Fall and winter estuarine recruitment of bluefish *Pomatomus saltatrix*: selectivity for large lipid-rich prey increases depleted energy levels

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ABSTRACT: The early life history of bluefish *Pomatomus saltatrix* follows a complex cycle with several migrations to and from estuarine nurseries. In contrast to spring and summer, little is known about fall and winter estuarine habitat use of juvenile bluefish. Here, we examined fall and winter estuarine ecology of juvenile bluefish in the Matanzas River Estuary in northeastern Florida over a 2 year period. Three distinct intra-annual cohorts of young-of-the-year (YOY), and age 1+ fish were identified through size frequencies and verified with otoliths. Estuarine recruitment was first observed in late October by spring-spawned and age 1+ fish, followed by summer-spawned YOY, and finally by the fall-spawned cohort with no new recruitment after February. Interannual differences in the timing of estuarine entry were likely due to variation in shelf cooling. A peak in relative abundance was observed in December. The highest relative abundances were found near the sandy inlets. Fish dominated the diet of all bluefish cohorts, mugilids by age 1+ and spring-spawned YOY bluefish, and engraulids by summer- and fall-spawned YOY. In contrast to previous studies, YOY and age 1+ bluefish were strongly selective for *Mugil* spp. prey. Bluefish lipid content increased over the fall and winter, peaking in January. A comparison of prey lipid levels across 30 potential prey species showed that *Mugil* spp. had the highest lipid content, 5 to 6× higher than lipid levels in other common prey items. We conclude that juvenile bluefish use Florida estuaries during the fall and winter to increase depleted lipids through selective feeding. Year class strength and cohort survival may be strongly related to the availability of selected prey items during this time.

KEY WORDS: Juvenile recruitment · Winter ecology · Lipid dynamics · Predator−prey

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INTRODUCTION

Many marine fishes migrate seasonally. In contrast to freshwater fish species, in temperate waters many marine or estuarine fish leave coastal and estuarine waters in the fall to avoid severe winter mortality and inhabit areas where survival rate will increase (Able & Fahay 1998, Hurst 2007). Several factors are responsible for controlling seasonal migration and estuarine recruitment including variations in water temperature, salinity, prey availability, and predation (Blaber 1987, Deegan 1990, Blaber et al. 1995, Livingston 1997).

The bluefish *Pomatomus saltatrix* (Linnaeus) is among the relatively few pelagic marine fish species to be globally distributed in subtropical inshore, coastal, and continental shelf waters (Briggs 1960) and has a similar migration pattern in all populations where it has been studied (Juanes et al. 1996). In the western North Atlantic, bluefish represent an important commercial and recreational fishery along much of the eastern USA (Oliver et al. 1989, Pottern et al. 1989, Shepherd & Packer 2006). The range of the northwest Atlantic population is extensive, spanning from the Gulf of Maine in the north

to Florida waters in the south (Collette & Klein-Macphee 2002).

Along the east coast of the USA, bluefish undergo repeated north–south movements along continental shelves, first as larvae (Hare & Cowen 1996, 1997), then as juveniles after the first summer of life (Buckel et al. 1999a, Munch & Conover 2000), and then as sub-adults and adults in later years (Lund & Maltezos 1970, Shepherd et al. 2006). These migrations appear to be largely regulated by environmental factors, primarily water temperature and prey availability (Olla et al. 1985, Hare & Cowen 1996). Spawning occurs annually in 2 distinct events. In early spring, adults first spawn in the South Atlantic Bight (SAB, ~27°N to 35°N) shelf waters between the months of March and May, which is coupled with a simultaneous northerly migration into the mid-Atlantic Bight (MAB, ~35°N to 40°N) (Juanes & Conover 1995). A portion of these spring-spawned larvae are then advected northward along the eastern Atlantic coast in waters associated with the Gulf Stream while others remain in the SAB (Hare & Cowen 1996). At sizes between 40 and 60 mm, larvae recruit into estuaries and coastal waters where a shift in diet occurs, from one consisting primarily of planktonic prey to one of piscine prey items (Marks & Conover 1993). A second spawning event takes place in the MAB during the months of June through August. These summer-spawned larvae also recruit into estuaries at similar sizes, and recruitment densities are comparable to the spring-spawned cohort (McBride & Conover 1991, Hare & Cowen 1996, Taylor & Able 2006, Wuenschel et al. 2012). A third but substantially smaller spawning event occurs during mid to late fall in the SAB, resulting in fall-spawned YOY which primarily recruit into SAB coastal waters (Collins & Stender 1987, McBride et al. 1993, Wuenschel et al. 2012).

By late summer/early fall, bluefish leave MAB estuaries and coastal waters and migrate southwards back into the SAB where they are thought to spend the winter (Munch & Conover 2000, Shepherd et al. 2006), and until recently little was known about their fall- and winter-time distribution, feeding habits, or physiological condition (Wuenschel et al. 2012). Previous research has primarily focused on distribution and abundance in the coastal waters of the MAB and northern SAB (Scharf et al. 2004, Taylor et al. 2006, Wuenschel et al. 2012). Much of this work has emphasized the locations and timing of estuarine recruitment as well as subsequent post-larval migrations during the spring and summer months. Only recently has work on winter ecology been completed (Morley et al. 2007, Slater et al. 2007, Murt & Juanes 2009).

Winter mortality can have a strong regulatory role in fish populations (Henderson et al. 1988) and is often size-dependent (Hurst & Conover 1998, Schultz et al. 1998) due to elevated size-specific metabolic rates of smaller fishes and their increased vulnerability to predation (Juanes 1994). Winter mortality can also be caused by lowered temperatures and chronic starvation due to loss of energy reserves (Schultz et al. 1998). Energy reserves, usually in the form of lipids, are typically expended in energetically demanding activities such as reproduction and migration, or in routine activities during periods of prey scarcity (Adams 1999, Shulman & Love 1999). However, the mechanisms responsible for replenishing depleted energy levels are unclear. Do overwintering individuals expend less energy by reducing activity and/or increasing feeding rates? These seem unlikely in a dynamic coastal system during relatively adverse environmental conditions. Could fish instead switch their diets to target lipid-rich prey ('nutrient-specific foraging'; see Mayntz et al. 2005) to build energy levels? Juvenile bluefish diets have been well studied, primarily in the MAB in the summer (Wuenschel et al. 2012) where YOY tend to be generalists and non-selective with respect to prey type (Juanes et al. 1993, Juanes & Conover 1995), but negatively size-selective (Juanes et al. 1994, Scharf et al. 2003, 2009). In contrast, little is known about diets, prey availability, or prey-type and -size selectivity during fall and winter months, and how variation in prey lipid content affects prey choice.

Results of a recent analysis using catch data collected by NMFS Northwest Atlantic fall cruises from 1972 to 2001 indicated that first year overwinter survival was a 'critical period' (sensu Hjort 1914) for bluefish that could dictate recruitment success (Wiedenmann & Essington 2006) and, thus, the relative abundance of spring- and summer-spawned cohorts. Those authors also concluded that research focused on the overwintering period is lacking but necessary. It is, therefore, important to understand the role SAB estuaries may play for juvenile bluefish survival during these times of potential stress.

Recent work has clarified fall and winter bluefish distributions in the SAB (Morley et al. 2007, Wuenschel et al. 2012) but, compared to the MAB, we still do not fully understand to what extent estuaries provide habitat during this period.

In North Carolina, YOY fish are collected year around; in some years, catches peak in early fall (October) and decline thereafter, in others, catches

peak in late fall/early winter (November/December) and are typically lowest in early winter (January) (Morley et al. 2007, Wuenschel et al. 2012). Historical tagging data suggest that Florida estuaries may provide winter habitat for bluefish (see Shepherd et al. 2006); however, no previous studies have focused on fall and winter estuarine use in Florida. The northeastern coast of Florida is also likely critical for older overwintering bluefish since it is the waters off the coast of Florida in the spring that are first used as spawning grounds (Kendall & Walford 1979).

