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Modeling Growth and Survival in an Age-0 Fish Cohort

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Abstract.—We applied an individual-based model to an age-0 cohort of smallmouth bass *Micropterus dolomieu* to simulate the cohort's growth and survivorship through its first growing season. The purpose was to determine whether the stock–recruitment characteristics of the age-0 fish could be predicted. The model smallmouth bass were exposed to size-dependent predation, size-independent mortality, and starvation mortality resulting from depletion of their prey supply. Survivorship curves were produced by model simulations. When survivorship at a given time was plotted against initial egg density during the early growing season, the curve resembled the peaked pattern of a Ricker-type curve. In contrast, curves for survivorship during the late growing season had no noticeable peak or maximum. Other results showed (1) strong density dependence of the mortality rate early in the growing season and density independence late in the growing season; (2) a distinct critical time (CT) during which the slope of the survivorship curve changed from a steep to a shallow decline, and (3) a decrease in CT as a function of the initial egg density. Competition for and overexploitation of prey during the early growing season produced these results. The model simulation results resembled patterns of some empirical data.

Stock–recruitment models have been used for decades as a means for studying and attempting to predict the characteristics of animal populations that reproduce at discrete intervals of time. These models have formed the theoretical basis for studies of fish population dynamics, the Ricker (1954) and Beverton and Holt (1957) models being the most widely recognized functions relating a reproductive population to progeny production. The basic question is: If there is a reproductive population of $N(t)$ at time t, how many recruits to the population (e.g., yearling animals) will there be a year later at time $t + 1$?

A characteristic feature of the stock–recruitment curves produced from these models is their nonlinearity as a function of the increasing number of spawners. The Beverton–Holt curve approaches an asymptote, signifying that increasing the number of spawners contributes less and less to increasing the number of recruits. This effect is sometimes termed "compensation." The Ricker curve represents a situation in which the number of recruits at first rises but then eventually starts to decrease as the number of female spawners continues to increase. Therefore, the curve has a maximum or a peak at some intermediate density of spawners. This effect is sometimes called "overcompensation" (e.g., McFadden 1977).

These models are not the only stock–recruitment models that have been developed, but they represent the class of models with a few parameters that are fit statistically to empirical data on reproductive population and recruit population sizes. Both the Ricker and Beverton–Holt models contain a negative feedback between the number of spawners—and of the initial number of their progeny—and the subsequent survival rate of these progeny. However, these models, while having an appearance of plausibility, are poor predictors of year-to-year variations in fish populations. Crecco and Savoy (1984), for example, showed that stock–recruitment models of Ricker (1954), Beverton and Holt (1957), and others could explain no more than 6.5% of the year-to-year variation in the abundance of American shad *Alosa sapidissima* in the Connecticut River. Part of the reason for this lack of success is that these models ignore the interactions between the populations and the changing abiotic and biotic environments. Another reason is that the causal relation between spawner and progeny density and mortality is more complex than is assumed in the models. As Hjort (1914) suggested, recruitment could be determined by events occurring when fish are in the egg and larval stages and more susceptible to environmental fluctuations. Models of the Ricker and Beverton–Holt types can be extended to account for effects of the environment (Crecco and Savoy 1984) by addition of parameters determined by regression against presumably key environmental characteristics, but these models remain phenomenological functions that do not attempt to represent mechanisms.

The objective of the present paper is to determine if a mechanistically based model can make good qualitative predictions of stock–recruitment relationships in terms of causal factors during a cohort's first growing season. The use of mechanistic modeling of fish populations is not new and several such models have been developed (e.g., Koonce et al. 1977; Serchuk et al. 1980; Beyer and Laurence 1981; Banks et al. 1989). The particular mechanistic approach used here, individual-based modeling, is relatively new, however.

Individual-based models explicitly simulate a population as an assemblage of interacting individuals (see Huston et al. 1988; Hogeweg and Hesper 1990; DeAngelis and Gross 1992 for overviews; see DeAngelis et al. 1979; Madenjian and Carpenter 1991; Trebitz 1991; MacKay 1992; Rose and Cowan 1993, for detailed applications). The survival, growth, and behavior of a large representative sample of individuals in the population or, in this case, an age-class cohort, are followed simultaneously. In principle, any relevant characteristics of individual organisms that can be quantified can be included in such a model: age, size, sex, spatial location, aggressiveness, competence at catching prey, and habitat preferences, for example. In practice, quantitative information suitable for modeling may be available for only a few such characteristics. In the model described below for age-0 smallmouth bass *Micropterus dolomieu*, the main characteristics modeled are fish lengths and weights.

An important reason for using the individual-based approach is that individuals in a cohort can differ greatly from one another both in intrinsic, genetically based characteristics and in environmentally conditioned responses such as hatching date and encounters with potential prey and predators. Our current model does not account for genetic differences between fish, but it allows their hatching dates to differ and their day-to-day encounters with prey to vary stochastically according to Monte Carlo simulation. By simulating simultaneously many individual fish, interacting through exploitation of prey, the model produces the collective characteristics of the population. Because individual age-0 fish in the population are simulated, the model makes explicit predictions regarding the daily feeding and growth of individuals and the changes in the overall size distribution of a cohort, which are often accessible to measurement.

The Fish Cohort Model

The model used here is meant to be a relatively generic one for seasonally spawning freshwater fish. However, in developing the model, we relied on specific information for smallmouth bass and for the environment of a typical temperate lake, Lake Opeongo, in southern Ontario. An individual-based model of smallmouth bass was developed and described by DeAngelis et al. (1991), and then fit to a set of lakes in southern Ontario (B. J. Shuter and others, unpublished). Because the model is described in detail in the first of those papers, only a brief summary is given here. Components of the model are specified in the Appendix. Although the model now is specific to smallmouth bass, its basic processes of growth and mortality may be relevant to other species and situations.

