, the benthic invertebrate fauna at the restored salt hay farm site in the lower bay has approached the assemblage structure typical of nearby reference marshes (G. Taghon pers comm.). For all analyses comparing regions of the bay, we pooled data that included both restored and natural sites in both regions.

RESULTS

Abundance and size structure

Abundance of the 3 transient sciaenids was generally higher in the lower bay than in the upper bay sites (Figs. 3, 4 & 5) while the opposite was true for *Morone americana* (Fig. 6). The patterns of abundance of the transient species were fairly similar across both years of sampling, with a few notable exceptions. *Leiostomus xanthurus* recruited strongly to the lower bay early in both years, recruited to the upper bay sites later in the summer in 1997, and failed to recruit to the upper bay at all in 1998 (Fig. 3). The later recruitment to the upper bay in 1997 can also be seen in the monthly size structure of *L. xanthurus* (Fig. 3). In April and May 1997, *L. xanthurus* were present only in the lower bay at sizes <50 mm. In June, they were present at sizes 20 to 100 mm in the lower bay, while the first small individuals appeared in the upper bay at about 30 to 40 mm. By August, and through the remainder of the summer, the sizes of individuals in both regions overlapped broadly. In 1998, *L. xanthurus* size structure was far narrower in every month compared to 1997.

Cynoscion regalis had very similar patterns of abundance in both regions in 1997, but recruited more strongly to the lower bay in 1998 (Fig. 4). In 1997, *C. regalis* were generally smaller in the lower bay than in the upper bay. While they first appeared in July in both regions in 1997, it appears that immigration continued into August in both regions, as the minimum size present decreased from July to August. In 1998, *C. regalis* were far smaller in the lower bay than in the upper bay, and mean size decreased from July through September, indicating the continual arrival of small individuals into the lower bay throughout the summer.

Micropogonias undulatus were 1 to 3 orders of magnitude more abundant at the lower bay sites than the upper bay, and recruited far more strongly overall in the spring of 1998 than 1997 (Fig. 5). Overall size structure in both regions was quite similar. In October 1997, the largest individuals appeared to emigrate first in both regions, as the mean size dropped dramatically from September to October.

Morone americana were far more abundant at the upper bay sites in both years (Fig. 6). Between June and September 1997, abundance dropped off sharply, while in 1998 abundance remained high during these months. Size structure in both regions and years was quite variable. *M. americana* were generally larger in the lower bay, particularly in 1998. There was no pattern of growth of a single cohort apparent in either year or region (Fig. 6) as there was for *Leiostomus xanthurus* (Fig. 3) and *Micropogonias undulatus* (Fig. 5).

