

## Accelerating the onset of piscivory: intersection of predator and prey phenologies

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Piscivorous fishes tend to be able to consume other fishes early in development and generally experience a dramatic increase in growth after the ontogenetic diet shift to piscine prey. Hence, an acceleration of the onset of piscivory may be favoured strongly by natural selection. Temperate freshwater piscivores, for example, becomes piscivorous at a relatively young age by spawning in advance of, and thereby achieving a size advantage over, the young of their piscine prey. Research in various North American estuaries suggests that young-of-the-year (YOY) bluefish *Pomatomus saltatrix*, an offshore-spawning estuarine-dependent marine fish, may accelerate the onset of piscivory by being advected to higher latitudes and timing their estuarine entry with the appearance of small coastal fishes. This hypothesis was tested by: (i) determining the annual recruitment date of YOY bluefish and their prey; and (ii) examining the diet and prey size preferences, and predator size–prey size relationships, of YOY bluefish in two different estuarine systems: Great South Bay, and the lower Hudson River. Results suggest that the relationships between bluefish and their prey are determined by a complex interplay between recruitment timing of both predator and prey, prey size availability, predator selectivities, and the timing of vernal warming. It is concluded that YOY bluefish migration into northern estuaries at an advanced size provides them with a predatory size advantage over their principal piscine prey thereby facilitating an early diet shift to piscivory while minimizing the time spent as planktivores.

Key words: bluefish; size selectivity; predator–prey relationships; piscivory.

### INTRODUCTION

Virtually no teleosts are piscivorous at hatching. The early life stages of most piscivores feed initially on zooplankton or other invertebrates and then undergo an ontogenetic shift to a diet of fish as larger size is attained (Popova, 1978; Keast, 1985a). Many species experience a dramatic increase in growth after the diet shift to piscine prey (Larkin *et al.*, 1957; Paloheimo & Dickie, 1966; Martin, 1966; Wicker & Johnson, 1987; Juanes & Conover, in press a). All else being equal, minimizing the time spent on an invertebrate diet would appear to increase fitness because it would allow for more rapid development through the juvenile stages. If so, the evolution of life history strategies in piscivores that minimize the duration of the planktivorous feeding stage is to be expected. One such strategy would be to match the timing and location of spawning with the availability of piscine prey.

Keast (1985a) observed that in temperate lakes, piscivore species tend to spawn earlier in the year than do other fishes. Some young-of-the-year (YOY) piscivores thereby attain sufficient size to enable consumption of the young of other fishes spawned later in the same year. Several studies of freshwater systems

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have shown that the availability of piscine prey of appropriate size greatly influences the growth rate, survival, and year class strength of piscivores (Keast & Eadie, 1985; Adams & DeAngelis, 1987; Wicker & Johnson, 1987; Buijse & Houthuijzen, 1992). Similar findings with respect to marine systems, however, are non-existent.

The bluefish, *Pomatomus saltatrix* L., is an estuarine-dependent marine piscivore of circumglobal distribution (LeGall, 1934; Briggs, 1960). Among temperate North American coastal fishes it is unique in the large size it attains at age 1 (Juanes, 1992), and it is the only fish to enter the U.S. coastal fishery in the YOY stage (i.e. at about 120 days) (Nyman & Conover, 1988). Spawning occurs offshore over different regions of the continental shelf at various times of the year (Kendall & Walford, 1979). Those fish spawned in the South Atlantic Bight in early spring are advected northward in waters associated with the Gulf Stream and then migrate abruptly into Middle Atlantic Bight estuaries at c. 60 mm fork length (F.L.) (Nyman & Conover, 1988). The offshore to inshore habitat shift coincides with both an abrupt increase in growth rate (McBride & Conover, 1991) and a feeding shift from planktivory to piscivory (Marks & Conover, 1993). Controlled diet studies in the laboratory suggest that the shift from invertebrate to piscine food is at least partially responsible for the increase in growth rate (Juanes & Conover, in press *a*). Although recruits are also produced at other times of the year, spring-spawned fish appear to be the main contributor to the adult stock (Chiarella & Conover, 1990; McBride & Conover, 1991).

In the present study, evidence is provided that the timing of juvenile inshore migration is matched with the availability of piscine prey of the appropriate size by comparing the timing of recruitment of bluefish and their prey in two New York estuaries, Great South Bay and the lower Hudson River. Bluefish diet and prey size selectivity are quantified and comparisons are made between estuaries. Potential morphological changes occurring in concert with the habitat and dietary shifts are also investigated.

