

Cohort splitting in bluefish, *Pomatomus saltatrix*, in the US mid-Atlantic Bight

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ABSTRACT

Atlantic bluefish exhibit cohort splitting, whereby two modes of juvenile recruits originate from spatially distinct spring- and summer-spawning regions in US Atlantic shelf waters. We evaluate the pattern of cohort splitting in a transition area (US Maryland coastal region and Chesapeake Bay) between the two major spawning regions. Spring and summer cohorts were differentially represented in Maryland estuarine (Chesapeake Bay) and coastal waters. The spring cohort was dominant in Chesapeake Bay, but was not well represented in the ocean environment, and the converse true for the summer cohort. We hypothesized that ocean temperatures control the bimodal spawning behavior and extent of cohort splitting. As evidence, we observed an intervening early summer cohort produced in years when shelf temperatures during early summer were suitably warm for spawning. In most years however, two dominant cohorts were evident. We propose that vernal warming dynamics in the mid-Atlantic Bight influence spawning behavior and the resultant bimodal pattern of seasonal juvenile cohort production commonly observed along the US east coast.

Key words: bluefish, phenology, recruitment, spawning, split cohort, temperature

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INTRODUCTION

In many important temperate marine species, discontinuous or episodic patterns in spawning result in differing recruitment outcomes. Termed pulsed recruitment (Nyman and Conover, 1988; Ebert *et al.*, 1993) or split cohorts (Post *et al.*, 1997), larval and juvenile fates that differ because of spawning time and place can serve to dampen high variability in recruitment that might otherwise occur (Secor, 2007). Split cohorts are well described for bluefish, *Pomatomus saltatrix*, in the northwestern Atlantic (McBride and Conover, 1991; McBride *et al.*, 1993; Taylor and Able, 2006).

Bluefish is a migratory continental shelf species exhibiting a worldwide temperate and subtropical distribution (Briggs, 1960; Juanes *et al.*, 1996). In the northwest Atlantic, genetic data suggest there is a single population of bluefish (Graves *et al.*, 1992). Spring spawning occurs on the outer shelf of the US SAB (South Atlantic Bight; Cape Canaveral, FL to Cape Hatteras, NC, USA) from March through May (Collins and Stender, 1987; Hare and Cowen, 1993). Adults then migrate northward to the US MAB (Middle Atlantic Bight; Cape Hatteras, NC to Cape Cod, MA, USA) during late May or early June. Summer spawning occurs in inner to mid-shelf waters of the MAB from June to August with a strong peak in July off New Jersey and Delaware Bay (Smith *et al.*, 1994; Berrien and Sibunka, 1999). Egg production is minimal offshore of the Chesapeake Bay mouth and moderate in the Maryland coastal region, although patches of high egg densities occur in some years (Berrien and Sibunka, 1999). A minor fall spawning peak is sometimes observed in SAB waters following a southern adult migration (Lund and Maltezos, 1970; Kendall and Walford, 1979; Collins and Stender, 1987).

In the MAB, most bluefish eggs have been collected when surface water temperatures are 18–26°C. Norcross *et al.* (1974) found that 18°C was the minimum temperature for the occurrence of bluefish eggs. Furthermore, in synoptic (10 yr, MAB shelf-wide) Marine Resources Monitoring, Assessment, and Prediction Program surveys, 97% of all collected

bluefish eggs and 95% of positive stations coincided with surface water temperatures $\geq 18^\circ\text{C}$ (Berrien and Sibunka, 1999, 2006). Thus, 18°C is used herein as the minimum temperature threshold at which spawning is expected.

Physical transport regimes of bluefish larvae and recruitment pathways differ between seasonal cohorts. Some spring-spawned bluefish recruit locally to estuaries of the SAB (McBride *et al.*, 1993), but the majority are likely entrained in Gulf Stream flow and advected northward to the MAB (Hare and Cowen, 1996). Warm-core ring streamers and wind-driven transport of larvae, and active swimming by early stage pelagic juveniles are proposed as important mechanisms delivering spring-spawned bluefish to nearshore nursery habitats in the MAB (Hare and Cowen, 1996; Munch, 1997). Summer-spawned bluefish are produced more proximate to nurseries; therefore, along-shore transport, wind-driven Ekman transport, and buoyancy-driven flows are most important in delivery of this cohort to nurseries (Epifanio and Garvine, 2001). One currently held view is that the consequence of pulsed-spawning behavior and larval dispersal is a consistent pattern of bimodal size and hatch date distributions of young-of-the-year (YOY) bluefish that arrive to inshore nursery habitats (Nyman and Conover, 1988; Chiarella and Conover, 1990; McBride and Conover, 1991).

Controls on spawning behaviors that lead to split cohorts in bluefish remain unknown. Indeed, debate remains on whether spawning is discrete or continuous. Conceivably, split cohorts could result from consistent selection against offspring spawned during early summer months. Still, the consistency across systems and years of an early summer gap in hatch dates (derived from otolith analysis of juvenile bluefish) is remarkable. This temporal gap (typically mid-May to mid-June) has been observed in New York and New Jersey estuaries (Nyman and Conover, 1988; McBride and Conover, 1991), and North and South Carolina estuaries (McBride *et al.*, 1993). Yet, evidence for discrete spawning remains circumstantial and other hypotheses are plausible; for example: selection against early spawned larvae because of unfavorable transport regimes (Hare and Cowen, 1993) or recruitment to regions where hatch dates have not been documented (Smith *et al.*, 1994).

The differential representation of split cohorts could have important consequences to overall recruitment amplitude and variability because of generational scale changes in climate and other oceanographic effects. Numerous studies have shown higher abundance and more consistent recruitment across years of spring-

versus summer-spawned bluefish in estuarine habitats of the MAB (Nyman and Conover, 1988; McBride and Conover, 1991; McBride *et al.*, 1995), Maine (Creaser and Perkins, 1994), and the SAB (McBride *et al.*, 1993). Further, it has been suggested that summer-spawned bluefish primarily utilize coastal ocean habitats as nurseries (Kendall and Walford, 1979; Able and Fahay, 1998; Able *et al.*, 2003), although the role of coastal ocean nurseries has not been as extensively studied. Interestingly, the representation of spring and summer cohorts of bluefish has been shown to oscillate over a multi-decadal time period (Munch and Conover, 2000; Conover *et al.*, 2003).

We examined the following hypotheses related to the causes and consequences of cohort splitting in bluefish:

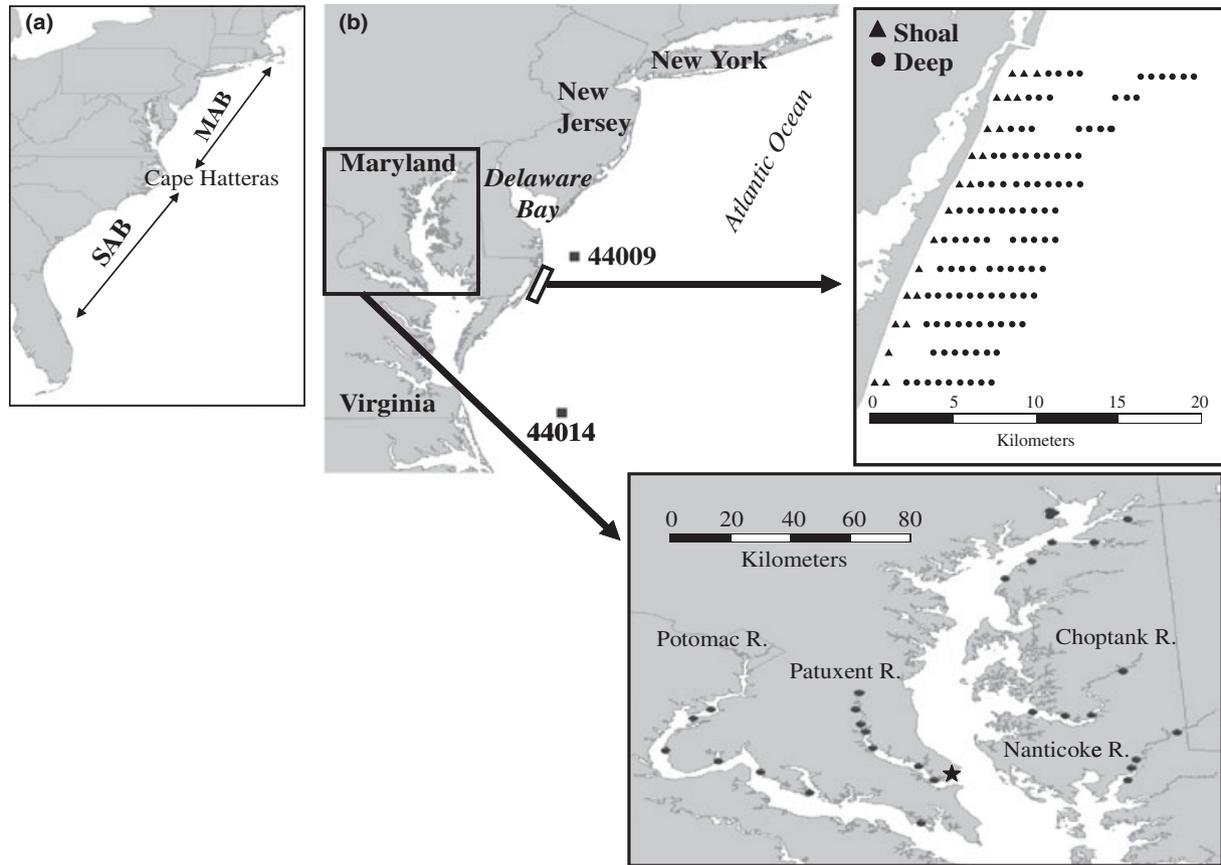
1. The pattern of split cohort production in the MAB is controlled by ocean temperatures. In a transition region between the two principal spawning habitats, local production of larvae can occur when temperatures are suitably warm ($\geq 18^\circ\text{C}$).
2. The two dominant seasonal cohorts exhibit different patterns of nursery dependence. Spring-spawned juveniles predominate in Chesapeake Bay and summer-spawned juveniles predominate in ocean waters.

