Recruitment Patterns and Habitat Use of Young-of-the-Year Bluefish along the United States East Coast: Insights from Coordinated Coastwide Sampling

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Protracted spawning and pulsed juvenile production are common in coastal spawning fishes, the phenology of which determines potential environmental effects on recruitment. This article examines bluefish (Pomatomus saltatrix), a cosmopolitan coastal spawning species that produces multiple cohorts of juveniles utilizing both estuarine and coastal habitats as nurseries along the U.S. east coast. To determine recruitment on a coastwide basis, ocean (bottom, neuston, and surfzone) and estuarine habitats were sampled in Florida and North Carolina south of Cape Hatteras in the South Atlantic Bight, and Maryland, New Jersey, and New York in the Middle Atlantic Bight. This coordinated sampling effort across multiple habitats with multiple gears on a coastwide basis allowed the resolution of the occurrence, growth, and movement of cohorts along the coast. Production of the spring-spawned cohort occurred in both South Atlantic Bight and Middle Atlantic Bight habitats, while summer-spawned cohort production was limited to the Middle Atlantic Bight. Information from the present study is synthesized with prior research to develop a conceptual model of the seasonal patterns of YOY bluefish habitat use and to emphasize the value of coordinated sampling at a large spatial scale in understanding recruitment processes in this and potentially other important marine species.

Keywords bluefish Pomatomus saltatrix, recruitment, cohort, habitat, young-of-the-year

INTRODUCTION

Most marine fishes produce large numbers of pelagic eggs that experience high mortality (Houde, 1989; Winemiller and Rose, 1993). In addition, many migratory marine fishes spawn over large geographic areas; therefore, recruitment variability in these species is influenced by complex processes acting over
multiple temporal and spatial scales during egg, larval, and juvenile stages (Houde, 2008, 2009). Environmental uncertainty promotes the evolution of complex life histories, which can include temporal and spatial spreading of reproductive output. Spawning that varies temporally or spatially (i.e., bet-hedging) potentially dampens variability in recruitment by spreading survival risk over time and space (Armstrong and Shelton, 1990; Winemiller and Rose, 1993; Fogarty et al., 2001; Secor, 2007). Multiple cohorts within a year-class are found in numerous fishes, including engraulids (Leak and Houde, 1987), clupeoids (Lambert, 1984; Gamble et al., 1985), fundulids (Kneib, 1993), atherinids (Rountree and Able, 1993), moronids (Secor and Houde, 1995; Secor et al., 1998), and pomatomids (Able and Fahay, 1998; Munch and Conover, 2000). Bet-hedging in a temporal sense is common for many of the fishes listed above through protracted spawning. Some highly mobile fishes are capable of spatial bet-hedging associated with seasonal migration in response to fluctuating environmental conditions. The east coast of the United States is characterized by extreme annual ranges in sea surface temperature (~20°C; Conover, 1992), which restricts the spawning and growing season for many fishes.

Bluefish (Pomatomus saltatrix, Pomatomidae) is a cosmopolitan species, occurring in subtropical to tropical waters of the Atlantic, Indian, and western Pacific Oceans (Nelson, 2006). Bluefish are an important recreational and commercial species throughout its near-circumglobal range, including the U.S. east coast (Klein-MacPhee, 2002; Shepherd and Packer, 2006), Brazil (Lucena et al., 2002; Silvano and Begossi, 2005); Australia (Lenanton et al. 1996; Silvano and Begossi, 2005); the Black and Mediterranean Seas (Ceyhan et al., 2007), and Africa (Potts et al., 2009). These populations occur in systems that are either strongly influenced by western boundary currents that transport warm water from the tropics toward the poles (southeast coast of the United States, eastern Australia, eastern South America, and south eastern Africa) or by variable shelf currents (middle Atlantic coast of the United States, Black and Mediterranean Seas, northwestern Africa, and western Australia) (Juanes et al., 1996). Several life history characteristics are common across many of these populations, including seasonal migrations to lower latitudes during winter, seasonal exploitation of temperate latitudes during summer, and alongshore transport of early life stages that is poleward in western boundary systems but generally toward the equator in other systems (see Juanes et al. [1996] for review). Not surprisingly, however, differences exist across populations.

Along the U.S. east coast, bluefish undergo seasonal migrations and spawn over a protracted period, producing multiple cohorts at multiple locations along the U.S. east coast (Deuel et al., 1966; Norcross et al., 1974; Kendall and Walford, 1979; Collins and Stender, 1987; Chiarella and Conover, 1990; Hare and Cowan, 1993, 1996; Shepherd et al., 2006; Robillard et al., 2008). There has been much research on this species due to its importance to recreational and commercial fisheries and as a dominant predator in estuarine and coastal systems (Hartman and Brandt, 1995; Buckel et al., 1999a,b,c). Historically, this population has exhibited wide fluctuations in abundance (Baird, 1873; Bigelow and Schroeder, 1953). More recently, bluefish abundance was high in the early 1980s, declined to a low in the mid-1990s, and began increasing thereafter (Shepherd and Nieland, 2010). For bluefish, the measurement of juvenile production requires an understanding of both spatial and temporal patterns of abundance for each cohort.

Knowledge of the life history and ecology of the U.S. east coast bluefish population is extensive (see reviews by Able and Fahay [1998, 2010], Fahay et al., [1999], and Shepherd and Packer [2006]). Bluefish spawning times and location have been inferred from egg and larval collections in ocean habitats. Generally, spawning is thought to occur in the South Atlantic Bight (SAB; Cape Hatteras, North Carolina, to Cape Canaveral, Florida) near the Gulf Stream in spring and in the Middle Atlantic Bight (MAB; Cape Cod, Massachusetts, to Cape Hatteras, North Carolina) on the continental shelf in summer (Kendall and Walford, 1979; Collins and Stender, 1987; Hare and Cowen, 1993, 1996; Smith et al., 1994; Taylor and Able, 2006). Additional limited spawning in the SAB in fall, presumably after adults return south, has been documented from collections of eggs, larvae, and small juveniles (Collins and Stender, 1987; McBride et al., 1993; Murt and Juanes, 2009); yet, egg and larval abundance in the SAB during fall are much lower than in spring and summer (Hare and Cowen, 1993). Juveniles from the main spawning events in spring and summer have been collected both in estuarine and ocean habitats in the MAB and SAB (Nyman and Conover, 1988; McBride and Conover, 1991; McBride et al., 1993; Taylor et al., 2007); spring-spawned recruits are known to occur in both MAB and SAB habitats ( McBride et al., 1993), but summer-spawned fish were not observed until October in the SAB ( McBride et al., 1993). It is thought that YOY bluefish in the MAB move south into SAB habitats to overwinter (Long Island tagging study; Lund and Maltezos, 1970). Even with the large amount of research efforts to date, understanding and interpreting many aspects of the ecology of early life stages of bluefish remain uncertain or controversial. Several of these uncertainties have implications for management and therefore warrant more comprehensive investigation.

