

**FORAGING TACTICS OF YOUNG-OF-THE-YEAR BLUEFISH  
IN THE HUDSON RIVER:  
THE INFLUENCE OF BODY SIZE ON PREDATOR MODE  
CHOICE AND PREY PROFITABILITY**

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## ABSTRACT

In the last decade, convincing evidence has been presented linking size-dependent predation on fishes during early life stages to differential survival rates among individuals, suggesting predation plays a major role in determining ultimate year class strength. However, the majority of research directed at understanding the causes of variation in recruitment success has centered on eggs and larval fishes, whereas the juvenile stage of the life history has been relatively ignored. The bluefish (*Pomatomus saltatrix*) is an important predator on a variety of juvenile fishes on the east coast of the U.S. Here, we determine empirically the rate of capture success, handling time, and prey profitability as a function of prey length/predator length ratio for age-0 bluefish feeding on juvenile striped bass (*Morone saxatilis*) and Atlantic silversides (*Menidia menidia*). Laboratory feeding trials (n = 83) were conducted using groups of 3 bluefish and 10 prey fish. For each prey species, bluefish capture success declined linearly and handling time increased exponentially with increasing prey length/predator length ratio. However, relative to juvenile striped bass, Atlantic silversides were always easier to capture and induced lower handling times over the range of prey length/predator length ratios used in the experiment. These differences in predation components led to disparate prey profitability curves for each prey species. Further, prey specific differences in morphology and behavior likely led to differences in prey size/predator size ratios that led to shifts in foraging mode by bluefish from swallowing prey fish whole to consumption of fish in pieces. Our results suggest that for juvenile fishes, prey specific differences in morphology and behavior can have significant effects on relative prey vulnerability to predation and may present important implications for recruitment success in fishes.

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## INTRODUCTION

Recruitment success in fish populations can exhibit substantial variation on both temporal and spatial scales. Most research directed towards understanding the underlying mechanisms that regulate recruitment success has focused on the larval period of the life history (Miller et al. 1988, Houde 1989, Paradis et al. 1996). However, a growing body of evidence exists indicating that factors contributing to year class strength may also involve the juvenile stage (Ansell and Gibson 1993). Therefore, an improved knowledge of the causes of variation in recruitment success may be gained through more complete information on juvenile life history.

Predator-prey interactions involving fish at early stages in the life history have been strongly linked to recruitment success in fishes (Houde 1989, Bailey and Houde 1989, Pepin et al. 1992). Specifically, size dependent processes of predation play an important role in determining the abundance and size-structure of prey and predator populations. The outcome of size-structured interactions between prey and predator populations that are growing simultaneously are often complex (Werner and Gilliam 1984, Stein et al. 1988, Rice et al. 1993). Hence, specific components of size-structured predator-prey interactions are typically determined from laboratory experiments using individual predator-prey combinations or small groups. Information obtained from laboratory trials may then be incorporated into size dependent foraging models used to predict the outcome of population level interactions (Adams and DeAngelis 1987, Wilbur 1988, Rice et al. 1993). Therefore, laboratory derived components of individual predator-prey interactions may provide important knowledge towards a better understanding of population processes.

Knowledge of predator and prey characteristics leading to changes in predator feeding modes may also enhance our understanding of population-level interactions. Predators that are capable of shifting modes of search, capture, or ingestion in response to changes in prey abundance, distribution, or size-structure may have greater effects on prey resources relative to predators with restricted feeding capabilities, thus potentially affecting recruitment success of both predator and prey. Specifically, fish predators with the ability to alter their modes of handling or ingesting prey, in order to reduce prey size, may reduce limitations imposed by gape or mouth width and exploit prey of larger size (Helfman and Winkelman 1991, Scharf et al. in press). Hence, the incorporation into foraging models of complete information on both causes and effects of predator foraging mode shifts may yield more precise estimates of interactions between size-structured predator and prey populations (Helfman 1990).

The bluefish (*Pomatomus saltatrix*) is an important piscivore on the east coast of the US. Larvae are spawned in the South Atlantic Bight in early spring and are advected northward in Gulf Stream waters (Kendall and Walford 1979). Within approximately two months, juveniles between 40-60 millimeters fork length migrate into estuaries of the Middle Atlantic Bight where they remain throughout summer and early fall (Nyman and Conover 1988, McBride and Conover 1991). Entry into estuaries is accompanied by a shift in bluefish diet from zooplankton to fish (Marks and Conover 1993). The estuarine waters of the lower Hudson River (New York) represent one such estuary inhabited by juvenile bluefish during summer months, as well as containing a diverse fish assemblage including several species of recreational and commercial importance (Beebe and Savidge 1988). Recent work has indicated that juvenile bluefish consume a variety of fish species

during summer residence in the Hudson River (Juanes et al. 1993, Juanes et al. 1994). Previous laboratory analyses of the feeding behavior of juvenile bluefish have found that they often sever prey fishes with frequent losses of prey fish pieces to other bluefish within the group (i.e., pirating) (Juanes and Conover 1994). Analyses of stomach contents data indicate a similar frequency of the occurrence of severed fish prey and suggest that prey length relative to predator length is an important factor leading to shifts in handling mode (Scharf et al. in press).

Here, we determine empirically prey length/predator length ratio specific rates of capture success, handling times, and prey profitabilities for young-of-the-year bluefish feeding on two prey species with contrasting morphologies and behaviors, namely juvenile striped bass (*Morone saxatilis*) and the Atlantic silverside (*Menidia menidia*). To determine the effect of prey morphology on predator mode choice, we examine bluefish foraging mode shifts from swallowing prey fish whole to consumption of pieces of fish in terms of prey size/predator size ratios when feeding on each prey species.

## METHODS

Juvenile bluefish, striped bass, and Atlantic silversides were collected in the Haverstraw Bay region of the Hudson River during June through August of 1996 using beach seines. Additional bluefish and Atlantic silversides were collected from Great South Bay in Patchogue, NY, and Flax Pond in Old Field, NY, which are marine embayments on the south and north shores of Long Island, respectively. Additional striped bass were collected in the Hudson River by the New York State Department of Environmental Conservation during a juvenile striped bass survey.

Fish were immediately transported to the Flax Pond Marine Laboratory in Old

Field, NY, and allowed to acclimate for at least one week prior to use in experiments. All fish were maintained in tanks with a continuous flow of sea water at ambient temperatures and salinities and natural photoperiod throughout the experiments. Because bluefish feeding trials were conducted during a five week period of mid summer (10 July to 14 August 1996), water temperatures, salinities, and photoperiod remained relatively constant throughout the experiments.

A total of 53 bluefish ranging from 80-155 millimeters (mm) total length were used in the feeding trials. Bluefish were separated by size and held in three 800 liter (l) holding tanks while being fed a combination of live and frozen fish prey throughout the experimental period. Bluefish were sampled randomly from the holding tanks and were mildly anesthetized with MS-222 (tricaine methanesulfonate) and sorted into groups of three similarly sized individuals to ensure that length differences between any two members of the group did not exceed five mm. The three bluefish were then placed in 200 l tanks and starved for a 24-hour period to standardize hunger levels across feeding trials. Bluefish were then placed in one of four 215 l experimental chambers, which were derived from equal partitioning of two 430 l tanks each equipped with a transparent plexiglass viewing window, and allowed to acclimate for at least eight hours prior to the initiation of a feeding trial.

