Diet Composition of Young-of-the-Year Bluefish in the Lower Chesapeake Bay and the Coastal Ocean of Virginia

JAMES GARTLAND,* ROBERT J. LATOUR, AIMEE D. HALVORSON, AND HERBERT M. AUSTIN

Department of Fisheries Science, Virginia Institute of Marine Science, College of William and Mary, Post Office Box 1346, Gloucester Point, Virginia 23062, USA

Abstract.--The lower Chesapeake Bay and coastal ocean of Virginia serve as an important nursery area for bluefish Pomatomus saltatrix. Describing the diet composition of young-of-the-year (hereafter, age-0) bluefish in this region is essential to support current Chesapeake Bay ecosystem modeling efforts and to contribute to the understanding of the foraging ecology of these fish along the U.S. Atlantic coast. The stomach contents of 404 age-0 bluefish collected from the lower Chesapeake Bay and adjacent coastal zone in 1999 and 2000 were examined as part of a diet composition study. Age-0 bluefish foraged primarily on bay anchovies Anchoa mitchilli, striped anchovies Anchoa hepsetus, and Atlantic silversides Menidia menidia. Other fishes such as striped bass Morone saxatilis, white perch Morone americana, Atlantic menhaden Brevoortia tyrannus, and bluefish were seasonally important. Crab zoea and megalope Callinectes spp. and amphipods Gammarus spp. were the most important invertebrate prey. A seasonal dietary shift from Atlantic silversides to anchovies was evident. Overall, small pelagic and littoral schooling fishes, particularly engraulids and atherinids, predominated in the diet of the age-0 bluefish collected for this study. Although the results presented here were similar to the diet composition of age-0 bluefish reported in previous studies, some notable differences were probably due to spatial and temporal differences in prey assemblages.

Bluefish *Pomatomus saltatrix* are a highly migratory coastal pelagic species that occurs in temperate and subtropical waters throughout the world, except for the eastern Pacific. In the United States, bluefish are found seasonally along the eastern coastline from Maine to Florida (Kendall and Walford 1979) and in the northern Gulf of Mexico (Ditty and Shaw 1995). Genetic analyses have shown that bluefish along the U.S. Atlantic coast comprise a single unit stock (Graves et al. 1992), which is managed by the Mid-Atlantic Fishery Management Council (MAFMC) and the Atlantic States Marine Fisheries Commission (ASMFC) accordingly.

Historically, the Atlantic coast bluefish stock has experienced periods of great abundance interspersed with decades in which these fish were nearly absent from the coastal waters (Baird 1873; Bigelow and Schroeder 1953). Recent trends in biomass estimates and landings have raised concerns that the stock is currently in a period of decline (Lewis 2002). Factors including overfishing, declining habitat quality and reproductive success, altered migratory patterns, competition with increased populations of striped bass *Morone saxatilis*, and shifts in feeding ecology have been identified as possible causes of these trends (MAFMC 1998).

The perception of a decline in the abundance of Atlantic coast bluefish, combined with a realized lack of fundamental population dynamics information, has prompted a number of research activities in recent years. Several studies have focused on quantifying various aspects of the biology and ecology of youngof-the-year (age-0) bluefish; the potential importance of this life stage in determining future stock size of fishes is well documented (Sissenwine 1984; Wicker and Johnson 1987; Fogarty et al. 1991; Buijse and Houthuijzen 1992). Specifically, diet composition, feeding behavior, and resource competition have received considerable attention (Juanes et al. 1993; Juanes and Conover 1994; Buckel and Conover 1997; Buckel et al. 1999a; Buckel and Stoner 2000; Buckel and McKown 2002; Scharf et al. 2002; Able et al. 2003, Scharf et al. 2004), and collectively, these studies have contributed greatly to our understanding of age-0 bluefish feeding ecology. Although the diet composition of these fish has been investigated in several U.S. Atlantic coast estuaries, few attempts have been made to quantify bluefish diet in Chesapeake Bay, the largest of these estuaries and, along with Virginia's coastal ocean, an important bluefish nursery area (Austin et al. 1997).

