Hurry Up and Wait: Growth of Young Bluegills in Ponds and in Simulations with an Individual-Based Model

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Abstract.–The growth of young-of-the-year bluegills *Lepomis macrochirus* was measured in six experimental ponds and simulated with an individual-based model. In the ponds the young bluegills grew at a rate of about 0.6 mm/d for 3-4 weeks. An abrupt reduction in growth rate to about 0.2 mm/d occurred when total zooplankton density (exclusive of rotifers) decreased below about 50 organisms/L, and growth rate decreased to nearly zero by September. The model included daily foraging for several sizes of open-water or benthic prey and a revised set of bioenergetics parameters for bluegill. The simulations suggest that the initially rapid growth rate was near the limit set by maximum daily ration; the fish may have obtained full rations even with suboptimal foraging during this phase. Over a wide range of fry densities, the time of growth reduction and the average final fish size at the end of the growing season were strongly density dependent, both in the simulations and the ponds. Two natal cohorts started 10 d apart in the simulations. The size-frequency distributions produced by this individual-based model showed that these two cohorts remained distinct at starting densities below about 1 fish/m^3, but tended to overlap in size at higher densities.

Knowledge of the density-dependent processes occurring in the early life stages of fish is important for understanding recruitment and population dynamics. Individual-based models can help elucidate these density-dependent processes (Huston et al. 1988; Madenjian and Carpenter 1991). Individual-based models are used for studying a population's responses to various factors by simulating the responses of many individuals and aggregating the results as means or distributions for the population. Compared to other modeling approaches, an individual-based model can be easier to construct, easier to explain and interpret, and easier to parameterize. In some situations, it may be the only proper model. A model of many individuals may be required in cases where strong local interactions occur between individuals or where stochastic effects at low population sizes can predominate. For example, if only a few predators are stocked into a pond, the consequences for predator growth and prey behavior and survival may depend greatly on the particular sizes of individuals stocked, particularly on the extreme sizes. For another example, the chance that a predator's attack will be successful may depend on the sizes of the predator and the prey, and this chance may

differ from the average success rate for all predators.

Bioenergetics analyses have helped to identify factors that influence food consumption by and growth of fish (Kitchell et al. 1977; Rice et al. 1983; Hewett and Stewart 1989). Individual-based models extend bioenergetics models, linking them with dynamic prey models via foraging theory and incorporating mechanisms of prey selection.

In this paper I use an individual-based model to explain patterns in the timing and density dependence of growth of young-of-the-year bluegills *Lepomis macrochirus* in ponds and the response of invertebrate prey to bluegill predation. Included is a new summary of bioenergetics parameters for bluegill. The objectives of this paper are to describe an individual-based model of age-0 bluegill foraging and growth, to use this model to explain some patterns in the growth of young bluegills in ponds, and to explore some of the implications of those patterns.

The model helps explain the two-phase growth seen in ponds: an initial period of rapid growth followed by a second period of much slower growth. The size-frequency distributions produced by the model show that natal cohorts remain distinct when fish density is low but tend to become overlapping in size when fish density is higher; at the highest densities a later cohort can be lost due to starvation. Such results could not be produced by a model that simulated only the average individual.

Methods

Pond experiments

Growth of age-0 bluegills was measured in six experimental ponds at the Saline Fisheries Research Station, Saline, Michigan, as part of an experiment to evaluate the effect of yearlings on bluegill reproductive success. Ponds approximately 0.25 hectare in area and 1 m in average depth were stocked with adult bluegills (102-152 mm total length, TL) in April 1990 at a density of 56 kg/hectare. Two of these ponds also received yearlings (25-50 mm

TL) at a density of 5.6 kg/hectare. Reproduction occurred in these six ponds. A 2.5-m seine (mesh size, 1x3 mm) was used to sample age-0 bluegills every 3-4 d in June, about every 14 d in July and August, and once in September.

Young bluegills obtained on each sampling date were preserved in 95% ethanol and later measured to the nearest 0.1 mm. Natal cohorts and growth rates were determined by analysis of the size-frequency data. Each natal cohort included individuals born over a period less than 1 week. On several occasions fish were taken for measurement of length, wet weight (without alcohol preservation, to the nearest 0.1 mg) and dry weight. Dry weight was measured after approximately 24 h of drying at 55°C. Fry less than 20 mm were weighed on an electrobalance to the nearest 0.01 mg.

Zooplankton were sampled weekly by vertical tows with a 30-cm-diameter, 20-mm-mesh plankton net. Samples were taken at four fixed locations in each pond and pooled (Gray 1991). Samples were stained with eosin Y and preserved in 5% formalin with sucrose. Subsamples were counted at 40x magnification and zooplankton was identified to the following groups: *Bosmina*, *Ceriodaphnia*, *Chydorus*, copepod nauplii, older copepod stages, *Daphnia*, *Diaphanosoma*, ostracods, and rotifers.

Model

The individual-based model estimates daily growth of age-0 bluegills through their first summer of life. Each day individual bluegill fry forage stochastically for prey in open-water or benthic habitats, and then grow according to a bioenergetics submodel. Within each habitat, prey of several size-classes grow according to a logistic equation, and they are subject to mortality due to fish predation.

Bioenergetics parameters.–The bioenergetics component of the model uses the equations of Hewett and Johnson (1987, 1992) to account for the energy ingested and lost or stored as growth. The daily change in wet weight (W, g) is computed from weight-specific rates ($g \cdot g^{-1} \cdot d^{-1}$)

of consumption (C), respiration (R), egestion (F), and excretion (U):

$$\frac{\Delta W}{W \Delta t} = C - (R + F + U); \qquad (1)$$

t is time (d) and D denotes "change in." The rates are first calculated in energy terms ($J \cdot g^{-1} \cdot d^{-1}$) and then converted to the weight terms used in equation (1) by dividing by the energy density of the fish (E_{BG}, J/g) (Table 1). Reproductive losses are omitted for these juvenile fish.

The types and numbers of prey consumed are determined in the foraging submodel discussed below, with the constraint that the total mass of prey consumed daily is not permitted to exceed the maximum daily ration (MR, g/d):

$$MR = W \cdot C_{max} \cdot f(T); \qquad (2)$$

$C_{max} = CA \cdot W^{CB}$ is the maximum weight-specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$) at the optimal temperature for consumption, and $f(T)$ adjusts for the effect of temperature (T, °C):

$$f(T) = V^X e^{X(1-V)};$$

$$V = \frac{(CTM - T)}{(CTM - CTO)};$$

$$X = \frac{Z^2 \left(1 + (1 + 40/Y)^{\frac{1}{2}}\right)^2}{400};$$

$$Z = (CTM - CTO)\log_e(CQ);$$

$$Y = (CTM - CTO + 2)\log_e(CQ);$$

and CTM, CTO, and CQ are constants (Table 1; Kitchell et al. 1977). The total energy ingested is the product of the biomass of each prey type ingested times the energy density of each prey type, summed over all prey types.

One modification of Hewett and Johnson (1987, 1992) is that the equation for the rate of activity-dependent respiration (R_{S+A}) (Rice et al. 1983; Adams and Breck 1990) in the present model assumes that a fish swims at a fixed number of body lengths (BL) per second rather than at a fixed speed in centimeters per second:

$$R_{S+A} = RA \cdot W^{RB} e^{RQ \cdot T + RTO \cdot SC};$$

$SC = 0.1 \cdot TL \cdot SS$ is the calculated swimming speed (cm/s), SS is the specified swimming speed (BL/s), and RA, RB, RQ, and RTO are constants (Table 1). Under this assumption the absolute swimming speed will increase as the fish grows in length, as has been observed (Blaxter 1986), rather than being constant. This consideration is more important for age-0 fish because their change in length during the growing season is proportionately greater than that of older fish.

The respiration rate (R) is the sum of the activity-dependent respiration rate and the costs associated with processing and assimilating ingested food, usually called specific dynamic action:

$$R = R_{S+A} + SDA(C - F);$$

SDA is the dimensionless coefficient for specific dynamic action.

