Contrasting patterns of resource utilization between juvenile estuarine predators: the influence of relative prey size and foraging ability on the ontogeny of piscivory

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Abstract: In aquatic systems, ontogenetic patterns of resource utilization strongly influence growth and survival, particularly during early life stages. We compared prey resource use and evaluated potential factors affecting the timing of the shift to piscivorous feeding in two juvenile estuarine fish predators: striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*). In New York Bight estuaries, bluefish shift to piscivory earlier in ontogeny and consume larger relative prey fish sizes compared with striped bass. Predator gape allometries are similar and did not determine maximum prey sizes eaten. Experimental results revealed marked differences in foraging abilities between predators, with bluefish realizing much greater foraging efficiency compared with striped bass feeding on identical fish prey. Both predators demonstrated lower feeding efficiency and grew relatively poorly when feeding on invertebrates compared with fish prey. When held together under limited prey conditions, bluefish exploited a greater proportion of available prey at the expense of striped bass. Our findings highlight the importance of the availability of appropriately sized forage fishes to the ontogeny of piscivory and provide evidence that predator–prey size relationships and disparate foraging abilities can generate inter- and intra-specific variation in patterns of resource utilization and predator growth.

Résumé : Dans les systèmes aquatiques, les patrons ontogéniques d'utilisation des ressources influencent fortement la croissance et la survie, particulièrement durant les premiers stades de la vie. Nous comparons l'utilisation des ressources en proies et évaluons les facteurs potentiels qui affectent le moment du changement vers un régime alimentaire piscivore chez deux jeunes poissons prédateurs estuariens, le bar rayé (*Morone saxatilis*) et le tassergal (*Pomatomus saltatrix*). Dans les estuaires du golfe de New York, les tassergals deviennent piscivores plus tôt dans leur ontogénie et consomment des proies de taille relativement plus grande que les bars rayés. Les allométries de l'ouverture de la bouche sont semblables et ne déterminent pas la taille maximale de proie consommée. Des données expérimentales indiquent des différences marquées dans l'habileté de recherche de nourriture entre ces prédateurs et les tassergals atteignent une efficacité de recherche de nourriture beaucoup plus grande que celle des bars rayés qui se nourrissent des mêmes poissons proies. Lorsqu'ils s'alimentent d'invertébrés plutôt que de poissons, les deux prédateurs montrent une efficacité alimentaire réduite et croissent relativement mal. Gardés ensemble en présence de proies limitées, les tassergals exploitent une proportion plus élevée des proies disponibles au détriment des bars rayés. Nos résultats soulignent l'importance de la disponibilité de poissons fourrage de taille adéquate dans l'ontogénie de l'ichtyophagie et démontrent que les relations de taille entre les prédateurs et les proies, ainsi que les différences d'habileté de recherche de nourriture, peuvent produire des variations inter- et intra-spécifiques dans les patrons d'utilisation des ressources et la croissance des prédateurs.

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Introduction

Ontogenetic niche shifts maximize growth and survival and are thought to be adaptive (Werner and Gilliam 1984). The diet shift from invertebrate to fish prey by piscivorous fishes is known to be an important transitional stage that results in markedly increased growth rates for many species (Juanes and Conover 1994; Olson 1996; Galarowicz and Wahl 2005). Predators that shift to fish prey early in ontogeny benefit from larger body size at a young age, which can provide a refuge from size-dependent sources of mortality (e.g., predation and overwinter starvation; Sogard 1997; Hurst 2007). Because of advantages in growth and survival conferred during early life, the timing of the onset of piscivory has been implicated as a major determinant of year

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class strength for freshwater piscivores (Buijse and Houthuijzen 1992; Olson 1996). Given the likely strong selective pressures to shift to a fish diet, what are the factors that affect the timing of the onset of piscivory? Timing of spawning, water temperature, predator morphology, growth rates during the invertebrate feeding stage, and predator and prey population dynamics have all been shown to influence the shift to piscivory (e.g., Buijse and Houthuijzen 1992; Amundsen et al. 2003; Galarowicz et al. 2006). These factors may often operate synergistically to generate community patterns of prey fish density and predator–prey size relationships, which contribute principally to the encounter and capture probabilities that appear most critical in determining the ability of a predator to forage on fish prey (Juanes et al. 2002).

In a multispecies review of the ontogeny of piscivory, Mittelbach and Persson (1998) noted that size-specific information on diets and growth rates was often lacking for many freshwater piscivores, which made detecting general interspecific patterns difficult. Among several predator species, the authors did identify traits such as size at hatch and gape size that were broadly related to the timing of the shift to piscivory. However, they did not find differences in the sizes of prey fishes consumed by different piscivore species, which they attributed partly to the shortage of more refined measures (e.g., size-dependent capture success and attack rates) of piscivore foraging ability. They concluded that to determine the extent of variation in the onset of piscivory among species, as well as determine the principle factors responsible for this variation, would require more focused studies that combined field comparisons with laboratory experimentation. Given that the timing of the shift to piscivory has been found to contribute largely to the eventual success of piscivore cohorts (e.g., Buijse and Houthuijzen 1992; Olson 1996), there is a clear need for comparative ontogenetic information to more fully understand the environmental, behavioral, and morphological causes of inter- and intra-specific variation.

Striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix*) are predatory fishes found in western North Atlantic estuarine and continental shelf waters (Bigelow and Schroeder 1953; Kendall and Walford 1979). Striped bass are anadromous and spawn in several river systems on the US east coast (e.g., the Hudson River, several Chesapeake Bay rivers, and the Roanoke River – Albemarle Sound system). Juvenile striped bass from the Hudson River population occupy several New York Bight estuaries and occur predominantly in these systems during their second summer of life (i.e., at age-1). Juvenile bluefish also occupy New York Bight estuaries during their first summer of life (i.e., at age-0). Following spawning by adults in oceanic waters, juvenile age-0 bluefish from a spring spawning event recruit to estuaries in June, while those from an early to mid-summer spawning event recruit in August–September (McBride and Conover 1991). Along the US Atlantic coast, the adult stages of both species are primarily piscivorous in their feeding habits (Hartman and Brandt 1995a; Walter et al. 2003). However, diet studies of juvenile bluefish and striped bass in New York Bight estuarine environments provide evidence for an early and abrupt shift to piscivory by age-0 bluefish (Juanes and Conover 1995) and a later and

gradual shift to piscivory by age-0 and age-1 striped bass (Gardinier and Hoff 1982; Buckel and McKown 2002; Jordan et al. 2003). Since a large body of ecological evidence suggests the likelihood of strong selective pressures for an early onset of piscivory (see above), why do striped bass exhibit a delayed onset of piscivory compared with the early shift to piscivorous feeding by sympatric bluefish? Prey availability alone would not seem to explain the interspecific differences, since the fish prey that are available to bluefish in New York Bight estuaries should also be available to striped bass.

