

Gastric Evacuation Rates of Piscivorous Young-of-the-Year Bluefish

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Abstract.—Estimates of gastric evacuation rates (GER) are needed to calculate consumption rates of fish from field-collected data on stomach contents. The results of 16 GER experiments designed to determine the effects of body size, prey type, and temperature on the GER in young-of-the-year (age-0) bluefish *Pomatomus saltatrix* are presented. The linear, square-root, and exponential GER models similarly fit the data. Temperature had a highly significant effect on age-0 bluefish GER. However, there was no significant difference in GER between small (5.14 g wet weight) and large (35.99 g wet weight) age-0 bluefish. Among the three different prey types tested (age-0 striped bass *Morone saxatilis*, bay anchovy *Anchoa mitchilli*, and age-0 Atlantic menhaden *Brevoortia tyrannus*) there was no significant difference in GER. The exponential relation between bluefish GER and temperature can be used in estimating age-0 bluefish consumption rates in the field.

Along the Atlantic coast of the southern U.S., bluefish *Pomatomus saltatrix* spawn in continental shelf waters beginning in early spring, about 2 months before the spawning of most estuarine fishes in the Middle Atlantic Bight. When young-of-the-year (age-0) bluefish migrate into estuaries along the Middle Atlantic Bight at about 60 d of age, they are considerably larger than estuarine age-0 fishes that become their principal prey. The offshore-to-inshore habitat transition is coincident with a shift in bluefish diet from zooplankton to almost exclusively small fishes (Marks and Conover 1993). Juanes et al. (1994) and Juanes and Conover (1995) hypothesize that this life history pattern has evolved to allow an early onset of piscivory.

One east coast estuary where juvenile bluefish are particularly abundant in early summer is the lower Hudson River (Nyman and Conover 1988; McBride and Conover 1991). In the Hudson River estuary, age-0 bluefish prey includes the age-0 stages of many important anadromous species such as striped bass *Morone saxatilis* and American shad *Alosa sapidissima* (Juanes et al. 1993, 1994; Buckel and Conover, unpublished data). The estuarine juvenile stage of bluefish may strongly affect the mortality rate of these and other prey species for two reasons. First, the consumption and growth rates of bluefish appear to be exceedingly high (Juanes and Conover 1994; Buckel et al. 1995). Second, total prey consumption by juvenile stages tends to exceed that of adult stages. The latter occurs because cohort biomass tends to peak at ages prior to maturity when weight-specific con-

sumption is also highest (Stewart and Binkowski 1986; Yáñez-Arancibia et al. 1993).

This paper is part of a larger study to estimate the impact of bluefish predation on the mortality rates of their prey. Making field-based determinations of predation impacts requires accurate estimates of the predator's consumption rate. Consumption rates of fishes in the field are estimated from knowledge of gastric evacuation rates (GERs) and stomach content weight (Eggers 1979; Elliott and Persson 1978).

Here we determine the GER of age-0 bluefish. A variety of factors are known to affect the GER of fishes, including temperature, predator size, meal size, prey type, prey size, number of meals, time since previous meal, and force-feeding (Windell 1978; Jobling 1981, 1986; Durbin et al. 1983; Bromley 1994). Our study focuses on the effects of temperature, predator size, and prey type. Because our ultimate goal is to use a predictive GER function to aid in calculation of bluefish consumption rate in the Hudson River estuary, we used prey types and meal sizes that reflect those found at this site. Effects of salinity on GER are also evaluated.

Methods

Field collection and acclimation.—Age-0 bluefish were collected during early summer and mid-summer in Great South Bay and Long Island Sound, New York, with a 30-m beach seine. Larger fish caught later in the season were also angled with hook and line. Fish were immediately transported to the Flax Pond Marine Laboratory of the State University of New York (SUNY) at Stony

Brook, Old Field, New York, where all laboratory experiments were conducted. Upon arrival, bluefish were placed in 680-L flow-through seawater tanks at ambient temperature and salinity ($\sim 21^{\circ}\text{C}$ and $\sim 28\text{‰}$) and were fed ad libitum amounts of live Atlantic silversides *Menidia menidia*.

In our first year of experiments, laboratory stocks of bluefish were acclimated for at least 1 week to either low temperature ($\sim 22.5^{\circ}\text{C}$) or high temperature ($\sim 28.5^{\circ}\text{C}$) and to low salinities ranging from 5‰ to 10‰. These salinities are similar to those typically found in our Hudson River study site (mean, 7‰; range, 5–15‰) based on our unpublished data. During this period, ad libitum amounts of Atlantic silversides were provided as food. Prior to all experiments, bluefish were further acclimated to experimental temperatures (21 or 24°C for fish acclimated to low temperatures and 27 or 30°C for fish acclimated to high temperatures) and tanks for at least 48 h. The time since a previous meal ranged from 12 to 48 h. Because experiments the first year demonstrated that salinity had no measurable effect on GER, all experiments the second year were conducted at ambient Flax Pond salinity (28‰).