Losses due to egestion (F) and excretion (U) are modeled as fractions of consumption and assimilation, respectively:

$$F = FA \cdot C;$$

$$U = UA(C - F);$$

FA and UA are dimensionless constants.

The bioenergetics parameters for bluegill are revised from those presented by Breck and Kitchell (1979, used with slight modification by Hewett and Johnson 1987). The earlier values for bluegill respiration rate ($g \ O_2 \cdot g^{-1} \cdot d^{-1}$) as a function of weight and temperature produce overestimates of respiration rate compared to empirical results for sunfish species (bluegill: Wohlschlag and Juliano 1959 and O'Hara 1968; pumpkinseed *Lepomis gibbosus*: Evans 1984; redbreast sunfish *Lepomis auritus*: Shepard 1988). Revised estimates for metabolism parameters RA, RB, and RQ (Table 1; notation

follows Hewett and Johnson 1987) were taken from Evans (1984) and combine his "overall" values. I tried to fit the laboratory data of Savitz (1971) for starving bluegills using the parameters derived from Evans (1984). When I set swimming speed to zero for starving fish, set the starting weight at 73.9 g, and made energy density fall linearly from 5,480 to 4,480 J/g on day 29, the simulated fish did not starve fast enough. When the metabolism coefficient RA was doubled to the value shown in Table 1, the calibration runs gave reasonable results for the starvation experiments of Savitz (1971) and Schneider (1973). The coefficient for swimming speed (RTO) was estimated from Brett and Sutherland (1965). The age-0 bluegills are assumed to swim at a constant speed, SS = 1 BL/s, a typical value for fish larvae (Blaxter 1986). The factor converting oxygen consumed to joules used (13.56 J/mg O_2) was taken from Elliott and Davison (1975).

Only one of the parameters for consumption rate was changed from Breck and Kitchell (1979), who estimated CA and CB from data of McComish (1971) for bluegills fed ad libitum rations at 20°C, and CQ, CTO, and CTM from data in Beitinger (1974). In preliminary simulations, young bluegills would not grow fast enough until the maximum daily ration was increased 50%, from 0.182 to 0.273 g·g^{-1}·d^{-1} (Table 1).

The fraction of ingested energy lost due to egestion (FA) was obtained from Brett and Groves (1979) for fish consuming prey with a hard exoskeleton. Assimilated energy is the energy consumed minus the energy egested. The fraction of assimilated energy lost due to excretion (UA) was obtained from Brett and Groves (1979).

As fish grow in weight, the model increments length to follow an appropriate weight-length regression from Table 2. Fish length is not allowed to decrease. If weight decreases, length remains the same until weight returns to the regression's weight for that length (Rice et al. 1983).

Morphological parameters.–A wet weight-length relationship was determined for bluegills ranging from 4.4 mm to 31.2 mm TL (Table 2). A dry weight-length relationship was determined for fish of at least 8.0 mm (Table 2). The dry weight of fry less than 6 mm was approximately 10% of wet weight; the median value for larger fry was 18%. Using Craig's (1977) relationship between dry weight and energy density, I estimated that age-0 bluegills had about 2,300 J/g wet weight (Table 1).

Bluegill gape was estimated with the regression of Werner (1974). I used Beckman's (1948) factor of 1.278 to convert standard length to total length, and the equation of Murphy et al. (1991) for bluegill standard weight.

Fish numbers.–The model follows 100 individual fish in the simulations presented here. The weight (W_k) and length (TL_k) of each of these fish (k = 1, ..., 100) are followed separately as state variables. Each of these individuals represents NS_k identical fish in the population [NS_k = (fish density)(pond volume)/100]. Initially the number of fish represented is the same for each of the k individuals, but differences in the NS_k accrue through mortality.

Fish mortality.–Fish in the model can die due to size-independent "natural mortality" or due to starvation. The daily probability of dying due to "natural" causes (P_M) is a constant, calculated from the annual survival rate (S):

$$P_M = 1 - S^{\frac{1}{365}}.$$

The annual survival rate for yearling and older bluegills in these ponds was estimated to be 35% (Clark and Lockwood 1990), so that P_M = 0.0029. This is in the center of the range of daily mortality rates estimated by Beard (1982) for age-0 bluegills in two experimental Wisconsin lakes, measured from day 4 after dispersal from the nest until the fall. This value is lower than the May-October mortality rates measured by Krumholz (1946), who stocked bluegill yolk-sac fry (5.0-5.8 mm) into hatchery ponds. Because fish individual k represents NS_k other fish in the population, the number of those fish dying each day is chosen from a binomial

distribution with parameters P_M and NS_k according to the algorithm of Press et al. (1986).

Starvation occurs when the wet weight of an individual decreases below 20% of the standard weight (Murphy et al. 1991). If starvation occurs for individual k, then all NS_k fish represented by individual k also starve. The total number of fish dying each day is the sum of the deaths occurring for each of the 100 individuals modeled.

Prey dynamics.–Prey dynamics are incorporated in the model to provide a mechanism by which fish growth can respond – indirectly, via food supply – to fish density. Prey occur in two habitats, an open-water habitat containing cladocerans, and a benthic habitat containing midge larvae. Each of several prey types grows according to a logistic growth model, and is subjected to mortality due to fish predation:

$$\frac{\Delta N_i}{\Delta t} = N_i r_i \left(1 - \frac{N_i}{K_i} \right) - M_i \; ;$$

N_i is the density of prey type i (number/m^3 for zooplankton, number/m^2 for benthic prey), r_i is the intrinsic per capita rate of increase for prey type i (d^{-1}), K_i is the carrying capacity for prey type i (number/m^3 for zooplankton, number/m^2 for benthic prey), and M_i is the total number of type i prey consumed by all fish during 1 d.

Multiple sizes of prey are included so that fish have additional prey resources available to them as they grow. The simulations reported here use eight open-water prey types, representing zooplankton of different sizes, and eight benthic prey types, representing midge larvae of different sizes. The eight open-water prey types ($i = 1, ..., 8$) have lengths (L_i) of 1.2, 1.0, 0.8, 0.6, 0.5, 0.4, 0.3, 0.2 mm, and were arbitrarily assigned carrying capacities of 3, 4, 6, 10, 90, 100, 40, and 80 organisms/L, respectively. Their energy densities (E_i) are set at 2,300 J/g wet weight. The eight sediment prey types ($i = 9, ..., 16$) have lengths of 20, 15, 12, 9, 7, 5, 4, and 3 mm, and were arbitrarily assigned carrying capacities of 800, 850, 900, 1,000, 1,200, 2,000, 2,400, and 3,000 organisms/m^2, respectively. Their energy

densities are set at 2,510 J/g wet weight. Both these energy densities are about 10% higher than the values estimated by Mittelbach (1981).

An allometric equation for the ratio of production to mean biomass (Peters 1983: Figure 8.4, invertebrates) is used to estimate the weight-specific intrinsic rate of increase (r_i) for each prey size. The following equation includes a conversion of units to g·g^{-1}·d^{-1} from Watts/kg (Peters 1983):

$$r_i = 0.5789 (0.001 \, W_i)^{-0.37} E_i^{-1} \; ;$$

W_i is the wet weight of prey type i (g), and E_i is the energy density of prey type i (J/g). Each prey type's weight is estimated from its specified length with Mittelbach's (1981) regressions for these different types of prey:

$$W_i = 0.00012 L_i^{2.63}, \quad i = 1, ..., 8 \; ,$$

and

$$W_i = 0.00003 L_i^{2.35}, \quad i = 9, ..., 16 \; ;$$

wet weight is assumed to be 10 times the dry weight. Mittelbach's third prey category, epiphytic prey, was not used in these simulations because aquatic vegetation was very sparse in the experimental ponds.

Foraging.–The model allows for variation among fish in the number of prey encountered and consumed each day. Both encounter rate and mean handling time depend on prey type, prey size, and fish size. Mean handling time is the average time from encounter with a prey item until search resumes, and it includes the time required for and the probability of successfully completing the stalk, strike, manipulation and swallowing of the prey. The model has an option to allow optimal foraging by each fish: that is, to allow the fish to select the encountered prey types that maximize the rate of energy intake (Mittelbach 1981).

