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SPORT FISH RESTORATION

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Abstract.-An individual-based model, LakeMod, was developed to synthesize information and to help answer questions raised in the management of freshwater fish communities, particularly ponds and lakes containing bluegills and largemouth bass or walleyes. The daily model accounts for size-specific interactions between predators and prey, selection among multiple prey types, energetics of growth, changes in body composition, and seasonal water temperature. Sources of fish mortality include predation, starvation, and other causes. Because of the importance of energy density to fish growth and survival, a new model has been developed for dynamic changes in energy density, body composition, and relative weight. This model explains the common observation that both percent lipid and energy density show a linear relationship with percent water, and also explains the difference in vulnerability to starvation among fish of different sizes. Because of the abundance of forage fish compared to their predators, each "individual" bluegill in the model represents many identical fish in a lake or pond, whereas each largemouth bass in the model may represents one or more fish in a pond. The model has been used to explain patterns in the density-dependent growth of bluegills and largemouth bass, and to examine predator-prey interactions. Simulations of pond experiments involving different densities of largemouth bass show that the numbers and mean lengths of surviving bluegills reflect size-dependent and density-dependent processes that are readily represented in an individual-based model. Simulations show the strong interactions between growth of forage fish and growth and survival of piscivores. Understanding these complex response patterns should improve the ability of fisheries managers to determine appropriate sizes and densities of predators and prey in warmwater fish communities.

Bluegills *Lepomis macrochirus* are of special interest to fisheries scientists because they are the ecologically dominant fish species in many Michigan warmwater lakes, often exceeding 50% of the total fish biomass (Schneider 1973a, 1981). They are of interest to fisheries managers because bluegills are among the most popular panfish for anglers.

Slow-growing bluegill populations are a common problem in southern Michigan lakes. Various management actions have been tried in an attempt to provide long-term improvements in growth and size structure of slow-growing populations. Such actions have included chemical treatment to remove juveniles, manual removal to thin the population, harvesting macrophytes to increase predation on juveniles, special regulations, and stocking of predators. In recent years there has been increased interest in managing warmwater lakes as entire fish communities, rather than on a species by species basis. To manage warmwater lakes most effectively, we need to understand interactions within the fish community.

One of the most important ecological interactions in fish communities is predation, including predation by piscivores on fish populations of interest, predation by fish populations on their various prey, and predation on conspecifics. There is more to learn about using predators in the management of prey populations. Using predators to reduce the density of juvenile bluegills would seem to be an effective way to improve bluegill growth, but determining the proper numbers and sizes of predators is not straightforward. The work of Swingle (1950), Jenkins (1979), Hackney (1979), Ney and Orth (1986), and others has demonstrated that both the density and size distribution of predators are important in maintaining good growth of predators and prey (Forsythe 1977; Forsythe and Wrenn 1979; Beyerle 1983). Lawrence (1958), Hambright (1991), Schneider and Breck (1996), and others have identified predator gape and prey body depth as critical limits for the predator-prey interaction. The size of prey selected by predators can have a strong effect on the size-specific survival of the prey (Schneider 1975; Swenson 1977; Popova 1978; Knight et al. 1984; Wahl and Stein 1988; Rice et al. 1993; Crowder et al. 1994; Rice et al. 1997).

Another important ecological interaction is competition, including competition with conspecifics and competition with other species. The growth of bluegill is density dependent due to intraspecific competition for food. The population dynamics of several centrarchid fish species are linked because of competition among the juveniles in the littoral zone (Mittelbach and Chesson 1987; Mittelbach and Osenberg 1992). Recent studies have shown that small juveniles of predators such as largemouth bass *Micropterus salmoides* compete with juvenile bluegills, complicating the interactions between populations of predators and prey (Olson et al. 1995; Olson 1996; Holt and Polis 1997). A fish community model can help explore the implications of these factors for the population and growth dynamics of predators and prey.

Individual-based models can help in understanding population dynamics and predator-prey interactions. In this relatively new modeling approach (Huston et al. 1988; DeAngelis and Gross 1992), many individuals are simulated, not just the average individual. The responses of the population are determined by combining the responses of many individuals, and these individuals can differ in size and other attributes, and some can experience conditions much different than average. This modeling approach is showing promise in fisheries biology and management (Madenjian 1991; Madenjian and Carpenter 1991; Trebitz 1991; Breck 1993a; Rose and Cowan 1993; additional papers accompanying Van Winkle et al. 1993; Beyer and Lassen 1994; Crowder et al. 1994; Cowan et al. 1996; Letcher et al. 1996b; Rice et al. 1997; Wang et al. 1997; Ridgway and Shuter 1997; Fryxell and Lundberg 1998). Rykiel (1996) and others have discussed validation of ecological models, and Bart (1995) proposed acceptance criteria for use of individual-based models in management.

A model of fish community dynamics in freshwater lakes should account for major processes, including predation, competition, individual growth and reproduction. These processes are typically density-dependent, strongly size-dependent, and vary with water temperature. Predation is especially size-dependent, including forage fish preying on invertebrates and piscivores feeding on forage fish (Werner 1974, 1977; Breck 1993b). Individual-based models can readily incorporate size-, density- and temperature-dependent processes, and this suggests that such models can be helpful in understanding the complex interactions in fish communities of ponds and lakes.

Many individual-based fish models published to date have used fixed patterns of mortality due to piscivores or fixed growth patterns of prey (Madenjian 1991; Madenjian and Carpenter 1991; but see Trebitz 1991). Several recent fish models have used dynamically changing densities of multiple prey types (Breck 1993a and other papers discussed by Van Winkle et al. 1993). Few individual-based models have been developed that combine dynamic invertebrate prey, dynamic forage fish, and dynamic predators. This is the approach used in this study.

The purpose of this study is to synthesize information about warmwater fish communities to better understand the processes affecting the dynamics of fish numbers and biomass. The approach is to develop an individual-based model for explaining patters in the growth and survival of bluegills in lakes and ponds containing various densities of competitors and predators such as largemouth bass. The model is intended to describe and help understand the critical factors determining the size-frequency distributions, relative abundance, growth, and survival of important fish species in warmwater lakes and ponds. The goal is to improve the management of fish communities by understanding the likely responses to alternative management actions.

Model Rationale and Description

The computer model used in this study is named LakeMod. It is a modification of the model described fully in Breck (1993a). LakeMod is coded in object-oriented Pascal, using Borland® Delphi™ for Windows, and runs on a microcomputer.

The model is intended to describe growth and survival of interacting fish species during a growing season, not the long-term dynamics of fish populations. The model is intended to be used to examine factors influencing growth, survival, and condition of warmwater fishes, and to gain insight into the ecological factors of most importance and the management actions most likely to influence fish abundance and size structure in bluegill populations.

The model represents multiple fish populations in a lake or pond (Figure 1). There are three trophic levels. The top level is composed of piscivores, such as largemouth bass, walleye *Stizostedion vitreum*, or northern pike *Esox lucius*. The middle trophic level contains the fish species of primary interest, the bluegill. This middle trophic level can also contain competitors of bluegill, such as pumpkinseed *Lepomis gibbosus* or yellow perch *Perca flavescens*. The lowest trophic level in this model contains several invertebrate prey types, which occur in specific habitats in the littoral and pelagic zones.

The distinction between pelagic and littoral zones is ecologically important because juvenile fishes of many species, including bluegill, are generally restricted to the vegetated littoral zone by the presence of piscivores until they reach a size too big for most predators (Werner et al. 1983a; Werner and Gilliam 1984; Mittelbach 1986). For bluegill this size is about 96 mm total length (75 mm standard length; Mittelbach and Chesson 1979). This restriction of juveniles to the littoral zone means that adult bluegills have access to resources not available to juveniles – pelagic zooplankton (Mittelbach and Osenberg 1992; Osenberg et al. 1993) and sublittoral benthic prey. Thus in lakes with pelagic zooplankton and with juveniles restricted to a refuge in the vegetation, growth and survival rates of adult bluegill can vary independently of the growth and survival rates of juvenile bluegill (Mittelbach and Chesson 1979; Mittelbach and Osenberg 1992; Osenberg et al. 1993).

For pumpkinseeds, the superior shell-crushing ability of adults means that they have access to a resource not available to juveniles or bluegills – larger snails (Mittelbach 1984). Thus the growth and survival rates of adult pumpkinseed can vary independently of the growth and survival rates of juvenile pumpkinseed. But the population dynamics of pumpkinseed and bluegill are linked because of the competition among juveniles of both species that occurs in the littoral zone (Mittelbach 1986; Osenberg et al. 1993).

Model structure

Figure 2 shows a flow chart with the processes included in LakeMod. The model is designed so that multiple runs can be set up at one time. For example, successive simulations can evaluate different stocking densities of predators. Output from each run is stored on computer disk for analysis.

For each simulation, the model executes for a specified number of simulated days. On each day, the model computes water temperature and day length, and then calculates the daily increments of change in the state variables for each individual fish of each species and for each prey type. After the increments have been computed for all fish and all prey, then all state variables are updated using the calculated increments, and the daily reports are printed to disk and to screen windows. After the last day, final reports are printed and the program loops to begin the next run.

Prey types

Simulation of a warmwater lake will typically include three types of prey habitats in the littoral zone and two types in the pelagic zone (Figure 1, Tables 1 and 2). In the littoral zone, prey can be found in the water column (primarily crustacean zooplankton, such as *Daphnia* and *Bosmina*), in vegetation (epiphytic prey such as damselflies and amphipods), and in or on the sediment (benthic prey such as midge larvae) (Mittelbach 1981). In the pelagic zone, water-column prey are also predominantly crustacean zooplankton, often including larger sizes of *Daphnia* than usually occur in the littoral zone. Benthic prey occur in the sediment below the pelagic zone, though not in areas devoid of oxygen. The number of foraging habitats in the model can be changed to represent different lakes or ponds; the pelagic habitats may be missing in small ponds or shallow lakes.

In this model, each habitat contains prey of different sizes (Tables 1 and 2). The size-structure of prey populations, especially zooplankton, generally reflects the intensity of fish predation and can be related to patterns of bluegill growth (Theiling 1991). The purpose of multiple habitats and prey sizes is, first, to enable model behavior to include fish's diet shifts to less-preferred prey and foraging shifts to less profitable habitats that occur as the growing season progresses (Werner and Hall 1979; Mittelbach 1981; Werner et al. 1983b; Werner and Gilliam 1984). The second purpose is to incorporate a mechanism allowing late-season slow-down in fish growth rate, especially for age-0 bluegills, without causing elimination of all prey followed by mass starvation of predators (Breck 1993a).

The size categories of prey are fixed (Tables 1 and 2). The energy densities were assigned to be representative of the general prey type (550 cal/g for littoral and pelagic zooplankton, 600 cal/g for littoral benthic prey, 800 cal/g for vegetation prey, 850 cal/g for sublittoral benthic prey; Breck 1993a). Numerical density (number/m^3 for zooplankton or vegetation prey, number/m^2 for benthic prey) is the single state variable for each prey type. Invertebrate prey grow according to a discrete logistic equation, subject to mortality due to fish predation.

$$N_{t+1} = N_t + r N_t \left(1 - \frac{N_t}{K} \right) - M_t \,,$$

where N_t is the prey density of a given size and type of prey on day t (number/m^3 or number/m^2), r is the intrinsic rate of natural increase for that prey (d^{-1}), K is the carrying capacity for that prey (number/m^3 or number/m^2), and M_t is the total number/m^3 or number/m^2 of prey of that size and type consumed by all fish on day t. The intrinsic rate of natural increase for a particular prey type is size dependent (see Breck 1993a). The carrying capacity for each size prey can be adjusted by specifying a multiplier for the relative K values in Tables 1 and 2.

The width of each prey type is used to determine if the prey can be ingested by fish with a given gape. Prey maximum body width is set at a constant fraction of prey length; this fraction is assumed to be 0.70 for zooplankton, 0.18 for benthos, and 0.30 for vegetation prey.

Fish populations

A population of each fish species is composed of multiple "individuals" in each of several age classes (Figure 1). Each modeled "individual" represents a certain number of identical fish in the lake or pond. As mortality occurs, each modeled "individual" represents fewer and fewer fish. There may be 200 or more model individuals per fish species. Because year-class strength may be set in the early years of life, it is usual to have larger numbers of model individuals for the younger age classes and fewer numbers of model individuals for the older age classes in a population.

Each modeled "individual" fish has three state variables: L (total length, mm), W (wet weight, g), and N (the number of identical fish in the lake currently represented by a given model individual). For each individual on each day, the model executes procedures (or subroutines) to forage (selecting the prey habitat with the highest energetic reward), metabolize energy (using a bioenergetics model to compute net energy intake), grow (allocating energy to body structure and body reserves), and die (see description of fish mortality, below).

The following sections will describe how LakeMod implements the processes of foraging, metabolism, energy allocation, and mortality.

Fish Foraging

Foraging by planktivores in LakeMod uses encounter rates that depend on prey size, planktivore swimming speed and visual acuity (Breck 1993a). Encounter rate for each prey size is a product of prey density and fish search volume. Search volume is assumed to be a cylinder with a radius equal to the reactive distance for that prey size, and a length equal to the distance that the fish could swim during daylight (Breck 1993a). Encounter volume increases with fish size because of improvements in visual acuity and because of increased swimming speed.

Foraging theory has been well developed for planktivorous fish, but is much less developed for piscivores (Werner and Mittelbach 1981; Crow 1982; Breck 1993b). For planktivores, optimal prey size is typically determined by the maximum ratio of E/H, where E is energy per item, and H is handling time given attack. This type of analysis has been done for piscivores (e.g., Hoyle and Keast 1987). For piscivores, however, a growing body of evidence is suggesting that this ratio needs to be multiplied by the probability of capture given encounter (Crow 1982; Folkvord and Hunter 1986; Breck 1993b; Rice et al. 1993; Crowder et al. 1994). Quantification of the size preference of predators of bluegills, such as largemouth bass, should enable better estimation of the size distribution of predators required to achieve a desired change in bluegill sizes and densities (Hoyle and Keast 1987).

The general approach used for piscivore foraging in LakeMod is similar to that used for planktivore foraging. I assumed that prey fish were encountered by piscivores in proportion to prey fish density and the relative volume of water searched. For each modeled prey individual, relative search volume was computed from the square of prey length, predator swimming speed, and a factor for relative encounter rate, which incorporates effects due to piscivore visual acuity and the probability of capture given encounter.

The maximum size of prey fish ingested by piscivores is determined by piscivore gape and the maximum body depth of the forage fish. I fit an equation to the data of Lawrence (1958), who measured the gape (G, mm) of largemouth bass:

$$G = 3.209 + 0.05155L + 1.593 \cdot 10^{-4} L^2 ,$$

where L is bass total length (mm), $N = 23$, $r^2 = 0.999$. The equation for maximum body depth (D, mm) of bluegills is from Breck and Schneider (1996):

$$\log_{10} D = -0.863 + 1.190 \log_{10} L ,$$

where $N = 416$, $r^2 = 0.997$, for bluegill L ranging from 18.5 to 220 mm. Maximum body depth of largemouth bass was estimated as 27.3% of length.

For each modeled piscivore, the number of forage fish encountered and ingested is calculated. The calculation starts with the forage density represented by the largest modeled forage fish and ends with the smallest forage fish, thus giving a preference to larger prey. The calculation ends if the maximum daily ration is attained. After going through the list of forage fish, piscivores next go through the list of smaller conspecifics, so cannibalism is possible for model piscivores. If less than 80% of a full daily ration has been obtained, then the model piscivores forage for invertebrate prey.

Metabolism

A bioenergetics model (Hewett and Johnson 1992; Breck 1993a) is used to determine net energy intake based on current weight, water temperature, and the energy value of ingested prey. The model accounts for maximum daily ration, egestion, excretion, activity-dependent respiration, and specific dynamic action. After accounting for energy losses and expenditures, the model calculates the net energy gained that is available for growth in length or condition, as discussed in the next section. The bioenergetics parameters for bluegill (Breck 1993a) were estimated considering information from several sources (Wohlschlag and Juliano 1959; Brett and Sutherland 1965; O'Hara 1968; Savitz 1971; Schneider 1973b; McComish 1971; Elliott and Davison 1975; Kitchell et al. 1977; Breck and Kitchell 1979; Rice et al. 1983; Evans 1984; Shepard 1988; West et al. 1997).

Body Composition, Energy Density, Relative Weight, and Energy Allocation

Background and rationale.–This section begins with a rationale for including a model of energy density in a fish community model. Then a new model is developed that allows dynamic changes in fish energy density, body composition, and relative weight with changes in food availability. This model is an extension of the recent work by Broekhuizen et al. (1994) on compensatory growth in salmonids.

Energy density of a fish and its prey are very important factors influencing the dynamics of fish growth. Energy density is measured in kcal/g or kJ/g (1 joule = 4.185 calories), usually on a wet weight basis. For bioenergetics models of fish growth, sensitivity analysis suggests that energy density of the fish and its prey are among the most influential factors affecting predicted consumption and growth. Although energy density of fish and prey were not explicitly included in the sensitivity analyses of Kitchell et al. (1977) or Bartell et al. (1986), those analyses indicated that factors proportional to consumption (like energy value of food) have the greatest influence on predicted fish growth.

To demonstrate the influence of energy density on predicted fish growth, I did two sets of simulations using the bioenergetics model for largemouth bass of Hewett and Johnson (1992). In the first set of runs, I varied prey energy density from 1.0 to 1.8 kcal/g of prey. This represents a range of prey types from large invertebrates and small juvenile fish to adult forage fish. Other input values were held constant among runs: initial bass weight = 100 g, bass energy density = 1.4 kcal/g (Niimi 1972), temperature = 26°C, and daily ration = 2% body weight/d for 60 d. Figure 3 shows the dramatic effect of prey energy density on the amount of weight gained in 60 d. Even though the daily ration was the same in terms of weight of food consumed (2% body weight/d), prey with an energy density of 1.0 kcal/g caused bass to lose about 5 g in 60 d, whereas prey with an energy density of 1.8 kcal/g caused bass to gain about 60 g.

In a second set of runs, I held prey energy density constant at 1.4 kcal/g and varied energy density of largemouth bass from 1.0 to 1.8 kcal/g (Figure 4). This represents a range from juvenile bass to lipid-rich adult bass. Other input values were the same as before. It requires more energy to add a g of energy-rich tissue than to add a g of energy-poor tissue. A fish with an energy density of 1.8 kcal/g requires 1.8 kcal of energy to add 1 g body weight; a fish with an energy density of 1.0 kcal/g requires 1.0 kcal of energy to add 1 g body weight. If both fish receive meals resulting in a net gain of 1.4 kcal, then the fish with the higher energy density will add fewer g body weight. So, if energy density of the fish does not change, then, everything else being equal, fish with a higher energy density will grow more slowly. Figure 4 shows that simulated growth of largemouth bass decreases with increasing bass energy density. Fish with an energy density of 1.0 kcal/g gained about 37 g in 60 d, whereas fish with an energy density of 1.8 kcal/g gained only 18 g. These two sets of simulations show that energy density of prey and fish can have a great influence on fish growth.

Fish energy density can influence survival and reproduction as well as growth. Energy level in late fall can affect over-winter survival (Oliver et al. 1979; Shuter et al. 1980; Thompson et al. 1991). Energy level at the end of winter may influence the timing of reproduction. Cargnelli and Gross (1997) have shown that larger male bluegills emerge from winter in better condition, with higher levels of lipid than smaller males. They suggest that this may explain why larger individuals of both sexes tend to breed earlier than smaller individuals in several sunfish species (Ridgeway et al. 1991; Danylchuck and Fox 1994). In some fish species, adults may skip one or more years of reproduction in order to attain sufficient energy reserves (e.g., Arctic charr, Dutil 1986; sturgeon, Doroshov 1985).

