Diet composition of large striped bass (*Morone saxatilis*) in Chesapeake Bay*

John F. Walter III
Herbert M. Austin
Virginia Institute of Marine Science
School of Marine Science
The College of William and Mary
PO Box 1346, Gloucester Point, Virginia 23062
E-mail address (for J. F. Walter): jfwalter@vims.edu

Abstract—Large (>458 mm) striped bass (*Morone saxatilis*) are dominant predators in Chesapeake Bay. In recent years, the Chesapeake Bay stock of striped bass has increased dramatically, raising concerns about their predatory impact and their forage requirements. In response to these concerns and the need for more recent ecological studies, this investigation was conducted to characterize feeding habits of large striped bass in Chesapeake Bay. Stomach contents from 1225 striped bass from 458 to 1151 mm TL were examined in the spring and fall of 1997 and 1998. Striped bass consumed 52 different species of vertebrates and invertebrates; however, only a few species of clupeoid and sciaenid fishes dominated diets across both the seasons and size ranges of striped bass examined. Of finfish species, menhaden (*Brevoortia tyrannus*) was the dominant prey in most areas and gizzard shad (*Dorosoma cepedianum*) replaced menhaden in importance in lower salinity waters. Spot (*Leiostomus xanthurus*) and other sciaenid fishes and anadromous herrings (*Alosa* spp.) also contibuted large percentages of striped bass diet. Although pelagic schooling fishes formed the majority of the diet, benthic fishes contributed a higher percentage to the diet than in previous studies of striped bass diet composition.

Manuscript accepted 22 October 2002.
Manuscript received 9 January 2003 at NMFS Scientific Publications Office.
Fish. Bull. 101:414–423 (2003).

Along the Atlantic coast of North America, the striped bass is one of the most important commercial and recreational fishes (Richards and Rago, 1999). In the face of intense overfishing, the Atlantic Coast population of striped bass experienced drastic declines in the 1970s (Field, 1997; Richards and Rago, 1999). During these periods of intense harvesting, smaller fish dominated the stock composition and the fishery (Koo, 1970). With the relaxation of fishing pressure and the implementation of regulations designed to protect older age classes, populations rebounded to the point where, currently, large, older fish comprise a high percentage of the population (Richards and Rago, 1999). The increased abundance of large striped bass has raised concerns over both the predatory impact and prey needs of this large population of seasonally abundant species in Chesapeake Bay.

Within Chesapeake Bay, historically a center of striped bass abundance and one of the largest sources of juvenile production for the Atlantic coast (Merriman, 1941; Berggren and Lieberman, 1978; Kohlenstein, 1981), striped bass are seasonally abundant upper trophic level predators. Chesapeake Bay striped bass are partitioned into a resident, primarily male or juvenile, group of fish found year-round and a migratory group consisting of older, larger (>711 mm total length) and often primarily female fish found in the spring and fall (Chapman, 1987). The Atlantic States Marine Fisheries Commission manages fish greater than 711 mm (28 inches) total length as migratory (ASMFC[1]) because the majority of these fish leave Chesapeake Bay and migrate throughout the Atlantic coast. Striped bass within Chesapeake Bay migrate during the spring when mature fish ascend tidal freshwater tributaries to spawn (Chapoton and Sykes, 1961; Dorazio et al., 1994). After spawning, these fish leave Chesapeake Bay and migrate northward along the Atlantic coast, returning to Chesapeake Bay in large numbers during the fall. With a major peak in March–April and a minor peak in October–November, the historical landings data reflect the migratory behavior and seasonal abundance of larger fish (Koo, 1970).

Diet studies represent the first step in determining the magnitude and direction of trophic interactions and are essential data for the management of both predators and prey (Livingston, 1985). For the management of multispecies fisheries, detailed information on fish food habits is required in order to account for the temporal, spatial, and ontogenetical nature of trophic interactions (Walters et al., 1999; Hollowed et al., 2000; Whipple et al, 2000). Although the feeding habits of resident juvenile and early adult striped bass have received considerable study in Chesapeake Bay (Hollis, 1952; Markle

* Contribution 2507 of the Virginia Institute of Marine Science, School of Marine Science, The College of William and Mary, Gloucester Point, VA 23062.

[1] ASMFC (Atlantic States Marine Fisheries Commission). 2000. Public information document for Amendment 6 to the Interstate Fishery Management Plan for striped bass, 17 p. ASMFC, 1444 Eye Street NW. Washington, DC 20005. http://www.jcaa.org/PID.htm (March 2001).

and Grant, 1970; Setzler et al., 1980; Boynton et al., 1981; Limburg et al., 1997; Hartman and Brandt, 1995a) and in other locations (Schaefer, 1970; Manooch, 1973; Rulifson and McKenna, 1987), no studies have included enough specimens larger than 600 mm total length to adequately characterize the diet of migratory fish. The absence of dietary information for these larger striped bass may have been due to the difficulty in sampling larger striped bass and also to the relative scarcity of large striped bass in Chesapeake Bay during times of severe overfishing (Koo, 1970). Nevertheless, the absence of diet data represents a gap in our knowledge of the trophic dynamics of large striped bass that form the major portion of the spawning stock, are prized fisheries targets and, through successful fisheries management, have emerged as a significant seasonal predatory force within Chesapeake Bay. We specifically address the diet composition of large (458–1151 mm) striped bass in Chesapeake Bay to determine the important species in their diet during the spring and fall periods of abundance.