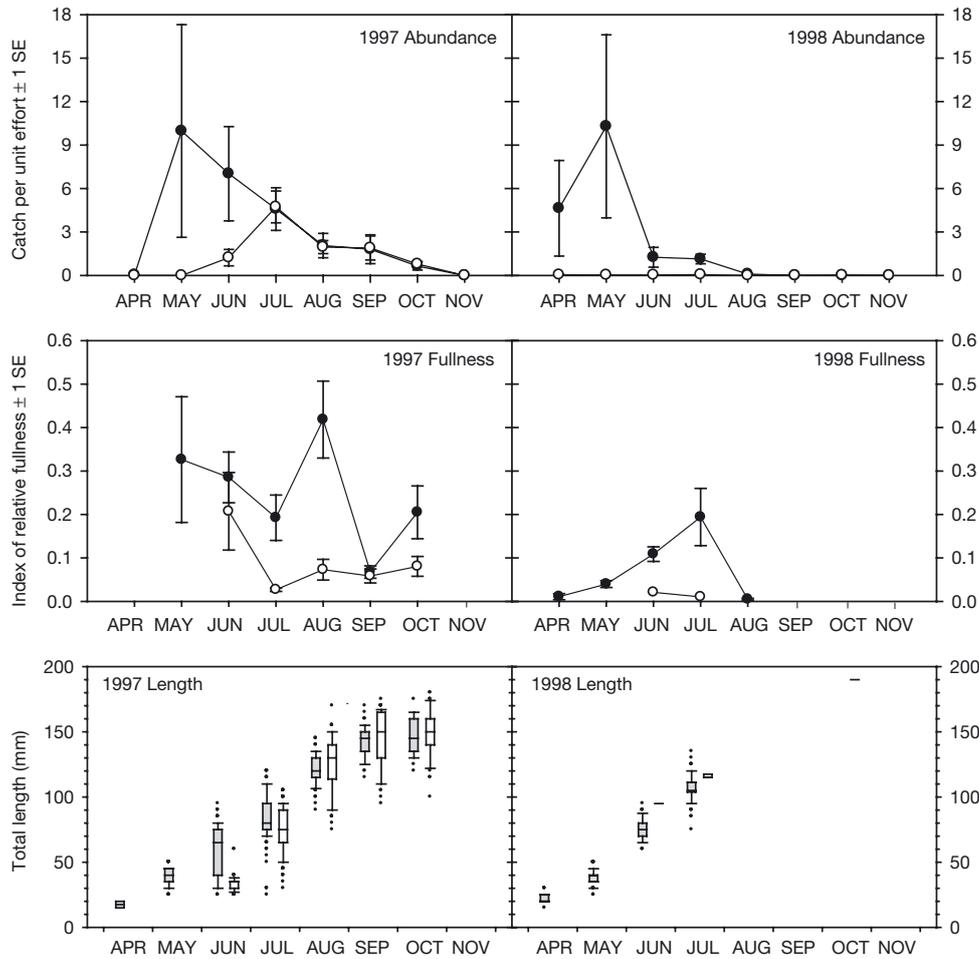


Fig. 3. *Leiostomus xanthurus*. Abundance, stomach fullness, and lengths of spot collected from Delaware Bay marsh creek sites during 1997 and 1998. Filled circles and shaded box plots are data from lower bay sites; open circles and box plots are data from upper bay sites. In box plots, center line represents median length, ends of box 25th and 75th percentile lengths, and ends of whiskers 10th and 90th percentile lengths; dots represent individual outliers

Bootstrap weighting function

Prey diversity was lowest in samples with the stomach contents of only 1 fish and increased until the number of fish in a sample reached 8, after which it declined slightly (Fig. 2). The variability of mean total stomach contents weight per fish was greatest across samples containing the stomach contents of 1 fish and decreased until reaching a minimum at samples of 11 fish (i.e. variability of mean total contents weight for samples of 12 fish was higher than that for samples of 11 fish). Variability of mean total contents weight was probably high in samples containing the contents of only 1 or a few fish because small sample handling and weighing errors were a larger fraction of the total weight of these samples than of samples containing the contents of more fish. These results (discounting the trends in the very largest samples) indicate that samples containing a large number of fish were a more

accurate indicator of the true diet of the predator. The step function hand-fitted to the prey accumulation and sample variability curves resulted in an increasing, asymptotic likelihood that samples representing more fish were resampled (Fig. 2).

Diet composition

Cynoscion regalis. Crustaceans, mysids and fishes dominated diets, with substantial and significant site based differences (Table 3). Piscivory was highest at Dennis/Moores (45.5%) and at Mill Creek (44.3%), intermediate at Mad Horse Creek (20.4%) and almost absent from Browns Run (1.9%)¹. Mysid consumption was similar across Dennis/Moores (26.0%), Browns

¹ Only mean values are used in the text; means and upper and lower 95% CIs are given for each species in Table 3

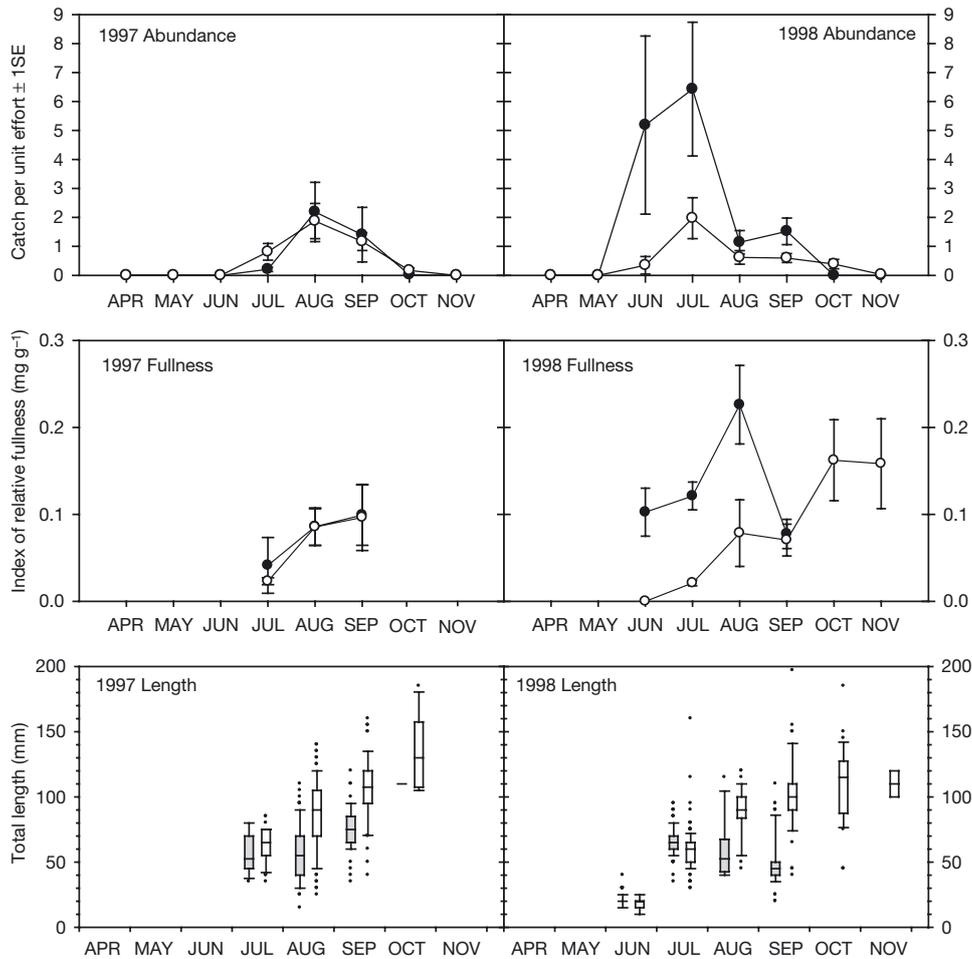


Fig. 4. *Cynoscion regalis*. Abundance, stomach fullness and lengths of weakfish collected from Delaware Bay marsh creek sites during 1997 and 1998. Further details as in Fig. 3