Feeding trials were conducted during early morning and late afternoon throughout the experimental period. Each feeding trial consisted of a group of three bluefish to allow for schooling while still allowing individuals to be distinguished (Juanes and Conover 1994). Bluefish were presented with a group of ten striped bass or ten Atlantic silversides with length differences not exceeding 2.5 mm between any two prey fishes in a group.

Juvenile striped bass used ranged in size from 25-80mm total length, whereas Atlantic silversides ranged from 20-85mm total length. Throughout the five week experimental period, various combinations of prey and predator length groups were used to generate a database with a continuous range of prey length/predator length ratios ranging from 0.20 to 0.65 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 and allowed to acclimate to chamber conditions for at least five minutes before the cylinder was removed and the bluefish had access to the prey. Each experimental chamber was illuminated during feeding trials using a 150-watt halogen light positioned approximately 1 meter (m) above the chamber and continuous sea water flow was maintained. Each feeding trial was video recorded using a standard Hi-8 camera mounted on a tripod at a distance from the viewing window of approximately 1 m and lasted 15 minutes, at which time 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 to avoid the effects of potential learned behavior by the bluefish resulting from continuous holding in the experimental chambers for extended time periods. Our experimental procedure for random sampling of bluefish from the holding tanks, placement into tanks for a 24-hour starvation period, and subsequent placement into feeding 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 hours for any given bluefish.

Capture success was determined from the proportion of bluefish capture attempts

that resulted in prey consumption and expressed as a percent. 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. Capture success was calculated for bluefish feeding on each prey species for each 0.05 interval of prey length/predator length ratio by pooling the numbers of successful and total capture attempts across individual feeding trials within each ratio interval. The potential effect of changes in bluefish hunger level during feeding trials was examined by calculating capture success for the first capture attempt and separately for all subsequent capture attempts within each feeding trial and pooling trial data for each 0.05 interval of prey length/predator length ratio. Least squares regression analysis was used to determine the relationship between capture success and prey length/predator length ratio for each prey species. Analysis of covariance (ANCOVA) was employed to compare regressions between prey species and within each prey species between first capture attempts and all subsequent attempts (Sokal and Rohlf, 1995).

Handling time, defined as total ingestion time from initial bluefish contact with a given prey fish until swallowing activity ceased, was estimated to the 30<sup>th</sup> of a second (s) for each successful capture. Mean handling times were calculated for each 0.05 interval of prey length/predator length ratio by pooling trial data within each interval. For each prey species, mean handling times were determined for prey fishes swallowed whole, for the first pieces severed and ingested by each original attacking bluefish, and for the complete consumption of a given prey fish, regardless of the number of prey pieces or the number of participating bluefish. Nonlinear least squares regression models were fit to

mean handling times for prey fishes swallowed whole and prey fishes consumed in pieces when the entire prey fish was eaten using the exponential relationship,  $y = ae^{bx}$  (StataCorp, 1995). Normal least squares regression analysis was used to determine the relationship between mean handling time for the first piece of a severed prey fish and prey length/predator length ratio for each prey species. Nonlinear regression coefficients of handling time curves were compared between prey species using a t-test with unequal sample sizes (Sokal and Rohlf, 1995).

Profitability estimates for each prey species were calculated as the ratio of prey weight ingested to bluefish weight per unit handling time (s) multiplied by percent capture success for each 0.05 interval of prey length/predator length ratio. Estimates were generated using instances when only the entire prey fish was consumed, whether it was swallowed whole or ingested in pieces. Least squares regressions were fit to profitability estimates for each prey species.

Bluefish foraging mode shifts were examined by plotting the relative percent frequency of each prey species swallowed whole and consumed in pieces for each 0.05 interval of prey length/predator length ratio. Midpoints of relative percent frequencies were calculated for each 0.05 ratio interval. The ratio interval within which relative percent frequency became skewed toward partial rather than whole prey consumption as well as the immediately preceding ratio interval were identified. The boundaries of these two ratio intervals were then considered to best approximate the range of prey length/predator length ratios leading to a shift in bluefish foraging mode from primarily swallowing prey fishes whole to partial consumption. To examine further the effects of differences in prey morphology, bluefish foraging mode shifts were analyzed in terms of

prey weight/predator weight ratios and prey body depth/predator mouth width ratios using weight-length and depth/mouth width-length conversions (Table 1). To maintain relatively uniform numbers of observations within each ratio interval, data presented in terms of prey weight/predator weight ratios were grouped in 0.02 intervals up to a relative weight ratio of 0.10, and 0.05 intervals thereafter. Data presented in terms of prey body depth/predator mouth width ratios were grouped in 0.10 intervals.

### RESULTS

A total of 83 bluefish feeding trials were conducted which generated 485 observed attacks resulting in 261 successful prey captures. Bluefish attacks were always directed posteriorly resulting in tail-first ingestion of prey fishes. Of successful prey captures, 51 involved severing of prey and consumption of pieces of fish. Posterior pieces of prey fishes (i.e., those including the tail) were swallowed tail-first, whereas anterior pieces of prey fishes (i.e., those including the head) were manipulated in order to allow head-first swallowing. More than half of the successful prey captures that necessitated prey severing by bluefish involved pirating of prey fish pieces by other bluefish within a group. Moreover, only 22% of captures involving prey severing resulted in the original attacking bluefish consuming the entire prey fish.

Bluefish capture success declined linearly with increasing prey length/predator length ratio when feeding on each prey species (striped bass:  $y = 1.21 - 2.11x$ ,  $p < 0.0001$ ,  $r^2 = 0.98$ ; Atlantic silverside:  $y = 1.30 - 1.62x$ ,  $p < 0.0001$ ,  $r^2 = 0.92$ ) (Fig. 1). Regression slopes were not statistically different ( $F = 2.292$ ,  $0.10 < p < 0.25$ ), however, elevation of Atlantic silverside capture success was significantly higher than that of striped bass

Table 1. - Linear regression equations estimating weight (W) and body depth (BD) or mouth width (MW) from total length (TL) for Atlantic silverside, juvenile striped bass, and juvenile bluefish. Length measurements are in millimeters; weight is measured in grams. All regressions are highly significant ( $p < 0.0001$ ).  $S_b$  = standard error of regression coefficient;  $r^2$  = coefficient of determination;  $n$  = number of fish measured.