This pattern of pulsed recruitment on the U.S. east coast is different from populations of bluefish occurring elsewhere in the world (Miskiewicz et al., 1996; Ward et al., 2003, Vasconcellos et al., 2010). Part of the cause for this difference may reside in the diverse temperatures and oceanographic conditions (SAB versus MAB) along the U.S. east coast in comparison to other populations. Thus migration, spawning, and juvenile production spans across latitudes with an extremely wide range of temperatures on an annual basis (Conover, 1992). Seasonal migration and protracted spawning of adults deliver juveniles to nurseries throughout the entire coastal range of U.S. Atlantic waters, but these migrations can also result in potential mismatches between juvenile bluefish and their prey (Juanes and Conover, 1995; Scharf et al., 2006). This synthesis examines
the pattern of juvenile bluefish recruitment on the U.S. east coast in the context of life history evolution to widely ranging thermal and oceanographic environments, which is relevant to other species in this system and elsewhere. Specifically, several remaining uncertainties in bluefish ecology on the U.S. east coast related to spawning, cohort structure and contribution to the adult population, regional patterns in YOY production, and habitat utilization patterns within regions are addressed.

Uncertainty persists whether the spawning period is continuous from February to September (with higher survival during spring and summer periods) or discontinuous with a hiatus in spawning between the spring and summer periods (McBride and Conover, 1991; Hare and Cowen, 1993; Smith et al., 1994; Callihan et al., 2008). For bluefish and other coastal spawning fishes, where continuous spawning during migrations is expected, variable survival of eggs, larvae, and young juveniles can result in discontinuous (pulsed) production of juveniles. Although this study did not address spawning of adults directly, it can, for the first time, be addressed whether there are previously undersampled habitats along the U.S. east coast (estuarine and ocean) that contain “intervening” bluefish cohorts between the spring- and summer-spawned cohorts. If spawning is continuous, is the apparent absence of intervening cohorts the result of under-sampling certain regions, or do such cohorts exist only at early life stages before succumbing to high early mortality rates? If spawning is discontinuous, does cohort structure reflect temperature-mediated migratory behavior (and subsequent spawning locations) of adults in spring and summer?

Juvenile productions in a pulsed manner can be expected to differ in their subsequent survival and spatial fates (Limburg, 2002). For bluefish on the U.S. east coast, the relative contribution (based on scale back-calculation of size at age 1) of spring- and summer-spawned cohorts to the adult population differs between a study conducted in the SAB (Lassiter, 1962; equal contribution of spring and summer) and two studies conducted in the MAB at a different time period (Chiarella and Conover, 1990; Conover et al., 2003; spring-cohort dominated). In contrast, for recent years of the longest time series of YOY monitoring data examined in the MAB, the summer cohort typically comprises a greater proportion of YOY (Munch and Conover, 2000; Conover et al., 2003; spring-cohort dominated). Does sampling over a coastwide scale (both MAB and SAB) still lead to the conclusion that the there is a greater proportion of summer-spawned cohorts? Is there evidence for distinct survival/growth differences between spring- and summer-spawned cohorts?

Recruitment apparently differs among cohorts of juveniles but also could potentially differ among latitudinal regions where bluefish spawn. The cohort-specific contributions of MAB and SAB habitats to coastwide production have not yet been evaluated. Research has historically been directed in the MAB, with a paucity of abundance estimates in comparable SAB habitats. Do inshore SAB habitats function comparably to MAB habitats? Are SAB habitats only important in winter?

Juvenile bluefish are often assumed to be estuarine dependent (McHugh, 1966, 1967; Munch, 1997), and a world-wide review also indicates that estuaries are important for this widely distributed species (Juanes et al., 1996). Still, it has become apparent that YOY bluefish use both ocean and estuarine waters that may vary by cohort (Able et al., 2003, Taylor and Able, 2006; Taylor et al., 2007). Although individual researchers and states have sampled YOY in nearshore (shallow) ocean environments, sampling has not been performed concurrently throughout the range of recruitment along the east coast of the United States to date. Are YOY bluefish abundances in nearshore (shallow) ocean habitats similar to those collected in estuarine habitats?

A fisheries independent index of recruitment is useful when modeling the population dynamics and effects of exploitation in marine fishes. However, indexing recruitment in a broadly ranging coastal species with protracted and pulsed juvenile production is a particular challenge. It is evident that production in both MAB and SAB waters may be important in indexing abundance of YOY bluefish for the U.S. east coast population. Recent assessments have included both autumn bottom trawl survey data (Northeast Fisheries Science Center; NEFSC) from the MAB that collects many age-0 bluefish, and spring bottom trawl survey data (Southeast Area Monitoring and Assessment Program; SEAMAP) in the SAB that captures largely age-1 bluefish (assuming a 1 January birth date); however, given seasonal migration patterns, the degree to which these indices capture bight-specific versus total production is uncertain. Are monitoring surveys of YOY bluefish abundance in the MAB adequate for indexing YOY bluefish coastwide production, or does YOY bluefish production in the SAB need to be indexed as well?

To address these questions, YOY bluefish were sampled coastwide (from Florida to New York on the U.S. east coast) in ocean (bottom, neuston, and surfzone) and estuarine habitats. This contribution summarizes multiple years (2005–2007) of coordinated sampling effort in multiple habitats on a coastwide basis using multiple identical gears. Additionally, previously published work is synthesized pertaining to bluefish recruitment and habitat use along the U.S. east coast to aid in interpretation of these data. The results provide insight into the complexities of recruitment processes in this, and potentially other, marine species that spawn over broad geographic areas, and they demonstrate the utility of coordinated sampling across a large spatial scale to resolve uncertainties in the interpretation of data collected regionally. It is the hope of the authors that this information will aid in developing recruitment indices that are more appropriate for bluefish stock assessments and a fuller understanding of habitat use patterns throughout the east coast.

**METHODS**

**Sampling Approach**

Standardized sampling occurred in both estuarine and the nearshore coastal ocean habitats (<30-m depth) of the MAB (New York, New Jersey, and Maryland in 2005 and 2006) and
the SAB (North Carolina south of Cape Hatteras in 2005 and 2006 and Florida in 2006 and 2007) (Figure 1); the nearshore (shallow) coastal ocean and ocean beaches represent potential habitats that had been under-represented in prior bluefish recruitment studies. Only the SAB portion of North Carolina waters was sampled in the present study; therefore, unless stated otherwise, any hereafter reference to North Carolina waters is to that portion within the SAB. The timing of surveys within each region was chosen to correspond with anticipated high abundances of YOY bluefish, and the number of tows varied due to a number of factors (size of survey area, weather conditions, and available vessel time); the months of sampling in each location for each year can be found in Table 1. Combining all surveys, sampling occurred throughout the year. To evaluate habitat use by the multiple cohorts expected for YOY bluefish, abundances across regions and habitats were sampled with three gear types (Methot trawl, beach seine, otter trawl) (Table 1). In all surveys, YOY were defined by characteristic lengths (<300-mm fork length [FL]) based on earlier studies in the region (see Able and Fahay, 1998; Munch and Conover, 2000; Able et al., 2003; Conover et al., 2003; Callihan, 2005) and further assigned to specific cohorts (see below).

Ocean Bottom

YOY bluefish were collected from inner continental shelf habitats (<30 m) with a 20-min duration otter trawl (30-m head rope, 6-mm codend) tows during the day. For New York, New

Figure 1  Map of U.S. east coast showing study areas (insets; New York, New Jersey, Maryland, North Carolina, Florida) in the coastwide sampling program and buoys utilized for hydrographic data (left). The locations sampled are shown for each habitat (ocean bottom, ocean surface, ocean beach, and estuary beach) from New York (top row) to Florida (bottom row).
Table 1 Summary of monthly sampling effort (number of seine hauls, estuary and ocean beach; number of tows, ocean bottom, and ocean surface) in each habitat within each state

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The months listed are January 2005 through December 2006 for New York, New Jersey, Maryland, and North Carolina; January 2006 through December 2007 for Florida.

