

Selective feeding in a generalist invertivore, age-0 striped bass

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Abstract – Age-0 striped bass (*Morone saxatilis*) and potential benthic and epibenthic invertebrate prey were collected at three sites in the mid-estuarine region of the Hudson River, New York, USA. Diet was related to prey availability to investigate the role of selectivity in feeding behaviour. The effects of prey availability and selectivity on stomach fullness were also examined. Gammarid amphipods and chironomid larvae were most numerous as stomach contents; and chironomid larvae, polychaetes, and isopods were the most numerous invertebrates captured. When selective feeding occurred, gammarid amphipods, *Crangon* spp. shrimp, and chironomid larvae were most commonly the preferred prey. Selective feeding correlated with higher stomach fullness. Fullness was also higher when the preferred prey was categorized as epibenthic versus benthic. Interaction between prey availability and environmental conditions appears to be an important determinant of age-0 striped bass feeding behaviour.

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Key words: prey selectivity; feeding behaviour; turbidity; striped bass

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Introduction

Fish feed opportunistically yet are often selective in their diets (Ehlinger & Wilson 1988, Gerking 1994, Fry et al. 1999). Selective feeding behaviour results from internal factors that may be anatomical, physiological or behavioural, and from external factors such as prey encounter and catchability (Juanes 1994, Juanes et al. 2002). The interaction and dynamics of these factors can result in variable and non-random feeding behaviour even in species often considered generalists. Feeding behaviour at the level of prey selection can have implications at the individual (Fraser et al. 2007), population (Herwig & Zimmer 2007), and community levels (Schleuter & Eckmann 2007).

Striped bass, *Morone saxatilis* (Walbaum, 1792), is important commercially and recreationally along the eastern coast of the United States (ASMFC 2005) and is often considered to be a feeding opportunist (Markle & Grant 1970, Boynton et al. 1981, Cooper et al. 1998, Hurst & Conover 2001). Age-0 striped bass are abundant in the Hudson River estuary (Boreman & Klauda 1988, McKown & Gelardi 2000) where they

provide an important trophic link as both predators and prey (Buckel et al. 1999). Age-0 striped bass in the Hudson River eat a variety of benthic (infaunal) prey, including oedicerotid amphipods, chironomid larvae, polychaetes, and isopods; and epibenthic (hyperbenthic) prey including gammarid amphipods, decapod shrimp and crabs, and mysid shrimp (Hurst & Conover 2001, Jordan et al. 2003). Their diets vary spatially and temporally (Jordan et al. 2003), but it is unknown how much of this variation reflects prey availability or is a function of prey selectivity.

In this study, we sampled age-0 striped bass stomach contents and potential benthic and epibenthic prey on four dates between July and October, 2000 at three locations in the mid-estuarine portion of the Hudson River. We then related prey consumption to prey availability to investigate the role of selectivity in feeding behaviour. We also examined stomach fullness to investigate the potential implications of prey availability and selectivity on feeding success. Striped bass are visual predators and the visual environment in estuarine habitats is dynamic, we therefore also tested the hypothesis that turbidity affects striped bass feeding behaviour.

Materials and methods

Study area

Striped bass and potential prey were sampled concurrently at three locations: Manitou, Croton Point and Dobbs Ferry, in the mid-estuarine portion of the Hudson River (Fig. 1) in 2000. These sites were chosen because they are spaced roughly equidistantly along the section of the river where age-0 striped bass are known to be abundant and because they were likely to differ in prey available and physical characteristics. The substrate at Manitou included heavily embedded, large rocks composing <25% of the surface area and mud mostly layered with organic debris. Croton Point was largely densely packed coarse sand and pebbles along with patches of finer sand. At Dobbs Ferry, the substrate was mainly packed finer sand interspersed with patches of organic debris and plant matter.

