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Influence of habitat on diet and distribution of striped bass (Morone saxatilis) in a temperate estuary

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INFLUENCE OF HABITAT ON DIET AND DISTRIBUTION OF STRIPED BASS (*MORONE SAXATILIS*) IN A TEMPERATE ESTUARY

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ABSTRACT

Striped bass (*Morone saxatilis*) are recreationally and commercially valuable finfish along the Atlantic seaboard of North America including the Chesapeake Bay estuary. Habitat use patterns for striped bass in relation to biogenic habitat types in Chesapeake Bay tributaries are poorly described although it is widely acknowledged that these piscivorous fishes use estuarine habitat for nursery and feeding grounds during development. Striped bass diet and distribution patterns were examined in relation to a gradient of biogenic habitats ranging from complex three-dimensional oyster reef through flat oyster bar to sand bottom habitat in the Piankatank River, Virginia. Striped bass were more abundant at both sites with oysters and oyster shell substrate than at the site with sand substrate. Striped bass in association with the three-dimensional oyster reef were larger and consumed more teleosts (e.g., naked gobies) than fish at either of the non-reef sites. Striped bass estuarine habitat use is positively correlated with the presence of oyster reef habitat that includes physical structure and food resources via complex trophic communities centered on the oyster reef.

Striped bass (*Morone saxatilis*) are apex predators commonly found in estuarine and coastal waters along the Atlantic and Pacific coasts of North America (Raney, 1952). These large anadromous fish are highly sought after by both commercial and recreational fishermen throughout their range. Chesapeake Bay and Hudson River striped bass stocks are the major contributors to the North American Atlantic coast spawning stock (Merriman, 1941; Raney, 1952; Berggren and Lieberman, 1978; Kohlensten, 1981). Relative contributions of each stock to the fishery are partially dependent on year-class strength and can be highly variable (Van Winkle et al., 1988).

Estuarine habitats such as Chesapeake Bay provide spawning, nursery, and feeding grounds for multiple life history stages of striped bass. These anadromous predators spawn in tidal freshwater areas of Chesapeake Bay tributaries from early April–early June (Raney, 1952; Uphoff, 1989; Grant and Olney, 1991; Olney et al., 1991). As larvae develop post-hatching, they are commonly found in shallow nearshore areas (Boynton et al., 1981; McGovern and Olney, 1996; Robichaud-LeBlanc et al., 1998). During their first summer, striped bass gradually move downriver into more saline waters (e.g., Markle and Grant, 1970; Setzler-Hamilton et al., 1981; Robichaud-LeBlanc et al., 1998). Most Chesapeake Bay juvenile and sub-adult striped bass remain in their natal estuaries for approximately two years post-hatching and then leave the estuaries to participate in seasonal coastal-estuarine migrations (Mansueti, 1961; Massmann and Pacheco, 1961; Setzler-Hamilton and Hall, 1991). Adult fish overwinter in estuarine waters and return to coastal waters after spring spawning events (Hollis, 1952; Setzler-Hamilton and Hall, 1991).

Given their status as apex predators, striped bass are an important trophic component for estuarine communities. Recreationally and commercially important pelagic fishes including striped bass, bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) use feeding and nursery grounds provided by Eastern oyster (*Crassostrea virginica*) reef communities (Harding and Mann, 1999; Breitburg, 1999; Coen et al., 1999; Harding and Mann, 2001b). Historically in Chesapeake Bay, oysters were a keystone species responsible for both benthic-pelagic coupling and the creation of three-dimensional reef structures (Newell, 1988; Kennedy et al., 1996 and references therein). Oyster reefs provide both food and habitat resources for complex estuarine food webs including apex predators e.g., striped bass, bluefish, weakfish. Long-term environmental degredation in the Chesapeake Bay watershed, combined with overfishing and disease, has caused a decline of the resident oyster population (Hargis, 1999) that has consequences affecting all trophic levels including apex predators such as bluefish (Harding and Mann, 2001a) and striped bass. Current natural oyster aggregations in Chesapeake Bay are much smaller in terms of vertical relief and basal extent (Hargis, 1999). Oyster restoration efforts focus on renewal of this keystone species (Luckenbach et al., 1999; Mann 2000; Coen and Luckenbach, 2000) through reconstruction of physical habitat. The argument is proffered that provision of structure accelerates development of ecological communities associated with oyster reefs towards climax or equilibrium states. One barometer of progress towards such an equilibrium is the development of reef fish assemblages towards stability in numbers, species richness, species composition, or trophic composition (Sale, 1980). Current monitoring programs of oyster reef restoration efforts have adopted this expanded trophic level approach to describe the temporal sequence of community development (Harding and Mann, 1998; Nestlerode et al., 1998; Breitburg, 1999; Coen et al., 1999; Harding and Mann, 1999; Posey et al., 1999; Coen and Luckenbach, 2000; Harding and Mann, 2000; Harding and Mann, 2001a; Harding and Mann, 2001b) with comparisons of habitat use by pelagic fishes of restored reef versus natural habitat as a major theme. The objective of this study was to compare striped bass diet and distribution across a gradient of habitats ranging from hard sand bottom to restored oyster reef within the same estuary across seasonal, diurnal, and tidal scales.