Experimental protocol.—All GER experiments were conducted in an identical manner. Experiments were performed in $30 \times 60 \times 100\text{-cm}$ tanks that were filled to a height of 30 cm and contained one fish per tank. A single prey item was fed to each bluefish. After the prey item was ingested, the bluefish was assigned a digestion period ranging from 0.25 h to 11 h. At the end of this period the tank was drained and the fish was anesthetized with MS-222 (tricaine methanesulfonate) to prevent regurgitation during capture. Fish were then killed with an overdose of MS-222. Total length (TL) and fork length (nearest millimeter) and weight (nearest 0.01 g) were measured. Stomach contents were removed, blotted dry, and weighed to the nearest 0.001 g. Sample sizes per experiment ranged from 11 to 20 bluefish.

Effects of body size, temperature, and salinity.—During the first year (1992), experiments were designed to determine the effects of temperature and bluefish size on GER. Small and large age-0 bluefish were fed a single live age-0 striped bass ($N = 99$) or white perch *M. americana* ($N = 6$). Age-0 striped bass were chosen as prey because of their importance as both a resource species and predominant prey type in the Hudson River. These experiments were performed at 5–10‰ and four different temperatures (21, 24, 27, and 30°C), which cover the range of temperatures observed

TABLE 1.—Experimental design for bluefish gastric evacuation experiments. Mean values of bluefish total length (TL) and wet weight, prey wet weight, and prey wet weight/bluefish wet weight (PW/BW) are presented (raw data are available on request); N is the number of bluefish per experiment. Bluefish sizes are small (S; 69–106 mm TL), large (L; 126–206 mm TL), or not applicable (NA). Prey types are striped bass (SB), bay anchovy (BA), and Atlantic menhaden (AM).

Year	Size	Prey	Temperature ($^{\circ}\text{C}$)	Bluefish			Prey weight (g)	PW/BW (%)
				N	TL (mm)	Weight (g)		
1	S	SB	21	17	82.8	4.51	0.287	6.77
1	S	SB	24	16	81.6	4.61	0.254	5.68
1	S	SB	27	11	84.1	5.08	0.309	6.44
1	S	SB	30	11	95.4	6.96	0.335	5.25
1	L	SB	21	14	161.9	37.20	1.455	4.13
1	L	SB	24	13	159.2	36.03	1.737	4.90
1	L	SB	27	12	156.8	35.61	1.811	4.88
1	L	SB	30	11	155.3	34.73	1.480	3.94
2	NA	BA	21	20	114.6	12.40	0.572	5.55
2	NA	BA	24	18	128.6	17.57	0.838	4.89
2	NA	BA	27	15	127.7	17.41	0.782	4.65
2	NA	BA	30	12	108.8	10.06	0.546	5.91
2	NA	AM	21	19	98.1	7.28	0.508	7.30
2	NA	AM	24	15	110.1	11.27	0.514	5.17
2	NA	AM	27	14	120.0	14.53	0.774	6.01
2	NA	AM	30	13	98.9	7.53	0.486	6.56

during the summer months in the Hudson River (Cooper et al. 1988). Two bluefish sizes were examined across four temperatures for a total of eight experiments. Fish sizes in the four small bluefish treatments were as follows: mean bluefish TL = 85.2 mm (range = 69–106 mm), mean wet weight = 5.14 g, prey mean wet weight = 0.291 g, mean prey wet weight/predator wet weight = 6.08% (Table 1). Fish sizes in the four large bluefish treatments were as follows: mean bluefish TL = 158.5 mm (range = 126–206 mm), mean wet weight = 35.99 g, prey mean wet weight = 1.618 g, mean prey wet weight/predator wet weight = 4.47%. The relationship between exponential GER (R_e , \log_e -transformed) and temperature for the two bluefish sizes were compared by analysis of covariance (ANCOVA) after testing for homogeneity of slopes (Sokal and Rohlf 1995). In addition to this analysis, we also examined the effect of bluefish size by comparing the slopes (R_e , calculated from nonlinear regression analyses) of small and large treatments within individual temperatures by means of a t -test (Zar 1984).

To evaluate the effects of salinity on GER, we performed an experiment that was similar to one performed earlier at the Flax Pond Laboratory by Juanes and Conover (1994), except that ours was conducted at salinities of 5–10‰, whereas Juanes

and Conover (1994) used salinities of ~28‰. Juanes and Conover (1994) performed their experiment in 1990 with the following fish and meal sizes and environmental conditions: mean bluefish TL = 133.4 mm ($N = 18$, range = 121–143 mm), mean wet weight = 19.85 g, prey mean wet weight = 0.279 g, mean prey wet weight/predator wet weight = 1.41%; temperature = 21–22°C, salinity ~28‰. Our experiment was conducted in 1992 with similar fish and meal sizes and environmental conditions: mean bluefish TL = 125.8 mm ($N = 13$, range = 108–140 mm), mean wet weight = 16.75 g, prey mean wet weight = 0.295 g, mean prey wet weight/predator wet weight = 1.87%; temperature = 21°C, salinity = 5–10‰. In both of these experiments live Atlantic silversides were used as prey. We examined the effect of salinity on bluefish GER by comparing the slopes (R_e) of the low- and high-salinity treatments with a t -test.

