COHORT STRUCTURE, GROWTH, AND ENERGY DYNAMICS OF JUVENILE BLUEFISH IN THE HUDSON RIVER ESTUARY

A Final Report of the Tibor T. Polgar Fellowship Program

David G. Stormer

Polgar Fellow

Department of Natural Resources Conservation
University of Massachusetts
Amherst, Massachusetts 01003

Project Advisor:

Francis Juanes
Department of Natural Resources Conservation
University of Massachusetts
Amherst, Massachusetts 01003

ABSTRACT

The mechanisms of recruitment in marine fishes have been topics of much interest for several decades. Estuaries serve as nursery areas for their inhabitants by providing resources for fast growth, energy and protection against predation, ultimately increasing recruitment potential. Bluefish, *Pomatomus saltatrix*, is a species that uses the Hudson River estuary as a nursery area through summer and early fall.

In this study, the cohort structure of juvenile bluefish was investigated during summer residency in the Hudson River estuary by determining individual hatch-dates and examining length-frequency distributions. Growth rates and lipid content of white muscle were compared between the spring- and summer-spawned cohorts of juvenile bluefish through the summer of 2008.

Peak hatch-dates for the spring and summer cohorts occurred in mid-April and late June respectively. Spring-spawned juvenile bluefish comprised the entire catch until late July when the first summer-spawned fish was captured in the estuary. The summer cohort recruited to the estuary by mid-August, making up approximately half of the juvenile abundance (61% by the end August). The spring and summer cohorts exhibited similar growth rates. Lipid content of both cohorts was also similar when all time periods were combined. However, spring-spawned fish entered summer with higher lipid content and depleted energy reserves through the summer, whereas the summer cohort accumulated lipid content over time.
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INTRODUCTION

In fishes, small changes in growth rates of juveniles can have large impacts on the number surviving to the adult population (Taylor et al. 2007). Estuaries vary greatly in their biotic and abiotic characteristics with direct implications to fish populations. Variability in temperature, salinity and productivity has been associated with small-scale changes in growth for many species that reside in estuaries during early life stages (Castro and Cowen 1991; McBride et al. 1995; Cooper et al. 1998).

During estuarine residency, temperate and tropical fishes also accumulate energy reserves in the form of lipids and this energy acquisition is often essential for survival (Schultz and Conover 1999). For migratory fishes, foraging is greatly reduced or ceases during migration, and energy reserves are rapidly depleted. As a result, migrating species must rely on the stored energy acquired during estuarine residency to survive (Morley et al. 2007). For juveniles that spend the summer and early fall in estuaries, it is critical that adequate energy reserves are accumulated and available for the migration and over-winter survival.

One such species that uses estuaries extensively during early life-history stages is bluefish, *Pomatomus saltatrix*. Bluefish is a highly migratory species found worldwide in subtropical and temperate waters, except for the eastern Pacific (Juanes et al. 1996). In the United States, bluefish occur seasonally along the eastern coastline from Maine to Florida (Kendall and Walford 1979).

Bluefish reproduce multiple times along the eastern coast of the U.S. during annual spawning migrations. Although the exact temporal and spatial patterns of bluefish spawning remains uncertain, at least two cohorts (spring and summer) are evident as a
result of spawning over the continental shelf (Hare and Cowen 1996). Eggs and larvae develop offshore, and juveniles recruit to nearshore and estuarine waters (Nyman and Conover 1988). Multiple cohorts are rare in many species but may contribute to dampened recruitment variability in bluefish.

From the early 1970s to the mid-1990s, spring-spawned bluefish have dominated juvenile abundances, corresponding to a healthy adult population (Conover et al. 2003). However, for reasons unknown, a shift in recruitment dynamics from the mid-1990s through the turn of the century has appeared to favor the summer-spawned cohort, which has been implicated in the decline of the adult population (Conover et al. 2003). The coast-wide cohort structure from 2000 to the current time is unresolved.

Increased size-dependent mortality of summer-spawned bluefish could be contributing to decreased recruitment potential and subsequent declining adult stock size. Mortality during periods of cold stress is often related to size, with smaller individuals suffering higher mortality rates (Sogard 1997). Conover et al. (2003) observed greater abundances of age-0 summer-spawned bluefish than spring-spawned fish along the southern and mid-Atlantic coast, but found little evidence of the summer cohort in the adult population. Size-related over-winter starvation of small summer-spawned juvenile bluefish, and subsequent cohort-specific recruitment failure, were implicated in the recent decline of adult stock abundance (Conover et al. 2003). Differences in body size and energy acquisition between the spring and summer cohorts during estuarine residency coupled with an apparent shift in cohort structure may be associated with variable juvenile survival and recruitment potential (Slater et al. 2007). One explanation for this
disparity in relative abundance could be that many summer-spawned bluefish do not have the energy reserves to survive their first winter migration.