In the early 1990s, Hartman and Brandt (1995) documented the age-specific diet of bluefish ranging from ages 0 to 2 in Chesapeake Bay, though sampling was limited to the Maryland portion of the bay. More recently, Harding and Mann (2001) quantified bluefish feeding in the lower Chesapeake Bay; however, this study examined mostly age-1 fish from an oyster reef in the Piankatank River, Virginia. Although these studies provided valuable insights into bluefish foraging ecology in Chesapeake Bay, neither characterized

^{*} Corresponding author: jgartlan@vims.edu

Received January 31, 2005; accepted November 6, 2005 Published online February 10, 2006

the age-0 bluefish diet in the lower bay or Virginia's coastal ocean. Such an investigation would provide critical trophic interaction data necessary to support current Chesapeake Bay ecosystem modeling efforts (Latour et al. 2003). Further, this information, when combined with results from previous studies, would contribute to a more comprehensive, coastwide depiction of bluefish feeding ecology during their first year of life.

In this paper, we present the results of a diet composition study of age-0 bluefish inhabiting the lower Chesapeake Bay and the coastal ocean of Virginia to fill the aforementioned data gaps. Spatial, interannual, and intraannual diet variations were evaluated to provide a more detailed description of predator–prey trophic interactions.

Methods

Field collections.—Age-0 bluefish were sampled from the lower Chesapeake Bay and the coastal ocean of Virginia in 1999 and 2000 (Figure 1). A bag seine $(30.5 \times 1.8 \text{ m}, 6.4\text{-mm-bar mesh})$ was used to collect specimens biweekly during the months of May through October each year. Sampling was conducted at 11 fixed stations on Virginia's Eastern Shore and Southside beaches. Select sites on Virginia's tributaries were also sampled approximately biweekly from July to September during these years. All age-0 bluefish (identified by specimen length) were immediately preserved in 10% buffered formalin upon capture to minimize digestive losses. Additional specimens were collected from the lower main-stem Chesapeake Bay and its tributaries by the Virginia Institute of Marine Science Juvenile Fish and Blue Crab Trawl Survey, which conducts cruises monthly throughout the entire year (Geer and Austin 2000). This survey tows a 9.1-m semiballoon otter trawl (38.1-mm stretched-mesh body, 6.4-mm stretched-mesh cod end liner) along the bottom for 5 min at each sampling location. Age-0 bluefish captured by this survey were held on ice to minimize digestive losses and preserved upon return to the laboratory at the end of each day. All seine and trawl collections were conducted during daylight hours.

Laboratory procedures.—In the laboratory, each specimen was removed from the preservative and rinsed with freshwater. Fork length (mm) and location and date of capture were recorded. Each stomach was opened, and the inner walls were scraped with the tip of a scalpel to collect all contents. Prey items were sorted, identified to the lowest possible taxon, and weighed (0.001 g, wet weight) after blotting excess fluid.

General diet description.-In support of ecological



FIGURE 1.—Map of the lower Chesapeake Bay and coastal ocean of Virginia, showing the locations (solid dots) where age-0 bluefish were collected for a diet study in 1999 and 2000.

modeling efforts in the Chesapeake Bay region (Latour et al. 2003), the percent weight index was selected to categorize the main prey in the diet of age-0 bluefish (Hyslop 1980). Both the seine and trawl collections yielded a cluster of bluefish at each station, so this index was calculated using a cluster sampling estimator (Buckel et al. 1999a, 1999b).

The contribution of each prey type *k* to the diet by weight $(\% W_k)$ was calculated by

$$\%W_k = \frac{\sum_{i=1}^n M_i q_{ik}}{\sum_{i=1}^n M_i} \cdot 100$$

where

$$q_{ik} = \frac{w_{ik}}{w_i}$$

and M_i is the number of bluefish collected at sampling location *i*, w_i is the total weight of all prey items found in the stomachs of bluefish collected from sampling location *i*, and w_{ik} is the total weight of prey type *k* in these stomachs.

