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HABITAT USE AND COMPETITIVE BOTTLENECKS IN SIZE-STRUCTURED FISH POPULATIONS

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Habitat Use and Competitive Bottlenecks

in Size-structured Fish Populations

By

James F. Gilliam

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ABSTRACT

HABITAT USE AND COMPETITIVE BOTTLENECKS IN SIZE-STRUCTURED FISH POPULATIONS

By

James F. Gilliam

This thesis deals with two current problems in the ecology of size-structured populations. By size-structured populations, I mean populations which consist of an array of sizes, and in which different sizes have different ecological characteristics. The first problem is the question of optimal habitat choice when habitats differ not only in the foraging rates obtainable in them, but also in the mortality risk to which an animal is exposed while foraging. The second problem involves an interaction between two species, say A and B, in which A preys upon B when A is large, but A competes with B when A is small.

The first chapter deals with the problem of foraging under mortality risk. This chapter is completely theoretical. Using optimal control theory, I derive decision rules for animals given a "choice" of a number of growth rates and mortality rates, where the choice of a higher growth rate during a day brings with it a higher probability of being preyed upon. For juveniles in populations near equilibrium, the rule is very simple: an animal should choose the habitat or behavior which minimizes the ratio of mortality rate to growth rate. For adults or animals in increasing or decreasing populations, the results can be expressed as degrees of departure from the rule just stated. The second chapter concerns the problem of the predator-prey "bottleneck." The chapter contains some work on the implications of a bottleneck's effect on the demography and population dynamics of the system, but most of the chapter is an investigation of the potential for this type of effect between the largemouth bass (<u>Micropterus</u> <u>salmoides</u>) and the bluegill sunfish (<u>Lepomis macrochirus</u>). The largemouth bass preys upon the bluegill over much of its life, but when small the bass and bluegill consume similar prey. I conclude that the bluegills probably reduce the growth rates of small bass in one lake but not another, and quantify the effect of four bluegill densities on bass growth rates in an experimental pond.

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CHAPTER 1

Foraging Under Mortality Risk In Size-Structured Populations

INTRODUCTION

For most animals, fitness is clearly related both to an ability to obtain food and to avoid predators. However, many circumstances arise in which these two components of fitness conflict. For example, the most profitable habitats for foraging may also be the most dangerous, or certain foraging tactics may make a forager more vulnerable to predators. It is often concluded that predation risk strongly affects the evolution of a forager's behavior (e.g. Rosenzweig 1974; Sih 1980; Nelson and Vance 1979; see Stein 1979 and Morse 1980 for reviews). Further, some work has shown that the behaviors can be plastic since foragers show a reduction in foraging rate when predators or predator models are present (Stein and Magnuson 1976; Milinski and Heller 1978; Caraco, Martindale, and Pulliam 1980; Shaffer and Whitford 1981; Fraser and Cerri 1982). Werner, Gilliam, Hall, and Mittelbach (1983) have shown that small bluegill sunfish shift to energetically less profitable but apparently safer habitats when a predator is present, and, further, that the shift results in reduced growth rates for the survivors. Thus, the presence of a predator introduces a cost to a forager, the risk of predatory death, which the forager may partially offset by incurring a second cost, a

reduced foraging (growth) rate. Collectively, the above studies show that at least some ants, fish, birds, and mammals do in some way facultatively balance a tradeoff between mortality risk and foraging rate.

Since habitat use and prey selection within a habitat are central to competitive processes, a method of predicting foraging behavior under predation risk is an essential element in a predictive theory of community organization. In this paper I present a basis for predicting behavior when the maximization of foraging rate and short-term survivorship conflict. The major question asked is: Given a "choice" of a number of foraging rates, each with an associated mortality rate, which choice maximizes fitness? In particular, given an array of habitats, each with an associated foraging rate and mortality rate, in which one(s) should an animal forage?