Methods

Study Sites.—Field work was conducted at three field sites in the Piankatank River, Virginia, U.S. (Fig. 1): Palace Bar oyster reef, an oyster shell bar (Ginney Point), and a sand bar (Roane Point). Palace Bar reef (N 37° 31′41.69, W 76° 22′25.98) is a three dimensional, intertidal oyster reef (210 × 30 m, reef depth range of 0.5 m above MLW to 3 m below MLW) adjacent to the Palace Bar oyster grounds. Palace Bar reef was built in 1993 by the Virginia Marine Resources Commission (VMRC) Shellfish Replenishment program as a series of 18 shell mounds centered on and around an east-west centerline 300 m long (Mann et al., 1996). Approximately 70% of the reef (0.63 ha) is composed of oyster shell, while the remaining area (0.27 ha) is crushed clamshell. Palace Bar reef has supported oyster densities similar to those observed on natural (i.e., not constructed) oyster bars in the Piankatank River since 1997 (Harding and Mann, 1999; R. Mann, unpubl. data). The Ginney Point site (N 37° 31′ 52.78, W 76° 24′ 08.40) is a flat oyster bar (approximately 400 × 50 m, depth range 2–5 m; Fig. 1) that also receives annual oyster spat settlement. The Roane Point site (N 37° 31′ 37.48, W 76° 22′ 39.63) includes a sand bar south and inshore of Palace Bar reef (approximately 400 × 15 m; depth range 1.5–4 m; Fig. 1). Mean tidal range in the Piankatank River is approximately 0.4 m. Water temperature and salinity were recorded weekly from May–October 1997 at Ginney Point and Palace Bar reef (Fig. 2) to provide comparative habitat information. Water samples were taken at the surface and just above the bottom with a Niskin bottle. Temperature was measured immediately with a thermometer and salinity was measured with a refractometer.

Sampling Periodicity and Methods.—Sampling events incorporated seasonal, tidal, and diurnal variation and were conducted during nine, 36 hr periods from May–September on the new and full moon (May 22–23, June 5–6, June 19–20, July 2–3, July 17–18, August 4–5, August 18–19, Sep-

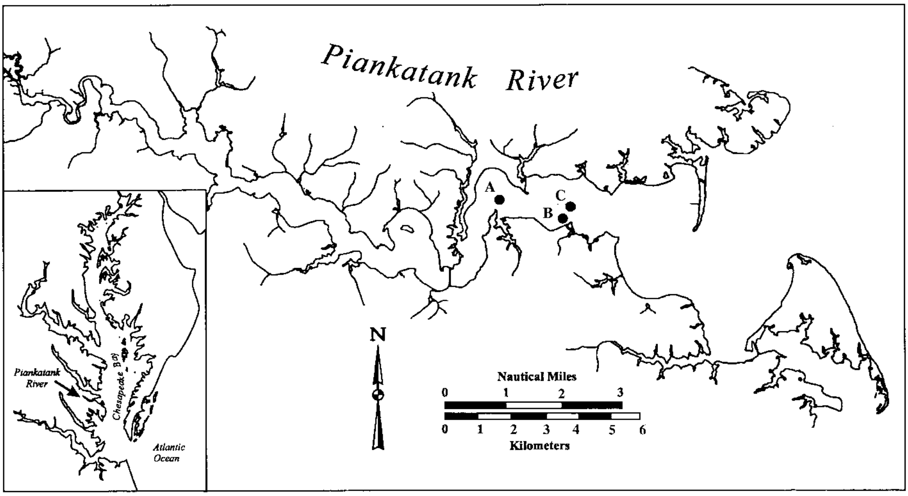

Figure 1. Map of the Piankatank River, Virginia, U.S. in relation to the Chesapeake Bay showing sampling locations. Palace Bar oyster reef (C) was sampled in relation to two non-reef sites representing a gradient in habitat complexity: Ginney Point, an oyster bar (A) and Roane Point, a sand bar (B) from Harding and Mann (1999).

tember 2–3 and September 15–16, 1997). During a single sampling event, all three sites (reef and non-reef) were sampled for 36 consecutive hours at three-h intervals corresponding to changes in tidal stage: flood, slack onto ebb, ebb, and slack onto flood. Digestion rates of six–eight hrs for copepods and amphipods have been reported for striped bass < 114 mm fork length (Heubach et al., 1963); sampling intervals of three hours made it less likely that invertebrate or vertebrate gut contents were lost due to digestion and/or evacuation.

