Abstract.–Along the U.S. east coast, the bluefish *Pomatomus saltatrix* spawns in offshore continental shelf waters during at least two distinct periods: spring and summer. Juveniles migrate to inshore nurseries where they complete the first growing season. Previous studies have shown that diet during the oceanic larval stage consists of copepods, while older juveniles captured inshore feed largely on teleost prey. To determine timing of the ontogenetic shift in diet to piscivory, we examined the feeding habits of 189 early-juvenile bluefish (18–74 mmTL). Samples were collected from continental shelf waters of the Middle Atlantic Bight (MAB) during spring and summer of 1988 and 1989. Spring- and summer-spawned *P. saltatrix* differed in body size, prey size, and in the proportions of prey types consumed. Copepods were the most common prey type in fish <60 mm. Teleost prey appeared initially in the diet of 30 mm individuals and became the major dietary item in spring-spawned fish >40 mmTL. Gut fullness and incidence of piscivory peaked in late afternoon and were positively correlated with daylight hours. There was no evidence of an abrupt increase in mouth width associated with this ontogenetic shift in diet. Because juvenile bluefish migrate inshore soon after becoming piscivores, their impact as predators on the abundance of other young fishes is probably focused on inshore/estuarine, rather than offshore species.

Ontogenetic shift in the diet of young-of-year bluefish *Pomatomus saltatrix* during the oceanic phase of the early life history*

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The bluefish, *Pomatomus saltatrix* (Linnaeus), occurs along the Atlantic coast of North America from Florida to the Gulf of Maine. Throughout its range the species is found from shallow coastal waters to the outer, continental shelf at various times of the year (Bigelow & Schroeder 1953, Lund & Maltezos 1970, Kendall & Walford 1979, Nyman & Conover 1988). *Pomatomus saltatrix* is an important component of the recreational fishery along the east coast of North America (NMFS 1991).

Two major spawning concentrations exist in the western Atlantic. Spring spawning occurs in the South Atlantic Bight (SAB) during March–May, with a peak in April. Summer spawning occurs in the Middle Atlantic Bight (MAB) during the months of June–September, with a peak in July (Kendall & Walford 1979, Nyman & Conover 1988, McBride & Conover 1991).

The spring-spawned larvae move northeastward in waters associated with the Gulf Stream. Juveniles cross shelf waters at an age of 40–70 d, and enter bays and estuaries of the mid-Atlantic coast in late spring (Kendall & Walford 1979, Nyman & Conover 1988). Summer-spawned larvae may either spend most of the summer at sea or inhabit the inshore nursery areas of the MAB for a brief period before the onset of autumn, when both cohorts move southward to wintering grounds in the SAB (Kendall & Walford 1979, Nyman & Conover 1988).

Once inshore, *P. saltatrix* feed almost exclusively on piscine prey (Lassiter 1962, Richards 1976, Naughton & Saloman 1978, McDermott 1983, Smale & Kok 1983, Smale 1984, Olla et al. 1985, Friedland et al. 1988). Very little is known, however, about the diet of young *P. saltatrix* at sea. In the only published account, the diet of newly-hatched *P. saltatrix* was found to consist mainly of copepods (Kendall & Nalpin 1981). Hence, at some point during ontogeny there must be a shift in diet from zooplankton to fish. If the diet shift occurs early in development, then juvenile *P. saltatrix* may be important predators of larval fishes on the shelf. On the other hand, the shift from a zooplankton to a fish-dominated diet may occur coincidentally with the habitat shift to estuarine waters.