Run (31.1%) and Mad Horse Creek (33.6%) and negligible at Mill Creek (0.6%). Crustacean consumption was significantly higher at Browns Run (66.2%) than at any of the other sites (28.2 to 35.6%).

Leiostomus xanthurus. Annelids strongly dominated the diet at Dennis/Moores (77.9%), but accounted for only 23.9% at Browns Run and 31.5% at Mad Horse Creek (Table 3). Meiobenthos was a common prey type at all 3 sites, although consumption of this category was significantly higher at Browns Run (29.2%) than at either at Dennis/Moores or Mad Horse Creek (both 12.4%). Crustacean consumption was significantly higher at both Browns Run (19.6%) and Mad Horse Creek (19.1%) than at Dennis/Moores (3.3%). In general, the diet of *L. xanthurus* was more diverse at the 2 upper bay sites where it was captured (it was absent from Mill Creek) compared to Dennis/Moores.

Micropogonias undulatus. Individuals had a fairly diverse diet that varied among sites (Table 3). Annelid con-

sumption was quite high and similar at all sites (32.0 to 50.6%). Crustacean consumption was high at upper bay sites (15.3 to 34.5%) but low at Dennis/Moores (3.8%). Mysid consumption was high only at Dennis/Moores (45.8%) and at Mad Horse Creek (33.1%) and almost absent at the other 2 sites (0 to 2.2%). *M. undulatus* consumed substantial amounts of insects (15.1%) and zooplankton (19.8%) only at Mill Creek, while piscivory was most prevalent at Dennis/Moores (9.2%) and at Mill Creek (3.4%).

Morone americana. The diets of small (<140 mm) and large (≥ 140 mm) individuals differed substantially (Table 3). The diet of small *M. americana* (60 to 139 mm) varied across the sites and was dominated by crustaceans, mysids, zooplankton and insects, depending upon site. These fish consumed similar amounts of crustaceans at all sites (33.7 to 48.7%), while zooplankton consumption was very similar at Browns Run and Mill Creek (24.8 and 24.7%, respectively), and higher than at either Mad Horse Creek (10.8%) or at

