

Seasonal and Interannual Patterns of Distribution and Diet of Bluefish within a Middle Atlantic Bight Estuary in Relation to Abiotic and Biotic Factors

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ABSTRACT: Seasonal and interannual patterns in the spatial distribution of bluefish (*Pomatomus saltatrix*) within a Middle Atlantic Bight estuary were examined using multipanel gillnets fished biweekly at 14 fixed stations in the Sandy Hook Bay-Navesink River estuary during May–November of 1998 and 1999. To characterize habitats along the estuarine gradient, we measured several abiotic and biotic variables concurrently with gillnet sampling. Juvenile (age-0 and age-1+) bluefish were captured regularly during both years along with large numbers of Atlantic menhaden (*Brevoortia tyrannus*), which were confirmed by diet analyses to be bluefish's primary forage species. The date of initial appearance of age-0 bluefish and menhaden in the estuary varied between years and may have been related to interannual differences in seawater temperatures on the continental shelf during spring. Delayed estuarine arrival of prey fishes may have contributed to variability in bluefish diets between years. Within the estuary, bluefish spatial distributions were consistent across seasons and years: bluefish were most common in areas associated with high concentrations of suspended materials and the presence of menhaden. Community analyses also indicated habitat overlap between bluefish and menhaden. Spatial distribution patterns revealed the consistent occurrence of piscivorous bluefish in shallow estuarine habitats that retained suspended materials and aggregated prey fishes. Foraging success of bluefish and other estuarine piscivores may be closely linked with the availability of these productive habitats, highlighting the need for future study of biological interactions and the governing physical processes.

Introduction

Shallow estuarine and marine ecosystems are highly productive and support abundant and diverse animal populations. For juvenile fishes, the advantages of refuge from predation and available food resources are thought to promote increased growth and survival making estuarine habitats critical for recruitment success (Gunter 1967; Boesch and Turner 1984; Miller et al. 1985; Kneib 1997; Jenkins and Wheatley 1998). The widely assumed decrease in predation pressure afforded by shallow estuarine habitats has been questioned recently (Sheaves 2001). In addition to larger piscivores (e.g., Manderson et al. 2000; Scharf and Schlicht 2000), abundant populations of small piscivorous fishes have been found to occupy shallow, near-shore habitats (Buckel and Conover 1997; Rooker et al. 1998). The evidence indicates that our un-

derstanding of the distribution of piscivorous fishes and associated predation mortality within estuarine systems is incomplete and should provoke re-evaluation of the notion that shallow water consistently provides a refuge from predation (Sheaves 2001). Given the important role of piscivorous fishes in aquatic food webs and their potential impact on freshwater and marine communities (Juanes et al. 2002), knowledge of the factors affecting their distribution in shallow estuaries should enable better evaluation of the potential refuge provided by these habitats.

The validity of the nursery-role concept as it relates to estuaries has also been revisited (Beck et al. 2001). Although entire estuarine ecosystems have long been thought to represent nursery areas for juvenile fish and invertebrates, variability may exist in the quality of specific habitats (e.g., seagrass beds, oyster reefs, marshes) within each system. The need to identify specific estuarine habitats that contribute disproportionately to adult recruitment has been emphasized in order to achieve better conservation and management of these habitats (Beck et al. 2001). Identification of

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critical habitats for a given species requires knowledge of patterns of seasonal use and the factors that may be important in generating those patterns.

The bluefish (*Pomatomus saltatrix*) is a marine piscivore of circumglobal distribution that uses shallow marine and estuarine waters as both juveniles and adults (Collette and Klein-MacPhee 2002). Along the United States Atlantic coast, spawning occurs on the continental shelf in spring and summer, followed by movement inshore by small juveniles (approximately 40–60 mm TL; Kendall and Walford 1979; Nyman and Conover 1988). During summer and early fall, juvenile bluefish achieve rapid growth rates, due primarily to high consumption rates on fish prey (Juanes and Conover 1994), and have been shown to have significant impacts on local prey fish populations (Buckel et al. 1999). After spending summer months in Middle Atlantic Bight estuaries and coastal areas, juveniles migrate to southern latitudes to overwinter. Although adult bluefish frequent shallow coastal waters during warmer months, juveniles are believed to be especially dependent upon nearshore shallow water habitats for feeding and growth during their first year of life, given that cohort success may be linked to body size prior to fall migration (Munch and Conover 2000). During estuarine residence, juvenile bluefish have been found to occupy shallow nearshore waters during the day and deeper waters, further from the beach, at night, with movement patterns associated with feeding periodicity (Buckel and Conover 1997). Little is known about the seasonal movement of bluefish across entire estuaries and the factors that contribute to estuarine distribution patterns.

We report the results of a 2-yr study designed to examine the biotic and abiotic factors that influence the spatial patterns of bluefish abundance within a Middle Atlantic Bight estuary. We used a multipanel gillnet survey to determine patterns of abundance of bluefish and prey species across the estuary from late spring through fall in consecutive years. Bluefish diets were determined and bluefish size-prey size relationships were evaluated to verify dominant prey during the study period. Several abiotic factors measured during the gillnet survey were combined with abundance estimates for dominant bluefish prey to evaluate potentially important factors contributing to bluefish spatial distributions within estuarine systems.