Fish energy density changes in response to recent feeding history. Energy density declines during starvation (Savitz 1971; Niimi 1972; Elliott 1976), including starvation over winter (Oliver et al. 1979), and increases as daily ration increases (Brett et al. 1969; Niimi and Beamish 1974; Elliott 1976; Weatherley and Gill 1983; Brown and Murphy 1991; Tyler and Dunn 1976; Heidinger and Crawford 1977). Energy density of yellow perch was observed to increase following a reduction in density of competing white sucker *Catostomus commersoni*, which apparently made more food available to yellow perch (Hayes and Taylor 1994). Because energy density is so closely linked to growth, changes in the amount of food should lead to changes in the growth response.

Ontogenetic changes in body composition are commonly observed. Fish larvae tend to have higher water content than juveniles and adults (Tarby 1977; Henderson and Ward 1978; Machiels and Henken 1986). Ash content is higher in larger fish (McComish 1974; Niimi 1974; Focken and Becker 1993) For many species, percent lipid tends to increase with body size (Elliott 1976; Rottiers and Tucker 1982; Van Pelt et al. 1997; but see Craig 1977). Because energy density is so closely linked to growth, changes in nominal energy density across life stages should lead to ontogenetic differences in the growth response.

In a fish community model with interacting predators and prey, food availability to fish changes through time. This suggests the need for a model to predict changes in fish energy density in response to food availability and metabolic demands.

Energy density reflects proximate body composition in terms of lipid, protein, carbohydrate, ash, and water. Assuming that lipid level has been measured using appropriate methods (Randall et al. 1991), energy density can be calculated using standard values for the energy value of lipid, protein, and carbohydrate (Elliott 1976; Brett and Groves 1979). The amount of carbohydrate in fish is usually negligible (less than 0.06%; Craig et al. 1978). Brett and Groves (1979) recommend a value of 9.45 kcal/g for typical fish lipid. The recommended energy value of fish protein as measured by bomb calorimetry is 5.65 kcal/g protein, but the metabolizable energy value of protein to fish is only 4.80 kcal/g protein, because most fishes break down protein to ammonia as a nitrogenous waste, so not as much energy is obtained as when the protein is completely oxidized in a bomb calorimeter (Brett and Groves 1979). A model for fish energy density should be consistent with observed patterns in body composition.

Various approaches to specifying energy density of fish and prey have been used in typical applications of bioenergetics models, in which the pattern of fish growth through time is known in advance and the models are used to calculate fish consumption of prey. For example, the bioenergetics models of Kitchell et al. (1977), Stewart et al. (1983; Stewart and Ibarra 1991), Rice et al. (1983), and Hewett and Johnson (1992) predict consumption for a single population at a time, given initial and final fish sizes. For each group of fish modeled, the energy density is assumed to be constant through the year (Kitchell et al. 1977), or changing as a function of fish body size (Stewart et al. 1983), or changing seasonally in a specified and predetermined pattern (Hewett and Johnson 1992). However, these approaches are less applicable in dynamic models of predators and prey, because prey density can vary during simulation runs and from run to run, so the seasonal pattern of predator ration – which affects energy density and growth – is not known in advance.

It would be useful for a fish community model to be able to compute body condition or relative weight of predators and prey so that the model could be used to determine expected responses under alternative scenarios (Rice et al. 1983; From and Rasmussen 1984; Van Winkle et al. 1997). Examination of the average body condition of predators and prey has been proposed as a means of assessing the predator-prey status of lakes and ponds (Wege and

Anderson 1978; Anderson and Gutreuter 1983; Murphy et al. 1991; Liao et al. 1995). Relative weight (or condition factor) is positively correlated with energy density (Brown and Murphy 1991; Jonas et al. 1996) and growth (Willis et al. 1991), and negatively correlated with percent water (McComish 1974). In order for a model to make predictions about body condition (or relative weight) of predators and prey, the model must relate relative weight to some dynamic variable, such as energy density.

In summary, there are several reasons why a fish community model with predators and prey should include a model for dynamic changes in energy density, body composition, and relative weight. First, predicted growth is very sensitive to energy density of fish and their food, as shown in the bioenergetic runs. Second, energy reserves influence survival and reproduction. Third, energy density can change in response to recent feeding history. Fourth, energy density changes with ontogeny. Fifth, a fixed pattern of energy density would not be appropriate for a model in which food availability can change dynamically. Sixth, relating energy density and body composition to relative weight would enable the model to be used to determine expected responses in relative weight to alternative scenarios.

Body composition.–A new model was developed for simulating dynamic changes in body composition and energy density during starvation and growth. The approach is briefly summarized here and the equations are derived in Appendix 1. This model for energy density can explain two common observations related to body composition of fish during starvation and growth: (1) there is a linear relationship between percent lipid and percent water, and (2) there is a linear relationship between energy density and percent water. Using only two state variables, the model predicts changes in wet weight, relative weight, body composition (lipid, protein, ash, water) and energy density based on the net energy obtained each day during growth, or the net energy used each day during starvation.

The model for changes in energy density has three assumptions. First, assume that during starvation a constant fraction (s) of required energy comes from stored lipid and the rest ($1-s$) comes from stored protein. Niimi (1972) and others have shown that during starvation, fish use energy from both lipid and protein, and Niimi estimated that s was approximately 0.6 for starving largemouth bass, and a similar value (0.61) can be estimated for bluegill from the data in Savitz (1971). Second, assume that there is a fixed amount of water (z) associated with each g of lipid, and a fixed amount of water (y) associated with each g of protein. Gerking (1955, citing Newburgh et al. 1945) notes that about 0.1 gram of water is associated with a gram of lipid (z is about 0.1), and about 3 grams of water are associated with a gram of protein (y is about 3). Jobling (1994, p. 147) notes that deposition of 1 g lipid “leads to a weight increase of 1 g,” suggesting that very little water is added and that z must be much smaller than 1 (or perhaps $z = 0$), whereas deposition of 1 g protein “leads to the deposition of 3-4 g water,” suggesting that y is about 3-4. Third, assume that the amount of ash does not change during starvation. Then, based on the known energy densities of lipid and protein and the assumptions that s, z, and y are constant, one can use the daily energy expenditure to compute the change in body composition (lipid, protein, water, ash), energy density (kcal/g), and relative weight (see Appendix 1 for details).

During the initial period of starvation, a fish’s loss of weight and stored energy may be relatively rapid. But after some period of starvation, fish metabolic rate decreases, slowing the rate of loss in body energy and weight. Following the approach of Broekhuizen et al. (1994), I assume that when body reserves decrease to some threshold (0.75 of the nominal level), the fish enters a “hungry” state, in which maximum daily ration increases by a factor of 2.0 (Hayward et al. 1997) and swimming speed increases by a factor of 1.5 above nominal levels (see Madon and Culver 1993). After a further decrease in reserves to a level of 0.10 of the nominal level, the fish enters a “torpid” state, in which the nominal value of metabolic rate is modified by a factor of 0.3, maximum daily ration by a factor of 0.8, and swimming speed by a factor of 0.5. As the fish starves, body composition changes as the fish depletes lipid and protein to meet metabolic demands (ash is constant). An example of a fish starving according to model assumptions is shown in Figures 5 and 6. The rate changes on d 9 are due to the fish becoming torpid and reducing metabolic rate. The differences in the loss rates of lipid, protein, and water are due to differences in rate of depletion of these body components as determined by *s*, *z*, and *y*.

This example shows that even though there is a decrease in total weight, lipid and body water (Figure 5), there is an increase in percent water (Figure 6), because body water decreases more slowly than total weight. It is difficult to compare the absolute weight of body components (fat, protein, water, ash) among individuals that differ in weight. For this reason, body composition is generally reported as percent of wet or dry weight. But this can lead to confusion. During starvation, percent lipid decreases and percent water increases (e.g., Niimi 1972) (Figure 6). But this is *not* due to water replacing lipid, as has sometimes been said. In starving fish, the nearly universal observation is that the weight of lipid, protein, and water all decrease (the amount of ash remains approximately constant) (Figure 5). Lipid decreases at the fastest rate, protein decreases more slowly, and water decreases even more slowly. In almost all cases, the fish loses total body weight faster than it loses water. When body components are compared as a percent of body weight, percent water *increases* even though the amount of water is decreasing. So during starvation, percent lipid decreases, percent protein may change only modestly, percent ash increases, and percent water increases even though the amounts of all components (except ash) are decreasing.

One consequence of the three assumptions above is that starving fish will have a negative linear relationship between percent lipid and percent water, and also between energy density and percent water. The equations for these relationships are completely specified by *s*, *z*, and *y*, the known energy densities of lipid and protein, and reference levels of percent lipid (or energy density) and percent water (see Appendix 1). This appears to be the first time that such assumptions have been used to quantitatively explain these two common observations.

In the body composition of fishes, levels of lipid, water, and energy density are highly correlated. Both lipid level and energy density have a strong negative correlation with percent water (Brett et al. 1969; Elliott 1976; Craig 1977; Rottiers and Tucker 1982; Machiels and Henken 1986, 1987; Thompson et al. 1991; Murphy and Brown 1991; Hartman and Brandt 1995; Van Pelt et al. 1997). These observations are not only for starvation conditions, but also include situations where fish are growing.

Growth is not just anti-starvation. The situation is complicated by the fact that fish not only gain energy and weight, but also increase in length. A full analysis of energy dynamics must account for the allocation of energy to increasing in length as well as adding to stored energy reserves.

Energy allocation.–The new model for energy allocation used in these simulations is an extension of the model by Broekhuizen et al. (1994), who modeled compensatory growth of salmonids. The first addition to their model allows prediction of dynamic changes in body composition (lipid, protein, water, ash), not just total weight. The second addition allows simulations of the total range of fish sizes (larvae to adults), not just large juveniles and adults. The model is described in detail in Appendix 1 and is briefly summarized here.

There are three main assumptions for this model of energy allocation; the first two assumptions were also made by Broekhuizen et al. (1994). The first is that a fish's body tissues can be categorized as either structural or reserve tissues. The usefulness of this assumption has been demonstrated by Gurney et al. (1990), Kooijman (1993), and Broekhuizen et al. (1994). Reserve tissues are those that can be mobilized and depleted during starvation. These include nonpolar lipids (e.g., triacylglycerols), protein reserves, and associated water. Structural tissues are not mobilized, and so do not decrease during starvation. Structural tissues include structural protein, ash (associated primarily with skeleton and scales), and associated water. Structural tissues could also include polar phospholipids associated with cell membranes. The amount of structural tissues determine fish length; increases in structural tissues mean increases in length.

The second model assumption involves allocation of net energy intake. Net energy intake is the difference between total ingested energy and total energy losses and expenditures. Energy losses and expenditures are estimated using a bioenergetics model (Hewett and Johnson 1992; Breck 1993a). The second assumption is that the current ratio of reserve to structural energy (r) determines how net energy intake is allocated between reserve and structural tissues (Figure 7). When reserve energy is high relative to structural energy, then a large fraction of net energy intake is allocated to increasing body structure – growing in length; the rest is allocated to increasing reserve energy. Conversely, when reserve energy is low relative to structural energy, then a large fraction of net energy intake is allocated to increasing reserve tissue. As explained in Appendix 1, the energy allocation relationship (Figure 7) is specified so that when r is at its nominal value (r_0), then both reserve and structure increase in such a manner that the ratio r remains the same.

The third model assumption is that the nominal ratio of reserve to structural energy (r_0) increases with fish length. This assumption is required to account for the large differences observed in body composition as fish increase in length. Larval fish tend to have very little ash or lipid, and a relatively high percentage water (80-90%). They have a relatively low energy density and are vulnerable to starvation (Letcher et al. 1996a). Compared to larvae and juveniles, adult fish tend to have much greater lipid levels, more ash, a lower percentage water (about 75%), a higher energy density, and they are much less vulnerable to starvation (McComish 1974; Niimi 1974, Love 1980; Focken and Becker 1993). Figure 8 shows the proposed relationship between the nominal ratio of reserve to structural energy (r_0) and bluegill length.

The differences in nominal body composition with fish size produce differences in the expected relationship between percent lipid and percent water. Both the slope and intercept are expected to change with body size (Figure 9).

This new approach to modeling body composition, energy density, and relative weight, allows the simulations to account for widely observed patterns that have a potentially large influence on fish growth and survival. This approach may be especially influential in an individual-based model, because it provides a mechanism by which individual differences in foraging experience (energy intake) can produce differences in growth and survival compared to the cohort average.

Fish mortality

Death can occur in the model in three ways: (1) by predation; (2) by starvation, when body reserves are completely depleted; or (3) by an additional “natural” factor that has a constant daily probability of death. The background “natural” mortality rate (i.e., in addition to predation and possible starvation) is implemented as a daily probability of survival. The daily probability of dying from “natural” causes (p_n) is computed as

$$p_n = 1 - (1 - A)^{1/365},$$

where A is the fraction of the population dying from “natural” causes each year. Each simulated “individual” represents N_t identical fish in the lake or pond at time t. For each simulated “individual” the daily number of fish dying from “natural” causes (N_n) is a random number chosen from a binomial distribution with parameters p_n and N_t using the algorithm of Press et al. (1986).

For each simulated “individual,” the number of identical fish represented as surviving to the next day (N_{t+1}) accounts for losses to predation (N_p), starvation (N_s), and “natural” causes (N_n):

$$N_{t+1} = N_t - N_p - N_s - N_n .$$

Bluegill Reproduction

Because the focus of the present version of the model is on fish growth and survival within a year, fish reproduction has been implemented only as a constant annual number of recruits. In order to make model projections over several years, or to examine long-term population dynamics, there are several details of bluegill reproduction that should be incorporated. These include the effect of male and female body size and condition on readiness to begin nesting (Ridgway et al. 1991; Danylchuk and Fox 1994;

Cargnelli and Gross 1997; Bohlin et al. 1994), size-dependent spawning and nesting success of male bluegills (Gross 1982, 1984; Jennings et al. 1997), the effect of water temperature on probability of nest desertion (Claussen 1991) and rate of development of eggs and fry (Beard 1982), the effect of female size on fecundity (Ulrey et al. 1938; Mayhew 1956; Latta and Merna 1976; Breck 1996), the effect of food availability on female body condition and fecundity (Scott 1962; Hester 1964; Baganal 1969; Wooton 1973, 1977; FitzGerald and Keenleyside 1978; Kuznetzov and Khalitov 1978; Dahlgren 1979; Deacon and Keast 1987; Breck 1996), the vulnerability of nesting males to angling (Philipp et al. 1997; Ridgway and Shuter 1997; Beard et al. 1997), movement of fry between littoral and pelagic habitats (Werner 1967, 1969), and the effect of cannibalism by juvenile bluegills on number of fry surviving to age 1 (Clark and Lockwood 1990; Breck 1996).

Model Applications

Application to pond experiment of Howick et al.

In this application, initial conditions of the model were set to simulate the experiment of Howick et al. (1993). These investigators evaluated the effects of stocking different numbers of fingerling largemouth bass on the growth and survival of bluegills and bass in 0.04-ha earthen ponds containing high densities of macrophytes. Adult bluegills were stocked in April, and age-0 bluegills were present after spawning occurred in late May. Fingerling largemouth bass were stocked in April at 0, 10, 20, 40, and 80 individuals per pond in duplicate ponds. The ponds were drained in December and the fish were recovered and measured.

Because of the many macrophytes in the ponds of Howick et al. (1993), epiphytic prey types were added to the model of Breck (1993a), making three types of prey: littoral zooplankton, benthic invertebrates (primarily dipteran midge larvae), and epiphytic prey (“vegetation prey”, primarily damselfly naiads, Mittelbach 1981). I assumed there was no pelagic zone in such small ponds. There were eight size classes of each prey type (Table 1). The initial densities of zooplankton and benthic invertebrate prey types were modified from values in Breck (1993a) by decreasing the density of the larger prey sizes (to slow fish growth) and increasing the density of the smaller sizes (to reduce fish starvation).

Total pond volume was set at 400 m^3, with 100 m^3 as zooplankton habitat and 300 m^3 of vegetation containing epiphytic invertebrates. The pond was assumed to be 1 m deep, with 400 m^2 of sediment for the benthic invertebrates. Water temperature was assumed to follow an annual sine curve which has a maximum temperature of 28°C on d 200 (July 19) and a low of 0°C, but the curve was truncated at a minimum temperature of 3°C.

Howick et al. (1993) stocked fingerling largemouth bass into duplicate ponds, using 0, 10, 20, 40, and 80 bass per pond. Simulations of this experiment using LakeMod involved stocking 0, 1, 2, 3, 5, 10, 20, 40, 60, and 80 individual largemouth bass (L = 115±4 mm) into replicate 0.04-ha ponds (N = 3 per stocking density) containing 16-mm bluegill. The total number of simulated bluegills was 16,000 per pond, represented by 200 model “individuals,” each initially representing 80 identical fish in the pond. To represent spawning bouts every 10 d (Claussen 1991), 4,000 age-0 bluegills (50 “individuals”) became available to bass on days 0, 10, 20, and 30 of the 175-d simulation. The background “natural” mortality rate (i.e., in addition to predation and possible starvation) was assumed to be 33% per year, implemented as a daily probability of survival.

Starvation of simulated fish is assumed to occur when an individual’s reserve tissue is depleted (see Appendix 1). The bioenergetics parameters for largemouth bass follow Rice et al. (1983) and those for bluegill follow Breck (1993a), with the modifications discussed earlier. The energy density of both bluegills and largemouth bass was allowed to vary dynamically (see Appendix 1).

A preliminary series of 25 simulations was performed to find reasonable values for the relative encounter rate between largemouth bass and bluegill and also for the relative carrying capacity of the invertebrate prey types. If the encounter rate between piscivores and their prey is too low, then the piscivores grow very slowly or even starve. If the encounter rate is too high, then the piscivores find and consume all the available forage fish. For bluegill growth and survival, piscivore encounter rate interacts with invertebrate carrying capacity (*K*) because bluegill growth is density dependent. The bluegill density at which growth slows to zero depends on carrying capacities of the invertebrate prey types. For a prey population growing according to the logistic equation, total population growth rate is maximized when density is 0.5 *K*.

These 25 preliminary simulations used five values of prey relative carrying capacity (PreyNK = 0.1, 0.3, 1.0, 3.0, 10.0) at each of five values of piscivore relative encounter rate (EncKnob = 0.01, 0.03, 0.1, 0.3, 1.0). The value of PreyNK was multiplied by the value of Relative K in Table 1 to determine carrying capacity, *K*, for each prey type. The initial number of age-0 bluegills was 16,000 and the number of juvenile bass was 20.