Effects of prey type and temperature.—Two additional prey types were examined in our second year of experiments (1993). Pieces of previously frozen adult bay anchovy *Anchoa mitchilli* or fresh age-0 Atlantic menhaden *Brevoortia tyrannus* were used as prey at four temperatures (21, 24, 27, and 30°C) for a total of eight experiments. Fish sizes in the four bay anchovy treatments were as follows: mean bluefish TL = 120.4 mm (range = 87–146 mm), mean wet weight = 14.55 g, prey mean wet weight = 0.689 g, mean prey wet weight/predator wet weight = 5.22% (Table 1). Fish sizes in the four Atlantic menhaden treatments were as follows: mean bluefish TL = 105.9 mm (range = 82–141 mm), mean wet weight = 9.84 g, prey mean wet weight = 0.564 g, mean prey wet weight/predator wet weight = 6.33%. The relationship between R_e (\log_e -transformed) and temperature for bay anchovy, Atlantic menhaden, and striped bass (small and large bluefish treatments pooled) were compared by ANCOVA after testing for homogeneity of slopes (Sokal and Rohlf 1995). In addition to this analysis, we also tested for the effect of prey type by comparing all possible combinations of the three slopes within individual temperatures with t -tests.

Model selection.—We used three different mathematical models to estimate age-0 bluefish GER, a linear model (Swenson and Smith 1973; Olson and Boggs 1986):

$$W_t/W_0 = b - R_l t;$$

a square-root model (Jobling 1981):

$$\sqrt{W_t/W_0} = b - R_s t;$$

and an exponential model (Elliott and Persson 1978):

$$\log_e(W_t/W_0) = b - R_e t.$$

For all models, W_t is the final wet weight of the prey at time t , W_0 is the original wet weight of the prey at time 0, b is the intercept, and R_l , R_s , and R_e are the linear, square-root, and exponential gastric evacuation rates, respectively.

Comparisons of the coefficient of determination (r^2) from linear regression analysis have typically been used by researchers to evaluate which model provides the best fit to the GER data. Such comparisons are invalid because the units of the dependent variable for these models are not identical (Sokal and Rohlf 1995). An improved method of comparison has been the use of a deviation index that is based on the differences between observed and predicted dependent variables in the untransformed space (Jobling 1986). However, this method is not without problems because there is a bias associated with back-transforming the predicted variable (Beauchamp and Olsen 1973). Therefore, we used nonlinear regression analysis to fit the three GER models (above equations, but rearranged to obtain identical dependent variable units) to the age-0 bluefish data. Choice of evacuation model was based on evaluation of r^2 values and residual patterns.

Results

Model Selection

Coefficients of determination from the linear (mean $r^2 = 76.8$, range = 52.9–91.8), square-root (mean $r^2 = 76.9$, range = 52.6–91.6), and the exponential (mean $r^2 = 76.1$, range = 50.8–90.8) model fits were similar (Table 2). An analysis of residual patterns did not indicate that any single model was superior. All three GER models gave equally good fits to the age-0 bluefish data. We chose the exponential GER model for all analyses below because of its widespread use in estimating daily ration (Elliott and Persson 1978; Bromley 1994).

Effects of Body Size, Temperature, and Salinity

Gastric evacuation rates in small and large bluefish treatments, representing early and late summer Hudson River bluefish sizes, were not significantly different (Figure 1A–D; Table 2). The slopes and the intercepts of the regressions between R_e (\log_e -transformed) and temperature for small and large

TABLE 2.—Nonlinear regression statistics for linear, square-root, and exponential gastric evacuation models. Coefficients of determination (r^2), y-intercepts (b), gastric evacuation rates (slope, R) and SEs of the slopes are presented for all experiments (raw data are available on request). Bluefish sizes are small (S; 69–106 mm TL), large (L; 126–206 mm TL), or not applicable (NA). Prey types are striped bass (SB), bay anchovy (BA), and Atlantic menhaden (AM).

