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ARTICLE

Spatial and Temporal Diet Patterns of Subadult and Small Adult Striped Bass in Massachusetts Estuaries: Data, a Synthesis, and Trends across Scales

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Abstract

Subadult and small adult (375–475 mm total length) striped bass *Morone saxatilis* are abundant and represent an important component of the recovered U.S. Atlantic coast stocks. However, little is known about these large aggregations of striped bass during their annual foraging migrations to New England. A quantitative understanding of trends in the diets of subadult and small adult migrants is critical to research and management. Because of the complexity of the Massachusetts coast, we were able to compare diets at multiple spatial, temporal, and taxonomic scales and evaluate which of these provided the greatest insights into the foraging patterns of this size of fish. Specifically, during spring through autumn, we quantified the diets of 797 migratory striped bass collected from 13 Massachusetts estuaries distributed among three geographic regions in two biogeographic provinces. Our data provided three useful results. First, subadult and young adult striped bass ate a season-specific mixture of fish and invertebrates. For example, more juvenile Atlantic herring *Clupea harengus* were eaten in spring than in summer or autumn, more juvenile Atlantic menhaden *Brevoortia tyrannus* were eaten in autumn than in spring or summer, amphipods were eaten primarily in the southern biogeographic province, and shrimp *Crangon* sp. were eaten in all locations and seasons. Second, examining diets by season was essential because of the temporal variability in striped bass prey. Grouping prey by fish and invertebrates revealed the potential for predictable differences in growth across geographic locations and seasons, based on the output from simple bioenergetics simulations. Third, of the three spatial scales examined, region provided the most quantitative and interpretable ecological trends. Our results demonstrate the utility of comparing multiple scales to evaluate the best way to depict diet trends in a migrating predator that seasonally uses different geographic locations.

Despite the popularity of migratory striped bass *Morone saxatilis* as a sport fish, little is known about the diets of a common size-class (375–475 mm total length [TL]) composed of subadults and small adults that forage seasonally along the

Atlantic coast. Striped bass, a highly mobile predator in estuaries and coastal waters, have been historically important to both fisheries and ecosystem dynamics (Fay et al. 1983; Richards and Rago 1999). The U.S. Atlantic coast striped bass stocks spawn

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TABLE 1. Summary of peer-reviewed studies on coastal subadult and young-adult striped bass diets.

Study	System name ^a	Major coastal areas ^b	Years	Management period ^c	Season				Sizes	Synthesis across					Scales ^d		
					Spring	Summer	Autumn	Winter		Major coastal areas	Years	Management periods	Seasons	Sizes	Multiple sites	Spatial scales	Largest Middle Smallest
1. Schaefer (1970)	LI	N	1964	H	X	X	X		275–940				X	X			
2. Gardiner and Hoff (1982)	HR	N	1974–1977	H	X	X	X		<76–>800		X		X	X			
3. Dew (1988)	HR	N	1973–1975	H	X				400–1,050								
4. Dunning et al. (1997)	HR	N	1986–1994	C				X	<200–>300					X			
5. Rulifson and McKenna (1987)	BF	N	1985	C	X	X	X		69–520				X	X			
6. Nelson et al. (2003)	MA	N	1997–2000	R	X	X	X		290–1,162				X	X	X	Rg	Ha
7. Hollis (1952)	CB	M	1936–1937	H	X	X	X	X	180–485				X		X		U–D
8. Dovel (1968)	CB	M	1962	H				X									
9. Griffin and Margraf (2003)	CB	M	1955–1959	H	X	X	X	X	170–1,219				X	X			
10. Hartman and Brandt (1995a)	CB	M	1990–1992	C	X	X	X	X	Age 0–3 +				X	X			
11. Walter and Austin (2003)	CB	M	1997–1998	R	X		X		458–1,151				X	X	X		U–D
12. Harding and Mann (2003)	CB	M	1997	R	X	X	X		210–400				X	X	X		Ha
13. Overton et al. (2009)	CB	M	1998–2001	R	X	X	X	X	107–>700				X	X	X		U–D
14. Tupper and Able (2000)	DB	M	1998	R	X	X	X		212–670				X		X	Mr	Ck
15. Trent and Hassler (1966)	RR	S	1963–1965	H	X										X		U–D
16. Manooch (1973)	AS	S	1970–1971	H	X	X	X	X	125–714				X	X	X		E–W
17. Rudershausen et al. (2005)	AS	S	2002–2003	R	X	X	X		121–620		X		X	X			
18. Overton et al. (2008)	VA, NC	M, S	1994–2007	R				X	373–1,250		X			X			
19. Walter et al. (2003)	A	A	A	A	X	X	X		150–1,183	X			X	X	X		C
This study	MA	N	1999	R	X	X	X		375–475				X		X	X	Bio Rg Est

^aLI = Long Island Sound; HR = Hudson River; BF = Bay of Fundy; MA = coastal Massachusetts; CB = Chesapeake Bay; DB = Delaware Bay; RR = Roanoke River; AS = Albemarle Sound; VA, NC = Virginia and North Carolina; A = all.

^bN = North of Long Island; M = Delaware and Chesapeake bays; S = North Carolina.

^cH = historical (<1981); C = crisis (1981–1994); R = recovered (≥1995).

^dRg = region; Ha = habitat; U–D = up–downstream; Mr = marsh; Ck = creek; E–W = east–west; Bio = biogeographic break; Est = estuary; C = coastal.

primarily in the Chesapeake Bay, Delaware River, and Hudson River; migrate north along the Atlantic coast in late spring, feed off New England and southern Canada in summer, and return south in autumn (Waldman et al. 1990; Mather et al. 2009; Pautzke et al. 2010). Previous diet studies have not focused on the complex of subadult and small adult striped bass that migrate and feed as adults, nor have previous studies compared insights about diets obtained by examining multiple spatial, temporal, and taxonomic scales.

The coastal stocks of striped bass have undergone a dramatic decline and recovery that has altered the structure of this migratory population (Richards and Rago 1999; Hartman and Margraf 2003). During the late 1970s and 1980s, overfishing, recruitment failures, and poor water quality in Chesapeake Bay led to the collapse of the migratory population. These fish were restored in the mid-1990s (Field 1997) following a series of successful management actions. The recovered U.S. Atlantic

coast striped bass stocks are very abundant (e.g., 43 million in 2002 compared with 5 million in 1980). One reason for this recovery is that 8 of 14 recent year-classes have been moderately strong (>10,000,000: 1992, 1994, 1995, 2000, 2006) or very strong (>15,000,000: 1996, 2001, 2003; NEFSC 2008). This has resulted in an abundance of subadult and young adult migratory striped bass (>2 years), many of which participate in the coastal migration. Consequently, subadult and small adult striped bass migrants have been seasonally abundant predators in New England waters for more than a decade.

Although the diets of Atlantic coastal striped bass (>2 years) have been examined in 19 previous peer-reviewed studies (Table 1), synthesis is lacking. These striped bass diet studies were undertaken in nine systems representing three major coastal areas of the North Atlantic Ocean: (1) northern (north of and including Long Island; six studies); (2) middle (Delaware and Chesapeake Bays; eight studies); and (3) southern (North

Carolina; three studies); in addition data were collected in one study spanning the middle and southern coastal areas. Only a single study synthesized data across all major coastal areas (Walter et al. 2003; Table 1). Data used in these 19 studies were collected between the years of 1936 and 2007, fish data often being collected over multiple years (Table 1). However, only three studies assessed annual variation. These 19 peer-reviewed diet studies spanned the management periods: historical (before 1981; 8 studies), crisis (1981–1994; 3 studies), and recovered (after 1995; 7 studies). One study pooled data across all three periods (Walter et al. 2003; Table 1), but no study has compared temporal trends across management periods. Most studies collected and synthesized data from multiple seasons. These 19 studies examined a range of sizes (69 mm–1250 mm), most included some migratory subadult and young-adult fish, and many studies (14 of 19) compared diets across sizes. No previous study, however, focused exclusively on the often abundant, migratory subadult and small adult sizes.

The sampling design of these peer-reviewed striped bass diet studies varied. Less than half of the existing studies (9 of 19) explicitly examined spatial variation across multiple sites (Table 1). These studies compared (1) habitats within a system (Harding and Mann 2003), (2) within-system gradients (e.g., upstream-downstream, west-east gradients; Hollis 1952; Trent and Hassler 1966; Manooch 1973; Walter and Austin 2003; Overton et al. 2009), (3) within-system and across-system patterns such as creeks within marshes (Tupper and Able 2000) and habitats within regions (Nelson et al. 2003), and (4) major coastal areas (Walter et al. 2003). Unfortunately, the lack

of standardization in design across these studies, limits insights about how striped bass diets vary across locations, and only 2 of the 19 studies (Tupper and Able 2000; Nelson et al. 2003) sampled at multiple scales.