Jersey, and Maryland, the same vessel (R/V Seawolf, 24.4 m) and identical sampling gear was utilized. In North Carolina and Florida, trawls of the same size and manufacture were used, and set times (20 min) and tows speeds (3 knots) matched those aboard the R/V Seawolf. Sampling occurred aboard the F/V Capt. David (22.9 m) in North Carolina, and the F/V Kevin and Chad (16 m) was used in Florida. Otter trawl sampling in New Jersey occurred in cooperation with the New Jersey Department of Environmental Protection (NJDEP) and the Rutgers University Marine Field Station (RUMFS) in depth-stratified (0–10, 10–20, 20–30 m) random sampling over an area of 4,600 km² from the entrance to New York Harbor to the entrance of Delaware Bay (Byrne, 1994). The same depth-stratified random approach was used to survey New York state waters (Dunton et al., 2010). In Maryland, each survey consisted of randomly selected stations arrayed across two depth strata (5–9 m, 10–18 m). The 48-km-long survey grid was located between the Ocean City inlet and Maryland–Virginia border off Assateague Island. Due to hard bottom habitats in North Carolina and Florida, fixed transects over known towable bottom types were used. In North Carolina, two depth strata (5–9, 10–18 m) were sampled (three stations per strata) along each of two transects extending 8 km from shore; one off Masonboro Inlet (77°47'W, 34°13'N) and the other off Beaufort Inlet (76°36'W, 34°39'N). In Florida, two depth strata (5–9, 10–18 m) were sampled (two stations per strata) along each of four transects spaced 24 km apart between St. Augustine 29°05'W, 81°20'N) and Daytona Beach, FL (29°05'W, 80°54'N). Within each region and month, the number of tows varied (Table 1). Surface and bottom temperature, salinity, and dissolved oxygen were determined at each station throughout the survey. The FL and, in some cases, total length (TL), were measured immediately (nearest cm).

Ocean Surface

Neustonic YOY bluefish were collected with 10-min-duration surface Methot trawl consisting of a square 5-m² mouth (Methot, 1986; Hare and Cowen, 1994; Taylor and Able, 2006), with a 13-m-long net of 3.5-mm mesh leading to a tapering canvas collar and 0.165-m-diameter codend with the same 3.5-mm mesh (Able et al., 2011). The trawl was towed at the surface (0–2 m depth), with the top of the frame approximately 0.25 m out of the water and in a large arc so as to avoid the wake of the ship. A General Oceanics flowmeter was attached to the frame along a lower corner to determine the volume of water sampled (approximately 5,000 m³ per tow). Frame trawls appear efficient at capturing small juvenile fishes based on in situ observations (Itaya et al., 2001). All samples were sorted onboard and fish placed in 95% ethanol. For large samples with abundant gelatinous zooplankton (scyphomedusa, ctenophores, and larvaceans), the remaining sample was placed in 10% formalin and sorted for additional fish in the laboratory. Fish from these samples were identified to the lowest possible taxon and measured to the nearest 0.1 mm standard length (SL) under a
dissecting microscope. Larger YOY were measured to the nearest 1.0 mm FL. Within each region, the distribution and selection of sampling sites (Figure 1) was similar to that for otter trawls (above); however, station locations did not always coincide with otter trawl stations in the same month, and the amount of tows varied (Table 1). Temperature and salinity were recorded for each tow. 

Ocean and Estuarine Beaches

To quantify the importance of estuarine and ocean beach habitats, YOY bluefish were sampled in these habitats using a bag seine (30 × 1.8 m, 6-mm mesh; Rowe et al., 2002; Able et al., 2003). Sites that were suitable for seining were sampled monthly during periods of expected bluefish occurrence (Table 1). Sites were generally sampled once per month; however, in some cases, additional tows were made on different days. Seines were carried offshore until either of the following conditions was met: a depth of 1.5 m or a distance of 50 m from shore was reached, resulting in a range of maximum depths sampled of 0.8–1.5 m. Seines were then deployed parallel to shore and hauled into the beach. Temperature and salinity were collected for each haul, and captured fishes were measured immediately (FL in mm).

Cohort Identification and Growth

Traditionally, there have been two cohorts described for bluefish: summer spawned and spring spawned (Kendall and Walford, 1979; Nyman and Conover, 1988). Based on modes and antimodes of length frequencies and daily age and growth studies of U.S. east coast bluefish, monthly length ranges were established to demarcate the spring and summer cohorts (reported as the mid-monthly values, Table 2). These length ranges were further refined by examining the aggregate length frequencies across regions. Individual bluefish across all regions sampled were classified as spring or summer spawned when their FL was greater than or equal to the minimum FL but less than the maximum FL for the month of capture. See “Methods” section for further explanation on cohort assignment and calculation of cohort specific CPUE. Within each habitat sampled, bluefish abundance was evaluated across cohorts, regions, and months. Survey- and buoy-based (National Oceanic and Atmospheric Administration [NOAA] Buoy) hydrographic data were utilized to evaluate how climate and oceanographic factors contributed to the movements and abundance of YOY bluefish cohorts within and across regions. Finally, a conceptual model of bluefish early life history over the entire U.S. east coast was developed by combining published information with new findings from this coastwide sampling effort.

Water temperature data near the five sampling locations on the U.S. east coast were obtained from the National Data Buoy Center website (www.ndbc.noaa.gov). Data from January 2005 to December 2006 were obtained from inshore and offshore locations at New York, Delaware, North Carolina, and Florida. Water temperature for New Jersey came from an inshore sampling location. Locations were as follows: New York inshore (41.048 N, 71.016 W), New York offshore (40.691 N, 72.046 W); New Jersey inshore (39.355 N, 74.418 W); Delaware inshore (38.782 N, 75.120 W), Delaware offshore (38.464 N, 74.702 W); North Carolina inshore (34.703 N, 76.670 W), North Carolina offshore (34.476 N, 77.280 W); and Florida inshore (29.857 N, 81.265 W), Florida offshore (30.041 N, 80.533 W) (Figure 1). Mean monthly water temperature was calculated from daily records.

The relative contribution of MAB and SAB habitats to production of both spring- and summer-spawned bluefish was evaluated in several ways. First, the mean CPUE (overall) of spring-spawned bluefish collected in MAB and SAB waters (ocean and estuarine beaches and ocean bottom and surface habitats) from May through July were compared. Similarly, the overall mean CPUE of summer-spawned cohort in MAB versus SAB habitats August through October were compared. These periods...
were chosen to capture patterns of abundance that would indicate regional (i.e., within bight) production before migration of each cohort while they are still susceptible to the sampling gears (spring-spawned cohort) and before the influx of migrants produced elsewhere (both cohorts).

