Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture

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Abstract

We conducted a series of size-structured laboratory experiments to quantify and compare the susceptibility of several estuarine and marine forage fishes to attack and capture by piscivorous predators. Size-dependent estimates of capture success, handling time, and prey profitability were generated from single-species experiments offering bay anchovy, Atlantic menhaden, Atlantic silverside, and age-0 striped bass to piscivores. Bay anchovy and Atlantic menhaden were most susceptible to capture and yielded high profitability compared to Atlantic silverside and age-0 striped bass prey. Variation in capture success among forage species was particularly influential in generating disparate profitability functions. Although morphological differences among forage species contributed to variation in susceptibility to predation, behavioral analyses indicated that variable reaction distances to approaching predators and activity levels of prey may explain a large fraction of the observed differences in susceptibility. When several forage species were offered to predators simultaneously in larger enclosures, mortality was highest and occurred earlier for bay anchovy and Atlantic menhaden compared to other prey, which points to the strong influence of predator capture success on overall forage fish vulnerability. Our results demonstrate species-specific differences among forage fishes in the ability to avoid attack and capture by piscivores, and we conclude that the

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expression of antipredator behaviors contributes significantly to variation in forage species vulnerability.

1. Introduction

Predation may represent the largest source of mortality for juvenile fishes. Understanding the factors that impact vulnerability to predation during early life is essential, particularly given the evidence for several species indicating that variable, density-dependent mortality during the juvenile stage can contribute to population regulation of marine fishes (Myers and Cadigan, 1993; Steele, 1997). In fact, mounting interest in the application of more holistic, ecosystem-based approaches to fisheries management will require detailed knowledge of the controlling mechanisms and relative strengths of trophic interactions during critical life stages (Link, 2002).

Prey vulnerability can be defined as the product of encounter probability and susceptibility to attack and capture once encountered (Greene, 1986; Bailey and Houde, 1989). The vulnerability of young fishes to predation is a function of morphological and behavioral traits that develop during ontogeny (Fuiman and Magurran, 1994), and is often taxon-specific, depending on both prey and predator species. Further, body size relationships between predator and prey fishes often reflect consistent patterns indicative of their important role in trophic interactions of many species (Scharf et al., 2000). The evidence supporting the importance of relative body size to the outcome of predator–prey interactions among both larval and juvenile fishes is unequivocal (Werner and Gilliam, 1984; Miller et al., 1988; Pepin et al., 1992; Fuiman, 1994; Juanes and Conover, 1994; Paradis et al., 1996; Rice et al., 1997; Scharf et al., 1998; Lundvall et al., 1999) and indicates that the morphological and behavioral traits that contribute to interspecific variation in prey vulnerability must be examined within a framework that incorporates the relative sizes of predator and prey.

Species interactions operate on a fine spatial scale and identifying the mechanisms that govern prey vulnerability often requires direct behavioral observation in a laboratory setting. Several studies examining predation on larval and juvenile fishes have demonstrated the effective use of size-dependent information obtained from laboratory experiments to predict the outcome of interactions among size-structured populations (Rice et al., 1993; Cowan et al., 1996). Individual-based foraging models have allowed researchers to examine dynamic processes, occurring among individuals, that impact the organization of fish communities. However, although nested within a body size framework, the results of interactions among predators and prey are often species-specific (Webb, 1986; Wahl and Stein, 1988; Scharf et al., 1998). Since variation in predation components has been shown to have large effects on model predictions (Adams and DeAngelis, 1987), accurate estimation of these components is critical for model success.

Recently, there has been increased interest in the population dynamics of forage fishes in both freshwater and marine ecosystems (Bogstad and Mehl, 1997; Donovan et al., 1997;

Stephenson, 1997). This increase stems from the realization that fluctuations in year-class strength and abundance of harvestable predator species may be directly linked to variation in population structure and abundance of key forage species. In freshwater systems, researchers have used knowledge of size-structured predator–prey interactions during early life to predict recruitment success of native and stocked piscivores more accurately (Donovan et al., 1997). Changes in size structure and abundance of marine forage fish populations may reduce the availability of vulnerable prey to juvenile piscivorous fishes and have implications for piscivore growth and cohort success. Prediction of population-level effects of changes in the forage base depends upon knowledge of the factors that determine size-specific vulnerability of forage species.

Here, we quantify the susceptibility of several marine forage species to attack and capture in order to evaluate potential mechanisms producing variation among species as well as the relative contribution of prey susceptibility to overall vulnerability of forage species. Piscivore capture success and handling times are estimated for several forage species as functions of relative prey and predator sizes. Capture and handling components are combined with relative prey mass ingested to generate size-dependent profitability functions, which serve as an index of predator foraging efficiency. Predation components are then compared among forage species to assess their relative susceptibility to predation. We also evaluate antipredator behaviors of prey, including reaction distance and burst escape velocity, to identify potential behavioral mechanisms explaining variation in susceptibility of different forage species to predation. In a separate experiment conducted in large enclosures, we calculate mortality rates of prey offered in mixed-species assemblages to determine if variation among forage species in susceptibility to predation estimated from single-species foraging experiments can predict species-specific survival patterns in a multiple-prey environment.

2. Methods

Forage species and piscivorous predators were chosen based on known trophic linkages in estuarine and marine systems of the US east coast and because many of the species chosen support valuable commercial and recreational fisheries. Juvenile bluefish (*Pomatomus saltatrix*) and striped bass (*Morone saxatilis*) are seasonally abundant piscivores that have been shown to have strong impacts on prey fish populations in large estuarine systems such as the Chesapeake Bay and the Hudson River (Hartman and Brandt, 1995a; Buckel et al., 1999). In addition, both species support large recreational and commercial fisheries in several Atlantic coast states. The forage species chosen were small, juvenile fishes that are highly abundant throughout the east coast of the US, and included bay anchovy (*Anchoa mitchilli*), Atlantic menhaden (*Brevoortia tyrannus*), Atlantic silverside (*Menidia menidia*), and striped bass. These forage species represent the primary prey fishes consumed by bluefish and striped bass predators during summer months and are a critical component of estuarine and marine food webs in the western Atlantic (Baird and Ulanowicz, 1989; Hartman and Brandt, 1995b; Buckel et al., 1999).