The results of the preliminary simulations demonstrate how piscivore relative encounter rate and relative carrying capacity of invertebrate prey interact to influence the total numbers of bluegill eaten, starved, and surviving, and the final length of simulated bluegills and largemouth bass (Figure 10). As the bass' encounter rate increased, more bluegills were eaten and fewer bluegills starved (Figure 10a, b). The number of bluegills starving also decreased as invertebrate carrying capacity increased (Figure 10b). Because of these nearly complementary changes in sources of bluegill mortality, the total number of bluegills surviving changed only slowly with bass encounter rate (Figure 10c). Bluegill growth was density dependent (Figure 10d). Bass growth varied both with encounter rate and invertebrate carrying capacity (Figure 10e). In the following simulation of the experiment of Howick et al. (1993), piscivore relative encounter rate was set at 0.3 and relative carrying capacity of invertebrates was set at 1.0

Results.–For both the pond experiments and the simulations, the number of surviving bluegill decreased as the number of stocked predators increased. Reading from a graph in Howick et al. (1993), they recovered about 3,300 and 4,700 bluegill in the ponds without predators, about 6,000 and 3,000 bluegill in ponds stocked with 20 predators, and about 2,000 and 1,200 bluegill in ponds stocked with 80 predators. In the simulations, there were 4,865±183 (mean±SE, *N* = 3) survivors with 0 predators per pond, 2,717±216 survivors with 20 predators per pond, and 201±5 survivors with 80 predators per pond (Figure 11). The variation among simulated replicates reflects the stochastic processes of encounters with predators and prey, and chance variations in background mortality.

Mean length of surviving bluegill was about 25 and 33 mm in the ponds without predators, about 25 and 27 mm in ponds stocked with 20 predators, and about 33 and 41 mm in ponds stocked with 80 predators (Howick et al. 1993). In the simulations, the mean length of surviving bluegill increased slightly as the number of stocked predators increased from 0 to 20, but survivors were much larger in ponds stocked with 40, 60, or 80 predators (Figure 12). Average length was 47.1±0.5 mm (mean±SE, *N* = 3) with 0 predators, and 50.5±1.0 mm with 20 predators, 71.2±0.1 mm with 40 predators, and 63.4±0.2 mm with 80 predators (Figure 12).

In Howick's pond study, mean length of surviving largemouth bass was about 226 and 194 mm in ponds stocked with 10 bass, 203 and 184 in ponds stocked with 20 bass, and 133 and 130 in ponds stocked with 80 bass. In the simulations, there was not much difference in mean final length for ponds stocked with 20 or fewer bass, but mean length was smaller at higher stocking densities (Figure 13). Mean length of surviving largemouth bass was 187.3±0.5 mm (mean±SE, *N* = 3) with 10 predators, and 190.6±0.8 mm with 20 predators, and 121.9±2.1 mm with 80 predators (Figure 13).

One big advantage of individual-based models is that they make it possible to examine the distribution of model variables, not just the mean values. Figures 14 and 15 show size-frequency distributions for surviving bluegill and largemouth bass for several model runs. Figure 14 shows the distribution of bluegill lengths from 1 simulated pond for each of seven stocking densities of bass. The general patterns is for mean bluegill length to increase with predator stocking density, but the pattern is complex. In the top two panels of Figure 14, representing ponds receiving 0 and 5 bass, note that a very small number of bluegill reached a length of 80 and 81 mm, whereas the rest of the bluegills reached only 37-54 mm. This result would not be observed in a model that only simulated the average individual.

The simulated distribution of final bass lengths is shown Figure 15. A length close to 190 mm is reached in ponds in which the stocking density is 20 or fewer. Competition among the bass results in smaller final sizes when the stocking density is higher.

Discussion.–The simulations are able to capture the qualitative trends observed in the pond experiment. For both the experimental ponds and the simulations, as the number of stocked predators increased, there was a decrease in the number of surviving bluegill, an increase in mean bluegill length, and a decrease in mean bass length.

The simulation results are less variable than the duplicate ponds reported by Howick et al. (1993; Deutsch et al. 1992). This is due in part to unavoidable differences among experimental ponds, and in part due to differences in the amount of bluegill reproduction occurring in each pond. The investigators stocked adult bluegills, which spawned; the investigators did not stock a fixed number of age-0 bluegills, as was done in the simulations.

Fingerling largemouth bass in the simulations grew more slowly than bass in the experimental ponds. Bluegill in the simulations grew to larger sizes than fish in the experimental ponds. These quantitative differences could be reduced by additional calibration.

Bluegill population in a 10-hectare lake

To demonstrate some of the output the model can produce, LakeMod was used to simulate an entire bluegill population in a 10-ha lake. Each of 10 model runs simulated 15 years (5475 days). In each model run, a constant number of age-0 recruits was added each year; total annual recruitment was varied among simulations from 60 to 60,000 (i.e., 6 to 6,000 ha^{-1}). In the model, 15 “individuals” were added every year, with each “individual” initially representing 4 to 4,000 fish in the lake. Surviving individuals were removed from the population when they exceeded a maximum age of 12. Average annual non-starvation mortality rate was set at 33%. The value for theta (θ), a parameter influencing energy allocation between growth in length and growth in relative condition, was set at 1.0 in all 10 simulations (see Appendix 1).

Five types of prey were included in the model: littoral zooplankton, littoral benthic invertebrates (primarily dipteran midge larvae), littoral epiphytic prey (vegetation-dwelling prey, primarily damselfly naiads, Mittelbach 1981), pelagic zooplankton, and sublittoral benthic invertebrates (including midge larvae and burrowing mayflies of the genus *Hexagenia*; energy density was set at 850 cal/g). There were eight size classes of each prey type (Tables 1 and 2).

The method of ranking foraging habitats was changed for this set of simulations. On each day, each simulated fish forages in the habitat that it ranks the highest. In the above application to the experiments of Howick et al. (1993), simulated fish ranked foraging habitats daily according to the fraction of the daily ration that could be obtained (total biomass of prey ingested if foraging in habitat *i* / maximum daily ration). But in these runs the fish ranked foraging habitats daily according to the net amount of energy that could be obtained. This increased simulated fish growth because of differences in energy density among prey types (Tables 1 and 2).

Total volume of the 10-ha lake was set at 150,000 m^3, for a mean depth of 1.5 m. The littoral zone (1 m deep) contained 25,000 m^3 as littoral zooplankton habitat, 25,000 m^3 of vegetation containing epiphytic invertebrates, and a sediment area of 50,000 m^2. The pelagic zone (2 m deep) contained 50,000 m^2 of sublittoral sediment area and 100,000 m^3 of open water. Water temperature was assumed to follow an annual sine curve which has a maximum temperature of 26°C on d 200 (July 19) and a low of 0°C, but the curve was truncated at a minimum temperature of 4°C.

Model results are shown for March 31 of year 15 (day 5031) of each simulation. Preliminary runs indicated that relative weight was usually lowest at the end of the third month of the model year, reflecting energy losses during winter.

Results.–Bluegill population density in year 15 increased linearly as number of recruits increased from 60 to about 20,000 (Figure 16). Over this range the observed population density reflects the average non-starvation mortality rate of 33%/y. Above 20,000 recruits/y the number of survivors decreased due to starvation of some individuals.

From 60 to about 2,000 recruits/y, increases in recruitment produced nearly linear increases in population biomass (kg/ha) (Figure 17). Above this level, population biomass reached a maximum of about 50 kg/ha. This level of biomass occurred over a five-fold range in recruitment, from about 6,000 to 30,000 recruits/y.

At 30,000 or more recruits/y there were several weak or missing year classes due to starvation (Figure 18). A weak or missing year class was often followed by a stronger year class.

Bluegill growth was strongly density dependent, as expected (Figure 19). Individual growth reached a maximum for recruitment levels less than or equal to 195 fish/y (Figure 19, see 0.2k and 0.06k recruits/y). In those simulations in which starvation eliminated some year classes, growth of other fish in the population increased greatly (Figure 19, see 30k and 60k recruits/y). The mean length of age-1 and age-2 bluegills was closest to the Michigan state average growth (Laarman et al. 1985) when total annual recruitment was 10,000/y in the simulated 10-ha lake. Additional calibration could make the correspondence even closer, especially for older fish.

Relative weight generally declined with age (Figure 20). Relative weight at a given age tended to increase as recruitment increased, except when starvation of young fish caused missing year classes.

Discussion.–The simulations of bluegill populations with different levels of recruitment demonstrated that the model could reproduce several phenomena important in warmwater lakes and ponds. The model clearly showed density dependent growth of bluegills, a maximum population biomass limited by food availability, variation in relative weight with age and density, and growth responses to weak and strong year classes. The model demonstrated compensation in bluegill population biomass over a 5-fold range in recruitment.

Several model components would benefit from additional calibration. The vulnerability of benthic prey to bluegills could be increased, both in littoral and sublittoral habitats. Because the vulnerability of benthos was assumed to decrease with increasing prey size (Breck 1993a), large benthic items were consumed only rarely in these simulations and were not appreciably depleted, even at the highest bluegill densities.

In simulations with high levels of bluegill recruitment, starvation reduced some year classes and caused complete elimination of others (Figure 18). In studies at the Saline Fisheries Research Station, occasional year-class failure has been observed in ponds containing only bluegills (Clark and Lockwood 1990). However, in subsequent experiments to examine the cause of such year-class failures, starvation of an entire year-class was not observed, even when the number of age-0 bluegills exceeded 100,000 ha^{-1}(Breck 1996; Gray 1991; Gray et al. 1998). In those experiments the first natal cohort was not observed to starve. But the later natal cohorts sometimes disappeared during their first summer, perhaps due to starvation, perhaps due to cannibalism (Breck 1996). Although it is clear that growth of young bluegill is strongly density dependent (Krumholz 1946; Latta and Merna 1976; Breck 1996), it appears that real age-0 bluegills are somewhat less vulnerable to starvation than the current model's bluegills, indicating the need for additional calibration.

The maximum standing crop biomass is set by food availability. Total prey production could be adjusted to increase the standing crop biomass of fish closer to the value of 204 kg/ha reported by Schneider (1973) for lakes with slow-growing bluegills, in which bluegills made up an average of 82% of the total biomass.

Contrary to the pattern observed in these simulations, relative weight is expected to increase in older, larger fish (Cargnelli and Gross 1997; Baylis et al. 1993; Breck 1996). It is expected that some very large prey items will only be available to the largest bluegills. Such prey might include yearling crayfish, other large invertebrates, or even juvenile fish. It may be possible to find a set of prey sizes and densities that produce higher relative weight in larger fish. In addition, metabolic costs per unit mass are lower in larger fish (West et al. 1997), so the energetic cost of maintaining condition should be lower. It may be possible to find a set of constant values of the parameters related to energy allocation that would increase the correspondence between the simulated and expected patterns in relative weight. If such a set of constant parameters cannot be found, then perhaps these patterns change with age. It would certainly be expected that energy allocation parameters would change after the fish reaches sexual maturity.

The variation among bluegill individuals in length at age is too low in the model compared to observed variation in natural lakes. For fish such as bluegills that consume a large number of small prey per day, a relatively small variation in growth among individuals might be expected due to chance effects on the daily number of prey encountered (Breck 1993b); this source of variation is included in the model. Some variation in length at age must be due to differences in date of hatch. Claussen (1991) reported that in five years of observation in Lake Opinicon, Ontario, the length of the bluegill reproductive season (from first to last day of spawning) varied from 37 to 47 days. The model includes multiple bouts of reproduction spanning 20 to 30 days, so some variation from this source is included. Robinson et al. (1996) provide evidence that some of the variation among individuals in condition and growth rate is due to morphological variation among individuals. Some of the variation in length at age may be due to genetic differences. But I suspect that the greatest differences in length at age within a single lake population may be caused by spatial heterogeneity in food availability. Spatial heterogeneity in food availability could be added to a future version of the model.

Bluegill and largemouth bass populations in a 10-hectare lake

LakeMod is capable of simulating interacting populations of bluegill and largemouth bass. In the present version of the model, annual recruitment of each species is constant. A set of six runs was made with annual recruitment of largemouth bass held constant at 0, 45, 150, 450, 1,500, and 4,500 recruits/y. Bluegill recruitment in the simulated 10-ha lake was constant at 10,000 recruits/y. For both largemouth bass and bluegill, the number of annual recruits was divided among fifteen new model “individuals” each year. Individuals were dropped from each population when they exceeded the maximum age of 12 y, so the total number of model “individuals” per species could be as high as 180 (=15 x 12) in these runs. Average annual non-starvation, non-predatory mortality was set at 33% for bluegill and 25% for largemouth bass. The five prey habitats were the same as those used in the simulations with only bluegill. The value for theta (q), a parameter influencing energy allocation between growth in length and growth in relative condition, was set at 0.3 in all 6 simulations (see Appendix 1). As above, model results are shown for March 31 of year 15 (day 5031) of each simulation.

Results.–As expected, bluegill population density and biomass decreased, due to predation by bass, as largemouth bass recruitment increased (Figure 21). Density and biomass of largemouth bass increased as recruitment increased, except at the two lowest levels of recruitment (Figure 21). Bass growth was faster at 150 recruits/y than at 45/y, leading to increased cannibalism and a somewhat lower population density and biomass.

Bluegill growth increased as bass recruitment increased (Figure 22a). Even the predation due to 45 bass recruits per year caused a substantial improvement in bluegill growth compared to the simulation without bass. Intraspecific competition was reduced enough that the length of ages 1-5 was above the Michigan average for bluegill (Laarman et al. 1985).

The growth pattern for largemouth bass was more complex than the pattern for bluegill (Figure 22b). For largemouth bass ages 1-4, length at age increased as recruitment increased. In contrast, for the oldest bass, length at age was greatest at low levels of recruitment. With 4,500 recruits/y, growth was rapid for the first 3-4 y, but very few bass ever exceeded 370 mm. With 45 recruits/y, initial growth was slower, but age-12 bass reached 549 mm.

Bluegill relative weight decreased with age for all levels of bass recruitment (Figure 23a). Older fish approached a lower limit of about 0.6. This lower limit for relative weight is determined by the set of parameters related to energy allocation and the state of health of individual fish (e.g., the threshold ratios of reserve energy to structural energy at which a fish's condition changes from healthy to hungry or hungry to torpid; see Appendix 1 and Broekhuizen et al. 1994).

Relative weight of largemouth bass decreased with age (Figure 23b). The trends in relative weight with recruitment mirrored the trends in growth. Among younger bass, increased recruitment was associated with lower relative weight; among older bass, increased recruitment was associated with higher relative weight.

The relative age-frequency of the largemouth bass population changed with recruitment (Figure 24). At the highest level of recruitment, over 4,000 of the 4,500 new recruits were cannibalized during the first year of life by larger bass. A much smaller fraction of new recruits was cannibalized at lower levels of recruitment. At 4,500 recruits/y the relative frequency of older age classes was much more even than at lower levels of recruitment.

Discussion.–These simulations of bluegill and largemouth bass demonstrate one of the trade-offs often observed by fisheries managers: conditions favoring good growth of bluegills are often associated with abundant, small largemouth bass. In the simulation with 4,500 bass recruits/y, bluegill growth was most rapid and bluegills reached the greatest length (Figure 22, lines for 4,500 bass recruits/y). At this level of recruitment, however, few bass grew beyond 370 mm. In contrast, bass reached the greatest length at the lowest level of recruitment (45 recruits/y), while bluegill growth was relatively slow compared to higher levels of bass recruitment.

The results of these simulations suggest some of the rich range of behavior that the model is capable of producing. Additional simulations and analyses should provide insight into the complex patterns expected in the predator-prey dynamics of warmwater fish communities.

Conclusions

Several ecological ideas were suggested during the process of model development. First, growth of age-0 bluegills slows during summer without causing massive starvation. In the first attempts at modeling growth of age-0 bluegill, it was very tricky to find search parameters and prey densities that would allow coexistence of both fish and prey. For many parameter combinations, either the young bluegill grew well until they eliminated their prey and then starved, or else the young bluegill could not find enough prey to grow and thus starved. Parameter combinations that allowed young bluegill to grow at observed rates often led to the fish eliminating their prey and then starving. Parameter combinations that allowed persistence of prey generally caused bluegill growth rates lower than observed. This problem was solved by including a greater variety of prey in the model, including a several sizes of each prey type. Because encounter rates depend strongly on the size of the prey, the smaller prey were encountered at lower rates and were also less energetically valuable to the fish (fewer calories per individual prey item). So as larger prey types were depleted, fish consumed smaller prey of lower energetic value, ingested fewer calories per day, and grew at a lower rate. Thus, fish growth rate slowed without leading to massive starvation. The idea that predators prefer the energetically optimal prey is well known. The seasonal switch to less-preferred prey appears to be common among generalist predators. But the implications of seasonal prey switching for changing seasonal growth rate of generalist predators seem not to be commonly recognized.

In preliminary model runs, the size-frequency distribution of age-0 bluegill lengths in the fall was too narrow – there was not enough variation among individuals. In ponds and lakes the variation in size among age-0 bluegills is often quite great (Krumholtz 1946; Forsythe and Wrenn 1979; Breck 1993a). Within a group of bluegills hatching on the same day (a natal cohort), there is some divergence in size through time due to chance variations in encounter rates with prey, but for fish that tend to eat a large number of small prey items per day, this effect is small (Breck 1993b). Although genetic differences could theoretically produce growth-rate differences among age-0 individuals, this did not seem to have a large effect in experimental ponds; rather, members of natal cohorts tended to be very similar in size all through the summer (Breck, unpublished data). The factor having the greatest influence on variation in fall size appears to be variation in hatching date. When fish survive from a wide range of hatching dates, there will be a wide range in size of age-0 fish in the fall. This result can be seen both in data from experimental ponds and in model results (Breck 1993a).

Use of laboratory-derived parameters for encounter rates with damselfly larvae and midge larvae caused model fish to rapidly eliminate these prey items; the laboratory-derived encounter rates were much too high. Mittelbach (1981) probably collected insects from ponds with high invertebrate densities, and these were probably ponds without fish, which would have contained species adapted to fishless conditions and much more vulnerable to fish predators (McPeek 1990, 1998).

Fish may learn the locations of higher densities of prey within territories or individual foraging areas (D. S. Wilson and students). So average densities of invertebrates measured by humans may not reflect the prey densities perceived by resident fish. This could be part of the explanation for differences between models and real aquatic systems.

Because the area and volume of the littoral and pelagic zones are explicit parameters in this model, LakeMod could be used to evaluate assumptions about the effects of lake morphology on fish community dynamics. In particular, growth and survival of juvenile fishes are expected to depend on the littoral zone’s size, food production, and ability to serve as a refuge from predators, whereas the growth and reproductive potential of adults may depend more heavily on the characteristics of the pelagic zone (Mittelbach and Chesson 1987; Mittelbach and Osenberg 1992; Osenberg et al. 1993). The model could also be used to evaluate the consequences of changes in invertebrate production caused, for example, by changes in nutrient loading to a lake.

Individual-based models of fish communities hold promise as a way to gain understanding into seasonal and inter-annual patterns of fish growth and survival. The results of the size- and density-dependent interactions in such models can be complex. Understanding the patterns should improve our ability to manage warmwater fish communities.