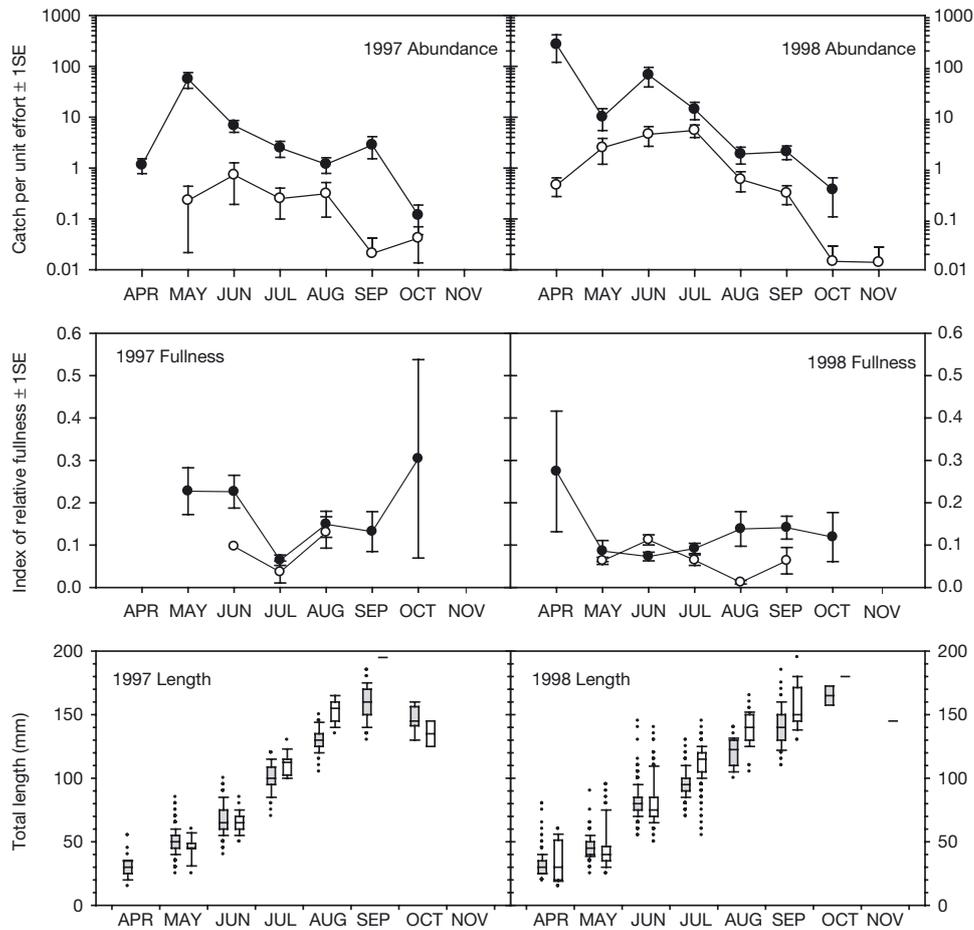


Fig. 5. *Micropogonias undulatus*. Abundance, stomach fullness and lengths of Atlantic croaker collected from Delaware Bay marsh creek sites during 1997 and 1998. Further details as in Fig. 3. Note log scale on abundance graphs

Dennis/Moores (0.2%). Mysid consumption was highest at Dennis/Moores (48.3%) and Mad Horse Creek (32.2%), greatly exceeding that at the other 2 sites (1.3 to 3.4%). Insects were consumed by small *M. americana* only at Mill Creek, where they accounted for 23.4% of the diet.

Larger *Morone americana* (140 to 299 mm) differed from small individuals primarily in the inclusion of more fishes in their diet (Table 3). However, the degree of piscivory in *M. americana* was highly variable, with wide CIs. Piscivory was highest at Mill Creek (66.3%) but this differed significantly only from the site with the least piscivory, Dennis/Moores (10.5%). Browns Run (41.8%) and Mad Horse Creek (35.4%) had intermediate amounts of piscivory. Crustacean consumption was similar at Dennis/Moores (53.4%), Browns Run (53.9%) and Mad Horse Creek (39.0%) and very low at Mill Creek (1.1%). Mysids were consumed only at Dennis/Moores (36.0%) and at Mad Horse Creek (22.7%) while insects were consumed only at Mill Creek (29.8%).

Stomach fullness

The 3 transient, sciaenid species generally had fuller stomachs at Dennis/Moores than at the upper bay sites (Figs. 3, 4 & 5). This was true for *Leiostomus xanthurus*, and *Cynoscion regalis* during every month sampled during both years, and for *Micropogonias undulatus* in every month but 1. Although this trend toward higher fullness at Dennis/Moores occurred across almost every month, the difference was significant for *L. xanthurus* only in July and August 1997, *C. regalis* in July and August 1998, and *M. undulatus* in August 1998 (Wilcoxon 2-sample rank sum test, $p < 0.05$). *M. undulatus* captured at the upper bay sites in June 1998 had fuller stomachs than those captured at Dennis/Moores (Wilcoxon 2-sample rank sum test, $p < 0.05$). In 1997, *Morone americana* stomach fullness was variable, with generally similar to higher fullness in the upper bay except for in May when fullness was higher at the lower bay sites (Fig. 6). In 1998, too few *M. americana* were caught in the lower bay to allow stomach fullness comparisons