On each day of the simulation, the number of planktonic prey encountered by each fish is chosen randomly from a Poisson distribution with a mean equal to the product of the volume

of water searched and the mean density of that prey type (number/m^3). The volume of water searched by each fish is different for each prey size; the larger the prey items, the greater the distance at which fish react to them. The reactive distance (RD) for each prey size was calculated from the equation in Breck and Gitter (1983) for bluegills feeding on cladocerans. The water volume searched is computed as the volume of a cylinder with a radius equal to the reactive distance and a length equal to the distance the fish could swim in 15 h at a speed of 1 BL/s (Confer and Blades 1975).

For benthic prey, the mean of the Poisson distribution is the product of the prey density (number/m^2), the sediment area searched (I assumed that the RD for sediment prey is equal to that for a cladoceran 36% as long as the midge larva), and the proportion of the prey that are available to bluegills, discussed below. The sediment area searched is assumed to be a rectangle with a length equal to the distance the fish swims in 15 h at 1 BL/s and a width equal to 2RD·sin(p/3) (the fish is assumed to swim 0.5RD above the sediment). Larger instars of *Chironomus* midge larvae tend to burrow deeper in the sediment (Shiozawa and Barnes 1977), which probably accounts for the apparent selection of smaller midge larvae by bluegills (Werner et al. 1983). I assumed that the proportion of benthic prey available to fish (P_{BAv}) varied with prey length (L_{BP}, mm) in the following way:

$$P_{BAv} = 0.01 \exp(-4.2864 - 0.3188\, L_{BP}),$$

so that P_{BAv} is 0.0001 for 1-mm larvae and 0.000003 for 12-mm larvae.

For each fish, the mean handling time (t_h) for each prey type is computed daily from the following equation based on the sequence of events that occur during foraging (see Stephens and Krebs 1986); though t_h and its components differ for each prey type and individual fish, such subscripts are omitted to simplify the notation:

$$
\begin{aligned}
t_h = (1 - P_f)t_{noStalk} + P_f \Big\langle t_{Stalk} + \\
\left(1 - P_s\right)t_{noStrike} + P_s\Big\{ t_{Strike} + \\
\left(1 - P_c\right)t_{noCap} + P_c\Big[t_{Adjust} + \\
\left(1 - P_i\right)t_{noIngest} + P_i\left(t_{Process}\right)\Big]\Big\}\Big\rangle \; ;
\end{aligned}
$$

P_f is the probability of stalking the prey item given an encounter, P_s is the probability of attempting a strike given a stalk, P_c is the probability of prey capture given a strike, P_i is the probability of prey ingestion given a capture, $t_{noStalk}$ is the time to resume search given a decision not to stalk, t_{Stalk} is the time to stalk an encountered prey, $t_{noStrike}$ is the time to resume search given a decision not to strike, t_{Strike} is the time to strike at a stalked prey, t_{noCap} is the time to resume search given the strike fails to capture the prey, t_{Adjust} is the time to adjust the captured prey for ingestion, $t_{noIngest}$ is the time to resume search given the captured prey is not ingested, and $t_{Process}$ is the time to process ingested prey before search resumes. Stalking, striking and adjusting prey can be important for piscivores (Crow 1982), but these components are much less important for fish feeding on zooplankton and midge larvae.

For these simulations I assume that P_s and P_i = 1, t_{Stalk} and $t_{Adjust} = 0$, and $t_{noStalk}$, $t_{noStrike}$, t_{noCap}, and $t_{noIngest} = 0.1$ s. I assume that feeding is attempted ($P_f = 1$) only if the prey size is less than or equal to the fish's mouth gape (or else $P_f = 0$); for benthic prey, the critical prey size is assumed to be one-tenth of the total prey length, because midge larvae can be swallowed end first. Calculation of t_{Strike} presumes the fish strikes over a distance RD at a speed of 2 BL/s. The probability of capture (P_c) is assumed to be 1 for prey whose critical size is less than 75% of the gape; P_c declines linearly to 0 as the critical prey size becomes equal to the gape. The $t_{Process}$ is computed with the "handling time" equations of Mittelbach (1981) for open-water prey and benthic prey; his equations account for the effects of fish size (TL) and prey size (L):

$$t_{Process} = 0.536 e^{\frac{18.488\, L}{TL}},$$

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for planktonic prey when $L/\text{TL} \geq 0.034$ (otherwise $t_{\text{Process}} = 1.02$ s) and

$$t_{\text{Process}} = 2.364 e^{\frac{6.492\,L}{\text{TL}}},$$

for benthic prey when $L/\text{TL} \geq 0.220$ (otherwise $t_{\text{Process}} = 9.63$ s) (Mittelbach 1981).

This foraging model permits optimal foraging by each fish. The available prey types ($P_f > 0$) are ranked according to their energy per unit handling time: that is, by $W_t E_i / t_h$ (Werner 1974; Mittelbach 1981). Starting with the most profitable prey types, additional prey types are added to the diet as long as the total energy intake rate does not decrease. This calculation is done separately for open-water prey and benthic prey, and the individual fish then forages for that day in the habitat providing the higher energy intake rate. If the optimal foraging option is not used, the available prey are taken in the proportions in which they are encountered, in the habitat providing the higher energy intake rate.

Water temperature.–The daily water temperature in the model follows a truncated sine curve. The parameters were chosen to approximate the seasonal pattern of water temperature in the Saline ponds:

$$T_{\text{sine}} = 13.0 + 13.0 \sin\left[\left(\text{DY} - 200 + \frac{365}{4}\right)\text{PD}\right],$$

$$T = \max\left(T_{\text{sine}},\ 4\right); \tag{4}$$

T_{sine} is the temperature calculated from the sine function (°C), DY is the day of the year, PD = $2\pi/365$, T is the water temperature (°C), and the function max(.) keeps the temperature from dropping below 4°C. The water temperature reaches a maximum of 26°C on July 19 (DY = 200).

The starting point for these simulations is near the time when bluegill fry leave the nest and begin feeding. This generally occurs at a length of about 5 mm (Toetz 1966; Beard 1982) and first occurs in late May or early June in southern Michigan. For these simulations the initial length of each individual was chosen stochastically from a normal distribution with a mean of 6.0 mm and a standard deviation of 0.5 mm; this standard deviation is close to the value observed for the first group of bluegill fry produced in the Saline ponds in 1990. Two natal cohorts are modeled, and 50 fish represent each cohort. The cohorts begin to grow on June 5 and June 15, respectively. The simulations terminate on October 3, after 120 d. I used a simulated pond volume of 7,100 m³ so that at least 100 individuals will be present at densities as low as 0.014 fish/m³.

A series of simulations was performed in order to determine the effects of density of age-0 bluegills on their size at the end of the growing season. Simulations were done at densities ranging from 0.014 to 25.8 fish/m³. Additional simulations were done to compare fish growth when the optimal foraging and suboptimal foraging algorithms were used. The simulated fish size was expressed in length because length is the customary field measure of size. The results were compared with information from the experimental ponds.

Results

Pond experiments

Age-0 bluegills in ponds had two growth phases: rapid for the first 30 or 40 d and much slower later (Figure 1). In the first phase length increased approximately linearly at about 0.6 mm/d. This rapid growth continued for about 10 d longer in the two ponds containing yearlings. In the first growth phase, it was generally easy to identify the natal cohorts in size-frequency plots (Figure 2). In each of the six ponds, two to four natal cohorts could be distinguished. The first two natal cohorts were strongest; their length modes were about 6 mm apart, suggesting that spawning occurred about 10 d apart. In the second growth phase, however, it was harder to consistently identify separate cohorts (Figure 2). In some of the ponds, a few age-0 fish grew more rapidly during phase two than the other fish (see the size-frequency plots for August 21 and September 21 in Figure 2).

In the ponds, large cladocerans were generally depleted first, then smaller prey (Figure 3) (Gray 1991). At first feeding, bluegill fry cannot ingest the larger cladocerans. However, after reaching 13.5 mm the fish have a gape just large enough to consume 1.2-mm cladocerans (Table 2; Werner 1974). By the time the biomass of fish is large enough to have a big effect on prey density, the fish can consume the larger cladocerans (Werner 1974), causing those prey to decrease in density.