## MATERIALS AND METHODS

Great South Bay (GSB) is an embayment on the south shore of Long Island, New York, U.S.A. (40°10' N, 73°10' W). Relatively little freshwater runoff enters the bay and the fish assemblage is therefore dominated largely by atherinid and engraulid fishes (Juanes, 1992). Four stations within the bay, ranging from Smith Point Park on the easternmost end to Seatuck on the westernmost end, were sampled to obtain fish for gut content analyses and to assess relative predator and prey recruitment dates. Collections were made with a 30 × 2 m beach seine (6 mm mesh in wings, 3 mm mesh bag) approximately biweekly from May until October 1988, 1989 and 1990. Three successive hauls were completed at each station. All fish species collected were sorted by species and enumerated. All bluefish and subsamples of the other contents of the net (potential prey) were collected, kept on ice in the field, and frozen upon return to the laboratory.

The lower Hudson River is one of several major estuaries along the east coast of the U.S.A. (41°00' N, 73°54' W). It represents a nursery area for a diverse ichthyofaunal community consisting of several anadromous (clupeid and percichthyid) and estuarine (engraulid and atherinid) fishes (Beebe & Savidge, 1988). Collections were conducted approximately biweekly from mid-June until November 1992 and 1993, from sites which extended over a 24 km section of the Hudson River estuary (see Juanes *et al.*, 1993 for

specific locations). Collections from mid June to mid July were conducted by the authors at eight sites whereas those from mid July to November were conducted by the New York State Department of Environmental Conservation at 25 sites. All collections in the Hudson River were made with a 61 × 3 m beach seine (13 mm mesh wings and a 6 mm mesh bag). One seine haul was conducted at each station. All bluefish and subsamples of the other contents of the net (potential prey) were collected and preserved in 10% buffered formalin.

Diets of bluefish captured throughout the sampling season were quantified but only those representing their initial appearance and peak in abundance in GSB and Hudson River are presented here. Bluefish were measured for total length (T.L.) and their stomachs extracted. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed ( $\pm 0.01$  g), and measured (T.L.  $\pm 1.0$  mm). Two indices were computed to describe diets (see Hyslop, 1980): (1) number of stomachs in which a taxon occurred, expressed as a percentage of the total number of stomachs containing food (%F=per cent frequency of occurrence), and (2) weight of taxon, expressed as a percentage of the total weight of food items (%W=per cent weight).

Relative abundances of bluefish and their main prey items were calculated as the number of animals caught per seine haul [=catch per unit effort (cpue)]. YOY bluefish cpues were compared to the cpues of their main prey items to assess relative recruitment dates and peaks in abundance. In GSB, similar comparisons were also made for 1987 (data obtained from McBride, unpublished).

Subsamples of the main prey items, Atlantic silversides *Menidia menidia* L. and striped bass *Morone saxatilis* W. from GSB and Hudson River, respectively, were measured (mm T.L.) to obtain prey length-frequency distributions. Prey size-selection was determined by comparing median prey lengths in the field with median prey lengths from guts of bluefish collected on that date. Field and gut prey medians were compared using a median test (Zar, 1984), a non-parametric test used due to the high frequency of non-normal prey size distributions in both gut and field samples (see Juanes, 1992).

The relationships between prey size (T.L.) and predator size (T.L.) were determined using regression analysis. Analysis of covariance (ANCOVA) was used to compare prey size and bluefish size relationships between the main prey species in each estuary.

Ontogenetic diet shifts in fishes are often characterized by abrupt changes in morphology. For example, increases in mouth gape often lead to shifts to larger prey sizes. To assess morphological changes coinciding with the estuarine entry, regressions of bluefish maximum body depth against total length and mouth width against total length were compared between YOY bluefish collected in offshore waters before estuarine entry and those collected in GSB using ANCOVA. Mouth widths were measured as the outside distance between the posterior of the maxillaries. Fineness ratios, also implicated as being important in determining the success of piscivorous predation (Harper & Blake, 1988), were calculated as total length divided by maximum depth.

## RESULTS

From collections of bluefish immediately after their appearance in GSB, a total of 157 fish was examined for gut contents in 1988 and 1989. A total of 163 fish was examined for gut contents from initial collections in the Hudson River in 1992 and 1993. Overall, about 75 to 90% of the diet by weight in both estuaries was fish (Tables I and II). Diet in GSB was dominated by silversides in both 1988 and 1989 (Table I), when it was also the most abundant fish in the seine collections (Juanes, 1992). In the Hudson River, striped bass dominated the diet by frequency and weight in both 1992 and 1993 and was also the most abundant YOY fish collected together with bluefish in these seine hauls. Invertebrates (zoa and copepods) were important parts of the diet by frequency but less so by weight (Table II). In both estuaries a large proportion of the diet