Experiment			Linear model				Square-root model				Exponential model			
Temperature (°C)	Size	Prey	r^2	b	R_l	SE	r^2	b	R_s	SE	r^2	b	R_e	SE
21	S	SB	80.1	0.84	-0.065	0.008	81.1	0.90	-0.048	0.006	81.7	0.97	-0.144	0.020
24	S	SB	82.1	0.91	-0.102	0.013	81.3	0.98	-0.076	0.011	78.0	1.05	-0.211	0.036
27	S	SB	76.0	0.83	-0.105	0.020	73.2	0.84	-0.073	0.016	70.3	0.88	-0.197	0.047
30	S	SB	84.7	0.98	-0.170	0.024	81.5	1.06	-0.120	0.021	78.5	1.16	-0.334	0.080
21	L	SB	52.9	0.75	-0.050	0.014	53.0	0.77	-0.036	0.010	53.2	0.81	-0.105	0.032
24	L	SB	80.8	0.85	-0.065	0.010	79.5	0.86	-0.043	0.007	77.7	0.89	-0.112	0.020
27	L	SB	82.0	1.00	-0.127	0.019	85.1	1.12	-0.097	0.015	85.0	1.24	-0.267	0.044
30	L	SB	54.2	0.90	-0.103	0.032	52.6	0.95	-0.072	0.024	50.8	0.99	-0.194	0.074
21	NA	BA	65.3	0.82	-0.071	0.012	68.5	0.86	-0.054	0.010	70.4	0.93	-0.157	0.031
24	NA	BA	91.8	0.84	-0.099	0.007	91.6	0.86	-0.071	0.006	90.3	0.89	-0.199	0.020
27	NA	BA	74.3	0.80	-0.104	0.017	79.4	0.86	-0.087	0.014	83.2	0.95	-0.273	0.043
30	NA	BA	89.8	0.85	-0.155	0.017	91.0	0.90	-0.124	0.014	90.8	0.97	-0.376	0.052
21	NA	AM	85.3	0.97	-0.089	0.009	84.2	1.00	-0.059	0.007	81.8	1.03	-0.149	0.021
24	NA	AM	65.6	0.82	-0.087	0.018	63.6	0.81	-0.057	0.001	61.2	0.83	-0.147	0.035
27	NA	AM	86.4	0.86	-0.119	0.014	89.0	0.93	-0.097	0.012	90.0	0.96	-0.298	0.039
30	NA	AM	77.6	0.80	-0.138	0.022	76.1	0.82	-0.100	0.019	74.5	0.85	-0.284	0.065

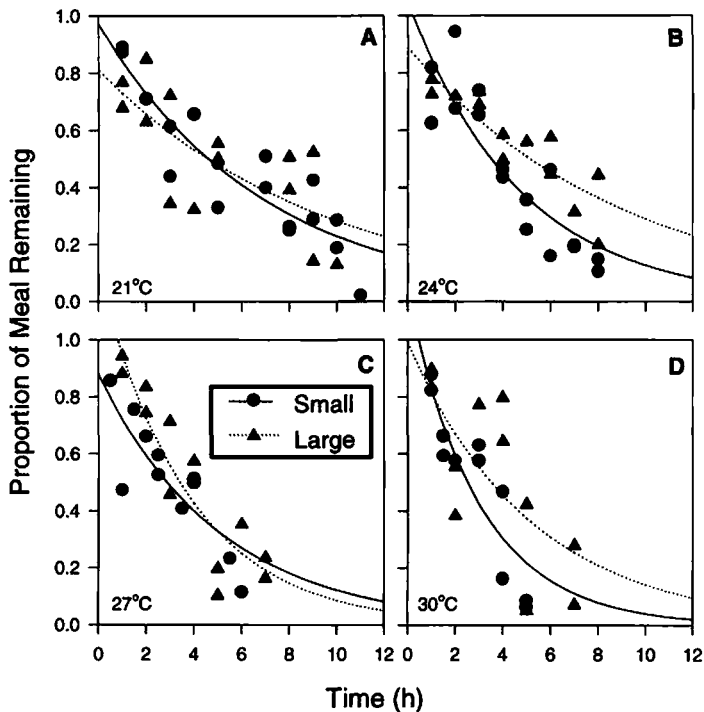


FIGURE 1.—Proportion of meal remaining versus time for small (69–106 mm) and large (126–206 mm) age-0 bluefish feeding on age-0 striped bass at 21, 24, 27, and 30°C. The eight experiments conducted in 1992 are shown. See Tables 1 and 2 for experimental design and results from regression analyses for these experiments.