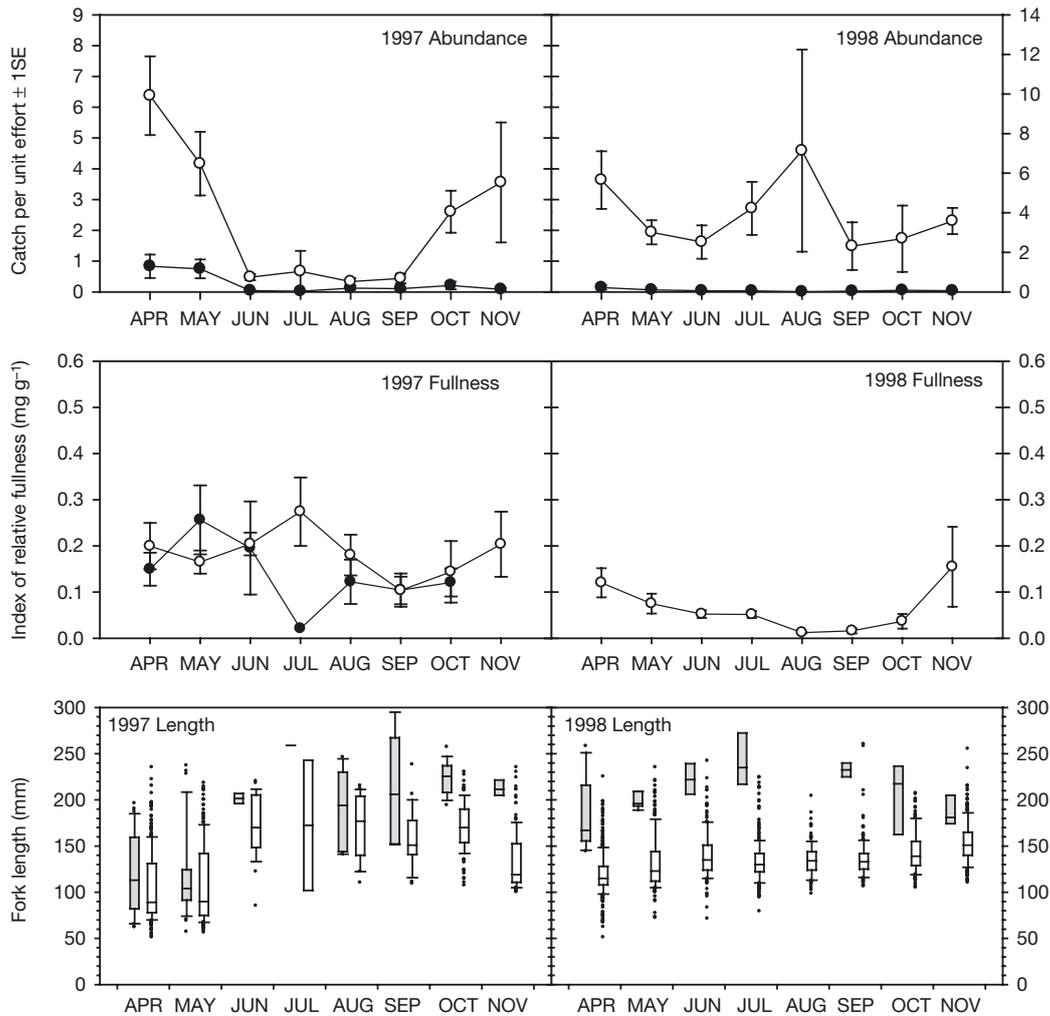


Fig. 6. *Morone americana*. Abundance, stomach fullness and lengths of white perch collected from Delaware Bay marsh creek sites during 1997 and 1998. Further details as in Fig. 3

DISCUSSION

The sample sizes in this food habits study were among the largest ever assembled for an estuary (see Livingston 1982, Smith et al. 1984, Barry et al. 1996); the study covered a wide spatial area, and included 2 yr of sampling. This has allowed us to examine detailed patterns of spatial variability in feeding by the dominant predator species in this system and thus speculate about the mechanisms underlying the distribution of these species in the estuary. We are aware that these inferences are correlative and that the mechanisms themselves have not been tested. Nonetheless, the large size and extent of this study lend substantial power to such inferences. Furthermore, synoptic, observational studies such as this are an important prerequisite to the formation of testable hypotheses (Underwood et al. 2000).

Diet composition

Most species exhibited spatial variability in their diets. This was particularly true for *Leiostomus xanthurus*, which consumed significantly more annelids at Dennis/Moores (77.9%) than at either of the other 2 sites where it was captured (23.9 to 31.5%). However, *Micropogonias undulatus*, which also consumed substantial quantities of annelids, consumed similar quantities at all sites (32.0 to 50.6%). This level of consumption is similar to that of *L. xanthurus* in the upper bay sites (23.9 to 31.5%). Annelids have been reported to be a preferred prey of *L. xanthurus* (Miltner et al. 1995), while *M. undulatus* generally consume more mobile, epibenthic prey (Chao & Musick 1977, Sheridan 1979, Currin et al. 1984). Therefore, it is possible that annelids are more available in the lower bay and that both predators were able to find enough annelids to meet about 30% of their dietary needs at all sites,

Table 3. *Cynoscion regalis*, *Leiostomus xanthurus*, *Morone americana* and *Micropogonias undulatus*. Proportional consumption by predator species and sampling site. Mean: mean gravimetric percentage consumption of prey type; Lower CL, Upper CL: lower and upper bootstrap 95% confidence limits, respectively. See Table 1 for sample sizes and Fig. 1 for sampling locations