TABLE I. Stomach contents of juvenile bluefish T.L. &lt;90 mm captured during their initial appearance in Great South Bay in 1988 and 1989

Prey type	1988		1989	
	%F	%W	%F	%W
<i>Menidia menidia</i>	54.69	70.24	25.86	42.37
<i>Anchoa mitchilli</i>			5.17	10.45
<i>Gasterosteus aculeatus</i>	3.12	4.60		
<i>Lucania parva</i>			1.72	5.63
Fish eggs	3.12	1.36	1.72	0.05
Unidentified fish remains	21.21	11.50	41.38	16.89
<i>Crangon</i> and <i>Palaemonetes</i>	24.24	11.51	6.89	12.25
Zoea			22.41	6.63
Unidentified shrimp remains	1.51	0.79	13.79	5.72
Total fish	85.94	87.70	65.62	75.40
Total stomach analysed		83		74
Number containing prey		64		58
Dates which bluefish were collected	June 8–July 1		June 8–July 26	

%F, frequency of occurrence, %W, percent wet weight.

TABLE II. Stomach contents of juvenile bluefish T.L. &lt;110 mm captured during their initial appearance in the Hudson River in 1992 and 1993

Prey type	1992		1993	
	%F	%W	%F	%W
<i>Morone saxatilis</i>	20.00	24.70	23.26	41.65
<i>Menidia menidia</i>			2.33	2.53
<i>Anchoa mitchilli</i>	2.00	17.71		
<i>Alosa aestivalis</i>			2.33	4.50
<i>Alosa</i> spp.	6.00	17.97		
Unidentified fish remains	54.00	27.48	41.86	41.13
<i>Palaemonetes</i> spp.	2.00	3.86		
Zoea and copepods	20.00	8.29	37.21	10.23
Other			4.65	0.46
Total fish	82.00	87.86	69.77	89.81
Total stomachs analysed		106		57
Number containing prey		50		43
Dates which bluefish were collected	June 18–July 7		June 30	

%F, frequency of occurrence, %W, percent wet weight.

was unidentified fish remains which were probably comprised of the dominant fish prey in each estuary: silversides in GSB and striped bass in the Hudson River.

The recruitment of bluefish to GSB occurred just after the appearance of juvenile silversides each year from 1987 to 1990 [Fig. 1(a)]. The peak in bluefish abundance appeared to lag behind the peak in abundance of silversides by 1–2