Summer-spawned bluefish are considerably smaller than the spring-spawned group when they first appear in the Hudson River estuary (Juanes et al. 1993), but there can be considerable overlap in the length distributions between the two cohorts. Juanes et al. (1993) suggested that cohort structure of juvenile bluefish may display considerable variation, and recommended a thorough examination of the cohort structure to better understand bluefish recruitment dynamics.

Length-frequency analysis has typically been the method used in evaluating cohort-specific recruitment success of juvenile bluefish. However, the examination of otolith microstructure may provide better resolution in cohort identification by counting daily growth rings to elucidate hatch-dates. Additionally, otoliths can provide an estimate of daily growth rate by back-calculating daily growth increments. Otolith microstructure analysis has recently been validated for aging juvenile bluefish (Roemer and Oliveira 2007), and has been used to examine cohort structure and estimate growth rates for juvenile bluefish inhabiting oceanic and estuarine environments (Taylor and Able 2006; Taylor et al. 2007; Roemer and Oliveira 2007). This aging technique can provide the same information as long-term mark-recapture studies or costly laboratory experiments in age determination and growth rate estimation (Roemer and Olivera 2007). However, otolith microstructure analysis has not been used to examine cohort structure or estimate growth rates for juvenile bluefish residing in the Hudson River estuary.

Examination of lipid content has proved a powerful approach in assessing the energy dynamics of freshwater and marine fishes (Miranda and Hubbard 1994; Griffiths...
Temporal dynamics, cohort structure, and environmental characteristics have been implicated in the differences in energy acquisition and depletion observed for juvenile bluefish during the over-wintering period (Morley et al. 2007; Slater et al. 2007). Slater et al. (2007) examined over-winter survival of the spring- and summer-spawned juvenile bluefish in mesocosm, but suggested a thorough investigation of lipid content in wild fish to estimate energy levels prior to the fall migration.

In this study, the hypothesis was tested that smaller individuals of the summer cohort accumulate lipids more rapidly or efficiently than larger spring-spawned bluefish at the time of estuarine egress. The specific objectives were to examine otolith microstructure to determine hatch-dates and cohort structure, and to compare cohort-specific growth rates of juvenile bluefish inhabiting the Hudson River estuary. Also, pre-winter energy reserves were assessed for juvenile bluefish during summer residency in the Hudson River estuary.

**METHODS**

Fish sampling was conducted biweekly from early July to late August 2008 at 30 stations over a 65 kilometer (km) section of the lower Hudson River estuary (Figure 1). Bluefish were collected with a 61 meter (m) x 3 m beach seine with 13 millimeter (mm) stretched mesh wings and a 6 mm stretched mesh bag. Seine hauls were set from a boat and parallel to shore. Catches were processed on shore, with juvenile bluefish preserved frozen for subsequent age and lipid analysis. Hydrographic (temperature, salinity, and
dissolved oxygen), and habitat (depth, tidal stage and substrate type) measurements were recorded for each seine haul.

Figure 1. Area of the Hudson River estuary selected for sampling juvenile bluefish. Straight lines terminating at river margin indicate sampling locations.

Cohort structure, and growth

Juvenile bluefish were aged by enumerating growth increments on sagittal otoliths. Whole otoliths were fixed, concave side down, to glass microscope slides and embedded in Crystalbond glass adhesive (SPI supplies). To facilitate interpretation,
embedded otoliths were ground by hand on 1,200-grit silicon carbide sandpaper and polished with alumina micropolish until growth increments were visible. Hatch-dates and daily increments were enumerated by viewing photographic images of sectioned otoliths produced by an Olympus compound microscope (Olympus America, Inc.) at a magnification of 400x. The images were transferred to image analysis software (Image J) for augmentation of growth increments. Hatch-dates were calculated by subtracting the number of otolith increments (age in days) from the date on which juvenile bluefish were collected in the field.

