

Relative contribution of spring- and summer-spawned bluefish cohorts to the adult population: effects of size-selective winter mortality, overwinter growth, and sampling bias

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Abstract: Length distributions of juvenile bluefish (*Pomatomus saltatrix*) are bimodal, consisting of spring- and summer-spawned fish. Research during the 1990s from the northeastern United States suggested that the summer cohort contributes little to the adult population and that overwinter mortality may limit their survival. We examined length distributions of juvenile bluefish from before and after winter and found that the mean length of the summer cohort increased during winter. Based on a winter-growth experiment and temperatures from the two winters examined, changes in mean length were due to size-selective mortality for one year class and growth for the other. Despite evidence for winter mortality, summer-spawned bluefish were commonly caught at age 1. We reexamined the relative contribution of each cohort to the adult population using archived scales from North Carolina fisheries. Cohort origin of adults was determined by back-calculating length at age 1. One-third of adults consisted of summer-spawned fish, contrasting with previous research from the northeast. The differences in relative cohort abundance between the northeastern and southeastern United States arise from size-based migration in age-1 and age-2 bluefish (the dominant age groups sampled in these studies) and the size-selective gear and sampling season in which they were collected.

Résumé : Les distributions de la longueur des tasserzals (*Pomatomus saltatrix*) juvéniles sont bimodales, comprenant des poissons issus des fraies printanier, d'une part, et estival, d'autre part. Des travaux réalisés dans les années 1990 dans le nord-est des États-Unis donnaient à penser que l'apport de la cohorte estivale à la population adulte était faible et que la mortalité hivernale pouvait limiter la survie de cette cohorte. Nous avons examiné les distributions de la longueur de tasserzals juvéniles avant et après l'hiver et constaté que la longueur moyenne de la cohorte estivale augmentait durant l'hiver. À la lumière des résultats d'une expérience de croissance hivernale et des températures pour les deux hivers étudiés, il appert que la variation de la longueur moyenne soit due à une mortalité dépendant de la taille pour une classe d'âge et à la croissance pour l'autre. Bien que certaines observations indiquent la présence d'une mortalité hivernale, les prises comptaient de nombreux tasserzals d'un an issus du frai estival. Nous avons réexaminé la contribution relative de chaque cohorte à la population adulte à l'aide d'échelles archivées provenant de pêches en Caroline du Nord. La cohorte d'origine des adultes a été déterminée par rétrocalcul de la longueur à l'âge d'un an. Un tiers des adultes étaient des poissons issus du frai estival, des résultats qui tranchent avec ceux des travaux antérieurs pour le nord-est. Les différences sur le plan de l'abondance relative des cohortes entre le nord-est et le sud-est des États-Unis découlent de la migration dépendant de la taille chez les tasserzals d'un an et de deux ans (les principaux groupes d'âge échantillonnés dans le cadre de ces études), ainsi que des engins qui sélectionnent en fonction de la taille des poissons et de la saison durant laquelle les données ont été obtenues. [Traduit par la Rédaction]

Introduction

Many species of fish exhibit bet-hedging strategies for reproduction by varying spawning output temporally and spatially (Collins and Stender 1987; Secor 2007). By spreading out reproductive effort, these species increase the chance of producing offspring that will encounter favorable conditions, because mortality of early life stages in fishes varies temporally (Rice et al. 1987; Rutherford and Houde 1995) and spatially (Scharf 2000; Secor 2007). Variability in mortality is often examined at the larval and early juvenile stages, and sources of mortality may differ among cohorts spawned at different times of the year. For some species, cohorts spawned later in the season experience warmer temperatures, which enhances survival through increased growth rates and a subsequent reduction in the time larvae and juveniles spend at small, vulnerable sizes (Rice et al. 1987; Rutherford and Houde 1995). However, making conclusions about juvenile mortality that

are based solely on these early life stages may be misleading; cohorts spawned early in the season typically reach a larger size by the end of the year and as a result may have an advantage in surviving winter (Cargnelli and Gross 1996; Ludsin and DeVries 1997). One of the most effective ways to examine the relative value of different intra-annual cohorts, or spawning regions, is to sample adult fish and determine their temporal or spatial spawning origins using scales or otoliths (Cargnelli and Gross 1996; Thorrold et al. 2001; Conover et al. 2003). However, obtaining an unbiased sample of adult fish can be challenging, especially in marine systems (Hilborn and Walters 1992).

Bluefish (*Pomatomus saltatrix*) is a migratory species that has historically been difficult to manage owing to their complex life history and bet-hedging reproductive strategy (Wilson and Degenbol 2002; Conover et al. 2003; Wuenschel et al. 2012). Adult bluefish are batch spawners with a prolonged spawning season (Robillard et al.

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2008). Based on catches of eggs and larvae, spawning occurs throughout most of the year (Kendall and Walford 1979; Smith et al. 1994; Hare and Cowen 1996), but the majority of juveniles come from two spawning periods. The first group of juveniles each year is the spring-spawned cohort, with hatch dates typically between late March and early May (McBride and Conover 1991; Taylor et al. 2007; Callihan et al. 2008). The spring cohort originates from spawning in the South Atlantic Bight (SAB), which is defined by Cape Hatteras, North Carolina, and Cape Canaveral, Florida (Kendall and Walford 1979; Robillard et al. 2008). Juveniles from the spring cohort occur along the entire east coast because of larval transport in the Gulf Stream (Kendall and Walford 1979; Hare and Cowen 1996; Wuenschel et al. 2012). The second group of juveniles is the summer-spawned cohort, with hatch dates in late June and July (McBride and Conover 1991; Taylor et al. 2007; Callihan et al. 2008). Summer spawning of bluefish mostly takes place off the northeast coast (Smith et al. 1994; Robillard et al. 2008), so juveniles from the summer cohort mostly occur in coastal habitats of the Middle Atlantic Bight (MAB), which is defined by Cape Cod, Massachusetts, and Cape Hatteras, North Carolina (Wuenschel et al. 2012). The distinct spring and summer spawning periods result in bimodal length distributions of juveniles, and the two cohorts are easily identified (Munch and Conover 2000; Able et al. 2003). During the fall, juveniles in the MAB migrate south to overwinter in the SAB (Shepherd et al. 2006; Morley et al. 2007; Wuenschel et al. 2012).

Recent evidence suggests that the overwinter period of juvenile bluefish may be important in determining year class strength. Wiedenmann and Essington (2006) compared abundance of young-of-the-year (YOY) bluefish during the fall migration period with age-1 abundance the following year. They found an asymptotic relationship suggesting density-dependent mortality during the winter. Morley et al. (2007) addressed several questions related to overwintering in juvenile bluefish. Owing to the large difference in size between spring- and summer-spawned fish, their overwintering strategies differ. Summer-spawned fish accumulate less energy stores during the fall, and they incur a greater energetic deficit during severe winters. Also, evidence for negative size-selective mortality of the summer cohort was found. This suggests that winter mortality may be greater for the summer cohort. However, Morley et al. (2007) was only able to examine one year class for size-selective mortality, so its prevalence and the influence of winter severity is uncertain. Further, the assumption that YOY bluefish do not grow during the winter has not been experimentally tested; if growth occurs, analysis of size-selective mortality would be biased.

If mortality rates differed greatly between the spring and summer cohorts during winter, their relative abundance in the adult population may not be related to their abundance as juveniles. The difference in size between cohorts at the end of their first year allows the cohort identity of adult fish (age 1+) to be determined by back-calculating length at the time of first annulus formation (i.e., length at age 1). Lassiter (1962) was the first to do this using scales from adult bluefish captured off North Carolina in 1960–1961; around one-third of the adult fish belonged to the summer cohort. Chiarella and Conover (1990) examined the 1981–1984 year classes using adults from the MAB and found almost entirely spring-spawned fish. However, recruitment of the summer cohort was relatively low for those year classes (Conover et al. 2003). Most recently, Conover et al. (2003) examined the 1991–1998 year classes using adults from the MAB. They also found poor contribution by summer-spawned fish, which was surprising because recruitment of the summer cohort was strong during those years. They hypothesized that decadal scale changes in overwinter mortality of the summer cohort may influence their contribution to the adult population. For example, low winter mortality of juvenile summer-spawned fish during Lassiter's (1962) study may explain why he found more of them in the adult population. An alternative explanation is that the sampling location for adults influ-

ences estimates of the relative contribution of the spring and summer cohorts. For example, summer-spawned fish may be less likely to migrate north into the MAB at younger ages owing to their smaller size. The majority of adults examined by Lassiter (1962) and Conover et al. (2003) were ages 1 and 2.