In the ponds, the slow-growth phase started after total zooplankton density (exclusive of rotifers) declined to about 50/L (Gray 1991). At that time the zooplankton comprised copepods and a few small cladocerans such as *Bosmina* spp. Stomachs of young bluegills examined during this slow-growth phase contained midge larvae, copepods, small cladocerans, and ostracods (Gray 1991).

Model Results

The simulated age-0 bluegills also had two growth phases. In the first phase they increased approximately linearly in length, averaging 0.61 mm/d (Figure 4). Growth was the same in both natal cohorts. The daily ration was very close to the maximum during this phase.

Final length was independent of density at 0.8 fish/m^3 and lower (Figures 4, 5). At these levels the final length was limited by time and temperature, not by food. These fish were still growing at the end of the simulations and the prey had not yet crashed, though the fish were growing slowly because the temperature had decreased to 16.4°C (Figure 4). The two natal cohorts remained distinct throughout the 120 d (Figure 5).

Final length was highly density dependent above 2.5 fish/m^3 (Figures 4, 5). The growth rate during phase one was the same for all densities simulated. However, at higher densities the period of rapid growth ended sooner, so that the final lengths were less (Figure 4). Above 2.5 fish/m^3 there was a greater spreading of the size-frequency distributions of each natal cohort than at lower densities, resulting in some overlap between the cohorts (Figure 5).

Mortality due to nonspecific causes was about 28% during this 120 d period, independent of density. Starvation occurred only at densities of 8.2, 14.2, and 25.8 fish/m^3; additional mortalities were 16%, 65%, and 80%, respectively. At densities of 14.2 and 25.8 fish/m^3, the entire second natal cohort starved (Figure 5).

The strong density dependence of growth in the simulations can be clearly seen by examining the final mean length of the young fish (Figure 6). Data collected in 1966 and 1968 from the same experimental ponds (Latta and Merna 1977) show a similar pattern with respect to density of young bluegills (Figure 6). Over part of the range of densities simulated, the log-log plot shows a nearly linear decrease in final mean length with increasing fish density. A 10-fold increase in fish density from 1.42 to 14.2 fish/m^3 produced a 47% decrease in final fish length.

In the simulations, the duration of the rapid-growth phase was strongly density dependent. Figure 7 shows the day of the simulation on which growth rapidly decelerated for most individuals. A 10-fold increase in fish density reduced the duration of rapid growth by a factor of about 2.8. No points are shown for densities below 2.5 fish/m^3 because growth continued throughout the 120-d simulations at those fish densities.

The mean and maximum final lengths were greatest at densities of 1.1 and 1.4 fish/m^3 (Figures 4-6). At these critical densities, the bluegills are abundant enough to deplete the zooplankton and force a switch to benthic prey, but not abundant enough to severely deplete the benthic prey during the simulation. Because the model sets a limit on the grams of prey that can be consumed per day (equation 2), and because the energy density of the benthic prey is greater than that of the zooplankton, the fish consume more energy on a maximum ration of benthos than on a maximum ration of zooplankton. These fish therefore grow larger than the fish that continue to consume maximum rations of zooplankton. This interpretation was confirmed with additional simulations in which the energy

density of the benthic prey was made the same as that of zooplankton; the fish at these critical densities then achieved a final length no greater than the fish growing at lower densities.

In the simulations the fish were able to obtain maximum rations during phase one even though the suboptimal foraging algorithm was used and the fish consumed prey types in the proportions in which they were encountered. The larger prey types were depleted first even though there was no active selection for them (Figure 8a). Larger prey were differentially consumed because their larger sizes meant increased reactive distances and, therefore, increased encounter rates.

In the simulations employing optimal foraging, fish maintained maximum growth by switching prey types. Available prey (prey detected and small enough to be ingested) with high values of energy per handling time were depleted first, then less preferred prey (Figure 8b). With optimal foraging, the zooplankton were depleted in order of size, with the exception of the 1.2-mm prey. The 1.0- and 0.8-mm prey were depleted before the 1.2-mm prey because the fish were not large enough to ingest 1.2-mm prey until about day 17. The smallest zooplankton type (0.2 mm) persisted much longer with optimal foraging than with suboptimal foraging.

Zooplankton densities go to zero on days 30-35 in Figure 8a, and on days 19-32 for all but the 0.2-mm prey in Figure 8b. With either type of foraging, fish growth continued for several days after the crash of the zooplankton because the fish switched to foraging on benthic prey. These simulations indicate that if sufficient alternative prey are available, rapid fish growth can continue even after depletion of large cladocerans.

Discussion

The simulation model reproduces the approximately linear increase in fish length observed in the ponds in the first phase of age-0 growth. This growth pattern appears to be the result of the combined allometric functions of maximum daily ration, fish length, and metabolic rate.

The simulation results suggest that the initial growth of age-0 bluegills in the Saline ponds was near the maximum rate possible given the water temperature and the caloric value of the available prey. The simulated bluegills initially obtained maximum daily rations, or just slightly less because they were constrained to consume an integer number of prey items each day.

The maximum mean length attained by the first natal cohort in these simulations was about 65 mm TL, for initial densities of 1.4 fish/m^3. Age-0 bluegills can grow larger than this under certain conditions. Krumholz (1946) stocked bluegill yolk-sac fry at four densities into hatchery ponds near Kalamazoo, Michigan. The 5.0-mm fry stocked at the lowest density (0.6 fish/m^3) into a fertilized pond on May 31, 1941, had the best survival (39.3%) and attained a mean length of 99 mm by the week of October 24, about 146 d later. The larger final size might be explained by warmer water temperatures and prey with a higher energy density than assumed in my simulations.

Optimal foraging, in terms of diet breadth, may not be critical for age-0 bluegills during the rapid-growth phase. Growth during this phase may be limited by temperature or digestion rate or other physiological parameters, not by rate of energy intake. In such conditions, suboptimal foraging may be adequate to supply a maximum daily ration. Optimal diet breadth may not be critical during the slow-growth phase, because the prey density is so low that all available prey that are encountered can be consumed. At sufficiently low prey density, consumption of all encountered prey *is* the optimal behavior.

The relative value of suboptimal foraging is suggested by simulations in which the fish took available prey in the proportions in which they were encountered in the habitat providing the higher energy intake rate (Table 3). When suboptimal foraging was used, diet breadth was increased, foraging was not concentrated on just a few prey types, and the prey types were eliminated less quickly than when diet breadth was optimally narrow (Figure 8). Fish density had a much greater effect on final fish length

than the type of foraging used (Table 3). I had expected the optimal foraging algorithm to have a bigger effect. But apparently the period when it would have made the most difference (the period when prey densities are low enough that fish can not obtain a maximum ration but not so low that it is optimal to take all prey encountered) was too short to have a large effect on final length.

Because the percent dry weight is lower for age-0 bluegills (median of 18%) than for adults (about 24%; McComish 1971), each unit of net energy intake produces a larger increase in weight and length of young fish than of adults. A rapid increase in length is very important for these small fish (Miller et al. 1988), so their lower percent dry weight is very advantageous. An increase in length means an increase in gape and an increase in the availability of larger food items. If size-dependent mortality is occurring, an increase in length means that the fish are exposed to lower mortality rates and probably have greater overwinter survival.

Rapid growth of age-0 fish has major implications for prey survival. As age-0 bluegills grow from 5 to 25 mm their weight increases by a factor of about 220. According to the weight-length regression in Table 2, a 5-mm bluegill weighs 0.00081 g, whereas a 25-mm bluegill weighs 0.18 g. A rapid increase in fish weight implies a similar increase in daily consumption of prey and daily prey mortality. The increase implies a rapid change from a nearly insignificant prey mortality rate to an overwhelming prey mortality rate. The prey population cannot persist for long with a high mortality rate, and the population quickly crashes. The simulation model reproduces this phenomenon observed in the ponds.