Since the importance of estuaries to age-0, juvenile, and adult bluefish recruitment is unknown during the winter, particularly at the southern edge of the North American distribution, determining the significance of estuarine recruitment by bluefish in Florida warrants attention. We expect that during late fall and early winter juvenile bluefish will use Florida estuaries to feed on abundant estuarine fishes and continue to exhibit decreased energy levels until the spring. The objectives of this study are to examine the use of a SAB estuary by juvenile bluefish during fall and winter by assessing habitat use and
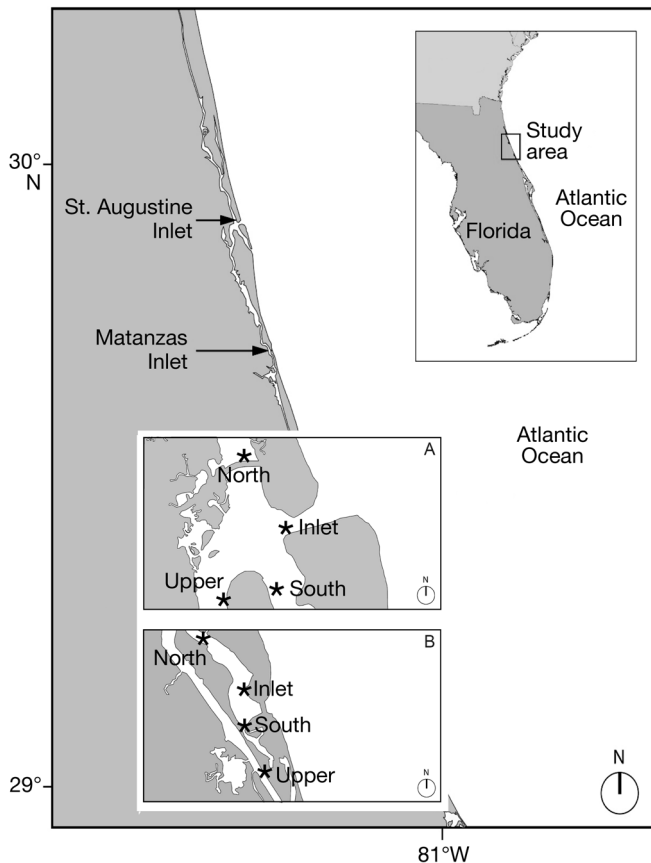

Fig. 1. Location of the Matanzas River estuary, (A) Saint Augustine Inlet site and (B) Matanzas Inlet site. Sampling locations (★) are identified at each site

distribution, feeding ecology, and energy levels of bluefish and their prey.

MATERIALS AND METHODS

Field sampling

Sampling took place in the Matanzas River estuary located in northeast Florida (Fig. 1). The Saint Augustine and Matanzas inlets served as northern and southern study sites respectively (Fig. 1), and are joined by the intra-coastal waterway. We used 2 gear types to sample across all age classes. Gillnets were 91 m long, consisting of 5 panels, each 18 × 2 m, with mesh size progressing from 13 mm to 203 mm stretch. A progression of mesh size from small to large allowed the collection of available prey items in addition to a range of bluefish sizes, although primarily larger bluefish were collected with gillnets. A 30 m beach seine constructed with 7 mm stretch mesh wings with a 6 mm mesh bag was also used and primarily collected smaller bluefish as well as potential prey items. Sampling was conducted over the course of 2 consecutive winters. In Year 1, sampling began on November 9, 2002 and ended on February 24, 2003. In Year 2, we sampled from October 13, 2003 to January 16, 2004. Four fixed gillnet sampling stations were established in each site with 3 random locations at each station for a total of 12 net deployments at each site (Fig. 1). Both sites were sampled twice a week with gillnets and once a week with beach seines during daylight hours and randomly during the tidal cycle. Gillnets were deployed and soaked for a minimum of 1 h each. Fixed seining stations were identified and overlapped as far as possible with our gillnet stations. Where access or substrate topography did not allow for direct overlap sampling, a station in close proximity was established and sampled instead. Several seine sites were tidally dependent and were sampled as allowed during the tidal cycle. At each seine station, 2 hauls were completed, for a total of 8 hauls per site. Each of the 4 stations located within a site was identified by proximity to the inlet proper and by benthic habitat. Stations within each site were identified as an inlet station, north of inlet (upriver from the particular inlet station), south of inlet, and upper estuarine (west of all other stations). Specific net locations were recorded during each net deployment using GPS coordinates to ensure that fixed stations were sampled repeatedly. Depth was recorded using a Hummingbird Depth recorder.

Temperature, salinity, and dissolved oxygen were measured just below the water surface during each net set with a multi-parameter YSI-80 meter. Turbidity was measured using a Secchi disk. Estuarine temperatures were compared to temperature data collected from National Marine Fisheries Service buoys in continental shelf waters in the MAB (Station 44009, Delaware Bay, 26 nautical miles SE of Cape May, New Jersey) and SAB (Station 41012, 40 nautical miles ENE of St. Augustine, Florida).

All captured fish were identified and sorted by species, enumerated, and measured for length (±1 mm); all species other than bluefish were returned to the water unless further identification was needed. In such cases, representative size ranges were retained and preserved in 95% ethanol. Bluefish were either immediately gutted, and stomach contents preserved, or preserved whole in 95% ethanol.

Bluefish were grouped by intra-annual cohorts of spring, summer, and fall-spawned YOY, and age 1+ fish using length-frequency histograms, consistent with frequency distributions found in MAB and other SAB estuaries, and later verified by otolith analyses (Murt & Juanes 2009). Based on previous age and growth estimates in MAB estuaries, YOY maximum size is 300 mm fork length (FL) at the end of the summer, and fish grow an additional ~60 mm during the fall and winter, to a maximum of 360 mm FL in the first year of life (Lassiter 1962, McBride & Conover 1991, Salerno et al. 2001). We therefore designated fish in the SAB occurring during the fall and winter as YOY when FL was less than 360 mm (and age 1+ fish, FL ≥360 mm). Based on length frequency distributions and previous work in the SAB (Lassiter 1962, McBride et al. 1993, Morley et al. 2007), spring-spawned YOY fish included FL = 226–359 mm, summer-spawned YOY fish FL = 80–225 mm, and fall-spawned fish FL ≤79 mm.

To collect prey fish for lipid analyses, we used the same seine net as above. Monthly sampling was conducted at 4 fixed sampling sites: St. Augustine Inlet, Matanzas Inlet, and 2 sites further south, Gamble Rogers State Park and Ponce De Leon Inlet. Three stations were sampled in each inlet site during each sampling trip: inside the inlet, in the mouth of the inlet, and on the ocean beach. Gamble Rogers State Park was sampled only in the intra-coastal canal. A minimum of 2 seine hauls were sampled at each station for a total of 114 hauls between October 27, 2005 and January 29, 2006. Where possible, different size classes of each prey species were selected for lipid extractions to allow for variability in lipid content amongst sizes.

Relative abundance and distribution

Relative abundance of bluefish and their main prey items were calculated using a catch per unit effort (CPUE) index by calculating the number of fish collected per hour of gillnet deployment or the number of fish collected per seine haul for each sampling month within each year. Data were pooled for stations and sites for each year but remained separate for individual years to enable between year variability comparisons.

Dietary analysis

Diets of spring-, summer-, and fall-spawned YOY and age 1+ bluefish were quantified. Summer- and fall-spawned YOY bluefish were immediately measured for length (±1 mm FL) preserved whole in 95% ethanol and weighed (±0.01 g) prior to extracting stomachs in the laboratory. Spring-spawned YOY and age 1+ bluefish were processed in the field, whole stomachs were preserved in 95% ethanol while the gutted bodies were retained in ice and measured for wet weight in the laboratory. Stomach contents were identified to the lowest possible taxon, enumerated, blotted dry, weighed (±0.01 g), and, when possible, measured for length (±1 mm). Identification of well-digested partial remains of fish prey was aided by the inspection of scales, otoliths, and jaw morphology. Two indices were calculated to describe diet composition (Hyslop 1980): (1) number of stomachs in which a taxon occurred, expressed as a percentage of the total number of stomachs containing food (%FO = percent frequency of occurrence), and (2) weight of a taxon, expressed as a percentage of the total weight of food items found in all stomachs examined (%W = percent weight). To assess cohort-specific diets, bluefish were classified by cohorts as described above.

