

Cohort-specific Winter Growth Rates of YOY Bluefish, *Pomatomus saltatrix*, in Northeast Florida Estuaries: Implications for Recruitment

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Abstract

Age and growth were determined from otoliths for 181 juvenile bluefish (*Pomatomus saltatrix*), collected using a variety of gear in northeast Florida during 2003 and 2005. Three distinct cohorts were identified recruiting to the near shore waters during spring, summer and autumn. Growth rates were high regardless of cohort or season. To compare pre- and post-recruitment growth rates, models were fit to individual growth trajectories using change point analysis. Post-estuarine growth rates were generally higher. Growth rates and hatching times were within the range of those obtained in other bluefish studies conducted at higher latitudes. As this is the only area where winter recruitment of bluefish has been observed, coastal Florida habitats may be essential for the bluefish stock and will need to be carefully monitored in future studies.

Keywords: bluefish, coastal Florida, estuary habitat, hatch dates, otolith, winter recruitment

Introduction

Recruitment to estuaries is considered an important part of the early life history of many fish species (Boehlert and Mundy, 1988). In Chesapeake Bay, the largest estuary in the U.S, some 267 species have been recorded (Murdy *et al.*, 1997). Of these 267 species only 32 are year round residents, while 235 species migrate in and out from both fresh water and marine systems.

Bluefish (*Pomatomus saltatrix*) are a highly migratory species found in semi tropical waters (Briggs, 1960; Juanes *et al.*, 1996). The northwest Atlantic population ranges from Florida to Nova Scotia depending on season (Murdy *et al.*, 1997; Juanes *et al.*, 2002; Collette and Klein-Macphree, 2002). Adult bluefish migrations are coupled with spawning aggregations which first occur during the spring in the South Atlantic Bight (SAB) (Lassiter, MS 1962). The majority of spring-spawned juvenile bluefish, assisted by the advective current of the Gulf Stream, recruit to the Mid Atlantic Bight (MAB) to feed in estuarine and near shore environments (Nyman and Conover, 1988; McBride and Conover, 1991; Hare and Cowen, 1996). Concurrent with this passive migration, adults actively migrate north to the MAB and Gulf of Maine. A second spawning event during the summer results in summer-spawned juveniles which also recruit to

MAB estuaries (McBride and Conover, 1991). Throughout the summer and autumn estuaries provide an abundance of juvenile prey fish (Murdy *et al.*, 1997). High consumption rates allow bluefish to exhibit extraordinarily fast growth before their southerly migration back to the SAB, presumably to over-winter (Juanes and Conover, 1994; Scharf *et al.*, 2004). In late autumn, a third, less important, cohort is produced from spawning in northeast Florida (McBride *et al.*, 1993) and recruits directly to SAB estuaries (Clarke, MS 2006).

Age and growth of bluefish has been studied from Massachusetts (Roemer and Oliveira, 2007) to South Carolina (McBride *et al.*, 1993), with the MAB receiving the majority of study effort (Nyman and Conover, 1988; McBride and Conover, 1991; Able *et al.*, 2003; Takata, MS 2004; Callihan, MS 2005). In contrast to the MAB, where spring and summer growth has been well documented, little is known about winter growth of the autumn-spawned cohort which recruits directly to SAB estuaries in late autumn, or winter growth in general, especially at the southern edge of their range.

The spring cohort is often identified as the dominant contributor to the overall bluefish population (Munch and Conover, 2000). More recently Conover *et al.* (2003) found a shift in cohort dominance from spring-spawned

to summer-spawned in the New York area. Lower recruitment of spring-spawned individuals to the overall population has been offset by higher summer-spawned recruitment. The autumn cohort, which has thus far failed to be detected in MAB sampling and aging studies, could serve a similar role in years of poor recruitment for the spring and summer cohorts.

There is variability in the timing of bluefish recruitment to estuaries, but it generally occurs at lengths between 40 and 70 mm (Nyman and Conover, 1988). Hare and Cowen (1995) identified stage specific growth rate effects using otoliths instead of growth rate comparisons among cohorts as has been done previously (McBride *et al.*, 1993; 1995). However, the bluefish used in Hare and Cowen (1995) were pre-recruitment larval and pelagic juveniles, and could not be used to compare estuarine growth to prior oceanic growth. Moreover, no previous studies have compared growth between the two habitats and the consequences for recruitment. Understanding growth rates in both habitats will not answer whether bluefish are estuarine dependent or not (Able *et al.*, 2003) but will likely shed some light on the growth consequences of variation in estuarine residency on recruitment.

The autumn-spawned cohort contributes less to the overall population structure than the spring- and summer-spawned cohorts (McBride *et al.*, 1993). Lower production, as well as being potentially resident to the SAB (Shepherd *et al.*, 2006), has made the autumn-spawned cohort less studied than the earlier spawned cohorts. It is essential that the autumn cohort be studied and its role understood because it likely has a smaller geographic distribution than the spring and summer cohorts (perhaps restricted to the SAB). Human development and use of estuarine environments increases every year, impacting this already small range, with northeast Florida being one of the most developed shorelines on the east coast of the United States. This study is the first to analyze growth rates for all three cohorts at the southern end of their range through the autumn and winter.

The objectives of this study are to identify whether all 3 YOY bluefish cohorts recruit to estuaries and near shore waters of northeast Florida, to compare growth among cohorts and seasons, and between pre- and post-estuarine entry, and to assess the potential importance of winter growth on cohort-specific recruitment.