In this paper we estimate the relative contribution of two intra-annual cohorts to the adult bluefish population and examine mechanisms responsible for differential contribution. First, we expand upon the work of Morley et al. (2007) in looking for evidence of size-selective winter mortality of the summer cohort over multiple years by comparing length distributions from before and after winter. To ensure the accuracy of this approach, we tested the assumption that growth does not occur during the winter with a laboratory experiment. The second component of this paper tests the hypothesis that the relative abundance of spring- and summer-spawned bluefish in the adult population differs between the MAB and SAB. We examined archived scale samples from adult bluefish collected off North Carolina and compared the relative cohort abundance from the same year classes that were sampled in the MAB by Conover et al. (2003). We also examined how size-based migration strategies of age-1 and age-2 bluefish may lead to spatial and temporal sampling bias when estimating relative cohort contribution to the adult population. Last, the back-calculation technique assumes that the first annulus is formed on scales at the beginning of the second growing season. We validate this assumption with marginal increment analysis using scales from age-1 bluefish.

Materials and methods

Size-selective overwinter mortality of field-caught bluefish

Field sampling to examine the potential for size-selective mortality in juvenile bluefish was conducted monthly with otter trawls (30 m head rope) of 20 min duration between November 2004 and April 2008. During this period, there was a hiatus in sampling between January and October 2007. Trawling was conducted in Onslow Bay, North Carolina, on two transects, each oriented perpendicularly to the shore. Tows were conducted at 3 knots (1 knot = 0.514 m·s⁻¹), parallel to shore, at six different locations on each transect: 0.4, 0.8, 1.6, 3.2, 5.6, and 8 km from shore. Temperature was recorded throughout the sampling period at 30 min intervals with a data logger placed on the Suloid wreck in Onslow Bay, which is located 15 km from shore (P.E. Whitfield and G.G. Purifoy, Jr., NOAA Beaufort Laboratory, North Carolina, unpublished data).

Negative size-selective winter mortality of the summer-spawned cohort was examined for the 2004, 2005, and 2007 year classes. The sampling hiatus in spring of 2007 prevented examination of the 2006 year class. We compared length frequency histograms from catches before and after winter. An increase in the mean fork length (FL) and a decrease in variance over the winter indicate higher mortality of small individuals, provided that no growth occurs. Based on examination of monthly length distributions, growth of the summer cohort ceases in November and resumes in April or early May (Morley et al. 2007; Wuenschel et al. 2012). We pooled fish caught between November and January for our prewinter length distributions because the timing of our largest catches of summer-spawned juveniles varied among years. Further, the southward migration of YOY in the fall is size dependent, and the larger individuals from the summer cohort arrive earlier in North Carolina (Morley et al. 2007; Wuenschel et al. 2012). Therefore, by pooling multiple months we get a better representation of cohort length structure. Postwinter length distributions came from sampling in late March and April. To ensure growth had not resumed prior to our postwinter sampling, scale samples from a subset of fish were examined to determine whether an annulus had formed.

The cohort structure of age-1 bluefish from the 2004 and 2005 year classes was examined by scale analysis (see below for methods); FL at annulus 1 was back-calculated, and estimated age-1 length distributions were compared with observed age-1 lengths taken from April trawl-catch data. For the 2004 year class, we used scales collected from trawl-caught fish between June and September 2005. For the 2005 year class, trawling did not take place in June, so scales were collected between July and September 2006. Additional samples were obtained by hook and line for the 2004 year class between June 2005 and January 2006 from Beaufort Inlet and near Cape Lookout, North Carolina. Scales were taken from the area between the lateral line and the spinous dorsal fin.

Winter consumption and growth experiment

Summer-spawned juvenile bluefish were caught by 30 m beach seine in Bogue Sound, North Carolina, between 16 November and 2 December 2006. Fish were transported to the Center for Marine Sciences and Technology (CMAS) Fisheries Research Laboratory and held in 540 L circular tanks with flow-through seawater from Bogue Sound. During the acclimation period, fish were fed daily to satiation with thawed *Menidia menidia*. Ambient light from windows was used throughout the experiment. On 30 January 2007, fish were anesthetized with MS-222, measured for FL (mm), weighed (0.01 g), and randomly allocated to six tanks, with six fish per tank. Three temperature treatments were used, 10, 12, and 14.5 °C, with two replicate tanks for each. Mean FL was 152 mm (range 136–170 mm); there was no significant difference in initial mean FL between treatments (ANOVA: $SS_{\text{treatment}} = 3.90$, $SS_{\text{error}} = 67.3$, $F_{[2,3]} = 0.086$, $P = 0.92$). Temperatures in tanks were adjusted from ambient conditions of 11.5 °C to treatment levels at 1 °C-day⁻¹. Data loggers recorded temperature in each tank at 10 min intervals.

To compare our work to a prior study, bluefish were fed, and consumption was determined, in a similar fashion to the maximum consumption experiments conducted by Hartman and Brandt (1995). Fish were fed twice daily to satiation using thawed *Menidia menidia* at 0800 and 1700 h. The mass of food added to each tank was recorded. After the second feeding, uneaten food was removed with a dip net and weighed. We chose to remove uneaten food only once per day, unlike Hartman and Brandt (1995), who did so twice, to minimize stress for the fish. However, we developed a correction factor to account for the mass change of uneaten food that resulted from remaining submerged in the tanks. Using tanks without fish, we duplicated our feeding protocol and created a regression comparing mass of food added to mass retrieved

$$FA = 0.045 + 0.908FR \quad R^2 = 0.99, n = 24$$

where FA is mass (g) of food added to tank, combining the morning and evening quantities, and FR is mass of food removed at the end of the day. Using this equation we estimated the initial mass of uneaten food and subtracted that value from the mass of food added to the tank to calculate daily consumption per tank.

On day 22 of the experiment, one fish from a 14.5 °C tank died. Based on the FL of this fish, it was easily identified from the initial lengths of fish for the tank, and it was eliminated from growth calculations. A fin-clipped bluefish (155 mm) from an extra tank was added to replace the mortality; this fish was not included in growth analyses. Consumption values for all tanks on this day were excluded from analyses. Our experiment ended on 1 March, after 30 days. Fish were sacrificed with a lethal dose of MS-222, then measured and weighed. We used the change in mean FL and mass from initial values in each tank to determine daily growth rate in length and mass. The effect of temperature on growth rate in length was examined using ANOVA; growth rate was log-transformed to meet assumptions of homogeneity of variance.

The effect of temperature on growth rate in mass was examined using a nonparametric Kruskal–Wallis test, because transformations did not improve the heteroscedasticity of residuals.

We determined daily mass-specific consumption (C_{max}) per tank by dividing consumption by the collective mass of bluefish, divided by the number of days. As bluefish were not weighed during the experiment, we used the geometric mean of initial and final bluefish masses. ANOVA was used to compare mean daily C_{max} across temperatures. To determine whether a seasonal effect on consumption exists, we compared our results from February with predictions from a C_{max} versus temperature model derived from experiments conducted between May and December (Hartman and Brandt 1995). Hartman and Brandt's (1995) model yields C_{max} values based on bluefish mass and temperature; we used a 50.9 g bluefish with their model, which was the mean mass of all fish during our experiment.

Does the relative abundance of spring- and summer-spawned bluefish in the adult population differ between the MAB and SAB?

To compare the relative contribution of spring- and summer-spawned bluefish to the adult population using samples taken from the SAB versus the MAB, we obtained archived scales from adult bluefish collected by the North Carolina Division of Marine Fisheries (SAB samples) and back-calculated age-1 length to compare with the results of Conover et al. (2003), who used MAB samples. The SAB samples came from commercial and recreational catches throughout North Carolina every month of the year between 1997 and 2000. These sampling years were chosen because they would allow us to examine many of the same year classes of Conover et al. (2003). Catches from multiple fishing gears were sampled: gill net ($n = 635$), beach seine ($n = 282$), hook and line ($n = 95$), trawl ($n = 82$), and pound net ($n = 33$). FL of bluefish were measured, sex was determined, and scales were removed from the area below the lateral line and posterior to the base of the pectoral fin. During scale analysis, each sample was aged and FL at annulus 1 was back-calculated (see below for methods). While bluefish have been shown to lay down an annulus each year (Wilk 1977; Robillard et al. 2009), using scales to age older fish is difficult. Based on comparisons between scale impressions and sectioned otoliths, age estimates of bluefish from scales appear accurate up until age 5 (Chiarella and Conover 1990; Sipe and Chittenden 2002; Robillard et al. 2009), so we excluded age-6+ fish.

