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The Trophic Dynamics Of Summer Flounder (Paralichthys Dentatus) In Chesapeake Bay

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Abstract—Data on the trophic dynamics of fishes are needed for management of ecosystems such as Chesapeake Bay. Summer flounder (*Paralichthys dentatus*) are an abundant seasonal resident of the bay and have the potential to impact foodweb dynamics. Analyses of diet data for late juvenile and adult summer flounder collected from 2002–2006 in Chesapeake Bay were conducted to characterize the role of this flatfish in this estuary and to contribute to our understanding of summer flounder trophic dynamics throughout its range. Despite the diversity of prey, nearly half of the diet comprised mysid shrimp (*Neomysis* spp.) and bay anchovy (*Anchoa mitchilli*). Ontogenetic differences in diet and an increase in diet diversity with increasing fish size were documented. Temporal (inter- and intra-annual) changes were also detected, as well as trends in diet reflecting peaks in abundance and diversity of prey. The preponderance of fishes in the diet of summer flounder indicates that this species is an important piscivorous predator in Chesapeake Bay.

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Summer flounder (*Paralichthys dentatus*) are found along the eastern seaboard of North America from Nova Scotia to Florida, but are most abundant between Massachusetts and North Carolina (Ginsberg, 1952; Leim and Scott, 1966; Gutherz, 1967). This species supports both commercial and recreational fisheries throughout southern New England and the Mid-Atlantic Bight. The commercial fishery for summer flounder has historically accounted for about 60% of the annual landings and occurs mainly in the offshore waters of the continental shelf during late fall and winter. The majority of the recreational fishery, which on occasions has exceeded the commercial harvest, takes place in state waters (i.e., estuaries and the coastal waters out to 3 nautical miles) during summer and early fall. Both fisheries contribute millions of dollars to economies on local and regional scales (Terceiro, 2002).

The trophic dynamics of summer flounder have been fairly well studied (Poole, 1964; Smith and Daiber, 1977; Powell and Schwartz, 1979; Roundtree and Able, 1992; Link et al., 2002; Staudinger, 2006). However, the majority of these investigations have documented the diet of summer flounder in coastal waters or in more northern estuarine environments, rather than in the southern estuaries. The latter ecosystems support a high abundance of summer flounder and provide vital summertime habitats for this species (Desfosse, 1995).

The Chesapeake Bay is the largest estuary in the summer flounder range. No known studies have been undertaken to document summer flounder diet in these waters, and thus there has been a gap in our understanding of the feeding habits of this species within an important area of its range. Further, there is growing awareness regionally, nationally, and internationally of the importance of ecosystem-based approaches to fisheries management (EBFM). A necessary element in support of EBFM is nontraditional types of fisheries data, including information on the trophic dynamics of fishes.

In this article, we present the diet composition of summer flounder collected in Chesapeake Bay from 2002 through 2006 to explore ontogenetic, interannual, and intra-annual variability in diet using canonical correspondence analysis (CCA). Collectively, this information provides insight into the role of summer flounder in the Chesapeake Bay foodweb, and contributes to our understanding of the trophic dynamics of this species throughout its range.

Materials and methods

Field collections

The data presented in this article were collected from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), which is a bottom trawl survey program designed to sample late-juvenile and adult fishes in the mainstem Chesapeake Bay (i.e., nontributary waters). During 2002–2006, a total of 25 ChesMMAP cruises were conducted (March, May, July, September, and November annually) and approximately 80 to 90 sites were sampled during each cruise. Sampling locations were chosen according to a stratified random design, and strata were defined by water depth (3–9 m, 9–15 m, and >15 m) within five 30-latitudinal minute regions of the bay. The locations sampled in each stratum of each region were randomly selected and the number of locations was in proportion to the surface area of that stratum. At each sampling location, a 13.7-m 4-seam balloon otter trawl (15.2-cm stretch mesh in the wings and body and 7.6-cm stretch mesh in the cod end) was towed for 20 min at approximately 6.5 km/h. The catch from each tow was sorted and individual lengths (total length, TL) were recorded according to species or size-class if distinct classes within a particular species were evident. Stomachs were removed from a subsample of each species or size-class and immersed in preservative for diet composition analysis after each cruise.

Identification of stomach contents

The contents of each stomach were removed for identification to the lowest possible taxon. Prey encountered in the esophagus and buccal cavity were included for identification (and assumed not to be the result of net feeding because of a lack of retention of prey in large mesh gear), whereas prey in the intestines were ignored because of the difficulty associated with identifying digested prey items in advanced stages of decomposition. All prey items were sorted, measured (either fork or total length, as appropriate and when possible), and the wet weight (0.001 g) of each was recorded.

General diet description

To summarize the diet composition of summer flounder in the mainstem of Chesapeake Bay, a measure of percent weight was calculated for each prey type (Hyslop, 1980). Because the ChesMMAP trawl collections yielded a cluster of summer flounder at each sampling location, the aforementioned percentages were calculated by using a cluster sampling estimator (Bogstad et al., 1995; Buckel et al., 1999). Therefore, the contribution of each prey type to the diet by weight ($\%W_k$) was

$$\%W_k = \frac{\sum_{i=1}^{n} M_i q_{ik}}{\sum_{i=1}^{n} M_i} * 100 , \qquad (1)$$

where $q_{ik} = \dfrac{w_{ik}}{w_i}$,

and where n = the number of trawls containing summer flounder;
M_i = the number of summer flounder collected at sampling site i;
w_i = the total weight of all prey items encountered in the stomachs of summer flounder collected from sampling location i; and
w_{ik} = the total weight of prey type k in these stomachs.

The variance estimate for $\%W_k$ was given by

$$\mathrm{var}(\%W_k) = \frac{1}{n\bar{M}^2} \frac{\sum_{i=1}^{n} M_i^2 (q_{ik} - W_k)^2}{n-1} \times 100^2 , \qquad (2)$$

where $\bar{M} = \dfrac{\sum_{i=1}^{n} M_i}{n}$ is the average number of summer flounder collected at a sampling location.

