

**ESTIMATING PISCINE PREY SIZE FROM PARTIAL REMAINS: TESTING
FOR SHIFTS IN FORAGING MODE BY BLUEFISH IN THE HUDSON RIVER**

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ABSTRACT

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 height 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. The ratio at which shifting occurred was approximately equal for three different prey species. These results suggest 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 provide bluefish with an expanded prey size range which may increase their potential effect on prey populations.

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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 (Sissenwine 1984; Houde 1987; Luecke et al. 1990). Further, piscivores are known to feed selectively based on prey body size (Ursin 1973; Hart and Hamrin 1988; Tonn et al. 1991) with a consistent pattern of selection for small-sized prey (Juanes and Conover 1994b; Juanes 1994; Paszkowski and 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; Rice et al. 1993; Wright et al. 1993). Accurate assessments of predator 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 potential predator effects and community structure.

Investigation of the methods 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 behaviour with predator choice and feeding mode being related to availability, behaviour, and size of the prey as well as competition and predation risk (Dill 1983; Crowder 1985; O'Brien et al. 1989). Foraging mode plasticity also influences the types and sizes of prey consumed and may provide an adaptive mechanism which 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 only prey fish which 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 and Keast 1988; Hambright 1991). Helfman and Clark (1986) however, concluded that anguillid eels were able to reduce the constraints of gape 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 available for consumption. Consequently, a piscivore that is able to reduce its gape limits by ingesting prey in smaller, more manageable pieces may have potentially greater effects on prey populations and community structure.

The bluefish (*Pomatomus saltatrix*) is a piscivorous predator that displays flexibility in the foraging mode it uses to ingest its prey and therefore presents an ideal opportunity to study the potential effects of such mode shifts on prey populations. In North America, adult bluefish spawn in the South Atlantic Bight in early spring and the larvae are advected northward in waters associated with the Gulf Stream (Nyman and Conover 1988; McBride and Conover 1991). In early summer, at sizes of approximately 40-60mm fork length, juveniles migrate across continental shelf waters and enter estuaries of the Middle Atlantic Bight (McBride and Conover 1991). Coincident with a habitat shift from offshore to inshore waters is a shift in diet from one dominated by zooplankton offshore to a diet that is predominantly composed of fish inshore (Marks and Conover 1993). One east coast estuary that juveniles inhabit during their first summer of life is the Hudson River estuary wherein their diet is composed of many recreationally and commercially important fish species including striped bass (*Morone saxatilis*), American shad (*Alosa sapidissima*), and bay anchovy (*Anchoa mitchilli*) (Juanes et al.

1993; Juanes et al. 1994). A second wave of bluefish recruits is typically produced in the Middle Atlantic Bight in early summer but appears to contribute only marginally to the adult stock (Chiarella and Conover 1990; McBride and Conover 1991).

In contrast to most piscivores (Hoyle and Keast 1987; Hart and Hamrin 1988; Hambright 1991), bluefish are capable of severing prey fishes into pieces to facilitate the swallowing process (Lux and Mahoney 1972; Juanes and Conover 1994b). In addition to swallowing prey fishes whole, bluefish frequently employ this alternative foraging mode which is made possible by the existence of large, canine teeth that are interdigitated on the upper and lower jaws. The interdigitation of upper and lower teeth not only allows bluefish to grasp prey items but also permits the severing of prey (W. Bemis, personal communication). This foraging strategy creates a unique problem when determining sizes of prey recovered from bluefish stomachs. Further, it may provide a means for bluefish to increase the maximum prey size they can consume, thereby potentially increasing the effects of bluefish predation on prey populations.

Here, we describe a method to estimate the original sizes of prey fishes that were ingested in pieces by juvenile bluefish. We examine the size-selective feeding patterns of bluefish and we explore differences in prey size and prey body form for several fish species consumed by bluefish. In addition, we determine prey length/predator length ratios that lead to a shift in foraging mode from primarily swallowing prey fish whole to consuming prey fish mainly in pieces. Lastly, we discuss the potential implications of this atypical feeding behaviour for prey populations.