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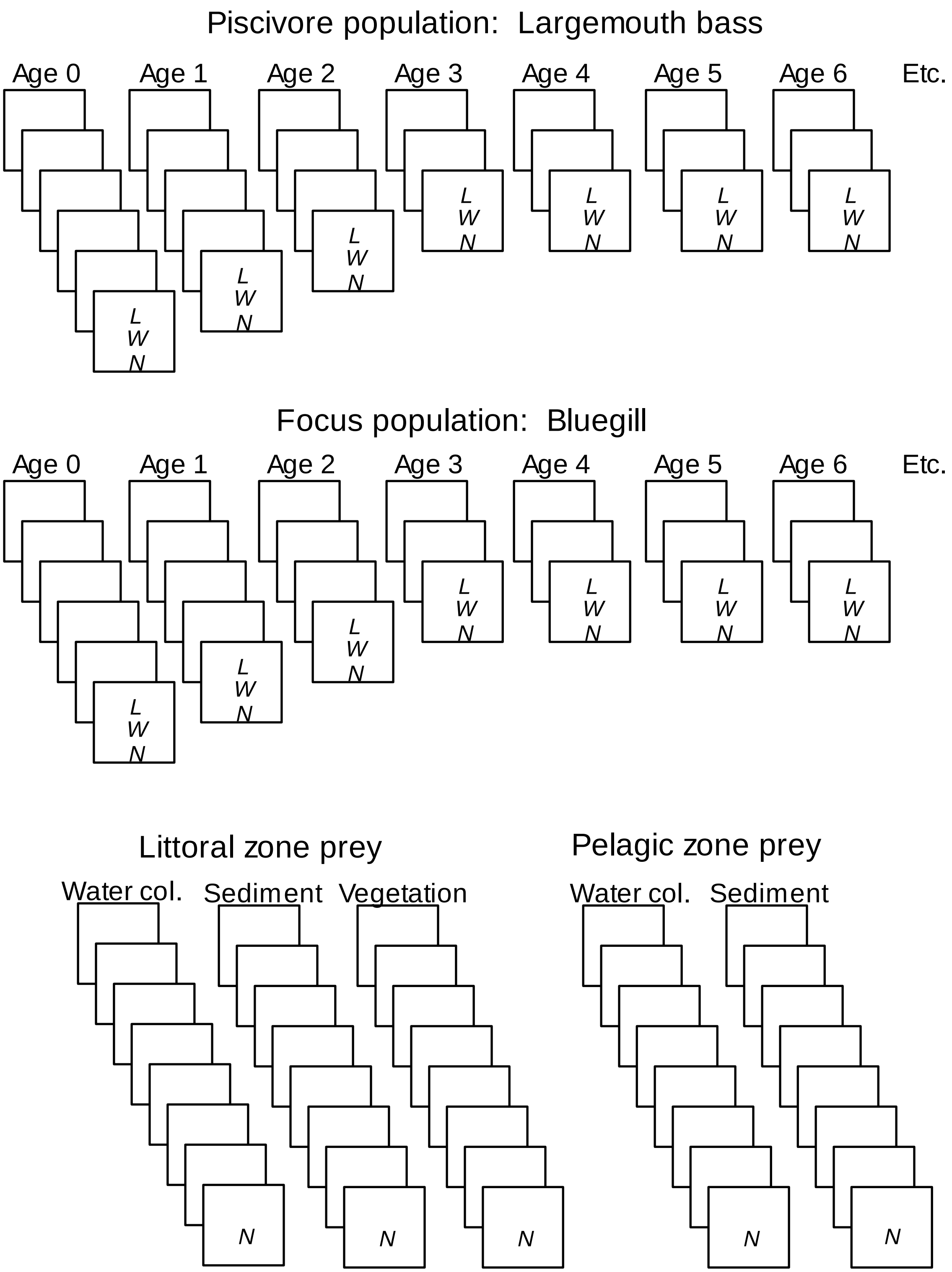

Figure 1.–The components of LakeMod include a population of piscivores, such as largemouth bass; the focus population of bluegill; and five habitat types containing fixed sizes of invertebrate prey. The total number of "individual" fish in the model may be several hundred, each with three state variables: *L* = length, *W* = weight, and *N* = number of identical fish in the lake represented by the modeled "individual." For each of the eight fixed size categories of prey in a habitat type, the state variable *N* = number of prey per unit area or volume.

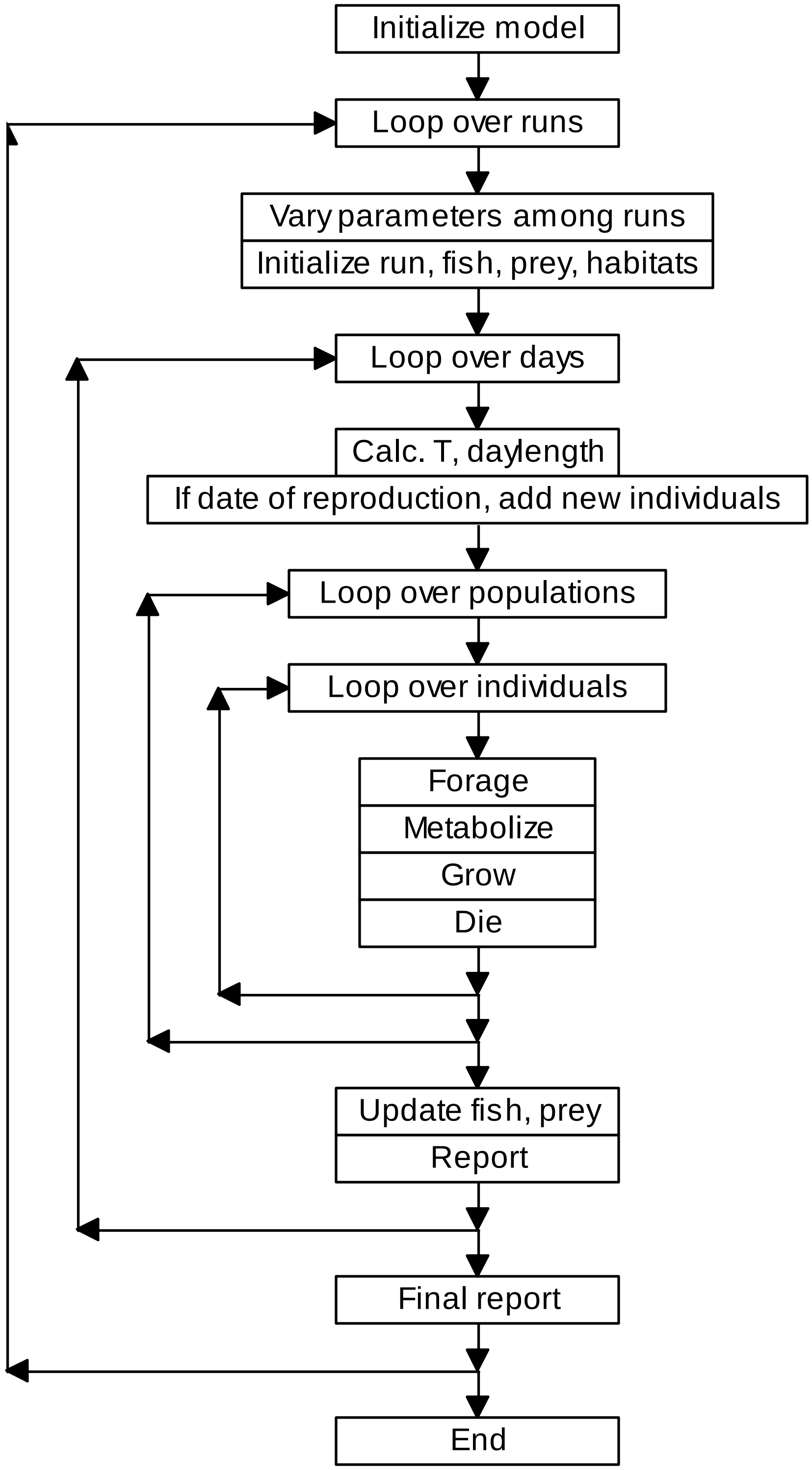

Figure 2.–Flow chart showing the major processes included in LakeMod.

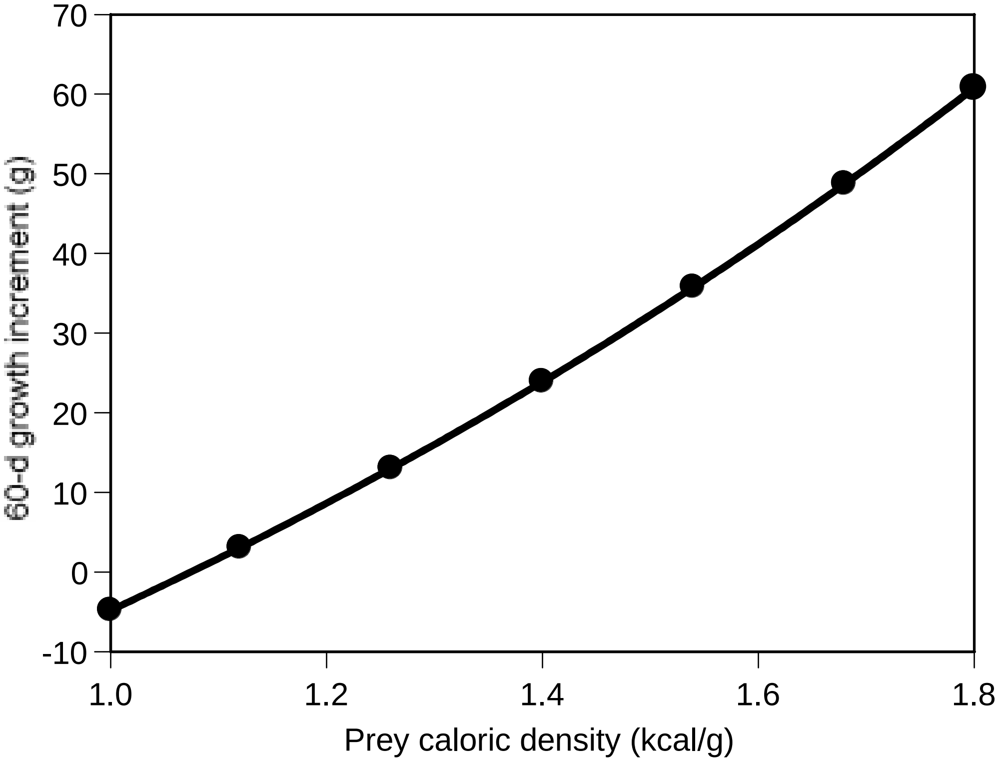

Figure 3.–Simulated growth of largemouth bass increases with prey energy density. Simulations used the bioenergetics model for largemouth bass in Hewett and Johnson (1992), with initial weight = 100 g, bass energy density = 1.4 kcal/g, temperature = 26°C, and ration = 2% body weight/d for 60 d; prey energy density varied among simulations from 1.0 to 1.8 kcal/g of prey.

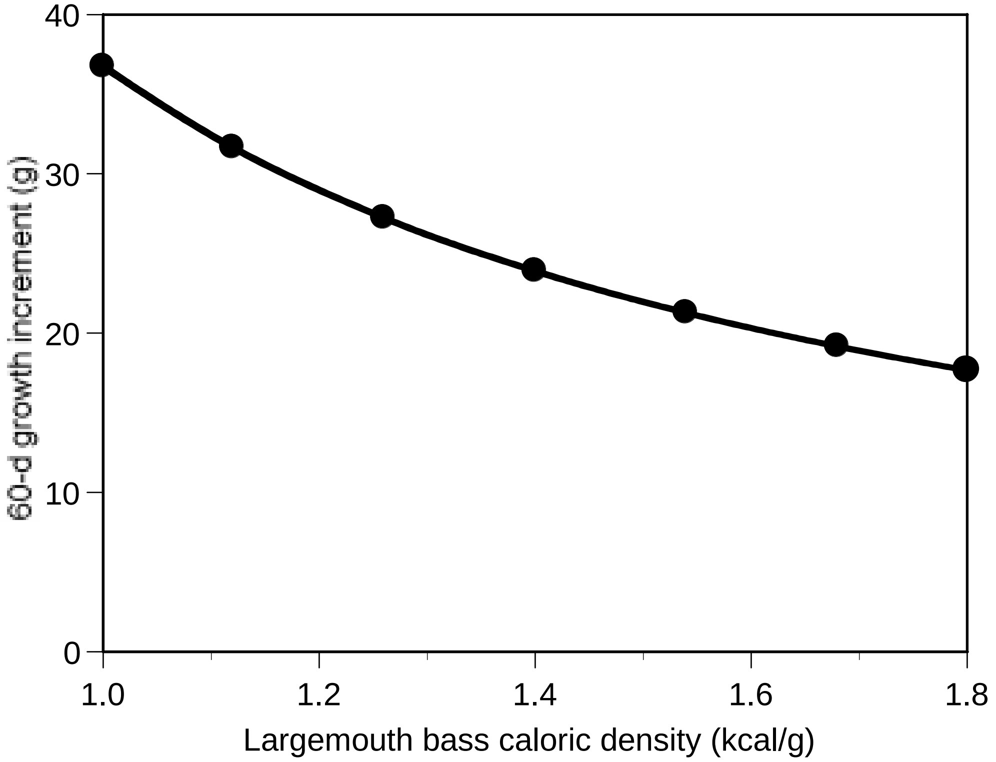

Figure 4.–Simulated growth of largemouth bass decreases with increasing bass energy density. A net daily increase of 1.8 kcal represents a gain of 1.8 g for a fish with 1.0 kcal/g body weight, but represents a gain of only 1.0 g at 1.8 kcal/g body weight. Simulations used the bioenergetics model for largemouth bass in Hewett and Johnson (1992), with initial weight = 100 g, prey energy density = 1.4 kcal/g, temperature = 26°C, and ration = 2% body weight/d for 60 d; bass energy density varied among simulations from 1.0 to 1.8 kcal/g of fish.

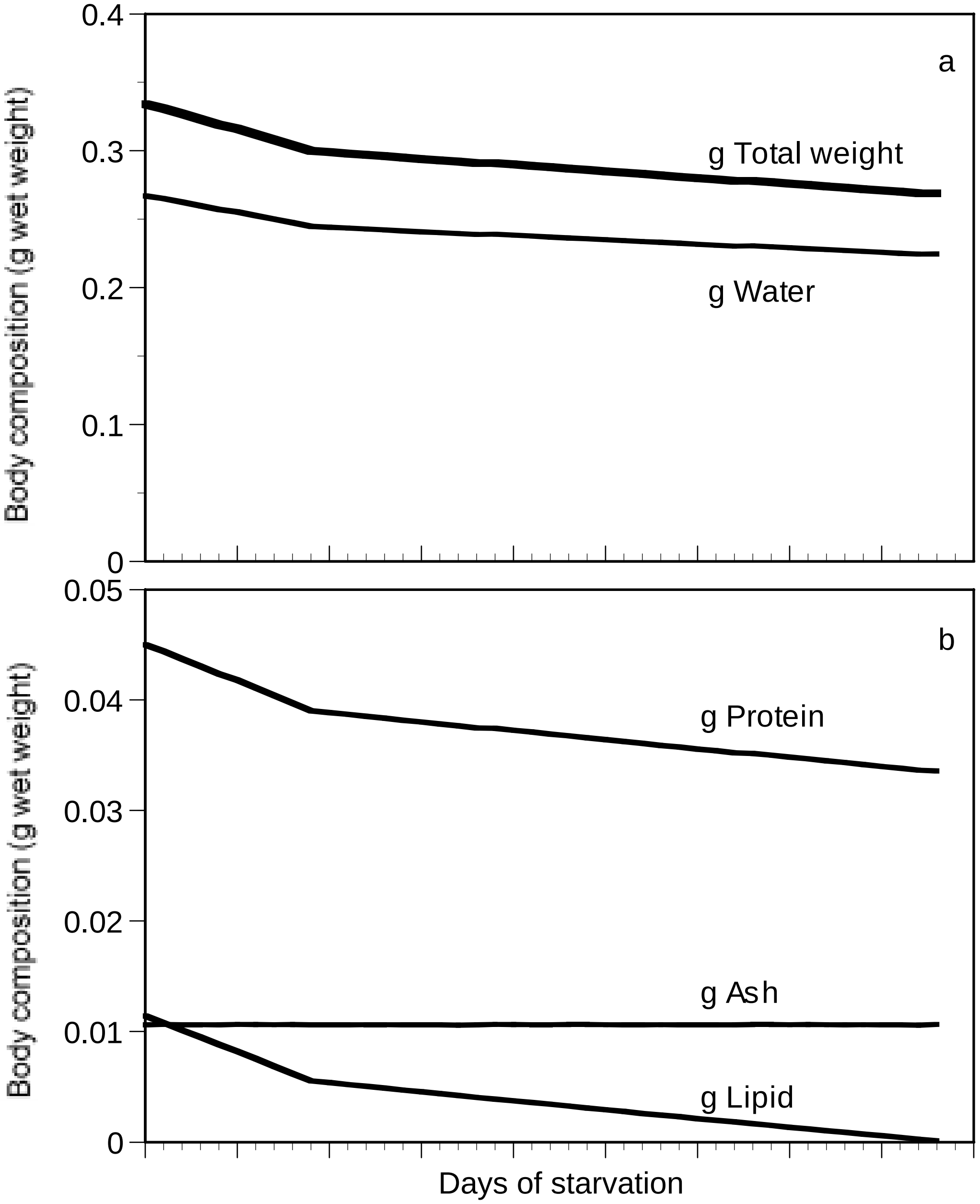

Figure 5.–For a fish starving according to model assumptions, (a) total weight and water mass decrease, (b) lipid mass approaches zero, protein mass decreases, and ash mass is constant. Results are shown for a 30-mm bluegill starting at standard weight (0.334 g) and starving at 25°C. The change in slope at d 9 occurs because the fish becomes "torpid" and reduces respiration rate. The simulated fish was dead on d 44.

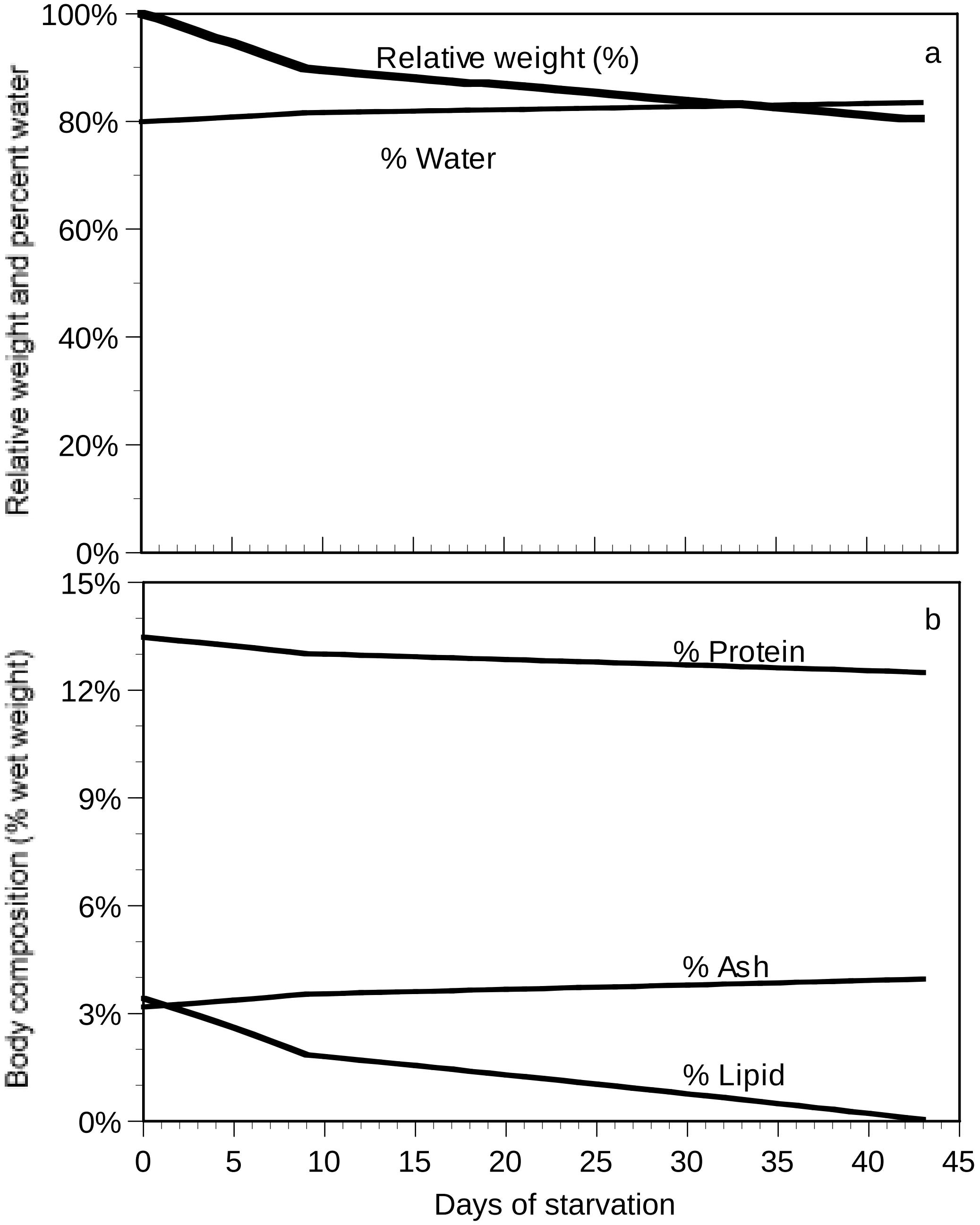

Figure 6.–For a fish starving according to model assumptions, (a) relative weight decreases, percent water increases, (b) percent lipid approaches zero, percent protein is nearly constant, and percent ash increases. Results are shown for a 30-mm bluegill starting at standard weight (0.334 g) and starving at 25°C. The change in slope at d 9 occurs because the fish becomes “torpid” and reduces respiration rate. The simulated fish was dead on d 44.