Ontogenetic and temporal changes in diet

Canonical correspondence analysis (CCA; ter Braak, 1986), a multivariate direct gradient analysis technique, was used to explore the relationship between summer flounder diet and three factors: fish size (mm), year (2002, 2003, 2004, 2005, 2006), and month (March, May, July, September, November). Spatial variations in summer flounder diet were not explored because the distribution of summer flounder in Chesapeake Bay is restricted primarily to the polyhaline (>18 ppt) region of the bay (Fig. 1).

The summer flounder collected ranged in size from 148 to 712 mm TL (Fig. 2). To examine the effect of fish size on diet using CCA, we grouped summer flounder into size categories such that all members of a given category exhibited a relatively consistent diet composition. Summer flounder were grouped into 25-mm size-classes, and diet was calculated for each with Equation 1. After trimming 10% of the observations (i.e., 25-mm size-classes) on account of low probability density in order to minimize outliers, cluster analysis (Euclidean distance, average linkage method) was used to group size-classes with similar diet compositions into broader categories. A scree plot indicated the presence of four clusters (Fig. 3A) (McGarigal et al., 2000), corresponding to four broad size-categories: <225 mm TL (small), 225–374 mm TL (small–medium), 375–574 mm TL (large–medium), and >574 mm TL (large) (Fig. 3B).

For the CCA, each element of the response matrix was the mean percent weight of a given prey type at a given sampling site in a particular size, month, and year combination. The matrix was log-transformed (ln[x+1]) to account for the log-normal distribution

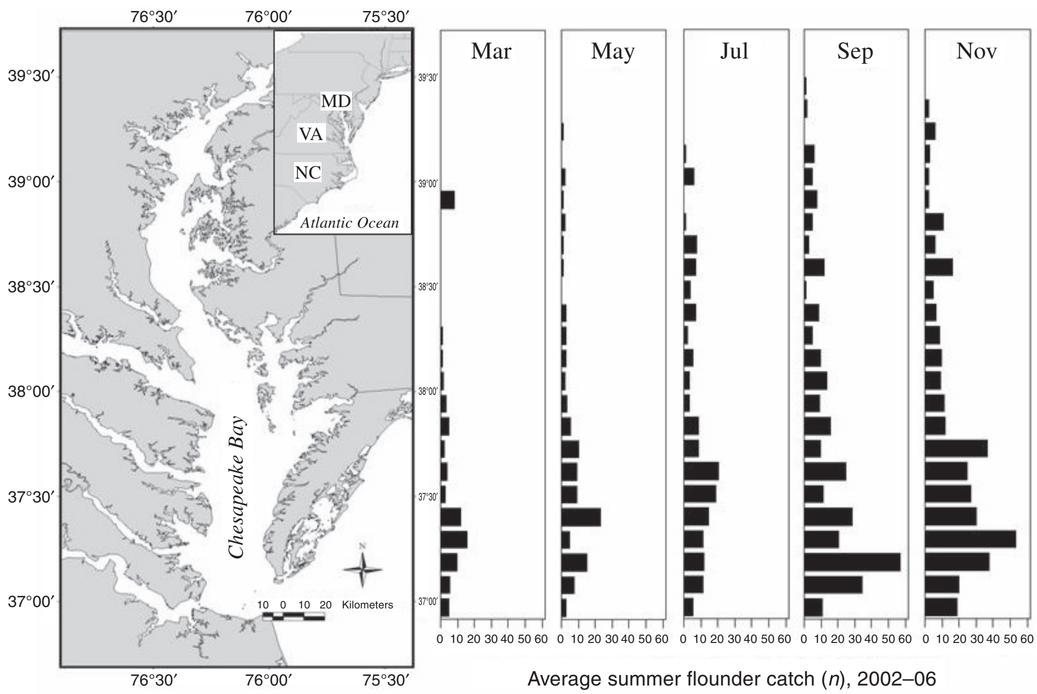


Figure 1

Average catch of summer flounder (*Paralichthys dentatus*) in the mainstem (i.e., nontributary waters) of Chesapeake Bay by sampling month (Mar, May, Jul, Sep, Nov) from 2002 through 2006. Horizontal histograms represent raw catch data by 0.1 latitudinal degrees corresponding to the map scale.

of the data (Garrison and Link, 2000). Size, month, and year were coded by using ordinal variables. Observations (sampling sites) containing fewer than three summer flounder and explanatory variable blocks (size, month, year categories) containing fewer than three observations were excluded to eliminate variance issues related to small sample size.

The CCA was used to determine the amount of variability in the summer flounder diet explained by the canonical axes, which are linear combinations of the three explanatory variables correlated to weighted averages of prey within blocks (ter Braak, 1986; Garrison and Link, 2000). The significance of the ontogenetic and temporal factors was determined by using permutation tests (ter Braak, 1986). A prey species-explanatory factor biplot was constructed to examine the correlations between the factors and the canonical axes and to explore the dietary trends associated with these variables. Detailed diet descriptions were then generated for each of the significant factors identified by the CCA. The CCA was performed with the program CANOCO, vers. 4.5 (Microcomputer Power, Ithaca, NY).

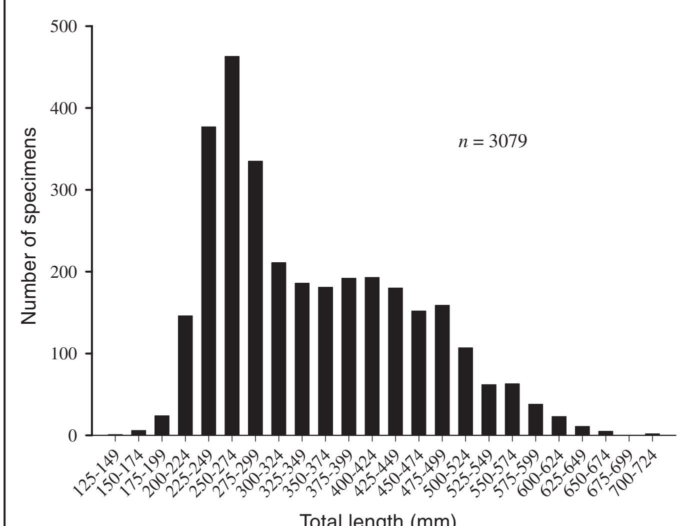


Figure 2

Size frequency of summer flounder (*Paralichthys dentatus*) sampled in the mainstem (i.e., nontributary waters) of Chesapeake Bay from 2002 through 2006.

