

Rapid Growth, High Feeding Rates, and Early Piscivory in Young-of-the-Year Bluefish (*Pomatomus saltatrix*)

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The bluefish (*Pomatomus saltatrix*) is an offshore-spawning estuarine-dependent fish that is abundant along the east coast of North America. Young-of-the-year bluefish undergo a habitat shift from offshore waters to inshore nursery areas at about 40–70 mm total length which coincides with an increased growth rate and a diet shift from planktivory to piscivory. Here, we measure growth of young-of-the-year bluefish on different diets and estimate consumption rates both in the field and in the laboratory. Growth on a fish diet is significantly higher than that on a zooplanktivorous diet. Bluefish have among the highest evacuation (5–7 h), consumption (20–30% body weight/d), and specific growth rates (1–2 mm/d) reported for temperate fishes and are similar to those for pelagic tropical species. These results suggest that bluefish may exhibit a tropical feeding physiology in temperate estuarine nurseries as a way to achieve rapid growth rates.

Le tasserger (*Pomatomus saltatrix*) est un poisson estuarien frayant au large qui est abondant le long de la côte est de l'Amérique du Nord. Le jeune de l'année quitte son habitat au large pour gagner les viviers le long de la côte lorsqu'il atteint environ 40–70 mm de longueur totale, ce qui coïncide avec une augmentation du taux de croissance et une modification du régime alimentaire, de planctivore à piscivore. Ici, on mesure la croissance du jeune tasserger sur différents régimes, et on évalue la consommation dans la nature et au laboratoire. La croissance sur un régime à base de poisson est significativement plus rapide que sur un régime zooplanctivore. Les taux d'évacuation (5–7 h), de consommation (20–30% du poids corporel/d) et de croissance spécifique (1–2 mm/d) du tasserger sont parmi les plus élevés des poissons vivant en eau tempérée et sont semblables à ceux que l'on observe chez les espèces tropicales pélagiques. Ces résultats indiquent que le tasserger peut manifester un comportement alimentaire tropical dans des viviers estuariens tempérés de manière à croître plus rapidement.

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The bluefish (*Pomatomus saltatrix*) is a highly migratory species with a worldwide distribution (Le Gall 1934; Briggs 1960; Champagnat 1983). Along the east coast of North America, bluefish appear to have two distinct major spawning seasons and locations: a spring spawning in the South Atlantic Bight and a summer spawning in the Middle Atlantic Bight (Norcross et al. 1974; Kendall and Walford 1979; Chiarella and Conover 1990). Spring-spawned fish are advected northwards along the edges of the Gulf Stream and move into estuaries of the Middle Atlantic Bight in May and June. Summer-spawned fish recruit to these same estuaries in mid- to late August (Nyman and Conover 1988; Shima 1990; McBride and Conover 1991). Young-of-the-year (YOY) bluefish undergo the habitat shift from offshore waters to inshore nursery areas at about 40–70 mm total length (TL) (Nyman and Conover 1988; McBride and Conover 1991; Juanes 1992). This habitat shift coincides with a diet shift from planktivory to piscivory (Marks and Conover 1993) and with an increase in growth rate (McBride and Conover 1991). These estuarine growth rates are unusually high for a temperate inshore fish

(1.2–1.8 mm/d, Nyman and Conover 1988; McBride and Conover 1991) and allow YOY bluefish to attain a larger size at age 1 than any other morphologically similar species in this area (Nyman and Conover 1988; Chiarella and Conover 1990).

The primary goal of this study was to examine how the rapid growth of YOY bluefish is achieved. First, we asked whether bluefish may increase their growth rate as a consequence of the diet shift to piscivory. We tested this hypothesis by determining if growth on a fish diet is greater than growth on an invertebrate diet. Second, we explored the physiological bases for this rapid growth. The distribution of bluefish is generally restricted to waters warmer than 15°C, suggesting that it is a warmwater species and may exhibit physiological traits more characteristic of tropical than temperate fishes (Le Gall 1934; van der Elst 1976). Tropical fishes are characterized by relatively high digestion and consumption rates (Fänge and Grove 1979; Pandian and Vivekanandan 1985; Pauly 1989). Hence, the rapid growth of YOY bluefish may be a consequence of high rates of feeding and digestion. We thus estimated consumption and gut evacuation rates in the laboratory and also assessed consumption rates in the field from diel variations in weight of stomach contents on two dates during the summer. These estimates were then compared with published results for temperate and tropical species.

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Material and Methods

Diel Diet and Gut Fullness

Samples of YOY bluefish were collected on June 28–29 and July 26–27, 1989. Collections were made every 4 h starting at 06:00 with three hauls of two 30-m seine nets at two adjacent beaches in Great South Bay (GSB) near Islip, Long Island, N.Y. (40°10'N, 73°10'W). All bluefish collected were immediately frozen on dry ice.

In the laboratory, bluefish were thawed, measured (± 1.0 mm TL), and weighed (± 0.01 g wet weight). Gut contents were weighed (± 0.01 g), measured (± 1.0 mm TL), and identified to the lowest possible taxon. Gut fullnesses were calculated as the wet weight of the gut contents divided by the wet weight of the eviscerated bluefish. Mean lengths of bluefish captured at each time were compared using ANOVA after testing for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Bartlett's test). If treatment effects were significant, mean lengths were further compared using a Tukey HSD multiple comparison test. To assess whether feeding increased through the day, correlations between time of day and gut fullness for daylight hours were evaluated using a Pearson correlation coefficient.

Sunrise and sunset occurred at about 05:30 and 20:30, respectively, on both sampling dates. The moon was in its last quarter on both dates, although the moonrise occurred later during the first sampling period (on June 29 at 01:30, and on July 26 at 23:57). Water temperatures were measured at both sites before each series of net hauls using a thermometer. Mean water temperature was significantly higher on July 26–27 ($27.67 \pm 1.21^\circ\text{C}$ (SD)) than on June 28–29 ($25.83 \pm 0.82^\circ\text{C}$) ($t = 0.075$, $df = 10$, $p = 0.0117$).