In this paper we examine the feeding ecology of young juvenile *P. saltatrix* prior to their arrival in the nursery areas of the MAB. We document the predator size at which teleost prey initially appear in the diet and whether or not this shift to piscivory occurs coincidentally with the habitat shift inshore. Since fish are considered gape-limited predators (Hartman 1958, Ross 1978, Hunter 1980, Roberts et al. 1981), we examine mouth width for abrupt changes that may accompany an ontogenetic shift in diet.
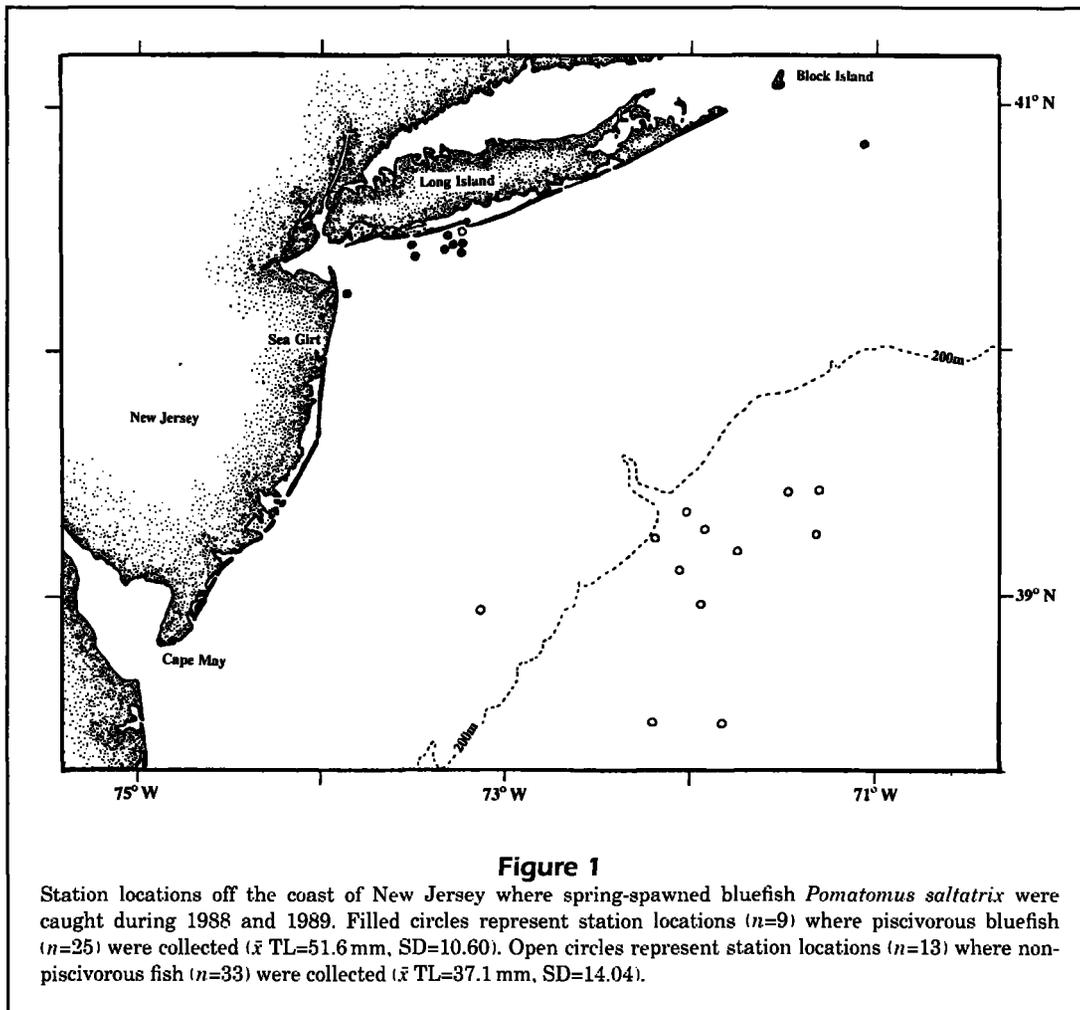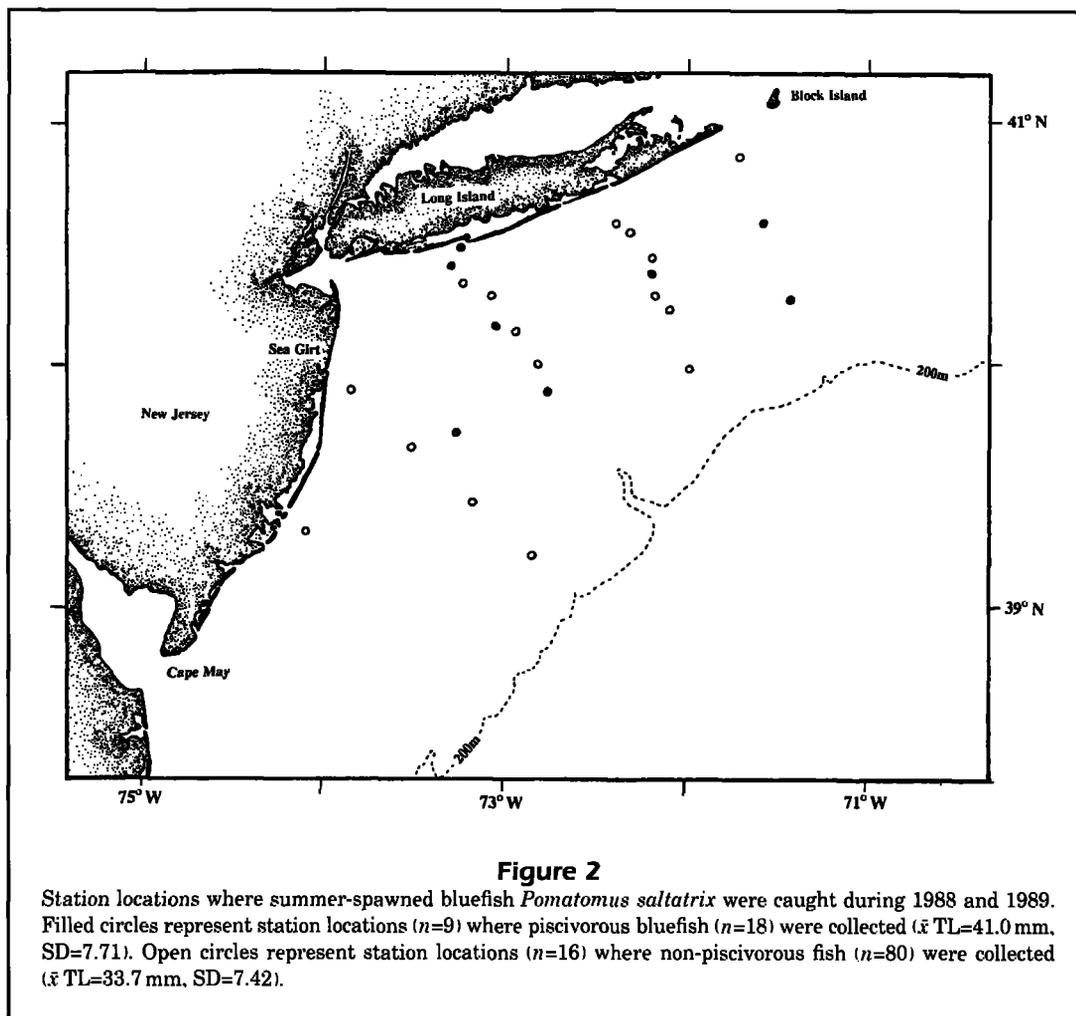
Methods