Back-calculated age-1 length distributions were examined by year class, and each was partitioned into spring- and summer-spawned fish based on the location of the antimode between the two cohorts. For some year classes the location of the antimode was not clear, so we used a minimum and maximum value (175 and 210 mm FL) to represent a range in relative cohort contribution. The minimum and maximum values for the antimode were based on results from the present study and from previous studies that have shown bimodal back-calculated age-1 distributions (Lassiter 1962) or actual length distributions of bluefish at the end of winter (Morley et al. 2007). To determine how sampling region affects estimates of summer cohort contribution, we combined year classes to determine a mean back-calculated length distribution for SAB- and MAB-caught fish. To correct for differences in sample size between year classes, we determined the percent abundance for each 10 mm length bin within each year, and then determined the mean percentage across year classes for each length bin. Only the year classes that overlapped between our study and that of Conover et al. (2003) were used. DataThief software (Tummers 2006) was used to extract data from MAB bluefish using length distributions from Conover et al. (2003) and Gilmore (2000).

The archived scales were also used to gain a better understanding of the seasonality of cohort-specific abundance in the SAB. We

plotted monthly mean back-calculated age-1 length separately for age-1, age-2, and pooled age-3 to age-5 bluefish. For age-1 fish that had not yet formed an annulus, we used FL at capture. We used three-factor ANOVA to examine differences in back-calculated age-1 length between season of capture (winter: January–April versus summer: June–September), age groups (age-1 vs. age-2), and gear of capture (gill net vs. combined beach seine and trawl). Age-3+ fish were excluded because they were absent from summer catches. Gear type was included in the model because differences in fishing gear among seasons and ages may bias results. Variance among treatments was not homogenous according to Levene's test ($P < 0.01$), and transformations of the response variable were not helpful. However, ANOVA has been shown to be robust to violations of the homogenous variance assumption, provided that treatment means are not correlated to variance (Lindman 1974); we found no such relationship (slope not different from zero: $t_{[6]} = 0.263$, $P = 0.80$), so we proceeded with the analysis.

If summer spawning in the MAB is the primary reason that adult bluefish migrate north, then immature age-1+ fish may remain in the SAB. Male bluefish mature at a smaller size than females (Salerno et al. 2001; Robillard et al. 2008) so we would expect the ratio of males to females to decrease during summer in the SAB. Using the data on bluefish sex that was provided with the archived scales, we compared the male to female ratio of adult bluefish sampled in winter (January–March) versus summer (July–September) using a χ^2 test of association with a 2×2 contingency table. This analysis was restricted to bluefish between 340 and 440 mm because in this range a majority of males are mature, but most females are immature (Salerno et al. 2001; Robillard et al. 2008). Significant results would suggest maturity influences migration, which would have important implications for relative cohort abundance in the MAB versus SAB.

Scale analysis

To back-calculate FL at age-1, actual scales were examined (i.e., not pressings) with a microfiche reader at $32\times$ magnification. Between 8 and 12 scales were examined per fish. Regenerated scales and scales that showed evidence of curling, by not entirely coming into focus, were excluded. Only fully formed annuli were counted when ageing the fish. Measurements of scales followed Conover et al. (2003), measuring from the focus to the first annulus (S_1) and to the margin (S_c). The measurements were made in the anterior field of the scale at a 20° angle from the dorsoventral axis.

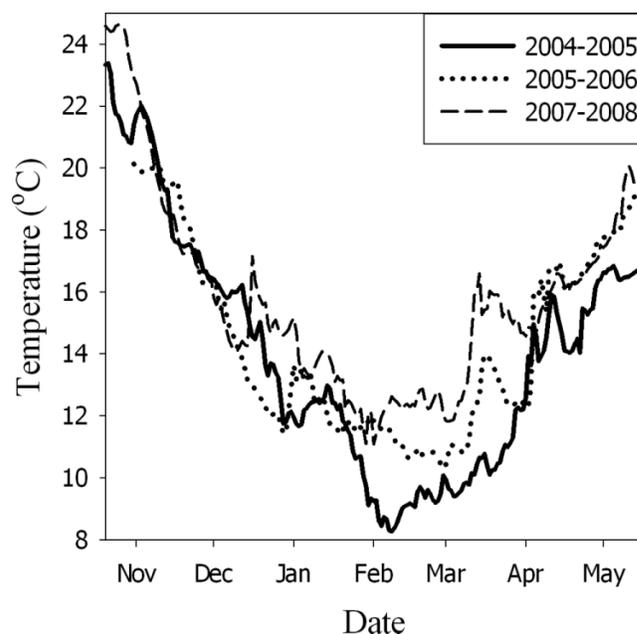
For back calculating length at age-1 we used the Fraser–Lee equation

$$L_1 = \alpha + \left(\frac{L_c - \alpha}{S_c} \right) S_1$$

where L_1 is the length at age-1, L_c is the length at capture, and α is the intercept from a regression of length against scale size (Fraser 1916; Lee 1920). Carlander (1982) advocated using standard intercept (α) values within a species to facilitate comparison among studies. For the 2004 and 2005 year classes we took scale samples from the same dorsal region as Lassiter (1962), so we used his value of $\alpha = 10.49$ mm for those samples. For archived scales we used $\alpha = 5.02$ mm, as determined by Conover et al. (2003), because they used scales taken from the same lateral region. Size at age-1 was calculated with two different scales, and the mean of the readings was used. For 15% of samples, the age-1 length estimates from the two scales differed by over 15 mm. For these samples a third scale was examined, and the two closest readings were used or the sample was rejected; <5% of samples were rejected.

To confirm the timing of annulus formation on age-1 bluefish scales, we conducted a marginal increment analysis using archived scales of age-1 fish, which included the 1996–1999 year

Fig. 1. Ocean-bottom temperatures in Onslow Bay, North Carolina, 15 km from shore during three winter sampling periods.



classes. Marginal increments were calculated as the distance between the scale margin and either the focus or the annulus, if present. The marginal increment from two scales per fish was measured, and the mean value was used. Bluefish from each half month were pooled, and mean values were plotted against date.

To ensure that our results are comparable with previous studies that used slightly different methods to back-calculate length, we conducted two regression analyses. First, a subset of age-1 bluefish from the 2005 year class were used to compare back-calculated lengths from both dorsal and lateral scales, each with the appropriate α value. Second, a subset of archived scales from fish between ages 1 and 5 (mean age = 2.4) were used to compare estimated length at age 1 using acetate scale impressions versus estimates using actual scales. For each comparison, regression was used to compare age-1 length estimates and determine whether the relationship differed from 1:1; Student's t tests were used to determine whether the intercept differed from zero and whether the slope differed from one.