Materials and Methods

FIELD SAMPLING

All sampling was completed in the Sandy Hook Bay-Navesink River estuary located along the cen-

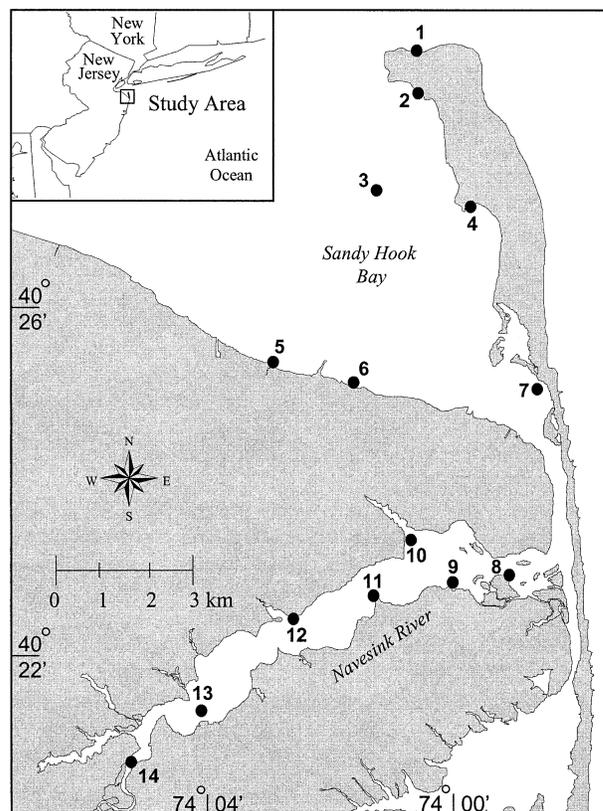


Fig. 1. Map of the study area indicating gillnet sampling stations in Sandy Hook Bay and the Navesink River.

tral coast of New Jersey, U.S. Shallow water habitats, defined as subtidal depths <1 m at mean low water (mean tidal range = 1.4 m), account for approximately 40% of the total surface area of this estuarine system based on National Ocean Service (NOS) digital elevation models (NOS models available for viewing at <http://spo.nos.noaa.gov/bathy/>). Gillnets (45.7 m in length by 2.4 m depth, with 6 equal length [7.6 m] panels of ascending sizes of square mesh [1.3, 1.9, 2.5, 3.8, 5.1, and 7.6 cm]) were fished biweekly from early May through the end of October during 1998 and 1999 (Fig. 1). Gillnets were fished at 7 fixed stations in the Navesink River and 7 fixed stations in Sandy Hook Bay. Stations were located along a spatial gradient within the estuary and habitat characteristics, including temperature, salinity, sediment grain size, and distance from the mouth of the estuary, differed among stations. To control for tidal stage and depth, all gillnets were set in waters ranging 1.5–3.0 m depth ($x \pm SD = 2.23 \pm 0.45$), and 1–2 h before mean high water and were fished for 2 h. To capture predatory fishes just after the morning crepuscular period, when feeding activity may be heightened, sampling was completed on mornings

when high tide occurred no more than 4 h after sunrise. Gillnets regularly fished the entire water column because most station depths were <3 m. Surface (<1 m depth) water temperature (°C) and salinity (‰) were measured at each station during net deployment. After 2 h, gillnets were retrieved and all fish and macroinvertebrates were removed from each net, sorted by mesh size, counted, and measured for length (total length for fishes; carapace length or width for shrimp and crabs). The stomachs of piscivorous fishes were removed and preserved in a 10% formalin solution. Stomach contents were examined and fish and macroinvertebrate prey items were identified to the lowest taxonomic level possible (often to species). Wet weights (g) and lengths (mm) were recorded for individual prey recovered from bluefish stomachs.

DATA ANALYSIS

We explored the relationship between bluefish distribution and habitat characteristics during each year using Generalized Additive Models (GAMs) with Poisson link functions (Hastie and Tibshirani 1990; Venables and Ripley 1997), which we fitted using S-Plus software. Numbers of bluefish collected in gillnets served as the dependent variable. Water temperature, salinity, the abundance of Atlantic menhaden (*Brevoortia tyrannus*) prey, and sediment grain size (ϕ) were considered as independent variables. Sediment grain size was used as an index of current velocity because fine grain sediments are associated with low flow, depositional areas, and coarse sediments are typically found in areas of rapid current flow and high energy. Water temperature, salinity, and Atlantic menhaden abundance at each station were measured concurrently with bluefish sampling during 1998 and 1999. An estuary-wide survey completed during 1997 provided estimates of sediment grain size at each of our stations (Stoner et al. 2000). We constructed each GAM with forward stepwise selection using a cubic spline with 4 degrees of freedom, which produced moderate smoothing of the relation between bluefish numerical abundances and factors of interest (Hastie and Tibshirani 1990; Venables and Ripley 1997). The independent variable added to the model at each step resulted in the largest significant (approximate χ^2 test, $p < 0.05$) reduction in residual deviance when compared with the previous model (Hastie 1992). We calculated deviance (variance) explained as:

$$\text{Deviance}_{\text{explained}} = \frac{(\text{Deviance}_{\text{null}} - \text{Deviance}_{\text{residual}})}{\text{Deviance}_{\text{null}}}$$

First-order interactions between significant independent variables were also tested. Partial additive effects of the independent variables on bluefish

abundance were plotted with ± 2 SE confidence bands. The same y-axis scale was used for each significant independent variable, allowing for visual assessment of the relative importance of each factor. GAM functions that demonstrate the largest deviation from 0 along the y-axis represent independent variables with the largest effects on bluefish abundance.