Evacuation Rates

Three gut evacuation experiments were conducted using different-sized bluefish and the Atlantic silverside (*Menidia menidia*) as prey. Small bluefish were used on September 11, 1990 (mean bluefish TL = 74.20 mm, range = 57–96, mean weight = 3.207 g, $n = 10$; prey mean wet weight = 0.127 g; mean prey weight/predator weight = 3.972%). Medium bluefish were tested on August 6, 1990 (mean TL = 133.83 mm, range = 121–143, mean wet weight = 19.85 g, $n = 17$; prey mean wet weight = 0.279 g; mean prey weight/predator weight = 1.407%). Large bluefish were used on September 2, 1988 (mean TL = 154.82 mm, range = 128–199, mean wet weight = 31.53 g, $n = 11$; prey mean wet weight = 1.08 g; mean prey weight/predator weight = 3.425%). Bluefish were placed in individual tanks 2 d before the experiment and deprived of food in order to standardize hunger levels. Individual bluefish were then fed one silverside of a predetermined size. Time of ingestion was noted. Bluefish were then chosen randomly at 30- or 60-min intervals. Their stomach contents were removed, measured, weighed, and expressed as percentage of prey weight remaining. A similar experiment using sand shrimp as prey (*Crangon septemspinosus*, mean wet weight = 0.522 g, mean prey weight/predator weight = 3.265%) was conducted on medium bluefish (mean TL = 125.8 mm, range = 110–142, mean wet weight = 15.98 g, $n = 10$) on August 3, 1990. All these experiments were conducted at temperatures ranging from 21 to 22°C.

Evacuation rates were estimated by computing regressions between percent prey remaining in the gut and time

after ingestion using linear, exponential, and square root models. The relationship between percent prey remaining and time after ingestion for the three Atlantic silverside digestion experiments were compared using an ANCOVA after testing for homogeneity of slopes.

Field Consumption Rates

Daily rations are commonly measured as functions of gut evacuation rates determined in laboratory studies and diel variations of stomach contents of field-collected fish. Because none of the available models for estimating daily ration (Jobling 1986; Persson 1986; Adams and Breck 1990; Wootton 1990) appeared to be particularly applicable to a warmwater piscivore eating relatively small prey, we used the four most appropriate and widely used models:

Eggers (1979) model:

$$C_{\Delta 24} = 24 \cdot r_e \cdot W_{\Delta 24}$$

Elliott and Persson (1978) model:

$$C_{\Delta t} = \frac{(\bar{W}_t - \bar{W}_{t-1} \cdot e^{-r_e t}) \cdot r_e t}{1 - e^{-r_e t}}$$

Pennington (1985) model:

$$C_{\Delta t} = 2 \cdot r_{0.5} \cdot \sum_{i=1}^n \left(\frac{\sqrt{W_i}}{n} \right) + \frac{(\bar{W}_t - \bar{W}_{(t-1)})}{t - (t-1)}$$

Olson and Boggs (1986) model:

$$\hat{r} = \left(\sum_{i=0}^l \frac{\bar{W}_i}{A_i} \right) \cdot 24$$

where $C_{\Delta t}$ is food consumption between sampling periods at time t and $t - 1$, W_t is average prey weight at time t , W_i is the prey weight in an individual bluefish at time t , n is the number of bluefish, r_e is the exponential evacuation rate, $r_{0.5}$ is the square root evacuation rate, A_i is the integral of the evacuation function, W_i is the mean stomach contents per predator, l is the number of prey types, and \hat{r} is the feeding rate (grams per hour). Daily meal is calculated by multiplying \hat{r} by 24 h, and daily ration is the daily meal expressed as a percent of body weight. The Eggers (1979) and Elliott and Persson (1978) models both assume exponential gastric evacuation. The Pennington (1985) model is usually used with a square root evacuation model, although this model can accommodate any form of the evacuation function. The Olson and Boggs (1986) model also does not require any specific form of the gastric evacuation function, but has commonly been used with a linear evacuation rate. Because fish were collected over a 20-h period (06:00–02:00), for those models that require 24-h sampling (Elliott and Persson and Pennington), we assumed the following 06:00 gut fullness to be similar to the previous 06:00 gut fullness.

Consumption, Growth and Gross Efficiency in the Laboratory

A 20-d-long experiment was conducted in 1990 to estimate short-term growth rates, mean feeding rates, and gross growth efficiency on four natural diets. The experiments were conducted with four groups of three bluefish in separate tanks ($75 \times 75 \times 30$ cm). Each group was randomly selected to

