



ARTICLE

Premigration Patterns of Growth, Condition, and Resource Use by the Spring-Spawned and Summer-Spawned Cohorts of Juvenile Bluefish in the Hudson River Estuary, New York

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Abstract

In fish populations with multiple age-classes of similar size and close proximity, interactions between age-classes may be an important source of density-dependent population structuring if there is a disparity in competitive ability, creating a competitive bottleneck. However, intercohort competitive interactions within a single year-class have rarely been investigated and may have implications for recruitment success. Bluefish *Pomatomus saltatrix* produce at least two cohorts (spring- and summer-spawned) of offspring each year, and juveniles of this species are abundant in the lower Hudson River estuary, New York, during summer and early autumn. Our objectives were to evaluate the potential for a competitive bottleneck between these spring and summer cohorts by assessing the cohort-specific growth, condition, and patterns of resource use prior to the autumn migration in 2008 and 2009. The size advantage gained by the spring cohort resulting from earlier hatching dates was maintained throughout both summers. However, the summer juveniles achieved higher lipid content by the end of each summer. When the two cohorts inhabited the estuary at the same time, they exhibited high diet overlap and low spatial overlap. Although Bay Anchovy *Anchoa mitchilli* predominated the prey base, the two Bluefish cohorts exhibited cohort-specific size-selective feeding, such that the spring cohort preyed upon larger Bay Anchovy than the summer cohort, probably corresponding to different Bay Anchovy year-classes. In this large estuary, the two juvenile Bluefish cohorts exhibited unique strategies with respect to growth and condition, which widened the competitive bottleneck by separating their niches spatially and by foraging on different age-classes of Bay Anchovy.

For temperate migratory fishes, achieving a minimum size and energy storage level during the summer may be required to survive the autumn migration and subsequent overwinter period. The summer is often brief in temperate regions and can be resource-limited, creating the potential for competitive interactions between individuals (Huss et al. 2008). Within a population, fish may face periods of intraspecific competition for shared resources, particularly if the resources are limited.

For example, age-0 juveniles migrating into a nursery habitat may compete for food and space with other members of the same cohort and/or individuals of older year-classes (Caddy 2007). For species with multiple age-classes of similar size and close proximity, interactions between age-classes may be an important source of density-dependent population structuring, especially if there is a disparity in competitive ability between the cohorts (Webster 2004). Competition within

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size-structured populations can play an important role in recruitment dynamics (Persson and Leonardsson 1998; Classen et al. 2000).

According to the juvenile competitive bottleneck theory (Werner and Hall 1979), young fish of one species that exhibit a higher foraging efficiency than individuals of a competing species may force the competitors into an earlier ontogenetic niche shift than if the competitive interaction were not present. This competition can be revealed in a cost to growth and energy accumulation to the less efficient species, while potentially increasing the risk of predation to one or both species. Bottlenecking has been evident between two competing native species (Cardona et al. 2008), among groups of native and nonnative species (Walsworth et al. 2013), and across age-classes within a single species (Machias and Labropoulou 2002). The degree to which bottlenecking influences the vital functions of the competing species is associated with age-specific growth rate, year-class structure, and recruitment timing (Scharf et al. 2006). The juvenile bottleneck theory could apply within a year-class of a single species if two or more cohorts are produced. However, intercohort competitive interactions within a single year-class have rarely been investigated and may have implications for recruitment success.

One species that produces multiple cohorts of offspring each year is the Bluefish *Pomatomus saltatrix*. Bluefish reproduce along the eastern coast of the USA during annual spawning migrations. Although the exact temporal and spatial patterns of Bluefish spawning remain uncertain, at least two cohorts (spring and summer) of offspring are produced as a result of spawning over the continental shelf (Hare and Cowen 1996; Wuenschel et al. 2012). The spring-spawned (March–May) cohort results from Bluefish reproduction in the South Atlantic Bight (SAB) from Cape Hatteras, North Carolina, to Cape Canaveral, Florida, and the summer-spawned (June–August) cohort originates from spawning along the mid-Atlantic Bight (MAB) from Cape Hatteras to Cape Cod, Massachusetts (McBride and Conover 1991). Bluefish eggs and larvae develop offshore, and juveniles subsequently recruit to nearshore and estuarine waters of the MAB (Nyman and Conover 1988). Upon entry into MAB estuaries, juvenile Bluefish of both cohorts occupy more constricted habitat than in the open ocean and are primarily piscivorous (Juanes and Conover 1994), creating the potential for intercohort competition for space and food.

The Hudson River estuary in southeastern New York is composed of a seasonal assemblage of marine, freshwater, and estuarine fishes, including Bluefish (Beebe and Savidge 1988). Juvenile Bluefish typically recruit to the lower Hudson River estuary in pulses. The spring-spawned cohort first appears in late June, while the summer-spawned cohort arrives by early August; both cohorts are abundant in the estuary throughout summer and early autumn (Juanes et al. 1994). Juvenile Bluefish emigration from the lower Hudson River estuary may be linked to water temperature and generally occurs from early to mid-October (Juanes et al. 1993).

Increasing water temperature in the lower Hudson River estuary has been implicated in the recent decline of several fish species (Seaby and Henderson 2008), some of which are known prey of juvenile Bluefish. The relative abundance of juvenile Blueback Herring *Alosa aestivalis*, Alewife *Alosa pseudoharengus*, Atlantic Tomcod *Microgadus tomcod*, and White Perch *Morone americana* in the Hudson River have declined by over 50% since 1990 (Heimbuch 2008), and Schultz et al. (2006) reported a 10-fold decline in the abundance of Bay Anchovy since the late 1980s. Bay Anchovy is an important forage fish for both cohorts of juvenile Bluefish and represents the primary prey base for the summer cohort (Juanes et al. 1993; Scharf et al. 2002).

Simulation modeling of prey abundance and the time of Bluefish entry into the estuary indicate that even modest fluctuations in prey densities could generate considerable variation in prey consumption and the growth realized by the summer cohort, but the spring cohort was less affected by prey-specific abundance and timing (Scharf et al. 2006). The Hudson River estuary represents an excellent system to evaluate the potential for a juvenile competitive bottleneck between the spring and summer cohorts of juvenile Bluefish because it provides for a unique opportunity to examine intercohort interactions prior to the fall migration. For juvenile Bluefish occupying the lower Hudson River estuary during the summer and early autumn of 2008 and 2009, our objectives were to evaluate the potential for a juvenile competitive bottleneck by comparing the energy content and growth and determining the degree of food and habitat overlap or partitioning between the spring and summer cohorts.

METHODS

Field sampling and fish processing.—Field sampling was conducted as part of the New York State Department of Environmental Conservation (NYSDEC) juvenile fish survey biweekly from late July to early November 2008 and 2009 at 25 fixed stations over a 65-km section of the lower Hudson River estuary (Figure 1). Bluefish were collected with a beach seine (61 m × 3 m) with 13-mm stretched mesh wings and 6-mm stretched mesh center bag. Seine hauls were set from a boat and parallel to shore. Catches were processed on shore, and juvenile Bluefish and representative forage fishes were preserved frozen for subsequent laboratory analysis. Water temperatures of the lower Hudson River estuary were obtained from the Hudson River Environmental Conditions Observing System (HRECOS), an environmental monitoring network of high-frequency (15-min) hydrographic recording stations geographically distributed along the estuary. The George Washington Bridge hydrographic station was selected because it was located closest to the field sampling sites (Figure 1).

