

Estimating piscine prey size from partial remains: testing for shifts in foraging mode by juvenile bluefish

Frederick S. Scharf¹, Jeffrey A. Buckel², Francis Juanes¹ & David O. Conover²

¹Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003-4210, U.S.A.

²Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, U.S.A.

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Synopsis

Knowledge of prey sizes consumed by a predator aids in the estimation of predation impact. Young-of-the-year bluefish, *Pomatomus saltatrix*, attack their prey tail-first and often bite their prey in half; this poses a unique problem in determining prey sizes from stomach content analysis. We developed a series of linear regressions to estimate original prey lengths from measurements of eye diameter and caudal peduncle depth for striped bass, *Morone saxatilis*, bay anchovy, *Anchoa mitchilli*, American shad, *Alosa sapidissima*, blueback herring, *Alosa aestivalis*, Atlantic silverside, *Menidia menidia*, and white perch, *Morone americana*. We then used these regressions to estimate original prey sizes from pieces of prey found in stomachs of bluefish collected in the Hudson River estuary from 1990–1993. Lengths of prey that were swallowed whole were compared to estimated lengths of prey that were consumed in pieces. Lengths of prey that were consumed in pieces were larger than prey that were consumed whole. We determined the prey length/predator length ratio at which bluefish began shifting from swallowing their prey whole to partial consumption. Shifting occurred at a ratio of approximately 0.35 irrespective of prey species, suggesting that prey length plays an important role in predator foraging decisions and may contribute to gape limitations. Shifts in foraging mode effectively reduce gape limitation and allow bluefish to consume larger prey sizes which may increase their effect on prey populations.

Introduction

Fish community dynamics are strongly influenced by the effects of piscivorous predators. Recruitment success of prey species may be limited by predation on the early life history stages when prey vulnerability is high (Nielsen 1980, Sissenwine 1984, Houde 1987, Lyons & Magnuson 1987, Luecke et al. 1990, Tonn et al. 1992). Further, piscivores are known to feed selectively based on prey body size

(Ursin 1973, Hart & Hamrin 1988, Tonn et al. 1991) with a consistent pattern of selection for small-sized prey (Juanes & Conover 1994a, Juanes 1994, Paszkowski & Tonn 1994). Size-selective feeding patterns in fishes may cause substantial variability in the survival and size distributions of prey populations with much of this variability being contingent on the size structure of predator populations (Vince et al. 1976, Tonn & Paszkowski 1986, Rice et al. 1993, Wright et al. 1993). Accurate assessments of preda-

tor impact on recruitment success and size distributions of prey populations are dependent on prey size information. Therefore, knowledge of size relationships between predators and their prey are essential to understanding predator effects on prey populations.

Investigation of the modes used by predators to locate, capture, and consume their prey may provide important details on the vulnerability of specific prey and potential impact of predators. Fish have been shown to display a high degree of flexibility in foraging behavior with predator feeding mode being related to availability, behavior, and size of prey (Dill 1983, Cooper et al. 1985, Crowder 1985, Miller 1987, Chapman et al. 1989, O'Brien et al. 1989, Helfman 1994). Foraging mode plasticity also influences the types and sizes of prey consumed and may provide an adaptive mechanism that enables predators to forage in a variable environment (Helfman 1990). Because most piscivorous fishes lack the necessary dentition to sever their prey they are restricted to capturing and ingesting sizes that can be swallowed whole. Hence, piscivore gape width is often identified as the upper limit to maximum prey size available for consumption (Lawrence 1958, Hoyle & Keast 1988, Hambright 1991). Helfman & Clark (1986) however, concluded that anguillid eels were able to reduce the constraints of gape width limitation through the use of alternative prey handling modes. The ability of anguillid eels to consume large prey items by tearing off small pieces led to a direct increase in the maximum size of prey that eels were able to consume. Consequently, a piscivore that is able to reduce its gape limits by ingesting prey in smaller, more manageable pieces, may increase the range of prey sizes and consequently, the diversity of prey types it consumes.