In the laboratory, individual juvenile bluefish were measured to ± 1.0 mm fork length (mm FL; measured from the tip of the jaw or tip of the snout with closed mouth to the center of the fork in the tail) and weighed (± 0.1 grams wet weight). Juvenile bluefish growth was derived from regression slopes of age-length relationships. Differences in the slopes of the linear regressions between body size and otolith increment counts (hatch-date or age) were analyzed with analysis of covariance (ANCOVA) models, with age in days (d) as the covariate and cohort (spring and summer) as the explanatory variables.

*Lipid content*

Approximately 2-4 grams (g) of white muscle were removed from individual bluefish representing each cohort and time of residency. White muscle was selected for lipid content analysis because this tissue is an appropriate proxy for overall energy content of juvenile bluefish (Slater et al. 2007). Tissue samples were weighed (± 0.001 g), dried at 60 °C for at least 72 hours, and reweighed to determine dry weight and percent water weight per sample. Dry tissue was transferred to pre-weighed porous
Alundum (fused alumina) thimbles for lipid extraction. An automated soxhlet extractor with di-ethyl ether was used to dissolve neutral lipids with a method similar to Shahidi (2001). Soxhlet extraction was used to remove the soluble components (lipids) from a solid sample (dried muscle tissue). The soxhlet extractor consisted of a flask which contained the solvent. As the flask was heated the solvent vapor rose (passing through the extraction thimble), and entered a water-cooled condensor, and liquified. When the liquid level in the extractor reached the top a siphon tube returned it as an extract-enriched solvent to the flask and this process was repeated until the entire lipid was dissolved. The extraction time was between 2-5 hours depending on the sample aggregation distillation rate. After extraction, the thimbles were dried again at 60 °C for 24 hours to ensure evaporation of remaining solvent prior to final weighing. Weights of post-extracted dry tissue and pre-extracted dry tissue were used to determine lipid content. Lipid levels were expressed as a proportion of the sample dry weight. Analysis of variance (ANOVA) and ANCOVA were used to compare lipid content between the spring and summer cohorts and among 4 time periods. Data were natural log (ln) transformed to meet assumptions of normality and homogeneity of variances. A significance level of ≤ 0.05 was considered statistically significant.

RESULTS

Cohort structure, and growth

A total of 269 juvenile bluefish were collected from the Hudson River estuary from 15 July 2008 to 27 August 2008, ranging in size between 43 – 192 mm FL (mean
FL = 125 mm; # of seine hauls = 156). Otolith microstructure was used to determine ages (d) of juvenile bluefish and ranged between 33 and 165 d (mean = 76 ± 33 d; n = 47). Back-calculated hatch-date distributions were bimodal, indicating the occurrence of spring and summer cohorts (Figure 2). Juvenile bluefish with hatch-dates on or before 15 May 2008 were assigned to the spring cohort and individuals with hatch-dates after 15 May 2008 were classified as summer-spawned. Peak hatch-dates for the spring and summer cohorts occurred in mid-April and late June respectively (Figure 2).

![Hatch-date distributions of juvenile bluefish collected from the Hudson River estuary during summer 2008, aged by otolith microstructure analysis.](image-url)

Figure 2. Hatch-date distributions of juvenile bluefish collected from the Hudson River estuary during summer 2008, aged by otolith microstructure analysis.
Hatch-date to length relationships of 47 juvenile bluefish were used to construct age-length keys for the remaining bluefish collected (n = 222) during each sampling event (15 July = T1; 29 July = T2; 13 August = T3; 27 August = T4; Figure 3). These data

Figure 3. Length-frequency distributions of spring-spawned (gray bars) and summer-spawned (black bars) juvenile bluefish collected from the Hudson River estuary on: (a) T1: 15 July 2008, (b) T2: 29 July 2008, (c) T3: 13 August 2008, and (d) T4: 27 August 2008.
corroborated the presence of two major spawning periods (spring and summer). In early summer (T1), all juvenile bluefish collected resulted from spring spawning (Figure 3a). Summer-spawned bluefish first appeared in the Hudson River estuary in late July (T2), and constituted approximately 50% of the bluefish catch by mid-August (T3). In late summer (T4), multiple pulses of summer-spawned bluefish were evident as the length frequency distribution of this cohort resulted in 2 modes (mean = 101 mm FL, mode 1; mean = 120 mm FL, mode 2; Figure 3d).

Growth was estimated from the slope of the linear regression between juvenile bluefish size and age for the spring and summer cohorts. Covariate analysis showed that growth was similar between the cohorts (ANCOVA; age x cohort: $F = 1.24, df = 1, P = 0.27$; Figure 4).