Predator–prey size relationships

The relationship between prey size (mm FL for fish) and predator size (mm FL) was determined by regression analysis using dominant prey items. To assess how maximum and minimum prey sizes changed with predator size, we estimated the upper and lower bounds of the scatter using quantile regression (Scharf et al. 1998b, 2000, Juanes 2003). Often, bluefish guts contained only partial pieces of digested remains of prey. Regressions between FL and eye diameter (ED, ±0.1 mm) or caudal peduncle depth (CP,

±0.1 mm) were used to reconstruct original prey length (FL) for *Anchoa mitchilli* bay anchovy (see regression equations in Scharf et al. 1997) and *Mugil curema* white mullet, the most common prey items. The resulting regressions for mullet were FL = 0.0488 × ED + 1.271 (n = 22, r^2 = 0.8306, p < 0.0001, FL range = 104–249 mm) and FL = 0.0514 × CP − 4.544 (n = 11, r^2 = 0.5166, p < 0.0001, FL range = 97–249 mm).

Prey selectivity

To assess bluefish prey type selectivity, we compared the relative abundance of the 4 most prevalent prey items found in the gut contents (measured as frequency of occurrence) with the corresponding relative abundance of those species in the field. Relative prey abundance in the field was calculated using seine haul collection data, and was computed as the number of fish collected per haul. Seine collections represented 94% of total potential prey sizes within the size range of bluefish collected. Maximum prey size range was estimated from previous work on bluefish predator–prey size relationships (Scharf et al. 2002, 2004). We quantified bluefish prey selectivity using Chesson's (1983) index,

$$\alpha_i = \frac{r_i \, / \, p_i}{\sum_{j=1}^{m} r_j \, / \, p_j}, \; i = 1, \ldots, m \qquad (1)$$

where α_i is the selectivity for prey type i, r_i is the relative abundance of prey type i in bluefish stomachs, p_i is the relative abundance of prey type i in the environment, and m is the number of prey types available. Random feeding occurs when $\alpha_i = 1/m$. In this study, values of $\alpha_i > 0.25$ or $\alpha_i < 0.25$ represent 'selection' and 'avoidance' of prey respectively. For this analysis, we lumped together spring-spawned and age 1+ fish, and summer- and fall-spawned YOY respectively as they had similar diets. For most prey types, selectivities were calculated for the entire season (i.e. one value for r, and one for p in each year). For prey that occurred over most months in stomachs and the environment, we calculated mean monthly selectivities (α_i) and tested whether they were statistically different from 0.25 using *t*-tests.

Lipid analysis

We used a Soxhlet extractor to determine lipid content of dry white muscle tissue. Previously weighed wet white muscle was placed in a 60°C drying oven

and, after at least 72 h, reweighed to determine tissue dry weight and percent water weight. The dry tissue was transferred to pre-weighed porous Alundum thimbles for lipid extraction. An automated Soxhlet extractor with petroleum ether was used to dissolve the neutral lipids of up to 32 samples at a time. We used an extraction period of 5 h, allowing for at least 20 cycles of clean petroleum ether. Thimbles were then placed in a 60°C drying oven for a period of 24 h to ensure the evaporation of remaining solvent prior to final weighing. Lipid content was determined from the difference in weights between pre- and post-extraction tissues.

The composition of each fish was expressed as the weight of water and neutral lipids. Lipid levels, expressed as a percentage of muscle dry mass, were compared across months by converting the sample date to day of the year (with January dates attached to the previous year, i.e. dates > 365) and performing linear regressions. We also assessed the relationship between bluefish length and % lipids, and bluefish length and day of the year using linear regression.

Because of the small size of most prey, lipid analyses were performed on whole individuals rather than only white muscle. The extraction process was as above. Prey were divided by species before extractions. Distinguishing white mullet *Mugil curema* from striped mullet *Mugil cephalus* juveniles proved to be extremely difficult for fish <40 mm. Therefore, all mugilids <40 mm were categorized as juvenile mullet. Where possible, multiple extractions were carried out on the same species, but when sample sizes and body sizes were small, multiple fish from the same species were combined into one sample. As for bluefish, all lipid results for prey species are presented as % dry weight and compared among prey species using an analysis of variance (ANOVA).

RESULTS

Water temperature

Surface temperatures in the Matanzas River estuary declined from October (~24°C) through January (~14°C) (Fig. 2A). Offshore buoy data obtained from NMFS buoys showed that in October 2002, continental shelf waters of the Mid-Atlantic Bight reached a mean of 20°C, and by November dropped to a mean of 14°C (Fig. 2B). In contrast, during that same year, shelf waters off Florida in the SAB experienced mean temperatures of 27°C in October and 25°C in November (Fig. 2B). Year 2 followed a similar trend al-
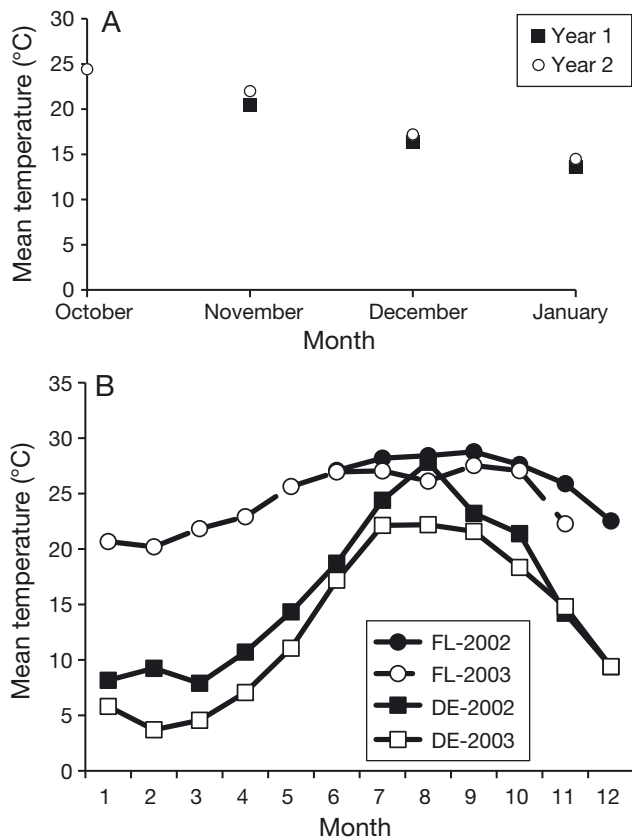
Fig. 2. (A) Average water temperatures in the Matanzas River estuary (Year 1: Nov 2002–Jan 2003; Year 2: Oct 2003–Jan 2004) and (B) buoy temperature off Cape May, New Jersey, 2002–2003 (DE) and St. Augustine, Florida, 2002–2003 (FL). Note that there are no Florida buoy data for Jan–May 2002, and Dec 2003

though shelf temperatures were on average lower, particularly in the MAB (Fig. 2B). Dissolved oxygen varied from 3.5 to 8.5 mg l^{-1}, Secchi disk depth from <1–4 m, and salinity from 22 to 36 ppt (data not shown).

Relative abundance and distribution

Age 1+, and spring-spawned YOY bluefish were primarily captured with gillnets, summer and fall-spawned YOY bluefish with seine nets. In both years, the first bluefish to be captured were age 1+ (≥360 mm FL) individuals. This was followed shortly during the same month by the appearance of YOY fish (<359 mm FL) in our samples (Fig. 3). In both years, the onset of recruitment into the estuary began in late fall, and estuarine use ceased by mid-winter. However, the specific month of initial appearance of YOY and age 1+ fish differed between years. During

Year 1, age 1+ and YOY bluefish were first captured in late November in 3 distinct size modes representing fall-spawned YOY (size range = 53–71 mm FL, mean ± SD = 58 ± 8.8 mm FL), spring-spawned YOY (244–353 mm FL, 298 ± 39.4 mm), and an age 1+ cohort (360–418 mm FL, 381 ± 18.6 mm). In December, the samples consisted of spring-spawned YOY (232–355 mm FL, 311 ± 31.3 mm), with only a few individuals identified as age 1+ fish (360–463 mm FL, 379 ± 23.1 mm). In January, only one size mode was observed, consisting of spring-spawned YOY (243–358 mm FL, 307 ± 24.9 mm). Sampling efforts in February during the first year produced no bluefish.

In Year 2, the onset of estuarine recruitment began in October with the collection of spring-spawned YOY fish (258–355 mm FL, 324 ± 33.4 mm) and a few age 1+ fish (370–454 mm FL, 409 ± 40.9 mm). In November, samples yielded both summer- (80–111 mm FL, 97 ± 7.2 mm) and spring-spawned YOY cohorts (235–358 mm FL, 315 ± 38.1 mm), in addition to several age 1+ fish (360–456 mm FL, 391 ± 28.9 mm). In December, spring- and summer-spawned YOY were collected (274 ± 38.2 mm and 216 ± 8.3 mm FL respectively), and fall-spawned YOY appeared for the first time (40–55 mm FL, 47 ± 4.5 mm). January sampling produced only 4 spring-spawned YOY (261–286 mm FL, 275 ± 11.6 mm).