Piscivorous age-0 bluefish and age-1 striped bass were collected in beach seines during June 1999 and 2000 in estuaries located in western Long Island, NY (Jamaica, Little Neck,

and Manhasset Bays; approximately 40°40′ N, 73°45′ W). Bluefish were also captured periodically during summer months in Sandy Hook Bay, NJ (40°24′ N, 74°00′ W). Forage species were captured mainly by beach seine in Sandy Hook Bay during summer 1999 and 2000. Age-0 striped bass were captured in estuarine waters of the lower Hudson River (Haverstraw Bay region) during both summers. Fishes were transported in ambient seawater to the James J. Howard Marine Science Laboratory (National Marine Fisheries Service, Northeast Fisheries Science Center) in Highlands, NJ, where all fishes were held and experiments performed. After capture and transport, fishes were transferred to circular aquaria (1500 l; 1.8 m diameter, 0.6 m depth) to acclimate for at least 1 week prior to use in feeding experiments. Predators were fed a combination of live and frozen fish prey twice daily, and forage species were fed a combination of live cultured and frozen brine shrimp, and commercial flake and pellet foods twice daily. All fishes were maintained throughout the experimental period in ambient flow-through seawater at temperatures (19–21 °C), salinities (22–27 ppt), and photoperiods (14:10 light:dark cycle) similar to environmental conditions during summer in Sandy Hook Bay.

Laboratory experiments were conducted using sizes of both predators and forage species that matched those fish sizes that naturally occur simultaneously in US mid-Atlantic Bight estuaries during summer and early fall (see size ranges in Tables 1 and 2). Size-dependent predation components were quantified for bluefish predators feeding on bay anchovy, Atlantic menhaden, Atlantic silverside, and age-0 striped bass (Table 1), and

Table 1
Number of foraging trials completed for bluefish predators feeding on four forage fish species across the range of relative prey sizes tested during summer 1999 and 2000

Relative prey size	Species tested			
	Bluefish predators vs. Bay anchovy prey	Bluefish predators vs. Atlantic silverside prey	Bluefish predators vs. Atlantic menhaden prey	Bluefish predators vs. Age-0 striped bass prey
	Number of foraging trials			
0.20–0.25	4	6	3	2
0.25–0.30	8	7	8	9
0.30–0.35	9	6	5	6
0.35–0.40	5	7	5	6
0.40–0.45	7	5	9	5
0.45–0.50	5	3	8	3
0.50–0.55	3	3	5	0
0.55–0.60	3	2	0	0
0.60–0.65	3	0	0	0
Total number of foraging trials	47	39	43	31
Prey TL range (mm)	30–65	25–65	25–60	25–55
Predator TL range (mm)	90–180	90–180	70–135	90–160

Size ranges of bluefish and forage species used throughout experiments are indicated.
TL = total length.

Table 2
Number of foraging trials completed for striped bass predators feeding on two forage fish species across the range of relative prey sizes tested during summer 1999 and 2000

	Species tested	
	Striped bass predators vs. Bay anchovy prey	Striped bass predators vs. Atlantic silverside prey
Relative prey size	Number of foraging trials	
0.10–0.15	0	6
0.15–0.20	10	7
0.20–0.25	11	14
0.25–0.30	6	11
0.30–0.35	5	11
0.35–0.40	5	6
0.40–0.45	3	7
0.45–0.50	3	3
0.50–0.55	3	0
Total number of foraging trials	46	65
Prey TL range (mm)	25–65	17–65
Predator TL range (mm)	120–190	120–190

Size ranges of striped bass and forage species used throughout experiments are indicated.
TL = total length.

for striped bass predators feeding on Atlantic silverside and bay anchovy (Table 2). For each predator species, the choice of forage species studied was based on diet information identifying dominant fish prey for age-0 bluefish and age-1 striped bass. The size ranges of predators and prey used in the experiments allowed foraging components to be measured across a range of relative fish sizes (prey/predator length ratios of 0.10–0.65). Throughout the summer, predators used in feeding experiments were randomly sampled with replacement from laboratory populations of 50–60 individuals of each species. A total of 160 feeding trials were completed with bluefish predators (three individuals per trial); thus, each bluefish within the laboratory population was used for multiple feeding trials (about 8–10, assuming random sampling resulted in approximately equal numbers of feeding trials across individuals). Similarly, 111 feeding trials were completed with striped bass predators, with each striped bass expected to have been used in about six to eight feeding trials during the summer. Laboratory populations of forage fishes were replenished throughout the summer and new individuals were used for each feeding trial.

Feeding trials to quantify predation components were conducted in flow-through seawater tanks (475 l; $1.05 \times 0.76 \times 0.60$ m depth) each with a clear Plexiglass front for viewing. Tank bottoms were covered with a thin layer (10 mm) of coarse sand, and two 150-W halogen bulbs positioned 1.0 m above each tank provided lighting. All experimental feeding trials were recorded using either Hi-8 or digital video cameras positioned 1.0 m in front of each tank. Each feeding trial consisted of a group of three size-matched (10 mm TL range) predators being offered a group of 10 size-matched (5 mm TL range) prey. Predators were starved for at least 12 h and acclimated to experimental tanks for up to 8 h prior to feeding trials. Prey were added to each tank and contained within a clear Plexiglass holding chamber for a 10- to 15-min acclimation period before being exposed to

predators. All feeding trials lasted 15 min, at which time all fish were removed and remaining prey were counted. Within each feeding trial, predator capture success was calculated as the number of attacks resulting in prey ingestion. Handling time was measured as the difference between the time of initial contact with the prey and cessation of rapid opercular movement. Handling times for all prey eaten during a single feeding trial were averaged to obtain a mean handling time per trial.