METHODS

Young-of-the-year (YOY) bluefish were collected in the summers of 1992 and 1993 approximately biweekly from mid-June through late October. Additional bluefish collected from 1990-1993 were provided by the New York State Department of Environmental Conservation (NYDEC). The study area consisted of a 24-km section of the lower Hudson River estuary (Fig. 1). Eight sites were sampled in 1992 and 1993 by personnel at the Marine Sciences Research Center (MSRC), Stony Brook, NY and twenty-five sites were sampled from 1990-1993 by NYDEC personnel.

All fish were captured using a 61m x 3m beach seine (13mm mesh wings and a 6mm mesh bag) set from a boat. YOY bluefish were immediately preserved in 10% buffered formalin for later diet analysis. Subsamples of important prey species were preserved in 10% buffered formalin to generate prey length frequency distributions and construct predictive equations. All other fish captured were sorted by species, counted, and subsequently returned to the river.

Bluefish were weighed to the nearest 0.01g (wet weight) and measured for total length and fork length to the nearest 0.01mm. Stomachs were removed with incisions just anterior to the intestine and just posterior to the pharynx and the contents were identified to the lowest taxon possible, counted, weighed and measured. Although bluefish frequently sever their prey, the pieces are normally large and therefore prey fish were often identified to species. Preserved subsamples of prey fish were similarly weighed and measured.

Predictive equations were constructed relating prey fish measurements of eye diameter and caudal peduncle height (dorsoventral height) to prey total length using