In the model, numbers and sizes of adults that spawn to produce the age-0 population are prescribed as input variables. The day on which a male smallmouth bass begins guarding fertilized eggs on the nest is predicted from an empirical regression by Ridgway et al. (1991). This regression plots the number of accumulated degree-days needed for commencement of guarding as a function of male length. The duration of the spawning season in the model is typically about 2 or 3 weeks. The length of time from egg fertilization to swim-up of larvae from the nest and initiation of feeding in the water column is also described by accumulated degree-days (see DeAngelis et al. 1991). The age-0 fish are modeled as individuals only after they have reached the swim-up stage. Initial lengths of swim-up smallmouth bass were chosen randomly in the interval 8.5–9.5 mm based on data from Friesen (1990). Larval and postlarval smallmouth bass were assumed to stay near the nest for 21 d after swim-up or until they reached a length of 20 mm, whichever came first (Ridgway and Friesen 1992).

We assumed that smallmouth bass began to forage immediately at the time of swim-up (Friesen 1990). Foraging was modeled as random (Monte Carlo) encounters with prey. A mean probability of encounter with prey, based on predator searching volume and current prey density, was calculated for each prey type on each day. The number of prey actually encountered was determined through the use of pseudorandom numbers. Each smallmouth bass searched a larger volume of water as its own body size increased as a result of increases in both swimming speed and reactive distance (the distance at which a fish can perceive prey of a particular size) that typically parallel increases in fish body size (Breck and Gitter 1983). An age-0 individual was assumed to feed preferentially on the largest prey size-classes that its own gape allowed it to consume head first. However, if necessary, the individual could increase its breadth of selected prey towards smaller size-classes until it first either achieved its maximum possible intake or consumed all prey encountered. Age-0 fish switched from feeding in the water column to feeding on benthos when they reached a size at which benthivory was energetically more profitable than planktivory. Because the daily feeding of each fish was determined by Monte Carlo simulation, prey intake varied from day to day and from fish to fish.

The modeled prey were divided into seven size-classes of zooplankton in the water column and 18 size-classes of benthos, of which the smaller insect prey became available to age-0 fish late in the growing season. This prey structure was somewhat arbitrary, but it represented the wide variety of prey sizes typically available to age-0 smallmouth bass. The prey population in each size-class was described by a discretized version of the logistic equation with daily time steps. A carrying capacity was specified for each prey size-class such that the total carrying capacity was 70 $mg \cdot m^{-3}$ dry weight for all zooplankton and 49 $g \cdot m^{-2}$ dry weight for all benthic prey. These weights were chosen to agree on the average with data on zooplankton (G. Morgan, Ontario Ministry of Natural Resources, personal communication) and benthic prey (Rasmussen, McGill University, personal communication) for southern Ontario. The turnover or regeneration rates of these prey species were based on data from oligotrophic lakes in southern Ontario (Plante and Downing 1989) as well as on losses due to daily consumption by age-0 predators. Losses of prey to other predators were not considered. Feeding by age-0 smallmouth bass removed prey from the exploited size-classes so that the predators were capable of depressing the levels of abundances of the various prey types and size-classes.

Growth of each age-0 individual was predicted by a bioenergetics model that used daily food intake and mean daily temperature as input data to compute the daily gains in weight. This model was developed for the smallmouth bass by Shuter (DeAngelis et al. 1991). In this bioenergetics model, when fish weight increases, length increases allometrically. When weight decreases as a result of low prey consumption by the fish, length remains fixed and both weight and condition factor of the fish thus decline. When the condition factor, measured as ash-free dry weight at a given length divided by the ash-free dry weight of a growing fish at the same length, declines below a critical level, the fish dies of starvation.

We allowed mortality to affect both individuals on the nest (pre-swim-up) and free-swimming individuals. For simplicity, losses of pre-swim-up larvae and possible losses of whole nests were ignored. Mortality of post-swim-up individuals occurred through both starvation and a variety of external agents lumped together as size-dependent and size-independent factors. Predation is probably the most important external agent (Miller et al. 1988). Size-dependent mortality was assumed to be stronger than size-independent mortality and fell off as $0.2\exp(-0.4L)$, where L is the length of a given individual (Houpt 1991). It is known that young smallmouth bass have a very poorly developed repertoire of antipredator behavior after swim-up, but that their defense improves substantially with increasing size (Brown 1985).

Although the model of smallmouth bass incorporates rather specific assumptions and detailed submodels for reproduction, foraging, growth, and mortality, the basic processes occurring are fairly general to a variety of freshwater fish species that have a relatively short spawning season, suffer size-dependent and size-independent mortality, and can depress their prey supply.

Model Simulations

Our model simulations were designed to investigate the relationship between the initial number of fertilized eggs in a spawning area and the survival and size distribution of age-0 fish through the growing season. To accomplish this, we performed a sequence of simulations in which the number of eggs was successively increased. We used a simulated male spawning population of 100

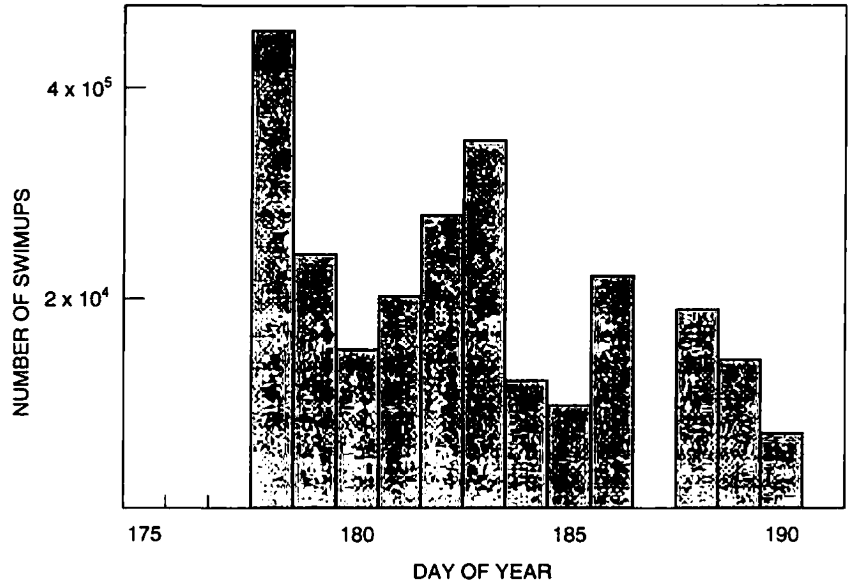

FIGURE 1.—Model simulation of numbers of larval smallmouth bass swimming up on various days during the reproductive season, based on temperature-dependent relationships of spawning and egg and early larval development. The same temporal pattern of swim-up was used in every simulation leading to Figure 2, although absolute numbers of swim-up fish varied because the number of eggs per nest was varied from simulation to simulation.

males with the approximate range of lengths (240–450 mm) of males known to have spawned in Jones Bay, Lake Opeongo, in a given year. The number of eggs per nest was successively increased, representing either more eggs per spawning female or more females depositing eggs per nest. With this approach, the initial number of eggs in the whole spawning area ranged from 50,000 to 2,000,000. All nests were assumed to be in a 10-hectare area, and the age-0 fish remained in that area through the rest of the growing season. Age-0 fish had access to all the prey available in this area; that is, the prey were assumed to be well mixed in the 10-hectare area.