![Figure 4. Body size (mm FL) to age (# of otolith increments) relationships of juvenile bluefish as a function of cohort (spring and summer).](image-url)
Lipid content

Total neutral lipids constituted between 2.0 and 8.2 % (mean ± standard error = 5.42 ± 0.19 %, n = 46) of dried muscle for the spring and summer cohorts combined. Lipid content ranged from 2.0 – 8.2 % of dried muscle for the spring cohort (mean ± standard error = 5.43 ± 0.24; n = 31) and from 3.0 – 7.2 % (mean ± standard error = 5.34 ± 0.32; n = 15) for the summer cohort. The lipid percentage in dried muscle did not differ between the spring and summer cohorts of juvenile bluefish inhabiting the Hudson River estuary after pooling time periods (F = 0.04, df = 1, P = 0.85; Figure 5).

![Figure 5](image.png)

Figure 5. Mean (±SE) lipid content of white muscle for spring- and summer-spawned juvenile bluefish cohorts over all time periods combined.

To examine the effect of time period on lipid content of the spring and summer cohorts combined, T1 was omitted because no summer-spawned individuals were collected.
Lipid content was similar among times 2 – 4 (F = 0.33, df = 2, P = 0.72) for the spring and summer cohorts of juvenile bluefish combined. Lipid content declined modestly with increasing bluefish length when cohorts were combined (r² = 0.10, P = 0.04; Figure 6).

Figure 6. Lipid content as a function of length (mm FL) for the spring and summer cohorts of juvenile bluefish inhabiting the Hudson River estuary during summer 2008 combined (n = 46).

Cohort-specific lipid content of juvenile bluefish over time was examined using ANCOVA. The slope coefficient of the lipid content to time period relationship differed between the cohorts (t = 2.33, P = 0.02). Lipid content of spring-spawned juvenile bluefish was highest during the first time period and decreased through the summer. The
summer-spawned cohort exhibited the lowest lipid content levels upon arrival into the Hudson River estuary and increased over time (Figure 7).

Figure 7. Mean (± SE) white muscle lipid content for the spring and summer cohorts of juvenile bluefish residing in the Hudson River estuary as a function of time period.

DISCUSSION

Cohort structure, and growth

This study supports the function of the Hudson River estuary as an important juvenile bluefish nursery area, as the estuary is used by the spring and summer cohorts of juvenile bluefish throughout the summer. Juvenile bluefish have previously been classified as estuarine dependent (Kendall and Walford 1979); however, the summer cohort may preferentially inhabit the coastal ocean zone during late summer and early fall.
(Able et al 2003). The results of this study indicate estuarine use by the 2 cohorts of juvenile bluefish throughout the summer. Ocean sampling was not included in this study, but would be necessary to determine cohort-specific habitat selection. Further, movement between the coastal ocean and estuary by juvenile bluefish during summer and fall remains largely unresolved. Nevertheless, it was evident by consistent abundances of the spring and summer cohorts that the Hudson River estuary provided adequate resources for summer-long residency of juvenile bluefish.

In early summer, the entire catch of juvenile bluefish in the Hudson River estuary was comprised of spring-spawned individuals, while the summer cohort did not ingress until late July. These findings were consistent with previous observations of bluefish recruitment to the Mid-Atlantic Bight (MAB) (Wilber et al. 2003; Taylor and Able 2006). By late summer, catches of summer-spawned bluefish were greater than the spring cohort providing evidence for summer-spawned cohort dominance of the age-0 year class as suggested by Conover et al (2003). Estimates of cohort-specific abundance in the Hudson River estuary and associated coastal ocean zone through fall are required to further elucidate the pre-migration cohort structure. Examination of otolith microstructure allowed for hatch-date distributions and corresponding age-length keys to be constructed, which corroborated the identification of two principal bluefish spawning events (Figure 2). Mean hatch-dates of mid-April and late June indicated the two spawning events occurred in spring and summer respectively. The timing of spawning periods was consistent with previous studies of juvenile bluefish recruitment dynamics in other Atlantic coast estuaries (Taylor et al. 2007; Callihan et al. 2008).
Length-frequency distributions (Figure 3) were consistent with a previous study that indicated the presence of at least 2 cohorts with the possibility of multiple intra-summer-spawned cohorts of juvenile bluefish inhabiting the Hudson River estuary (Taylor and Able 2006). Concomitant with earlier hatch-dates of the spring cohort, and similar cohort-specific growth rates, members of the spring cohort (mean = 147 mm FL) were larger in absolute size than summer-spawned bluefish (mean = 94 mm FL) by the end of August. The disproportionately low contribution of summer-spawned individuals to the adult bluefish population observed by Conover et al. (2003) could result from size-selective mortality of summer-spawned individuals as they emigrate from inshore nurseries to over-wintering waters of the South Atlantic Bight.