Understanding the patterns of variation in subadult and young adult striped bass diets within and across scales can aid research and management. Because of the natural complexity of coastal Massachusetts, we had the unique opportunity to simultaneously collect data on migratory subadult and small adult striped bass diets at multiple scales. These scales included the estuary, region, and biogeographic province from spring through autumn, using both prey grouped by specific categories and prey pooled as fish or invertebrates. Here we examined diet data at a variety of aggregations to address the following questions: (1) what are subadult and young adult striped bass (375–475 mm TL, 3–5 years) eating and how do their diets compare with diets of other sizes of coastal striped bass reported in the literature, (2) within Massachusetts, do striped bass diets vary geographically, and (3) what spatial, temporal, and taxonomic scales provide the clearest insights?

METHODS

To concurrently examine three spatial scales (estuary, region, and biogeographic province), we chose 13 medium-sized estuaries (7–21 km from the mouth of the estuary to the first dam) located along the coast of Massachusetts (Figure 1). These 13 estuaries can be grouped into three distinct regions of the Massachusetts coast (Figure 1): North Shore (estuaries 1–4),

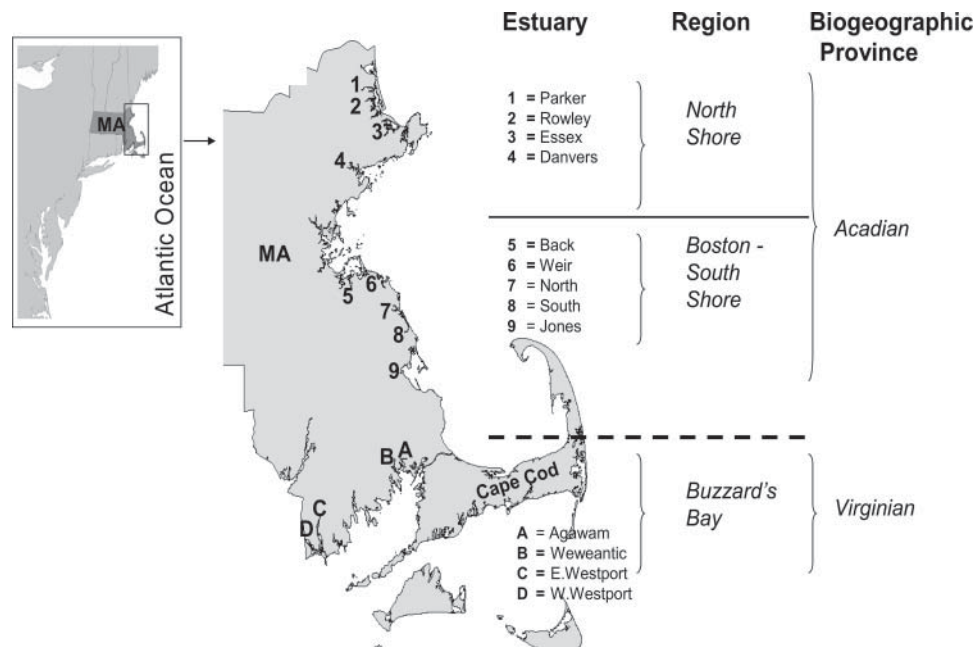


FIGURE 1. Map of the study area showing the three spatial scales considered in sampling striped bass: estuary, geographic region, and biogeographic province (the dashed horizontal line separates the two provinces in question).

Boston–South Shore (estuaries 5–9), and Buzzards Bay (estuaries A–D). These three regions represent two biogeographic provinces (Figure 1): the Acadian (estuaries 1–9; region north of Cape Cod) and the Virginian (region south of Cape Cod; estuaries A–D; Briggs 1974). Although many species were common to all estuaries, the prey assemblage north of the biogeographic break included subarctic fauna, whereas southern Massachusetts included warm temperate species (Ayvazian et al. 1992). Mean tide heights were 2.4–3.6 m north of Cape Cod but only 1.2 m south of Cape Cod. Eliminated from consideration were (1) uniquely large estuaries (>50 km from the estuary mouth to headwaters), (2) systems with limited foraging habitat for coastal striped bass (e.g., a dam <6 km from the estuary mouth), and (3) systems that were logistically difficult to sample because of distance and human travel time (estuaries on Cape Cod). We chose study sites in this way to maintain standardization in sampling. We prioritized standardization as a critical criterion for comparing spatial and temporal variation in striped bass diets across estuaries of similar size. If we had included large estuaries, the entire extent of small estuaries, or estuaries that required extended travel time, we would not have been able to sample all estuaries within the same time frame.

We collected striped bass in three seasons: spring (May–June), summer (July–August), and autumn (September–October) 1999. Foraging striped bass were captured by fly angling within the lower 6 km of each estuary, an area in which migrating fish were common. Fly angling was used because it was a very efficient method of sampling feeding striped bass. A professional fly fishing guide familiar with each estuary and a second experienced fly angler (>15 years experience) fished for 4 h at first light on ebbing tides for 2 d in each estuary in each season. All estuaries were sampled within a 3-week period in each season. Salinity was similar among estuaries (range, 10–30‰) in the 6-km study area within and across seasons. Angling equipment consisted of barbless single hooks (i.e., generic juvenile fish imitations). Bait was never used. Scientists oversaw onboard data collection, enforced standardized collection protocols, and processed diets. Fishing time, casts/h, and fly type were similar in all estuaries and seasons. Because protocols were the same, we could compare diets across locations and seasons.

We obtained striped bass diets using gastric lavage, a non-lethal diet sampling method in which pressurized water is flushed into fish stomachs to force out contents (Foster 1977; Light et al. 1983). To reduce handling stress, we first anesthetized fish with clove oil (1.5 ml/L; Munday and Wilson 1997; Keene et al. 1998). After stomach pumping, all striped bass were allowed to recover then released back into the estuary. For each striped bass, flushed prey items were bagged, stored on ice, and then frozen. In the laboratory, when possible we identified all prey fish to species via exterior morphometric features and backbone counts (Weiss 1995; Able and Fahay 1998; Collette and Klein-MacPhee 2002). All digested fish and backbones were

TABLE 2. Prey categories and specific components used for summarizing striped bass diets.

Category	Components
	Fish
1. Menhaden	Atlantic menhaden <i>Brevoortia tyrannus</i>
2. Clupeids	Atlantic herring <i>Clupea harengus</i> Blueback herring <i>Alosa aestivalis</i> Alewife <i>Alosa pseudoharengus</i> American shad <i>Alosa sapidissima</i> Highly digested clupeids
3. Silverside	Atlantic silverside <i>Menidia menidia</i>
4. Rare and unidentified fish	Unidentified fish and fish parts Atlantic cod <i>Gadus morhua</i> and hake (Phycidae) Rainbow smelt <i>Osmerus mordax</i> American eel <i>Anguilla rostrata</i> Northern pipefish <i>Syngnathus fuscus</i> Other rare species
5. Sand lance	American sand lance <i>Ammodytes americanus</i>
6. Mummichog	Mummichog <i>Fundulus heteroclitus</i>
	Invertebrates
7. Crangon sp.	Sevenspine bay shrimp <i>Crangon septemspinosa</i>
8. Crab	Decapod crabs
9. Small crustaceans	Amphipods Isopods Mysids
10. Rare and unidentified crustaceans	Unidentified decapoda Grass shrimp <i>Paleomonetes</i> spp. Mud shrimp <i>Thalassinidea</i>
11. Other invertebrates	Gastropods Bivalves Polychaetes
	Other
12. Miscellaneous fish and invertebrates	Inseparable fish and invertebrate parts

identified to the lowest taxonomic level possible using vertebral counts. Heavily digested fish and invertebrate prey were reconstructed to original weight and length through a series of linear regressions (Hartman and Brandt 1995a; Able and Fahay 1998). Commonly encountered, undigested invertebrates were identified to species. Uncommon and partially digested invertebrates were identified to family or order (Gosner 1971; Williams 1984; Weiss 1995). Empty stomachs were included in all calculations. We grouped prey into 12 categories, reflecting eight functional groups (e.g., important, identifiable groups, 1–3, 5–9 in Table 2) and four groups of unidentified, miscellaneous, or other species (4, 10–12 in Table 2). We examined diets in six ways, including

an analysis of all 797 examined fish together, and five different combinations of spatial, temporal, and taxonomic scales. In these last five comparisons, diets were calculated as the average wet weight (g) eaten per individual striped bass.