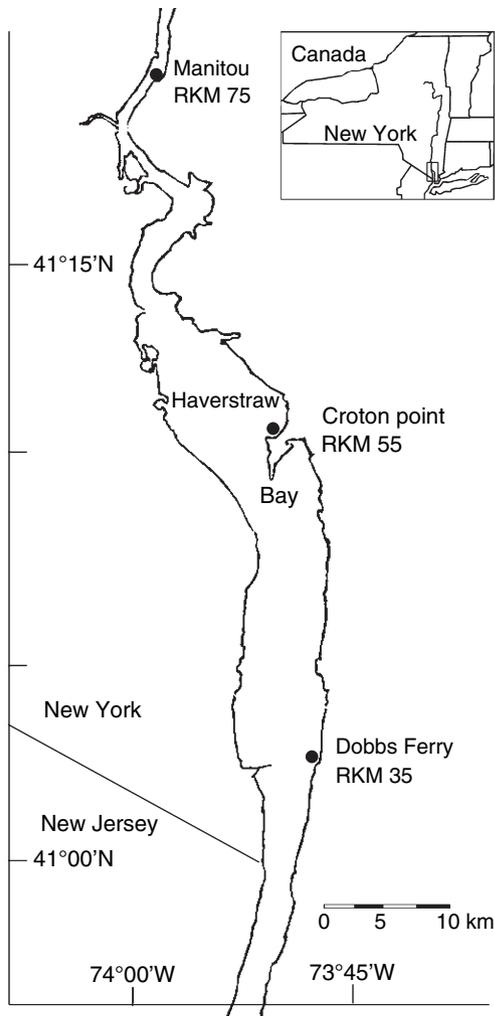


Fig. 1. Map of the Hudson River indicating location (RKM = River kilometer) of the three collection sites.

Fish sampling and diet analysis

At each location, samples were collected on one day and night during three periods, 30–31 July, 22–23 August and 16–17 September, and during the day only on 21 October. Sampling occurred as close to low tide as possible. Salinity, water and air temperature, dissolved oxygen and turbidity (formazine turbidity units, FTU) were recorded. Fish were seined with a 50 m, 7-mm mesh seine until five hauls were completed or 30 age-0 striped bass were captured. Total length ($TL \pm 1$ mm), standard length ($SL \pm 1$ mm) and weight (± 0.01 g) were measured on location and striped bass were decapitated and placed in formalin for later stomach content analysis. Decapitation enabled rapid fixing of stomach contents. Striped bass lengths were compared by site using ANOVA. In the laboratory, stomach contents were identified and percent number (%N), i.e., the ratio of the number of items in a given prey category to total number of consumed prey items expressed as a percent, was calculated. Fullness was calculated as stomach content weight (± 0.001 g) divided by fish weight – stomach content weight. Empty stomachs were included to most realistically characterize and compare feeding success. Fish stomachs were most commonly empty in night samples, which were either separated from day samples or not used in parametric tests.

Invertebrate sampling

Potential benthic and epibenthic prey were collected using a D-framed sampling net and a sand auger following the protocol designed by Hicks (1999). Sampling locations were randomly assigned along five transects parallel to the shore and equally spaced out to 1 m water depth. Three transects were used for net sweeps and two for auger cores. A flow meter was attached to the net and used along with net dimensions to determine the surface area covered by the net sweeps. Sweep lengths were approximately 3–4 m and the net was towed over the substrate along the transect. If an impassable obstruction impeded the tow, a new transect was established over undisturbed substrate. Average substrate surface area sampled by three sweeps was $3.63 \text{ m}^2 \pm 0.87 \text{ SD}$. The auger was twisted into the substrate to a maximum depth of 8 cm, and four cores were taken per transect. The substrate surface area sampled by 12 auger cores totaled 0.18 m^2 . Captured organisms were placed in 10% buffered formalin for later identification. To combine organism counts from the two methods, counts from the auger were extrapolated to the area sampled by the net for the given sampling event. This estimate was then converted to numbers of individuals/ m^2 .