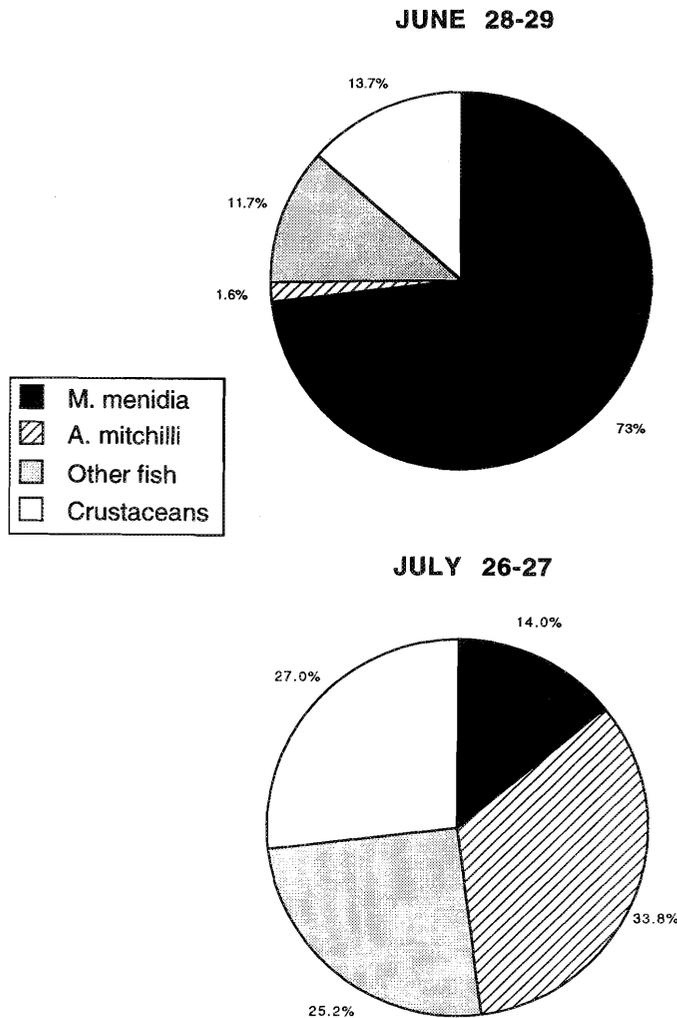


FIG. 1. Diet description by weight of the June 28–29 and July 26–27 samples of YOY bluefish. “Crustaceans” category includes grass and sand shrimp (*Palaemonetes vulgaris* and *Crangon septemspinosa*, respectively), zoea, and unidentified shrimp remains. “Other fish” category includes rainwater killifish (*Lucania parva*), northern puffer (*Sphoeroides maculatus*), permit (*Trachinotus falcatus*), winter flounder (*Pleuronectes americanus*), unknown fish species, and unidentified fish remains.

be fed one of four live diets: adult brine shrimp (*Artemia* sp.), sand shrimp, and small (20–40 mm TL) or medium (50–70 mm TL) Atlantic silverside. Fish were kept under a constant light regime (14 h light : 10 h dark) and temperature (range = 20–23°C, mean = 21.45°C (SD = 1.13)). All bluefish were anaesthetized with MS-222, weighed, and measured before they were put into tanks. Individuals within each tank were marked by clipping small portions of the caudal fin. Members of each tank were selected to be as similarly sized (within 1–3 mm) as possible. All bluefish were starved for 24 h before being fed for the first time. Live shrimp and Atlantic silverside were added after measuring, weighing, and counting. *Artemia* were blotted dry before weighing. Enough food was added to exceed daily ration requirements (calculated in previous experiments). On each successive day, remaining shrimp and Atlantic silverside prey were counted, and enough additional prey individuals were added to again exceed calculated daily rations. Dead prey were collected from the bottom of the tank,

weighed, and subtracted from the previous day’s consumption total. Tanks were checked daily for potential bluefish mortality. All bluefish survived the period of the experiment and prey were never totally consumed within any treatment. After 19 d, all prey were removed, and bluefish were starved for 24 h, before weighing and measuring.

Daily specific growth rate (G) of each fish was calculated as

$$G = \left[\frac{\ln Wt_f - \ln Wt_i}{d} \right] \cdot 100$$

where Wt_f = final wet or dry weight, Wt_i = initial wet or dry (calculated from the wet weight/dry weight regression, see below) weight, and d = number of feeding days (=18).

Daily specific feeding rates were calculated by dividing the overall amount of food consumed within each tank by the average size of bluefish during the experiment in each tank (calculated as $(\ln Wt_f + \ln Wt_i)/2$). Feeding rates were expressed in terms of wet weight (grams per gram), dry weight (grams per gram), and energy (kilojoules per kilojoule, calculated from dry weights, see below). Gross growth efficiency (K) was calculated as the total fish weight gain per prey weight consumed. The mean daily number of prey consumed per tank was calculated from daily counts of remaining Atlantic silverside and shrimp. Daily numbers of *Artemia* ingested were calculated as the total consumption divided by the average weight of an individual.

Mean daily specific growth rates, feeding rates, growth efficiencies, and numbers of prey items consumed (three tanks or replicates per diet treatment) were compared among diet treatments using ANOVA after testing for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Bartlett’s test). If treatment effects were significant, means were further compared using a Tukey HSD multiple comparison test.

A range of Atlantic silverside, shrimp, and bluefish sizes were dried in an oven (at 60°C) until a constant weight was achieved (usually 24 h). The regressions relating wet weight (WW, grams) to TL (millimetres) and dry weight (DW, grams) to wet weight were as follows:

Bluefish:

$$DW = 0.211 \times WW^{1.039}, n = 54, r^2 = 0.999, p < 0.0001$$

$$WW = (1.483 \times 10^{-6}) \times TL^{3.347}, n = 54, r^2 = 0.996, p < 0.0001$$

Shrimp:

$$DW = 0.247 \times WW^{0.969}, n = 21, r^2 = 0.990, p < 0.0001$$

$$WW = (8.685 \times 10^{-6}) \times TL^{3.00}, n = 21, r^2 = 0.984, p < 0.0001$$

Atlantic silverside:

$$DW = 0.250 \times WW^{1.016}, n = 55, r^2 = 0.995, p < 0.0001$$

$$WW = (4.303 \times 10^{-6}) \times TL^{3.034}, n = 55, r^2 = 0.994, p < 0.0001.$$

Five 1-g samples of *Artemia* were also dried for 24 h to obtain a dry weight to wet weight conversion:

$$1 \text{ g WW} = 0.065 \pm 0.0007 \text{ (SD) g DW}, n = 5.$$

In addition, four sets of 50, 40, 30, and 20 individuals were

dried to obtain the average dry weight of an individual *Artemia* ($=0.00338 \pm 0.000162$ (SE) g).

Estimates of the caloric value of Atlantic silverside (21.2 kJ/g dry weight), sand shrimp (16.2 kJ/g dry weight), and bluefish (20.8 kJ/g dry weight) were obtained from Steimle and Terranova (1985). The caloric content of *Artemia* (24.5 kJ/g dry weight) was obtained from Leger et al. (1986).

