

# Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability

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**Abstract:** Capture success, handling time, prey vulnerability, and prey profitability were examined as a function of prey length/predator length ratio for age-0 juvenile bluefish (*Pomatomus saltatrix*) feeding on juvenile striped bass (*Morone saxatilis*) and Atlantic silverside (*Menidia menidia*). For each prey species, bluefish capture success declined linearly and handling time increased exponentially with increasing length ratios between 0.20 and 0.65. However, bluefish capture success was lower and handling times increased at a faster rate when feeding on juvenile striped bass compared with Atlantic silverside. Prey vulnerability, measured as bluefish predation rate, declined exponentially with increasing length ratios for each prey species. Profitability curves were dome shaped for each prey species; however, profitability values and the location of dome peaks differed between prey species. Capture success functions were combined with field length distributions to generate expected frequency distributions of length ratios included in bluefish diets. Comparisons resulted in good agreement between expected and observed sizes in bluefish diets, illustrating the importance of capture success in determining piscivore diets. Our results indicate that, for juvenile fishes, prey-specific morphological and behavioral differences can have significant effects on the outcome of predator-prey interactions and that size-based predation components are best represented as continuous functions of relative fish size.

**Résumé :** On a examiné le taux de capture, le temps de manipulation, la vulnérabilité des proies et la profitabilité des proies comme fonction du ratio longueur de la proie à longueur du prédateur dans le cas de tassergals (*Pomatomus saltatrix*) juvéniles d'âge 0 se nourrissant de juvéniles de bars rayés (*Morone saxatilis*) et de capucettes (*Menidia menidia*). Pour chaque espèce de proie, le taux de capture du tassergal diminuait linéairement et le temps de manipulation augmentait exponentiellement quand les ratios de longueurs s'accroissaient entre 0,20 et 0,65. Cependant, le taux de capture était plus faible et le temps de manipulation s'accroissait plus rapidement avec des bars rayés juvéniles qu'avec des capucettes comme proies. La vulnérabilité des proies, indiquée par le taux de prédation des tassergals, diminuait exponentiellement quand augmentaient les ratios de longueurs pour chacune des espèces proies. Les courbes de profitabilité étaient en forme de cloche pour chaque espèce proie, mais les valeurs de profitabilité et la position des sommets des courbes différaient d'une espèce proie à l'autre. On a combiné les fonctions de taux de capture avec les distributions des longueurs sur le terrain pour générer des distributions de fréquences attendues des ratios de longueurs dans le régime alimentaire des tassergals. Les comparaisons ont montré qu'il y avait une bonne correspondance entre les tailles attendues et observées des proies composant le régime alimentaire du tassergal, ce qui témoigne de l'importance du taux de capture dans la détermination du régime alimentaire des poissons piscivores. Nos résultats montrent que, pour les poissons juvéniles, les différences morphologiques et comportementales chez les différentes proies peuvent avoir des effets importants sur l'issue des interactions prédateurs-proies, et que les paramètres de la prédation ayant trait à la taille sont le mieux représentés par des fonctions continues de la taille relative des poissons.

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## Introduction

Predator-prey interactions during early life history stages have important effects on survival and recruitment processes of fishes (Bailey and Houde 1989). Specifically, size-dependent predation can play a major role in determining the abundance and size structure of prey and predator populations. However, the outcome of size-structured interactions between prey and predator populations that are growing simultaneously is often complex (Werner and Gilliam 1984; Stein et al. 1988; Rice et al. 1993). Therefore, specific components of size-structured predator-prey interactions are typically determined from laboratory experiments using individual predator-prey

combinations or small groups. Previous work has demonstrated the potential effectiveness of size-dependent information obtained from laboratory predation experiments in predicting the outcome of population-level interactions (Adams and DeAngelis 1987; Rice et al. 1993).

The mechanisms of size-dependent predation processes must be clearly defined to use individual-based laboratory results to aid in predicting the dynamics of fish populations. Individual-based approaches to modelling fish interactions require accurate information on each component of the predation process (Rice et al. 1997). However, laboratory experiments necessary to generate required predation information are often not conducted, but rather, values for species-specific parameters are estimated from best available data or are replaced with those of a similar species. In particular, success or failure of predator capture during individual encounters with prey has often been estimated by using a single discrete threshold value of prey to predator size ratio (Adams and DeAngelis 1987; Madenjian et al. 1991). The use of a discrete value of relative fish size to determine capture success ignores the dynamic nature of size-dependent predation processes. Adams and DeAngelis (1987) indicated that only a 10% change in the value of the capture success parameter resulted in significant differences in mean length of predator populations in their model output.

Several empirical studies have used single predator and prey species to examine size-structured predation on larval (Folkvord and Hunter 1986; Pepin et al. 1992) and juvenile fishes (Rice et al. 1993; Juanes and Conover 1994a). Others have examined the vulnerability of single species of larval fishes to a variety of predator types (Bailey and Houde 1989; Cowan et al. 1996; Paradis et al. 1996). However, recent studies examining predation components for multiple prey species are relatively uncommon (Bailey and Batty 1984; Webb 1986; Wahl and Stein 1988), despite the potential importance of prey morphology and behavior in determining prey vulnerabilities and their effect on the outcome of predator-prey interactions (Sih and Moore 1990).