Spatial and temporal diet variability.-Canonical correspondence analysis (CCA; ter Braak 1986), a multivariate direct gradient analysis technique, was used to explore the relationship between age-0 bluefish diet and three factors: location (estuary versus coastal ocean, referred to as spatial), year of capture (interannual), and month of capture (intraannual). Although potentially informative, the inclusion of additional factors, such as cohort (spring-spawned versus summer-spawned) and gear (seine versus trawl), to the analysis was precluded by small sample size. Each element of the response matrix was the mean percent weight of a given prey type for a given sampling location, year, and month combination, weighted by sample size (i.e., number of bluefish collected at a sampling site). The matrix was logtransformed $(\log_{e}[x+1])$ to account for the lognormal distribution of the data (Garrison and Link 2000). Explanatory variables were coded using nominal variables, and location-year-month blocks containing fewer than three observations were excluded to eliminate variance issues related to small sample size. The CCA analysis was performed using CANOCO 4.52 (ter Braak 2003).

Specifically, the CCA was used to reveal the amount of variability in the bluefish diet explained by the canonical axes, 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 factors was determined using forward selection (ter Braak 1986). A species–factor biplot was constructed to examine the correlations between the explanatory factors and the canonical axes and to explore the dietary trends associated with these variables. Additional diet descriptions were then generated based on the perceived trends.

Results

General Diet Description

Prey were encountered in 331 of the 404 (81.9%) age-0 bluefish stomachs processed for diet analysis. Of the 17 identifiable prey types, 11 were fishes and 6 were invertebrates. Small, pelagic and littoral schooling fishes were the main prey of age-0 bluefish (Figure 2). Taken together, bay anchovy Anchoa mitchilli, striped anchovy Anchoa hepsetus, and Atlantic silverside Menidia menidia accounted for 74.7% of the diet by %W. When combined with Anchoa spp. (i.e., anchovies that could not be identified to species), engraulids and atherinids composed 77.2% of the diet. Of these prey, bay anchovies were predominant (%W = 33.5%), followed by striped anchovies (23.3%) and Atlantic silversides (17.9%). Invertebrate prey were of secondary importance and were consumed mainly by smaller specimens. Crab zoea and megalope (Callinectes spp.; %W = 2.9%) and amphipods (*Gammarus* spp.; %W =2.7%) were the most important invertebrates in the diet.

The %W values for the 12 remaining identifiable prey types were each less than 2.0% and included the juvenile stage of several economically and ecologically important species: striped bass, bluefish, white perch *Morone americana*, Atlantic herring *Clupea harengus*, Atlantic menhaden *Brevoortia tyrannus*, Atlantic brief squid *Lolliguncula brevis*, opossum shrimp *Neomysis americana*, and sand shrimp *Crangon septemspinosa*. The unknown categories, especially unknown fish and unknown prey, composed a substantial portion of the diet. Many of the unknown items encountered in stomachs containing identifiable prey probably reflected the identified species composition, but they were classified as unknown to preclude potential error in diet descriptions.

Spatial and Temporal Diet Variability

The CCA indicated that the hypothesized explanatory variables explained 6.7% of the variance in the age-0 bluefish diet composition, and the first two canonical axes accounted for 85.5% of this variability. The first axis was correlated with the month of capture and represented an intraannual shift in the bluefish diet (r = 0.678; P = 0.001; Figure 3). The second axis was correlated with both location (r = 0.434; P = 0.249) and



FIGURE 2.—Diet composition of age-0 bluefish collected from the lower Chesapeake Bay and coastal ocean of Virginia in 1999 and 2000.

year of capture (r = -0.298; P = 0.444), but neither of these variables were significant.

Based on the results of the CCA, the age-0 bluefish diet was partitioned by month to explore the intraannual diet variability (Table 1). Atlantic silversides, unidentifiable fish eggs, and crab zoea and megalope were the main prey of bluefish upon arrival to the Chesapeake Bay region in May. Silversides continued to predominate in June and July, accounting for approximately 50% by weight each month. Striped bass and brief squid were of secondary importance in June, and bay and striped anchovy, white perch, and opossum shrimp were minor components. Anchovies increased in importance in July, composing 21.8% of the diet, and some cannibalism was observed at this time. Sand shrimp and crab zoea and megalope were the main invertebrates consumed.