In this study, the following questions are addressed: Are there consistent differences in the timing of the onset of piscivory between bluefish and striped bass in estuarine environments of the New York Bight? Might differences in predator morphology or foraging ability contribute to diverse patterns in the use of fish prey by these predators? And finally, do differences in foraging ability result in differential predator growth in a mixed-species environment with limited fish prey? To address these questions, we combined new experimental evidence with previously published field data on feeding habits and a re-examination of behavioral evidence from published laboratory experiments. Specifically, we examined accumulated field data on the diets and prey sizes eaten by juvenile age-1 striped bass and age-0 bluefish in New York Bight estuaries to generate a synthetic view of the timing of the shift to piscivory in these two species. We compared predator gape allometries to assess whether morphological limitations may be important in determining prey sizes eaten. To evaluate interspecific differences in predator foraging ability and related behavioral mechanisms while feeding on common prey, we compared predator capture success and handling times, prey profitabilities, and predator attack behavior based on a re-examination of data from previously conducted laboratory experiments. To confirm differences in predator growth due to prey quality observed previously for juvenile bluefish, we conducted a new experiment to determine growth rates for striped bass when fed unlimited rations of fish versus invertebrate prey. Finally, we completed an additional experiment that tested for the existence of differential foraging abilities in a mixed-predator assemblage through an examination of growth rates realized in a limited prey environment.

Materials and methods

Diet, prey size, and predator morphology

A synopsis of juvenile bluefish and striped bass diets in New York Bight (USA) estuaries was developed from fish collected in the lower Hudson River (41°00′N, 73°54′W) (1974: Gardinier and Hoff 1982; 1990–1993: Buckel et al. 1999) and western Long Island bays (40°40′N, 73°45′W) (1997–1998: Buckel and McKown 2002) during summer and fall of several years. For each study, the percentage of prey by stomach (Gardinier and Hoff 1982) or frequency of occurrence (% FO, all other studies) were standardized to 100% by month and percent invertebrate and fish prey calculated. These values were used to determine a monthly mean for both bluefish and striped bass.

Prey size data for two prey fish species (Atlantic silverside (*Menidia menidia*) and bay anchovy (*Anchoa mitchilli*))

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common to the diets of both predators were examined from bluefish collected in the lower Hudson River during 1990–1993 (Scharf et al. 1997) and Great South Bay, New York (40°10′N, 73°10′W) during 1989 (Juanes and Conover 1995), as well as from bluefish and striped bass collected in western Long Island bays during 1997–1998 (Buckel and McKown 2002). Quantile regression analysis was used to determine the upper bounds (maximum prey size) of bivariate relationships between both bay anchovy and Atlantic silverside total length (TL) and predator TL (Scharf et al. 1998). To determine if the upper bounds for each prey type differed between bluefish and striped bass, we applied an ad hoc test statistic based on the standard errors of the quantile regression coefficients that at least asymptotically approaches an F distribution (Scharf et al. 1998).

Prey body depths were estimated from regressions relating bay anchovy and Atlantic silverside TL to body depth (Scharf et al. 1997). Striped bass gape height was measured as the distance between the anterior-most points of the lower and upper jaws with the mouth completely open, and throat width was measured as the distance between the cleithrum bones when stretched open to their maximum width. Bluefish gape height and throat width were determined previously from similar measurements and reported in Juanes and Conover (1995) and Scharf et al. (2002). Gape allometries between species were compared using analysis of covariance (ANCOVA).

Laboratory experiments

Size-dependent foraging ability and behavior

The results of single-species experiments to quantify size-dependent foraging ability of bluefish and striped bass have been reported previously in Scharf et al. (2002 and 2003), which evaluated the influence of prey-specific traits (e.g., size, morphology, and behavior) on their vulnerability to predation. Here, we re-examined the results of several of these experiments to evaluate the relative foraging ability of bluefish and striped bass when feeding on common prey. Details of fish capture, transport, laboratory acclimation, and maintenance are carefully outlined in Scharf et al. (2002, 2003). The design and execution of the laboratory experiments that generated some of the data re-examined in this study are also described in a previous publication (text in Methods and tables 1 and 2 in Scharf et al. 2003). All experiments were completed at the NOAA Fisheries James J. Howard Marine Sciences Laboratory at Sandy Hook, New Jersey, USA. We completed additional single-species foraging experiments with striped bass predators feeding on sand shrimp (*Crangon septemspinosa*) between 10 and 35 mm TL that were captured along sandy beaches using 1 m beam trawls and fed pieces of previously frozen fish during laboratory holding. The results of the foraging experiments using striped bass predators and sand shrimp prey have not been reported previously.

Relationships between predator capture success and relative prey size (prey length/predator length ratio) were compared between bluefish and striped bass when feeding on each prey species using ANCOVA. Mean handling times as a function of relative prey size (linearized using $\log_e$ transformation) were compared similarly. Profitability, an index

of size-dependent predator foraging efficiency, was also compared qualitatively between predators feeding on each prey type as a function of relative prey size. Profitability was calculated as prey-specific energetic content (kJ·g^{-1}) × relative prey mass (prey mass (g) per predator mass (g)) × % capture success × mean handling time^{-1}. Because tank volumes were moderate (475 L) and water clarity was high during single-species experiments, we assumed that encounter probability was close to one at all times, and therefore energetic costs for searching activities were low and independent of prey type or size for both predators. Data for bluefish foraging on sand shrimp presented in Juanes et al. (2001) were compared with experimental results for striped bass foraging on sand shrimp obtained during this study.

Predator foraging behavior was characterized from the video-recorded observations made during the laboratory feeding experiments. Predator schooling behavior, movement patterns within the experimental arena, prey inspection behavior, and attack behaviors were assessed qualitatively. Predator attack velocities as a function of body size were quantified for a random sample of attacks based on distance traveled and the number of video frames (~0.03 s·frame^{-1}) elapsed during the attack. Velocities were only measured for individuals moving in a plane orthogonal to the camera. Traveled distances were measured using a grid system positioned within each aquarium and were adjusted for the distance of individuals from the front of aquaria. Least squares regressions were generated to determine the relationship between predator attack velocity and body size for each predator species and were compared using ANCOVA.

Predator growth on shrimp versus fish prey

A 20-day growth experiment was conducted in 2001 to test for an effect of prey type on age-1 striped bass growth. Striped bass were collected in New York Bight estuaries using beach seines. All fish were immediately transported to the Howard Laboratory and acclimated in round tanks (1.8 m diameter × 0.6 m deep) supplied with flow-through seawater from Sandy Hook Bay. Fish were maintained at ambient temperatures (19–22 °C), salinities (23–27 ppt), and photoperiod (14 h light:10 h dark) during the experimental period.