Field collections

Spring- and summer-spawned juvenile *P. saltatrix* were sampled from transects across the MAB in 1988 and 1989. The area sampled extended along the eastern U.S. coast from Cape May, New Jersey northeast to Montauk, New York and to 125 miles offshore. Cruises were conducted during two time-periods: 4 April 1988–8 August 1988, and 4 April 1989–8 August 1989. A total of 275 stations were sampled during 16 cruises. Juvenile *P. saltatrix* were collected at 46 of these stations (Figs. 1,2). Offshore stations were located 10 nmi (18.52 km) apart, and several coastal stations were located within 1 mi (1.85 km) of the shoreline (for comprehensive cruise track maps, see Hare & Cowen 1991, Marks 1991). Cruise duration was 3–7 d with tows conducted at regular intervals, 24 h/d. Tows consisted of a 10 min net deployment filtering approximately 3500 m^3 of seawater, at a ship speed of 3–4 kn.

Samples were collected using a modified Methot Frame Trawl (Methot 1986). The opening of the trawl was 5 m^2 and the mesh was 2 mm. Total net length was 13 m. Because juvenile *P. saltatrix* are often found near the surface (Kendall & Nalpin 1981, Collins & Stender 1987), trawls were conducted with the top 30 cm of the net above the water surface. All specimens were preserved in 70% ethanol.

Figure 1

Station locations off the coast of New Jersey where spring-spawned bluefish *Pomatomus saltatrix* were caught during 1988 and 1989. Filled circles represent station locations (n=9) where piscivorous bluefish (n=25) were collected (x̄ TL=51.6 mm, SD=10.60). Open circles represent station locations (n=13) where nonpiscivorous fish (n=33) were collected (x̄ TL=37.1 mm, SD=14.04).

Figure 2

Station locations where summer-spawned bluefish *Pomatomus saltatrix* were caught during 1988 and 1989. Filled circles represent station locations (n=9) where piscivorous bluefish (n=18) were collected ($\bar{x}$ TL=41.0 mm, SD=7.71). Open circles represent station locations (n=16) where non-piscivorous fish (n=80) were collected ($\bar{x}$ TL=33.7 mm, SD=7.42).

Laboratory analysis

Preserved *P. saltatrix* were wet weighed (±0.001 g) and measured (total length, TL, to ±0.1 mm). Fish in the 18–74 mm size-range were examined for diet comparisons. The minimum size represents the stage at which metamorphosis into the juvenile phase is completed (Norcross 1974). The maximum fish size represents the largest specimen collected.

Stomachs were removed from the pharynx and anterior to the intestine, cut longitudinally, and the contents transferred to a petri dish. The gut cavity was then washed to remove any adhering particles. Prey items were identified to species or lowest taxon possible, enumerated, and measured for total length using a dissecting scope equipped with an ocular micrometer.

Weighted mean prey length was calculated for each stomach to provide an accurate representation of prey length consumed. Individual bluefish often consumed several small prey (e.g., copepod) and one large prey (e.g., teleost). Computation of the weighted mean is equivalent to adding up all the original measurements and dividing the sum by the total number of measurements. Hence, the most common prey type will influence the weighted mean length in proportion to its numerical occurrence (see Sokal & Rohlf 1981).

Protocol for determining various prey length was defined as follows: (1) largest diameter for hydrated oocytes, (2) metasome + cephalosome for copepods, (3) anterior edge of head to anterior edge of caudal rami for fish lice (*Caligus* spp.), (4) anterior edge of eye to anterior edge of uropod for amphipods, (5) base of rostrum to anterior edge of telson for other crustacea, and (6) total length for polychaetes, ostracods, pteropods, squid (*Loligo* spp.), and teleost prey.

Fish scales were present in <5% of the guts and were not regarded as a prey type, but were used to indicate the occurrence of piscine prey. The presence of any teleost part (e.g., otolith, spine, fin ray) was recorded as piscine prey.