The bluefish, *Pomatomus saltatrix*, is a piscivorous predator that displays flexibility in the foraging mode it uses to ingest prey. On the east coast of the US, adults spawn in the South Atlantic Bight in early spring and the larvae are advected northward in waters associated with the Gulf Stream (Kendall & Walford 1979, Hare & Cowen 1996). In early summer, at sizes of approximately 40–60 mm fork length, juveniles migrate across continental shelf waters and enter estuaries of the Middle Atlantic

Bight where they remain until southward migration in early fall (Nyman & Conover 1988, McBride & Conover 1991, Hare & Cowen 1996). Coincident with a habitat shift from offshore to inshore waters, juvenile bluefish diet shifts from one dominated by zooplankton to a diet that is predominantly composed of fish (Marks & Conover 1993). One east coast estuary that juveniles inhabit during their first summer of life is the Hudson River estuary. The Hudson River is inhabited by a diverse fish assemblage composed of many recreationally and commercially important species (Beebe & Savidge 1988). Previous studies have shown that bluefish consume a variety of prey fish species during summer residence in the Hudson including striped bass, *Morone saxatilis*, American shad, *Alosa sapidissima*, and bay anchovy, *Anchoa mitchilli* (Juanes et al. 1993, Juanes et al. 1994). In contrast to most piscivores (Hoyle & Keast 1987, Hart & Hamrin 1988, Hambright 1991), bluefish are capable of severing prey fishes into pieces (Lux & Mahoney 1972, Juanes & Conover 1994a). Strong adductor musculature and large, canine teeth that are interdigitated on the upper and lower jaws allow bluefish to grasp and sever prey (W. Bemis personal communication). However, bluefish also at times swallow their prey whole. This mixed foraging tactic creates a unique problem when determining sizes of prey recovered from bluefish stomachs. Moreover, it may increase the maximum prey size that bluefish consume.

Here, we describe a method to estimate the original sizes of prey fishes that were ingested in pieces by juvenile bluefish. We also examine the size-selective feeding patterns of bluefish on several different prey. We explore differences in prey size and prey body form for several fish species consumed by bluefish and determine prey length/predator length ratios that lead to a shift in foraging mode from primarily swallowing prey fish whole to consuming prey fish in pieces.

Methods

Young-of-the-year bluefish and samples of prey species were collected in the Hudson River estuary

from late June to late October between 1990–1993 by the New York State Department of Environmental Conservation and personnel from the Marine Sciences Research Center at The State University of New York at Stony Brook. Fish were captured using 30×2 m and 61×3 m beach seines. Specific station locations and additional methods of fish collections and stomach content analyses are outlined in Juanes et al. (1993) and Juanes et al. (1994).

Predictive equations were constructed relating prey fish measurements of eye diameter and caudal peduncle depth (dorsoventral depth) to prey total length (TL) using least-squares regression analysis. Equations were generated for striped bass, American shad, bay anchovy, blueblack herring, *Alosa aestivalis*, Atlantic silverside, *Menidia menidia*, and white perch, *Morone americana*. These prey species make up a significant portion of the diet of juvenile bluefish in the Hudson River estuary (Juanes et al. 1993, Juanes et al. 1994).

Regression equations were then used to reconstruct original prey length from prey remains for prey fish that were consumed in pieces. Prey fish were recovered in three conditions: (1) whole, indicating the entire prey fish was recovered as a single unit; (2) in pieces, indicating the entire prey fish was recovered in multiple units; (3) incomplete remains, indicating recovery of something less than

the entire prey fish (e.g. head or tail). For purposes of this study, all prey items recovered in any condition other than whole were termed partial prey.

Predator size-prey size scatterplots were examined to determine if differences existed between the sizes of prey swallowed whole and the reconstructed sizes of partial prey. For each prey species, least-squares regression analysis was employed to determine the relationship between prey length and predator length for whole and partial prey. Analysis of covariance (Sokal & Rohlf 1995) was used to test for differences between whole and partial prey sizes.

For bay anchovy, striped bass, and Atlantic silverside, threshold prey length/predator length ratios that led to a shift in juvenile bluefish foraging mode from swallowing prey whole to consuming prey in pieces were estimated. Relative frequencies of prey length/predator length ratios were compared for whole and partial prey. Midpoints of combined relative frequencies (whole prey + partial prey) were calculated at 0.05 intervals over the range of prey length/predator length ratios. Midpoints were fit using third-order least-squares regressions and intersections of third-order regressions with x-axes were determined to represent approximate prey length/predator length ratios associated with foraging mode shifts by juvenile bluefish for each prey species (e.g. Figure 3).

Table 1. Linear regression equations estimating prey total length (TL) from prey measurements of eye diameter (ED) and caudal peduncle depth (CP) for six prey species occurring in juvenile bluefish diets. All measurements are in millimeters. All regressions are highly significant ($p < 0.0001$). Syx = standard error of regression coefficient; r^2 values represent coefficients of determination; n = number of fish measured.