Young fish do not always have a strong effect on zooplankton (Hewett and Stewart 1989; Dettmers and Stein 1992). As demonstrated here, the outcome depends on fish density and time. Early in the season the total consumption by the year class represents a trivial source of mortality for zooplankton. Just a few weeks later, due to exponential growth in weight by the young fish, the total consumption of zooplankton by fish can represent an overwhelming source of mortality. Whether or not the age-0 fish have a dominant affect on the zooplankton depends on many factors, including the mortality rate of the fish, which could keep their peak total prey consumption relatively low, or the movement of age-0 fish from the pelagic zone into the littoral zone, as young bluegills move in lakes (Werner 1967, 1969). Also, refuges can reduce the availability of zooplankton to fish (Tessier and Welser 1991).

In this individual-based model, the growth compensation seen in Figures 4-6 occurs because the prey are overwhelmed by a certain mortality rate, which corresponds to a particular rate of consumption by the fish. A lower fish density allows prey production to occur for a longer period of time, so that the fish grow larger. This formulation is consistent with the observations of Werner and Hall (1979) and Werner et al. (1981) that sunfish deplete the most favored prey types and then switch to a different habitat with different prey.

The type of two-phase growth described here may be more common in shallow ponds and unstratified lakes than in stratified lakes. Stratified lakes with an oxygenated hypolimnion can provide a refuge for large cladocerans (Tessier and Welser 1991) so that these prey are less likely to be eliminated by age-0 fishes.

Recent work with individual-based models of piscivorous walleye *Stizostedion vitreum* indicates that age-0 growth rate can be very sensitive to prey density (Madenjian and Carpenter 1991). Results with that piscivore, which feeds on a few relatively large prey each day, appear to be different than the results for age-0 bluegills, which feed on many small prey each day. This study suggests that production of young bluegills in ponds is more like a batch-culture process with rapid initial growth, reset each spring, than like a continuous growth process with the growth rate dependent on prey density.

While the model can reproduce the pattern of rapid fish growth during the first phase (e.g., Figure 4), it did not reproduce the pattern of slow (about 0.2 mm/d) growth during the second phase. Based on other simulation runs, it appears that unless the prey densities are within certain narrow bounds, either the modeled fish starve or they grow too much.

Perhaps the additional, larger, infrequently encountered prey types need to be added to the model to reproduce the slow growth in midsummer.

Additional insights into the processes of recruitment and population dynamics are likely to be gained by considering additional age groups, predators (Forsythe and Wrenn 1979), and competitors. This research is underway.
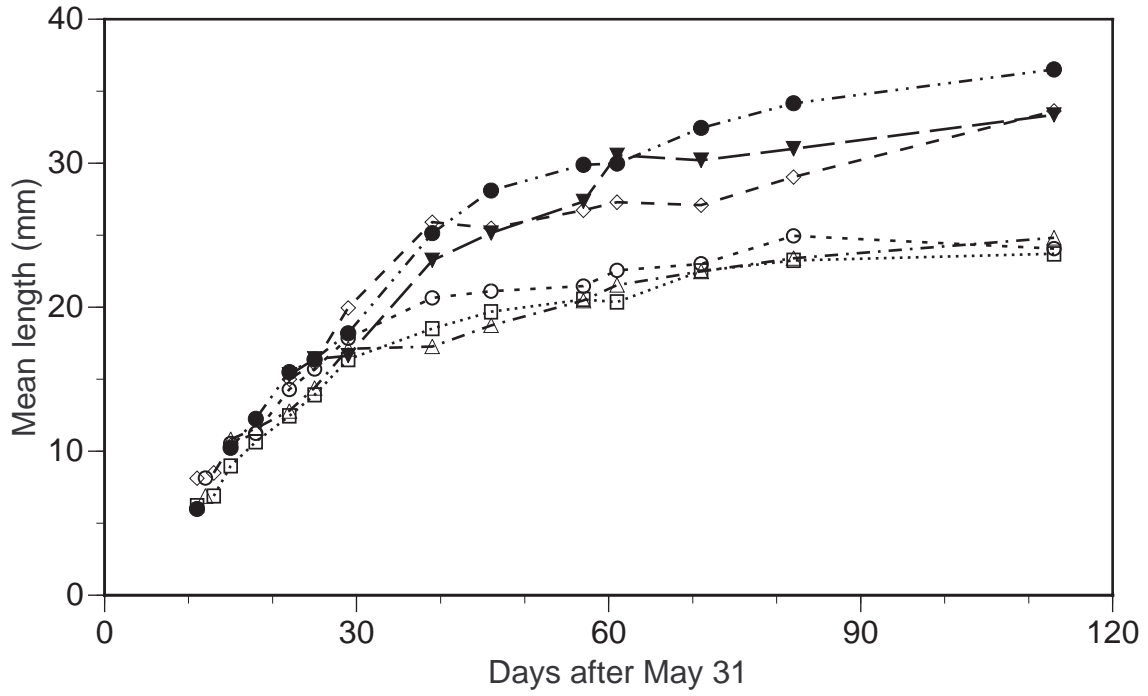
Acknowledgments