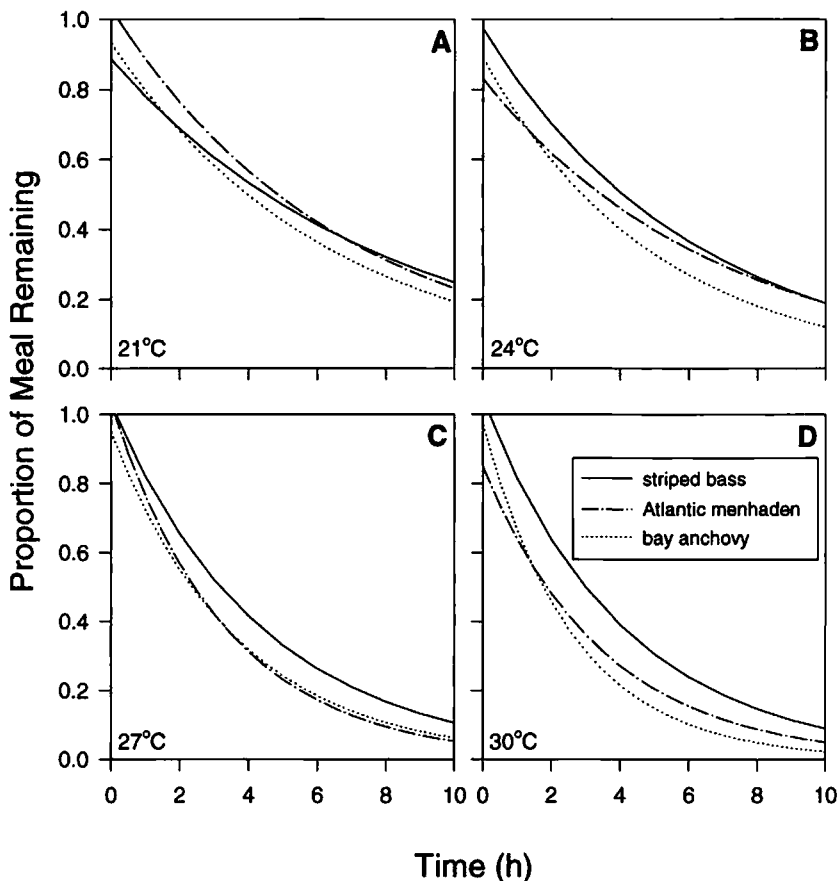


FIGURE 2.—Exponential model fits of proportion of meal remaining versus time for age-0 bluefish fed age-0 striped bass, bay anchovy, and age-0 Atlantic menhaden at 21, 24, 27, and 30°C.

bluefish were statistically indistinguishable (slopes: $F = 0.017$; $df = 1, 4$; $P = 0.903$; intercepts: $F = 2.985$; $df = 1, 5$; $P = 0.115$). In addition, no significant differences were found between small and large bluefish GER at 21°C ($P = 0.294$), 27°C ($P = 0.290$), or 30°C ($P = 0.215$). However, there was a significant difference between small and large bluefish GER at 24°C ($P = 0.033$). Temperature had a significant effect on bluefish GER in these experiments ($F = 8.449$; $df = 1, 6$; $P = 0.027$).

We found no difference between GER estimates from one of our experiments conducted at low salinity: $W_t/W_0 = 1.196e^{0.374t}$, $N = 13$, and $r^2 = 89.1$ ($t =$ time in hours) and a comparable past experiment conducted at high salinity in our laboratory (Juanes and Conover 1994): $W_t/W_0 = 0.819e^{0.262t}$, $N = 18$, and $r^2 = 46.6$ (t -test: $t = 1.034$; $df = 27$; $P = 0.310$).

Effects of Prey Type and Temperature

Prey type did not have a significant effect on GER in age-0 bluefish. The slopes and intercepts of the regressions between R_e (\log_e -transformed) and temperature for bay anchovy, Atlantic menhaden, and striped bass (small and large bluefish treatment pooled; Table 2) were statistically indistinguishable (slopes: $F = 0.039$; $df = 2, 10$; $P = 0.962$; intercepts: $F = 1.980$; $df = 2, 12$; $P = 0.181$). In addition, no significant differences ($P > 0.05$) were found between any of the possible comparisons between bay anchovy, Atlantic menhaden, and striped bass treatments at 21, 24, 27 or 30°C. This can be seen visually by examining the exponential regression model fits to these data (Figure 2). For the bay anchovy and Atlantic menhaden experiments, as in those with striped bass, temperature had a significant effect on bluefish GER ($F = 30.946$; $df = 1, 6$; $P = 0.001$).

Discussion

Model Selection

Linear GERs have been found in a wide variety of piscivores. Walleye *Stizostedion vitreum* (Swenson and Smith 1973), largemouth bass *Micropterus salmoides* (Adams et al. 1982), Sacramento squawfish *Ptychocheilus grandis* (Vondracek 1987), mountain whitefish *Prosopium williamsoni* (McKone 1971), and yellowfin tuna *Thunnus albacares* (Olson and Boggs 1986) evacuate their guts in a linear fashion. However, not all piscivorous fish have a linear GER. Hayward and Bushmann (1994), for example, found that juvenile largemouth bass did not have a linear GER. Juvenile coho salmon *Oncorhynchus kisutch* (Ruggerone 1989) and brown trout *Salmo trutta* (Elliott 1991) had exponential GERs when fed piscine prey.