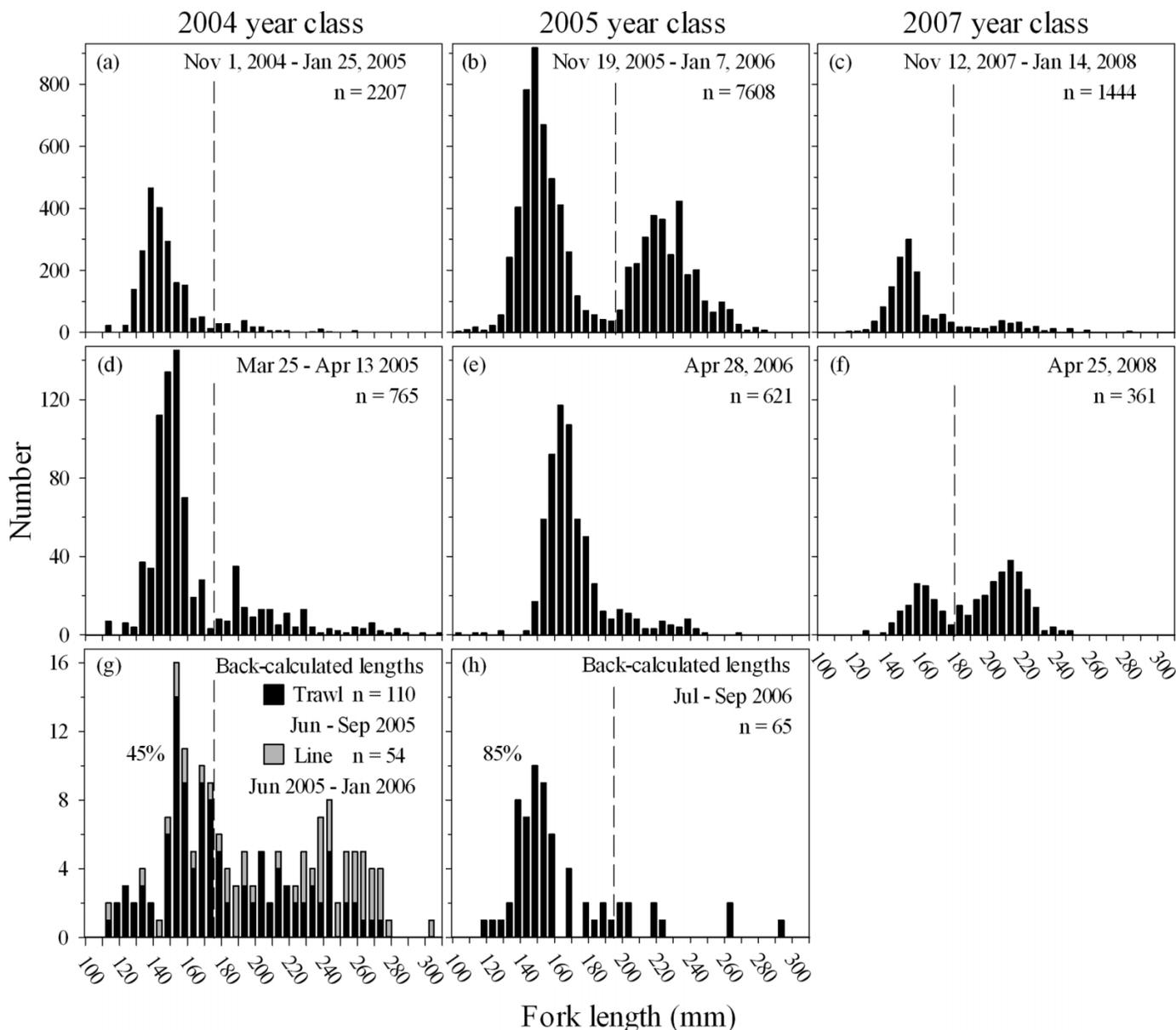
Results

Size-selective overwinter mortality of field-caught bluefish

Water temperatures varied among the three winters (Fig. 1). The 2004 year class experienced the harshest conditions, with 73 days below 12°C and 40 days below 10°C . The 2005 year class experienced 59 days below 12°C , and the temperature never dropped below 10°C . The 2007 year class experienced a mild winter, with only 11 days below 12°C .

The antimode between the spring- and summer-spawned cohorts during the late fall months ranged between 175 and 195 mm (Figs. 2a–2c). Based on spring catches, winter survival of the summer cohort was evident for each year class (Figs. 2d–2f). Based on scale examinations from April-caught bluefish, growth in spring 2006 had started before our sampling took place, so the 2005 year class was not included in the size-selective mortality analyses. Evidence for size-selective mortality was found in one of the other two year classes. The mean length of the 2004 year class increased from 144.8 to 149.9 mm over the winter (t test: $P < 0.001$) and the variance decreased (F test: $P = 0.012$), which suggests that size-selective mortality occurred. Mean length of the 2007 year class increased from 153.9 to 159.9 mm (t test: $P < 0.001$), but the de-

Fig. 2. Length frequency distributions of bluefish caught by bottom trawl off North Carolina. The 2004, 2005, and 2007 year classes are represented in column 1 (a, d, g), 2 (b, e, h), and 3 (c, f), respectively. Plots in the first row (a, b, c) show prewinter lengths from each year class, the second row (d, e, f) postwinter lengths, and the third row (g, h) back-calculated lengths to the first annulus of trawl-caught age-1 bluefish. Some samples were also obtained by hook and line in panel (g). The broken lines show the location of the antimode used to separate the spring and summer cohorts. No broken line is present in panel (e) because growth had resumed prior to collection and no analysis was performed. The percent value in panels (g) and (h) shows the relative contribution of summer-spawned bluefish to age-1 adults.



crease in variance was not significant (F test: $P = 0.188$), which indicates that size-selective mortality did not occur.

Age-1 bluefish collected during our trawl sampling were dominated by the summer cohort and had back-calculated length distributions that were similar to actual lengths from the previous winter. For the 2004 year class, the summer cohort comprised 57% of age-1 fish and had a mean back-calculated length of 155 mm (Fig. 2g), which was similar to the mean value of 150 mm for the summer cohort in early spring (Fig. 2d). The summer cohort comprised 85% of age-1 fish from the 2005 year class and had a mean back-calculated length of 153 mm (Fig. 2h). Growth had resumed prior to our spring sampling of the 2005 year class (Fig. 2e), but the mean length of the summer cohort in late fall was also 153 mm (Fig. 2b). The estimated contribution by the summer cohort de-

ended on sampling gear used for age-1 fish; only 20% of line-caught fish were from the summer cohort (Fig. 2g). However, this apparent difference in sampling gear may be a result of different sampling dates between gears; the hook and line caught fish that were sampled between June and August ($n = 12$) had a mean back-calculated FL of 177 mm, whereas the fish sampled between late October and January ($n = 42$) had a mean age-1 FL of 232 mm.

Winter consumption and growth experiment

Mean temperatures by treatment were 10.0, 11.9, and 14.3 °C. Bluefish fed at all temperatures (Fig. 3a), and mean daily C_{max} showed a significant temperature effect (Table 1). The coldest temperature treatment had significantly lower C_{max} than higher tem-

Fig. 3. Results from a 30-day consumption and growth experiment conducted at three temperatures during winter with juvenile bluefish (mean FL = 152 mm). (a) Mass-specific consumption ($C_{\max} \pm \text{SE}$) where feeding occurred twice daily to satiation. The line shows C_{\max} values of the same-sized bluefish during the summer and fall, as determined from a laboratory-derived mass and temperature predictive consumption model (Hartman and Brandt 1995). Mean ($\pm \text{SE}$) daily growth in length (b) and mass (c) were also calculated.

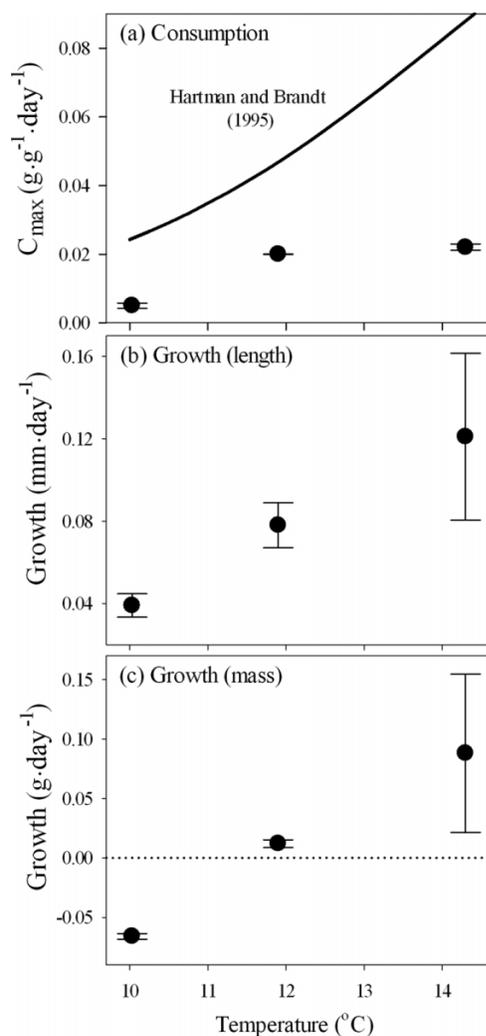
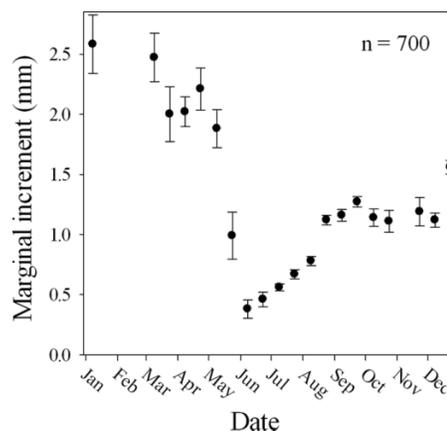


Table 1. Analysis of variance models with temperature (10.0, 11.9, and 14.3 °C) as the independent variable and juvenile bluefish consumption ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$) and growth ($\log(\text{mm}\cdot\text{day}^{-1})$) as dependent variables.