	—Dennis/Moores—			— Browns Run—			— Mad Horse Creek—			— Mill Creek—		
	Lower CL	Mean	Upper CL	Lower CL	Mean	Upper CL	Lower CL	Mean	Upper CL	Lower CL	Mean	Upper CL
<i>Cynoscion regalis</i>												
Annelids		0.1			0.5		2.9	4.8	7.9		0.1	
Crustaceans	26.3	28.2	40.5	56.6	66.2	76.6	32.0	39.3	46.3	19.9	35.6	48.3
Fishes	29.5	45.5	47.1	1.4	1.9	2.4	12.4	20.4	24.6	25.3	44.3	49.0
Insects		0.0			0.2			0.0			0.8	
Meiobenthos		0.0			0.1	0.2	0.4	0.9	1.6		0.9	
Mollusks		0.0			0.0			0.0			0.0	
Mysids	20.6	26.0	33.2	20.5	31.1	40.7	25.5	33.6	43.4		0.6	
Zooplankton	0.1	0.1	0.3		0.0		0.3	0.9	1.8	12.2	17.7	38.0
<i>Leiostomus xanthurus</i>												
Annelids	70.7	77.9	81.9	16.1	23.9	30.6	27.7	31.5	44.0			
Crustaceans	3.7	3.3	8.4	17.7	19.6	33.1	14.9	19.1	25.6			
Fishes		0.3			0.0		0.3	1.0	2.7			
Insects	0.5	1.1	2.3	0.4	2.5	3.9		0.2				
Meiobenthos	8.4	12.4	16.7	26.5	29.2	43.1	12.8	12.4	20.4			
Mollusks	0.8	1.5	3.2	8.9	20.3	24.7	1.2	7.7	8.3			
Mysids	1.3	2.9	5.3		0.1		5.6	13.7	13.5			
Zooplankton		0.5		2.3	4.3	5.6	9.4	14.4	19.5			
<i>Micropogonias undulatus</i>												
Annelids	23.9	32.5	33.9		50.6		33.2	41.1	47.3	18.1	32.0	33.3
Crustaceans	27.1	29.7	38.5		36.1		24.2	30.6	36.2	18.4	21.5	29.0
Fishes	6.1	9.2	11.9		1.0		0.2	1.2	1.8	1.2	3.4	6.2
Insects	0.5	0.8	1.1		2.7		0.0	0.4	1.0	11.9	15.1	25.3
Meiobenthos	0.2	0.4	0.5		3.0		0.2	0.9	1.7	3.2	3.8	5.4
Mollusks	3.2	4.4	6.3		5.7		0.1	0.3	0.5	0.8	2.1	3.1
Mysids	19.2	22.0	24.9		0.2		19.1	23.8	31.5	0.7	2.2	3.7
Zooplankton	0.6	1.0	1.5		0.9		0.6	1.8	4.1	16.5	19.8	24.6
<i>Morone americana</i> 60–139 mm												
Annelids		0.2		5.1	6.7	12.5	7.6	10.9	15.6	3.1	5.6	8.6
Crustaceans	19.1	48.7	50.2	35.6	41.8	59.8	26.9	35.4	43.0	25.6	33.7	37.8
Fishes		0.1		0.2	15.0	20.5	0.8	8.5	13.2	3.2	7.7	13.3
Insects				0.7	1.5	3.2		0.1		18.3	23.4	31.3
Meiobenthos		0.1			0.9			0.2		2.0	3.2	5.3
Mollusks	0.0	2.6	3.7	3.7	5.9	9.5	1.0	2.0	4.5		0.4	
Mysids	47.2	48.3	76.2	2.7	3.4	6.2	23.0	32.2	42.3	0.0	1.3	4.3
Zooplankton		0.2		17.4	24.8	31.8	8.0	10.7	14.9	20.9	24.7	31.2
<i>Morone americana</i> 140–295 mm												
Annelids				1.5	3.9	6.9	1.0	4.8	12.0	0.0	1.0	10.2
Crustaceans	32.3	53.4	70.0	44.7	53.9	81.9	25.0	39.0	58.7	0.2	1.1	9.2
Fishes	0.0	10.5	19.3	11.5	39.5	48.7	8.7	33.1	42.4	24.6	66.3	71.4
Insects					0.2					25.9	29.8	58.0
Meiobenthos		0.0			0.1			0.1		0.1	1.2	1.4
Mollusks		0.0			0.2			0.3				
Mysids	22.8	36.0	56.1	0.5	1.4	3.1	10.0	22.7	38.0		0.2	
Zooplankton		0.0			0.8			0.0			0.5	

but that *L. xanthurus*, which may target annelids more directly, were able to exceed this amount only at the lower bay sites.

Several other prey categories appeared to be restricted in their distribution across the sites based on predator diets. This was particularly true for mysids—which were

consumed regularly at Dennis/Moores and at Mad Horse Creek by all species, only by *Cynoscion regalis* at Browns Run, and very rarely at Mill Creek—and insects, which were consumed regularly only at Mill Creek, the least saline site (Table 3). Because mysids are a preferred prey for *C. regalis* in Delaware Bay (Greccay & Targett

1996, Lankford & Targett 1997), it is possible that only this species, which actively targets this prey source, captured it in quantity at Browns Run, while the general scarcity of mysids at this site made it rare in the diets of the other species. Mysids were almost never consumed at Mill Creek and are probably rare at this site. Both size classes of *Morone americana* consumed large quantities of insects at Mill Creek (up to 29.8%), while *Micropogonias undulatus* consumed 15.1% insects. Insect consumption never exceeded 1.5% at any other site and insect prey can be assumed to be relatively rare at these sites, probably due to their higher salinity.

Fish consumption also varied across sites, but not consistently for the individual predator. It appears that differences in prey abundance and size structure influenced the degree of piscivory exhibited by *Cynoscion regalis* and *Morone americana*. Piscivory by *C. regalis* was very low at Browns Run (1.9%), yet ranged from 20.4 to 45.5% at the other sites. The second most piscivorous predator, *M. americana*, consumed relatively high levels of fishes at Browns Run compared to the other sites (Table 3). As *C. regalis* generally consumed smaller fish prey than *M. americana* (D. M. Nemerson unpubl. data), it is possible that a lack of suitable small fish prey for *C. regalis* at the Browns Run site accounted for this discrepancy. The smaller sized *C. regalis* generally consumed the small bay anchovy *Anchoa mitchilli* as prey, while larger individuals preyed upon the small mummichog *Fundulus heteroclitus* (Nemerson 2001); *M. americana* generally consumed somewhat larger specimens of *F. heteroclitus* (D. M. Nemerson pers. obs). Small *A. mitchilli* were far less abundant at Browns Run than at either Mill Creek or Dennis/Moores (D. M. Nemerson unpubl. data), and *F. heteroclitus* were significantly larger at Browns Run than at any of the other sites (ANOVA, Tukey multiple comparison test, $p < 0.05$, D. M. Nemerson unpubl. data).