The simulations were carried out from the beginning of the spawning season to the end of the growing season. The relative numbers of swim-up fish on each day of the spawning season are shown in Figure 1. This pattern resulted from the assumed distribution of male spawner sizes and the relationship described by Ridgway et al. (1991) between male size and spawning date, and it is consistent with data from southern Ontario lakes (Shuter and others, unpublished).

The simulations did not explicitly simulate every age-0 fish, because the 486 personal computer we used could not readily keep track of 50,000–2,000,000 individuals. In each simulation, 600 age-0 fish were simulated, representing the whole cohort in each case via a scaling factor; that is, one simulated fish represented many fish. The 600 simulated fish comprised the "model sample" population. Each time an individual simulated fish died, it was replaced by another individual drawn randomly from the model sample population on that day. Thus the model sample population was kept at 600 fish even though the cohort may have suffered heavy mortality from day to day. However, the scaling factor was decreased following mortalities on each day, so that each of the 600 modeled fish represented fewer other fish. This simulation technique, which we call "renormalization," has been shown to produce accurate results. Rose and Cowan (1993) simulated populations using this technique with 500 fish and then with up to 500,000 individuals (without renormalization). The results agreed well.

Results

The relationship between the number of fertilized eggs and the simulated number of surviving age-0 fish (for the baseline scenario with parameters listed in the Appendix) differed between a time early in the growing season, July 20, and a time at the end of the growing season, November 1 (Figure 2). The relationship on July 20 had a

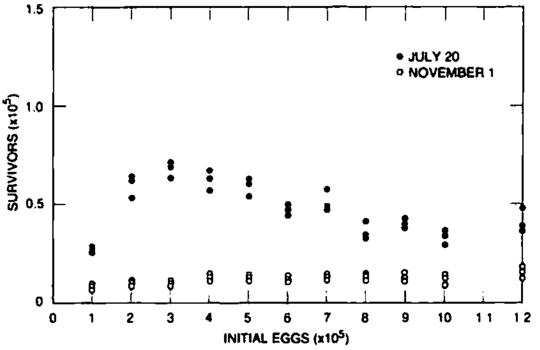

FIGURE 2.—Modeled numbers of surviving age-0 smallmouth bass on July 20 and November 1 versus the initial egg numbers (identical to the numbers of swim-up fish) when swim-up occurred over 2 weeks. Three simulations were made for each initial egg number.

maximum, somewhat like a Ricker curve (Ricker 1954). We do not identify this curve with a Ricker curve, because it is based on an entirely different modeling approach, but the shape does suggest overcompensation. The relationship for November 1 had no apparent maximum.

In his 22-year study of brown trout *Salmo trutta* in Black Brows Beck in the English Lake District, Elliott (1989) measured survivorship early (May–June) and late (August–September) in the growing season. Patterns of survival in relation to egg density were similar to ours: the data had a distinct maximum early in the growing season, but not later (Figure 3).

There have been numerous studies of survival of age-0 fish, including those of Serns (1984) for smallmouth bass, van der Veer (1986) for plaice *Pleuronectes platessa*, Hume and Parkinson (1987) for steelhead *Oncorhynchus mykiss*, and others discussed by Hume and Parkinson (1987) and Cushing (1988). However, Elliott's work on age-0 brown trout has the most relevant data for detailed comparison with our model, and we have restricted our comparisons to his data. Although there are major differences between a salmonid species in a stream and a centrarchid species in a lake, we believe that the density-dependent factors influencing growth and mortality in an age-0 fish cohort may be general enough to apply to both species in a similar way, though the specifics of how they operate may differ.

To assess the effects that might be caused by details of the spawning and swim-up scenarios, we also performed simulations in which the spawning season was compressed and all age-0 fish were assumed to swim up on the same day (July 3). Survivorship computed on July 20 and November 1 showed the same qualitative pattern as before (Figure 4). Survivorship was somewhat higher when all the fish swam up on July 3 than when the spawning season was extended, probably because the average age-0 fish was spawned at a

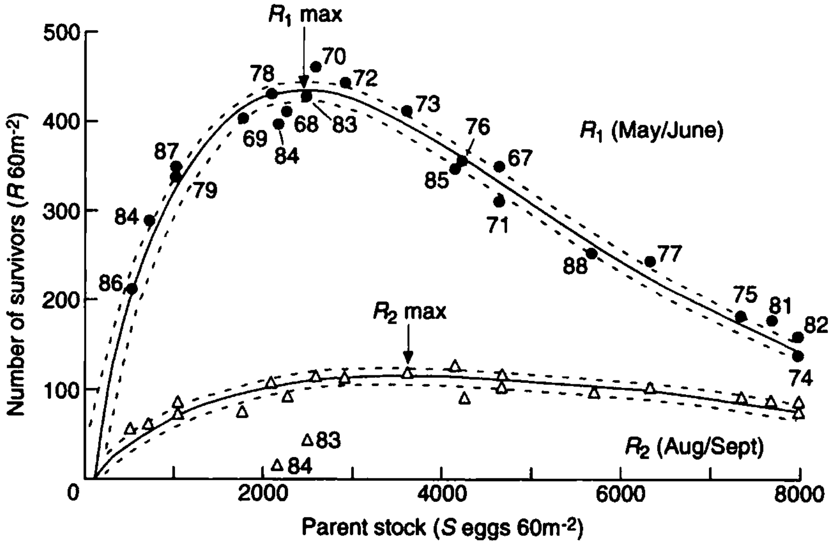

FIGURE 3.—Empirical data on brown trout survival at two times during their first growing season as a function of egg density. Broken lines are 95% confidence intervals; numbers along curves are years. (Redrawn from Figure 1 of Elliott 1989 with permission from the author and the British Ecological Society.)