To evaluate potential antipredator behaviors of forage fishes affecting susceptibility to attack and capture, swimming speeds and reaction distances were quantified for each species. Burst escape velocities were calculated for a random sample of prey escape attempts as the distance traveled (cm) per elapsed video frame (0.03 s). Reaction distances were measured as the distance (mm) separating an approaching predator from a single forage fish immediately before the prey initiated an escape response, and were estimated for a random sample of prey escape attempts. Because the video setup could accurately quantify movement in only two dimensions, burst velocities and reaction distances were measured only when prey and predators were moving in a plane perpendicular or approximately perpendicular to the camera. Distances traveled during prey bursts and reaction distances separating predators and prey prior to escape responses were measured using a grid system positioned within the tanks and adjusted based on relationships between actual fish sizes and fish sizes measured on video.

Additional feeding experiments were completed to assess the effect of container volume on predator capture success. Predation trials with bluefish feeding on Atlantic silverside were conducted in 900-l tanks in addition to the experiments carried out in 475-l tanks described above. Feeding trials in 900-l tanks were conducted using a similar experimental protocol, with three predators being offered 10 prey, and were video-recorded. Bluefish capture success was estimated for a range of relative prey sizes and results were compared among 900- and 475-l tanks and to previously published results completed in 215-l tanks (Scharf et al., 1998).

Experiments to determine mortality rates of forage species when presented simultaneously in mixed-species assemblages were conducted in large, circular tanks (2400 l; 2.4 m diameter × 0.6 m depth). Groups of three size-matched predators (10 mm TL range; mean bluefish TL = 165 mm; mean striped bass TL = 175 mm) were acclimated to the experimental tanks and starved for at least 12 h to standardize hunger levels. Predators were simultaneously presented with groups of 10 size-matched individuals (5 mm TL range; mean prey sizes = 50–55 mm TL) of each forage species. Four forage species (Atlantic menhaden, Atlantic silverside, bay anchovy, and age-0 striped bass) and 40 total prey fishes were simultaneously offered to bluefish predators. Three forage species (Atlantic silverside, bay anchovy, and mummichogs, *Fundulus heteroclitus*) and 30 total prey fishes were simultaneously offered to striped bass predators. Mummichog prey were included in striped bass experiments in order to offer three, rather than only two, size-matched forage species simultaneously. Preliminary data indicated that mummichog was intermediate between Atlantic silverside and bay anchovy in susceptibility to capture by striped bass predators (F.S. Scharf, unpublished data). Forage species were introduced into tanks simultaneously and allowed to acclimate within a circular, opaque container for 15 min before containers were lifted and predators had access to prey. Mortality rates of each forage species were assessed based on visual counts of the number of each forage species

remaining after 15 min, 30 min, 1 h, 2 h, 3 h, 6 h, 9 h, 12 h, and 24 h, at which time the feeding trial was terminated and all remaining prey were counted. Four replicate feeding trials were completed using striped bass predators and six replicate feeding trials were completed using bluefish predators.

For single-species feeding experiments, linear regressions were generated to estimate capture success as a function of prey length/predator length ratio for each predator and forage species combination. Mean handling times were log-transformed (ln) before regressions were completed for mean handling time as a function of prey length/predator length ratio.

Forage species profitability was estimated as a function of prey length/predator length ratio by calculating relative prey mass ingested (prey weight/predator weight) × handling time^{-1} × capture success for all predator–prey species combinations. Relative prey mass ingested represents energetic intake, and handling time and capture success represent energetic costs. For the forage species tested, prey mass is probably a reasonable estimate of energetic intake because caloric content (cal g^{-1}) for these species does not vary considerably (Steimle and Terranova, 1985). Standard errors for profitability functions calculated from three variables ($AB^{-1}C$) were approximated using:

$$\text{S.E.}(\text{prof}) \approx \frac{1}{B^2}\left[C^2\text{S.E.}(A) + A^2\text{S.E.}(C) + \frac{A^2C^2}{B^2}\text{S.E.}(B)\right]$$

where A = relative prey mass; B = handling time; and C = capture success. Peak profitability values were compared among forage species using a variance ratio test.
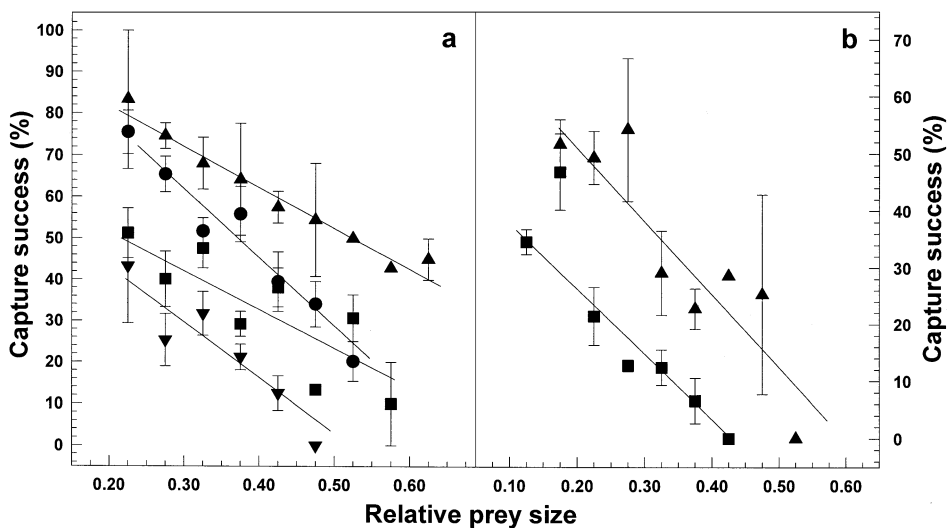

Fig. 1. (a) Bluefish and (b) striped bass capture success as a function of relative prey size (prey total length/predator total length ratio) for several forage species. Regression lines are based on data from all individual feeding trials and means (± 1 S.E.) are presented for all trials within each 5% interval of relative prey size for illustrative purposes. ANCOVA statistics are given in Tables 3 and 4. (▲) Bay anchovy; (●) Atlantic menhaden; (■) Atlantic silverside; and (▼) age-0 striped bass.