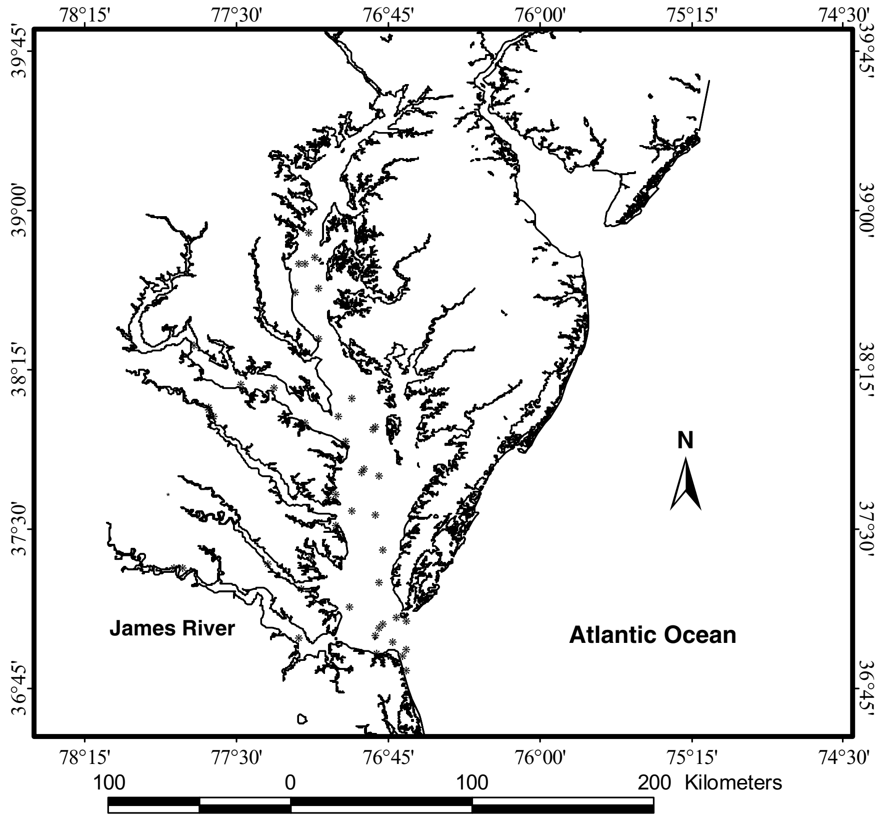

Figure 1

Map of Chesapeake Bay showing spatial distribution of striped bass samples from March 1997 to May 1998.

Methods

From March 1997 to May 1998, 1225 striped bass were collected from various localities in Chesapeake Bay, its Virginia tributaries, and the Chesapeake Bay mouth (Fig. 1). Fish were collected from recreational fishermen, charterboat captains, and seafood dealers, as well as from scientific monitoring programs in the spring (48.5%) and fall (51.5%), corresponding to seasonal migration patterns and fishing seasons. Fish ranged in size from 458 to 1151 mm TL (mean 653.7mm) and were 0.91–17.6 kg in weight (mean 3.69 kg). Hook-and-line gear, gill nets, fyke nets, and otter trawls were used to capture fish. Fish captured in pound nets were excluded from this analysis because of complications introduced by the confinement of the fish in pound nets. Fish captured by hook and line were recorded as such in order that the bait and chum used with this gear could be excluded from the diet analyses. Total length (±1.0 mm), sex, and weight (±0.001 kg wet weight) were recorded for each fish, as well as location, date, and method of capture. Stomachs were removed by cutting the alimentary canal anterior to the stomach and posterior to the pylorus and the contents were frozen until processed. In some cases, stomachs of fish donated by charterboat captains and recreational fishermen were removed by the fisherman.

Fish stomachs were thawed and emptied, and their contents were blotted dry and weighed. Contents were sorted and identified to the lowest possible taxon, weighed, counted, and measured. Diet composition was analyzed by using three measures described in Hyslop (1980): percent frequency of occurrence, percent weight, and percent number. These values were combined to give an index of relative importance (Pinkas et al., 1971). The index of relative importance for a particular prey category i (IRI_i) is expressed as

$$IRI_i = (\%N + \%W) \times \%F,$$

where $\%N$ = the percentage of a prey species by number;
$\%W$ = the percentage of a prey species by weight; and
$\%FO$ = the percent frequency of occurrence of a prey species.

IRI values were calculated as percent IRI values (Cortes, 1997). In calculating IRI values, we excluded several items appearing in the stomachs, such as chum (ground menhaden), bait, trash and plant material because they were deemed to be non-naturally occurring food items. Several prey species were combined either because of difficulties in identification of partially digested prey to species or because of ecological or taxonomic similarity. Both bay anchovy (*Anchoa mitchilli*) and striped anchovy (*Anchoa* *hepsetus*) were combined into a single-prey category. In addition, gizzard and threadfin shad (*Dorosoma cepedianum* and *D. petenense*), and blueback and alewife herring (*Alosa aestivalis* and *A. pseudoharengus*) were treated as single-prey categories. Unidentified prey consisted primarily of unidentified fish remains and were recorded as such.

Striped bass were categorized by fish length and month of capture. Fish were partitioned into two size classes corresponding to mixed resident and migratory fish (458–710 mm total length) and coastal migrant fish (711–1255 mm total length) based on the Atlantic States Marine Fisheries Service classification of fish 711 mm and above as fully recruited to the coastal migratory stock. For spatial analysis of feeding habits, each fish was placed into one of two salinity regimes: tidal freshwater (0–5 ppt) or mesohaline waters (6–28 ppt). Tidal freshwater-waters include the upper reaches of the James, York, Rappahannock, and Potomac rivers. Mesohaline waters include the open waters of Chesapeake Bay and the lower reaches of most rivers. No fish were collected in the fall from tidal freshwater. For both monthly and spatial analyses, diet was quantified by weight only.

To measure intensity of feeding, a stomach fullness index (SFI) was calculated according to Hureau (1969):

$$SFI = \frac{Stomach\ content\ weight}{Fish\ weight} \times 10.$$

SFI values were calculated for all fish regardless of the presence or absence of stomach contents.

A regression of striped bass total length versus prey total length was fitted by least-squares linear regression of the untransformed values. Prey lengths were reconstructed from partially digested backbones by using regressions of backbone length on total length obtained from samples collected in 1998 by the authors and those given by Hartman and Brandt (1995a).