We used a multivariate analysis of variance (MANOVA) to examine how fish and invertebrate prey in striped bass diets changed with geographic location. When multiple dependent response variables are measured, MANOVA is the appropriate general linear model (Scheiner 2001; Quinn and Keough 2002), and MANOVA has been used to examine fish diets elsewhere (Chipps and Garvey 2007). The response variables (amounts of fish and invertebrate prey eaten) were log transformed. Because we had a large sample ($n = 797$), only two response variables, and few empty stomachs (15%), the assumptions of MANOVA were met (O'Rourke et al. 2005). Three MANOVAs were run to examine the effect of location within each spatial scale (estuary, region, biogeographic province). If these results were significant, we ran an analysis of variance (ANOVA) on the individual fish and invertebrate responses (McGarigal et al. 2000). To evaluate location-related differences at each spatial scale, we compared MANOVAs, ANOVAs, and plots.

We collected water temperature data using HOBO Temp Loggers (Onset Computer Corporation). Temperature data were not available for all days for all 13 systems because of logistical and mechanical problems. We obtained usable temperature data for 7 estuaries in spring, 11 estuaries in summer, and 12 estuaries in autumn. Daily means were calculated as the average of all measurements collected within each 24-h period for three representative estuaries: the Rowley River, North River, and East Westport River (Figure 1). These data provided a detailed view of the thermal complexity that striped bass encounter, especially extreme high and low temperatures of short duration. Seasonal means were calculated for all estuaries for which temperature data were available by averaging all measurements across each season. We compared our data with two temperature thresholds described in the literature for adult striped bass: (1) temperatures where growth could be greater than 2% body weight/d if unlimited food resources are available (12–25°C; Hartman and Brandt 1995b), and (2) temperatures selected by striped bass in the field (21°C; Coutant 1985).

To identify whether empirically based differences in the relative amount of food, type of prey eaten, and estuary-specific temperatures could cause differences in striped bass growth across seasons and estuaries, we used the Fish Bioenergetics Model 3.0 (Hanson et al. 1997). This model has been parameterized for adult striped bass (Hartman and Brandt 1995b). For bioenergetic simulations, we chose the longest possible overlapping temperature records for each season. Because of limited availability of shared daily temperature records, we could only compare bioenergetics simulations for select estuaries during specific periods: spring (19 d, 6 estuaries), summer (30 d, 8 estuaries), and autumn (24 d, 6 estuaries). Hartman and Brandt (1995b) fed striped bass twice per day during model development, and striped bass in Massachusetts estuaries fed at least

twice a day (daylight ebb and flood tide; Ferry, unpublished data). For these reasons, to compare possible scenarios across seasons and estuaries, we calculated the proportion of maximum consumption by assuming that modeled striped bass ate twice the empirically derived amount and type of prey during each day of the simulation. We then combined our season-specific and estuary-specific data on temperature and prey with literature values for predator energy density (Hartman and Brandt 1995c), physiological characteristics of striped bass (Hartman and Brandt 1995b), and energy density of two types of prey (benthic malacostraca = 5,400 J/g wet mass, pelagic fish = 6,300 J/g wet mass; Steimle and Terranova 1985). Initial striped bass weight was 650 g, the mean weight of striped bass in spring. The response of interest was potential growth (hereafter called growth) or the amount of weight that could be gained per day, given the simplifying assumptions we used.

To further explore how temperature and diet might influence predicted growth across estuaries and seasons, we varied seasonal temperature inputs to the bioenergetics model while holding estuary-specific diet constant. That is, for a subset of estuaries, we sequentially examined the combination of spring, summer, and autumn temperatures with spring diets, repeated this using summer diets, and then using autumn diets. We also varied diets across seasons while holding estuary-specific temperatures constant. That is, we sequentially examined the combination of spring, summer, and autumn diets with spring temperatures, repeated this using summer temperatures, and then using autumn temperatures. If the model output changed in these simulations, we concluded that the parameter being varied (temperature or diet respectively), could influence growth across estuaries and seasons. Our use of the bioenergetics model had a very specific and limited application (i.e., to assess what might happen when empirically based diet amounts, prey types, and temperatures were combined). This use assumed that our empirically derived diets, collected with standardized methods, reflected system-specific and season-specific differences in consumption across a 24-h period.

RESULTS

We collected 14–129 striped bass per estuary, 153–388 in each of three regions, and 153 and 644 in the two biogeographic provinces (Table 3). Food was present in 85% of the stomachs, and empty stomachs were observed in all three seasons. Sizes of the striped bass we examined were similar: mean total length = 426 mm (SE = 2), mean wet weight = 843 g (SE = 14), 60% were 400–450 mm, and 83% were 375–475 mm. Of the fish examined, 94% were aged 3–5 years, based on a size-age key for striped bass caught in Massachusetts (G. Nelson, Massachusetts Division of Marine Fisheries, Annisquam River Marine Fisheries Station, personal communication).

One common metric for analyzing diets, percent composition by weight, yielded complex trends for striped bass feeding in three representative estuaries (Figure 2). For 12 prey

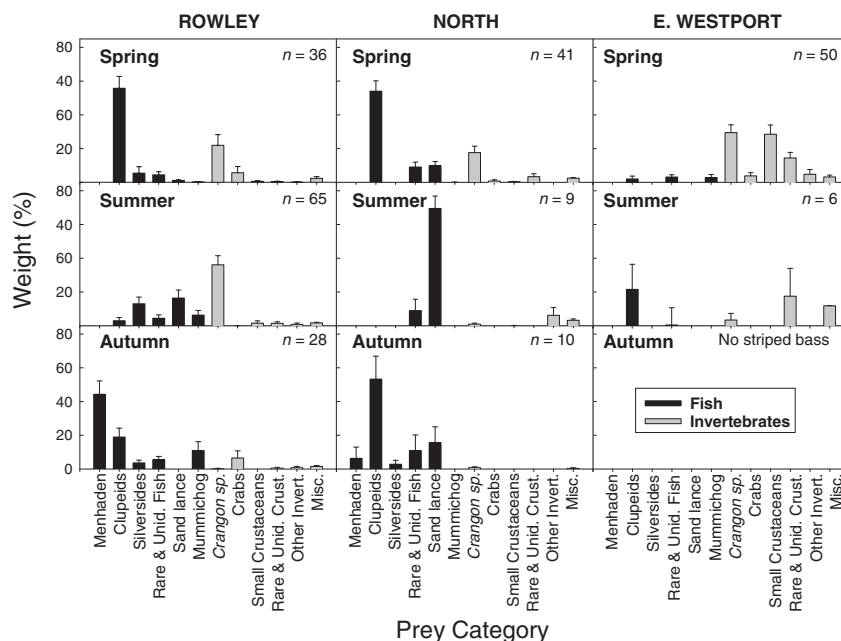
TABLE 3. Number of striped bass stomachs examined at three spatial scales (estuary, region, and biogeographic), by season (spring [SP], summer [SU], and autumn [AU]).

Estuary						Region					Biogeographic				
Estuary	ID ^a	SP	SU	AU	Subtotal	Region	SP	SU	AU	Subtotal	Province	SP	SU	AU	Subtotal
Parker	1	8	39	9	56	North Shore	119	162	107	388	Acadian	246	241	157	644
Rowley	2	36	65	28	129										
Essex	3	56	22	50	128										
Danvers	4	19	36	20	75										
Back	5	11	33	2	46										
Weir	6	10	4	0	14										
North	7	41	9	10	60										
South	8	42	9	26	77										
Jones	9	23	24	12	59	Boston–South Shore	127	79	50	256					
Agawam	A	15		1	16										
Weweantic	B	29	8	0	37										
East Westport	C	50	6	0	56										
West Westprt	D	40	3	1	44										
Subtotal		380	258	159		Subtotal	380	258	159		Subtotal	380	258	159	
Total					797	Total				797	Total				797

^aSee Figure 1.

categories, in spring in the Rowley and North estuaries, juvenile nonmenhaden clupeids (e.g., mostly Atlantic herring based on vertebrae counts) and shrimp *Crangon* sp. predominated in the striped bass diets (Figure 2). In summer, striped bass in the Rowley estuary ate primarily *Crangon* sp. fish prey in the diet declined (Figure 2). In the North estuary in summer, striped bass

ate sand lance (Figure 2). In autumn, juvenile Atlantic menhaden was the most common prey eaten by weight in the Rowley and North estuaries (Figure 2). In contrast, striped bass from the East Westport ate mainly *Crangon* sp. and small crustaceans (<2 mm; amphipods, isopods) throughout the spring (Figure 2), and some juvenile Atlantic menhaden were also eaten in

FIGURE 2. Percent composition by weight and standard errors for each of 12 fish and invertebrate prey groups found in striped bass diets in three Massachusetts estuaries (see Figure 1), by season. In each panel, n = the number of striped bass stomachs examined.