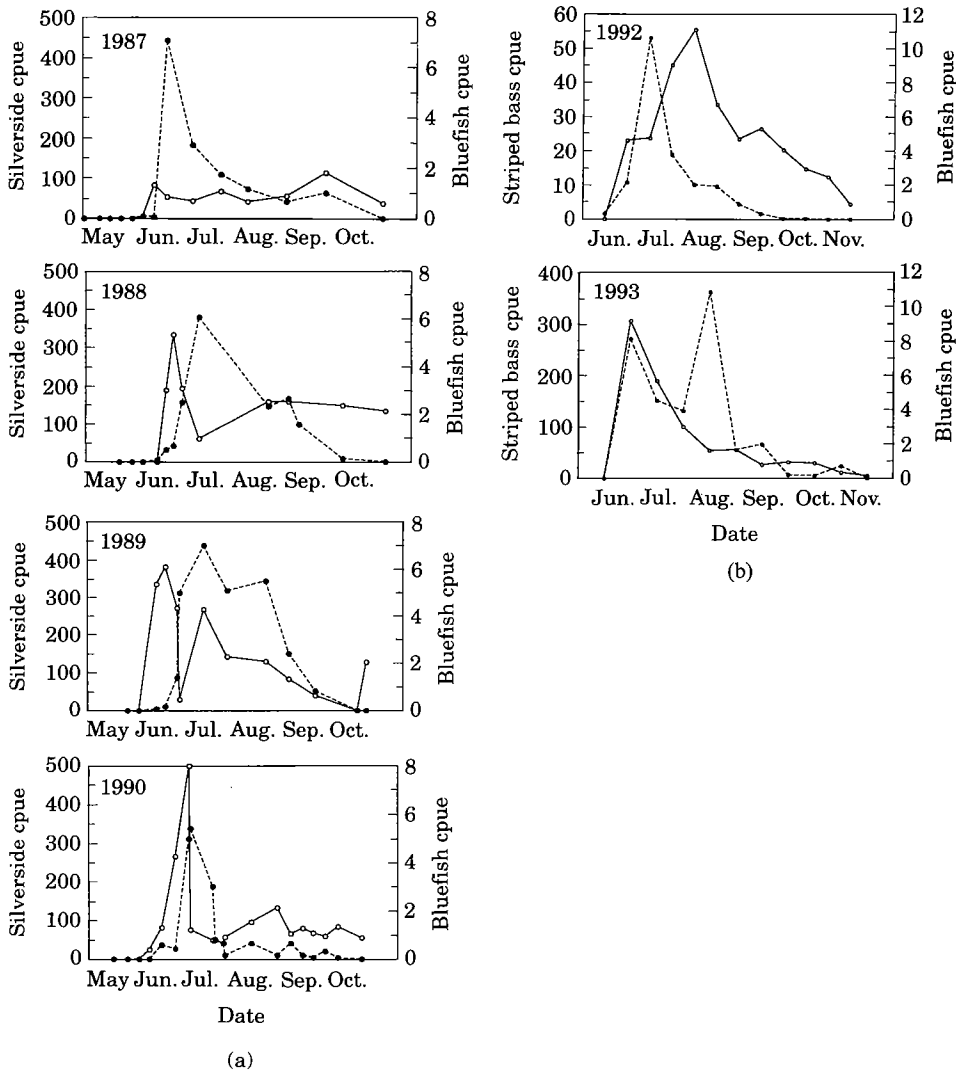


FIG. 1. Comparison of spring-spawned bluefish catch per unit effort (cpue) vs cpue of their main prey item. (a) Juvenile Atlantic silversides *Menidia menidia* in Great South Bay for 1987 to 1990. The 1987 data are from McBride (unpublished). (b) Juvenile striped bass *Morone saxatilis* in the Hudson River for 1992 to 1993. cpue was measured as the mean number of fish per haul. ○, Silversides or Striped bass; ●, bluefish.

weeks. In the Hudson River, the initial appearance of both bluefish and juvenile striped bass occurred simultaneously in 1992 and 1993 [Fig. 1(b)]. In 1992, the peak in bluefish abundance occurred 4 weeks before the peak in *M. saxatilis* abundance. In 1993, there were two peaks in the abundance of bluefish. The initial peak occurred coincidentally with the peak abundance of *M. saxatilis*. The second peak in cpue of bluefish in August 1993 was caused by unusually high catches at two of the 25 sites. Generally, peaks in abundance were followed by steady declines in relative numbers of predator and prey through the remainder of the sampling season in both GSB and Hudson River.