Results

General diet description

From 2002 through 2006, summer flounder were collected at 877 sampling locations, and at 688 of these locations at least one summer flounder had prey in its stomach. Overall, prey were encountered in 1780 (57.8%) of the 3079 stomachs collected. The total observed diet was composed of 123 prey types, 70 of which were identifiable to the species level (24 fishes and 46 invertebrates). In an effort to present summer flounder diet composition in the most efficient manner, prey types contributing relatively little to the overall diet were combined at higher taxonomic levels.

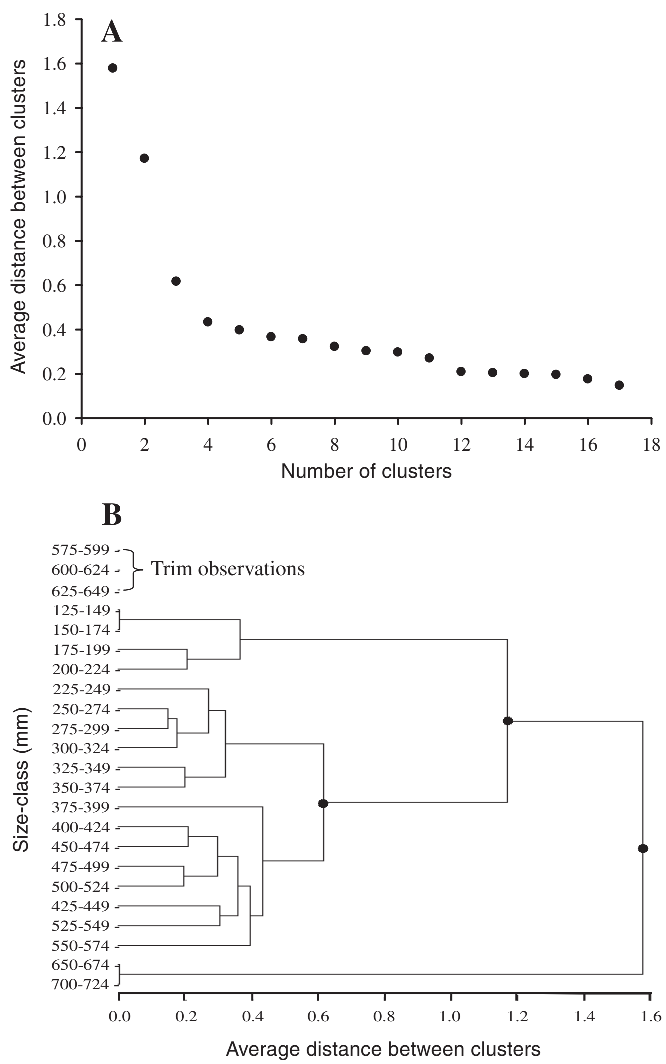


Figure 3

(**A**) Scree plot depicting average distance between clusters versus the number of clusters which was used to identify the number of clusters into which 25-mm size-classes of summer flounder (*Paralichthys dentatus*) should be grouped (four size groups were selected since the curve leveled out at five or more clusters), (**B**) cluster diagram representing the relationships among the diet compositions of 25-mm size-classes of summer flounder. Trim observations represent the 25-mm size-classes omitted from the analysis because of low probability density, and average distance represents the coefficient used as a measure of dissimilarity among size-classes.

Mysid shrimp (*Neomysis* spp.) and bay anchovy (*Anchoa mitchilli*) were the main prey of the summer flounder, accounting for approximately 42% combined (24.1% and 17.9%, respectively, Fig. 4) of the diet by weight, and mantis shrimp (*Squilla empusa*—11.2%) and weakfish (*Cynoscion regalis*—11.1%) were of secondary and nearly equal importance. Of the remaining prey types, spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and spotted hake (*Urophycis regia*) were the most important fishes, and sand shrimp (*Crangon septemspinosa*) was the main invertebrate prey. Each of these species represented between 2% and 7% of the diet. All other identifiable prey types each contributed <2% to the diet.

Unidentifiable prey items (i.e., unidentifiable fish and unidentifiable material) were prevalent, likely because of the shearing action of the teeth of these predators, and composed 6.0% of the diet by weight. Although many of the unidentifiable items were encountered in stomachs along with identifiable prey and were likely the same species as the latter, they were, however, classified as unidentifiable so as to provide a conservative diet description.

Ontogenetic and temporal changes in diet

The CCA indicated that summer flounder dietary changes by fish size, month, and year were statistically significant. Taken together, the aforementioned factors explained 6.0% (P=0.001) of the variability in diet; the first and second canonical axes accounted for 51.2% and 34.5% of the explainable variation, respectively. Fish size (r=−0.459; P=0.001) more closely corresponded to the first canonical axis than the second and, of the three variables examined, accounted for the greatest portion of the variation that was explicable. Month (r=−0.481; P=0.001) and year (r=−0.094; P=0.001) were more closely correlated to the second axis (Fig. 5).

The amount of fish in the diet of summer flounder increased with increasing size (Fig. 6A). Mysid shrimp, sand shrimp, and mantis shrimp accounted for approximately 79% of the diet of the summer flounder <225 mm TL. Bay anchovy (9.5%) and weakfish (2.3%) were the main fish prey of these individuals. The diet of summer flounder ranging from 225 to 374 mm TL was also dominated by mysid shrimp. The contribution of sand shrimp to the diet of these fish was approximately the same as in the smallest size-category, whereas that of mantis shrimp increased. Fishes were again of secondary importance and were represented mainly by bay anchovy, weakfish, and Atlantic croaker. Weakfish was the primary prey of the large-medium summer flounder and, although the contribution of bay anchovy declined, anchovy still represented 15.4% of the diet. The contribution of spot to the diet of summer flounder increased from less than 1% in the small-medium fish to 13% in the 375–574 mm TL size-group. Mantis shrimp was the most important invertebrate prey of the large-medium fish. Sciaenids (i.e., spot, weakfish, and Atlantic croaker) were the main prey of of the largest summer flounder and accounted for 67.3% of the diet. Our representation of the diet composition of these fish should be viewed as preliminary because of the small cluster sample size (n_c=23).