Dietary indices of percent frequency of occurrence (%FO) and percent by weight (%W) were calculated for each prey category recovered from bluefish stomachs. Diets of age-1 and older fish were analyzed separately from diets of age-0 fish for each year, with age classes separated on the basis of length. Relationships between prey size and bluefish size were determined using least squares and quantile regression analyses.

Bluefish spatial distributions through time (sample dates) and patterns of habitat overlap between bluefish and their primary prey, Atlantic menhaden, were assessed using niche overlap analysis performed with EcoSim software (Gotelli and Entsminger 2001). We generated Monte Carlo randomizations from the observed matrix of species distributions (relative abundance data), calculated overlap indices, and statistically evaluated the probability of obtaining the overlap patterns observed in the data. To evaluate significance of the observed overlap indices, 1,000 iterations were performed using a randomization algorithm that retained niche breadth within the matrix and reshuffled the zero values (Gotelli and Entsminger 2001). These iterations yielded a frequency distribution of niche overlap indices for all possible matrices with a particular niche breadth. An overlap index (Pianka 1973) was calculated for the observed data and compared with the distribution of 1,000 overlap indices calculated for the randomized matrices. Significance (p value) was determined from the proportion of iterations (out of 1,000) that produced an overlap index higher than the overlap index of the actual matrix. Since we used relative abundance data, significant niche overlap is based on correlated catch rates, rather than simple presence-absence matrices that are typically used to assess patterns of animal co-occurrence. Based on the consistent occurrence of pelagic bluefish and Atlantic menhaden and the relatively low number of stations (14), co-occurrence analysis using presence-absence data would have yielded very high estimates of spatial overlap that were mostly uninformative. The niche overlap analysis we employed represents a more conservative approach for evaluating patterns of association among animal spatial distributions.

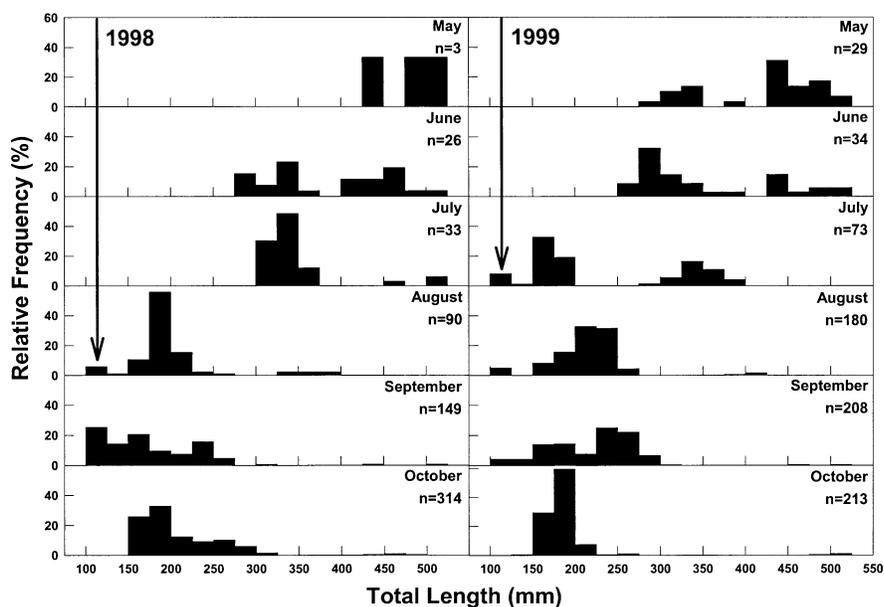


Fig. 2. Bluefish length frequency plots for 1998 and 1999. The total number of bluefish captured in gill nets per month is indicated in the upper right of each panel. Arrows indicate the time of recruitment of the age-0 cohort to the sampling gear each year.

Results

Bluefish were present in the Sandy Hook Bay-Navesink River estuary during all sampling months in 1998 and 1999 (Fig. 2). Small numbers of larger fish (>300 mm TL, age-1+) were captured in late spring before age-0 fish recruited to the sampling gear in mid-summer at a body size of about 100 mm TL. These larger bluefish were only rarely captured within the estuary after July during each year. The date of initial appearance of age-0 bluefish differed between years. The first age-0 fish were not captured until early August 1998, whereas the age-0 cohort was first detected in mid-July 1999. Relative abundance of age-0 bluefish as measured by our gillnets was similar during 1998 and 1999 and length-frequency plots indicated the presence of age-0 fish into October.

Atlantic menhaden was the most abundant forage species captured during both years and displayed patterns similar to bluefish in the timing of appearance of multiple cohorts (Fig. 3). Only larger menhaden (>250 mm TL) were captured during late spring, and these fish were rarely captured after July of each year. The age-0 cohort first recruited to the sampling gear at about 75 mm TL, and the date of their initial appearance in the estuary varied between years. Similar to age-0 bluefish, age-0 menhaden were not detected until early August 1998, but were first captured in mid-July in 1999. Age-0 menhaden were present in the estuary in large numbers through October of both years.

Bluefish spatial distributions within the estuary

were consistent across sampling periods within years and between sampling years. In both years, more bluefish were captured in the Navesink River than in Sandy Hook Bay. High numbers of bluefish were routinely captured at two stations in the Navesink River (stations 10 and 13) during both years (Fig. 4). Although catch rates were lower in Sandy Hook Bay, station 6 along the southern shoreline produced more bluefish than other bay stations during both years. Temporal patterns of bluefish habitat use within each year yielded niche overlap values of 0.461 and 0.491 for 1998 and 1999. These indices represent a measure of habitat (station) use for the various sampling periods in a given year. The average of 1,000 overlap indices calculated for the randomized matrices was 0.267 and 0.251 for 1998 and 1999, with none of the 1,000 randomized matrices generating an overlap index greater than the observed overlap index during either year ($p < 0.001$). These highly significant overlap indices imply that bluefish consistently used the same habitats (stations) in the estuary throughout the sampling period.

