Abstract.–Young-of-the-year (YOY) bluefish, *Pomatomus saltatrix,* were collected during the summers of 1992 and 1993 in the Hudson River estuary with beach seine, surface trawl, and gill nets. The temporal and spatial patterns of catch-per-unit-of-effort (CPUE) and gut-fullness values were used to infer bluefish movement and feeding periods, respectively. Estimates of daily ration were made from gut-fullness values and previously published estimates of gastric evacuation rate. Nearshore beach-seine CPUE was highest during day collections and lowest at night. Offshore gill-net CPUE was highest during crepuscular or night periods and lowest during day sets. Hence, YOY bluefish appear to occupy nearshore environments during the day and move away from shore at night. Gut-fullness values for bluefish captured with beach seines were highest at diurnal and crepuscular periods and declined at night; however, there were indications of night feeding on some dates. The magnitude and pattern of daily ration estimates of YOY bluefish in the Hudson River estuary were similar to values measured in previous studies with other methods. Interannual differences in the magnitude of daily ration were observed and may be a result of day-to-day variation in feeding or differences in available prey type and size. Clupeids, striped bass, and bay anchovy were important prey in 1992, whereas striped bass, bay anchovy, and Atlantic silversides were the dominant prey of YOY bluefish in 1993. Improved understanding of the spatial and temporal patterns of bluefish feeding, as well as fine-scale temporal resolution of estimates of bluefish consumption rates, will aid in assessing the impact of YOY bluefish predation on fish populations within the Hudson River estuary.

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Movements, feeding periods, and daily ration of piscivorous young-of-the-year bluefish, *Pomatomus saltatrix*, in the Hudson River estuary*

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The movements of fishes are controlled by both biotic and abiotic phenomena. In estuaries, fish may move in relation to the availability of prey and to reduce the risk of predation, as well as in response to fluctuations in light, tide, salinity, temperature, and dissolved oxygen levels (Miller and Dunn, 1980). Fish distribution is often controlled by the interacting effects of these factors (Miller and Dunn, 1980; Gibson et al., 1996). An understanding of the factors that govern the movements and distributions of predators and prey is prerequisite to quantifying predator-prey interactions.

The bluefish, *Pomatomus saltatrix,* is a marine piscivorous predator of circumglobal distribution. On the U.S. east coast, spawning occurs offshore over the continental shelf, but young-of-the-year (YOY) migrate abruptly into estuaries at ~60 mm fork length (Kendall and Walford, 1979; Nyman and Conover, 1988; McBride and Conover, 1991; Juanes and Conover, 1995). Bluefish spawned in the South Atlantic Bight in the spring (spring-spawned) are advected northward in waters associated with the Gulf Stream (Hare and Cowen, 1996) and move into New York-New Jersey estuaries in June (Nyman and Conover, 1988; McBride and Conover, 1991). A second wave of recruits made up of summer-spawned fish (spawned in the Middle Atlantic Bight) appear in nearshore waters in mid- to late-summer. The habitat shift from oceanic waters to estuarine areas coincides with a shift from feeding that is zooplanktivorous to one that is piscivorous (Marks and Conover, 1993).

This study is part of a larger project designed to estimate the predatory impact that YOY bluefish have on their piscine prey populations in the Hudson River estuary. Young-of-the-year bluefish are known to prey on larval and juvenile fishes in marine embayments and estuaries along the U.S. east coast (Grant, 1962; Friedland et al., 1988; Juanes et al., 1993; Creaser and Perkins, 1994; Hartman and Brandt, 1995a; Juanes and Conover, 1995). In the Hudson River estuary, YOY bluefish prey include the young of several resource species such as striped bass, *Morone sax-*

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atilis, and American shad, *Alosa sapidissima* (Juanes et al., 1993; 1994). Mortality caused by YOY bluefish predation may be intense given the relatively high consumption rates of this species (Juanes and Conover, 1994; Buckel et al., 1995). In order to assess the effect of YOY bluefish predation, an understanding of the location and timing of bluefish prey interactions, as well as accurate and fine-scale temporal measurements of bluefish consumption rates, are needed.

Consumption rates of fish are measured with direct methods (laboratory- or field-based) and indirect methods. The field-based method requires measurements of gut fullness over a diel cycle coupled with estimates of gastric evacuation rate (Elliott and Persson, 1978; Eggers, 1979). The indirect method most widely used is a bioenergetic approach that requires knowledge of the predator's growth trajectory, physiological parameters, and environmental data (Kitchell et al., 1977). Because all of these methods have their drawbacks and their use is controversial (Hewett et al., 1991; Boisclair and Leggett, 1991), we used a combination of different techniques in order to compare methods and cross-validate results.

Juanes and Conover (1994) and Buckel et al. (1995) measured YOY bluefish consumption rates in the laboratory. Steinberg (1994) estimated daily ration of Hudson River YOY bluefish with a bioenergetics modeling approach. However, the only two field estimates of bluefish consumption rates that exist were made in Great South Bay, NY (Juanes and Conover, 1994), an environment that differs from the Hudson River estuary.

Here we report on the results of diel field collections of YOY bluefish during the summers of 1992 and 1993 in the Hudson River estuary. These collections allowed us to determine temporal and spatial (e.g. inshore vs. offshore) patterns of YOY bluefish movements and feeding. Gut-fullness values were coupled with previously determined estimates of gastric evacuation rates (Buckel and Conover, 1996) to estimate YOY bluefish daily ration.

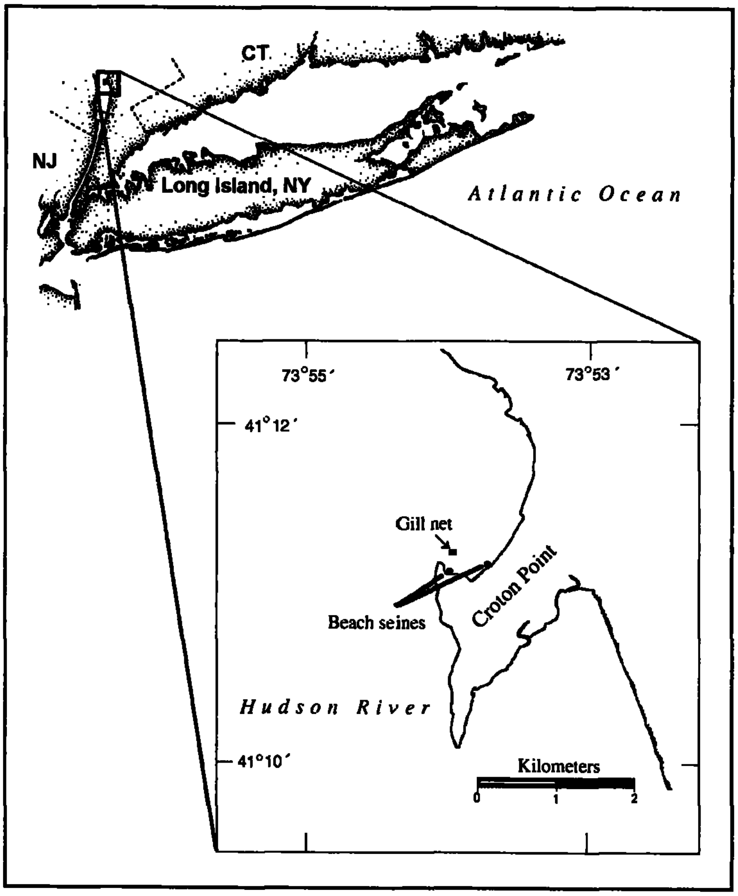

Figure 1

Locations where beach seines and gill nets were used at Croton Point, New York, in the lower Hudson River estuary.