During both years, relative abundance of all size classes of bluefish was highest during December (Fig. 4). In Year 1, bluefish abundance reached a peak quickly during December with only a few collections occurring in November and slowly declining during the month of January until recruitment into our sampling gear ceased. Year 2 abundance experienced a gradual increase to a peak in December and abruptly declined in January (Fig. 4).

Juvenile bluefish spatial distributions within the Matanzas River estuary varied between years and sites but were similar across sampling locations (Fig. 5). The Matanzas Inlet site was cumulatively more productive than the Saint Augustine site for YOY and age 1+ bluefish during Year 1 with more bluefish caught at stations nearest the inlets (Fig. 5). Conversely, Year 2 sampling produced more YOY bluefish in the Saint Augustine site, but, consistent with the previous year, the most productive stations were those found nearest the inlet (Fig. 5).

Diets

We examined the stomach contents of 384 bluefish (age 1+ n = 43, spring-spawned YOY n = 277, sum-

mer-spawned YOY n = 60, and fall-spawned YOY n = 14), ranging in size from 40 to 463 mm FL. Of the stomachs examined, 74% contained prey and all were dominated by teleost fish (Table 1). In both years, spring-spawned YOY/age 1+ fish and sum-
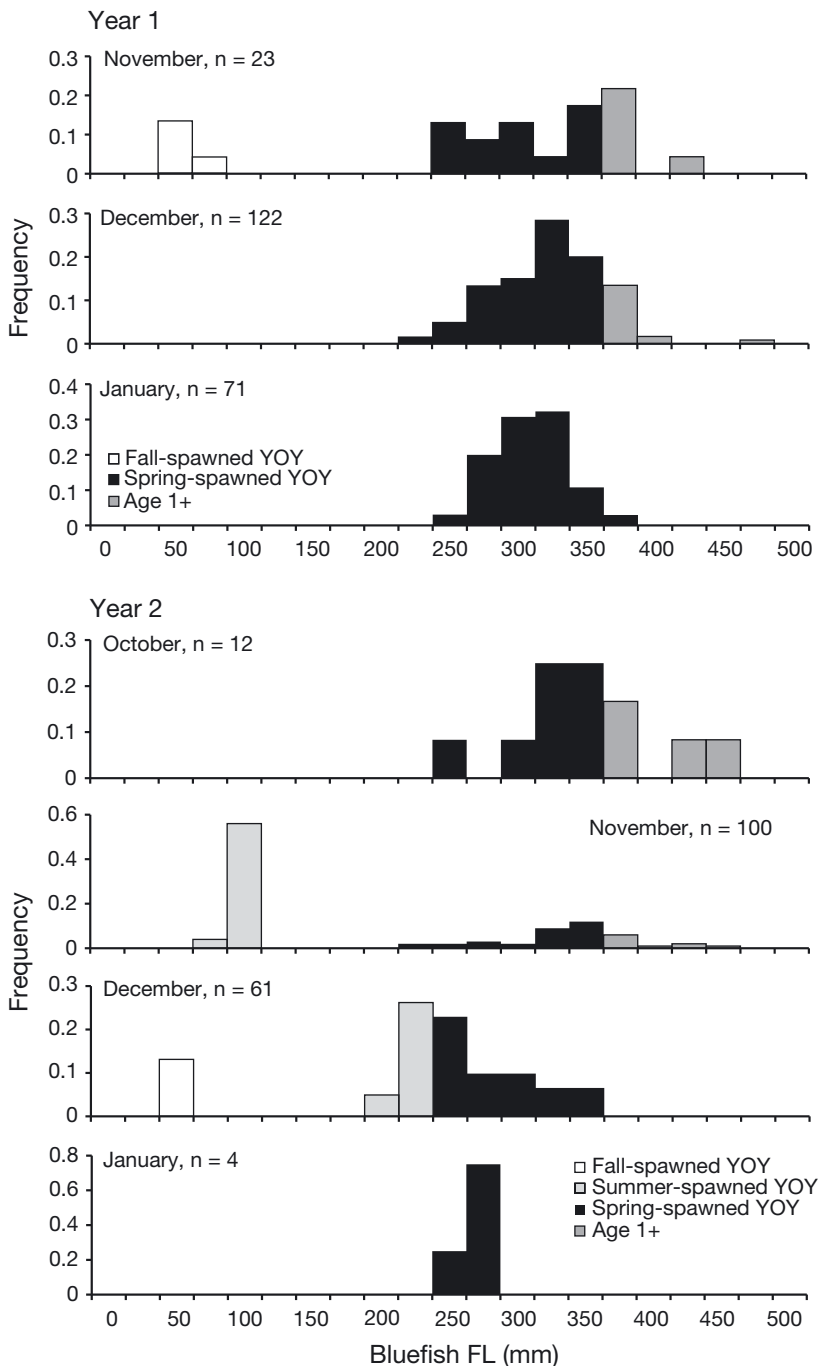

Fig. 3. *Pomatomus saltatrix*. Length-frequency distributions of bluefish for Year 1 (Nov 2002–Jan 2003) and Year 2 (Oct 2003–Jan 2004) by cohort captured in the Matanzas River estuary. All age 1+, and spring-spawned YOY (young-of-the-year) bluefish were captured with gillnets, summer-spawned and fall-spawned YOY bluefish with seine nets

mer/fall-spawned YOY differed in prey composition but were similar across years within these age classes (Table 1). Diets of both spring-spawned YOY and age 1+ fish consisted almost exclusively of a mixture of mullets, *Mugil curema* and *M. cephalus*, which when combined accounted for 50–77% by frequency of occurrence (FO) and 74–99% by weight (W) (Table 1). The few summer-spawned YOY collected in the first year and the fall-spawned fish collected in Year 2 also had a diet dominated by piscine prey. Summer-spawned fish diets consisted of similar amounts of engraulids (25% FO, 39% W), sciaenids (25% FO, 33% W) and a few mysid shrimp (25% FO, <0.01% W) (Table 1). Fall-spawned YOY diets were dominated by engraulids (82% FO, 72% W), with a few occurrences of sciaenids (22% FO, 15% W), and, to a lesser degree, mugilids (13% FO, 8% W) (Table 1). In contrast, the diet composition of summer-spawned YOY in Year 2 was dominated by invertebrate prey, particularly mysid shrimp and white shrimp (62% FO, 33% W), but also including lesser amounts of engraulids (12% FO, 18% W) and sciaenids (13% FO, 34% W) (Table 1).

Predator–prey size relationships

We found a positive linear relationship between bluefish length and prey length (bluefish length = 0.486 × prey length − 24.453, r^2 = 0.737, n = 179, p < 0.0001) (Fig. 6). As predator size increased, so did the range of prey sizes that was found in the stomach reflecting the cohort-specific prey types consumed, from relatively small sciaenids and engraulids for bluefish <120 mm, to primarily mugilids for larger bluefish. Minimum and maximum prey sizes for summer/fall spawned YOY ranged from 1 to 24 mm FL, while maximum prey size for the larger age 1+ and spring spawned YOY was 265 mm FL. The large slope (0.486) indicated that bluefish consumed prey that averaged almost 50% of their body length. Quantile
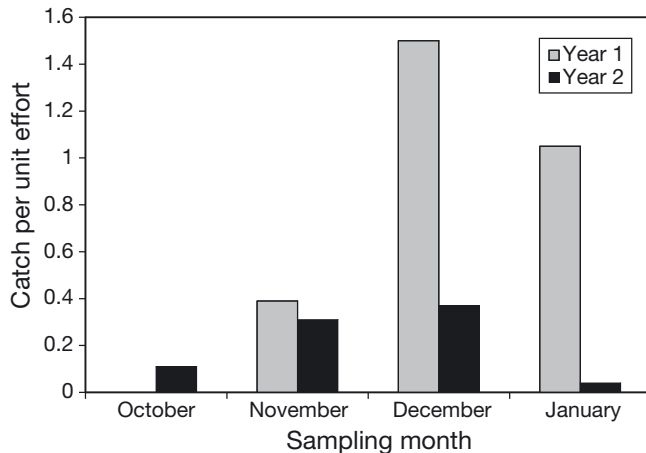
Fig. 4. *Pomatomus saltatrix*. Catch per unit effort (CPUE) of bluefish captured in gillnets by month in each of 2 years in the Matanzas River estuary. Catch is total numbers of juvenile bluefish captured that month; effort is the total number of hours of gillnet deployment for that month. Year 1: Nov 2002–Jan 2003; Year 2: Oct 2003–Jan 2004