Our exploratory GAM analysis suggested that bluefish were most common in depositional habitats where Atlantic menhaden prey were also relatively abundant. Bluefish abundance was significantly related to sediment grain size (current velocity), Atlantic menhaden abundance, salinity, and seawater temperature, which combined to account for 46% and 59% of the total deviance in 1998 and 1999 (Table 1). During both years sedi-

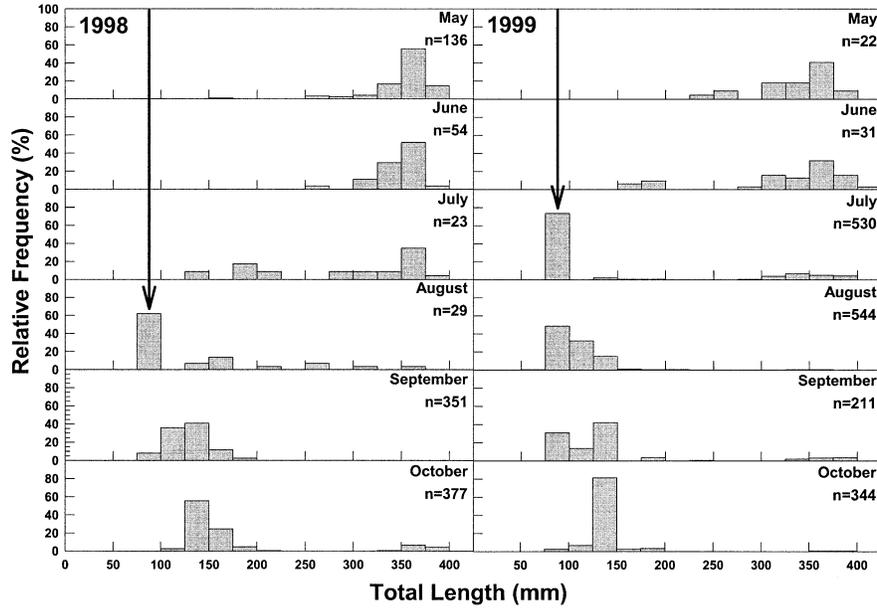


Fig. 3. Atlantic menhaden length frequency plots for 1998 and 1999. The total number of menhaden captured in gill nets per month is indicated in the upper right of each panel. Arrows indicate the time of recruitment of the age-0 cohort to the sampling gear each year.

ment grain size had the strongest independent effects and bluefish were collected in greater numbers in areas with fine grain sediments, indicating a preference for depositional habitats with relatively low current velocities (Fig. 5). Bluefish were also consistently present at sites and times when estuarine temperatures ranged from 14–25°C. The re-

lationship of bluefish abundance to salinity and menhaden abundance was somewhat inconsistent, perhaps as a result of interannual variation in the degree to which the habitat variables were correlated (Table 1). In 1998, the independent effects of salinity were strong and bluefish were commonly collected in waters where salinity values ranged

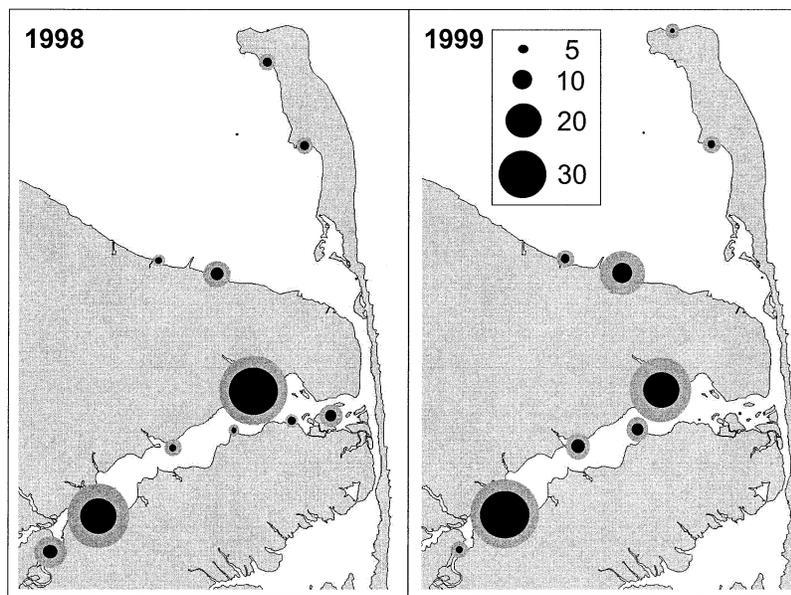


Fig. 4. Spatial distribution of bluefish within the estuary averaged across all sampling dates during 1998 and 1999. Darkened circles represent the mean relative abundance (% frequency) of bluefish captured at each of 14 sample stations. Gray outer circles represent one standard error of the mean.

TABLE 1. Generalized additive models for bluefish abundance during 1998 and 1999. The Null model deviance is equal to the sum of the squared deviations about the mean. The Null model assumed that bluefish abundance was not explained by habitat parameters.