Species	Equation	$S_b$	$r^2$	$n$
Atlantic silverside	$W = 5.08 \times 10^{-6} TL^{3.055}$	0.000	0.98	53
	$BD = 0.694 + 0.138 TL$	0.000	0.00	38
Striped bass	$W = 3.53 \times 10^{-6} TL^{3.273}$	0.000	0.99	84
	$BD = -0.788 + 0.232 TL$	0.000	0.00	71
Bluefish	$W = 1.48 \times 10^{-6} TL^{3.347}$	0.000	0.99	54
	$MW = 0.840 + 0.129 TL$	0.000	0.00	.00

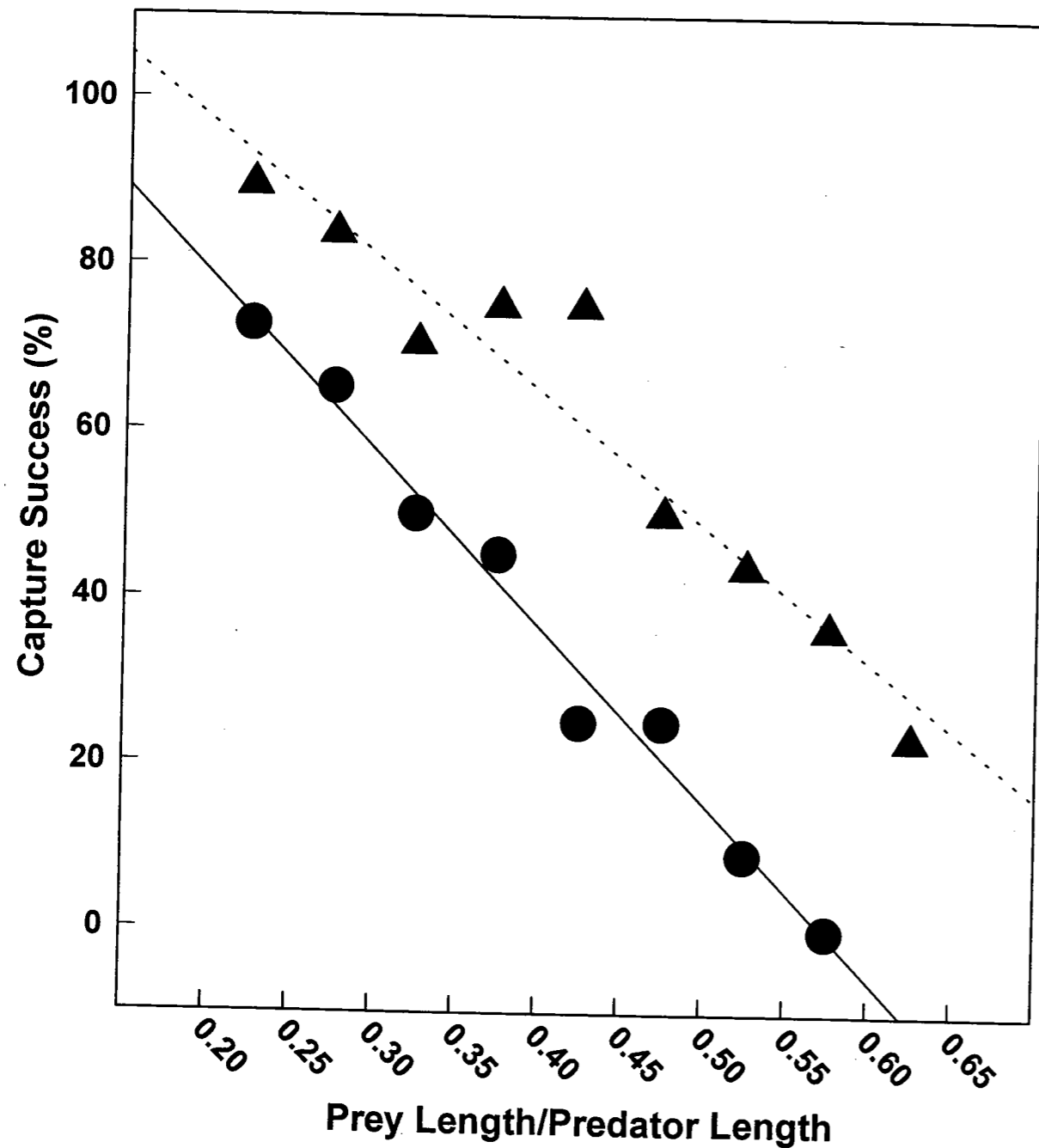


Figure 1. - Percentage of successful captures as a function of prey length/predator length ratio for juvenile bluefish feeding on striped bass (●) and Atlantic silversides (▲).

( $F = 86.662$ ,  $p < 0.001$ ). Capture success of first attacks within each feeding trial also declined linearly with increasing prey length/predator length ratio for each prey species (striped bass:  $y = 1.09 - 1.83x$ ,  $p < 0.005$ ,  $r^2 = 0.77$ ; Atlantic silverside:  $y = 1.44 - 1.74x$ ,  $p < 0.0005$ ,  $r^2 = 0.83$ ) (Fig. 2). Similarly, capture success for all attacks other than first attacks within each feeding trial exhibited a linear decline (striped bass:  $y = 1.23 - 2.17x$ ,  $p < 0.0001$ ,  $r^2 = 0.98$ ; Atlantic silverside:  $y = 1.28 - 1.62x$ ,  $p < 0.0001$ ,  $r^2 = 0.92$ ). For striped bass, regressions explaining capture success of first attacks and all other attacks were not significantly different (slopes:  $F = 0.310$ ,  $p > 0.50$ ; elevations:  $F = 0.054$ ,  $p > 0.75$ ) (Fig. 2a). For Atlantic silversides, regression slopes were not statistically different ( $F = 0.064$ ,  $p > 0.75$ ), however, elevation of capture success for first attacks was significantly higher than elevation of capture success for all other attacks ( $F = 5.988$ ,  $0.025 < p < 0.05$ ) (Fig. 2b).

Bluefish mean handling times calculated for prey fish swallowed whole increased exponentially with increasing prey length/predator length ratio for each prey species (striped bass:  $y = 0.679e^{9.087x}$ ,  $p < 0.0005$ ,  $r^2 = 0.99$ ; Atlantic silverside:  $y = 2.318e^{3.248x}$ ,  $p < 0.0005$ ,  $r^2 = 0.99$ ) (Fig. 3a). Slope comparisons indicated a significantly higher rate of increase in bluefish handling time when feeding on striped bass ( $t = 12.564$ ,  $p < 0.001$ ). Mean handling times calculated for the first pieces severed and ingested by each original attacking bluefish did not change significantly with increasing prey length/predator length ratio for each prey species (striped bass:  $p = 0.059$ ; Atlantic silverside:  $p = 0.576$ ) (Fig. 3b). Similar to bluefish handling times for prey fish swallowed whole, mean handling times calculated for the complete consumption of a given prey fish, regardless of the number of prey pieces or the number of participating bluefish, increased exponentially