Results

Diet and Gut Fullness

A total of 256 YOY bluefish were collected during the two sampling periods. Because both of the collection dates took place before any summer-spawned bluefish appeared (Juanes 1992), only spring-spawned bluefish were sampled. On both dates, bluefish diets consisted mainly of fish (86.3% on June 28–29 and 73.0% on July 26–27) although composed of different prey species (Fig. 1). The first diel sample occurred early in the estuarine phase, when bluefish were still relatively small (mean bluefish TL = 98.06 mm, mean wet weight = 9.357 g, Fig. 2) and when their diet was dominated by Atlantic silverside (73.04% by weight, Fig. 1). The percentage of fish by weight in the diet remained fairly constant through the sampling period and the crustacean part of the diet was composed mainly of crab zoea (see Juanes 1992). On July 26–27, bluefish were significantly larger (mean TL = 135.45 mm, mean wet weight = 26.08 g; $t = 7.450$, $df = 86$, $p < 0.001$), having grown about 1.37 mm/d (and 0.62 g/d) between sampling dates. On this second sampling date, the diet was composed mainly of bay anchovy (*Anchoa mitchilli*) (34%), shrimp (21%), and Atlantic silverside (14%) (Fig. 1). The percentage of fish by weight in the diet was fairly constant throughout the sampling period except for the 10:00 sample when 85% of the diet was composed of the two species of shrimp (Juanes 1992). Although bluefish were significantly larger on July 26–27, mean teleost prey size was similar on both dates (June 28–29: mean prey TL = 28.17 ± 1.91 (SE) mm, $n = 35$; July 26–27: mean prey TL = 30.06 ± 1.74 , $n = 53$; $t = 0.7139$, $df = 86$, $p = 0.477$).

On June 28–29, gut fullness increased through the day, peaked at 18:00, and then decreased through the night (Fig. 2). This pattern was mirrored by the percentage of empty guts at each time period: low during the day ($\approx 20\%$) and higher at night ($\approx 60\%$). There was a positive significant correlation between fullness and time of day for daylight hours ($r = 0.184$, $p = 0.044$), and similarly sized bluefish were collected at each time period (ANOVA $p = 0.166$). Gut fullness also increased during the daylight hours on July 26–27 ($r = 0.365$, $p = 0.002$). However, a second peak was observed at the 02:00 sample (Fig. 2). On this date, the percentage of empty guts was generally lower ($\approx 10\%$) throughout the day. In addition, the two night samples (22:00 and 02:00) were composed of significantly larger bluefish than those collected during the daylight hours (ANOVA $p = 0.007$, followed by a Tukey HSD multiple comparison; Fig. 2).

Evacuation Rates

Evacuation rates of YOY bluefish were uniformly high. Time to 90% digestion of prey for the three bluefish body sizes varied from 5.5 to 7 h. Both the slopes and the ele-

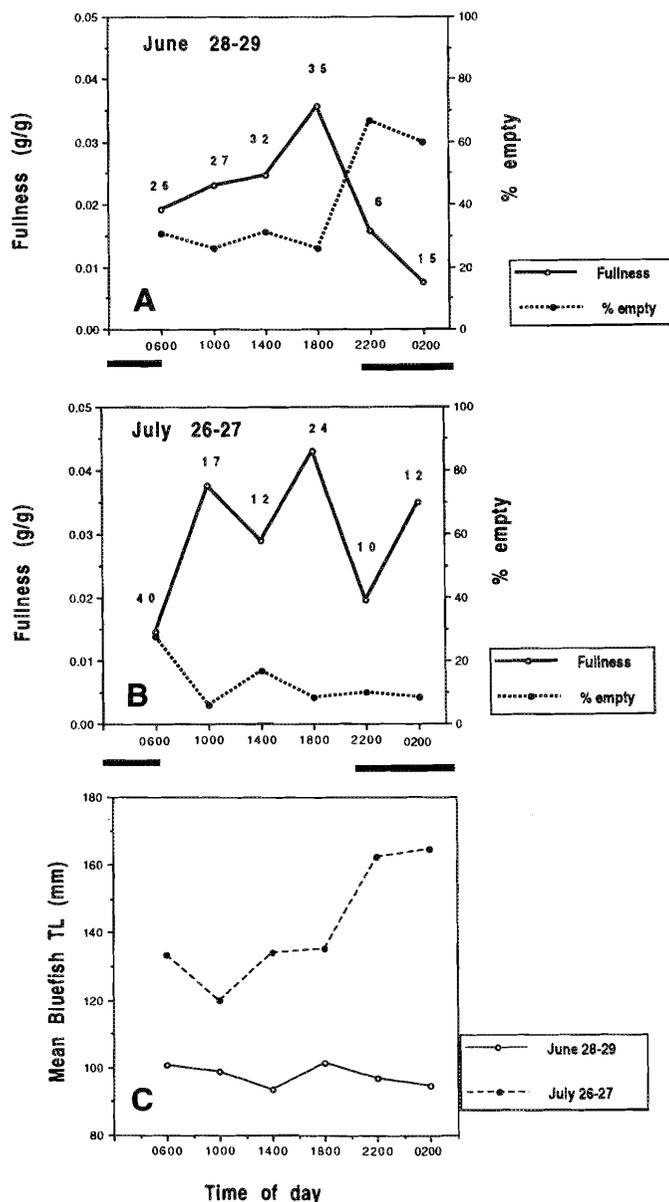


FIG. 2. (A and B) Diel gut fullness patterns and (C) mean bluefish sizes collected during June 28–29 and July 26–27, 1989. Dark bands represent periods of darkness. Numbers above points are sample sizes.

variations of the regressions between percent prey remaining and time after ingestion for the three *Menidia* digestion experiments were statistically indistinguishable (slopes: $F = 0.454$, $df = 34$, $p > 0.05$; intercepts: $F = 2.344$, $df = 36$, $p > 0.05$; Fig. 3). The data for these three experiments were thus combined for further analyses. These combined data were then used to calculate the three types of evacuation rates, linear, exponential, and square root:

Linear:

$$(\%rem) = 67.933 - 9.535t, r^2 = 0.497, p < 0.0001, n = 39$$

Square root:

$$\sqrt{(\%rem)} = 8.416 - 0.812t, r^2 = 0.492, p < 0.0001, n = 39$$

Exponential:

$$1 - n(\%rem) = 4.372 - 0.306t, r^2 = 0.444, p < 0.0001, n = 39.$$

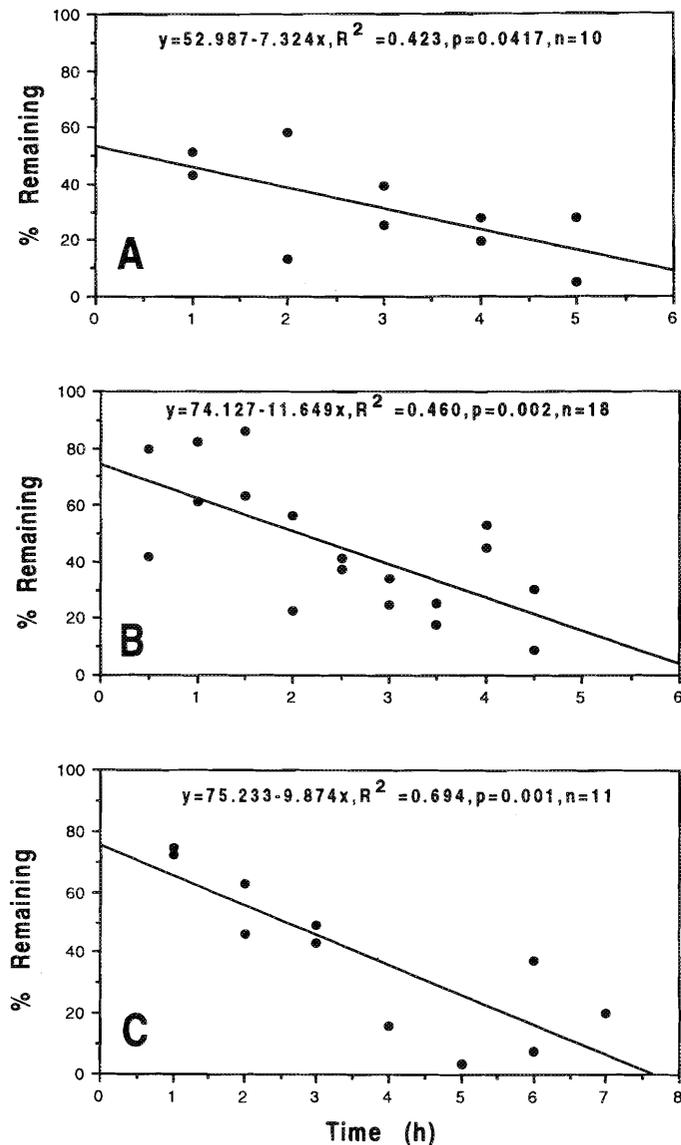


FIG. 3. Relationships between percent prey remaining and time for YOY bluefish feeding on Atlantic silverside. (A) September 11, 1990: mean bluefish TL = 74.20 mm, range = 57–96, mean weight = 3.207 g, $n = 10$; prey mean wet weight = 0.127 g; prey weight/predator weight = 3.972%; (B) August 6, 1990: mean TL = 133.83 mm, range = 121–143, mean wet weight = 19.85 g, $n = 17$; prey mean wet weight = 0.279 g; prey weight/predator weight = 1.407%; (C) September 2, 1988: mean TL = 154.82 mm, range = 128–199, mean wet weight = 31.53 g, $n = 11$; prey mean wet weight = 1.08 g; prey weight/predator weight = 3.425%.

The resulting (linear) regression equation for the shrimp digestion was (Fig. 4)

$$\%rem = 98.157 - 11.921t, r^2 = 0.606, p = 0.008, n = 10.$$

When Atlantic silverside and shrimp linear evacuation rates were compared, their slopes were statistically indistinguishable ($t = 0.6149$, $df = 45$, $p < 0.05$).

Field Consumption Rates

The evacuation rate parameters were then incorporated into the four models for estimating daily ration in the field (i.e., linear, Olson and Boggs; square root, Pennington;

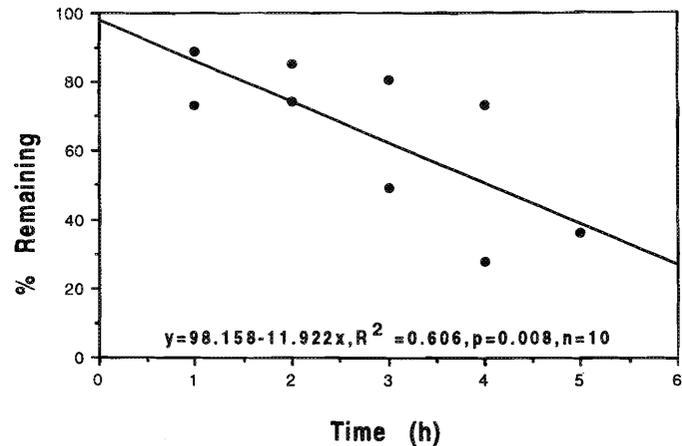


FIG. 4. Relationship between percent prey remaining and time for YOY bluefish feeding on sand shrimp. The experiment was conducted on August 3, 1990 (mean bluefish TL = 125.8 mm, range = 110–142, mean bluefish wet weight = 15.98, $n = 10$, mean prey wet weight = 0.522 g, prey weight/predator weight = 3.265%).

TABLE 1. Daily ration estimates (% body weight/d) from field-collected bluefish on two dates in 1989, using four consumption models.

Model	June 28–29	July 26–27
Eggers	16.78	24.40
Elliott and Persson	16.78	24.40
Pennington	32.88	28.81
Olson and Boggs	22.69	32.93
Mean TL (mm)	98.85	135.45

exponential, Eggers and Elliott and Persson). The four models generated similar estimates of consumption: daily meal ranged from 1.57–3.07 g (16.78–32.88% body weight) on June 28–29 to 6.36–8.55 g (24.40–32.73% body weight) on July 26–27 (Table 1). The Olson and Boggs model incorporates prey-specific evacuation rates. When consumption was calculated using both shrimp and fish evacuation rates and incorporated the different amounts of these items consumed on the respective dates, the results were very similar to those obtained using only fish evacuation rates (June 28–29: 21.29%, July 26–27: 29.35%). The reasons for this consistency are likely to be the similar evacuation rates and the proportionally low amounts of shrimp consumed.