MATERIALS AND METHODS

Field sampling

We sampled juvenile bluefish over their reported period of occurrence in the MAB, May to October (Nyman and Conover, 1988; McBride and Conover, 1991; Takata, 2004) during 2003–04. Our oceanic sampling domain encompassed waters just outside the surf zone to 6–7 km offshore ($75^\circ 10' 15''$ – $74^\circ 59' 46''$ W) along Maryland's coast ($38^\circ 18' 37''$ – $38^\circ 08' 13''$ N); the total study area was ca. 150 km^2 (Fig. 1). Because depth is an important factor influencing juvenile bluefish abundance in coastal waters (Takata, 2004), we employed a depth-stratified simple random sampling design with strata 5–9 and 10–18 m (Fig. 1) (Callihan, 2005). A random subset of stations was chosen for each cruise from the possible grid of stations, whereby adjacent stations were separated by 2 km latitudinally and 500 m longitudinally to ensure independence of sampling units. We conducted daytime monthly trawl sampling aboard commercial fishing vessels in 2003 (May–October) and 2004 (July–November), and typically performed 16 twenty-minute tows each cruise. Beyond these two principal comparison years, ancillary samples were obtained from mid-water trawl (MWT) sampling (12 tows per

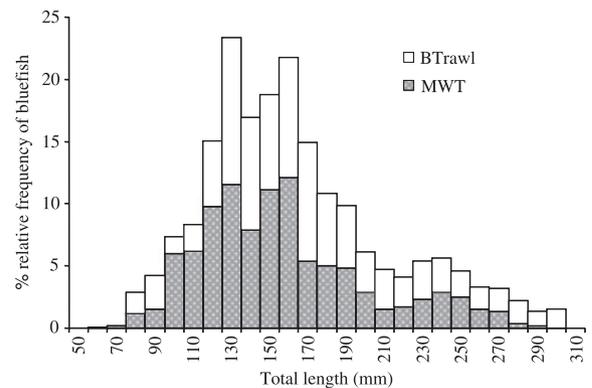
Figure 1. (a) Delineation of Atlantic coastal waters into South Atlantic Bight (SAB) and Mid-Atlantic Bight (MAB). (b) Study areas and sampling sites. Primary sampling site in Chesapeake Bay (Chesapeake Biological Laboratory research pier) is represented by a star. The grid of all possible stations is shown for the coastal ocean by depth stratum. Squares indicate the locations of NOAA buoys utilized for temperature analyses.



month) during 2000 (August, September) and 2001 (June, August, and September).

Different trawls were used between years for ocean sampling. In 2000, 2001, and 2003, we used an 18 m² mouth-opening MWT with 6 mm cod end mesh. The MWT was fished obliquely from surface to bottom in 2-min stepped intervals for a total duration of 20 min. In 2004, we used a bottom trawl with specifications: 25 m headrope, 30 m footrope, 6 mm cod end mesh, and 3.0–3.5 m vertical spread. We compared length frequency distributions of YOY bluefish, ≤300 mm total length (TL), between gear types using MWT data pooled across years and cruises for 2000, 2001, 2003, and bottom trawl data for 2004 pooled across cruises (Fig. 2). Length frequency distributions were statistically distinguishable ($P < 0.0001$, two sample Kolmogorov–Smirnov test); medians were within 10 mm of one another (146 and 155 mm TL for MWT and bottom trawl, respectively), yet significantly different ($P < 0.0001$, Wilcoxon two-sample test). Despite differences in the median sizes selected, each gear

Figure 2. Comparison of length frequency distributions for juvenile bluefish collected with mid-water trawl (MWT), pooled across years 2000, 2001, and 2003 versus bottom trawl (BTrawl), pooled across cruises for 2004.



selected for the same range of bluefish sizes (Fig. 2); also, Takata (2004) demonstrated that data from the MWT was consistent with semi-continuous hatch date distributions similar to those observed for bottom trawl

surveys. Therefore, although gears selected for slightly different sized YOY (ca. 10 mm difference), we assumed that hatch date distributions were not confounded by this difference.

In 2004, some tows were reduced to 10 min when extremely large catches (particularly *Cynoscion regalis*) were encountered. Also, the total number of tows per cruise was less than our target ($n = 16$) during August (because of large catches) and November (weather). Accordingly, we developed stratum-specific tow duration multipliers based on systematic sampling during September 2004, when four paired-comparison 10- and 20-min tows were conducted within each depth stratum. Multipliers, or catch ratios for 20 : 10 min tow durations, were: 2.00X and 1.56X for bluefish ≤ 200 mm TL in shoal and deep strata, respectively; 1.59X and 1.63X for bluefish 201–300 mm TL in shoal and deep strata, respectively. We used these multipliers to yield standardized (16 twenty-minute tows per cruise) abundances and lengths (Callihan, 2005) to which age-length keys (ALKs) were applied (see below) to obtain hatch date distributions.

Sampling in Chesapeake Bay occurred in littoral zones (<1.5 m depth) of sub-estuary tributaries (Patuxent, Potomac, Choptank, and Nanticoke Rivers; the upper Bay) located in Maryland's portion of Chesapeake Bay (Fig. 1). Weekly seine collections were conducted at the Chesapeake Biological Laboratory research pier from May to October in 1999–2001 and 2003–04. Also, samples were obtained from monthly (July–September) bay-wide seine sampling by the Maryland Department of Natural Resources in all years except 2003. The seine used in both surveys was a 30.5 m \times 1.5 m non-tarred beach seine.

Otolith microstructure analysis and age determination

We utilized otolith microstructure analysis to age juvenile bluefish and generate hatch date distributions. Immediately upon sampling, all juvenile bluefish were enumerated, measured (TL) to the nearest mm, and preserved by 'flash-freezing' with dry ice. Samples from 2003 and 2004 were collected over the entire recruitment period in both estuarine and oceanic systems, facilitating robust comparisons of cohort splitting and representation within and between systems across years. Hatch date distributions based on directly aged individuals, ≤ 200 mm TL (at larger sizes aging precision was poor), were used in modal analyses to investigate cohort splitting; but tests of cohort representation (spring versus summer) between systems also incorporated age estimates of larger juveniles derived from ALKs. Hatch dates from 1999 to 2001

collections were used as ancillary evidence because in those years sampling occurred throughout the entire recruitment period in Chesapeake Bay, but not in the coastal ocean.

Otolith preparation methods followed those presented by Secor *et al.* (1992). We interpreted ages from sagittal otoliths for fish ≤ 200 mm TL ($N = 617$) because otolith sections from larger fish were difficult to interpret because of the prevalence of secondary growth centers and decreased contrast of peripheral increments. Otoliths were prepared using a 'triple-grinding-polishing' technique (Callihan, 2005) to attain thin transverse sections yielding highly resolved daily increments.

Daily increment formation in juvenile bluefish has been validated (Nyman and Conover, 1988). We determined the mean number of increment counts as the average of blind triplicate, non-successive counts for each otolith, requiring counts to fall within 10% of the mean. If this condition was not met a fourth count was conducted and the outlier count discarded (Nyman and Conover, 1988; Takata, 2004). Mean age was calculated by subtracting 1 day from the mean of counts because the first increment forms at hatching (Hare and Cowen, 1994). Hatch dates were back-calculated by subtracting mean age from the date of capture. They are expected to closely track spawning dates as incubation time is 46–48 h at 18–22°C (Deuel *et al.*, 1966).