Most research directed towards understanding the effects of size-structured predator-prey interactions on fish populations has focused on the larval period of the life history (Miller et al. 1988; Paradis et al. 1996) whereas the juvenile period has received comparatively less attention (Rice et al. 1993; Wright et al. 1993; Juanes and Conover 1995). Recent evidence indicates that size-related differences in survival rates of juvenile fishes may significantly affect year-class strength (Campana 1996). Therefore, an improved knowledge of the causes of variation in prey and predator abundances may be gained through a more complete understanding of the processes that influence juvenile survival.

The bluefish (*Pomatomus saltatrix*) is an abundant marine piscivorous fish along the Atlantic coast of the United States. Juvenile bluefish have been shown to be important estuarine piscivores during summer months, as their diet consists of a variety of fish species of commercial and recreational importance (Friedland et al. 1988; Juanes et al. 1993). Several studies have demonstrated that juvenile bluefish feed selectively based on prey size, with smaller prey sizes occurring consistently in the diet (Juanes et al. 1994; Juanes and Conover 1995; Scharf et al. 1997). Based on prey choice experiments conducted using Atlantic silverside (*Menidia menidia*) as prey,

Juanes and Conover (1994a) suggested that juvenile bluefish attack all prey sizes at equal rates, but consume mainly smaller fishes because of higher capture efficiencies.

Here, we determine empirically the rate of capture success, handling time, prey profitability, and prey vulnerability as a function of prey length/predator length ratio for young-of-the-year bluefish feeding on juvenile striped bass (*Morone saxatilis*) and Atlantic silverside. These two prey species frequently occur in the diet of juvenile bluefish in U.S. east coast estuaries and differ considerably in morphology and behavior, with striped bass being a deep-bodied, facultative schooling species with well-developed dorsal and anal fin spines and Atlantic silverside being a slender-bodied, obligate schooling species that lacks well-developed fin spines. We then generate expected frequency distributions of prey to predator size ratios included in bluefish diets using bluefish capture success functions and predator and prey size availability data and compare these distributions with actual prey to predator size ratio distributions occurring in bluefish diets during summer months in two U.S. Atlantic coast estuaries.

## Methods

Juvenile bluefish, striped bass, and Atlantic silverside were collected in the Haverstraw Bay region of the lower Hudson River, N.Y. (41°11'N, 73°54'W), during June–August of 1996 by using beach seines. Additional bluefish and Atlantic silverside were collected from Great South Bay, N.Y. (40°10'N, 73°10'W), and Flax Pond, N.Y. (40°57'N, 73°07'W), marine embayments on the south and north shores of Long Island, respectively. Additional striped bass were collected in the lower Hudson River by the New York State Department of Environmental Conservation as part of a juvenile striped bass survey.

Fish were immediately transported to the Flax Pond Marine Laboratory in Old Field, N.Y., and allowed to acclimate for at least 1 week prior to use in experiments. All fish were maintained in tanks with a continuous flow of seawater at ambient temperatures and natural photoperiod throughout the experiments. Because bluefish feeding trials were conducted during a 5-week period in midsummer (10 July to 14 August 1996), water temperatures (20–23°C) and photoperiod (14 h light : 10 h dark) remained relatively constant throughout the experiments.

A total of 53 bluefish ranging from 80 to 155 mm total length (TL) were used in the feeding trials. Bluefish were held in three 800-L holding tanks while being fed a combination of live and previously frozen fish prey throughout the experimental period. Bluefish were sampled randomly from the holding tanks and were mildly anesthetized with tricaine methanesulfonate (MS 222) before being sorted into groups of three to allow for schooling (Juanes and Conover 1994a). Individuals were sorted by size to ensure that TL differences between any two members of the group did not exceed 5 mm. Each group of three bluefish was then placed in a 200-L tank and starved for 24 h to standardize hunger levels across feeding trials. Each group of three bluefish was then placed in one of four 215-L experimental chambers, each equipped with a transparent plexiglass viewing window, and allowed to acclimate for at least 8 h prior to the initiation of a feeding trial.

Each feeding trial consisted of a group of three bluefish presented with a group of 10 striped bass or 10 Atlantic silverside with TL differences not exceeding 2.5 mm between any two prey fish in a group. Juvenile striped bass prey ranged in size from 25 to 80 mm TL whereas Atlantic silverside ranged from 20 to 85 mm TL. Throughout the 5-week experimental period, various combinations of prey and predator length groups were used to generate a continuous range of prey length/predator length ratios from 0.20 to 0.65 for each prey

species (Table 1), which represents a natural range of length ratios occurring in the field (Scharf et al. 1997). Both large and small bluefish were used to obtain prey length/predator length ratios at each end of this range for each prey species. Prey were added to chambers already containing bluefish using a hollow, transparent plexiglass cylinder that was placed vertically into the chamber. Prey were placed within the cylinder and allowed to acclimate for at least 5 min before the cylinder was removed and bluefish had access to the prey. Experimental chambers were illuminated during feeding trials using a 150-W halogen light positioned about 1 m above each chamber. Each 15-min feeding trial was recorded using a standard Hi-8 video camera mounted about 1 m from the viewing window. After each trial, all live prey fishes were counted and removed and bluefish were returned to the 800-L holding tanks.