Methods

Diel collections—beach seine

Spring- and summer-spawned YOY bluefish (cohorts easily identified by size) and their prey were collected from the lower Hudson River estuary in 1992 and 1993 on the north shore of Croton Point (41°11'N, 73°54'W; Fig. 1). Ten diel beach-seine collections were made: five in 1992 (16–17 July, 28–29 July, 13–14 August, 26–27 August, and 19–20 September) and five in 1993 (7–8 July, 20–21 July, 4–5 August, 18–19 August, and 11–12 September). Collections were made every three hours beginning at 1200 h and ending at 1200 h the following day. Sampling began 30 min before and ended 30 min after each time point (e.g. sampling for the 1200 time point began at 1130 and ended at 1230). A 60 × 3 m beach seine (13-mm-mesh wings, 6-mm-mesh bag) and a 30 × 2 m beach seine (6-mm-mesh wings, 3-mm-mesh bag) were used for nearshore sampling. The 60-m seine was set by boat. A minimum of two 60-m seine hauls were made during each one-hour sampling period. Additional seine hauls were sometimes made to increase bluefish sample size. Bluefish and samples of prey were immediately preserved in 10% formalin. Catch-per-unit-of-effort (CPUE) of bluefish was calculated as the number of fish caught per seine haul in the first two 60-m seine hauls. Potential prey were counted from one haul of each of the 60- and 30-m seines in 1993. Temperature (thermometer), salinity (refractometer), and dissolved oxygen (modified Winkler's method) were measured at each time point. Periodic functions were used to obtain quantitative values of tide and light levels for statistical analyses. Tides at the study site are semidiurnal and the tidal amplitude is ~1.5 m. The state of tide (T) for any given time point was calculated from the following equation:

$$T = \cos\left(\left((2\pi/12.42)\times \text{time of day}\right)-\theta\right),$$

where θ = the time of high tide in radians.

A value for illumination (watts/cm^2) was calculated for each time point on each specific date (Kuo-Nan, 1980).

The effects of light, tide, salinity, dissolved oxygen, and temperature on CPUE of spring-spawned bluefish were examined with a forward step-wise multiple regression. Data from 1992 and 1993 were analyzed separately and $\log_e(x+1)$ transformed to remove heterogeneity of variances.

Diel collections—gill net and surface trawl

A 90 × 2 m (4-cm-stretch, 2-cm-square) monofilament surface gill net was used to collect spring-spawned YOY bluefish from offshore shoal areas. One end of the gill net was anchored approximately 30 m east of the northernmost tip of Croton Point at a depth of ~3 m (low tide) and set parallel to the north shore of Croton Point (see Fig. 1). The nearest beach-seine site was ~200 m away in the cove just south of the gill-net set location. Gill-net collections were made concurrently with diel beach-seine collections on 20–21 July (approximate mid-set times were 1500, 2100, 0600), 4–5 August (2100, 0130, 0600), and 18–19 August (1500, 2100, 0130, 0600) in 1993. Soak times always lasted two hours. After net retrieval, bluefish were removed and immediately frozen on dry ice. Fish from gill-net collections were not used in the calculation of daily ration. Relative abundances of bluefish were calculated as the number of fish caught per hour of soak time (CPUE).

A surface trawl collection (8.2-m head-rope, 6.7-m foot-rope, 0.9-m-opening height, 2.5-cm-mesh net, 0.6-cm-mesh codend) towed between two boats was made on 15–16 July 1993. It was conducted 1) to supplement night beach-seine collections, 2) to determine YOY bluefish movement patterns, and 3) to estimate daily ration. Collections were made every three hours beginning at 1230 and ending at 1230 the following day. Two to three ten-minute tows were made at each time point. Tow speed was approximately 4 knots. Bluefish and prey were immediately preserved in 10% formalin. Relative abundances of bluefish were calculated as the number of fish caught per trawl (CPUE).

Diel collections—"movement collection"

A combination gill-net and beach-seine collection was made on 11–12 August 1993 with the sole purpose of examining bluefish movement at crepuscular periods. Fish from these collections were not used in the calculation of daily ration. Collections with beach seines were performed at 1200, 2400, and one hour before and after sunrise (0520 and 0720) and sunset (1900 and 2100). The temporal resolution of this sampling scheme with respect to sunrise and sunset was higher than that of evenly spaced intervals of beach seining described above (every three hours). Gill-net collections lasted two hours and were made throughout the diel cycle.

Feeding period

Values of gut fullness were used to examine the feeding periods of beach-seine-collected YOY bluefish. Gut-fullness values (F) were calculated as

$$F = G/W,$$

where G = prey wet weight; and
W = bluefish wet weight (total weight minus prey wet weight; see "Diet analysis" below).

Arc-sin square root and $\log_e(x+1)$ transformations of individual gut-fullness values did not remove heteroscedasticity; therefore, the effect of time on gut-fullness values from beach-seine data (excluding 11–12 Aug and 11–12 Sep 1993) was examined with a nonparametric Kruskal-Wallis ANOVA. If treatment effects were significant, a nonparametric multiple comparison test for unequal sample sizes (Zar, 1984) was used to compare means.

Daily ration estimates

Values of gut fullness for spring-spawned bluefish from beach-seine (five dates in 1992 and four dates in 1993) and surface trawl (15–16 July 1993) collections were used in estimating daily ration. Daily ration was also estimated for summer-spawned bluefish captured during beach-seine collections (19–20 Sept. 1992). The Elliott and Persson (1978) food consumption model was used to estimate bluefish daily ration:

$$C_{\Delta t} = \frac{(\overline{F}_{t_2} - \overline{F}_{t_1} \cdot e^{-R_e t}) \cdot R_e t}{1 - e^{R_e t}}$$

where $C_{\Delta t}$ = food consumption between sampling periods at time t_2 and t_1;
$\overline{F}_{t_2}$ and $\overline{F}_{t_1}$ = the geometric mean gut-fullness values (back-transformed from $\log_e (x+1)$) at these time points (time points with $n <$ 3 fish were not used in daily ration calculation);
R_e = the exponential gastric evacuation rate; and
t = $t_2 - t_1$.

Daily ration was calculated by summing estimates of $C_{\Delta t}$.

The method of Boisclair and Marchand (1993) and Trudel and Boisclair (1993) was used to estimate 95% confidence intervals for daily ration estimates. There were four steps in the analysis. First, an estimate of exponential evacuation rate (R_e) was made from the average water temperature during a given sampling period. Estimates of R_e were calculated from the equation

$$R_e = 0.015e^{(0.103T)},$$

where T = water temperature (°C) from Buckel and Conover (1996).