Age-0 bluefish foraged primarily on bay and striped anchovies from August to October, which accounted for more than 80% of the diet each month. The diversity of identifiable prey consumed peaked in August. Atlantic silversides were no longer the main prey, and the %W value for this species was nearly equal to that of amphipods and crab zoea and megalope. Cannibalism was again evident. Bluefish fed almost exclusively on bay and striped anchovy in September and October. Atlantic herring, Atlantic menhaden, and Atlantic silversides were minor components of the diet in September, and brief squid and rough silversides *Membras martinica* were the only other identifiable prey in the stomachs of bluefish in October. Bluefish diet was 95.7% bay anchovy by weight in November, and the remaining 4.3% was Atlantic silversides and sand shrimp.

Discussion

This study provides an accurate depiction of the foraging ecology of age-0 bluefish inhabiting the lower Chesapeake Bay and nearshore waters of Virginia in 1999 and 2000 because these predators were sampled throughout their entire nursery period from numerous localities in the bay, its tributaries, and the adjacent coastal ocean. Small pelagic and littoral schooling fishes predominated the diet of the age-0 bluefish collected from this area. Bay anchovies, striped anchovies, and Atlantic silversides were the main prey



FIGURE 3.—The canonical correspondence analysis biplot used to explore the spatial and temporal variability in the diet of age-0 bluefish collected from the lower Chesapeake Bay and coastal ocean of Virginia in 1999 and 2000. The arrow represents the significant explanatory factor, and points represent prey types.

by weight. Although the dietary contribution of each of the seven other identifiable fish prey species was minor, combined they accounted for 5.1% by %W, suggesting that the contribution of prey consumed occasionally is relatively important as a whole. Further, the diversity of fishes composing the diet attests to the piscivorous feeding nature of bluefish. Invertebrates (i.e., several species of crabs, shrimps, and amphipods) were a relatively small component of the diet, but they were found in bluefish stomachs throughout the entire investigation.

The description of age-0 bluefish diet in the lower Chesapeake Bay and coastal ocean of Virginia is consistent with other findings on age-0 bluefish feeding in estuarine and coastal waters—that is, that pelagic and littoral schooling fishes were the main prey and invertebrates, mostly crustaceans, were of secondary importance (Breeder 1922; Grant 1962; Lassiter 1962; Juanes et al. 1993; Juanes et al. 1994; Hartman and Brandt 1995; Juanes and Conover 1995; Buckel and Conover 1997; Buckel et al. 1999a; Scharf et al. 2004). Similar to our findings for the lower Chesapeake Bay and adjacent coastal waters, age-0 bluefish in New York's Hudson River and Great South Bay fed primarily on engraulid and atherinid fishes during the period of estuarine residency (Juanes et al. 1993; Juanes et al. 1994; Juanes and Conover 1995; Buckel and Conover 1997; Buckel et al. 1999a).

Although pelagic and littoral schooling fishes predominated in the diet reported in our study and most previous investigations, analysis of the species compositions of these diets did yield several differences. Most notably, anadromous fishes—specifically, striped bass, American shad *Alosa sapidissima*, and blueback herring *Alosa aestivalis*—were important prey of age-0 bluefish inhabiting the Hudson River (Juanes et al. 1993; Juanes et al. 1994; Buckel and Conover 1997; Buckel et al. 1999a), whereas we found