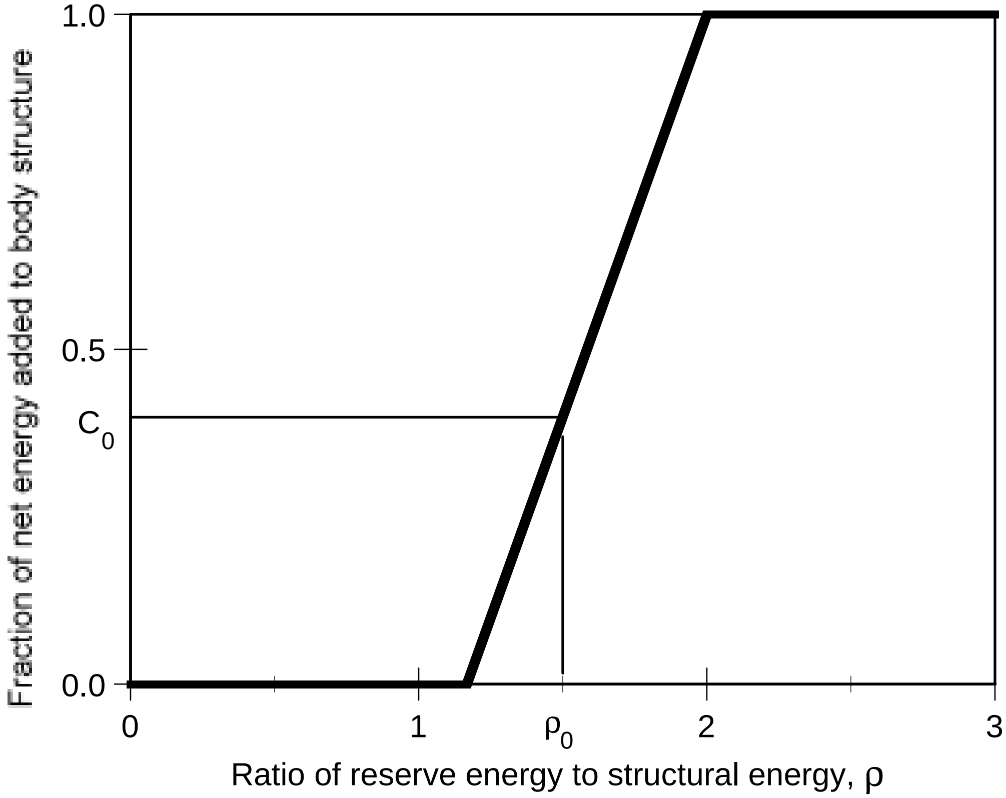

Figure 7.–Energy allocation model assumes that the fraction of net energy added to body structure depends on ρ, the ratio of reserve energy to structural energy (Broekhuizen et al. 1994).

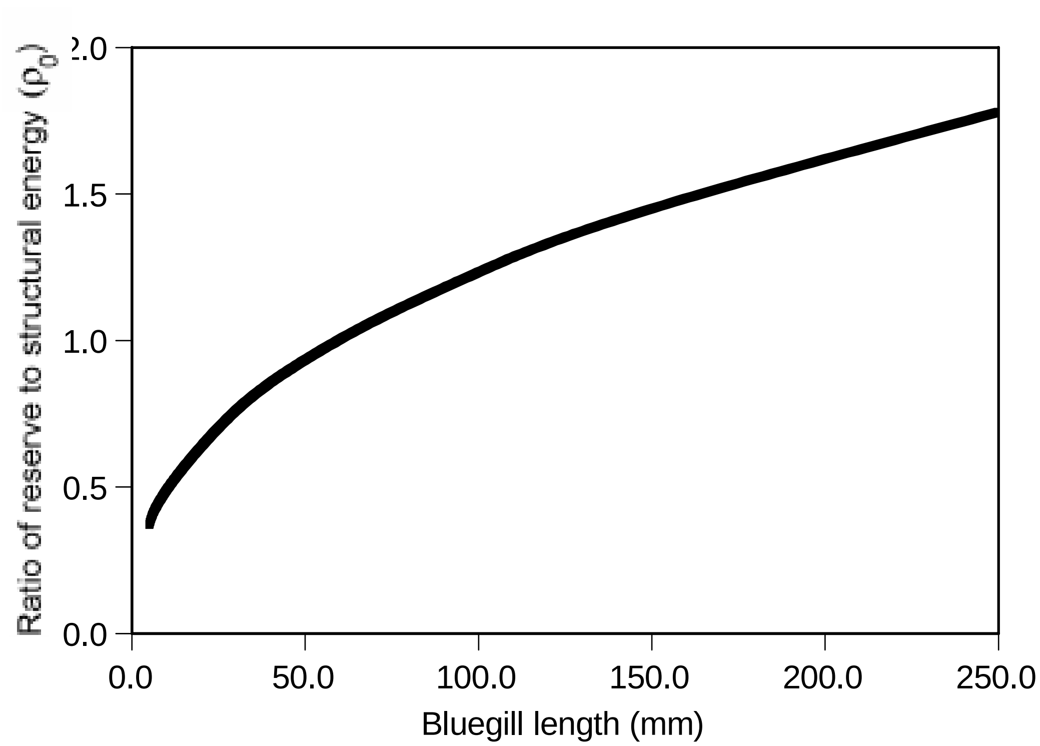

Figure 8.–The nominal ratio of reserve energy to structural energy (ρ_0) is assumed to increase with body size in bluegill and other fish species.

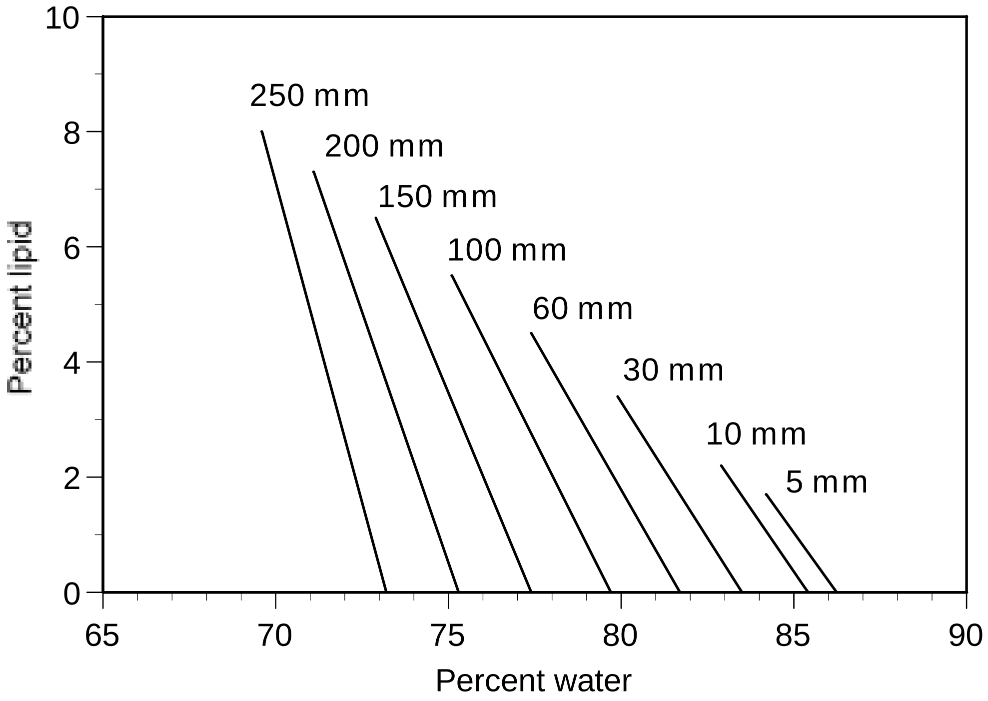

Figure 9.–During starvation, a linear relationship is expected between percent lipid and percent water if two conditions hold: (1) the proportions of energy coming from lipid and protein are constant, and (2) a constant amount of water is lost per gram of lipid and protein mobilized. The slope and intercept of the relationship depend on the nominal body composition, which is assumed to vary with body size in bluegill.

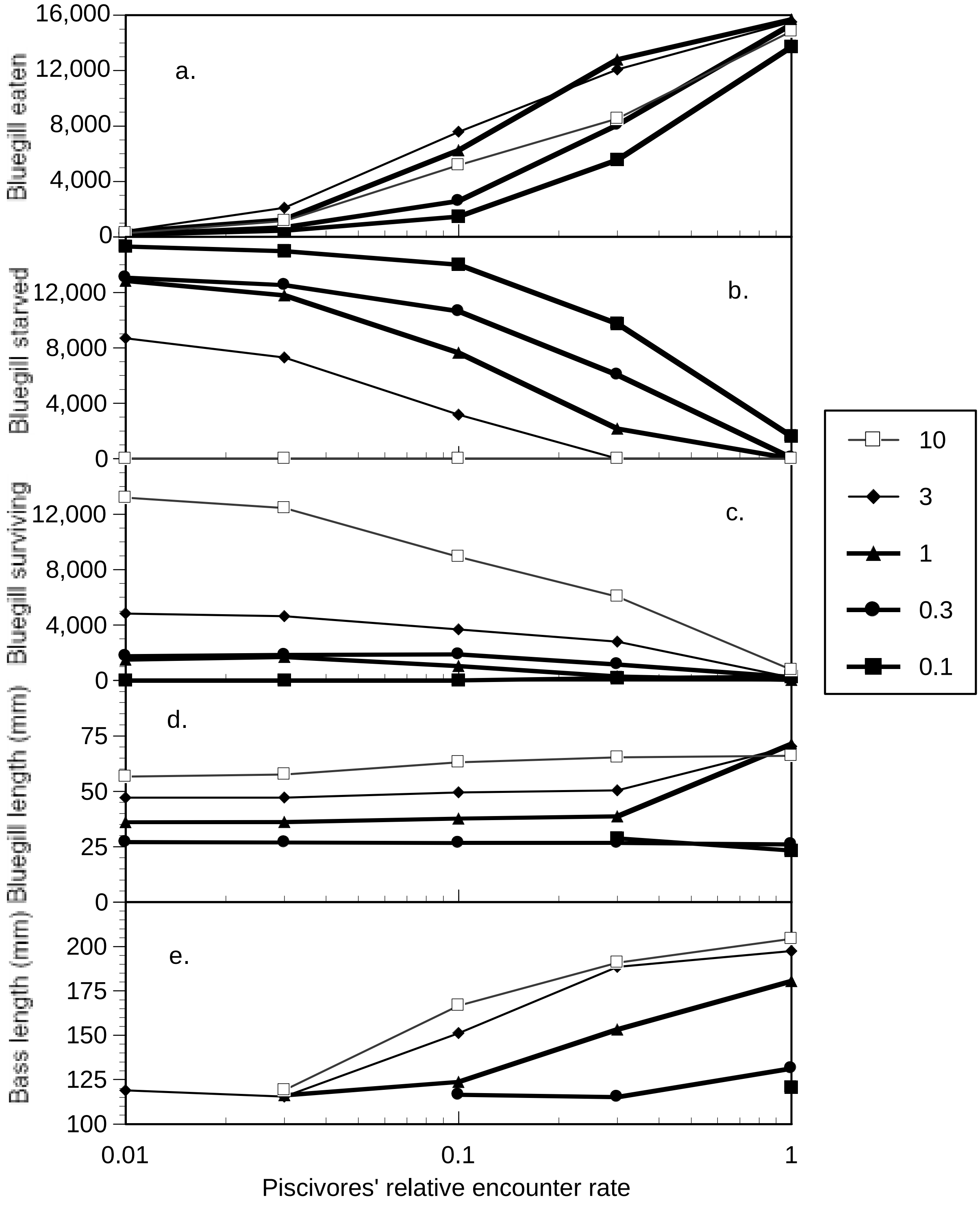

Figure 10.–Effect of piscivores' relative encounter rate and relative carrying capacity of invertebrate prey on: (a) number of bluegill eaten, (b) number of bluegill starving, (c) number of bluegill surviving, (d) final bluegill length, and (e) final length of largemouth bass in the 175-d simulations. Five levels of relative carrying capacity of invertebrate prey (10, 3, 1, 0.3, 0.1) were used at each of five levels of piscivores' relative encounter rate (0.01, 0.03, 0.1, 0.3, 1.0).

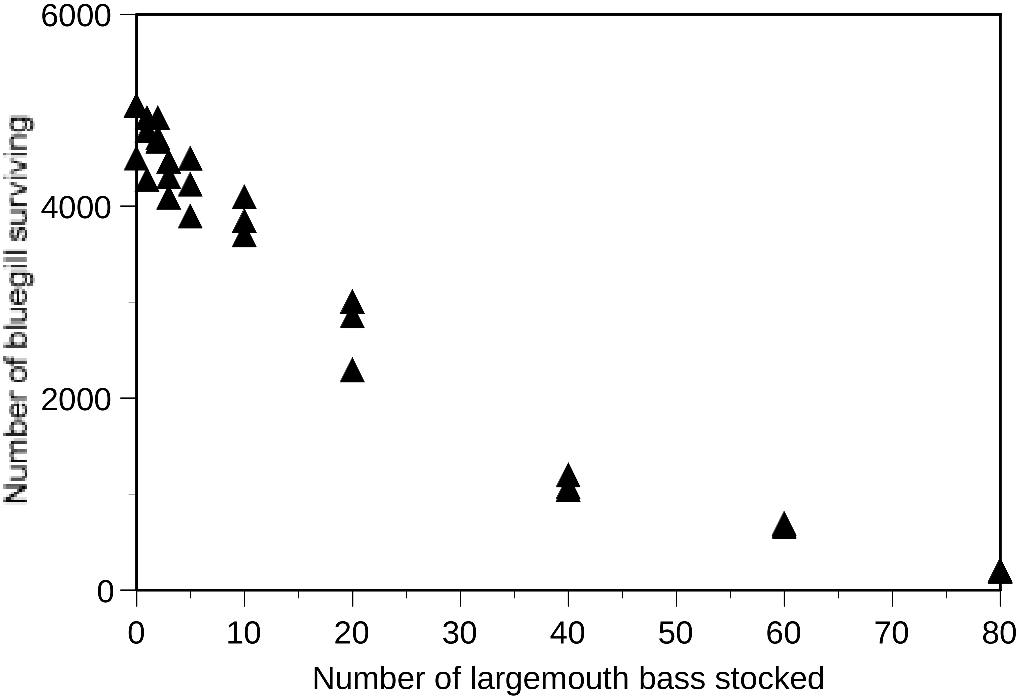

Figure 11.–Number of age-0 bluegill surviving in model simulations of the pond experiments of Howick et al. (1993). The model simulated stocking 0, 1, 2, 3, 5, 10, 20, 40, 60, and 80 largemouth bass (*L* = 115±4 mm) into replicate 0.04-ha ponds (*N* = 3 per stocking density) containing 16-mm age-0 bluegill.

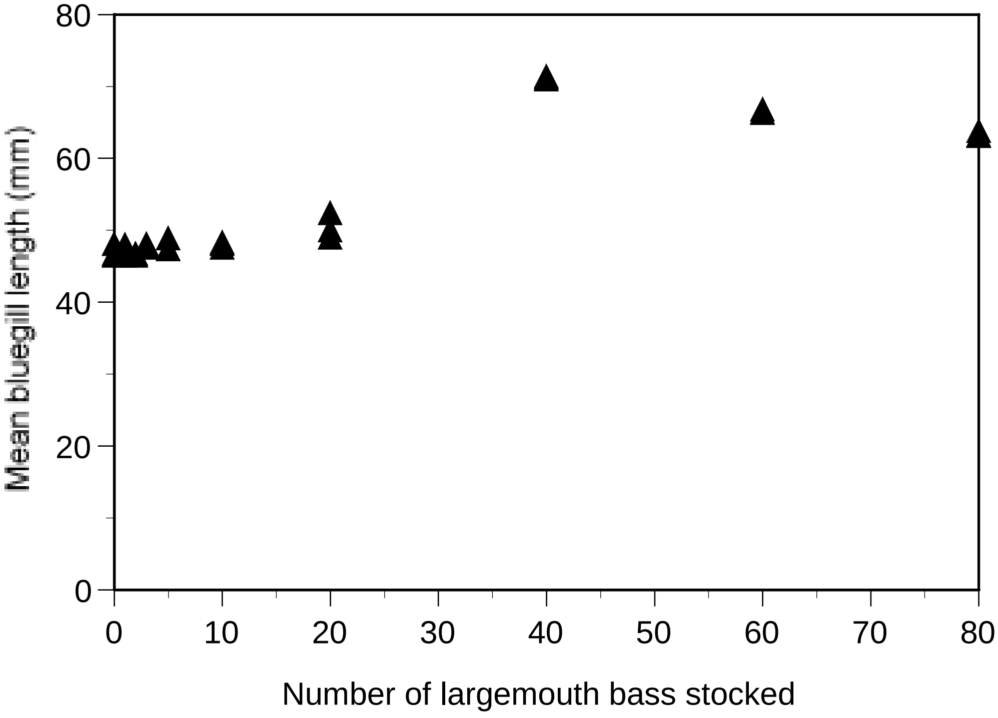

Figure 12.–Mean final length of age-0 bluegill surviving in model simulations of the pond experiments of Howick et al. (1993). The model simulated stocking 0, 1, 2, 3, 5, 10, 20, 40, 60, and 80 largemouth bass (*L* = 115±4 mm) into replicate 0.04-ha ponds (*N* = 3 per stocking density) containing 16-mm age-0 bluegill.