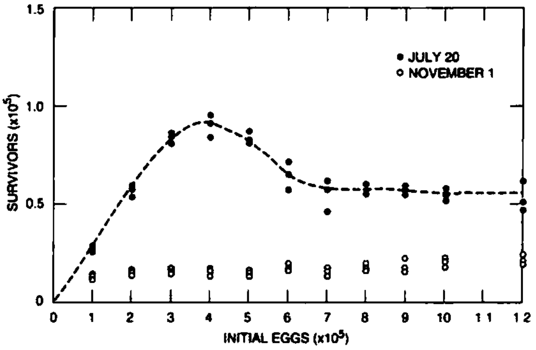

FIGURE 4.—Modeled numbers of surviving age-0 smallmouth bass on July 20 and November 1 versus the initial egg numbers when swim-up occurred on one day.

later date and so was exposed to mortality for a shorter time.

When number of survivors was plotted against time, three distinct patterns of mortality were evident (Figure 5). First, a relatively slow decline in numbers occurred just before the end of the swim-up period (phase I). Size-dependent mortality was large during this period because the mortality rate $0.2\exp(-0.4L)$ is large for small values of fish length L, but starvation mortality was slight because the fish had little time to lose weight. Also, mortality in phase I was confounded by the arrival of new swim-up fish (fish are not counted in the population until they have swum up). Second, a rapid decline in numbers lasted a few weeks (phase II). Starvation mortality was dominant during this period. A much reduced mortality rate, lasting the remainder of the growing season, marked phase III. These results are similar to Elliott's (1989) for brown trout (Figure 6). One can roughly estimate the transition from phase II to phase III by fitting regression lines to the respective survivorship data and determining where they intersect. Following Elliott (1989), we call the time from swim-up to this intersection point the critical time, CT. Values of CT decreased with increasing initial egg number both in our simulations (Figure 7) and in Elliott's empirical study (Figure 8b).

One further result resembling Elliott's was obtained by plotting the daily mortality rates, Z, early and late in the growing season as a function of initial egg density. These mortality rates were approximated from the slopes of the lines in Figure 5, divided by the average number of age-0 fish present during the respective mortality phases. Daily mortality showed a strong positive relationship to initial egg density in the early period, but it was independent of egg density in the late period (Figure 9), a result very similar to Elliott's (1989), shown in Figure 8a. The strong density dependence suggests that heavy exploitation of prey by age-0 fish had a feedback effect on fish mortality. A similar pattern of density-dependent mortality of age-0 plaice was noted by van der Veer (1986) (his results are reprinted in Figure 5.3 of Cushing 1988).

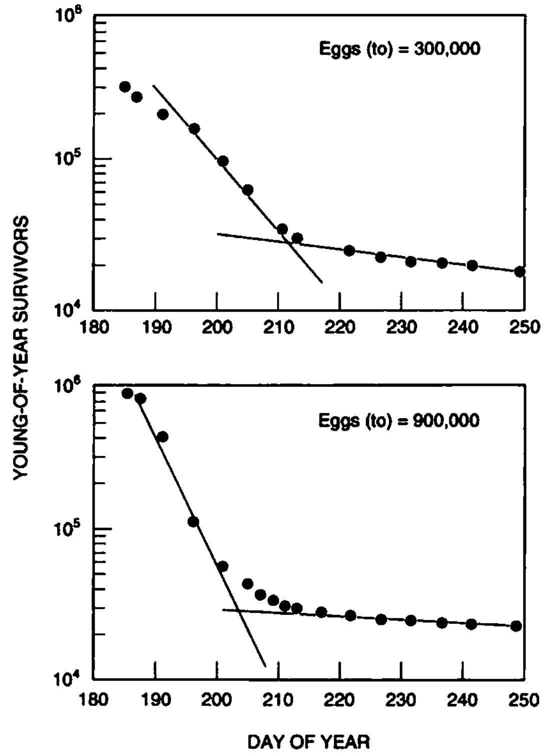

FIGURE 5.—Modeled age-0 smallmouth bass survivorship as a function of time for two initial (t_0) egg numbers: 300,000 (top) and 900,000 (bottom). Least-squares regression lines were fit to two segments of the survivorship curves: (1) the part of the curve for later than day 220 and (2) the four days on which the rate of mortality seemed to be the highest (days 196, 201, 205, 210 for 300,000 eggs, and days 188, 191, 196, 201 for 900,000 eggs). The intersections of the lines were computed to be 30.5 d (top) and 20.5 d (bottom) from day 183.

To provide a further context for understanding these patterns, a brief sensitivity analysis was performed by changing the assumptions on some of the parameters to see how they affected results.

Increase in prey regeneration rate.—It might be expected that prey availability would play a role in age-0 survival. When the prey regeneration rate was doubled from the baseline (Appendix), sur-