The effect of diet on striped bass growth was tested using two diet treatments that consisted of shrimp (sand shrimp) or fish (Atlantic silverside) prey. Each treatment was replicated three times. Eighteen striped bass were measured (TL; ±1 mm), weighed (±0.01 g), and placed in groups of three into one of six 565 L circular aquaria (1.2 m diameter × 0.5 m depth) supplied with flow-through seawater. Aquaria were assigned randomly to either shrimp- or fish-fed treatments. Live shrimp and fish prey of similar size (prey/predator TL ratios = 0.15–0.30) were provided in unlimited quantities throughout the experimental period, and measurements of striped bass (TL (mm) and weight (g)) were made at the start (day 0), midpoint (day 10), and end (day 20) of the experiment. Dead, uneaten prey were removed and weighed, and temperature and salinity were measured daily.

Striped bass growth between shrimp- versus fish-fed treatments was compared using a repeated-measures analysis of variance (ANOVA) with weight as the dependent variable and day as the independent variable. Results for striped

bass growth were compared with previously published data for bluefish growth when fed fish versus shrimp diets (Buckel et al. 2004).

Foraging ability in a mixed-predator assemblage

A 50-day experiment was conducted to test for differences in foraging ability among predator species in a mixed-predator assemblage. Bluefish and striped bass, independent from predators used in foraging behavior experiments, were collected, transported, and acclimated to laboratory conditions using methods identical to those used for prior experiments. Fish were measured (TL; ± 1 mm), weighed (±0.01 g), and assigned (see below) to nine circular, experimental mesocosms (2360 L; 2.4 m diameter × 0.6 m depth) supplied with flow-through seawater at ambient conditions. Three experimental treatments, each replicated three times, were employed: six bluefish (single-species), six striped bass (single-species), and three bluefish + three striped bass (mixed-species). Individual predators were assigned randomly to either single- or mixed-species treatments, and measurements (TL (mm) and weight (g)) were made every 10 days. In maintaining equal fish densities across treatments, the experiment employed a substitutive design to measure the relative foraging ability of bluefish versus striped bass (Fausch 1998; Weber and Fausch 2003). For our purposes, the use of a substitutive design eliminated any effect of an overall increase in density and allowed us to measure whether the effect on one species of adding a separate species was distinct from the effect of simply adding more conspecifics. If growth rates in a mixed-predator assemblage differ from expected patterns based on the observations from single-species treatments, one can infer differences in foraging ability (Weber and Fausch 2003).

Prey fish were provided in limited quantities to detect differences in growth rate between mixed- versus single-species treatments if diverse foraging abilities existed in a mixed-predator assemblage. Rather than feed both predator species the same limited ration, we took advantage of known bioenergetic information that enabled us to estimate species-specific limited rations equaling 50% of maximum consumption rates (C_{max}). Specifically, the amount of prey (weight (g)) fed to single-species treatments was equal to 50% of the estimated maximum consumption based on size and species (bluefish or striped bass) of the six individual fish in each mesocosm. Each mixed-species mesocosm received amounts of prey equal to 50% of the estimated maximum consumption of three bluefish and three striped bass. The maximum consumption rates we used were based on relationships between C_{max}, fish size, and water temperature determined experimentally for bluefish and striped bass by Hartman and Brandt (1995b). Ration levels were adjusted every 10 days based on updated predator size data. Each treatment mesocosm was fed weighed amounts of live fish prey daily (Atlantic silversides and mummichog (*Fundulus heteroclitus*)). Dead fish prey were removed and weighed daily. Mortalities of bluefish ($n = 1$) and striped bass ($n = 1$) occurred between days 10 and 20 and were replaced with fin-clipped fish of similar size. The new additions kept any density-dependent influences on feeding and growth rate constant throughout the experiment. Growth of

Fig. 1. Diet data pooled across prior studies in New York Bight estuaries for (*a*) age-1 striped bass and (*b*) age-0 bluefish), illustrating utilization of fish (solid bars) and invertebrate (open bars) prey resources during summer and early fall months. Ranges in total length by month across years are as follows: age-1 striped bass: May (77–261 mm), June (78–207 mm), July (96–241 mm), August (96–241 mm), September (164–296 mm), and October (164–296 mm); age-0 bluefish: June (51–99 mm), July (59–176 mm), August (69–256 mm), and September–October (118–260 mm). Size range data by month were not available in Gardinier and Hoff (1982).
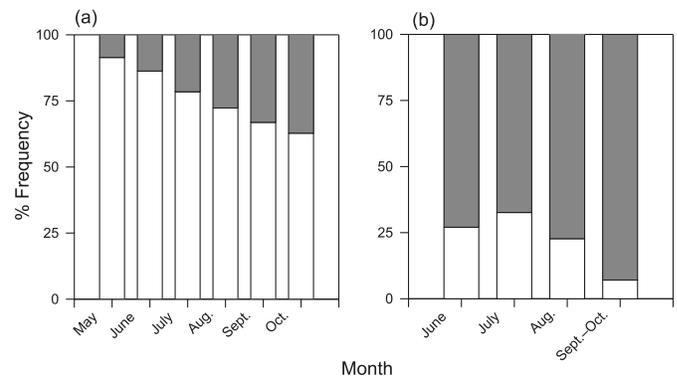
the original fish was monitored separately from the new additions.

The mixed- versus single-species treatments were compared using repeated-measures ANOVA with weight as the dependent variable and day as the independent variable. The analysis was performed separately for bluefish and striped bass. The specific growth rate during the 50-day experiment was calculated as $(\ln Wt_f - \ln Wt_i)/d \times 100$, where Wt_f is final wet weight (g), Wt_i is initial wet weight (g), and d is number of days. Means and standard errors for specific growth were calculated for each treatment. Prey availability was indexed for each treatment as the average biomass of fish prey available to individual predators and was calculated as the biomass of fish prey fed to each mesocosm over the 50-day experiment divided by the number of predators. Prey fish availability in single- versus mixed-species treatments and the observed growth rates in the single-species treatments were used to formulate expected growth patterns for the mixed-species treatment.

Results

Diet, prey size, and predator morphology

When examined synoptically across multiple summer–fall periods, age-0 bluefish diets were consistently dominated by fish, while age-1 striped bass included considerably more invertebrate prey in their diets (Fig. 1). Striped bass showed a trend of increased fish prey utilization during late summer and early fall, which coincided with increasing predator body size. In contrast, bluefish consistently foraged mainly on fish prey from the outset of summer through fall. The collective diet data confirm that age-0 bluefish demonstrate an earlier onset of piscivory and consume considerably more fish prey compared with similarly sized age-1 striped bass in New York Bight estuaries.