Periods of declining gut fullness can be used as a validation of laboratory-based gastric evacuation rates (see Parrish and Margraf, 1990) and were used for seven out of ten diel beach-seine collections with the same data analysis techniques as those described in Buckel and Conover (1996). The mean field-derived estimate of R_e for these dates was 0.241/h, and the laboratory-derived estimate was 0.201/h (± 0.038 SE).

Second, a normal distribution of 1,000 pseudo values of R_e were calculated as

$$R_e^* = R_e + (SE_{Re} \times RN),$$

where R_e^* = the pseudo value of evacuation rate;
R_e = the estimated mean evacuation rate;
SE_{Re} = the standard error of R_e (Buckel and Conover 1996); and
RN = a random number (different for each calculation) from a normal distribution with a mean of 0 and standard deviation of 1.

Third, a normal distribution of 1,000 pseudo values of gut fullness (F) were calculated for each time point as

$$F_t^* = F_t + (\mathrm{SE}_{Ft} \times RN),$$

where F_t^* = the pseudo value of gut fullness;
F_t = the mean $\log_e(F+1)$ transformed gut fullness;
SE_{Ft} = the standard error of F_t; and
RN = a random number (different for each calculation) from a normal distribution with a mean of 0 and standard deviation of 1.

Fourth, Monte-Carlo simulations were used to estimate $C_{\Delta t}$ from the above equations by randomly choosing values of R_e^*, $F_{t_1}^*$, and $F_{t_2}^*$ from the distributions of 1,000 pseudo values (values of $F_{t_1}^*$ and $F_{t_2}^*$ were back-transformed before calculation of $C_{\Delta t}$). Simulated values of $C_{\Delta t}$ were generated for each of the eight time intervals (nine sampling points; less if a time point had n<3 fish) and summed to estimate a daily ration. This calculation was repeated 1,000 times. The 2.5 and 97.5 percentiles of these daily ration estimates were taken as the 95% confidence intervals.

Diet analysis

Diets of bluefish captured with beach seines, surface trawls, and gill nets were quantified. In the laboratory, bluefish were measured for total length (TL, ± 1.0 mm), weighed (± 0.01 g), and their stomachs were extracted. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (± 0.01 g), and measured (TL, ± 1.0 mm; eye diameter, ± 0.1 mm; caudal peduncle depth, ± 0.1 mm). Regressions relating prey eye-diameter and caudal peduncle depth to TL were used to estimate prey TL from prey pieces (see Scharf et al., 1997). A reference collection of Hudson River fish species (whole fish, scales, and bones) was used to aid in identification of digested prey. Two indices were computed to describe diets (see Hyslop, 1980). The indices were 1) number of stomachs in which a taxon was found, expressed as a percentage of the total number of stomachs containing food (%F=percent frequency of occurrence), and 2) weight of taxon, expressed as a percentage of the total weight of food items (%W=percent weight).

Results

Diel collections—beach seine

A total of 1,204 spring-spawned and 64 summer-spawned bluefish were collected during diel beach-seine collections. There were five successful diel collections in 1992 (571 spring- and 64 summer-spawned) and four in 1993 (633 spring-spawned fish). The sample size of bluefish from the 11–12 September 1993 beach-seine collection was too small (n=23) for all analyses except diet.

In the forward stepwise multiple-regression analysis, illumination of the surface waters was the only factor that explained a significant amount of the variation in spring-spawned bluefish CPUE for both 1992 (P=0.006) and 1993 (P<0.001). The influence of illumination on CPUE of spring-spawned bluefish was positive in both 1992 and 1993 (Fig. 2, A and B): more bluefish were captured by day than by night but daytime CPUE was more variable. The CPUE pattern was also seen with summer-spawned bluefish (Fig. 2A).

The number of prey captured in the 60- and 30-m seine hauls at each time point ranged from 1 to 1,910 in 1993. On three out of the four dates examined, the relation between numbers of prey and bluefish (from identical seine hauls) was positive; however, none of these correlations were significant.

Diel collections—gill net and surface trawl

A total of 154 bluefish were captured in gill-net sets on three diel collections in 1993. Mean CPUE was highest during sunset and midnight collections and lowest during afternoon and sunrise sets (Fig. 2C). A total of 94 bluefish were captured during surface trawl collections on 15–16 July 1993. Bluefish surface trawl CPUE was highest during the day (1500) and lowest at sunset (2100)(Fig. 2D).

Diel collections—"movement collection"

Gill nets and beach seines captured 29 and 47 bluefish on 11–12 August 1993, respectively. Gill-net CPUE was low during midday, increased through the evening to a peak at midnight (Fig. 2E), and then declined to zero by morning. Beach-seine CPUE was high during the day and low at night: the drop and increase in CPUE corresponded with sunset and sunrise, respectively.

Feeding period

Time of collection had a highly significant (Kruskal-Wallis ANOVA, P<0.001) effect on the gut-fullness values of spring-spawned bluefish in 1992 and 1993 (Figs. 3, A–F, and 4, A–E). Mean gut-fullness patterns from seine-collected bluefish in 1992 increased throughout the afternoon, peaked in late afternoon or evening, decreased throughout the night, and increased during the morning hours (Fig. 3A).

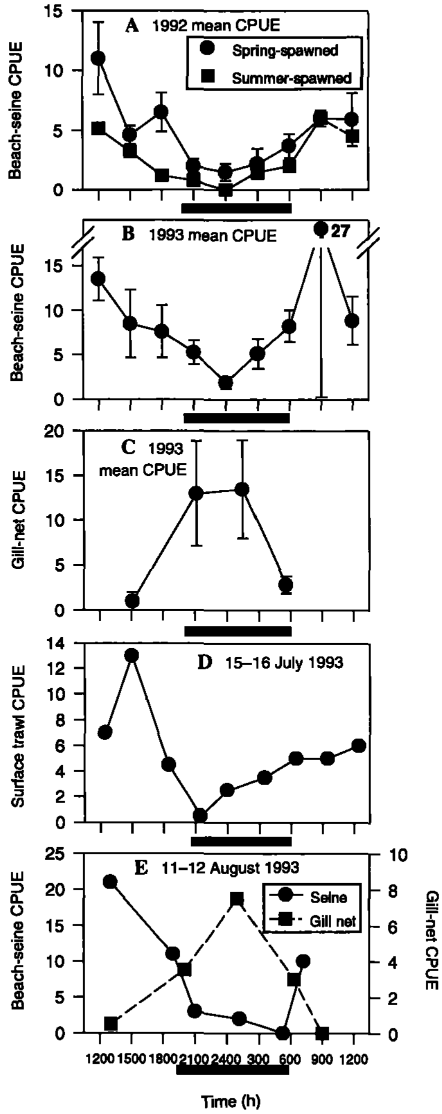

Figure 2

Catch-per-unit-of-effort (CPUE) of bluefish, *Pomatomus saltatrix*, versus time of capture during 1992 and 1993 diel collections. (A) Mean 1992 beach-seine CPUE (circles; ± SE) of spring-spawned bluefish averaged over all dates of collection (16–17 July, 28–29 July, 13–14 August, 26–27 August, and 19–20 September) and summer-spawned bluefish CPUE (squares) on 19–20 September. (B) Mean 1993 beach-seine CPUE (± SE) of spring-spawned bluefish averaged over all dates of collection (7–8 July, 20–21 July, 4–5 August, and 18–19 August). (C) Mean 1993 gill-net CPUE averaged over all dates of collection (20–21 July, 4–5 August, and 18–19 August). (D) Surface trawl CPUE on 15–16 July 1993. (E) CPUE of spring-spawned bluefish during the beach-seine (circles, solid line) and gill-net (squares, broken line) "movement collection" on 11–12 August 1993. The time periods from sunset to sunrise are indicated by dark horizontal bars.