Materials and Methods

Field sampling

YOY and age 1+ bluefish were collected in northeast Florida (Fig. 1) using gill netting, beach seining, and cast

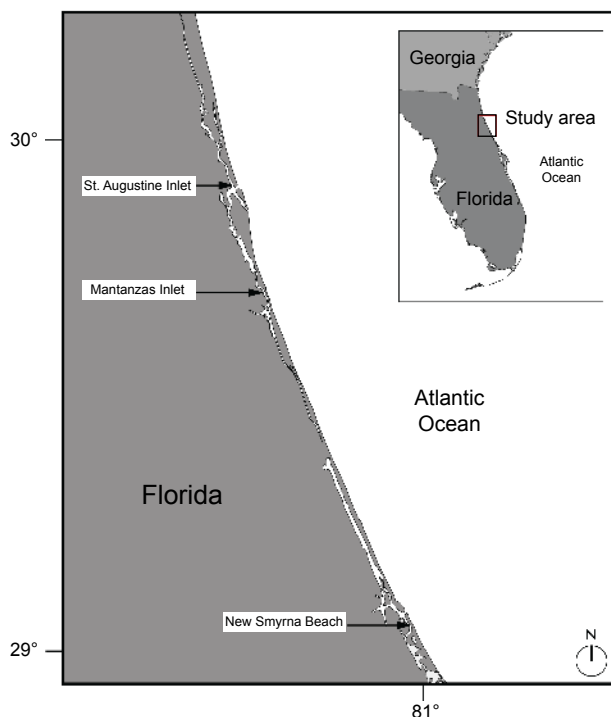


Fig. 1. Study Area located in northeast Florida between St. Augustine Inlet and New Smyrna Beach.

netting techniques. Collections were made in the summer, autumn and winter to allow growth rate comparisons among the spring, summer and autumn-spawned cohorts. Bluefish were sampled on 9 November 2002–24 February 2003, and 6–9 June 2003 (“Year-1”), 13 October 2003–16 January 2004 (“Year-2”), and 26–29 June 2005 (“Year-3”). Catch per unit effort for Year-1 and Year-2 and spatial distributions are reported in Clarke (MS 2006).

Three sampling locations were identified at each site, inside the inlet, in the mouth of the inlet, and on the ocean beach outside the inlet. Two seine hauls were conducted at each location per month. Lengths (± 1 mm) were recorded for all species captured in the sampling gears.

Bluefish carcasses less than 160 mm Fork Length (FL) were stored in 95% ethanol, whereas bluefish greater than 160 mm FL had their heads removed in the field and were frozen for future otolith analysis. Year-3 bluefish were preserved whole in 95% ethanol in the field.

Laboratory methods - Otolith processing

After removing the cranium with a scalpel both sagittae were removed from beneath the posterior end of the brain case for all YOY bluefish. Due to the fragility of bluefish otoliths and the frequency of breakage, one sagittae from each fish was processed for aging, while the remaining otoliths were preserved in 95% ethanol

for backup. Otoliths were cleaned with distilled water to remove excess tissue. Sagittae were then glued concave side down to glass microscope slides using Crystalbond™ 509. Once the glue had set otoliths were sanded down using 600–1200 grit wet/dry sand paper. Once the nucleus had been reached otoliths were polished with 0.3 micron levigated alumina polishing compound on a polishing cloth. Due to the difficulty of holding glass slides on a polishing wheel it proved more practical to polish them by hand. Polishing cloths were glued to the worktop and alumina polishing compound was added to them with water. Slides were placed face down and otoliths were polished in a circular motion. Once one side had been sanded and polished slides were placed on a hot plate. Heating the Crystalbond™ 509 to 80°C allowed the bonding agent to melt permitting otoliths to be flipped. The same sanding and polishing method was used for both sides of the otolith.

Microstructural analysis of YOY bluefish otoliths has demonstrated daily growth rings in sagittal otoliths (Nyman and Conover, 1988; Roemer and Oliveira, 2007). To enhance the definition of daily growth increments a drop of immersion oil was added to each polished otolith. Otoliths were then viewed and photographed under an Olympus™ BH2 compound microscope with a Canon™ A95 digital camera and measured using an ocular micrometer to the nearest micron. Digital images were taken at 40× and 100× magnifications. Multiple 100× magnified images had to be taken of the same otolith to allow the whole image to be observed. These images were stitched together using the “merge photo” tool in Adobe™ Photoshop. Once images had been stitched they were imported into Adobe Illustrator and daily rings were counted concurrently on the computer screen as well as under the microscope. A transect was first drawn from the center of the otolith core to the outer tip of the rostrum, this allowed for the longest transect possible. For every seven rings that were counted under the microscope a mark was placed along the transect at the corresponding point using Adobe Illustrator. Bluefish ages were estimated by counting the number of daily increments present on the polished otolith. Otolith daily increment widths tend to be autocorrelated, therefore interpolation was often needed to estimate the outer increment. Interpolation did not exceed 5% of the total counts deemed acceptable by Campana (1992). All images were saved as illustrator and jpeg files.

Stevenson and Campana (1992) infer that the major source of otolith increment width measurement bias occurs during focus adjustment in light microscopy. Since the focal plane of one increment is not necessarily the same for an adjacent increment, adjustments to the focus can cause apparent width changes in daily increments. By measur-

ing weekly increments the overlap error which occurs during refocusing was minimized as fewer measurements were needed. The otolith jpeg files with the weekly ring counts were opened in Image J™, calibrated using total otolith length and the width between weekly marks was measured. Daily otolith growth was calculated by dividing the weekly growth width by seven. Unfortunately this technique has an averaging effect whereby it assumes that growth remains constant for the whole week, not allowing for daily growth variability. More commonly, daily increments are individually measured in YOY fish (Secor *et al.*, 1992; Stevenson and Campana, 1992) allowing for daily growth variability but increasing daily growth error.

Statistical analysis

Total increments were counted on one sagittal otolith from each bluefish with each increment representing one day (Nyman and Conover, 1988; Roemer and Oliveira, 2007). One day was subtracted from each total count as the first increment is formed at hatching (Hare and Cowen, 1994). Hatch dates were sorted into bi-weekly hatch bins. For all cohorts, first hatch, last hatch and number of days between first and last hatch were recorded.