Discrete estimates of cohort-specific growth (spring cohort = 1.15; summer cohort = 1.49 mmFLd^{-1}, Figure 4) were comparable with juvenile bluefish growth rates observed elsewhere in the MAB (McBride and Conover 1991; Able et al. 2003). However, the range of growth rates estimated in this study was lower than reported for juvenile bluefish in the Chesapeake Bay, Maryland (Callihan 2005). This discrepancy may be explained by spatial and inter-annual variation in water temperature between the Hudson River estuary and the Chesapeake Bay. Bluefish growth is optimized at a water temperature of approximately 24 °C (Hartman and Brandt 1995), and it is likely (Callihan 2008) that the Chesapeake Bay area maintains sea surface temperatures closer to this optimum for a longer period through the summer than the Hudson River estuary, thus maximizing growth potential. All the same, this study reaffirms that bluefish growth rates are among the fastest of any temperate fish species (Able and Fahay 1998).
Summer-spawned bluefish may be expected to exhibit faster growth than spring-spawned juveniles to compensate for the size advantage incurred by earlier hatch-dates and dietary shift to piscine prey of the spring cohort (Juanes and Conover 1995). Taylor et al. (2007) reported faster growth of summer-spawned juvenile bluefish than the spring cohort in New Jersey waters, but the observed growth rate differences corresponded to habitat whereby growth rates were higher in the coastal ocean than the estuary irrespective of cohort classification. In this study, growth rates of the spring and summer cohorts of juvenile bluefish residing in the Hudson River estuary during summer were similar.

**Lipid dynamics**

For many fishes, accumulation of lipids in muscle has been associated with increasing body length (Hutchings et al. 1999). Juvenile bluefish do not seem to follow these patterns as lipid content declined with increasing length when individuals of each cohort were examined together (Figure 6). However, when examined separately, larger body size of the spring cohort conferred higher energy content at the beginning of the summer, and subsequently declined with length, while the summer cohort exhibited increasing lipid reserves with length (Figure 7). The observed cohort-specific lipid content to length relationships corresponded to the growth rate estimations and length-frequency analyses. The summer cohort did not exhibit an increased rate of size-specific compensatory growth, indicating considerable resource intake to energy storage in the form of lipids.

The lipid content in dried muscle of the spring and summer juvenile bluefish cohorts inhabiting the Hudson River estuary were similar after pooling time periods.
(Figure 5). However, a significant time effect was evident, revealing a decline in energy content of the spring cohort, and an accumulation of lipids in summer-spawned juvenile bluefish through the summer of 2008 (Figure 7). Morley et al. (2007) reported higher energy content in the spring cohort than summer-spawned bluefish at the beginning of summer from the nearshore waters of North Carolina. However, over-summer lipid dynamics were not examined, and June was the final time period analyzed by the investigators (Morley et al. 2007). In this study, the summer cohort did not appear in the Hudson River estuary until late July, and approximately 1 month after spring-spawned bluefish. It is possible that an earlier dietary shift by the spring cohort from low energy prey to a more lipid rich fish diet (Juanes et al. 1994) resulted in higher initial energy content of spring-spawned fish, while the summer cohort suffered from an early summer lipid accumulation deficit.

**CONCLUSION**

A risk tradeoff between migration (or over-winter starvation) and predation may explain the observed cohort-specific growth rates and differences in lipid allocation versus mobilization strategies (Post and Parkinson 2001). If adequate energy storage is not obtained prior to the fall migration, energy depletion and starvation may increase natural mortality. Conversely, smaller individuals are at greater risk to predation than larger conspecifics, and could suffer higher predation mortality by allocating a greater proportion of energy intake to lipid storage over somatic growth (Sogard 1997). Results of this study indicated that the spring and summer cohorts of juvenile bluefish inhabiting the Hudson River estuary grew at similar rates and that summer-spawned fish
accumulated lipids while the spring cohort depleted energy reserves over time. Perhaps, energy acquisition was selected over growth in the summer cohort in preparation of the fall migration. Consequently, size-specific predation mortality rather than starvation during migration may explain the recruitment failure exhibited by the summer cohort of juvenile bluefish to the adult population.
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