Growth, Consumption, and Gross Efficiency in Laboratory Experiments

ANOVAs performed on specific growth rates calculated from wet weight and dry weight detected a significant effect of diet (wet weight: $p = 0.027$, $df = 3, 8$, $F = 5.235$; dry weight: $p = 0.028$, $df = 3, 8$, $F = 5.206$). The general pattern was for growth to be highest on the fish diets, intermediate on the shrimp diet, and lowest on *Artemia* (Fig. 5; Table 2). Tukey HSD multiple comparisons revealed significantly higher growth on the fish diets than on the *Artemia* diet but no significant differences in growth between shrimp and fish or among the two fish size classes. When examining absolute growth in length during the experiment, similar results were obtained, with the addition that the shrimp diet also produced significantly higher growth than the

Artemia diet ($p < 0.001$, $df = 3,8$, $F = 17.846$). However, growth was relatively high on all diets, ranging from 1.2 mm/d on *Artemia* to 2.0 mm/d on *Menidia* of medium size.

ANOVAs performed on the daily specific feeding rates (i.e., consumption) indicated a significant treatment effect (wet weight: $p < 0.001$, $df = 3,8$, $F = 29.266$; dry weights: $p = 0.007$, $df = 3,8$, $F = 8.446$; energy: $p = 0.001$, $df = 3,8$, $F = 14.477$). Highest feeding rates were on *Artemia*, followed by small Atlantic silverside, medium Atlantic silverside, and shrimp (Fig. 5; Table 2). Multiple comparison tests performed on dry weight consumption indicated highest feeding rates on small Atlantic silverside and *Artemia* diets, intermediate rates on medium *Menidia*, and lowest on shrimp (significantly different from both *Artemia* ($p = 0.011$) and small Atlantic silverside feeding rates ($p = 0.015$)).

Gross growth efficiencies were also dependent on diet (wet weight: $p < 0.001$, $df = 3,8$, $F = 85.063$; dry weight: $p < 0.001$, $df = 3,8$, $F = 40.085$; energy: $p < 0.001$, $df = 3,8$, $F = 59.888$). Comparisons of means (based on dry weight) showed highest efficiencies on shrimp and medium *Menidia*, lower efficiencies on small *Menidia* (significantly different from all other diets), and lowest efficiencies on *Artemia* (significantly different from all other diets) (Fig. 5; Table 2).

The mean number of daily prey consumed per individual also depended on diet ($p < 0.001$, $df = 3,8$, $F = 317.778$). An individual bluefish consumed an average of 142.0 ± 7.7 (SE) *Artemia*, 4.9 ± 0.3 shrimp, 7.7 ± 0.6 small Atlantic silversides, or 2.6 ± 0.3 medium Atlantic silversides per day. Comparison of these means revealed that only the number of *Artemia* consumed was significantly different from the numbers of other prey ingested ($p < 0.0001$). If *Artemia* consumption was excluded, the ANOVA was still significant ($p < 0.001$, $df = 2,6$, $F = 42.258$) and all means were significantly different from each other (all $p < 0.016$).

Discussion

Diel Diet and Gut Fullness

YOY bluefish diets generally reflect prey relative abundances and prey-size availability (Juanes 1992; Juanes et al. 1993). In this study, the diet was predominantly piscivorous and was dominated by Atlantic silverside in the first sample and by bay anchovy and other fishes in the second sample (Fig. 1).

Feeding by YOY bluefish was continuous, but tended to be lowest just after sunrise and peaked in late afternoon. On July 26–27, a second peak was observed at 02:00. However, this sample contained significantly larger fish than those collected during daylight hours (Fig. 2). In addition, because the moon rose earlier on this second sampling date, there may have been sufficient light for visual foraging. Although bluefish are considered visual predators (Marks and Conover 1993), with activity peaking during daylight hours (Olla and Studholme 1972, 1978), laboratory experiments have shown that they are able to feed in complete darkness (F. Juanes, unpublished data).

Evacuation Rates and Field Consumption Estimates

YOY bluefish evacuate food from their stomachs faster than most other piscivorous fishes studied (Magnuson 1969; Windell 1978; Fänge and Grove 1979). Only yellowfin

