FORAGING TACTICS OF YOUNG-OF-THE-YEAR BLUEFISH

IN THE HUDSON RIVER:

THE INFLUENCE OF BODY SIZE ON PREDATOR MODE

CHOICE AND PREY PROFITABILITY

by

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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

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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

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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 30th 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.

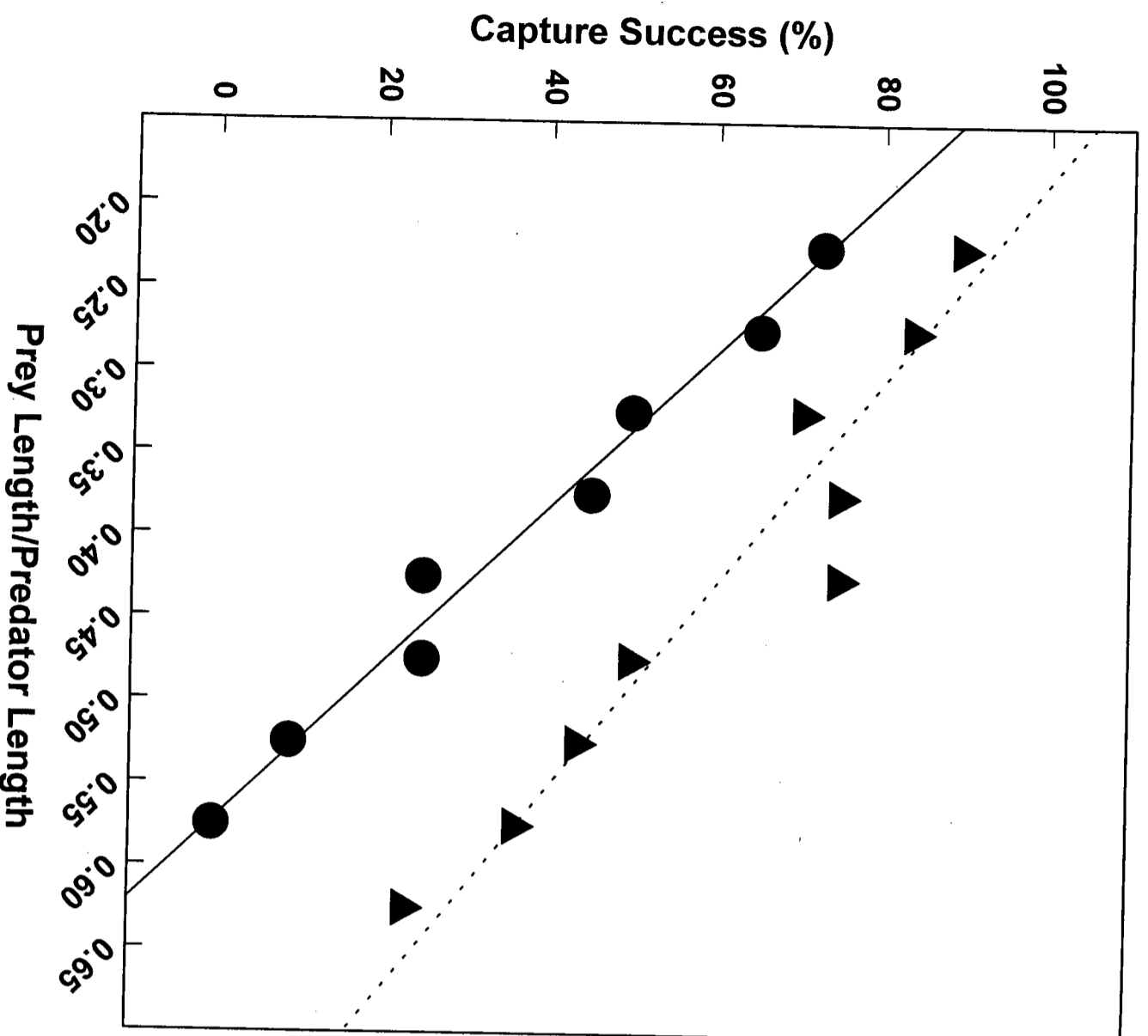| Species	Equation	S_b	r^2	n
Atlantic silverside	$W=5.08 \times 10^{-6} TL^{3.055}$	0.000	0.98	53
	$BD=0.694+0.138TL$	0.000	0.00	38
Striped bass	$W=3.53 \times 10^{-6} TL^{3.273}$	0.000	0.99	84
	$BD=-0.788+0.232TL$	0.000	0.00	71
Bluefish	$W=1.48 \times 10^{-6} TL^{3.347}$	0.000	0.99	54