Traditional ALKs, utilizing proportions at age within length bins (Westrheim and Ricker, 1978), were applied to 2004 samples because of the large number of juveniles captured (ca. 2300 fish ≤ 200 mm TL). We developed cruise-specific ALKs based on ages obtained from direct aging of a total of 64 juveniles per cruise that were equally distributed across 10 mm size bins. Ages were assigned as the midpoint of weekly age bins; the number of fish within each length class was multiplied by the corresponding proportions at age to generate age distributions and associated hatch date distributions. For 2003 ocean samples, the age sampling rate (i.e., % of fish ≤ 200 mm TL directly aged) was high at 76%. Hence, we relied upon an age-length regression to estimate ages of the remaining 24% of fish (collected in September and October), according to the summer cohort ALK:

$$\text{Age} = 0.27 \times \text{TL} + 39.59, r^2 = 0.54, \\ \text{summer cohort} \leq 200 \text{ mm}, n = 74 \quad (1)$$

Composite ocean hatch date distributions for each year were attained by summing hatch dates from

directly aged fish with those derived from ALKs. The age sampling rate was high for 2003–04 Chesapeake Bay samples: 100% in 2003 and 70% in 2004. Therefore, we assumed corresponding hatch date distributions adequately reflected those of the juvenile population in Chesapeake Bay. For ancillary 1999–2001 samples, the age sampling rate ranged from 14% to 62% per system/year combination; thus, regression-based ALKs were also applied to these samples to obtain ages of individuals not directly aged.

For ocean samples, no fish larger than 200 mm TL exhibited an annulus for 2003; monthly maximum YOY size thresholds for 2004 were determined as: 200 mm for July, 250 mm for August, and 300 mm for September–November. The maximum YOY size achieved by fall found in this study, 300 mm TL, is similar to that utilized in other studies (Munch, 1997; Munch and Conover, 2000). Larger YOY (200–300 mm TL) represented 25% and 17% of all collected juveniles in 2003 and 2004, respectively; their ages were calculated using the age at length relationship of the spring cohort based on direct aging:

$$\begin{aligned} \text{Age} &= 0.36 \times \text{TL} + 50.30, r^2 = 0.64 \\ \text{spring cohort 2003, } n &= 48 \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Age} &= 0.28 \times \text{TL} + 44.62, r^2 = 0.54 \\ \text{spring cohort 2004, } n &= 93 \end{aligned} \quad (3)$$

Composite hatch date distributions used in hypothesis testing of cohort representation were obtained by summing hatch dates of larger YOY with those ≤ 200 mm.

Hatch date analysis

All hatch date distributions were corrected for cumulative mortality differential. The premise for this adjustment is that older individuals collected on a given date will have experienced greater cumulative mortality than younger fish. We used a daily instantaneous natural mortality rate of 0.01 per day based on a literature review of juvenile stage mortality rates of marine fishes (Callihan, 2005). The exponential decay model was used to account for mortality between the actual sampling date and the standardized final sampling date (Campana and Jones, 1992) for each year to obtain a composite age distribution, to which the following equation (Brown and Bailey, 1992) was applied to correct for differences in the amount of cumulative mortality experienced:

$$N_{i,j} = \frac{N_i}{e^{-M(i-j)}} \quad (4)$$

where $N_{i,j}$ is the abundance of cohort of daily age i corrected for cumulative mortality, N_i is the standardized abundance of daily cohort age i on the final capture date not corrected for cumulative mortality, M is the daily instantaneous natural mortality rate, and j is the youngest age represented on the final sampling date.

Observed modes in hatch date distributions of respective system/year combinations (2003–04 samples) were skewed and not normally distributed (Kolmogorov–Smirnov goodness of fit tests). However, gaps between modal groupings were present in most distributions, thus facilitating cohort identification. Furthermore, median and mean hatch dates for each cohort were very similar, typically falling within the same hatch week. Therefore, we used the NORMSEP procedure (FiSAT II software ver. 1.2.1, Rome, Italy), an iterative maximum likelihood technique that assumes normal component distributions, to discern whether hatch modes were distinct. Two modes were considered distinct if they were separated by twice the largest standard deviation of the two modes (Abramson, 1971).

Three-way contingency table analysis (cohort \times system \times year) was used to test for system and year effects on cohort representation. The Cochran–Mantel–Haenszel test (Agresti, 1996) was used to test for conditional independence between cohort and system, controlling for year. The Breslow–Day statistic was used to test for homogeneous association (i.e., equal odds ratios) of the cohort \times system relationship across years. Odds ratios are useful in discerning the directions of relationships in contingency table analyses, which generally cannot be used to determine the direction of significant differences (Agresti, 1996).

Retrospective analyses

To evaluate the relationship between cohort splitting and ocean temperatures, we analyzed sea surface temperature (SST) records for the month of June (typical hatch date gap) in MAB shelf waters. National Oceanic and Atmospheric Administration (NOAA) buoys #44014 (36°36'40"N, 74°50'11"W) and #44009 (38°27'49"N, 74°42'07"W) are located in mid-shelf waters off Chesapeake Bay and Delaware Bay, respectively (Fig. 1), encompassing the region where highest catches of pelagic bluefish eggs have been observed during June (Berrien and Sibunka, 1999). Daily average sea surface (upper m) temperatures over the entire month of June were analyzed for years 2000, 2001, 2003, and 2004. Temperature data from buoy #44014 were not available for 2000, thus for this year only data from the Delaware Bay region were analyzed. Non-parametric procedures were used to test

for differences in June temperatures among years for a given region because homoscedasticity assumptions were not met for analysis of variance.

Historical hatch dates of bluefish in Chesapeake Bay were reconstructed for a long-term (1966–present) seine survey conducted by the Maryland Department of Natural Resources. Monthly sampling was conducted in this survey during July, August, and September; replicate seine hauls were performed at each of the 22 sites throughout the upper Chesapeake Bay, Potomac, Choptank, and Nanticoke Rivers (Fig. 1). Sites in the Patuxent River (Fig. 1) were added to the standard sampling regime after 1983. Gear specification and deployment methods were similar to those described above. Lengths were not recorded for all bluefish; in some instances only the minimum and maximum lengths of fish collected in a given haul were recorded. Minimum/maximum lengths were only considered to be representative if four or less fish were captured in the haul, and only such hauls were retained in the analysis. Hatch dates were only reconstructed for years in which 45% or more bluefish were measured, resulting in exclusion of years 1974, 1979, 1989, and 1990. Also, no bluefish were collected in 1966. Samples for which length data were available (83% of bluefish samples) were distributed evenly across sampling events and locations.

To estimate historical hatch dates of bluefish in Chesapeake Bay, a regression-based ALK was developed based on ages obtained from direct otolith aging of juveniles. Age and length data were pooled across years 1999, 2001, and 2004 to generate the ALK (Eqn 5) because the slope and intercept of the age-at-length relationship were not significantly different among these years ($P = 0.75$ and 0.58 , respectively, ANCOVA).

$$\text{Age} = 0.36 \times \text{total length (mm)} + 32.43, \\ r^2 = 0.81, n = 133 \quad (5)$$

The ALK was used to estimate ages (hatch dates) of all YOY bluefish including those >200 mm TL (11.6% of all bluefish). Hatch date distributions are presented as composite distributions, uncorrected for cumulative mortality effects, for 5-yr periods from 1966 to 2006.

RESULTS

Cohort splitting

Hatch date distributions for each system/year (2003, 2004) were bimodal, with distinct modes (as indicated by NORMSEP) corresponding to spring and summer cohorts (Fig. 3). The degree of cohort splitting was considerably greater in 2003 than 2004 across systems. A salient feature, contributing to the extent of cohort splitting, was that bluefish with June hatch dates were rare in 2003 and common in 2004, especially in the coastal ocean (Fig. 3). The proportion of bluefish with June hatch dates in the coastal ocean was significantly higher in 2004 (25.8%) than 2003 (6.8%) (odds ratio or $\theta_{2004:2003} = 4.8$, $P < 0.0001$).