Prey dry weights were obtained either from the literature or measured directly after oven-drying for 24 h at 60°C. Where individual prey weights were very low or existed as exoskeleton material, dry weights were obtained by drying a known number of fresh prey items to obtain an average weight per prey item (see Grossman 1980, Ryer & Orth 1987).

Dry weights of 49 bluefish (17–74 mm) with empty guts were determined by oven-drying at 60°C until recording constant weight. The time required for a constant measure was 24–48 h, depending on individual fish size. The regression equation (Log Y=3.128 × Log X–6.059) was used to predict the dry weights of all bluefish in this study (Marks 1991). Gut fullness was measured using a ratio of prey dry weight to individual *P. saltatrix* dry weight.

Mouth width measurements were taken to detect morphological changes during ontogeny. Mouth width was measured as the width at the posterior tip of the maxillaries using digital calipers (±0.01 mm) (see Hartman 1958, Ross 1978, Hunter 1980, Hunter & Kimbrell 1980). Additionally, body depth of prey fish was measured at the widest location.

Diet analysis

Diet was analyzed using the methods outlined by Hyslop (1980) (see also Lassiter 1962, Naughton & Saloman 1978, Friedland et al. 1988): Total number of stomachs in which a food item occurred divided by the total number of stomachs (%F); total number of individuals of a taxon divided by the total number of food items (%N); and total dry weight of a taxon divided by the total dry weight of all food items (%W).

Bluefish were grouped by spring- and summer-spawned cohorts based on size and date of capture (Kendall & Walford 1979, Nyman & Conover 1988, McBride & Conover 1991). Trophic ontogeny was examined by arbitrarily splitting bluefish into size groupings and using percent dry weight of prey categories to assess dietary importance.

Results

General diet description

A total of 189 *P. saltatrix* were examined for gut content (Table 1). Approximately 84% had food present in the stomachs. Spring-spawned bluefish consumed

an average of 31 prey items per individual compared with 85 prey items for summer-spawned fish.

Spring-spawned fish were found to be significantly larger (Table 1; *t*-test for means with unequal variances, $t_s=5.24$, df=156, $P \leq 0.001$,) and had a greater mouth width ($0.01 < P < 0.05$, $t_s=2.39$) than did summer-spawned fish.

Overall, copepods were the dominant prey, accounting for 50% and 94% of the diet by weight (Table 2) of

Table 1

Comparison of sample characteristics from the spring- and summer-spawned cohorts of *Pomatomus saltatrix*. (*0.01<P<0.05, ***P<0.001; numbers in parentheses are ±1SD.)

Sample characteristics	Spring-spawned	Summer-spawned
Sample size	63	126
Percentage with prey	92	79
Mean mm TL (±1SD)	42.9 (14.57)	34.7 (7.84)***
Size range (mm)	19.0–74.0	18.0–64.0
Mean mouth width (mm)	2.38 (1.040)	2.05 (0.499)*
Mouth width range (mm)	0.85–5.18	0.99–3.93
Mean prey length (mm)	2.67 (2.548)	1.12 (0.565)***
Prey length range (mm)	0.27–36.0	0.29–12.62

