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Aspects of Fish Growth and Predator-Prey Interactions: Modeling Relative Weight, Predicting Maximum Prey Size, and Evaluating Predator Growth and Prey Survival in Experimental Ponds

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Aspects of Fish Growth and Predator-Prey Interactions: Modeling Relative Weight, Predicting Maximum Prey Size, and Evaluating Predator Growth and Prey Survival in Experimental Ponds

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Abstract.–Increased understanding of fish growth and predator-prey interactions can advance the scientific basis for fisheries management. This study addresses several topics involving fish growth, predators, and prey. First, two laboratory experiments assessed how largemouth bass *Micropterus salmoides* allocate new tissue to growth in weight and growth in length. Results show that when fish condition is good, increases in weight are primarily allocated to increasing in length while maintaining condition, whereas when condition is poor, increases in weight are primarily allocated to improving condition. Second, a mathematical model was developed to help summarize the information from these experiments in terms of changes in relative weight in relation to recent growth rate. For juvenile largemouth bass, relative weight appears to be a useful index of average growth rate and food consumption over the previous few weeks. Third, because larger bluegills *Lepomis macrochirus* can be predators on smaller bluegills, measurements were made on the gape and maximum body depth of a wide size range of bluegills; laboratory experiments evaluated the predicted gape limitation. New equations were developed to relate gape of bluegills as predators and maximum body depth of bluegills as prey. Fourth, pond experiments were conducted to assess juvenile walleye *Sander vitreus* and adult bluegill predator growth and predation rates in the presence of different densities of juvenile bluegills as prey. Average growth of individually marked walleyes generally increased with density of bluegill prey. An experiment in ponds over winter indicated that adult bluegills are not likely to cause appreciable predatory mortality when age-0 bluegills are potential prey.

Increased understanding of fish growth and predator-prey interactions can advance the scientific basis for fisheries management. Fish are gape-limited predators, so predator body size affects the sizes of prey that can be ingested. Fish growth rate determines size and gape at a given age and growth rate is influenced by food availability. Increased knowledge of growth rate and size-specific predator-prey interactions has the potential to help in managing the size distributions of predators and prey in fish communities.

Growth rate may affect fish condition as measured by relative weight (Wege and Anderson 1978; Blackwell et al. 2000). Increased understanding of how fish allocate new tissue to growth in length and growth in condition can give insight into the expected relationship between relative weight and growth rate. In order to interpret field measurements of relative weight, information is needed on how quickly relative weight changes in response to changes in growth rate or food consumption. For example, if relative weight reflects long-term average food consumption, then relative weight would be expected to correlate with annual growth rate. On the other hand, if relative weight reflects shortterm average food consumption, then relative weight would not be expected to correlate with annual growth rate.

Broekhuizen et al. (1994) presented a model of energy allocation in fish based on a distinction between storage (or reserve) tissues, which can be mobilized when net energy intake is negative, and structural tissues, which cannot. In their approach, an increase in the amount of structural tissues (which include the skeleton and nervous system) produces an increase in fish length. An increase in storage tissues (which include nonpolar lipids and some proteins) produces an increase in condition (plumpness or weight for a given length). They propose that fish allocate new tissue to storage and structural tissues according to the current ratio of storage tissue:structural tissue. If this ratio is below some set value, then a larger fraction of the new tissue is allocated to storage and the ratio increases. Conversely, if this ratio is above the set value, then a larger fraction of the new tissue is allocated to structure and the ratio decreases. This model has the advantage of allowing a fish to regulate its ratio of storage:structure about some set value. Two important observations are not addressed by this model. First, fish condition (which is related to the storage:structure ratio) tends to vary with ration level. Second, fish condition (and the storage:structure set value) tends to increase with fish size. This was not included in the Broekhuizen et al. (1994) model, which was applied to a limited size range of salmonids.

Recent studies by Rob Hayward at the University of Missouri, Columbia, and his colleagues have demonstrated the importance of fish condition and recent feeding history in determining the amount of food that fish consume and the rate of growth in length and weight (Whitledge and Hayward 1997; Whitledge et al. 1998, 2003; Bajer et al. 2003). This effect could have a large influence on the predictions of predator-prey models such as those used to predict effects of potential fishing regulations.

My project addressed several topics related to predator-prey interactions. First, two laboratory experiments assessed how largemouth bass *Micropterus salmoides* allocate new tissue to growth in weight and growth in length. Second, a mathematical model was developed to help summarize the information from these experiments in terms of changes in relative weight in relation to recent growth rate. Third, because larger bluegills *Lepomis macrochirus* can be predators on smaller bluegills, measurements were made on the gape and maximum body depth of a wide size range of bluegills and laboratory experiments were used to evaluate the predicted gape limitation. Fourth, pond experiments were conducted with juvenile walleyes *Sander vitreus* and adult bluegills as predators. The walleye experiment assessed predator growth and predation rates in the presence of different densities of age-0 bluegills as prey. The adult bluegill experiment evaluated the potential for predation by adults on juvenile bluegills over winter.

Methods

Model for Growth in Length, Weight, and Condition

A preliminary model was developed to describe the allocation of new biomass to increasing length or changing condition. The model begins from the equation defining relative weight (W_r), introduced by Wege and Anderson (1978), which expresses fish wet weight (W) relative to a defined standard weight (W_s).

$$W_r = \frac{W}{W_s}, \qquad \text{Equation 1}$$

Relative weight will be 1.0 when weight is equal to the standard weight. Standard weight (W_s) for a given length is calculated as

$$W_s = a \cdot L^b, \qquad \text{Equation 2}$$

where *a* and *b* are species specific constants (Murphy et al. 1991; Blackwell et al. 2000). For largemouth bass, the values used in this report are a = -5.316 and b = 3.191 for length in mm and weight in g (Anderson and Gutreuter 1983; Murphy et al. 1991). For bluegill, the values used in this report are a = -5.374 and b = 3.316 for length in mm and weight in g (Anderson and Gutreuter 1983; Murphy et al. 1991). These two equations can be combined.

$$W = W_r \cdot a \cdot L^b \qquad \text{Equation 3}$$

We can now take the derivative of both sides of the equation and rearrange terms to show the relationship between the length-specific rate of change in length (dL/Ldt), the weight-specific rate of change in weight (dW/Wdt), and the relative-weight-specific rate of change in relative weight (dW_r/W_rdt).

$$\frac{dL}{Ldt} = \left(\frac{1}{b}\right) \cdot \frac{dW}{Wdt} - \left(\frac{1}{b}\right) \cdot \frac{dW_r}{W_r dt} \qquad \text{Equation 4}$$

This equation indicates that if relative weight remains constant, that is, if the rate of change in relative weight (dW_r/dt) is zero, then the length-specific rate of increase in length (dL/Ldt) will be equal to the weight-specific rate of increase in weight (dW/Wdt) divided by b, the exponent of length in the definition of standard weight. Alternatively, if the rate of change in length is zero, then the relative rate of change in relative weight (dW_r/W_rdt) will be equal to the weight-specific rate of change in weight (dW/Wdt).

A model was developed to describe changes in weight, length, and condition that were observed in the first experiment. The form of the model was determined after studying the results of the experiment.

Laboratory Experiments on Predator Growth in Length, Weight and Condition

Experiment 1: Growth by ration and condition.–A lab experiment was conducted in summer 2004 to measure the amount of growth in length and weight for largemouth bass fed different ration sizes using fish that differed in initial condition. The experiment used a 3x3 cross-classified design, involving fish in three levels of body condition fed at three ration levels for 7 weeks. In the pre-treatment phase of the experiment, three levels of body condition were established by feeding fish at three different ration levels. In the second phase of the experiment, fish from each of the three levels of body condition were assigned to three ration levels for a total of nine treatment combinations. Thus, some fish that had been fed at a high ration in the first phase were switched to medium or low rations in the second phase, some that had been on a low ration were switched to medium or high rations, etc., and some stayed at the same ration. The three ration levels in each phase were one, two, or four fathead minnows *Pimephales promelas* per day (low, medium, and high rations, respectively). Each treatment had three replicate fish for a total of 27 fish, held in individual 10-gallon aquaria. Length (nearest 1 mm) and weight (nearest 0.1 g) were measured weekly. Water temperature was measured daily in two aquaria on opposite sides of the lab. The average water temperature during the experiment was 21.7°C. During the treatment phase of the experiment, wet weight (nearest 0.01 g) of fathead minnows added to each tank was measured daily, as well as the wet weight of any unconsumed minnows from the previous day. During one week, feces were collected daily from each tank, dried 24 h at 55°C, and weighed to the nearest 0.01 g. On several occasions throughout the experiment, a subsample of minnows was measured for length and wet and dry weight (dried 24 h at 55°C).

I obtained 36 juvenile largemouth bass (size range 187–191 mm) from Pond 2 at the Saline Fisheries Research Station on April 22, 2004, and held them in the lab in individual aquaria. Fish were acclimated to the lab for 5 d and feeding was started on fathead minnows. Fish were randomly assigned to one of the three feeding levels to produce 12 fish per feeding level. Then for a 37-d pre-treatment period, fish were fed low, medium, or high daily rations of fathead minnows in order to produce 12 fish in each of three levels of condition for the start of the experiment. There was no mortality during acclimation or the subsequent experiment although one fish was replaced after 8 d in the lab due to fungus growth. One-way ANOVA was used to evaluate whether the three levels of body condition were significantly different.

The second (treatment) phase of the experiment began on June 4, 2004. At this time nine randomly selected fish (three fish per condition level) were sacrificed, measured for length, weight, and gonad weight, and frozen for subsequent determination of dry weight. The remaining 27 fish were randomly reassigned to produce three fish from each condition level at each of the three feeding levels. During the treatment period, fish were measured weekly to determine growth in length and weight and consequent change in condition as measured by relative weight (Equation 1). After 42 d, all fish were sacrificed and measured for length, weight, and gonad weight, and frozen for subsequent determination of dry weight. Dry weight was measured by drying fish at 60°C until constant weight was achieved. Two-way ANOVA was used to evaluate whether final relative weight was influenced by the three levels of initial body condition and the three ration levels of the second (treatment) phase of the experiment.

Experiment 2: Growth by fish size and feeding regime.–A second lab experiment was conducted in summer 2005 to measure the amount of growth in length and weight for largemouth bass that differed in starting size and daily feeding regime. Feeding regimes varied in total amount of food offered and in timing of the amount offered. I hypothesized that fish might be able to extract more energy from a meal if it remained longer in the digestive tract, and that meals might remain in the digestive tract longer if no additional food was consumed the next day (Karasov and Martinez del Rio 2007). This hypothesis suggests that fish with feeding regimes with 2 or 3 d of no food in a 4-d cycle might have higher assimilation efficiency and therefore a higher growth rate than fish fed a similar total amount of food but fed as an equal amount of food each day.

The experiment used a 3x4 cross-classified design, involving largemouth bass grouped into three size classes fed at one of four feeding regimes for 8 weeks. Fish were assigned to one of three size categories according to initial length. Fish 103–133 mm (13.5–26.9 g) were “small”; fish 140–186 mm (32.6–90.8 g) were “medium”; fish 189–213 mm (86.6–123.1 g) were “large.” Fish in each size category were randomly assigned to one of four feeding groups. Group one was fed one fathead minnow every day, for a total of four minnows every 4 d (1, 1, 1, 1). Group two (2, 2, 2, 2) was fed two minnows every day, for a total of eight minnows every 4 d. Group three (4, 0, 0, 0) was fed four minnows on one day, then nothing for the next 3 d, for a total of four minnows every 4 d. Group four (4, 0, 4, 0) was fed four minnows on one day, nothing on the next day, four minnows the next day, and nothing on the next day, for a total of eight minnows every 4 d.

Three replicate bass at each of the twelve treatment combinations made a total of 36 fish. Fish were held in individual 10-gallon aquaria. Length (nearest mm) and weight (nearest 0.1 g) were measured weekly before feeding. A data logger recorded water temperatures every 30 minutes in four aquaria around the lab. Daily mean temperature during the experiment was 24.1 ± 1.5°C (mean ± SD). Wet weight (nearest 0.01 g) of fathead minnows added to each tank was measured daily, as well as the wet weight of any unconsumed minnows from the previous day. On several occasions throughout the experiment, a subsample of minnows was measured for length and wet and dry weight (dried 24 h at 60°C). The experiment started on June 30, 2005, and concluded on August 25, 2005.

After 56 d, all fish were sacrificed and measured for length, weight, liver, and gonad weight, and then frozen for subsequent determination of dry weight. Dry weight was measured by drying fish at 60°C until constant weight was achieved. Two-way ANOVA was used to evaluate whether final relative weight was influenced by the three size categories and the four feeding regimes.

Gape Limitation of Bluegills as Predators

The purpose of this set of experiments was to compare the observed maximum size of prey ingested by bluegills with the maximum size predicted from predator mouth gape and prey maximum body depth. Juvenile bluegills were used as prey. Previous studies have indicated that bluegills can be cannibalistic (Gray 1991; Breck 1996).

First gape experiment.–Laboratory experiments were conducted at the Saline Fisheries Research Station in December 1996, to evaluate the probability of capture of juvenile bluegills of various sizes by ten adult bluegills 148–191 mm total length (TL). The experiments were conducted in 10-gallon aquaria at room temperature. Approximately three times per week, one juvenile bluegill was offered as prey to each adult bluegill. If the prey was consumed, then a slightly larger juvenile bluegill was offered the next feeding day. It was intended that some juvenile prey bluegills be too large for the adults to ingest. The experiment continued until no larger juvenile bluegills were available in the laboratory.

Observed maximum prey sizes from this laboratory experiment were compared with predicted maximum prey sizes. Bluegill gape (G, mm) was first estimated using the regression of Werner (1974).

$$G = 0.217 + 0.093 \cdot \left(\frac{L}{1.278} \right) \qquad \text{Equation 5}$$

The factor of 1.278 from Beckman (1948) was used to convert total length (L, mm) to standard length as used by Werner (1974). Predicted maximum prey size was assumed to be the length of bluegills having a maximum body depth equal to the predator's gape.

The predicted length of bluegills having a given maximum body depth (D, mm) was calculated using an equation from Schneider and Breck (1997):

$$\log_{10} L = 0.728(\pm 0.017) + 0.8383(\pm 0.0020)\log_{10} D, \qquad \text{Equation 6}$$

where $r^2 = 0.997$, $N = 416$, for bluegills 19–220 mm total length, with maximum body depths 4–89 mm.

Second gape experiment.–During summer and fall 1998 a second lab experiment was conducted to evaluate gape limitation by adult bluegills preying on juvenile bluegills of various sizes. The purpose, again, was to compare the observed maximum size of prey ingested by bluegills with the maximum size predicted from predator mouth gape and prey maximum body depth (equations 5 and 6). Twelve adult bluegills 154–253 mm TL were held in individual 10-gallon aquaria from June 2 to November 9, 1998. They were fed juvenile crayfish *Orconectes virilis*, fathead minnows, and juvenile bluegills during acclimation to lab conditions and between periods of data collection. The experiments took several months because only the first prey item consumed each trial day gave useful data. A fish that had consumed one or more prey items was much less likely to attack and ingest a second large prey item that day, although smaller prey items would often be accepted. The adult bluegills needed to be hungry to obtain useful measures of the maximum size of prey that they would ingest. Fish were starved about 24 h between trials, longer over weekends. If a prey was offered that was too large, the fish often refused similar-sized prey offered the same day. Larger and larger prey (juvenile bluegills) were offered as the first prey of the day. If within 1 h a prey item was not attacked, or was attacked but not ingested, then smaller prey were offered on the next occasion.

Pond Experiments on Predator Growth

Adult bluegills as predators and juvenile bluegills as prey.–A pond experiment attempted to evaluate overwinter predation (cannibalism) by large adult bluegills on age-0 bluegills. Five ponds were stocked on December 11, 1996, with age-0 bluegills and three of these ponds were stocked with large adults as predators (Tables 1 and 2). The overwinter experiment was terminated after about 15 weeks in spring 1997 (Tables 1 and 2). The five ponds were drained on March 26, 27, and April 1, 1997.

Adult bluegills were individually marked by clipping one of the soft rays on the dorsal fin, leaving a stub of about 2 mm to prevent movement of the adjacent rays. Clipping a soft-dorsal ray worked well to mark individual adult bluegills over winter. Overwinter predation was evaluated by draining the ponds after 15 weeks, counting the surviving juvenile bluegills, and comparing the percent survival between the ponds with versus without adult bluegills as predators.

A recording digital thermometer was deployed in Pond 7 on September 13, 1996, and retrieved on March 26, 1997. (The logger was also deployed earlier in the summer of 1996 for a different experiment.) Tied between a float and a weight, the sensor of the temperature logger was located about 0.5 m below the surface. Hourly temperature measurements were summarized as daily means (Table 3). The average water temperature during the 105-d experiment was 3.2°C.

Juvenile walleyes as predators and juvenile bluegills as prey.–During fall 1997 a 6-week experiment was conducted to evaluate predation by juvenile walleyes on juvenile bluegills. The purpose was to measure growth of walleyes as a function of bluegill density. Eight ponds were stocked in October with similar-sized juvenile bluegills (24.6 ± 3.6 mm, 0.17 ± 0.09 g, mean ± SD, $N = 200$). Ponds were stocked with juvenile bluegills and walleyes in October 1997. Bluegills were stocked in the ratios 0, 1, 2, 4, 8, and 16 into six treatment ponds containing walleyes, and 5.6 in two control ponds without walleyes, where a value of 1 represented 449 g/ha, an estimated 2,583 bluegills per hectare (Table 4). The six treatment ponds were stocked with 10 juvenile walleyes (203 ± 10 mm, 62.5 ± 9.3 g, $N = 60$) per pond. Predators were given individual marks by clipping one or two rays of the soft dorsal fin. This visible mark persisted to the end of the experiment. This experiment was terminated by draining the eight ponds in late November and early December 1997. The change in bluegill biomass was measured by subtracting initial from final bluegill biomass. Individual walleye growth during the experiment was determined by subtracting initial weight from final weight. Average walleye growth as a function of bluegill stocking density was determined by regression.

Results

Laboratory Experiments on Predator Growth in Length, Weight, and Condition

Experiment 1: Growth by ration and condition.–Manipulating ration during the pre-treatment period produced three groups of largemouth bass with significantly different relative weight (One-way ANOVA, $P < 0.001$). At the end of the pre-treatment period (beginning of the treatment), average relative weight (mean ± SE) for the three feeding groups was as follows: high ration: 0.992 ± 0.012; medium ration: 0.958 ± 0.007; low ration: 0.874 ± 0.008 ($N = 12$ per group) (Figure 1).

By the end of the treatment, relative weight reflected the treatment ration, not the pre-treatment ration. A two-way ANOVA showed a highly significant effect of treatment ration on final W_r ($P < 0.001$), but no significant effect of initial relative weight on final W_r ($P = 0.16$). At the end of the experiment, average relative weight for the three feeding groups was as follows: high ration: 1.015 ± 0.016; medium ration: 0.961 ± 0.008; low ration: 0.872 ± 0.011 ($N = 9$ per group) (Figure 2).

A regression analysis demonstrated that final relative weight was dependent on the average weight-specific growth rate (*dW/Wdt*) during the 6-week treatment period (Figure 3).

$$W_r = 0.910 + 16.489 \cdot \left(\frac{dW}{Wdt} \right), \qquad \text{Equation 7}$$

where $N = 27$ and $r^2 = 0.65$, $P < 0.001$. Based on this equation, fish with a weight-specific growth rate of 0.0055 d^{-1} would be expected to achieve a relative weight of 1.0, that is, to reach standard weight for their length. This equation also predicts that fish on a maintenance ration ($dW/Wdt = 0$) would reach a relative weight of 0.91.

Experiment 2: Growth by fish size and feeding regime.–When three sizes groups of largemouth bass were fed fathead minnows in different feeding regimes, fish size category had a large effect on final relative weight. A two-way ANOVA using three size categories and four feeding regimes indicated a highly significant effect of size category on final relative weight ($P < 0.001$), and no significant effect of feeding regime ($P = 0.10$). Because the food items were live whole minnows, a given feeding regime (e.g., one minnow per day) represented a smaller daily ration (as percent body weight) for the large bass than for the smaller bass, so the large bass grew more slowly and developed a lower relative weight than the smaller bass (Figure 4).

Model for Growth in Length, Weight, and Condition

Trajectories of relative weight over the time course during the first relative-weight experiment indicated that after 6 weeks the largemouth bass were close to a steady-state value for relative weight (Figure 5). It was also very clear that the steady-state value for relative weight increased with average growth rate of the fish (Figure 3). The simplest model to describe this assumes that the steady-state value for relative weight (W_{rSS}) is linearly related to the weight-specific growth rate (*dW/Wdt*). This is the linear relationship described by Equation 7. The relationship can be normalized so that $W_{\mathrm{rSS}} = 1$ when $dW/Wdt = g_s$; in other words, g_s is the weight-specific growth rate at which the fish attains a relative weight of 1.0.

$$W_{rSS} = \left(\frac{dW}{Wdt} - g_s \right) \cdot m + 1 \ , \qquad \text{Equation 8}$$

Based on the linear regression of data from the first laboratory experiment, $g_s = 0.0055$ d^{-1} and $m = 16.5$ (Equation 7 and Figure 3). When the weight-specific growth rate is larger than g_s, the steady-state value will be greater than 1.0, and when the weight-specific growth rate is smaller than g_s, the steady-state value will be less than 1.0.

The data in Figure 5 suggest that the rate of approach to W_{rSS} slows as W_r gets closer to W_{rSS}. Equation 9 is a simple way to model this observed behavior.

$$\frac{dW_r}{dt} = k \cdot W_r \left(W_{rSS} - W_r \right) \qquad \text{Equation 9}$$

In this equation, when $W_r = W_{rSS}$, then the rate of change in relative weight (dW_r/dt) will be zero, and W_r will be constant. The equation was simultaneously fitted to the trajectories of all 27 fish, starting at the initial value of W_r for each fish and ending at the observed final value for each fish. This resulted in a fitted value of k = 0.59 d^{-1} (Figure 5). So, for this model, the weight-specific growth rate (dW/Wdt) determines the steady-state value of relative weight (W_{rSS}), which then affects the rate of change in relative weight (dW_r/W_rdt). The values of dW/Wdt and dW_r/W_rdt then determine the length-specific rate of change in length (dL/Ldt), as indicated by Equation 4.

Gape Limitation of Bluegills as Predators and Prey

First gape experiment.–Unexpectedly, the adult bluegills in this experiment ingested all available sizes of juvenile bluegills offered as prey (Table 5). This made it impossible to use this experiment to define the maximum prey size for adult bluegills. I developed new predictive equations for prey length and body depth before proceeding to experiment 2.

One explanation for these results may be that the juvenile bluegills used as prey were in poor condition and consequently had a reduced body depth. The juvenile bluegills used as prey were taken from ponds in December and had not yet converted to feeding in the lab. They may have had a smaller body depth than the bluegills used to develop the original regression. A new regression was performed using both body depth and relative weight as predictor variables for bluegill length:

$$\log_{10} L = 0.7025(\pm 0.0051) + 0.8362(\pm 0.0031)\log_{10} D - 0.3034(\pm 0.0162)\log_{10} W_r\,, \quad \text{Equation 10}$$

where r^2 = 0.994, N = 450, for bluegills 51–220 mm TL, with maximum body depths of 13–89 mm and W_r of 0.55–1.04. It can be important to account for the effect of relative weight when estimating the sizes of prey that can be ingested by piscivores. Equation 10 indicates that for body depths (and predator gapes) 11–14 mm, the predicted maximum bluegill length varies by 7–9 mm as relative weight changes from 0.60 to 1.10.

The corresponding new equation for predicting maximum body depth from length and relative weight is:

$$\log_{10} D = -0.8259(\pm 0.0090) + 1.1887(\pm 0.0043)\log_{10} L + 0.3592(\pm 0.0194)\log_{10} W_r\,, \quad \text{Equation 11}$$

where r^2 = 0.994, N = 450.

Second gape experiment.–A sufficiently large size range of juvenile bluegills was offered as prey so that the maximum ingestible prey size could be estimated (Table 6). For all 12 bluegills tested, the maximum size of prey successfully ingested by these adult bluegills was larger than predicted by the gape equation from the literature (Equation 5) and the length-depth relationship described by Equation 6 (Figure 6, Table 6).