Selectivity and fullness

PREFER v. 5.1 (Pankratz 1994) was used to test for selectivity. PREFER applies the non-parametric approach described in Johnson (1980) to compare resource utilization and availability. Waller and Duncan (1969) multiple comparison tests are used by PREFER to find the sources of heterogeneity if selectivity is detected. Percent number of prey individuals by taxon in each striped bass stomach comprised the prey utilization data, and percent number of individuals by taxon in the respective habitat represented the prey availability data. We used numbers of prey items rather than weights because of the difficulty in separating mixed stomach contents and error associated with weighing small or incomplete prey items. We categorized samples in which striped bass had fed selectively as either benthic or epibenthic based on the highest ranking prey item. We used Mann–Whitney (two-sided) and Kruskal–Wallis tests to compare stomach fullness by location and time of collection and *t*-tests (two-tailed) to relate feeding behaviour to turbidity and stomach fullness. Only day caught striped bass were used in the test of the effect of presence or absence of selectivity on fullness because fullness differed between day and night. Linear regression was used to correlate turbidity with stomach fullness. Samples were separated into day and night and means of stomach fullness by site were used in the analysis. A significance level of 0.05 was used in all tests.

Results

We collected 331 age-0 striped bass ranging in TL from 34 to 110 mm. Total lengths did not differ among sites overall (ANOVA, d.f. = 317, *F* = 2.55, *P* = 0.08). No striped bass were captured at Manitou during the first sampling event. Striped bass were generally most abundant at Croton Point and only once did we capture 30 striped bass in five seine hauls at another site (Table 1). Twice at Croton Point, we captured 30 or more striped bass in just four hauls. The most striped bass we retained from a single haul was 14. In general, fewer striped bass were collected during the night than during the day. Water temperature did not differ by location (Kruskal–Wallis, *H* = 0.30, d.f. = 2, *P* = 0.863); salinity decreased with latitude (Table 1). Turbidity at Croton Point averaged less than half than at the other sites, and this site was also the most highly oxygenated (Table 1).

Striped bass food habits

Stomach contents were well preserved and were almost entirely identifiable. At all sites striped bass consumed

Table 1. Total bass captured, salinity (ppt), turbidity (formazine turbidity units), dissolved oxygen (ppm) and percent oxygen saturation (%Sat) at each site by week and time.

Site	Week	<i>n</i>	Salinity	Turbidity	H ₂ O (°C)	DO	%Sat
Manitou	2D	5	1.0	34.6	24.5	7.4	88.0
Manitou	2N	10	1.0	18.7	22.0	6.8	77.0
Manitou	3D	13	0.3	81.0	22.0	7.8	88.0
Manitou	3N	4	0.3	19.8	22.0	7.2	81.0
Manitou	4D	8	0.3	60.0	17.0	8.7	92.0
Croton	1D	32	3.0	7.0	23.0	8.4	96.0
Croton	1N	32	1.8	17.0	23.0	6.4	75.0
Croton	2D	32	2.5	8.3	22.0	9.7	110.0
Croton	2N	17	2.0	6.3	23.0	8.0	91.0
Croton	3D	32	3.3	46.7	22.5	9.0	103.0
Croton	3N	6	3.5	14.9	19.5	9.3	100.0
Croton	4D	30	3.8	31.1	17.5	9.8	101.0
Dobbs	1D	32	5.5	14.0	23.0	6.5	75.0
Dobbs	1N	5	5.5		23.0	6.4	74.0
Dobbs	2D	25	4.0	80.0	22.0	7.7	84.0
Dobbs	2N	28	5.0	39.0	23.0	7.4	87.0
Dobbs	3D	13	6.5	84.0	23.5	8.3	93.0
Dobbs	3N	5	6.0	31.9	21.0	10.5	82.0
Dobbs	4D	2	7.5	25.1	16.0	8.7	88.0

D and N refer to day and night.

gammarid and oedicerotid amphipods, chironomid larvae, *Crangon septemspinosa* (sand shrimp), and polychaete worms (Table 2). *Palaemonetes* spp. (grass shrimp), mysid shrimp (possum shrimp), fish, isopods and copepods were eaten at Dobbs Ferry and Croton Point but not Manitou. Portunid crabs (blue crabs) were consumed only at Dobbs Ferry. Stomach fullness did not differ among sites except on the nights of the second and third weeks (Table 3, Kruskal–Wallis *P* = 0.027 and 0.014, respectively).