For 2003, bluefish with hatch dates on or before June 17 were classified as the spring cohort, and those with hatch dates afterwards as the summer cohort. For 2004, a similar cohort delineation date of June 10 was used. In 2003, peak hatch dates of the spring cohort (early May) and summer cohort (late July) coincided between systems (Fig. 3). In 2004, peak hatch dates of the spring cohort were 1 month earlier in Chesapeake Bay (mid-April) than in the coastal ocean (mid-May). Peak hatch dates of the summer cohort in 2004 were early July and late June in the coastal ocean and

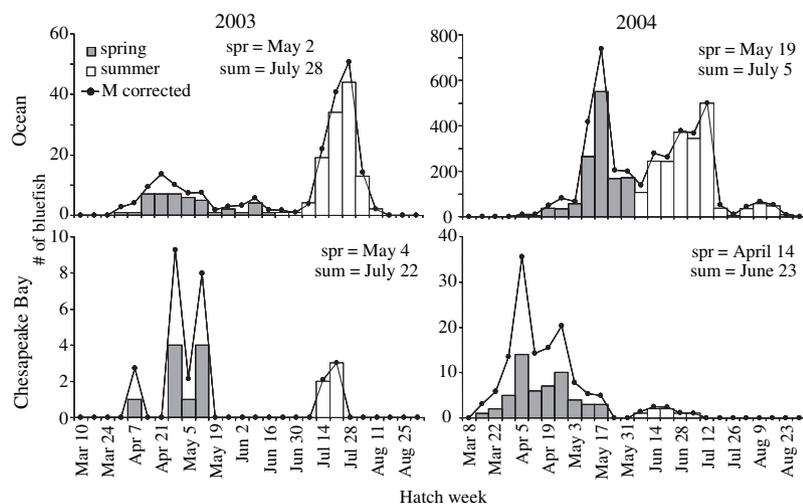


Figure 3. Hatch date frequencies of juvenile bluefish (2003–04) in Maryland coastal waters and Chesapeake Bay. Spring cohort represented by gray stippled bars, summer cohort white bars, and frequencies adjusted for cumulative mortality illustrated by black line. Median hatch dates reported for spring (spr) and summer (sum) cohorts.

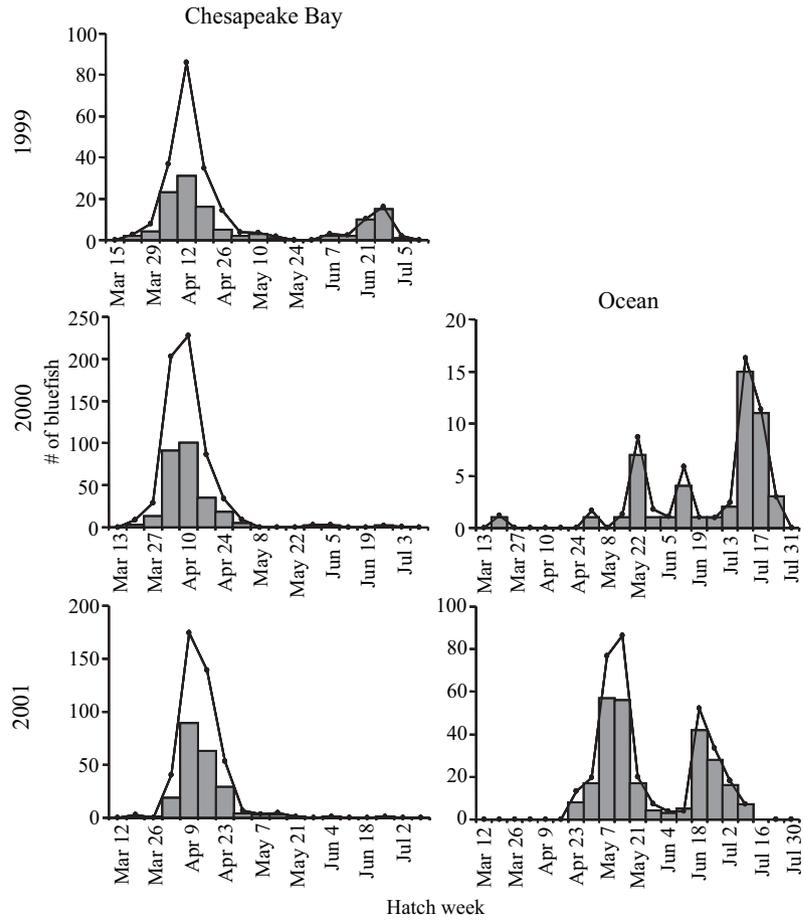


Figure 4. Hatch date frequencies of juvenile bluefish in Chesapeake Bay (1999–2001) and Maryland coastal waters (2000–01). Solid line represents frequencies corrected for cumulative mortality.

Chesapeake Bay, respectively. More importantly, peak hatch dates of the summer cohort were ca. 1 month earlier in 2004 than 2003, irrespective of system (Fig. 3).

Hatch date distributions from 1999 to 2001 showed that peak hatch dates for the spring cohort in Chesapeake Bay were consistently mid-April across years, similar to 2004 (Fig. 4). Further, for bluefish collected in the coastal ocean during August and September, hatch dates spanned from late April to July and recruits with June hatch dates were more common in 2001 (26.6%) than 2000 (17.2%) (Fig. 4).

Shelf temperatures

Median June temperatures differed significantly among years (Kruskal–Wallis test, $P < 0.0001$). Specifically, median June temperatures were significantly lower in 2003 than 2004 and 2001 in both regions (Delaware and Virginia), and lower, but not significantly so, in 2003 than 2000 off Delaware (Table 1). Accordingly, 2003 surface temperatures off Delaware were below the spawning threshold (18°C) for the entire month of June, except the last week; off Virginia, temperatures

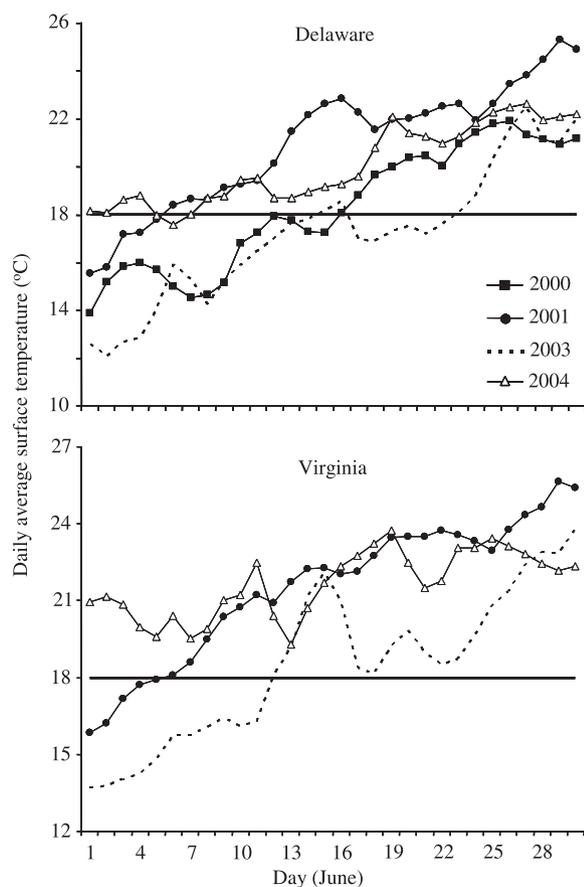
Table 1. Comparison of average June sea surface temperatures among years for shelf waters off Delaware and Virginia.

Year	Average June SST (°C)	
	Delaware	Virginia
2000	18.0 ^a	N/A
2001	20.9 ^b	22.1 ^a
2003	17.2 ^a	18.6 ^b
2004	19.5 ^b	21.7 ^a

SST, sea surface temperature. Mean June temperatures with different letters (within each region) are significantly different based on non-parametric Tukey-type multiple comparisons using the Nemenyi test.

were below 18°C (June 1–15) or hovered slightly above the threshold (June 16–30) (Fig. 5). Conversely, in 2004, surface temperatures were well above 18°C during the entire month of June in both regions (Fig. 5). In 2001, surface temperatures remained above 18°C after the first week of June in both regions; in 2000 off Delaware, surface temperatures were above the threshold during the latter half of June (Fig. 5).

Figure 5. Daily average surface water temperatures during the month of June for various years, recorded at mid-shelf locations off Delaware (NOAA buoy #44009) and Virginia (NOAA buoy #44014). The solid reference line at 18°C represents the minimum temperature at which bluefish eggs have been collected.



Cohort representation

Controlling for year, relative cohort frequencies depended on system (Cochran–Mantel–Haenszel test, $P < 0.0001$). The similar direction of the odds ratio of the cohort \times system relationship each year indicated that relative cohort frequencies differed between systems in a similar manner, with spring and summer cohorts more common in Chesapeake Bay and the coastal ocean, respectively. However, the magnitude of the odds ratio for the cohort \times system relationship differed significantly across years as indicated by a homogenous association test (Breslow–Day test, $P = 0.009$). The odds of capturing a summer– rather than spring-spawned bluefish were 3.3 times (2003) and 15.2 times (2004) higher in the coastal ocean than in Chesapeake Bay; it follows that the odds of capturing a spring– rather than summer-spawned bluefish

Table 2. Cohort frequencies of young-of-the-year bluefish (corrected for cumulative mortality) by year and system.