Prey type	May (6)	Jun (53)	Jul (50)	Aug (142)	Sep (86)	Oct (38)	Nov (29)
Anchoa spp.	0	0	0	5.6	2.3	0.7	0
Atlantic herring	0	0	1.5	0	1.2	0	0
Atlantic menhaden	0	0	0	0	1.2	0	0
Atlantic silverside	33.3	52.1	47.6	7.3	9.1	0	3.3
Bay anchovy	0	5.4	12.9	30.0	42.6	49.8	95.7
Bluefish	0	0	4.4	2.2	0	0	0
Fish egg	31.0	0	0	0	0	0	0
Rough silverside	0	0	0	1.7	0	0.5	0
Striped anchovy	0	3.8	8.9	26.3	38.6	44.3	0
Striped bass	0	10.7	0	0	0	0	0
White perch	0	4.0	1.2	0	0	0	0
Atlantic brief squid	0	10.5	0	0	0	1.6	0
Crab zoea and megalope	16.6	< 0.1	2.6	6.6	0.1	1.6	0
Gammarid amphipod	0	0	0.1	7.5	0	0	0
Lady crab	0	0	0	0.8	0	0	0
Opossum shrimp	0	4.2	0.2	0.9	0	0	0
Sand shrimp	0	0.2	4.3	< 0.1	0	0	1.0
Unknown fish	0	7.7	15.7	5.8	3.5	3.0	0
Unknown invertebrate	0	1.3	0	0	0	< 0.1	0
Unknown prey	19.0	0	0.5	5.4	1.5	< 0.1	0

TABLE 1.—Monthly diet composition expressed as percent weight of age-0 bluefish collected from the lower Chesapeake Bay and coastal ocean of Virginia in 1999 and 2000. Sample size is given in parentheses beside each month.

striped bass were a minor component and American shad and blueback herring were absent. Age-0 bluefish rarely venture into the Chesapeake Bay's upper and middle tributary nursery areas occupied by these age-0 anadromous fishes, which probably explains the minimal predator–prey interactions between bluefish and anadromous fishes in this region (Austin et al. 2001).

Although the diet composition from our study generally resembled that reported by Hartman and Brandt (1995), appreciable differences in prey species composition were again evident. They reported that Atlantic menhaden was one of the main prey of age-0 bluefish, whereas we found this prey species was of minor importance. Indices of relative abundance for age-0 Atlantic menhaden in Chesapeake Bay have declined steadily throughout the 1990s, which may explain these differences in diet composition (ASMFC 2004). The overall diet diversity in this study was greater than that reported by Hartman and Brandt (1995). Several of the main prey in this study (e.g., Atlantic silversides, striped anchovies, and crab zoea and megalope) were either of minor importance or absent from the description provided by Hartman and Brandt (1995). These inconsistencies are probably due to differences in the sampling locations (mesohaline versus polyhaline environments) and the periods (early 1990s versus late 1990s) of the studies.

The CCA accounted for 6.7% of the variability in the diet of age-0 bluefish, which is reasonable when considering the similarities to previous applications of this method to finfish diet data and given the number of biotic and abiotic factors potentially influencing the

feeding ecology of finfish (Link et al. 2002; Link and Garrison 2002). Of the three hypothesized explanatory variables, season was the only significant factor. This result is not unexpected given the well-documented, acute seasonal faunal shifts in Chesapeake Bay (Murdy et al. 1997). The shift from a predominantly Atlantic silverside diet in the late spring and early summer to one mainly composed of anchovies by midsummer was also observed by Juanes and Conover (1995) in Great South Bay. Hartman and Brandt (1995) also found that age-0 bluefish foraged primarily upon bay anchovies in the upper Chesapeake Bay during late summer but did not observe the early summer predominance of Atlantic silversides (our study)—again, perhaps because of differences in sampling locations.

With the addition of the present study, we now have a more complete coastal assessment of bluefish feeding ecology. Collectively, age-0 bluefish diet investigations ranging from New York to North Carolina indicated that the engraulids and atherinids are important food sources in each of these nursery areas. Furthermore, although prey fish species composition varied among these regions, all prey were usually small, pelagic and littoral age-0 and age-1 fishes, and bluefish diet differences probably reflected spatial and temporal variations in these prey assemblages.