In the laboratory, individual juvenile Bluefish collected during field sampling were measured (mm; FL) and weighed (0.1 g wet weight). Cohort assignments were determined by

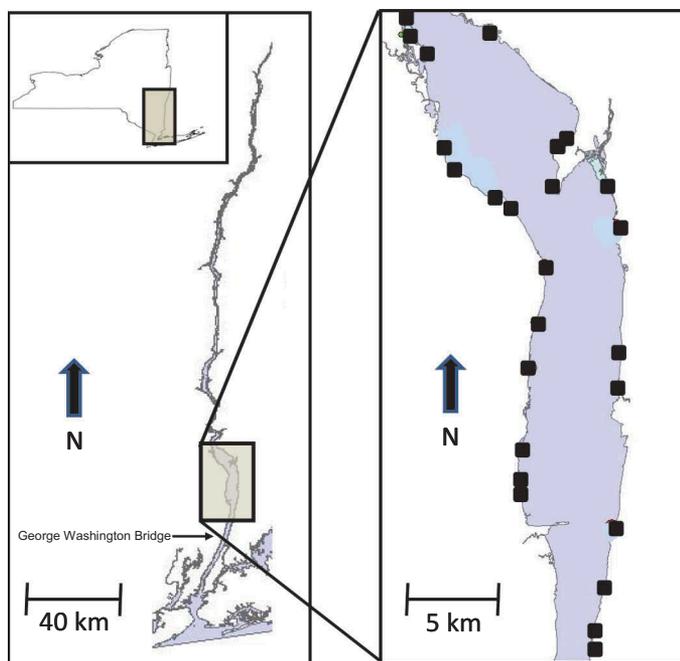


FIGURE 1. Map of the study area in the lower Hudson River estuary, New York, showing the fixed stations (solid black squares) sampled by the New York State Department of Environmental Conservation.

enumerating daily growth increments on sagittal otoliths from a randomly selected subsample of 87 juvenile Bluefish collected during each biweekly field sampling event in the summer and early autumn in 2008 and 2009. The deposition of daily growth increments on otoliths has been validated for juvenile Bluefish (Roemer and Oliveira 2007). Whole otoliths were extracted and fixed to glass microscope slides with Crystalbond glass adhesive (SPI Supplies), ground by hand on silicon carbide sandpaper (600–1,200 grit), and polished with alumina micropolish until the daily growth increments were visible under transmitted light at magnifications of 40–100 \times . All microscopy and image analyses were performed with Olympus instruments (Olympus Canada Inc., Richmond, Ontario)

The diet contents of juvenile Bluefish were examined by extracting and weighing (0.01 g) the stomachs and removing all of the stomach contents. The inner walls of each stomach were scraped with a scalpel to remove any remaining contents and reweighed, and prey items were enumerated, identified to the lowest possible taxon, and blotted dry. Whole prey fishes were measured to total length (0.1 mm) and weighed (0.001 g). For juvenile Bluefish stomachs that contained partial, but identifiable remains of fish prey, otoliths were extracted from the remains and measured (0.001 mm) with a dissecting stereomicroscope connected to a digital camera. The representative forage fishes that were collected along with juvenile Bluefish during each biweekly sampling period were measured

(0.10 mm; TL), and 50 otoliths per species were extracted and measured (0.001 mm) to reconstruct whole fish total lengths (mm) from the partial prey found in juvenile Bluefish stomachs (similar to Harvey et al. 2000).

The energy content of juvenile Bluefish was determined by extracting the total neutral lipid content. White muscle was selected for energy content analysis because this tissue is an appropriate proxy for overall lipid storage in juvenile Bluefish (Slater et al. 2007). Approximately 2–4 g of white muscle tissue was removed from individual juvenile Bluefish representing each cohort and time of residency. Tissue samples were weighed (0.001 g), dried at 60 $^{\circ}$ C for at least 72 h to remove the water content, and reweighed to determine dry weight and percent water weight per sample. The dry tissue was transferred to preweighed porous Alundum (fused alumina) thimbles for lipid extraction. An automated Soxhlet extractor with di-ethyl ether was used to dissolve neutral lipids following a method similar to Shahidi (2001). After extraction, the thimbles were dried again at 60 $^{\circ}$ C for 24 h to ensure evaporation of any remaining solvent prior to final weighing. Weights of postextracted dry tissue and preextracted dry tissue were used to determine lipid content.

Statistical analysis.—Differences in the monthly water temperatures of the lower Hudson River estuary between years were assessed with a Kruskal–Wallis one-way analysis of variance on ranks. January and February 2008 water temperature data were not available from HRECOS and were excluded from the analysis. March-to-June water temperature data were included in the analysis to test for differences in the water temperature of the lower Hudson River estuary between years prior to the arrival of juvenile Bluefish.

Hatch dates were calculated for the subsample of juvenile Bluefish by subtracting the number of otolith increments (age in days) from the date on which juvenile Bluefish were collected in the field. Juvenile Bluefish with hatch dates prior to June 21 (the summer solstice) were assigned to the spring-spawned cohort and fish with hatch-dates after June 21 were assigned to the summer-spawned cohort. Hatch dates were estimated for all remaining juvenile Bluefish not selected for dissection via age–length keys, and cohort was used in subsequent analyses. The cohort-specific catch per effort (CPE) of juvenile Bluefish and Bay Anchovy, the primary prey species, was calculated by dividing the number of Bluefish from each cohort and Bay Anchovy collected by the number of seining events during each biweekly sampling period.

The metrics computed for the stomach contents analysis of juvenile Bluefish included (1) frequency of occurrence (the number of stomachs in which a prey type occurred, expressed as a frequency of the total number of stomachs in which prey were present), (2) percent prey composition by wet weight (the total weight of a prey taxon, expressed as the percentage of the total stomach content weight), and (3) percent prey composition by number (the number of individuals of a prey taxon, expressed as a percentage of the total number of prey).

For juvenile Bluefish with stomachs that contained food, a gastrosomatic ratio (GSR) was calculated as the proportion of the stomach content weight to Bluefish body weight: $GSR = (FSW - ESW)/EW$,

where FSW = the wet weight of the stomach and its contents, ESW = empty stomach weight, and EW = eviscerated Bluefish weight. Two-way ANOVA was used to investigate the effects of cohort and sampling date and their interaction on the GSR and number of prey per stomach within each year. If a significant interaction was detected, a Bonferroni correction ($P = 0.05/n$) was applied to account for the pairwise type I error rate, where n was equal to the number of comparisons. The percentage of empty Bluefish stomachs was compared between cohorts and among sampling periods using chi-square goodness-of-fit tests. To examine the relationships between predator size and prey size for the spring and summer cohorts, partial prey lengths were converted to whole prey lengths via least-squares linear regressions between otolith length (OL) and total length ($TL = \alpha + \beta \times OL$) of the representative forage fishes collected from the lower Hudson River estuary. Converted prey sizes (TL) were compared between the juvenile Bluefish cohorts and between years with a two-way ANOVA. The relationship between Bluefish size (FL) and prey size was examined for the spring and summer cohorts with least-squares linear regression.

The size (FL) of juvenile Bluefish was compared between the spring and summer cohorts during each cohabitated biweekly sampling period with one-way ANOVA. The cohort-specific growth rate (mm/d) was determined by least-squares linear regressions of mean size over time and compared between the two cohorts via ANCOVA, with the biweekly sampling date as the covariate and cohort (spring or summer) as the explanatory variable. Fork lengths were log-transformed to homogenize the variances.

The water content in the white muscle of juvenile Bluefish was similar between years and cohorts; thus, the lipid levels were expressed as a proportion of the sample dry weight of white muscle. Within each year, lipid content was compared between the spring and summer cohorts and among time periods with two-way ANOVA. The Fisher's least-significant-difference (LSD) test was used to evaluate pairwise differences in lipid content. The lipid content values of all samples were arcsine-square-root-transformed prior to analysis due to nonnormality and heterogeneous variances.

The level of competitive interaction in feeding and habitat between the spring and summer cohorts was assessed using cohort-specific diet content and spatial distribution feeding. Habitat overlap between the spring and summer cohorts was determined using Schoener's index (Schoener 1970):

$$\alpha = 1 - 0.5 \left[\sum_{i=1}^n |p_{ij} - p_{ik}| \right],$$

where p_{ij} = the proportion of i th resource (prey type or sampling station) used by cohort j , and p_{ik} = the proportion of the i th resource used by cohort k . The Schoener's index value ranges from 0 to 1. Values that exceeded 0.6 were considered to represent ecologically significant overlap in resource use. Diet and habitat overlap were restricted to dates when the spring and summer cohorts had both recruited into the Hudson River estuary.