Results

Of the 1225 striped bass examined, 688 (56%) contained items in the stomachs (Table 1). Thirty-four different species of fish and 18 species of invertebrates were observed in the diet. Overall, clupeid fishes dominated the diet and menhaden, in particular, accounted for 44% of the weight and occurred in 18% of all stomachs (Table 2). Menhaden ranged in length from 103 to 360 mm total length. A % IRI value of 58.3 for menhaden was higher than that for all other species combined. Anchovies were numerically the most abundant (22%) of all prey items and were equal to spot (*Leiostomus xanthurus*) in % IRI, both sharing a value of 12.3. Other prey in order of decreasing %IRI were gizzard shad (genus *Dorosoma*) with a % IRI of 6.7, and blue crab (*Callinectes sapidus*) with %IRI values of 3.4. Atlantic croaker (*Micropogonius undulatus*) and summer flounder (*Paralichthys dentatus*) had %IRI values of 1.1 and 1.0, respectively.

All other prey categories had %IRI values <1 and appeared relatively unimportant in the overall diet of striped bass, although some increased in relative importance at certain times and locations. Invertebrates were relatively minor constituents of the overall diet of large striped bass, providing only 4.4% of the total IRI. In contrast, clupeid fishes contributed 65% of the IRI and both sciaenid and engraulid fishes combined contributed over 25% of the total IRI.

Clear seasonal and spatial patterns in diet corresponded with the migratory behavior of large striped bass. Striped bass in both sizes classes, 458–710 mm and 711 mm and above, migrated into tidal freshwater to spawn in the months of March, April, and May. Striped bass fed in the tidal freshwater region, although at a reduced intensity as evidenced by the lower stomach fullness values and the lower percentages of nonempty stomachs compared to those at other times and locations (Table 1). Gizzard shad, white perch (*Morone americana*), and anadromous herrings (*Alosa pseudoharengus* and *Alosa aestivalis*) were the main constituents of the diet of both sizes of striped bass in the tidal freshwater region (Table 3, Fig. 2).

During spring, striped bass also pass through the mesohaline waters of Chesapeake Bay prior to and after spawning, during which time they feed fairly heavily as indicated by higher than average stomach fullness values and percentages of nonempty stomachs (Table 1). Approximately 83% of the striped bass sampled from mesohaline waters during this time had food in the stomachs indicating active feeding during the pre- and postspawning migration. Menhaden dominated the diets by weight of both size classes of striped bass from mesohaline waters in the spring. Striped bass of both size classes also consumed croaker, blue crab, and white perch (Table 3, Fig. 2); however, the size classes differed in that smaller fish consumed bay anchovy and juvenile spotted hake (*Urophycis regia*) and larger striped bass consumed anadromous herrings.

Large striped bass are generally absent from Chesapeake Bay in significant numbers in the summer and return in the fall to mesohaline waters of Chesapeake Bay and its lower tributaries. The fall return is essentially a feeding migration and the high stomach fullness values and high percentages of nonempty stomachs (Table 1) indicate active feeding. Striped bass of both size classes fed predominantly upon menhaden, which had percent weight values between 53% and 58 % (Fig. 3). Sciaenid fishes, including spot, Atlantic croaker, and weakfish (*Cynoscion regalis*) combined provided between 23% and 31% of the diet by weight for both size classes of fish. Notable differences occurred in the high percentage of summer flounder (*Paralichthys dentatus*) found in the diets of larger striped bass (15% by weight) and in the high percentage of both butterfish (*Peprilus triacanthus,* 4%) and gizzard shad (11%) found in the diets of smaller fish (Fig. 3). The only invertebrates found in abundance in the diets during this time were blue crabs, which contributed 70% of the diet by weight for the smaller size class of striped bass in September (Table 3). The greatest number of species occurred in the diet in fall with forty-four different species of prey items observed, although many were isolated occurrences of rare prey and only a few species contributed to the overall diet at this time.

Table 1

Distribution of striped bass collections by month with location, capture method, percentage of nonempty (% full) stomachs, and stomach fullness index.

Month	Location	Method	Total	% full	Stomach fullness index	Standard deviation
Striped bass, 458–710 mm total length						
Feb	Potomac River	gill net	14	64.3%	1.13	1.73
Mar	York,Rappahannock, James River	gill net, fyke net	116	47.4%	0.36	0.79
Apr	York, Rappahannock, James River	gill net, fyke net	159	25.2%	0.38	1.52
May	Upper York River	electroshock	28	71.4%	1.15	1.80
Jun	Middle Bay	gill net, hook and line	77	93.5%	4.85	3.87
Sep	Middle Bay	hook and line, gill net	74	27.0%	0.30	0.62
Oct	Lower Bay	hook and line, gill net	245	58.4%	1.06	1.93
Nov	Lower Bay	hook and line, gill net	114	74.6%	2.08	3.08
Dec	Lower Bay	hook and line, gill net, trawl	12	91.7%	1.48	1.24
Striped bass 711–1255 mm total length						
Mar	York, Rappahannock, James River	gill net, fyke net	12	50.0%	0.31	0.69
Apr	York, Rappahannock, James River	gill net, fyke net	85	31.8%	0.60	1.44
May	Upper York River	electroshock	7	85.7%	0.82	1.74
Jun	Middle Bay	hook and line	66	81.8%	2.75	2.14
Sep	Middle Bay	hook and line, gill net	20	25.0%	0.21	0.24
Oct	Lower Bay	hook and line, gill net	45	42.2%	0.71	1.52
Nov	Lower Bay	hook and line, gill net	95	74.7%	1.69	2.80
Dec	Lower Bay	hook and line, gill net	56	80.4%	1.23	1.66
Total	all	all	1225	56.1%	1.00	2.03

Table 2

Stomach contents of striped bass from Chesapeake Bay, 1997–98 (n=688, total number of stomachs with quantified contents).