Acknowledgments

This study was presented in partial fulfillment of a master of science degree, School of Marine Science at the College of William and Mary by J.G. Thesis committee members Deborah A. Bodolus, Mark E. Chittenden, Jr., David A. Evans, and John A. Musick are acknowledged for their guidance. We also thank the numerous staff and students who participated in the beach seine sampling efforts. The Virginia Institute of Marine Science (VIMS) Juvenile Striped Bass Seine Survey and the VIMS Juvenile Fish and Blue Crab Trawl Survey extended the geographic sampling range of this study by providing additional specimens. These programs received funding from the Wallop–Breaux expansion of the Sportfish Restoration and Enhancement Act and the Virginia Recreational Fishing Advisory Board, respectively, during the period of this investigation. This is contribution number 2706 of the Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point.

References

- Able, K. W., P. Rowe, M. Burlas, and D. Byrne. 2003. Use of ocean and estuarine habitats by young-of-the-year bluefish (*Pomatomus saltatrix*) in the New York Bight. Fishery Bulletin 101:201–214.
- ASMFC (Atlantic States Marine Fisheries Commission). 2004. Atlantic menhaden stock assessment report for peer review. ASMFC, Report 04-01 (Supplement), Washington, D.C.
- Austin, H. M., A. D. Estes, and D. M. Seaver. 2001. Estimation of juvenile striped bass relative abundance in the Virginia portion of Chesapeake Bay. Report of the Virginia Institute of Marine Science to the Virginia Marine Resources Commission, Newport News.
- Austin, H. M., D. M. Seaver, and C. M. Wagner. 1997. Monitoring juvenile recreational fishes on the Eastern Shore of Virginia with special focus on developing a bluefish, *Pomatomus saltatrix*, young-of-the-year index in Virginia. Report of the Virginia Institute of Marine Science to the Virginia Marine Resources Commission, Newport News.
- Baird, S. F. 1873. Natural history of some of the more important food fishes of the south shore of New England. Report to the U.S. Commission of Fish and Fisheries for 1871–1872. U.S. Government Printing Office, Washington, D.C.
- Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. U.S. Fish and Wildlife Service Fishery Bulletin 53:383–389.
- Breeder, C. M. 1922. Observations on young bluefish. Copeia 106:34–36.
- Buckel, J. A., and D. O. Conover. 1997. Movements, feeding periods, and daily ration of piscivorous young-of-theyear bluefish, *Pomatomus saltatrix*, in the Hudson River estuary. Fishery Bulletin 95:665–679.
- Buckel, J. A., D. O. Conover, N. D. Steinberg, and K. A. McKown. 1999a. Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in Hudson River estuary: evidence for density-dependant loss of juvenile striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 56:275–287.
- Buckel, J. A., M. J. Fogarty, and D. O. Conover. 1999b. Foraging habits of bluefish, *Pomatomus saltatrix*, on the

U.S. East coast continental shelf. Fishery Bulletin 97:758–775.