The limited time-series of fall MAB and SAB abundances (two years) of the present study limits direct comparison of trends in overall abundance to other recruitment indices (e.g., NEFSC autumn bottom trawl survey). However, given the complex cohort structure in YOY bluefish, the goal was to compare the cohort composition (percentage spring and summer cohorts) collected in 2005 and 2006 to that from the NEFSC trawl survey (inshore strata 1–45). For this comparison, ocean bottom trawl abundances from the coastwide survey in September (prior to large-scale fall migration), which coincide with dates of the annual NEFSC survey were used. The coastwide sampling survey was not stratified with equal effort or area along the coast; therefore, cohort composition in September was calculated by first averaging monthly CPUE for spring and summer cohorts in each region sampled in September (New York, New Jersey, Maryland, and North Carolina). The monthly averages by region were then weighted by the area surveyed by each region in September (New York, 1,035 km²; New Jersey, 1,581 km²; Maryland, 150 km²). The two transects sampled in North Carolina were assumed to be representative of the area bounded by Cape Lookout to Cape Fear, from the coastline out to 8 km from shore (1,467 km²). Earlier work that included four transects in this area indicated that bluefish abundances were similar across transects (Morley, 2004). Florida did not sample in September, and was not included in the calculation of coastwide cohort composition. The estimate of cohort proportions (COASTWIDE) was then calculated as the average of cohort proportions from the weighted mean monthly CPUE data (i.e., mean of weighted regional means):

\[
\text{COASTWIDE} = \left(0.245 \cdot \frac{\overline{N_T}}{\overline{N_J}} + 0.373 \cdot \frac{\overline{N_J}}{\overline{N_T}} + 0.035 \cdot \overline{MD} + 0.347 \cdot \overline{NC}\right)
\]

Also calculated were mean catches within only MAB regions (MAB, weighted by area sampled as above) to compare directly to the NEFSC autumn bottom trawl survey that samples limited stations below Cape Hatteras in the SAB:

\[
\text{MAB} = \left(0.374 \cdot \frac{\overline{N_T}}{\overline{N_J}} + 0.571 \cdot \frac{\overline{N_J}}{\overline{N_T}} + 0.054 \cdot \overline{MD}\right).
\]

These two estimates of percent contribution from this survey provide alternate estimates of cohort proportions to compare to those estimated from the NEFSC autumn bottom trawl survey at the same time period. The same length-based criteria were used to determine cohort membership in the two datasets (Table 2, i.e., 140 and 260 mm for maximum FL of summer- and spring-spawned bluefish collected in September).

**RESULTS**

**Seasonal and Spatial Variation in Temperature**

As expected, inshore and offshore temperatures were warmer and less seasonally variable in the southermost study site in Florida relative to locations to the north (Figure 2). The coldest temperatures occurred in winter in New York and New Jersey, but these varied annually with lower temperatures in the winter of January–March 2005. These same areas varied in summer temperature with those in 2006 cooler than in 2005. North Carolina temperatures were intermediate to these extremes in the winter of 2005 but were as warm as Florida in the summer. In the SAB, water temperatures were suitable for spawning (> 18°C) throughout the year in Florida and from April–November in North Carolina. Temperatures suitable for spawning in MAB waters occurred June–October.

**Patterns of Cohort Structure and Abundance**

A total of 2,465 tows were completed in this coastwide sampling effort in estuary beach (608), ocean beach (470), ocean bottom (836), and ocean surface (551) habitats, capturing 21,001 YOY bluefish. The two dominant cohorts of YOY bluefish (spring and summer spawned) were sampled consistently at multiple locations and in multiple gear types in this sampling program (Figures 3–8). Across regions however, catch rates of bluefish were highly variable, as might be expected for
Figure 3  Composite length frequency distributions for bluefish collected in ocean and estuarine habitats in New York (2005 and 2006). The percent frequency of each 10-mm length bin is shown for each habitat (ocean bottom, ocean beach, estuary beach, and ocean surface) and the total numbers caught indicated in each panel. The mid-monthly size ranges of spring-spawned cohort (diagonal hatching) and summer-spawned (horizontal hatching) YOY are shown. Months sampled with zero catches are not plotted; ND indicates habitats not sampled that month (color figure available online).

Figure 4  Composite length frequency distributions for bluefish collected in ocean and estuarine habitats in New Jersey (2005 and 2006). The percent frequency of each 10-mm length bin is shown for each habitat (ocean bottom, ocean beach, estuary beach, and ocean surface) and the total numbers caught indicated in each panel. The mid-monthly size ranges of spring-spawned cohort (diagonal hatching) and summer-spawned (horizontal hatching) YOY are shown. Months sampled with zero catches are not plotted; ND indicates habitats not sampled that month (color figure available online).
Figure 5  Composite length frequency distributions for bluefish collected in ocean and estuarine habitats in Maryland (2005 and 2006). The percent frequency of each 10-mm length bin is shown for each habitat (ocean bottom, ocean beach, estuary beach, and ocean surface) and the total numbers caught indicated in each panel. The mid-monthly size ranges of spring-spawned cohort (diagonal hatching) and summer-spawned (horizontal hatching) YOY are shown; ND indicates habitats not sampled that month (color figure available online).

Figure 6  Composite length frequency distributions for bluefish collected in ocean and estuarine habitats in North Carolina (2005). The percent frequency of each 10-mm length bin is shown for each habitat (ocean bottom, ocean beach, estuary beach, and ocean surface) and the total numbers caught indicated in each panel. The mid-monthly size ranges of spring-spawned cohort (diagonal hatching) and summer-spawned (horizontal hatching) YOY are shown. Months sampled with zero catches are not plotted; ND indicates habitats not sampled that month (color figure available online).
schooling, highly mobile species that are patchily distributed. The catch variability and low sample sizes within region, month, and habitats made it difficult to identify cohort breakpoints at this level (not all cohorts were sampled in most cases). The more general length-based cohort designations (Table 2) based on this and prior studies allowed the evaluation of patterns of abundance for the two dominant cohorts of YOY bluefish described in what follows.

Small spring-spawned YOY bluefish (<75-mm FL) initially showed up in low numbers in North Carolina in April in ocean surface and estuarine and ocean beach habitats (Figures 6 and 7). This cohort became more abundant, peaked in abundance in June, and remained in estuarine and ocean beach habitats of North Carolina throughout the summer (Figures 9 and 10). This cohort, very likely the result of spawning in the SAB, was not present in the other (more northern) regions until June–July, where they were present at lengths generally greater than 50-mm FL. Spring-spawned bluefish occurred in ocean and estuarine beach habitats throughout the New York to North Carolina portion of the study area through the summer (Figures 3, 4, and 5). Summer abundances of the spring-spawned cohort in beach habitats were similar in the SAB (North Carolina) and the MAB (New York and New Jersey), except for Maryland where few individuals were collected. In the fall, catches of this cohort declined in the northern regions (New York and New Jersey), but they showed up in abundance in ocean bottom habitats at more southerly locations, notably in September in Maryland and September–November in North Carolina. This suggested a fall, southern movement of the spring cohort from New York and New Jersey coastal waters to Maryland and North Carolina waters. The continued fall southern dispersal from the MAB is supported by the strong representation of this cohort in North Carolina ocean bottom samples in November and December.

Summer-spawned YOY bluefish first occurred in low numbers in the northern regions (New York, New Jersey, and Maryland) in July, peaked in abundance August to September before declining in October, and were a major component of YOY bluefish abundance in those regions. There was a progression of peak in ocean bottom abundances southward from New York in August to New Jersey and Maryland in September (Figures 3, 4, and 5), suggesting a fall, southern dispersal within the northern MAB. The summer-spawned cohort was not collected in North Carolina until November, after they presumably moved south from MAB waters along with additional spring-spawned individuals (Figures 6 and 7). Ocean surface sampling indicated the presence of continued spawning in late summer in the MAB (fish <50-mm FL sampled during August through October); however, these occurred in low abundance with respect to the other cohorts. Based on sampling ocean surface waters with the Methot trawl, there was no evidence of summer spawning in the SAB.