Invertebrate abundance

In general, Manitou had the least diversity and lowest overall density of prey, with chironomid larvae and gammarid amphipods being the most consistently available and reaching the highest densities of prey taxa at the site. Chironomid larvae were also among the most abundant invertebrates at Croton Point, reaching densities up to 15 times higher there than at Manitou. Isopods also reached high densities at that site. Shrimp abundance was low at both Manitou and Croton Point, but was slightly higher at Croton Point than at Manitou. All shrimp types and oedicerotid amphipods were most abundant at Dobbs Ferry. Gammarid abundance at Dobbs Ferry did not differ from Manitou (two-sample *t*-test, *t* = -0.31, d.f. = 8, *P* = 0.762). Dobbs Ferry ranked highest in polychaete abundance and it was the only site with portunid crab larvae.

Table 2. Striped bass prey selectivity.

Taxon	Site	Day1		Night1		Day2		Night2		Day3		Night 3		Day 4	
		%N	D	%N	D	%N	D	%N	D	%N	D	%N	D	%N	D
CR(E)	M							11.1		0	0.3	0			
GA(E)	M					77.8	2.3	77.8	3.3	57.1	9.9	80	10.5	73.1 ^b	22.2
MY(E)	M														
PA(E)	M														
PO(E)	M														
CH(B)	M					22.2	11.3	11.1	19.5	21.4 ^a	3.1	20	6.9	11.5 ^b	0.3
IS(B)	M					0	0.6	0	5.9	21.4 ^a	3.1	0	0.5	0c	5.4
OD(B)	M					0	0.9	0	1					11.5 ^a	1.0
PC(B)	M					0	5.4	0	10.8					3.9 ^b	0
CR(E)	C	0.1 ^a	0	1.1	0.3	0.4 ^b	0							4.8 ^b	0.1
GA(E)	C	1.6 ^a	0.5	12.8	7.5	2.9 ^a	0.1	40 ^a	0	4 ^b	0.2	27.1	0.7	33.7 ^d	0
MY(E)	C													3.8 ^c	6.2
PA(E)	C			0	0.3	0.2 ^b	0	0	0.6	0.6 ^c	0.1	1.2	0		
PO(E)	C														
CH(B)	C	97.6 ^b	78.9	85.1	54.3	93.3 ^c	45.7			89 ^a	0.3	50.6	5.4	17.3 ^f	304.2
IS(B)	C	0.4 ^c	21.9	1.1	16.2	2.7 ^f	96.3	20 ^a	0.3	6.2 ^b	0.2	11.8	0.1	34.6 ^d	65.7
OD(B)	C					0.4 ^d	8.1	20 ^a	0.1			9.4	0	0.0 ^a	10.8
PC(B)	C	0.3 ^b	5.4	0	10.8	0 ^e	37.9	20 ^a	0.4	0.3 ^b	0.1			5.8 ^d	10.8
CR(E)	D	29.3 ^a	0.5	16.7	0	12.1 ^b	0.3			1.6	0.5	0	3.9	8.3	0
GA(E)	D	16.4 ^c	21.5	83.3	0	33.3 ^b	0.5	38.9 ^b	1.8	13.1	21.6	9.5	23.7		
MY(E)	D			0	5.4			0.0 ^b	0.4	4.9	1.5	4.8	8.3	83.3	19.8
PA(E)	D	48.3 ^b	4.6			12.1 ^a	0	6.9 ^b	0.7					8.3	0.6
PO(E)	D					3.0 ^c	0.5	11.1 ^c	2.1	18.0	1.2	0	5		
CH(B)	D	2.6 ^b	1.5			15.2 ^a	0	1.4 ^a	0	52.5	1.2				
IS(B)	D			0	0.4	15.2 ^d	21.7	8.3 ^d	49.4	0	23.1	19	17.7		
OD(B)	D					6.1 ^d	9.1	26.4 ^c	49.1	9.8	58.0	61.9	91.8		
PC(B)	D	3.4 ^d	43.6			3.0 ^e	37.9	4.2 ^e	97.8	0	22.1	4.8	86.6		

CR, *Crangon*; GA, gammarid; MY, mysid; PA, *Palaemonetes*; PO, Portunid; CH, chironomid; IS, isopod; OD, oedicerotid; PC, polychaete. 'E' or 'B' following taxa indicates categorization as either epibenthic or benthic. Prey %N as stomach contents and abundance per m² (D) are shown. Superscripts indicate results of the Waller–Duncan procedures and show order of preference when selectivity was detected. Items sharing the same superscript do not differ significantly.