Year	System	Cohort	
		Spring (%)	Summer (%)
2003	Ocean	184 (57.5)	136 (42.5)
	Chesapeake Bay	22 (81.5)	5 (18.5)
2004	Ocean	2541 (50.9)	2455 (49.1)
	Chesapeake Bay	126 (94.0)	8 (6.0)

Observed cell counts and row percents reported.

were 3.3 times (2003) and 15.2 times (2004) higher in Chesapeake Bay than in the coastal ocean. Relative cohort proportions showed the same pattern of spring cohort dominance in Chesapeake Bay and were eight to nine times higher for the spring cohort across years (Table 2). In contrast, spring and summer cohorts appeared to contribute roughly equally to abundance in the coastal ocean across years (Table 2).

Reconstructed historical hatch dates for bluefish in Chesapeake Bay indicated that the spring cohort dominated in this estuarine system across a multi-decadal period. Hatch date distributions were generally unimodal (with the arguable exception of the 1975–79 period) and right skewed, spanning from late March to early July (Fig. 6). Peak hatch dates for spring-spawned bluefish were generally late April/early May, with the exception of the 2000–06 period, when earlier (mid-April) peak hatch dates were observed (Fig. 6). Early summer-spawned bluefish with June hatch dates constituted 10% of all bluefish across years; the proportion of bluefish with July hatch dates was only 2%.

Supplementary hatch dates based on 1999–2001 samples further supported the trend of dominance of the spring cohort in Chesapeake Bay and prevalence of the summer cohort in the coastal ocean. In Chesapeake Bay, the summer cohort was apparently absent in 2000 and 2001. In 1999, the summer cohort was present at 15% relative frequency and fish with June hatch dates were fairly common (Fig. 4). In the coastal ocean, the relative proportion of the summer cohort (mid-June through July hatch dates) was higher in 2000 (74%) than 2001 (35%) (Fig. 4).

DISCUSSION

The bimodal hatch date distributions of juvenile bluefish recruits to Maryland coastal waters and Chesapeake Bay found in this study corroborate results from previous bluefish recruitment studies concluding that two major spawning events, spring and summer,

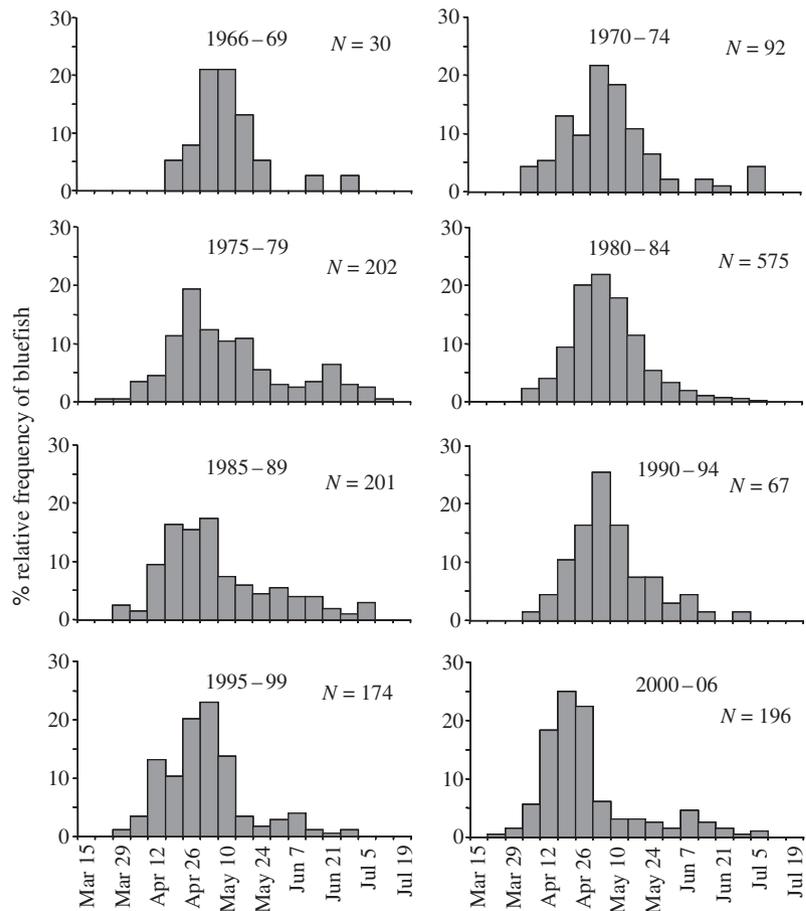


Figure 6. Historical hatch date frequencies of juvenile bluefish in Chesapeake Bay. N = number of bluefish whose hatch dates were estimated in each 5-yr time period.

contribute to juvenile production each year along the US east coast. Still, our results do not fully support either of the opposing contemporary views that: (i) spring- and summer-spawning episodes are strictly 'discrete' with no spawning occurring in the interim (Chiarella and Conover, 1990; McBride and Conover, 1991; Juanes and Conover, 1995) or (ii) spawning is 'continuous' with higher mortality of progeny from late spring/early summer (Hare and Cowen, 1993). We aged juveniles recruiting to a transitional region (between the two principal spawning grounds) where bluefish hatch dates have not been documented previously. Late spring/early summer (May–June) shelf temperatures appeared to influence the local production of young bluefish in this region, as recruits with June hatch dates were rare in 2003 when temperatures were below those required for spawning activity and common in 2004 when temperatures were suitable for spawning. Hence, the incidence of early summer spawning, which is dependent on suitable temperatures, may control the pattern of split cohort production.

Cohort representation differed between estuarine and oceanic macrohabitats. Hatch dates from 1999 to 2001, 2003 to 2004, and the historical hatch date reconstructions all clearly showed that the spring cohort dominated in Chesapeake Bay. The summer cohort was only prevalent in ocean habitats, where the spring cohort was also present.

Temperature control on spawning behavior

Most mature bluefish make north-south seasonal migrations between the MAB and SAB, migrating north to the MAB during spring and south during fall to primary SAB over-wintering areas off North and South Carolina. Various lines of evidence suggest the northern spring migration occurs during May, when commercial catches and recaptures of tagged fish show northward shifts in distribution from the SAB to the MAB (Lund and Maltezos, 1970; Shepherd *et al.*, 2006). Further, surface temperatures on the MAB shelf during late May are suitable for adults as historical NOAA buoy temperature data (Delaware 1984–85, 1987–96, 1998–2006; Virginia 11 yr from 1991 to

2005) indicated that SSTs typically reached the minimum of the preferred temperature range of adult bluefish (14°C) (Bigelow and Schroeder, 1953; Lund and Maltezos, 1970; Shepherd and Packer, 2006) during the latter half of May.

If surface water temperatures are conducive for spawning (>18°C) when bluefish arrive in MAB shelf waters during late May to early June, then spawning may continue as an extension of spring spawning that began in the SAB, which peaks in April and proceeds north during May as bluefish commence their migration to the MAB. Otherwise, if temperatures upon arrival to the MAB are too cool for spawning, there may be a cessation of spawning until temperatures are suitably warm. During June, bluefish continue their northward transit and move through the Virginia–Maryland–Delaware corridor of the MAB to the principal summer-spawning grounds off New Jersey. Spawning may continue through June if temperatures remain suitably warm. As evidence, we observed that bluefish with June hatch dates were rare in 2003 when shelf temperatures off both Virginia and Delaware were below the spawning threshold for almost the entire month of June; yet in 2004, when shelf temperatures were above the spawning threshold for the entire month of June, recruits with June hatch dates (i.e., the ‘intervening cohort’) were common. Furthermore, surface waters off Delaware reached 18°C 10 days earlier in 2001 (June 6) than 2000 (June 16);

accordingly recruits with June hatch dates were more common in 2001. Also, the highest proportions of June recruits in Chesapeake Bay were observed in 1999 and 2004, years when shelf temperatures were above 18°C the entire month of June in both regions. Hence, late spring/early summer SST trends in the MAB shelf region from Virginia to Delaware appear to influence spawning incidence of bluefish as they migrate from major spawning grounds in the SAB to those in the MAB.