When feeding on bay anchovy and Atlantic silversides,

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Fig. 2. (*a*) Prey total length versus predator total length (PredTL) for bluefish (○) and striped bass (●) feeding on bay anchovy and Atlantic silversides (both prey species pooled). The 90th quantiles for bluefish (Max prey = 0.42PredTL + 1.60) and striped bass (Max prey = 0.20PredTL + 14.71) represent the relationship between maximum prey size consumed and predator size. (*b*) Prey body depth (bay anchovy and Atlantic silversides pooled) and gape allometries as a function of PredTL. Allometric equations: bluefish gape height = 0.13PredTL + 2.43, $r^2 = 0.89$; bluefish throat width = 0.13PredTL + 0.84, $r^2 = 0.92$; striped bass gape height = 0.13PredTL – 1.27, $r^2 = 0.99$; striped bass throat width = 0.10PredTL – 0.46, $r^2 = 0.99$. Bluefish gape height was originally reported in Juanes and Conover (1995); bluefish throat width was originally reported in Scharf et al. (2002).
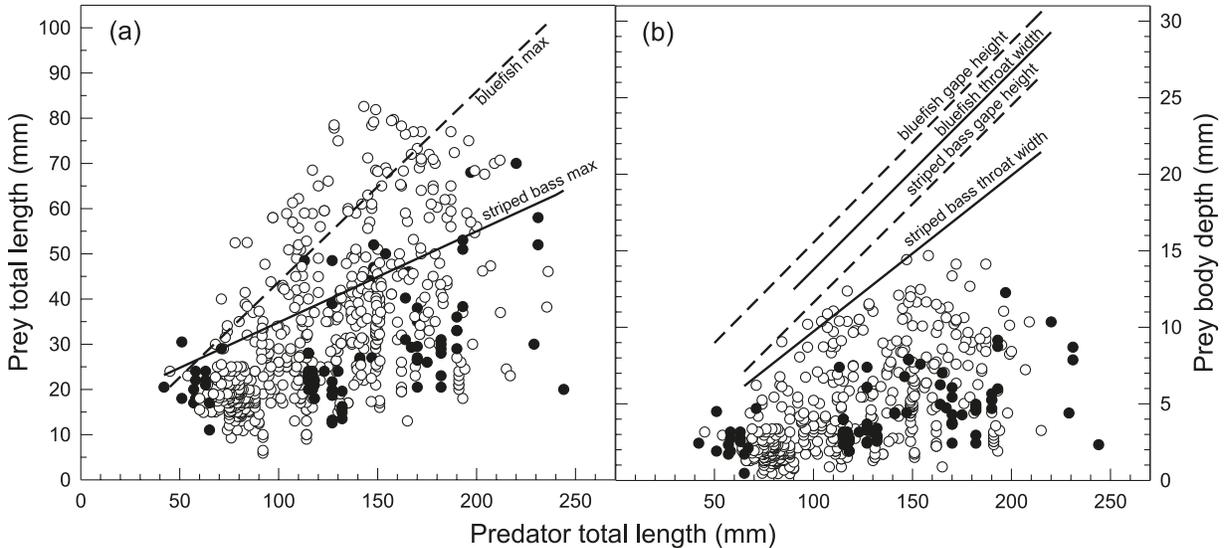
maximum prey sizes consumed in the field by bluefish increased at a faster rate (steeper slope) with increasing predator size compared with maximum prey sizes eaten by striped bass (Fig. 2*a*; comparison of quantile regression slopes: $F = 11.09$; $P < 0.001$). Thus, at a given predator body size, bluefish were able to consume substantially larger prey than striped bass across the range of body sizes examined. Allometric relationships indicated that predator gape size did not represent a morphological limitation for maximum prey size, since body depths of bay anchovy and Atlantic silverside prey were smaller than maximum ingestible prey sizes predicted from predator gape allometries, especially for larger predators (Fig. 2*b*). Although bluefish gape sizes at a given body length were larger compared with striped bass (ANCOVA$_{gape\ height}$: $F = 131.39$, $P < 0.001$; homogeneity of slopes$_{throat\ width}$: $F = 10.88$, $P < 0.005$), striped bass were clearly morphologically capable of ingesting larger prey sizes than those observed in their diet.

Laboratory experiments

Size-dependent foraging ability and behavior

Bluefish capture success was significantly higher compared with striped bass for both prey fish species (ANCOVA$_{bay\ anchovy}$: $F = 87.56$, $P < 0.001$; ANCOVA$_{Atlantic\ silverside}$: $F = 65.58$, $P < 0.001$). Differences in percent capture success demonstrated that bluefish were often two–three times more likely to capture a given prey fish, with increasing disparities between predators at larger relative prey sizes (Fig. 3*a*). Striped bass handling time increased at a significantly faster rate for larger relative prey sizes compared with bluefish for both prey fish species (homogeneity of slopes$_{bay\ anchovy}$: $F = 26.81$, $P < 0.001$; homogeneity of slopes$_{Atlantic\ silverside}$: $F = 7.81$, $P = 0.007$). Prey fish handling times were generally

similar for bluefish and striped bass feeding on either prey fish species at small to intermediate relative body sizes; however, striped bass experienced much longer handling times for larger relative prey sizes (Fig. 3*b*). For both prey fish species, peak bluefish profitability was close to four times higher than that for striped bass and was located at substantially larger relative prey sizes (Fig. 3*c*).

When feeding on sand shrimp prey, striped bass capture success was high (40%–60%) at small relative prey sizes (0.10–0.20), but declined rapidly to 25%–30% above relative prey sizes of 0.20 and was close to zero above relative prey sizes of 0.30. The time required for striped bass to handle sand shrimp prey also increased considerably as relative prey sizes increased above 0.20 and was greater than the time required to handle fish prey at all sizes. Striped bass profitability when feeding on shrimp peaked at lower relative prey sizes and was lower compared with feeding on fish prey at all relative prey sizes above 0.15. Similarly, data presented in Juanes et al. (2001) indicated that bluefish realized higher capture success, lower handing times, and higher profitability when feeding on fish prey compared with similarly sized sand shrimp prey.

Both predator species schooled tightly during feeding experiments, with bluefish generally occupying the middle to upper water column and striped bass staying mainly in the lower portions of the feeding arena. Both predator species frequently attacked solitary prey individuals that had become separated from prey schools and approached prey at rapid speeds. Maximum attack velocities for bluefish were significantly higher compared with striped bass within the range of body sizes tested (ANCOVA: $F = 49.29$, $P < 0.001$). Maximum bluefish attack velocities ranged from 150 to 225 cm·s^{-1}, while maximum attack velocities for striped bass were between 125 and 160 cm·s^{-1} (Fig. 4).