Effect	df	SS	F	P
Consumption				
Temperature	2	0.000329	178.34	<0.001
Error	3	0.000003		
Growth rate				
Temperature	2	0.225	5.46	0.1
Error	3	0.062		

peratures (Bonferroni test: $P < 0.01$), but the two higher temperatures did not differ significantly ($P = 0.17$). When compared with C_{\max} values from the Hartman and Brandt (1995) model, which was parameterized during the summer and fall

Fig. 4. Marginal increments of scales from age-1 bluefish from the 1996–1999 year classes caught off North Carolina with commercial and recreational gear. Values shown are means ($\pm \text{SE}$) from the first and second half of each month.



months, our February values were much lower (Fig. 3a). Further, we saw very little increase in consumption between 11.9 and 14.3 °C, while C_{\max} values from the Hartman and Brandt (1995) model almost doubled. Growth rates were low for all treatments (Figs. 3b and 3c), and we saw no significant effect of temperature on growth in length (Table 1) or mass (Kruskal–Wallis test: $H_{[2]} = 4.597$, $P = 0.1$), although a positive trend in growth with increasing temperature was evident. At the lowest temperature, mean FL increased by 1.2 mm over the 30-day experiment, despite a loss of body mass; length increased by 3.6 mm at 14.3 °C.

Does the relative abundance of spring- and summer-spawned bluefish in the adult population differ between the MAB and SAB?

Marginal increment analysis showed that age-1 bluefish lay down their first annulus in May and early June (Fig. 4). However, it was evident that a majority of fish began to lay their annulus down in late April, although these typically are not fully formed around the circumference of the scale and so were not counted. Thus, back-calculated sizes at age 1 represent bluefish lengths during spring of their second year.

We were able to examine the relative cohort contribution of adult bluefish to the North Carolina fishery from the 1994 through 1999 year classes. Back-calculated age-1 length distributions were distinctly bimodal for the 1995 year class, which had 30% summer cohort contribution (Fig. 5b), and the 1999 year class, which had 39% summer cohort contribution (Fig. 5f). We were not able to objectively locate the antimode in the four remaining year classes, so minimum and maximum values were used. Despite the lack of a clear antimode, summer cohort contribution appeared to be important for the 1994 year class, ranging between 21% and 45% (Fig. 5a), and the 1998 year class, ranging between 28% and 59% (Fig. 5e). Back-calculated distributions for the two remaining year classes did not appear to be bimodal; summer cohort contribution ranged between 2% and 38% for the 1996 year class (Fig. 5c) and between 5% and 27% for the 1997 year class (Fig. 5d). The relative cohort contribution did not appear to be related to the age of fish that were examined (Fig. 5). For example, the 1995 and 1999 year classes had similar distributions despite examining differently aged fish. Further, contribution of the summer cohort appeared much stronger in the 1998 year class compared with the 1996 and 1997 year classes, despite examining similarly aged fish.

Five of the six year classes we examined (1994–1998) were also sampled by Conover et al. (2003). Back-calculated length distributions from these pooled year classes were not bimodal for either SAB or the MAB (Fig. 6). However, the two distributions differed

Fig. 5. Back-calculated age-1 length distributions of adult bluefish caught off North Carolina with commercial and recreational gear for the (a) 1994, (b) 1995, (c) 1996, (d) 1997, (e) 1998, and (f) 1999 year class. For each year class, the range in age of fish used to back-calculate length is shown, along with the mean age in parentheses. The two broken lines indicate the potential location of the antimode and thus the potential range in relative summer cohort abundance. For distributions where the location of the antimode was obvious (b and f), only one broken line is present.

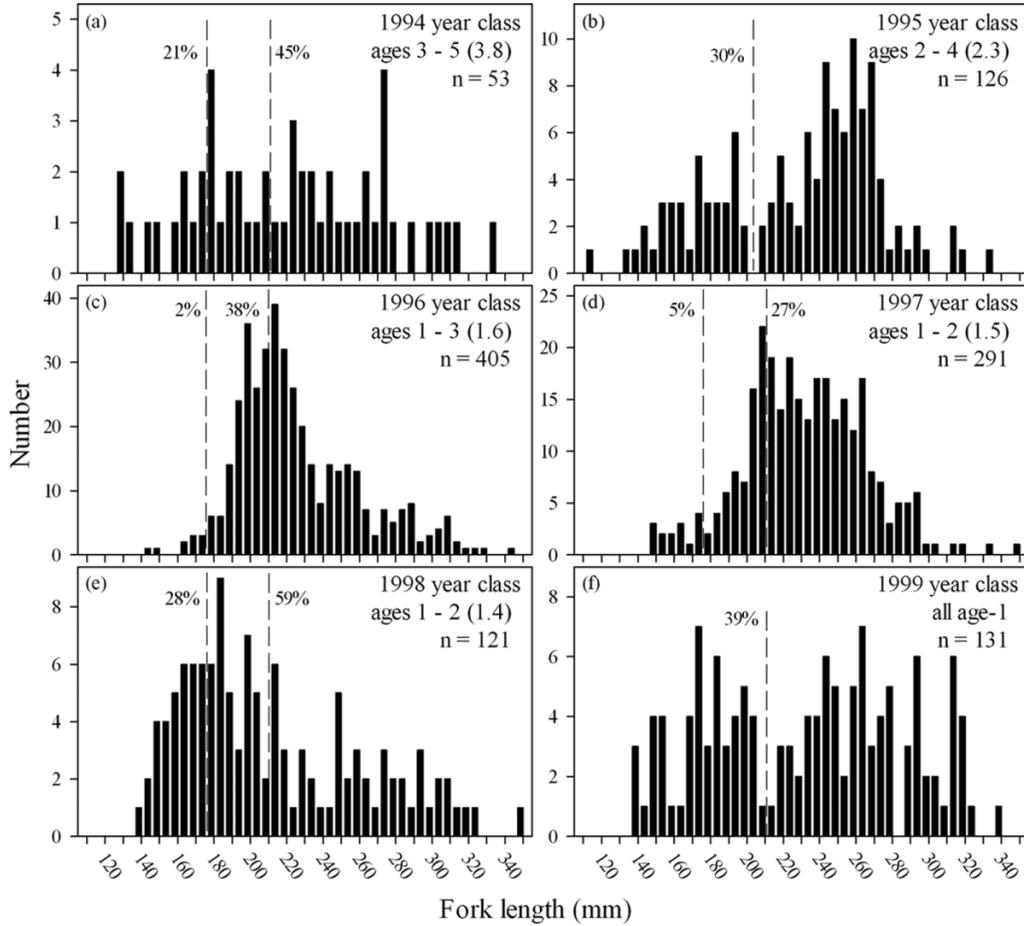
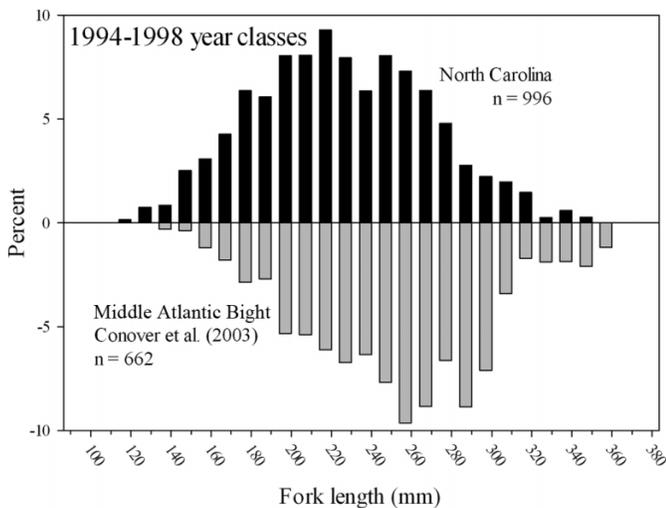


Fig. 6. Pooled back-calculated age-1 length distributions of adult bluefish from the 1994–1998 year classes for North Carolina fisheries (positive axis) and fish captured from the Middle Atlantic Bight from a fishery-independent trawl survey and commercial fishery (negative axis). Values for each length bin are mean percentages across year classes. Data from the Middle Atlantic Bight were taken from Conover et al. (2003).



significantly (Kolmogorov–Smirnov test: $D = 0.235$, $P < 0.01$). The distribution from North Carolina had a greater proportion of smaller bluefish, suggesting that the relative abundance of summer-spawned bluefish is greater in southern regions. The mean age-1 length of North Carolina bluefish from these five year classes was 227.8 mm, and 32.2% were <200 mm. The mean age-1 length of MAB bluefish from the same year classes was 256.0 mm, and only 14.5% were <200 mm.