Prey	Equation	Syx	r^2	n
Bay anchovy	TL = 16.009ED + 1.257	0.447	0.97	44
	TL = 11.312CP + 2.662	0.354	0.96	44
Striped bass	TL = 14.602ED - 0.985	0.392	0.94	84
	TL = 10.604CP + 2.464	0.174	0.98	84
American shad	TL = 14.410ED + 0.637	0.485	0.94	55
	TL = 12.206CP + 0.159	0.349	0.96	55
Atlantic silverside	TL = 22.262ED - 20.745	0.849	0.93	53
	TL = 13.603CP + 0.264	0.766	0.86	53
Blueback herring	TL = 14.727ED + 1.820	1.271	0.88	21
	TL = 11.598CP + 3.733	0.957	0.89	21
White perch	TL = 14.911ED - 2.923	0.389	0.97	42
	TL = 9.991CP + 2.427	0.246	0.98	42

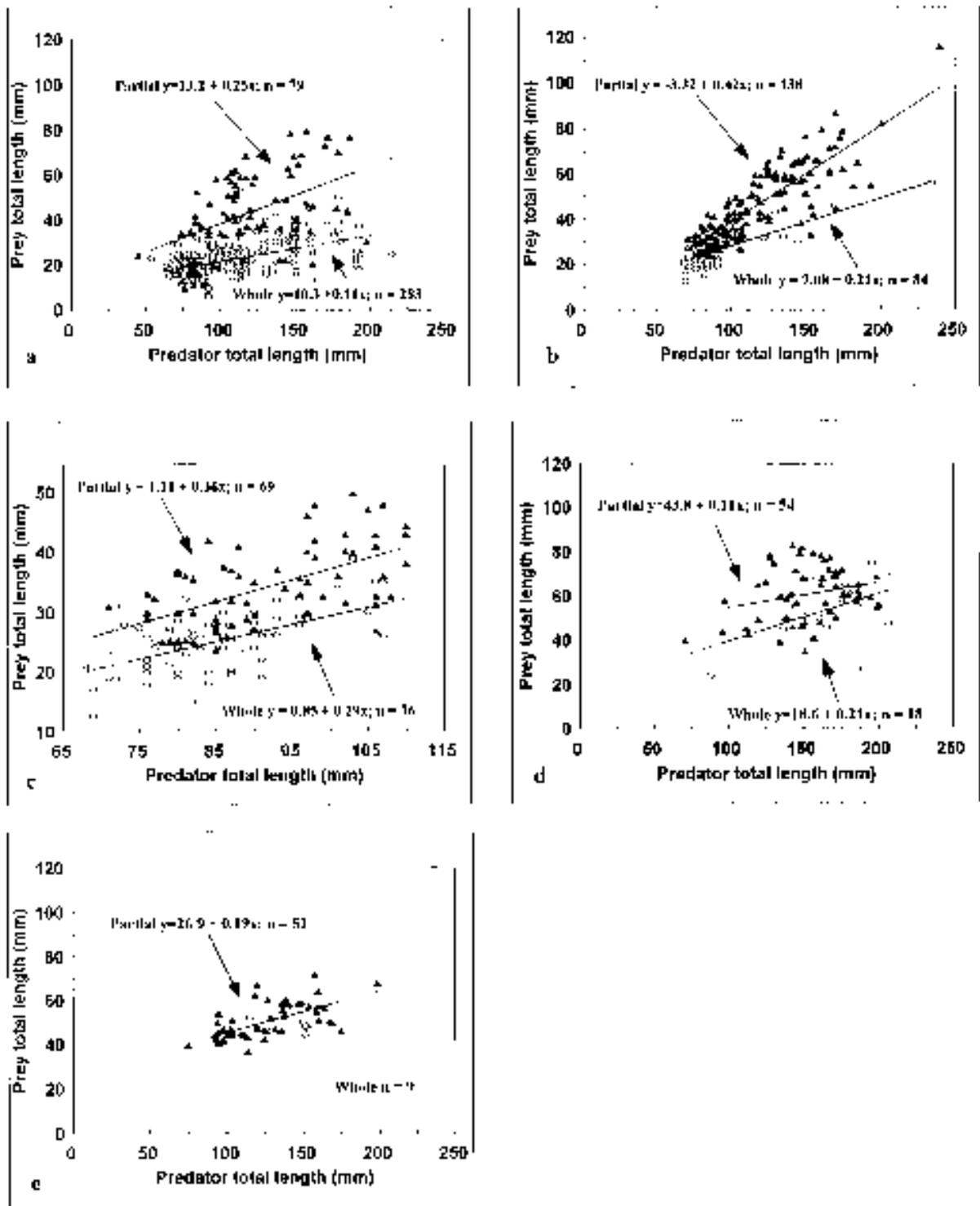


Figure 1. Prey length vs. bluefish length scatterplots for bay anchovy (a), striped bass (b), striped bass for bluefish < 110 mm TL (c), Atlantic silverside (d), and American shad (e). Least-squares regression equations are given for whole (⊖) and partial (⊕) prey for each prey species. n = measured number of fish recovered from bluefish stomachs.