Fig. 3. (*a*) Capture success, (*b*) mean predator handling time, and (*c*) profitability (defined in Materials and methods) of bluefish (solid lines) and striped bass (dashed lines) when feeding on common estuarine fish prey (bay anchovy and Atlantic silversides). The single dotted line in each panel represents the relationship for striped bass foraging on sand shrimp. Comparable data for bluefish feeding on sand shrimp are presented in Juanes et al. (2001), but could not be added to this figure, since experimental animals were categorized only as small or large, and thus exact sizes of individuals were not recorded for each trial. Least squares regression lines presented are based on analysis of all foraging trials completed. Note the difference in the scale of the *x* axis for panel (*c*).
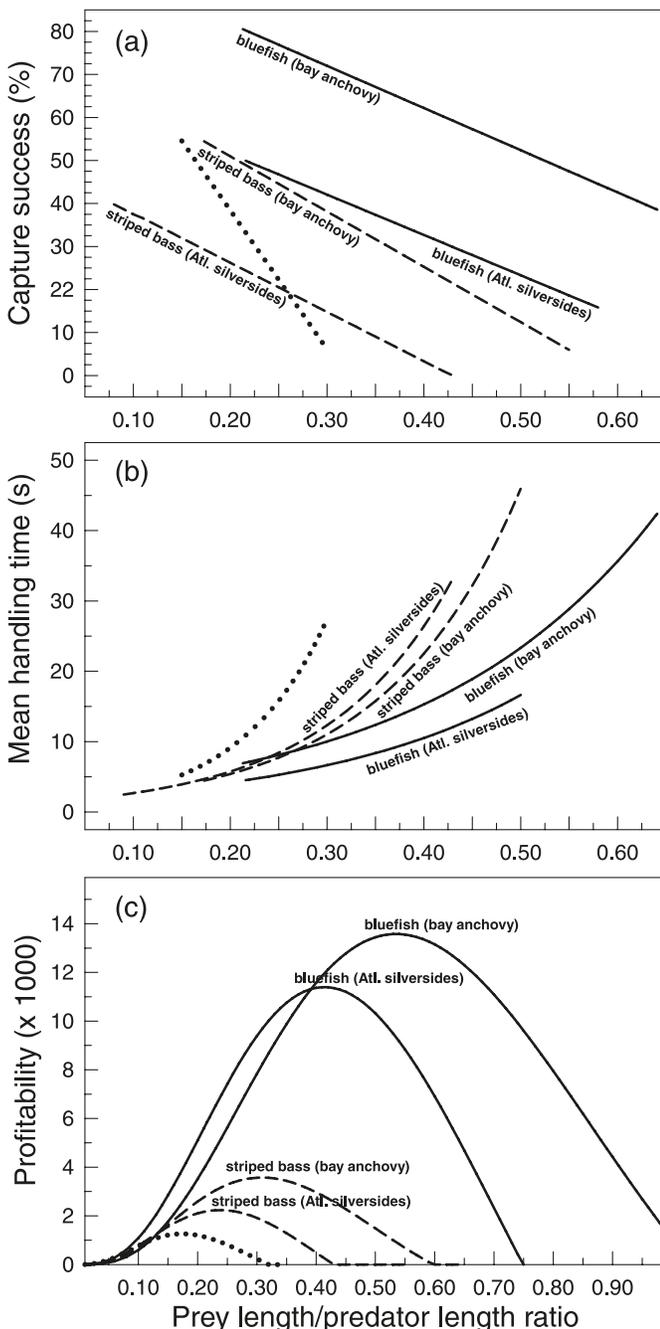
Fig. 4. Maximum attack velocity for bluefish (○) and striped bass (●) predators. Means and standard errors for each 10 mm total length (TL) range are indicated.
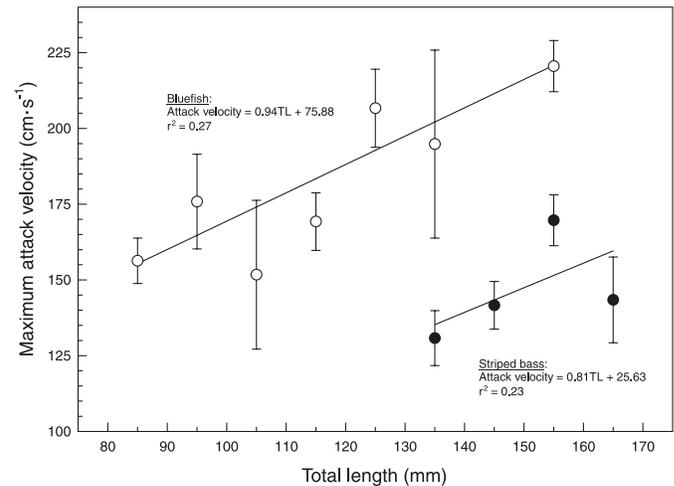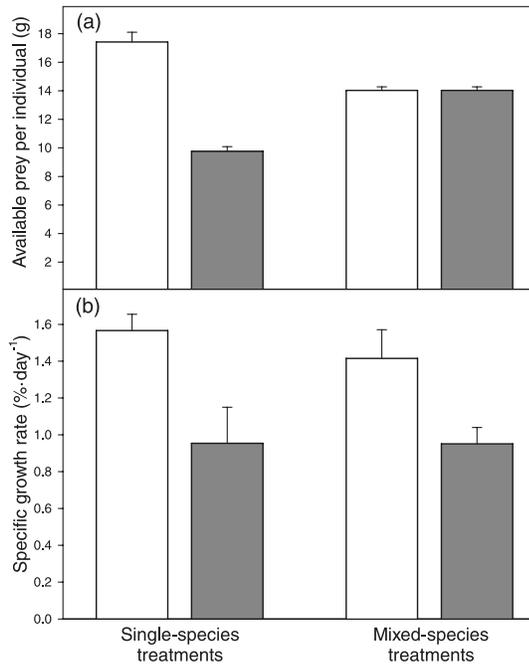

Predator growth on shrimp versus fish diet

The initial mean weights (± standard error, SE) of striped bass in the shrimp- and fish-fed treatments were 40.0 g (±0.7 g) and 40.9 g (±2.3 g), respectively, and did not differ among treatments ($t = -0.399$, df = 4, $P = 0.710$). After 20 days, repeated measures ANOVA revealed a marginally significant (interaction term, $P = 0.057$) difference in growth of striped bass fed a fish versus a shrimp diet. Striped bass in fish-fed tanks were an average of 5.2 g heavier at the end of the experiment than striped bass that were fed a shrimp diet. Fish-fed striped bass had an average instantaneous growth rate of 0.017 (1.7%·day^{-1}) compared with an instantaneous growth rate of 0.013 (1.3%·day^{-1}) for shrimp-fed striped bass, a difference of 30%. Previously published experimental results for bluefish demonstrated that when fed a fish diet, bluefish were more than 16 g heavier, on average, at the end of 60 days than bluefish fed a shrimp diet (see Buckel et al. 2004 for experimental details). Bluefish instantaneous growth rates were 0.041 (4.1%·day^{-1}) on a fish diet and 0.032 (3.2%·day^{-1}) on a shrimp diet, a difference of 28% (Buckel et al. 2004). Both bluefish and striped bass realized higher growth rates when consuming piscine prey compared with shrimp prey.