Season of capture, age of fish examined, and fishing gear influenced the back-calculated age-1 lengths of adult bluefish caught off North Carolina (Table 2). However, both the effect of gear and season were dependent on age. The only significant difference between gear types occurred with age-1 fish during the summer, where gill net caught fish had larger back-calculated lengths than trawl and beach seine caught fish (Bonferroni post hoc: $P < 0.05$; Fig. 7a). Further, among gill net caught adults, age-2 bluefish had smaller back-calculated lengths than age-1 fish within each season ($P < 0.05$; Figs. 7a and 7b). Within each gear type, there was a significant decline in back-calculated age-1 lengths from winter to summer for both age-1 and age-2 bluefish ($P < 0.05$), with the exception of gill net caught age-2 fish (Figs. 7a and 7b). This suggests that the larger individuals from each age-class are more likely to migrate from the area during the spring. Age-3+ bluefish were not included in the ANOVA because only two individuals were sampled during the summer months, presumably owing to low catches of larger bluefish at this time (Fig. 7c). The seasonal and age related-trends in back-calculated length described here would probably be more pro-

Table 2. Analysis of variance using North Carolina caught bluefish with capture gear (gill net versus combined beach seine and trawl), season of capture (winter versus summer) and bluefish age at capture (age-1 versus age-2) as independent variables and back-calculated age-1 length as the dependent variable.

Effect	df	SS	F	P
Gear	1	10595	6.85	0.009
Season	1	93904	60.70	<0.001
Age	1	95376	61.65	<0.001
Gear × season	1	5141	3.32	0.069
Gear × age	1	6708	4.34	0.038
Season × age	1	8719	5.64	0.018
Gear × season × age	1	3222	2.08	0.149
Error	788	1219001		

nounced for other year classes. This is because 57% of the age-1 samples and 71% of age-2 samples for this analysis came from the 1996 and 1997 year classes; these two year classes showed the least evidence of contribution by the summer cohort.

Our hypothesis that maturity (based on males maturing earlier than females) influences migration strategy was supported. The ratio of males to females declined significantly from winter to summer ($n_{\text{winter}} = 109$; $n_{\text{summer}} = 164$; $\chi^2 = 5.94$; $P = 0.02$). During winter, 40.4% of sampled bluefish between 340 and 440 mm were male, compared with only 25.6% in summer.

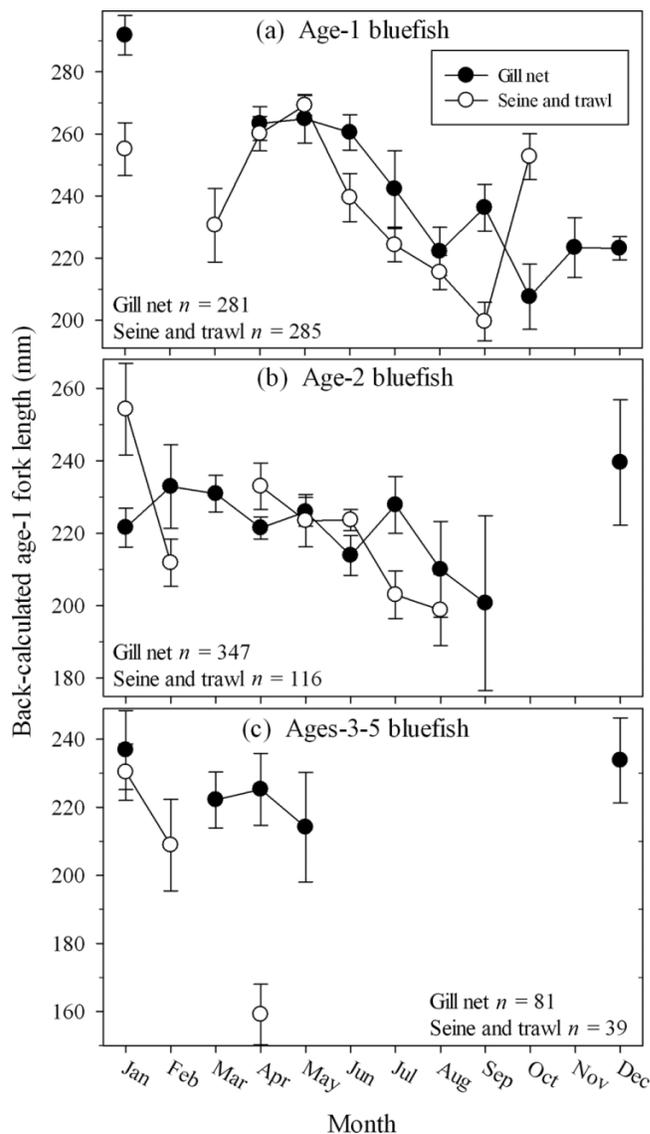
The regression equation comparing back-calculated FL at age 1 from dorsal versus lateral scales was not significantly different from a 1:1 relationship ($y = -7.09 + 1.03x$; $n = 24$; $R^2 = 0.98$; t test for intercept = 0: $t_{[22]} = 1.28$, $P = 0.21$; t test for slope = 1: $t_{[22]} = 1.0$, $P = 0.33$). The mean difference between age-1 size estimates from the two scale regions was only 2 mm. Thus, our results for the 2004 and 2005 year classes (Figs. 2g and 2h) are comparable to the archived scale samples (Fig. 5) and previous studies that used lateral scales. The regression equation comparing back-calculated size at age 1 from scale pressings versus actual scales was also not significantly different from a 1:1 relationship ($y = 5.94 + 0.96x$; $n = 41$; $R^2 = 0.95$; t test for intercept = 0: $t_{[39]} = 0.68$, $P = 0.50$; t test for slope = 1: $t_{[39]} = 1.06$, $P = 0.30$). The mean difference between back-calculated length estimates from pressings and actual scales was only 3.3 mm. Thus our use of actual scales to back-calculate length does not bias comparisons with previous studies that used scale pressings.

Discussion

Size-selective overwinter mortality of field-caught bluefish

Based on empirical findings, Wiedenmann and Essington (2006) hypothesized that overwinter mortality may be an important source of mortality in juvenile bluefish. Further, Conover et al. (2003) hypothesized that winter mortality may limit contribution of the summer cohort to the adult population. We did find evidence of size-selective overwinter mortality within the summer cohort in one of the two year classes examined, but this mortality did not result in complete loss of the cohort. The mean length of the summer cohort increased by 5–6 mm during the winter for the two year classes we examined. Based on the results from our winter growth experiment, the temperature between sampling intervals must be considered to determine whether this shift in mean length could have been caused by growth. For the 2004 year class the increase in mean length was probably due to size-selective mortality. This is because 97% of our prewinter lengths for that year class came from January, and by this date water temperature had already declined to 12 °C. Further, the mean water temperature between our January and April catches was 10.9 °C, a temperature at which maximum growth in mass is negative. There is also no evidence to suggest that the antimode between the spring and summer cohorts increased during that

Fig. 7. Monthly mean (\pm SE) back-calculated age-1 lengths of bluefish from the 1994–1999 year classes, sampled from two fishing gears from the North Carolina fishery at (a) age 1, (b) age 2, and (c) ages 3 through 5.



time. Conversely, for the 2007 year class there was a much greater chance that winter growth biased our results. This year class experienced a mild winter, and 80% of our prewinter lengths came from November, when water temperatures were still mild. Further, our sampling in spring took place in late April. Morley et al. (2007) found greater evidence for size-selective mortality in the 2002 year class, which increased by 11 mm. The 2002 year class experienced a severe winter (76 days <12 °C; 38 days <10 °C) that was similar to that experienced by the 2004 year class, and the fish collected in early spring were in poor energetic condition. The impact that size-selective mortality has on the contribution of the summer cohort to the adult population is uncertain. Ricker (1969) demonstrated that it takes a large degree of selective mortality to produce a detectable increase in mean length and decrease in variation. This would suggest that although we only observed small increases in mean length over the winter, size-selective mortality may be important at the population level.