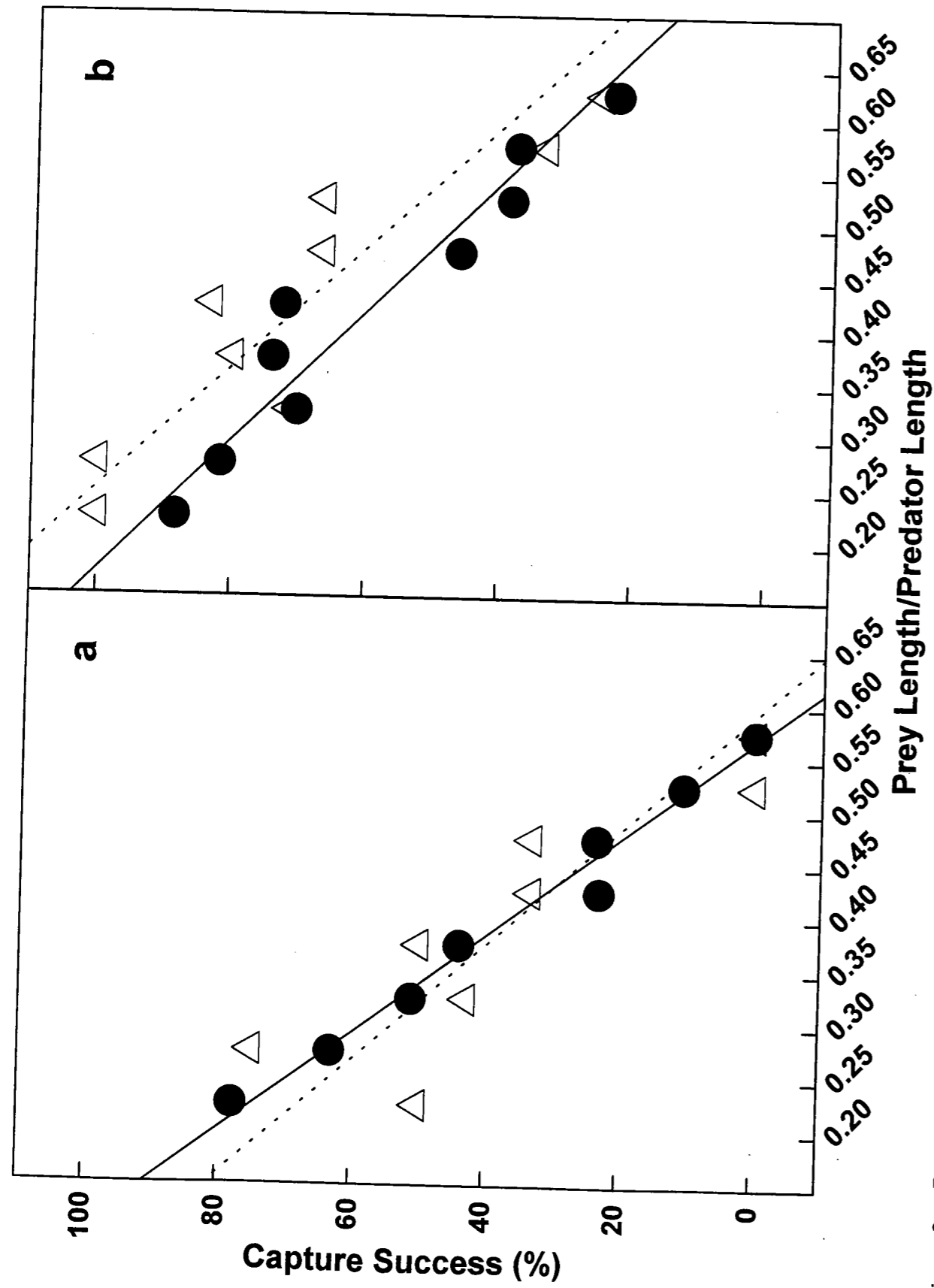


Figure 2. - Percentage of successful captures by juvenile bluefish feeding on striped bass (a) and Atlantic silversides (b) as a function of prey length/predator length ratio for first strike attempts within each feeding trial ( $\Delta$ ) and for all other strike attempts ( $\bullet$ ) excluding first strike attempts.

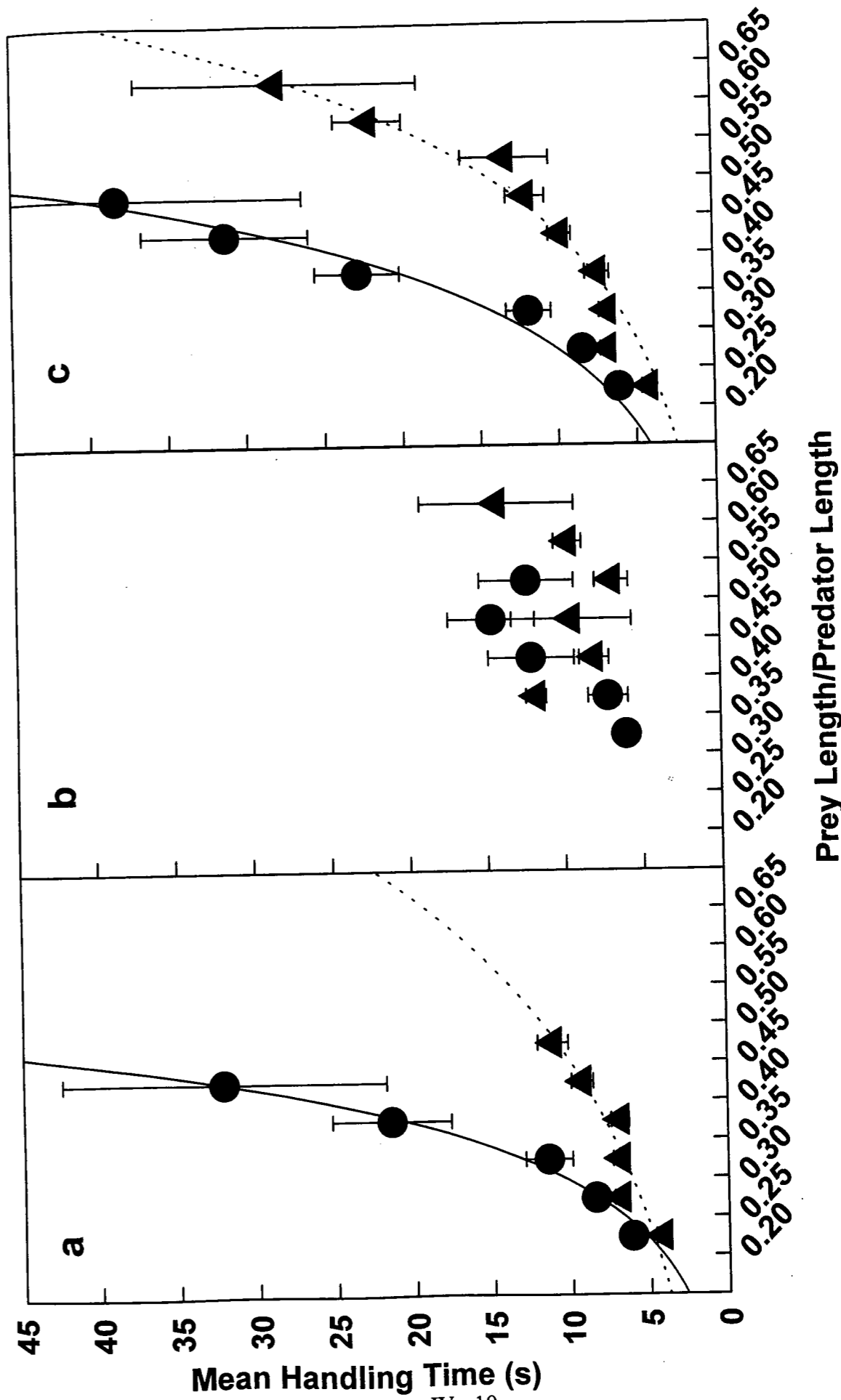


Figure 3. - Mean handling time in seconds as a function of prey length/predator length ratio for bluefish feeding on striped bass ( $\bullet$ ) and Atlantic silversides ( $\Delta$ ). Data points represent means  $\pm$  1 SE. (a) Handling time for prey swallowed whole. (b) Handling time only for first piece (always posterior end of prey) ingested by original attacking bluefish. (c) Handling time for entire prey fish to be consumed regardless of the number of pieces or the number of participating bluefish.

with increasing prey length/predator length ratio for each prey species (striped bass:  $y = 1.464e^{6.978x}$ ,  $p < 0.0005$ ,  $r^2 = 0.99$ ; Atlantic silverside:  $y = 1.160e^{5.038x}$ ,  $p < 0.0001$ ,  $r^2 = 0.99$ ) (Fig. 3c). Bluefish handling time when feeding on striped bass increased at a significantly higher rate than when feeding on Atlantic silverside ( $t = 4.864$ ,  $p < 0.001$ ).