Table 3. Mann–Whitney and Kruskal–Wallis tests of striped bass stomach fullness.

Site	\bar{x}	n	SD	Site	\bar{x}	N	SD	Test
Week 1	Day			Night				
Croton	0.030	32	0.029	Croton	0.002	31	0.003	Z = 0.66
Dobbs	0.021	31	0.015	Dobbs	0.003	5		P = 0.509
Week 2								
Manitou	0.011	5	0.002	Manitou	0.003	10	0.007	$\chi^2 = 7.19$
Croton	0.008	32	0.007	Croton	0.005	13	0.004	P = 0.027
Dobbs	0.008	24	0.006	Dobbs	0.013	28	0.011	
Week 3								
Manitou	0.002	11	0.002	Manitou	0.002	4	0.004	$\chi^2 = 8.48$
Croton	0.011	32	0.010	Croton	0.021	5	0.009	P = 0.014
Dobbs	0.006	11	0.003	Dobbs	0.004	3	0.002	
Week 4								
Manitou	0.015	5	0.018					
Croton	0.011	32	0.010					
Dobbs	0.029	2	0.002					

Z scores are reported for the Mann–Whitney tests; χ^2 values for the Kruskal–Wallis tests.

Selectivity

Selective feeding was detected in 10 of 19 samples overall (Table 2). Of five collections at Manitou, striped bass in two collections had fed selectively

(Day 2: $F = 45.24$, $P < 0.001$; Day 4: $F = 58.22$, $P = 0.001$). Chironomid larvae were the preferred prey, accompanied by either oedicerotids or polychaetes. Gammarids, the most abundant potential prey items in those samples, were eaten in disproportionately low numbers. Isopods were found in four of five benthic samples at Manitou, but were never found in striped bass stomachs. Polychaetes were found in three benthic samples, and found in striped bass stomachs in only one sample.

At Croton Point, selective feeding occurred in all four day samples and in one night sample (Day 1: $F = 146.81$, $P < 0.001$; Day 2: $F = 637.44$, $P < 0.001$; Night 2: $F = 191.63$, $P < 0.001$; Day 3: $F = 9.66$, $P = 0.003$; Day 4: $F = 88.93$, $P < 0.001$). On the first, second and fourth days, Gammaridae was the preferred taxon, although not differing significantly from *Crangon* spp. on the first day. Chironomid larvae were the highest ranking prey taxon on the third day. In the night sample showing selectivity, gammarids ranked highest in %N, although the difference among the top four prey items was not significant. At Dobbs Ferry, three of seven samples indicated selectivity (Day 1: $F = 83.24$, $P < 0.001$; Day 2: $F = 82.84$, $P < 0.001$;

Night 2: $F = 128.06$, $P < 0.001$). *Crangon* shrimp, chironomid larvae, and chironomid larvae plus *Palaemonetes* shrimp were preferentially consumed. Polychaete worms, while most numerous in the invertebrate samples on those occasions, ranked lowest in preference. Isopods were also numerous at Dobbs Ferry, most notably during the second and third sampling periods, but consistently ranked low as ingested prey.

Relationships among turbidity, fullness and selectivity

We found no effect of turbidity on whether or not striped bass had fed selectively ($P = 0.607$, Table 4). Mean turbidity, however, was significantly higher for samples in which the highest ranking prey item was benthic versus epibenthic ($P < 0.001$). Stomach fullness was different between striped bass from samples in which selectivity occurred and in which selectivity did not occur ($P = 0.017$). Stomach fullness was also different between striped bass in the benthic and the epibenthic categories ($P = 0.026$). We found a significant inverse relationship between turbidity and stomach fullness during the day ($P = 0.027$), but not in nighttime samples ($P = 0.806$) (Fig. 2).