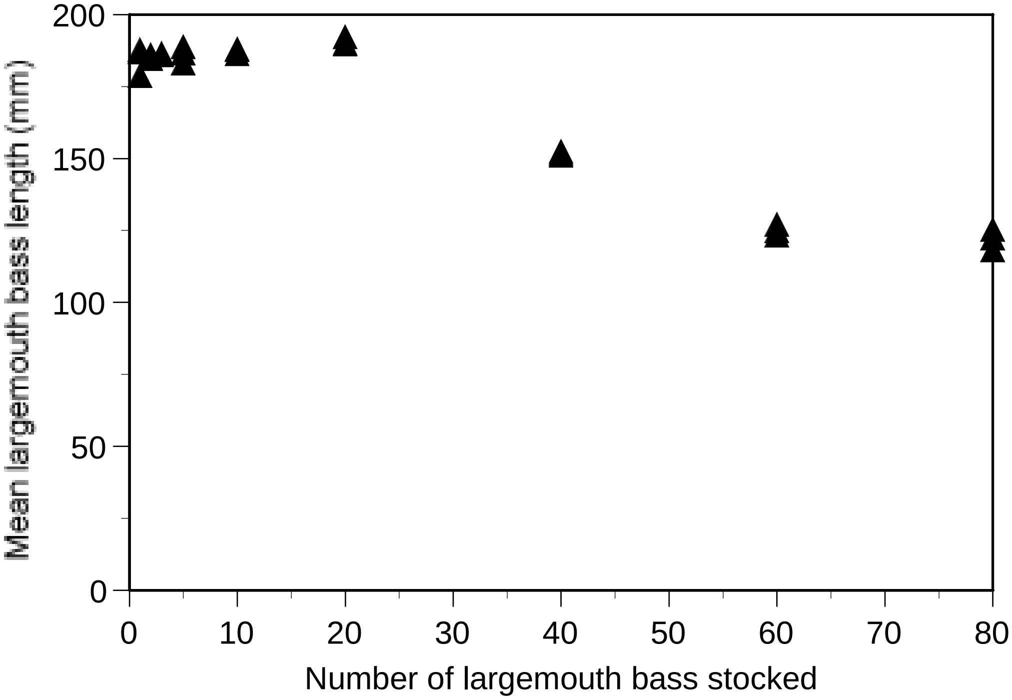

Figure 13.– Mean final length of largemouth bass surviving in model simulations of the pond experiments of Howick et al. (1993). The model simulated stocking 0, 1, 2, 3, 5, 10, 20, 40, 60, and 80 largemouth bass (*L* = 115±4 mm) into replicate 0.04-ha ponds (*N* = 3 per stocking density) containing 16-mm age-0 bluegill.

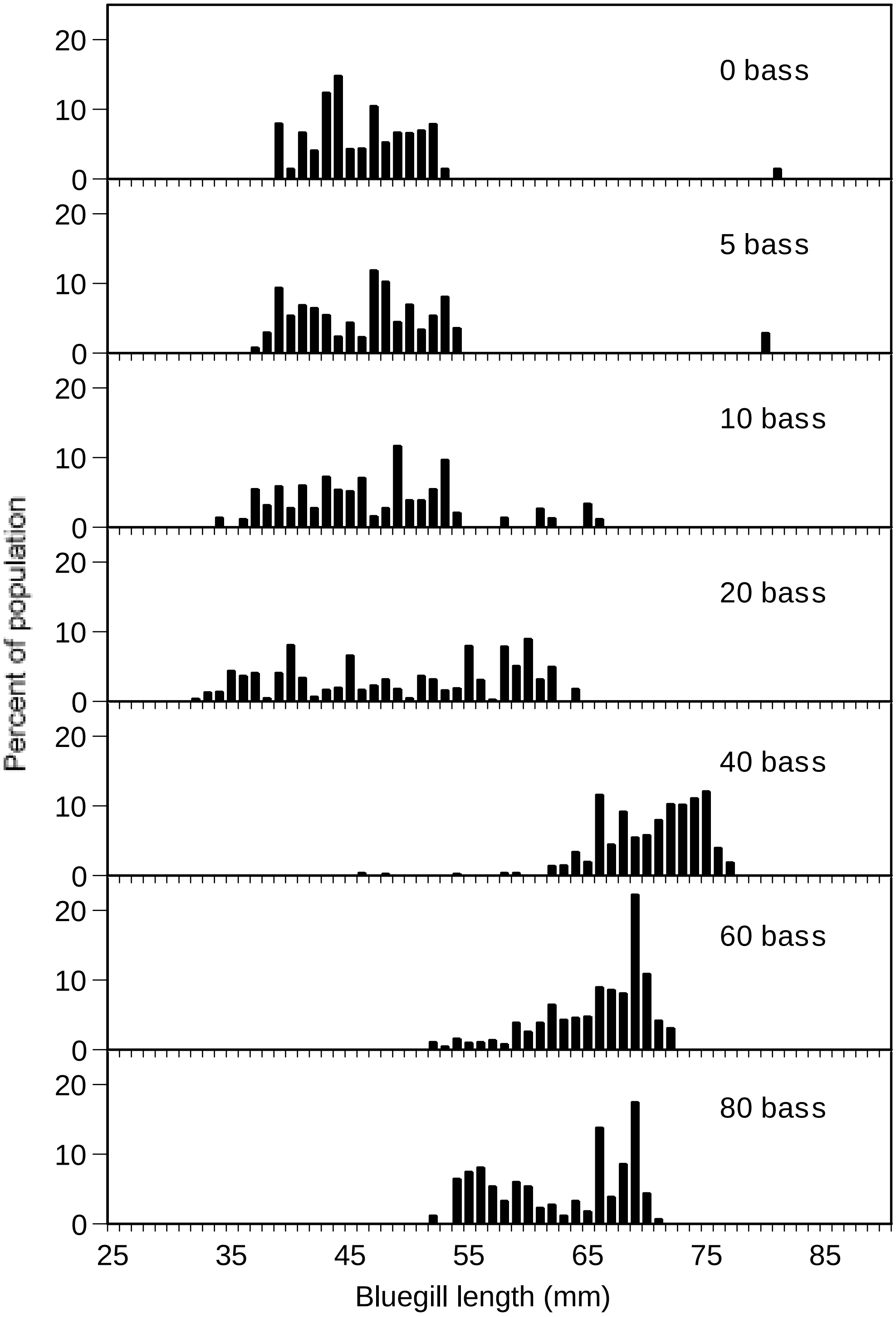

Figure 14.–Size-frequency distributions of age-0 bluegill surviving in model simulations of the pond experiments of Howick et al. (1993). Results are shown for a single replicate of simulated stocking of 0, 5, 10, 20, 40, 60, and 80 largemouth bass (L = 115±4 mm) into 0.04-ha ponds containing 16-mm age-0 bluegill.

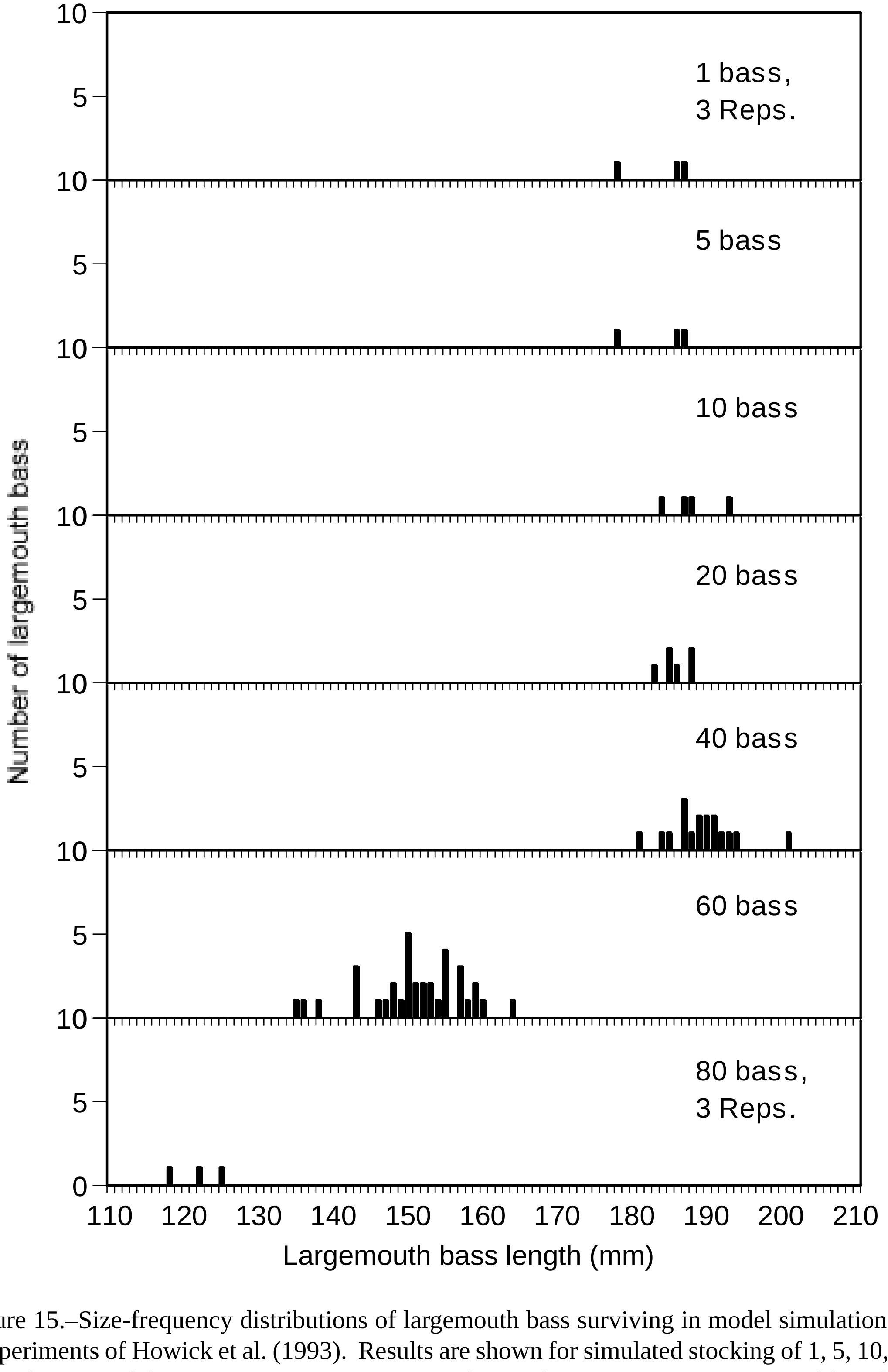

Figure 15.–Size-frequency distributions of largemouth bass surviving in model simulations of the pond experiments of Howick et al. (1993). Results are shown for simulated stocking of 1, 5, 10, 20, 40, 60, and 80 largemouth bass (*L* = 115±4 mm) into 0.04-ha ponds containing 16-mm age-0 bluegill. Each panel shows results from a single model run, except for bass stocking densities of 1 and 80, where results for three runs are combined.

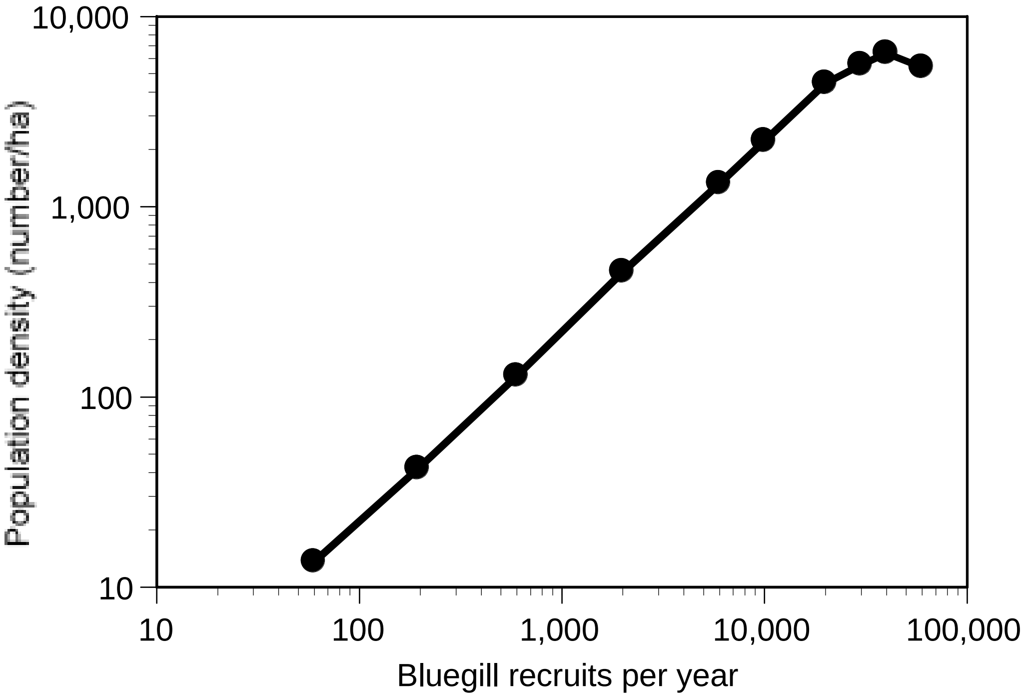

Figure 16.–Bluegill population density increases linearly with recruitment until starvation begins to occur. Constant annual recruitment was varied from 60 to 60,000 age-0 bluegills in a simulated 10-ha lake. Density is shown for March 31 of year 15 (day 5031) of the simulations. Average annual non-starvation mortality was set at 33%.

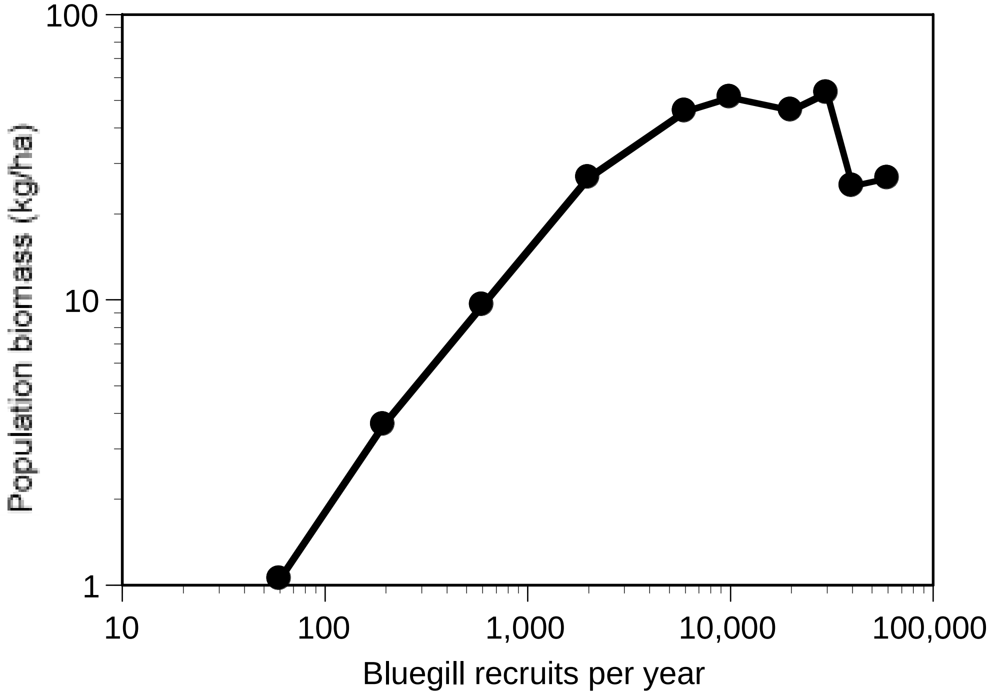

Figure 17.–Bluegill population biomass increases with recruitment to a level (about 50 kg/ha) set by food availability. At the highest levels of recruitment, population biomass is reduced by starvation. Constant annual recruitment was varied from 60 to 60,000 age-0 bluegills in a simulated 10-ha lake. Biomass is shown for March 31 of year 15 (day 5031) of the simulations.

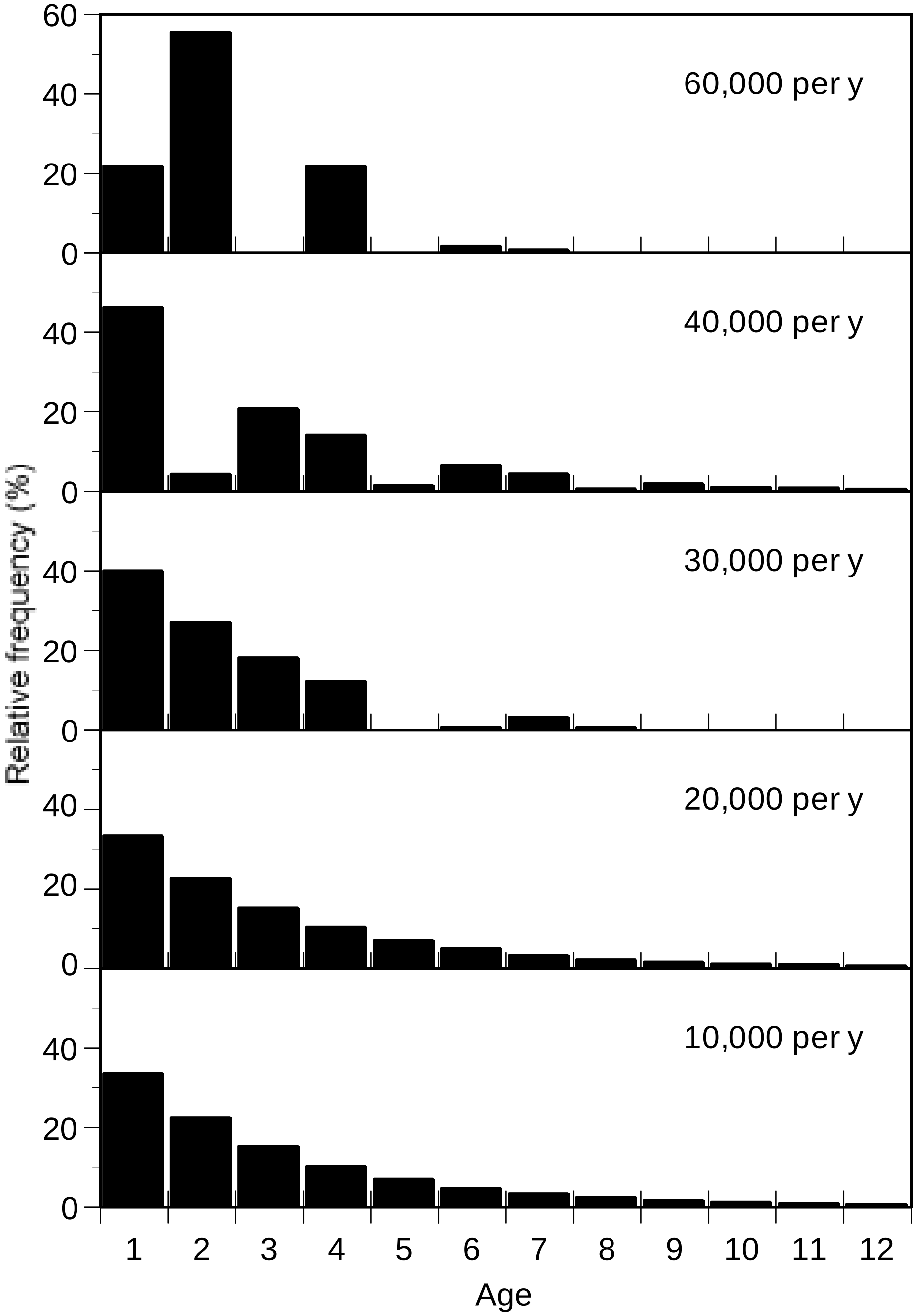

Figure 18.–Relative frequency of bluegill of ages 1-12 in simulations with constant annual recruitment of 10,000 to 60,000 age-0 bluegills in a 10-ha lake. Some very weak age classes are present with 40,000 annual recruits, and some age classes are missing in simulations with 30,000 and 60,000 recruits. Data are shown for March 31 of year 15 (day 5031) of the simulations. Average annual non-starvation mortality was set at 33%.