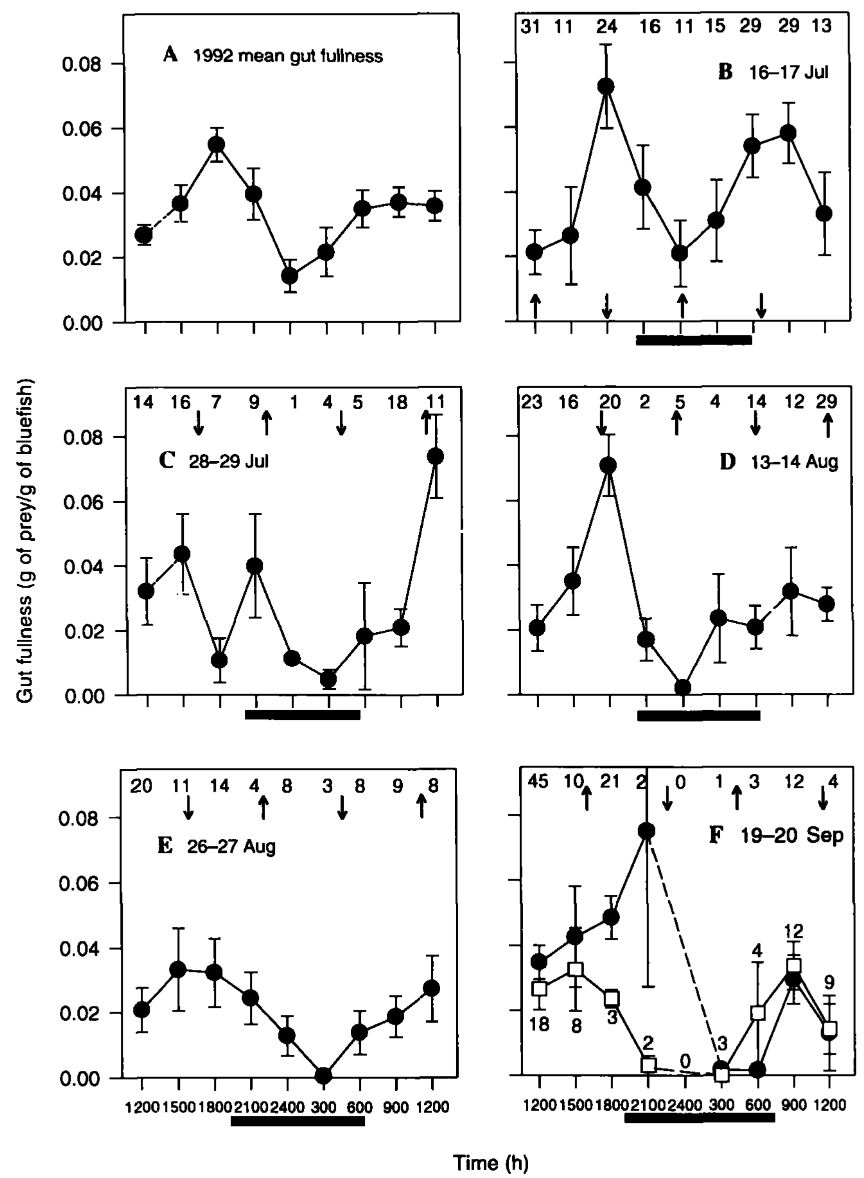

Figure 3

Gut-fullness values (mean ± SE) of spring-spawned bluefish, *Pomatomus saltatrix*, versus time of capture during 1992 diel beach-seine collections. (**A**) Mean gut fullness (± SE) averaged across all dates of collection: (**B**) 16–17 July, (**C**) 28–29 July, (**D**) 13–14 August, (**E**) 26–27 August, and (**F**) spring-spawned (closed circles) and summer-spawned (open squares) bluefish versus time of capture during diel beach-seine collections on 19–20 September. The time periods from sunset to sunrise are indicated by dark horizontal bars. Numbers above (or near, for summer-spawned) each gut-fullness estimate represent bluefish sample size. Upward and downward facing arrows represent the time of high and low tide, respectively.

One potential problem in the above analysis is the potential lack of independence of gut-fullness estimates between time points. This lack of independence is mainly a concern with adjacent time points (spaced 3 hours apart) because gastric evacuation in bluefish is ~6–8 hours (Juanes and Conover, 1994; Buckel and Conover, 1996). Therefore, gut-fullness estimates at time points that are separated by at least six hours are more likely to be independent of each other. We used post-hoc comparisons to examine for statistical differences between such pairs.

The gut-fullness value at 1800 was significantly higher (nonparametric multiple-comparison test, $P<0.001$) than the gut-fullness value at 1200, 2400, and 0300. A similar pattern was seen for summer-spawned fish (Fig. 3F). The gut-fullness values of 1993 beach-seine-collected bluefish differed from those seen in 1992 (Fig. 4A); decline in gut fullness at night was not as dramatic. Gut-fullness values at 1200 were significantly lower ($P<0.01$) than values from morning (0600 and 0900) and evening (2100) collections. However, the lowest night gut-fullness value (0300) was not significantly different from the highest day (0600) gut-fullness value ($P>0.05$).

Daily ration estimates

Daily ration estimates for YOY spring-spawned bluefish during 1992 beach-seine collections were highest on our first sampling date 16–17 July at 22.2% body weight/d (95% confidence interval (CI) 13.3–32.3) and dropped to 7.3% body weight/d (1.7–13.6) by 19–20 September (Fig. 5A). Although there was a decline in daily ration, these values had overlapping CI's and were therefore not statistically different. In 1993, daily ration values from beach-seine-captured spring-spawned bluefish were highest on 20–21 July at 14.7% body weight/d (8.5–21.6) and lowest on 7–8 July at 10.1% body weight/d (6.7–14.0) (Fig. 5B). The diel collection made with surface trawls on 15–16 July 1993 yielded a daily ration estimate of 8.6% body weight/d (4.7–12.8).

Estimates of daily ration in 1993 were not statistically different from each other. Daily ration of summer-spawned fish on 19–20 September 1992 was 5.7% body weight/d (2.6–9.4).

Diet analysis

Diets of YOY bluefish collected with beach seines during 1992 and 1993 were dominated by fish. Fish prey represented 97–100% of bluefish diet by weight (Table 1 and 2).