Foraging ability in a mixed-predator assemblage

The initial mean weights (±SE) of bluefish were 26.2 g (±0.8 g) and 27.8 g (±0.7 g) in the single- and mixed-species treatments, respectively. Initial mean weights of striped bass were 25.3 g (±1.3 g) in the single-species treatments and 28.3 g (±1.6 g) in the mixed-species treatments. Values of initial mean weight did not differ within species for the mixed- versus single-species treatments (bluefish: $t = -1.53$, df = 4, $P = 0.201$; striped bass: $t = -1.48$, df = 4, $P = 0.212$) and also did not differ between species within the mixed-species treatment ($t = -0.27$, df = 4, $P = 0.802$). Temperature and salinity were stable throughout the 50-day experiment (mean temperature = 19.9 °C, range = 17.7–21.5 °C; mean salinity = 23.6 ppt, range = 21.8–25.5 ppt).

To interpret the growth data, expected growth rates in the mixed-species treatments were based on the absolute amount

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Fig. 5. Mean (+1 standard error, SE) (*a*) prey fish biomass available per individual predator and (*b*) specific growth rate for bluefish (open bars) and striped bass (solid bars) in single- and mixed-species treatments during foraging ability experiment. Under the assumption of no difference in foraging ability between predator species and equal amounts of prey biomass available per individual in the mixed-species treatment, we hypothesized growth in the mixed-species treatments would be lower for bluefish and higher for striped bass relative to observed growth rates for each species in the single-species treatments.

Table 1. Repeated measures analysis of variance with treatment (single- versus mixed-species) and time as independent variables and weight as the dependent variable for bluefish and striped bass.

Effect	df	SS	F	P
Bluefish weight				
Treatment	1	4.52	0.13	0.735
Time	5	3808.71	438.93	<0.0001
Treatment×time	5	12.90	1.49	0.239
Striped bass weight				
Treatment	1	199.34	4.09	0.113
Time	5	1073.26	148.36	<0.0001
Treatment×time	5	6.07	0.84	0.537

Note: Nonsignificant P values for the treatment $\times$ time interaction terms indicates no statistical difference in growth trajectories between single- and mixed-species treatments for each predator species.

served growth rates in the mixed-species treatment did not match expectations that assumed equivalent foraging abilities; bluefish grew faster than expected, while striped bass grew more slowly than expected. To produce the observed growth pattern, bluefish would have required nearly two-thirds of the available prey in the mixed-species treatment. Therefore, when held in mixed-predator assemblages, bluefish displayed greater foraging ability and were able to exploit prey fish resources at the expense of striped bass in a limited prey environment.

Discussion

Patterns of resource utilization

Our synoptic examination of diet data from New York Bight estuaries indicates that age-0 bluefish become piscivorous earlier and consume more fish prey compared with age-1 striped bass of similar size. The feeding habits of bluefish and striped bass in New York Bight estuaries are similar to patterns observed for these species in other US Atlantic coast estuaries located at northern latitudes. Age-0 bluefish diets consist mainly of fish prey upon estuarine arrival in early summer (Juanes and Conover 1995; Buckel and Conover 1997; Buckel et al. 1999), while age-1 striped bass diets are dominated by invertebrates in early summer with a trend towards increased piscivory in late summer and early fall (Schaefer 1970; Gardinier and Hoff 1982; Buckel and McKown 2002).

Variation in the onset of piscivory has been documented in freshwater systems both among piscivorous species and within a single species across years and systems (Keast 1985; Mittelbach and Persson 1998; Graeb et al. 2005). Among freshwater piscivores, some appear structurally adapted for an early shift to piscivory, while others do not begin eating fish prey until much later in life (termed ''specialist'' and ''secondary'' piscivores, respectively, by Keast 1985). The early onset of piscivory in age-0 estuarine bluefish would characterize them as a specialist piscivore; however, striped bass are difficult to categorize. The secondary piscivores in freshwater systems studied by Keast (1985) generally did not include considerable amounts of fish prey in the diet until ages 3 or 4. The striped bass in New York Bight estuaries, in contrast, typically include moderate amounts (up to 30% FO) of fish prey in their diets by the fall of age 1 and have been observed in some instances to

of prey available (Fig. 5*a*) and observed growth in the single-species treatments (left side of Fig. 5*b*). We limited rations to 50% of per capita (g·g^{-1}·day^{-1}) maximum consumption, which differs between bluefish (~10% body mass per day) and striped bass (~6.5% body mass per day) based on bioenergetic experiments conducted for these life stages (Hartman and Brandt 1995*b*). Therefore, the three treatments received different absolute amounts of prey over the course of the experiment, necessitating that expected growth rates for the mixed-species treatment were based on these differences coupled with observed growth in the single-species treatments (Fig. 5). On average, bluefish in mixed-species treatments had access to less prey per individual compared with bluefish in single-species treatments, and striped bass in mixed-species treatments had access to more prey per individual compared with striped bass in the single-species treatments. Thus, the following growth rate predictions were made for the mixed-species treatment assuming equal foraging abilities of bluefish and striped bass: bluefish in the mixed-species treatment would grow slower than bluefish in the single-species treatment, while striped bass in the mixed-species treatment would grow faster than striped bass held in the single-species treatment.

Both bluefish and striped bass grew significantly over time (Table 1, Fig. 5*b*). However, we detected no significant differences in growth of bluefish or striped bass between single- and mixed-species treatments (Table 1, Fig. 5*b*). Ob-

eat small amounts (<10% FO) of fish prey during their first year (age-0 fish) (Buckel and McKown 2002; Jordan et al. 2003). Although the trend for striped bass at northern latitudes indicates a gradual increase in piscivorous feeding during their second and third summers (age-1 and age-2 fish), considerable variation in the timing and extent of piscivory in striped bass has been observed along the US Atlantic coast. In the Chesapeake Bay, located south of the New York Bight, fish prey constituted >60% of the biomass of prey eaten by age-1 striped bass by midsummer (Hartman and Brandt 1995*a*). Similarly, Markle and Grant (1970) found that fish occurred in >20% of the stomachs containing food and represented >50% by volume of the diet of juvenile striped bass between 30 and 150 mm TL from three major tributaries in the southern region of Chesapeake Bay. Moreover, striped bass appear to make an even earlier shift to piscivory at more southern latitudes, as age-1 striped bass in the Albemarle Sound estuary, North Carolina, were found to be completely piscivorous (>95% FO and % weight) by June of their second summer during two independent studies separated by more than 30 years (Manooch 1973; Rudershausen et al. 2005). Larger body sizes at age-1 for striped bass at southern latitudes (Rudershausen et al. 2005) provide a greater size advantage over piscine prey and may be mostly responsible for an earlier shift to a piscivorous diet in these systems.