	$MW=0.840+0.129TL$	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 significantly 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
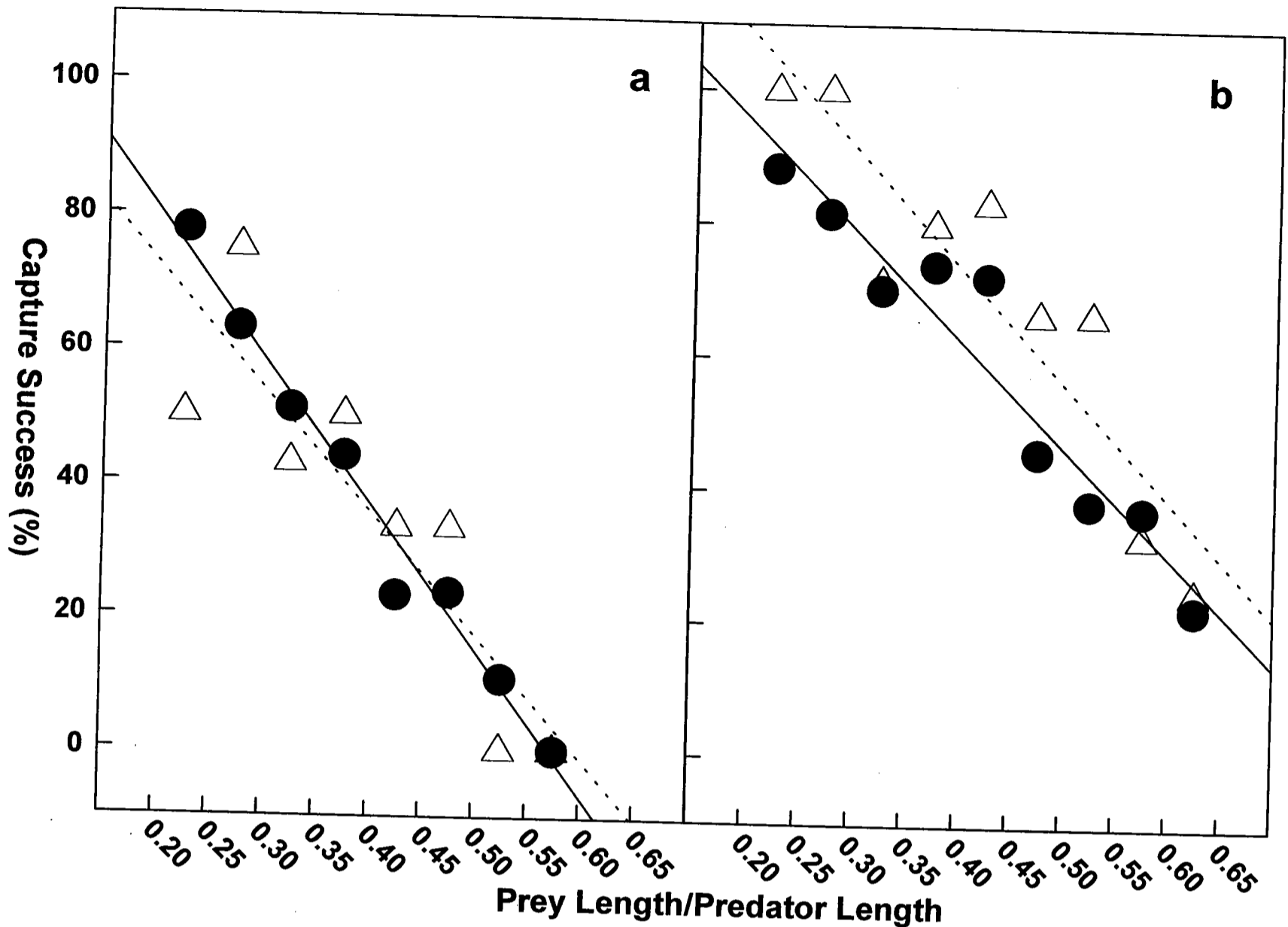
Figure 2. - Percentage of successful captures by juvenile bluefish feeding on striped bass (a) and Atlantic silversides (b) as a function of prey length/predator length ratio for first strike attempts within each feeding trial (△) and for all other strike attempts (●) excluding first strike attempts.