Seasonal changes in summer flounder diet likely mirrored the temporal variability of prey assemblages in Chesapeake Bay. The contribution of sand shrimp and spotted hake peaked in the spring and early summer (Fig. 6B). Atlantic brief squid (*Lolliguncula brevis*), Atlantic croaker, mantis shrimp, silver perch (*Bairdiella chrysoura*), spot, and weakfish accounted for a greater portion of the diet throughout the summer and autumn. Bay anchovy and mysid shrimp were always two of the top three main prey types in the diet of summer flounder from May to November.

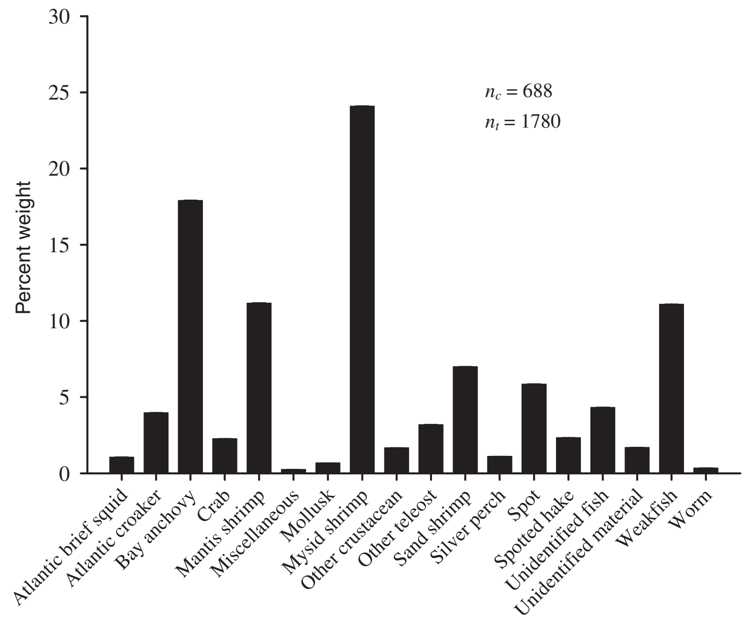


Figure 4

Percent weight of prey types present in the diet of summer flounder (*Paralichthys dentatus*) collected from the mainstem of Chesapeake Bay from 2002 through 2006. The total number of clusters collected is given by n_c, and n_t represents the total number of specimens included in this study. Standard error estimates, represented by error bars, were calculated from cluster sampling variance estimates and all were less than 0.03%.

The diet of summer flounder was dominated by mantis shrimp and bay anchovy in 2002, whereas mysid shrimp was the main prey from 2003 through 2006 (Fig. 6C). Atlantic brief squid, crab, mantis shrimp, and spotted hake generally decreased in importance over this time period, whereas the contribution of mysid shrimp and spot generally increased.

Predator-prey size relationships

The available data on sizes of whole prey consumed by summer flounder (the primary prey types excluding mysid shrimp) were examined with respect to summer flounder size. For all prey types, the size of the prey consumed increased significantly with increasing summer flounder size (P<0.05, Fig. 7). With respect to Atlantic croaker and spot, the majority of the individuals consumed were likely young-of-the-year (YOY), and a few of the larger individuals were age-1. However, summer flounder appear to have preyed exclusively on YOY weakfish. At a given size of summer flounder, the sizes of bay anchovy, mantis, and sand shrimp consumed were more variable than the sizes of the sciaenid prey, and this finding may indicate less probability of a size-modulated predator-prey relationship.

Discussion

Summer flounder feed on a diverse array of prey in Chesapeake Bay, as evidenced by over 120 prey types encountered in the diet. However, despite this diversity, approximately half of the diet comprised only two prey types, mysid shrimp and bay anchovy. The other half of the diet consisted of a few fishes (sciaenids-weakfish, spot, and Atlantic croaker) and invertebrates (mantis and sand shrimps). Similar results have been reported for other upper trophic level predators in Chesapeake Bay (i.e., striped bass [*Morone saxatilis*] bluefish [*Pomatomus saltatrix*] and weakfish)—results that further support the notion that although the Chesapeake Bay food web is complex, the number of prey species supporting these predators is relatively few (Hartman and Brandt, 1995).

Mysid shrimp dominate the diets of summer flounder in other estuarine and coastal habitats (Smith and Daiber, 1977; Link et al., 2002). Our study shows that mysid shrimp also play an important role in the trophic dynamics of summer flounder in Chesapeake Bay.

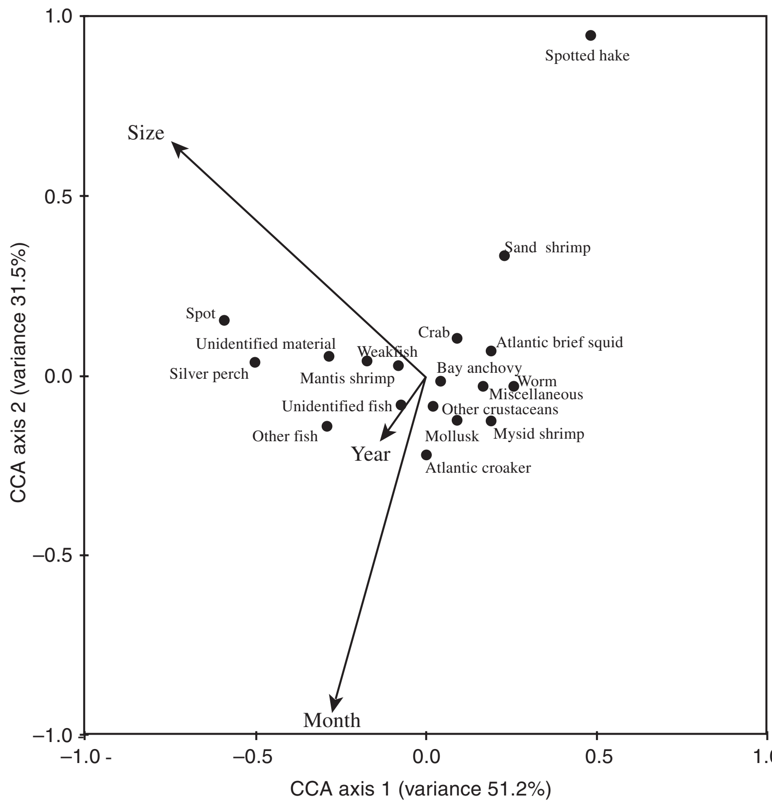


Figure 5

Canonical correspondence analysis (CCA) biplot for summer flounder (*Paralichthys dentatus*) diet in the mainstem of Chesapeake Bay from 2002 through 2006. Arrows represent the significant explanatory factors and dots represent prey types. The canonical axes represent linear combinations of the three explanatory variables (fish size, month, and year).