Term	1998 Nonparametric Effects					1999 Nonparametric Effects				
	df	Chi-square	p	Deviance Accounted For	Independent Effects (%)	df	Chi-square	p	Deviance Accounted For	Independent Effects (%)
Null model				1,803.53					1,923.18	
Temperature	3	84.05	<0.001	189.99	10.53	3	94.47	<0.001	87.24	4.54
Salinity	3	17.28	<0.001	210.23	11.66	3	23.51	<0.001	27.63	1.44
Sediment grain size	3	121.70	<0.001	253.88	14.08	3	18.35	<0.001	183.38	9.54
Menhaden abundance	3	29.05	<0.001	55.62	3.08	3	103.62	<0.001	176.69	9.19
Sum of independent effects				709.72	39.35				474.94	24.70
Intercorrelated effects				123.21	6.83				662.49	34.44
Total deviance explained				832.93	46.18				1,137.43	59.14

from 23–27‰. During the same year bluefish were only marginally more abundant at sites and times when menhaden prey were also common (Table 1, Fig. 5). In 1999, the relationship between bluefish abundance and salinity was weak while the effect

of Atlantic menhaden prey abundance was relatively strong and positive.

Diet analyses revealed that bluefish consumed mainly fish prey during both years, but with a stronger invertebrate component in 1998 compared with 1999. Total fish prey represented 92.1% and 97.8% by weight of age-0 bluefish diets during 1998 and 1999. Age-0 diets were dominated by Atlantic menhaden, with menhaden constituting 44.0% and 58.5% of the diet by weight during 1998 and 1999 (Table 2). Atlantic silversides (*Menidia menidia*) represented an important prey in 1998, but were less important in 1999. Common sand (*Crangon septimspinosa*) and grass shrimp (*Palaemonetes* spp.) were recovered from age-0 bluefish stomachs with some regularity during 1998 (% FO = 10.3% and 12.6%), but were rare in 1999 (% FO = 1.4% and 0.6%).

Atlantic menhaden were also an important component of age-1+ bluefish diets, ranking second in %W during 1998 (18.6%) and dominating the diet in 1999 (%W = 41.0). Total fish prey represented a significant fraction (34.3% by weight in 1998 and 80.0% by weight in 1999) of age-1+ bluefish diets. Common sand and grass shrimp were also present consistently in age-1+ bluefish diets during 1998 (% FO = 26.9% and 13.5%) and 1999 (% FO = 32.8% and 20.9%). The dominant prey of age-1+ bluefish during 1998 was blue crab (*Callinectes sapidus*), occurring in 26.9% of stomachs with food and representing 44.6% of the diet by weight. This prey was relatively rare in the diet of age-1+ bluefish during 1999.

The predator-prey size relationship between bluefish and Atlantic menhaden illustrated that larger bluefish consumed larger mean prey sizes (Fig. 6). Large age-1+ bluefish collected in late spring consumed mainly larger menhaden present in the estuary at that time, whereas age-0 bluefish fed exclusively on the age-0 cohort of menhaden that recruited to the estuary in early to mid-summer. The maximum prey size consumed by age-0

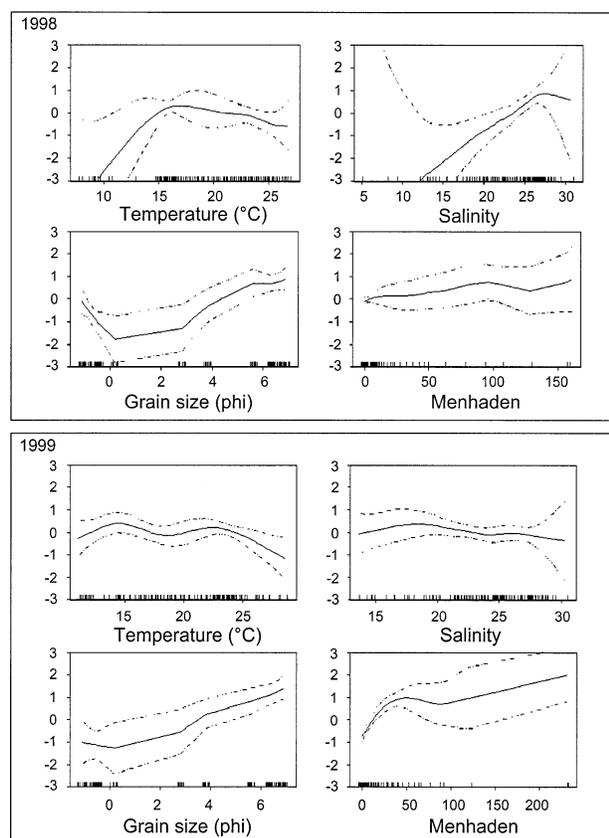


Fig. 5. Deviance plots generated from generalized additive models for 1998 and 1999 showing the partial additive effects of seawater temperature, salinity, sediment grain size, and menhaden abundance on the abundance of bluefish in the estuary. Vertical dashes along the abscissa indicate the distribution of values for each factor. Dashed lines represent 2 SE confidence bands.

TABLE 2. 1998 and 1999 diet composition of age-0 and age-1+ bluefish in the Sandy Hook Bay-Navesink River estuary expressed as percent wet weight (%W) and percent frequency of occurrence (%FO). UID = unidentified. Other includes algae (*Ulva*, *Gracilaria*, *Agardhiella*, and *Enteromorpha* spp.), shell, plastic, and rock.