In 1992, the diet of YOY bluefish was dominated by clupeids, moronids, and bay anchovy *Anchoa mitchilli* (Table 1). Clupeids (American shad, blueback herring [*Alosa aestivalis*], alewife [*Alosa pseudoharengus*], and *Alosa* spp.—clupeids that could not be identified to species) were the dominant prey of 1992 bluefish collected by beach seine and were found in 30% of stomachs containing prey and represented 27% of bluefish prey weight (Table 1). Striped bass, white perch, *Morone americana*, and *Morone* spp. (moronids that could not be identified to species) were found in 19% of bluefish stomachs and made up 27% of their diet by weight. Bay anchovy were an important component of the diet on 19–20 Sept, representing 47% of the diet by weight (41%*F*). Atlantic silversides, *Menidia menidia*, and Atlantic tomcod, *Microgadus tomcod*, were found in bluefish diets during August and September. Invertebrates (zoeae, copepods, and sand shrimp) were a small component of bluefish diet (Table 1).

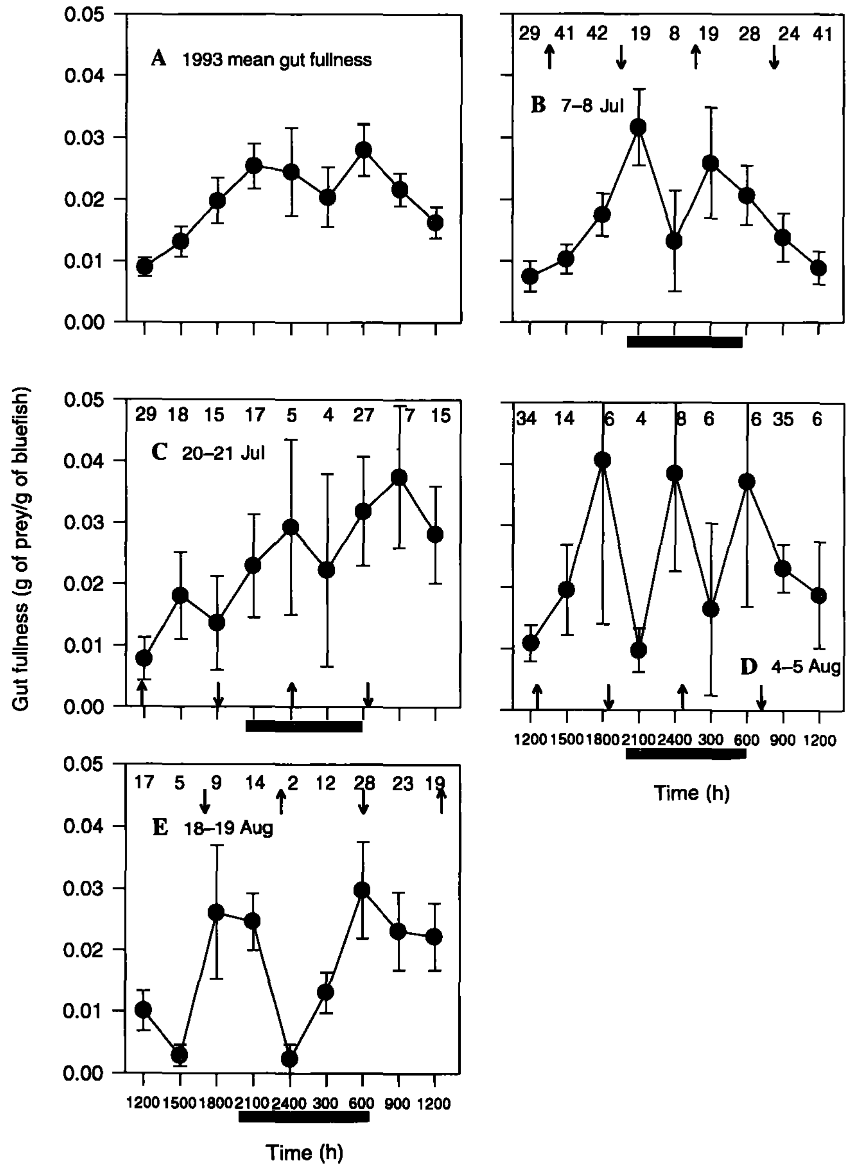

Figure 4

Gut-fullness values (mean ± SE) of spring-spawned bluefish, *Pomatomus saltatrix*, versus time of capture during 1993 diel beach-seine collections. (**A**) Mean gut fullness (± SE) averaged across all dates of collection: (**B**) 7–8 July, (**C**) 20–21 July, (**D**) 4–5 August, and (**E**) 18–19 August 1993. The time periods from sunset to sunrise are indicated by dark horizontal bars. Numbers above each gut-fullness estimate represent bluefish sample size. Upward and downward facing arrows represent the time of high and low tide, respectively.

In 1993, the diet of YOY bluefish was dominated by striped bass, bay anchovy, and Atlantic silversides (Table 2). Striped bass was the dominant prey of YOY bluefish in 1993 beach-seine collections, i.e. in 22% of bluefish stomachs and accounting for 37% of their diet by weight. Bay anchovy was also a major prey of bluefish in 1993 (11%*F*, 22%*W*), particularly during the July collections. The Atlantic silverside became an important prey in August (Table 2). As in 1992, invertebrates were a small component of bluefish diet.

Striped bass (17%*F*, 35%*W*) and Atlantic silversides (24%*F*, 27%*W*) were dominant prey items of YOY bluefish captured with the gill net in 1993 (Table 3).

Clupeids and bay anchovy were also important prey items of YOY bluefish captured in the gill net. Diets of YOY bluefish captured in the surface trawl on 15–16 July 1993 were dominated by bay anchovy (56%*F*, 52%*W*) and striped bass (7%*F*, 20%*W*) (Table 3).

Discussion

Diel movements

We found large differences in the CPUE of bluefish with the diel cycle in beach-seine, gill-net, and surface trawl collections. There are several mechanisms that could account for these patterns. Rountree and Able (1993) distinguished two types of diel sampling bias: 1) direct avoidance of the gear or 2) a change in fish behavior. They further divided the second bias into diel movement between habitats (into or away from the gear sampling area) and diel changes in local activity (e.g. foraging).

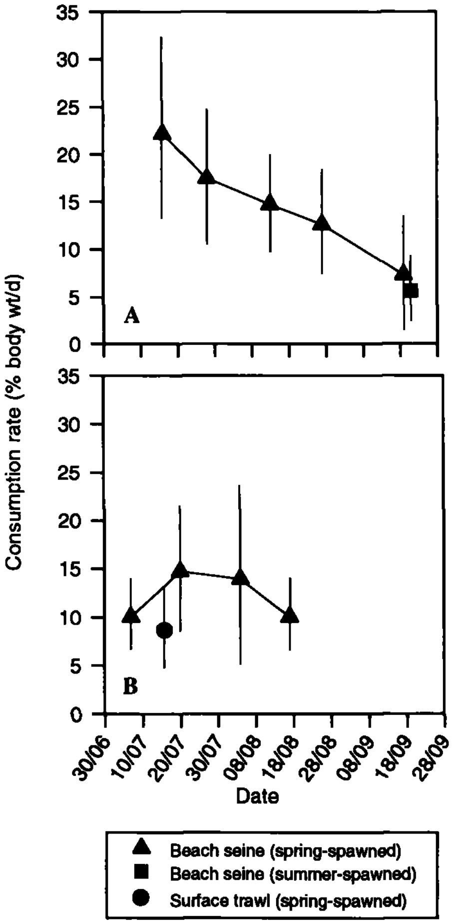

Figure 5

Estimates of consumption rates versus date for spring-spawned (triangles) and summer-spawned (squares) bluefish, *Pomatomus saltatrix*, captured by beach seines in 1992 (**A**) and for spring-spawned bluefish captured by beach seine (triangles) and surface trawling (circles) in 1993 (**B**). Bars represent 95% confidence intervals.