All three GER models described our data equally well. This is most likely a result of the high variability associated with our GER data. Past GER studies with marine piscivores have also found high variability in GER data. For example, r^2 values were relatively low ($r^2 = 0.50-0.73$) in a study of yellowfin tuna GER (Olson and Boggs 1986). This variability can arise from the several factors that have been shown to affect GER in prior studies (see list above). Therefore, it is important to control for as many of these variables as possible when examining the influence of a specific factor on GER. For example, although we attempted to control for several variables, we did not use a fixed starvation period. Our starvation periods varied from 12 to 48 h and may be a potential source of variability. However, Juanes and Conover (1994) used a fixed starvation period of 48 h and had a larger amount of variability (mean $r^2 = 54.5$, range = 42.3–69.4) than we had in our study (mean $r^2 = 76.8$, range = 52.9–91.8). A second potential source of variability in our study was the effect of tank confinement or biomass density. Two out of the four experiments we conducted on large fish had the lowest r^2 values of all 16 experiments. Buckel et al. (1995) found that growth and consumption rates of large bluefish were depressed in small tanks compared to similar-sized fish held in larger tanks. It is possible that the increased variability in the experiments with large fish is due to stress of tank confinement.

Effects of Body Size, Temperature, and Salinity

With increasing fish size, GER has been observed to decrease (Hunt 1960; Smith et al. 1989;

Hayward and Bushmann 1994), increase (Swenson and Smith 1973; Cochran and Adelman 1982), or be unaffected (Elliott 1972; dos Santos and Jobling 1991). As Boisclair and Leggett (1991) and Bromley (1994) point out, these contradictory results are most likely due to differences in units and methods. For example, relative GERs ($\text{g prey remaining} \cdot \text{g}^{-1} \text{ prey initial} \cdot \text{h}^{-1}$; R_f) in our experiments with small and large bluefish at 21°C were similar, 0.065 and 0.050, respectively (Figure 1A; Table 2). However, the absolute GER ($\text{g prey} \cdot \text{h}^{-1}$) for the small and large bluefish treatments were very different: 0.030 and 0.167, respectively. Special attention should be made to units when comparing different GER studies. He and Wurtsbaugh (1993) analyzed the effects of predator size, prey size, and temperature on exponential GER from 121 published GER estimates. Although temperature and prey size had a significant effect on GER in their empirical model, predator size did not.

For a fixed amount of food, dos Santos and Jobling (1991) found that gastric evacuation time (GET) in Atlantic cod *Gadus morhua* declined with increasing fish size. However, these authors also noted that when cod are fed meals of the same relative size ($100 \times \text{g prey/g predator}$), gastric evacuation time is independent of body size. Our experiments support this finding; GER and time to 90% evacuation were similar for small and large age-0 bluefish when fed comparable ration sizes (Figure 1). Juanes and Conover (1994) also found no difference in GER between small, medium, and large bluefish that were fed fish prey.

We did not test for meal size effects on GER. In our experiments, bluefish were fed meals that were similar in relative size to those observed for bluefish in the field. In bluefish, full stomachs are representative of a recently consumed meal, and we assume that full stomachs represent meal sizes of age-0 bluefish in the field. Of 459 age-0 bluefish captured from July 17 to October 24, 1990, in the Hudson River, 50 fish had stomachs which were ranked as full (Hyslop 1980) based on our previously unpublished qualitative observations. The mean gut fullness ($100 \times \text{g prey/g predator}$) of these bluefish was 6.90%. Mean meal size used in our laboratory experiments was 5.57% (Table 1).

We found no effect of salinity on bluefish GER. This finding is in agreement with recent work that found no difference in bluefish growth or consumption rate at salinities of 5‰ and 25‰ (Buckel et al. 1995).

Effects of Prey Type and Temperature

Differences in prey type can have a significant effect on GER (Fänge and Grove 1979; see Bromley 1994 for review). Yellowfin tuna had similar evacuation rates for three of four prey types; chub mackerel *Scomber japonicus* was evacuated at a significantly slower rate compared with surf smelt *Hypomesus pretiosus*, California market squid *Loligo opalescens*, and the anchovy species, nehu *Stolephorus purpureus* (Olson and Boggs 1986). MacDonald et al. (1982) fed three prey types (clams, worms, and amphipods) to four different fish species (cod, ocean pout *Macrozoarces americanus*, winter flounder *Pleuronectes (=Pseudopleuronectes) americanus*, and American plaice *Hippoglossoides platessoides*); clams were evacuated at a slower rate compared to worms and amphipods in all four fish species. From these studies, it appears that food types that are very different in morphology, energy content, or both cause differences in GER. The lack of prey type effect on bluefish GER in our study may reflect the only slight energy content differences in the types tested (Steimle and Terranova 1985). However, Juanes and Conover (1994) found no difference in age-0 bluefish GER between fish (Atlantic silverside) and shrimp (*Crangon septemspinosa*) meals.