Throughout the experimental period, bluefish were sampled randomly with replacement from the holding tanks. This was done to avoid the effects of potential learned behavior by the bluefish resulting from continuous holding in the experimental chambers for extended periods. Our experimental procedure for random sampling of bluefish from the holding tanks, placement into tanks for a 24-h starvation period, and subsequent placement into experimental chambers ensured that once used in a feeding trial, bluefish of a given group could not be used during the next two trials. This translated into a minimum time between use in feeding trials of 36 h for any given bluefish. Given the high consumption and gut evacuation rates exhibited by juvenile bluefish during estuarine residency (Juanes and Conover 1994b; Buckel et al. 1995), we felt that our experimental protocol was sufficient to minimize potential predator learning while maintaining adequate hunger levels.

Capture success was calculated as the proportion of bluefish capture attempts that resulted in prey consumption. A capture attempt was defined as a directed strike at a prey fish, wherein a single bluefish oriented toward an individual prey fish and exhibited a burst in swimming speed culminating in a lunge in an attempt to grasp the given prey fish. Handling time, defined as the time from capture of a given prey fish until swallowing activity ceased, was estimated to within 0.03 s for each successful capture. The vulnerability of each prey species to bluefish predation was assessed by plotting predation rate as a function of prey length/predator length ratio. Predation rate was calculated as the percentage of prey offered that was eaten per number of predators per unit time ( $\% \text{ prey eaten} \times \text{no. predators}^{-1} \times \text{hours}^{-1}$ ).

For each prey species, relationships between capture success and relative fish size were analyzed by using least squares regressions (StataCorp. 1995). Handling times and prey vulnerabilities were linearized by using logarithmic transformations and analyzed as a function of prey length/predator length by using least squares regressions. Least squares regressions were compared by using analysis of covariance (Sokal and Rohlf 1995). Nonlinear least squares regression models fit to the exponential relationship  $y = ae^{bx}$  (StataCorp. 1995) are presented for handling time and prey vulnerability relationships because back-transformation of linearized functions is subject to bias (Beauchamp and Olsen 1973). Means ( $\pm 1$  SE) were calculated at each 0.05 interval of prey length/predator length ratio for bluefish capture success, handling time, and prey vulnerability and are illustrated in the figures for simplification. We wanted to ensure that the prey to predator size ratio, and not predator size alone, was the variable responsible for our results. To accomplish this goal, residuals of linear regressions for bluefish capture success, handling time, and prey vulnerability were regressed against bluefish TL to examine the relationship between predation components and bluefish body size across the range of predator lengths used in the experiments.

Profitability was estimated for each prey species as a function of prey length/predator length by combining functions derived from the feeding trials for relative prey mass ingested, handling time, and capture success (prey mass/predator mass  $\times$  handling time $^{-1}$   $\times$  capture probability). To examine the influence of capture success,

**Table 1.** Number of bluefish feeding trials conducted at each interval of prey length/predator length ratio using striped bass and Atlantic silverside as prey.

Prey length/predator length ratio	Striped bass	Atlantic silverside
0.200–0.249	4	3
0.250–0.299	4	4
0.300–0.349	7	7
0.350–0.399	6	5
0.400–0.449	7	7
0.450–0.499	4	5
0.500–0.549	5	5
0.550–0.599	4	3
0.600–0.649	0	3
Total	41	42

profitability was also estimated with capture success functions removed from the equations.

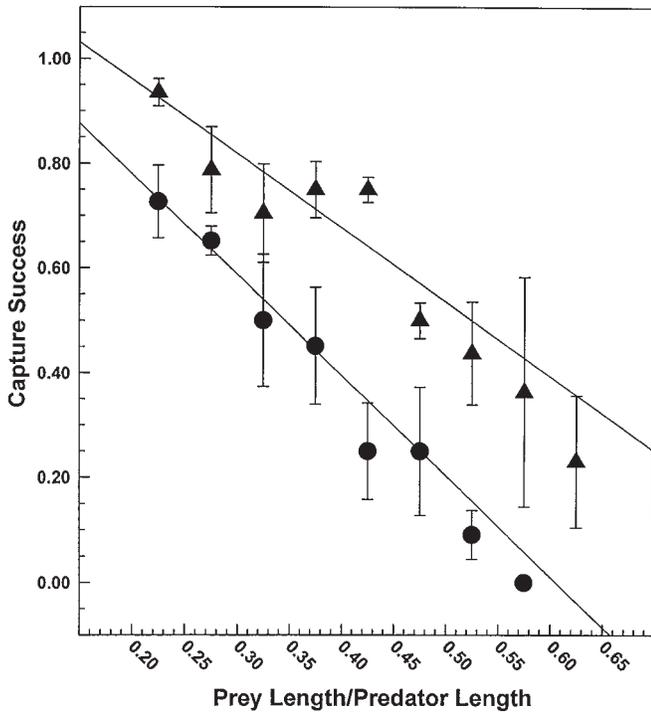
For each prey species, bluefish and prey length distributions observed in the field from early July to mid-August were combined to generate a probability distribution of prey length/predator length ratios occurring in the field during this time period. Prey and predator sizes were obtained for this time period to ensure that size distributions of predator and prey coincided with those used in the laboratory experiments. Bluefish capture success functions were combined with each probability distribution to generate an expected frequency distribution of prey length/predator length ratios included in bluefish diets for each prey species. Expected frequency distributions were generated for Atlantic silverside using predator and prey length distributions occurring in Great South Bay, N.Y., on four dates from 5 July to 9 August in 1989 and for juvenile striped bass using length distributions occurring in the lower Hudson River, N.Y., on five dates from 7 July to 4 August in 1993. Expected frequency distributions were compared with actual frequency distributions of length ratios consumed by bluefish in the field at the same sampling locations on the dates indicated by using chi-square analysis.