Figure 1.–Mean lengths of the first natal cohort of age-0 bluegills in six experimental ponds. Solid symbols indicate ponds stocked with yearling bluegills at 5.6 kg/hectare; open symbols indicate ponds without yearlings.
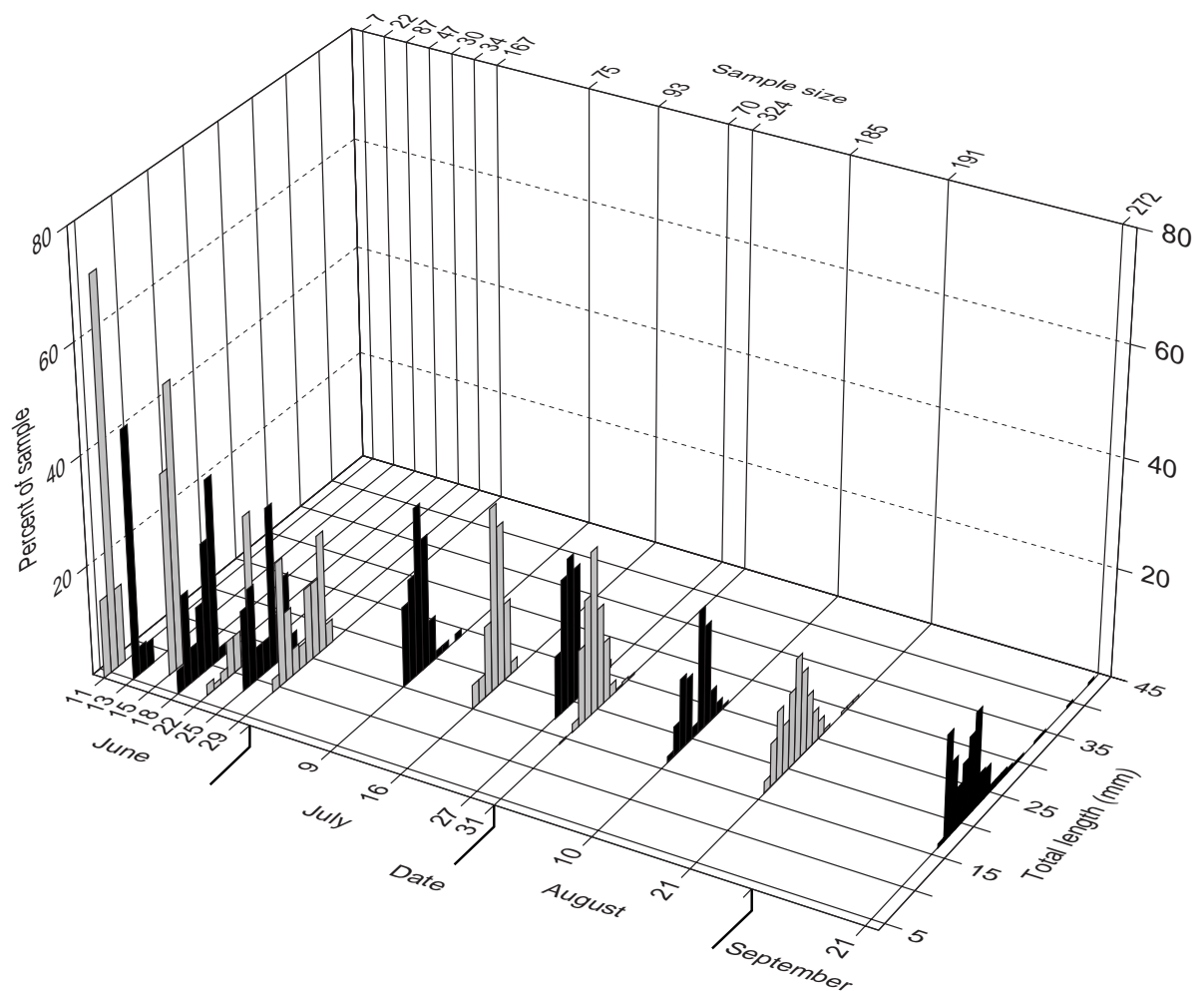
Figure 2.–Size-frequency distributions and sample sizes of age-0 bluegills in one of the experimental ponds without yearlings on 14 dates in 1990. For clarity, the shading pattern alternates on successive sampling dates.
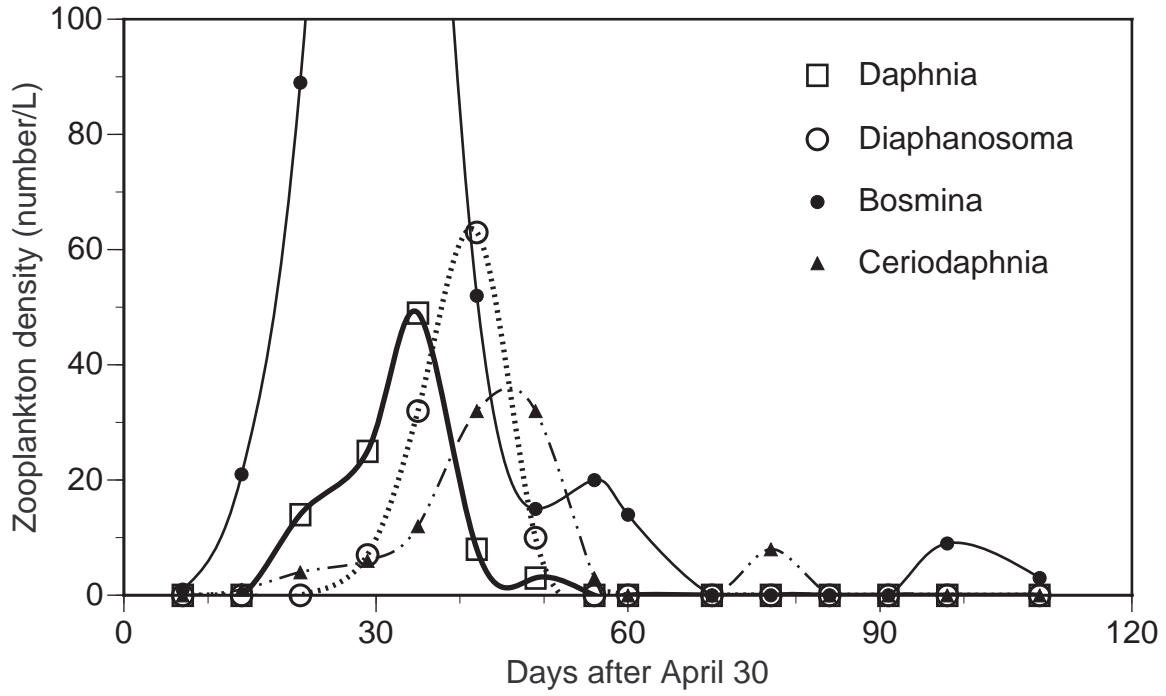
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Figure 3.–Zooplankton densities from May through August in a pond where bluegill spawning took place near the end of May. Open symbols indicate genera of large cladocerans, solid symbols small cladocerans. Data from Gray (1991).
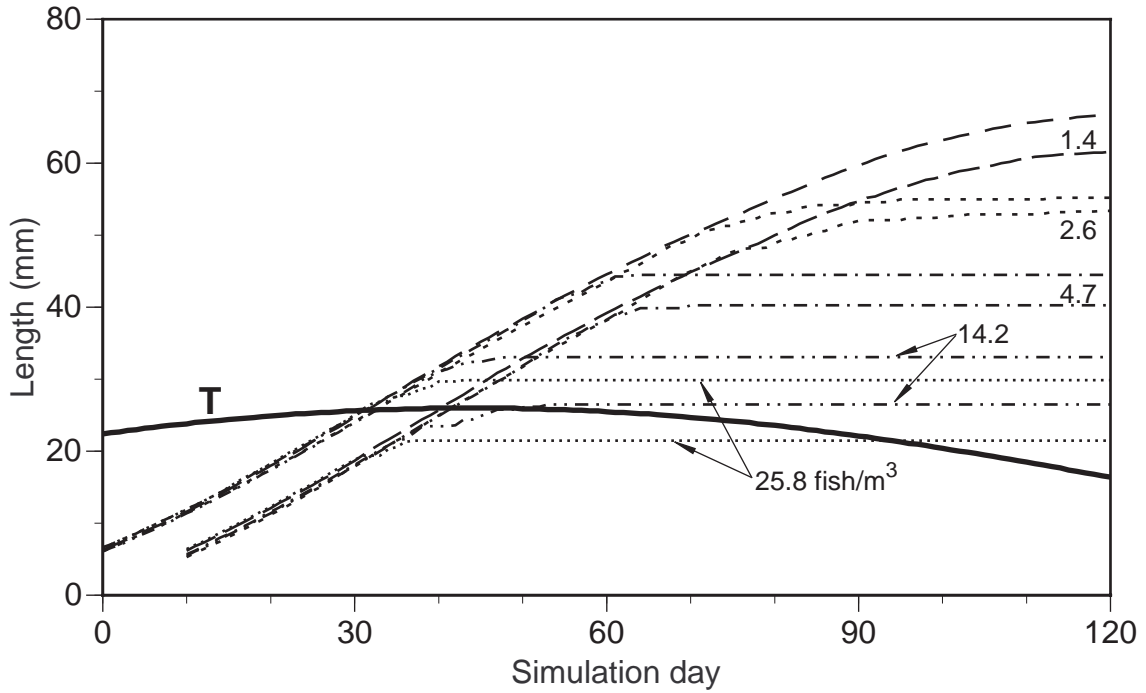
Figure 4.–Simulated growth of two individual age-0 bluegills, one from each natal cohort, at each of five densities. Starting lengths in the simulations were chosen randomly from a normal distribution with a mean of 6.0 mm and an SD of 0.5 mm. Growth during the first 30 d averaged 0.61 mm/d. The solid line indicates the water temperature (°C) from equation (4); temperature (T) has the same scale as length.
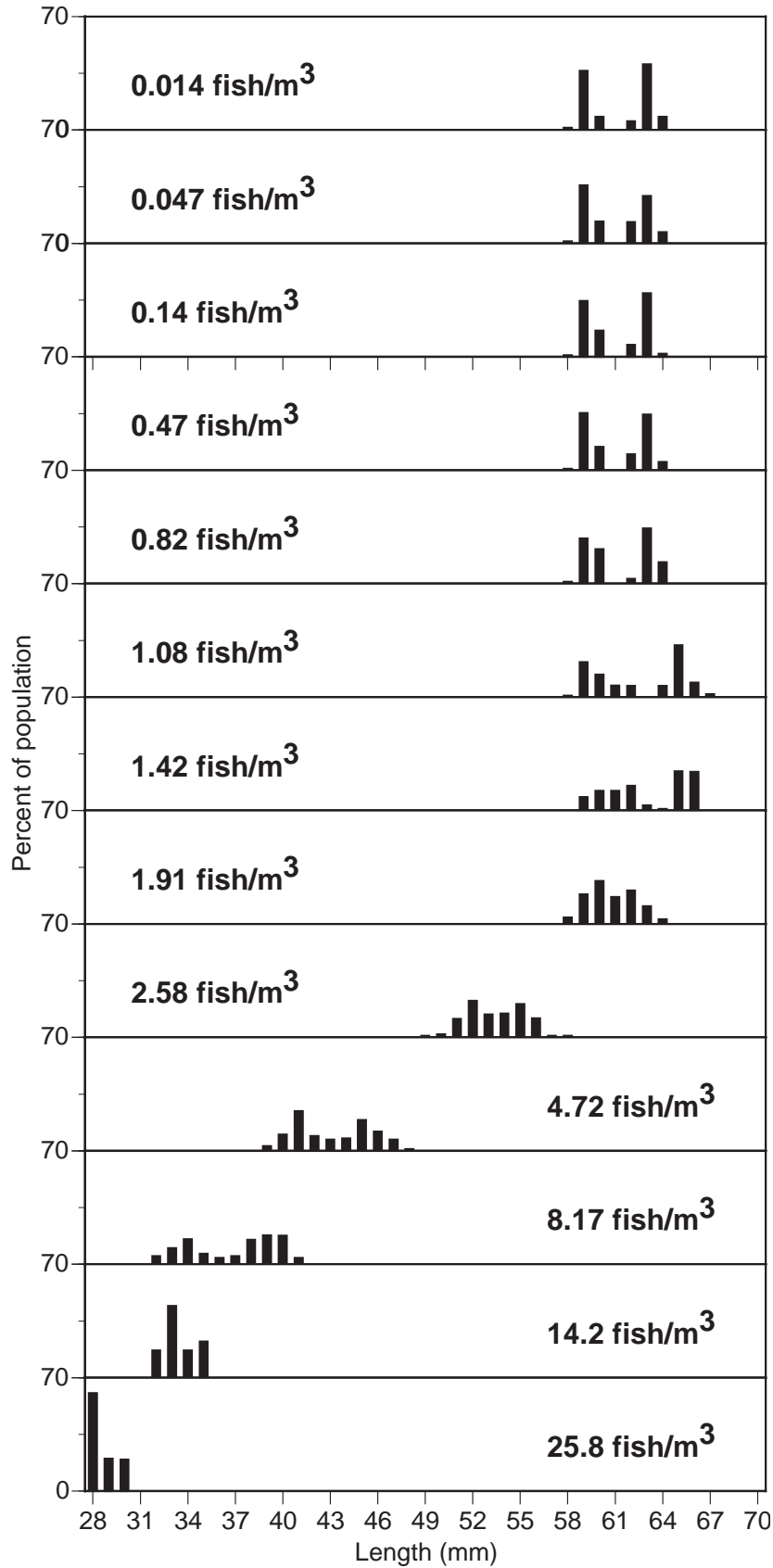
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Figure 5.–Size-frequency distributions of simulated age-0 bluegills after 120 d of growth, for different initial densities.
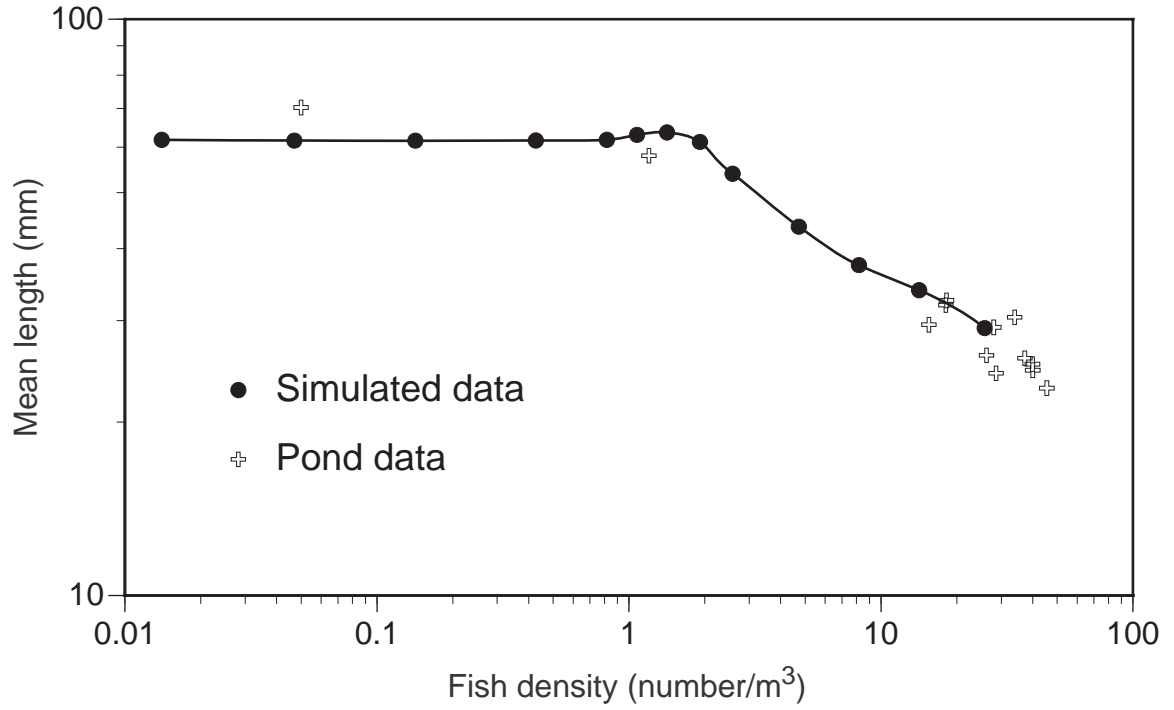
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Figure 6.–Density dependence of the final length of simulated age-0 bluegills compared with empirical lengths of pond bluegills measured by Latta and Merna (1977).