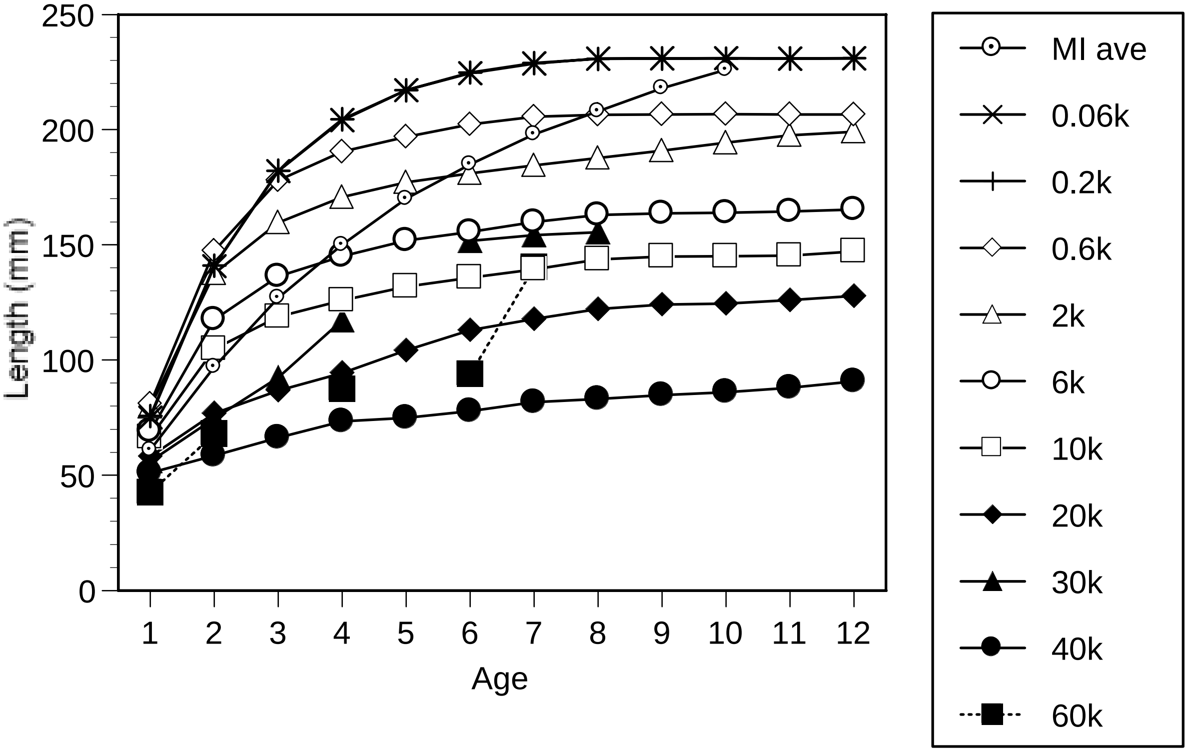

Figure 19.–Bluegill length at age decreases as annual recruitment increases from 60 to 60,000 age-0 bluegills in a simulated 10-ha lake. Results overlap for the two lowest levels of recruitment. Some age classes are missing due to starvation in the simulation with 30,000 and 60,000 recruits. Lengths are shown for March 31 of year 15 (day 5031) of the simulations. The dotted line indicates the Michigan average length at age (Laarman et al. 1985).

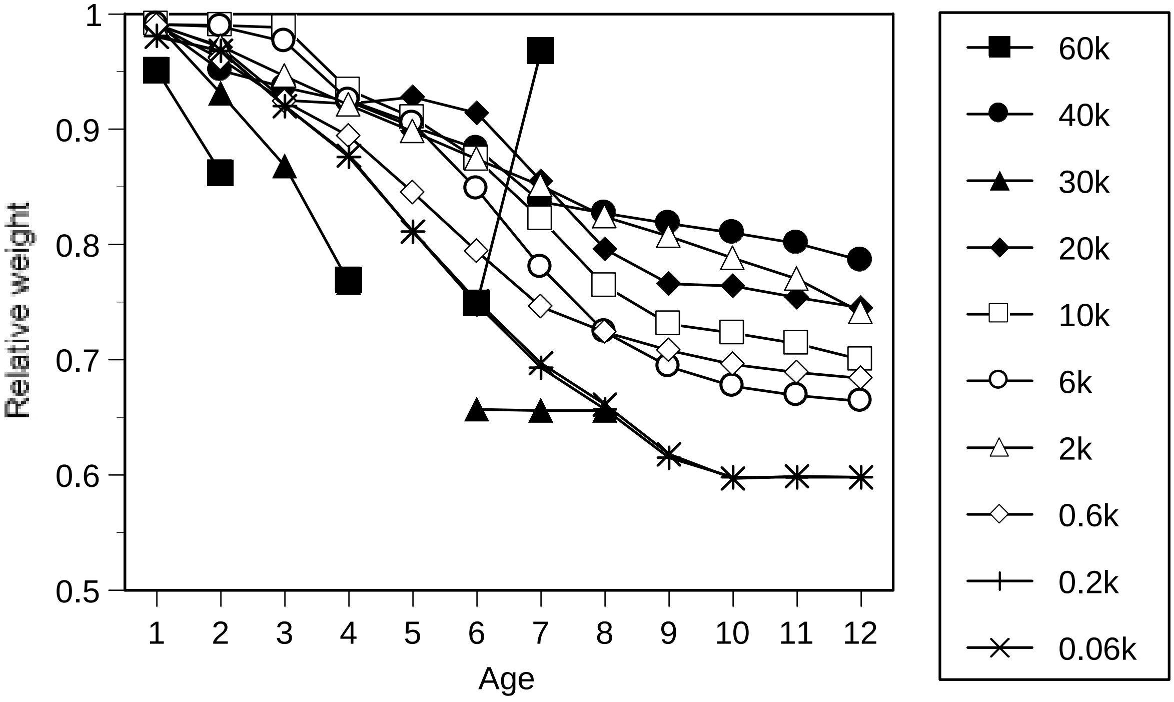

Figure 20.–Relative weight of bluegill of ages 1-12 in simulations with constant annual recruitment of 60 to 60,000 age-0 bluegills in a 10-ha lake. Results nearly overlap for the two lowest levels of recruitment, some very weak age classes are present with 40,000 annual recruits, and some age classes are missing in the simulations with 30,000 and 60,000 recruits. Data are shown for March 31 of year 15 (day 5031) of the simulations.

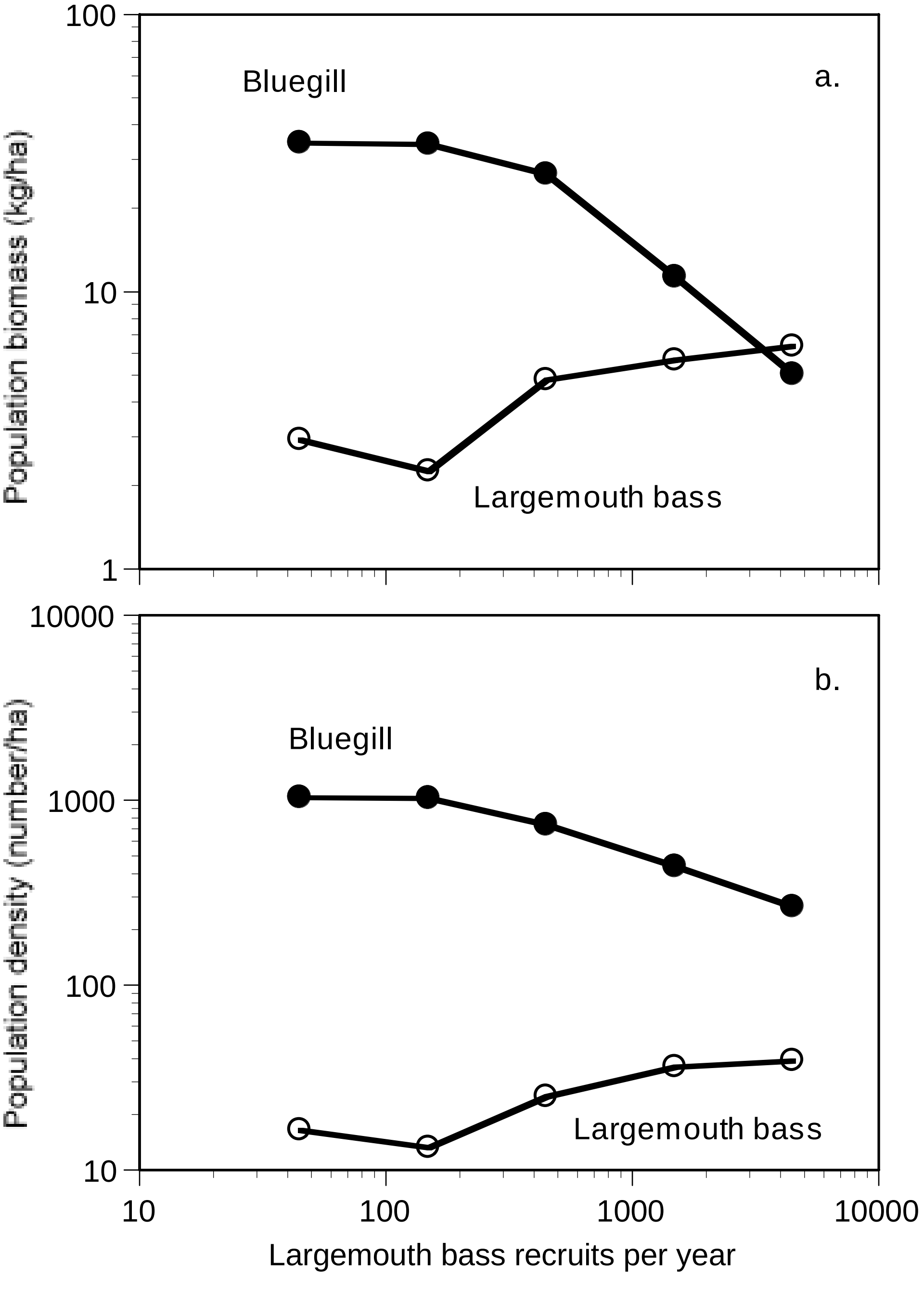

Figure 21.–Population biomass and population density of simulated populations of bluegill and largemouth bass in a 10-ha lake. Bluegill annual recruitment was held constant at 10,000; largemouth bass annual recruitment was varied from 45 to 4,500. Data are shown for March 31 of year 15 (day 5031) of the simulations.

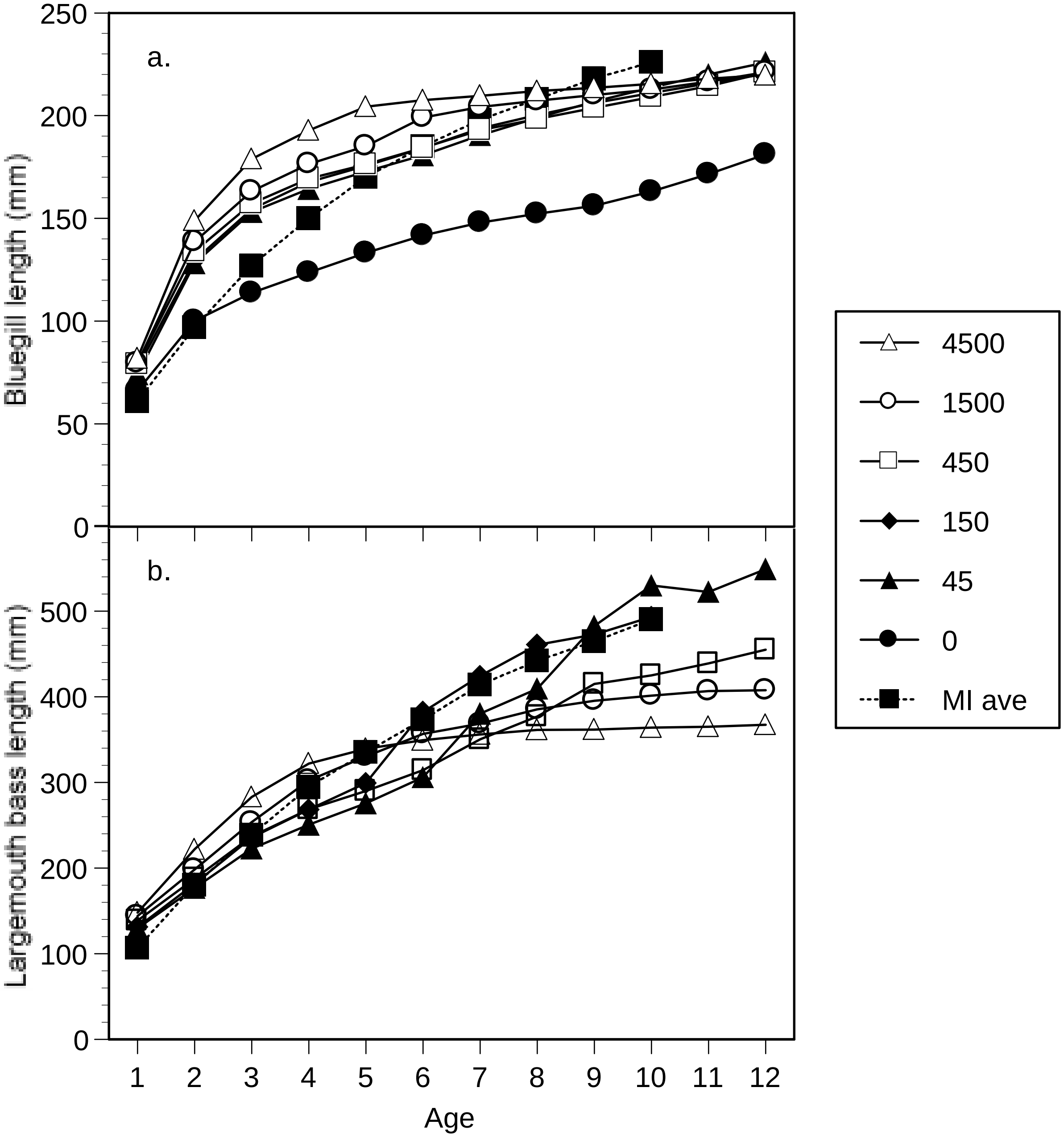

Figure 22.–Length at age of simulated populations of (a) bluegill and (b) largemouth bass in a 10-ha lake. Bluegill annual recruitment was held constant at 10,000; largemouth bass annual recruitment was varied from 45 to 4,500. Data are shown for March 31 of year 15 (day 5031) of the simulations. The dotted lines indicate the Michigan average length at age (Laarman et al. 1985).

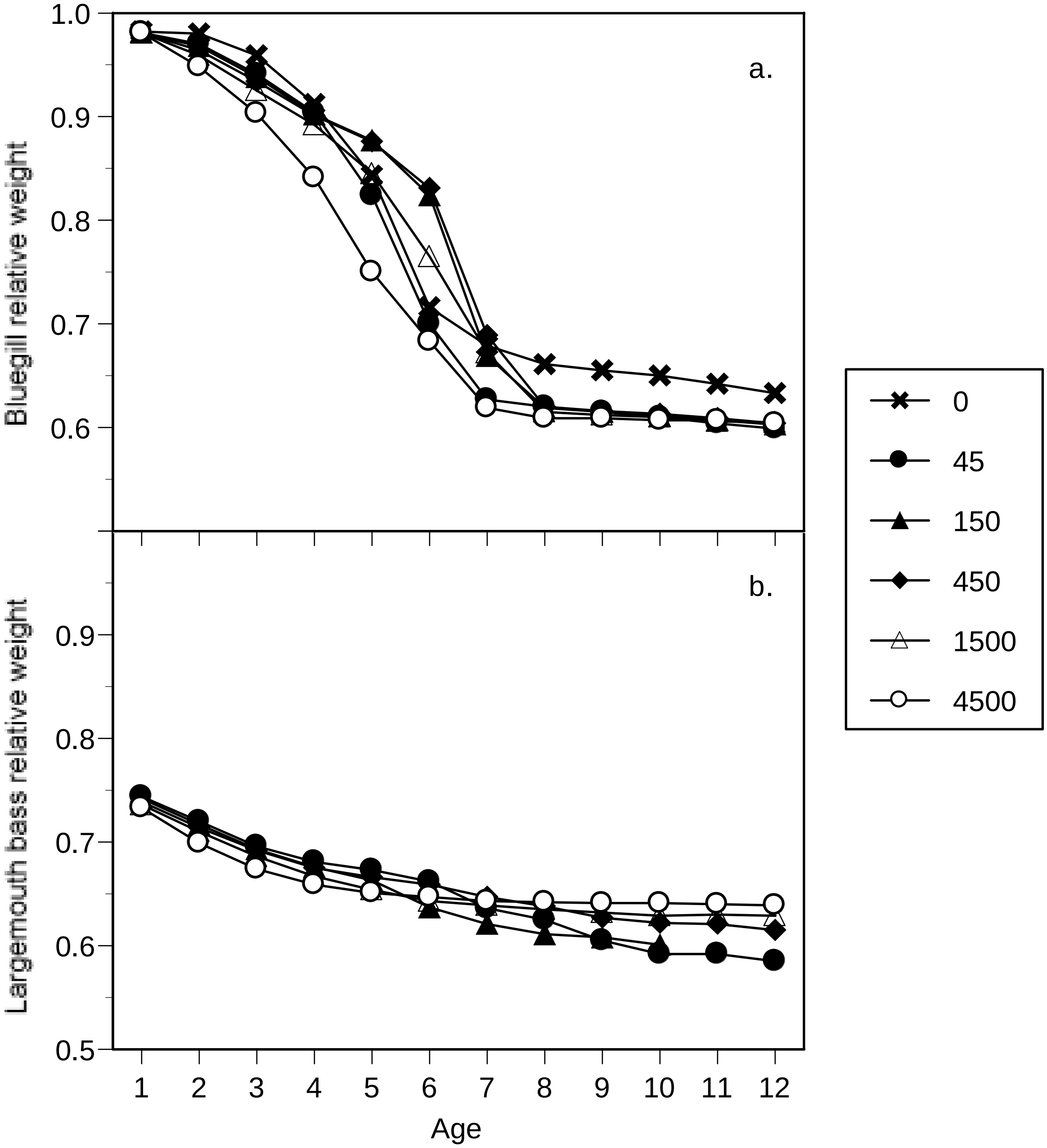

Figure 23.–Relative weight of simulated populations of (a) bluegill and (b) largemouth bass in a 10-ha lake. Bluegill annual recruitment was held constant at 10,000; largemouth bass annual recruitment was varied from 45 to 4,500. Data are shown for March 31 of year 15 (day 5031) of the simulations.