## Results

A total of 83 bluefish feeding trials were conducted that generated 485 observed attacks resulting in 261 successful prey captures. Bluefish capture success declined linearly with increasing prey length/predator length ratio when feeding on each prey species (striped bass:  $y = 1.166 - 1.926x$ ,  $p < 0.001$ ,  $r^2 = 0.41$ ; Atlantic silverside:  $y = 1.245 - 1.419x$ ,  $p < 0.001$ ,  $r^2 = 0.42$ ) (Fig. 1). Regression slopes were not statistically different ( $F_{1,72} = 0.591$ ,  $p > 0.25$ ); however, elevation of Atlantic silverside capture success was significantly higher than that of striped bass ( $F_{1,75} = 30.719$ ,  $p < 0.001$ ). There was no significant linear relationship between residuals of capture success versus prey length/predator length regressions and bluefish total length for either prey species (striped bass:  $p = 0.406$ ; Atlantic silverside:  $p = 0.721$ ).

Bluefish handling times increased exponentially with increasing prey length/predator length ratio for each prey species (striped bass:  $\ln(y) = 0.112 + 7.108x$ ,  $p < 0.001$ ,  $r^2 = 0.54$ ; Atlantic silverside:  $\ln(y) = 0.588 + 3.933x$ ,  $p < 0.001$ ,  $r^2 = 0.41$ ) (Fig. 2). Regression slopes were significantly different, with bluefish handling time increasing at a faster rate when feeding on striped bass ( $F_{1,239} = 7.968$ ,  $p < 0.005$ ). There was no significant linear relationship between residuals of handling time

**Fig. 1.** Proportion of successful captures as a function of prey length/predator length ratio for juvenile bluefish feeding on striped bass (●) and Atlantic silverside (▲). Data points represent means  $\pm 1$  SE. Lines represent linear regression equations presented in the text.

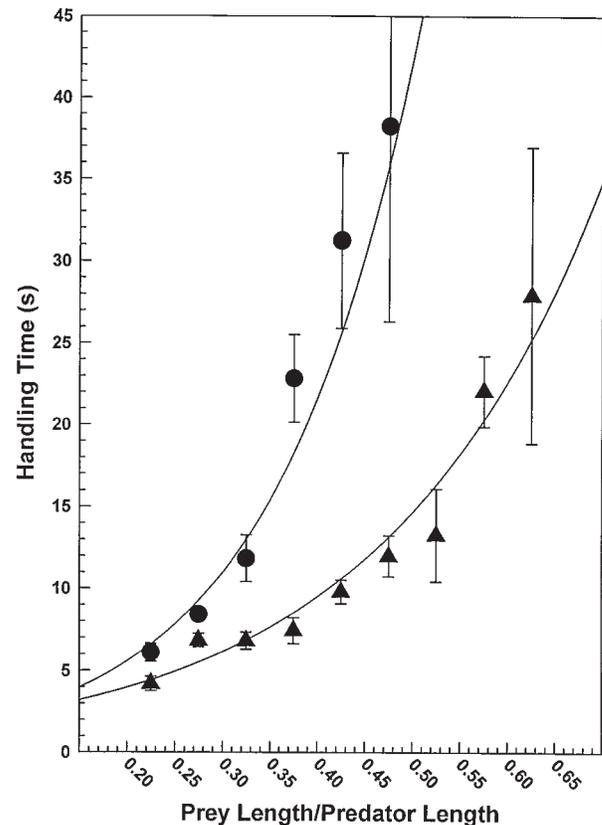


versus prey length/predator length regressions and bluefish total length for either prey species (striped bass:  $p = 0.618$ ; Atlantic silverside:  $p = 0.156$ ). For future predictive purposes, unbiased nonlinear least squares regression models were generated for bluefish handling time feeding on each prey species (striped bass:  $y = 1.442e^{6.768x}$ ,  $p < 0.001$ ,  $r^2 = 0.78$ ; Atlantic silverside:  $y = 1.671e^{4.342x}$ ,  $p < 0.001$ ,  $r^2 = 0.83$ ).