Vernal warming patterns in a given year may be an integral factor influencing the extent of cohort splitting in bluefish. For instance, under conditions of intense and/or advanced vernal warming, surface waters could support spawning and the production of the intervening cohort, leading to less discrete cohorts. Conversely, when vernal warming is slow and/or delayed, cooler waters could lead to a longer cessation of spawning, contributing to a greater degree of cohort splitting. In 2003 and 2004 off Virginia and Delaware, vernal surface warming began in mid-April when warming trends of surface waters began to closely parallel local air temperatures (Fig. 7). Water temperatures increased through late April and were similar, between years, in respective regions by early May. However, a profound difference between years was the divergence of surface temperatures during May in both regions, whereby water temperatures essentially ‘stalled’ during May in 2003 but increased rapidly

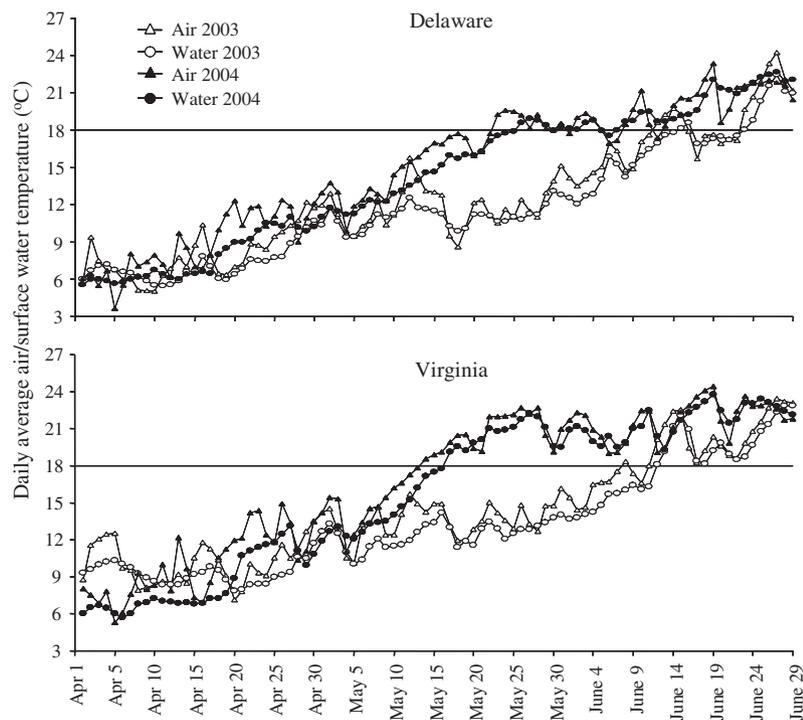


Figure 7. Daily average air and surface water temperatures (April–June) off Delaware (NOAA buoy #44009) and Virginia (NOAA buoy #44014). The solid reference line at 18°C represents the minimum temperature at which bluefish eggs have been collected.

throughout May in 2004 (Fig. 7). Air temperatures appeared to drive this trend as May air temperatures were 4–5°C cooler in 2003 than 2004.

Interannual variability in the timing and intensity of vernal warming, driven chiefly by mesoscale solar heating dynamics, may determine the spawning window for bluefish in the southern MAB during late spring/early summer. Interestingly, Jossi and Benway (2003) found that the highest interannual variability (2–3°C) in SSTs in the MAB for given biweekly intervals occurred during the first two weeks of June. The amount of coastal runoff and dynamics of buoyant plumes from Chesapeake and Delaware Bays may also influence the magnitude (more than timing) of vernal warming. Specifically, the upper water column becomes more stabilized under conditions of decreased surface salinity (i.e., increased runoff) and decreased wind mixing, facilitating more rapid warming of surface waters (Mountain and Taylor, 1998).

To characterize 'typical' vernal warming patterns in the southern MAB, we analyzed historical SST data (May through June: Delaware 1984–85, 1987–96, 1998–2006; Virginia 11 yr from 1991 to 2005). Temperatures exhibited a steady increase during the warming period, and rarely dropped below the 18°C spawning threshold once this benchmark was reached. Across years within each region, the average date at which SSTs exceeded 18°C was June 5 off Virginia and June 10 off Delaware. Because more years of data were available for the Delaware region, these data were used to develop an index to predict spawning behaviors of bluefish based on temperature trends. During most years (15 of 21 or 71%), surface temperatures off Delaware did not warm to 18°C until the second or third week of June, hence, there is likely a cessation of spawning during late spring/early summer in most years. During the other 6 yr, temperatures reached 18°C by late May (1991, 2002, and 2004) or early June (by June 4 for 1989, 1995, and 1999). Interestingly, 2003 and 2004 were the most anomalous years on record in terms of the date at which the spawning threshold was exceeded, the earliest date occurred in 2004 and the latest date occurred in 2003. This was similarly true for the Virginia temperature record. Therefore, the hatch date patterns we observed in 2003 (a 7-week gap from late May through early July) and 2004 (a continuous distribution) may represent the extremes of a continuum of potential cohort splitting patterns in bluefish.

Our temperature hypothesis predicts that the intervening cohort should be abundant when vernal warming is considerably advanced and virtually absent when vernal warming is substantially delayed. Con-

ceivably, patterns of cohort splitting of bluefish could be predicted by analyzing buoy- or satellite-derived (e.g., Advanced Very High Resolution Radiometer) shelf temperatures during late spring/early summer in the MAB region.

Tagging and commercial catch data indicate that some larger bluefish may not undertake north-south migrations between the SAB and MAB, but rather are resident to the MAB and undergo inshore–offshore migrations, moving inshore to shelf waters during spring from offshore over-wintering areas near the shelf-break or beyond (Lund and Maltezos, 1970; Wilk, 1977; Shepherd *et al.*, 2006). Our temperature hypothesis would also apply to this group of fish, which under suitable temperature regimes could contribute to production of the intervening and/or summer cohorts. We expect that 'year-round' MAB adults would move into shelf waters as early as the beginning of May (Lund and Maltezos, 1970), but would not spawn until surface temperatures were sufficiently warm.

In addition to controlling production of the intervening cohort, SST trends also appeared to influence the timing of peak summer spawning, with earlier peak activity under warmer conditions. Peak hatch dates of the summer cohort were more than 3 weeks earlier, across systems, in 2004 than 2003, when vernal warming was advanced and higher SSTs (ca. 2°C) continued throughout July. Similarly, Norcross *et al.* (1974) suggested that cool temperatures (17–19°C) during June 1960 delayed bluefish spawning offshore of the Chesapeake Bay mouth in comparison with June 1961 when SSTs were 21–22°C. SST warming trends may also influence timing of the onset and peak spring spawning in the SAB. However, ichthyoplankton collections in the SAB have not been as synoptic and systematic as those in the MAB, and only larvae have been noted in SAB ichthyoplankton collections (Fahay, 1975; Powles, 1981; Kendall and Walford, 1979; Collins and Stender, 1987). Hence, exact spawning locations of bluefish in the SAB are unknown. Furthermore, while the 18°C spawning threshold used herein for the MAB may be general for the Atlantic bluefish, insufficient temperature data exist to test this relationship for the SAB. Consequently, these data limitations precluded us from analyzing relationships between hatch dates of the spring cohort observed in this study and SST trends in the SAB.

One caveat of using hatch dates to infer spawning patterns is the assumption that mortality of larval and juvenile bluefish is fairly constant (i.e., minimal selective mortality). Possible agents of selective mortality include physical transport processes, predation

pressure, and competition. We examined June wind data recorded from the same buoys used in temperature analyses to examine whether the difference in representation of the intervening cohort between years 2003 and 2004 might be due to differing wind-driven transport regimes. Daily average wind vectors were predominantly directed towards the northwest to northeast and of similar magnitude ($2\text{--}8\text{ m s}^{-1}$) in both years for each region. Hence, larval transport pathways were likely similar between years and did not contribute to the observed interannual difference in the contribution of the intervening cohort.

Predominantly northward winds during summer over mid-shelf waters of the MAB found in this study and others (Boicourt, 1982; Epifanio *et al.*, 1989; Epifanio and Garvine, 2001) would lead to retention of larval bluefish produced during June and curtail flux to the SAB. Most bluefish eggs collected during June have been observed in mid-shelf waters from Cape Hatteras to southern New Jersey (Berrien and Sibunka, 1999). Expected patterns of larval drift, accounting for Ekman drift of surface waters, would be north to northeast in the MAB. Using the conversion factor from Epifanio and Garvine (2001) – that 1.6 cm s^{-1} of surface current is generated for every 1 m s^{-1} of alongshelf wind and the average alongshelf wind magnitude across years for Delaware and Virginia of 4.3 m s^{-1} – expected surface currents during June in mid-shelf waters of the MAB would be 5.9 km day^{-1} . Assuming that larval bluefish metamorphose to juveniles at 18–25 days (Hare and Cowen, 1994) and completely passive transport (i.e., minimal larval swimming), the potential recruitment range of the intervening cohort would be from southern Virginia to northern New Jersey, an area encompassing our sampling domain. Active swimming can modify expected passive transport pathways and distances, particularly for more competent or late stage larvae. Juveniles likely rely on swimming as the chief mechanism to cross the shelf to reach nearshore nursery grounds.

Another caveat in this study was the possible error in estimating hatch dates with ALKs. However, the interannual difference in contribution of the intervening cohort was not an artifact of hatch date estimation methods because raw hatch dates also showed that the intervening cohort was rare in 2003 (6% of coastal ocean samples had June hatch dates) and common in 2004 (23%).