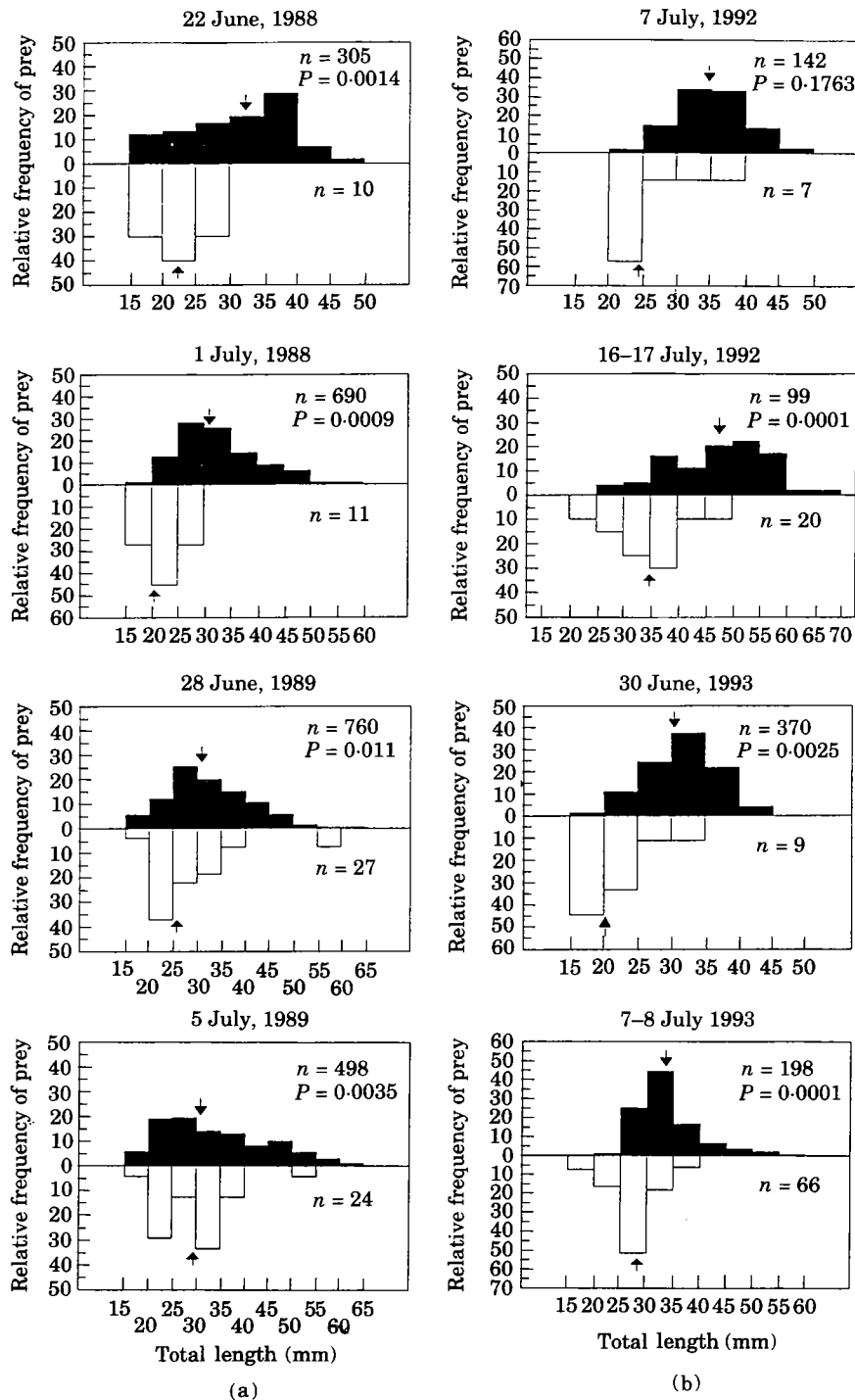


FIG. 2. Comparison between the length-frequency distributions (with medians indicated by arrows) of prey found in bluefish guts ( $\square$ ) and the same prey species collected in the field ( $\blacksquare$ ) on those dates.  $n$  the number of fish measured and  $P$  the probability value of the median test. (a) Silversides, Great South Bay 1988 to 1989. (b) Striped bass, Hudson River 1992 to 1993.

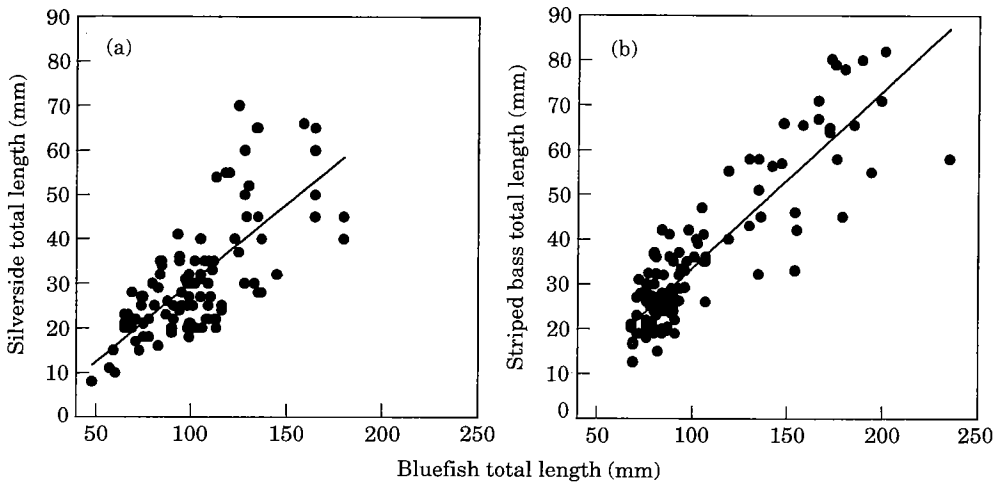


FIG. 3. Relationships between: (a) silverside prey total length and bluefish total length in Great South Bay, 1988 to 1989 ( $r^2=0.495$ ,  $P<0.001$ ,  $n=110$ ); (b) striped bass prey total length and spring-spawned bluefish total length in the Hudson River, 1992 to 1993 ( $r^2=0.797$ ,  $P<0.0001$ ,  $n=132$ ).

In all median test comparisons for silversides in GSB, the median prey lengths from guts were significantly different from the median prey lengths in the field [Fig. 2(a)]. In the Hudson River, three out of the four median tests detected a significant difference between gut prey length medians and field prey length medians [Fig. 2(b)]. For all comparisons, the medians of the prey length–frequency distributions in the gut were smaller than the medians of prey length–frequency distributions sampled in the field on that date (Fig. 2).

A significant positive linear relationship between prey size and bluefish size existed for both silversides and striped bass (Fig. 3). The silverside size against bluefish size regression slope was statistically indistinguishable from the striped bass size slope ( $t=1.1362$ , d.f.=238,  $P>0.05$ ), although the elevations were significantly different ( $t=3.1189$ , d.f.=239,  $P<0.05$ ).