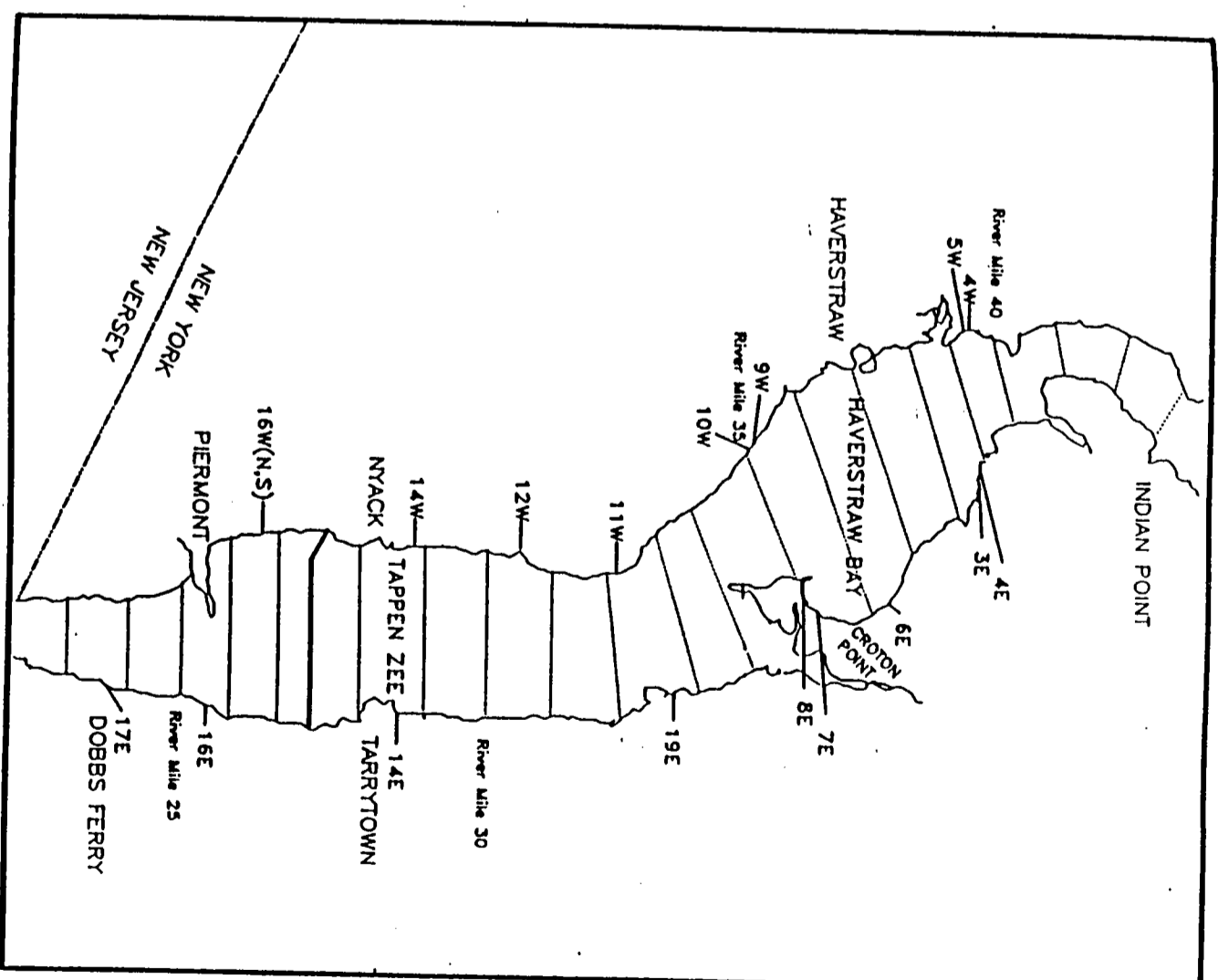


Figure 1. Map of the lower Hudson River. Numbers correspond to sampling stations of the New York State Department of Environmental Conservation. Bluefish and prey samples were collected at several of these sampling stations.

least-squares regression analysis. Additional equations describing total length-weight relationships were similarly constructed. Equations were generated for six species collected in the Hudson River estuary. These include striped bass, American shad, bay anchovy, blueback 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 during their residence in Middle Atlantic Bight estuaries (Friedland et al. 1988; Juanes et al. 1993; Hartman and Brandt 1995). Regression equations were then used to reconstruct original prey total 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 and were thus pooled as such.

Size-selective feeding patterns were assessed through comparison of prey size frequency distributions in bluefish diets and the environment. Length frequency distributions were produced from bluefish stomach contents and field samples for the four prey species with sufficient data (prey species mentioned previously, excluding blueback herring and white perch). All subsequent analyses were undertaken using these four prey species. Samples from two dates were analyzed for each prey species except Atlantic silverside for which only one date was analyzed. Because prey length frequencies were generally not distributed normally, a Median test (Zar, 1984) was applied to compare medians of prey length frequency distributions recovered from bluefish stomachs to

medians of prey length frequency distributions collected in the field for the same date, time, and location.

Predator size-prey size scatterplots were examined to determine if differences existed between the sizes of prey swallowed whole and the sizes of prey consumed in pieces. Prey sizes for partial prey refer to total lengths reconstructed from regression equations. Least-squares regression analysis was employed to determine the relationship between predator size and prey size for whole and partial prey. Analysis of covariance (ANCOVA) was used to test for differences between whole prey sizes and partial prey sizes.

To further explore differences in prey sizes of whole and partial prey we calculated prey length/predator length ratios for both prey conditions. Ratios were calculated using total lengths for each predator-prey pair and were then transformed using an arcsine transformation (Zar, 1984) in order to test for differences. Because transformed ratios were not all distributed normally (Shapiro-Wilk test) and displayed heterogeneity among variances (Bartlett's test), a Wilcoxon two-sample test (Sokal and Rohlf 1995) was employed to test for differences between the prey length/predator length ratios of whole and partial prey items. Prey length/predator length ratios for partial prey were compared across species using a Kruskal-Wallis test (Sokal and Rohlf 1995) to test for similarities in predator size-prey size relationships for prey consumed in pieces. Maximum size of prey swallowed whole was compared to maximum size of prey consumed in pieces for a range of bluefish sizes using a sign test for each prey species. Maximum partial prey sizes refer to prey lengths reconstructed from regression equations.