In addition to including greater proportions of fish in their diet, we found that for a given predator body size, bluefish were able to consume larger sizes of identical prey species compared with striped bass. Since some of our bluefish prey size data was compiled from different years and estuaries than striped bass prey size data, spatial and temporal differences in prey size availability could partially explain these differences. However, based on the similarity in relative prey sizes eaten by striped bass in estuaries outside of New York Bight, this explanation does not appear likely. Manooch (1973) and Rudershausen et al. (2005) each found that striped bass consumed small relative prey sizes (prey/predator size ratios (PPR) = 0.13–0.27 (Manooch 1973); PPR = 0.19–0.27 (Rudershausen et al. 2005); mean PPR = 0.21 for both studies) in Albemarle Sound, North Carolina. These relative prey sizes were nearly identical to those observed for age-1 striped bass in New York Bight estuaries, suggesting that juvenile striped bass along the US Atlantic coast consume mostly small prey relative to their body size that are smaller than the relative prey sizes eaten by juvenile bluefish.

Morphological and behavioral explanations

Factors that can influence the timing and extent of piscivory may often do so indirectly through their effect on predator–prey body size relationships and include timing of spawning of predator and prey species, water temperature, growth rates during the invertebrate feeding stage, and predator and prey fish densities. To ensure the size advantage necessary to achieve piscivory, Keast (1985) noted that specialist freshwater piscivores spawned sufficiently earlier than their piscine prey. Indeed, bluefish utilize warm waters off the southeastern US continental shelf to spawn ahead of, and gain a size advantage over, their primary prey species, which are restricted to later spawning periods

in more northern estuaries (Juanes and Conover 1995). This spawning strategy enables age-0 bluefish to feed on fish prey during their first summer. However, age-1 striped bass also achieve a considerable size advantage over potential prey fishes, since they are spawned a full year ahead of the forage fish available to them during their second summer of life. In fact, age-1 striped bass are larger than age-0 bluefish when they each enter estuaries in early summer, an indication that the difference in spawning timing should not be a primary factor explaining disparities in consumption of fish prey between these predators.

Gape allometry also did not appear to limit maximum prey sizes that predators were able to consume. Both predators possessed sufficiently large gapes to consume larger prey than were included in their diets, indicating that the sizes of forages fishes eaten were not morphologically constrained. Several studies have noted the importance of predator gape allometry in regulating prey sizes eaten (Persson et al. 1996; Scharf et al. 2000). However, evidence is equally available indicating that the sizes of prey eaten by many predators do not approach gape limitations, with limits instead being potentially set by prey behavior and availability (Gaughan and Potter 1997; Scharf et al. 2000; Galarowicz et al. 2006). In their review, Mittelbach and Persson (1998) found freshwater piscivores with larger mouth gapes switch to piscivory at smaller sizes and were larger at age-1. For bluefish and striped bass, gape sizes did not appear to be responsible for observed differences in the timing and extent of piscivory.

Foraging abilities of bluefish and striped bass exhibited size-dependent patterns typical of piscivorous fish predators, with linear declines in capture success, exponential increases in handling time, and dome-shaped patterns of profitability as relative prey size increased. However, there were striking differences in foraging ability between piscivore species. Bluefish capture success was generally two–three times higher than striped bass capture success on equal sized prey. Differences were greatest at large relative prey sizes, implying that the availability of relatively small forage fishes is likely of paramount importance to the ontogeny of piscivory in striped bass. The rapid increases in prey handling time demonstrate the potential for increased foraging costs to striped bass when prey sizes are large. Using large amounts of time to handle prey can be energetically costly and may also increase the risk of interactions with potential predators and competitors (e.g., Nilsson et al. 2000). When feeding on sand shrimp prey, both predator species realized lower profitabilities compared with feeding on similar-sized fish prey, an indication that neither species obtains an advantage in foraging efficiency when feeding on a common benthic invertebrate prey. Reduced foraging efficiency and growth rate in bluefish and striped bass when feeding on shrimp prey combine to suggest that there should be strong selection for an accelerated shift to piscivory in both predators.

Profitability functions serve as an index of predator feeding efficiency and probably constitute the most complete measure of piscivore foraging ability when prey are readily available. The measure does not account for differences in predator encounter rates with potential prey that may be related to differences in predator search strategy, activity

level, or visual acuity, but rather combines capture success and handling time functions with the mass and energetic content of prey ingested to generate a relative estimate of size-dependent feeding efficiency. We assumed that search costs were negligible and encounter probabilities were essentially 100% in our experiments, regardless of predator and prey species or size, because of the moderate tank volumes, abundant light, and high water transparency (Mazur and Beauchamp 2003; Turesson and Brönmark 2007). For each prey fish species, peaks in bluefish profitability were nearly four times higher than those of striped bass, indicating that bluefish are more efficient at capturing and manipulating fish prey for ingestion. More importantly, bluefish profitability peaked at larger relative prey sizes compared with striped bass, illustrating the ability of bluefish to forage effectively on even relatively large fish prey and further establishing the limitations for striped bass when small forage fishes are not available.

Behavioral observations revealed that bluefish and striped bass employed similar attack strategies, but that bluefish attained substantially higher burst velocities when attacking prey compared with striped bass. Strike tactics of both predators involved approaching prey at low swimming velocities (30–40 cm·s^{-1}) followed by rapid acceleration from an "S-start" position to strike at prey with high velocity (125–200 cm·s^{-1}). Webb (1984) observed variation in strike speeds among predators employing different attack strategies and concluded that predators likely optimized attack speeds to minimize closure times. Bluefish and striped bass attack behaviors did not exhibit obvious differences; thus, higher strike velocities by bluefish may have contributed to higher capture efficiencies. Moreover, striped bass swimming velocity often peaked slightly ahead of the strike, which may have negatively affected prey capture success. Bluefish tooth morphology could also contribute to their greater foraging ability. Bluefish possess large, sharp, deeply socketed teeth, a suite of dentition characters shared by other vertebrate groups that display extreme carnivory on large, active prey (Bemis et al. 2005). Tooth structure and attachment in bluefish allow larger prey to be severed into smaller pieces, whereas striped bass have small cardiform teeth and must swallow prey whole. The ability of bluefish to sever prey also reduces handling time on larger prey (Scharf et al. 1997), thus increasing overall foraging efficiency.