Moreover, mysid shrimp have dominated the diets of other teleost piscivores in the bay over the past several years, which indicates that this prey represents a crucial linkage between lower and upper trophic level production. Despite the importance of mysid shrimp in the diets of fishes, very little is known about the population dynamics and abundance of this species (when compared to other prey types, e.g., bay anchovy) in Chesapeake Bay. Data on mysid shrimp abundance would be instrumental to better understanding not only trophic interactions of summer flounder, but those of other top teleost predators in this estuary.

Significant ontogenetic changes in the diet were documented; small flounder mainly consumed small invertebrates and bay anchovy. The diversity of the diet in terms of numbers and sizes of prey types increased with increasing summer flounder size. Medium-size flounder continued to consume prey types found in the diet of small flounder, but the diet of medium-size flounder appeared to be an expansion of rather than a shift from the diet of small flounder. Fishes (primarily sciaenids) were found almost exclusively in the diet of the largest summer flounder, and because bay anchovy and the aforementioned invertebrate prey types were absent in the stomachs of these fish, there appeared to be a diet shift at approximately 575 mm TL. Although similar changes in the diet of summer flounder (>500 mm TL) have been documented in offshore waters (Link et al., 2002), cephalopods were the primary prey type as opposed to fishes. This contrast in the diets of the larger summer flounder is likely due to the lack of an abundant and comparable large soft-bodied invertebrate prey in Chesapeake Bay.

Seasonal trends in summer flounder diet composition were not surprising given the well documented spatiotemporal patterns of summer flounder prey. Sand shrimp and spotted hake abundance generally peaks during late winter and early spring in the mainstem of the lower bay; hence, it follows that they composed appreciable fractions of the summer flounder diet during this season (Haefner, 1976; Murdy et al., 1997). Faunal diversity in Chesapeake Bay reaches a maximum during late August and September and corresponds with a highest diversity of prey types in the diet of summer