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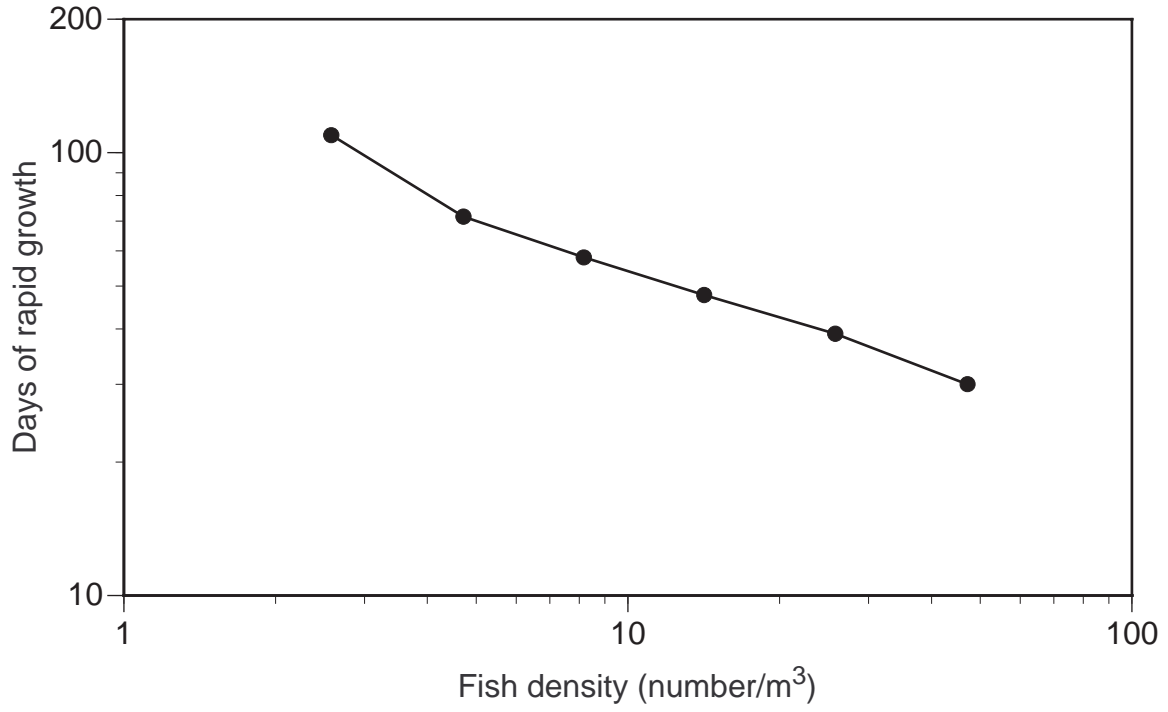
Figure 7.–Density dependence of the duration of the initial rapid-growth phase of simulated age-0 bluegills. The number of days of rapid growth is plotted against fish density.