Prey	Occurrences	% frequency of occurrence	Number	% by number	Weight in grams	% by mass	%IRI
Class Osteichthyes							
Clupeidae							
Brevoortia tyrannus	132	20.63	319	18.11	14757.03	44.40	58.34
Alosa spp.	7	1.09	20	1.14	977.38	2.94	0.20
Dorosoma spp.	43	6.72	142	8.06	4623.73	13.91	6.68
Unknown clupeid	18	2.81	21	1.19	134.56	0.40	0.20
Moronidae							
Morone saxatilis	1	0.16	1	0.06	19.46	0.06	0.00
Morone americana	19	2.97	24	1.36	750.09	2.26	0.49
Sciaenidae							
Leiostomus xanthurus	86	13.44	179	10.16	3315.84	9.98	12.25
Bairdiella chrysoura	13	2.03	17	0.97	244.61	0.74	0.16
Cynoscion regalis	15	2.34	19	1.08	835.62	2.51	0.38
Micropogonias undulatus	20	3.13	21	1.19	2123.82	6.39	1.07
Unknown scieanid	14	2.19	21	1.19	61.41	0.18	0.14

continued

A significant relationship between striped bass total length and prey total length ($P<0.05$, $r^2=0.26$) was observed which indicated that larger and older striped bass ate larger prey (Fig. 4). The fit of the regression was poor, indicating that, although larger striped bass did consume larger prey, they also consumed smaller prey.

Table 2 (continued)

Prey	Occurrences	% frequency of occurrence	Number	% by number	Weight in grams	% by mass	%IRI
Engraulidae							
Anchoa spp.	74	11.56	399	22.66	256.29	0.77	12.26
Other fish							
Paralichthys dentatus	17	2.66	30	1.70	2256.59	6.79	1.02
Membras martinica	1	0.16	15	0.85	26.17	0.08	0.01
Menidia menidia	12	1.88	25	1.42	27.00	0.08	0.13
Anguilla rostrata	10	1.56	21	1.19	544.48	1.64	0.20
Symphurus plagiusa	9	1.41	40	2.27	111.59	0.34	0.17
Peprilus triacanthus	6	0.94	12	0.68	385.88	1.16	0.08
Urophycis regia	3	0.47	26	1.48	400.00	1.20	0.06
Notropis spp.	3	0.47	5	0.28	8.45	0.03	0.01
Trinectes maculatus	5	0.78	5	0.28	23.56	0.07	0.01
Pomatomus saltatrix	3	0.47	3	0.17	184.21	0.55	0.02
Eucinostomus argenteus	3	0.47	3	0.17	39.92	0.12	0.01
Gobiosoma bosc	1	0.16	1	0.06	0.10	0.00	0.00
Synodus foetens	2	0.31	2	0.11	68.54	0.21	0.00
Strongylura marina	1	0.16	3	0.17	67.96	0.20	0.00
Scophthalmus aquosus	1	0.16	1	0.06	14.42	0.04	0.00
Mugil curema	1	0.16	1	0.06	36.08	0.11	0.00
Sphoeroides maculatus	1	0.16	1	0.06	4.80	0.01	0.00
Hypsoblennius hentzi	1	0.16	1	0.06	4.15	0.01	0.00
Fundulus heteroclitus	1	0.16	1	0.06	3.39	0.01	0.00
Unidentified fish remains	56	8.75	71	4.03	128.37	0.39	1.75
Class Crustacea							
Callinectes sapidus	55	8.59	129	7.33	439.81	1.32	3.36
Neomysis americana	13	2.03	90	5.11	11.09	0.03	0.47
Squilla empusa	23	3.59	35	1.99	174.26	0.52	0.41
Ovalipes ocellatus	13	2.03	15	0.85	103.68	0.31	0.11
Lironeca ovalis	6	0.94	6	0.34	0.54	0.00	0.01
Callinectes spp.	4	0.63	7	0.40	28.83	0.09	0.01
Penaeus setiferus	5	0.78	5	0.28	13.00	0.04	0.01
Crangon septemspinosa	3	0.47	5	0.28	1.34	0.00	0.01
Paleamonetes pugio	4	0.63	9	0.51	2.24	0.01	0.01
Cancer irroratus	1	0.16	1	0.06	7.73	0.02	0.00
Upogebia affinis	1	0.16	1	0.06	0.59	0.00	0.00
Class Bivalvia	*	*	*	*	2.00	*	**
Mytilus edulis	*	*	*	*	2.00	*	**
Crossostrea virginica							
Class Gastropoda							
All gastropods	1	0.16	1	0.06	0.39	0.00	0.00
Class Polychaeta							
All polychaetes	4	0.63	4	0.23	7.92	0.02	0.01
Class Hydrozoa							
All hydroids	2	0.31	2	0.11	0.00	0.00	0.00
Phylum Porifera							
All sponges	1	0.16	1	0.06	2.29	0.01	0.00
Miscellaneous items							
Chum (ground menhaden)	159	*	*	*	*	*	**
Bait (menhaden, spot, etc)	28	*	*	*	*	*	**