The source of mortality for overwintering juvenile bluefish is uncertain and may involve multiple biotic factors that interact

with winter severity and duration. Acute cold stress is probably not important; in the lab, juvenile bluefish have been shown to survive temperatures as low as 6 °C for short periods (Slater et al. 2007). Further, juvenile bluefish appear to effectively avoid water <11 °C (Morley et al. 2007; Wuenschel et al. 2012). However, low temperatures appear to force summer-spawned juveniles farther from shore, potentially into less suitable habitat (Morley et al. 2007). The exhaustion of energy reserves is often cited as a cause of size-selective winter mortality (Hurst 2007), and it may be of importance to the summer cohort because they maintain lower energy stores throughout the winter (Morley et al. 2007). Further, there is evidence that the summer cohort experiences a greater energy deficit than spring-spawned fish during harsh winters, suggesting that size-selective mortality would be stronger in those years (Morley et al. 2007). Predation can also be a major source of mortality during the winter (Santucci and Wahl 2003; Garvey et al. 1998), and it is often selective for smaller fish (Sogard 1997).

Winter consumption and growth

The results from the laboratory experiment can be interpreted with respect to winter temperatures in which bluefish are caught. The temperatures that bluefish experienced during our experiment ranged from the lower limit (10 °C) at which bluefish have been caught (Munch and Conover 2000; Wuenschel et al. 2012) up to mild winter temperatures experienced by the summer cohort (Morley et al. 2007). During winter on the continental shelf of the SAB, water temperatures are generally uniform along isobaths, and near-shore temperatures generally range between 10 and 14 °C between North Carolina and northern Florida (Atkinson et al. 1983). There is also a strong cross-shelf temperature gradient associated with the Gulf Stream (Atkinson et al. 1983). However, the summer cohort has been shown to stay within 2 km of shore during winter unless temperature drops below 11 °C, which may force them farther from shore (Morley et al. 2007). Some summer-spawned fish are caught as far south as Florida during winter, where temperatures are milder (Wuenschel et al. 2012), but the largest catches of this cohort off North Carolina are typically in December (Morley et al. 2007; Wuenschel et al. 2012), so only a small portion may reach Florida. Further, based on 10 years of trawl survey data in the SAB, densities of YOY bluefish in April and May are more than an order of magnitude greater off the Carolinas than off Georgia and Florida (South Carolina Department of Natural Resources 2000).

The goal of our experiment was to determine the physiological maximum capacity for growth during the winter, under ideal conditions of unlimited food and low activity. In the wild, growth would likely be lower at these temperatures because prey may be limited and fish would be expending more energy to forage, avoid predators, and migrate. The trends in growth we observed have important implications for analyzing size-selective mortality during winter. Bluefish held at 10 °C were able to feed, but not enough to maintain body mass, and growth in FL was within the bounds of measurement error. This supports Hartman and Brandt's (1995) study, which found a negative scope for growth at this temperature. Physiological limitations of feeding and growth at this low temperature would explain why survey catches of juvenile bluefish at <11 °C are rare (Wiedenmann and Essington 2006; Morley et al. 2007; Wuenschel et al. 2012). At 11.9 °C, growth in mass was negligible, suggesting that fish in the wild at this temperature probably do not grow. At the highest temperature tested, one of the treatments showed marked growth in length and mass. While the growth that we observed at 14.3 °C is low compared with what is found during the spring and summer (McBride and Conover 1991; McBride et al. 1995), it still may lead to an increase in the mean length of overwintering fish. Therefore, when looking for evidence of size-selective mortality, the temperature between sampling dates needs to be considered.

The difference in C_{max} values between our experiment (conducted in winter) and Hartman and Brandt's (1995) experiment (conducted during summer and autumn) suggests a seasonal effect on consumption that is independent of temperature. This supports many laboratory studies that have shown fish to exhibit endogenous seasonal patterns in appetite (Metcalfe et al. 1988; Simpson et al. 1996), metabolism (Evans 1984; Karas 1990), growth (Metcalfe et al. 1988; Karas 1990), and activity (Sandström 1983) that occur independently of temperature or food availability. The adaptation of submaximal consumption in overwintering fishes may result from a feeding strategy designed to maintain adequate energy reserves for winter survival rather than growth (Bull et al. 1996; Hurst and Conover 2001). Further, the strategy of reduced feeding motivation and growth during winter may be the result of consistent prey limitations (Foy and Paul 1999) or poor growth efficiency at low temperatures (Hardewig and van Dijk 2003; Bermudes et al. 2010).

Does the relative abundance of spring- and summer-spawned bluefish in the adult population differ between the MAB and SAB?

The relative abundance of spring- and summer-spawned bluefish in the adult population differed between samples obtained from the SAB versus those obtained from the MAB. Estimates of summer cohort contribution from the SAB were greater than MAB estimates by more than a factor of two. The magnitude of this difference was influenced by collection gear, season of capture, and ages of fish sampled. We will discuss how these three factors influenced our estimates of relative cohort contribution and how they bias comparisons among previous studies. For our SAB samples, we found the contribution of the summer cohort to be 21% or more in four of the six year classes examined from archived scales. This is a conservatively low estimate because (i) it is based on the lowest value that has been observed as an antimode (see Methods) between the summer and spring cohorts during the winter and (ii) a majority of our scale samples came from bluefish captured by gill net, which is a gear that may select for larger age-1 and age-2 individuals (Lucena and O'Brien 2001; this study). When we pooled age-1 lengths from the 1994–1998 year classes, the resulting distribution was not bimodal, despite strong summer cohort contribution in 3 of the 5 years. This is probably the result of small interannual differences in both the mean length attained by the summer cohort by the end of their first year, and the location of the antimode between cohorts. Conversely, Lassiter (1962) found a bimodal age-1 distribution when he pooled year classes. However, he only sampled during 2 years, and two-thirds of his bluefish were age 1. Therefore his pooled distribution would have been biased towards only one or two year classes.

Size selectivity of sampling gear can lead to misleading information about population size structure (Hilborn and Walters 1992), and this is important to consider when comparing our results with those of previous studies that have examined bluefish cohort structure. Bottom trawls and seines tend to select for smaller individuals, while gill nets are more selective for an intermediate length, depending on the mesh used (Hilborn and Walters 1992). These general statements have been confirmed for bluefish; Lucena and O'Brien (2001) examined commercial bluefish catches off Brazil and found bottom trawls to select for the smaller individuals in each age class, while gill nets selected for the larger age-1 and age-2 fish and smaller individuals from older ages. Our data support the conclusion that gill nets select larger age-1 individuals compared with those caught by trawl and seine. However, there was no effect of gear among our back-calculated lengths for age-2 fish. The mean length of the spring and summer cohort differs by 120 mm at age 1 and by 70 mm at age 2 (Lassiter 1962). Therefore the potential for gear selectivity biasing estimates of relative cohort contribution in bluefish is strong, especially considering that over half of the scale samples used in

Lassiter (1962), Conover et al. (2003), and our study came from age-1 and age-2 fish. The National Marine Fisheries Service autumn bottom trawl survey, which is designed to sample juvenile fishes, provided 54% of the bluefish samples used by Conover et al. (2003). The smaller summer-spawned bluefish would have been more vulnerable to this gear, especially at age 1, as we showed with our trawl sampling of age-1 fish from the 2004 and 2005 year classes. Therefore, their results that suggest poor contribution of the summer cohort are surprising. Further, our examination of the year classes from the 1990s using bluefish captured off North Carolina found a much higher contribution of summer-spawned fish, despite the fact that a majority of our samples came from commercial gill nets. Therefore, we believe the differences between our estimates of summer cohort contribution off North Carolina and those of Conover et al. (2003) from the MAB are conservative and are probably the result of size-based migration strategies among age-1 and age-2 bluefish.