Vulnerability of striped bass to bluefish predation declined with increasing prey length/predator length ratios ( $\ln(y + 1) = 0.812 - 1.384x$ ,  $p < 0.001$ ,  $r^2 = 0.30$ ). Atlantic silverside vulnerability also declined with increasing relative prey size ( $\ln(y + 1) = 1.373 - 2.061x$ ,  $p < 0.001$ ,  $r^2 = 0.47$ ) (Fig. 3). Slopes of vulnerability equations were not significantly different between prey species ( $F_{1,76} = 0.922$ ,  $p > 0.25$ ). Elevations were significantly different ( $F_{1,79} = 26.719$ ,  $p < 0.001$ ), with Atlantic silverside being more vulnerable to bluefish predation across the range of length ratios used in the experiments. There was no significant linear relationship between residuals of predation rate versus prey length/predator length regressions and bluefish total length for either prey species (striped bass:  $p = 0.873$ ; Atlantic silverside:  $p = 0.921$ ). For future predictive purposes, unbiased nonlinear least squares regression models were generated for prey vulnerabilities (striped bass:  $y = 2.375e^{-5.035x}$ ,  $p < 0.05$ ,  $r^2 = 0.44$ ; Atlantic silverside:  $y = 11.598e^{-7.200x}$ ,  $p < 0.001$ ,  $r^2 = 0.72$ ).

Profitability as a function of prey length/predator length ratio was calculated using the capture success and handling time functions given above, as well as functions describing the relationship between prey mass/predator mass and prey length/predator length for each prey species (striped bass:  $y =$

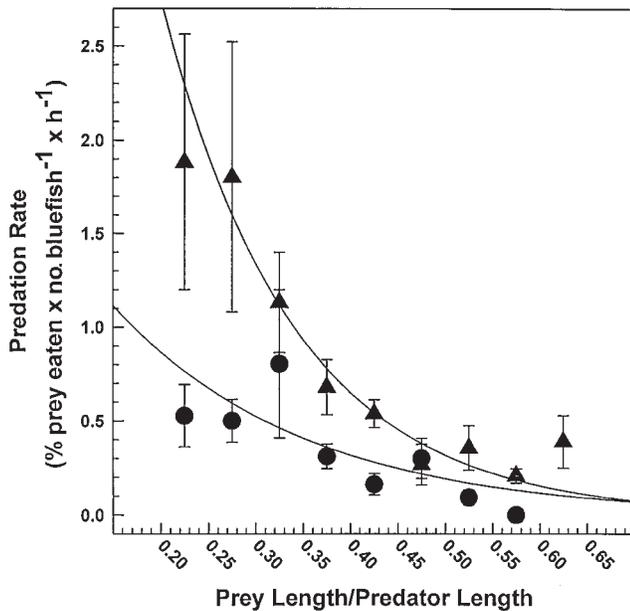
**Fig. 2.** Bluefish handling time as a function of prey length/predator length ratio for bluefish feeding on striped bass (●) and Atlantic silverside (▲). Data points represent means  $\pm 1$  SE. Curves represent nonlinear regression equations presented in the text.



$1.686x^{3.280}$ ; Atlantic silverside:  $y = 0.854x^{3.072}$ ). Profitability curves calculated both with and without capture success functions were dome shaped for each prey species (Fig. 4). However, profitability estimates incorporating capture success were much lower, extended over a narrower range of length ratios, and had peaks at lower length ratios than estimates that did not incorporate capture success. Striped bass profitability peaked at a length ratio of about 0.30 (Fig. 4a), much lower than Atlantic silverside profitability, which peaked at a length ratio of about 0.40 (Fig. 4b).

Probability distributions of prey length/predator length ratios occurring in the field peaked at ratios between 0.40 and 0.45 for striped bass as prey and at ratios between 0.20 and 0.25 for Atlantic silverside as prey during midsummer of 1993 and 1989, respectively (Figs. 5a and 6a). For both prey species, multiplying the probability distributions of length ratios occurring in the field by species-specific capture success functions yielded higher relative frequencies at lower prey length/predator ratios in the resulting expected frequency distributions (Figs. 5b and 6b). Chi-square analysis did produce a significant difference between expected and actual (Fig. 5c) distributions of length ratios included in bluefish diets for striped bass as prey ( $\chi^2_9 = 64.500$ ,  $p < 0.001$ ). Similar analyses did not result in a significant difference between expected and actual (Fig. 6c) distributions of length ratios included in bluefish diets for Atlantic silverside as prey ( $\chi^2_{16} = 10.142$ ,  $0.75 < p < 0.90$ ).

**Fig. 3.** Bluefish predation rate on striped bass (●) and Atlantic silverside (▲) as a function of prey length/predator length ratio. Data points represent means  $\pm$  1 SE. Curves represent nonlinear regression equations presented in the text.