Table 3
Least squares regression equations relating bluefish capture success and mean handling time to relative prey size for each of four species of forage fishes

| Forage species | Regression equation | Capture success | Multiple comparisons |
		ANCOVA statistics	
Bay anchovy[1]	$y = 1.01 - 0.98x$ ($p < 0.001$; $r^2 = 0.50$)	$F_{slopes}(3,102) = 2.104$; $p = 0.104$	1 vs. 2, $p < 0.001$
Atlantic silverside[2]	$y = 0.70 - 0.94x$ ($p < 0.001$; $r^2 = 0.33$)	$F_{adjusted\ means}(3,105) = 53.556$; $p < 0.001$	1 vs. 3, $p < 0.001$
Atlantic menhaden[3]	$y = 1.12 - 1.66x$ ($p < 0.001$; $r^2 = 0.63$)		1 vs. 4, $p < 0.001$
Age-0 striped bass[4]	$y = 0.70 - 1.34x$ ($p < 0.001$; $r^2 = 0.48$)		2 vs. 3, $p < 0.001$
			2 vs. 4, $p < 0.001$
			3 vs. 4, $p < 0.001$

| Forage species | Regression equation | Handling time | Multiple comparisons |
		ANCOVA statistics	
Bay anchovy[1]	$y = 2.81e^{4.23x}$ ($p < 0.001$; $r^2 = 0.86$)	$F_{slopes}(3,96) = 0.758$; $p = 0.520$	1 vs. 2, $p < 0.001$
Atlantic silverside[2]	$y = 1.68e^{4.58x}$ ($p < 0.001$; $r^2 = 0.69$)	$F_{adjusted\ means}(3,99) = 27.311$; $p < 0.001$	1 vs. 3, $p < 0.001$
Atlantic menhaden[3]	$y = 3.08e^{4.80x}$ ($p < 0.001$; $r^2 = 0.68$)		1 vs. 4, $p < 0.005$
Age-0 striped bass[4]	$y = 2.26e^{5.73x}$ ($p < 0.001$; $r^2 = 0.56$)		2 vs. 3, $p < 0.001$
			2 vs. 4, $p < 0.001$
			3 vs. 4, $p = 0.715$

Results of ANCOVAs and Tukey multiple comparison tests are presented. Each forage species is numerically labeled when referring to multiple comparison test results.

For each predator, capture success and handling time regressions were compared across forage species using analysis of covariance (ANCOVA). The effect of tank size on bluefish capture success was assessed by comparing linear regressions across different tank

Table 4
Least squares regression equations relating striped bass capture success and mean handling time to relative prey size for each of two forage species

| Forage species | Regression equation | Capture success |
		ANCOVA statistics
Bay anchovy	$y = 0.77 - 1.29x$ ($p < 0.001$; $r^2 = 0.59$)	$F_{slopes}(1,65) = 0.191$; $p = 0.664$
Atlantic silverside	$y = 0.49 - 1.15x$ ($p < 0.001$; $r^2 = 0.39$)	$F_{adjusted\ means}(1,66) = 55.549$; $p < 0.001$

| Forage species | Regression equation | Handling time |
		ANCOVA statistics
Bay anchovy	$y = 1.30e^{7.14x}$ ($p < 0.001$; $r^2 = 0.88$)	$F_{slopes}(1,69) = 0.356$; $p = 0.553$
Atlantic silverside	$y = 1.08e^{7.62x}$ ($p < 0.001$; $r^2 = 0.78$)	$F_{adjusted\ means}(1,70) = 0.686$; $p = 0.410$

ANCOVA results are presented.

volumes using ANCOVA. Forage species burst velocities were also determined as functions of body size and regressions compared across species using ANCOVA. Mean reaction distances were estimated for each forage species and tested for differences using analysis of variance (ANOVA). When forage species were offered to predators simulta-neously, mortality rates were evaluated and compared using survival analysis (Cox and Oates, 1984). Time-dependent mortality of forage species was modeled by assuming a Weibull distribution, with comparisons among forage species based on log-likelihood estimates.

3. Results

For each of four forage species, capture success of piscivorous bluefish declined linearly with increasing relative prey size (Fig. 1a; Table 3). ANCOVA results indicated that regression slopes were not statistically distinct; however, elevations (adjusted means) were significantly different. Post-hoc multiple comparisons revealed significant differ-ences between all pairwise combinations of regression elevations. Bluefish capture success was highest on bay anchovy, reaching 80% at the smallest relative prey sizes, and was nearly as high for Atlantic menhaden prey, especially at small relative prey sizes. Capture success on Atlantic silverside prey was intermediate, with age-0 striped bass being the
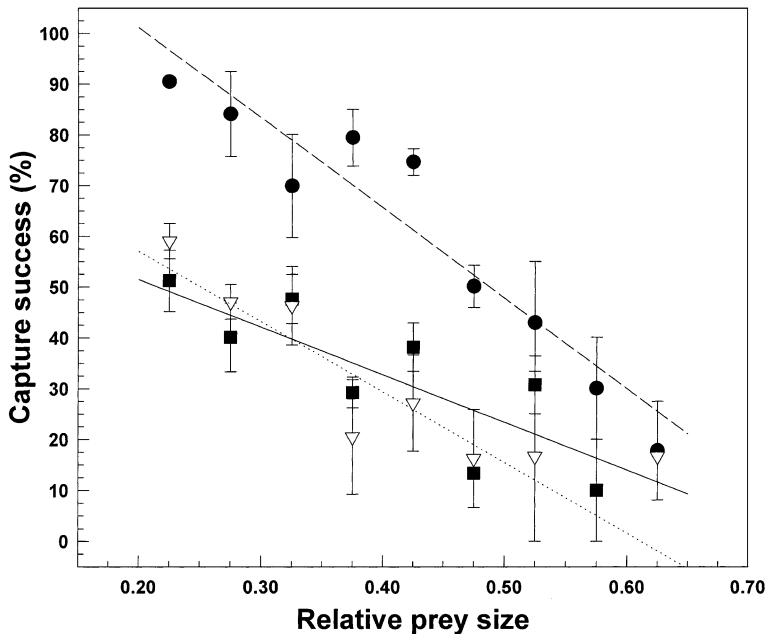