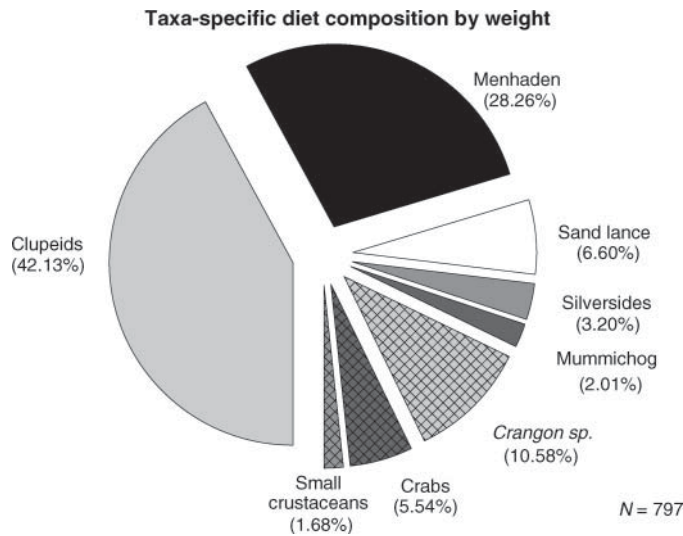


FIGURE 3. Composition by weight of eight prey categories consumed by 797 striped bass from 13 Massachusetts estuaries over the three seasons combined. Prey categories are defined in Table 2.

summer (Figure 2). In autumn in the East Westport, no striped bass were caught, presumably because they were present in lower numbers or not feeding.

To simplify these trends, we examined eight specific prey categories for all 797 striped bass combined (Figure 3). By weight, striped bass ate both fish (82.2%) and invertebrates (17.8%). A more detailed but still understandable view of subadult and young adult striped bass diets emerged when the amounts of fish and invertebrates eaten (g) per individual fish were examined for three spatial scales. For all seasons combined, striped bass in the Acadian biogeographic province ate mostly fish (Figure 4A). In the Virginian biogeographic province, they ate primarily invertebrates. The total amount eaten in the Virginian province was less than in the Acadian province. By region, more prey and dominantly fish prey were eaten in the North Shore and Boston–South Shore regions than in the southern Buzzards Bay region. In this southern region, the prey type eaten, again, was predominated by invertebrates (Figure 4B). Across estuaries north of the biogeographic break, the total amount of food eaten per striped bass varied (estuaries 1–9 in Figure 4C) but generally exceeded 10 g of mostly higher-energy fish prey. In estuaries in the region south of the biogeographic break, individual fish ate about 3 g of prey on average, mostly lower-energy invertebrates.

For all striped bass, in spring the amount of food eaten by individual striped bass exceeded 10 g and was dominated by fish prey (Figure 5). In summer, striped bass ate less than 5 g of both fish and invertebrate prey, in similar proportions. In autumn, striped bass ate greater than 13 g of mostly fish prey. These seasonal trends in the weight of fish and invertebrate prey eaten changed with location at all three scales (MANOVA, $P < 0.001$; Table 4). In the North Shore region, the most food present per individual striped bass occurred in spring, followed by autumn, then summer (Figure 5B). In the Boston–South Shore region,

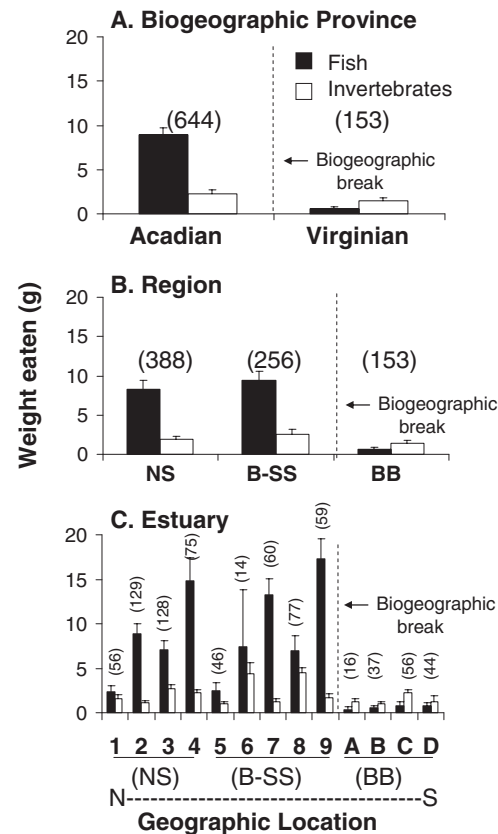


FIGURE 4. Mean weights of fish and invertebrate prey eaten by striped bass over all seasons grouped from north (left) to south (right) by (A) biogeographic province, (B) region (NS = North Shore, B-SS = Boston–South Shore, and BB = Buzzards Bay), and (C) estuary (see Figure 1). The error bars represent ± 1 SE; the numbers in parentheses above the bars are the numbers of striped bass stomachs examined.

the amount of food eaten per individual striped bass was highest in autumn, followed by spring; the least prey present was again in summer (Figure 5C). In both the North Shore and Boston–South Shore regions the spring and autumn diets were mostly fish prey, whereas in summer, fish and invertebrates were eaten in similar amounts. Individuals in the southern Buzzards Bay region had less than 2 g of stomach contents in spring and about 3 g of primarily invertebrate prey in summer. Fish prey were eaten by the few striped bass caught in this southern region in autumn (Figure 5D).

Some prey categories were consistently eaten more than others. In spring the North Shore and Boston–South Shore striped bass ate predominately nonmenhaden clupeids (e.g., mostly juvenile Atlantic herring; Figure 6A). Less than 5% of the prey eaten by striped bass in the clupeid category was anadromous alosines. In summer, striped bass from these two northern regions continued to eat a variety of prey, including *Crangon* sp. (Figure 6B) and some Atlantic menhaden. In autumn the North Shore and Boston–South Shore striped bass ate fish prey, mostly juvenile menhaden (Figure 6C). In Buzzards Bay, south of the Cape Cod biogeographic break, diets were primarily benthic

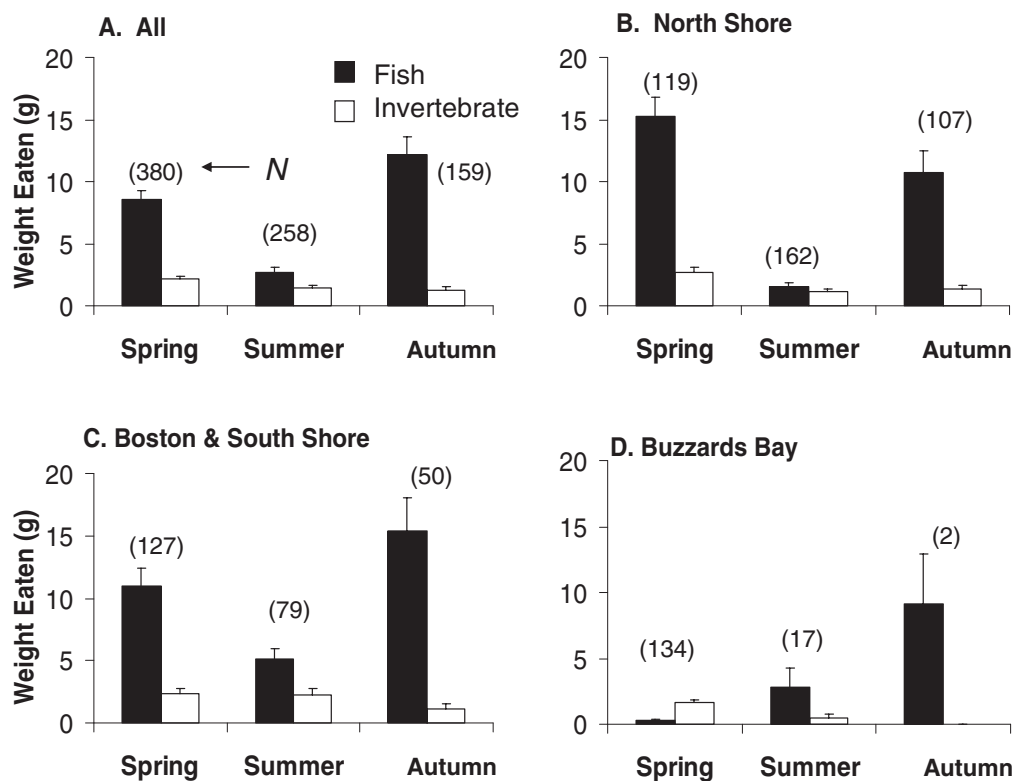


FIGURE 5. Mean weights of fish and invertebrate prey eaten by striped bass in spring, summer, and autumn in (A) all regions combined and the (B) North Shore, (C) Boston–South Shore, and (D) Buzzards Bay regions separately. The error bars represent ± 1 SEs; the numbers in parentheses are the numbers of striped bass stomachs examined.

invertebrates (*Crangon* sp., small crustaceans) in spring, adding juvenile menhaden in the summer and autumn.