Profitability estimates for striped bass declined linearly with increasing prey length/predator length ratio ( $y = 0.319 - 0.513x$ ,  $p < 0.0005$ ,  $r^2 = 0.91$ ) (Fig. 4a). In contrast, Atlantic silverside profitability estimates were dome shaped ( $y = -0.802 + 5.599x - 6.465x^2$ ,  $p < 0.005$ ,  $r^2 = 0.84$ ) (Fig. 4b). Only slight differences in profitability estimates were observed between prey species at low values of prey length/predator length ratio ( $< 0.35$ ), however, at intermediate and high values, Atlantic silverside estimates of profitability were always greater than estimates for striped bass.

Bluefish shifted from swallowing prey fish whole to consumption of pieces of fish at prey length/predator length ratios between 0.35 and 0.45 when feeding on striped bass, whereas bluefish foraging mode shifts occurred at length ratios between 0.45 and 0.55 when feeding on Atlantic silverside (Fig. 5a). When bluefish foraging mode was examined in terms of prey weight/predator weight ratios, shifts were observed at weight ratios between 0.06 and 0.10 when feeding on striped bass and between 0.08 and 0.10 when feeding on Atlantic silverside (Fig. 5b). When plotted in terms of prey body depth/predator mouth width ratios, results between prey species were opposite to those produced using prey length/predator length ratios. Bluefish shifted from whole to partial prey at depth/mouth width ratios between 0.50 and 0.70 when feeding on striped bass and between 0.40 and 0.60 when feeding on Atlantic silverside (Fig. 5c).

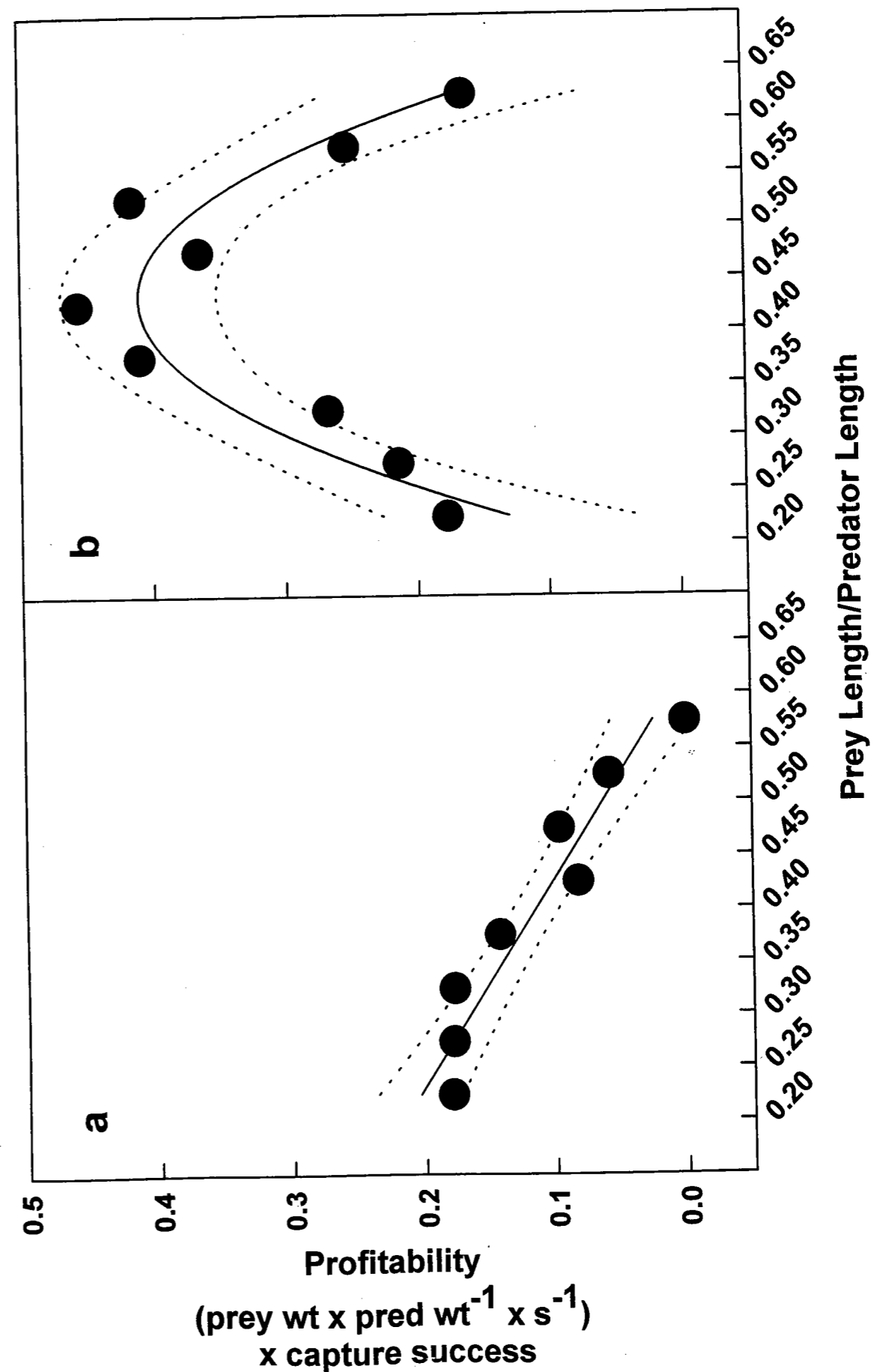


Figure 4. - Prey profitability multiplied by capture success as a function of prey length/predator length ratio for striped bass (a) and Atlantic silversides (b). Profitability calculated using only entirely consumed prey regardless of whether prey fish was swallowed whole or consumed in pieces.