Although sampling did not occur in Florida in 2005, previous work (2002–2004) sampling only estuaries has shown that multiple cohorts occur in late fall and early winter in this region.
The spring-spawned cohort was encountered first in November followed by the summer- and fall-spawned cohorts in December (Figure 8). Catches peaked in December and age-1 bluefish remained in the region through March. Although no YOY bluefish were encountered in estuarine and ocean beach habitats in the present study, Clarke (2006) collected YOY bluefish using gillnets in Florida estuaries October through January.

Overall, the coastwide abundance data indicates a northern shift in the center of abundance of the spring-spawned cohort from North Carolina (ocean surface and beaches) in May–July to Maryland waters in July (ocean bottom) to New Jersey and New York waters in August (Figures 9 and 10). This is followed by a southern migration from New York, New Jersey, and Maryland waters to North Carolina waters from September to November. After occurring in the SAB ocean bottom in fall, spring-spawned bluefish were absent in 2005 and dropped in number in 2006 from nearshore ocean bottom habitat in North Carolina. Catches of the two cohorts in the ocean bottom were also similar in relation to water depth, with most catches occurring in shallow areas less than 20 m (Figure 11). Both cohorts were less frequently collected in slightly deeper waters (20–30 m). Although the seine surveys produced highly variable catch rates, several patterns emerged across the sampling areas. In the SAB, based primarily on the extensive seine efforts in North Carolina, spring-spawned bluefish recruited to both ocean and estuarine beaches in spring (April–July), with catches diminishing in summer, possibly due to escapement from the sampling gear. There does not appear to be a difference in utilization by spring-spawned bluefish in estuarine versus ocean beaches in North Carolina in the spring based on abundance. In September of both years, the summer-spawned cohort occurred in low numbers in North Carolina, where they were slightly more common in ocean versus estuary beaches. Very few YOY bluefish were collected in either estuarine or ocean beaches in Maryland, limiting a comparison for this region; however, bluefish were collected in nearby shallow coastal waters (inner shelf) and also at a nearby ocean inlet beach (D. H. Clarke, 2006). The spring-spawned cohort was encountered first in November followed by the summer- and fall-spawned cohorts in December (Figure 8). Catches peaked in December and age-1 bluefish remained in the region through March. Although no YOY bluefish were encountered in estuarine and ocean beach habitats in the present study, Clarke (2006) collected YOY bluefish using gillnets in Florida estuaries October through January.
Secor, unpublished data). The high energy nature of the ocean surf zone and tidal changes in beach exposure can make this a difficult habitat to sample consistently. In Maryland, due to the nature (slope etc.) of the beaches sampled, ocean beach hauls were limited to 15–20 m from shore (compared to 15–50 m in other regions). Given that bluefish were rarely collected at ocean beach sets less than 20 m from shore at the other locations, it is believed that the lack of bluefish collected at Maryland ocean beaches was due to this inability to adequately sample behind the breaking waves. Further north (New Jersey and New York), spring-spawned bluefish were found in comparable numbers at both estuarine and ocean beaches in June and July. Summer-spawned bluefish occurred in August in New York and New Jersey, where they were more abundant at ocean beach sites compared to estuarine beaches, as has been reported previously in New Jersey (Able et al., 2003). Summer-spawned bluefish were collected in large numbers in the nearshore ocean bottom August through October, indicating significant use of this habitat during summer. As noted earlier, the decline in catches of spring-spawned bluefish in seines in late summer may be due to limitations of the sampling gear, potentially underestimating the utilization (and importance) of these habitats for those sizes and months. Growth rates of spring- and summer-spawned bluefish were rapid (inferred from increases in modal size) during summer but slowed or stopped during fall months.

**MAB Versus SAB Production**

The abundances (Ln(number + 1) tow⁻¹) of the spring cohort collected in spring (May through July) were similar in ocean (0.47–0.97) and estuarine beaches (0.46–0.86) across MAB and SAB sites (Figure 12). Abundances of the spring cohort in beach habitats were generally higher in 2005 as compared to 2006, except for SAB ocean beaches. The summer cohort collections in the period August through October were generally restricted to MAB waters (0.17–0.87), with the exception of lesser numbers of the summer-spawned cohort collected in SAB ocean beaches (0.01–0.22; Figure 12). The abundance of the summer cohort in these months was higher in 2006 than in 2005, except in ocean.
Figure 10  Monthly cohort-specific CPUE and sampling effort from New York (top row) to Florida (bottom row) over two years in ocean beach (left column) and estuary beach (right column) habitats. The months listed are January 2005 through December 2006 for New York (NY), New Jersey (NJ), Maryland (MD), and North Carolina (NC) and January 2006 through December 2007 for Florida (FL). CPUE was log transformed. Diagonal hatching indicates spring-spawned cohort; horizontal hatching indicates summer-spawned cohort.

The relative proportion of the spring cohort (of total YOY) in 2005 of the present study (COASTWIDE) was greater (58%) than the proportion estimated from MAB alone (36%) and the NEFSC autumn bottom trawl survey (40%). The pattern in estimates of relative proportions derived from this study were similar in both years, with the proportion of spring-spawned cohort in COASTWIDE > MAB. In 2006, the proportion of spring-spawned cohort was slightly higher in both COASTWIDE (65%) and MAB (46%) estimates from this study, and much greater as estimated by the NEFSC survey (73%). In both years, the SAB September ocean bottom trawl catches (North Carolina, Figures 6 and 7) were comprised solely of spring-spawned cohort, while large numbers of summer spawned bluefish were collected in the MAB in September. Thus, estimated cohort proportions across only the MAB collections of this study (New York, New Jersey, and Maryland) indicated greater proportions of summer-spawned bluefish.

**DISCUSSION**

**Patterns of Cohort Structure and Abundance**

The consistency of the split cohort structure of juvenile bluefish would seem surprising given the species protracted and spatially distributed spawning behavior. Bluefish have a complex life history, with differential migration among age groups, shifting from largely north–south movements at younger ages to onshore–offshore movement in older fish (Shepherd et al., 2006). One component of mature bluefish spawn in SAB waters in spring and migrate long distances to join the onshore–offshore migrating component of the stock (older age-classes) in MAB waters, where both groups spawn in summer. Juveniles recruit to various estuarine and ocean habitats in the SAB and MAB during spring–summer before undergoing their own southward migration in fall. Various mechanisms have been proposed to explain the largely bimodal (two cohort) pattern in bluefish, including oceanographic conditions (Hare and Cowen, 1993, 1996), discrete spawning stocks (Kendall and Walford, 1979), and behavioral differences (Callihan et al., 2008).
the possibility of discrete spawning stock has been tested and shown to be false (see Chiarella and Conover, 1990; Conover et al., 2003; Graves et al., 1992), rigorous tests of other potential mechanisms causing bimodal recruitment of YOY bluefish are lacking. Similar multiple cohort patterns have been described for other MAB fishes, e.g., Scophthalmus aquosus (Neuman and Able, 2003), Urophycis regia (Able and Fahay 1998; 2010), and Peprilus triacanthus (Rotunno and Cowen, 1997; Able and Fahay, 1998, 2010). However, the causes of these observed patterns, which may be the result of variable environments acting on egg and larval stages or reproductive partitioning (bet hedging) on the part of adults, are likely species specific.