Temperature Effects and Summary

Given that temperature was the only factor tested to significantly influence bluefish GER, we used regression analysis to develop a predictive equation for GER based on temperature alone. This was done by fitting an exponential function to the GER estimates from all 16 experiments (pooling across bluefish sizes and prey types; Tables 1, 2). The resulting equation, $R_e = 0.022e^{0.087T}$ ($N = 16$, $P < 0.001$; $T =$ temperature), had a r^2 value of 0.643. After removal of a single outlier at 30°C the resulting equation ($N = 15$, $r^2 = 0.803$; Figure 3),

$$R_e = 0.015 \cdot e^{0.1037T}$$

was highly significant ($F = 39.642$; $df = 1, 13$; $P < 0.001$).

Based on the rule of "input equals output" (see Bromley 1994), rough estimates of consumption rate of bluefish can be made by using absolute GER. If we assume that bluefish are feeding continuously over the entire diel cycle, then, based on the input-output rule, the 21°C small and large bluefish treatments give daily feeding rates of 0.72 and 4.01 g/d (15.98% and 10.79% body weight/d), respectively. These rates compare favorably to pre-

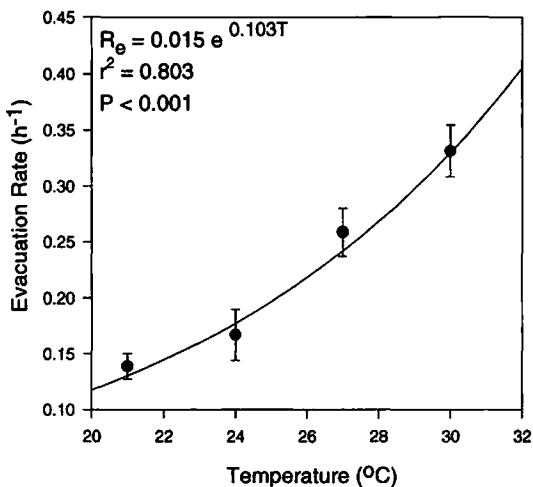


FIGURE 3.—Predictive equation describing the effects of temperature (°C) on exponential evacuation rate (R_e) for age-0 bluefish fed age-0 striped bass, bay anchovy, and age-0 Atlantic menhaden. The mean (\pm SE) of the exponential evacuation rates for all treatments is plotted.

vious estimates of age-0 bluefish consumption rates measured in the laboratory and field (Juanes and Conover 1994; Buckel et al. 1995).

Juanes and Conover (1994) described age-0 bluefish as having a "tropical physiology in a temperate environment" because of their rapid GER, high consumption rates, and rapid growth rates. We also found that age-0 bluefish have extremely rapid GERs. Time to 90% evacuation ranged from ~5 h at 30°C to ~10 h at 21°C. Therefore, age-0 bluefish are capable of feeding two to four times a day. Gut fullness data from diel field collections support this calculation. At different times of the year juvenile bluefish appeared to feed either at crepuscular time periods, continuously throughout the day, or continuously over a 24-h time period (Juanes and Conover 1994; Buckel and Conover, unpublished data). Such flexibility in feeding schedule allows bluefish to achieve very high daily consumption rates and makes them a potentially important predator in estuarine systems (Juanes and Conover 1994; Buckel et al. 1995).