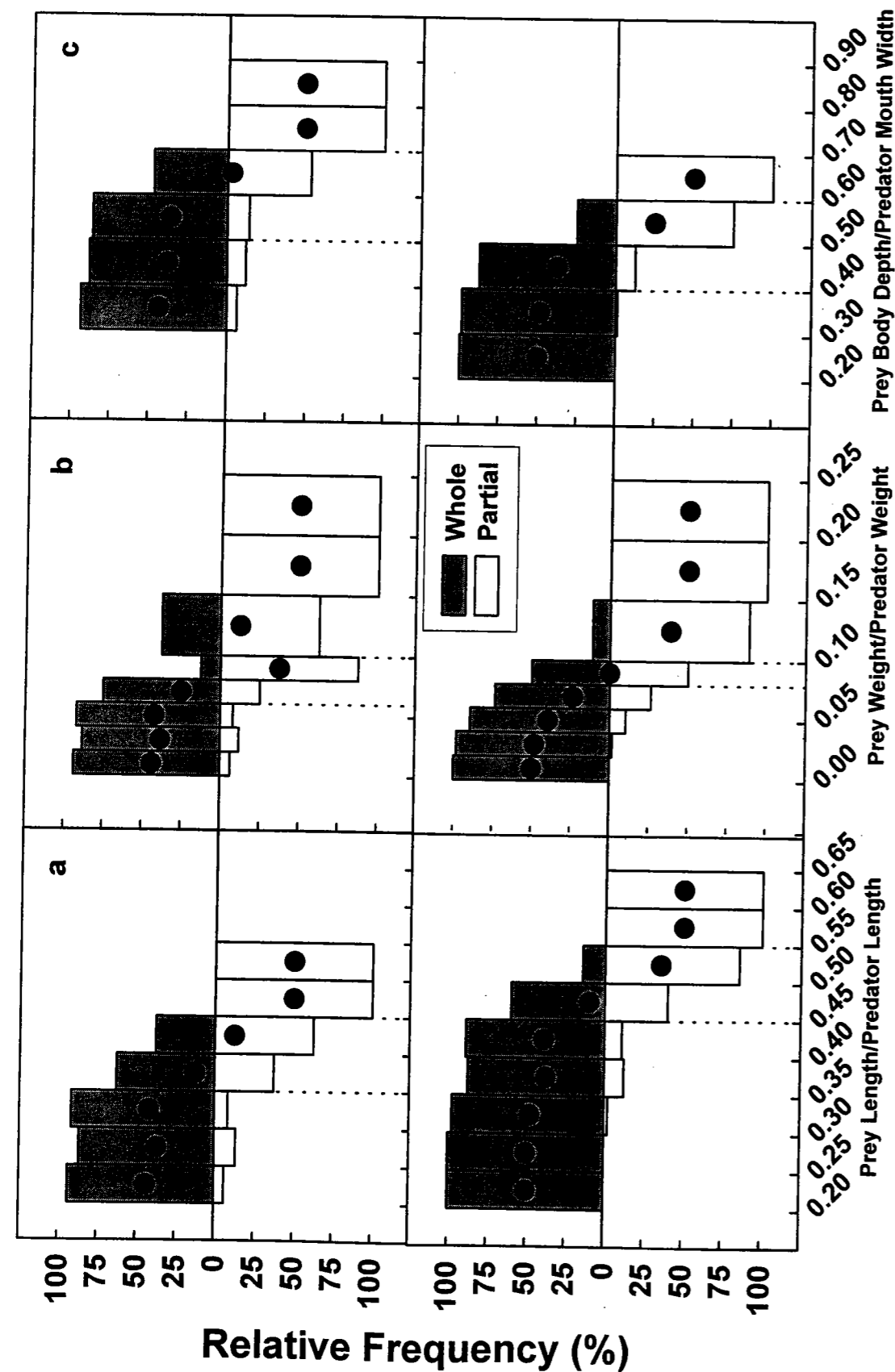


Figure 5. - Relative proportions of prey fish swallowed whole and consumed in pieces as a function of prey length/predator length ratio (a), prey weight/predator weight ratio (b), and prey body depth/predator mouth width ratio (c). Data for bluefish feeding on striped bass are displayed in the upper panels and data for bluefish feeding on Atlantic silversides are displayed in the lower panels of each prey size/predator size ratio combination. Midpoints (●) are plotted for each 0.05 increment of relative length ratio, each 0.02 or 0.05 increment of relative weight ratio, and each 0.10 increment of depth/mouth width ratio. Vertical dashed lines represent the boundaries of the two ratio intervals within which the midpoint becomes skewed toward partial prey and indicate the approximate range of prey size/predator size ratios leading to a shift from whole to partial prey consumption.

## DISCUSSION

The results of our bluefish predation experiments using juvenile striped bass and Atlantic silversides as prey revealed declining capture probabilities coupled with increasing handling times as prey fish size increased relative to bluefish size, which are patterns typical of most studies of predation on fishes (Werner 1974, Miller et al. 1988, Juanes 1994). Although observed patterns of bluefish capture efficiency and handling time for each prey species demonstrated similar functional relationships, Atlantic silversides were always easier to catch and induced lower handling time costs relative to striped bass. These prey specific differences in predation components resulted in disparate profitability curve shapes for each prey species. Moreover, dissimilarities in prey morphology likely caused differences in prey size/predator size ratios leading to bluefish shifts in foraging mode from swallowing prey fish whole to consumption of prey fish in pieces.

Consistent with our findings, several other studies have shown piscivore capture success to be negatively related to prey size (Miller et al. 1988, Litvak and Leggett 1992, Juanes and Conover 1994a). Juanes (1994) proposed that the apparent selection by piscivores of small prey fishes when presented with a range of prey sizes may represent a passive process that is strongly influenced by size-dependent differences in capture efficiency, rather than active predator choice. The consistent inclusion of small prey fishes in piscivore diets may thus be a function of their increased susceptibility to capture relative to large prey (Juanes 1994). For larval prey fishes, Miller et al. (1988) revealed consistent patterns between predator capture success and larval prey size across several taxa. Our results concur with those of Juanes and Conover (1994a) for capture success

relationships of young-of-the-year bluefish feeding on juvenile fishes, however, to determine if patterns can be generalized across prey and predator taxa, susceptibility to capture needs to be determined empirically for juvenile fishes with representatives from several prey and predator taxa.

We observed no change in bluefish capture efficiency between first attacks and all other attacks within a feeding trial when feeding on striped bass and only slight differences when feeding on Atlantic silversides (Fig. 2). Increased levels of predator satiation are generally thought to negatively affect attack rates; however, evidence for similar effects on predator capture success has not been noted. Heatherly (1993) observed constant capture probabilities for initial attacks within each feeding trial of bluefish feeding on spot (*Leiostomus xanthurus*) for a range of prey length/predator length ratios, whereas bluefish capture success declined as prey length/predator length ratio increased when examining all attacks. In our experiment, Atlantic silversides were slightly easier to catch during initial capture attempts by bluefish, but capture success for these first attempts still declined as a function of increasing prey length/predator length ratio. Based on observation of video recorded feeding trials, Atlantic silversides appeared to respond more slowly to predator presence relative to striped bass and did not usually demonstrate evasive behavior when initially exposed to bluefish predators, although visual detection of bluefish was ensured prior to exposure through the use of a transparent cylinder. Therefore, we speculate that slightly higher initial success rates by bluefish were a function of prey behavior rather than predator satiation levels.

Bluefish handling time increased exponentially with increasing prey length/predator length ratio when feeding on each prey species (Fig. 3a and 3c). These

results are consistent with previous studies in demonstrating the link between relative prey body size and the time needed to manipulate and ingest it (Werner 1974, Mittelbach 1981, 1984, Stein et al. 1984, Juanes and Conover 1994a, Hirvonen and Ranta 1996). We did, however, observe significant differences in the slopes of the handling time curves between prey species, with striped bass handling time accelerating at a faster rate relative to Atlantic silversides. Largemouth bass (*Micropterus salmoides*) handling time was found to vary for six 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, which concurs with our findings. The handling time necessary to ingest the first piece of a severed prey fish was not, however, related to prey length/predator length ratio for either prey species. Similar handling times for pieces of prey fish of different species across a range of prey length/predator length ratios suggests that the size of the first piece severed was fairly constant for all instances of partial prey consumption.