Here, I investigate the above questions for iteroparous size-structured populations. By "size-structured" populations, I mean populations in which an individual's salient ecological properties, notably its foraging abilities, vulnerability to predators, and fecundity, can be regarded as functions of the individual's size rather than its age. I also allow the animal's foraging rate and mortality rate to be under behavioral control; that is, the animal's daily foraging and mortality rates are functions of both its size and its behavior (e.g. habitat use, times of feeding, swimming speed). The fecundity rate is taken to be a function of the animal's size (reproductive effort questions are not considered here). This dependence of ecological characteristics on size rather than age appears to be a reasonable representation for many animals which

exhibit indeterminant growth, as many fish, reptiles, amphibians, and invertebrates.

I first consider optimal behavior in populations near equilibrial population size, and then investigate the cases of increasing and decreasing populations. Initially, I assume that the foraging, mortality, and fecundity rates are not explicit functions of time. That is, these rates are functions of time only to the extent that body size is a function of time. The important biological consequence of this assumption is that this implies a constant environment and continuous reproduction. This allows an analytical solution to the problem which provides a starting point from which consequences of alternative assumptions can be explored.

The Nature of the Tradeoff:

A Representative Problem and a Generalization

As an example of the growth-mortality tradeoff, consider the problem of ontogenetic habitat shifts by fish. As fish grow, they typically exhibit marked shifts in prey utilization, as documented by a huge literature on fish diets (Carlander 1977). Habitat shifts often accompany the changes in diets. For example, juvenile bluegill sunfish (Lepomis macrochirus) travel from shallow littoral nests to the limnetic zone upon hatching and feed upon zooplankton (Werner, 1966). They then usually return to the littoral zone after reaching a size of about 20 mm standard length and prey primarily upon insects and crustaceans. In lakes in southwest Michigan, the bluegills typically forage among littoral vegetation until reaching 60-100 mm length (3 to 4 years old), at which time they switch habitats again, and most of their time is subsequently spent foraging on open-water

Figure 1. Size-specific growth (g_1) and mortality $({}^{\mu}{}_1)$ rates in habitats 1 and 2. b(s) is the birth rate.





zooplankton (pers. obs.; Mittelbach, 1981).

Mittelbach (1981) has presented evidence that the bluegills in the littoral zone would usually exhibit higher growth rates if they instead foraged in the open limnetic zone. He suggested that small fish may remain among vegetation because the structure affords protection from predators, and that larger fish can utilize the open water with less danger because their vulnerability is lower than small fish. Further, Werner, Gilliam, Mittelbach, and Hall (1983) have experimentally confirmed that small bluegills shift to greater use of a vegetated habitat in the presence of predators versus their use in the predators' absence, but larger non-vulnerable bluegills do not show the habitat shift.

A simple representation of vital rates associated with ontogenetic habitat shifts is shown in Figure 1 (see Werner 1982 for a similar treatment of habitat shifts when habitats do not vary in mortality risk). At a particular resource level, a fish of a given size foraging in Habitat 1 is depicted to grow (gm/day, cal/day, or mm/day) at a rate g_1 and incur a mortality rate (probability of death/day) of μ_1 . In Habitat 2, the fish would experience growth and mortality rates of g_2 and μ_2 , respectively. Thus, Habitat 2 is always the more dangerous habitat, but large fish can grow faster there. μ_1 and μ_2 are shown as declining functions of fish size, which will usually be true if larger fish are less vulnerable to predators, though μ_1 or μ_2 may increase over some range if the predators are positively size-selective. As drawn, the growth functions, g_1 and g_2 , indicate that, on a particular resource, the growth rate first increases and then declines to zero. This happens when the animal's

gross foraging rate increases with size, but at large sizes metabolic costs increase faster than increases in foraging capabilities. The details of the growth and mortality functions are not important to the conceptual development of the problem; Figure 1 simply represents a seemingly common case.