Recent studies on the movement patterns (Shepherd et al., 2006) and reproductive condition (Robillard et al., 2008) of adult bluefish have provided additional insights to the occurrence of early life stages in SAB and MAB waters. In general, there is growing support for the hypothesis that bluefish spawn over a very long period, typical of batch-spawning species with asynchronous oocyte development, with a probable suspension of or reduction in spawning during the spring migration north. In this sense, the cohort structure of YOY bluefish is influenced by temperature-mediated migratory behavior of adults in spring and summer. The latitudinal differences and seasonal shifts of temperature in the study area (Figure 2) are evident and provide the mechanism for these shifts in reproduction and migration. Movement rates of adult bluefish are greatest in spring and fall (Shepherd et al., 2006) and are related to changes in day length and temperature effects (Olla et al., 1985; Stehlik, 2009). In the MAB, there is some evidence of offshore rather than southward migration of adult bluefish in fall, particularly for larger sized fish (Klein-MacPhee, 2002; Shepherd et al., 2006). The spring migration of younger adults from SAB to MAB waters bisects reproductive effort into two dominant periods and regions for this component of the stock. If the shift in migration pattern with age from across both MAB to SAB to entirely within the MAB (Shepherd et al., 2006) is strong enough, this implies older mature fish only contribute to summer spawning (in the MAB). Therefore, the abundance of the summer cohort may be related to the abundance of older age-classes and the degree to which the age structure of the population is truncated.

Bluefish have asynchronous oocyte development and are capable of producing and spawning multiple batches of eggs over a protracted spawning period (Van der Elst, 1976; Robillard et al., 2008). This type of spawning pattern is common in low-latitude pelagic fishes, e.g., Hemiramphus brasiliensis and H. balao (McBride and Thurman, 2003; McBride et al., 2003), Coryphaena hippurus (Schwenke and Buckel, 2008), Acanthocybium solandri (Maki-Jenkins and McBride, 2009), and Etrumeus teres (Plaza et al., 2007). Robillard et al. (2008) hypothesized an inverse relation between average monthly
movement rates reported in Shepherd et al. (2006) and spawning for adult bluefish. The poor condition of adult bluefish when they arrive in MAB waters in May–June (anecdotal evidence from fisherman) might limit egg production (smaller and/or less frequent batches) after the energetically costly period of spring spawning and northward migration. An analysis of length–weight relationships for bluefish collected in NEFSC bottom trawl surveys in the MAB in spring and fall indicated significantly lower condition in spring (Wigley et al., 2003). The three-fold range in estimates of batch fecundity at length reported for bluefish (Robillard et al., 2008) indicates that batch fecundity is largely dependent on factors other than length. Condition has been shown to influence batch size and/or batch frequency in other batch spawning fishes (Somarakis et al., 2004; Takasuka et al., 2005; Murua et al., 2006; Murua and Motos, 2006; Dominguez-Petit and Saborido-Rey, 2010). Reductions in batch size or frequency during the spring migration of bluefish, either due to poor condition or encountering temperatures below the spawning threshold (18°C) upon their arrival in MAB waters or both, would result in a bimodal distribution of egg production. Callihan et al. (2008) provided evidence for the latter hypothesis in the southern MAB; June hatch-dates were rare in one year when temperatures in the area (Delaware–Maryland–Virginia peninsula) were below those required for spawning, while they were common the following year when temperatures were suitable.

Historical larval abundances, however, do not show a clear bimodality, as might be expected if a hiatus or significant reduction in spawning occurs (Hare and Cowen, 1993). It should be noted, however, that the data presented in Hare and Cowen (1993) was pooled over 11 years for the MAB and 8 years for the SAB. They showed an April to May peak in SAB larval density, followed by a July peak in the MAB that was approximately twice that of the SAB densities. The ocean surface samples collected in the present study included later life stages (pelagic juveniles in the Methot trawl versus larvae in the bongo net); therefore, it is not surprising that the observed peaks in abundance overlapped their peaks and were more prolonged in the present study (Figure 9). Similar to the data summarized in Hare and Cowen (1993), this study’s catches of early-stage (pelagic juvenile) summer-spawned bluefish in the MAB were much greater than catches of similar stages of spring-spawned early life stages in the SAB (Figures 9 and 12). The different oceanographic conditions present in SAB versus MAB spawning areas (Gulf Stream versus shelf) likely affect the dispersal and/or retention of eggs and larvae and, therefore, their measured densities. Normalization to maximum catches observed in each (SAB and MAB) would result in a more distinctly bimodal distribution. Given the annual variability in timing of temperatures suitable for spawning (Figure 2), potential breaks in spawning, and the lunar periodicity observed in back-calculated hatch dates (Taylor and Able, 2006), larval summaries aggregated over

**Figure 12** Mean abundances of spring-spawned bluefish collected from May to July (2005 and 2006) in MAB and SAB estuary and ocean habitats (left) and mean abundances of summer-spawned bluefish collected August to October in MAB and SAB estuary and ocean habitats (right). Error bars represent the standard errors; ND indicates habitats not sampled during the period.
multiple years (as in Hare and Cowen, 1993) may obscure breaks in larval production occurring at slightly different times in different years. Further evaluation of lunar periodicity and temperature effects on bluefish spawning and recruitment is warranted.

The results of this study suggest limited late-summer to fall spawning (inferred from larval and juvenile collections), similar to previous studies (Collins and Stender, 1987; Hare and Cowen, 1993; McBride et al., 1993; Clarke, 2006; Taylor et al., 2006; Murt and Juanes, 2009), possibly resulting from adults in good condition continuing to spawn on the southward migration or after they arrive in the SAB. This reproductive effort appears limited, however, to a small fraction of the stock (possibly larger and older fish) and may therefore be dependent on stock size, composition (diversity of age-classes present), and physiological condition. Abundances of bluefish in the ocean surface in fall were much lower than in spring and summer, similar to the findings of Collins and Stender (1987) and Hare and Cowen (1993). The presence of this late-spawned cohort is largely limited to larval and early juvenile collections, in contrast to the two dominant cohorts that were consistently collected through later juvenile stages. Therefore, owing to overall low abundance and inferred limited survival, it is unlikely the fall spawned bluefish contribute significantly to the stock.

Although the issue of continuous versus discontinuous spawning cannot specifically be addressed, one of the outstanding hypotheses presented by Smith et al. (1994) was that an intervening cohort might exist in Virginia or southern MAB estuaries (areas not sampled in their study). The present extensive sampling efforts throughout the MAB failed to reveal such intervening cohorts, although Callihan et al.’s (2008) analysis observed earlier hatch dates of the summer-spawned cohort when early warming produced suitable temperatures for spawning in the southern MAB. Further evidence for a lack of an intervening cohort can be found when examining late fall and winter catches of juveniles off North Carolina. During this time, growth has ceased (Morley et al., 2007), and YOY are mostly concentrated on the continental shelf, allowing for an accurate examination of cohort structure as resident juveniles emigrate and fish from the MAB migrate through to overwinter in the SAB. Morley et al. (2007) found a clear distinction between summer- and spring-spawned cohorts over two winter seasons off North Carolina, and this is supported by the present study. When all of the available data on reproduction of bluefish are considered together (pattern of oocyte development, batch spawning, seasonal migration, variable relative condition), it becomes plausible that bluefish (at the individual and population level) are capable of prolonged spawning, with a potential reduction or hiatus in spawning in late spring when adults are in poor condition following long-distance migration and recent spawning. In addition, although a proportion of the spring-spawned cohort is mature at age 1 (Salerno et al., 2001), it is doubtful whether these individuals are ready to contribute to spring spawning in the SAB (i.e., they more likely join the spawning stock biomass during the summer in the MAB, thereby contributing to production of the summer cohort in MAB waters).