Table 2

Stomach contents of spring- and summer-spawned juvenile bluefish *Pomatomus saltatrix* collected in the Middle Atlantic Bight. (%F=percent frequency of occurrence; %N=percent numerical abundance; %W=percent dry weight).
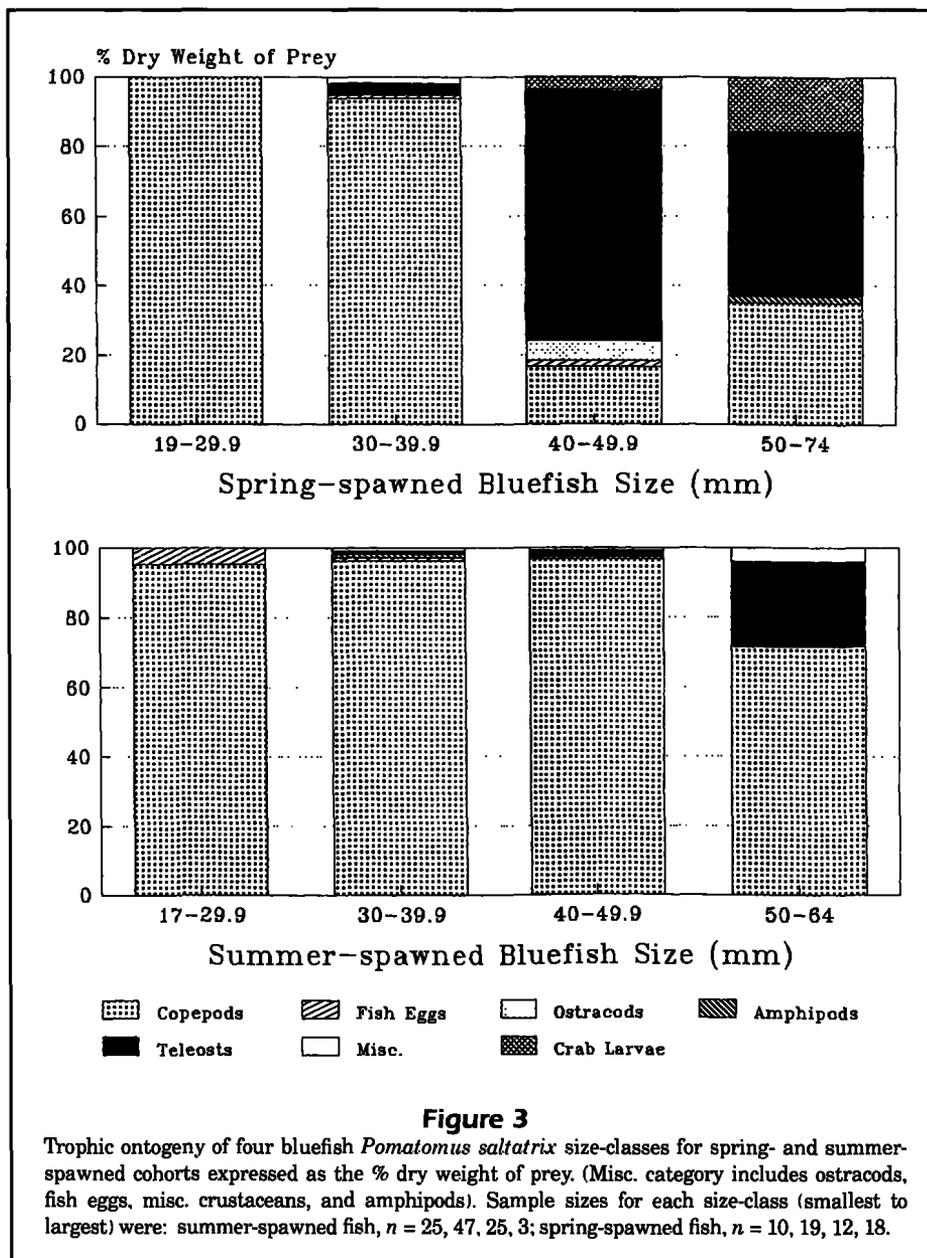
Prey taxa	Spring-spawned %F	%N	%W	Summer-spawned %F	%N	%W
Polychaeta						
Unidentified Maldanidae	1.7	0.0	0.0	0.0	0.0	0.0
Crustacea						
Calanoid copepods	89.7	88.6	50.0	99.0	97.6	93.9
Cyclopoid copepods	1.7	0.0	0.0	0.0	0.0	0.0
Fish lice (*Caligus* spp.)	1.7	0.0	0.0	0.0	0.0	0.0
Ostracods	8.6	2.0	1.1	4.0	0.1	0.2
Gammarid amphipods	5.2	0.2	0.7	1.0	0.0	0.1
Hyperiid amphipods	1.7	0.0	0.1	5.0	0.1	0.8
Mysid shrimp	3.4	0.1	0.1	1.0	0.0	0.0
Lucifer shrimp (*Lucifer* spp.)	1.7	0.0	0.1	4.0	0.0	0.1
Euphausids	3.4	0.1	0.1	7.0	0.1	0.2
Zoea	34.5	4.4	5.3	4.0	0.1	0.2
Megalopae	19.0	1.4	3.7	1.0	0.0	0.0
Unidentified crustacea	1.7	0.1	0.1	5.0	0.0	0.1
Gastropoda						
Unidentified pteropod	0.0	0.0	0.0	1.0	0.0	0.0
Cephalopoda						
Squid (*Loligo* spp.)	0.0	0.0	0.0	1.0	0.0	0.1
Teleostei						
Fish larvae and juveniles	39.7	1.9	37.5	17.0	0.2	1.8
Fish eggs (Unidentified)	17.2	0.9	0.8	37.0	1.6	2.4

spring- and summer-spawned fish, respectively. Teleosts were the next most-abundant prey type. Fish prey constituted 37% by weight of the diet of spring-spawned bluefish. Summer-spawned bluefish, by comparison, consumed a much smaller amount (1.8%). The majority of teleosts consumed were hakes (*Urophycis* spp.) or other unidentifiable gadids. There were also limited occurrences of engraulids and triglids (*Prionotus* spp.). Based on number and weight, all other prey types were relatively unimportant except crab larvae (zoea and megalopae). A low proportion by weight was comprised of hydrated oocytes which were frequently present in stomachs. Rare prey included *Caligus* spp., *Loligo* spp., a maldanid polychaete and a pteropod.

Onset of piscivory

We pooled data by size-class within cohorts to provide an overall view of diet changes with body size. The smallest size-class of summer-spawned *P. saltatrix* (17–29.9 mm) fed exclusively on copepods and fish eggs (Fig. 3). The 30.0–39.9 mm size-class expanded their diet to include teleosts, amphipods, and miscellaneous crustaceans. Bluefish in the 40.0–49.9 mm class also

Figure 3

Trophic ontogeny of four bluefish *Pomatomus saltatrix* size-classes for spring- and summer-spawned cohorts expressed as the % dry weight of prey. (Misc. category includes ostracods, fish eggs, misc. crustaceans, and amphipods). Sample sizes for each size-class (smallest to largest) were: summer-spawned fish, n = 25, 47, 25, 3; spring-spawned fish, n = 10, 19, 12, 18.

continued to feed mostly on copepods. The largest size-class of summer-spawned bluefish increased their consumption of fish prey and continued to take copepods and miscellaneous crustaceans.