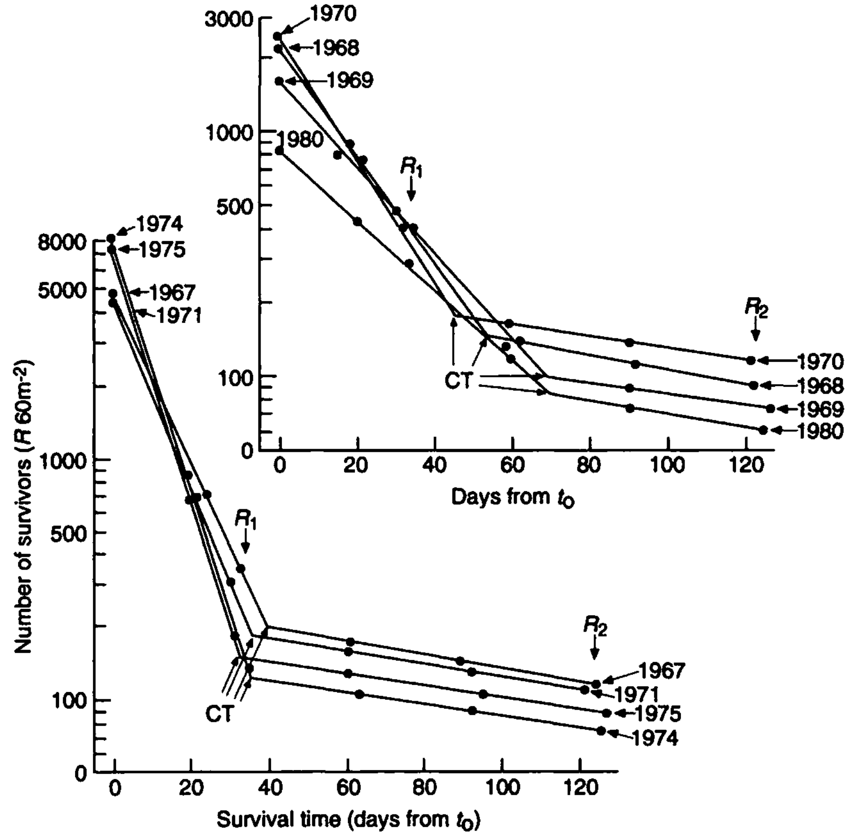

FIGURE 6.—Empirical survivorship of age-0 brown trout hatching at time t_0 from eggs spawned at several densities (see Figure 3); R_1 is May–June and R_2 is August–September. (Redrawn from Figure 3 of Elliott 1989 with permission of the author and the British Ecological Society.)

vivorship on July 20 was generally higher at high egg numbers than at baseline and only a moderate maximum in the survivorship curve developed (Figure 10).

Decrease in size-dependent mortality.—Changes in the size-dependent mortality rate had a smaller effect on the July survivorship maximum than did changes in the prey regeneration rate, though some effect was observed. A decrease to 25% of the baseline mortality value (Appendix) made the maximum of the survival curve somewhat less pronounced (Figure 11a). A doubling of the baseline value of size-dependent mortality sharpened the peak by decreasing the survivorship at higher density (Figure 11b).

Support for the idea, suggested by Figure 9, that the large age-0 mortality during phase II in the model was a density-dependent effect of overexploiting prey can be obtained by looking at the biomass density of the model zooplankton, which were the sole prey during that period. Depletion

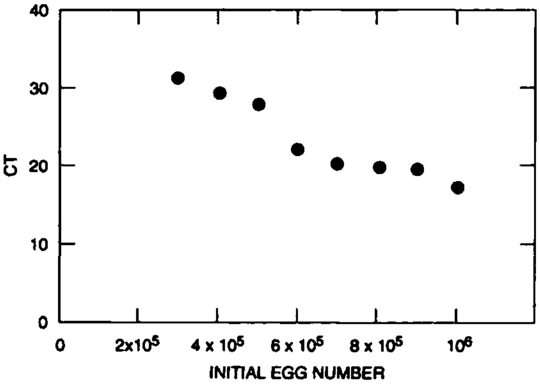

FIGURE 7.—Critical time (CT), the approximate number of days following swim-up before the sharp decrease in the mortality rate, modeled in relation to initial number of smallmouth bass eggs and computed from survival plots such as those shown in Figure 5. The critical time is measured from day 183 (approximately the middle of the swim-up period) to the intersection of high- and low-mortality regressions (see Figure 5).

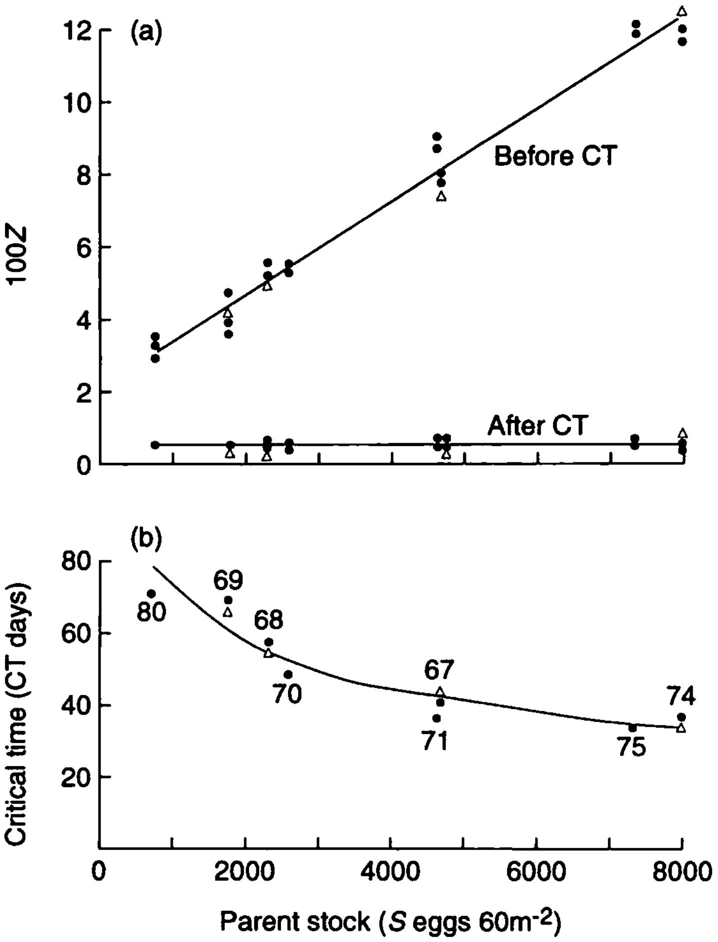

Figure 8.—(a) Empirical values of daily brown trout mortality rate, Z, in the early and late parts of the growing season as a function of initial egg number. (b) Empirical values of the critical time (CT) for brown trout. Numbers along the curve denote years. (Redrawn from Figure 5 of Elliott 1989 with permission of the author and the British Ecological Society.)