Table 4. Results of two-tailed *t*-tests comparing turbidity and fullness by feeding behaviour (selectivity vs. no selectivity, epibenthic vs. benthic).

x	y	Means	d.f.	P
Selectivity +/-	Turbidity	$\bar{y}_1 = 37.3, \bar{y}_2 = 30.8$	16	0.607
	Fullness	$\bar{y}_1 = 0.017, \bar{y}_2 = 0.009$	24	0.017
Epibenthic/benthic	Turbidity	$\bar{y}_1 = 61.3, \bar{y}_2 = 13.6$	8	0.002
	Fullness	$\bar{y}_1 = 0.015, \bar{y}_2 = 0.009$	8	0.026

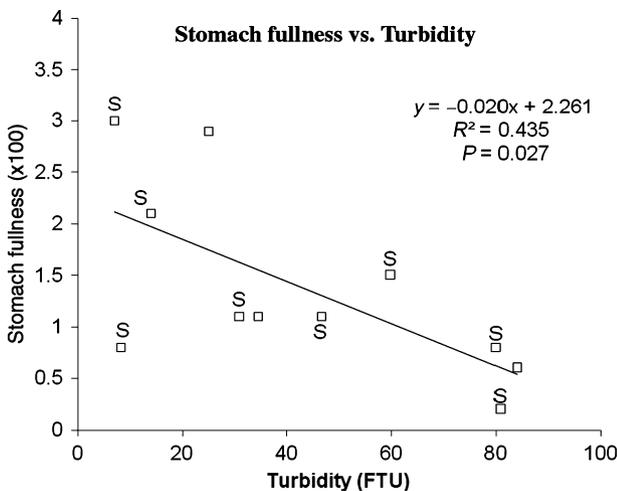


Fig. 2. Regression of stomach fullness on turbidity. As the regression for night samples was not significant, only the results for day caught striped bass are shown. Points represent the mean fullness of each subset of striped bass. For reference, subsets in which selectivity was detected are marked with 'S'.

Discussion

The diets described here are similar in prey composition to those previously reported for striped bass in the Hudson River (Gardinier & Hoff 1982, Hurst & Conover 2001, Jordan et al. 2003) and for other locations on the east coast of North America (Boynton et al. 1981, Cooper et al. 1998, Harding & Mann 2003, Walter et al. 2003). This is the first time to our knowledge; however, where prey selectivity has been assessed for post-larval age-0 striped bass using field-derived estimates of prey availability, necessary to quantify selectivity (Juanes 1994, Juanes et al. 2002).

Sampling methodology and prey patchiness

Assessing prey availability for such a fish is difficult because of the variety of lifestyles of the prey and their patchy distribution. Using two methods, we were able to collect all prey types ingested by striped bass. On a few occasions, prey density was low in comparison to presence in stomachs and at times there was a disparity between day and night prey densities. Although we captured striped bass in shallow water, they may have been feeding in deeper water, especially at Croton Point where turbidity was low. During the day, however, striped bass were observed feeding near shore. Although we made every attempt to repeat prey sampling in the same location, the distance from shore of the 1 m depth line varied more greatly at Croton Point even close to the point of low tide.

Another possibility is that striped bass and other fish had markedly reduced prey populations. Evidence suggestive of such an effect by predators is strongest at Croton Point, especially on the second day and third night. At other times, prey densities remained sufficiently high to enable reasonable conclusions about trends in preference. The low abundances at Croton Point also raise the possibility that age-0 striped bass and other fish might be prey limited at times in the Hudson River. A benthic sampling strategy that extracted a larger surface area and which took more samples might improve assessment of prey density, although these measures might limit sampling to one location per day.