Trends in prey categories were easier to interpret at the regional than the estuary scale (Figure 7). For striped bass feeding in the North Shore and Boston–South Shore regions across all seasons, fish prey in the clupeid category and menhaden dominated diets with some sand lance, silversides, mummichog, *Crangon* sp., and other small crustaceans present (Figure 7). Among estuaries, striped bass diets exhibited substantial variation in fish prey categories eaten. For example, (1) more clupeids were eaten in estuaries 2–4 and 6–9, (2) more menhaden were eaten in estuaries 2, 4, and 9, and (3) more sand lance were eaten in estuaries 7, 8. Conversely, the amounts of *Crangon* sp. and crab eaten were similar across estuaries (Figure 7B). In Buzzards Bay, patterns were similar at the region and estuary scales, probably because striped bass in all four southern estuaries (A–D) ate small amounts of homogeneous prey (Figure 7B).

Mean daily temperatures varied across seasons both within and across systems (Figure 8). For the northern Rowley estuary, mean daily temperatures in spring (June) and summer (July and August) were within the first threshold, 12–25°C, the range for more than 2% striped bass growth (Hartman and Brandt 1995b). However, spring temperatures in the Rowley estuary frequently

exceeded the second threshold, 21°C, a preferred temperature based on habitat selection (Coutant 1985). In spring and summer, mean daily temperatures in the centrally located North estuary were within the range for high growth, 12–25°C, and always below the preferred temperature of 21°C. In the southern East Westport estuary, rapid warming in late spring caused summer temperatures to exceed both maximum conditions for growth (25°C) and preferred conditions, 21°C. During autumn, water temperatures dropped coastwide.

Across systems, seasonal mean water temperatures ranged from 14.5°C to 23.2°C in spring, from 16.6°C to 24.9°C in summer, and from 11.2°C to 18.9°C in autumn (Figure 8). In spring and summer, marked regional differences in temperature developed north and south of the Cape Cod biogeographic break. On average, southern estuaries were 2–9°C warmer than northern estuaries in spring and 2–8°C warmer in summer. In all estuaries north of Cape Cod (systems 1–9), spring and summer mean temperatures were within the suitable range for high growth (12–25°C; Hartman and Brandt 1995b) and at or below the preferred temperature for habitat selection (21°C; Coutant 1985). In the three of the four estuaries south of Cape Cod with temperature data (systems A–C), spring and summer mean temperatures neared or exceeded the upper threshold for growth (25°C) and consistently exceeded the preferred temperature (21°C). In

TABLE 4. Statistical results summarizing how geographic location at three scales influenced the amount of fish and invertebrate prey eaten when prey were examined in combination (MANOVA) and individually (ANOVA). The MANOVA statistic is Roy's greatest root (RGR). The three scales were analyzed separately, and the response variables were log transformed; MS = mean square.

MANOVA						ANOVA						
Variable (X)	RGR	F	df		P	Variables		df	Type III MS	F	P	
			Numerator	Denominator		Y	X					
Estuary												
Estuary (E)	0.0211	13.42	12	762	<0.0001	Fish prey	Estuary	12	162.27	14	13.06	<0.0001
Season (S)	0.051	19.49	2	762	<0.0001		Season	2	34.26	17	16.54	<0.0001
E × S	0.259	9.88	20	762	<0.0001		E × S	20	197.647	9.9	9.54	<0.0001
						Invertebrate prey	Estuary	12	48.806	3.9	8.41	<0.0001
							Season	2	7.711	3.9	8.31	0.0003
							E × S	20	32.215	1.6	3.47	<0.0001
Region												
Region (R)	0.044	11.66	3	785	<0.0001	Fish prey	Region	3	24.24	8.1	6.39	0.0003
Season (S)	0.024	9.7	2	785	0.0001		Season	2	17.36	8.7	6.86	0.0011
R × S	0.1	13.2	6	785	<0.0001		R × S	6	95.219	16	12.54	<0.0001
						Invertebrate prey	Region	3	5.09	1.7	3.14	0.0247
							Season	2	10.439	5.2	9.66	<0.0001
							R × S	6	9.346	1.6	2.88	0.0087
Biogeographic												
Biogeographic province (B)	0.006	2.47	2	790	0.08	Fish prey	Biogeographic province	1	2.23	2.2	1.63	0.2
Season (S)	0.018	7.48	2	791	0.0006		Season	2	10.5	5.3	3.84	0.02
B × S	0.039	15.71	2	791	<0.0001		B × S	2	42.53	21	15.55	<0.0001
						Invertebrate prey	Biogeographic province	1	1.3	1.3	2.36	0.12
							Season	2	8.13	4.1	7.38	0.0007
							B × S	2	0.18	0.1	0.17	0.85

autumn, except for the Parker and Essex estuaries, mean conditions were within the range where high growth could occur (Figure 8).

Modeled daily mean growth across all estuaries was moderate in spring (0.008 g/g of body weight per day, SE = 0.009), slower in summer (0.00007 g/g per day, SE = 0.003), and fastest in autumn (0.021 g/g per day, SE = 0.004). The most pronounced differences in potential weight gain occurred in the estuaries within regions separated by the biogeographic break. In spring, the bioenergetics model predicted high but variable growth for estuaries in the two northern regions (estuaries 2, 3, 7) and weight loss in estuaries in the southern Buzzards Bay region (estuaries A–C; Figure 9A). Summer growth was reduced everywhere compared with spring, was sometimes negative in the North Shore region (estuaries 2, 4), and always negative in the Buzzards Bay region (estuaries B, C; Figure 9). In autumn, because striped bass in our study ate higher-energy fish prey at temperatures within the range where growth could occur, potential weight gain was faster everywhere (Figure 9).

Varying empirically derived temperatures and diet rations reinforced the observed patterns. When spring diet was held constant for individual estuaries north of Cape Cod (estuaries 2, 3, 7), growth did not change when spring temperatures were replaced with higher summer or cooler autumn temperatures (Figure 10). When the empirically derived diets observed in estuaries south of Cape Cod in spring and coastwide in summer were held constant, warmer temperatures (spring diet, summer temperatures) accelerated weight loss (Figure 10; estuaries B–C) and cooler fall temperatures (e.g., spring diet, fall temperatures) reduced weight loss (Figure 10, estuary A). Thus, at low diet rations, higher temperatures south of Cape Cod in spring and coastwide in summer reduced growth. In autumn, when the empirically derived diet ration was large, higher temperatures (e.g., autumn diet, spring temperature versus autumn diet, summer temperature) increased growth (Figure 10). When temperatures were held constant and diet ration was varied (Figure 10), runs using summer diet rations had the lowest growth, reinforcing our previous finding that food was limiting