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References

- Adams, S. M., R. B. McLean, and M. M. Huffman. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1175-1184.
- Beauchamp, J. J., and J. S. Olsen. 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology* 54:1403-1407.
- Boisclair, D., and W. C. Leggett. 1991. If computers could swim or fish could be programmed: a response to comments by Hewett et al. (1991). *Canadian Journal of Fisheries and Aquatic Sciences* 48:1337-1344.
- Bromley, P. J. 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries* 4:36-66.
- Buckel, J. A., N. D. Steinberg, and D. O. Conover. 1995. Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. *Journal of Fish Biology* 47:696-706.
- Cochran, P. A., and I. R. Adelman. 1982. Seasonal aspects of daily ration and diet of largemouth bass, *Micropterus salmoides*, with an evaluation of gastric evacuation rates. *Environmental Biology of Fishes* 7:265-275.
- Cooper, J. C., F. R. Cantelmo, and C. E. Newton. 1988. Overview of the Hudson River estuary. Pages 11-24 in L. W. Barnhouse, R. J. Klauda, D. S. Vaughan, and R. L. Kendall, editors. *Science, law, and Hudson River power plants: a case study in environmental impact assessment*. American Fisheries Society, Monograph 4, Bethesda, Maryland.
- dos Santos, J., and M. Jobling. 1991. Factors affecting gastric evacuation in cod, *Gadus morhua* L., fed single-meals of natural prey. *Journal of Fish Biology* 38:697-713.
- Durbin, E. G., A. G. Durbin, R. W. Langton, and R. E. Bowman. 1983. Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. U.S. National Marine Fisheries Service Fishery Bulletin 81: 437-454.
- Eggers, D. 1979. Comments on some recent methods for estimating food consumption by fish. *Journal of the Fisheries Research Board of Canada* 36:1018-1019.
- Elliott, J. M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta*. *Freshwater Biology* 2:1-18.
- Elliott, J. M. 1991. Rates of gastric evacuation in piscivorous brown trout, *Salmo trutta*. *Freshwater Biology* 25:297-305.
- Elliott, J. M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology* 47:977-990.
- Fänge, R., and D. Grove. 1979. Digestion. Pages 161-260 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. *Fish physiology*, volume 8. Academic Press, New York.
- Hayward, R. S., and M. E. Bushmann. 1994. Gastric evacuation rates for juvenile largemouth bass. *Transactions of the American Fisheries Society* 123: 88-93.
- He, E., and W. A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. *Transactions of the American Fisheries Society* 122:717-730.
- Hunt, B. P. 1960. Digestion rate and food consumption of Florida gar, warmouth and largemouth bass. *Transactions of the American Fisheries Society* 89: 206-210.
- Hyslop, E. J. 1980. Stomach contents analysis—a review of methods and their applications. *Journal of Fish Biology* 17:411-429.
- Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *Journal of Fish Biology* 19:245-257.
- Jobling, M. 1986. Mythical models of gastric emptying and implications for food consumption studies. *Environmental Biology of Fishes* 16:35-50.
- Juanes, F., J. A. Buckel, and D. O. Conover. 1994. Accelerating the onset of piscivory: intersection of predator and prey phenologies. *Journal of Fish Biology* 45(A):41-54.
- Juanes, F., and D. O. Conover. 1994. Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish, *Pomatomus saltatrix*. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1752-1761.
- Juanes, F., and D. O. Conover. 1995. Size-structured piscivory: advection and the linkage between predator and prey recruitment in young-of-the-year bluefish. *Marine Ecology Progress Series* 128:287-304.
- Juanes, F., R. E. Marks, K. A. McKown, and D. O. Conover. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River estuary. *Transactions of the American Fisheries Society* 122:348-356.
- MacDonald, J. S., K. G. Waiwood, and R. H. Green. 1982. Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macro-*

- zoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*). Canadian Journal of Fisheries and Aquatic Sciences 39:651-659.
- Marks, R. E., and D. O. Conover. 1993. Ontogenetic shift in the diet of young-of-the-year bluefish *Pomatomus saltatrix* during the oceanic phase of the early life history. U.S. National Marine Fisheries Service Fishery Bulletin 91:97-106.
- McBride, R. S., and D. O. Conover. 1991. Recruitment of young-of-the-year bluefish *Pomatomus saltatrix* to the New York Bight: variation in abundance and growth of spring- and summer-spawned cohorts. Marine Ecology Progress Series 78:205-216.
- McKone, D. 1971. Rate at which sockeye salmon alevins are evacuated from the stomach of mountain whitefish (*Prosopium williamsoni*). Journal of the Fisheries Research Board of Canada 28:110-111.
- Nyman, R. N., and D. O. Conover. 1988. The relation between spawning season and recruitment of young-of-the-year bluefish, *Pomatomus saltatrix* to New York. U.S. National Marine Fisheries Service Fishery Bulletin 86:237-250.
- Olson, R. J., and C. H. Boggs. 1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Canadian Journal of Fisheries and Aquatic Sciences 43:1760-1775.
- Ruggerone, G. T. 1989. Gastric evacuation rates and daily ration of piscivorous coho salmon, *Oncorhynchus kisutch* Walbaum. Journal of Fish Biology 34:451-463.
- Smith, R. L., J. M. Paul, and A. J. Paul. 1989. Gastric evacuation in walleye pollock, *Theragra chalcogramma*. Canadian Journal of Fisheries and Aquatic Sciences 46:489-493.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd edition. Freeman, New York.
- Steimle, F. W., Jr., and R. J. Terranova. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. Journal of Northwest Atlantic Fishery Science 6:117-124.
- Stewart, D. J., and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Transactions of the American Fisheries Society 115:643-661.
- Swenson, W. A., and L. L. Smith. 1973. Gastric digestion, food consumption, feeding periodicity and food conversion efficiency in walleye, (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 30:1327-1336.
- Vondracek, B. 1987. Digestion rates and gastric evacuation times in relation to temperature of the Sacramento squawfish, *Ptychocheilus grandis*. U.S. National Marine Fisheries Service Fishery Bulletin 85:159-163.
- Windell, J. T. 1978. Digestion and the daily ration of fishes. Pages 159-183 in S. D. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, UK.
- Yáñez-Arancibia, A., A. L. L. Dominguez, and D. Pauly. 1993. Coastal lagoons as fish habitats. Pages 339-351 in B. Kjerfve, editor. Coastal lagoon processes. Elsevier Science Publishers, Elsevier Oceanography Series 60, Amsterdam.
- Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey.