Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish

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Consumption and growth rates of juvenile bluefish *Pomatomus saltatrix* increased with increasing temperature and decreased with increasing fish size in short-term (7 days) experiments. Salinity had no effect on growth or consumption rate in a short-term experiment. In a long-term (90 days) mesocosm experiment, consumption and growth rates declined with increasing body size. Predictive equations developed from short-term experiments did not adequately predict observed consumption rates in the mesocosm experiment. However, growth in the mesocosm experiment was similar to field growth. Also, mesocosm consumption rates and consumption rates calculated using field growth and mesocosm growth efficiencies were similar to published independent field estimates of consumption rate. Our results indicate that experiments to determine the effects of temperature and the allometry of body size on growth and consumption rates should be conducted over long time periods simulating field conditions. Juvenile bluefish have rapid growth and their individual cumulative consumption is large. This result suggests that bluefish may have a large effect on their prey populations. This effect has yet to be quantified. © 1995 The Fisheries Society of the British Isles

Key words: bluefish; consumption; growth; temperature; allometry; salinity.

INTRODUCTION

Predation on early life history stages is one process that is believed to regulate recruitment in fishes (Sissenwine, 1984; Houde, 1987; Bailey & Houde, 1989). In Middle Atlantic Bight estuaries of the east coast of the U.S., juvenile bluefish *Pomatomus saltatrix* L., are predators on larval and juvenile fish (Grant, 1962; Friedland *et al.*, 1988; Juanes *et al.*, 1993). Juanes *et al.* (1994) hypothesized that the early life history of bluefish has evolved to allow juveniles to accelerate the onset of piscivory by being advected north from their South Atlantic Bight spawning area to take advantage of appropriate sized prey in northern estuaries. In the Hudson River, a major east coast estuary, prey of juvenile bluefish includes larvae and juveniles of important resource species such as striped bass *Morone saxatilis* Walbaum, and American shad *Alosa sapidissima* Wilson (Juanes *et al.*, 1993).

Accurate measurements of juvenile bluefish consumption rates are needed to quantify their effect on prey in the Hudson River. Consumption rates of fish are measured using direct laboratory- or field-based methods and indirect methods. The field-based method requires measurements of gut contents over a diel cycle coupled with estimates of gastric evacuation rate (Elliott & Persson, 1978; Eggers, 1979). The indirect method most widely used is a bioenergetic approach

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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; Boisclar & Leggett, 1991), it is necessary to use a combination of different techniques in order to evaluate results.

Here we report on the results of short-term experiments to estimate maximum consumption rates of young-of-the-year (YOY) bluefish as a function of temperature and body size. We also report on long-term mesocosm experiments used to estimate consumption and growth of juvenile bluefish over the length of the growing season and compare results with previously published estimates for Great South Bay, New York.

MATERIALS AND METHODS

SHORT-TERM EXPERIMENTS

YOY bluefish were collected with a 30-m beach seine from Great South Bay, Long Island, New York. Fish were transported immediately to the Flax Pond Marine Laboratory of the State University of New York at Stony Brook, Old Field, NY, where all laboratory experiments were conducted. Upon arrival, bluefish were stocked first in 680-l, ambient water flow-through tanks at about 20° C and 30‰ and were fed live Atlantic silversides *Menidia menidia* L. These bluefish were then gradually acclimated to low salinity (5–10‰) and one of two temperatures: moderate (*c.* 22·5° C) and high (*c.* 28·5° C). Acclimation to low salinity was carried out in order to conduct experiments in conditions similar to the Hudson River. The rate of temperature change was approximately 1–2° C day^{-1} and salinity change was about 5‰ day^{-1}. Prior to formal experiments, bluefish were further acclimated to specific experimental temperatures. Fish acclimated to moderate temperatures were assigned to 17, 21 or 24° C and high temperature fish to 27 or 30° C for at least 48 h before testing.

Short-term (7 day) consumption experiments were performed at five temperatures (17, 21, 24, 27 and 30° C) on three bluefish body sizes [small, $\bar{x}=2{·}6$ g (1·85–7·7); medium, $\bar{x}=10{·}16$ g (4·74–19·05); large, $\bar{x}=24{·}12$ g (13·32–34·19)]. Bluefish lengths and wet weights were measured after a 12 h non-feeding period at the beginning and end of each experiment. Initial mean sizes of medium ($F=0{·}26$, $P=0{·}116$) and large ($F=2{·}43$, $P=0{·}26$) fish did not differ between temperature treatments. There was a marginally significant difference between small fish initial mean sizes ($F=4{·}40$, $P=0{·}026$); however, a Tukey's multiple comparison test did not detect a difference between means. Temperatures were regulated by immersion of tanks in temperature-controlled water baths. Photoperiod was maintained at 14 h light : 10 h dark. Each temperature × body size treatment was replicated three times; each replicate consisted of three fish in a 75 × 30 × 75 cm tank filled to a height of 30 cm. Water was changed as often as every 2 days in higher temperature tanks. Each day, bluefish were fed *ad libitum* weighed amounts of live *M. menidia* in size distributions reflecting those encountered by bluefish in the field. Live prey were never allowed to be depleted completely. Dead prey were removed and weighed daily.

EFFECTS OF SALINITY

A short-term (7 day) experiment was conducted to determine the effect of salinity on growth and consumption rates. Trials were conducted at two salinities, 5 and 25‰. Fish were acclimated to these salinities over 4 days. Tanks and feeding conditions were identical to those used in the short-term experiment described above. Each salinity treatment was replicated three times and each replicate consisted of three fish. Experiments were conducted at 24° C. Initial mean fish size [5‰, $\bar{x}=9{·}58$ g (6·3–13·0); 25‰, $\bar{x}=9{·}22$ g (7·5–11·6)] did not differ between salinity treatments ($t=0{·}419$, $P=0{·}703$).

MESOCOSM EXPERIMENTS

Fish collection and acclimation to laboratory conditions were similar to the above procedures with the exception of temperature and salinity acclimation. The fish were held in 680-l flow-through circular tanks with ambient water from Flax Pond, an adjacent salt marsh pond, with temperatures ranging from 18 to 24° C and salinities ranging from 26 to 31‰. Because fish from Great South Bay normally encounter similar temperatures and salinities, no acclimation period was necessary. Growth and consumption were measured over a 90-day period on three groups of five fish [initial mean size=2·10 g (1·15–2·70)]. Photoperiod was adjusted approximately every 2 weeks to match natural photoperiod. A known weight of live *M. menidia* was placed into each tank daily. These prey were captured in the field by beach seining and represent size distributions encountered by bluefish in the field. Dead prey were removed and weighed daily. Bluefish lengths and weights were measured every 10 days.

ANALYSIS

Daily specific growth rate (G) was calculated as $G=[(\ln Wt_f - \ln Wt_i)/d \times 100]$, where Wt_f=final wet weight (g), Wt_i=initial wet weight (g), and d=number of days. Daily consumption rate was calculated as amount of prey consumed (g)/mean fish weight (g)/day. Gross growth efficiency (K) was calculated as $K=$[fish weight gain (g)/prey biomass consumed (g)]. Mean fish weight was calculated as, $[(\ln Wt_i + \ln Wt_f)/2]$, where Wt_i=initial wet weight, Wt_f=final wet weight. In the short-term experiment, growth rate and consumption rate were calculated for replicates within each body size and temperature treatment.

The effect of temperature and fish size on growth and consumption rate was assessed with two-way ANOVA (SAS, 1989). The effect of salinity on growth and consumption rate was determined using a *t*-test (Sokal & Rohlf, 1981). Multiple regression analysis was used to develop predictive equations from which growth and consumption rates could be estimated from fish size and temperature (SAS, 1989). For every 10-day interval of the mesocosm experiment, mean bluefish body size, specific growth rate, consumption rate, cumulative consumption, and gross growth efficiency were calculated.

COMPARISONS AMONG EXPERIMENTS AND FIELD DATA

The results of the short-term experiment and the mesocosm experiment were compared using the predictive equation derived for consumption from the short-term experiment. Average fish weight and temperature over 10-day intervals in the mesocosm tanks were used in the regression equation to predict consumption rates in the mesocosm. The predicted consumption rates were then compared to those observed in the mesocosm tanks.

The mesocosm experiments were compared to field populations in two ways. First the growth trajectory from the mesocosm was compared with field growth (fork length, mm) for juvenile bluefish in Great South Bay during 1985, a year when the longest time series of mean lengths was available (Nyman & Conover, 1988). Second, the mesocosm gross growth efficiency estimates were used to estimate consumption rates in 1989, a year when direct estimates using gastric evacuation techniques were available (Juanes & Conover, 1994*a*). Estimates of field consumption were calculated as [growth increment (g)/K]. Efficiency-derived consumption rates as well as the actual mesocosm consumption rates were then compared to the direct field estimates of consumption rates.

RESULTS

SHORT-TERM EXPERIMENTS

Mean consumption rate increased with increasing temperature in the medium and large size classes but did not increase above 27° C in the small size class.

TABLE I. Experimental conditions and resulting consumption and growth rates in short-term experiments

Temperature (°C)	Size class	Mean weight (g)	Consumption rate (% body weight day^{-1})	Growth rate (% day^{-1})
17	S	3·39 (0·41)	19·48 (1·47)	4·59 (0·53)
	M	12·06 (1·61)	6·49 (0·43)	1·42 (0·09)
	L	24·10 (0·62)	3·45 (1·22)	0·72 (0·60)
21	S	3·86 (0·19)	31·52 (4·18)	9·25 (0·26)
	M	10·45 (0·57)	10·71 (1·76)	2·73 (0·59)
	L	30·03 (3·32)	3·55 (1·53)	0·86 (0·42)
24	S	5·02 (0·13)	33·18 (1·54)	11·01 (0·22)
	M	11·56 (1·06)	13·41 (0·94)	2·74 (0·37)
	L	25·62 (2·51)	9·43 (0·61)	2·86 (0·57)
27	S	5·48 (0·41)	36·71 (1·24)	10·49 (0·27)
	M	11·57 (1·01)	17·37 (0·92)	4·53 (0·51)
	L	22·11 (0·43)	12·30 (0·61)	3·13 (0·16)
30	S	5·21 (0·12)	36·53 (1·11)	9·95 (0·14)
	M	13·03 (1·17)	21·65 (0·63)	4·83 (0·62)
	L	25·72 (2·42)	13·14 (2·22)	3·20 (0·25)

Mean weights, consumption rates, and growth rates are means ($\pm$ s.e.) of three replicates containing three fish each. S, Small; M, medium; L, large.

Highest consumption rates were observed in the small fish group with values ranging from 19·48% body weight day^{-1} at 17° C to 36·71% body weight day^{-1} at 27° C (Table I). The medium fish treatment had consumption rates ranging from 6·49% body weight day^{-1} at 17° C to 21·65% body weight day^{-1} at 30° C. The large fish treatment consumption rates ranged from 3·17% body weight day^{-1} at 17° C to 13·14% body weight day^{-1} at 30° C. Two replicates, a 17° C medium and 17° C large, were not included in the analysis because of mortality. Both temperature ($F=29·412$, $P<0·0001$) and fish size ($F=254·687$, $P<0·0001$) had significant effects on consumption rate and there was no interaction of fish size and temperature ($F=1·959$, $P=0·090$).

Mean growth rate increased with increasing temperature in the medium and large size classes but did not increase above 24° C in the small size class. Highest growth rates were observed in the small fish group with values ranging from 4·59% day^{-1} at 17° C to 11·01% day^{-1} at 24° C (Table I). Growth rates of medium fish ranged from 1·42% day^{-1} at 17° C to 4·83% day^{-1} at 30° C. Growth rates for large fish ranged from 0·72% day^{-1} at 17° C to 3·20% day^{-1} at 30° C. Both temperature ($F=38·661$, $P<0·0001$) and weight ($F=398·478$, $P<0·0001$) had significant effects on growth rate and there was an interaction of body weight and temperature ($F=6·835$, $P<0·0001$). The predictive equations developed from these experiments were,

$\log_{10}$[consumption rate (day^{-1})]$= -0·974 + 0·044T - 0·890 \log_{10}(W)$, $r^2=0·90$ [Fig. 1(a)], and $\log_{10}$[growth rate (day^{-1})]$= -1·653 + 0·052T - 1·021 \log_{10}(W)$, $r^2=0·79$ [Fig. 1(b)],

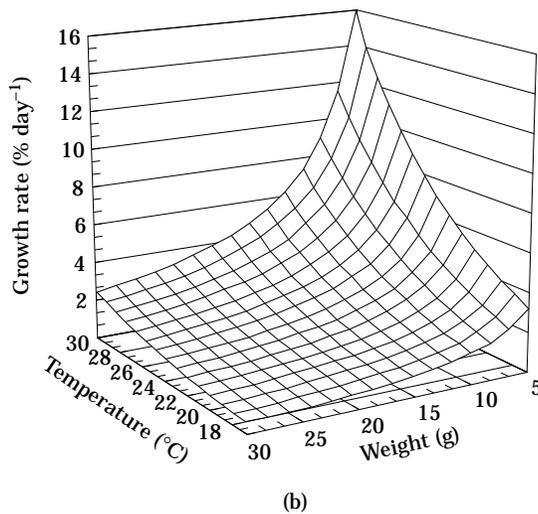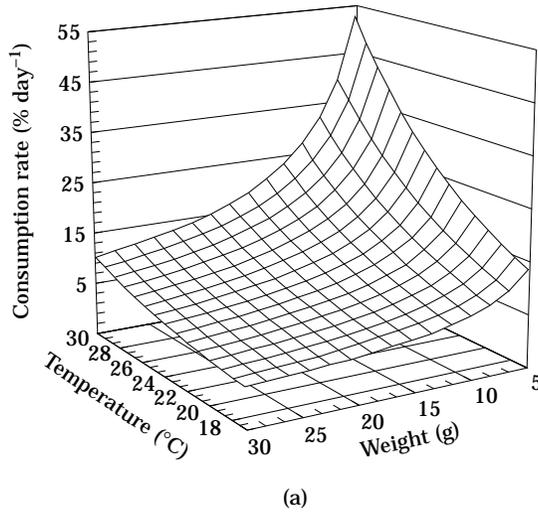where, $T=$temperature (° C) and $W=$weight (g).

(a)

(b)

F<small>IG</small>. 1. Response-surface diagram of consumption rate (a) and growth rate (b) of juvenile bluefish as a function of temperature and bluefish weight in short-term experiments. Values calculated from multiple regression equations presented in text.

EFFECTS OF SALINITY

In the short-term salinity experiment, mean consumption rate was 19·47% body weight day^{-1} at 5‰ and 21·35% body weight day^{-1} at 25‰. A 25‰ replicate was lost due to mortality. Mean growth rate was 4·67% day^{-1} at 5‰ and 4·69% day^{-1} at 25‰. Salinity had no significant effect on consumption ($t=0·641$, $P=0·567$) or growth rate ($t=0·025$, $P=0·982$).

MESOCOSM EXPERIMENTS

During the first 30 days of the experiment, mean specific growth rate [Fig. 2(a)] was 4–7% day^{-1} and dropped to 1–2% day^{-1} during the final 10 days of the
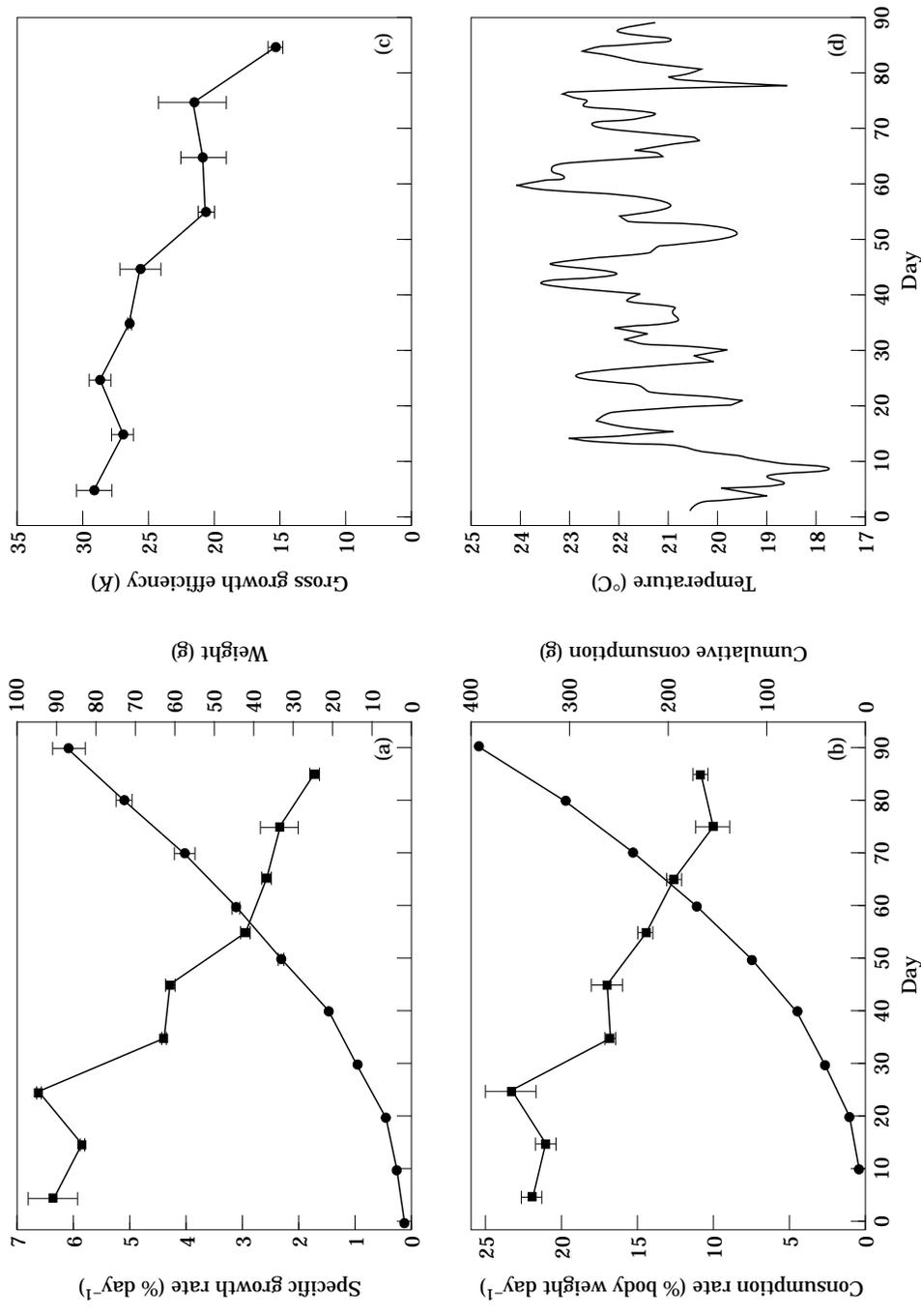
FIG. 2. Juvenile bluefish mean specific growth rate (■) and mean weight (●) (a), mean consumption rate (■) and mean cumulative consumption (●) (b), mean gross growth efficiency (c), and mean daily temperature (d) from mesocosm experiments (error bars represent ± 1 S.E.)
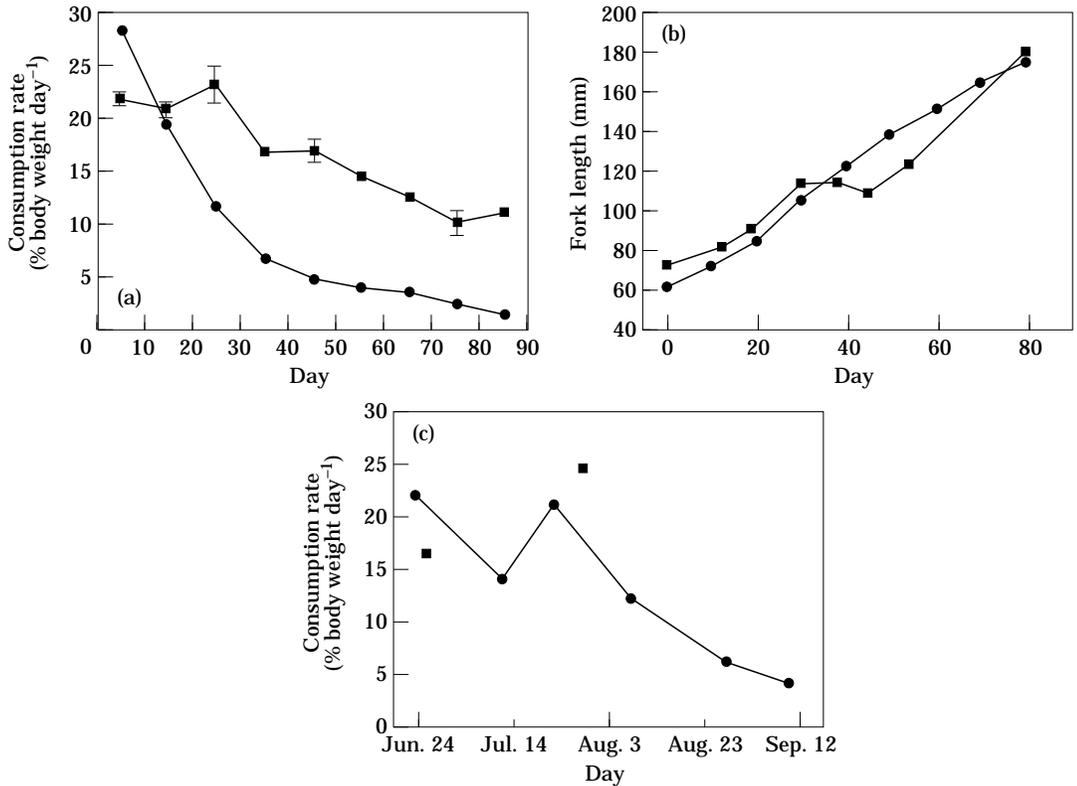
FIG. 3. Comparisons of (a) observed mesocosm consumption rates (■) (± 1 s.e) and short-term experiment multiple regression predicted consumption rates, (●) (b) fork length of fish in mesocosm (●) and of fish collected in Great South Bay, NY by Nyman & Conover (1988; Day 0=June 28 1985) (■), and (c) mesocosm efficiency calculated consumption rates from field growth increments (●) and field calculated (■) consumption rate estimates from Juanes & Conover (1994*a*).

experiment. Two of the three tanks had a single death during the course of the experiment. Mean consumption rate [Fig. 2(b)] during the first 30 days of the experiment was about 20% body weight day^{-1} and decreased to a mean of about 10% body weight day^{-1}. The mean cumulative consumption over 90 days [Fig. 2(b)] per YOY bluefish was 389 g of prey. Gross growth efficiency [Fig. 2(c)] was initially *c.* 28·0% and dropped throughout the experiment to values *c.* 20·0%.

COMPARISONS AMONG EXPERIMENTS AND FIELD DATA

Estimates of consumption rate calculated from the short-term predictive equation were generally lower than actual values observed in the mesocosm experiment [Fig. 3(a)]. The growth trajectory in the mesocosm was similar to observed field growth for Great South Bay in 1985 [Fig. 3(b)]. Consumption rates calculated by using field growth and mesocosm efficiencies were similar to those seen in the mesocosm [Fig. 3(a), (c)]. Estimated consumption rates were similar to independent field estimates of consumption from Juanes & Conover [1994*a*; Fig. 3(c)].

DISCUSSION

Juvenile bluefish may be important predators of larval and juvenile fish in Mid-Atlantic Bight estuaries (Juanes *et al.*, 1993). Accurate measurements of consumption rates of fish are needed to estimate the effect that predators have on prey populations. The results of both the short-term and mesocosm experiment support previous findings that juvenile bluefish have relatively high growth and consumption rates (Juanes & Conover, 1994*a*). Estimates of consumption rate from the short-term small tank experiments underestimated the observed values in the mesocosm experiments. However, growth and consumption rates of bluefish in the mesocosms were similar to field growth and independent field consumption rate measurements.

Temperature and fish size had a significant effect on consumption and growth in the short-term experiment. Growth rates of medium and large fish continued to increase at higher temperatures whereas growth of small fish did not increase above 24° C. The significant interaction term indicates that the joint effects of temperature and fish size on growth were non-additive. Consumption rates for medium and large fish also continued to increase at higher temperatures. Consumption of small fish plateaued at 27° C in a similar manner to small fish growth. However, in this case the interaction between temperature and body size was not significant. Juanes & Conover (1994*a*) performed a 20-day growth and consumption rate experiment to determine differences in growth rate of bluefish fed an invertebrate and fish (*M. menidia*) diet. The initial sizes of their fish were similar to initial sizes within our small fish treatment. Their estimates of consumption rates (22·61–29·98% body weight day^{-1}), growth rates (5·75–6·10% day^{-1}), and gross growth efficiencies (20·05–28·28%) are similar to our estimates for small fish.

Estimates of mesocosm consumption rates and growth rates declined throughout the experiment. The ambient temperature in these experiments increased slightly as consumption and growth rates declined [Fig. 2(d)]. The decline in these rates was most likely due to the increase in fish size as was observed in the short-term experiments. This observation is similar to other workers' findings with juvenile fish (Boehlert & Yoklavich, 1983; Hawkins *et al.*, 1985; Hartman & Brandt, 1993).

To assess the validity of the short-term experiments we predicted consumption rates for the mesocosm from fish size and temperature relations derived from the short-term experiments. With the exception of the observed estimates for the smallest fish, the predicted values were lower than the observed values in the mesocosms [Fig. 3(a)]. There are several possible explanations. First, the short-term experiments were carried out in much smaller tanks than those used in the mesocosm experiments and the stress of confinement may have affected consumption in larger fish. Second, acclimation times may not have been sufficient and the duration of the short-term experiments may have been too brief. Third, the short-term experiments were conducted in static tanks compared to the flow-through system in the mesocosm tanks. Although water was changed frequently in the static tanks, increased disturbance or lower water quality may have affected appetite of the fish. Fourth, the short-term experiments were conducted at lower salinities (*c.* 5–10‰) compared to the higher salinities (*c.* 30‰) in the mesocosm. In our salinity experiment, however, we

found no difference in growth or consumption rate at 5 and 25‰. Although several of these factors could have affected the outcome of the short-term experiments, it seems most likely that tank size or biomass density may have been most important because predictions of consumption rate when fish were small were similar to the observed values in the mesocosm.

Estimates of consumption and growth rates in the mesocosm experiment were similar to those estimated in the field. Juvenile bluefish that Nyman & Conover (1988) held in a cage during an otolith marking experiment also had similar growth rates to fish in the field. This is perhaps surprising given that activity levels in captive fish might be expected to be lower than those in the field. Activity in fish is receiving increasing attention as a determinant of fish growth (Boisclair & Leggett, 1989) and its importance in bioenergetic models has been debated vigorously (Boisclair & Leggett, 1991; Hewett *et al.*, 1991). Our mesocosm experiments were designed to mimic field bluefish activity in two ways. First, circular tanks were used to allow greater opportunity for prey escape. Second, live prey were fed to bluefish in size distributions similar to prey size distributions in the field. Bluefish expend considerable energy in pursuing and capturing prey. Juanes & Conover (1994*b*) found that although juvenile bluefish attacked all prey sizes offered, their prey capture success in rectangular tanks was only about 25% when feeding on large prey and about 65% when feeding on small prey. However, this difference in capture success does not appear to have growth consequences. Juanes & Conover (1994*a*) found that juvenile bluefish had similar growth rates when fed two different sizes of prey (20–40 mm *v.* 50–70 mm *M. menidia*).

Data on the allometry and temperature-dependence of growth and consumption are necessary for the parameterization of bioenergetic models such as those of Hewett & Johnson (1992). Sensitivity analyses performed on this model have shown that the temperature-dependent exponents of consumption and metabolism are the most error-sensitive components of the model (Hartman & Brandt, 1993 and references therein). Therefore, these values need to be measured accurately in order to construct a valid model. Temperature-dependent exponents from experiments performed on large fish which are extrapolated to small size fish such as age-0 have been shown to be erroneous (Post, 1990; Madon & Culver, 1993). Hartman & Brandt (1993) found that experimental design had major effects on physiological parameter estimation in their experiments on juvenile striped bass. Our results suggest that mesocosm-like experimental regimes give more realistic consumption and growth rates and should be used in estimation of physiological parameters for bioenergetic models.

In the mesocosm experiment, the cumulative consumption of 389 g over a 90-day period resulted in YOY bluefish weighing approximately 90 g. The mesocosm experiment ended during the second week in September. Juvenile bluefish migrate out of Mid-Atlantic Bight estuaries when temperatures are *c.* 20° C. This migration occurs from mid-September to mid-October in New York estuaries (Nyman & Conover, 1988). Therefore, the cumulative consumption for an individual fish would be *c.* 400 g at a minimum and *c.* 750 g if we extrapolate the cumulative consumption curve out to mid-October [Fig. 1(b)]. Juanes *et al.* (1994) found that the mean size of two prey types in two different

Mid-Atlantic Bight estuaries was *c.* 35 mm which equals approximately a 0·5 g prey. Hence, a single bluefish consumes roughly 800 to 1500 prey fish by the end of the growing season in Mid-Atlantic Bight estuaries. Relatively small densities of bluefish could therefore have a large effect on prey mortality. The effects of this predator on prey populations remains to be quantified.

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