Striped bass were sampled using multi-panel experimental gill nets (one 30.5 m × 1.8 m and two 30.5 m × 3.0 m nets all with one 7.6 m panel each of stretch square mesh monofilament of 57.2, 63.5, 73.0, and 76.2 mm) deployed such that the entire water column was sampled (e.g., the smallest net at the shallowest site) and were retrieved at three hour intervals corresponding with changes in tidal stage. Fishes were removed from the gill nets immediately upon retrieval, measured (fork length (FL), to the nearest mm), and gutted. The entire gastrointestinal tract of each fish was removed and immediately preserved in seawater formalin for subsequent gut content analyses. In the laboratory, striped bass gut contents were enumerated and identified to the nearest practical taxon.

Data Analyses.—Significance levels for all statistical tests were established at $P = 0.05$ a priori. Assumptions of homogeneity of variance were tested using Bartlett's test, while assumptions of normality were tested with the Ryan-Joiner test. When data did not meet these assumptions, nonparametric Kruskal-Wallis tests were followed by Dunn tests for post-hoc multiple comparisons (Zar, 1996). Tukey's test was used for post-hoc parametric multiple comparisons (Zar, 1996).

Water Temperature and Salinity Data.—Water temperature and salinity data were transformed (natural logarithm) prior to analyses and satisfied assumptions of both homogeneity of variance and normality prior to analyses with ANOVAs.

Abundance.—The total numbers of striped bass caught in the Piankatank River satisfied the assumptions of both homogeneity of variance and normality after transformation with the reciprocal transformation (per Zar, 1996). The transformed data were compared with an ANOVA incorporating site, day of the year, time of day, and tidal stage.

Length-frequency Data.—Striped bass fork lengths (FL, mm) for individual fish captured with gill nets in the Piankatank River did not satisfy the assumptions of homogeneity of variance or normality regardless of the transformation (logarithm, natural logarithm, square-root, reciprocal).