One explanation for these results is that the effective gape of bluegills is actually larger than predicted by Equation 5, which is based on Werner (1974). Further investigation confirmed that gape was underestimated, especially for large bluegills, by the equation obtained from the literature. In my measurements of bluegill gape, I recorded both the vertical and horizontal dimensions of a fully opened mouth. Two new gape equations were developed that included data on both vertical and horizontal gape of bluegills up to 255 mm TL.

$$\log_{10}(G_V) = 0.245 - 0.348 \cdot \log_{10}(L) + 0.350 \cdot \left(\log_{10}(L)\right)^2 \qquad \text{Equation 12}$$

$$\log_{10}(G_H) = 0.962 - 1.254 \cdot \log_{10}(L) + 0.606 \cdot \left(\log_{10}(L)\right)^2 \qquad \text{Equation 13}$$

where G_V (mm) is gape measured in the vertical dimension, $N = 79$, adjusted $r^2 = 0.98$, and G_H (mm) is gape measured in the horizontal dimension, $N = 79$, adjusted $r^2 = 0.98$, for bluegills 43–255 mm in length (Table 6). According to these equations, the horizontal gape is greater than the vertical gape for fish larger than 183 mm (Figure 6). Using these new gape equations to estimate maximum prey size, the predicted gape was larger than the observed maximum prey body depth for 8 of the 12 predators tested, and the difference was quite small for the remaining four predators (Table 6). In a comparison of several data sets with measurements of both bluegill predator size and bluegill prey size, about 90% of the prey consumed were smaller than the predicted maximum size using the new gape equations (Figure 6). Some discrepancy remains for bluegills near 150–160 mm, but the new equations do a good job of estimating maximum prey size.

Pond Experiments on Predator Growth

Adult bluegills as predators and juvenile bluegills as prey.–Although there were problems with one of two control ponds and one of the three treatment ponds, it seems clear from the relatively high survival of juveniles that adult bluegills are unlikely to be significant predators of age-0 bluegills during winter (Table 1). In this overwinter predation experiment, only three of five ponds produced useful estimates of juvenile bluegill survival. Juvenile survival was 90% and 96% in two ponds containing adult bluegills, and 95% in a pond without adult bluegills (Table 1). The remaining ponds did not produce useful estimates because one control pond was contaminated with other small bluegills and the third predator pond had a heavy growth of *Chara* preventing complete recovery of juveniles (Table 1). If the adult bluegills had all survived and had consumed juveniles at the rate observed by Schneider and Breck (1997) for yellow perch (0.27% body weight/d) or walleyes (0.38%BW/d), they might have consumed 18% or 25% of the juveniles in Pond 16, and 24% or 34% of the juveniles in Pond 15. Using the geometric mean biomass of adults during the experiment, the estimated consumption might have been 13% or 18% of the juveniles in Pond 16, and 15% or 21% of the juveniles in Pond 15.

Although no significant change was observed in mean weight of the adult bluegills that were recovered, this observation must have resulted from the death of below-average individuals. The average initial weight (mean ± SD) of the adult bluegills was 180 ± 35 ($N = 21$); average relative weight was 0.82 ± 0.07. The average final weight of the survivors was 183 ± 34 ($N = 8$); average relative weight was 0.79 ± 0.05. Individual marks made it possible to show that all eight adult bluegills recovered alive had lost weight. The average loss was 3.3 ± 1.8% of their body weight in December. Juvenile bluegills also showed only slight changes in mean length, mean weight or relative weight (Table 2), which may also have been due to slight differential loss of below-average individuals. Adult survival was poor. Only eight of twenty-one (38%) stocked adults were recovered alive.

Juvenile walleyes as predators and juvenile bluegills as prey.–Despite a low walleye recovery (43% survival), marking of individual predators made it possible to demonstrate that the average change in weight of walleyes increased with bluegill stocking density (Table 7). The average walleye lost weight at the two lowest bluegill stocking densities but gained weight at the three highest bluegill stocking densities. The change in walleye weight corresponded roughly with the reduction in bluegill biomass, suggesting that it was the difference in consumption of bluegills that produced the change in weight. The three ponds that lost the most bluegill biomass during the experiment were ponds where the average change in walleye weight was positive, and the two walleye ponds that lost the least bluegill biomass were ponds where the average change in weight was negative. The two control ponds without walleyes had changes in bluegill biomass of 8.6% and -2.8% (Table 7). A linear regression of change in walleye individual weight on stocking density of juvenile bluegills was not significant (P = 0.095), suggesting that these juvenile walleyes were feeding on other prey items in addition to any bluegills they consumed.

Survival of juvenile walleye predators was low. Of the original 60 walleyes, a total of 26 were recovered, for 43% survival. I believe that most missing walleyes were consumed by great blue herons *Ardea herodias* as the ponds were drained.

Discussion

Growth in length depends on condition, often measured as relative weight. When condition is poor, increases in weight are primarily allocated to improving condition. When condition is good, increases in weight are primarily allocated to increasing in length while maintaining condition. This pattern observed here with largemouth bass is consistent with results for salmonids summarized in the model by Broekhuizen et al. (1994). Over several weeks, condition changes to reflect the current average ration. In the first laboratory experiment, by the end of the six-week experimental treatment, relative weight of the bass reflected their average current ration; there was no significant effect of their relative weight (and the previous ration) six weeks earlier. This temporal pattern is consistent with the largemouth bass study by Heidinger and Crawford (1977) indicating that liver:somatic index (liver weight as a fraction of total body weight) changes to reflect the ration level of the previous few weeks.

Ration level also influences proximate composition. The early experiments of Gerking (1955) with bluegills show that feeding a larger ration leads to increases in percent lipid and decreases in percent water within three weeks. The effect of ration size on body composition has been demonstrated in sockeye salmon (Brett et al. 1969), largemouth bass (Niimi 1974; Niimi and Beamish 1974), brown trout (Elliott 1976), rainbow trout (Weatherley and Gill 1983), and other species. One next step in modeling relative weight would be to use a more detailed model that also accounted for such changes in energy density and proximate composition. Work on such a model has begun.

In their recent review, Blackwell et al. (2000) report different standard-weight constants for largemouth bass: a = -5.528 and b = 3.273 for length in millimeters and weight in grams, citing the Master’s thesis of Henson (1991). Use of different values for the standard-weight constants would cause minor changes in the quantitative predictions for trajectories.

Yearling bluegills are generally found in the littoral zone, where they typically remain until they are large enough to avoid being captured by most predators, such as largemouth bass (Mittelbach 1986; Mittelbach and Chesson 1987). But yearling bluegills can themselves be predators on smaller bluegills. Age-0 bluegills move to open water after leaving the nest, and only return to the littoral zone after they have grown to 21–25 mm (Werner 1967, 1969). Based on the gape and body-depth measurements and experiments of this study, this is a size at which the age-0 bluegills could avoid being captured by most of the juvenile bluegills that would be present in the littoral zone (Figure 6).

This study developed a model for changes in relative weight and length in relation to rate of growth in wet weight. This approach can be can be used to extend current bioenergetics models of fish growth to enable them to predict growth in length and changes in relative weight in addition to changes in wet weight (Breck 1993, 1998). This should help advance our understanding of how spatial and temporal differences in prey availability lead to differences among lakes and seasons in predator growth rate and relative weight.

Management Implications

Relative weight is expected to be a useful index of recent food availability to largemouth bass over the past few weeks. This study’s laboratory experiments on growth of largemouth bass indicate that relative weight reflects the average ration and growth rate experienced by fish during the previous 6 weeks or less. Relative weight would not be expected to correlate strongly with annual growth unless food availability had remained relatively constant during the past year, an unlikely occurrence.

The measurements and laboratory experiments on gape and body depth indicate the sizes of smaller bluegills that are vulnerable to predation by larger bluegills.

Earlier studies indicated that yellow perch might be important predators of age-0 bluegills during winter (Schneider and Breck 1997). In contrast, the winter pond study reported here suggests that adult bluegills are not likely to be important predators of age-0 bluegills during winter.