Fig. 2. Capture success of bluefish feeding on Atlantic silverside prey in (●) 215-l, (■) 475-l, and (▽) 900-l tanks. Regression lines are based on data from all individual feeding trials and means (± 1 S.E.) are presented for all trials within each 5% interval of relative prey size for illustrative purposes. Data for 215-l tank size from Scharf et al. (1998). ANCOVA statistics are given in the text.
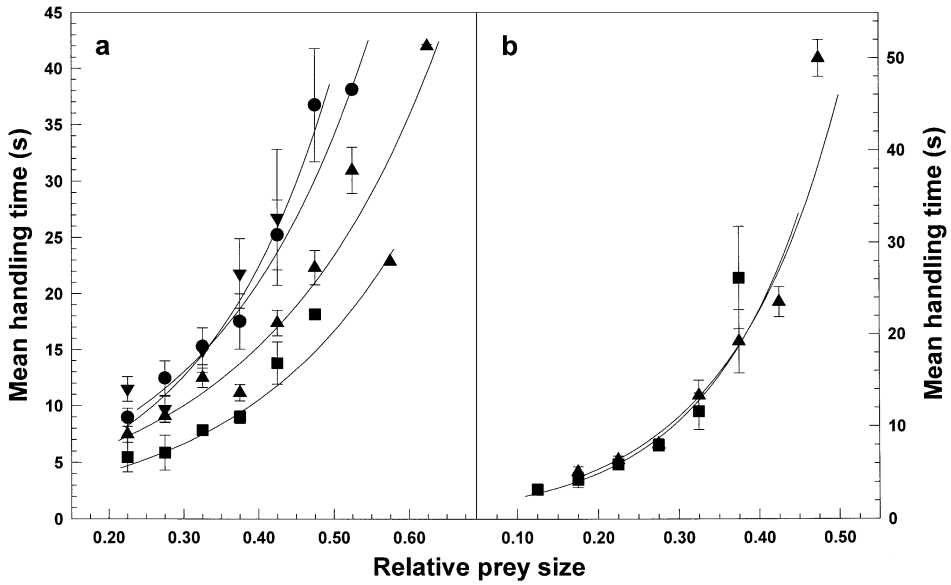
Fig. 3. Mean handling time as a function of relative prey size for (a) bluefish and (b) striped bass predators feeding on several forage species. Regression lines are based on data from all individual feeding trials and means (± 1 S.E.) are presented for all trials within each 5% interval of relative prey size for illustrative purposes. ANCOVA statistics are given in Tables 3 and 4. (▲) Bay anchovy; (●) Atlantic menhaden; (■) Atlantic silverside; and (▼) age-0 striped bass.
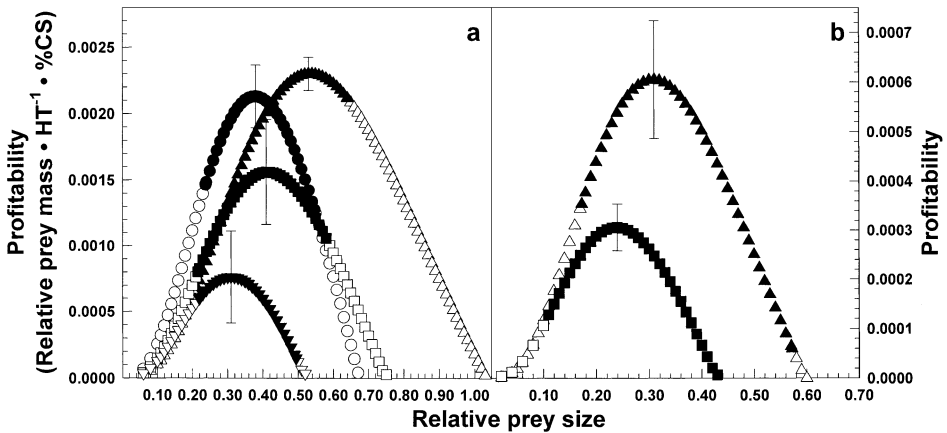

Fig. 4. Profitability of several forage species consumed by (a) bluefish and (b) striped bass as a function of relative prey size. Filled symbols represent the range of relative prey sizes tested in this study. Open symbols represent the extrapolation of profitability estimates to the *x*-axis. (▲) Bay anchovy; (●) Atlantic menhaden; (■) Atlantic silverside; and (▼) age-0 striped bass. HT = mean handling time; %CS = capture success.

most difficult prey for bluefish to catch. Capture success of striped bass predators also declined linearly with increasing relative prey size (Fig. 1b; Table 4). Comparisons of striped bass capture success between bay anchovy and Atlantic silverside prey indicated no differences among regression slopes and significant differences among elevations. For the range of relative prey sizes tested, bay anchovy were significantly easier for striped bass to capture compared to Atlantic silverside prey.

Experiments to evaluate the effects of container volume on predator capture success indicated that the decline in capture success with increasing relative prey size was linear for each container volume tested (Fig. 2). Regression slopes were not statistically different [ANCOVA$_{slopes}$: $F(2,87) = 2.867$; $p = 0.06$], but there was considerable variation. Differences in elevation were highly significant among container volumes [ANCOVA$_{adjusted\ means}$: $F(2,89) = 54.096$; $p < 0.001$]. Post-hoc multiple comparisons revealed that capture success in 215-l tanks was significantly higher than in 475-l tanks (Tukey $q = 12.68$; $p < 0.001$) or 900-l tanks (Tukey $q = 12.07$; $p < 0.001$), and that capture success was not different between 475- and 900-l arenas (Tukey $q = 0.26$; $p > 0.50$).