- Buckel, J. A., and K. A. McKown. 2002. Competition between juvenile striped bass and bluefish: resource partitioning and growth rate. Marine Ecology Progress Series 234:191–204.
- Buckel, J. A., and A. W. Stoner. 2000. Functional response and switching behavior of young-of- the-year piscivorous bluefish. Journal of Experimental Marine Biology and Ecology 245:25–41.
- Buijse, A. D., and R. P. Houthuijzen. 1992. Piscivory, growth, and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). Canadian Journal of Fisheries and Aquatic Sciences 49:894–902.
- Ditty, J. G., and R. F. Shaw. 1995. Seasonal occurrence, distribution, and abundance of larval bluefish, *Pomatomus saltatrix* (Family: Pomatomidae), in the northerm Gulf of Mexico. Bulletin of Marine Science 56:592–601.
- Fogarty, M. J., M. P. Sissenwine, and E. B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends in Ecology and Evolution 6:241–246.
- Garrison, L. P., and J. S. Link. 2000. Diets of five hake species in the northeast United States continental shelf system. Marine Ecology Progress Series 204:243–255.
- Geer, P. J., and H. M. Austin. 2000. Estimation of relative abundance of recreationally important finfish in the Virginia portion of Chesapeake Bay. Report of the Virginia Institute of Marine Science to the Virginia Marine Resources Commission, Newport News.
- Grant, G. C. 1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Science 3:45–47.
- Graves, J. E., J. R. McDowell, A. M. Beardsley, and D. R. Scoles. 1992. Stock structure of bluefish, *Pomatomus saltatrix*, along the mid-Atlantic coast. Fishery Bulletin 90:703–710.
- Harding, J. M., and R. Mann. 2001. Diet and habitat use by bluefish, *Pomatomus saltatrix*, in a Chesapeake Bay estuary. Environmental Biology of Fishes 60:401–409.
- Hartman, K. J., and S. B. Brandt. 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Transactions of the American Fisheries Society 124:520–537.
- Hyslop, E. J. 1980. Stomach contents analysis: a review of methods and their application. Journal of Fish Biology 17:411–429.
- Juanes, F., J. A. Buckel, and D. O. Conover. 1994. Accelerating the onset of piscivory: intersection of predator and prey phenologies. Journal of Fish Biology 45:41–54.
- Juanes, F., and D. O. Conover. 1994. Piscivory and size selection in young-of-the-year bluefish: predator preference or size-dependent capture success. Marine Ecology Progress Series 114:59–69.
- Juanes, F., and D. O. Conover. 1995. Size structured piscivory: advection and the linkage between predator and prey recruitment in young-of-the-year bluefish. Marine Ecology Progress Series 128:287–314.
- Juanes, F., R. E. Marks, K. A. McKown, and D. O. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous

fishes in the Hudson River estuary. Transactions of the American Fisheries Society 122:348–356.

- Kendall, A. W. Jr., and L. A. Walford. 1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the East Coast of the United States. Fishery Bulletin 77:213–227.
- Lassiter, R. R. 1962. Life history aspects of bluefish, *Pomatomus saltatrix* (Linnaeus), from the coast of North Carolina. Master's thesis. North Carolina State College, Raleigh.
- Latour, R. J., M. J. Brush, and C. F. Bonzek. 2003. Toward ecosystem-based fisheries management: strategies for multispecies modeling and associated data requirements. Fisheries 28:10–22.
- Lewis, M. 2002. 2002 review of the Atlantic States Marine Fisheries Commission fishery management plan for bluefish (*Pomatomus saltatrix*). Atlantic States Marine Fisheries Commission, Washington, DC.
- Link, J. S., K. Bolles, and C. G. Milliken. 2002. The feeding ecology of flatfish in the Northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 30:1–17.
- Link, J. S., and L. P. Garrison. 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast U.S. continental shelf. Marine Ecology Progress Series 227:109–123.
- MAFMC (Mid-Atlantic Fishery Management Council). 1998. Amendment I to the Bluefish Management Plan. MAFMC, Dover, Delaware.

- Murdy, E. O., R. Birdsong, and J. A. Musick. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, D.C.
- Scharf, F. S., J. A. Buckel, and F. Juanes. 2002. Sizedependent vulnerability of juvenile bay anchovy (*Anchoa mitchilli*) to bluefish predation: does large body size always provide a refuge? Marine Ecology Progress Series 233:241–252.
- Scharf, F. S., J. P. Manderson, M. C. Fabrizio, J. P. Pessutti, J. E. Rosendale, R. J. Chant, and A. J. Bejda. 2004. Seasonal and interannual patterns of distribution and diet of bluefish within a Middle Atlantic Bight estuary in relation to abiotic and biotic factors. Estuaries 27:426– 436.
- Sissenwine, M. P. 1984. Why do fish populations vary? Pages 59–94 in R. M. May, editor. Exploitation of marine communities. Springer-Verlag, Berlin.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.
- ter Braak, C. J. F. 2003. CANOCO, version 4.52. Wageningen University and Research Centre, Wageningen, The Netherlands.
- Wicker, A. M., and W. E. Johnson. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. Transactions of the American Fisheries Society 116:264–271.