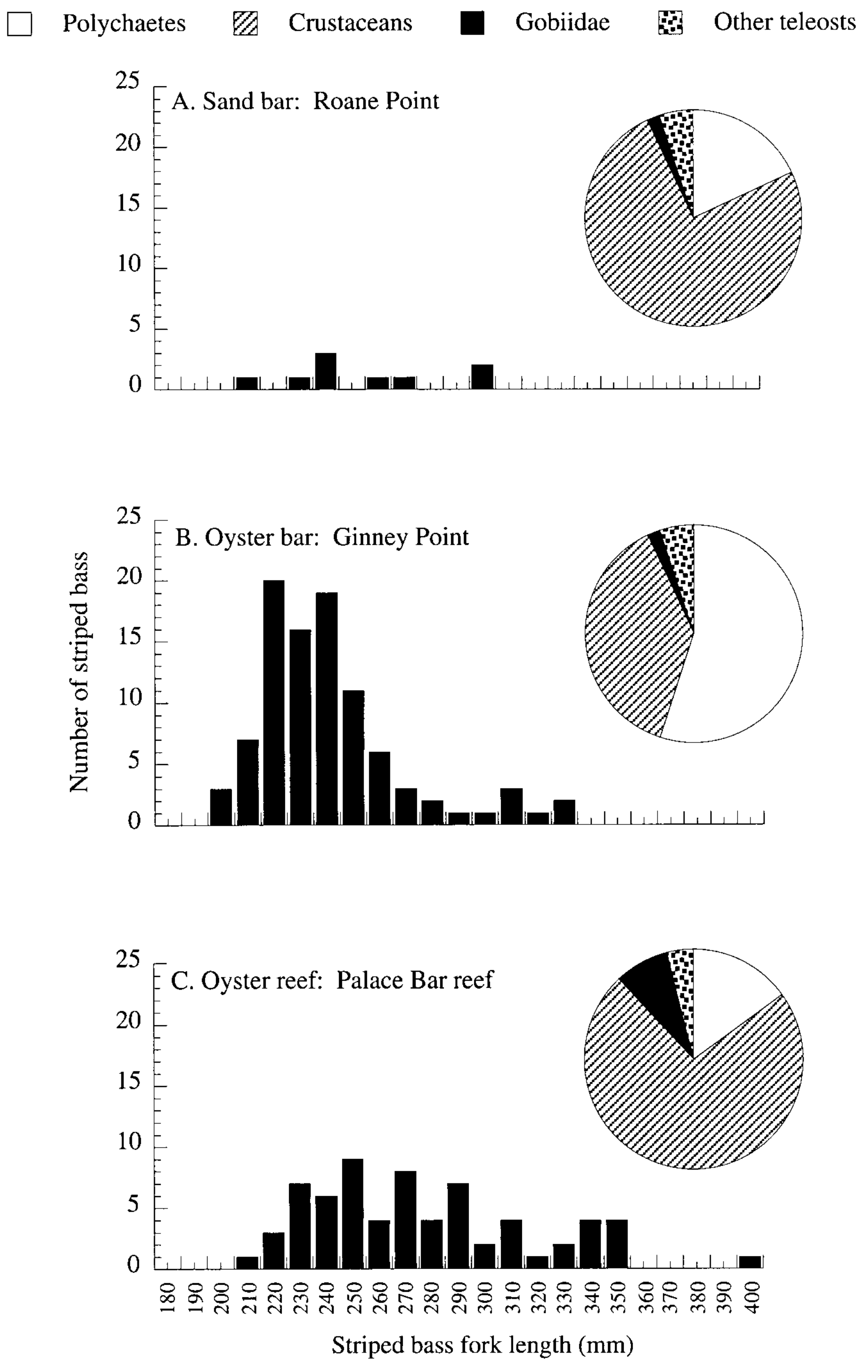

Figure 2. Site-specific length frequency distribution (bar graph) and percent numerical abundance (%N) of major prey taxa in the diets (pie charts) for Piankatank River striped bass. Fish with damaged or empty guts were not included in dietary analyses. Palace Bar reef (n = 67 caught/47 examined for diet), Ginney Point (n = 95/79), and Roane Point (n = 10/10) were sampled.

Thus, Kruskal-Wallis tests were used to compare striped bass fork lengths in relation to site, day of the year, time of day, and tidal stage.

Dietary Analyses.—Neither fish with empty guts (n = 11) nor fish with damaged guts [usually due to blue crab (*Callinectes sapidus*) predation in the gill nets; n = 36] were used for dietary analyses. Two prey indices were calculated for striped bass: frequency of occurrence (%F) or the percentage of fish, which consumed a particular category of prey and numerical abundance (%N) or the percentage of each prey type in relation to the total number of prey.

The total number of prey items per striped bass did not satisfy the assumptions of homogeneity of variance or normality even after transformation ((logarithm, natural logarithm, square-root, reciprocal) and were compared with Kruskal-Wallis tests incorporating site, day of the year, time of day, and tidal stage.

The percentages of fishes in the diets of individual striped bass were compared between site, day of the year, time of day, and tidal stage with Kruskal-Wallis tests since the data satisfied neither the assumption of normality nor homogeneity of variance even with transformation (arcsin, natural logarithm, square-root).

Results

Water Temperature and Salinity Data.—Neither water temperatures nor salinity values were significantly different between sampling sites (Table 1). Recorded weekly water temperatures during 1997 were similar to those observed weekly at the same sites during 1993–96 (Harding and Mann, 1999). Ranges of Piankatank River temperature (17–28° C) and salinity (11–18 psu) were similar to temperature and salinity ranges reported from other estuarine striped bass studies e.g., Hollis, 1952, Markle and Grant, 1970, and Boynton et al., 1981.

Abundance.—Striped bass were significantly more abundant at Palace Bar reef (n = 68) and Ginney Point (n = 96), sites with oyster shell substrate, than at Roane Point (n = 10), the sand bottom site (Table 1, Fig. 2). Day of the year, time of day, and tidal stage did not significantly affect striped bass abundance (Table 1).

Length-frequency Data.—Striped bass caught at Palace Bar oyster reef (mean fork length (FL) = 279.9 mm ± standard error (S.E.) of 4.9 mm) were significantly larger than fish caught at either of the other two sites (Table 1, Fig. 2). Roane Point fish (mean FL = 263.4 ± 10.2 mm) were larger than fish caught at Ginney Point (mean FL =244.8 ± 2.8 mm; Table 1, Fig. 2). Fish caught during late afternoon and early evening hours (4 pm–12 am EDT) were significantly larger (n = 59; mean FL = 276.3 ± 4.6 mm) than fishes caught during early morning (12–4 am EDT; n = 33; mean FL = 262.0 ± 7.9 mm) as well as fishes caught from 4 am–4 pm EDT (n = 80; mean FL = 246.1 ± 3.3 mm; Table 1). Striped bass caught on the flood tide (n = 33; mean FL = 276.5 ± 7.4 mm) were significantly larger than those caught at any other tidal stage (n = 139; mean FL = 255.5 ± 3.0 mm ; Table 1). All of the striped bass caught at these three Piankatank River sites were in the length range for Age 1 (92% of Piankatank River fish; 200–322 mm FL; Sadler et al., 1997) or Age 2 (8% of Piankatank River fish; 323–412 mm FL; Sadler et al., 1997) fish from the lower Chesapeake Bay.