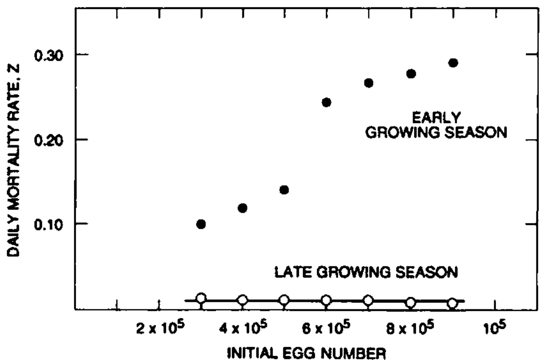

Figure 9.—Modeled values of daily smallmouth bass mortality rate, Z, in early and late parts of the growing season as a function of initial egg number.

of the zooplankton in the water column coincided with the end of phase I (see Figure 12, which shows the zooplankton biomass for a typical simulation at high initial egg density). The steep decline in age-0 fish during phase II was caused primarily by starvation, though detailed results from the simulation showed there was also some mortality from size-dependent predation. When phase II ended, the age-0 population had declined so much that partial recovery of the prey population was possible (compare the slight increase in zooplankton during this phase in Figure 12 with the decline of the age-0 fish in Figure 5, bottom). The time from swim-up to the end of phase II is what Elliott (1989, 1990a, 1990b) referred to as the critical time. During phase III, starvation mortality declined to a very small fraction of its value during phase II. Some size-dependent mortality continued to occur, but size-independent mortality became a much more important component of the overall mortality.

Discussion

The early-season maxima that occur in the curves of survivorship versus egg density for both modeled and empirical data (Figures 2, 3) indicate the effect of density on survival early in the growing season, resulting in overcompensation. Many studies of age-0 survivorship show density-dependent survival, including Sern's (1984) of smallmouth bass in Nebish Lake, Wisconsin, and several cited by Hume and Parkinson (1987) and Cushing (1988). Because Elliott's study (1989, 1990a, 1990b, and earlier papers) on brown trout provided much information that could be compared in detail with our model, we focused on that study. Although we developed our model for smallmouth bass, the model should be at least a good analog for other species because age-0 fish of many species can be expected to undergo similar patterns of growth and survival.

The close agreement of model results with empirical information does not mean, of course, that the mechanisms in the model are necessarily the explanation for cohort growth and survival characteristics in the field. Conditions in the field are more complex, and somewhat different mechanisms can act. For example, the high phase II mortality in the model simulations was due largely to starvation. Whether such fish in the field would actually reach the starvation point or other sources of mortality (e.g., disease, parasitism, predation) would remove the fish first is open to debate. But any mechanism by which age-0 fish are rapidly lost from a population due to causes directly or indirectly related to a loss in body weight should produce a behavior like that observed in phase II of the model simulations. The precise mechanism by which they are lost should not affect this result. Elliott (1990b) offered a different explanation for the survivorship shown in Figure 6 based on the strong empirical evidence that some age-0 brown trout are able to occupy territories whereas others are not. The number of trout without territories experienced a rapid decline to zero by the end of the critical period. Our model fish were not territorial, so Elliott's explanation is not possible for our case. However, the mechanism of death because of exclusion from territories, though differing from our model results of a rapid decline due directly to starvation, should produce analogous results. Perhaps a variety of mechanisms can produce results similar to Elliott's empirical findings and our model results.

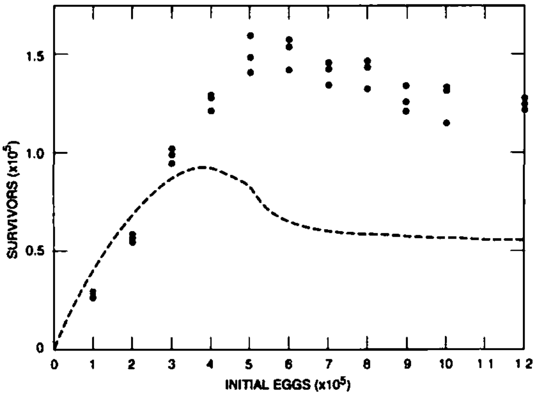

FIGURE 10.—Number of smallmouth bass survivors on July 20 versus initial egg numbers for double the baseline prey regeneration rate. An outline of the survivorship curve from Figure 2 is shown for comparison.

The importance of body size may be the factor that makes the brown trout and smallmouth bass systems similar. With respect to brown trout, body size and territory possession were the link between density-dependent survival and size-dependent mortality (Elliott 1990b). Competition for territories was most pronounced when trout were below the critical body size (40 mm), which largely defined the end of the critical period (Elliott 1990b). With respect to modeled smallmouth bass, vulnerability to starvation was also linked to body size, the small size-classes suffering nearly all the starvation mortality. Body size is important throughout larval fish ecology. Size and recruitment have been linked by Miller et al. (1988) in an integrating framework that suggests recruitment mechanisms vary with fish size in ways similar to what we observed in our model simulations.

Different initial densities of eggs (and thus of swim-up fish) gave rise to different survivorship curves. The general patterns produced by six such curves for low, intermediate, and high initial egg densities are shown in Figure 13. The duration of phase I increases with decreasing initial densities, because fewer fish take longer to deplete the same initial supply of zooplankton. The mortality rate during phase II is also lower for small initial densities, because when phase I is long, fish have reached a larger size when they enter phase II, the period of great food limitation. Therefore, the in-