Growth rate comparisons

Growth rates were compared using analysis of covariance (ANCOVA). The null hypothesis that the growth rates were not different was tested using a significance value of $p < 0.05$. To test whether otolith growth is related to fish length we used linear regression to correlate fish length against otolith length for each cohort.

Oceanic versus estuarine growth

Juvenile bluefish recruit to estuaries at fork lengths (FL) of 40–70 mm (Marks and Conover, 1993) although there is cohort- and population-level variability (Juanes *et al.*, 1996). As no recruitment mark was observed on bluefish sagittae we took the midpoint of the recruitment size range (55 mm) and calculated age using the pooled regression equation for fork length versus age, resulting in a recruitment age of 44.67 days or approximately 6 weeks. We considered growth before 6 weeks to be oceanic and any growth after six weeks to be estuarine.

Change point analysis was used to distinguish the point at which a slope diverges from the original slope. If the change point is already known it can be used to test whether there is any difference before and after the change point.

Five models using change point analysis were compared to see which produced the best fit for YOY bluefish

growth across cohorts. All intercepts are assumed to pass through the origin. Model 1 ($y = \beta_1 x$) assumed that growth was the same for all cohorts (y = otolith radius growth, β = slope, x = age). Model 2 ($y = \beta_{1i} x$) plotted individual growth for the three cohorts. Model 3 ($y = \beta_1 x + \beta_2 I(x-x_c)(x-x_c)$) assumed the change point occurred at 6 weeks and plotted the combined data before and after this point (x_c = age at change point). The I represents an indicator function which depends on $x > x_c$ to include the second part of the model, but if $x < x_c$ the second part of the model was not added. Model 4 ($y = \beta_1 x + \beta_{2i} I(x-x_c)(x-x_c)$) assumed that before the change point growth was the same across cohorts and after the change point growth rates were different (β_2 = slope change). Model 5 ($y = \beta_{1i} x + \beta_{2i} I(x-x_c)(x-x_c)$) assumed that individual cohort growth rates were different before and after the change point. The best fitting model was selected using Akaike's Information Criterion (AIC) which is a measure of the goodness of fit of an estimated statistical model. The AIC is a way of trading off the complexity of an estimated model against how well the model fits the data (Akaike, 1987).

Pre- and post-estuarine recruitment growth was compared for each cohort using a paired t -test. To control for size bias we standardized weekly otolith growth by dividing by total otolith radius for individual cohorts. A $p < 0.05$ was considered statistically significant.

Results

A total of 327 bluefish were available for this study. Of these, 179 YOY and age 1+ bluefish were sampled in Year-1 and Year-2, 132 YOY were sampled

during June 2003, and 16 YOY were sampled in June 2005.

Due to difficulty reading daily increments from otoliths of bluefish > 110 mm FL, only otoliths from bluefish < 110 mm FL were considered for aging, reducing the sample size to 213 (all YOY). Thirty seven otoliths (17.3% of the fish < 110 mm) broke during removal and preparation further reducing the available otoliths to 176, all of which were successfully aged. However, we used cohort-specific regression equations developed for the directly aged otoliths to estimate ages for the 37 samples with broken otoliths. Reader bias was quantified and shown to be less than 10%.

Hatch date analysis

Daily otolith increments allowed the three cohorts to be clearly differentiated through back calculation: hatch date = capture date – (# of increments – 1) (days). For the spring-spawned cohort, hatching first occurred on 8 April 2003 and lasted 22 days. The summer-spawned cohort first hatched on 11 August 2003 and lasted for 19 days. Autumn-spawned YOY first hatched on 22 October 2003 and lasted for 9 days. The 2005 spring-spawned cohort hatched slightly later than the 2003 spring-spawned cohort, hatching first on 14 April 2005 and lasting for 17 days. Mean length at capture was largest for the summer-spawned cohort at 95.57 mm and smallest for the autumn-spawned cohort at 47.13 mm.

Growth rate

Juvenile bluefish mean growth rates ranged from 1.35 to 1.52 mm per day for 2003 (Fig. 2). However, there were

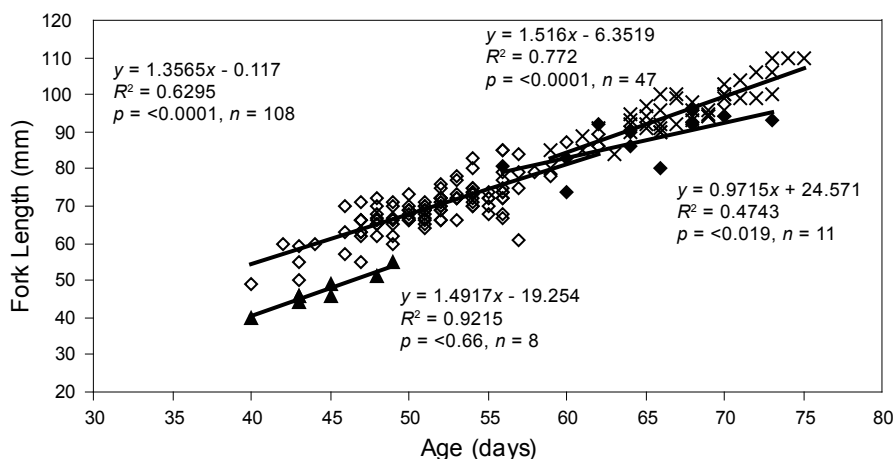


Fig. 2. Relationship between size and age for juvenile bluefish. 2003 Spring-spawned fish are depicted by hollow diamonds, 2003 summer-spawned fish by x's, 2003 autumn-spawned fish by solid triangles and 2005 spring-spawned by solid diamonds. Regression equations and statistics are included for each cohort.

no significant differences in the slopes ($p = 0.64$), but a significant difference in the adjusted means ($p < 0.0001$) with summer-spawned fish being largest and autumn-spawned the smallest. Cohort growth rates could thus not be pooled. The otolith length versus age ANCOVA showed similar results, slopes were not significantly different ($p = 0.70$) but the intercepts were ($p < 0.0001$). R^2 values showed fork length to be good predictor of age (All $R^2 > 0.47$) (Fig. 2) as was otolith length (All $R^2 > 0.57$) (Fig. 3).