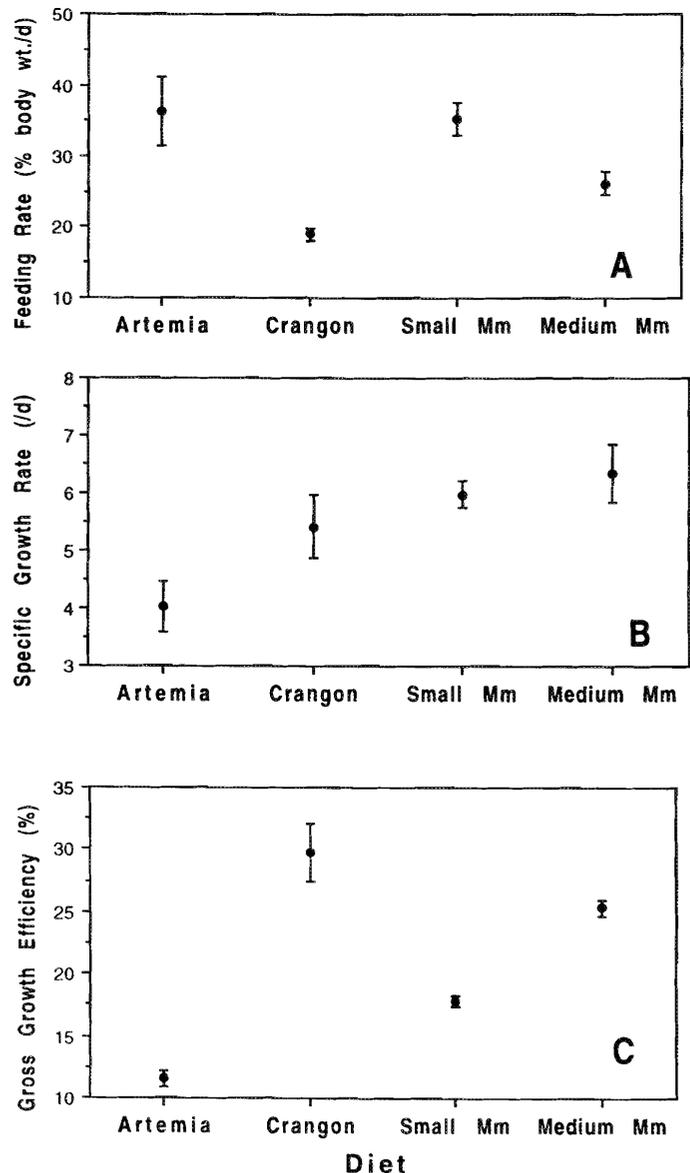


FIG. 5. Mean (A) feeding rate, (B) specific growth rate, and (C) gross growth efficiency of YOY bluefish fed on four live diets for 18 d. Each point represents the mean of three replicates. Calculations were based on dry weights. Each replicate was composed of three bluefish. Error bars are standard errors. Diets were *Artemia* adults, sand shrimp (*Crangon septemspinosa*), small *M. menidia* (Mm) (20–40 mm TL), and medium Mm (50–70 mm TL).

(*Thunnus thynnus*) and skipjack tuna (*Katsuwonus pelamis*) (Magnuson 1969; Olson and Boggs 1986) and juvenile piscivorous coho salmon (*Oncorhynchus kisutch*) (Ruggerone 1989) have been shown to have comparable evacuation times (ranging from 10 to 12 h). Similarly, the daily consumption of YOY bluefish on fish diets appears to be larger than that estimated for other piscivorous fishes (usually <5% body weight/d). The only comparable rates are for juvenile sablefish (*Anoplopoma fimbria*), an open-water epipelagic species that consumes about 30% wet body weight/d (Shenker and Olla 1986), juvenile blue marlin (*Makaira nigricans*) (30–45%, Gorbunova and Lippskaya 1975), and skipjack tuna (28–35%, Kitchell et al. 1978). Bluefish consumption estimates lie in the middle of the range outlined for tropical

TABLE 2. Results of laboratory growth experiments. *F*, feeding rate (%body weight or energy content/d); *G*, specific growth rate (*d*); *E*, gross growth efficiency (%); *n*, number of individuals consumed per day; BTL, bluefish size (mm) at the end of the experiment. *Mm*, *Menidia menidia*. WWT, DWT, kJ, and TL refer to measurements made using wet weights, dry weights, kilojoules, and total lengths (absolute values), respectively. See text for measurement formulas.

	Method	Diet							
		<i>Artemia</i>		<i>Crangon</i>		Small <i>Mm</i>		Medium <i>Mm</i>	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>F</i>	WWT	122.78	18.11	20.40	0.81	29.98	1.71	22.61	1.37
	DWT	36.32	4.82	19.03	0.84	35.34	2.22	26.30	1.66
	kJ	14.25	1.89	4.94	0.22	12.01	0.75	8.94	0.56
<i>G</i>	WWT	3.87	0.42	5.21	0.53	5.75	0.23	6.10	0.48
	DWT	4.03	0.44	5.42	0.55	5.98	0.24	6.34	0.49
	TL	21.56	0.99	30.33	1.07	32.22	1.64	36.00	1.90
<i>E</i>	WWT	3.18	0.19	26.69	2.26	20.05	0.46	28.28	0.92
	DWT	11.55	0.69	29.81	2.31	17.88	0.45	25.34	0.71
	kJ	9.80	0.58	38.27	2.96	17.54	0.44	24.85	0.69
<i>n</i>		142.01	7.66	4.88	0.26	7.70	0.56	2.64	0.27
BTL		101.55	4.07	117.33	2.80	123.00	3.33	126.44	7.85

fishes (Pandian and Vivekanandan 1985). The combination of relatively high evacuation and feeding rates might be expected, since interspecific comparisons reveal an exponential relationship between gastric evacuation rate and feeding rate (Pandian and Vivekanandan 1985).

The evacuation rates and consumption rates calculated here are likely to be underestimates, since the experiments were conducted at lower temperatures than those regularly measured in GSB and temperature is known to consistently increase evacuation rates and thus daily ration estimates (Windell 1978; Persson 1982). However, evacuation rates obtained in the laboratory can also be affected by other factors such as stress and enforced starvation periods (Swenson and Smith 1973; Windell 1978; Talbot 1985).

Linear, exponential, and square root forms of the evacuation model provided similar fits to the data collected in this study. These preliminary results also indicate little effect of predator size or prey type on gastric evacuation rates. More rigorous experiments using shorter intervals (15 or 30 min), more replicates, and varying meal sizes might resolve the best form of the evacuation curve with which to describe warmwater, continuously feeding predators such as bluefish. The rapid evacuation times exhibited by bluefish precluded the use of Diana's (1979) cold-water piscivore model because it assumes digestion periods of days. In addition, because bluefish feed fairly continuously during the day and the original sizes of prey could not always be reconstructed, the Adams et al. (1982) model for warmwater piscivores could not be applied.