RESULTS

Water Temperature

Overall, the March–October water temperature of the lower Hudson River estuary was warmer in 2008 than in 2009 ($H_{15} = 4,339.7$; $P < 0.001$). Four (April, June, July, and October) of the eight months prior to and during juvenile Bluefish residency in the lower Hudson River estuary were warmer in 2008 than in 2009, while none of the 2009 monthly mean water temperatures were significantly higher than in the preceding year (Figure 2).

Cohort Structure and Abundance

A total of 788 juvenile Bluefish were collected from the Hudson River estuary during the summer and early autumn in 2008 ($n = 310$) and 2009 ($n = 478$). Hatch date–length relationships of subsamples of juvenile Bluefish representing each biweekly sampling period in 2008 ($n = 47$; $r^2 = 0.93$; $P < 0.001$) and 2009 ($n = 40$; $r^2 = 0.97$; $P < 0.001$) were used to construct total cohort-specific hatch date distributions for the remaining Bluefish collected in each year. In both years, back-calculated hatch date distributions were bimodal, indicating

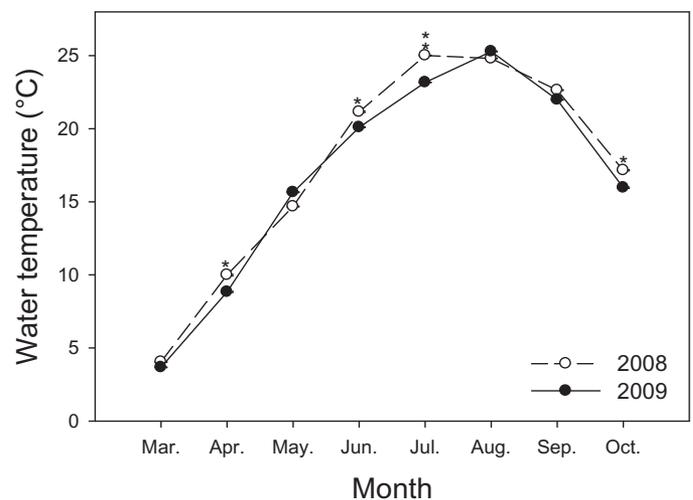


FIGURE 2. Water temperature profiles of the lower Hudson River estuary from March through October 2008 and 2009 recorded by the Hudson River Environmental Conditions Observing System's George Washington Bridge hydrographic station. Differences in mean monthly water temperatures are represented by single ($P < 0.01$) or double asterisks ($P < 0.001$).

the occurrence of spring and summer cohorts of juvenile Bluefish. Peak hatch dates for the spring and summer cohorts occurred in mid-April and late June, respectively, in 2008 and averaged 2 weeks later for each cohort in 2009 (Figure 3).

In 2008, the combined CPE of both juvenile Bluefish cohorts was more than three times higher in July than in August, September, and October, and the overall cohort-specific catch rates of spring Bluefish ($CPE_{total} = 1.72$ fish/seine) were higher than those for the summer cohort ($CPE_{total} = 0.81$ fish/seine). Only spring fish were collected during the first sampling event in mid-July 2008, and catches of this cohort declined throughout the remainder of the summer in 2008, while summer juveniles arrived in the lower Hudson River estuary in late July 2008 and were collected from the estuary until early October (Figure 4).

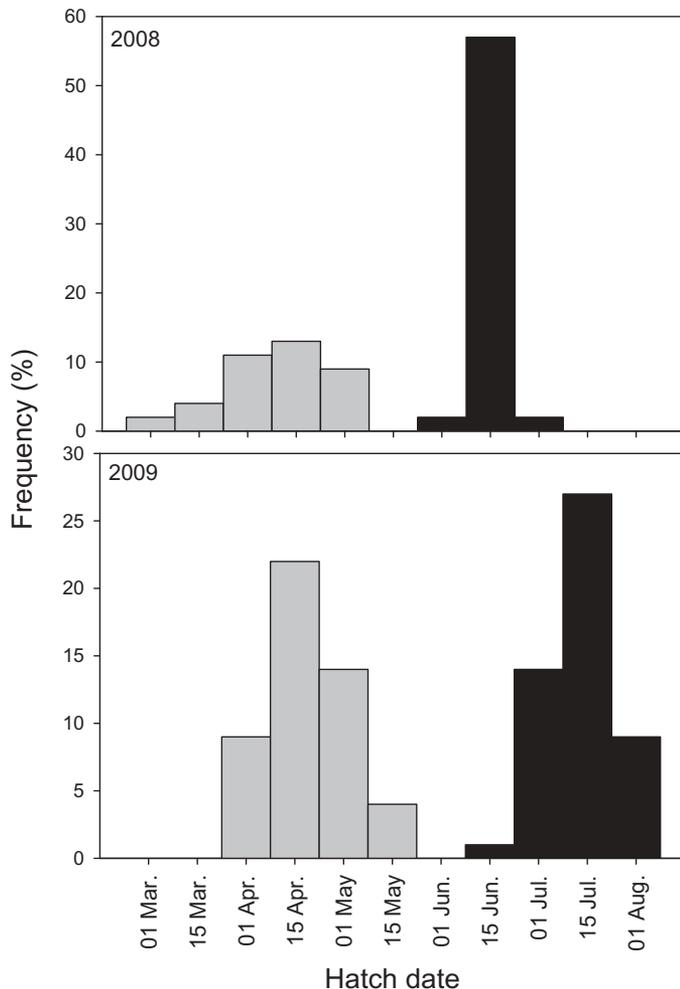


FIGURE 3. Hatch-date distributions of juvenile Bluefish collected from the lower Hudson River estuary in 2008 ($n = 47$) and 2009 ($n = 40$). Gray bars represent the spring-spawned cohort and black bars represent the summer-spawned cohort. Bar widths span 15 d and the given dates represent the midpoints for the 15-d periods.

In 2009 the greatest catch rates of juvenile Bluefish occurred more than 1 month later than in 2008, and the overall cohort structure was predominated by summer Bluefish ($CPE_{total} = 2.62$ fish/seine). Bluefish CPE was predominated by summer fish until the end of the study period. Catch rates of both cohorts combined were nine times greater in October 2009 ($CPE = 0.71$ fish/seine) than in October 2008 ($CPE = 0.08$ fish/seine), and Bluefish were still being collected through the middle of October in both years (Figure 4).

Feeding Habits and Prey Phenology

Bay Anchovy was the most abundant prey species of juvenile Bluefish in 2008 and 2009, contributing to over 70% of the stomach contents across all diet indices (Table 1). The second most abundant prey was Striped Bass *Morone saxatilis*, occurring in only 5.5% of Bluefish stomachs. No other prey fish species contributed more than 5% to the diets in any of the diet indices.

During the summer of 2008, the GSR decreased in the spring cohort and increased in the summer cohort, while the GSR decreased over time in both cohorts in 2009 (Table 2). Juvenile Bluefish of both cohorts had 1.0–1.5 prey in their stomachs, and the number of prey items per stomach was similar between the two cohorts in both years ($F_{2, 315} = 1.23$, $P = 0.31$). The percentage of empty stomachs was higher in the summer cohort (40.0%) than the spring cohort (26.8%) in 2008, while in 2009 more spring fish (52.0%) had empty stomachs than did summer fish (35.3%).

Bay Anchovy was the single important (>70.0%; no other prey > 6%) prey fish found in the stomachs of juvenile Bluefish. Consequently, the linear regression between OL and TL used for reconstructing whole prey size was calculated only for this species: $TL = 32.1 + (7.9 \times OL)$, where $n = 57$, $r^2 = 0.97$, $P < 0.001$. In 2008 and 2009 combined, the spring cohort consumed Bay Anchovy approximately two times larger (mean TL = 66.3 mm, $n = 197$) than those consumed by the summer cohort (mean TL = 32.9 mm, $n = 110$; $t = 21.2$, $P < 0.001$; Figure 5). Across both years a positive predator–prey size relationship ($r^2 = 0.22$, $P < 0.01$) was observed between the summer cohort and Bay Anchovy, while no relationship in size was evident between the spring cohort and Bay Anchovy prey (Figure 6).