## Discussion

### Capture success, handling time, and prey vulnerability

In our study, juvenile bluefish capture success declined with increasing prey length/predator length ratios for juvenile striped bass and Atlantic silverside. Juanes and Conover (1994a) also observed a decline in juvenile bluefish capture success with increased size of Atlantic silverside prey. Similarly, Heatherly (1993) found that capture success of juvenile bluefish feeding on spot (*Leiostomus xanthurus*) declined with increases in prey length/predator length ratios for a range of length ratios similar to that used here. Previous studies have demonstrated a strong negative relationship between piscivore capture success and prey size for several taxa (Miller et al. 1988; Litvak and Leggett 1992). However, these studies focused on experiments conducted using larval fishes as prey. Capture success information for juvenile prey fishes representing several taxa is not available.

For the range of prey length/predator length ratios examined here, juvenile bluefish had higher capture success on Atlantic silverside compared with striped bass. Bailey and Batty (1984) found differences in capture success of medusae predators feeding on four species of larval fishes. They suggested that observed differences in predator capture efficiency resulted from prey-specific differences in reactivity to encounters with predators. For piscivorous fish predators, both increased prey body depth and the presence of spines have been shown to negatively affect predator capture efficiencies (Hoogland et al. 1956; Webb 1986; Wahl and Stein 1988). Our results support previous findings that reveal the potential importance of prey morphology and behavior in affecting the outcome of predator-prey encounters. Video observations indicate that considerable morphological differences between striped bass and Atlantic silverside combined with earlier

reactions to bluefish attacks by striped bass produced the observed differences in bluefish capture success.

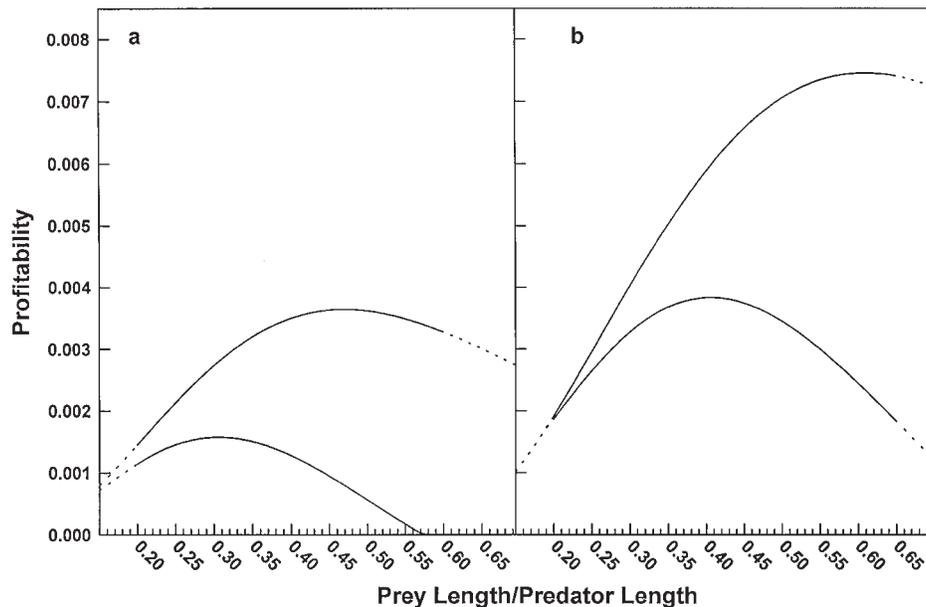
Bluefish handling time increased exponentially with increasing prey length/predator length ratio for both prey species. These results are consistent with previous studies in demonstrating the link between predator and prey size and the time needed to manipulate and ingest prey (Werner 1974; Mittelbach 1981; Juanes and Conover 1994a). Significant differences occurred in the slopes of the handling time curves between prey species, with bluefish handling time accelerating at a faster rate for striped bass than for Atlantic silverside. Largemouth bass (*Micropterus salmoides*) handling time was also found to vary among prey types with contrasting morphologies (Hoyle and Keast 1987). Among fish prey, Hoyle and Keast (1987) observed the fastest rate of increase in handling time for prey with the greatest body depth relative to length. Our findings agree with this result.

Vulnerability of juvenile striped bass and Atlantic silverside to bluefish predation declined exponentially with increasing prey length/predator length ratios, suggesting that the smallest prey sizes were most susceptible. In a review of the effects of body size on larval fish vulnerability, Paradis et al. (1996) show that larval vulnerability to predation by fishes is dome shaped, with maximum vulnerability occurring at prey length/predator length ratios of about 10%. Researchers have argued that dome-shaped vulnerability of larval fishes may arise because, as prey size increases, probabilities of predator encounter and (or) attack increase, while larval susceptibility to predator capture declines (Litvak and Leggett 1992; Pepin et al. 1992). For juvenile fishes, our results indicate that, relative to predator size, the smallest prey sizes are most vulnerable to predation by piscivorous fishes. Except for only the largest prey length/predator length ratios, the range of length ratios examined in this paper extends over the entire range of length ratios occurring in the field during midsummer months for bluefish feeding on these two prey species. Unlike interactions between larval fish prey and fish predators, wherein prey length/predator length ratios are typically less than 20% (Miller et al. 1988; Paradis et al. 1996), prey length/predator length ratios for interactions between juvenile fish prey and fish predators are usually higher than 20% (Rice et al. 1993), ranging from 15 to 85% for bluefish and their prey in our study. Based on our results, vulnerability curves of juvenile fishes to fish predators may peak at the smallest prey length/predator length ratios and decline continuously thereafter, which may simply represent a continuation of the vulnerability curves of larval fishes to fish predators similar to those presented by Paradis et al. (1996).