More detailed information on the condition, size-dependent migration, and spawning patterns (batch fecundity and frequency) of adults is needed to fully accept this interpretation.

The reproductive strategy of bluefish may not seem to be well adapted to present-day patterns of biogeography and circulation (see discussion by Hare and Cowen [1993]); however, the adaptive value of spring spawning by bluefish at the edge of the Gulf Stream in the SAB has been demonstrated to provide both transport to (Hare and Cowen, 1993) and early piscivory on locally produced prey in the MAB (Juanes and Conover, 1994; Juanes et al., 1994; Juanes and Conover, 1995; Buckel et al., 1998). Summer-spawning on the MAB shelf was argued to be adaptive as well, by promoting retention and not advection off the shelf. The benefits of early piscivory for the summer cohort are much reduced, as only anchovies (at least inshore) are an available piscine prey of the right size (Juanes and Conover, 1995; Buckel et al., 1999a; Scharf et al., 2006). This size dependency of predator–prey interactions also appears to extend into the fall, when the summer cohort may be too small to feed on most of the available piscine prey on the shelf relative to the spring cohort (Buckel et al., 1999b). Variability in abundance and recruitment timing of each cohort can have important implications for cohort-specific growth and survival (Scharf et al., 2006). Further, it is evident that there are decadal scale shifts in the abundance of the spring versus summer cohort (as measured in the NEFSC Autumn Bottom Trawl Survey) that have been documented in Munch and Conover (2000) and Conover et al. (2003). So there must be adaptive benefits to producing both cohorts in terms of other environmental forcing factors that are not yet understood.

**Conceptual Model of Bluefish Reproduction and Early Life History**

The data collected in this study was synthesized with previously published studies of bluefish on the U.S. east coast (Able and Fahay, 1998, 2010; Fahay et al., 1999; Shepherd et al., 2006, and references therein) to develop a conceptual model of bluefish early life history to illustrate spawning locations and habitat use by YOY bluefish cohort for four different three-month time periods during the year (Figure 13). During March to May, adult bluefish spawn in continental shelf waters south of Cape Hatteras near the Gulf Stream, and small spring-spawned juveniles begin utilizing nearshore ocean bottom and ocean and estuarine beach habitats of the SAB. Spawning by adult bluefish also occurs in continental shelf waters of the MAB from June to August. During these summer months, spring-spawned juveniles continue to use SAB habitats but also use those same habitats (nearshore ocean bottom and ocean and estuarine beaches) in the MAB; however, newly recruited summer-spawned bluefish are found in high abundances only in MAB estuarine and nearshore ocean habitats (inner shelf and beaches) at this time, an observation consistent with earlier studies off New Jersey (Able et al., 2003; Taylor et al., 2006, 2007; Taylor and Able, 2006). During
Figure 13 Conceptual model for bluefish early life-history stages showing spawning locations and habitat use by YOY bluefish cohorts along the U.S. east coast throughout the year. Plotted are occurrence of spawning and cohorts in estuary and ocean beaches and the coastal ocean in spring (a), summer (b), fall (c), and winter (d) for each three-month time period. Stippled areas indicate spawning, diagonal hatching indicates spring-spawned cohort, and horizontal hatching indicates summer-spawned cohort (color figure available online).
September to October, the bulk of spawning has concluded, and spring- and summer-spawned bluefish are migrating south and are found in both MAB and SAB nearshore ocean and estuarine habitats. During the December-to-February period, spring- and summer-spawned bluefish are found exclusively in SAB habitats; these habitats include nearshore ocean bottom (present study) and estuary in December but are limited to ocean waters during later months in this time period.

Measurements of Cohort Production and Contribution to the Adult Stock

The highly mobile and schooling nature of both adults and YOY bluefish often results in highly variable catch rates, making it difficult to determine patterns in abundance and movement over short temporal or spatial scales. Although YOY abundance has been positively correlated with age-1 abundance the following year in the NEFSC bottom trawl survey (Munch and Conover, 2000), this survey fails to capture YOY bluefish production in the SAB. In addition, abundances of the summer cohort may be over-represented, as they have experienced lower cumulative mortality (due to their younger age) and are potentially more vulnerable to the survey gear relative to the larger spring-spawned cohort. In contrast, the abundance and/or presence of fall-spawned cohorts is likely under-represented, as these only begin to recruit during the September–October sampling period of the NEFSC survey. Assuming that recruitment of the spring cohort is correlated at large spatial scales (across both SAB and MAB), the NEFSC survey would provide a sufficient annual index for assessment models without accounting for SAB production. In contrast, if SAB and MAB production of spring-spawned bluefish are not correlated, surveys restricted to the MAB might fail to track coastwide recruitment despite adequately measuring abundance of the summer-spawned cohort. The present study indicates that the MAB and SAB locations sampled produced similar numbers of spring cohort bluefish, but summer cohort production was limited to the MAB, with the exception of limited production at SAB ocean beaches (Figure 12). Additional years of data would be needed to evaluate the temporal stability of the patterns observed.

As in prior studies (Munch, 1997; Able et al., 2003; Callihan, 2005; Wiedenmann and Essington, 2006), YOY bluefish were more common in shoal areas <20 m than in deeper ocean waters (Figure 11). The Northeast Area Monitoring and Assessment Program (NEAMAP) survey continues to sample inshore strata previously sampled by NEFSC trawl surveys but not sampled since 2009 with the new survey vessel (FSV H. B. Bigelow). Although the NEFSC trawl survey includes a limited number of stations (>25-m depth) south of Cape Hatteras, North Carolina, the NEAMAP survey is only north of Cape Hatteras, making it difficult to evaluate to what extent shallow waters south of Cape Hatteras contribute to overall juvenile production. The two years of sampling effort described here suggest major concentration areas for YOY bluefish in both northern SAB and MAB estuaries and nearshore coastal waters. Northern, then southern, coastal migration of the spring cohort and southern coastal migration of the summer cohort is inferred from the comparison of monthly abundances from New York, New Jersey, Maryland, and North Carolina. In addition, a later (fall) cohort was collected in both years in low numbers and small sizes; however, this cohort did not appear to persist and contribute significantly to the population. The multiple-gear, multiple-habitat, concurrent coastwide sampling described in this study reinforce and clarify the observations of many other studies that have described YOY bluefish from collections that were more limited in time or space.

A combination of daily aging and length frequency distributions has allowed the identification of cohorts and comparisons of growth rates in the MAB from late spring, summer, and early fall collections (Nyman and Conover, 1988; McBride and Conover, 1991; Taylor and Able, 2006; Callihan et al., 2008). In the MAB, summer-spawned bluefish had faster growth rates over the first 60 days of life as compared to spring-spawned bluefish (Nyman and Conover, 1988; McBride and Conover, 1991). Presumably, summer-spawned bluefish experience warmer temperatures throughout their first two months in the MAB compared to spring-spawned bluefish that transit from warmer SAB spawning locations to cooler (but warming) MAB waters in spring. In the present study, however, across all regions, the two cohorts were collected at similar temperatures (Figure 11). Although daily increment formation has been validated for fast-growing juvenile bluefish (Nyman and Conover, 1988; Roemer and Oliveira, 2007), the interpretation of daily increments through the first winter has proven more difficult. Likely due to slowed growth during fall migrations (see below), daily aging of YOY bluefish during late fall, winter, and spring collections (see Morley et al., 2007) was not successful (due to the apparent lack of daily ring production from month-to-month samples within the same cohort; P. J. Rudershausen and J. A. Buckel, North Carolina State University, unpublished data); thus, the identity of cohorts (i.e., spring versus summer) was unknown in the Morley et al. (2007) study. This study’s coastwide synoptic sampling has aided in the identification of these cohorts. The two cohorts that dominate in late fall, winter, and spring sampling off North Carolina (and, to some degree, Florida) are spring- and summer-spawned bluefish; this is inferred from the departure of those cohorts from the MAB and their arrival in large numbers in the SAB. The reduced growth in YOY during fall migration occurs even though water temperatures are suitable for growth (Buckel et al., 1995; Fahay et al., 1999); this may be a result of the cost of migration and/or decreased feeding during southward migrations.