Similarly, no significant difference was detected between spring-spawned growth rates across the 2 years ($p = 0.18$). However, the spring-spawned 2005 cohort adjusted mean was significantly larger at age than the spring-spawned 2003 cohort ($p < 0.0001$).

Good relationships were observed between fish length and otolith length for all three cohorts (All $r^2 > 0.68$) suggesting that otolith growth is relative to somatic growth in this species. However, cohorts could not be pooled because the y intercepts were significantly different ($p < 0.0001$).

All indirectly aged samples belonged to spring- ($n = 27$) or summer-spawned ($n = 10$) cohorts. Indirectly aged spring-spawned samples were aged using the regression equation $Length = 1.3565 \text{ age} - 0.117$, and indirectly aged summer-spawned samples were aged calculated using the regression equation $Length = 1.516 \text{ age} - 6.3519$, both of which were calculated from directly aged samples (Fig. 2). Hatch dates of the indirectly aged bluefish were then combined with those estimated for the directly aged bluefish (Fig. 4).

Oceanic versus estuarine growth

Daily incremental otolith measurements showed similar growth among 2003 cohorts (Fig. 5), with the 2005 spring-spawned cohort experiencing very little increase in growth between week 4 and 8 (Fig. 5D). The initial observation after the sixth week showed that the spring 2003 cohort continued to grow at a steady rate, whereas the summer 2003 and spring 2005 cohorts growth rates slowed, and the autumn cohort growth rate increased (but based on only one week's growth). All five models were fitted to individual bluefish otolith growth (Fig. 6). The change point analysis suggested that Model 5 provided the best fit demonstrating different growth among all cohorts both before and after recruitment (Fig. 7).

Discussion

This study has identified for the first time three cohorts of YOY bluefish recruiting to the near shore waters of northeast Florida. The inclusion of the autumn-spawned cohort makes the SAB unique in terms of recruitment

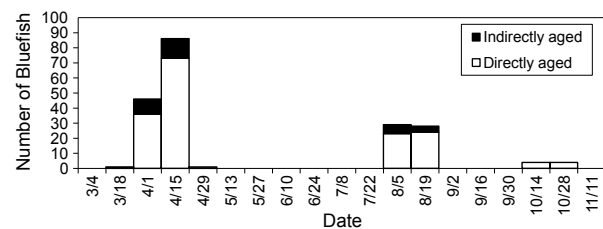


Fig. 4. Bi-weekly hatch dates for 2003 YOY bluefish including directly and indirectly aged fish.

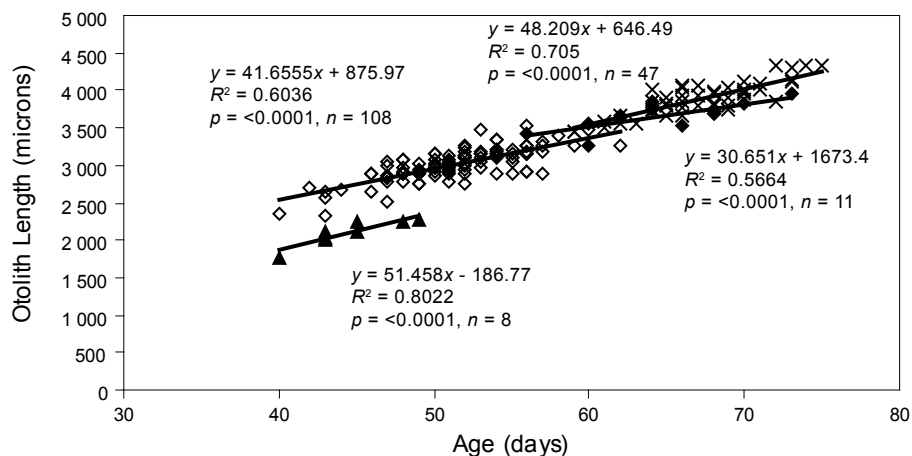


Fig. 3. Relationship between otolith length and age for juvenile bluefish. 2003 spring-spawned fish are depicted by hollow diamonds, 2003 summer-spawned fish by x's, 2003 autumn-spawned fish by solid triangles and 2005 spring-spawned fish by solid diamonds. Regression equations and statistics are included for each cohort.