Threshold prey length/predator length ratios that constituted a shift in juvenile bluefish foraging mode from primarily swallowing prey fish whole to consuming prey fish mainly in pieces were approximated for the three prey species with sufficient data, namely bay anchovy, striped bass, and Atlantic silverside. 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 or 0.10 intervals over the range of prey length/predator length ratios. Midpoints were fit using a 3rd order polynomial regression equation and intersections of 3rd order curves 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. Relationships between total length and maximum body width were generated for each prey species to examine the importance of prey body form in predator foraging mode choice. Maximum body width was equal to maximum dorsoventral body width. Measurement locations for width varied among prey species. Striped bass width 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 width was measured as the linear dorsoventral distance just posterior to the operculum.

RESULTS

A positive linear relationship existed between prey eye diameter and prey caudal peduncle height 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. Similarly, a significant relationship existed relating prey total length to prey weight for each prey species (Table 2). Coefficient of determination values (r^2) ranged from 0.90 to 0.98.

For six of 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 (Fig. 2). The results were independent of prey species as well as prey size range and were consistent across three years of sampling. The majority of prey sizes present on given sampling dates were within bluefish gape limitations (see below) and therefore available for consumption. Thus, juvenile bluefish were selectively feeding on smaller prey sizes when presented with a range of available prey sizes.

Prey sizes consumed increased significantly with increasing bluefish size across prey species for whole and partial prey (Fig. 3; p-values were less than 0.0001 for all regressions except those involving Atlantic silverside (Fig. 3D) which were only marginally significant at the 0.05 alpha level for whole prey and significant at the 0.10 alpha level for partial prey). Significant differences were detected between regression coefficients for 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 yielding larger slopes for both species (Fig. 3A and 3B). Therefore, tests for differences in elevations between whole and partial prey could not be administered for these two species. However, a substantial

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

Prey	Equation	r^2	n
Bay Anchovy	TL=16.009ED + 1.257	0.97	44
	TL=11.312CP + 2.662	0.96	44
Striped Bass	TL=14.602ED - 0.985	0.94	84
	TL=10.604CP + 2.464	0.98	84
American Shad	TL=14.410ED + 0.637	0.94	55
	TL=12.206CP + 0.159	0.96	55
Atlantic Silverside	TL=22.262ED - 20.745	0.93	53
	TL=13.603CP + 0.264	0.86	53
Blueback Herring	TL=14.727ED + 1.820	0.88	21
	TL=11.598CP + 3.733	0.89	21
White Perch	TL=14.911ED - 2.923	0.97	42
	TL=9.991CP + 2.427	0.98	42

Table 2. - Length-weight relationships for six prey species occurring in juvenile bluefish diets. Equations estimate prey weight (W) in grams from prey total length (TL) in millimeters. All regressions are highly significant ($p < 0.0001$). r^2 values represent coefficients of determination; n = number of fish measured.

Prey	Equation	r^2	n
Bay Anchovy	W=0.000000166TL ^{3.328}	0.99	44
Striped Bass	W=0.000000353TL ^{3.273}	0.99	84
American Shad	W=0.000000279TL ^{3.244}	0.99	55
Atlantic Silverside	W=0.000000508TL ^{3.055}	0.98	53
Blueback Herring	W=0.000000300TL ^{3.196}	0.90	21
White Perch	W=0.000000242TL ^{3.409}	0.99	42