Dietary Analyses.—Neither fish with empty guts (n = 11) nor fish with damaged guts [usually due to blue crab (*Callinectes sapidus*) predation in the gill nets; n = 36] were used for dietary analyses. Striped bass diets from all three sites included crustaceans (38% F, approximately 65% N; Table 2, Fig. 2), polychaetes (72% F, 30% N; Table 2, Fig. 2), and fishes (45% F, approximately 10% N; Table 2, Fig. 2). Crustaceans (predomi-

Table 1. Summary of statistical tests performed on water temperature, salinity, striped bass abundance, distribution, length (FL, mm) and diet data from the Piankatank River. Parametric multiple comparisons were made with the Tukey test. Non-parametric multiple comparisons used Dunn's test. Astericks indicate significance at the P = 0.05 level. Computation of interaction effects was impossible given the unbalanced nature of the data.

Date type	Statistical test	Factor(s)	df	P-value	Multiple comparison results
Water temperature	ANOVA	Site	1	0.79	
Salinity	ANOVA	Site	1	0.85	
Abundance	ANOVA	Site	2	0.01*	Palace Bar reef, Ginney Point > Roane Point
		Day of the year	7	0.88	
		Time of day	5	0.52	
		Tidal stage	3	0.11	
Length (FL, mm)	Kruskal-Wallis	Site	2	<0.01*	Palace Bar reef > Roane Point > Ginney Point
		Day of the year	7	0.40	
		Time of day	5	<0.01*	4 pm–12 am > 12–4 am > 4 am–4 pm
		Tidal stage	3	0.03*	Flood > Ebb > Slack-ebb, Slack-flood
Total number of prey items per fish	Kruskal-Wallis	Site	2	0.06	
		Day of the year	7	<0.01*	Sept. > May, June 1–15, July; June 15-30 > May
		Time of day	5	<0.01*	4–8pm > 4-8 am
		Tidal stage	3	0.54	
Percentage of teleost prey	Kruskal-Wallis	Site	2	0.24	
		Day of the year	7	<0.01*	July 1–15 > May, June; July 1–15 > Sept. 1–15
		Time of day	5	0.01*	8 pm–12 am> 4–8 am,12–4 pm; 8 am–12 pm > 4–8 am
		Tidal stage	3	0.06	

nantly the mysid shrimp *Neomysis americana*) composed the bulk of fish diets from both Palace Bar oyster reef (32% F, 73% N) and Roane Point (44% F, 73% N; Table 2, Fig. 2). Polychaetes were major diet items for Ginney Point fish (83% F, 55% N; Table 2, Fig. 2). Striped bass guts from Palace Bar reef and Roane Point contained identifiable remains of striped blennies (*Chasmodes bosquianus*); fish from all three sites consumed naked gobies (*Gobiosoma bosc*, Table 2). Atlantic menhaden (*Brevoortia tyrannus*) were found in Ginney Point fish (Table 2).

The total number of prey items consumed per fish was not significantly affected by site or tidal stage (Table 1). Striped bass consumed significantly more prey items from 4–8 pm EDT than from 4–8 am EDT (Table 1). Significantly more prey items were consumed by striped bass during September 1–15 than during May, June 1–15 and July (Table 1). The percentage of teleosts consumed by striped bass was significantly higher from July 1–15 than during May and June as well as September 1–15 (Table 1). More teleosts were consumed by striped bass during evening hours (8 pm–12 am EDT; Table 1).

Table 2. Gut contents of striped bass collected from May through September 1997 in the Piankatank River, Virginia, U.S. Striped bass were collected from Palace Bar reef (PBR), Roane Point (RP), and Ginney Point (GP). Fish with damaged or empty guts were not used in these analyses. The percentage of feeding fish was calculated by dividing the number of feeding fish by the total number of fish caught with intact guts (n). Data are presented in terms of percent frequency of occurrence (%F) and percent numerical abundance (%N).