The diet of spring-spawned bluefish (19.0–39.9 mm) was similar to the diet of same-sized fish from the summer-spawned cohort. There was a marked difference, however, in the amount of fish prey consumed by the 40.0–49.9 mm size-class. This difference was also evident in the largest size-class, despite small sample sizes in both cohorts. The diet of the two largest size-classes of spring-spawned bluefish also contained a relatively high percentage of crab larvae.

Mean prey length increased significantly with predator size in both spring- and summer-spawned bluefish (Fig. 4). Variance about the regression, however, was much greater for spring-spawned fish. Since transformation did not correct for inequality in the variances, we did not attempt further statistical analyses of these data.

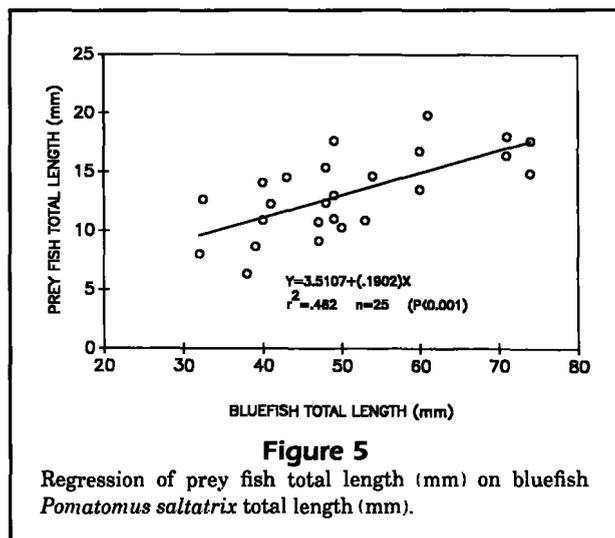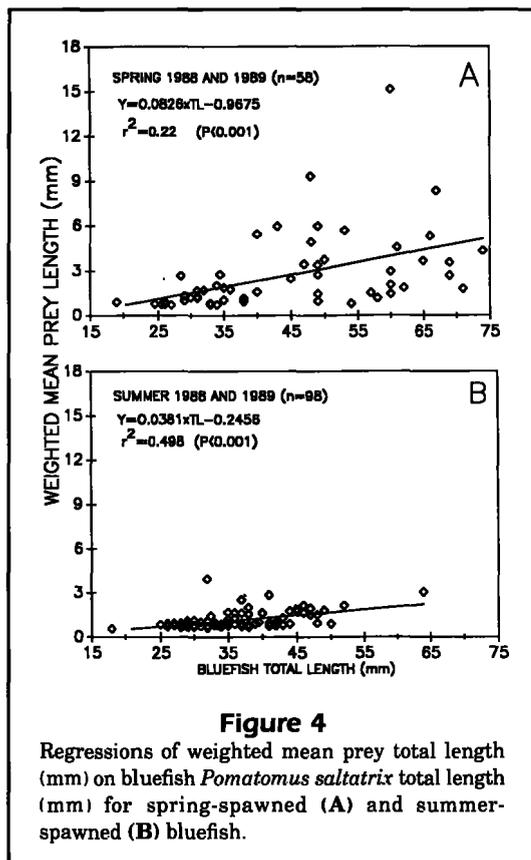Bluefish belonging to the spring-spawned cohort were caught either close to shore

(<8 km) or at distances >100 km from shore (Fig. 1). Piscivorous individuals from this cohort were larger in size ($\bar{x}$ TL=51.6 mm) and generally captured closer to shore than non-piscivorous individuals ($\bar{x}$ TL=37.1 mm). The difference between the mean TL for piscivorous fish versus non-piscivorous fish was significant ($P<0.001$, df=50, $t_s=6.22$).
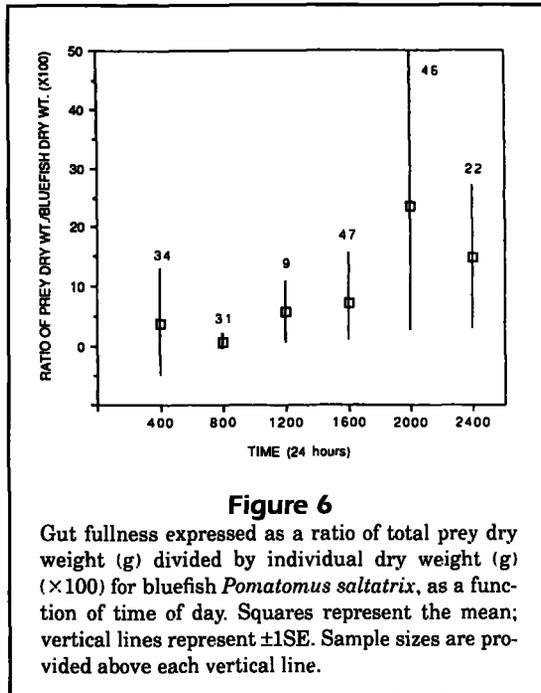
In comparison, piscivorous bluefish from the summer-spawned cohort were more evenly dispersed across the shelf (Fig. 2). Mean TL of piscivorous individuals (41.0 mm) was significantly greater than that of non-piscivorous fish ($\bar{x}$ TL=33.7, $P<0.001$, df=92, $t_s=5.04$).