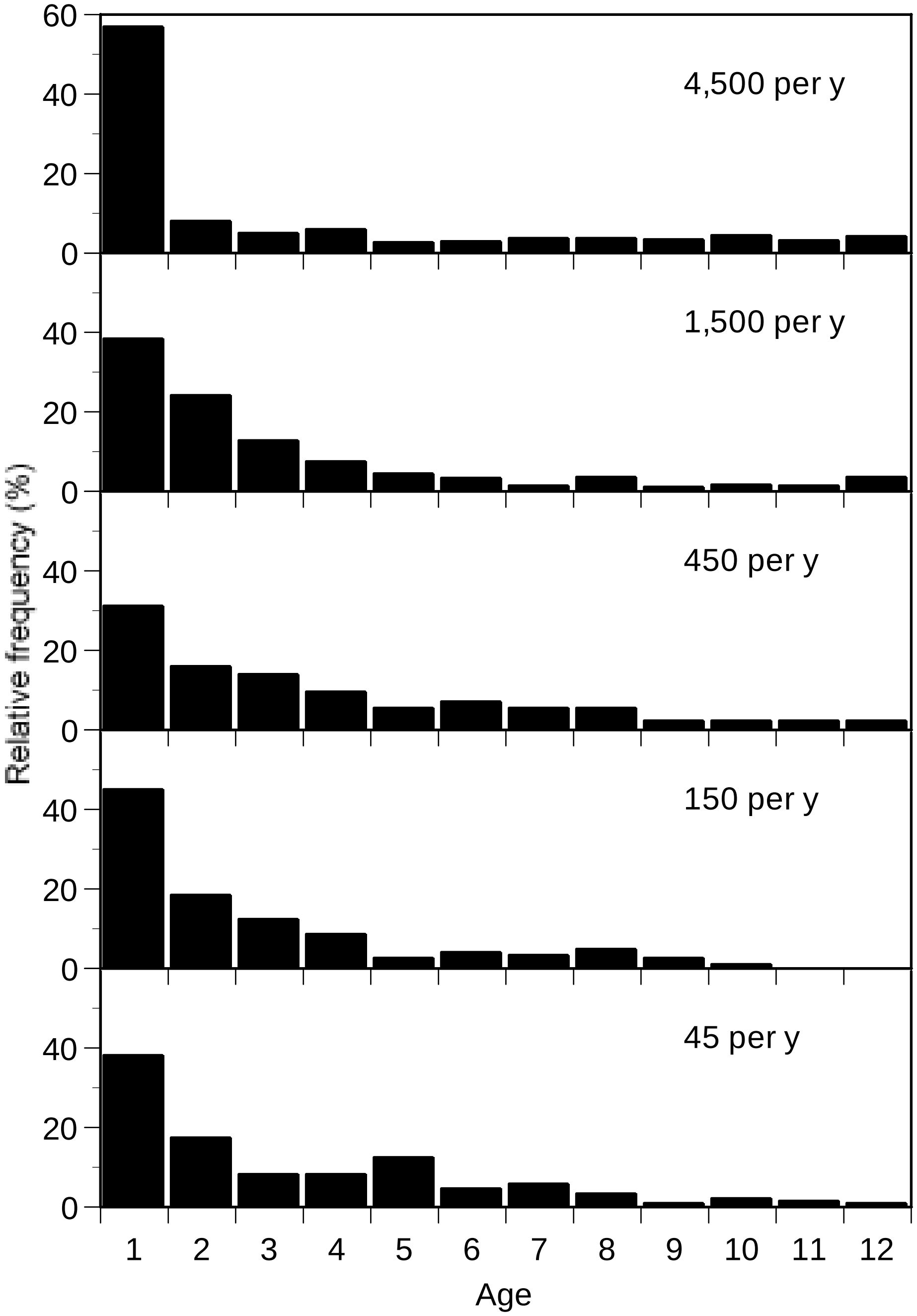

Figure 24.–Relative frequency of largemouth bass of ages 1-12 in simulations with constant annual recruitment of 45 to 4,500 age-0 bass in a 10-ha lake containing bluegill. Age classes are missing only in the simulation with 150 recruits. Data are shown for March 31 of year 15 (day 5031) of the simulations. Average annual non-starvation mortality was set at 25%.

Table 1.–Characteristics of three types of littoral invertebrate prey used in LakeMod. Carrying capacity in the logistic growth equation is set by multiplying a constant times the value for Relative K. Water-column prey represent zooplankton such as *Daphnia*, *Bosmina*, copepod nauplii, and rotifers; benthic prey represent midge larvae such as *Chironomus*; epiphytic (or vegetation-dwelling) prey represent damselfly nymphs.

Length (mm)	Weight (mg)	Relative K (number/m^3)[a]	Intrinsic rate of increase, *r* (d^{-1})	Energy density (cal/g)
		Water-column prey		
1.2	0.1938	2,000	0.077	550
1.0	0.1200	3,000	0.091	550
0.8	0.0667	6,000	0.114	550
0.6	0.0313	8,000	0.150	550
0.5	0.0194	20,000	0.180	550
0.4	0.0108	40,000	0.223	550
0.3	0.0051	80,000	0.295	550
0.2	0.0017	400,000	0.438	550
		Benthic prey		
30	88.79	60[a]	0.007	600
25	57.85	100[a]	0.009	600
20	34.24	150[a]	0.010	600
15	17.42	250[a]	0.013	600
12	10.31	400[a]	0.016	600
9	5.24	1,000[a]	0.021	600
7	2.90	1,500[a]	0.026	600
5	1.32	4,000[a]	0.035	600
		Epiphytic prey		
20	32.30	40	0.008	800
17	22.74	80	0.009	800
14	14.95	160	0.011	800
11	8.88	240	0.013	800
9	5.76	320	0.015	800
7	3.34	600	0.018	800
5	1.62	1,600	0.024	800
4	1.00	3,900	0.029	800

[a] For benthic prey, the units for density are number/m^2.

Table 2.–Characteristics of pelagic and sublittoral invertebrate prey used in LakeMod. Carrying capacity in the logistic growth equation is set by multiplying a constant times the value for Relative K. Water-column prey represent zooplankton such as *Daphnia*, *Bosmina*, copepod nauplii, and rotifers; sublittoral benthic prey represent midge larvae such as *Chironomus*, and burrowing mayflies such as *Hexagenia*.

Length (mm)	Weight (mg)	Relative K (number/m^3) [a]	Intrinsic rate of increase, r (d^{-1})	Energy density (cal/g)
		Water-column prey		
3.0	2.1578	1,000	0.031	550
2.5	1.3359	2,000	0.038	550
2.0	0.7428	3,000	0.047	550
1.6	0.4131	4,000	0.058	550
1.3	0.2393	6,000	0.071	550
1.0	0.1200	8,000	0.091	550
0.8	0.0667	20,000	0.114	550
0.6	0.0313	40,000	0.150	550
		Benthic prey		
30	88.79	60 [a]	0.007	850
25	57.85	100 [a]	0.009	850
20	34.24	150 [a]	0.010	850
15	17.42	250 [a]	0.013	850
12	10.31	500 [a]	0.016	850
9	5.24	1,000 [a]	0.021	850
7	2.90	1,500 [a]	0.026	850
5	1.32	4,000 [a]	0.035	850

[a] For benthic prey, the units for density are number/m^2.

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Appendix 1. Dynamic model for body composition, energy density, and energy allocation of fish during starvation and growth.

A fish's body composition determines its energy density (kJ/g or kcal/g), influences its growth rate and starvation time, and specifies its energy value for its predators. Predicted values of fish growth rate that are estimated with bioenergetics models are very sensitive to the specified energy density of the food and the fish. Body composition and energy density change dramatically during starvation, and vary with ration level during non-starvation conditions. In fish communities, where prey availability changes dynamically, body composition and energy density are expected to change dynamically and influence growth and condition of predators and prey. The purpose of this appendix is to describe a new model for simulating the dynamic changes in body composition, energy density, and energy allocation during starvation and growth.

This model for energy density can explain two common observations related to body composition of fish during starvation and growth: (1) the linear relationship between percent lipid and percent water, and (2) the linear relationship between energy density and percent water. This model also accounts for the changes in body composition (especially percent water and percent lipid) as fish grow in size from larvae to juveniles to adults. Using only two state variables (length and weight), the model predicts changes in wet weight, relative weight, body composition (lipid, protein, ash, water) and energy density based on the net energy obtained each day during growth (or the energy used each day during starvation).

Fraction lipid and fraction water

During fish starvation, energy used for metabolism comes predominantly from lipid, but some also comes from protein (e.g., Niimi 1972). According to Brett and Groves (1979), an average energy value for fish lipid is 9.45 kcal/g lipid. When measured in a bomb calorimeter, an average energy value for fish protein is 5.65 kcal/g protein, but because proteins are not oxidized as completely when metabolized by fish, the average metabolizable energy is 4.80 kcal/g protein (Brett and Groves 1979).

Let s represent the fraction of energy coming from lipid during starvation conditions, and let (1-s) represent the fraction of energy coming from protein. Assume that s is a constant. The grams of lipid used per kcal metabolized is, therefore, s/D_f, where D_f is the energy density of lipid (kcal/g lipid). The grams of protein used per kcal metabolized is $(1\text{-}s)/D_p$, where D_p is the energy density of protein (kcal/g protein). The ratio (R) of these two quantities represents the change in protein per unit change of lipid (g protein/g lipid).

$$R = \frac{D_f}{D_p} \cdot \frac{(1-s)}{s}$$

Let z represent the g of water associated with each g of lipid, and let y represent the g of water associated with each g of protein. For each g of lipid metabolized, R g of protein will be used, and there will be a change in body water due to the loss of lipid-associated water (z) and protein-associated water (yR).

$$\Psi = z + yR\,,$$

where Ψ is the change in water per unit change in lipid (g water/g lipid). This loss of lipid, protein, and water produces a change in wet weight.

$$Q = 1 + R + \Psi\,,$$

where Q is the change in wet weight per unit change in lipid (g weight/g lipid); this equation makes the reasonable assumption that the change in ash during starvation is negligible.

Let ΔE be the change in body energy (kcal) after 1 day of starvation. (During starvation, ΔE will be negative.) Then the change in body lipid (ΔF, g lipid) will be

$$\Delta F = \left(\frac{s}{D_f} \right) \Delta E ,$$

the change in body water (ΔH, g water) will be

$$\Delta H = \Psi \ \Delta F ,$$

and the change in body weight (ΔW, g total weight) will be

$$\Delta W = Q \ \Delta F .$$

Define f_0 as the fraction lipid and h_0 as the fraction water at some reference condition:

$$f_0 = \frac{F_0}{W_0} ,$$

$$h_0 = \frac{H_0}{W_0} \ ,$$

where F_0 is the amount of lipid (g), H_0 is the amount of water (g), and W_0 is the wet weight (g) at the reference condition. As starvation proceeds, the body composition will change, and the new values for fraction lipid (f) and fraction water (h) will be

$$f = \frac{F_0 + \Delta F}{W_0 + \Delta W} ,$$

$$h = \frac{H_0 + \Delta H}{W_0 + \Delta W} .$$

If s, z, and y are constants, then the above assumptions produce a linear relationship between fraction lipid (f) and fraction water (h) as starvation proceeds. The linear relationship can be determined from two points, representing the fraction lipid and fraction water at some reference time (f_0, h_0) and after some starvation (f, h).

$$f = h m_1 + b_1 ,$$

where the slope (m_1) is

$$m_1 = \frac{f - f_0}{h - h_0} ,$$

and after some algebra,

$$m_1 = \frac{f_0 Q - 1}{h_0 Q - \Psi} ,$$

and the intercept (b_1) is

$$b_1 = \frac{f_0 \Psi - h_0}{h_0 Q - \Psi} .$$

To my knowledge, this is the first time that someone has derived an equation based on underlying mechanisms to explain the commonly observed linear relationship between fraction lipid and fraction water.

According to the linear relation given above, the fraction lipid will reach zero when the fraction water reaches the threshold value h_{f0}.

$$h_{f0} = \frac{f_0 \Psi - h_0}{f_0 Q - 1} .$$

Energy density and fraction water

There is a decrease in energy density during starvation because of the changes in the amounts of lipid, protein and water (but not ash). The above assumptions imply a linear relationship between energy density (d) and fraction water (h) during starvation. The energy density (d_0, kcal/g) at some reference time is the total energy contained in lipid and protein, divided by body weight.

$$d_0 = \frac{F_0 D_f + P_0 D_p}{W_0},$$

where P_0 is the amount (g) of body protein at the reference time. The energy density after some starvation is

$$d = \frac{\left(F_0 + \Delta F\right) D_f + \left(P_0 + \Delta P\right) D_p}{W_0 + \Delta W},$$

where $\Delta P = R\Delta F$. Note that during starvation all the deltas (ΔF, ΔP, ΔW) will be negative. After some algebra, a linear relation is derived between d and h based on the two points (d_0, h_0) and (d, h).

$$d = h m_2 + b_2,$$

where the slope (m_2) is

$$m_2 = \frac{d - d_0}{h - h_0},$$

and after some algebra

$$m_2 = \frac{d_0 \Phi - 1}{h_0 \Phi - \beta},$$

and the intercept (b_2) is

$$b_2 = \frac{h_0 - d_0 \beta}{h_0 \Phi - \beta},$$

where β represents the change in water per unit change in energy (g water/kcal),

$$\beta = \frac{zs}{D_f} + \frac{y(1-s)}{D_p},$$

and Φ represents the change in wet weight per unit change in energy (g weight/kcal), and is the sum of changes in water, lipid, and protein per unit change in energy.

$$\Phi = \beta + \frac{s}{D_f} + \frac{(1-s)}{D_p}$$

$$= \frac{s(1+z)}{D_f} + \frac{(1-s)\left(1+y\right)}{D_p}.$$

Note that both β and Φ are constant if s, z, and y are constant. Again, to my knowledge, this is the first time that someone has derived an equation based on underlying mechanisms to explain the commonly observed linear relationship between energy density and fraction water.

Energy allocation

If a fish ingests less than a maintenance ration, then the fish uses some energy stored in body reserves, and the body composition changes as described above. If a fish ingests more than a maintenance ration, then some of that energy can be allocated to increasing body reserves and some can be allocated to increasing body structure. This section describes the method used to allocate energy to body reserves and body structure. It is an extension of the model developed by Broekhuizen et al. (1994).

Following Broekhuizen et al. (1994), I assume that all fish tissue can be categorized as either body reserves or body structure. Body reserves are those tissues that can be mobilized to supply energy during starvation; this includes nonpolar lipids, some body protein, and associated water. Tissues making up the body stucture are not mobilized during starvation. Structural tissues include the remaining body protein, body ash, and associated water. Body structure could also include polar phospholipids that make up cell membranes.

The second assumption is that the allocation of energy depends on the current ratio (ρ) of reserve energy to structural energy.

$$\rho = \frac{E_r}{E_s},$$

where E_r is the energy value of body reserves (kcal), and E_s is the energy value of body structure (kcal).

Let ΔE be the daily net energy intake, the difference between the daily total ingested energy and total energy losses and expenditures. If ΔE is positive, then it may be termed excess assimilate. Expressing the model of Broekhuizen et al. (1994) as a difference equation (because of the daily time step used in LakeMod),

$$\Delta E_s = C(\rho)\ \max(\Delta E, 0),$$

where ΔE_s is the amount of energy (kcal) allocated to structural tissues, $C(\rho)$ is the fraction of excess assimilate allocated to structural tissues, and $\max(\Delta E, 0)$ is excess assimilate. The expression $\max(\Delta E, 0)$ is used to ensure that ΔE_s is never negative, to be consistent with the assumption that fish do not metabolize body structure and do not shrink in length. After specifying the amount of energy allocated to structural tissues, the remainder goes to reserve tissues.

$$\Delta E_r = \Delta E - \Delta E_s$$

If ΔE is negative, then ΔE_s is zero, and ΔE_r will be negative, representing the energy shortfall to be made up from body reserves.

Broekhuizen et al. (1994) define the following relationship for $C(\rho)$:

$$C(\rho) = \min\{1, C_0 \max[0, 1 + \theta(\rho - \rho_0)]\},$$

where $C_0 = 1/(1 + \rho_0)$, the fraction allocated to structural tissues when $\rho = \rho_0$; ρ_0 is the ideal or nominal ratio of reserve energy to structural energy; and θ is a parameter influencing how quickly ρ approaches ρ_0. Figure 7 shows how $C(\rho)$ changes with ρ, for $\rho_0 = 1.5$, so that $C_0 = 0.4$. Broekhuizen et al. (1994) use a value of $\theta = 3.0$, but my simulations suggest that a lower value (perhaps 1.0 or 0.3) may be more appropriate for representing growth of fish under field conditions.

In attempting to apply this approach to an entire fish population, it became clear that the model needed to be extended to allow ρ_0 to vary with fish size. Body composition changes dramatically from larval fish and small juveniles to adults. In very small fish the energy reserves are relatively low, the fraction water is relatively high (80-90%), and the time to starvation is just a few days. In adults the energy reserves are much greater, the fraction water is closer to 75%, and the time to starvation is a few weeks or even months.

In extending this approach to a full range of fish sizes, I made some simplifying assumptions. I assumed that all body lipid is included in reserve tissues, all ash is included in structural tissues, and that structural protein was a constant fraction of standard weight.

If no lipid is included in structural tissues, then all energy in structural tissue comes from protein.

$$P_s = k_{ps} W_{std} \,,$$

$$E_s = P_s D_p \,,$$

where P_s is the amount of protein in structural tissues (g), k_{ps} is a constant, W_{std} is standard weight (g) (Murphy et al. 1991).

$$\log_{10} W_{std} = a + b \log_{10} L \,,$$

where L is fish length (mm), and for bluegill, a = -5.374 and b = 3.316 (Murphy et al. 1991).

McComish (1974; Niimi 1974) documents that the amount of ash (A, g) in bluegills increases with fish length:

$$A = \exp(-16.309 + 3.459 \ln L) \,.$$

Assume that the nominal fraction lipid (f_0, fraction wet weight) increases with fish length:

$$f_0 = \exp(a_f + b_f \ln L) \,,$$

where a_f = -4.740 and b_f = 0.401 for the case that the fraction lipid increases from 0.022 in 10-mm bluegill to 0.080 in 250-mm bluegill. Then the nominal amount of lipid (F_{r0}, g) will be

$$F_{r0} = f_0 W_{std} \,.$$

Because all lipid is assumed to be in reserve tissue, with a body composition as given above, the total nominal energy in reserve tissue is

$$E_{r0} = \frac{F_{r0} Q}{\Phi} \,,$$

and the nominal energy ratio is

$$\rho_0 = \frac{E_{r0}}{E_s} \,,$$

or

$$\rho_0 = f_0 \left(\frac{Q}{\Phi k_{ps} D_p} \right) .$$

Note that the term in parentheses is independent of fish length. So under these assumptions it is only f_0 that causes ρ_0 to increase with fish length.

Two state variables

Given the assumptions made above, the changes in fish body composition and energy density during starvation and growth can be computed using just two state variables: wet weight (W, g) and length (L, mm). As described above, length alone (using various constant parameters) determines standard weight (W_{std}), nominal fraction lipid (f_0), nominal energy ratio (ρ_0), amount of structural protein (P_s), amount of ash (A), nominal weight of reserve tissues (W_{res0}),

$$W_{res0} = Q f_0 W_{std} \,,$$

and weight of structural tissues (W_s):

$$W_s = W_{std} - W_{res0} \,.$$

The second state variable (W) is also needed to compute the current weight of reserve tissues (W_{res}):

$$W_{res} = W - W_s,$$

and relative weight (W_r):

$$W_r = \frac{W}{W_{std}}.$$

Using various constant parameters and the two state variables L and W, current values can be computed for body components as follows:
fraction lipid (f):

$$f = \frac{W_{res}}{QW},$$

fraction protein (p):

$$p = \frac{k_{ps} W_{std} + \frac{W_{res} R}{Q}}{W},$$

fraction ash (a):

$$a = \frac{A}{W},$$

fraction water (h):

$$h = 1 - (f + p + a),$$

and energy density (d):

$$d = f D_f + p D_p.$$

So in this model, two state variables, length and weight, contain all the information necessary to specify relative weight, energy density, and proximate composition of a simulated fish.