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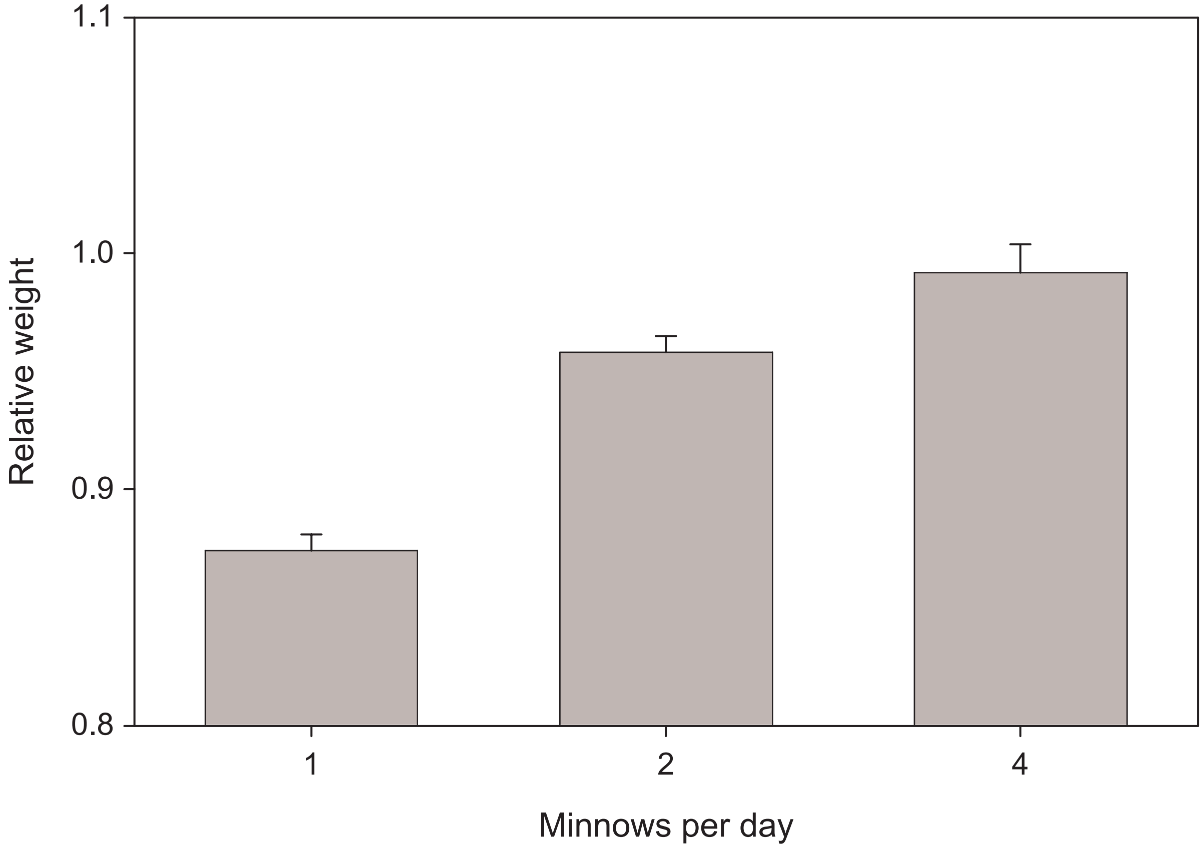

Figure 1.–Relative weight of three ration-size groups of largemouth bass at the beginning of the treatment (end of the pre-treatment period). Individual bass were fed one, two, or four minnows per day for the 37-d pre-treatment period. Error bars represent 1 SE; $N = 12$ bass per group. The three groups were significantly different in the mean value of relative weight.

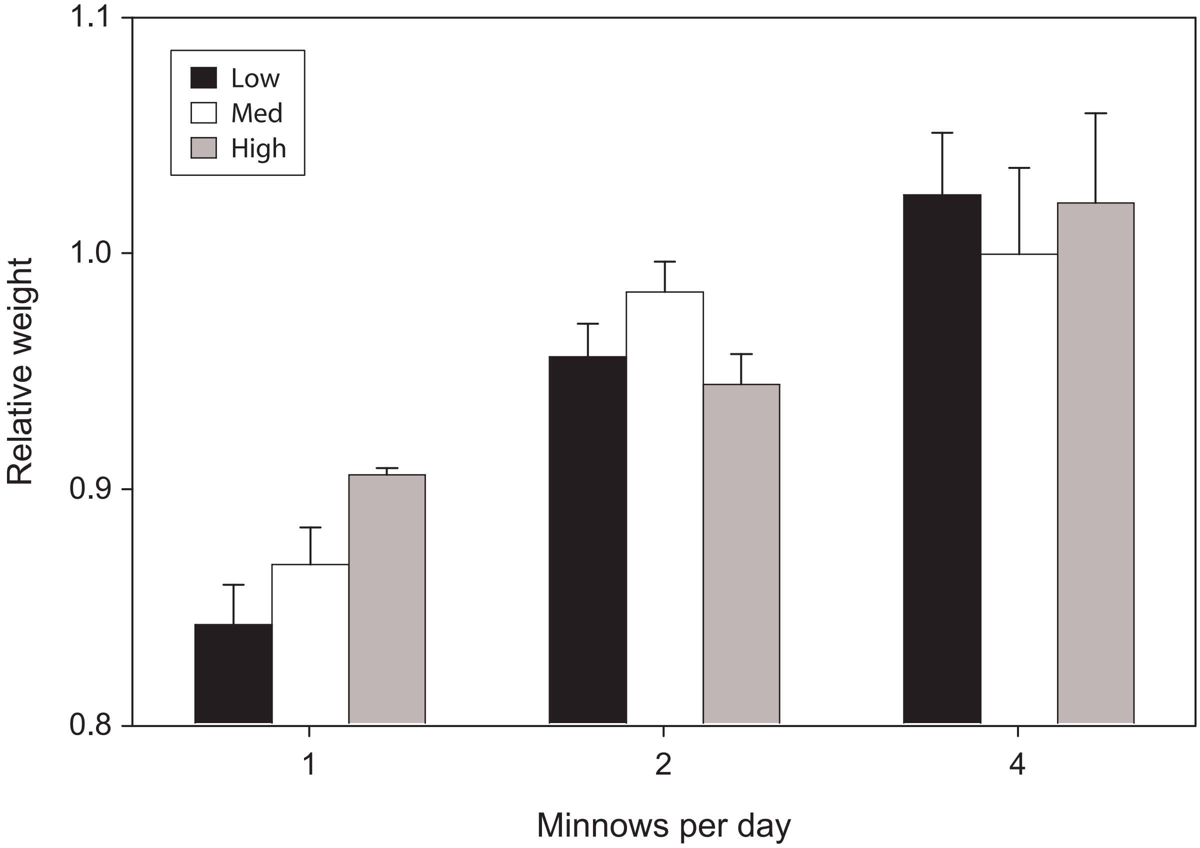

Figure 2.–Relative weight of nine groups of largemouth bass at the end of the treatment period. Shading indicates each group's relative weight at the start of the treatment period as low, medium, or high (see Figure 1). Individual bass from each of the three pre-treatment groups were fed at one of three rations (one, two, or four minnows per day) for the 42-d treatment period. Error bars represent 1 SE; *N* = 3 bass per treatment group.