regression showed that the predator–prey scatter was typically triangular in shape (Juanes et al. 2002) with minimum prey sizes increasing slower than maximum prey sizes, but both lower and upper bounds increasing at relatively high rates (slopes = 0.19 and 0.70, respectively).
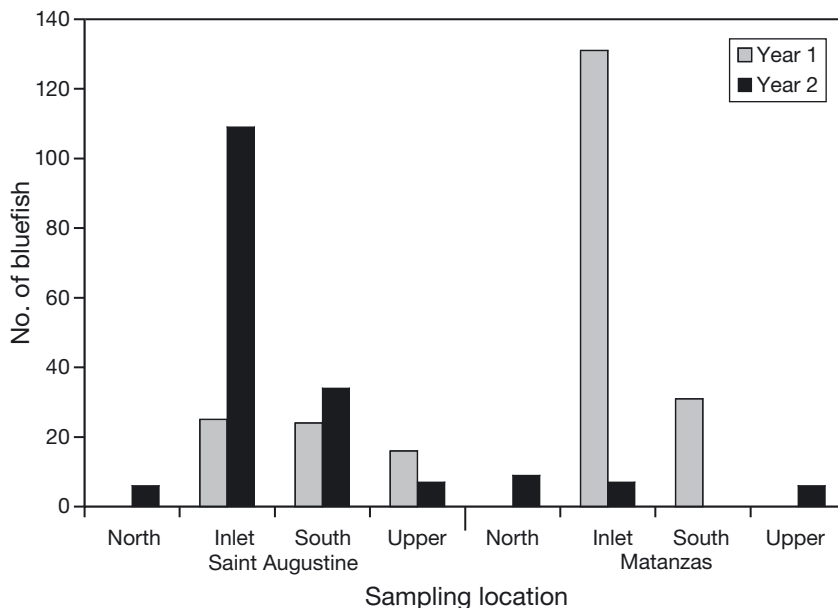

Fig. 5. *Pomatomus saltatrix*. Total number of bluefish captured at each sampling location with all gears, in each of 2 years in the Matanzas River estuary. Sampling effort (gillnet plus seine net) was similar across locations each year, so that reported total numbers are proportional to total CPUEs. Year 1: Nov 2002–Jan 2003; Year 2: Oct 2003–Jan 2004

Prey selectivity

Analysis of our gear types indicated that the majority of potential bluefish prey, ranging in size from 1 to 265 mm, were collected in seine hauls. In contrast, gillnets were found to be most useful for the capture of primary piscivores in the system, including spring-spawned YOY and age 1+ bluefish in addition to several other co-occurring predatory species such as spotted sea trout *Cynoscion nebulosus*, weakfish *Cynoscion regalis*, Spanish mackerel *Scomberomorus maculatus*, ladyfish *Elops saurus*, catfish *Arius felis*, summer flounder *Paralichthys dentatus*, and several shark species *Carcharhinidae*. Our results indicated that spring-spawned YOY and age 1+ individuals exhibited selective feeding on mugilids during Year 1 while avoiding gerrids, engraulids, and atherinids (Table 2). In Year 2, similar results were obtained for age 1+ and spring-spawned YOY fish with the addition of slight selectivity towards sciaenids (Table 2). We only had sufficient stomach content data for summer and fall-spawned YOY individuals in Year 2 to perform selectivity analysis. Our results for these cohorts show selectivity for sciaenids, random feeding for mugilids, and avoidance of atherinids and engraulids (Table 2).

Lipid analysis

Lipid content analysis of white muscle tissue was performed on 101 bluefish fish ranging in size from 230 to 463 mm FL. These lengths represented spring-spawned YOY (n = 84, FL = 230–359 mm) and age 1+ individuals (n = 17, FL > 360 mm); preservation methods used for smaller fish did not allow for the extraction of lipids from their tissues. Samples were pooled over both years in in order to achieve comprehensive length distributions throughout the months sampled. Spring-spawned YOY and age 1+ bluefish exhibited an increase in energy storage between the onset of recruitment in October and the end of estuarine use in January (slope = 0.0656, p = 0.0219) (Fig. 7). Mean lipid content was 6.6% in October and 6.7% in November. By December, storage levels rose to over 7.3% also

Table 1. Year 1 (Nov 2002–Jan 2003) and Year 2 (Oct 2003–Jan 2004) diet composition of bluefish in the Matanzas River estuary expressed as percent frequency of occurrence (% FO) and percent wet weight (% W). YOY: young-of-the-year

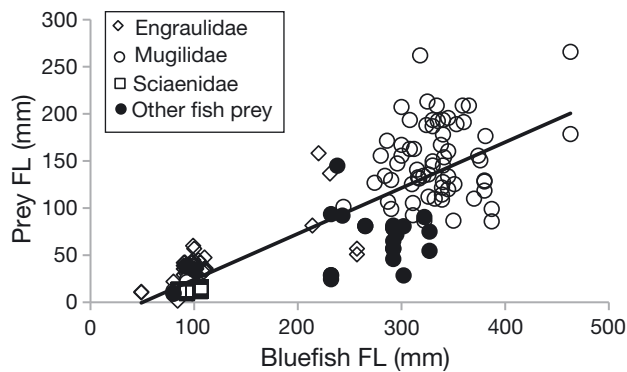| Bluefish cohort	Prey type	Species name	Year 1 % FO	Year 1 % W	Year 2 % FO	Year 2 % W
Age 1+	Mullet	*Mugil* spp.	77.27	99.55	20.00	29.31
	Unidentified fish remains		13.64	0.25	20.00	0.18
	White shrimp	*Penaeus setiferus*	4.55	0.20		
	Organic matter		4.55	0.00	10.00	0.39
	Atlantic menhaden	*Brevoortia tyrannus*			10.00	2.94
	White mullet	*Mugil curema*			30.00	58.12
	Pinfish	*Lagodon rhomboides*			10.00	9.05
Spring YOY	Mullet	*Mugil* spp.	54.24	78.33	51.61	49.36
	Unidentified fish remains		19.49	0.57	3.23	0.10
	White shrimp	*Penaeus setiferus*	10.17	6.21	1.61	0.53
	Mojarra	*Eucinostomas* spp.	5.08	3.13		
	Unidentified anchovy		4.24	0.27	12.90	1.17
	Unidentified organic matter		3.39	0.60		
	Atlantic silverside	*Menidia menidia*	2.54	1.34	1.61	0.00
	Isopod	*Aega psora*	1.69	0.02		
	Atlantic needlefish	*Strongylura marina*	1.69	0.38		
	Striped anchovy	*Anchoa hepsetus*	1.69	0.41	1.61	0.57
	Bluefish	*Pomatomus saltatrix*	1.69	0.03		
	Sheepshead	*Archosargus probatocephalus*	1.69	3.92		
	Unidentified herring		0.85	0.79		
	Long finned squid	*Loligo pealeii*	0.85	0.48		
	White mullet	*Mugil curema*	0.85	1.56	8.06	19.99
	Unidentified drum		0.85	0.06	4.84	1.09
	Spot	*Leiostomus xantharus*	0.85	0.00	8.06	16.27
	Inorganic matter		0.85	1.91		
	Sand		0.85	0.00		
	Inland silverside	*Menidia beryllina*			1.61	0.00
	Silversides	*Menidia* spp.			1.61	1.35
	Atlantic menhaden	*Brevoortia tyrannus*			3.23	3.04
	Striped mullet	*Mugil cephalus*			1.61	5.55
	Polychaete worm	Opheliidae			1.61	0.49
	Red drum	*Sciaenops ocellatus*			1.61	0.36
	Inshore lizardfish	*Synodus foetens*			1.61	0.00
	Squid				1.61	0.14
Summer YOY	Unidentified fish remains		50.00	27.78	25.00	14.20
	Drum	Sciaenidae	25.00	32.78	12.50	33.95
	Mysid shrimp	Mysidae	25.00	0.00	37.50	17.28
	Unidentified anchovy	*Anchoa* spp.	25.00	39.44	12.50	18.52
	White shrimp	*Penaeus setiferus*			25.00	16.05
Fall YOY	Unidentified anchovy	*Anchoa* spp.			75.00	60.39
	Drum	Sciaenidae			21.67	15.46
	Mullet	*Mugil* spp.			13.33	7.61
	Unidentified fish remains				8.33	0.70
	Bay anchovy	*Anchoa mitchilli*			6.67	10.34
	Atlantic silverside	*Menidia menidia*			1.67	1.02
	Atlantic menhaden	*Brevoortia tyrannus*			1.67	1.38
	Striped anchovy	*Anchoa hepsetus*			1.67	2.23
	White mullet	*Mugil curema*			1.67	0.59
	Mysid shrimp	Mysidae			1.67	0.15
	White shrimp	*Penaeus setiferus*			1.67	0.11
	Total stomachs analyzed		211		173	
	Number containing prey		143		149	
	Mean ± SE bluefish FL (mm)		315 ± 4		217 ± 9	
	FL range (mm)		53–463		40–456	