Consequences for predator growth

Growth rates of fishes can increase considerably after switching from an invertebrate to a fish diet (Buijse and Houthuijzen 1992; Buckel et al. 1998; Galarowicz and Wahl 2005). We found about a 30% increase in specific growth rate for age-1 striped bass fed a fish diet versus a shrimp diet, and we believe that the marginal statistical significance was mostly a result of the short duration of the experiment. A previous study (Buckel et al. 2004) demonstrated a similar pattern for juvenile bluefish and observed a 28% increase in specific growth rate for bluefish that were fed fish compared with those fed shrimp. Thus, both bluefish and striped bass suffer lower growth rates during the juvenile period when their diet is dominated by a common invertebrate prey. Friedland et al. (1988) observed

lower condition in field-captured age-0 bluefish during summers when benthic invertebrates (mostly small shrimp) were more prevalent in the diet and concluded that benthic invertebrates likely represented an energy-poor prey relative to fish. Indeed, mean energy content has been determined to be considerably lower for sand shrimp (3.7 kJ·g wet weight^{-1}) than bay anchovy (5.9 kJ·g^{-1}) or Atlantic silversides (7.3 kJ·g^{-1}) (Steimle and Terranova 1985) and contributes to lower profitability.

In an earlier study, Buckel and McKown (2002) found evidence for resource (habitat and diet) partitioning between bluefish and striped bass in New York Bight estuaries and concluded that resource partitioning could have resulted from past (sensu Rosenzweig 1981) competition (interference or exploitative) or that it could be an indication that these two species do not compete. Their laboratory experiments with mixed-predator assemblages and unlimited prey confirmed that interference competition was unlikely between these two species; however, they did not examine resource utilization under limited prey conditions. In this study, using limited prey rations determined bioenergetically, we observed that bluefish consumed nearly two-thirds of the available forage and thus were able to exploit prey fish resources at the expense of striped bass in a limited fish prey environment. Our findings suggest that exploitative competition is a potential mechanism leading to differences in habitat and prey use in New York Bight estuaries; future field studies should further investigate this possibility.

Divergent patterns of resource utilization are often caused by differences in foraging abilities between sympatric predators. For example, juvenile roach (*Rutilus rutilus*) attack and capture zooplankton prey more efficiently than European perch (*Perca fluviatilis*), leading to greater resource limitation, reduced growth, and lower survival in perch when the two species co-occur in lake systems with depressed prey resources (Persson et al. 2000). Eklöv and Diehl (1994) concluded that growth differences between piscivorous adult perch and northern pike (*Esox lucius*) fed fish prey and held separately under identical conditions resulted from differences in predator morphology, attack efficiency, and behavior; however, the authors concluded that differences may be altered if pike and perch were held together in mixed-predator assemblages. The differences in foraging ability that we found likely contribute to disparities in growth between juvenile bluefish and striped bass observed in natural systems. Long-term (1986–1998) field data in New York Bight estuaries demonstrate consistently lower growth rates for age-1 striped bass ($\bar{x}$ = 0.95 mm·day^{-1}) compared with age-0 bluefish ($\bar{x}$ = 1.43 mm·day^{-1}) during summer months (K.A. McKown, unpublished data). Higher estuarine growth rates observed for age-0 bluefish compared with age-1 striped bass are likely due primarily to an earlier shift to piscivory by bluefish, which is facilitated to a large degree by their exceptional foraging abilities when feeding on fish.

The consistently lower growth rates and large non-fish component of age-1 striped bass diets suggest that striped bass have limited access to fish prey during their second summer in northern US Atlantic coast estuaries. We stress that access to fish prey resources in these systems is not necessarily limited by low absolute densities of forage

fishes, but rather is restricted by having access to only a small fraction of the available prey fish size distribution. Juvenile striped bass should feed most efficiently on prey fishes that are 20%–30% of their body size, mainly because of difficulty in capturing forage fishes at larger relative sizes. Age-1 striped bass begin their second summer at smaller body sizes in northern US Atlantic coast estuaries compared with systems further south (Rudershausen et al. 2005), meaning that the primary forage fish species (e.g., atherinids, clupeids, and engraulids) may quickly grow beyond the most vulnerable sizes. Research in freshwater systems has highlighted the importance of predator–prey body size relationships to the growth and survival of piscivores (Donovan et al. 1997; Cyterski and Ney 2005). Our findings suggest that latitudinal variation in diet and growth of juvenile striped bass are also influenced by predator–prey body size relationships, which ultimately determine prey fish availability.

Although the effect on diet of variable prey densities was not examined in this study, the relative densities of benthic invertebrate and fish prey may also contribute to delayed piscivory in striped bass. In early summer, sand shrimp densities can be considerably higher than densities of forage fishes in northern US Atlantic coast estuaries, leading to higher encounter rates with shrimp prey and inclusion in predator diets (Juanes et al. 2001). However, even when fish prey were at lower relative densities, juvenile bluefish showed positive selection for fish prey and negative selection for shrimp that was related mainly to higher bluefish capture success on fish prey (Juanes et al. 2001). We discounted our profitability index by multiplying by the percentage of successful capture attempts, but the actual energetic consequences of failed strikes may represent a much greater cost. At small relative body sizes (10%–20%) in early summer, shrimp prey may represent a relatively profitable prey for juvenile striped bass because of high encounter rates and their relative ease of capture compared with larger fish prey. Estimates of the energetic costs of failed capture attempts (e.g., Selch and Chipps 2007) would enable a greater mechanistic understanding of the patterns of prey selection by bluefish and striped bass.

We conclude that contrasting patterns of resource utilization in northern US Atlantic coast estuaries between these two predators may be driven largely by differences in foraging ability. Juvenile striped bass have limited capture abilities when prey fishes are relatively large; thus, piscivory is delayed until the relative size of prey fishes is reduced through predator growth, increased availability of relatively small prey fishes, or a combination thereof. The early shift to piscivory observed for juvenile striped bass at more southern latitudes indicates that this species will take advantage of the accelerated growth provided by a piscivorous diet if prey fish sizes are small relative to predator size. Our findings highlight the importance of the availability of appropriately sized forage fishes to the ontogeny of piscivory and provide evidence that predator–prey size relationships and disparate foraging abilities can generate variation in patterns of resource utilization and predator growth. The important growth consequences of patterns of resource utilization by piscivorous fishes call for more rigorous assessments of forage fish size distributions and quantitative evaluation of foraging behavior to identify the processes that contribute to inter- and intra-specific variation.

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