Linear equations relating body depth and total length were generated for each prey species to characterize body depth differences between prey species and examine the importance of prey body form in predator foraging mode choice. Body depth was measured as the maximum dorsoventral body depth with fins depressed. Measurement locations for depth varied among prey species. Striped bass depth measurements were taken as the linear distance from the base of the first dorsal fin to the pelvic girdle; Atlantic silverside were measured from the base of the first dorsal fin to the base of the anal fin; and bay anchovy depths were measured as the linear dorsoventral distance just posterior to the operculum.

Increases in maximum prey sizes consumed were examined further through comparisons of ratios of prey body depth to bluefish mouth width. Prey body depth was estimated for each prey length using equations described above. Mouth width for bluefish was measured as the linear distance separating the inside edges of the slightly stretched cleithra bones. Bluefish mouth widths were estimated for each bluefish length using equations relating mouth width to total length. Across prey species, maximum prey body depth to bluefish mouth width ratios for whole and partial prey were identified and compared.

Size-selective feeding patterns were assessed through comparison of prey length frequency distributions in bluefish diets to prey length frequency distributions in the environment for species and dates with sufficient data. Because prey length frequencies were generally not distributed normally a Median test (Zar 1984) was applied to compare medians of the two distributions.

Results

A positive linear relationship existed between prey eye diameter and prey caudal peduncle depth and prey total length for all six prey species examined (Table 1). Coefficient of determination values (r^2) ranged from 0.86 to 0.98.

Prey sizes consumed increased significantly with increasing bluefish size across prey species for

whole and partial prey (Figure 1; $p < 0.0001$ for all prey types except Atlantic silverside (Figure 1d): $p < 0.05$ for whole prey, and $0.05 < p < 0.10$ for partial prey). Significant differences were detected between regression coefficients of whole and partial prey for bay anchovy ($F = 15.245$; $p < 0.001$) and striped bass ($F = 32.574$; $p < 0.001$) with partial prey having larger slopes for both species (Figure 1a, b). Therefore, tests for differences in elevations between whole and partial prey could not be performed for these two species. However, a substantial clustering of the data was apparent for bluefish < 110 mm TL feeding on striped bass with only minimal data representing prey swallowed whole for bluefish exceeding this length (Figure 1b). To further examine this clustering of data, striped bass TL was plotted against bluefish TL for bluefish < 110 mm TL (Figure 1c). For these data, we did not detect significant differences between regression coefficients of whole and partial prey ($F = 0.875$; $p > 0.25$). However, elevations of whole and partial prey regressions were significantly different ($F = 67.044$; $p < 0.001$) with partial prey having a higher elevation. Similarly, significant differences between slopes could not be detected ($F = 0.749$; $p > 0.25$) for Atlantic silverside and elevation of partial prey was significantly higher than elevation of whole prey ($F = 6.773$; $p < 0.025$) (Figure 1d). American shad were consumed primarily in pieces by juvenile bluefish and therefore comparisons between partial and whole prey regressions could not be made (Figure 1e). Maximum sizes of each prey species consumed in pieces were larger than maximum sizes of each prey species swallowed whole over a range of bluefish sizes (Figure 2).

Prey length/predator length ratios that led to a shift in bluefish foraging mode from swallowing prey whole to consuming prey in pieces were approximately equal for three distinct prey species (Figure 3). These ratios ranged from 0.33 for bay anchovy to 0.39 for Atlantic silverside, with striped bass yielding a ratio of 0.35. For each prey species, prey lengths exceeding one-third predator length were primarily consumed in pieces while prey lengths less than one-third predator length were primarily swallowed whole. Significant differences were detected between the length-depth relation-

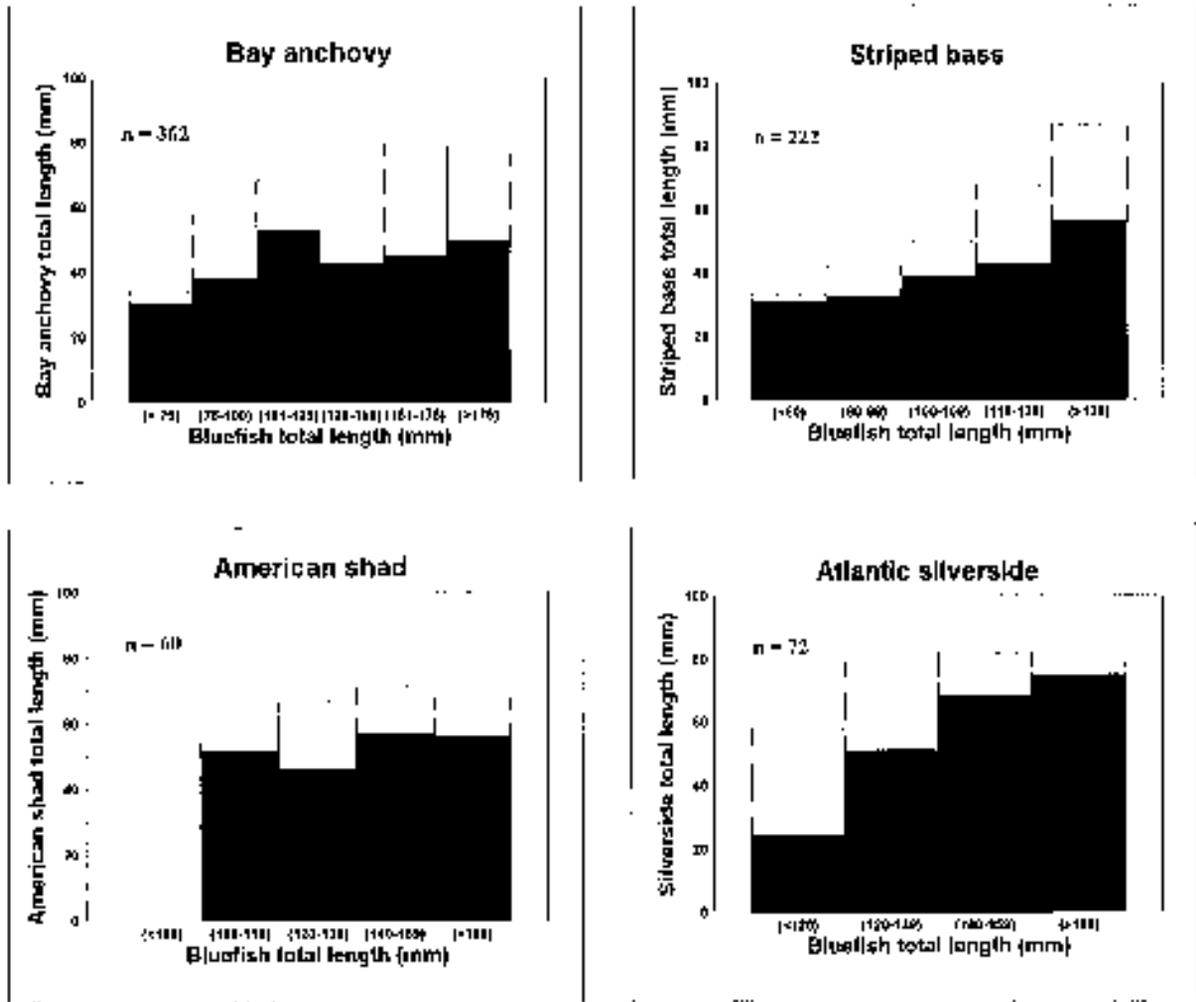


Figure 2. Maximum sizes of whole (j) and partial (n) prey consumed by juvenile bluefish. Differences between maximum sizes of whole and partial prey are illustrated for four prey species. Bluefish total length ranges from 50 mm to 250 mm and is partitioned into groups of widths equal to approximately 20 mm to 25 mm TL depending upon the number of fish measured (n).

ships of these three prey species (Figure 4; $F = 49.733$, $p < 0.001$; post-hoc tests indicated significant differences between all pair-wise combinations). Despite large differences in prey body depth, bluefish shifted from whole to partial prey at approximately the same prey length/predator length ratio for each prey species.

Across prey species, maximum prey body depth to bluefish mouth width ratios for prey swallowed whole ranged from 0.48 to 0.66, whereas maximum ratios for prey consumed in pieces were 28% to 37% larger, ranging from 0.66 to 0.86.

For six of the seven dates examined the median of prey length frequency distributions recovered from juvenile bluefish stomachs was significantly smaller than the median of prey length frequency distributions sampled in the field at the same location and time of day (Figure 5). The results were independent of prey species and were consistent across three years of sampling. The majority of prey sizes present on particular sampling dates were within bluefish gape width limitations (see below), indicating that bluefish were selecting small prey sizes from those available in the environment.

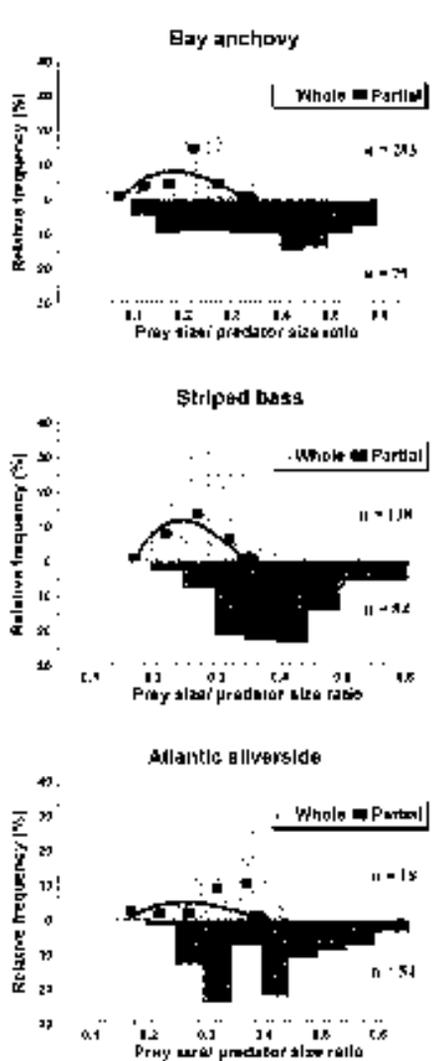


Figure 3. Comparison of frequency distributions of prey length/predator length ratios between whole and partial prey for three prey species consumed by juvenile bluefish. Bars represent 0.05 intervals of prey length/predator length ratios. Midpoints (\bar{x}) of combined frequencies (whole + partial) are fit using third-order regressions. Intersections of regressions with x-axes (\bar{d}) indicate approximate prey length/predator length ratios leading to a shift in bluefish foraging mode. Bay anchovy: ratio = 0.33; $y = 312.64 \times -1194.80 \times^2 + 1209.35 \times^3 - 16.48$; $p = 0.008$. Striped bass: ratio = 0.35; $y = 1777.56 \times -5624.74 \times^2 + 5410.30 \times^3 - 165.61$; $p = 0.017$. Atlantic silverside: ratio = 0.39; $y = 406.24 \times -1149.16 \times^2 + 955.60 \times^3 - 39.72$; $p = 0.207$. n = number of fish measured.

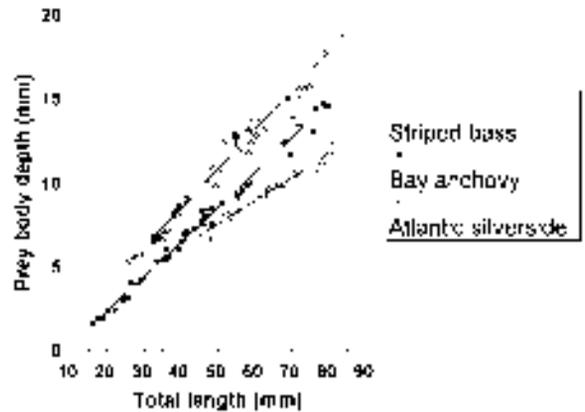


Figure 4. Length-body depth relationships for striped bass ($y = 0.232 \times - 0.788$; $n = 71$), bay anchovy ($y = 0.207 \times - 1.812$; $n = 46$), and Atlantic silverside ($y = 0.138 \times + 0.694$; $n = 38$).

Discussion

Measurements of prey eye diameter and caudal peduncle depth represent adequate predictors of original prey length for a variety of prey species recovered from bluefish guts (Table 1). Diagnostic bones including cleithra, dentaries, opercles, pharyngeal arches, and vertebrae have frequently been used to reconstruct original prey lengths from digested remains recovered from the stomachs of piscivores (Pikhu & Pikhu 1970, Newsome 1977, McIntyre & Ward 1986, Trippel & Beamish 1987, Hansel et al. 1988). The relatively large chunks of prey fishes consumed by bluefish permit the use of external morphological prey measurements to estimate original prey length. The ability to reconstruct original prey sizes is especially important when studying a predator that incorporates plasticity into the modes it uses to consume prey.

Shifts in foraging mode are common for a variety of animals with determinants of mode shifts and potential benefits being dependent on specific predator-prey combinations (Helfman 1990). Foraging theory predicts that animals will choose feeding alternatives in order to maximize energy gained relative to energy lost while acquiring food (Stephens & Krebs 1986, Schoener 1987). Hence, the incorporation of flexibility in the foraging process may provide animals with a means to increase fitness through appropriate decision-making in a variable foraging environment (Dill 1983).