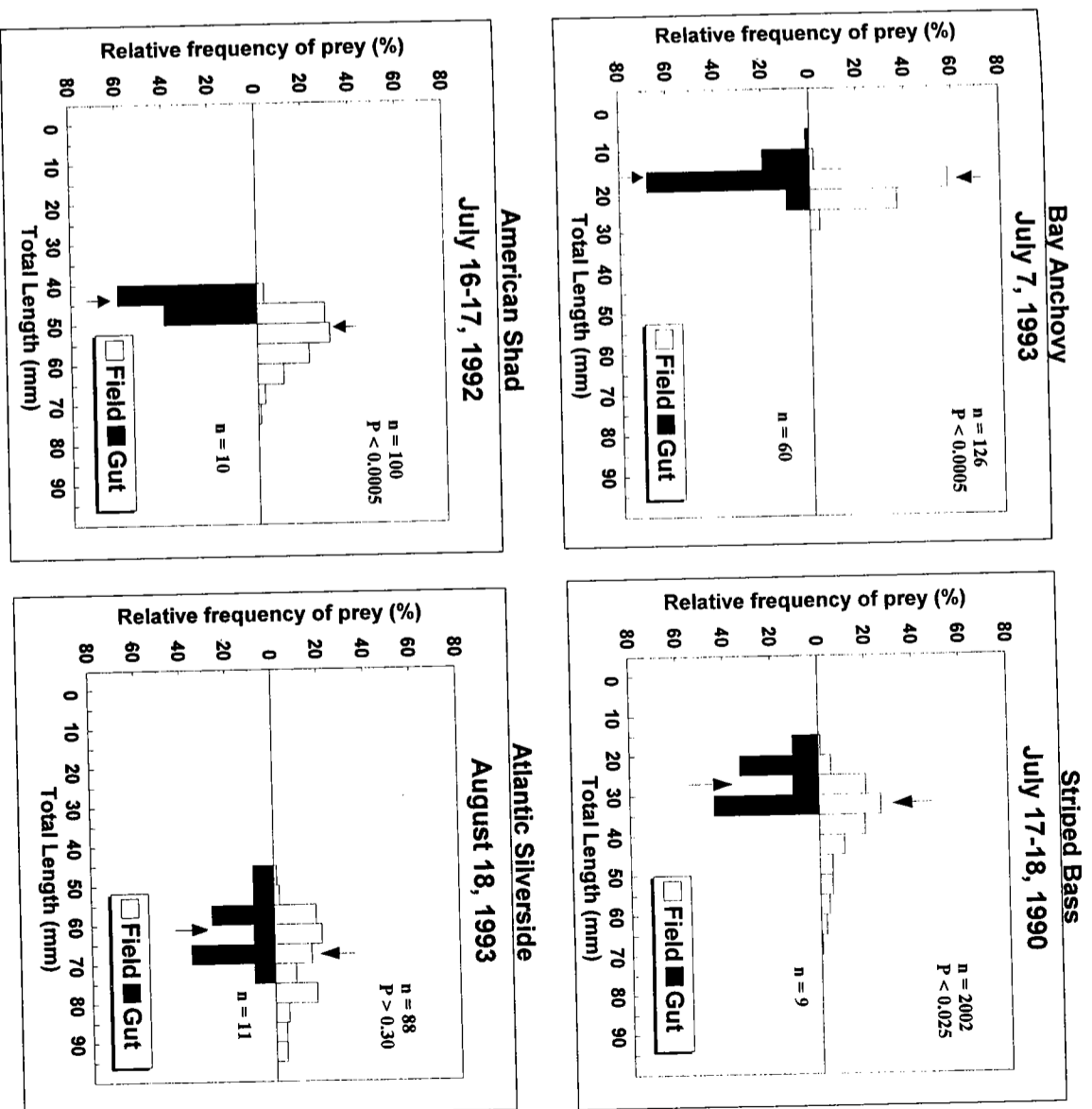


Figure 2. Comparison of length-frequency distributions of four prey recovered from bluefish guts with the same prey sampled in the field at the same locations on the dates indicated. Only four of the seven dates analyzed are shown. Medians of each distribution are indicated by arrows. n = number of fish measured. p = probability value of the median test.