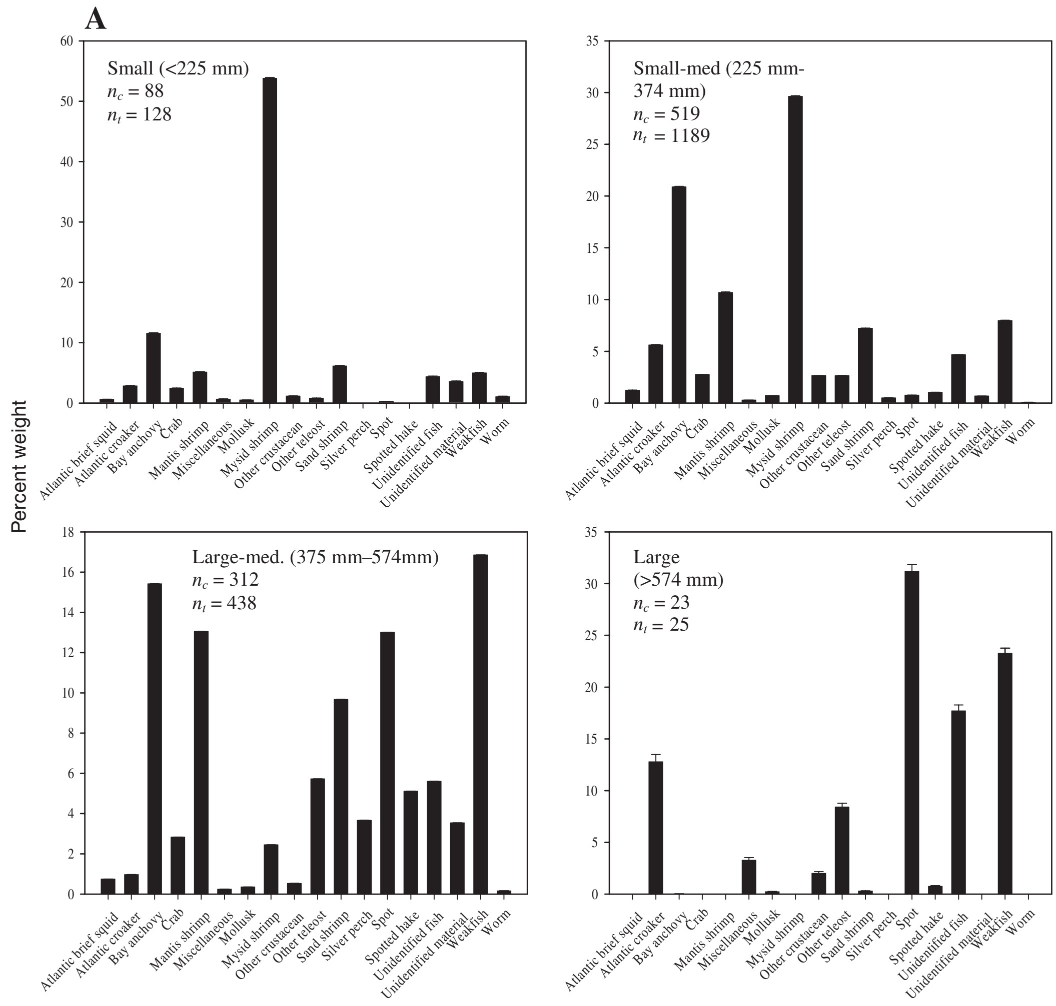
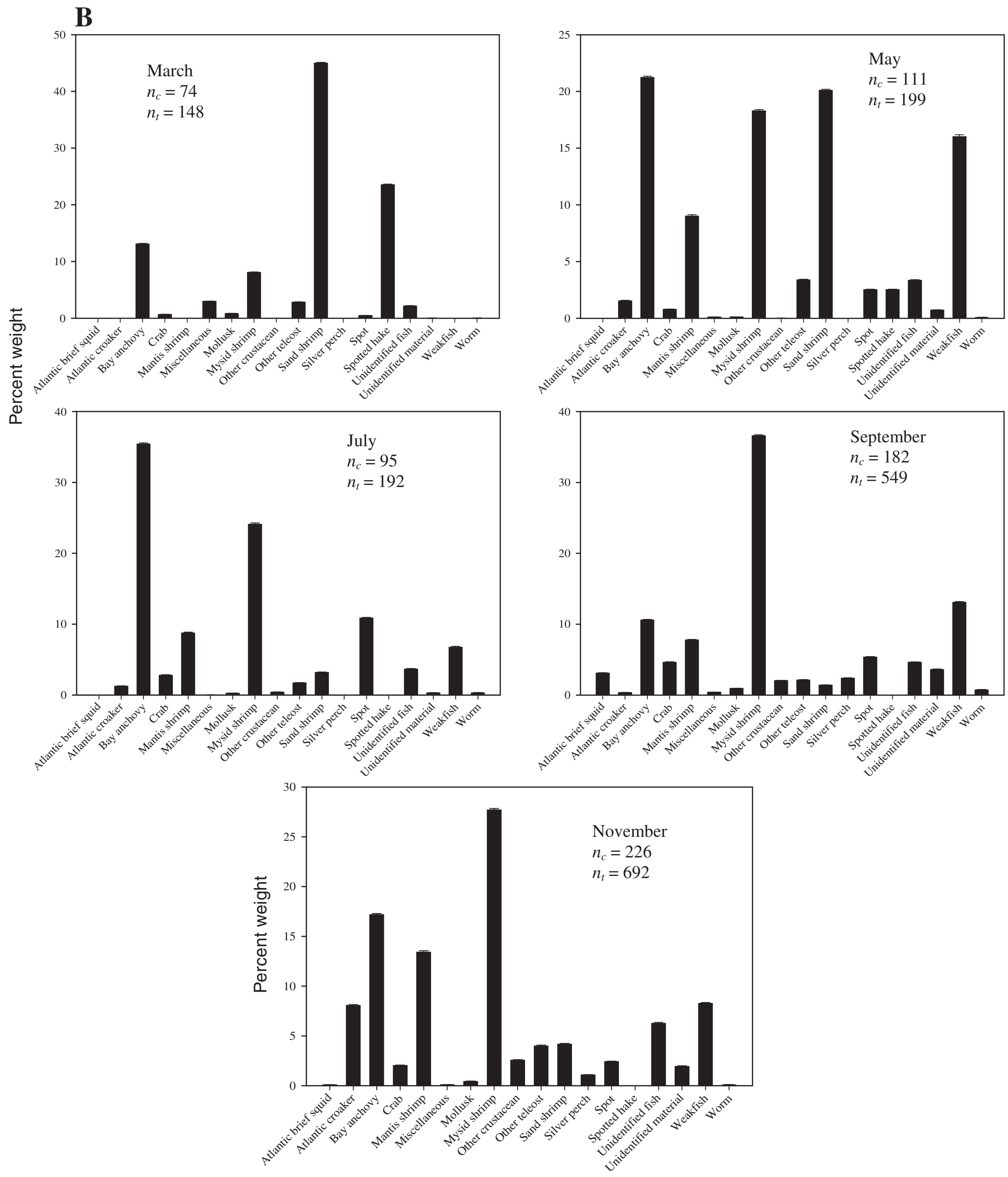


Figure 6

Diet composition (percent weight) of summer flounder (*Paralichthys dentatus*) collected from the mainstem of Chesapeake Bay, presented by (**A**) size-category, (**B**) month, and (**C**) year. The number of clusters collected in each subcategory is given by n_c, and n_t represents the total number of specimens. Error bars represent standard error of the percent weight values of each of the prey types encountered in the summer flounder diet, which were calculated from cluster sampling variance estimates.

flounder. Interannual variations in the diet of summer flounder generally followed fluctuations in the indices of relative abundance for several prey species routinely monitored by the Virginia Institute of Marine Science (VIMS) Juvenile Finfish and Blue Crab Trawl Survey. There was a weak visual correspondence between the trends in relative abundances of bay anchovy and YOY weakfish and their contributions to summer flounder diet throughout the study period. However, the diet of summer flounder more strongly mirrored trends in relative abundance of YOY spot.

In general, it is difficult to compare studies of diet composition of the same species because it is often the case that survey design (including gear types), indices reported (e.g., percent weight, %*W* vs. percent number, %*N*), and the methods used to calculate these indices (e.g., simple random vs. cluster sampling) vary among studies. Although these differences prohibit direct comparisons among investigations, it is still possible to draw some informative qualitative conclusions. For example, Smith and Daiber (1977), using the percent frequency of occurrence (%F) index, reported that the diet of summer flounder in Delaware Bay was dominated by invertebrates; yet their results also indicated that fishes composed an important part of their diet in the estuary. Poole (1964) reported that sand shrimp were the main prey by weight of summer flounder in Great South Bay, NY; however, fishes were also abun-