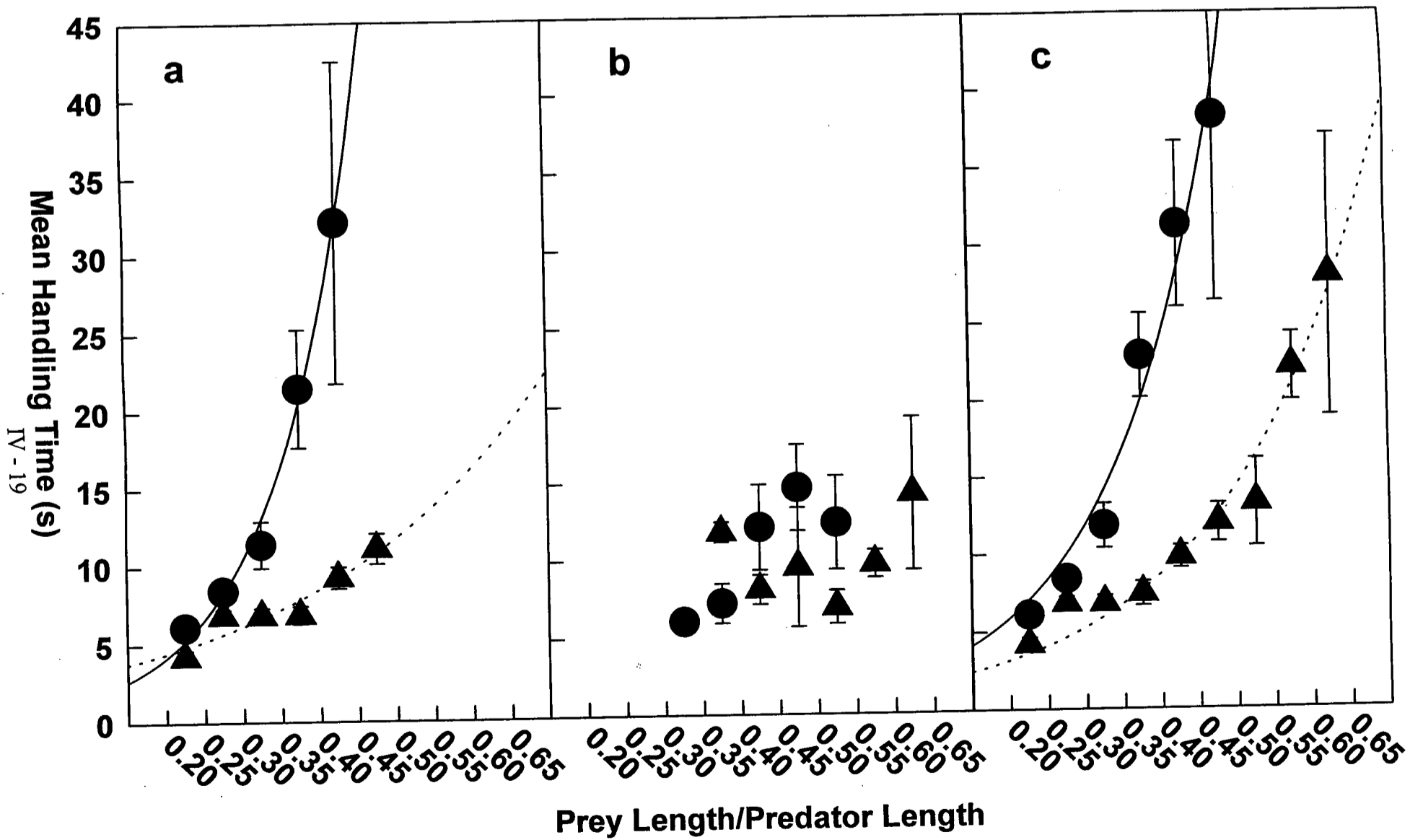
Figure 3. - Mean handling time in seconds as a function of prey length/predator length ratio for bluefish feeding on striped bass (●) and Atlantic silversides (▲). Data points represent means +/- 1 SE. (a) Handling time for prey swallowed whole. (b) Handling time only for first piece (always posterior 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).
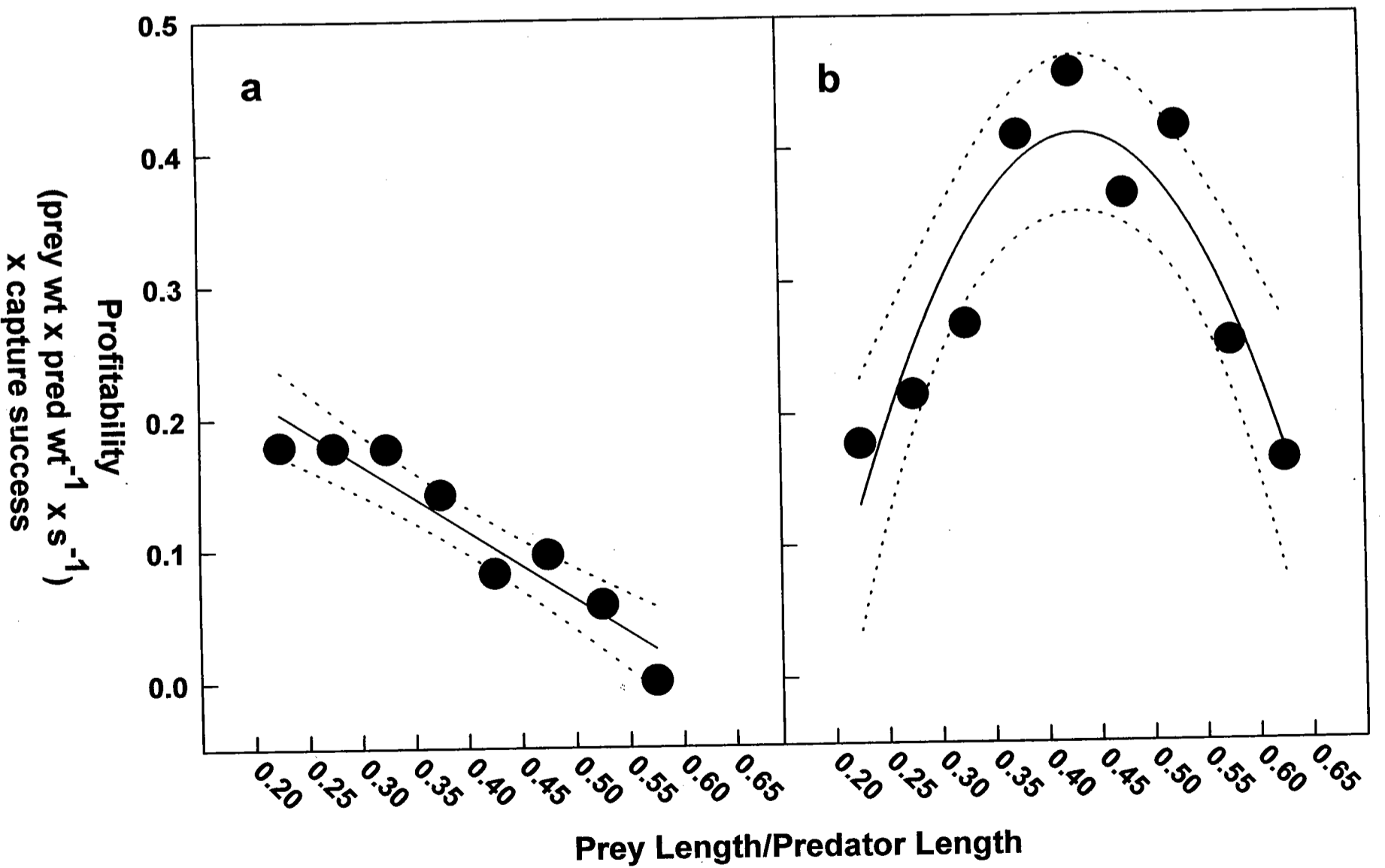