Catch-per-unit-of-effort of YOY bluefish (both spring- and summer-spawned cohorts) was higher during day beach-seine collections than during night collections in both 1992 and 1993 (Fig. 2, A–B). Fish would more likely detect and avoid beach-seine gear during the day than at night. Additionally, we used a boat to set the seine, which helped to standardize set time so that there were probably limited avoidance biases between diurnal and nocturnal collections due to "operator" efficiency. We therefore rule out direct avoidance of the gear (bias one) and accept a diel behavioral change (bias two) as an explanation for low night CPUE.

The surface trawl CPUE in 1993 was also highest during daylight hours (Fig. 2D). Because the pattern of CPUE in 1993 was not that expected if fish were visually avoiding the gear (bias one), we propose that a behavioral change that increases the susceptibility of bluefish to the surface trawl gear during the day is most likely responsible for the pattern.

Bluefish CPUE with the gill net was highest at sunset and night sets in 1993 (Fig. 2C). The pattern of gill-net CPUE was the opposite of what we saw with the 1993 beach-seine and surface trawl CPUE data. During the gill-net and beach-seine "movement collection" on 11–12 August 1993, beach-seine catches were higher an hour before sunset than an hour after (Fig. 2E). The opposite pattern was seen at sunrise. On this date, gill-net catches were low during the day and increased to a midnight peak before declining to zero after sunrise (Fig. 2E). We attempted to determine the direction of bluefish movement from the orientation of individual bluefish in the gill net; however, data were inconclusive.

According to beach-seine, surface trawl, and gill-net collections, bluefish occupy nearshore and surface waters during the day and then move offshore and below surface waters at night. Although we cannot rule out avoidance of gill-net gear (bias one) as a possible explanation of low day gill-net CPUE's, concomitant declines in beach-seine CPUE of bluefish in nearshore areas suggest that increased gill-net catches are at least partly a result of bluefish moving offshore. Support for our findings comes from field collections in other estuaries. Pristas and Trent (1977) found significantly higher catches of adult bluefish at night with monofilament and multifilament gill nets in shallow-water (0.7–1.1 m), mid-

Table 1

Stomach contents of spring- and summer-spawned bluefish, *Pomatomus saltatrix*, captured during diel beach-seine collections in the Hudson River estuary in 1992. %F = frequency of occurence, %W = percent wet weight.

		Spring-spawned										Summer-spawned		Spring-spawned	
Prey type		16–17 July		28–29 July		13–14 Aug.		26–27 Aug.		19–20 Sept.		19–20 Sept.		Total	
Species	Common name	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*	*%F*	*%W*
Anchoa mitchilli	bay anchovy	13.5	11.0	5.1	1.9	3.0	0.7	10.3	1.1	41.4	47.1	19.2	18.5	15.0	18.4
Morone saxatilis	striped bass	17.5	24.4	5.1	3.9	15.2	23.7	11.8	39.0	4.6	9.5			11.8	19.6
Morone americana	white perch	2.4	1.8	6.8	5.6	6.1	10.6	1.5	1.7	1.2	2.6			3.4	4.8
Morone spp.		5.6	2.3	3.4	1.5	5.1	4.3	2.9	1.9	1.2	1.0			3.9	2.2
Alosa sapidissima	American shad	6.4	15.6	15.3	24.1	5.1	7.3	7.4	6.6	9.2	9.7	2.1	9.3	8.0	10.5
Alosa aestivalis	blueback herring	3.2	4.9	15.3	12.7	1.0	1.4							3.2	2.1
Alosa pseudoharengus	alewife			3.4	7.1	1.0	3.0							0.7	1.5
Alosa spp.		21.4	22.9	25.4	26.1	18.2	17.4	17.7	8.7	10.3	5.4	14.9	26.4	18.5	13.0
Menidia menidia	Atlantic silverside	2.3	2.3			7.1	8.6	13.2	13.8	2.3	5.2	2.1	7.7	4.8	6.9
Microgadus tomcod	Atlantic tomcod	0.8	0.4			1.0	2.2	2.9	13.4	2.3	2.5			1.4	4.0
Other fish[1]						1.0	0.1	1.5	3.0					0.4	0.5
Unidentified fish remains		38.9	12.9	52.5	16.9	49.5	20.5	41.2	10.8	39.1	14.2	55.3	33.6	43.5	15.3
Total fish			98.5		99.8		99.8		99.5		97.2		95.5		98.8
Crangon spp.	sand shrimp							1.5	0.2	4.6	1.0	8.5	4.0	1.1	0.2
Zoeae and copepods		0.8	0.5	1.7	<0.1	2.0	<0.1	2.9	0.3	1.2	1.3			3.6	0.7
Other[2]				3.4	0.2	9.1	0.2	1.5	<0.1	8.0	0.5	14.9	0.8	4.9	0.3
Total stomachs analyzed		179		83		125		85		99		64		571	
Number containing prey		126		59		99		68		87		47		439	
Mean bluefish size (g) (SE)		4.48 (0.18)		11.30 (0.69)		25.04 (1.27)		41.16 (2.78)		43.71 (2.01)		10.29 (1.29)			

[1] "Other fish" include Atlantic menhaden, *Brevoortia tyrannus*, and bluefish, *Pomatomus saltatrix*.

[2] "Other" includes vegetation, gravel, sand, and rope fibers.

water (2.2–2.6 m), and deep-water (5.2–5.6 m) zones of a Florida estuary. Using a subtidal weir in a polyhaline marsh creek in New Jersey, Rountree and Able (1993) captured a significantly higher number of YOY bluefish during day sampling than during night sampling. They concluded that this CPUE pattern was a result of diurnal foraging or increased activity (or both). Juanes and Conover (1994) made two diel beach-seine collections in Great South Bay, NY. Although they made no comparison between night and day abundance, their mean diurnal catch was two to three times higher than their mean nocturnal catch. These field studies confirm that bluefish activity patterns are influenced by light and dark cycles and that this pattern exists in diverse environments beyond the Hudson River estuary.

Factors that may be responsible for changes in diel activity or movements of fishes include foraging (Sciarrotta and Nelson, 1977; Wurtsbaugh and Li, 1985), reduction in predation risk (Clark and Levy, 1988; see Hobson, 1991), spawning (Conover and Kynard, 1984), and thermoregulation (Caulton, 1978; Rountree and Able 1993; Neverman and Wurtsbaugh, 1994). These factors may be interdependent. For example, Neverman and Wurtsbaugh (1994) found that Bear Lake (Utah-Idaho) YOY sculpin were able to digest their gut contents in a short period (overnight) by moving into warm surface waters at night. By digesting their food overnight, these fish were able to feed the following day. Clark and Levy (1988) showed that the vertical migration of juvenile sockeye salmon in an Alaskan lake during the day could be explained as a tradeoff between foraging and predation risk. For juvenile estuarine fishes, Miller and Dunn (1980) considered foraging as the primary cause of diel movements.