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 (Fig. 3B). To further examine this clustering of data, striped bass TL was plotted against bluefish TL for bluefish less than 110mm total length (Fig. 3C). For these data, we did not detect significant differences between regression coefficients of whole and partial prey ($F = 0.875$; $p > 0.25$). Elevations of whole and partial prey were, however, significantly different ($F = 67.044$; $p < 0.001$) with partial prey yielding a higher elevation. Similarly, for Atlantic silverside significant differences between slopes could not be detected ($F = 0.749$; $p > 0.25$) and elevation for partial prey was significantly higher than elevation for whole prey ($F = 6.773$; $p < 0.025$) (Fig. 3D). American shad were consumed primarily in pieces by juvenile bluefish, thus, we lacked sufficient data for whole prey to make any comparisons between sizes of American shad swallowed whole and those consumed in pieces (Fig. 3E).

Prey length/predator length ratios for partial prey were significantly larger than prey length/predator length ratios for whole prey (Wilcoxon two-sample test; all p -values < 0.005) (Table 3). These results indicate that, relative to bluefish size, average prey size consumed in pieces was larger than average prey size swallowed whole over a range of bluefish sizes and prey species. Partial prey length/predator length ratios for each prey species were indistinguishable from one another (Kruskal-Wallis test; $p = 0.326$) (Table 3) suggesting similar predator size-prey size relationships for all partial prey, regardless of prey species.