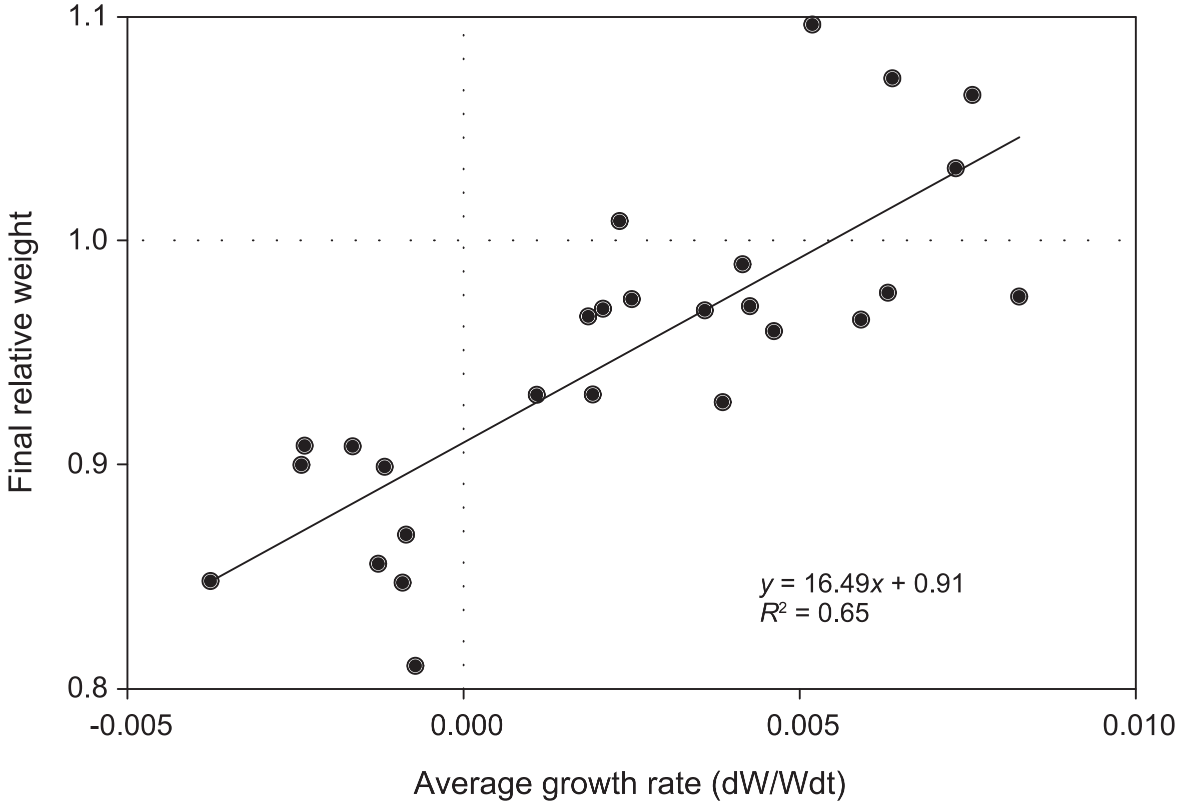

Figure 3.–Relative weight of individual largemouth bass at the end of the treatment period in relation to their average weight-specific growth rate (*dW/Wdt*) over the previous 6 weeks.

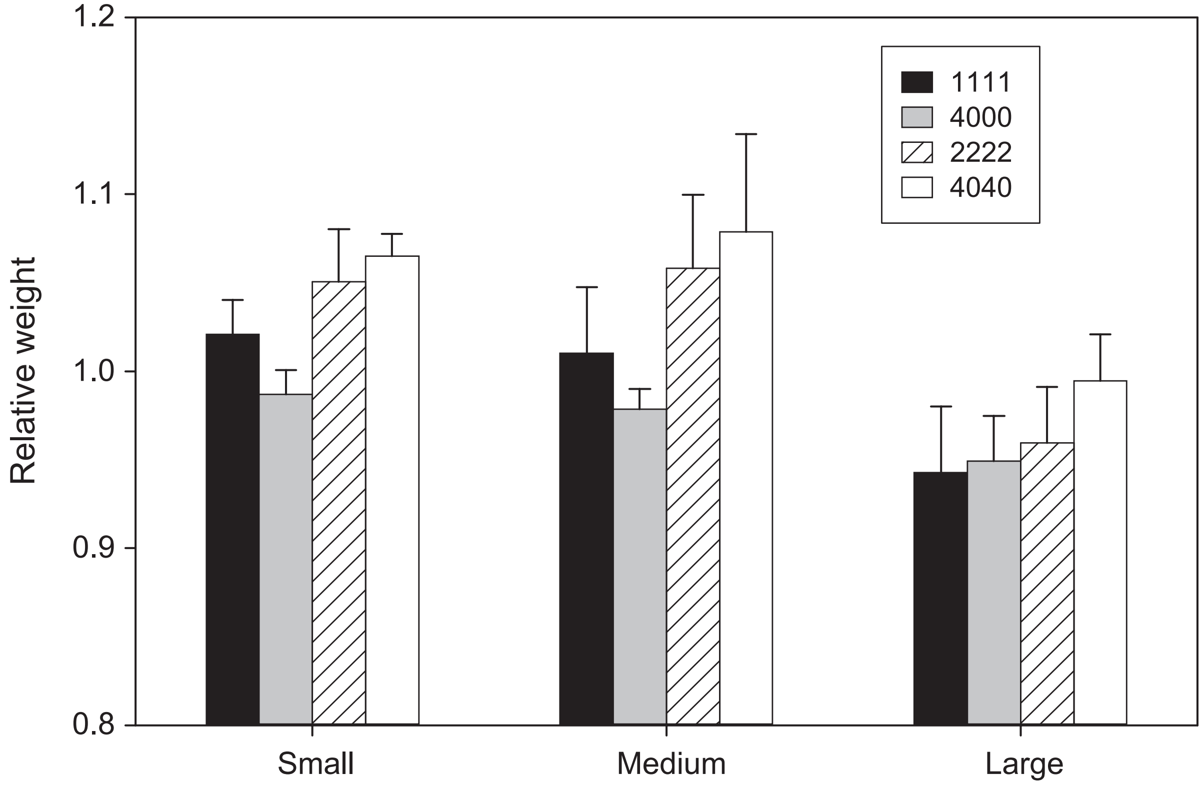

Figure 4.–Relative weight at the end of the treatment period for 12 groups of largemouth bass: three size classes and four feeding regimes. The legend indicates the feeding regime as the number of minnows fed to individual bass on each day of a 4-d sequence. Error bars represent 1 SE; *N* = 3 bass per group.

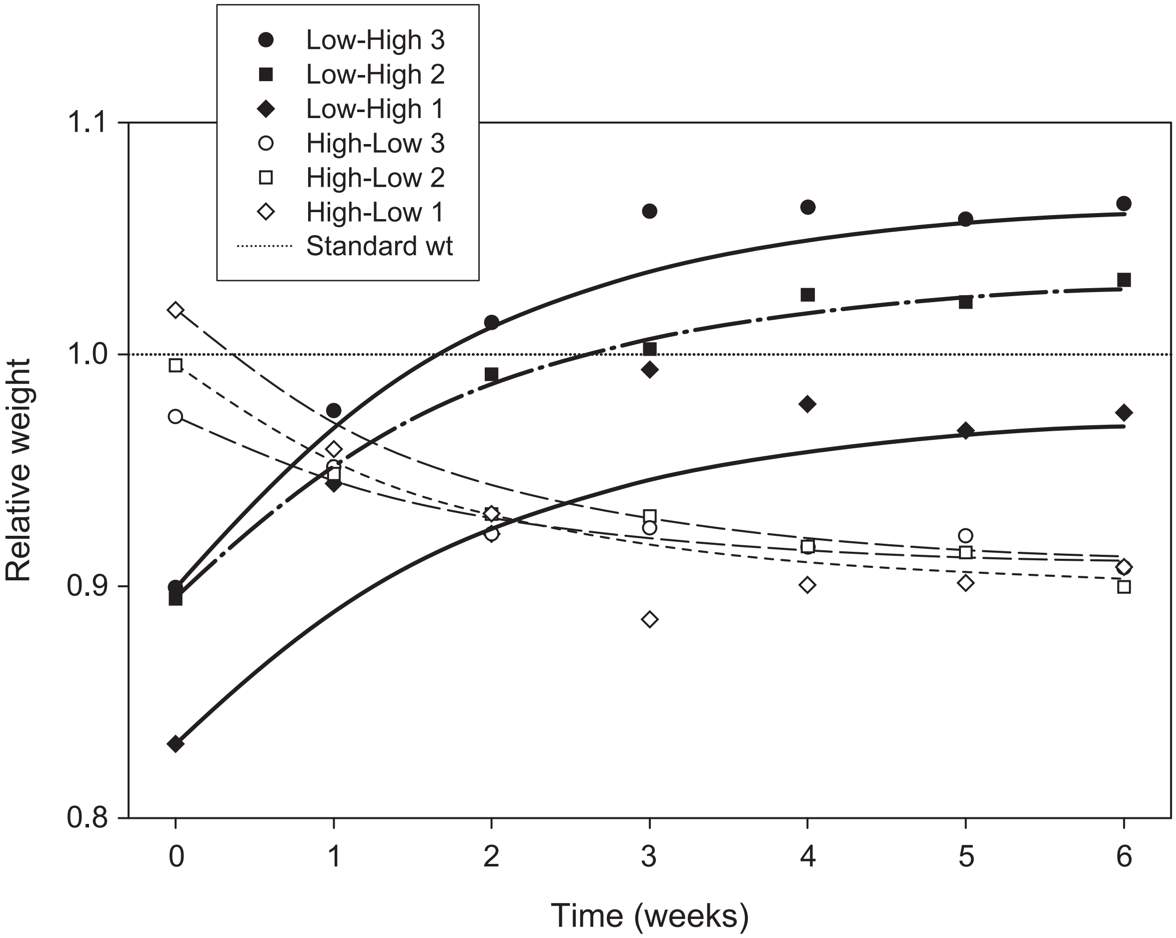

Figure 5.–Changes in relative weight of individual largemouth bass during the treatment period for two of the nine treatments. Solid symbols: fish from the low-ration pre-treatment group that were switched to a high ration for the treatment period; open symbols: fish from the high-ration pre-treatment group that were switched to a low ration for the treatment period; horizontal line indicates a relative weight of 1.0, which indicates the fish is at standard weight. The curved lines indicate trajectories of relative weight resulting from fitting *k* in Equation 9 to the treatment-period data for all 27 fish simultaneously, and starting the W_r for each fish at the observed value; this produced a fitted value of $k = 0.59\ d^{-1}$.