Similar to the interannual difference in the abundance of juvenile Bluefish in the lower Hudson River estuary, the overall CPE of Bay Anchovy was 16 times greater in 2009 than in 2008, and two peaks in the catches of Bay Anchovy were evident in both years, occurring approximately 2 weeks earlier in 2009 than in 2008 (Figure 7).

Size and Growth

In 2008, juvenile Bluefish sizes ranged from 43 to 192 mm FL (mean = 125 mm). The spring cohorts were larger than summer fish during all biweekly sampling periods ($F_{7, 198} = 33.8$, $P < 0.001$; Figure 8), but growth was greater in the

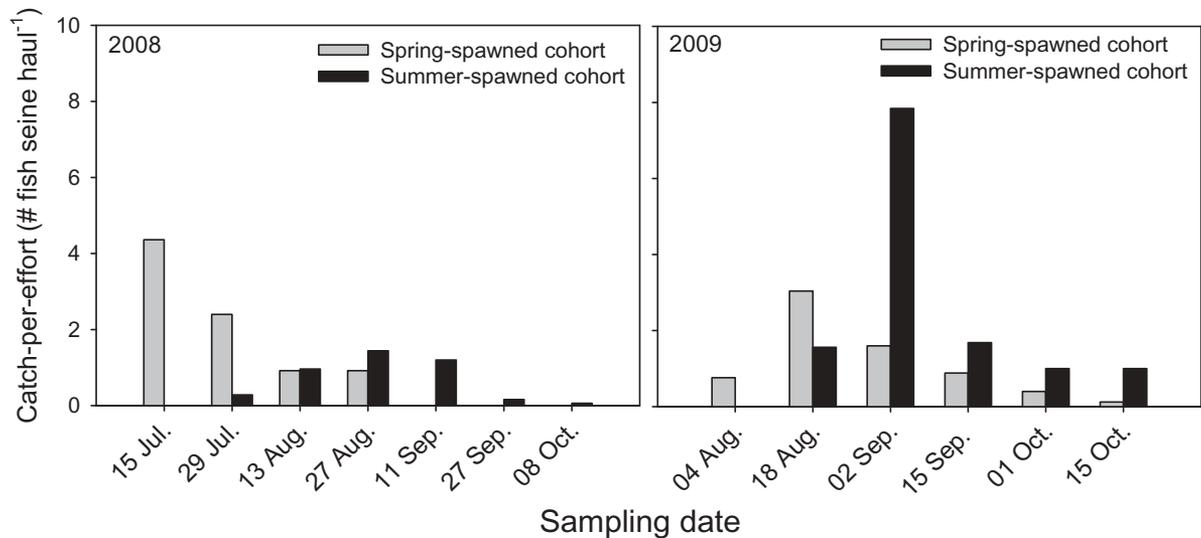


FIGURE 4. Catch per effort of juvenile Bluefish collected during biweekly sampling of the lower Hudson River estuary in 2008 and 2009.

TABLE 1. Diet composition of spring- and summer-spawned juvenile Bluefish collected from the lower Hudson River estuary in 2008 ($n = 204$ and 106, respectively) and 2009 ($n = 161$ and 317). Abbreviations are as follows: % N = the number of individuals of a prey taxon, expressed as a percentage of the total number of prey, % W = the total weight of a prey taxon, expressed as the percentage of the total Bluefish stomach content weight, and % FOO = the number of Bluefish stomachs in which a prey type occurred, expressed as a percentage of the total number of Bluefish stomachs in which prey were present.

Prey item	% N	% W	% FOO
Vertebrates			
Engraulidae			
Bay Anchovy <i>Anchoa mitchilli</i>	75.35	71.36	72.25
Striped Anchovy <i>Anchoa hepsetus</i>	0.40	2.05	0.52
Clupeidae			
American Shad <i>Alosa sapidissima</i>	0.40	0.10	0.52
Alewife <i>Alosa pseudoharengus</i>	0.59	0.78	0.79
Blueback Herring <i>Alosa aestivalis</i>	0.59	0.31	0.78
Atlantic Menhaden <i>Brevoortia tyrannus</i>	0.60	0.52	0.79
Unidentified Clupeidae	1.39	3.28	1.83
Moronidae			
Striped Bass <i>Morone saxatilis</i>	4.18	6.5	5.5
White Perch <i>Morone americana</i>	0.20	0.3	0.26
Pomatomidae			
Bluefish <i>Pomatomus saltatrix</i>	1.19	2.37	1.57
Gadidae			
Atlantic Tomcod <i>Microgadus tomcod</i>	0.99	2.09	1.31
Atherinidae			
Atlantic Silverside <i>Menidia menidia</i>	3.78	4.77	4.42
Fundulidae			
Banded Killifish <i>Fundulus diaphanus</i>	2.54	4.1	3.43
Unidentified fish	4.20	1.34	29.44
Invertebrates			
Amphipoda	3.00	0.12	5.24
Copepoda	0.38	0.01	0.52
Decapoda	0.20	0.01	0.26
Total	100	100	

TABLE 2. Feeding intensity of spring and summer juvenile Bluefish collected during biweekly sampling of the lower Hudson River estuary in 2008 and 2009. Significant differences in the gastroscopic ratio, number of prey per stomach, and percent empty stomachs among dates (columns) and between cohorts (rows) are represented by different lowercase and uppercase letters, respectively.

Date	Gastroscopic ratio		Number of prey per stomach		Empty stomachs (%)	
	Spring	Summer	Spring	Summer	Spring	Summer
2008						
Jul 15	2.49 z		1.22 z		21.2 y	
Jul 29	1.72 yZ	1.74 yZ	1.20 zZ	1.00 yZ	23.3 yY	100.0 zZ
Aug 13	1.23 xZ	1.99 yY	1.17 zY	1.46 zZ	26.5 yY	58.2 yZ
Aug 27	1.20 xZ	2.17 zY	1.16 zY	1.50 zZ	56.5 zZ	58.4 yZ
Sep 11		2.32 z		1.48 z		22.3 x
Average	1.66 Y	2.05 Z	1.20 Z	1.36 Z	26.8 Y	40.0 Z
2009						
Aug 4	3.57 z		1.25 yy		52.6 zy	
Aug 18	2.06 yZ	4.91 zY	1.20 zyZ	1.20 zZ	42.4 yZ	31.8 zZ
Sep 2	1.10 xZ	1.88 yY	1.00 yZ	1.25 zZ	60.0 zZ	37.8 zY
Sep 15	0.75 xZ	1.06 xZ	1.12 yZ	1.24 zZ	63.6 zZ	31.0 zY
Oct 1	1.41 yZ	2.15 yZ	1.50 zZ	1.20 zY	60.0 zZ	33.3 zY
Oct 15		2.65 y		1.47 z		32.0 z
Average	2.00 Z	2.10 Z	1.17 Z	1.30 Z	52.0 Z	35.3 Y

summer cohort (1.59 mm/d) than the spring cohort (1.0 mm/d) during estuarine occupancy. In 2009, Bluefish were modestly smaller (mean FL = 104 mm) than in 2008 and ranged from 46 to 210 mm FL. Similar to 2008, spring fish were larger than the summer cohort throughout the entire 2009 sample year ($F_{10, 476} = 155.9$, $P < 0.001$), but the growth rate of spring fish (1.25 mm/d) was greater than that of summer fish (0.89 mm/d).

Although sampling did not occur on the same date during each year of the study, within-cohort size differences were evident between years but only within the summer cohort. Summer fish arrived in the lower Hudson River estuary 3 weeks earlier in 2008 than in 2009 and were predictably smaller but grew fast in 2008 and were similar in size (mean FL = 117 mm) between years at the time of estuarine emigration. Spring fish were similar in size between years during all of the closest corresponding biweekly sampling periods.

Energy Content

The two-way ANOVAs showed that the lipid content of the juvenile Bluefish was influenced by both cohort and sampling date during both years of the study (Table 3). Overall, the percent lipid content of white muscle was higher in the summer cohort than the spring cohort across both years of the study ($t = 2.14$, $P = 0.03$). The significant interaction between cohort and sampling date in 2008 was driven by the higher lipid content during the sampling periods when only the spring

(July 15) or summer (September 11) cohort inhabited the estuary (Figure 9).