continued

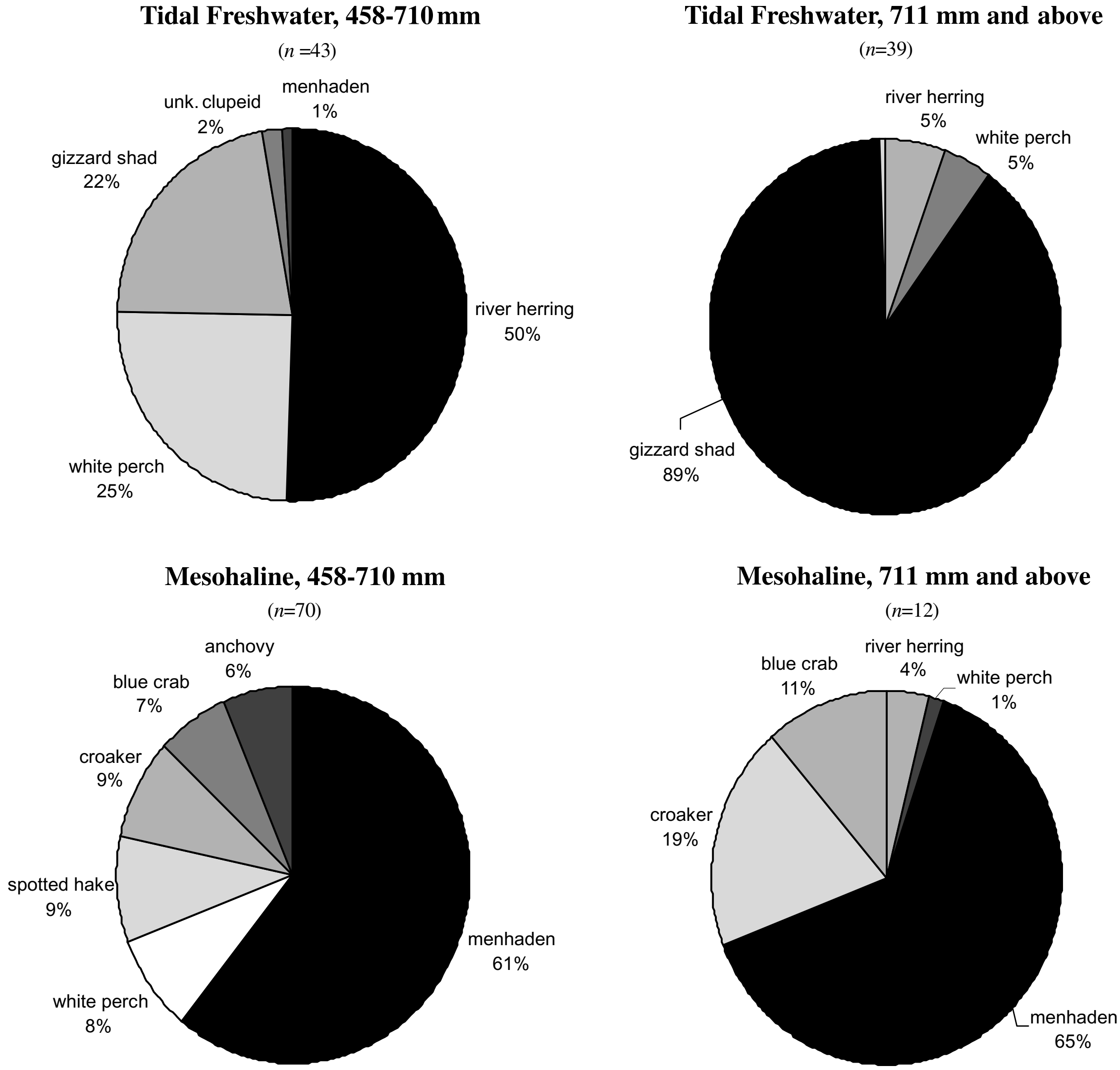

Figure 2

Percentage by weight of prey in the diets of striped bass captured in the spring (February–June). Note that only stomachs with contents other than bait were used in the construction of these figures.

Table 2 (continued)

Prey	Occurrences	% frequency of occurrence	Number	% by number	Weight in grams	% by mass	%IRI
Miscellaneous items (cont.)							
Plant material	11	*	*	*	*	*	**
Woody material	6	*	*	*	*	*	**
Plastic trash	1	*	*	*	*	*	**
Cigarette butts	2	*	*	*	*	*	**
Stones, gravel	2	*	*	*	*	*	**
Feathers	2	*	*	*	*	*	**

* Not quantified.
** Not included in IRI calculations.

Table 3

Seasonal diet composition by percent weight for striped bass from Chesapeake Bay, 1997–98. Sample sizes are listed in parentheses.

Month	Menhaden	*Dorosoma* spp.	White perch	*Alosa* spp.	*Callinectes* spp.	Spot	Other fish	Other invertebrates	Croaker	*Anchoa* spp.	Silversides
Striped bass 458–710 mm total length											
Feb (9)	0.0	43.1	56.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mar (55)	2.1	37.3	13.9	0.0	1.0	1.6	14.3	2.4	0.0	27.5	0.0
Apr (40)	0.0	23.4	27.4	18.9	1.6	0.0	25.1	2.0	1.0	0.5	0.0
May (20)	0.9	0.0	0.0	73.7	11.4	0.0	2.0	0.0	12.0	0.0	0.0
Jun (72)	78.2	0.0	10.6	0.0	4.4	0.0	0.0	0.0	6.8	0.0	0.0
Sep (20)	16.4	0.0	0.4	0.0	69.5	0.0	0.0	1.9	0.0	6.8	5.0
Oct (143)	38.0	22.0	0.1	0.0	2.7	21.0	14.2	0.6	0.0	0.9	0.5
Nov (85)	55.9	1.6	0.0	0.0	0.0	27.4	8.5	2.0	3.8	0.1	0.7
Dec (11)	44.1	0.0	0.0	0.0	0.0	33.7	1.0	0.0	0.0	20.7	0.4
Striped bass 711–1151 mm total length											
Mar (6)	0.0	96.5	0.1	0.0	0.1	0.0	3.3	0.0	0.0	0.0	0.0
Apr (27)	0.0	90.4	5.1	3.5	0.0	0.0	0.9	0.0	0.0	0.0	0.0
May (6)	0.0	22.2	0.0	77.1	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Jun (54)	61.9	0.0	1.1	3.9	14.3	0.0	0.0	0.0	18.7	0.0	0.0
Sep (5)	76.5	0.0	23.2	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Oct (19)	24.7	0.0	0.0	0.0	2.9	5.7	10.3	6.3	0.0	35.7	14.3
Nov (71)	43.1	2.2	0.0	0.0	0.2	6.8	5.9	1.2	14.6	3.8	22.1
Dec (45)	73.3	0.0	0.0	0.0	0.0	10.8	12.5	0.1	2.6	0.3	0.4

Discussion

Our study addresses the diet of striped bass above 458 mm total length in Chesapeake Bay. In previous studies of striped bass diet (Hollis, 1952; Hartman and Brandt, 1995a) in Chesapeake Bay and adjacent waters (Manooch, 1973), few fish above 458 mm were sampled. The comprehensive work by Hartman and Brandt (1995a) did not include fish above age 6. The current study focuses specifically on the diet of larger striped bass that previously were undersampled or were rare during periods of severe overfishing (Koo, 1970).