Cohort representation between systems

We observed that the two dominant bluefish cohorts exhibited consistently different recruitment outcomes, with the spring cohort primarily recruiting to Chesapeake

Bay and the summer cohort recruiting almost exclusively to Maryland coastal waters. Our findings agree with previous recruitment studies that have traditionally focused on estuaries (Nyman and Conover, 1988; McBride and Conover, 1991; McBride *et al.*, 1993, 1995; Creaser and Perkins, 1994) and add to a growing body of evidence, from more recent studies, that coastal ocean habitats function as important nurseries for summer-spawned bluefish (Able *et al.*, 2003; Taylor *et al.*, 2006).

Spawning geography and associated larval transport may explain the disparity in summer cohort representation between systems. During peak summer spawning in July, high egg densities are observed in inner shelf (to within 10 km of shore) to mid-shelf waters off New Jersey and Delaware Bay (Smith *et al.*, 1994; Berrien and Sibunka, 1999). The coastal current of the inner MAB shelf extends to ca. 20 km offshore and flows southward because of buoyancy-driven outflow from major MAB estuaries (e.g., Hudson River, Delaware Bay, and Chesapeake Bay) (Boicourt, 1982; Wong, 1999; Epifanio and Garvine, 2001). Accordingly, larval drift in the coastal current would be towards the south and veer toward the southwest (i.e., onshore) because of Ekman transport. Our ocean sampling area is within 50 km to the south of the epicenter of major summer spawning; therefore, we would expect high recruitment probability of the summer cohort because larvae would be swept southward towards Maryland in the coastal current. Conversely, recruitment probability of the summer cohort may be lower in Chesapeake Bay as the bay mouth is ca. 250 km south of the spawning epicenter, a distance well exceeding that of expected larval drift under typical coastal current flows of 5 cm s^{-1} (Wong, 1999). Hence, recruitment to Chesapeake Bay would require an extensive and possibly energetically taxing southern migration of juveniles.

Recruitment potential of the summer cohort may be higher in more northern estuaries (e.g., New Jersey and New York) than Chesapeake Bay. Specifically, larvae produced in mid-shelf waters (seaward of the coastal current) would be carried north of the spawning epicenter because surface flows in mid-shelf waters during summer are typically northward in association with prevailing winds (as described above). Still, low abundances and sporadic occurrences of the summer cohort have been reported in northern estuaries (Nyman and Conover, 1988; McBride and Conover, 1991; McBride *et al.*, 1995; Able *et al.*, 2003). One possibility explaining this discrepancy is that most of these studies occurred during the 1980s and early 1990s when the summer cohort reportedly

exhibited low coast-wide abundance (Conover *et al.*, 2003). However, all studies except Nyman and Conover (1988) did include some years in which coast-wide abundances were higher for the summer than spring cohort: 1988, 1992, and 1998 (see Conover *et al.*, 2003). Although McBride and Conover (1991) found higher abundance of the summer cohort during 1988 in New York and New Jersey estuaries, McBride *et al.* (1995) found higher abundances of the spring cohort in Narragansett Bay, Rhode Island that same year and also reported higher abundance of the spring versus summer cohort in 1992. Moreover, Able *et al.* (2003) found one to two orders of magnitude higher abundance of the summer cohort in ocean habitats than estuaries of New Jersey during 1998. Thus, across studies, evidence supports the view that the summer cohort predominates in oceanic nursery habitats.

Prey and temperature characteristics during the recruitment periods of spring and summer cohorts may explain the differences we observed in their utilization of macrohabitats. The chief prey item of juvenile bluefish in the coastal ocean is bay anchovy, *Anchoa mitchilli* (Buckel *et al.*, 1999; Callihan, 2005). We observed much higher abundances of bay anchovy, which were of a more appropriate size for predation (small YOY), during August–September (summer recruitment) than May–July (spring recruitment) in Maryland coastal waters across all years (Callihan, 2005). Furthermore, coastal water temperatures were much warmer during summer (20–22°C) than spring (13–19°C). Thus, an adequate forage base and suitable temperatures in the coastal ocean during late summer likely facilitate differential recruitment of the summer cohort to this habitat. Meanwhile, the spring cohort recruits primarily to estuaries probably because warmer temperatures and a more abundant and diverse forage base (e.g., *Menidia*, *Anchoa*, and *Clupea* sp.) exist therein during spring relative to ocean habitats.

Although the spring cohort appears to primarily utilize estuaries as nurseries, some individuals of the spring cohort will also use ocean habitats. As evidence, we observed moderate abundance of the spring cohort in Maryland coastal waters during July–September in 2003 and 2004; August–September in 2000 and 2001. Also, Able *et al.* (2003) collected spring-spawned bluefish (based on presumed sizes) in the coastal ocean off New Jersey from July to September, albeit at lower abundances than the summer cohort. However, the occurrence of spring-spawned bluefish in the coastal ocean does not necessarily imply residence, as these individuals may be *en route* to estuarine environments.

The degree to which juvenile bluefish reside in a particular macrohabitat is difficult to determine given their ability to rapidly disperse. Two recent studies provide evidence of minimal exchange between estuarine and oceanic environments after recruitment to a particular macrohabitat. Able *et al.* (2003) found no exchange of tagged (coded wire tags) YOY bluefish between oceanic and estuarine habitats of New Jersey; higher recapture rates occurred in estuaries (2.2%) than in surf-zone ocean habitats (0.04%). However, sampling rates and related power were expected to be quite low in this study. Takata (2004) employed otolith microchemical analyses (Sr : Ca ratios of life history transects) to evaluate habitat use. Her study indicated that all summer-spawned bluefish captured in Maryland coastal waters had remained resident in the coastal ocean throughout summer; the majority of spring-spawned bluefish collected in Chesapeake Bay exhibited Sr : Ca values indicative of estuarine residency. These results suggest that spring and summer cohorts persist in a given macrohabitat after initial recruitment to either estuarine or oceanic nurseries. Yet, it remains unclear whether spring-spawned bluefish in the coastal ocean remain resident there, are *en route* to estuaries or coastal bays, move to other regions of the coastal ocean, or move further offshore with increasing size. Opportunistic habitat use of the coastal ocean by the spring cohort could explain the higher than expected contributions (Table 2) and fluctuating monthly catches we observed for this cohort.

Differential recruitment patterns of seasonal, or split cohorts, have also been observed in the MAB for windowpane, *Scopthalmus aquosus* (Neuman and Able, 2003), and may exist for other coastal-spawning fishes upon further investigation (Secor, 2007). Spawning behaviors leading to temporally split cohorts which utilize different habitats as nurseries likely act as a bet-hedging strategy to buffer against both spatial and temporal variability in survival conditions during the first year of life. Furthermore, the fact that seasonal bluefish cohorts depend on different macrohabitats as nurseries highlights the need to protect both estuarine and nearshore oceanic environments in management plans for this important fishery species.