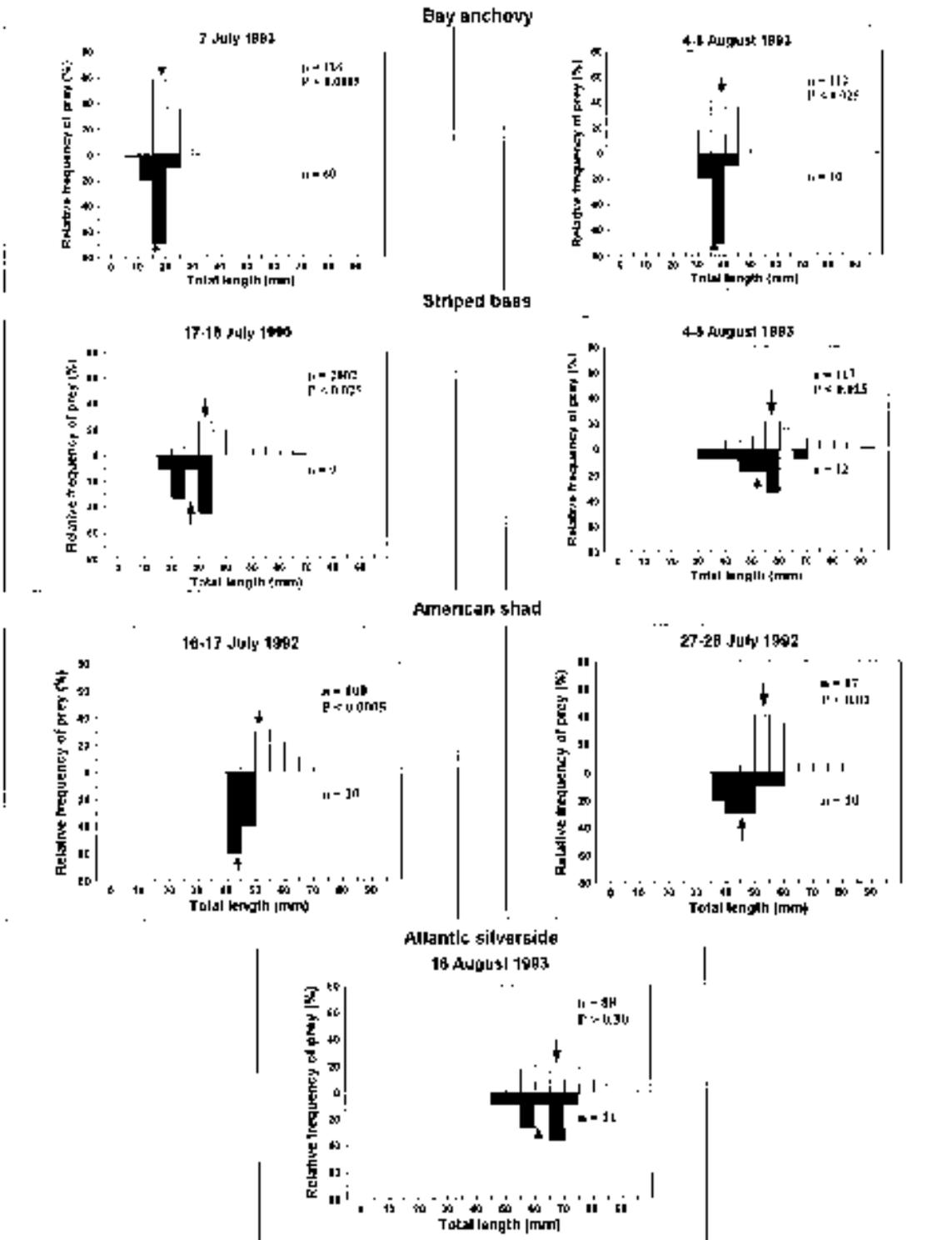


Figure 5. Comparison of length-frequency distributions of four prey species recovered from bluefish guts (j) with same species sampled in the field (h) at the same locations on the dates indicated. Medians of each distribution are indicated by arrows (n = number of fish measured, P = probability value of the median test).

The handling of prey is one component of the foraging process that entails flexibility (Miller 1987, Wainwright 1988, Helfman 1990, Helfman 1994). Prey handling refers to the manipulation of prey from the point of capture to ingestion and shifts in this feeding mode are frequently determined by prey escape ability and prey size (Helfman 1990). The ability to reduce predator gape width limitations and increase prey sizes consumed is demonstrated in the foraging mode flexibility of anguillid and muraenid eels (Helfman & Clark 1986, Miller 1989). However, Helfman & Winkelman (1991) proposed that although alternative handling modes represented an adaptive way for anguillid eels to expand diet breadth in terms of prey size, they were energetically expensive and were only employed when smaller prey were absent.