### Prey profitability and bluefish diet

Previous work directed at predicting predator diet using foraging theory suggests that even subtle differences in prey behavior and morphology can dramatically affect foraging relationships (Werner and Gilliam 1984; Sih and Moore 1990). For example, Wahl and Stein (1989) found that differences in taxon-specific movement patterns among esocids led to different levels of vulnerability to largemouth bass predation. We found prey-specific differences in profitability estimates and vulnerability to juvenile bluefish predation. Morphological differences resulted in striped bass providing greater benefits in terms of prey mass ingested relative to Atlantic silverside

**Fig. 4.** Prey profitability as a function of prey length/predator length ratio for (a) striped bass and (b) Atlantic silverside. Upper profitability curves calculated as (prey mass/predator mass  $\times$  handling time<sup>-1</sup>); lower profitability curves calculated as (prey mass/predator mass  $\times$  handling time<sup>-1</sup>  $\times$  % capture success). Solid line indicates the range of prey length/predator length ratios examined in this study.



of the same length. However, the increased mass per unit length of striped bass combined with prey behavioral differences in escape tactics also induced a much greater cost in terms of lower capture efficiency and increased handling time. The availability of prey with disparate levels of vulnerability to predation may have important effects on predator foraging success and prey survival.

Foraging theory has been developed extensively for planktivorous fishes and predicts that predators should include prey in the diet based on their ratio of net energy gain to handling time cost relative to other prey (Mittlebach 1981; Stephens and Krebs 1986). However, various authors have hypothesized that capture success is more important for piscivores than for planktivores and may be a critical determinant of piscivore diet (Breck 1993; Juanes 1994; Juanes and Conover 1994a). The inclusion of capture success functions in our calculation of profitability for each prey had significant effects on relative profitabilities. In addition to the expected lowering of profitabilities for each prey, the incorporation of capture success changed the relative values of profitability between prey species, with Atlantic silverside becoming even more profitable compared with striped bass. More importantly, profitability curves that included capture success extended over a narrower, and likely more realistic, range of prey length/predator length ratios and peaked at lower length ratios compared with curves without capture success.

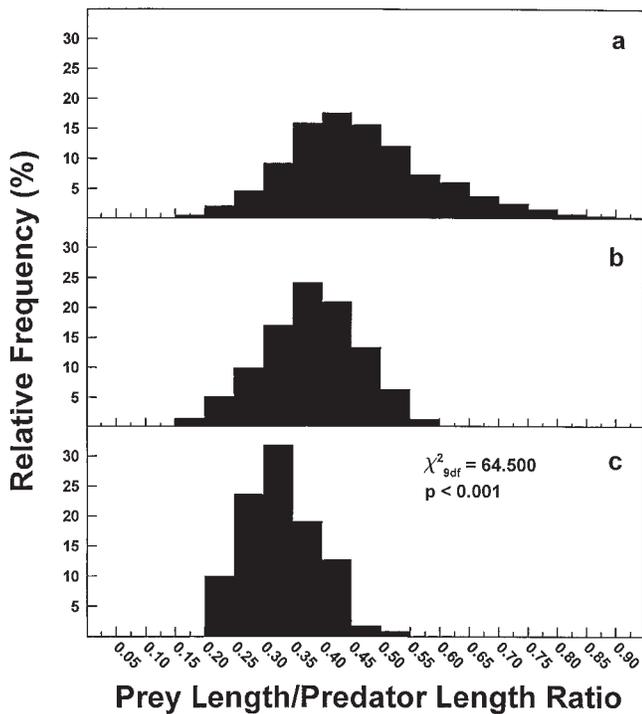
Relative frequency distributions of prey length/predator length ratios were generated from length ratios occurring in the field and laboratory-derived capture success functions. These predicted distributions showed good agreement when compared with distributions of prey length/predator length ratios actually consumed by juvenile bluefish in midsummer. Although a significant difference was detected between expected and observed length ratio distributions for bluefish feeding on juvenile striped bass, the peak of the expected

frequency distribution was only 5% higher on the prey length/predator length axis than the peak in the distribution of length ratios actually consumed. Our results indicate that estimates of the size composition of prey in bluefish diets may be obtainable from prey and predator length frequencies in the field and simple capture success functions. These findings support previous research on the importance of size-dependent capture success in determining the sizes of prey included in bluefish diets. For prey length/predator length ratios between about 0.15 and 0.60, Juanes and Conover (1994a) concluded that bluefish attack rates on Atlantic silverside are independent of prey size and suggest that observed size-selective feeding patterns of juvenile bluefish may result from differential size-based capture success rather than active predator choice. The influence of capture success on our estimates of prey profitability and the close match between predicted and observed distributions of length ratios in bluefish diets indicate that capture success is an important component of piscivore feeding and may be largely responsible for apparent predator selectivities. It is important to note that for diet predictions to be accurate, the size ranges of predator and prey used to estimate encounter and capture probabilities must closely approximate those occurring naturally in the environment. In our study, experiments were conducted using naturally occurring sizes of bluefish and prey during midsummer in U.S. east coast estuaries, and our comparisons with sizes of prey actually consumed in the field were done using only bluefish and prey captured during this time of the year.