Comparisons of morphometric features of offshore and inshore-collected YOY bluefish indicated little change, if any, coinciding with the habitat shift to inshore waters (Fig. 4). The slopes of the mouth gape against bluefish body length regressions for inshore and offshore bluefish were statistically indistinguishable ( $t=1.1707$ , d.f.=428,  $P>0.05$ ) [Fig. 4(b)], although the elevations were significantly different ( $t=6.0794$ , d.f.=429,  $P<0.05$ ). When the body depth against total length relationships were compared [Fig. 4(a)] no significant differences were found in either slopes ( $t=0.01501$ , d.f.=164,  $P>0.05$ ) or elevations ( $t=0.7309$ , d.f.=165,  $P>0.05$ ). Fineness ratios of the bluefish ranged from 3.7 to 5.3 with a mean of 4.2 (Fig. 5).

## DISCUSSION

Most of the juvenile bluefish that recruit to New York are products of spawning that takes place in March and April in the South Atlantic Bight, more than 500 km to the south (Nyman & Conover, 1988; McBride & Conover, 1991). In New York, water temperatures in March and April are in the range of

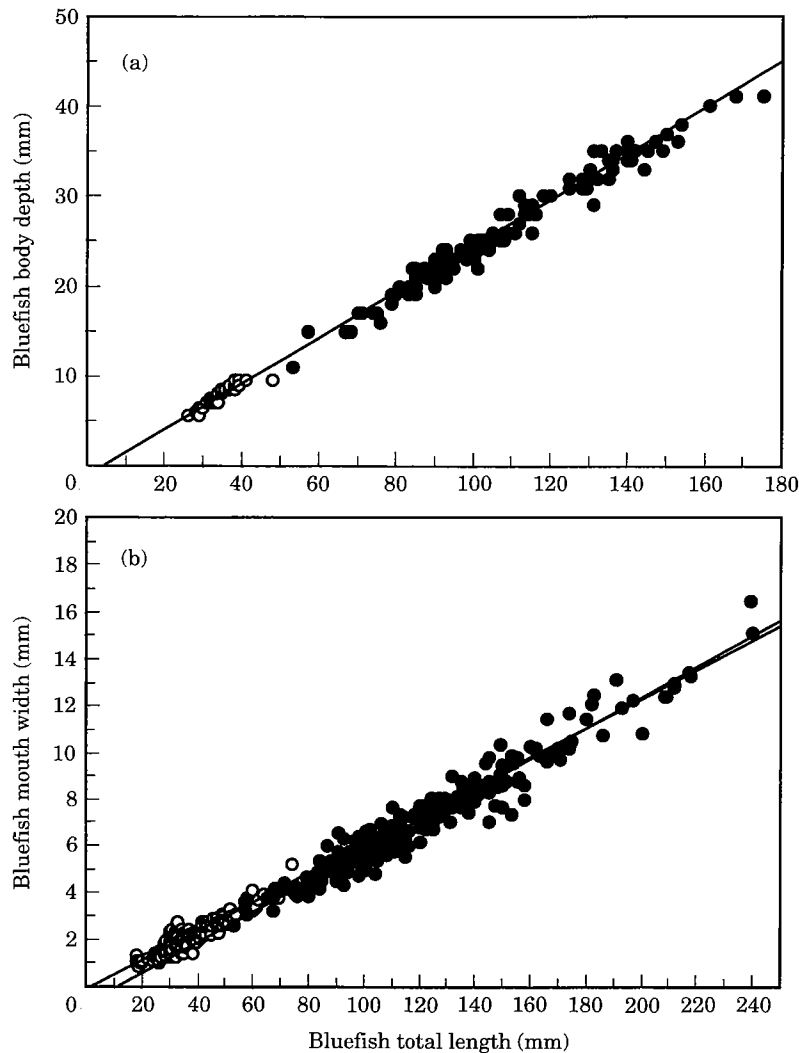


FIG. 4. Comparison of offshore (○) (data from Marks, unpublished) and inshore (●) collected (Great South Bay) bluefish morphology. (a) The relationship between bluefish body depth and total length (offshore:  $r^2=0.861$ ,  $P<0.0001$ ,  $n=138$ ; inshore:  $r^2=0.971$ ,  $P<0.0001$ ,  $n=130$ ). (b) The relationship between bluefish mouth width and total length (offshore:  $r^2=0.883$ ,  $P<0.0001$ ,  $n=188$ ; inshore:  $r^2=0.941$ ,  $P<0.0001$ ,  $n=244$ ).