Mean handling time for bluefish predators increased exponentially with increasing relative prey size for each of the four forage species tested (Fig. 3a; Table 3). ANCOVA results indicated that regression slopes were statistically similar, and that elevations were significantly different. Post-hoc multiple comparisons demonstrated significant differences between all pairwise combinations with the exception of handling times for Atlantic
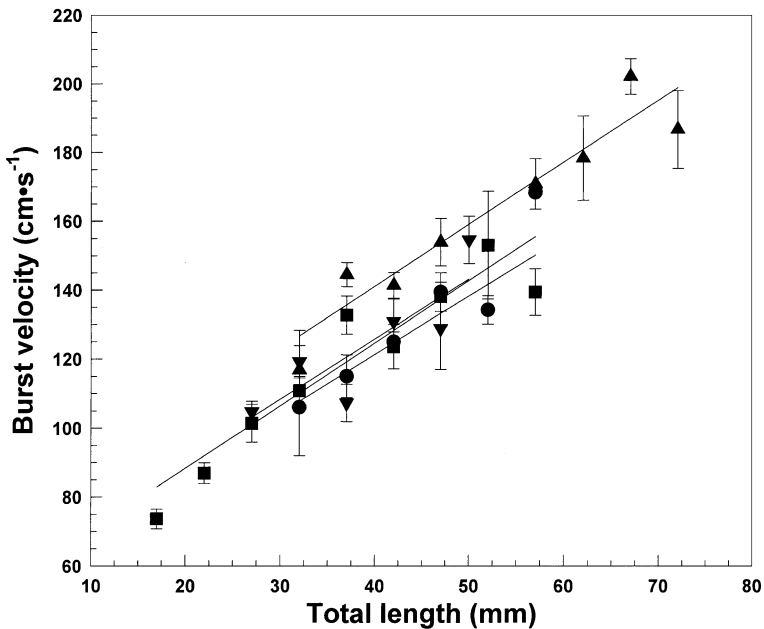

Fig. 5. Maximum burst velocity as a function of total body length for forage species. Regression lines are generated from all individual velocities calculated and means (± 1 S.E.) are presented for all velocities within each 5-mm interval of total body length for illustrative purposes. ANCOVA statistics are given in Table 5. (▲) Bay anchovy; (●) Atlantic menhaden; (■) Atlantic silverside; and (▼) age-0 striped bass.

menhaden and age-0 striped bass prey. Deeper-bodied striped bass and Atlantic menhaden required the longest time for bluefish to manipulate and ingest, while handling times were lower for bay anchovy and Atlantic silverside. Striped bass predators also displayed exponential increases in mean handling time as a function of increasing relative prey size for the two forage species tested (Fig. 3b; Table 4). ANCOVA detected no statistical differences among regression slopes or elevations for striped bass handling time on bay anchovy and Atlantic silverside prey.

Profitability of all forage species consumed by bluefish predators was dome-shaped with increasing relative prey size. Peak profitability values and the relative prey size at which peak profitability occurred varied considerably among forage species (Fig. 4a). Profitability of bay anchovy prey was maximized at a higher relative prey size compared to other forage species, and variance ratio tests indicated that bay anchovy peak profitability was significantly ($p < 0.05$) greater than peak profitability for Atlantic silverside or age-0 striped bass prey. Peak profitability for Atlantic menhaden prey was also significantly greater than peak profitability for age-0 striped bass prey. Profitability of forage species consumed by striped bass predators was also dome-shaped and varied between forage species (Fig. 4b). Bay anchovy profitability peaked at a higher relative prey size and was significantly greater than Atlantic silverside profitability.

Table 5
Maximum burst velocity regressions and mean reaction distance for four species of forage fishes

| Forage species | Regression equation | Burst velocity | | Multiple comparisons |
		ANCOVA statistics		
Bay anchovy[1]	$y = 1.80TL + 69.05$ ($p < 0.001$; $r^2 = 0.59$)	$F_{slopes}(3,227) = 0.026$; $p = 0.994$		1 vs. 2, $p < 0.001$
Atlantic silverside[2]	$y = 1.81TL + 52.09$ ($p < 0.001$; $r^2 = 0.51$)	$F_{adjusted\ means}(3,230) = 8.793$; $p < 0.001$		1 vs. 3, $p < 0.001$
Atlantic menhaden[3]	$y = 1.69TL + 53.66$ ($p < 0.001$; $r^2 = 0.34$)			1 vs. 4, $p < 0.001$
Age-0 striped bass[4]	$y = 1.74TL + 56.21$ ($p < 0.001$; $r^2 = 0.28$)			2 vs. 3, $p = 0.169$
				2 vs. 4, $p = 0.636$
				3 vs. 4, $p = 0.706$

| Forage species | Mean ($\pm$ S.E.) | Reaction distance | Multiple comparisons |
		ANOVA statistics	
Bay anchovy[1]	30.79 ($\pm$ 3.39)	$F(3,84) = 21.406$; $p < 0.001$	1 vs. 2, $p < 0.001$
Atlantic silverside[2]	79.78 ($\pm$ 9.08)		1 vs. 3, $p > 0.500$
Atlantic menhaden[3]	35.48 ($\pm$ 4.70)		1 vs. 4, $p < 0.001$
Age-0 striped bass[4]	77.39 ($\pm$ 4.83)		2 vs. 3, $p < 0.001$
			2 vs. 4, $p > 0.500$
			3 vs. 4, $p < 0.001$

Burst velocity in centimeters per second; TL = total body length in millimeters; reaction distance in millimeters. ANCOVA and ANOVA results and Tukey multiple comparison test results are presented. Each forage species is numerically labeled when referring to multiple comparison test results.
S.E. = standard error.