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

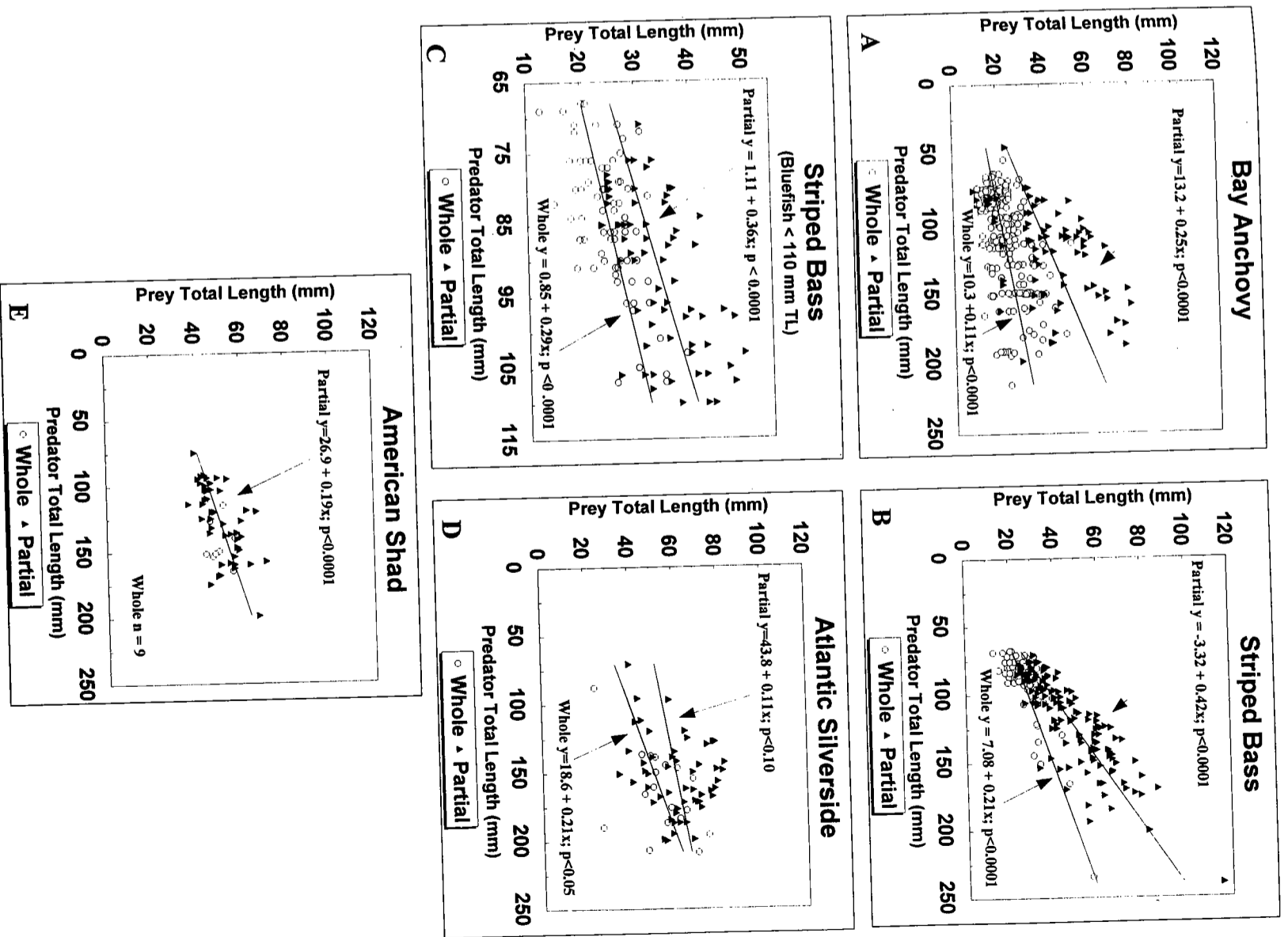


Figure 3. Prey length vs. bluefish length scatterplots for bay anchovy (A), striped bass (B), Atlantic silverside (D), and American shad (E). Least-squares regression equations are given for whole and partial prey for each prey species. Figure 1(C) represents striped bass length vs. bluefish < 110 mm TL.

Table 3.- Mean prey length/predator length ratios (+/- SE) for whole and partial prey for each prey species. Wilcoxon two-sample tests resulted in significant differences between ratios for whole and partial prey within each prey species ($p < 0.005$ for all prey species). A Kruskal-Wallis test did not detect significant differences between ratios for partial prey ($p = 0.3256$) among prey species. n = number of fish measured.

Prey Species	Mean prey length/predator length ratios		n	
	Whole	Partial	Whole	Partial
Bay Anchovy	0.214 ± 0.004	0.362 ± 0.015	283	79
Striped Bass	0.290 ± 0.005	0.386 ± 0.006	84	138
Atlantic Silverside	0.326 ± 0.016	0.405 ± 0.014	18	54
American Shad	0.356 ± 0.019	0.409 ± 0.009	9	51

(Fig. 4). Increases in maximum sizes of prey consumed in pieces over maximum sizes of prey swallowed whole represent an increase in the prey size range available for juvenile bluefish consumption.

Prey length/predator length ratios that led to a shift in bluefish foraging mode from primarily swallowing prey whole to consuming prey mainly in pieces were approximately equal for three distinct prey species (Fig. 5). These ratios ranged from 0.34 to 0.39, suggesting that prey lengths exceeding 1/3 predator length were consumed mainly in pieces while prey lengths less than 1/3 predator length were primarily swallowed whole. These results are suggestive of a general pattern in bluefish foraging with mode choice being primarily dependent upon prey length. Relationships between prey total length and maximum prey body width were generated to exemplify distinctions between prey species. Large differences were evident between the length-width relationships of the 3 prey species (Fig. 6), yet bluefish shifted from whole to partial prey at approximately the same prey length/predator length ratios further supporting the role of prey length as a decisive factor in foraging mode choice.

DISCUSSION

Bluefish have been described as "animated chopping machines" cutting large prey items into pieces to facilitate ingestion (Baird, 1873). The severing of prey confounds efforts to estimate the potential impact of bluefish predation on the recruitment success and size distributions of their prey species. 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