Distribution, abundance and stomach fullness

The 3 sciaenids were most abundant at Dennis/Moores in the lower bay, where they generally achieved the highest stomach fullness, while the resident, *Morone americana*, was most abundant in the upper bay, where it achieved somewhat lower feeding success (Figs. 3 to 6). These patterns, along with published data on the target species' physico-chemical preferences and the potential for predation in the upper and lower bay sites, allow us to make inferences about the relative value of these 2 regions as nursery habitat, and the factors that control their value, a continuing question in estuarine ecology (Craig & Crowder 2000, Beck et al. 2001, Gillanders et al. 2003).

While we have not directly measured all habitat attributes for each of our sites and target species, several direct and proxy measures are available. Total stomach fullness can serve as a proxy for resource availability (Gilliam & Fraser 1987), and the presence of large potential predators on the target species can serve as a proxy for predation risk. In our 4 yr of otter trawl sampling in Delaware Bay marsh creeks (1996 to 1999), potential large predators were not highly abundant in our samples, but were more common in our lower bay sites. For example, over this period we caught 88 *Morone saxatilis* (striped bass) and 10 *Paralichthys dentatus* (summer flounder) of >300 mm FL at our lower bay sites and only 6 *M. saxatilis* and 4 *P. dentatus* >300 mm FL at our upper bay sites, with similar sampling effort in the 2 regions (*M. saxatilis*: Nemerson 2001; *P. dentatus*: D. M. Nemerson unpubl. data). These totals may not accurately reflect the absolute abundance of large predators, as small otter trawls may not sample these fish well, but they do give an indication of the relative abundance of these predators in the lower and upper bay marsh creeks. In another study of *M. saxatilis* food habits at the same study sites, *Micropogonias undulatus* was the second most common fish prey, and accounted for about 13% of total gravimetric consumption (Nemerson & Able 2003). Several other investigators have concluded that potential predators on juvenile fishes, including larger *Cynoscion regalis*, *P. dentatus*, *Pomotomus saltatrix* (bluefish) and *M. saxatilis*, are generally more abundant in the more saline portions of estuaries, and consequently that predation rates may be higher in these areas (Weinstein & Walters 1981, Currin et al. 1984, Rozas & Hackney 1984, Miller et al. 1985, Paperno et al. 2000).

Earlier studies of spatial variation in feeding success and condition of *Cynoscion regalis* collected from open-bay locations in Delaware Bay agree in many respects with our results for this species collected from marsh creeks (Greco & Targett 1996, Paperno et al. 2000). In these studies, *C. regalis* collected from locations in the bay near our lower bay marsh creek sites (referred to as 'middle bay' stations in their studies) had fuller stomachs and were in better condition than fish collected farther up the bay near our 3 upper bay marsh-creek sites. While *C. regalis* were most abundant and achieved high feeding success at our lower bay sites, they were also present at upper bay sites, notably so at Mad Horse Creek, and they did experience reduced feeding success at these sites (Fig. 4). Given that laboratory evidence shows that physico-chemical conditions common at the upper bay sites are suboptimal for *C. regalis* (Lankford & Targett 1994), reduced predation pressure is an attractive explanation for their presence there, although this hypothesis has not been tested directly.

In a related study, *Cynoscion regalis*, along the long axis of Delaware Bay, had slower growth and shorter length-at-age in the lower-salinity areas of the upper bay (Paperno et al. 2000). However, Paperno et al. (2000) also found that mortality was lower in these habitats. Our results are somewhat equivocal relative to this study. In 1997, *C. regalis* recruited to both Dennis/Moores and our upper bay sites at the same time and in similar numbers, and the loss rate over time was very similar (Fig. 4). In 1998, *C. regalis* recruited far more strongly to Dennis/Moores where abundance peaked in July at 3 times the level found at the upper bay sites. However, subsequent loss was far greater at Dennis/Moores, resulting in similar abundance by the end of the nursery period, indicating the potential for higher mortality in lower bay marsh creeks.

Our findings of higher abundance and strong feeding success for *Cynoscion regalis* at Dennis/Moores may not be indicative, then, of overall higher habitat quality there, in the sense of producing the most recruits (Beck et al. 2001). Paperno et al. (2000) suggest that the potential for higher mortality in this region of the bay, presumably due to predation, may result in a smaller number of larger 'graduates' compared to the lower mortality but resource-poor upper bay. While our findings suggest that mortality, as estimated by loss from one sampling period to the next, may indeed be higher in lower bay creeks, particularly when *C. regalis* abundance is high, our length data do not support the concept of the production of larger recruits in these habitats. In both years, *C. regalis* were smaller at Dennis/Moores than at the upper bay sites, and even decreased in size with time in 1998 (Fig. 4), indicating the continued recruitment of small individuals to these sites. This suggests potentially even higher mortality in the lower bay, as the new recruits failed to bolster lower bay abundance later in the nursery period. We also saw no evidence of the presence of larger potential graduates in the lower bay toward the end of the nursery period.