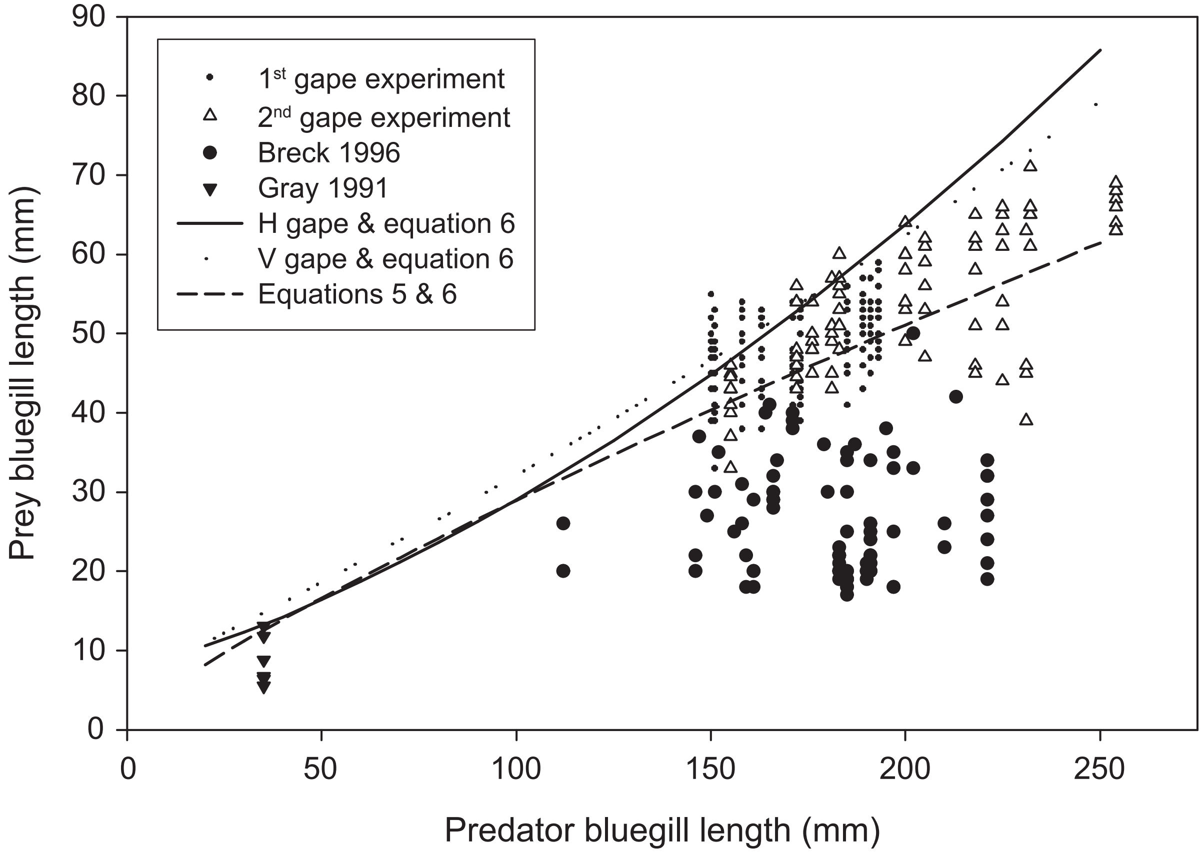

Figure 6.–Sizes of juvenile bluegills ingested by larger bluegills. The lines represent predicted maximum prey lengths, assuming maximum body depth of the prey (Equation 6; Schneider and Breck 1997) was equal to predator gape, for three estimates of predator gape. Dashed line: Equation 6 with gape from Equation 5 (Beckman 1948, Werner 1974); dotted line: Equation 6 with vertical gape, Equation 12, this study; solid line: Equation 6 with horizontal gape, Equation 13, this study. Points represent observations from several experiments. Small solid circles: first gape experiment, this study; open triangles: second gape experiment, this study; large solid circles: bluegill prey from stomachs of bluegills captured at pond draining (Breck 1996); solid triangles: lab experiments of Gray (1991).

Table 1.–Number of juvenile and adult bluegills stocked into five ponds on December 11, 1996, and recovered in spring 1997 for evaluation of overwinter predation by large adult bluegills.

Pond	Area (ha)	Stocked Juveniles	Stocked Adults	Date drained	Recovered Juveniles (number)	Recovered Juveniles (percent)	Recovered Adults (number)	Recovered Adults (percent)
Controls								
7	0.26	1,341	0	3/26/97	1,271	95	[a]	
17	0.24	1,770	0	3/26/97	6,303 [b]	356 [b]	[b]	
Large adults present								
14	0.21	1,094	6	3/27/97	619	57 [c]	2 [d]	33
15	0.29	1,454	8	4/01/97	1,392	96	3	38
16	0.24	1,770	7	3/27/97	1,594	90	4	57

[a] Other fish were found in Pond 7 at draining, including 15 juvenile largemouth bass (127–180 mm TL), 4 yellow perch (116–162 mm TL, all ripe males), 2 bluegills (111–115 mm TL), 2 brook sticklebacks, and about 20 fathead minnows.

[b] Adult bluegills had apparently been present in Pond 17 in late summer and produced a small year class. Four adult bluegills were found in the pond at draining (153, 155, 175, and 177 mm TL), as well as 32 other bluegills (80–107 mm TL).

[c] At pond draining, the macroalga *Chara* covered about two thirds of the bottom of Pond 14. Several dozen juvenile bluegills were retrieved from the *Chara* at draining, but an unknown number of bluegills remained.

[d] One of the two adults recovered at pond draining had recently died.

Table 2.–Average length, weight, and relative weight (mean ± SD) and sample size (*N*) of juvenile bluegills stocked into five ponds on December 11, 1996, and recovered in spring 1997.

Pond	Length ± SD (mm)	Weight ± SD (g)	Relative weight ± SD (%)	*N*
		Source pond, December 1997		
9	45.6 ± 4.8	1.20 ± 0.37	86.4 ± 5.3	156
		Control ponds, Spring 1997		
7	45.3 ± 4.9	1.13 ± 0.39	82.9 ± 4.4	200
17	37.2 [a] ± 7.7	0.67[a] ± 0.42	87.4 ± 7.1	104
		Ponds with large adults, Spring 1977		
14	48.0 ± 4.9	1.45 ± 0.45	88.5 ± 9.1	200
15	48.6 ± 4.6	1.45 ± 0.42	85.0 ± 5.3	200
16	47.3 ± 6.4	1.38 ± 0.80	85.3 ± 5.1	200

[a] Adult bluegills had apparently been present in Pond 17 in late summer and produced a small year class.

Table 3.–Daily mean water temperatures from May 25 to July 22, 1996, and from September 14, 1996, to March 1997, with monthly summaries, for Pond 7, Saline Fisheries Research Station. The monthly summaries are based on hourly values recorded with a digital thermometer (TempMentor S/N 902686, deployments 008 and 009). Pond 7 was drained on July 24, 1996, and on March 26, 1997.