Recent work directed at predicting predator diet using optimal 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 different levels of vulnerability to predation for three ecocids stocked in reservoirs. The availability of prey with disparate levels of vulnerability to predation may have important effects on predator foraging success and prey survival. We found differences between striped bass and Atlantic silversides in estimates of prey profitability (Fig. 4). Although striped bass provided greater benefits in terms of prey mass ingested relative to Atlantic silversides of the same length, they also

induced a much greater cost in terms of lower capture efficiency and faster rates of increase in handling time. The importance of capture success in determining piscivore diet has been noted by recent authors (Breck 1993, Juanes 1994, Juanes and Conover 1994a). However, predator handling time has been proposed to be of comparatively less importance to piscivores, relative to planktivorous fishes because absolute numbers of prey consumed per unit time are normally less for piscivores (Eggers 1977, Breck 1993, Wanzenböck 1995). This generalization may not apply to schooling piscivores such as bluefish, which typically attack schools of prey fishes, often consuming large numbers of prey in short time periods (Major 1978). Our results indicate that prey specific differences in predator handling time, when coupled with differences in capture success, may have a substantial influence on prey profitabilities and hence, predator diet.

Prey profitability estimates generated for Atlantic silversides in this study were dome shaped with intermediate prey length/predator length ratios being most profitable to bluefish (Fig. 4b). This result contrasts with that of Juanes and Conover (1994a) who observed increases in prey profitability for Atlantic silversides with increasing prey size regardless of bluefish size. In their experiment, bluefish and Atlantic silversides were separated into three groups of broad size range prior to feeding trials (i.e., small, medium, and large) (Juanes and Conover 1994a). Therefore, their results were obtained for discrete pairings of predator and prey size groups, rather than for a continuous range of prey length/predator length ratio, as obtained here. Because of the nature of the experimental design, Atlantic silverside profitability estimates obtained by Juanes and Conover (1994a) may not represent the upper end of the prey length/predator length information presented here, thus accounting for the observed differences.

In a review of foraging behavior for animal taxa, Helfman (1990) emphasized the need for information on foraging mode selection and switching and the incorporation of generalities regarding the use of different feeding modes into theoretical foraging models. Evidence has been presented indicating that feeding mode shifts generally may be dependent on the relative profitability of each feeding mode in terms of net energy intake (Crowder 1985, Helfman and Winkelman 1991), with shifts in modes used to handle and manipulate prey being linked to the relative sizes of prey and predator (Helfman and Clark 1986, Miller 1989, Scharf et al. in press). However, specific attributes of prey size that lead to shifts in handling mode are still in question. Bluefish shifted from whole to partial prey consumption at larger ratios of prey length/predator length when feeding on Atlantic silversides than when feeding on striped bass (Fig. 6a), whereas shifts occurred at relatively larger ratios of prey body depth/predator mouth width when feeding on striped bass (Fig. 6c). Shifts occurred at approximately equal ratios of prey weight/predator weight for each prey species (Fig. 6b). For a given length, striped bass are deeper bodied relative to Atlantic silversides, whereas for a given body depth, Atlantic silversides are much longer than striped bass. Therefore, for a given size bluefish, shifts in handling mode may not be determined solely from prey length as suggested by Scharf et al. (in press), but more so by an interplay between prey length and prey body depth.

These results may, however, be obscured by the considerable spinous fin rays of striped bass as the presence of spines has been shown to affect predator foraging success (Hoogland et al. 1957, Moody et al. 1983). Moreover, the location of bluefish severing often coincided with the position of the largest dorsal spine of striped bass. Our

perception that the spines of striped bass may have clouded the relationship between handling mode shifts and the relative length of prey and predator is further supported by the consistent handling times for the initial piece ingested from a severed striped bass, regardless of prey length/predator length ratio, suggesting severed pieces are of equal length (Fig. 3b). The use of prey with different body depth-length relationships both with and without the presence of spines may more clearly identify the morphological traits of prey leading to shifts in predator handling mode.

Attempts have been made to identify the determinants of various shifts in foraging modes of animals (Helfman 1990). However, the effects of shifts in predator foraging mode on the dynamics of both prey and predator populations has received little attention. Scharf et al. (in press) suggest that the ability of bluefish to sever large prey fishes may provide a means to effectively reduce gape width limitations and allow them to increase their maximum prey size. The ability of bluefish to consume larger prey fishes through shifts in handling mode may subsequently increase the diversity of prey fishes susceptible to bluefish predation with potential implications for community structure. Because of the widespread existence of foraging mode shifts in fishes (Dill 1983, Helfman 1994), the implications they present are most likely important in terms of foraging models and population-level interactions and should be the focus of more directed research efforts.

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 techniques, our ability to incorporate explicitly specific information on size-based interactions into foraging models has increased

significantly (DeAngelis and Gross 1992, Van Winkle et al. 1993, Cowan et al. 1996). However, the modelling of complex species interactions requires extensive size-specific data. Individual-based approaches presented in Adams and DeAngelis (1987) and Madenjian et al. (1991) each used threshold ratios of prey size/predator size to determine capture of juvenile fishes given an encounter with a piscivore, with models often being extremely sensitive to variation in this parameter (Adams and DeAngelis 1987). Our results indicate that juvenile prey fish capture and prey profitability are best represented as continuous functions of prey length/predator length ratio and incorporation into models of this type of information may lead to more accurate predictions of size-based interactions.

Recently, the generally accepted paradigm for fish larvae that large individuals are usually less susceptible to predation and have a higher chance of survival has come into question because certain instances have shown larger larvae to have higher vulnerabilities to predation relative to smaller individuals (Litvak and Leggett 1992, Pepin et al. 1992, Bertram 1996, Cowan et al. 1996). Cowan et al. (1996) propose that differences in predator attributes may influence larval survival more so than relative prey size. For juvenile prey fishes, our results indicate that differences in prey morphology and behavior can strongly affect predator success rates and hence, prey vulnerability over a range of relative fish sizes. Although we have not included the effects of prey type and size on predator encounter probability in our estimates of prey profitability, the relationships are strikingly different between prey species. However, predicting the outcome of size-structured interactions between bluefish and prey populations would require estimation of prey species and size specific encounter rate parameters for a given system through

further experiments (i.e., Rice et al. 1993) or the use of previous field-based results as model outcomes (Adams and DeAngelis 1987).

The unique life history strategy of bluefish allows them to accelerate the onset of piscivory by timing their estuarine entry with the appearance of appropriate sized prey fishes, thus resulting in extremely high growth rates during the juvenile stage (Juanes et al. 1994, Juanes and Conover 1995). This study indicates that prey specific differences in morphology and behavior may have important implications for the size structure and survival of both bluefish and their prey.