	All sites		Palace Bar reef		Ginney Point		Roane Point	
Total number of fish with intact guts (n)	136		47		79		10	
Percent of fish feeding	92		100		87		90	
Prey taxa	%F	%N	%F	%N	%F	%N	%F	%N
Polychaetes	72	30	62	15	83	55	33	18
Nematodes	2	< 1	6	< 1	1	< 1		
Crustaceans								
Amphipods	1	< 1			3	< 1		
Isopods	1	< 1					11	1
Mysid shrimp	30	60	32	73	26	36	33	73
Portunid crabs	2	< 1			10	1		
Paneid shrimp	1	< 1						
Xanthid crabs	3	< 1			4	1	11	1
Gastropods	1	< 1	2	< 1				
Bivalves	3	< 1	2	< 1	4	1		
Teleosts								
Blenniidae	2	< 1	4	< 1			11	1
Clupeidae	1	< 1			1	< 1		
Gobiidae	23	5	66	8	9	2	33	2
Unidentified teleostei	19	3	21	3	19	4	33	4

Discussion

In the Piankatank River, striped bass were more abundant at sites with oyster shell bottom (Palace Bar reef, Ginney Point) than at the site with a sand bottom (Roane Point). Larger fish were more abundant at Palace Bar reef than at either of the non-reef sites. Striped bass found in association with Palace Bar reef consumed more naked gobies than fish from other sites and 100% of reef striped bass examined contained food items. Age estimates based on fork lengths for striped bass from the lower Chesapeake Bay indicate that 92% of Piankatank River striped bass were Age 1 and all fish were Age 1 or 2. The percentages of Piankatank River fish feeding (87–100%) were higher than those reported by Stevens (1967), Boynton et al. (1981) and Robichaud-LeBlanc et al. (1997) for juvenile striped bass from the San Joaquin, Potomac, and Miramichi Rivers, respectively. By contrast, these percentages were similar to those from other Virginia Rivers: 89% of the yearling striped bass examined by Markle and Grant (1970) from the James, York, and Rappahannock Rivers were feeding while 88% of Age 1 and 2 striped bass from the lower Chesapeake Bay during 1997–98 were feeding (H. Austin, Dept. of Fisheries Science, VIMS, pers. comm.).

Palace Bar reef and Roane Point striped bass were larger and consumed more crustaceans than Ginney Point fish whose diets were dominated by polychaetes. Reef associated striped bass consumed other fishes more frequently than fishes from non-reef sites.

Observed differences in diet and fish size between sites relate to habitat-specific prey availability as influenced by both habitat complexity and productivity. The relative abundance of fishes in the diets of reef striped bass may be due to potentially higher abundance of small benthic fishes at the oyster reef in relation to other sites with lower degrees of substrate complexity and vertical relief. Habitats with oyster shell bottom (Ginney Point) provide greater substrate heterogeneity than sand bottom habitat (Roane Point). Three dimensional oyster reefs (Palace Bar reef) further enhance pelagic piscivorous fish feeding habitat by providing both heterogenous structure and vertical relief that may aggregate prey species. In the Piankatank River, striped bass were more abundant at sites with live oyster bottom and larger striped bass were more abundant at the reef site than at non-reef sites. Temperate oyster reef communities provide not only structure and vertical relief (habitat) but sustained food supplies; this combination attracts fishes from many different trophic levels much like tropical coral reefs (Roberts and Ormond, 1987; Ebeling and Hixon, 1991; Friedlander and Parrish, 1998; Harding and Mann, 1999; Breitburg, 1999, Coen et al., 1999). The availability of 32 finfish species, including species commonly consumed by striped bass e.g., naked gobies, spot, bay anchovies, and Atlantic menhaden (Hartman and Brandt, 1995) on, or in association with, Palace Bar reef during 1996–1997 (Harding and Mann, 1999; Harding and Mann, 2001b) render the site an attractive foraging ground for striped bass and other apex predators including bluefish and weakfish (Harding and Mann, 1998; Harding and Mann, 2001a,b).

Chesapeake Bay trophic pathways have been discussed by Baird and Ulanowicz (1989) and Hartman and Brandt (1995) in relation to apex predators including striped bass. Striped bass rely heavily on benthic production throughout their first year (Age 0), into midsummer of their second year (Age 1), and from May through June of subsequent years (Hartman and Brandt, 1995). Hartman and Brandt (1995) suggest that Baird and Ulanowicz (1989) may have underestimated the relative contribution of benthic production to striped bass production because of striped bass reliance on benthic trophic sources (including benthic fishes). This study, as well as Breitburg (1999) for Flag Pond oyster reef near the Patuxent River, Maryland, and similar data sets for bluefish (Harding and Mann, 2001a) in relation to Palace Bar Reef, document positive interactions between oyster reefs and these piscivorous fishes.