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REFERENCES

- Able, K.W. and Fahay, M.P. (1998) *The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight*. New Brunswick, NJ: Rutgers University Press, 342 pp.
- Able, K.W., Rowe, P., Burlas, M. and Byrne, D. (2003) Use of ocean and estuarine habitats by young-of-the-year bluefish (*Pomatomus saltatrix*) in the New York Bight. *Fish. Bull.* **101**:201–214.
- Abramson, N.J. (1971) Computer programs for fish stock assessment. *FAO Fish. Tech. Pap.* **101**:148 pp.
- Agresti, A. (1996) *An Introduction to Categorical Data Analysis*. New York: John Wiley and Sons, Inc., 290 pp.
- Berrien, P.L. and Sibunka, J.D. (1999) Distribution patterns of fish eggs in the U.S. northeast continental shelf ecosystem, 1977–1987. *NOAA Tech. Rep. NMFS* **145**:310 pp.
- Berrien, P.L. and Sibunka, J.D. (2006) *A Laboratory Guide to the Identification of Marine Fish Eggs on the Northeast Coast, 1977–1994*. Woods Hole, MA: Northeast Fisheries Science Center Reference Document 06-21.
- Bigelow, H.B. and Schroeder, W.C. (1953) Fishes of the Gulf of Maine. *Fish. Bull.* **74**:383–389.
- Boicourt, W.C. (1982) Estuarine larval retention mechanisms on two scales. In: *Estuarine Comparisons*. V. Kenn (ed) New York: Academic Press, pp. 445–458.
- Briggs, J.C. (1960) Fishes of worldwide (circumtropical) distribution. *Copeia* **1960**:171–180.
- Brown, A.L. and Bailey, K.M. (1992) Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. *Mar. Biol.* **112**:23–30.
- Buckel, J.A., Fogarty, M.J. and Conover, D.O. (1999) Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf. *Fish. Bull.* **97**:758–775.
- Callihan, J.L. (2005) *Ecology of Juvenile Bluefish (Pomatomus saltatrix) in Maryland Coastal Waters and Chesapeake Bay*, MS Thesis. College Park, MD: University of Maryland, 213 pp.
- Campana, S.E. and Jones, C.M. (1992) Analysis of otolith microstructure data. In: *Otolith Microstructure Examination and Analysis*. *Can. Spec. Publ. Fish. Aquat. Sci.* **117**. D.K. Stevenson & S.E. Campana (eds) Ottawa: Canada Communication Group-Publishing, pp. 73–100.
- Chiarella, L.A. and Conover, D.O. (1990) Spawning season and first-year growth of adult bluefish from the New York Bight. *Trans. Am. Fish. Soc.* **119**:455–462.
- Collins, M.R. and Stender, B.W. (1987) Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. *Bull. Mar. Sci.* **41**:822–834.
- Conover, D.O., Gilmore, T. and Munch, S.B. (2003) Estimating the relative contribution of spring- and summer-spawned cohorts to the Atlantic coast bluefish stock. *Trans. Am. Fish. Soc.* **132**:1117–1124.
- Creaser, E.P. and Perkins, H.C. (1994) The distribution, food, and age of juvenile bluefish, *Pomatomus saltatrix*, in Maine. *Fish. Bull.* **92**:494–508.
- Deuel, D.G., Clark, J.R. and Mansueti, A.J. (1966) Description of embryonic and early larval stages of bluefish, *Pomatomus saltatrix*. *Trans. Am. Fish. Soc.* **95**:264–271.
- Ebert, T.A., Schroeter, S.C. and Dixon, J.D. (1993) Inferring demographic processes from size frequency distributions: effect of pulsed recruitment on simple models. *Fish. Bull.* **91**:237–243.
- Epifanio, C.E. and Garvine, R.W. (2001) Larval transport on the Atlantic continental shelf of North America. *Estuar. Coast. Shelf Sci.* **52**:51–77.
- Epifanio, C.E., Masse, A.K. and Garvine, R.W. (1989) Transport of blue crab larvae by surface currents off Delaware Bay, USA. *Mar. Ecol. Prog. Ser.* **54**:35–41.
- Fahay, M.P. (1975) An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV Dolphin cruises between May 1967 and February 1968. *NOAA Technical Report NMFS*. Seattle, WA: SSRF-685, 39 pp.
- Graves, J.E., McDowell, J.R., Beardsley, A.M. and Scoles, D.R. (1992) Stock structure of the bluefish *Pomatomus saltatrix* along the mid-Atlantic coast. *Fish. Bull.* **90**:703–710.
- Hare, J.A. and Cowen, R.K. (1993) Ecological and evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. *Mar. Ecol. Prog. Ser.* **98**:1–16.
- Hare, J.A. and Cowen, R.K. (1994) Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). *Mar. Biol.* **118**:541–550.
- Hare, J.A. and Cowen, R.K. (1996) Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. *Limnol. Oceanogr.* **41**:1264–1280.
- Jossi, J.W. and Benway, R.L. (2003) Variability of temperature and salinity in the Middle Atlantic Bight and Gulf of Maine based on data collected as part of the MARMAP ships of opportunity program, 1978–2001. *NOAA Tech. Rep. NMFS* **172**:92 pp.
- Juanes, F. and Conover, D.O. (1995) Size-structured piscivory: advection and the linkage between predator and prey recruitment in young-of-the-year bluefish. *Mar. Ecol. Prog. Ser.* **128**:287–304.
- Juanes, F., Hare, J.A. and Miskiewicz, J.A. (1996) Comparing early life history strategies of *Pomatomus saltatrix*: a global approach. *Mar. Freshw. Res.* **47**:365–379.
- Kendall, A.W. and Walford, L.A. (1979) Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. *Fish. Bull.* **77**:213–227.
- Lund, W.A. and Maltezos, G.C. (1970) Movements and migrations of the bluefish, *Pomatomus saltatrix*, tagged in waters of New York and southern New England. *Trans. Am. Fish. Soc.* **4**:719–725.
- McBride, R.S. and Conover, D.O. (1991) Recruitment of young-of-the-year bluefish *Pomatomus saltatrix* to the New York Bight: variation in abundance and growth of spring and summer-spawned cohorts. *Mar. Ecol. Prog. Ser.* **78**:205–216.
- McBride, R.S., Ross, J.L. and Conover, D.O. (1993) Recruitment of bluefish *Pomatomus saltatrix* to estuaries of the U.S. *South Atlantic Bight. Fish. Bull.* **91**:395–398.

- McBride, R.S., Scherer, M.D. and Powell, J.C. (1995) Correlated variations in abundance, size, growth, and loss rates of age-0 bluefish in a southern New England estuary. *Trans. Am. Fish. Soc.* **124**:898–910.
- Mountain, D.G. and Taylor, M.H. (1998) Spatial coherence of interannual variation in water properties on the U.S. northeast shelf. *J. Geophys. Res.* **103**:3083–3092.
- Munch, S.B. (1997) *Recruitment Dynamics of Bluefish, Pomatomus saltatrix*, on the Continental Shelf from Cape Fear to Cape Cod, 1973–1995, MS Thesis. Stony Brook, NY: State University of New York, 127 pp.
- Munch, S.B. and Conover, D.O. (2000) Recruitment dynamics of bluefish (*Pomatomus saltatrix*) from Cape Hatteras to Cape Cod, 1973–1995. *ICES J. Mar. Sci.* **57**:393–402.
- Neuman, M.J. and Able, K.W. (2003) Inter-cohort differences in spatial and temporal settlement patterns of young-of-the-year windowpane, *Scophthalmus aquosus*, in southern New Jersey. *Estuar. Coast. Shelf Sci.* **56**:527–538.
- Norcross, J.J., Richardson, S.L., Massmann, W.H. and Joseph, E.B. (1974) Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginian coastal waters. *Trans. Am. Fish. Soc.* **103**:477–497.
- Nyman, R.M. and Conover, D.O. (1988) The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. *Fish. Bull.* **86**:237–250.
- Post, J.R., Johannes, M.R.S. and McQueen, D.J. (1997) Evidence of density dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. *Can. J. Fish. Aquat. Sci.* **54**:867–875.
- Powles, H. (1981) Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* **178**:207–209.
- Secor, D.H. (2007) The year-class phenomenon and the storage effect in marine fishes. *J. Sea Res.* **57**:91–103.
- Secor, D.H., Dean, J.M. and Laban, E.H. (1992) Otolith removal and preparation for microstructural examination. In: *Otolith Microstructure Examination and Analysis*. *Can. Spec. Publ. Fish. Aquat. Sci.* **117**. D.K. Stevenson & S.E. Campana (eds) Ottawa: Canada Communication Group-Publishing, pp. 19–57.
- Shepherd, G.R. and Packer, D.B. (2006) Essential Fish Habitat Source Document: Bluefish, *Pomatomus saltatrix*, life history and habitat characteristics. NOAA Tech. Rep. NMFS **198**:89 pp.
- Shepherd, G.R., Moser, J., Deuel, D. and Carlsen, P. (2006) The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries. *Fish. Bull.* **104**:559–570.
- Smith, W., Berrien, P. and Potthoff, T. (1994) Spawning patterns of bluefish, *Pomatomus saltatrix*, in the northeast continental shelf system. *Bull. Mar. Sci.* **54**:8–16.
- Takata, L.T. (2004) *Habitat Use and Cohort Recruitment Dynamics of Juvenile Bluefish, Pomatomus saltatrix*, in diverse Maryland nursery systems, MS Thesis. College Park, MD: University of Maryland, 110 pp.
- Taylor, D.L. and Able, K.W. (2006) Cohort dynamics of summer-spawned bluefish as determined by length–frequency and otolith microstructure analyses. *Trans. Am. Fish. Soc.* **135**:955–969.
- Taylor, D.L., Rowe, P.M. and Able, K.W. (2006) Habitat use of the inner continental shelf off southern New Jersey by summer-spawned bluefish (*Pomatomus saltatrix*). *Fish. Bull.* **104**:592–604.
- Westrheim, S.J. and Ricker, W.E. (1978) Bias in using an age–length key to estimate age–frequency distributions. *J. Fish. Res. Bd. Can.* **35**:184–189.
- Wilk, S.J. (1977) Biological and fisheries data on bluefish, *Pomatomus saltatrix*. NOAA Tech. Rep. NMFS **11**:55 pp.
- Wong, K.-C. (1999) The wind driven currents on the Middle Atlantic Bight inner shelf. *Cont. Shelf Res.* **19**:757–773.