Given the relations shown in Figure 1, a small fish would both maximize its growth rate and minimize its mortality rate by foraging in habitat 1. This would maximize its survivorship and size at each age and is clearly optimal in this framework. As the fish grows, at what size would a shift from habitat 1 to habitat 2 be favored by natural selection? A fish shifting a size s* would maximize its growth rate, but at the cost of raising its mortality rate from μ_1 (s*) to μ_2 (s*). Thus, at sizes greater than s*, the animal is faced with a growth rate-mortality rate tradeoff; maximization of growth during a day conflicts with the minimization of mortality risk (maximization of survivorship) during that day. Intuitively, one might surmise that a delay in the habitat shift would be favored by natural selection, since at sizes slightly larger than s*, the fish's mortality rate can be substantially lowered at the cost of a slightly lowered growth rate. However, a delayed switch to Habitat 2 would usually increase mortality at future ages, since the fish would be smaller at each future age than it would have if it had switched at s*. Also, the animal's fecundity at each future age will be lowered by the delay in switching since the animal will be smaller at each subsequent age. Clearly, the short-term tradeoff between mortality rate and growth rate can be restated to be a tradeoff between short-term survivorship (during a day) and long-term survivorship and

fecundity (over the rest of the animal's life).

Figure 2 represents a case similar to Figure 1, but depicts one habitat (in this case, a vegetated habitat) as being safer (lower μ) but less energetically profitable (lower g) than another habitat (an open water habitat with planktonic prey). This may crudely approximate the options often available to bluegill sunfish. Here, the question is not just when to switch habitats, but whether to switch, and how many times.

Now suppose that an animal may choose to split its time between the two habitats (the case for three or more habitats can also easily be constructed). Figure 3a depicts, for a fish of a given size, the overall daily growth and mortality rates as a function of the time spent in one of the habitats. Here, Habitat 1 is "dangerous" but "rich", and Habitat 2 is "safe" but "poor". The growth rate, g, is drawn as an increasing, concave function of the time spent in the rich habitat. The concavity is due to a concave relation between daily foraging rate and growth rate (Webb 1978). Other shapes of μ and g are certaily plausible. For example, g may decline over some range in Figure 3a if there are substantial travel costs between habitats; different shapes of curves can be easily accommodated in the model presented in this paper.

Since μ and g are both functions of behavior (the proportion of time in Habitat 1) for a fish of a given size, we can plot μ directly as a function of g, as in Figure 3b. This makes the tradeoff explicit; the animal must, in effect, choose a growth rate (via its habitat choice), and each increase in growth rate (a benefit) carries with it an increase in mortality (a cost). At other points in an

Figure 2. Hypothetical size-specific growth and mortality rates for bluegill sunfish in Lawrence Lake.



Figure 3. (a) Growth and mortality rates resulting from mixed habitat use. (b) The relationships in (a), replotted to express mortality rate as a function of growth rate.





animal's life history, μ may be a nonincreasing function of g. For example, fish smaller than s* in Fig. 1 simultaneously maximize growth and minimize mortality by foraging in Habitat 1.

The problem can now be generalized by defining three functions, as shown in Figure 4. The animal's birth rate, b(s), is a function of the animal's size. Also, there is a function, $g_{max}(s)$, which gives the animal's maximal growth rate obtainable under existing resource levels. The animal's mortality rate on a particular day is a function, $\mu(g,s)$, of the animal's size and the growth rate the animal "chooses" (Figure 4b). It will be convenient to refer to a "choice of growth rate" on each day, but, of course, this phrase really means that the animal behaves in a certain way (e.g. through its habitat choice, diel activity pattern, foraging speed, distance from a refuge), and that behavior, together with the animal's size, results in a growth rate and a mortality rate for that day.

The Selection Criterion

On each day an animal must adopt some behavior, and the behavior adopted will have associated growth and mortality rates. Taken together, the series of decisions across an animal's (or cohort's) lifetime results in a growth path. There exist an infinite number of possible growth paths, each with an associated survivorship and fecundity schedule, and the present task is to find the <u>particular</u> growth path which maximizes fitness.

The criterion of fitness used here is this: In a density-dependent population at equilibrium, find the series of decisions which result in $R_0 = 1$ (r = 0) when all other series of decisions results in $R_0 < 1$ (r < 0). Here, r is the instantaneous

Figure 4. (a) Size-specific birth and maximal growth rates.(b) Mortality rate, a function of size and "chosen" growth rate.