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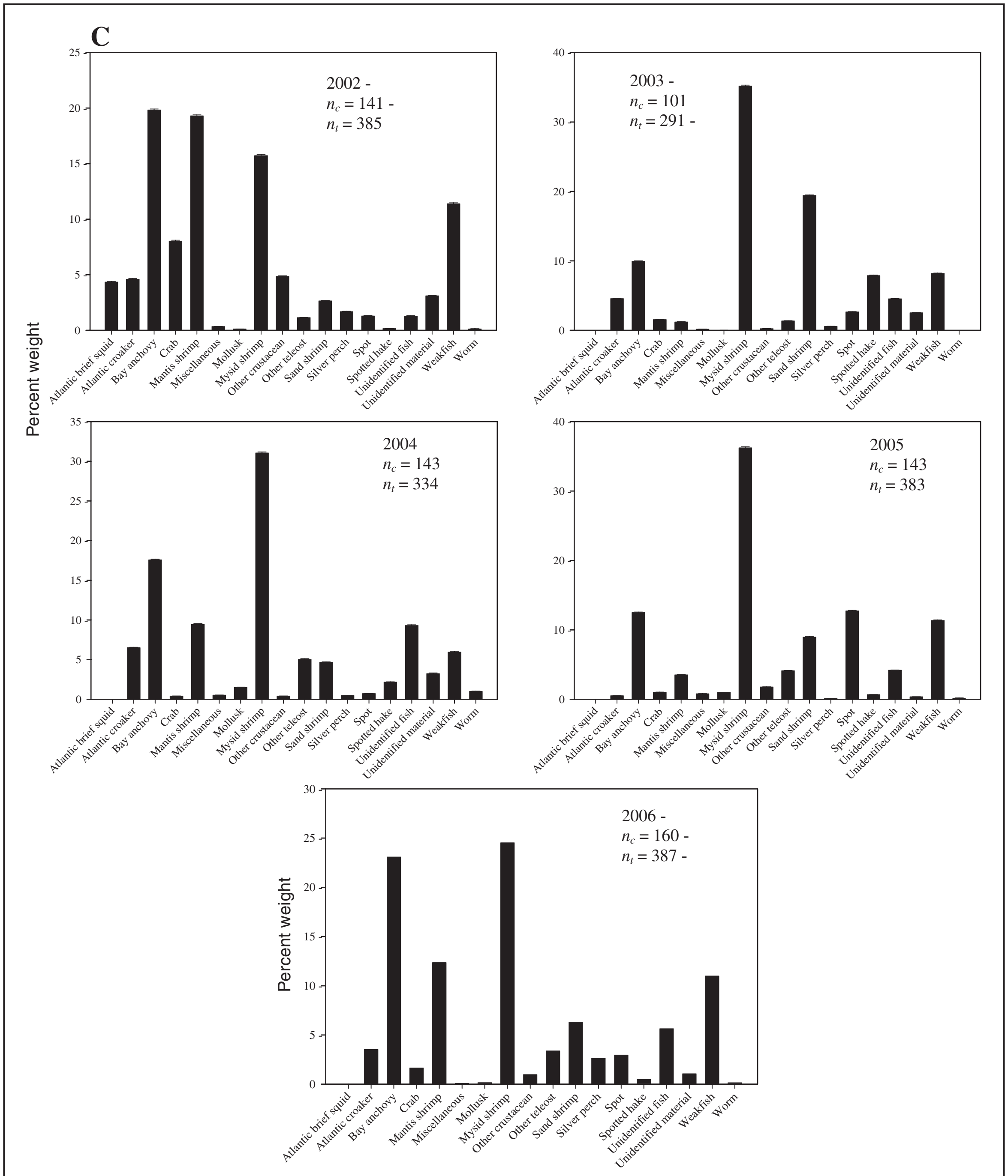
dant in the diet. The relative importance of specific fish species in the diet of summer flounder has varied across studies, likely because of spatial variations in prey assemblages and perhaps because of differences in study methods. Nevertheless, these studies in combination with the results of the present study indicate that summer flounder are piscivorous within estuarine environments throughout their range. Additionally, there appears to be appreciable similarity in the invertebrate taxa consumed by summer flounder in estuaries because sand and mysid shrimps have been found in the diet in multiple areas across decades (Poole, 1964; Powell and Schwartz, 1979).

Striped bass, weakfish, and bluefish represent the abundant upper trophic level teleost piscivorous predators in Chesapeake Bay (Dovel, 1968; Boynton et al.,



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1981; Hartman and Brandt, 1995), however, the preponderance of fishes in the diet of summer flounder indicates that this species also fits that characterization (i.e., fishes represent approximately 50% or more of the diet of summer flounder >225 mm TL). In terms of life history and estuarine dependence, appreciable abundances of summer flounder have been consistently present in our samples over the past several years. Hence, the sheer abundance, protracted use of estuarine habitat, and piscivorous diet of summer flounder combine to indicate that the impacts on piscine prey by this species have the potential to match those of the aforementioned three fishes. Piscivory was also documented in several size-classes of summer flounder within offshore habitats along the continental shelf (>10 m depth) from southern New England through the Mid-Atlantic Bight (Link