In 2008, lipid levels were similar between the cohorts upon the arrival of summer fish in the lower Hudson River estuary, but opposite trends were observed between the two cohorts throughout the remainder of the summer (Figure 9). A similarly inverse trend in the percent lipid content in dried white muscle of the two cohorts was observed during the summer of 2009. However, the lipid content of both cohorts declined in early autumn (October 1, 2009), particularly in the summer cohort, decreasing to the lowest percentage of white muscle by the last sampling date in mid-October (Figure 9).

Feeding and Habitat Overlap

In 2008, the spring and summer cohorts of juvenile Bluefish cohabited the lower Hudson River estuary from July 29 to August 27, but the evaluation of diet and habitat overlap was limited to the two sampling dates in August due to the low catch rates of the summer cohort on July 29. Diet overlap between the two cohorts was high (Shoener's $\alpha > 0.70$) during August, while spatial examination of the cohort-specific distribution showed low habitat overlap (Table 4). In 2009, both cohorts of juvenile Bluefish did not fully recruit to the estuary until mid-August, but a similar trend in the diet overlap was observed as in 2008. Although diet overlap between the two cohorts declined from August to early October 2009 due to the appearance of striped bass, Atlantic Silversides and Banded Killifish in the diets of spring-spawned Bluefish, the continued dominance of Bay Anchovy prey for both cohorts

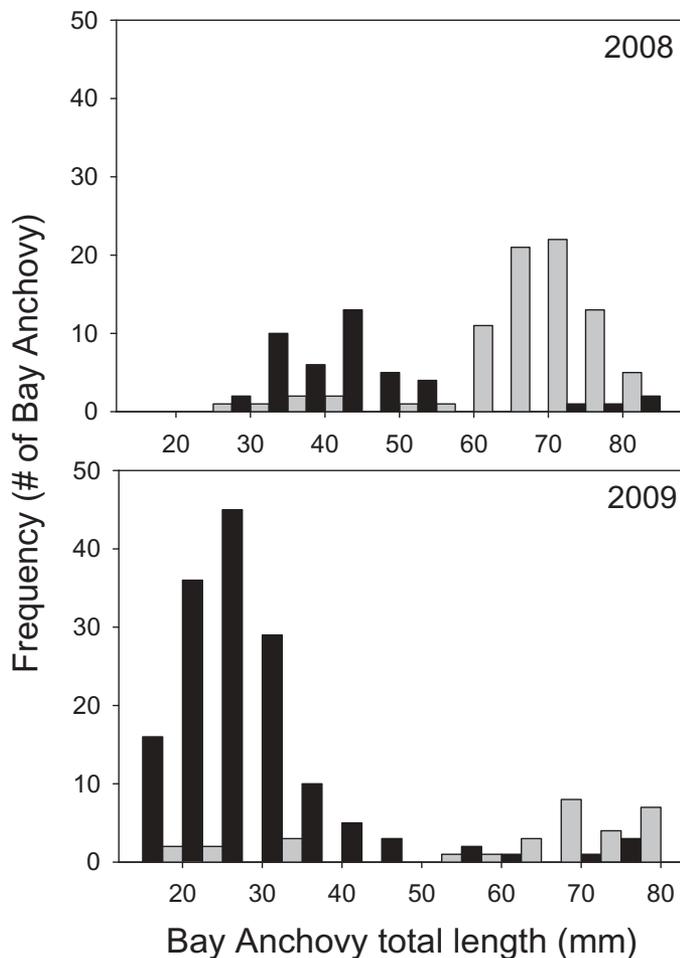


FIGURE 5. Size frequency distributions by the number of Bay Anchovy found in the stomachs of summer (black bars) and spring (gray bars) juvenile Bluefish collected from the lower Hudson River estuary in 2008 and 2009.

resulted in high overlap during early autumn. Similar to 2008, spatial overlap between the spring and summer cohorts of juvenile Bluefish was consistently low in 2009 (Shoener's $\alpha < 0.40$).

DISCUSSION

Juvenile Bluefish Cohort Structure

For fishes that reproduce within a discrete period and produce a single cohort of offspring, juvenile recruitment potential can be determined by stochastic environmental events, thus increasing interannual recruitment variability (Munch and Conover 2000). However, producing multiple cohorts of young across numerous spawning events dampens recruitment variability by spreading the mortality risk out over time and space (Secor 2007), and a single catastrophic environmental event is less likely to overwhelm an entire year-class. In the present study, peaks in the hatch-date distributions

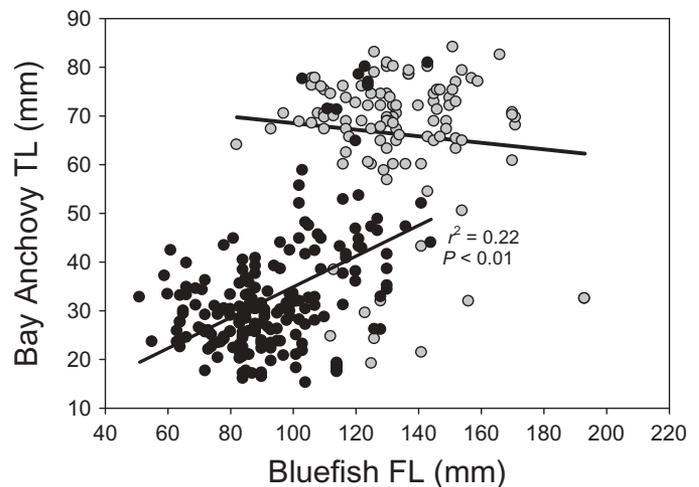


FIGURE 6. Predator-to-prey size relationships between juvenile summer (black circles) and spring (gray circles) Bluefish and Bay Anchovy collected from the lower Hudson River estuary in 2008 and 2009 combined.

of mid-April and late June to early July indicated that the juvenile Bluefish inhabiting the lower Hudson River estuary were produced from two primary spawning events in the spring and summer, respectively. The timing of these two spawning periods was consistent with previous investigations of Bluefish recruitment in other Atlantic Coast estuaries (Nyman and Conover 1988; McBride and Conover 1991; Taylor et al. 2007; Callihan et al. 2008) and may contribute to higher juvenile survival rates for Bluefish.

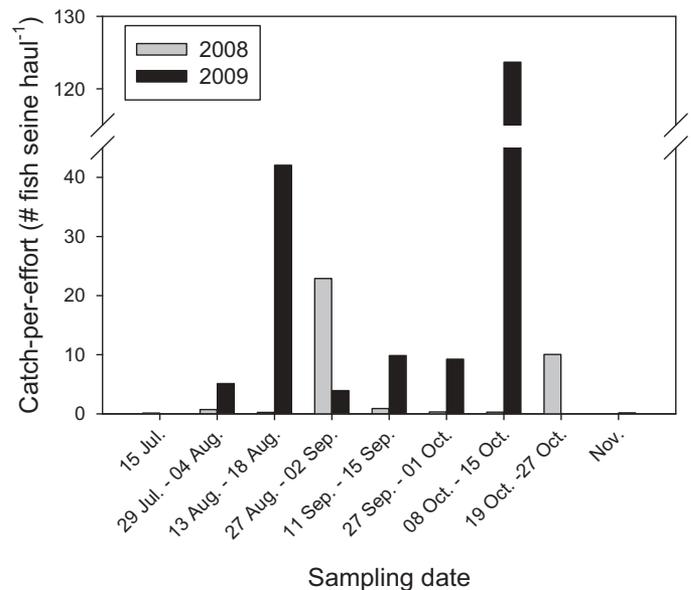


FIGURE 7. Catch per effort of Bay Anchovy collected during biweekly sampling of the lower Hudson River estuary. Each date range corresponds to the sampling dates of closest proximity between the 2008 and 2009 study years.