If bluefish movements are directly related to foraging, we might expect a strong correlation between the abundance of bluefish and their prey. Bluefish may congregate where prey density is high, or prey

Table 2

Stomach contents of spring-spawned bluefish, *Pomatomus saltatrix*, captured during diel beach-seine collections in the Hudson River estuary in 1993. %*F* = frequency of occurence, %*W* = percent wet weight.

		Date													
Prey type		7–8 July		20–21 July		4–5 Aug		11–12 Aug[1]		18–19 Aug		11–12 Sept[1]		Total	
Species	Common name	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Anchoa mitchilli	bay anchovy	27.9	13.5	30.2	27.3	15.1	8.9	15.4	5.9	12.2	7.8	12.5	3.2	21.7	9.9
Morone saxatilis	striped bass	32.0	67.8	17.4	41.2	16.3	37.0	7.7	13.8	13.0	28.9	12.5	23.9	20.7	32.2
Alosa sapidissima	American shad					2.3	8.5			1.0	1.4			0.6	2.4
Alosa spp.				2.3	5.8	5.8	5.0	2.6	0.5	4.1	4.0			2.5	3.3
Menidia menidia	Atlantic silverside	1.2	1.2	1.2	2.5	16.3	23.1	41.0	69.7	22.5	35.9	12.5	21.0	11.5	32.8
Other fish[2]						3.5	1.7			4.1	9.0	12.5	13.2	3.4	4.3
Unidentified fish remains		40.1	14.8	48.8	21.8	40.7	10.8	25.6	7.5	45.0	12.0	75.0	37.1	42.1	13.2
Total Fish			97.3		98.6		95.0		97.4		99.0		98.4		98.0
Crangon and *Palaemonetes* spp.	sand and grass shrimp					14.0	4.6	10.3	2.6	3.1	0.3	12.5	1.6	4.1	1.6
Zoeae and copepods		6.4	2.4	1.2	0.2					2.0	0.4				
Other[3]		5.2	0.3	11.0	1.2	7.0	0.4			10.2	0.3			7.0	0.4
Total stomachs analyzed		248		137		119		47		129		23		703	
Number containing prey		172		86		86		39		98		8		489	
Mean bluefish size (g) (SE)		4.96 (0.10)		8.96 (0.51)		19.84 (0.94)		23.29 (1.41)		33.41 (1.59)		75.67 (8.79)			

[1] Bluefish that were captured on 11–12 Aug and 11–12 September were not used to calculate daily ration.

[2] "Other fish" includes killifish, *Fundulus* spp., American eel, *Anguilla rostrata*, white perch, *Morone americana*, *Morone* spp., Atlantic menhaden, and unidentifiable sciaenids.

[3] "Other" includes vegetation, gravel, sand, and rope fibers.

may leave an area of high bluefish densities. However, we found no evidence of a correlation between prey and predator abundance; although positive relations between bluefish and prey abundance were found on three out of four dates in 1993, these correlations were nonsignificant.

Sea-surface illumination was the only environmental factor describing a significant amount of the variation in nearshore CPUE of YOY bluefish. Young-of-the-year fish of several shallow-water marine fishes move inshore at night (Keats, 1990; Burrows et al., 1994). We, however, observed an opposite pattern for bluefish in our study. Given that bluefish are visual predators, diurnal schooling and foraging in the nearshore zone is a possible explanation for relatively high and variable daytime beach-seine CPUE. Olla and Studholme (1972) found that adult bluefish in the laboratory had higher activity (swimming speed) and a larger schooling group size during the day than at night. The difference in diel activity was also seen in YOY bluefish and shown to be endogenous (Olla and Studholme, 1978). Olla and Marchioni (1968) found that photomechanical changes in the retina of YOY bluefish were also internally controlled and thus lessened the time required for light and dark adaptation. Such diurnal rhythms would offer a selective advantage for a predator dependent on vision for prey capture.

Feeding period

During 1992 and 1993, gut-fullness values from bluefish caught in beach seines were highest during day, evening, and morning collections. However, there were dates in 1993 when bluefish gut-fullness levels indicated nocturnal feeding; these dates occurred with a recent full moon (7–8 July, 4–5 August) and a new moon (20–21 July). Therefore, moonlight is not entirely responsible for the nocturnal feeding seen in 1993. In laboratory tanks, YOY bluefish are capable of feeding in complete darkness (Juanes and Conover, 1994). Tide may also influence the timing of feeding; however, the timing of low and high tide had no consistent influence on peaks in gut-fullness levels (Fig. 3–4).

Table 3

Stomach contents of spring-spawned bluefish captured during surface trawl and gill-net collections in the Hudson River estuary in 1993. %F = frequency of occurence, %W = percent wet weight.

		Date							
		Surface trawl		Gill net					
Prey type		15–16 July		20 July–4 Aug		11–12 Aug		18–19 Aug	
Species	Common name	%F	%W	%F	%W	%F	%W	%F	%W
Anchoa mitchilli	bay anchovy	56.3	51.7	3.0	5.9	6.3	10.1	2.6	0.6
Morone saxatilis	striped bass	7.0	20.4	18.2	47.6	25.0	33.9	18.4	33.3
Morone spp.				6.1	5.1				
Alosa sapidissima	American shad			3.0	5.1	12.5	19.8		
Alosa aestivalis	blueback herring							2.6	3.5
Alosa pseudoharengus	alewife					6.3	8.7		
Alosa spp.		1.4	2.5	15.2	8.5			5.3	2.8
Menidia menidia	Atlantic silverside			6.1	2.9	18.8	9.0	31.6	39.1
Other fish[1]		1.4	10.2	3.0	8.7	6.3	15.2	2.6	1.2
Unidentified fish remains		43.7	13.9	51.5	15.3	25.0	1.4	44.7	19.2
Total fish			98.7		99.2		97.9		99.7
Crangon spp.	sand shrimp			3.0	0.8	12.5	2.1	2.6	0.3
Zoeae and copepods		4.2	0.5						
Total stomachs analyzed		94		83		29		71	
Number containing prey		71		33		16		38	
Mean bluefish size (g) (SE)		6.83 (0.65)		50.93 (1.81)		55.25 (3.68)		52.95 (2.44)	

[1] "Other fish" are bluefish, Atlantic menhaden, unidentified sciaenid, and American eel.

Declining gut-fullness values probably represent periods when fish do not feed. In 1992, these periods occurred mostly after sunset during nocturnal hours for both spring- and summer-spawned bluefish (Fig. 3, B–F). In 1993, declining gut-fullness values were more variable and followed sunset or sunrise peaks in gut fullness, or else not at all (Fig. 4, B–E). Bluefish that Juanes and Conover (1994) captured during diel sampling showed peaks in gut-fullness values during crepuscular periods and a subsequent decline in gut-fullness values and a higher percentage of empty guts at night.

Many freshwater, estuarine, and marine fish species show periodicity in their daily feeding (Helfman, 1979; Miller and Dunn, 1980; Reis and Dean, 1981; Popova and Sierra, 1985; Wurtsbaugh and Li, 1985; Nico, 1990; Jansen and Mackay, 1992). This periodicity is exhibited in fish that feed either diurnally, nocturnally, or during crepuscular periods. Young-of-the-year bluefish appear to be mainly diurnal and crepuscular foragers but are also able to feed at night.