Figure 8.–Simulated zooplankton densities in a pond containing age-0 bluegills at a density of 14.2 fish/m³, for fish consuming prey types in the proportions in which they are encountered (a), and for fish selecting among the prey types encountered to maximize the energy intake rate (b). The zooplankton sizes (mm) are indicated.

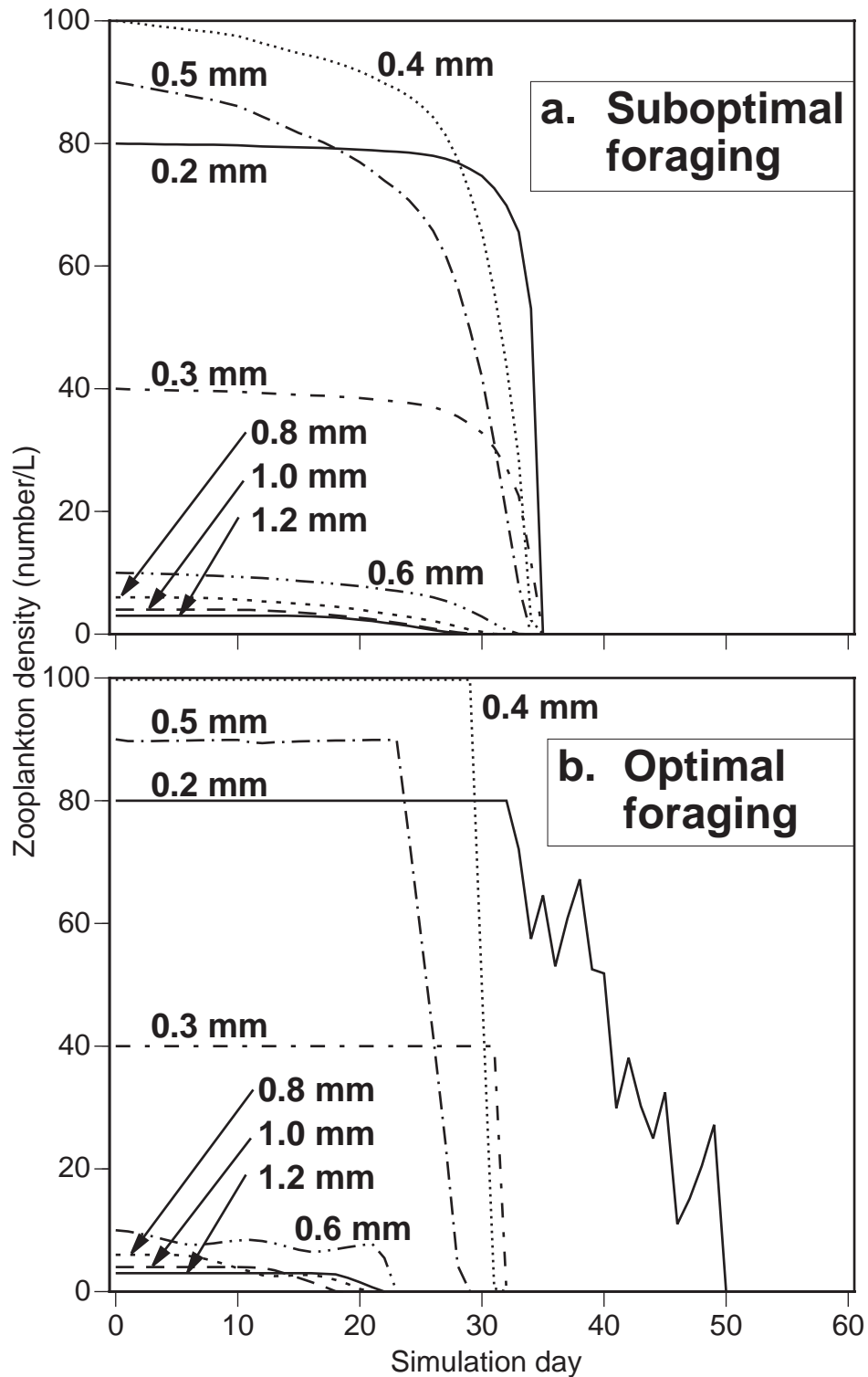Table 1.–Bioenergetics parameters for bluegill. Notation for the parameters follows Hewett and Johnson (1987).

Symbol	Description	Value
	Consumption (*C*)	
CA	Coefficient for maximum consumption, C_{max}, at 0°C[a]	0.273 $g \cdot g^{-1} \cdot d^{-1}$
CB	Exponent of weight for C_{max}	-0.274
CQ	Temperature dependence for C_{max}	2.3
CTO	Temperature at which consumption is maximum	31°C
CTM	High temperature at which consumption declines to 0	37°C
	Respiration (R_{S+A})	
RA	Coefficient for metabolism[b]	0.00272 $g\ O_2 \cdot g^{-1} \cdot d^{-1}$
RB	Exponent for effect of weight on metabolism	-0.269
RQ	Coefficient for effect of temperature on metabolism	0.0589 $(°C)^{-1}$
RTO	Coefficient for effect of swimming speed on metabolism	0.0562 s/cm
RTM	Coefficient for effect of temperature on swimming speed	0 $(°C)^{-1}$
RTL	Temperature above which RK1 and RK4 have effect	0°C
SS	Swimming speed[c]	1 BL/s
RK1	Coefficient for effect of weight on swimming speed[c]	4.201 cm/s
RK4	Exponent for effect of weight on swimming speed[c]	0.299
SDA	Coefficient for specific dynamic action	0.1531
	Egestion (*F*)	
FA	Fraction of consumed food egested	0.168
	Excretion (*U*)	
UA	Fraction of assimilated food excreted	0.0841
E_{BG}	Energy density of age-0 bluegill	2,300 J/g

[a] CA for age-0 bluegills was increased by a factor of 1.5 from the 0.182 estimated from data in McComish (1971) to 0.273.

[b] RA has been converted to $g\ O_2 \cdot g^{-1} \cdot d^{-1}$ from the units in the original reference.

[c] Specification of swimming speed, SS, with units BL/s, can replace Hewett and Johnson's (1987) RK1 and RK4; for the weight-length coefficients in Table 2, setting RK1 = 4.201 cm/s and RK4 = 0.299 is equivalent to specifying 1 BL/s.

Table 2.–Morphological parameters for young-of-the-year bluegills. (TL = total length, mm).

Variable	Equation	Reference
Wet weight (W, g)	$\log_{10} W = -5.430 + 3.345 \log_{10} TL$ for TL from 4.4 to 31.2 mm ($N = 141$, $r^2 = 0.99$)	This study
Dry weight (W_d, g)	$\log_{10} W_d = -6.279 + 3.426 \log_{10} TL$ for TL from 8.0 to 31.2 mm ($N = 136$, $r^2 = 0.99$)	This study
Standard weight (W_{std}, g)	$\log_{10} W_{std} = -5.374 + 3.316 \log_{10} TL$	Murphy et al. 1991
Standard length (SL, mm)	$SL = TL/1.278$	Beckman 1948
Gape (G, mm)	$G = 0.217 + 0.093\ SL$	Werner 1974

Table 3.–Final mean lengths of age-0 bluegills ($N = 100$) in simulations with and without optimal foraging, at different fish densities.

Fish density	Optimal foraging		Suboptimal foraging	
(number/m^3)	Length (mm)	SD (mm)	Length (mm)	SD (mm)
0.014	61.8	1.8	61.8	1.9
0.047	61.7	1.8	61.6	1.8
0.14	61.7	1.9	61.6	1.9
0.47	61.6	1.9	61.6	1.9
1.42	63.0	1.5	63.6	2.5
4.72	42.7	2.4	43.7	2.3
14.16	33.7	1.3	33.9	1.0
25.78	28.6	0.9	29.1	0.9

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