Species	Common Name	1998				1999			
		Age-0		Age-1+		Age-0		Age-1+	
		%W	%FO	%W	%FO	%W	%FO	%W	%FO
<i>Brevoortia tyrannus</i>	Atlantic menhaden	43.97	27.86	18.56	11.54	58.49	46.57	40.97	20.90
<i>Menidia menidia</i>	Atlantic silverside	21.29	20.61	2.05	9.62	4.55	8.86	1.58	5.97
<i>Anchoa mitchilli</i>	Bay anchovy	1.68	5.34			0.04	0.29	2.65	5.97
<i>Cynoscion regalis</i>	Weakfish	0.67	0.38					5.92	8.96
<i>Prionotus</i> spp.	Sea robin			1.58	1.92	0.62	0.57	2.22	5.97
<i>Pseudopleuronectes americanus</i>	Winter flounder			1.79	3.85	0.15	0.57		
<i>Pomatomus saltatrix</i>	Bluefish	2.88	1.53					6.76	2.99
<i>Fundulus</i> spp.	Killifish	0.63	0.38			0.32	0.29		
<i>Syngnathus fuscus</i>	Northern pipefish							0.28	1.49
<i>Anguilla rostrata</i>	American eel							6.33	1.49
<i>Stenotomus chrysops</i>	Scup							3.85	1.49
UID fish		21.00	33.59	10.32	23.08	33.65	56.86	9.42	28.36
<i>Crangon septimspinosa</i>	Sand shrimp	1.36	10.31	3.08	26.92	0.07	1.43	12.92	32.84
<i>Palaemonetes</i> spp.	Grass shrimp	4.88	12.60	2.80	13.46	0.07	0.57	0.61	20.90
UID shrimp		0.15	2.29	1.27	9.62	0.04	1.71	0.04	1.49
<i>Callinectes sapidus</i>	Blue crab			44.60	26.92			2.26	4.48
<i>Ovalipes ocellatus</i>	Lady crab			1.70	1.92			1.84	2.99
UID crab		0.50	1.53	9.30	15.38	1.98	1.43	0.83	5.97
<i>Gammaridea</i>	Amphipod	0.17	1.15			0.00	0.29	0.02	4.48
<i>Neomysis americana</i>	Mysid shrimp	0.00	0.38	0.04	1.92	0.00	0.29	0.01	2.99
<i>Isopoda</i>	Isopods							0.01	1.49
<i>Nereis</i> spp.	Clam worm	0.05	1.53					0.50	8.96
<i>Gastropoda</i>	Mud snail	0.19	0.38	2.27	11.54			0.52	4.48
Ctenophora	Comb jelly	0.56	0.38						
Other		0.03	0.76	0.64	15.38	0.01	0.29	0.47	7.46

bluefish increased with bluefish size at a faster rate than the mean prey size consumed (Inset, Fig. 6), indicating that young bluefish were continually able to feed on the largest members of the age-0 menhaden cohort.

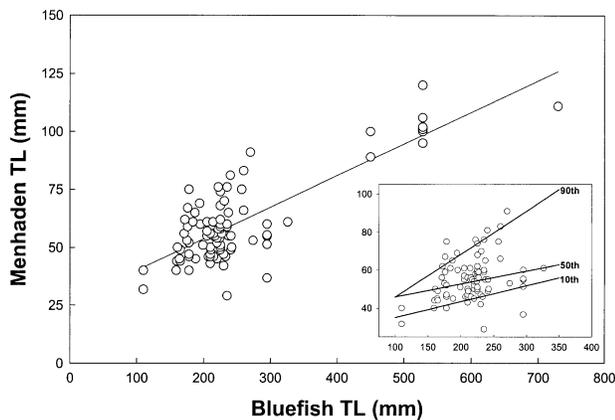


Fig. 6. Predator size-prey size relationship for bluefish predators and Atlantic menhaden prey. The single solid line represents the mean relationship generated from least squares regression. The inset box focuses on the relationship for bluefish < 300 mm TL (primarily age-0 fish) with lines representing minimum (10th quantile), median (50th quantile), and maximum (90th quantile) prey size relationships generated using quantile regression analysis.

Niche overlap analyses indicated habitat overlap between bluefish and their primary prey, Atlantic menhaden (Fig. 7). For 1998, our analysis produced an observed overlap index of 0.663, which was higher than the mean of 1,000 simulated overlap indices (0.541), but was not statistically significant ($p = 0.186$). For 1999, niche overlap analysis generated an observed overlap index of 0.906, which was significantly higher ($p = 0.002$) than the mean of 1,000 simulated overlap indices (0.464).

Discussion

Larger (age-1+) bluefish and Atlantic menhaden were present in the Sandy Hook Bay-Navesink River estuary in late spring and early summer, presumably entering the estuary from offshore waters once spring warming elevated coastal water temperatures sufficiently. The young of the year (age-0) of each species did not appear in our samples until at least mid-July, although the actual initial appearance of each cohort probably occurred up to 1 mo earlier. The smaller individuals (bluefish < 100 mm TL; menhaden < 75 mm TL) of each species were not susceptible to our gear. We detected both spring-spawned and summer-spawned cohorts of age-0 bluefish during each year, which is consistent with observations in other Middle Atlantic Bight estuaries (Nyman and Conover 1988;