Throughout the two size ranges of striped bass sampled and in both seasons and locations, schooling fishes dominated the diets in Chesapeake Bay. In particular, clupeid fishes (menhaden, gizzard shad) and the closely related anchovies exceeded all other prey species in frequency of occurrence, number, and biomass. Among other fishes, only spot rivaled the clupeids and anchovies in overall importance; however, white perch, croaker, weakfish, and summer flounder contributed important percentages of the diet in certain seasons. Hollis (1952), Manooch (1973) and Hartman and Brandt (1995a) and Overton (2002) also found that schooling clupeoid fishes formed the majority of the diets of striped bass from Chesapeake Bay and nearby Albemarle Sound.

There was a shift in the relative importance of smaller schooling fishes (anchovies) in striped bass 458–710 mm to larger schooling fishes (menhaden, gizzard shad) in striped bass 711–1151 mm. Although there was a tendency for larger striped bass to consume larger prey, this relationship should more accurately be described as one where larger striped bass have a greater size range of prey to consume (Fig. 4). The largest striped bass consumed prey ranging from several millimeters up to 400 mm in total length, corresponding to 40% of their total length and equaling the ratio of mean maximum forage length to striped bass length found by Manooch (1973). Similarly, smaller striped bass consumed prey that approached 40% of their total length; however, most prey consumed by all sizes of striped bass were smaller, young-of-the-year fishes—a finding corroborated by Overton (2002), who predicted an optimal prey size to be 21% of the striped bass length.

The predominance of fish in adult striped bass diets attests to the piscivorous nature of larger striped bass and corroborates the findings of other studies (Hollis, 1952; Manooch, 1973; Overton, 2002). Hartman and Brandt (1995a) and Gardinier and Hoff (1982) observed an ontogenetic shift at 200 mm TL

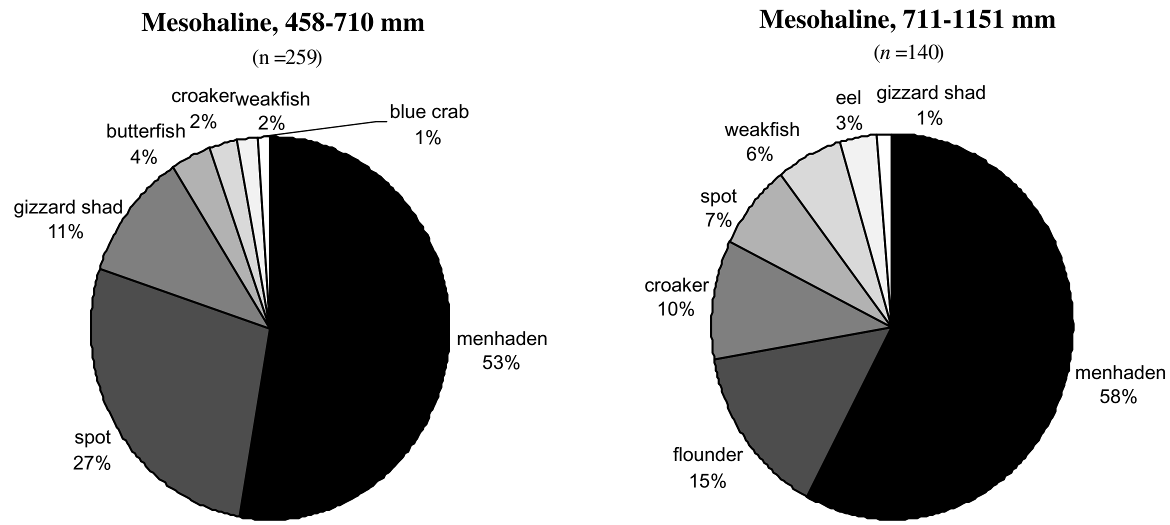

Figure 3

Percent by weight of prey in the diet of striped bass captured in the fall (September–December). Note that only stomachs with contents other than bait were used in the construction of these figures.

from invertebrate to vertebrate prey in the diet of smaller striped bass. In the present study, we sampled size ranges above 458 mm and found no clear ontogenetic dietary shift between vertebrate and invertebrate prey. Invertebrates, primarily blue crab, constituted a minor percentage of the overall diet and were significant in the diet only in May and September in mesohaline waters of Chesapeake Bay. This is in contrast to the high percentages of invertebrates found in the diets of large striped bass in New England waters and likely represents latitudinal differences in the availability of fish prey (Nelson et al.[2]).

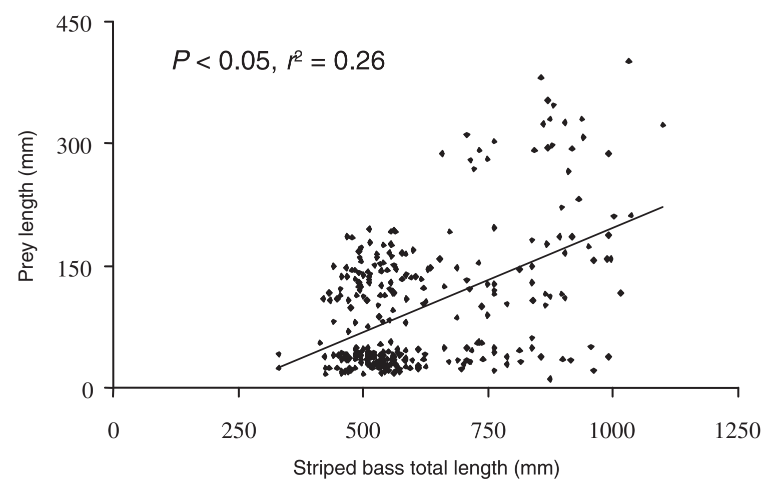

Figure 4

Plot of prey total length against total length for striped bass.