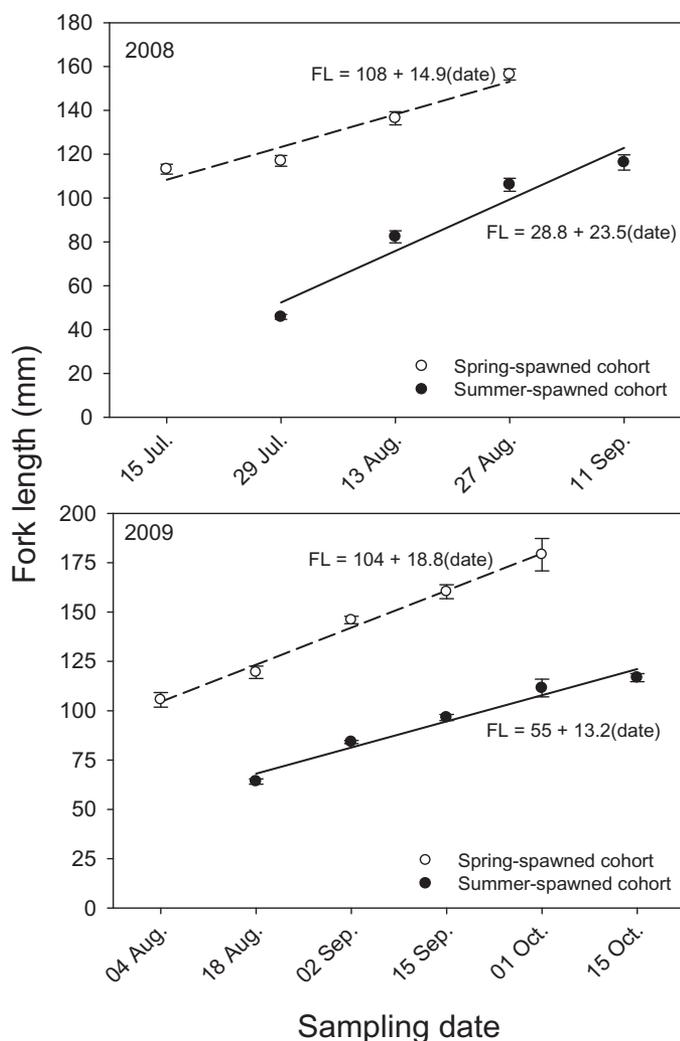


FIGURE 8. Least-squares linear regressions between sampling date and mean fork lengths of the spring and summer cohorts of juvenile Bluefish collected from the lower Hudson River estuary during the biweekly sampling dates in 2008 and 2009. Error bars represent standard errors.

We found that the cohort structure of juvenile Bluefish in the lower Hudson River estuary was dominated by spring-spawned fish in 2008 and summer-spawned fish in 2009. The contribution of the two cohorts to the western Atlantic adult Bluefish population has also varied over a multidecadal scale. During the 1950s, the relative abundance of the spring and summer cohorts was nearly equal (Lassiter 1962). From the mid-1970s through the 1980s spring Bluefish predominated the cohort structure in the MAB (Munch and Conover 2000). An apparent shift in Bluefish reproduction favored the summer cohort throughout much of the last 2 decades, but summer fish did not contribute proportionally to the adult population, and the low recruitment of this cohort has been implicated in the recent decline of the western Atlantic Bluefish stock (Conover et al. 2003). Consequently, incorporating the contribution of spring and summer Bluefish to juvenile abundance indices on an annual basis could contribute to better recruitment forecasts and, ultimately, improvements in Bluefish management (Wuenschel et al. 2012; Morley et al. 2013).

The peak hatch dates of the spring and summer cohorts of juvenile Bluefish occurred later in 2009 than in 2008, corresponding to similar delays in the arrival of the summer cohort in the lower Hudson River estuary and the later dates of maximum CPE for both cohorts. In the USA, Bluefish spawn in SAB and MAB waters as ocean temperatures surpass 18°C (Norcross et al. 1974). Larvae and juveniles are found in water temperatures between 18°C and 26°C (Kendall and Walford 1979) and do not tolerate water temperatures less than 13°C (Hare and Cowen 1996). Although the water temperatures in the lower Hudson River estuary corroborated the temperature preferences of juvenile Bluefish and were higher than 15°C through October in both years, temperatures during the period when the two cohorts occupied the estuary did not provide conclusive evidence for the differential cohort-specific phenology between the 2 years of the study. However, the average regional water temperature in the 4 months prior to the arrival of juvenile Bluefish was warmer in 2008 than 2009,

TABLE 3. Summary of the two-way ANOVA ($\alpha = 0.05$) on the effects of cohort and sampling date on the lipid content (percent dried white muscle) of juvenile Bluefish collected from the lower Hudson River estuary during the summer and early autumn of 2008 and 2009. Abbreviations are as follows: SS = sum of squares, MS = mean square; * $P \leq 0.05$; ** $P \leq 0.01$.

Year	Factor	df	SS	MS	F-value	P
2008	Cohort	1	8.49	8.49	6.00	0.017*
	Date	4	31.85	7.96	5.64	0.000**
	Cohort \times date	4	10.48	3.49	2.65	0.050*
	Error	40	55.03	1.31		
2009	Cohort	1	30.94	30.94	11.81	0.001**
	Date	5	62.38	12.48	3.84	0.004**
	Cohort \times date	5	16.67	4.17	1.59	0.189
	Error	54	146.75	2.62		

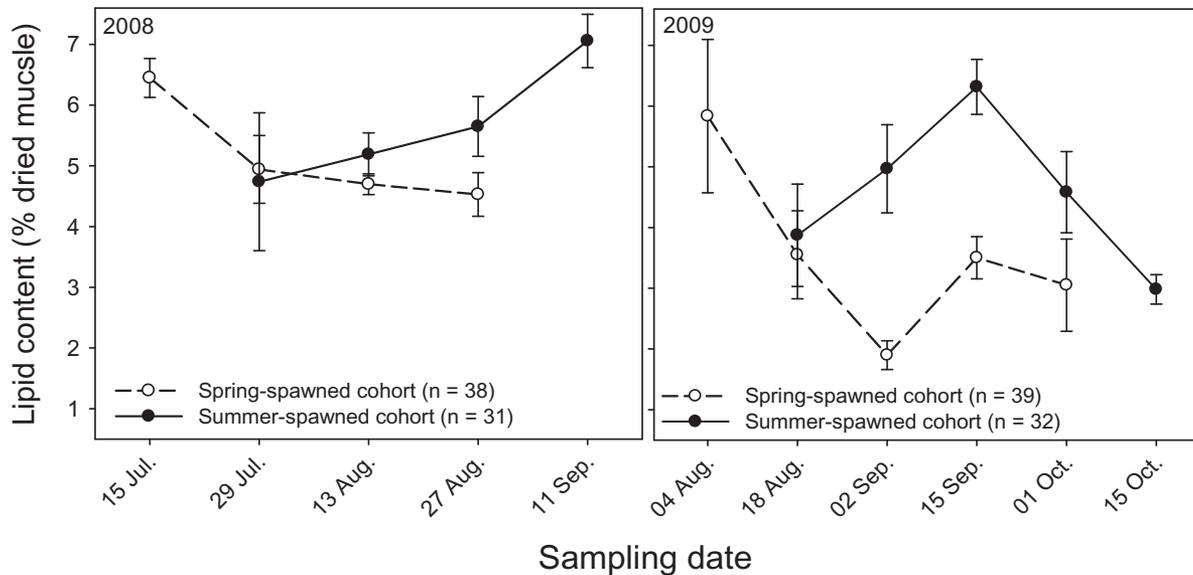


FIGURE 9. Lipid content of spring and summer juvenile Bluefish collected biweekly from the lower Hudson River estuary during the summer and early autumn of 2008 and 2009. Error bars represent standard errors.

particularly during the 2 months that corresponded to the peak hatch dates of the two cohorts, indicating a link between spring and early summer water temperatures and the timing of juvenile Bluefish entry into the estuary. Hence, monitoring the water temperature in regions to which juvenile Bluefish typically recruit after hatching, but in advance of their arrival, could be used as a tool to better understand Bluefish phenology in other regions.