Daily ration estimates

Daily ration estimates from this study are consistent with prior laboratory and field studies in which YOY bluefish were shown to have relatively high consumption rates for a temperate fish (Juanes and Conover, 1994; Buckel et al., 1995). Field estimates of bluefish consumption rates in the Hudson River estuary in early 1992 approached 25% body wt/d. In 1992, daily rations declined as fish grew. Largest values for consumption-rate rations occurred in mid-July (22.2%) and dropped to a low in mid-September (7.3%) (Fig. 5A). The pattern and magnitude of field estimates of consumption rate were similar to values of consumption rate from laboratory-mesocosm experiments made at the same time on similar-size fish (Buckel et al., 1995). In 1993, however, the early (10.1 %) and mid-July (8.6%) estimates of daily ration from 24-hour collections made with beach seines (7–8 July) and surface trawls (15–16 July) were lower than the mid-July beach-seine estimate in 1992 (16–17 July). The last three daily ration estimates in 1993 were similar to those estimated for similar dates in 1992 (Fig. 5, A and B). A comparison of these field consumption rate estimates with estimates from bioenergetic models (Steinberg, 1994; Hartman and Brandt, 1995b) is dealt with elsewhere (Steinberg and Conover[1]).

There are several possible explanations for the relatively low estimates of daily ration in early July 1993. First, these are point estimates of feeding rate that may not reflect average daily feeding over longer periods (see Smagula and Adleman, 1982; Trudel and Boisclair, 1993). Although Trudel and Boisclair (1993) found low day-to-day variation (7.0–16.3%) of daily ration for minnows in a field study, Smagula and Adelman (1982) found large day-to-day variation (30–40%) in daily ration estimates of piscivorous largemouth bass in the laboratory.

Alternatively, other factors known to affect fish consumption rates include temperature, fish size, prey availability, prey biomass, prey type and size composition, and risk of predation. Both temperatures and bluefish sizes were similar in 1992 and 1993 (Tables 1–4). Prey abundance was not recorded during diel collections in 1992 and thus cannot be compared, but there were differences in the types and sizes of prey consumed by bluefish in these years (Table 4). The much larger clupeid species were a dominant part of bluefish diet in 1992 but were not a dominant prey in 1993. This finding reflects riverwide relative abundance estimates from a separate beach-seine study (Buckel, 1997). In July 1992, clupeids, striped bass, and bay anchovy represented 90% of the available forage fish. Striped bass alone represented 63% of the available forage fish at this time in 1993. Moreover, striped bass and bay anchovy were larger for a given bluefish size in 1992 than in 1993. A combination of the size and type of prey available, along with the possible behavior differences between the prey (e.g. clupeids are more pelagic and less refuge oriented), may have caused the large differences in daily ration in July. We have no information on relative abundances of predators of juvenile bluefish in July 1992 and 1993 and therefore cannot discount predation risk as a potential mechanism explaining differences in daily ration in July.

Diet analysis

Diets of YOY bluefish in 1992 and 1993 were dominated by fish prey, confirming past studies in the Hudson River estuary that have shown YOY bluefish to be largely piscivorous (Texas Instruments, 1976; Juanes et al., 1993). Diets of YOY bluefish were dominated by important anadromous resource species: clupeids in 1992 and striped bass in 1993. Interannual variation in diet was also observed by Friedland et al. (1988) in their study of YOY bluefish in a New Jersey marine embayment. Because YOY bluefish are believed to be opportunistic predators (Friedland et al., 1988; Juanes et al., 1993), the diet differences we observed appear to be a result of the availability of different prey types in 1992 and 1993 (see riverwide abundances above). However, our diet data may be biased because spatial coverage was limited to the Croton Point region of the Hudson River.

Table 4

Percentages of fish with empty stomachs, prey types, mean prey size, and mean values of temperature and gut fullness for diel collections in 1992 and 1993 (beach-seine and the 15–16 July 1993 surface trawl collection (ST)). Prey types are C = clupeids; SB = striped bass; BA = bay anchovy; and AS = Atlantic silversides. Prey types are listed in their order of importance in bluefish diet on each date. Mean prey sizes follow the order of prey type.

Year	Date	% with empty stomach	Prey type	Mean prey size (mm)	Mean temp (°C)	Mean gut fullness (g of prey/g of bluefish) (%)
1992	16–17 June	29.6	C, SB, BA	42.9, 32.9, 27.3	25.6	4.31
	28–29 July	28.9	C	45.7	25.3	3.40
	13–14 Aug	20.8	C, SB, AS	50.9, 56.1, 68.3	25.0	3.26
	26–27 Aug	20.0	SB, C, AS	68, 52, 45.2	26.7	2.27
	19–20 Sept	12.1	BA, C	43.2, 60.2	22.4	3.62
1993	7–8 July	30.6	SB, BA	26.3, 16.5	26.9	1.52
	15–16 July (ST)	24.5	BA	20.4	25.6	1.69
	20–21 July	37.2	SB, BA	39.4, 24.5	26.1	2.13
	4–5 Aug	27.7	SB, AS, C, BA	52.5, 47.0, 57.3, 35.7	25.9	2.08
	18–19 Aug	24.0	SB, AS, BA	68.3, 61.5, 40.4	24.8	2.10

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[1] Steinberg, N. D., and D. O. Conover. 1997. Young-of-the-year bluefish (*Pomatomus saltatrix*) consumption in the Hudson River estuary: a bioenergetic modeling approach. Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000. Manuscr. in prep.

Bluefish collected by gill net and surface trawls had diets that were similar to those of bluefish captured with beach seines (Table 1–3). This finding suggests that YOY bluefish feed nearshore and then move offshore or that prey types in offshore shoal feeding areas do not differ from prey nearshore (or both). However, bluefish captured by surface trawls in 1993 had a larger amount of bay anchovy in their diet than did bluefish captured with beach seines during the previous week. This finding may reflect increased availability of bay anchovy in offshore surface waters than in nearshore environments.

Implications

This study provides an improved understanding of the temporal and spatial patterns of bluefish feeding ecology in the Hudson River estuary. Knowledge of the temporal and spatial scales at which predators forage is required for a variety of predator-prey studies. Densities of predator and prey at scales relevant to predator foraging should be used for calculations of prey-type selectivity (O'Brien and Vinyard, 1974), in encounter rate models (see Brandt and Mason, 1994), in functional and numerical response calculations (Peterman and Gatto, 1978), and in calculations of a predator's growth or impact (Brandt and Kirsch, 1993; Petersen, 1994).

Empirical data on the diel changes in spatial overlap of fish and their prey and the timing of foraging activity is often lacking from spatially explicit models of fish feeding and growth. For example, Brandt and Kirsch (1993) used estimates of prey density from offshore nighttime collections. If the sampling design for estimating the densities of YOY bluefish and their prey in the Hudson River were constrained to only offshore or night (or both), the peaks in feeding activity that occur during day and crepuscular periods in the nearshore would be missed. Clearly, a detailed understanding of the spatiotemporal movement and feeding patterns of predators and prey are necessary to produce realistic models of feeding and growth (Mason and Patrick, 1993).

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