	Daily mean temperature (°C)									
Day	May	Jun	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar
1		19.7	28.2		16.3	6.1	4.1	3.2	1.8	4.7
2		20.3	27.3		17.7	5.2	3.4	3.4	2.0	4.9
3		21.0	25.5		15.5	4.8	3.0	3.8	2.1	5.0
4		21.3	24.0		14.3	4.9	3.1	4.2	2.3	4.9
5		20.3	23.9		14.3	5.7	3.2	5.1	2.5	4.7
6		19.9	24.4		14.5	6.9	2.6	2.4	2.6	3.8
7		20.0	25.3		15.4	8.1	2.9	0.8	2.8	3.0
8		20.7	25.9		15.1	8.5	2.8	1.3	3.0	4.0
9		21.2	24.9		13.4	8.1	2.3	1.8	3.1	3.7
10		21.8	22.7		12.0	6.9	2.4	1.9	2.9	3.7
11		22.6	22.4		11.3	5.5	3.0	1.9	2.9	4.8
12		22.6	22.8		11.2	4.1	3.0	1.9	2.9	5.3
13		22.7	23.4		12.1	3.3	3.0	1.9	2.5	5.1
14		23.8	23.5	17.3	13.9	3.7	3.5	2.0	2.6	3.4
15		24.9	24.0	16.4	13.8	3.9	3.8	2.0	2.7	1.7
16		25.9	23.9	16.6	14.1	4.2	3.7	1.9	2.6	2.5
17		25.5	24.1	16.8	15.1	4.3	3.2	1.8	2.3	4.1
18		23.2	24.1	17.3	15.2	4.5	3.1	1.7	2.5	5.1
19		23.2	24.9	17.9	12.8	4.2	2.8	1.6	2.9	5.1
20		24.5	23.8	18.3	12.1	3.9	2.6	1.6	3.1	6.8
21		24.4	23.0	18.4	12.5	4.0	2.4	1.5	3.4	8.6
22		25.4	22.7	18.3	12.6	3.9	2.7	1.7	3.7	9.0
23		25.3		17.9	12.2	4.1	3.0	1.9	4.0	6.9
24		25.7		18.3	10.8	4.2	3.2	2.0	4.3	5.6
25	18.9	25.5		17.6	10.7	3.7	3.0	1.9	4.6	6.0
26	18.5	25.3		17.3	11.4	2.4	2.8	1.9	4.4	
27	17.5	25.8		17.2	12.8	2.2	2.5	1.9	4.8	
28	16.6	26.4		16.9	13.3	2.9	2.7	1.8	4.9	
29	17.4	27.3		15.8	11.8	3.2	3.1	1.7		
30	17.9	28.0		15.4	10.9	3.6	3.2	1.7		
31	18.9				7.8		3.2	1.7		
Monthly average	17.9	23.5	24.3	17.3	13.1	4.7	3.0	2.1	3.1	4.9
Monthly minimum	15.9	19.0	20.8	14.4	6.9	1.3	1.6	0.4	1.7	0.7
Monthly maximum	19.9	28.9	28.7	19.3	18.7	9.4	4.6	5.9	5.1	10.2
Average daily range	1.7	1.4	1.8	1.6	1.7	1.0	0.7	0.5	0.5	1.8
Cumulative degree days	125.6	704.2	534.7	293.6	406.8	141.2	93.1	66.1	86.3	122.3
Number of days	7	30	22	17	31	30	31	31	28	25

Table 4.–Total weight and estimated number of juvenile bluegills and average weight (*W*) and length (*L*) of juvenile walleyes stocked into eight ponds on October 13, 1997. Average bluegill size was 24.6 ± 3.6 mm, 0.17 ± 0.09 g, mean ± SD, $N = 200$. Ten walleyes were stocked into each treatment pond. A relative bluegill density of 1.0 = 444.8 g/ha.

		Bluegill			Walleye	
Pond	Area (ha)	Relative density	Total weight (g)	Estimated number	Mean *W* ± SD (g)	Mean *L* ± SD (mm)
Control						
6	0.28	5.6	709	4,082		
10	0.25	5.6	628	3,615		
Treatment, with 10 walleyes per pond						
9	0.27	0	0	0	60.1 ± 8.8	200 ± 8
15	0.29	1	129	743	60.1 ± 8.1	200 ± 9
8	0.25	2	224	1,290	66.4 ± 9.7	207 ± 9
7	0.26	4	470	2,706	60.8 ± 8.4	200 ± 8
5	0.30	8	1,071	6,166	62.7 ± 9.8	203 ± 11
16	0.24	16	1,708	9,833	65.1 ± 9.0	205 ± 9

Table 5.–Predator length, predicted gape, predicted maximum prey length, and prey sizes offered and consumed in laboratory experiments evaluating effects of prey size on prey capture. Both predators and prey were bluegills. All prey were consumed.

Predator		Predicted		
length (mm)	weight (g)	gape (mm)	max. prey length (mm)	Lengths of prey offered (mm)
148	50.9	11.0	39.9	39, 43, 45, 47, 48, 49, 50, 50, 52, 55
150	50.4	11.1	40.3	33, 39, 40, 41, 43, 45, 47, 48, 49, 51, 53
156	56.4	11.6	41.6	38, 41, 44, 46, 47, 49, 50, 52, 53, 53, 54
158	69.0	11.7	42.1	38, 42, 43, 44, 44, 47, 48, 51, 52, 52, 53
170	73.5	12.6	44.7	38, 41, 43, 45, 46, 47, 48, 48, 52, 54
171	87.8	12.7	44.9	39, 41, 42, 43, 44, 46, 47, 50, 52, 53, 53, 54
183	114.8	13.5	47.5	41, 45, 46, 48, 48, 49, 50, 53, 54, 56
184	79.7	13.6	47.7	43, 46, 48, 50, 51, 52, 53, 54, 55, 57
189	127.6	14.0	48.8	45, 47, 49, 50, 51, 51, 52, 53, 54, 57
191	105.8	14.1	49.2	47, 48, 49, 50, 52, 53, 54, 56, 58, 59

Table 6.–Final length, observed and predicted vertical and horizontal gape, and maximum prey depth and length ingested by adult bluegills in experiments conducted inside the lab at the Saline Fisheries Research Station from June to November, 1998.

	Observed gape (mm)		Predicted gape (mm)			Observed maximum prey	
Length (mm)	Vertical	Horizontal	Gape[a]	Vertical[b]	Horizontal[b]	*D* (mm)	*L* (mm)
154	15.4	13.8	11.5	13.66	13.11	13.1	46
168	17.4	15.0	12.7	15.14	14.83	17.5	56
177	17.7	15.7	13.0	16.12	16.00	15.8	50
180	17.4	16.8	13.4	16.46	16.40	17.5	57
186	18.5	18.3	13.5	17.13	17.22	18.0	60
199	18.7	21.0	14.8	18.63	19.07	20.0	64
206	18.4	19.4	15.1	19.45	20.12	19.3	62
217	21.1	22.3	16.1	20.78	21.82	20.5	65
224	21.8	23.1	16.6	21.64	22.95	20.4	66
226	21.6	24.5	17.0	21.89	23.27	20.7	63
229	23.1	26.2	17.1	22.27	23.77	23.2	71
253	25.6	29.2	18.7	25.37	27.97	23.0	69

[a] Predicted gape based on Werner (1974) and Beckman (1948).
[b] This study.

Table 7.–Biomass of juvenile bluegills and number and average change in weight of walleyes recovered in spring 1998 for ponds stocked with different densities of bluegills in fall, 1997. Change in bluegill biomass is final biomass minus initial biomass. Mean ΔW is the average (± SE) change in weight of individually marked walleyes recovered in each pond. A relative bluegill density of 1.0 = 444.8 g/ha.

		Bluegill			Walleye	
	Date	relative	biomass			
Pond	drained	density	Recovered (g)	Change (g)	*N*	Mean ΔW ± SE (g)
			Control			
6	11/29/97	5.6	770.2	61.2	0	
10	12/03/97	5.6	610.6	-17.4	0	
			Treatment, with 10 walleyes per pond			
9	12/08/97	0	0.0	0.0	9	-3.3 ± 1.7
15	11/26/97	1	24.0	-105.0	4	-1.0 ± 1.9
8	11/29/97	2	28.2	-195.8	0	
7	11/29/97	4	90.5	-379.5	3	1.8 ± 1.2
5	11/26/97	8	823.1	-247.9	2	3.2 ± 3.0
16	11/26/97	16	1,414.4	-293.6	8	0.8 ± 1.4

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