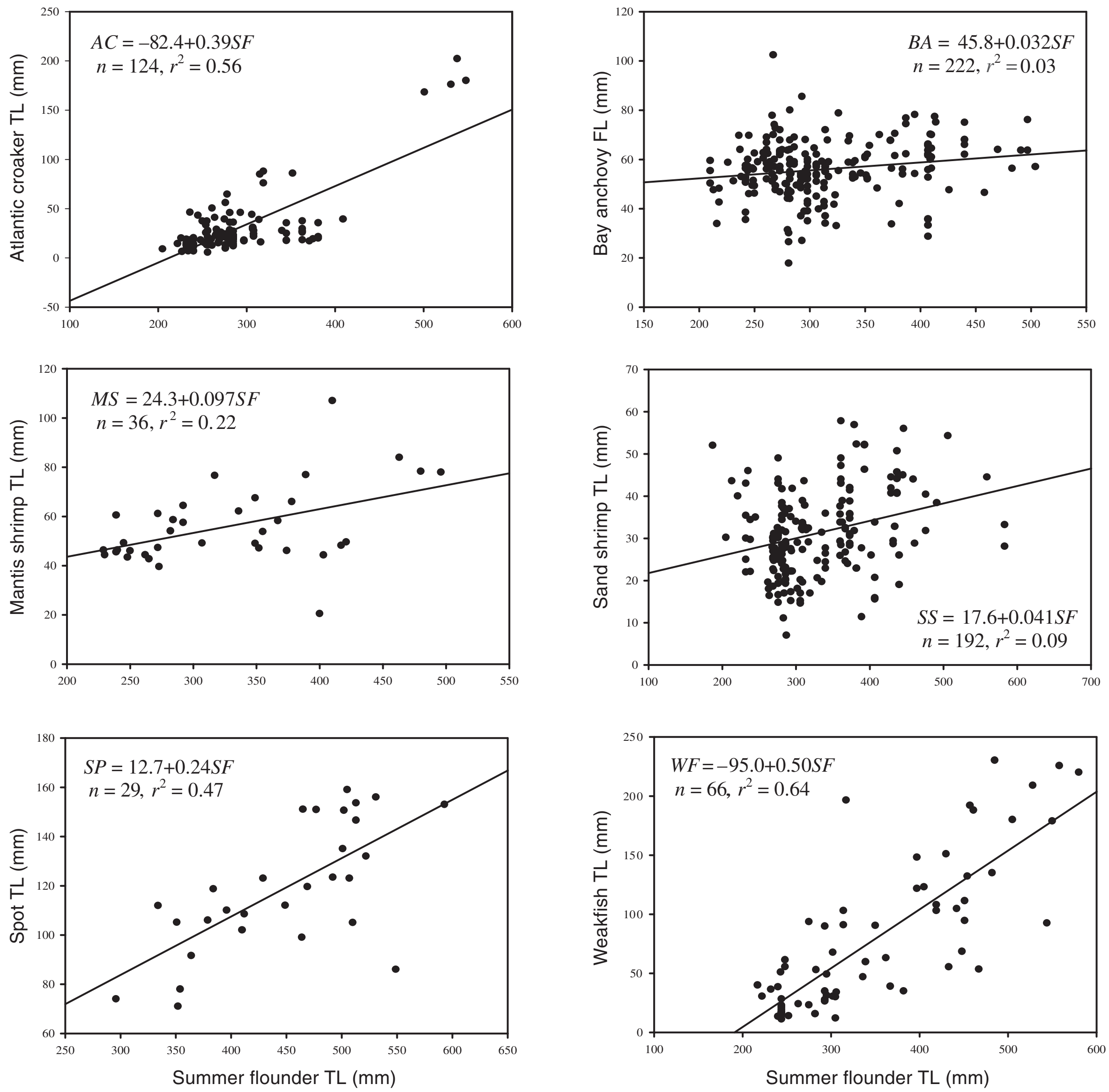

Figure 7

Relationship of prey size (whole prey items only) consumed by summer flounder (*Paralichthys dentatus*) in the mainstem of Chesapeake Bay from 2002 through 2006 versus summer flounder size (TL, mm). All regressions were significant ($P<0.05$).

et al., 2002; Staudinger, 2006). Hence, fishes represent an important component of summer flounder diet throughout its range implying that this species should be included in analyses designed to quantify pathways of production to piscivorous fishes.

Quantitative analyses of foodweb dynamics provide valuable insights into the structure of ecosystems and ultimately support the development of EBFM plans. However, these analyses require several data types, including information on the ontogenetic and temporal (intra- and interannual) changes in the trophic interactions of species within an ecosystem. This study provides fundamental trophic data for an important fish species in Chesapeake Bay and, taken with previous studies, contributes significantly to our understanding of the role of summer flounder as a predator throughout its range.

Acknowledgments

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Literature cited

Bogstad, B., M. Pennington, and J. H. Volstad.
1995. Cost-efficient survey designs for estimating food consumption by fish. Fish. Res. 23:36–47.

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.

Buckel, J. A., D. O. Conover, N. D. Steinberg, and K. A. McKown.
1999. Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass (*Morone saxatilis*). Can. J. Fish. Aquat. Sci. 56:275–287.

Desfosse., J. C.
1995. Movements and ecology of summer flounder, *Paralichthys dentatus* tagged in the southern Mid-Atlantic Bight. Ph.D. diss., 187 p. College of William and Mary, Williamsburg, VA.

Dovel, W. L.
1968. Predation by striped bass as a possible influence on population size of the Atlantic croaker. Trans. Am. Fish. Soc. 97:313–319.

Garrison, L. P., and J. S. Link.
2000. Diets of five hake species in the northeast United States continental shelf system. Mar. Ecol. Prog. Ser. 204:243–255.

Ginsberg, I.
1952. Flounders of the genus *Paralicthys* and related genera in American waters. Fish. Bull. 52:267–351.

Gutherz, E. J.
1967. Field guide to the flatfishes of the family Bothidae in the western North Atlantic, 47 p. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Circular 263, Washington, D.C.

Haefner, P. A., Jr.
1976. Seasonal distribution and abundance of sand shrimp *Crangon septemspinosa* in the York River-Chesapeake Bay estuary. Chesapeake Sci. 17:131–134.

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

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

Leim, A. H., and W. B. Scott.
1966. Fishes of the Atlantic Coast of Canada. Bull. Fish. Res. Board Can. 155:1–485.

Link, J. S., K. Bolles, and C. G. Milliken.
2002. The feeding ecology of flatfish in the Northwest Atlantic. J. North. Atl. Fish. Sci. 30:1–17.

McGarigal, K., S. Cushman, and S. Stafford.
2000. Multivariate statistics for wildlife and ecology research, 283 p. Springer, New York, NY.

Murdy, E. O., R. S. Birdsong, and J. A. Musick.
1997. Fishes of Chesapeake Bay, 324 p. Smithsonian Institution Press, Washington, D.C.

Poole, J. C.
1964. Feeding habits of summer flounder in Great South Bay. NY Fish Game J. 11:28–34.

Powell, A. B., and F. J. Schwartz.
1979. Food of *Paralichthys dentatus* and *P. lethostigma* (Pisces: Bothidae) in North Carolina estuaries. Estuaries 2:276–279.

Roundtree, R. A., and K. W. Able.
1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-the-year summer flounder in New Jersey. Trans. Am. Fish. Soc. 121:765–776.

Smith, R. W., and F. C. Daiber.
1977. Biology of the summer flounder, *Paralychthys dentatus*, in Delaware Bay. Fish. Bull. 75:823–830.

Staudinger, M. D.
2006. Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. Fish. Bull. 104:605–615.

ter Braak, C. J. F.
1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

Terceiro, M.
2002. The summer flounder chronicles: science, politics, and litigation, 1975–2000. Rev. Fish Biol. Fish. 11:125–168.