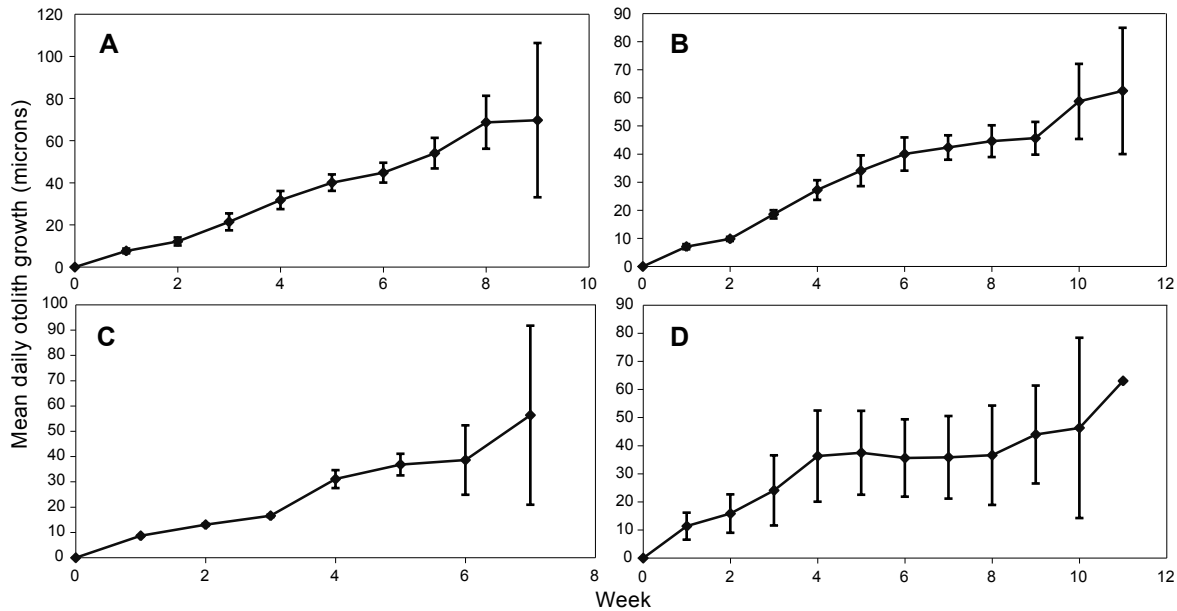


Fig. 5. Mean weekly otolith growth rates for juvenile bluefish. (A) 2003 Spring-spawned fish, (B), 2003 Summer-spawned fish, (C), 2003 Autumn-spawned fish, and (D), 2005 Spring-spawned fish. Error bars represent standard error of the mean.

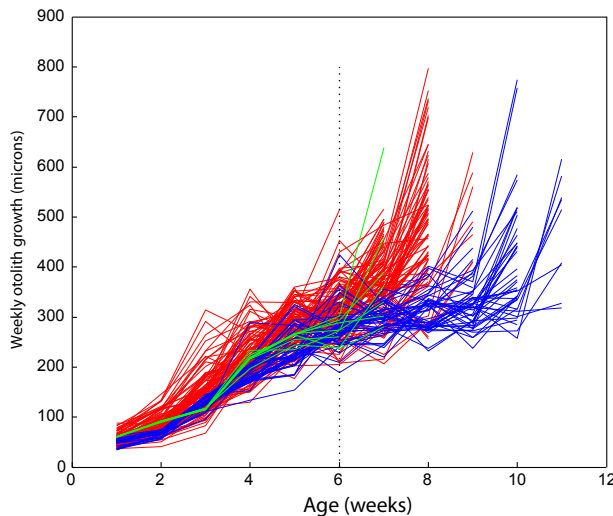


Fig. 6. Individual bluefish otolith growth used to fit all models. Spring cohort is represented in red, summer cohort is blue and the autumn cohort is green. The dashed line represents the mean age of estuarine recruitment of for bluefish.

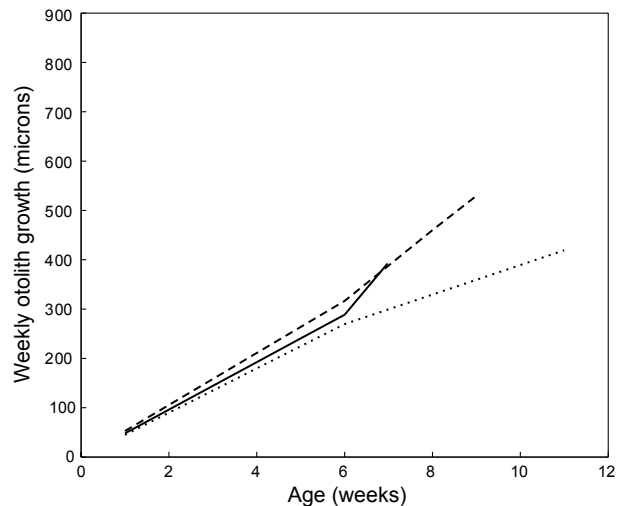


Fig. 7. Model 5 ($y = \beta_1 x + \beta_2 I(x-x_c)(x-x_c)$) fitted to 2003 bluefish growth data. A change point is inserted at 6 weeks for estuarine recruitment. The spring cohort is represented by the dashed line, the summer cohort by the dotted line and the autumn cohort by the solid line. This model was fit to data shown in figure 6.

as this cohort has not been detected in the MAB, where the majority of the population is present during summer. The growth rates calculated in this study were within the range of other growth studies performed on bluefish across its range, with significant differences in pre- and post-recruitment growth detected for all cohorts. Because of the observed winter recruitment of the autumn cohort and continued elevated growth of all cohorts, northeast

Florida estuaries are potentially very important to the overall bluefish population.

Hatch date

In contrast to studies in the MAB, where only two cohorts are recognized, we observed trimodal bluefish

TABLE 1. Cohort-specific bluefish hatch dates reported in previous studies.

Cohort			Reference
Spring	Summer	Autumn	
Mar + Apr	Jul + Aug		Kendall and Walford, 1979
Mar to May	Aug + Sep	Oct + Nov	Collins and Stender, 1987
Mar + Apr	Jul + Aug		Nyman and Conover, 1988
Mar to May	Jun to Sep		Marks and Conover, 1993
Mar to May	Jun to Aug	Sep to Jan	McBride <i>et al.</i> , 1993
Mar + Apr	Aug		Juanes and Conover, 1995
Mar to May	May to Aug	Sep to Nov	Hare and Cowen, 1996
Mar to May	Jul		Munch and Conover, 2000
Mar + Apr	Jun to Aug		Takata, MS 2004
Apr	Aug	Oct	This Study, 2008

recruitment. Cohort hatch dates from this study concurred with those produced from nine previous aging studies (Table 1) indicating that spring spawning starts in March, continues through April (4 of the studies) or into May (5 other studies). All of our spring-spawned bluefish hatched in April and are thus similar to previous results. Less agreement was found in the summer cohort hatch dates. The earliest hatch date was May (Hare and Cowen, 1996) and the latest was September (Marks and Conover, 1993). Despite the variation in the range of hatch dates, the majority of these studies centralize summer hatching around July and August, which agrees with our August summer-spawned hatching dates. The autumn cohort is only recognized in three of the studies, and all agree that autumn hatching starts in September, with two studies indicating it continues through November and one indicating it carries on through January (McBride *et al.*, 1993). Previous autumn hatching dates agree with our observed October autumn hatching dates.