Maximum burst swimming speeds of forage species increased linearly with body size and were relatively similar across species (Fig. 5). Burst velocities increased from about 100 cm s^{-1} at body sizes of 30 mm TL, to 150 cm s^{-1} at body sizes between 50 and 55 mm TL. Large bay anchovy (60–70 mm TL) were capable of reaching speeds of 180–190 cm s^{-1}. ANCOVA results indicated no statistical differences among regression slopes but significant differences among regression elevations (Table 5). Post-hoc multiple comparisons revealed that maximum burst velocities of bay anchovy were higher than other forage species. Mean reaction distances of forage species to approaching predators ranged from 30 to 80 mm and varied among species (Table 5). Bay anchovy and Atlantic menhaden reacted late, often allowing predators to approach within 30–40 mm before initiating an escape attempt. In contrast, Atlantic silverside and age-0 striped bass reacted more quickly and usually responded to predators approaching within 80–90 mm. ANOVA results indicated that mean reaction distances differed among forage species, and post-hoc multiple comparisons revealed that reaction distances of bay anchovy and Atlantic menhaden were significantly different from those of Atlantic silverside and age-0 striped bass (Table 5).

There were significant differences among forage species in time-dependent mortality from bluefish predation when offered in mixed-species assemblages (Fig. 6a). Each prey contributed significantly to the overall survival model, with the highest and earliest mortality experienced by bay anchovy, followed closely by Atlantic menhaden, with intermediate and low levels of mortality for age-0 striped bass and Atlantic silverside. Forage species displayed similar mortality patterns when exposed to striped bass predators
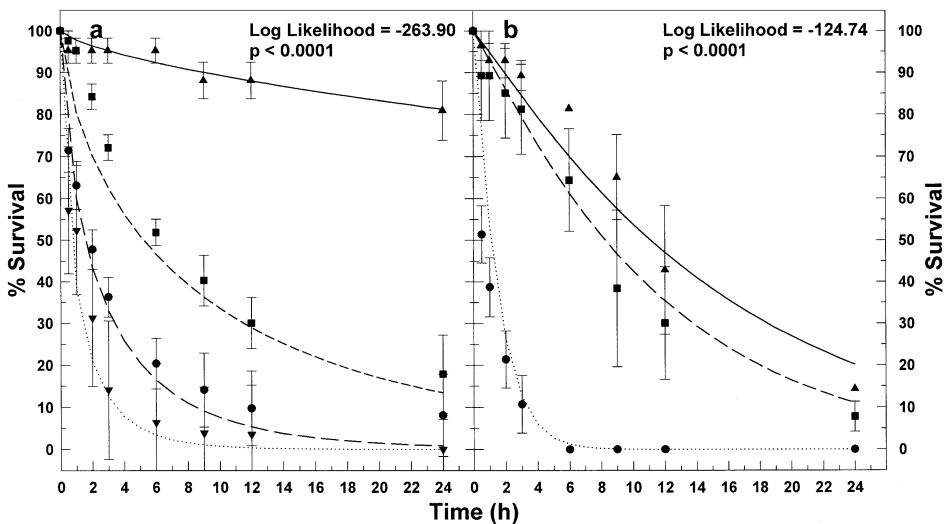

Fig. 6. Mean percent survival of forage species exposed to (a) bluefish and (b) striped bass predators in large enclosures over 24 h. Lines are fitted Weibull distributions to time-dependent mortality data. Log-likelihood and probability values are based on the full survival model. Dotted line, Bay anchovy; long dashed line, Atlantic menhaden; short dashed line, age-0 striped bass; and solid line, Atlantic silverside. In panel (b), long dashed line = mummichog.

(Fig. 6b). Bay anchovy experienced high mortality early in the feeding experiments, while mummichog and Atlantic silverside experienced much lower levels of mortality. Since mortality experiments were conducted using relative prey sizes of about 0.30, profitability functions predicted the earliest and highest mortality for Atlantic menhaden, followed by bay anchovy and Atlantic silverside, for which mortality patterns should have been similar, and the lowest mortality for age-0 striped bass when exposed to bluefish predators. Observed mortality schedules of forage species exposed to bluefish predators did not follow this order. When exposed to striped bass predators, mortality schedules of bay anchovy and Atlantic silverside did match predictions from prey profitability functions.

4. Discussion

Results of our laboratory experiments revealed clear differences in the abilities of several marine forage species to evade fish predators. Although differences between some species appeared to be related primarily to morphological traits (e.g., body depth, presence of dorsal spines), differences among others could be attributed directly to variable prey behavior (e.g., reaction distance). Species-specific morphological and behavioral traits combined to shape the antipredator abilities for each of the forage species examined in this study, generating considerable variation in their susceptibility to attack and capture. Our findings also reinforce the primary importance of capture success for explaining patterns of prey selection by piscivorous fishes and point to the effect of prey behavior on the distribution of predator attacks among simultaneously available prey.

The importance of prey morphology in determining relative vulnerability to predation is well established. In addition to predator gape size, which establishes upper limits on the sizes of prey that can be ingested, body depth of prey and the presence of spines can deter predator attacks and allow prey escapement during handling (Hambright, 1991; Einfalt and Wahl, 1997). Specifically, the central body location of dorsal spines and maximum body depth has been shown to redirect predator strikes away from the center of mass and to reduce capture success of freshwater piscivores (Webb, 1986; Wahl and Stein, 1988). In this study, the only forage species with robust dorsal spines, age-0 striped bass, was the most difficult for bluefish predators to capture. In addition, deep-bodied Atlantic menhaden were frequently able to escape from bluefish after being grasped. Over 18% of menhaden escapes occurred after being caught and held briefly by bluefish. Prey escapes after initially being captured represented less than 5% of escapes of other forage species, indicating that prey possessing morphological traits that require extensive predator manipulation prior to ingestion are often afforded higher escape success.