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#### References

- Adams, S.M., and D.L. DeAngelis. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. Pages 103-117 in W.C. Kerfoot and A. Sih, editors. Predation: direct and indirect effects on aquatic communities. University Press of New England, Hanover, New Hampshire.
- Ansell, A.D. and R.N. Gibson. 1993. The effect of sand and light on predation of juvenile plaice (*Pleuronectes platessa*) by fishes and crustaceans. *Journal of Fish Biology* 43:837-845.
- Bailey, K.M. and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 25:1-83.
- Beebe, C.A., and I.R. Savidge. 1988. Historical perspective on fish species composition and distribution in the Hudson River estuary. *American Fisheries Society Monograph* 4:25-36.
- Bertram, D.F. 1996. Size-dependent predation risk in larval fishes: mechanistic inferences and levels of analysis. *Fishery Bulletin* 94:371-373.
- Breck, J.E. 1993. Foraging theory and piscivorous fish, are forage fish just big zooplankton? *Transactions of the American Fisheries Society* 122:902-911.
- Cowan, J.H., E.D. Houde, and K.A. Rose. 1996. Size-dependent vulnerability of marine fish larvae to predation: and individual-based numerical experiment. *ICES Journal of marine Science* 53:23-37.
- Crowder, L.B. 1985. Optimal foraging and feeding mode shifts in fishes. *Environmental Biology of Fishes* 12:57-62.
- DeAngelis, D.L. and L.J. Gross. 1992. Individual-based models and approaches in

- ecology: populations, communities and ecosystems. Routledge, Chapman and Hall, New York.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Science* 40:398-408.
- Ebenman, B., and L. Persson. 1988. Size-structured populations: ecology and evolution. Springer-Verlag, Berlin.
- Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. *Ecology* 58:46-59.
- Heatherly, L.M. 1993. Size-dependent predation by young bluefish on juvenile estuarine fishes. M.Sc. Thesis. Department of Zoology. North Carolina State University.
- Helfman, G.S. 1990. Mode selection and mode switching in foraging animals. *Advances in the Study of Behavior* 19:249-298.
- Helfman, G.S. 1994. Adaptive variability and mode choice in foraging fishes. Pages 3-17 in D.J. Stouder, K.L. Fresh, and R.J. Feller, editors. *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia, South Carolina.
- Helfman, G.S., and J.B. Clark. 1986. Rotational feeding: overcoming gape-limited foraging in anguillid eels. *Copeia* 1986:679-685.
- Helfman, G.S., and D.L. Winkelman. 1991. Energy trade-offs and foraging mode choice in American eels. *Ecology* 72:310-318.
- Hirvonen, H. and E. Ranta. 1996. Prey to predator size ratio influences foraging efficiency of larval *Aeshna juncea* dragonflies. *Oecologia* 106:407-415.
- Hoogland, R., D. Morris, and N. Tinbergen. 1957. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and

- Esox*). *Behaviour* 10:205-236.
- Houde, E.D. 1989. Comparative growth, mortality and energetics of marine fish larvae: temperature, and implied latitudinal effect. *Fishery Bulletin* 87:471-496.
- Hoyle, J.A., and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 65:1972-1977.
- Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79-100 in D.J. Stouder, K.L. Fresh, and R.J. Feller, editors. *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia, South Carolina.
- Juanes, F., and D.O. Conover. 1994a. Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? *Marine Ecology Progress Series* 114:59-69.
- Juanes, F., and D.O. Conover. 1994b. Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). *Canadian Journal of Fisheries and Aquatic Sciences* 51:1752-1761.
- Juanes, F., and D.O. Conover. 1995. Size-structured piscivory: advection and the linkage between predator and prey recruitment in young-of-the-year bluefish. *Marine Ecology Progress Series* 128:287-304.
- Juanes, F., R.E. Marks, K.A. McKown, and D.O. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River estuary. *Transactions of the American Fisheries Society* 122:348-356.
- Juanes, F., J.A. Buckel, and D.O. Conover. 1994. Accelerating the onset of piscivory: intersection of predator and prey phenologies. *Journal of Fish Biology* 45(suppl.

- A):41-54.
- Kendall, A.W., Jr., and L.A. Walford. 1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fishery Bulletin 77:213-227.
- Litvak, M.K. and W.C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Marine Ecology Progress Series 81:13-24.
- Madenjian, C.P., B.M. Johnson, and S.R. Carpenter. 1991. Stocking strategies for fingerling walleyes: an individual-based model approach. Ecological Applications 1:280-288.
- Major, P.F. 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Animal Behaviour 26:760-777.
- Marks, R.E., and D.O. Conover. 1993. Ontogenetic shift in the diet of young-of-the-year bluefish (*Pomatomus saltatrix*) during the oceanic phase of the early life history. Fishery Bulletin 91:97-106.
- McBride, R.S., and D.O. Conover. 1991. Recruitment of young-of-the-year bluefish (*Pomatomus saltatrix*) to the New York Bight: variation in abundance and growth of spring- and summer-spawned cohorts. Marine Ecology Progress Series 78:205-216.
- Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries Aquatic Sciences 45:1657-1670.
- Miller, T. 1989. Feeding behavior of *Echidna nebulosa*, *Enchelycore pardalis*, and *Gymnomuraena zebra* (Teleostei: Muraenidae). Copeia 1989:662-672.
- Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.
- Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.
- Moody, R.C., J.M. Helland, and R.A. Stein. 1983. Escape tactics used by bluegills and fathead minnows to avoid predation by tiger muskellunge. Environmental Biology of Fishes 8:61-65.
- Nyman, R.M. and D.O. Conover. 1988. The relation between spawning season and the recruitment of young-of-the-year bluefish (*Pomatomus saltatrix*) to New York. Fishery Bulletin 86:237-250.
- Paradis, A.R., P. Pepin, and J.A. Brown. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and Aquatic Sciences 53:1226-1235.
- Pepin, P., T.H. Shears, and Y. deLafontaine. 1992. Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). Marine Ecology Progress Series 81:1-12.
- Rice, J.A., L.B. Crowder, and K.A. Rose. 1993. Interactions between size-structured predator and prey populations: experimental test and model comparison. Transactions of the American Fisheries Society 122:481-491.
- Scharf, F.S., J.A. Buckel, F. Juanes, and D.O. Conover. In press. Estimating piscine prey size from partial remains: testing for shifts in foraging mode by juvenile bluefish. Environmental Biology of Fishes.
- Sih, A. and R.D. Moore. 1990. Interacting effects of predator and prey behavior in determining diets. Pages 771-796 in R.N. Hughes, editor. Behavioural Mechanisms of

- Food Selection. Springer-Verlag, Berlin.
- Sokal, R.R., and F.J. Rohlf. 1995. Biometry. 3rd Ed. W. H. Freeman and company, New York.
- StataCorp. 1995. Stata Statistical Software: Release 4.0 College Station, TX: Stata Corporation.
- Stein, R.A., C.G. Goodman, and E.A. Marschall. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65:702-715.
- Stein, R.A., and seven coauthors. 1988. Size-structured interactions in lake communities. Pages 161-180 in S.R. Carpenter, editor. *Complex interactions in lake communities*. Springer-Verlag, New York.
- Van Winkle, W., K.A. Rose, and R.C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. *Transactions of the American Fisheries Society* 122:397-403.
- Wahl, D.H. and R.A. Stein. 1989. Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*) predation. *Canadian Journal of Fisheries and Aquatic Sciences* 46:2095-2103.
- Wanzenböck, J. 1995. Changing handling times during feeding and consequences for prey size selection of 0+ zooplanktivorous fish. *Oecologia* 104:372-378.
- Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada* 31:1531-1536.
- Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393-426.

- Wilbur, H.M. 1988. Interactions between growing predators and growing prey. Pages 157-172 in Ebenman and Persson, editors. *Size-structured populations: ecology and evolution*. Springer-Verlag, Berlin.