The clear separation in the tri-modal cohort distribution (Fig. 4) could mean one of two things; that there are three distinct spawning events whereby juveniles recruit to the near shore shortly after (as proposed for the spring- and summer-spawned cohorts by Kendall and Walford (1979)), or that there is a continuous spawning event starting in the spring and continuing into the autumn (as proposed by Hare and Cowen (1993)) and where observed recruitment patterns are a function of survival rates. No overlap was observed between cohort hatch dates in our 2003 samples, however, Takata (MS 2004) identified intermediate hatching between spring and summer cohorts in the MAB during the spring and summer for the same year which would suggest continuous spawning. We also found no overlap between the end of the summer-spawned and start of the autumn-spawned hatching with almost two months between hatch dates. It is clear that a larger

sample size would produce a wider hatch date distribution for each cohort, but the observed gap between cohorts is sufficiently large that even with an increased sample size it is unlikely that trimodal recruitment would be better described by continuous spawning.

Growth rate

Mortality during the first winter of juvenile fishes is often high due to thermal stress and starvation (Hurst, 2006). Individuals that are larger at the end of the first growing season likely experience lower winter mortality (Sogard, 1997). The migration from the MAB to the SAB is triggered when water temperatures drop below 15°C. Because northeast Florida estuaries maintain temperatures >20°C beyond November (Clarke, MS 2006), the southerly migration into these estuaries provides a lengthier growing season during which juvenile bluefish can continue to grow at high rates with the standard benefits of estuarine residency (*i.e.* low predation and high food resources) (Levin *et al.*, 1997). Our results show that all cohorts grow as well or better in the winter as they did previously either offshore or in MAB estuaries.

It is important to note however that for the three cohorts growth occurred at different times of the year and likely at different temperatures. Spring-spawned bluefish were collected during the summer when water temperatures were the highest, summer-spawned bluefish were collected during the autumn when water temperatures were dropping and the autumn-spawned cohort was collected during the winter when temperatures were lowest. We would therefore expect that since accumulated water temperatures often control growth (for example as determined using growth degree days (Neuheimer and Taggart, 2007)), the spring-spawned cohort would have grown fastest and the autumn-spawned cohort the slowest. Yet

in this study cohort growth increased upon recruitment for the spring- and autumn-spawned cohorts and decreased for the summer-spawned cohort.

Scharf *et al.* (2006) described the spring-spawned cohort growth as the most robust to fluctuations in prey dynamics as their early spawning temporally overlaps with an abundance of prey species. Our results agree with this finding as we observed little variability in growth detected between years. Comparisons could not be made between years for the summer and autumn cohorts as we only collected them during one year. Interestingly, Scharf *et al.* (2006) reported that summer spawned bluefish growth was more susceptible to prey fluctuations because of its dependence on a more limited diet. Much like the summer cohort in the MAB, the autumn cohort in Florida has a limited prey source (Clarke, MS 2006), as most prey species become either too large for juvenile bluefish to consume or are not present during late autumn and early winter, possibly making the autumn cohort even more susceptible to prey fluctuations. Scharf *et al.* (2006) also noted the importance of the relative timing of the spring and summer cohort to growth variability as a consequence of competition for prey. In northeast Florida, the presence of a third cohort suggests that more complex dynamics are possible; as the likelihood of cohort overlap increases so does the potential competition for shared prey resources. Detailed growth and diet studies over multiple years will be necessary to quantify such dynamics.

Growth rates of juvenile bluefish across their North American range have been shown to be highly variable across years, cohorts and locations (Table 2). The eleven studies highlighted in Table 2 have growth estimates ranging from 0.1–2.63 mm/d in the wild, with Roemer and Oliveira (2007) estimating a high of 3 mm/d in a tank-based study. Our observed growth rates in Florida were within the range for mean growth rates calculated from other latitudes. Although the highly migratory nature of bluefish makes latitude a difficult variable to consider when comparing growth rates across a large geographic area, some latitudinal patterns may be detected across the accumulated bluefish growth data. Excluding the tank-based study, fastest growth is achieved in mid-latitudes, in Maryland for both spring and summer cohorts (Takata, MS 2004). Otherwise, growth rates decline both north and south of Maryland. Heading north, maximum growth decreased with increasing latitude and heading south, maximum growth decreased with decreasing latitude (Table 2).

Oceanic versus estuarine growth

The diet transition from planktivory to piscivory occurs when YOY bluefish recruit to estuaries (Marks and Conover, 1993). During the oceanic larval phase, which lasts between 40 and 70 days, growth rates are described as rapid (*e.g.* Able *et al.* 2003). However, estuarine growth has been suggested to be faster (McBride and Conover,

TABLE 2. Cohort-specific bluefish growth rates (mm/day) reported from previous studies. Where cohorts were not identified, the same growth rate was assumed for all cohorts mentioned.