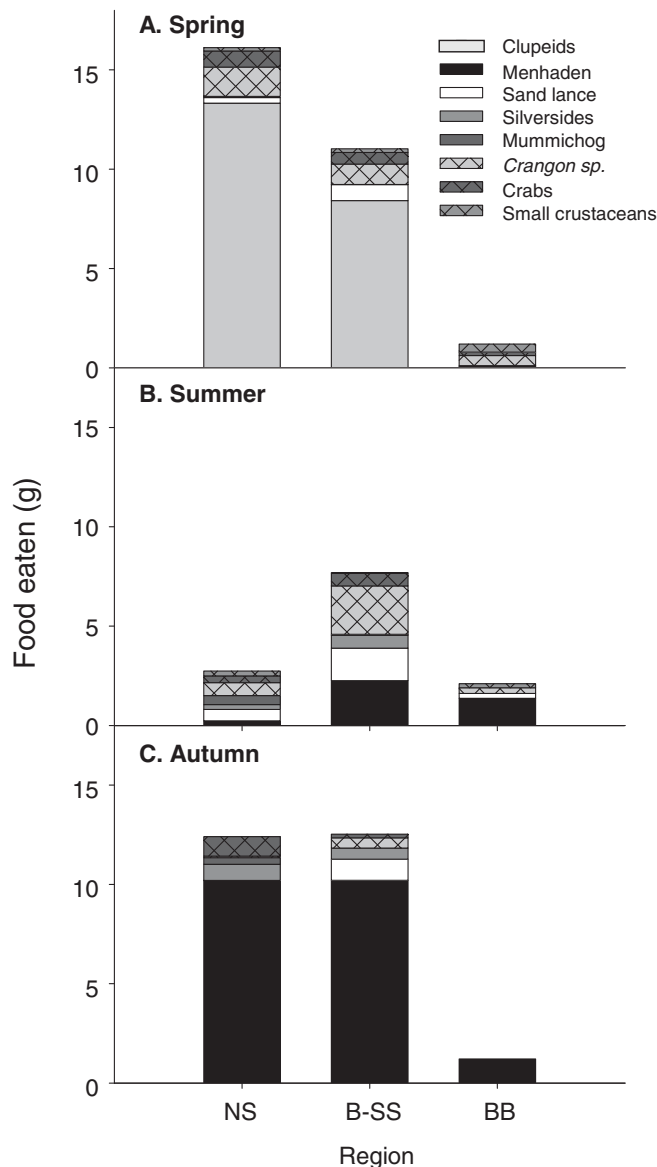


FIGURE 6. Mean weight of prey items eaten by striped bass in the three regions (NS = North Shore, B-SS = Boston-South Shore, and BB = Buzzard Bay) in (A) spring, (B) summer, and (C) autumn.

in this season. Autumn diet resulted in the highest potential growth in some estuaries and seasons, whereas spring diet resulted in the highest growth in others (Figure 10).

DISCUSSION

Overview

Our data from subadult and young-adult striped bass collected under standardized conditions during the “recovered” management time period (after 1995) yielded four insights into the feeding behavior of this abundant, consistently present size-class of predator. First, striped bass ate a season-specific mixture of fish and invertebrates in which some fish and invertebrate prey

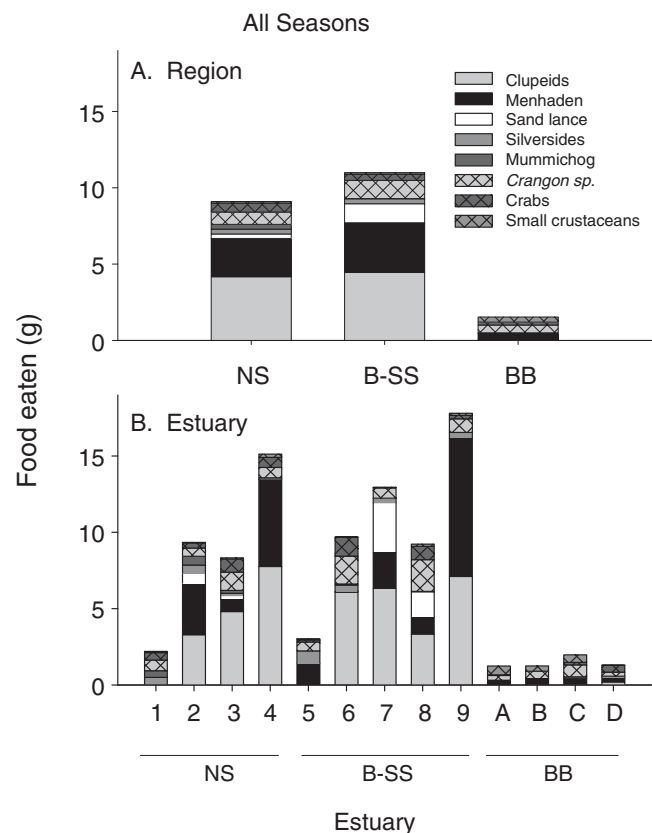


FIGURE 7. Mean weight of prey eaten by striped bass over all three seasons by (A) region (NS = North Shore, B-SS = Boston-South Shore, and BB = Buzzard Bay) and (B) estuary (see Figure 1). Data are the weights of prey eaten by average individual striped bass.

categories were eaten more often than others depending on location and season. Second, the patterns for these subadult and young-adult diets were similar to those observed for larger fish, as previously reported in the peer-reviewed literature. Within Massachusetts, diets of striped bass differed geographically along the coast, establishing the potential for predictable spatial heterogeneity in predator growth. Finally, the intermediate region scale provided the most quantitative, consistent, and interpretable trends in diet patterns.

Subadult and Small Adult Diets

Our subadult and small adult striped bass (average = 426 mm TL; 83% between 375 and 475 mm TL) ate a mixture of fish and invertebrate prey that varied predictably with location and season. In other diet studies, adult striped bass of a range of sizes also ate both fish and invertebrate prey. Unlike other estuary predators (Hartman and Brandt 1995a), striped bass often continue to eat invertebrates after the onset of piscivory (e.g., Schaefer 1970; Gardinier and Hoff 1982; Rulifson and McKenna 1987; Dew 1988; Hartman and Brandt 1995a; Dunning et al. 1997; Tupper and Able 2000; Walter et al. 2003; Nelson et al. 2003; Overton et al. 2009). The relative amount of fish and invertebrates eaten by striped bass differs across

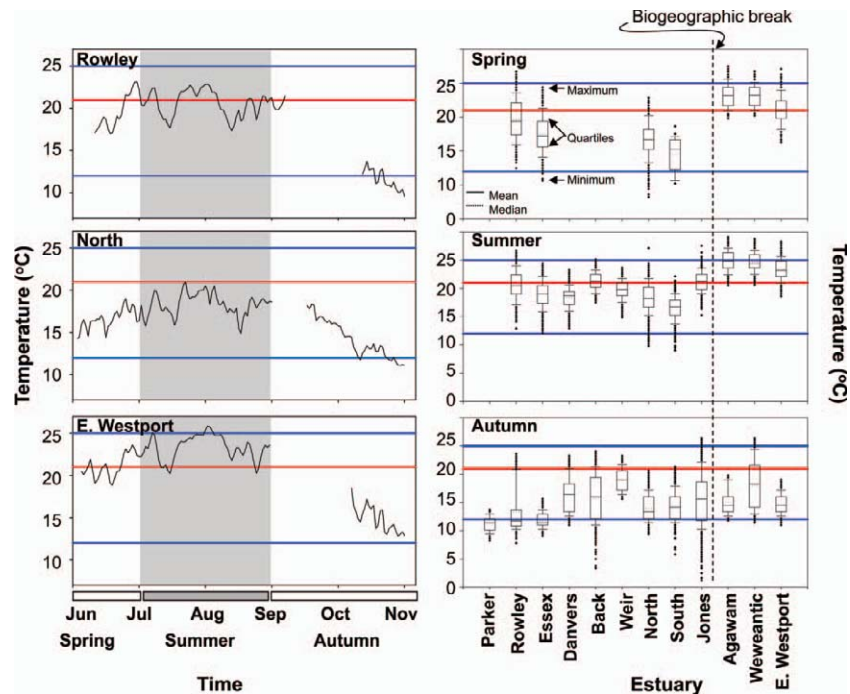


FIGURE 8. Daily mean temperature variations in 3 estuaries where striped bass were sampled (left-hand panels) and box-and-whisker plots of seasonal mean temperatures in all estuaries for which temperature data were available (right-hand panels). In each panel, the upper horizontal line is the upper boundary (25°C) for growth (2% of body weight per day at maximum consumption; Hartman and Brandt 1995a), the lower line is the lower boundary (12°C), and the middle line is the preferred temperature (21°C; Coutant 1985).

geographic areas of the Atlantic coast. Invertebrates are consistently present in striped bass diets in the northern North Atlantic area (Walter et al. 2003), where diets can be mostly invertebrates (Schaefer 1970; Rulifson and McKenna 1987; Dunning et al. 1997), mostly fish with few invertebrates (e.g., Gardinier and Hoff 1982; Dew 1988), or an even mix of both fish and invertebrates (Nelson et al. 2003). In contrast, in the middle North Atlantic (Hollis 1952; Dovel 1968; Hartman and Brandt 1995a; Griffin and Margraf 2003; Walter and Austin 2003; Overton et al. 2008, 2009) and southern North Atlantic (Trent and Hasler 1966; Manooch 1973; Rudershausen et al. 2005), striped bass older than age 2 ate mostly fish prey.