For bluefish, a general increase in prey size consumed with increasing bluefish size was observed for whole and partial prey across prey species (Figure 1). Average and maximum sizes of partial prey were larger than those for whole prey over a range of bluefish sizes for each prey species (Figures 1, 2). These results suggest that the ability of bluefish to sever large prey fish provides a means to effectively reduce gape width limitations and allows them to increase the maximum prey size and potentially the diversity of prey types they consume. Foraging mode shifts from swallowing prey whole to consuming prey in pieces occurred at similar prey length/predator length ratios for striped bass, bay anchovy, and Atlantic silverside (Figure 3). These three prey species diverge in their length-depth relationships (Figure 4) and in body form. Therefore, for prey sizes within gape width limits prey length, not prey body depth, may be the major determining factor in foraging mode choice by bluefish.

Recent studies have focused primarily on prey body depth (measured dorsoventrally) as the factor responsible for regulating maximum prey size ingested by a piscivore (Hoyle & Keast 1987, Hambricht 1991, Hambricht et al. 1991). Hoyle & Keast (1988) found that largemouth bass with mouth widths of 20 mm were capable of swallowing bluegill sunfish of up to 54 mm total length corresponding to a prey body depth of 15.5 mm (Lawrence 1958) and a prey body depth/mouth ratio of 0.775,

respectively. However, bass mouth width was measured as the inner dimension of the mouth at the angle of the jaws (Hoyle & Keast 1988). Lawrence (1958) showed that the exterior distance between the posterior tips of the maxillary bones best approximated the distance between the cleithra bones which was thought to regulate prey size. Hence, mouth width as measured by Hoyle & Keast (1988) probably underestimates true mouth width of largemouth bass leading to an overestimate of maximum prey body depth/mouth width ratio.

Maximum prey body depth/mouth width ratios for bluefish swallowing prey whole ranged from 0.48 to 0.66, whereas maximum ratios for bluefish consuming prey in pieces were substantially larger, ranging from 0.66 to 0.86. Assuming that mouth widths for largemouth bass were underestimated, maximum prey body depth/mouth width ratios for bass would more closely approximate maximum prey body depth/mouth width ratios for whole prey consumed by bluefish. This would be expected since bass lack specialized dentition and are confined to prey that they are able to swallow whole (Hoyle & Keast 1988). Because bluefish consume large prey fish in pieces, maximum prey body depth consumed increases relative to mouth width, thereby increasing the maximum size of prey they are capable of consuming. We argue that although prey body depth plays a critical role in determining the size of prey fishes available for predator consumption, prey length also limits available prey sizes, and that prey size limitations caused by prey length may be greater for piscivores that are restricted to swallowing prey fishes whole.

Although bluefish increased their maximum prey sizes by severing their prey, they consistently fed on prey sizes that were smaller than those available in the environment (Figure 5). Selection for smaller than average prey sizes is common among piscivorous fishes (Gillen et al. 1981, Knight et al. 1984, Hoyle & Keast 1987, Juanes 1994, Paszkowski & Tonn 1994). This pattern contrasts with observations of feeding behavior in planktivorous fishes which tend to ingest larger prey items preferentially (Brooks & Dodson 1965, Werner & Hall 1974, Langeland & Nost 1995). Piscivore foraging models have predicted that, similar to planktivorous fishes,

piscivores should select larger prey sizes to maximize feeding efficiency (Ivlev 1961, Harper & Blake 1988). The overestimation of optimal prey sizes in previous piscivore foraging models may be the result of failure to incorporate capture success rates into ratios of energy gain to handling time (Breck 1993, Juanes 1994). Hence, apparent preferences for small prey sizes by piscivores may represent a passive process mediated by differential size-based capture success, rather than active predator choice (Juanes 1994, Juanes & Conover 1994a). In this study, bluefish were able to consume larger prey through the use of an alternate foraging mode yet still did not preferentially ingest the largest prey sizes available in the field. Maximum prey sizes consumed in pieces approached, but did not equal bluefish gape width limits (defined in this study as the inside linear distance between the cleithra bones), indicating that size-dependent capture success may play a significant role in bluefish foraging.

Recent work directed at evaluating bluefish life history has determined that, for a temperate fish, bluefish exhibit extremely high growth rates during their first summer of life (McBride & Conover 1991, Juanes & Conover 1994b). These high rates of growth are thought to be due in large part to the rapid gastric evacuation and consumption rates exhibited by bluefish during estuarine residency (Juanes & Conover 1994b, Buckel et al. 1995, Buckel & Conover 1996). These attributes are strongly linked to an early ontogenetic change to a piscivorous lifestyle and the matching of estuarine arrival with the availability of appropriate sized prey (Juanes et al. 1994). Our results suggest that in combination with these life history traits, foraging mode shifts may increase potential effects of bluefish predation and present important implications for estuarine community structure.

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