COHORT			State/s	Reference
Spring	Summer	Autumn		
0.7–1.3	0.7–1.3		ME	Creaser and Perkins, 1994
0.4–3.0*			MA	Roemer and Oliveira, 2007
1.3			NY	Nyman and Conover, 1988
0.71–1.35	0.91–1.47		NY/NJ	McBride and Conover, 1991
0.1–2.2	0.1–2.2		NJ	Able <i>et al.</i> , 2003
	0.19–0.95		NJ	Taylor and Able, 2006
1.85–2.49	0.70–2.63		MD	Takata, MS 2004
1.78–1.95	1.98–2.39		MD	Callihan, MS 2005
1.2–1.9	0.9–1.13	1.06**	NC/SC	McBride <i>et al.</i> , 1993
0.97–1.35	1.52	1.49	FL	This study, 2008
0.9–2.1	0.9–2.1		East Coast	Juanes <i>et al.</i> , 1994

* Laboratory study.

** Based on one sample.

1991) likely due to the ontogenetic feeding shift to the abundant piscine prey, and the nutritional advantage of this prey type over plankton (Juanes and Conover, 1995; Juanes *et al.*, 1994). For the Florida bluefish collected in 2003, the change point inserted at six weeks marked a significant change in growth for all cohorts. The spring and autumn cohort's growth rates increased upon recruitment, whereas growth of the summer cohort decreased slightly (Fig. 7). However, it is more likely that recruitment of the summer cohort only occurred after 9–10 weeks, after which increased growth was observed (Fig. 6). Increased variability in the growth and the timing of estuarine entry of the summer cohort relative to the spring cohort has been noted in northern systems with important implications for cohort-specific recruitment (Scharf *et al.*, 2006).

Conclusion

Winter is often a stressful time for many species of marine fish where scarcity of prey is coupled with reduced growth rates and higher mortality (Schultz *et al.*, 1998). The growth rates observed in this study suggest that recruitment to northeast Florida estuaries is important for YOY bluefish during the winter as they continue to achieve high growth rates similar to those attained in the summer. Historically, the spring-spawned cohort has dominated recruitment to the overall population but more recently Conover *et al.* (2003) identified a shift in population structure to one dominated by the summer-spawned cohort as the overall population has declined. Presently very little is known about the autumn-spawned cohort, but its contribution to the population could become more important if the population decline continues. At present, northeast Florida is experiencing high population growth and development around its inlets, along with development comes increased fishing pressure and habitat degradation. As this is the only area where winter recruitment of bluefish has been observed, coastal habitats may be essential for the bluefish stock and will need to be carefully monitored in future studies. Similarly, winter recruitment of marine species into estuaries can be affected by the dynamics of the resident fauna. For example, Warlen and Burke (1990) observed winter recruitment of predominantly marine species, (*Brevoortia tyrannus*, *Leiostomus xanthurus*, *Micropogonias undulatus*, *Lagodon rhomboides*, and *Myrophis punctatus*) to North Carolina estuaries, identifying resident estuarine fishes lack of autumn/winter spawning as potentially less competition for resources for the marine larvae. The interaction between the dynamics of migrating and resident species, especially in the winter when resources are scarce, can therefore have implications for the recruitment of both life history types.

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References

- ABLE, K. W., P. ROWE, M. BURLAS, and D. BYRNE. 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.
- AKAIKE, H. 1987. Factor Analysis and AIC. *Psychometrika.*, **52**: 317–332. doi:10.1007/BF02294359
- BOEHLERT, G. W., and B. C. MUNDY. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. In: Larval fish and shellfish transport through Inlets. M. P. Weinstein (ed.). American Fisheries Society, Bethesda, MD, p. 51–67.
- BRIGGS, J. C. 1960. Fishes of worldwide (circumtropical) distribution. *Copeia*, **1960**: 171–180. doi:10.2307/1439652
- CALLIHAN, J. L. MS 2005. Ecology of juvenile bluefish, *Pomatomus saltatrix*, in Maryland coastal waters and Chesapeake Bay. M.S. Thesis, University of Maryland. 224 p.
- CAMPANA, S. E. 1992. Measurement and interpretation of the microstructure of fish otoliths. In: Otolith Microstructure examination and analysis. D. K. Stevenson and S.E. Campana (eds.). *Can. Spec. Publ. Fish. Aquat. Sci.*, **117**: 59–71.
- CLARKE, P. J. MS 2006. Winter ecology of young-of-the-year and age 1+ bluefish, *Pomatomus saltatrix*, in a northeast Florida estuary. M.S. Thesis, University of Massachusetts Amherst, 95 p.
- COLLETTE, B. B., and G. KLEIN-MACPHEE. 2002. (ed.). Bigelow and Schroeder's Fishes of the Gulf of Maine. 3rd ed. Smithsonian Institution Press, Washington, D. C., 748 p.
- COLLINS, M. R., and B. W. STENDER. 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., T. GILMORE, and S. B. MUNCH. 2003. Estimating the relative contribution of spring- and summer-spawned cohorts to the Atlantic coast bluefish stock. *Trans. Am. Fish. Soc.*, **132**: 1117–1124. doi:10.1577/T02-047
- CREASER, E. P., and H. C. PERKINS. 1994. The distribution, food, and age of juvenile bluefish, *Pomatomus saltatrix*, in Maine. *Fish. Bull.*, **92**: 494–508.
- HARE, J. A., and R. K. COWEN. 1993. Ecological and