Pomatomus saltatrix tended to feed on larger teleost prey with increasing size. A linear regression of prey fish length on predator length was highly significant ($r^2=0.46$, $n=25$, $P\leq0.001$; Fig. 5). With increasing body size, *P. saltatrix* also tended to feed on multiple teleost prey. More than one fish prey was found only in *P. saltatrix* >49 mm. The maximum number of intact teleost prey found in an individual predator (49 mm) was three. A *t*-test for the difference in means between the size of fish that consumed multiple fish prey (57.1 mm) and the size of those that fed on single prey (44.8 mm) was significant ($P<0.05$, df=30, $t_s=3.265$).

Diel cycle

Gut fullness pooled across all fish examined in the study versus time of day is depicted in Fig. 6. Gut fullness was evaluated as the ratio of total prey dry weight to individual *P. saltatrix* dry weight (×100). Feeding peaked during 1600–2000 h (the time of sunset during the study period ranged from 1945 to 2020 h). A nonparametric Spearman Rank Correlation test (Sokal & Rohlf 1981) resulted in a significant, positive relationship ($r_s=0.5818$, $P\leq0.001$, $n=189$) between time of day and gut fullness. The high proportion of food in the gut at approximately 2400 h may be attributed to food that was consumed during the evening crepuscular period, since prey from this time-period were generally in an advanced stage of digestion. Experimental laboratory data
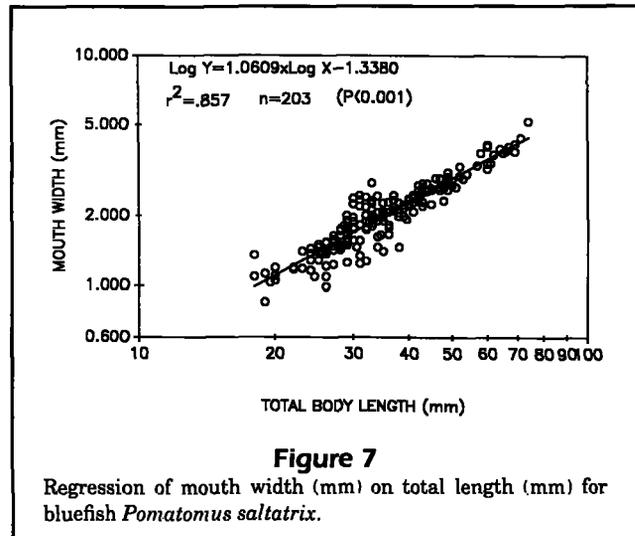

Figure 4
Regressions of weighted mean prey total length (mm) on bluefish *Pomatomus saltatrix* total length (mm) for spring-spawned (A) and summer-spawned (B) bluefish.

Figure 5
Regression of prey fish total length (mm) on bluefish *Pomatomus saltatrix* total length (mm).

Figure 6

Gut fullness expressed as a ratio of total prey dry weight (g) divided by individual dry weight (g) (×100) for bluefish *Pomatomus saltatrix*, as a function of time of day. Squares represent the mean; vertical lines represent ±1SE. Sample sizes are provided above each vertical line.

Figure 7

Regression of mouth width (mm) on total length (mm) for bluefish *Pomatomus saltatrix*.

showed that time to 90% digestion at 21°C is 5–7 h post-feeding in 57–199 mm bluefish (Marks 1991).

A two-way test for independence (adjusted G-statistic, $G_{adj}=5.98$, $P<0.05$; Sokal & Rohlf 1981) showed that the occurrence of fish in the stomachs depended on time of day. Piscivory was restricted to daylight hours, with some incidence recorded prior to 2400 h but none during 2400–0400 h. A slight increase (12%) was observed at 0800 h; the maximum evidence of piscivory (42%) occurred at 1600 h.

Mouth morphology

Teleost prey had the greatest maximum thickness of all prey types. The relationship between thickness of fish prey at the widest point and *P. saltatrix* mouth width was positive, but the regression was marginally non-significant ($P=3.91$, $n=23$, $0.05<P<0.1$).

The log-log regression of mouth width on total body length was highly significant ($r^2=.857$, $n=203$, $P<0.001$) and showed no evidence of an abrupt change in mouth width coincident with the onset of piscivory (Fig. 7). The regression slope (1.06) suggests isometric growth of mouth width in relation to body size. A SYSTAT piecewise linear-regression procedure (Wilkinson 1987) was employed to test

for the existence of more than one slope in the line. The test was run with an undetermined intersection as well as with an *a priori* intersection at 30 mm (the size of initiation of piscivory). No significant differences in slope were observed, and the conclusion was that a single regression line adequately described the relationship between mouth width and total body length.