*c.* 4–10° C, which is far too low to allow warm water fishes to commence spawning. While continental shelf waters warm in spring, bluefish are carried northward in warm waters associated with the Gulf Stream flow (Kendall & Walford, 1979). In late May and early June, they are found in relatively warm water near the edge of the continental shelf off the New York Bight (Shima, unpublished), and migrate across the shelf to inshore waters as soon as vernal warming permits. Otolith analyses show that these bluefish are about 60 days old when they arrive inshore in mid to late June (Nyman & Conover, 1988; McBride & Conover, 1991). In contrast, spawning of most estuarine fishes in



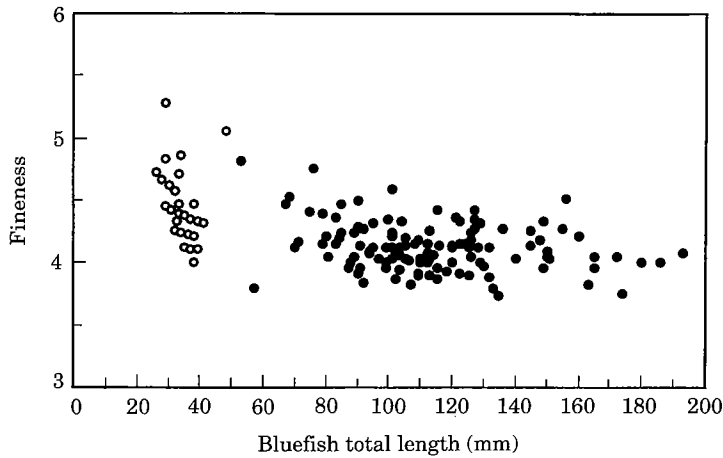


FIG. 5. The relationship between bluefish fineness ratio (calculated as the ratio of total length to maximum body depth) and total length for offshore (○) (data from Marks, unpublished) and inshore (●) fish (Great South Bay).

mid-Atlantic estuaries peaks in May and June (see Conover, 1990), about 2 months later than that of bluefish.

The present results show that the inshore migration of juvenile bluefish into two different Middle Atlantic Bight estuaries coincides with or closely follows the appearance of their principal prey. The dominant prey consumed, as well as dominant prey available, for juvenile bluefish upon arrival into GSB and the Hudson River are silversides and striped bass, respectively. In both estuaries, bluefish selected relatively small prey compared with what was available and the relationships between predator size and prey size in these two estuaries were similar.

Juvenile bluefish grow at an average rate of 0.75 to 1.0 mm day<sup>-1</sup> during the premigratory oceanic phase of their life history (Nyman & Conover, 1988) and are about 60 mm in F.L. when they arrive inshore in late June. Growth rates increase to 1.3 to 1.7 mm day<sup>-1</sup> after recruitment into estuaries and bluefish attain sizes exceeding 250 mm F.L. by the time they leave estuaries with the onset of autumn (McBride & Conover, 1991). This dramatic increase in growth rate and body size is probably due in part to the switch from a diet dominated by plankton to one dominated by fish. Marks & Conover (1993) found that oceanic spring-spawned fish fed exclusively on crustaceans (mostly copepods), until they neared the size of estuarine entry at which time piscine prey became a larger (c. 60% by weight) part of their diet. Juanes & Conover (in press *a*) found that juvenile bluefish had a significantly higher weight-specific rate of growth on a diet of fish compared to an invertebrate diet in the laboratory.

The advantage of earlier birth dates and the shift to a piscivorous diet is evident from comparison of size at age 1 and dominant prey type in several Middle Atlantic Bight fish (Juanes, 1992). The only species that reach lengths greater than 200 mm by age 1 are bluefish and summer flounder (*Paralichthys dentatus* L.) and these are also the only two species whose diet over the first summer of life is primarily fish (Rountree & Able, 1992; Juanes *et al.*, 1993).

Rapid morphological changes (e.g. increase in relative mouth gape) often accompany feeding shifts, particularly the feeding shift to piscivory (Keast & Webb, 1966; Popova, 1978; Keast, 1985b; Winemiller, 1989; Malmquist *et al.*, 1992). In this study no abrupt morphological changes were observed to coincide with the habitat shift from offshore to inshore (Fig. 4).

YOY bluefish fineness ratios approached the value of 4.5 proposed to minimize drag (Alexander, 1991) and were within the range of values (4.0–6.5) proposed to characterize many active piscivorous pelagic fish (Blake, 1983a, b). These results suggest that like other primary piscivores, juvenile bluefish are designed to be energetically efficient piscivorous predators relatively early in their ontogeny (Keast, 1985a). Since morphological traits that facilitate piscivory differ from those that facilitate other types of feeding (Werner, 1977; Werner & Hall, 1979; Persson, 1988), such an early morphological specialization is likely to hinder the ability to compete for zooplankton, creating an ontogenetic trade-off between feeding efficiency and future diet (Werner & Gilliam, 1984; Persson & Diehl, 1990). A potential result of such a trade-off might be to accelerate the onset of piscivory so as to minimize the time spent as a planktivore.