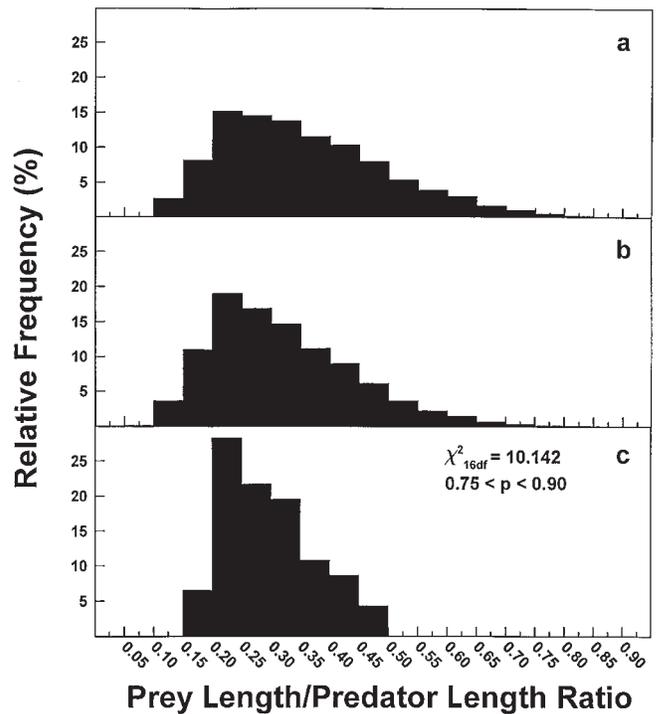
#### Foraging models and piscivores

Important advances have been made towards the understanding of size-structured species interactions and their role in population-level processes and community dynamics (Werner and Gilliam 1984; Ebenman and Persson 1988; Stein et al. 1988). With the advent of individual-based modelling

**Fig. 5.** Relative frequency distributions of prey length/predator length ratios for bluefish feeding on juvenile striped bass. Distribution *a* represents the relative probability of encounter for specific prey length/predator length ratios during 7 July to 4 August of 1993. Distribution *b* is generated through the multiplication of distribution *a* with the laboratory-derived capture success function for bluefish feeding on juvenile striped bass and represents the expected relative frequency distribution of prey length/predator length ratios occurring in bluefish diets during this time period based only on encounter and capture probabilities. Distribution *c* represents the relative frequency distribution of prey length/predator length ratios that were actually observed in the diets of bluefish feeding on striped bass during this time period. Chi-square statistics are presented for the comparison between distributions *b* and *c*.



**Fig. 6.** Relative frequency distributions of prey length/predator length ratios for bluefish feeding on Atlantic silverside. Distribution *a* represents the relative probability of encounter for specific prey length/predator length ratios during 5 July to 9 August of 1989. Distribution *b* is generated through the multiplication of distribution *a* with the laboratory-derived capture success function for bluefish feeding on Atlantic silverside and represents the expected relative frequency distribution of prey length/predator length ratios occurring in bluefish diets during this time period based only on encounter and capture probabilities. Distribution *c* represents the relative frequency distribution of prey length/predator length ratios that were actually observed in the diets of bluefish feeding on Atlantic silverside during this time period. Chi-square statistics are presented for the comparison between distributions *b* and *c*.



techniques, our ability to incorporate specific information on size-based interactions into foraging models has increased markedly (DeAngelis and Gross 1992; Van Winkle et al. 1993). However, the modelling of complex species interactions requires extensive size-specific data. Individual-based modelling approaches have often assumed threshold values of prey size/predator size ratios to determine capture of juvenile fishes given an encounter with a piscivore, with prey size/predator size ratios below threshold values resulting in 100% capture efficiency and those above always resulting in failed capture attempts (Adams and DeAngelis 1987; Madenjian et al. 1991). Our data suggest that using threshold values for capture success may not be realistic. This is particularly important, given that model outputs can be extremely sensitive to variation in this parameter (Adams and DeAngelis 1987). Cowan et al. (1996) proposed that differences in predator attributes such as swimming speed and search pattern may result in differential encounter rates with larval prey fishes, with considerable effects on larval survival rates. For juvenile prey fishes, differences in prey morphology and behavior may

strongly affect predator success rates and, hence, prey profitabilities and vulnerabilities over a range of relative fish sizes. Therefore, the outcomes of predator-prey interactions among juvenile fishes are likely to be species specific, with predation components best represented as continuous functions of relative prey and predator sizes such as those used by Rice et al. (1993). Our findings for bluefish suggest that the inclusion of specific sizes of prey fishes in the diets of piscivorous fish predators may be estimated with only knowledge of encounter and capture probabilities based on relative body size. The use of accurate field and laboratory information when estimating these parameters for foraging models should lead to more reliable predictions of size-based interactions.

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