Habitat relief and trophic complexity provided by living oyster reefs positively affect local habitat use and trophic partitioning patterns by striped bass during estuarine development. Within the Piankatank River, trophic patterns between benthic and pelagic pathways are illustrated on a local scale during 1997: reef striped bass were significantly larger and consumed more forage fish and crustaceans than non-reef bass. Equally important, at least five times as many striped bass used the three-dimensional oyster reef (Palace Bar reef) or flat oyster shell bottom (Ginney Point) habitat than the sand bottom (Roane Point) habitat. Oyster reefs with vertical relief provide habitat complexity that attracts benthic invertebrates and smaller fishes and subsequently increases the availability of ‘prey’ species for estuarine striped bass, at least on a local scale. Increased abundance of prey fishes in striped bass nursery estuaries have the potential to increase striped bass growth rates and survivorship during estuarine development.

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Literature Cited

Baird, D. and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay Ecosystem. Ecol. Monogr. 59: 329–364.

Bartol, I. and R. Mann. 1997. Small-scale settlement patterns of the oyster *Crassostrea virginica* on a constructed intertidal reef. Bull. Mar. Sci. 61: 881–897.

Berggren, T. J. and J. T. Lieberman. 1978. Relative contribution of Hudson, Chesapeake, and Roanoke striped bass, *Morone saxatilis*, stocks to the Atlantic coast fishery. U.S. Fish. Bull. 76: 335–345.

Boynton, W. R., T. T. Polgar and H. H. Zion. 1981. Importance of juvenile striped bass food habits in the Potomac estuary. Trans. Amer. Fish. Soc. 110: 56–63.

Breitburg, D. 1999. Are three dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? Pages 239–250 *in* M. W. Luckenbach, R. Mann and J. A. Wesson, eds. Oyster reef habitat restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Gloucester Point.

Coen, L., M. Luckenbach and D. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. Pages 438–454 *in* L. R. Benaka, ed. Fish habitat: Essential fish habitat and rehabilitation. American Fisheries Society, Symposium 22, Bethesda.

_______ and __________. 2000. Developing success criteria and goals for evaluating shellfish habitat restoration: Ecological function or resource exploitation? Ecol. Engin. 15: 323–343.

Ebeling, A. W. and M. A. Hixon. 1991. Tropical and temperate reef fishes: a comparison of community structures. Pages 509–563 *in* P. F. Sale, ed. The ecology of fishes on coral reefs. Academic Press, San Diego.

Friedlander, A. and J. Parrish. 1998. Habitat characteristics affect fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Biol. Ecol. 224: 1–30.

Grant, G. C. and J. E. Olney. 1991. Distribution of striped bass *Morone saxatilis* (Walbaum) eggs and larvae in major Virginia Rivers. U.S. Fish. Bull. 89: 187–193.

Harding, J. M. and R. Mann. 1998. Oyster reef restoration as a habitat enhancement tool for recreationally valuable finfishes. J. Shellfish Res. 17: 1302.

____________ and ________. 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. Bull. Mar. Sci. 65: 289–300.

____________ and ________. Estimates of naked goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*) and eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef. Bull. Mar. Sci. 66: 29–45.

____________ and _________. 2001a. Diet and habitat use by bluefish, *Pomatomus saltatrix*, in a Chesapeake Bay estuary. Env. Biol. Fishes. 60: 401–409.

____________ and _________. 2001b. Oyster reefs as fish habitat: Opportunistic use of restored reefs by transient fishes. J. Shellfish Res. 20: 951–959.

Hargis, W. J., Jr. 1999. The evolution of the Chesapeake oyster reef system during the Holocene epoch. Pages 5–23 *in* M. W. Luckenbach, R. Mann and J. A. Wesson, ed. Oyster reef habitat restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Gloucester Point.

Hartman, K. J. and S. B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Trans. Amer. Fish. Soc. 124: 520–537.

Heubach, W., R. Toth and A. McCready. 1963. Food of young-of-the-year striped bass (*Roccus saxatilis*) in the Sacramento-San Joaquin River system. Calif. Fish Game 49: 224–239.

Hollis, E. H. 1952. Variations in the feeding habits of the striped bass, *Roccus saxatilis* (Walbaum) in Chesapeake Bay. Bull. Bingham Oceanogr. Coll. 14: 111–131.

Kennedy, V., R. Newell, and A. Eble. 1996. The Eastern Oyster *Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland. 734 p.

Kohlenstein, L. C. 1981. On the proportion of the Chesapeake Bay stock of striped bass that migrates into the coastal fishery. Trans. Amer. Fish. Soc. 110: 168–179.

Luckenbach, M., R. Mann and J. A. Wesson. 1999. Oyster reef habitat restoration. A synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Gloucester Point. 366 p.

Mann, R. 2000. Restoring the oyster reef communities in Chesapeake Bay: a commentary. J. Shellfish Res. 19: 335–339.