The seasonal and spatial differences in the diet of striped bass correspond to the behavioral and seasonal migration patterns of the fish and reflect changes in the community composition at the location and time of capture. The major seasonal trend is spring feeding on gizzard shad, anadromous herrings, and white perch, corresponding to spawning migrations of both striped bass and their prey into tidal freshwater. Many spring samples came from upper river sites where gizzard shad and white perch are year-round residents and herrings are anadromous migrants (Murdy et al., 1997). This pattern of spring feeding on anadromous herrings and gizzard shads was also found by Trent and Hassler, 1966) in the Roanoke River, NC.

Striped bass captured in spring from the lower, more saline sections of the rivers exhibited high levels of feeding intensity and consumed primarily menhaden, sciaenids, anchovies, and blue (VIMS[3]) crabs. In the spring, Manooch

[2] Nelson, G. A., B. C. Chase and J. Stockwell. 2002. Feeding habits of striped bass (*Morone saxatilis*) from coastal waters of Massachusetts, 29 p. Massachusetts Department of Marine Fisheries Annisquam River Marine Fisheries Field Station 30 Emerson Ave. Gloucester, MA 01930.

[3] VIMS (Virginia Institute of Marine Science). 2002. Juvenile fish and blue crab trawl survey. VIMS, P. O. Box 1346 Gloucester Point, VA 23062. http://www.fisheries.vims.edu/vimstrawldata/. (March 2001)

(1973) found menhaden and anadromous herrings to be predominant (Homer and Boynton[4]) foods in brackish waters of Albemarle Sound and Hollis (1952) found menhaden as well as anchovies and blue crabs to be predominant food of striped bass in brackish waters of Chesapeake Bay. The predatory impact of migratory striped bass depends upon their residence time in these waters, as well as on striped bass population size and feeding rates. Carmichael et al. (1998) estimated that striped bass spend approximately one week in their upstream and one week in their downstream transit of the Roanoke River. There are no estimates of residence time in the open waters of Chesapeake Bay or Albemarle Sound; however, striped bass larger than 711 mm are captured in recreational fisheries in Chesapeake Bay into June, suggesting that they are present in Chesapeake Bay from March through June.

After leaving Chesapeake Bay and summering in New England waters, large striped bass return to the bay in fall (Dorazio et al., 1994) and fed primarily upon menhaden, spot, and anchovies. At this time, most fish were taken from open waters of Chesapeake Bay. In the lower bay during fall, large numbers of transient young-of-the-year (YOY) marine fishes (menhaden, spot, croaker, flounder, and weakfish) congregate in open waters of Chesapeake Bay prior to the fall out-migration, thus making them accessible prey for returning striped bass. Striped bass exhibited higher stomach fullness values and higher percentages of nonempty stomachs in November and December than in all other months, with the exception of June. This finding, in conjunction with observations of striped bass aggressively pursuing baitfishes in surface waters during the fall (Hollis, 1952, this study), indicates high feeding intensity. In bioenergetic simulations, striped bass growth potential and prey density peaked in October (Brandt and Kirsch, 1993). Because much of the annual growth (Hartman and Brandt, 1995a, 1995b) and gonadal development (Berlinsky and Specker, 1991) occur in the fall, this period is of primary importance both for the accumulation of body mass for overwintering and for the initial development of gonadal products.

Although pelagic fishes, notably anchovy and menhaden, provided the bulk of the diet for large striped bass, this study differs from the diet study of Hartman and Brandt (1995a) and the network analysis of Baird and Ulanowicz (1989) in that benthic fishes also contributed significantly to the diets. Baird and Ulanowicz (1989) estimated that striped bass obtained 91–100% of their diet from pelagic trophic pathways and Hartman and Brandt (1995a) estimated that 68–75% of the diet of age-2 to age-6 striped bass came from pelagic sources. These estimates contrast with the high percentages of benthic spot, croaker, summer flounder, and gizzard shad observed in this study and indicate that larger striped bass either prey to a greater extent upon benthic fishes or the overall diet has shifted towards benthic prey. Menhaden and bay anchovy juvenile abundance indices have declined over the past 10 years (VIMS[3]) suggesting that a dietary shift towards benthic prey may have occurred since the collections of Hartman and Brandt (1995a) and the studies cited in the Baird and Ulanowicz (1989) model. Without comprehensive and systematic annual diet sampling, it is difficult to separate dietary shifts from differences in the sizes of fish sampled or the sampling locations. Baird and Ulanowicz (1989) incorporated diet composition data from Hollis (1952), Gardinier and Hoff (1982), Manooch (1973), and Homer and Boynton[4] that included very few striped bass larger than >600 mm and their model included no linkages between striped bass and gizzard shad, spot, croaker, or summer flounder. Furthermore, the absence of gizzard shad in the Baird and Ulanowicz (1989) model represents a missing pathway that might link benthic detritus directly to piscivore production as occurs in freshwater impoundments where gizzard shad are the major prey of striped bass (Mathews et al., 1988) and play a pivotal role in the freshwater ecosystem (Stein et al., 1995).

[4] Homer, M., and W. R. Boynton. 1978. Stomach analysis of fish collected in the Calvert Cliffs region, Chesapeake Bay—1977. Rep. UMCEES 78-154 CBL, 363 p. Chesapeake Biological Laboratory, Univ. Maryland, Solomons, MD.

Acknowledgments

This work represents part of a thesis presented to the College of William and Mary (School of Marine Science) by the first author. We would like to thank the first author's committee members, David Evans, Robert Diaz, John Hoenig, and Thomas Munroe, for reviewing the thesis and this manuscript. We would like to acknowledge the many seafood dealers and recreational and commercial fisherman who provided fish samples. This research was funded by the Virginia Recreational Fishing Advisory Board and the Virginia Commercial Advisory Board (grant numbers RF-97-08 and CF-97-08).