Fig. 6. *Pomatomus saltatrix*. Relationship between bluefish fork length (FL) and prey FL collected in the Matanzas River estuary during both years of the study, Nov 2002–Jan 2004. Data are provided for all measurable fish prey by family. Linear regression is bluefish length = 0.486 × prey length – 24.453 (r^2 = 0.737, n = 179, p < 0.0001)

coinciding with the increase in relative abundance of bluefish recruiting into the estuary during this time. Lipid content peaked in January, with 11.8% of dry muscle weight devoted to storage lipids. There was a positive relationship between % lipid and bluefish length (slope = 0.0377, y-intercept = –4.2025, r^2 = 0.1217, n = 101, p = 0.0004; data not shown), although this was not a result of larger individuals being sampled later in the season (bluefish sizes decreased over the season: slope = 0.6018, y-intercept = 522.5, r^2 = 0.0511, n = 101, p = 0.0230; data not shown). Removing the effect of bluefish size on % lipids by analyzing the residuals showed a stronger positive relationship with date (slope = 0.0890, y-intercept =

–30.2881, r^2 = 0.1095, n = 101, p = 0.0007; data not shown).

A total of 480 prey samples from 30 different species were used for the prey lipid analysis. We detected a significant difference in lipid level across species (p < 0.0001). *Mugil curema* had the highest mean lipid content of all species (19.52%). Other common prey species from MAB bluefish diet studies, bay anchovy and Atlantic silverside, had intermediate lipid contents of 3.19% and 3.49% respectively (Table 3).

DISCUSSION

Winter can often be a time of increased mortality during the early life of fishes (see review by Hurst 2007). Several marine species undergo extensive migrations to maximize survival during this period of increased mortality (Able & Fahay 1998). Bluefish, an example of one of these species, migrates seasonally, during the fall following a southern route along the east coast of the USA into waters with relatively richer prey abundances (Fautin et al. 2010) and higher water temperatures than those found in the MAB especially during fall and winter periods (Wenner & Sedberry 1989, Love & Chase 2007). The migration of bluefish from shelf to estuary and in reverse is controlled primarily by abiotic factors such as temperature, and secondarily by the availability of suitable prey (Hare & Cowen 1996, Munch & Conover 2000, Callihan et al. 2008).

Most of the ecology of juvenile bluefish migration and habitat use in North America has been studied in MAB estuaries primarily during the summer (Creaser & Perkins 1994, Buckel et al. 1999b, Gartland et al. 2006, Taylor et al. 2007). While northern estuaries play an important role for juvenile recruitment, and particular habitat types such as low flow habitats are critical for juvenile bluefish survivorship in the MAB (Scharf et al. 2004), we know very little about the role of estuarine habitats at the southern edge of the bluefish range. As environmental conditions change, the likelihood of species requirements and preferences often also changes (Able 2005). Thus, it is likely that habitat use, feeding, and energetics might differ in fall and winter

Table 2. *Pomatomus saltatrix*. Prey selectivity analysis for the most common prey found in juvenile bluefish stomachs for those years and cohorts where enough data were available. Alpha value refers to the calculation of the Chesson index: random feeding occurs at α = 0.25, α > 0.25 represent 'selection', and α < 0.25 represent 'avoidance.' Monthly mean (SE) α were calculated for those cases where specific prey items occurred in every month. *Mean α were significantly different from 0.25

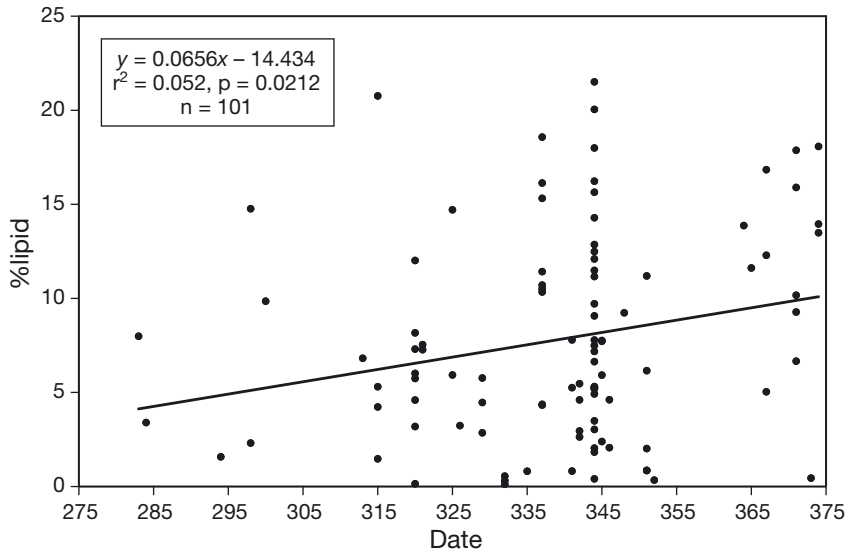| Year	Bluefish cohorts	Prey types	α	Mean α (SE)
1	Age 1+ and spring-spawned YOY	Mugilidae	0.85	0.77* (0.14)
		Gerridae	0.05	
		Engraulidae	0.02	
		Atherinidae	0.15	
2	Age 1+ and spring-spawned YOY	Mugilidae	0.52	0.68* (0.22)
		Sciaenidae	0.35	
		Engraulidae	0.03	
		Atherinidae	0.12	
2	Summer- and fall-spawned YOY	Mugilidae	0.21	
		Sciaenidae	0.62	0.74* (0.08)
		Engraulidae	0.14	0.25 (0.09)
		Atherinidae	0.02	

Fig. 7. *Pomatomus saltatrix*. Percent lipid vs. day of the year (with January dates attached to the previous year, i.e. dates > 365) of age 1+ and spring-spawned bluefish collected in the Matanzas River estuary pooled over both years (Nov 2002–Jan 2004)

habitats. However, until recently little was known about bluefish once they left their summer habitats.

Morley et al. (2007) and Slater et al. (2007) examined bluefish energetics, cohort structure, and survival off the North Carolina coast during fall and winter. Additionally, one year of winter sampling in the otherwise seasonally extensive SEAMAP program showed that bluefish could be abundant in Florida waters during the fall and winter months (Oct–Jan) (Wenner & Sedberry 1989). A long-term tagging study also showed that most juvenile bluefish tagged in northern waters in spring and summer were recaptured in Florida suggesting a fall and winter migration to the SAB (Shepherd et al. 2006). Our results document that multiple cohorts of juvenile bluefish use Florida estuarine habitats, where they feed on abundant fish prey and unexpectedly accumulate lipids during the fall and winter months. Aspects of their distribution, growth, and feeding appear different from those behaviors exhibited in more northern estuaries. Bluefish possess attributes of tropical fish, in that they seek temperatures that allow them to continue growing during the fall and winter by migrating from northern to southern waters, achieving optimal growth through continued feeding, rather than overwintering in colder waters and slowing growth as a means of retaining energy levels to maintain survival.

Relative abundance and distribution

During both years of this study, YOY and age 1+ bluefish were present in the Matanzas River Estuary, presumably after migrating from MAB and SAB estuaries and offshore waters when water temperatures in these regions dropped sufficiently to levels requiring movement (Shepherd et al. 2006). Although sampling in Florida was not conducted on a year-round basis, our sampling and results of the SEAMAP program (Wenner & Sedberry 1989) suggest limited, if any, estuarine use by bluefish of all size classes until late fall/early winter, and abruptly ending in January or February.