- evolutionary implications of the larval transport and reproductive strategy of bluefish *Pomatomus saltatrix*. *Mar. Ecol. Prog. Ser.*, **98**: 1–16. doi:10.3354/meps098001
1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces:Pomatomidae). *Mar. Biol.*, **118**: 541–550. doi:10.1007/BF00347500
1995. Effect of age, growth rate, and ontogeny on the otolith size-fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. *Can. J. Fish. Aquat. Sci.*, **52**: 1909–1922. doi:10.1139/f95-783
1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery areas. *Limnol. Oceanogr.*, **41**: 1264–1280.
- HURST, T. P. 2006. Causes and consequences of winter mortality in fishes. *J. Fish Biol.*, **71**: 315–345. doi:10.1111/j.1095-8649.2007.01596.x
- JUANES, F., J. A. BUCKEL, and D. O. CONOVER. 1994. Accelerating the onset of piscivory: intersection of predator and prey phenologies. *J. Fish Biol.*, **45**: 41–54.
- JUANES, F., J. BUCKEL, and F. SCHARF. 2002. Symposium review: ecology and life history of bluefish. *Rev. Fish Biol. Fish.*, **12**: 429–430. doi:10.1023/A:1025344418159
- JUANES, F., and D. O. CONOVER. 1994. Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). *Can. J. Fish. Aquat. Sci.*, **51**: 1752–1761. doi:10.1139/f94-176
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. doi:10.3354/meps128287
- JUANES, F., J. A. HARE, and A. G. MISKIEWICZ. 1996. Comparing life history strategies of *Pomatomus saltatrix*: a global approach. *Mar. Freshwat. Res.*, **47**: 365–379. doi:10.1071/MF9960365
- KENDALL, A. W., and L. A. WALFORD. 1979. Sources and distributions of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. *Fish. Bull.*, **77**: 213–227.
- LASSITER, R. MS 1962. Life history aspects of the bluefish, *Pomatomus saltatrix* from the coast of North Carolina. M.S. Thesis, North Carolina State College, 103 p.
- LEVIN, P., R. PETRIK, and J. MALONE. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia.*, **112**: 55–63. doi:10.1007/s004420050283
- MARKS, R., and D. CONOVER. 1993. Ontogenetic shift in the diet of young-of-the-year bluefish, *Pomatomus saltatrix*, during the oceanic phase of the early life history. *Fish. Bull.*, **91**: 97–106.
- MCBRIDE, R. S., and D. O. CONOVER. 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. doi:10.3354/meps078205
- MCBRIDE, R. S., J. L. ROSS, and D. O. CONOVER. 1993. Recruitment of bluefish (*Pomatomus saltatrix*) to estuaries of the South Atlantic Bight, U.S.A. *Fish. Bull.*, **91**: 389–395.
- MCBRIDE, R. S., M. D. SCHERER, and J. C. POWELL. 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. doi:10.1577/1548-8659(1995)124<0898:CVIASG>2.3.CO;2
- MUNCH, S. B., and D. O. CONOVER. 2000. Recruitment dynamics of bluefish (*Pomatomus saltatrix*) from Cape Hatteras to Cape Cod, 1973–1995. *ICES J. Mar. Sci.*, **57**: 393–402. doi:10.1006/jmsc.1999.0636
- MURDY, E. O., R. S. BIRDSONG, and J. A. MUSICK. 1997. Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington and London, 324 p.
- NEUHEIMER, A. B., and C. T. TAGGART. 2007. The growing degree-day and fish size-at-age: the overlooked metric. *Can. J. Fish. Aquat. Sci.*, **64**: 375–385. doi:10.1139/F07-003
- NYMAN, R. M., and D. O. CONOVER. 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.
- ROEMER, M. E., and K. OLIVEIRA. 2007. Validation of back-calculation equations for juvenile bluefish (*Pomatomus saltatrix*) with the use of tetracycline-marked otoliths. *Fish. Bull.*, **105**: 305–309.
- SCHARF, F. S., J. A. BUCKEL, K. A. ROSE, F. JUANES, and J. H. COWAN, Jr. 2006. Effects of variable prey and cohort dynamics on growth of young-of-the-year estuarine bluefish: Evidence for interactions between spring- and summer-spawned cohorts. *Trans. Am. Fish. Soc.*, **135**: 1266–1289. doi:10.1577/T05-075.1
- SCHARF, F. S., J. P. MANDERSON, M. G. FABRIZIO, J. P. PESSUTTI, J. E. ROSENDALE, R. J. CHANT, and A. J. BEJDA. 2004. Seasonal and interannual patterns of distribution and diet of bluefish within a middle Atlantic Bight estuary in relation to abiotic and biotic factors. *Estuaries*, **27**: 426–436. doi:10.1007/BF02803535
- SCHULTZ, E. T., D. O. CONOVER, and A. ETISHAM. 1998. The dead of winter: size-dependent variation and genetic differences in seasonal mortality among Atlantic silverside (Atherinidae: *Menidia menidia*) from different latitudes. *Can. J. Fish. Aquat. Sci.*, **55**: 1149–1157. doi:10.1139/cjfas-55-5-1149
- SECOR, D. H., J. M. DEAN, and E. H. LABAN. 1992. Otolith removal and preparation for microstructural examination. In: Otolith Microstructure examination and analysis. D. K. Stevenson and S.E. Campana (eds.). *Can. Spec. Publ. Fish. Aquat. Sci.*, **117**: 19–57.
- SHEPHERD, G. R., J. MOSER, D. DEUEL, and P. CARLSEN. 2006. The migration patterns of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries. *Fish. Bull.*, **104**: 559–570.
- SOGARD, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.*, **60**: 1129–1157.
- STEVENSON, D. K. and S. E. CAMPANA (ed.). 1992. Otolith microstructure examination and analysis. *Can. Spec. Publ. Fish. Aquat. Sci.*, **117**: 1–130.

- TAKATA, L. T. MS 2004. Habitat use and cohort recruitment patterns of juvenile bluefish (*Pomatomus saltatrix*) in diverse Maryland nursery systems. M.S. Thesis, University of Maryland, 115 p.
- TAYLOR, D. L., and K. W. ABLE. 2006. Cohort dynamics of summer-spawned bluefish as determined by length-frequency and otolith microstructure analysis. *Trans. Am. Fish. Soc.*, **135**: 955–969. doi:10.1577/T05-109.1
- WARLEN, S. M., and J. S. BURKE. 1990. Immigration of larvae of autumn/winter spawning marine fishes into a North Carolina estuary. *Estuaries*, **13**: 453–461. doi:10.2307/1351789
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