Previous work has also shown spatial variation in the density, growth and mortality of *Leiostomus xanthurus* across estuarine habitats, including specifically in marsh creek systems, where *L. xanthurus* can be very abundant. In Virginia, O'Neil & Weinstein (1987) found *L. xanthurus* to be twice as abundant in polyhaline than in meso-oligohaline marsh creeks. Based on equal otolith growth increments in the 2 areas, these authors also concluded that resources appeared adequate in both regions, although they did not measure stomach fullness directly. However, in another study, Weinstein & Walters (1981) concluded that *L. xanthurus* mortality was higher in polyhaline marshes than in oligohaline marshes in one year of the study and equal in the other year. In laboratory choice experiments,

food availability had a greater influence than predation risk on juvenile *L. xanthurus* distribution (Miltner et al. 1995). Our findings are in general accord, in that *L. xanthurus* were more abundant where they experienced the greatest feeding success (Fig. 3) and potentially faced the greatest predation threat.

Overall, our *Leiostomus xanthurus* data are somewhat equivocal with respect to the value of upper versus lower bay sites. In 1997, catch and length data (Fig. 3) indicate that these fish recruited to the upper bay creeks later in the summer and at larger sizes than the recruits to the lower bay earlier in the year. It is not clear whether these later-arriving upper bay fish were first present in the lower bay and then moved up-bay, or arrived directly from the ocean. This pattern of spatial recruitment is opposite to that reported in the Cape Fear estuary by Weinstein (1979), who concluded that the estuary 'filled up backwards,' indicating that these patterns vary spatially and may vary temporally at the same location. From July through the end of the nursery period in 1997, the loss rate of *L. xanthurus* was very similar in both regions, despite higher food consumption in the lower bay. By the end of the 1997 nursery period, there were similar quantities of *L. xanthurus* of roughly similar size in the creeks of both bay regions (Fig. 3).

The strong recruitment and subsequent decline and possible year class failure of *Leiostomus xanthurus* in 1998 is intriguing. In 1998, abundance of the confamilials *Cynoscion regalis* and *Micropogonias undulatus* was far higher than in 1997 (Figs. 4 & 5). Feeding success of *L. xanthurus* in 1998 was depressed relative to 1997, particularly in May and June (both months significant, Wilcoxon 2-sample rank sum test, $p < 0.05$, Fig. 3). This is perhaps indicative of inter-specific resource competition among these fishes resulting in reduced feeding and survival of *L. xanthurus*. Clearly, more data are needed to determine the potential for biotic interactions among juvenile sciaenids in these creeks.

Micropogonias undulatus had a similar pattern to both *Cynoscion regalis* and *Leiostomus xanthurus*, i.e. higher abundance and generally greater stomach fullness at Dennis/Moores than at the upper bay sites (Fig. 5). In both years, abundance was 1 to 3 orders of magnitude higher at Dennis/Moores than at the upper bay sites in the beginning of the sampling season, and declined at similar rates in both regions. While the rate of loss appears similar in both regions, the absolute loss of individuals was far greater at Dennis/Moores than at the upper bay sites (Fig. 5). Thus, overall loss (and potentially mortality) was higher at Dennis/Moores, consistent with the likelihood of more intense predation at these sites, although *M. undulatus* were more abundant in the lower bay sites in both years prior to the fall emigration.

The 1 estuarine resident species in the study, *Morone americana*, showed a different and less clear-cut pattern of abundance and feeding success (Fig. 6). In 1997, *M. americana* were most abundant in the upper bay in April and May and again in October and November. Stomach fullness appeared to increase somewhat during the period of low abundance in the upper bay (June to September; Fig. 6), suggesting that physico-chemical conditions and not lack of food availability caused these fish to leave the creek sampling sites during this summer. However, in 1998, abundance at the upper bay sites did not decrease during the summer and was always far higher than at Dennis/Moores (Fig. 6). Fullness was generally lower in 1998, as was fish size at the upper bay sites (Fig. 6).

The high abundance of *Morone americana* at Mill Creek does not appear to be due to the fish seeking a higher resource habitat, as feeding success was generally lower in 1998 when abundance was dominated by catches at Mill Creek, and may be a result of either low predation pressure, physico-chemical suitability, or another unrecognized factor. Because *M. americana* is primarily a brackish to freshwater species, with juveniles preferring salinities of <3 and adults <9 (Setzler-Hamilton 1991), it is likely that while intra-specific competition was low and feeding success high in the lower bay, physico-chemical conditions during the summer prevented these sites from being generally suitable to large numbers of *M. americana*.

In summary, all 4 species studied exhibited distinct patterns in the types and quantities of food consumed at the different study sites. Furthermore, the abundance of all species was related to total stomach fullness in ways that appear non-random. The current study provides compelling, indirect evidence about the roles of resource availability, predation pressure and physico-chemical suitability in controlling the distribution of 4 species that are common in Delaware Bay as juveniles.

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