Initial estuarine recruitment of bluefish in Florida was likely related to seawater temperatures before entry, specifically cooling of shelf waters, as has been shown in northern estuaries (Lund & Maltezos 1970, Hare & Cowen 1996). By November of both years, continental shelf water temperatures of the MAB had dipped to a mean of 14°C (Fig. 2), a temperature cold enough to initiate migration of bluefish southwards into warmer water (Lund & Maltezos 1970, Kendall & Walford 1979). In contrast, shelf waters in northern

Table 3. Mean (± SD) lipid content of common prey species collected in the Matanzas River estuary. For smaller species, each sample may have contained multiple individuals. Length is fork length for fishes, mantle length for squid, and total length for crustaceans. Only species with sample size (n) >1 are included

Species name	n	Length (mm)	Lipid content (%)
Mugil curema	11	100–164	19.52±5.83
Mugil spp.	3	25–35	15.70±6.99
Fundulus spp.	6	45–120	4.25±2.05
Lolliguncula brevis	3	25–44	3.88±1.66
Anchoa hepsetus	6	72–105	3.77±2.75
Cynoscion nebulosis	2	55–145	3.58±2.01
Eucinostomus spp.	4	20–86	3.56±1.15
Menidia menidia	4	35–80	3.49±1.17
Anchoa mitchilli	4	30–70	3.19±1.35
Sphyraena borealis	2	119–405	2.98±2.96
Sardinella aurita	6	60–94	2.85±1.54
Mentichirrus americanus	3	69–130	2.72±1.75
Trachinotus falcatus	2	25–120	2.46±1.05
Leiostomus xanthurus	2	70–115	2.36±0.91
Lagodon rhomboides	3	45–95	2.23±0.54
Paralichthys dentatus	3	40–166	2.09±0.69
Penaeus spp.	2	25–65	1.65±0.30
Synodus foetens	2	120–155	1.38±0.97

Florida experienced a mean temperature of 22 to 25°C in November, similar to estuarine temperatures, facilitating the onset of recruitment. As estuarine surface waters cooled below 15°C, bluefish stopped recruiting into our sampling gear, likely because they had moved out of the estuary and into the warmer shelf waters (D. Stormer & F. Juanes unpubl. data).

Distribution of YOY and age 1+ bluefish across sites varied between years; but within sites, highest catches consistently occurred near inlets and in sandy habitats, found almost exclusively near inlets, suggesting that while juvenile bluefish recruit into the Matanzas river estuary, estuarine use is limited to near oceanic inlet sites (Clarke 2006). This pattern of near exclusive use of inlets is different from other estuaries in the MAB where upper estuarine locations are often utilized (Buckel et al. 1999b, Scharf et al. 2004, Able 2005) and in the Chesapeake where highest abundances were found over oyster reef and bar habitats rather than sand habitats (Harding & Mann 2001). However, coastal and beach sampling has shown that YOY bluefish, especially the summer-spawned cohort, extensively uses continental shelf habitats and surf zones (Able et al. 2003, Taylor et al. 2006, Callihan et al. 2008, Wuenschel et al. 2012). Recent sampling of shelf habitats offshore from these Florida inlets has shown large concentrations of juvenile bluefish (D. Stormer & F. Juanes unpubl. data) perhaps indicating foraging migrations from offshore to the inlets to feed. White (or silver) mullet undergo seasonal spawning migrations from inshore Florida waters to offshore areas and back (Munyandorero et al. 2007). Juvenile mullet also migrate into Florida estuaries from the north when temperatures drop below 20°C (Mahmoudi 2002). It is likely that bluefish encounter abundant schools of migrating mullet, their main prey item in inshore Florida waters, at the inlets leaving or returning to the estuaries.

We observed multimodal recruitment into Florida estuaries. The presence of multi-modal spring-, summer-, and fall-spawned YOY cohorts in our length-frequency histogram distributions can be associated with the validated birth date verification of daily ring increments developed in other studies (Nyman & Conover 1988, McBride & Conover 1991, Murt & Juanes 2009). The observed cohort overlap was also observed by previous studies in North Carolina (Morley et al. 2007) and suggests that cohort structure at the southern range may be more complex than in the north. Recruitment to our gear was usually size-based with age 1+ fish captured first, followed in order by spring-, summer- and fall-spawned individuals. This is the first study to show overlapping habitat use of the 3 YOY cohorts along with age 1+ individuals. The habitat overlap may be due to the winter concentration of the bluefish population over a relatively small area compared to summer distributions and the fact that the fall-spawned individuals only recruit late in the year. The fall-spawned cohort is considered to be a minor component of the entire population and, as a third annual cohort, is unique when compared to other bluefish populations (Juanes et al. 1996). When growth was compared to the other YOY cohorts in Florida (using the fish collected here), fall-spawned individuals grew at similar rates, but appeared to enter estuaries at smaller sizes (Murt & Juanes 2009) perhaps due to the relative proximity of spawning areas (Collins & Stender 1987). The fall-spawned cohort is abundant in offshore Florida waters (D. Stormer & F. Juanes unpubl. data) and may, therefore, contribute primarily to Florida bluefish, especially if, as Shepherd et al. (2006) have suggested, Florida has a resident bluefish population.

Dietary analysis

Results from this study indicate that the YOY and age 1+ bluefish selectively feed on available prey items located within the estuary. The advection of larval bluefish from southern waters into northern waters during the spring has been attributed to the increase in potential prey availability, enabling YOY to profit from the recruitment of fish larvae in northern estuaries, by switching to piscivory upon estuarine entry (Marks & Conover 1993), leading to accelerated growth rates (Juanes et al. 1994, Juanes & Conover 1994a,b, 1995).

In northern Florida, diets of juvenile bluefish consisted almost entirely of piscine prey, as they are in most other locations where they have been studied (see review in Juanes et al. 1996). Fall- and summer-spawned fish diets were dominated by anchovies and larval sciaenids, whereas spring-spawned and age 1+ individuals consumed primarily mullet. Several other abundant potential prey species (mojarras *Eucinostomus* sp. and killifishes *Fundulus* sp.) falling into similar size ranges as those found dominating the diets were not consumed. More surprisingly was the negative selection towards abundant anchovy *Anchoa mitchilli* and silversides exhibited by spring-spawned and age 1+ fish; in more northern estuaries, these prey are readily consumed (Juanes & Conover 1995, Buckel et al. 1999b, Harding & Mann 2001, Gartland et al. 2006) and, in general, when examined, bluefish feed primarily on the most abundant

prey available with little prey type selection (Juanes et al. 1993, Juanes & Conover 1995).

Similar to most other piscivorous fishes (Juanes et al. 2002), prey size increased with bluefish size linearly. However, the slope of this relationship was about twice (~50%) what has been found in previous studies of juvenile bluefish feeding habits (Juanes et al. 1993, 1994, Buckel et al. 1999a, Scharf et al. 2004), indicating that, in Florida, juvenile bluefish consumed prey that on average were about half their body length. Based on laboratory studies using bluefish as predators and a variety of prey species (but not mullet), attacking and handling such large prey would incur severe time and energy costs as well as result in lowered capture success rates (Juanes et al. 1994, Scharf et al. 1998a, 2003, 2009). Such large costs incurred by consuming relatively large mullet prey would imply some other benefit not measured by time costs.

The occurrence of the dominant prey types and sizes found in diets may be correlated with habitat use overlap in Florida collected bluefish. While the dominant prey were not in the highest abundance, they may have been in higher abundance within the size range available, while the more abundant prey items may have been either larger than the capable size of consumable prey, or the smaller prey items are not encountered with the same frequency as larger ones. This is unlikely as the most abundant prey types were small forage fish that do not attain the size of the average consumed mullet. A second possibility for observed prey selectivity is gear-sampling bias. The relative abundance of mullet as calculated from the seine net collections may be artificially low because of gear bias. However, in gillnet collections, the relative abundance of mullet was also low, suggesting that this prey species had lower availability than others, yet were strongly selected for.