Because mortality rates decrease with increasing body size in fish (Gulland, 1965; Peterson & Wroblewski, 1984), the large size attained by bluefish at the end of the first growing season may increase survival during the following southward migration and winter. Werner & Gilliam (1984) proposed that the timing of ontogenetic shifts maximizes fitness by minimizing the ratio of mortality to growth and can thus be viewed as critical to survival. Therefore, an ontogenetic switch to piscine prey as early as possible in the life history of a piscivore may be favoured by natural selection.

Several temperate freshwater species appear also to have evolved specialized life history traits that allow them to have an early shift to piscivory. Juvenile stages of piscivorous fish in freshwater systems are able to consume prey fish juveniles because adult piscivores spawn in advance of their prey spawning. This has been observed in both largemouth bass *Micropterus salmoides* L., and northern pike *Esox lucius* L., feeding on centrarchids (Keast, 1985a); pike feeding on perch *Perca fluviatilis* L. (Frost, 1954); and walleye *Stizostedion vitreum* Mitchill, feeding on yellow perch *Perca flavescens* Mitchill. (Forney, 1971, 1976).

The spawning times of predator and prey, timing of feeding shifts, and the relative size and prey type distributions that result may be critical in determining year class strength. For example, Wicker & Johnson (1987) demonstrated that major reductions in abundance of juvenile largemouth bass in a Florida population were related to the lack of piscine prey at the time of the diet shift from planktivory to piscivory. Similarly, Buijse & Houthuijzen (1992) found that year-class strength of YOY pikeperch *Stizostedion lucioperca* L., was determined primarily by variability in the onset of piscivory over a 23-year period.

In marine environments, matching of the onset of piscivory with the availability of appropriate size prey is probably no less critical to recruitment, but the patterns are likely to be complicated by the influence of large scale advective forces such as the Gulf Stream. It has often been suggested that marine fish

spawn in locations that ensure transport to juvenile nursery areas at the appropriate time (Parrish *et al.*, 1981; Norcross & Shaw, 1984; Checkley *et al.*, 1988; Kotsikopoulous *et al.*, 1989; Jennings & Pawson, 1992; Walters *et al.*, 1992), but the importance of timing and interactions with the life histories of other species are poorly understood or not yet recognized.

The timing of estuarine entry by juvenile bluefish may be constrained by two factors, i.e. temperature and prey availability. Behavioural studies by Olla *et al.* (1985) suggest that young bluefish prefer temperatures  $>18^{\circ}\text{C}$  and so the inshore migration probably cannot occur until surface temperatures over the continental shelf have warmed to at least *c.*  $15^{\circ}\text{C}$ . Because the shallow waters close to shore warm faster than do those over the middle of the shelf, bluefish cannot cross into inshore waters until after the inshore species have already begun to spawn. Inshore temperatures are typically *c.*  $20^{\circ}\text{C}$  in late June when bluefish appear in estuaries (Nyman & Conover, 1988; McBride & Conover, 1991). The second constraint of the availability of small piscine prey means that if the bluefish arrive too late, the peak in prey abundance may be missed and prey sizes may become too large to maximize feeding efficiency. Our prey size selectivity results show that bluefish select smaller prey in both GSB and the Hudson River independent of prey type (Fig. 2). The similar relationships between bluefish size and prey size in two different estuaries with two different prey types (Fig. 3) further supports the importance of prey size over prey type. Laboratory experiments have shown that these selectivities for smaller prey sizes are a function of size-based differences in capture success rather than gape limitation (Juanes & Conover, in press *b*).

There is, in some years, a second wave of recruitment consisting of summer-spawned bluefish that migrate into estuarine waters in late summer. Because of their much later birth dates, summer-spawned bluefish reach only about half the size of the spring-spawned cohort at the end of year 1 (McBride & Conover, 1991). Summer recruits are usually much less abundant and appear to contribute little to the adult shock (Chiarella & Conover, 1990).

Hjort (1914) was the first to propose that the year class strength of marine fish populations is determined in the very early life stages (i.e. eggs and larvae) when mortality is high. In marine systems, matching of larvae with food availability has been hypothesized to explain year class variation in some planktivorous fish. The 'match-mismatch' hypothesis proposes that spawning is coupled with plankton production; however, larval stages are generally assumed to be the important early life history stage that is timed with proper food availability (Cushing, 1990). This study suggests that for piscivores it may be equally important to match the timing and location of spawning, and later ontogenetic shifts in habitat, with the phenology of prey production.

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