Discussion

Our results indicate that during the oceanic phase of the early life history, *P. saltatrix* gradually shifted its diet from small prey (crustaceans, mainly copepods) to fish and crab larvae. The diet appeared to shift over a size range that corresponds to the period of inshore migration.

The smallest juvenile *P. saltatrix* foraged predominately on copepods. A diet high in crustacean prey is characteristic of the larval and juvenile phases of many piscivorous fishes, including the Atlantic cod *Gadus morhua* (Last 1980) and the largemouth bass *Micropterus salmoides* (Keast 1985).

Overall, fish prey became a substantial component of the diet at about 40–60 mm. The majority of teleosts consumed were hakes (*Urophycis* spp.) or other unidentified gadids. Gadids are among the most-abundant icthyoplankton group found in the MAB during the spring (Kendall & Nalpin 1981, Morse 1989, Cowen et al. In press).

Crab larvae initially appeared in the diet of bluefish <40 mm and accounted for 9% of the diet by weight in bluefish >60 mm (Fig. 4). The appearance of crab larvae as the third most-abundant prey item is not surprising. The majority of crab larvae were found in spring-spawned bluefish captured close to shore. This may be a result of higher concentrations of crab larvae at frontal zones in the nearshore environment. Friedland et al. (1988) reported a high abundance of crustaceans in the diet of inshore juveniles.

There was a marked increase in the maximum size of prey consumed as spring-spawned bluefish size increased beyond 30 mm (Fig. 3). This is in agreement with the generalization that prey size increases with increasing predator size in fishes (Brooks & Dodson 1965, Tyler 1972, Ross 1977 and 1978, Hunter & Kimbrell 1980, Roberts et al. 1981, Smale 1984, Ryer & Orth 1987, Wetterer 1989, Persson 1990). There was, however, only a moderate increase in the maximum prey sizes consumed by summer-spawned bluefish. The reasons for this discrepancy are not clear, but may be a function of prey availability and differences in size at inshore migration. Summer-spawned bluefish appear inshore at smaller sizes than do spring-spawned bluefish (McBride & Conover 1991). The shift to larger prey items in summer-spawned fish may occur after inshore migration.

The onset of piscivory in the 30–70 mm size-range is similar to that reported for other teleosts: 40–60 mm for characids and 60–80 mm for pimelodids (Winemiller 1989), 23 mm for *Micropterus salmoides* (Keast 1985), and 60–100 mm for *Gadus morhua* (Bowman & Michaels 1984).

Piscivory in larval stages has been reported in some fishes, but apparently does not occur in bluefish. Hunter & Kimbrell (1980) found *Scomber japonicus* to be piscivorous at 8 mmSL. This could perhaps be attributed to the large mouth and strong, well-developed jaws that are characteristic of larval scombrids (Fahay 1983). Hunter (1980) also reported *Sphyraena argentea* to be piscivorous at 4.4 mm. Houde (1972) found evidence for piscivory in *S. borealis* at 9 mm. Despite having well-developed dentition at 4.3 mm (Fahay 1983), larval and postlarval *P. saltatrix* may lack either the jaw structure, visual acuity, or swimming speed necessary to feed on other fishes.

Pomatomus saltatrix are known to be visual predators (Olla & Marchioni 1968, Olla et al. 1970, Van der Elst 1976). It follows that reduced light levels after the evening crepuscular period should reduce feeding efficiency. Olla & Marchioni (1968) documented that *P. saltatrix* detect and attack prey visually, so it is not surprising that feeding appears to be correlated with daylight periods. Kjelson et al. (1975) also reported finding the lowest proportion of food in the gut of postlarval fishes during the evening hours.

Fish are considered "gape-limited" predators and are ultimately restricted by mouth size (Hartman 1958, Ross 1978, Hunter 1980, Roberts et al. 1981). Ontogenetic shifts in diet may be related to morphological changes in mouth size during development that allow for consumption of larger prey (Ross 1978, Grossman 1980, Roberts et al. 1981). Mouth width in *P. saltatrix*, however, appears to increase isometrically with body size. The inclusion of fish in the diet at a size of 30 mm

may be attributed to changes in feeding behavior with growth, or simply a result of the mouth reaching a size that permits fish ingestion.

The size at which teleost prey constitute a substantial portion of the diet is about 40–70 mm. This is also the size-range in which *P. saltatrix* juveniles recruit to the inshore waters of the MAB (Nyman & Conover 1988, McBride & Conover 1991). Hence, the dietary shift is largely coincident with a habitat shift. This is further supported by the observation that virtually all piscivorous spring-spawned *P. saltatrix* were captured close to shore. The limited occurrences of piscivory in the summer-spawned cohort were more evenly dispersed across the shelf. However, summer-spawned bluefish migrate inshore at a smaller size than do spring-spawned fish (McBride & Conover 1991) and may do so largely before the onset of piscivory. Our results suggest that the overall impact of predation by young bluefish on the abundance of other fishes is probably focused more on inshore rather than offshore species.

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