Lipid analysis

Lipid reserves in the form of neutral storage lipids are critical to fish undergoing migration and long-term overwintering efforts (Schultz & Conover 1999). Generally, in temperate environments, energy levels increase in the summer and decrease in the winter when feeding ceases due to cold temperatures (Adams et al. 1982, Foy & Paul 1999, Hurst et al. 2000). Contrary to our expectations, we found that energy reserves of YOY and age 1+ bluefish increased over the fall and winter. Despite the large individual variation, mean lipid levels doubled (from 6 to 12%) between October and January as temperatures declined. Although we found a relationship between bluefish size and % lipids (common in bluefish and other species, e.g. Ball et al. 2007, Morley et al. 2007), because average body size decreased from fall to winter, the temporal relationship was stronger when body size was accounted for statistically.

Morley et al. (2007) observed a depletion in lipid content, decline in abundances, and reduced feeding of YOY bluefish as winter progressed in North Carolina. Energy reserves peaked in November and were similar across cohorts by mid-winter, suggesting that larger bluefish deplete their energy stores at faster rates. Interestingly, lowest catches of spring-spawned YOY in North Carolina occurred in December and January when catches in Florida peaked. These patterns in abundance and energy content as well as long-term tagging data (Shepherd et al. 2006) suggest that bluefish pass through North Carolina in early fall with depleted energy contents, then recruit to Florida in late fall where feeding and growth increases (see Murt & Juanes 2009), and rebuild their lipid content through early winter before moving back offshore and in some cases back to North Carolina.

Our results show substantial variability in lipid content across the 30 prey species that we measured. Lipid content was highest for white mullet *Mugil curema* (19.52%) and juvenile mullet (*Mugil* spp.) (15.71%) compared to the other common prey species: striped anchovy (3.77%), bay anchovy (3.19%), Atlantic silverside (3.49%), and squid (3.88%). We do not know if the mullet lipid results reported here are unusually high compared to other locations as, to our knowledge, lipid content has not been previously measured for most of these prey species in US waters. Marais (1990) also reported high lipid levels in 2 mullets (*Valamugil cunnesius* and *Myxus capensis*) (14 to 16%) and low in a third (*Liza tricuspidens*) compared to other fish species in a South African estuary. In an earlier study comparing 4 species of mullet (*Mugil cephalus*, *Liza dumerili*, *L. richardsoni*, and *L. tricuspidens*), Marais & Erasmus (1977) found relatively low levels of fat content except for large individuals (>23 cm) with a general increase in lipid levels during the winter just ahead of spawning season.

It is reasonable to conclude that a diet dominated by mullets likely promotes faster lipid accumulation, increased energy storage, and higher overwinter survival of bluefish in Florida waters. However, detailed understanding of the role of mullet, and the mechanisms leading to selection of those prey and to over-

winter survival of bluefish warrants further study. We are not aware of any work on nutrient-specific foraging for wild fish, but brown bears are able to select salmon with higher energy content (Gende et al. 2004) and, in an aquaculture situation, trout can discriminate between feeds with different oil sources (Geurden et al. 2005).

Surviving winter is essential if a cohort is to contribute to the adult stock the following growing season. Conover et al. (2003) found that the summer-spawned YOY bluefish cohort was more abundant than the spring-spawned YOY cohort from 1992 to 2002, yet the summer cohort appeared to contribute little towards the adult stock based on back-calculated age 1+ scales. This lack of contribution could potentially be due to higher overwinter mortality experienced by the summer cohort relative to the spring cohort (Conover et al. 2003), as winter mortality is generally negatively size-selective, with smaller individuals experiencing higher rates of mortality (Sogard 1997, Schultz et al. 1998, Hurst 2007). In Florida, smaller bluefish cohorts (summer- and fall-spawned) generally selected the more abundant prey species available, primarily engraulids and sciaenids. Mullet are rarely small enough to be consumed by fish from these 2 cohorts and perhaps, as a consequence, these smaller bluefish may not exhibit the increase in lipid levels observed for the larger cohorts (we were only able to measure lipids in the larger fish). This lack of a lipid-rich diet combined with reduced lipid reserves (Morley et al. 2007, Slater et al. 2007), and the substantial amounts of invertebrate prey in their diet (which leads to reduced growth; see Friedland et al. 1988, Juanes & Conover 1994a), could contribute to higher winter mortalities of these smaller cohorts and help explain why they rarely contribute to the adult stock (Chiarella & Conover 1990, Munch & Conover 2000, Conover et al. 2003).

Implications for fisheries

Our results have important implications for both mullet and bluefish fisheries. Mugilids, both white and striped mullet, have considerable recreational and commercial importance in southern waters. If juvenile bluefish abundances are high, and given their large consumption rates (up to 40% per day; see Juanes & Conover 1994a, Buckel & Conover 1997), bluefish consumption could have a substantial impact on mullet populations as they have on striped bass in the Hudson River (see Buckel et al. 1999b).

On the other hand, if mullet are critical to overwinter lipid accumulation as our study suggests, then fluctuations in mullet abundance could strongly affect bluefish overwinter survival. Based on species-specific energetic differences, changes in the prey community have been shown to have important consequences for piscivorous fish, mammal, and bird predators in the Bering Sea, the Gulf of Alaska, and the North Sea (Payne et al. 1999, Iverson et al. 2002, Wanless et al. 2005, Ball et al. 2007). As bluefish do not represent a particularly important fishery in northern Florida, there are no good estimates of population abundance and, thus, their potential impact on mullet cannot be estimated. However, mullet are much more important and stock assessments of the species are routinely performed. The latest stock assessment for silver (white) mullet *Mugil curema* shows an increase in commercial and recreational landings (mainly used for bait) over the last 15 yr and suggests the stocks in Florida waters are 'healthy' (Munyandorero et al. 2007). The striped mullet *M. cephalus* fishery is much larger, primarily commercial, and is dominated by the roe fishery. The most recent assessment documents decreasing landings in Florida since the entangling net ban in 1995, so that current levels of fishing effort appear sustainable (Mahmoudi 2005). Much less is known about juvenile mullet ecology and the nature of the fingerling bait mullet fishery (B. Mahmoudi pers. comm.). Unfortunately, regulations on the mullet bait fishery are weakly enforced in Florida. As an example, 46% of the commercial catch off the Atlantic coast and 57.2% off the Gulf coast is represented by undersized mullet (minimum size limit is 11 inches [28 cm]) (Munyandorero et al. 2007). Competition with anglers for finger mullet could lead to bluefish feeding on less lipid-rich prey, not allowing the bluefish to accumulate the reserve lipids required for winter survival. In contrast, greater restrictions on mullet takes will help to rebuild the mullet populations and higher mullet abundances could likely result in more bluefish entering the estuaries to take advantage of the high-lipid prey. Longer term data on variability in mullet availability and condition will be necessary to quantify the potential effects on bluefish overwinter dynamics.

CONCLUSION

Migratory species can spend different parts of their annual cycles in widely separated locations. These periods and locations are ecologically linked and

their 'migratory connectivity' needs to be studied in order to understand how they influence survival (Webster et al. 2002). Modeling work to determine optimal conservation strategies for migrating species has shown that such strategies depend critically on knowledge of migratory connectivity (Martin et al. 2007). Our study contributes valuable information concerning fall and winter ecology of a highly migratory species. Our results show that during late fall and early winter, Florida estuaries provide bluefish with warmer water temperatures and higher abundances of prey resources than in northern coastal and estuarine waters. However, bluefish collected during the fall and winter in Florida are not using these estuaries as overwintering habitat where feeding rate is typically reduced and lipids depleted (Hurst 2007), instead they appear to be using these, and possibly other estuaries with similar attributes of prey density and temperature regime, as feeding and regeneration areas before continuing their migration either further south or possibly offshore to the continental shelf of Florida. Bluefish accomplish this by becoming strongly prey type selective for mullet, which is very high in lipids and likely allows bluefish to increase their lipid levels and maintain high growth rates (Murt & Juanes 2009). Because of its migratory lifestyle, this temperate marine piscivore extends its growing season by placing itself in environmental conditions conducive for continued growth, particularly higher water temperatures relative to the MAB and northern SAB, and estuaries with large densities of higher quality prey. The greater energetic demand of such a migration would need to be replenished before the onset of winter, or feeding would have to continue throughout the winter period to guarantee survival. The replenishment of stored energy through predation on lipid-rich mullet would likely increase winter survival of bluefish. However, competition with recreational anglers for available mullet could have wide ranging implications to overwinter survival of bluefish in Florida waters. Alternative prey species, although abundant, contain much lower lipid levels than mullet species and may not provide sufficient lipid reserves for bluefish to meet their minimum energy requirement for overwinter survival. Future management plans should consider how events occurring over the fall and winter interact, and how they influence survival.

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