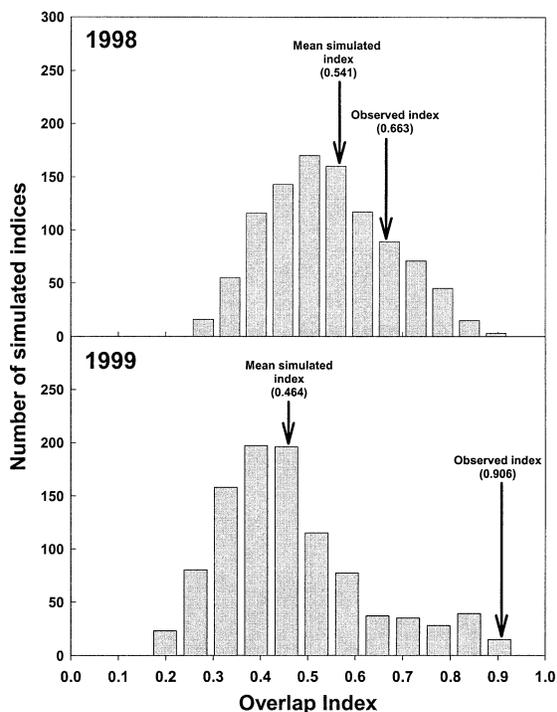


Fig. 7. The distribution of 1,000 simulated niche overlap index values between bluefish and Atlantic menhaden during 1998 and 1999. The mean of the simulated overlap index values and the actual observed overlap index are indicated. Detailed results of the analysis are presented in the text.

McBride and Conover 1991). The apparent difference of 2–3 wk in the initial appearance of age-0 bluefish observed between 1998 and 1999 also corresponds with previous studies that documented interannual variation in estuarine arrival of juvenile bluefish (Nyman and Conover 1988; McBride and Conover 1991; Hare and Cowen 1996). Variability in arrival timing of bluefish has been hypothesized to result from physical transport processes coupled with the rate of warming of continental shelf waters (Hare and Cowen 1996). Continental shelf waters in spring (April–June) were warmer in 1999 compared to 1998 (Fig. 8), which may be partly responsible for the differences in bluefish arrival times we observed. The similarities in recruitment timing for bluefish and Atlantic menhaden across years observed in this study supports the notion that larger scale oceanographic processes affecting development and transport of pelagic larvae, and thus estuarine arrival times of fishes spawned in continental shelf waters, may have similar effects on multiple species.

Interannual differences in bluefish arrival timing may have contributed to variation in bluefish diets in the estuary, particularly during late spring and early summer. Diets of older bluefish con-

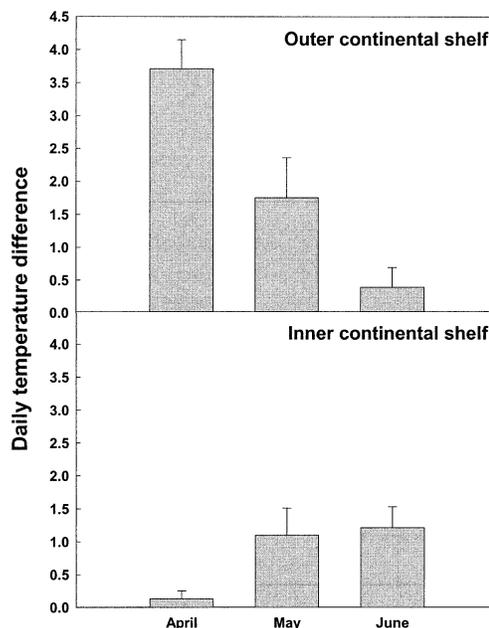


Fig. 8. Average daily seawater temperature difference on the outer continental shelf and the inner continental shelf between spring 1999 and spring 1998. Each bar represents the daily temperature difference (1999 minus 1998) averaged for April, May, and June ($n =$ approximately 30 for each month). Data provided from the National Oceanic and Atmospheric Administration National Data Buoy Center. Outer continental shelf data are from station 44004 located 200 nautical miles east of Cape May, New Jersey ($38^{\circ}50'N$, $70^{\circ}47'W$). Inner continental shelf data are from station 44025 located 33 nautical miles south of Islip, New York ($40^{\circ}25'N$, $73^{\circ}17'W$).

tained considerably more invertebrates during May–July 1998 compared with 1999. Friedland et al. (1988) also noted considerable interannual variation in the diets of bluefish collected from a small cove in Sandy Hook Bay. They found that juvenile bluefish consumed large quantities of invertebrates (mostly sand and grass shrimp) in some years and concluded that availability of fish prey in the estuary may have been an important factor determining bluefish diets (Friedland et al. 1988). In addition to bluefish and Atlantic menhaden, other forage fish species (e.g., Atlantic silversides) may have experienced a delay in estuarine arrival time during 1998. The delayed appearance of appropriately sized prey fish may have caused bluefish to depend more heavily on available invertebrates during spring and early summer. This phenomenon may also explain the unusually large biomass of blue crabs in the diet of age-1+ bluefish during 1998. Larger bluefish may not be able to sustain adequate growth while feeding on small sand and grass shrimp and may have substituted an alternative high energy prey (blue crab) until fish prey became available. Previous studies demonstrate

that bluefish achieve significantly higher growth rates on a fish diet compared with an invertebrate diet (Juanes and Conover 1994; Buckel et al. 1998). The effects of prey type on piscivore growth imply that interannual variation in the estuarine arrival timing of bluefish and their primary forage fishes may have important implications for bluefish growth and survival (Buckel et al. 1998).