Juvenile Bluefish typically emigrate from MAB estuaries en route to southern or offshore overwintering habitats as water temperatures fall below 15°C (Juanes et al. 1996) and are absent from MAB estuaries by mid-October (Able et al. 2003; Wuenschel et al. 2012). The water temperature of the lower

Hudson River estuary began to decline during September of both our study years, but remained above 15°C through October. Moreover, the average summer and early autumn water temperatures remained more than 1.0°C higher in 2008 than 2009. Accordingly, we expected longer residence times of both cohorts during 2008 than the cooler 2009, but the opposite timing of residency was observed. One possible explanation may be the temporal dynamics in the abundance of Bay Anchovy, the most important prey for juvenile Bluefish in both years. Taylor et al. (2007) showed a positive relationship between prey abundance and juvenile Bluefish CPE along the New Jersey coast but did not examine this relationship for each Bluefish cohort. In our study, Bay Anchovy CPE was low during all but two of the sampling events in 2008, the first peak occurring during the latest date that spring-spawned Bluefish inhabited the estuary and the second happening after both cohorts had already emigrated from the region. Conversely, Bay Anchovy were more abundant through mid-October of 2009, and the initial peak in CPE occurred 1–2 weeks prior to the greatest abundance of the spring and summer cohorts of juvenile Bluefish, respectively, corresponding to the longer residence time of both cohorts. Juanes et al. (1994) found that the arrival and peak CPE of Atlantic Silversides in the lower Hudson River estuary occurred just prior to the peak abundance of juvenile Bluefish over a 4-year period, suggesting that the timing of Bluefish ingress into juvenile nursery habitats is driven by the phenology of their prey. Our results indicate that the timing and duration of prey production in the estuary probably influences the timing of juvenile Bluefish egress as well, especially when water temperatures remain within the preferred range for this species.

TABLE 4. Schoener's overlap index (α) for diet (species) and habitat (station) between the spring and summer cohorts of juvenile Bluefish collected from the lower Hudson River estuary in 2008 and 2009. Alpha values greater than 0.6 were considered ecologically significant and are indicated by asterisks.

Sampling date	Diet type	Habitat
2008		
Aug 12	0.87*	0.30
Aug 27	0.93*	0.24
2009		
Aug 18	0.85*	0.24
Sep 02	0.79*	0.38
Sep 15	0.70*	0.30
Oct 01	0.57	0.40
Average	0.79*	0.27

Feeding Habits

The feeding behavior of juvenile Bluefish has been described in MAB waters (Buckel et al. 1999b; Able et al. 2003; Gartland et al. 2006), including the Hudson River estuary (Juanes et al. 1993, 1994; Buckel et al. 1999a). The selection for Bay Anchovy by juvenile Bluefish has been well documented (Buckel and Conover 1997; Woodland and Secor 2011), but our approach extended the regional diet description of Bluefish by examining the intercohort interaction in feeding ecology and the temporal trends in the feeding intensity of the two cohorts. The within-year decline and between-year difference in the GSR of spring fish reflected the interannual variability in Bay Anchovy abundance, while the opposite trend in the GSR of summer fish, particularly in 2008, indicated an interaction between the cohorts that was not explained by Bay Anchovy abundance alone. Juanes et al. (1993) used a size-based approach to summarize the cohort-specific diet content of juvenile Bluefish and showed an ontogenetic shift in prey species, from Bay Anchovy in small Bluefish to moronids and Atlantic Tomcod in medium to large-sized Bluefish. Although Striped Bass were found in 5.5% of Bluefish stomachs, we did not observe such a shift in prey type with increasing Bluefish size. The positive relationship between predator size and prey size has been well established for fishes (Juanes et al. 2002), including juvenile Bluefish (Juanes et al. 1994; Buckel et al. 1999b). Scharf et al. (2002) showed that juvenile Bluefish success in capturing Bay Anchovy declined with increasing Bay Anchovy size but remained relatively high up to anchovy sizes that were 50% of Bluefish sizes. Interestingly, we found that summer-spawned Bluefish consumed larger Bay Anchovy with increasing size, but spring-spawned fish preyed upon a relatively narrow range of Bay Anchovy sizes with a prey-to-predator size ratio of 50%. Although Scharf et al. (2002) did not separate juvenile Bluefish into spring and summer cohorts, their fish sampling was conducted in June, and hence, all of the Bluefish were probably spring individuals. The nonsignificant relationship we observed in size between spring Bluefish and Bay Anchovy represents a unique feeding strategy for this cohort.

The multimodal size distribution of prey consumed by the spring and summer cohorts indicated that the two cohorts selectively fed on different age-groups of Bay Anchovy. Larval and juvenile (age-0) Bay Anchovy in the lower Hudson River estuary are typically less than 55 mm TL (Hartman et al. 2004). Bassista and Hartman (2005) segregated the subadult and adult age composition of Bay Anchovy based on total lengths as age-1 fish < 65 mm, age-2 = 61–94 mm, age-3 = 79–92 mm, and age-4 > 93 mm, with age-2 and older fish constituting the spawning population. Our results showed that summer-spawned juvenile Bluefish preyed predominantly upon juvenile (age-0) and subadult (age-1) Bay Anchovy in 2008 and on smaller larval and juvenile Bay Anchovy in 2009, while the spring cohort consumed mostly

adult (ages 2 and 3) Bay Anchovy in both years. These findings have important implications for the recruitment dynamics of juvenile Bluefish and the population dynamics of Bay Anchovy, particularly if Bay Anchovy abundance is declining at a rate similar to that observed by Schultz et al. (2006). The impact of juvenile Bluefish on the population structure of Bay Anchovy will probably differ annually depending on the Bluefish cohort structure, while the bioenergetics of juvenile Bluefish will be influenced by the timing and magnitude of Bay Anchovy production.

Growth and Energetics

Fish mortality during periods of cold stress has been related to size, smaller individuals suffering higher mortality rates than their larger conspecifics (Sogard 1997; Hurst 2007). Consequently, summer-spawned juvenile Bluefish may be expected to grow faster than spring-spawned individuals in order to compensate for the size advantage resulting from the earlier hatching of spring fish (Juanes and Conover 1995). Faster growth rates of the summer cohort have been reported in other areas of the MAB, but spring fish were still larger than summer fish at the onset of the autumn migration (McBride and Conover 1991; Taylor et al. 2007). Similarly, we found that spring fish maintained the size advantage over the summer fish by the time of emigration from the estuary in both years, irrespective of the cohort-specific growth rate. The contribution of the summer cohort to the adult Bluefish population has been the topic of some debate and may be the result of size-selective overwinter mortality of small summer fish (Conover et al. 2003; Morley et al. 2013). If summer Bluefish are not contributing proportionally to the adult population, it may be attributable to the inability of this cohort to compensate in growth (i.e., compared with spring fish) by the time of the autumn migration.

The variable growth rates of spring and summer fish between years may have been associated with the densities of the two cohorts within each year. Scharf et al. (2006) demonstrated that the growth rates of early-arriving summer fish would be greater than those of late-arriving fish from the same cohort in years when the initial density of spring fish was low. We found that summer fish arrived earlier in 2008 than 2009, experiencing relatively high spring-spawned cohort densities, but grew faster in 2008 than in 2009 when arriving later and experiencing relatively low spring Bluefish densities. Further, the growth rate of summer fish was not affected by the presence of the spring fish during either year of the study. Moreover, the slowest growth rate of the summer fish occurred in 2009 at the highest density of summer fish, indicating that the summer Bluefish growth rates may have been less dependent on the density of spring fish than on the relative abundance of individuals from their own cohort.