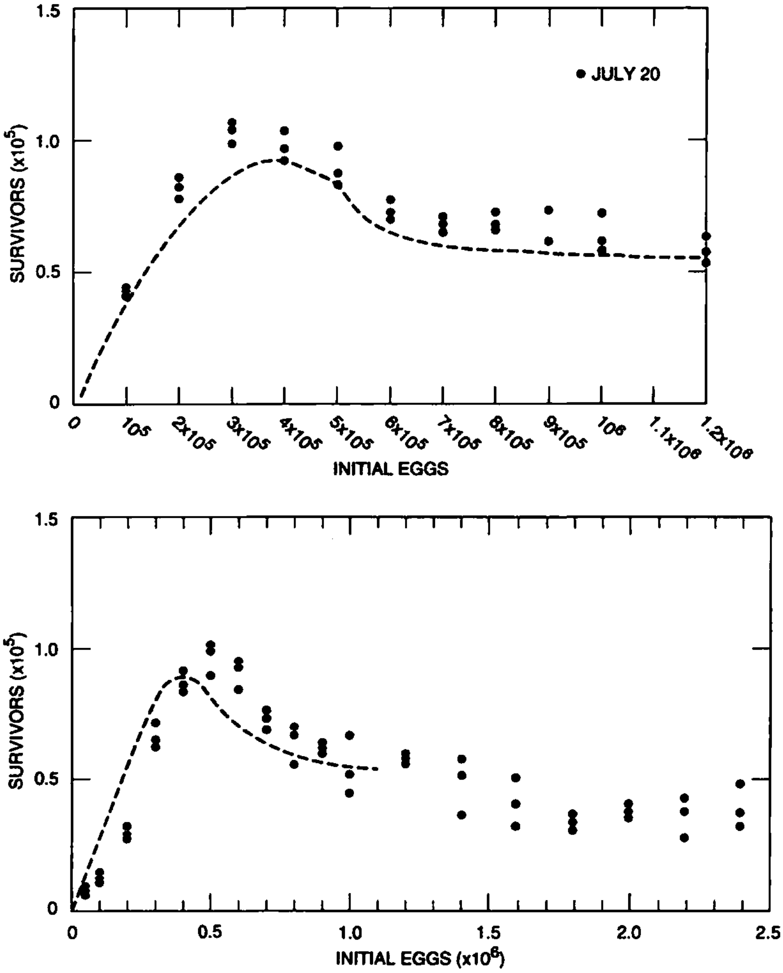

FIGURE 11.—Number of smallmouth bass survivors on July 20 versus initial egg numbers when size-dependent mortality was (a) reduced to 25% the baseline value and (b) increased to double the baseline value. An outline of the survivorship curve from Figure 2 is shown in each panel for comparison.

dividuals are less likely to starve and less likely to suffer size-dependent mortality. When initial egg densities are low enough, virtually no starvation occurs, as shown in the bottom three curves of Figure 13.

It can now be shown how peaked curves of survivors versus egg abundance (Figures 2, 3) originate. Choose some time, t_l, during the growing season within phase II of Figure 13 (denoted by a dotted line) and plot the number of survivors at that time versus the initial number of eggs. Starting from the smallest initial egg densities, the number of survivors at t_l increases with initial eggs. However, for the second highest initial egg density, survivors at t_l are fewer than for the third highest egg density, and survivors for the highest egg density are fewer still. In this way, a domed curve of survivors versus initial egg number is produced.

The peaked survivorship curve produced by overcompensation within phase II is not a true Ricker-type curve, for survivorship declines to a plateau for high densities rather than approaching zero. The reason is that even extremely high initial densities do not cause a complete collapse of age-0 cohorts. Two factors account for this. First, random variation in initial size and growth rate of smallmouth bass is built into the model, so the response of age-0 fish to food depletion also varies. Second, the model specifies several size-classes of prey, some of which may be vulnerable only to the larger age-0 fish. This means that the prey

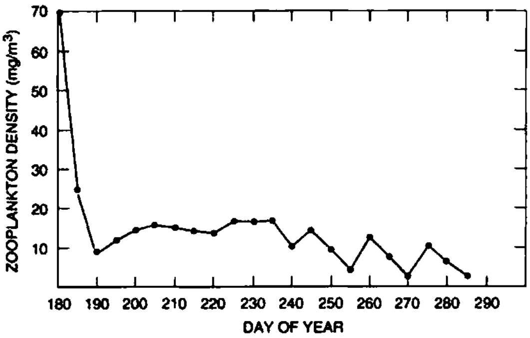

FIGURE 12.—Zooplankton numbers through time corresponding to the survivorship curves of age-0 smallmouth bass in Figure 5.

will not be totally depleted and that some of the larger fish may continue to grow, or at least not starve, during phase II. Thus, a substantial number of young usually will survive, even though the fraction surviving decreases as initial egg numbers increase.

The observed dependence of the length of the critical time, to the end of phase II, on initial egg density in the simulations (Figure 7) is a consequence of the strong effect of density on mortality. High age-0 density causes growth of nearly all fish and then a massive die-off of the fish, or a mortality "overshoot," so that the population may crash to low levels more quickly than an initially smaller age-0 population. How strong this effect will be depends on the resilience of the prey population. If the prey are able to bounce back to high levels, the effect will not be pronounced. However, if a high initial density of age-0 fish severely depresses the prey and the prey do not recover, the cohort crash would be very strong and an increase in the initial numbers of eggs would strongly decrease the critical time. In the smallmouth bass model, the zooplankton prey have a fast recovery rate, so as soon as mortality has removed an appreciable number of smaller age-0 fish, the rest are able to resume rapid growth on a replenished prey supply.

The model of smallmouth bass used in this study is an individual-based model, which we described earlier as fundamentally different from the traditional aggregated stock–recruitment models based on statistical fits to empirical data. It is different because it focuses on individual fish and what happens to them. The dynamics of the population as a whole come from summing the fates of individual fish. We do not claim that only this type of model can describe the results we found for age-0 fish or that the stochasticity in our model is essential to this general type of result. Beverton and Holt (1957) formulated a model for age-0 survival that incorporates three phases of mortality much like the ones we show in Figure 13 (see their page 50 and following pages), and they demonstrated the possibility of a recruitment curve with a peak. Our model, however, is able to produce these three phases automatically from basic mechanisms at the level of individual fish.

It is also possible much of the detailed complexity (e.g., the details of the feeding formulation)

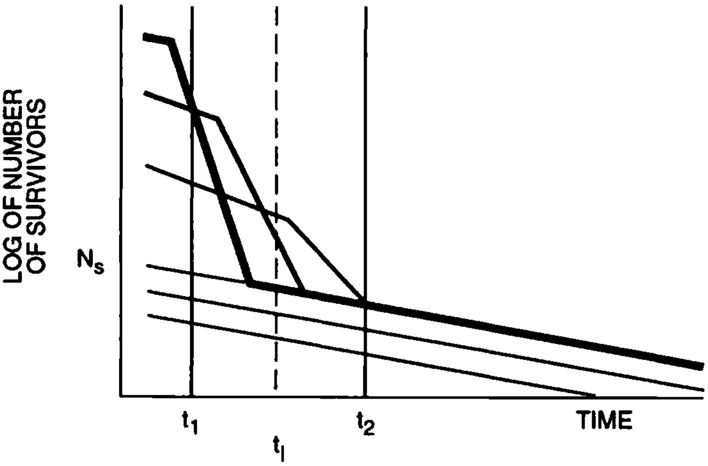

FIGURE 13.—Schematic illustration of three survivorship curve phases for six initial densities of smallmouth bass eggs. Fish stemming from the three lowest initial egg densities have no starvation phase (phase II). Fish from the highest initial egg density suffer the highest mortality rate during phase II.

could be removed from the individual-based smallmouth bass model without effect on the qualitative predictions discussed in this paper. However, this model was built with the intention of exploring other information available for age-0 smallmouth bass, including individual growth characteristics, variations in lengths, weights, and daily diets of individual fish, and possible correlations among hatching date, early growth rates, and survival to the end of the growing season. Simplification of models has many advantages, but individual-based models with sufficient complexity to be used with many types of available data should be useful tools for future studies of fish populations.