The behavior of prey can influence the likelihood of being detected, attacked, and captured by a predator (Sih and Moore, 1990), with several studies demonstrating the importance of prey fish behavior in determining their vulnerability to piscivorous fishes (Wahl and Stein, 1988; Eklov and Persson, 1995; Christensen, 1996a,b). Prey fish response thresholds to approaching predators and prey activity in the presence of predators have each been found to influence the probability of predator attack, which may result in attacks being directed disproportionately among multiple-prey species (Webb, 1986; Christensen and Persson, 1993). In this study, differences in burst swimming speeds

among forage species did not appear to explain differences in predator capture success, as bay anchovy actually demonstrated slightly higher swimming velocities compared to other prey, yet were the easiest prey to capture. However, we did not attempt to quantify differences in prey maneuverability possibly related to distinct body shapes and fin morphologies, which may contribute to overall prey evasiveness. Reaction distances did differ considerably among forage species and may represent an important behavioral mechanism for the capture success differences that we observed. Clupeiform prey (bay anchovy and Atlantic menhaden) displayed short reaction distances, allowing predators to approach closely before attempting an escape response. The timing of the behavioral response by prey is thought to be critical in deterring attacks and evading capture (Webb, 1986), and the association we observed between prey reaction distance and predator capture success is consistent with this notion.

The results of experiments conducted across multiple tank sizes suggest that the functional relationship between piscivore capture success and relative prey size may not be affected by container volume (similar slopes), but that smaller tank sizes can produce inflated estimates of predator capture rates. We caution, however, that our findings only represent preliminary data on the effects of enclosure size on capture success of predatory fishes. Clearly, future work is needed across a larger range of tank volumes; however, estimation of capture success is limited by video technology and becomes increasingly more difficult to measure accurately in large volumes of water. The effects of tank volume on predator capture success have important implications for models attempting to simulate field conditions that utilize species-specific capture success values (e.g., individual-based foraging models). For many species, estimating these parameters in the field is logistically impossible and most investigators rely on laboratory-generated parameters (Rice et al., 1993) or threshold values based on predator diets (Adams and DeAngelis, 1987). An empirically derived relationship between tank volume and predator capture rates would help to identify appropriate behavioral scales and improve our ability to utilize laboratory-generated parameters to predict the outcome of species interactions in the field.

Although predicted profitability was a dome-shaped function for each forage species we examined, there were substantial differences among prey in the magnitude of profitability, the relative prey size at which peaks in profitability occurred, and the range of relative prey sizes over which prey were profitable. Differences in prey body mass per unit length and handling time between deep- and shallow-bodied forage species were responsible for some of the variation observed. However, most of the variation in prey profitability were caused by differences in predator capture success among forage species. This is especially true for species that share similar body morphologies (i.e., deep- or shallow-bodied), for which capture success differences accounted for nearly all of the variation in profitability. For bluefish predators, prey-specific capture success relationships alone matched prey mortality patterns observed in multispecies experiments more closely than profitability functions, which is consistent with earlier studies recognizing the central role of capture success in defining prey fish vulnerability (Breck, 1993; Juanes and Conover, 1994). Model simulations conducted by Paradis et al. (1999) to examine factors contributing to vulnerability of larval fishes to predation also indicate a strong influence of susceptibility to predator capture. In this study, the influence of predator capture success on profitability and the close association between capture success and prey mortality

provide clear evidence that differential vulnerability of forage species to predation is directly linked to variation in susceptibility to capture.

The lack of agreement between predicted bluefish profitability and forage species mortality may also be related to differential prey behavior that results in some prey being attacked at disproportionately higher rates. Profitability functions do not account for differences in encounter rates among prey and simply provide an index of predator foraging efficiency when prey species are equally available (i.e., encounter probability = 1 for all prey). Encounter probabilities of 1 for each prey species were an assumption during our large enclosure experiments based on clear water and large reaction distances of visually hunting bluefish (Olla et al., 1970; F.S. Scharf, personal observations). Relative abundances of prey in the field, environmental conditions, and behavior of both predator and prey will affect overall prey encounter rates and, thus, vulnerability of forage species. In addition, although prey may be encountered, prey behavior can strongly affect the probability of predator attack (Eklov and Persson, 1995). In larger enclosures allowing greater behavioral expression, such as those used in our mortality experiments, behavior (e.g., level of activity) of some prey may result in higher exposure to predators and be more likely to elicit predator attacks compared to other prey, resulting in disparate attack rates across prey species despite prey being equally available. Such behavioral differences may explain the higher mortality rates suffered by striped bass prey compared to Atlantic silverside when presented in multispecies groups to bluefish predators. Lower bluefish capture success on striped bass prey in single-species experiments necessitates a much higher number of bluefish attacks on striped bass compared to Atlantic silverside prey during multispecies experiments to produce the observed differences in mortality. Higher predator attack rates on striped bass prey may be related to higher activity levels of striped bass in the presence of predators compared to Atlantic silverside, which demonstrate reduced activity and utilization of surface waters as a refuge (Scharf, 2001). When predators encounter multiple-prey species simultaneously, our findings suggest that antipredator behaviors such as reduced activity, which enables prey to avoid attacks, and low reaction thresholds, which reduce their susceptibility to capture, have a considerable effect on which prey are eaten. We contend that prey behavior in the presence of predators may be even more influential than prey morphology in determining species-specific patterns of mortality.

Our findings have obvious implications for understanding the dynamics of marine forage fish populations and their impact on feeding and growth of juvenile piscivorous fishes. Research in freshwater systems has provided abundant evidence for the impact of size structure and abundance of prey fish populations on diet shifts, growth, and survival of young piscivores (Olson, 1996; Donovan et al., 1997; Michaletz, 1997; Mason et al., 1998; Mittelbach and Persson, 1998). Results from this study suggest that annual fluctuations in the characteristics of forage fish populations could have a considerable effect on the foraging efficiency of estuarine piscivores, and may contribute to interannual variation in cohort growth and survival. A growing number of studies have focused on the interacting effects of fishing and predation, particularly as they relate to alterations in food web structure and prevention of ecosystem recovery to prefishing conditions (Christensen, 1996a,b; Spencer and Collie, 1997; Whipple et al., 2000; Bundy, 2001). Collectively, these studies indicate that knowledge of species interactions, particularly predator–prey rela-

tionships, is critical to the success of ecosystem-based approaches to fisheries management. Our findings reveal that the factors influencing trophic interactions among juvenile fishes can be complex and point to the need for a mechanistic understanding of the relative vulnerability of prey in order to predict the effects of changing prey populations on predator populations and effectively manage multispecies fisheries.

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