Predator behaviour and spatial variation in diet

Age-0 striped bass are generally considered 'opportunistic' predators suggesting little selectivity among prey types (Markle & Grant 1970, Boynton et al. 1981, Cooper et al. 1998, Hurst & Conover 2001). A recent review of age-0 striped bass diets concluded that there is little regional variation, but often high variability within a region and attributes this contrast to spatial and ontogenetic variation in feeding ecology

(Walter et al. 2003). Thus, diets reflect differences in ontogenetic habitat use which also lead to spatial variation in growth and trophic position (Wainwright et al. 1996). Our results suggest that spatial differences in growth and diet found in other studies could at least in part be a function of prey selectivity and thus predator behaviour.

Constraints on prey utilization

Selective feeding is a function of predator and prey morphological constraints as well as behavioural interactions between predator and prey (reviewed in Juanes et al. 2002). The age-0 striped bass in this study had eaten a variety of foods, but stomach contents commonly diverged from patterns in availability of invertebrates present in the habitat resulting in significant selectivity. Certain prey, such as isopods (*Cyathura* spp.) and polychaetes (*Marenzelleria* spp.) were largely avoided, even when common. These species may go undetected because of their colour and association with the benthos. Cryptic colouration might explain why ingestion of these taxa was somewhat more proportionate, yet still low, at Croton Point where water was clearest and the substrate least silted. These species may also be inefficient prey for age-0 striped bass because of their morphology. Both are elongated and dorso-ventrally flattened. *Cyathura* spp. has six pairs of walking legs and *Marenzelleria* has abundant chaetae that might make extraction from the substrate difficult.

Ontogeny and selectivity

Temporal and ontogenetic trends in age-0 striped bass diets have been noted previously (Jordan et al. 2003); however, in this study we noted no changes in selectivity with time. We also found no upward trend in ranking of large-bodied shrimp with predator age, which might be predicted given the pattern of increasing prey size reported in Jordan et al. (2003). Further, small-bodied prey taxa like gammarids and chironomid larvae typically ranked highly when present, even late in the season. It is possible, however, that the short-time scale in the present study was unable to capture a temporal or ontogenetic effect.

Cause of selectivity

Our results indicate that habitat-specific conditions including substrate and visibility can be factors in the selective feeding and prey choices of age-0 striped bass. Selective feeding occurred most often at Croton Point, raising the possibility that some condition there enables this behaviour. The sandy,

pebbly substrate at Croton Point might allow for more efficient prey capture compared with the mud and organic debris found elsewhere; thus, explaining the higher incidence of isopods and polychaetes in Croton Point diets. This site is located on the north side of a peninsula extending perpendicularly into the river, and is thus sheltered from wind and water currents. Also, the shallow water area is greater at Croton Point than at Dobbs Ferry and especially Manitou. These conditions might effectively increase foraging area and decrease the ability of prey to escape, particularly the often more preferred pelagic prey including shrimp and gammarid amphipods. Selectivity may also be triggered by some level of abundance of preferred prey. Decreased shelter for prey in areas with clear substrates might increase the abundance of prey perceived by the predator. Croton Point was the least turbid; however, we did not find a significant correlation between turbidity and selectivity.

Potential benefits of selectivity

Selectivity appears to be beneficial to age-0 striped bass as would be predicted by foraging theory when prey items differ in cost and benefits (Stephens & Krebs 1986). Feeding success, as measured by stomach fullness, was higher for striped bass that had fed selectively. Although turbidity appeared not to have promoted selective feeding, it did alter feeding behaviour in a way that has implications for growth. Higher turbidity correlated with higher ranking of infaunal types of prey, especially chironomid larvae. This benthic mode of selective feeding resulted in lower stomach fullness than when gammarids were the highest ranking prey. This loss may be offset by the higher caloric density of dipteran larvae versus amphipods, reported as 21% in Cummins & Wuycheck (1971). The strong preference for gammarid prey in clear water, however, suggests that this prey may offer some benefit over chironomids. In conclusion, our results suggest that previously observed spatial differences in diet and growth of juvenile striped bass (Cooper et al 1998, Wainwright et al. 1996, Harding & Mann 2003) might be a consequence of habitat-specific differences in selective behaviour. Future work should quantitatively examine the relationship between feeding efficiency, prey selectivity and growth.

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