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Appendix: Some Key Parameters of the Smallmouth Bass Model

Environmental conditions

Size of spawning zone: 10 hectares.

Temperature: typical daily temperatures (°C) of a southern Ontario lake (Figure A.1).

Reproduction

Average cumulative degree-days needed before male starts parental care of offspring (C_{DD}):

$$C_{DD} = \exp[9.188 - 0.85\cdot\log_e(L_{male})];$$

L_{male} = length of spawning male (cm).

Foraging

Foraging time per day: 12 h.

Average swimming speed: 0.5 body lengths$\cdot$s^{-1}.

Reactive distance (R_d: Breck and Gitter 1983):

$$R_d = L_{prey}/\Theta;$$

L_{prey} = prey length (mm);

Θ = $(2/21{,}600)\cdot\exp(\alpha)$;

α = $9.14 - 2.14\cdot\log_e(L_{fish}) + 0.229\cdot\log_e(L_{fish})$;

L_{fish} = fish (predator) length (cm).

Gape size (gs):

$$gs = 0.4\cdot L_{fish}^2/(L_{fish} + 2).$$

L_{fish} = fish (predator) length (cm).

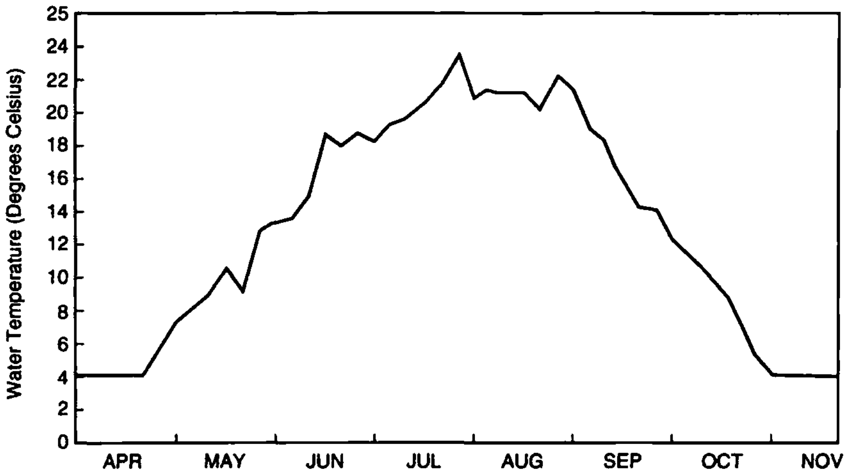

FIGURE A.1.—Water temperature data from Lake Opeongo, Ontario, 1989.

Prey availability

Zooplankton size-classes: 5., 10., 20., 40., 80., 120., and 250. μg dry weight.
Zooplankton carrying capacity (dry weight): 70 mg·m^{-3}.
Benthic prey size-classes: 0.25, 0.50, 1.0, 2.0, 4.0, 8.0, 16.0, 32.0, 64.0, 128.0, 256., 500., 1,000., 2,000., 4,000., 8,000., 16,000., and 32,000. mg dry weight.
Benthic prey carrying capacity (dry weight): 49 g·m^{-2}.
Prey regeneration rate (r_p; from Plante and Downing 1989):

$$r_p = 10^{0.06+0.25 \cdot \text{Tempav}} \cdot W_{\text{prey}}^{0.05}/365;$$

Tempav = average temperature (°C) during the growing season;
W_{prey} = prey weight (mg dry weight for zooplankton; mg dry weight for benthos).

Daily growth of age-0 fish (bioenergetics model of Shuter: DeAngelis et al. 1991):

$$\Delta W = \text{Con} - (\text{SDA} + \text{Res} + \text{Eg} + \text{Exc});$$

$$C_{\max} = 0.00016966 \cdot c^{\text{Temp}} \cdot L_{\text{fish}}^{1.9715};$$

ΔW = daily increment of wet weight (g);
Con = food consumption (g wet weight, from foraging);
SDA = specific dynamic action (g wet weight) = 0.16(Con − Eg);
Res = respiration (g wet weight) = $c^{\text{Temp}} \cdot a \cdot L_{\text{fish}}^{b}/\text{ratio}$;
Eg = egestion (g wet weight) = 0.104·Con;
Exc = excretion (g wet weight) = 0.68·Con;
$C_{\max}$ = maximum possible daily consumption (g wet weight);
c = 1.0806 when Temp ≤ 10°C and 1.1048 when Temp > 10°C;
Temp = mean daily temperature (°C);
L_{fish} = fish length (mm);
a = $0.32 \cdot 10^{-6}$ when Temp ≤ 10°C and $0.36 \cdot 10^{-6}$ when Temp > 10°C;
b = 1.929;
ratio = $0.1363 \cdot 10^{0.0499}$ when $L_{\text{fish}} < 51$ mm and 0.165 when $L_{\text{fish}} \geq 51$ mm.

Starvation

Starvation occurs when:

$$\text{ratio} \cdot W_{\text{fish}} < \text{AFDWS};$$

ratio = $0.1363 \cdot 10^{0.0499}$ when $L_{\text{fish}} < 51$ mm and 0.165 when $L_{\text{fish}} \geq 51$ mm;
W_{fish} = fish weight (mg dry weight);
AFDWS = starvation threshold of ash-free dry weight (mg) = $4.07 \cdot 10^{-7} \cdot L_{\text{fish}}{}^{3.21}$;
L_{fish} = fish length (mm).

Mortality

Size-dependent mortality: $0.2 \cdot \exp(-0.04 \cdot L_{\text{fish}}) \cdot d^{-1}$; L_{fish} is fish length (mm).
Size-independent mortality: $0.0002 \cdot d^{-1}$.