By season, the striped bass in our study ate a consistent amount of invertebrates at all times, with the addition of fish prey in some estuaries in spring and in all estuaries in autumn. Elsewhere, striped bass ate more invertebrates in the spring (Schaefer 1970), spring and summer (Hartman and Brandt 1995a), or summer (Overton et al. 2009). In autumn, regardless of location, striped bass overwhelmingly ate fish prey (e.g., Hollis 1952; Manooch 1973; Hartman and Brandt 1995a; Walter et al. 2003; Griffin and Margraf 2003; Walter and Austin 2003; Rudershausen et al. 2005; Overton et al. 2009). Our samples included a very narrow size range of striped bass (60% between 400 and 450 mm TL; 92% between 350 and 550 mm TL) preventing a meaningful examination of size-specific differences in diets. Elsewhere, for juveniles and very small subadults, the amount of

fish prey increases with size (Schaefer 1970; Rudershausen et al. 2005). However, large striped bass do not necessarily become more piscivorous (Nelson et al. 2003) and very large striped bass often add large invertebrates to their diet seasonally (>675 mm [Nelson et al. 2003]; >700 mm [Overton et al. 2009]).

The specific prey categories eaten by subadult and young-adult striped bass foraging along the coast of Massachusetts supported some insights from previous studies, identified novel diet patterns, and failed to confirm other previously reported trends. In many studies including ours, Atlantic menhaden was a key prey (Hollis 1952; Manooch 1973; Hartman and Brandt 1995a; Nelson et al. 2003; Walter and Austin 2003; Griffin and Margraf 2003; Walter et al. 2003; Overton et al. 2008, 2009; Rudershausen et al. 2005). The emigration of juvenile menhaden from estuarine nursery areas during late summer and autumn likely provides a highly abundant and easily captured prey for striped bass (Manooch 1973). In the "historical" and "crisis" management time periods, the abundance of Atlantic menhaden has been variable in New England (Reintjes and Pacheco 1966), but since 1995, large year classes of juveniles have consistently appeared along the Massachusetts coast, making these fish an important staple for migratory striped bass in autumn. The small crabs and crustaceans, including *Crangon* sp., consumed in our study, were also eaten by striped bass in other northern North Atlantic studies (Rulifson and McKenna 1987; Dew 1988; Schaefer 1970; Dunning et al. 1997; Tupper and Able 2000; Nelson

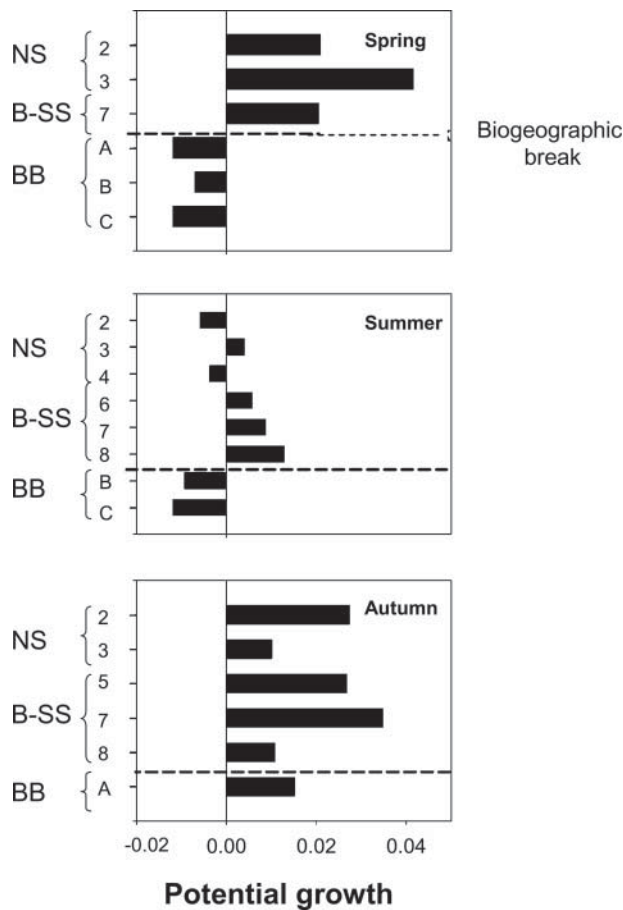


FIGURE 9. Potential growth (g/g of body weight per day) for adult striped bass in spring, summer, and autumn by region (NS = North Shore, B-SS = Boston-South Shore, and BB = Buzzard Bay), selected estuary, and biogeographic province. The solid vertical solid line represents no growth.

et al. 2003). In spring-summer, *Crangon* sp. comprised nearly one third of the diet (% weight) for individual striped bass in some of our estuaries. The preponderance of *Crangon* sp. in the diets suggests that striped bass could have a major impact on how energy flows and nutrients cycle in these estuaries, which are important nurseries for an array of marine fish.

Although adult Atlantic herring have been observed in striped bass diets (Overton et al. 2008), previous studies have not reported that subadult and young-adult striped bass eat a substantial amount of juvenile Atlantic herring in spring. This observation may be unique to the northern North Atlantic estuarine habitats in the time period that we sampled or may reflect recent changes in the estuarine community (Rulifson 1994; Overholtz and Friedland 2002; Wyda et al. 2002). In our study, in summer, nonclupeid fish such as sand lance contributed to striped bass diets in select systems and resident estuarine fishes such as mummichogs and silversides were consistently present in striped bass diets, albeit at low levels. Except for these, the prey fish important in previous studies were not important here. For ex-

ample, in many locations along the Atlantic coast, bay anchovy *Anchoa mitchilli* (Hollis 1952; Schaefer 1970; Manooch 1973; Hartman and Brandt 1995a; Griffin and Margraf 2003; Overton et al. 2009) and sciaenid fish were eaten by adult striped bass (Hollis 1952; Dovel 1968; Hartman and Brandt 1995a; Walter and Austin 2003; Walter et al. 2003; Overton et al. 2008). We did not see these prey as they are not common in the northern Acadian biogeographic province.

We observed few anadromous alosines in the diets of striped bass within our study estuaries at the time we sampled. The importance of anadromous alosines in striped bass diets in other studies also varies. Anadromous alosines were key prey in diet studies throughout the Atlantic coast in the “historical” and “crisis” time periods (Hollis 1952; Trent and Hassler 1966; Manooch 1973; Gardinier and Hoff 1982; Dew 1988; Dunning et al. 1997). Conversely, alosine prey were relatively rare or absent in diets of striped bass caught near Long Island, New York (Schaefer 1970), off the coast of Virginia and North Carolina in winter (Overton et al. 2008), and in some (e.g., Nelson et al. 2003), but not all (Walter and Austin 2003; Rudershausen et al. 2005) “recovered” period striped bass diet studies. These differences in the number of alosines eaten by striped bass may reflect spatial and temporal heterogeneity in predator diets, variation across coastal regions, changes across time periods, alternate foraging behaviors, or changes in the prey community (Rulifson 1994).

Geographic Patterns in Diets

Striped bass diets differed geographically along the Massachusetts coast. For the nine estuaries in the two northern regions within the Acadian biogeographic province, striped bass ate more food (mostly fish prey) than striped bass in the four estuaries in the southern region within the Virginian biogeographic province, for which the diet was mostly invertebrates. In spring, in the two northern regions, the amount of food eaten was high but variable across individual estuaries while little food of any prey category was eaten in the southern region. In summer and autumn, few regional differences were observed because striped bass ate little in summer in any estuary. Then in autumn, they added a high weight of fish prey to their diets in all estuaries. Only a subset of other striped bass diet studies have quantified any type of spatial variation. Tupper and Able (2000), Walter et al. (2003), Nelson et al. (2003) examined within and across-area variation in striped bass diets through comparisons of marsh restoration, multiple habitats within coastal regions, and across coastal areas. Five other existing striped bass studies examined within-system variation including upstream-downstream, and west-east gradients (Hollis 1952; Trent and Hassler 1966; Manooch 1973; Walter and Austin 2003; Overton et al. 2009). In all of these, partitioning within and across-system variability enhanced the clarity of feeding patterns. Documenting heterogeneity within and across-systems requires additional sampling, but this extra effort can reduce error in interpretation