Consumption Comparisons

The consumption estimates from field-collected bluefish are similar irrespective of the model used (Table 1). The only exception is the estimate from the Pennington model for the smaller fish (June 28–29 sample). A similar result was obtained by Ruggerone (1989) when comparing daily ration estimates based on linear, exponential, and square root evacuation models for juvenile coho salmon fed sockeye salmon

(*Oncorhynchus nerka*) fry. He found that the Eggers and the Elliott and Persson models resulted in very similar estimates of food consumption whereas the Pennington model tended to estimate slightly lower daily rations. Boisclair and Leggett (1988), after a series of ten 24-h samplings of yellow perch (*Perca flavescens*), found that the daily ration estimates derived from both the Eggers and the Elliott and Persson models did not differ significantly. This consistency occurred despite the lack of continuous feeding or equal gut fullnesses at the beginning and end of a 24-h sampling period. The authors concluded that the Eggers model is robust and can be applied to species that feed throughout the day on a range of food types, exhibit feeding peaks, and do not have rigid feeding periodicities. Hayward (1991) has recently shown that the estimates derived from these models (also on yellow perch) tend to vary as the sampling intervals become longer than 6 h. Although the various consumption models provided similar estimates, the results of this study cannot assess the appropriateness of a particular model, since various assumptions (such as continuous feeding, full 24-h samples, equal amounts of food in the gut at the beginning and end of the cycle) may have been violated.

Field estimates were generally lower than estimates derived from laboratory experiments (for the fish diets), although it is difficult to compare the results directly, since bluefish sizes differed (Tables 1 and 2). However, laboratory bluefish sizes overlapped with those from both field samples. Sizes at the beginning of the experiment were similar to those measured on June 28–29 whereas sizes at the end of the experiment resembled those of the second diel sampling (the experiment was conducted during the first 3 wk of July 1990). Moreover, results of the laboratory evacuation experiments showed no differences between bluefish sizes. Field values are likely to be underestimated because the temperatures during both diel samplings were higher than the average temperature during either the growth experiment or the evacuation trials. Other studies have also found field estimates to be lower than laboratory daily consumption estimates (Mann 1978; Worobec 1984; Canino et al. 1991).

Growth

Results of the laboratory growth experiments showed a significant effect of food type. Growth was highest on the fish diets, intermediate (although not significantly different from the fish diets) on shrimp, and lowest on *Artemia* (Fig. 5; Table 2). Thus, as predicted, growth on a fish diet was significantly higher than growth on a zooplanktivorous diet. Potential reasons for this growth rate difference are the increased foraging costs of feeding on *Artemia* (see below) and the higher dry to wet weight ratio of fish (0.259) and shrimp (0.231) prey as compared with *Artemia* (0.065) (Shenker and Olla 1986). Similar results were obtained by Martin (1966) when examining growth of planktivorous and piscivorous lake trout (*Salvelinus namaycush*). Those fish fed on a fish diet attained maximum weights at least 2.5 times higher than those that remained planktivorous.

Most studies of fish consumption have found a positive relationship between growth rate and feeding rate (often described as a negatively accelerated curve, Brett and Groves 1979; Wootton 1990). Recent evidence has suggested that this may not always be true. Boisclair and Leggett (1989a, 1989b, 1989c, 1989d), in a series of papers, showed a lack of correlation between field estimates of food consumption and relative growth rates of age 2 and 3 yellow perch across 12 lake populations. They suggested that differential activity costs rather than feeding rate led to the interpopulation growth differences (Boisclair and Leggett 1989d, 1990, 1991). In our study, feeding and growth rates were highest on fish diets (Fig. 5). However, the opposite pattern was found for fish fed on *Artemia*: high feeding rates but low growth rates (despite the similar caloric values of fish and *Artemia*). This result is likely due to the extreme differences between the average number of prey constituting the daily ration of each diet. Hence, *Artemia*-fed fish would incur increased foraging costs due to the increased number of feeding bouts resulting in lower growth (Mann 1978).

Despite the observed differences in growth, all the estimated growth rates were as high (*Artemia*) or higher (shrimp and fish) than that observed in the field (McBride and Conover 1991). Generally, laboratory-derived growth rates tend to be higher than those estimated from field collections because fish in the laboratory will feed at higher rates if given food ad libitum and tend to exhibit reduced activity levels from being confined to small spaces resulting in lower energy expenditures (Kerr 1971b; Mann 1978; Brett 1979; Brett and Groves 1979; Ricker 1979; Hawkins et al. 1985; Jobling 1985; Werner 1986). The growth rates of bluefish fed on fish diets observed in this study (1.8–2.0 mm/d) also rank among the highest measured for juvenile fishes (Shenker and Olla 1986; D'Amours et al. 1990; Szedlmayer et al. 1992).

Growth Efficiency

Gross growth efficiency is the ratio of growth to consumption. The results of this study show the highest efficiencies on a shrimp diet, intermediate on fish diets, and lowest on *Artemia* (Fig. 5; Table 2). All of the observed efficiencies based on dry weight (10–30%) lie in the range of those obtained for other juvenile marine fishes (Brett and Groves 1979; Lane et al. 1979; Smith et al. 1986; Malloy and Targett 1991). The comparatively low efficiencies of fish and *Artemia* diets as compared with the shrimp diet

may be a function of the well-described relationship between conversion efficiency and ration in fishes (Paloheimo and Dickie 1966; Kerr 1971a, 1971b; Brett and Groves 1979). This relationship produces a humped curve in which highest efficiencies are obtained at intermediate ration levels ("optimum rations"), while increased rations lead to reduced efficiencies (the "K-line"). Such a relationship suggests that bluefish were consuming near-optimal rations of shrimp but maximum rations of fish and *Artemia* resulting in lower growth efficiencies.

In conclusion, YOY bluefish show relatively high evacuation rates, feeding rates, and specific growth rates that are as high as those for pelagic warmwater fish species. These high rates, combined with more rapid growth after the shift from a zooplankton to a fish diet, explain how YOY bluefish, by pursuing a tropical life-style in a temperate environment, can achieve higher growth rates and hence much greater sizes at age 1 than any other morphologically similar species in this region (Nyman and Conover 1988; Chiarella and Conover 1990; McBride and Conover 1991). This life-style may also have other ecological implications, including potentially strong effects on prey populations, particularly if predation mortality is an important determinant of recruitment success (see Juanes et al. 1993 for an example in the Hudson River estuary).

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