_______, F. Perkins, J. Wesson and I. Bartol. 1996. Intertidal oyster reefs as a tool for estuarine rehabilitation and rejuvenation of the Virginia oyster fishery. Final Rpt. Dept. Environ. Quality, Virginia Coastal Resource Management Program, Richmond. 129 p.

Mansueti, R. J. 1961. Age, growth, and movements of the striped bass, *Roccus saxatilis*, taken in size selective fishing gear in Maryland. Ches. Sci. 2: 9–36.

Markle, D. F. and G. C. Grant. 1970. The summer food habits of young-of-the-year striped bass in three Virginia rivers. Ches. Sci. 11: 50–54.

Massmann, W. H. and A. L. Pacheco. 1961. Movements of striped bass tagged in Virginia waters of Chesapeake Bay. Ches. Sci. 2: 37–44.

McGovern, J. C. and J. E. Olney. 1996. Factors affecting survival of early life stages and subsequent recruitment of striped bass on the Pamunkey River, Virginia. Can. J. Fish. Aquat. Sci. 53: 1713–1726.

Merriman, D. 1941. Studies on the striped bass (*Roccus saxatilis*) of the Atlantic coast. U.S. Fish. Bull. 50: 1–77.

Nestlerode, J., M. Luckenbach and F. O' Beirn. 1998. Trends in early community development and trophic links on constructed oyster reefs. J. Shellfish Res. 17: 1309.

Newell, R. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? Pages 536–546 *in* M.P. Lynch and J. A. Mihursky, eds. Understanding the estuary: Advances in Chesapeake Bay research. Ches. Res. Cons. Publ. 129.

Olney, J. E., J. D. Field, and J. C. McGovern. 1991. Striped bass egg mortality, production, and female biomass in Virginia rivers, 1980–89. Trans. Amer. Fish. Soc. 120: 354–367.

Posey, M. H., T. D. Alpin, C. M. Powell, and E. Townsend. 1999. Oyster reefs as habitat for fish and decapods. Pages 229–237 *in* M. W. Luckenbach, R. Mann, and J. A. Wesson, eds. Oyster reef habitat restoration: A synopsis and synthesis of approaches. Virg. Inst. of Mar. Sci. Press, Gloucester Point.

Raney, E. C. 1952. The life history of the striped bass, *Roccus saxatilis* (Walbaum). Bull. Bingham Oceanogr. Coll. 14: 5–97.

Roberts, C. M. and R. F. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol. Prog. Ser. 41: 1–8.

Robichaud-LeBlanc, K. A., S. C. Courtenay and J. M. Hanson. 1997. Ontogenic diet shifts from age-0 striped bass, *Morone saxatilis*, from the Miramichi River estuary, Gulf of St. Lawrence. Can. J. Zool. 75: 1399–1309.

____________________, S. C. Courtenay and T. J. Benfey. 1998. Distribution and growth of young of the year striped bass in the Miramichi River estuary, Gulf of St. Lawrence. Trans. Amer. Fish. Soc. 127: 56–69.

Sadler, P., J. Olney, R. Harris Jr. and J. Davis. 1997. Evaluation of striped bass stocks in Virginia: Tagging and monitoring studies. Annual Rept. Virg. Mar. Res. Comm., Newport News. 38 p.

Sale, P. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 18: 367–421.

Setzler-Hamilton, E. M., W. Boynton, J. Mihursky, T. Polgar, and K. Wood. 1981. Spatial and temporal distribution of striped bass eggs, larvae, and juveniles in the Potomac estuary. Trans. Amer. Fish. Soc. 110: 121–136.

__________________ and L. Hall, Jr. 1991. Striped bass *Morone saxatilis*. Pages 13–31 *in* S. Funderbunk, S. Jordan, J. Mihursky and D. Riley, eds. Habitat requirements for Chesapeake Bay living resources, 2nd ed. Living Resources Subcommittee, Chesapeake Bay Program, Annapolis.

Stevens, D. E. 1967. Food habits of striped bass, *Roccus saxatilis*, in the Sacramento-San Joaquin Delta. California Department of Fish and Game, Fish Bull. 136: 68–96.

Uphoff, J. H. 1989. Environmental effects on survival of eggs, larvae, and juveniles of striped bass in the Choptank River, Maryland. Trans. Amer. Fish. Soc. 118: 251–263.

Van Winkle, W. K. Kumar, and D. Vaughan. 1988. Relative contributions of Hudson River and Chesapeake Bay striped bass stocks to the Atlantic coastal population. Amer. Fish. Soc. Monogr. 4: 255–266.

Zar, J. H. 1996. Biostatistical analysis, 3rd ed. Prentice Hall. New Jeresy. 662 p.

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