We captured bluefish regularly in waters less than 2 m depth from late spring through early fall of both study years. Bluefish have also been observed to occupy primarily shallow water habitats in other Mid-Atlantic estuaries, including the lower Hudson River, New York (Buckel and Conover 1997), and Little Egg Harbor in southern New Jersey (Rountree and Able 1997). In the lower Hudson River, bluefish were shown to be responsible for a large fraction of estimated prey mortality (Buckel et al. 1999), indicating that abundant bluefish populations may have considerable impacts on shallow water prey fish communities in other mid-Atlantic estuaries. Our findings also provide additional evidence on the general use of shallow water habitats by a variety of piscivorous fishes (Rooker et al. 1998; Manderson et al. 2000; Scharf and Schlicht 2000). Given the potential of large numbers of piscivorous fishes to affect prey populations, future studies will be required to reexamine the role of shallow water habitat as a predation refuge (Sheaves 2001).

The distribution of bluefish within the Sandy Hook Bay-Navesink River estuary was remarkably consistent across sampling periods within each year and across years. Our exploratory models suggested that of the variables we measured flow dynamics (based on variation in sediment grain size) had the largest influence on the distribution of bluefish within the estuary. Bluefish catches were consistently high at two stations in the Navesink River characterized by fine grain sediments, indicative of depositional environments with low current velocity. The high depositional rate of suspended matter associated with these stations implies that zones of turbidity maxima are likely to occur within this region of the estuary. During September 2000, hydrographic sampling was conducted in the Navesink River to generate turbidity profiles. Turbidity, salinity, and temperature were sampled using moored and shipboard LISST (Laser In Situ Sediment Scatterometer and Transmissometer), conductivity-temperature-depth (CTD), and OBS (Optical BackScatter). Both the OBS and the LISST provide proxies for total suspended sediment (TSS) concentration. Shipboard surveys were conducted along the main channel of the river and included stations that coincided with gillnet sampling locations in 1998 and 1999. Sampling was

conducted every 1–2 h over the course of several tidal cycles and produced quasi-synoptic sections that captured intratidal variations in the salinity and TSS fields. TSS fields were typically higher during the flood than on ebb, as expected in this flood-dominated system (Chant and Stoner 2001). During times of maximum TSS concentration there tended to be two regions of enhanced TSS, one in the upper river and a second in the lower river. We suggest that the high turbidity levels observed in the upper river were associated with high concentrations of fine particles related to freshwater discharge and the reworking of this material by the tide, whereas the periodic occurrence of high turbidity in the lower river was related to a transitional region of the estuary where sediment size changes rather abruptly to finer particles that are resuspended during the higher velocity flood currents (Chant and Stoner 2001).

Zones of turbidity maxima in other estuarine systems have been found to contain high abundances of zooplankton that are thought to result from high concentrations of food (detritus and phytoplankton) and circulation driven retention mechanisms (Kimmerer et al. 1998; Roman et al. 2001). The abundant supply of zooplankton and a potential refuge from visual predators provided by estuarine turbidity maxima are believed to support enhanced production of larval and juvenile fishes (Dodson et al. 1989; North and Houde 2001). In the Sandy Hook Bay-Navesink River estuary, the association of bluefish with maximum turbidity zones may be explained partly by the occurrence in these regions of their primary prey, Atlantic menhaden. The relative abundance of Atlantic menhaden was a significant factor affecting the numbers of bluefish captured at a given location in the estuary, and was pronounced during 1999 when patterns of spatial overlap were highly significant. Atlantic menhaden are filter feeders with juveniles grazing primarily on phytoplankton (Friedland et al. 1984), but also on zooplankton and detritus (Jeffries 1975). The distribution patterns of menhaden have been shown to be positively correlated with phytoplankton abundance and regions of turbidity maxima in other Mid-Atlantic estuaries (Friedland et al. 1989, 1996). Independent otter trawl surveys completed in the Sandy Hook Bay-Navesink River estuary during July 1998 and 1999 indicate that the distribution of other bluefish prey species, bay anchovy (*Anchoa mitchilli*), and Atlantic silverside, also coincided with estuarine zones of turbidity maxima in the upper and middle regions of the river (Meise unpublished data). Multiple forage species may respond similarly to zones of high productivity within estuarine systems, resulting in large aggregations of potential prey that appear to contribute

to the relatively consistent estuarine distribution patterns for bluefish observed across seasons and years.

Estuarine and coastal systems throughout the Middle Atlantic Bight contain abundant populations of juvenile bluefish (Hartman and Brandt 1995; Juanes and Conover 1995; McBride et al. 1995; Buckel et al. 1999), which contributes to the notion that entire estuaries or coastal bays are critical to growth and survival during early life. We found bluefish distributions within the estuary to be centered in specific areas throughout the study period, supporting recent claims that only certain habitats within estuarine systems may function as nurseries (Beck et al. 2001). Low net flow depositional areas (i.e., turbidity maximum zones) may serve to aggregate prey fishes and promote growth and survival of juvenile piscivores, such as bluefish, that use these areas. In the presence of such effects, we speculate that a disproportionate number of successful recruits may be associated with these areas relative to alternative estuarine habitats. Estuarine regions of enhanced turbidity will be difficult to designate for conservation purposes because their location may shift seasonally and annually, reflecting the effects of physical and biological processes. In this case, routine monitoring of estuarine physical properties will be required for proper identification of productive fish habitats. Bluefish foraging success may be linked to the occurrence and duration of habitats with high concentrations of suspended materials and points to the need for future research on the role of these habitats in year-class production.

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