Figure 4. - Prey profitability multiplied by capture success as a function of prey length/predator length ratio for striped bass (a) and Atlantic silversides (b). Profitability calculated using only entirely consumed prey regardless of whether prey fish was swallowed whole or consumed in pieces.
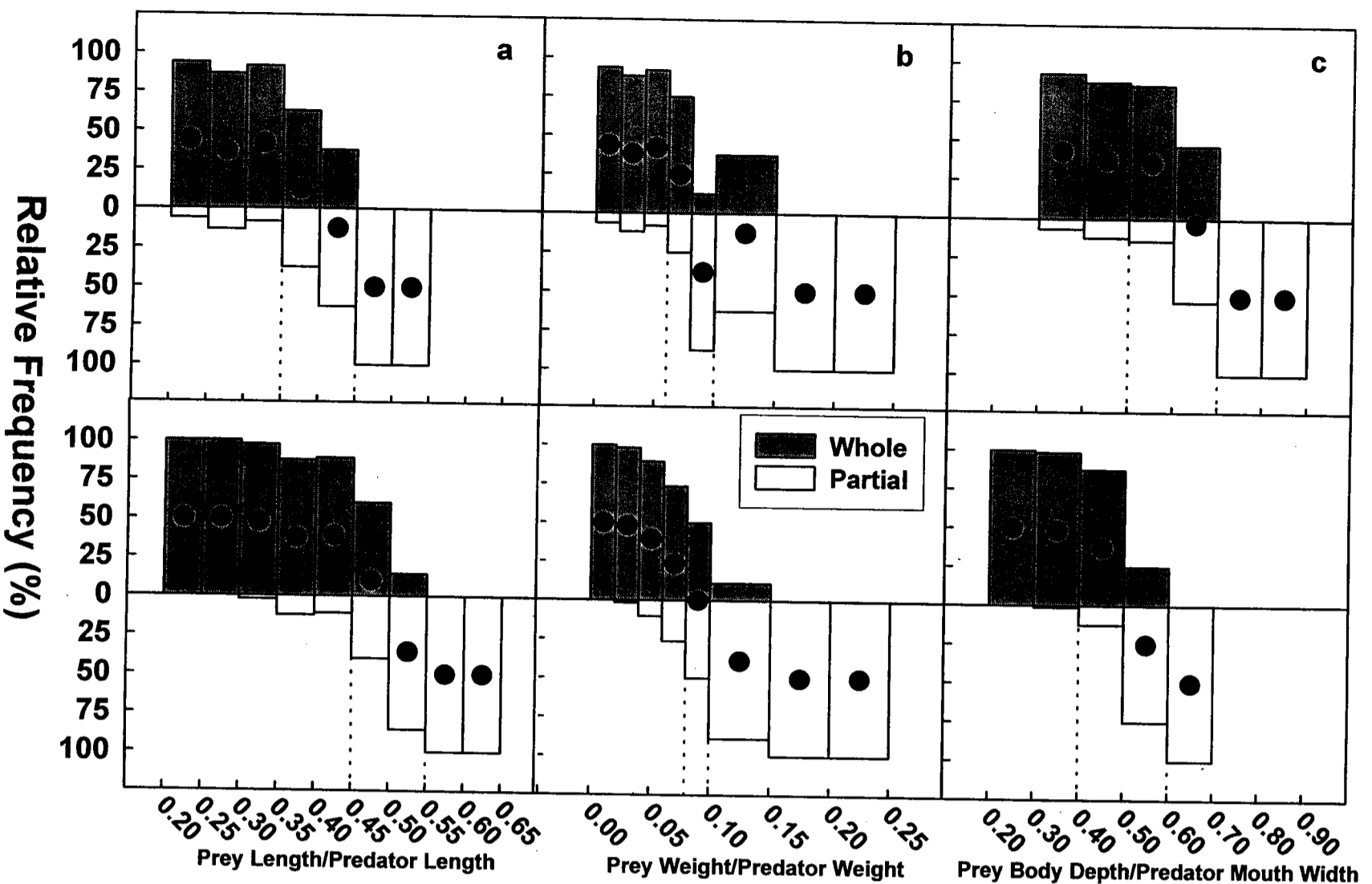
Figure 5. - Relative proportions of prey fish swallowed whole and consumed in pieces as a function of prey length/predator length ratio (a), prey weight/predator weight ratio (b), and prey body depth/predator mouth width ratio (c). Data for bluefish feeding on striped bass are displayed in the upper 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