•



SIZE, s



rate of increase of the population, and ${\rm R}_{\rm O}$ is the net reproductive rate,

$$R_{o} = o^{\int \widetilde{\ell}(x)b(x)dx}, \qquad (1)$$

where $\ell(x) = survivorship$ to age x, and b(x) = fecundity at age x. A morph with $R_0 = 1$ just replaces itself, and "invading" morphs with $R_0 < 1$ are eliminated.

This criterion is used implicitly in density-dependent models without age-structure, where the criterion is equivalent to the maximization of population density. The maximization of total population density cannot usually be used as a congruent criterion for size-structured populations, although Hastings (1978) has shown that it can be for the special case of the density-dependence at each age (size) depending only upon the total population size, and Charlesworth (1980) has shown that if a "critical age group" can be identified, the maximization of the density of that age group is equivalent to the criterion, $R_0 = 1$ when all alternatives yield $R_0 < 1$. The analysis in this paper assumes nothing about the details of density-dependence except that, for a population exhibiting an arbitrary series of behaviors, the population will establish an equilibrial size (and age) structure at which $R_0 = 1$, and the task is to depict the choice of a growth path (series of behaviors) which is noninvasable by alternative choices when $R_0 = 1$ for the "established" path.

I describe below the series of decisions which maximize R_0 for a given level of resources and mortality pressure, and note that the solution holds for the <u>particular</u> case of the resource levels and mortality pressures existing at equilibrium. That is, a population

exhibiting optimal behavior will have the property that $R_0 = 1$ at equilibrium, and all invading behaviors yield $R_0 < 1$. The case of increasing or declining populations will be considered subsequently.

A Solution

Mathematically, we want to find a function, g(x), which maximizes an integral, R_0 . This kind of problem can be solved with optimal control theory, a technique with its roots in the calculus of variations. Optimal control theory is certainly largely unfamiliar to most ecologists, though optimal control theory has been used in ecological contexts by some authors, especially recently (Katz 1974, Leon 1976, Sibly and McFarland 1976, Clark 1976, Mirmirani and Oster 1978, Oster and Wilson 1978, McCleery 1978, Vincent and Pulliam 1980, Goh 1980, Goodman 1982). Suggested introductions are contained in Intriligator (1971), Takayama (1974), and the original work of Pontryagin et al. (1964), as well as the papers cited above.

In the terminology of optimal control theory, the growth rate, g(x), is a control variable, whose value at each age is to be chosen so as to maximize the objective functional, R_0 . In addition, two state variables can be defined which describe the state of a cohort at age x. These state variables are the size at age x, s(x), and the integral of previous mortality rates, $D(x) = \int_0^x \mu(y) dy$, where y is a dummy variable. These two state variables completely specify $\ell(x)$ and b(x) since $\ell(x) = e^{-D(x)}$ and b(x) = b [s(x)]. Across age (time), the state variables change at a rate determined by the control variable and the state variables themselves:

$$\frac{dD}{dx} = \frac{d \int o \mu(y) dx}{dx} = \mu(x) = \mu[s(x), g(x)]$$
(2)

$$\frac{ds}{dx} = g(x) \tag{3}$$

Thus, at each age, the life historical effects of the choice of growth rate are expressed through the effects on the state variables.

There is also a constraint on the growth rate, g(x) < g_{max} [s(x)]. This can be incorporated either by explicitly entering the constraint in the problem, or by imposing an artificial penalty that effectively prevents g(x) from exceeding $g_{max}[s(x)]$. The latter method keeps the mathematics more transparent in this case and has no effect on the biological results, as will be seen in graphical solutions. The penalty is imposed by letting $\mu(g, s)$ turn arbitrarily sharply upward at $g_{max}(s)$. In Figure 4b, this could be depicted by drawing $\mu(g, s)$ as turning very sharply along the edge defined by $g_{max}(s)$, rather than terminating the surface as now drawn. Thus, strictly speaking, g(x) has no formal upper bound, but the penalty (greatly increased mortality rate) is set so great that in practice it will not exceed $g_{max}(s)$. The mathematics also require that b(s) be continually differentiable; accordingly, b(s) is taken to be very sharply sigmoid near the size of first reproduction, rather than a discontinuous function as depicted in Figure 4a.