Bluefish migration patterns are related to size (Shepherd et al. 2006), and adults occupy progressively more northern and offshore waters as they age (Salerno et al. 2001). Tagging studies have shown that age-1 bluefish may migrate north or remain in the SAB for their second growing season (Lund and Maltezos 1970; Shepherd et al. 2006), but the proportion of age-1 fish that migrate north and how it differs by cohort is uncertain. Age-1 bluefish appear more abundant off North Carolina than in the MAB during summer months (Wuenschel et al. 2012), which suggests a large proportion may remain in southern regions. The energetic cost of migration decreases with size (Nottestad et al. 1999), so the smaller summer-spawned bluefish may be less likely to migrate north at ages 1 and 2. Evidence for size-based migration can be seen in our analysis of seasonal trends in mean back-calculated length. There was a decline in mean age-1 length from winter to summer in both age groups. This suggests that larger age-1 and age-2 individuals (i.e., spring-spawned bluefish) migrate north in greater numbers. Additional support for this hypothesis comes from our hook and line samples of adult bluefish from the 2004 year class; age-1 bluefish collected during summer months were mostly from the summer cohort, and those collected in fall and winter were mostly spring-spawned fish. By age 3, a majority of the bluefish population appears to migrate north each year, based on the lack of samples collected in North Carolina during the summer from older fish. Different migration strategies between spring- and summer-spawned bluefish at younger ages leads to important consequences for studies that examine population level cohort structure, especially when a majority of samples come from age-1 and age-2 fish.

Maturity stage is probably an important factor influencing migration because a majority of summer spawning takes place in the MAB (Kendall and Walford 1979; Collins and Stender 1987; Smith et al. 1994). The difference in size at age between cohorts would lead to summer-spawned fish reaching maturity at a later age. Male bluefish reach 50% maturity at 339 mm (Salerno et al. 2001) and females at 480 mm (Robillard et al. 2008), and growth rate does not differ by sex. Based on cohort-specific age and growth data, spring-spawned fish reach maturity at age 1 for males and ages 2 or 3 for females (Lassiter 1962; Chiarella and Conover 1990); male summer-spawned fish typically reach maturity at age 2 and females at ages 3 or 4 (Lassiter 1962). Our analysis of seasonal changes in bluefish sex ratio shows that the relative abundance of mature males declines in summer off North Carolina. This supports the hypothesis that maturity stage influences migration and may result in the smaller summer-spawned fish remaining in the SAB at ages 1 and 2. Thus catches of younger adults in the MAB would be biased towards the spring cohort.

Lassiter's (1962) study off North Carolina has been used as a historic baseline for comparison among studies that examine cohort structure of adult bluefish. However, our study has revealed that Lassiter's (1962) sampling was biased towards catching

summer-spawned bluefish. Age-1 and age-2 fish constituted 78% of his samples, and based on the information he provided, most of these were collected by beach seine or bottom trawl. Further, his sampling was biased towards the summer months; as we discussed above, the mean back-calculated length of age-1 and age-2 fish declines during summer as the larger individuals move out of North Carolina and most likely migrate north. Also, Lassiter's samples were only 35% male, which is consistent with our results on seasonal changes in bluefish sex ratio. Our trawl-caught age-1 bluefish from the SAB in the summer match best with the timing, location, and gear type used by Lassiter (1962); back-calculated lengths of those age-1 fish have greater than 50% contribution by summer-spawned bluefish.

Assumptions of back-calculating length with scales

The use of the back-calculation technique to quantify relative cohort contribution in bluefish was originally based on the bimodal length distribution that Lassiter (1962) found for fish at age 1, which resembled length distributions of YOY bluefish during the fall migration (Chiarella and Conover 1990). Because Lassiter's age-1 distribution was bimodal, it was assumed that the spring and summer cohort remain distinctly different in length when their first annulus forms during spring. We found that the mean FL attained by the summer cohort at the end of their first growing season is consistently near 150 mm. Further, our laboratory and field results, combined with previous studies that examined length distributions throughout winter (Morley et al. 2007; Wuenschel et al. 2012), confirm that winter growth does not disrupt the bimodal pattern of spring- and summer-spawned bluefish.

Another important assumption for using this technique is that the first annulus is formed on scales at the beginning of the second growing season in early spring. This information is needed so we know that back-calculated age-1 distributions represent the lengths fish attained at the end of their first year and are comparable to cohort structure during the fall. We have confirmed that annuli typically start to form in late April and are complete in May and early June. This is supported by Wilk (1977), who gave anecdotal evidence that age-1 annulus formation on scales occurs in May. Similarly, Robillard et al. (2009) found annulus formation in otoliths to be complete in June for age-1 bluefish. Although annulus formation is not complete until May or June, the growing season of most age-1 bluefish begins earlier in the year. Based on monthly length frequency distributions during the early spring, growth appears to resume in late April or early May (Morley et al. 2007; Wuenschel et al. 2012). Annulus formation is associated with early spring growth, but they are not completely formed and thus countable, based on our criteria, until later in spring.

The use of the back-calculation technique on bluefish to estimate relative cohort contribution has been validated in two ways. First, Conover et al. (2003) conducted an experiment where spring- and summer-spawned bluefish were collected as YOY and held in tanks until the end of their second growing season. In blind tests using scales to back-calculate length, the cohort identity was correctly identified in 29 of 30 fish. The second validation comes from our comparison of YOY length distributions from the overwintering period of the 2004 and 2005 year classes with subsequent back-calculated length distributions from age-1 fish. For each year class we observed similar mean summer cohort lengths between back-calculated age-1 distributions and actual lengths from sampling at the end of the first growing season (Fig. 2). Last, support for use of the back-calculation technique on older bluefish comes from the 1995 year class (Fig. 4b); we found a distinctly bimodal distribution, and the scale samples came from age-2 to age-4 bluefish, suggesting that the accuracy of the technique is not limited to age-1 fish.

Management implications

The relative contribution of the summer cohort to the adult population has been an important topic for bluefish research and management (Munch and Conover 2000; Conover et al. 2003; Shepherd and Nieland 2010). Juvenile abundance indices are used in bluefish stock assessments to forecast changes in population size, which helps to inform decisions on annual fishing quotas (Shepherd and Nieland 2010). During some years, the summer cohort can dominate juvenile recruitment in the MAB (Conover et al. 2003), which is where a majority of juvenile abundance indices are derived (Shepherd and Nieland 2010). It has been suggested that juvenile abundance indices may be improved by reducing the importance of summer-spawned fish (Conover et al. 2003). This is based on evidence from year classes that had high abundance of summer-spawned juveniles, but poor contribution to the adult population. While our study supports the conclusion that the spring cohort contributes more to the population, the summer cohort consistently constitutes around one-third of adults captured in the SAB. The abundance of juvenile summer-spawned bluefish should still be considered when constructing recruitment indices.

One of the surveys used in bluefish stock assessments to calculate juvenile abundance indices is the Northeast Fisheries Science Center (NEFSC) fall bottom trawl, which is conducted mostly in the MAB (Shepherd and Nieland 2010). Length data from this survey have been used to separate juvenile abundance into spring- and summer-spawned bluefish (Munch and Conover 2000; Conover et al. 2003; Wiedenmann and Essington 2006). Based on these cohort-specific juvenile abundance indices, it appears that the relative cohort abundance of adult bluefish is not always in agreement with their abundance as YOY (Conover et al. 2003). For example, juvenile abundance of the summer cohort was low in 1995 and high in 1997, but this was not reflected in back-calculated age-1 lengths from adult fish in our study. The reason for this lack of agreement is important to resolve because it suggests that juvenile abundance may not always be an effective recruitment indicator. A number of explanations are plausible. First, overwinter mortality may decouple recruitment indices from contribution to the adult population (Wiedenmann and Essington 2006). Second, the abundance of summer-spawned juveniles may be over-represented by the NEFSC survey. NEFSC sampling excludes most of the SAB, where recruitment of the summer cohort is minimal, but spring-spawned recruitment occurs along the entire east coast, resulting in the potential for greater recruitment of the spring cohort (Wuenschel et al. 2012). There is also evidence from the MAB that spring-spawned fish may continue using estuarine habitat into the early fall, when the NEFSC survey operates (Taylor et al. 2007). Further, owing to size selectivity of bottom trawls (Hilborn and Walters 1992; Lucena and O'Brien 2001), summer-spawned fish may be more vulnerable to capture by the survey. This problem of estimating the juvenile abundance of species with protracted spawning using size-selective gear has been described for largemouth bass (Pine et al. 2000). Third, using a single trawl survey to estimate juvenile abundance of each cohort may result in a poor estimate in some years. The NEFSC survey operates in a large area, and regional bluefish recruitment within the MAB varies interannually (McBride and Conover 1991; McBride et al. 1995). Further, bluefish stock assessments also use trawl surveys off Connecticut, New Jersey, and Delaware to help estimate juvenile abundance (Shepherd and Nieland 2010). Recruitment indices from these state-level surveys do not always agree with NEFSC survey abundance estimates. Future efforts to compare cohort-specific juvenile abundance with relative contribution to the adult population would benefit from multiple juvenile surveys and adult collections along the entire east coast.

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