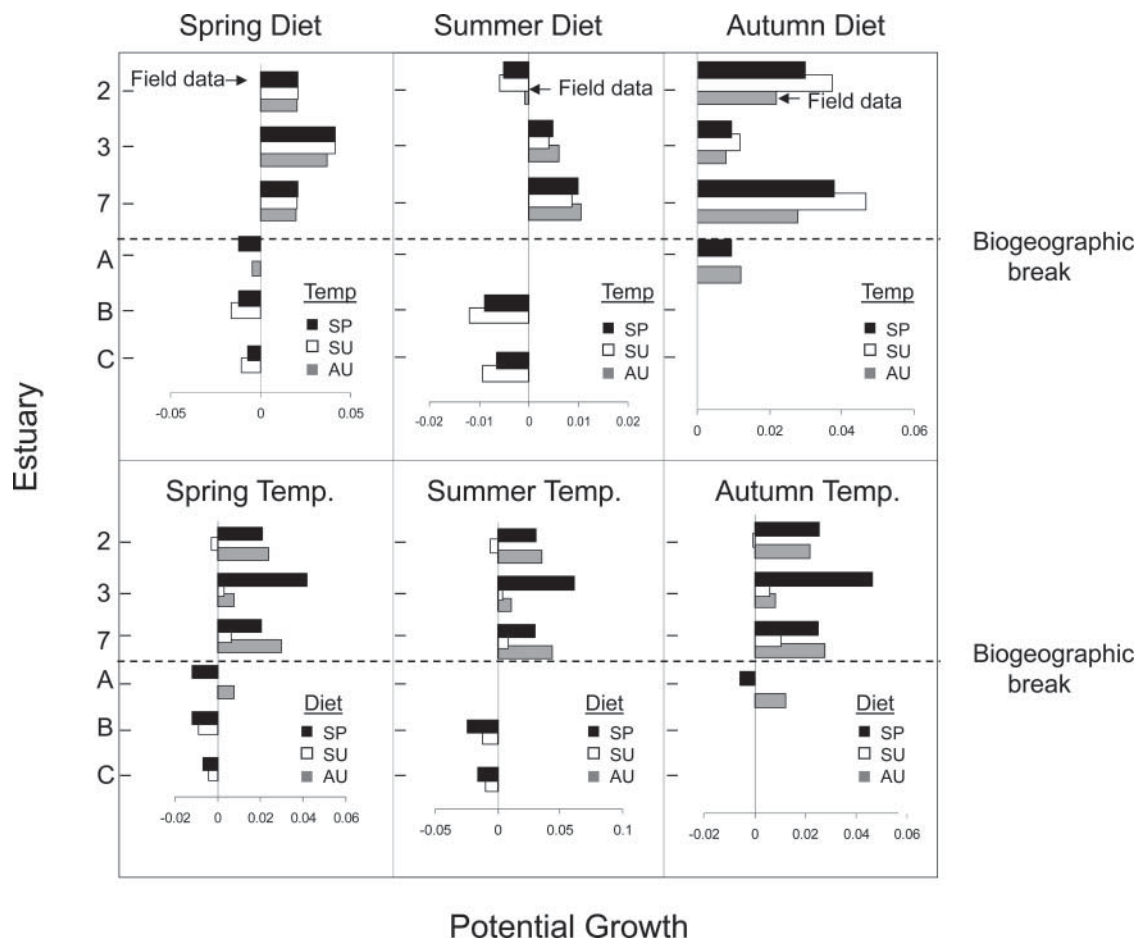


FIGURE 10. Potential growth (g/g body weight per day) for adult striped bass when the empirically derived diet for each estuary was held constant with estuary-specific temperatures in spring (SP), summer (SU), and autumn (AU) versus the potential growth when the empirically derived temperature for each estuary was held constant with estuary-specific diet rations. The designation “field data” refers to the combinations of diet and temperature that were actually observed and correspond to the simulation output in Figure 9. Note that the scale of the x-axis varies across plots.

(Petersen 1994; Kosa and Mather 2001) and improve sample design.

Heterogeneity in Modeled Growth

Coupled with temperature differences, the temporal and spatial heterogeneity in the amount and type of food can have consequences for striped bass growth. In other studies, the highest growth for striped bass in Chesapeake Bay occurs after mid-July (Hartman and Brandt 1995a) and as late as autumn (Brandt and Kirsch 1993), when striped bass diets are dominated by pelagic fish prey. In our estuaries, higher modeled growth occurred in spring and autumn because striped bass consumed large amounts of higher-energy, fish prey at moderate temperatures in both seasons. This trend contrasted with low modeled growth observed when fewer, lower-energy, invertebrate prey were eaten in warm water in summer. Geographically, lower modeled growth consistently occurred in the southern Virginian biogeographic province where limited quantities of lower-energy, invertebrate prey were consumed. The combination of high spring and sum-

mer temperatures south of Cape Cod, combined with a small diet ration composed of lower-energy invertebrate prey, contributed to the weight loss observed in the bioenergetics simulations in this region during these seasons. Within the higher-growth, Acadian province, across-estuary variation occurred in growth, especially in spring, probably because of variability in fish prey across individual estuaries. A tradeoff between dependable supplies of low calorie invertebrates versus highly variable but more nutritious fish may result in alternative risk-sensitive foraging strategies (Barkan 1990; Cartar 1991), with consequent growth variation.

Comparisons across Scales

The three spatial scales provided different levels of clarity. At the biogeographic province scale, both the numbers of estuaries and numbers of striped bass across provinces were uneven. At the regional scale, the numbers of estuaries sampled and fish examined were more similar. Low sample size was a problem at the estuary scale because relatively few fish were caught in some

estuaries within specific seasons. Although location-season interactions were significant at all scales, the biogeographic main effect was not, possibly because the data set was unbalanced at this scale. The high variation across individual systems made consistent biological interpretation challenging at the detailed estuary scale. On the other hand, regional trends were relatively easy to interpret. Few diet studies have compared results across scales as we have done here.

Thus, based on ecological and statistical considerations, the intermediate region scale provided the clearest trends. Because of the natural complexity of the Massachusetts coast, our data could be examined concurrently as 13 estuaries, three geographic regions, and two biogeographic provinces. This allowed us to compare taxonomic, spatial, and temporal scale that can both complicate and clarify trends for foraging predators. Because the choice of scale can affect the clarity of trends, understanding the role of scale in diet analysis has implications for management. Our results have several ecological implications related to interpreting the complexity associated with multiple scales. First, because of temporal changes in prey in estuaries, diet trends for migrant striped bass need to be examined by season. Second, if all data available are used to depict diet trends, the feeding pattern becomes too complex to be useful, but if too much detail is aggregated, important trends about foraging disappear. Third, several criteria should be considered when choosing a spatial scale for sampling and analysis including (a) the question being asked, (b) heterogeneity in physical conditions, and (c) statistical implications of the design (e.g., sample size and balance across treatments). For the results we presented here, we recommend using the regional scale. Although location is often considered in diet analyses, how spatial scale is segmented is not. A thoughtful decision on scale can make diet patterns clearer. We recommend considering the results of multiple analyses at multiple scales before the final decision on scale is made.

Implications and Limitations

Here we have compared the diets of subadult and young-adult migratory striped bass collected under standardized conditions. We have summarized the differences in fish versus invertebrate prey and specific prey categories eaten across three spatial scales and three seasons. For perspective, we have framed our results in light of previous diet studies of migratory striped bass. Our data on differences in diet across locations, seasons, and scales has added a new and useful perspective on what these abundant-sized predators are eating relative to other peer-reviewed studies from different locations and time periods. Although anecdotal information exists about when and where these popular sport fish feed, science-based data on their foraging in complex habitats are limited. We do know, however, that fish of different sizes collected with different gear at different times of day at different tides likely eat different prey. By using standardized methods (i.e., same protocols across all estuaries and seasons), we have

removed these concerns from our examination of trends across estuaries and seasons.

Our focused standardized sampling protocol had clear advantages for the question we asked, but it also had limitations. Our focus was rather narrow (e.g., two days in each season, one tidal stage, first light, fish collected in limited locations). We do not know if tidal differences in estuaries north and south of the Cape Cod biogeographic break affected foraging or if localized habitat differences existed in individual estuaries. Our sampling allowed us to contrast the specific conditions we tested in our sampling design, but, of course, does not allow for expansion of inferences to the entire population, especially for larger fish. Our focused use of the bioenergetics model suggested that differences in amount of food eaten and types of prey can have consequences at seasonally variable temperatures. However, we did not have empirically based consumption estimates, we did not have estimates of periodicity of striped bass feeding, and we do not know if periodicity differs across estuaries. Consequently, to test the generality of these results, additional bioenergetics modeling is needed that incorporates diel consumption data. Clearly, our simplified sampling and modeling have not answered all questions about how diets varied across all physical and temporal conditions. We view our research as a first step in developing a framework for comparative, multiscale analyses of diet trends.

SUMMARY

Our consistent focus on the mix of subadults and small adults that migrate and feed as adults has allowed us to partition diet variation across scales. The striped bass sizes we examined are not important components of the spawning biomass, and thus are often overlooked in management. Their growth and survival, however, may impact future harvest, local prey resources, and aquatic community structure. Consequently, knowing sources of variation in the diets of this size-group of striped bass is essential for both research and management.

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