The Hamiltonian function can now be formed:

$$H = e^{-D(x)} b[s(x)] + \lambda_D(x) \mu[g(x), s(x)] + \lambda_s(x)g(x)$$
(4)

The first term is the integrand of the objective functional. The second and third terms are each the product of an auxiliary variable (also called a costate variable, adjoint variable, or multiplier), and a state variable's rate of change. $\lambda_{\rm D}({\rm x})$ is an auxiliary variable

associated with the state variable D(x) and multiplies $\mu[g(x), s(x)]$, the value of dD/dx (see Eq. 2). Similarly, $\lambda_g(x)$ is associated with the state variable s(x) and multiplies g(x), the value of ds/dx (Eq. 3).

Pontryagin's Maximum Principle states that H is maximized at each x by the optimal g(x). Further, it is known that $dH/dx = \partial H/\partial x$. For this problem, $\partial H/\partial x = 0$ since x does not appear explicitly in the equation (e.g. b and μ depend only upon the state and control variables, not <u>explicitly</u> on age itself). Thus, the Hamiltonian is said to be autonomous and is in fact constant across all ages.

The fact that H is constant for all x can be used to good advantage in determining a solution. Since H is constant, its value can be determined by finding its value at any particular x, in this case when x is very large. It is known that when the objective functional's (R₀'s) limits of integration are from say, 0 to T, where T is finite, the values of the auxiliary variables at T are equal to zero if the final values of the state variables are unspecified (in this problem, we do not specify required final values for s and D). This is true for any arbitarily large but finite T. Surprisingly, perhaps, this result does not always hold for $T = \infty$, and counterexamples have been found (e.g. Takayama 1974, p. 625). It does appear that $\lambda_{D}(\infty) = 0$ and $\lambda_{g}(\infty) = 0$ for this system, but the general conditions for which this would hold are not known. However, we can circumvent this problem by taking the integral (R_0) from 0 to T, where T is very large but finite, rather than from 0 to ∞ . If T is sufficiently large, we can safely take $e^{-D(T)}b(T) = 0$, and since $\lambda_D(T)$ = $\lambda_s(T) = 0$, it follows that H(T) = 0. Thus, for all x, H = 0 for the optimal growth path, and H < 0 for suboptimal paths. This is reminiscent of the condition, r = 0 ($R_0 = 1$) for the optimal path and r < 0 ($R_0 < 1$) for all other paths.

The problem can now be stated succinctly within the structure of Pontryagin's Maximum Principle. The goal is to find the path of the control variable, g(x), which maximizes $R_0 = \int_0^T e^{-D(x)} b[s(x)]dx$, subject to the constraints on the state variables (Eqs. 2 and 3). For this problem, dropping the arguments of the functions for brevity,

$$H = e^{-D}b + \lambda_D \mu + \lambda_s g = 0$$
 (5)

Further, since H is maximized by the choice of g,

$$\frac{\partial H}{\partial g} = 0 = \lambda_D \frac{\partial \mu}{\partial g} + \lambda_s \text{ for each } x \tag{6}$$

The changes in the auxiliary variables are described by

$$\frac{d^{\lambda}D}{dx} = -\frac{\partial H}{\partial D} = e^{-D}b$$
(7)

$$\frac{d\lambda_{s}}{dx} = -\frac{\partial H}{\partial s} = -e^{-D} \frac{db}{ds} - \lambda_{D} \frac{\partial \mu}{\partial s}$$
(8)

The usual way of solving this type of problem would be to solve the differential equations, Eqs. 2, 3, 7, and 8 with two known initial values, D(0) = 0 and $s(0) = s_0$, and two known final values, $\lambda_D(T) = \lambda_g(T) = 0$. However, the observation that the Hamiltonian is constant and equal to zero allows us to circumvent this process and obtain useful results without having to specify the forms of the functions.