Long-distance migrations incur significant energetic costs to individuals (Nottestad et al., 1999). Bluefish are adapted to exploit seasonally productive habitats. This requires the ability (and energy) to move to and inhabit these areas when they are suitable for growth, and abandon them when they become unsuitable. Like many highly migratory pelagic marine fishes, bluefish are relatively stenothermal as compared to temperate estuarine resident fishes. These thermal constraints promote the
observed seasonal migrations in bluefish and many other species that are summer residents in the MAB (Able and Fahay, 2010). Swimming speed, swimming efficiency, and energy stores generally increase with size of fishes (Nottestad et al., 1999); therefore, it might be expected that the cost of the fall migration south would be greater for summer-spawned than spring-spawned bluefish. Morley et al. (2007) found larger YOY bluefish to have much greater energy storage in fall as compared to smaller YOY. In contrast to the spring cohort, which partially recruits directly to SAB habitats, very few summer-spawned bluefish recruit directly to SAB habitats (Figure 12); therefore, almost all summer-spawned bluefish must undergo fall migration.

The slowed growth observed here for summer-spawned cohort (inferred from length-frequencies) during fall, despite suitable temperatures for growth (Shepherd and Packer, 2006) and co-occurrence with many suitable YOY prey fishes leaving MAB estuaries in the fall (Able and Fahay, 1998, 2010), supports this hypothesis. Similar to the findings of Nyman and Conover (1988), there was substantial growth in summer-spawned bluefish in the MAB during September and October (Figures 3, 4, and 5); however, the sizes of this cohort in late fall in North Carolina was only slightly larger than those observed in the MAB in October. Following their arrival in North Carolina, the summer-spawned cohort did not increase in size from November to December in either year (Figures 6 and 7); in fact, there was a slight decrease in sizes that could be the result of size-dependent migration (smaller fish arriving later). This pattern is consistent with the study of Morley et al. (2007), which did not detect growth for the summer-spawned cohort from November through early April in North Carolina. The ability of YOY bluefish to increase energy storage in fall, in preparation for overwintering, has recently been well described (Morley et al., 2007; Slater et al., 2007). The shift in energy allocation from rapid growth to storage and migration is likely more pronounced for the summer-spawned cohort. Summer-spawned YOY bluefish appear adequately prepared to survive their first winter; however, this preparation (via lipid storage; Morley et al., 2007) coupled with the energetic cost of migration compromises their ability to maintain rapid growth rates. Therefore, while the energetic demands of spring migration of adults may cause an initial bimodal distribution in YOY (via reduction or suspension of spawning due to reduced condition or increased migration in May–June), the energetically costly (and necessary) southerly migration of juveniles in the fall (especially for summer-spawned cohorts) acts to maintain/reinforce these size differences. This could help explain why the summer use of MAB estuaries by spring-spawned bluefish is optimal. Detailed information on high-temperature physiology, movement rates of juveniles, and the energetic cost of swimming and migration are needed to more fully evaluate the trade-offs between growth and migration for both spring- and summer-spawned bluefish.

The coastwide nature of this study has allowed a detailed examination of the role of seasonal temperature change in the fall and winter movements of YOY bluefish into southern waters. YOY bluefish were consistently collected in nearshore ocean habitats (beaches and inner shelf), providing additional support for the importance of shallow ocean habitats as potential nurseries (Able et al., 2003); therefore, the role of these ocean habitats should receive further attention, particularly in New Jersey and New York. When considering total production by habitats, it should be noted that ocean beaches represent a small fraction (<10%) of total tidal shoreline in the region; therefore, bluefish densities in ocean beaches would have to be an order of magnitude greater than estuarine densities to match estuarine production. Nonetheless, it is believed that ocean beaches are important to the population dynamics of YOY bluefish. Further, these habitats may be impacted by potential modification of ocean habitats, such as from beach nourishment, coastal contamination by estuarine plumes, and other natural or anthropogenic disturbances. It is recognized that additional recruitment may exist in New England waters (Creaser and Perkins, 1994) and in the Gulf of Mexico, but the effort described here (coordinated sampling across >1,000 km of coastal and estuarine habitats) focused on the regions where most juveniles are produced.

Conover et al. (2003) provided evidence that spring-spawned bluefish cohorts contributed more than the summer-spawned cohorts, even when summer-spawned bluefish were more numerous in the NEFSC trawl survey. The results of this study provide strong evidence that spring-spawned bluefish are produced in both the MAB and the SAB, while summers-spawned bluefish are produced mostly in the MAB. If this result is consistent from year to year, this would suggest that spring-spawned bluefish production is greater than previously estimated, potentially explaining why earlier analyses of the adult population have identified a dominance of spring-spawned individuals (Chiarella and Conover, 1990; Conover et al., 2003). More complete quantification of SAB production of spring-spawned bluefish (which was limited to North Carolina in the present analysis) is needed to evaluate overall SAB contribution, which may help explain some of the observed differences in cohort proportions of year-classes across ages. Further, since the NEFSC survey samples only the MAB extensively, potentially missing significant SAB production of the spring cohort that remains in the SAB, caution should be exercised in assuming cohort proportions of YOY bluefish derived from that survey are representative of the overall stock. The degree to which annual abundances of the spring cohort in MAB and SAB are correlated through time should be evaluated to determine the suitability of recruitment indices derived in one region. Further, the influence of increasing ocean and estuary temperatures, as the result of climate change, may alter the timing of reproduction, pattern of larval supply, habitat use, and migration of the different cohorts in SAB and MAB waters differently.

In summary, this large-scale collaborative study allowed the determination of the patterns of habitat use and movement for multiple cohorts across along the U.S. east coast. In addition, the coastwide concurrent sampling approach described here is a necessary first step in an analysis of the factors affecting recruitment success for this species with contributions from multiple cohorts. In fact, the approach may, in the future, be used to...
address other coastal Atlantic species that originate from several cohorts, in which case, considering the diversity of spawning behaviors is critical to conservation and management. While consistent with previous, less comprehensive studies, the patterns observed in timing and abundance of YOY bluefish in 2005–2006 (Figures 3–8) are much less ambiguous owing to the temporal and spatial coverage of sampling and are believed to be representative of the annual pattern for juveniles across the broad study area. Despite differences in sampling effort in the different regions and years, when the data are considered in aggregate, a more complete picture emerges. Due to the possibility of annual variation and the complex nature of cohort structure for this highly mobile species, additional years of data would be needed to determine the linkages between regional cohort abundance and recruitment to the adult population. The data presented here indicate that production of spring-spawned juvenile bluefish in at least some regions of the SAB is comparable to production in the MAB, while production of the summer-spawned cohort is limited to the MAB. Future analyses of cohort proportions at later ages and recruitment indices for stock assessments will need to account for SAB production of the spring-spawned cohort, which has not previously been quantified.

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