Literature cited

Baird, D., and R. E. Ulanowicz.
1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Mono. 59(4):329–364.

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. Fish. Bull.76:335–342.

Berlinsky, D. L. ,and J. L. Specker.
1991. Changes in gonadal hormones during oocyte development in the striped bass, *Morone saxatilis*. Fish Phys. Biochem. 9:51–62.

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

Brandt, S. B., and J. Kirsch.
1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Trans. Am. Fish. Soc. 122: 845–869.

Carmichael, J. T., S. L. Haeseker, and J. E. Hightower,
1998. Spawning migration of telemetered striped bass in the Roanoke River, North Carolina. Trans. Am. Fish. Soc. 127:286–297.

Chapman, R. W.
1987. Changes in the population structure of male striped

bass spawning in three areas of the Chesapeake Bay from 1984 to 1986. Fish. Bull. 85:167–170.

Chapoton, R. B., and J. E. Sykes.
1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. Trans. Am. Fish. Soc. 90: 13–20.

Cortes, E.
1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: an application to elasmobranch fishes. Can. J. Fish Aquat. Sci. 54: 726–738.

Dorazio R. M., K. A. Hattala, C. B. McCollough, and J. E. Skjeveland.
1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. Trans. Am. Fish. Soc. 123:950–963.

Field, J. D.
1997. Atlantic striped bass management: Where did we go right? Fisheries 22:6–9.

Gardinier, M., and T. Hoff.
1982. Diet of striped bass in the Hudson River Estuary. N.Y. Fish Game J. 29:152–165.

Hartman, K. and S. Brandt.
1995a. Trophic resource partitioning, diets and growth of sympatric estuarine predators. Trans. Am. Fish. Soc. 124: 520–537.
1995b. Predatory demand and impact of striped bass, bluefish and weakfish in the Chesapeake Bay: applications of bioenergetics models. Can. J. Fish. Aquat. Sci. 52: 1667–1687.

Hollis, E. H.
1952. Variations in the feeding habits of the striped bass, *Roccus saxatilis*, in Chesapeake Bay. Bull. Bingh. Ocean. Coll. 14(1):111–131.

Hollowed, A. B., N. Bax, R. Beamish, J. Collie, M. Fogarty, P. Livingston, J. Pope, and J. C. Rice.
2000. Application of multispecies models in assessment of impacts of commercial fishing. Symposium proceedings in the ecosystem effects of fishing. ICES J. Mar. Sci. 57: 707–719.

Hureau, J. C.
1969. Biologie comparée de quelques poissons anarctiques (Nototheniidae). Bull. Inst. Oceangr. Monaco 68:1–44.

Hyslop. E. J.
1980. Stomach content analysis- a review of methods and their application. J. Fish Biol. 17:411–429.

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

Koo, T. S. Y.
1970. The striped bass fishery in the Atlantic states. Ches. Sci. 11:73–93.

Livingston, P. A.
1985. An ecosystem model evaluation: the importance of fish food habits data. Mar. Fish. Rev. 47:9–12.

Limburg, K. E., M. L Pace, and D. Fischer.
1997. Consumption, selectivity and use of zooplankton by larval striped bass and white perch in a seasonally pulsed estuary. Trans. Am. Fish. Soc. 126:607–621.

Manooch, C. S., III.
1973. Food habits of yearling and adult striped bass, *Morone saxatilis*, from Albemarle Sound, North Carolina. Ches. Sci. 14:73–86.

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

Mathews, W. J., L. G. Hill, D. R. Edds, J. J. Hoover, and T. G. Heger.
1988. Trophic ecology of striped bass, *Morone saxatilis*, in a freshwater reservoir (Lake Texoma, USA). J. Fish Biol.: 33:273–288.

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

Murdy, E. O., R. Birdsong, and J. A. Musick.
1997. Fishes of the Chesapeake Bay, 324 p. Smithsonian Institute Press, Washington, DC.

Overton, A. S.
2002. Striped bass predator-prey interactions in Chesapeake Bay and along the Atlantic Coast. Ph.D. diss., 226 p. Univ. Maryland Eastern Shore, Princess Anne, MD.

Pinkas, L.
1971. Food habits study. *In* Food habits of albacore, bluefin tuna and bonita in California waters (L. Pinkas, M. S. Oliphant, and I. L. K. Iverson, eds.), p. 47–63. Calif. Dep. Fish Game, Fish. Bull. 152.

Richards, R. A., and P. J. Rago.
1999. A case history of effective fishery management: Chesapeake Bay striped bass. N. Am. J. Fish. Manage. 19:356–375.

Rulifson, R. A., and S. A. McKenna.
1987. Food of striped bass in the upper Bay of Fundy, Canada. Trans. Am. Fish. Soc. 116:119–122.

Schaefer. R.
1970. Feeding habits of striped bass from the surf waters of Long Island. N.Y. Fish Game J. 17:1–17.

Setzler, E. M., W. R. Boynton, K. V. Wood, H. H Zion, L Lubbers, N. K. Mountford, P. Frere. L. Tucker, J. A. Mihursky.
1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). U.S. Dep. Commer., NOAA Technical Report NMFS Circ. 433, 69 p.

Stein, R. A., D. V. DeVries, and J. M. Dettmers.
1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Can. J. Fish Aquat. Sci. 52: 2518–2526.

Trent, L., and W. Hassler.
1966. Feeding habits of adult striped bass, *Roccus saxatilis*, in relation to stages of sexual maturity. Ches. Sci. 7: 189–192.

Walters, C., D. Pauly, and V. Christensen.
1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539–554.

Whipple, S. J., J. S. Link, L. P. Garrison, and M. J. Fogarty.
2000. Models of predation and fishing mortality in aquatic ecosystems. Fish Fisheries 1(1):22–40.