To our knowledge, our study represents the first examination of the lipid content in juvenile Bluefish from summer through early autumn in preparation for the southerly

migration. Migratory fishes inhabiting temperate waters typically accumulate energy stores in the summer, especially during periods of maximum feeding opportunities and optimal water temperature (Rikardsen et al. 2006; Chicharo et al. 2012). In the present study, the water temperature of the lower Hudson River estuary increased through August and was in the optimal range for juvenile Bluefish (Hartman and Brandt 1995) during the entire summer in both years. Thus, we expected the lipid levels in both cohorts to increase during this time in preparation for the autumn migration. We found this to be the case for the summer cohort in both years but not for spring-cohort in either year. Spring fish arrive in northern MAB estuaries from mid to late June (Nyman and Conover 1988; McBride and Conover 1991), so we probably missed the first collection of this cohort by at least one biweekly sampling period. Consequently, it was not possible to determine the energetics of the spring cohort upon arrival in the estuary, such as we were able to discern for summer fish. Nevertheless, the inverse trends in the percent lipid content of white muscle between the two cohorts over time warrants further consideration.

Within a species, the lipid levels of juvenile fish can be influenced by ambient temperature (Merayo 1996; Luzia et al. 2003), prey quality and quantity (Kiessling et al. 1989; Daly et al. 2010), somatic size (Copeman et al. 2008; Heermann et al. 2009), and physiological factors (Griffiths and Kirkwood 1995). Although the spatial overlap between spring and summer fish was low, the two cohorts probably experienced equivalent water temperatures while co-habiting the lower Hudson River estuary. Therefore, temperature could be effectively ruled out as a cause of the differential energetics between the two cohorts. In both years of the study, the summer cohort did not recruit to the estuary until at least 2 weeks after spring cohort; thus, it is possible that an earlier dietary shift by the spring cohort from low-energy invertebrate prey to a more lipid-rich fish diet (Buckel and Conover 1997; Buckel et al. 1998, 1999a) resulted in a higher initial energy content of spring fish, while the summer cohort arrived under a midsummer lipid deficit. A novel discovery of our study was the similarity in prey types between spring and summer fish while the two cohorts co-occurred in the estuary, in that both cohorts consumed Bay Anchovy almost exclusively. Although we did not report the whole-body lipid content of Bay Anchovy, it was determined as part of an associated project, and no relationship was evident between Bay Anchovy size and lipid levels. As a result, prey quality was also unlikely to be responsible for the different lipid-content dynamics of the two cohorts. In 2008, the GSR of the spring cohort decreased and the percentage of empty stomachs increased during the summer, while the opposite trends were observed in the summer cohort. The relationships between lipid content and feeding intensity were not as direct during the summer of 2009 as in 2008, but the general trends were maintained, suggesting that prey quantity was associated with the differential trends in

the percentage of lipid content of white muscle between the two cohorts.

With respect to size, the higher percentage lipid in the white muscle of the smaller summer fish conflicts with previous observations of the relationship between somatic size and energy content, wherein larger fish typically contain greater energy stores than smaller fish within the same year-class (Schultz and Conover 1997; Hurst and Conover 2003), including Bluefish (Juanes et al. 2013; Deshpande et al. 2016). Although we recognize that the spring cohort was larger than summer cohort throughout the summer and early autumn, and thus probably had more total white muscle lipid content, we were investigating how the percentage of lipid in white muscle differed between the two cohorts over time. The concept of smaller fish within a year-class having lower lipid content is thought to be due a higher mass-specific metabolic rate (Post and Lee 1996), particularly during winter. Morley et al. (2007) collected larger juvenile Bluefish with greater energy reserves from North Carolina waters in autumn, but the larger fish lost this energetic advantage during the winter due to faster energy depletion with increasing somatic size. Moreover, Slater et al. (2007) experimentally showed that the larger spring fish began the winter with greater proportional lipid content than summer fish, but that the two cohorts contained similar energy reserves by early spring. We found that the greatest difference in percentage lipid content between the summer and spring cohorts occurred at the end of the summer. This finding indicates that the dynamics of lipid accumulation may not be as size dependent as previously assumed, and perhaps there is a cohort-specific physiological trade-off or constraint between growth and energy utilization in juvenile Bluefish.

For temperate fishes, smaller juveniles within a year-class have been shown to allocate resource intake to growth rather than to energy storage in order to reduce their vulnerability to predation, while larger individuals typically dedicate resources to storing energy over growth as the size-selective predation risk declines (Sogard 1997; Post and Parkinson 2001). With this in mind, we expected the smaller summer cohort to dedicate as much resource intake as possible to growth over lipid accumulation during the summer. Summer Bluefish grew faster than spring fish in 2008, but they were still considerably smaller than spring fish by the end of the summer and stored a higher proportion of lipids in white muscle tissue than their larger conspecifics during the summer in both years. Although we did not evaluate predation risk in this study, juvenile Bluefish are already piscivorous when they arrive in the lower Hudson River estuary (Scharf et al. 2004) and probably do not experience high rates of predation during the summer (Sagarese et al. 2011). With the risk of predation low, juvenile Bluefish of both cohorts may have dedicated more food resources to energy storage than growth in preparation for the autumn migration, and the contrasting trends in energy utilization between the two cohorts during the summer of 2008

and 2009 were primarily attributed to the temporal differences in feeding intensity exhibited by each cohort.

Temperate fishes have been shown to deplete energy resources during autumn and winter due to reductions in feeding and temperature (Hurst et al. 2000; Brodersen et al. 2011). We found that the spring-spawned cohort of juvenile Bluefish emigrated from the lower Hudson River estuary during the summer of 2008 when water temperatures were still above 18°C, precluding the evaluation of premigration autumn energetics. However, concomitant with water temperatures declining below 18°C during autumn, the lipid levels of both cohorts declined through October 2009 until emigrating from the estuary. Juvenile Bluefish were shown to mobilize lipid content during the late autumn and winter in North Carolina and Florida (Morley et al. 2007; Juanes et al. 2013). Interestingly, the water temperatures during October and November in North Carolina waters (Morley et al. 2007; Wuenschel et al. 2012), and over the winter along the northern Florida coast (Juanes et al. 2013) were similar to those in the lower Hudson River estuary during the summer and within the preferred range (18–26°C) of juvenile Bluefish. Although it cannot be discounted that juvenile Bluefish with high lipid content emigrated from the Hudson River estuary earlier than fish with depleted energy reserves, our results indicate that a rapid decline in lipid content during early autumn in northern MAB estuaries like the lower Hudson River estuary may trigger juvenile Bluefish to begin a southerly migration. Subsequent declines in condition during late autumn to early winter in the southern MAB promotes movement farther south to overwinter in SAB waters, and is driven by both abiotic and biological factors.

CONCLUSIONS

According to the juvenile competitive bottleneck theory, a species with higher foraging efficiency may force another species to an earlier ontogenetic niche shift during the first summer of life, resulting in a cost to growth and energy accumulation (Werner and Hall 1979). Spring- and summer-spawned juvenile Bluefish have been observed moving between nearshore and offshore habitats of the Hudson River estuary over a diel cycle (Buckel and Conover 1997), but whether the two cohorts occupy the same habitat at the same time has remained unclear. We observed a high level of habitat partitioning between the spring and summer cohorts during the summer and early autumn in 2008 and 2009. Although we cannot rule out the possibility of the larger spring-spawned cohort forcing their younger and smaller conspecifics to alternative habitats in the lower Hudson River estuary (interference competition), neither cohort of juvenile Bluefish appeared to be resource limited during either year of this study, and a cost to growth and condition was not apparent in summer fish. Juvenile Bluefish are already upper-level predators upon arrival in the estuary;

thus, cannibalism would probably be the primary source of predation. Although cannibalism can influence the size structure of fish populations (Classen et al. 2000; Persson et al. 2004), it was not evident in 2008 and only observed during the first sampling period in 2009.

For species like Bluefish that produce two or more distinct cohorts within a year-class, the feeding preferences on a single prey species may be similar among the cohorts, leading to the appearance of high intra-specific competition. However, the age-class-selective feeding on Bay Anchovy of the two juvenile Bluefish cohorts that we observed resulted in the reality of low intraspecific competition. Our results indicate that in a large estuary like the lower Hudson River, the spring and summer cohorts reduced intraspecific competition by separating their niches in the spatial dimension and their feeding on different age-classes of Bay Anchovy. This niche separation widened or eliminated the juvenile competitive bottleneck, such that summer fish did not appear to suffer any negative consequences to occupying different habitats than their older conspecifics during the first summer of life.

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