One way to describe the relationship between $\boldsymbol{\mu}$ and g at the

optimal solution is to find $\partial \mu / \partial g$, which will be called the "marginal risk," at the optimum. Solving Eq. 6 for $\partial \mu / \partial g$ yields $\partial \mu / \partial g = -\lambda_{g}/\lambda_{D}$. Solving Eq. 5 for λ_{g} (this is where H = 0 is a crucial observation) and substituting into $\partial \mu / \partial g = -\lambda_{g}/\lambda_{D}$ yields

$$\frac{\partial \mu}{\partial g} = \frac{\mu + e^{-D}b/\lambda_D}{g} \text{ for each } x$$
 (9)

This equation is the central result of this paper. The meaning of this equation will be assessed below separately for juveniles and adults.

Optimal Decisions for Juveniles

For juveniles, b = 0 by definition. Hence Eq. 9 reduces to

$$\frac{\partial \mu}{\partial g} = \frac{\mu}{g} \tag{10}$$

In Figure 5, it can be seen by inspection that this relationship holds at only one value of g, denoted g_{opt} . That is, straight lines drawn through the origin depict points at which μ/g is constant, and the particular line which is tangent to μ defines the point at which $\partial \mu/\partial g = \mu/g$.

Figure 5 suggests an alternative statement of the condition for optimality. g_{opt} may be recognized graphically as the value of g which minimizes μ/g . This can be confirmed by solving $\partial(\mu/g)/\partial g = 0$ for $\partial \mu/\partial g$, which yields Eq. 10. Thus a simpler statement of the rule is "minimize μ/g at each age (size)."

The meaning of this rule becomes clearer when related to an expression for survivorship to a particular size. It has been shown (VanSickle 1977, Werner, Gilliam, Hall, and Mittelbach, 1982) that the Figure 5. Graphical solution of the optimal growth rate for juveniles.


survivorship to a particular size, s_1 , can be described by

$$\ell(s_1) = e^{-s_0} \frac{g(s)}{g(s)} ds$$
(11)

where $s_0 = size$ at birth. An animal which minimizes $\mu(s)/g(s)$ at each size thus maximizes its probability of reaching each size, in particular the probability of reaching reproductive size.

The simplicity of the rule (minimize μ/g) suggest that animals may evolve an ability to make decisions approximating optimal behavior. For example, if an animal must choose between two habitats, the first of which confers twice the growth rate as the other, the animal should just choose the first habitat unless it is twice as dangerous (µ twice as large). That is, "choose habitat 1 if $\mu_1/g_1 <$ μ_2/g_2 " can be rewritten as, "choose habitat 1 if $g_1/g_2 > \mu_1/\mu_2$." The animal does not have to judge the absolute levels of μ and g in each habitat, only the relative values of growth and "danger". Given the repeatedly demonstrated ability of animals to make some kind of decision when foraging rate and mortality rate conflict, this particular rule does not appear difficult to follow, whether through the evolution of inflexible behavior or the evolution of an ability to facultatively balance costs and benefits through some process. The simplicity of the rule also suggests that tests of this model are achievable if growth and mortality rates can be experimentally determined for alternate habitats.

The problem of ontogenetic habitat shifts can now be solved for juveniles. Figures 6a and 6b are solutions to the problems in Figures 1 and 2. Here, the switches are shown to be discrete, though a period of use of both habitats might be predicted in some cases (see below). Figure 6. (a) Optimal size (s_{opt}) for switching from habitat 1 to habitat 2. s^* is the size at which an animal maximizing its growth rate would switch. (b) Optimal switching sizes between plankton and vegetation. Fitness is maximized by foraging on plankton between sizes s_0 and s_1 , foraging among vegetation between sizes s_1 and s_2 , and returning to the plankton at size s_2 .



Other problems can be solved if the options can be depicted in the μ -g plane (either as a continuous function, as first modelled, or as any other set of points, since "minimize μ/g " is the general rule for juveniles). For example, if μ and g can be depicted as a function of movement rate, distance from a refuge, or duration of a crepuscular foraging bout, the options can be plotted in the μ -g plane. The optimal solution can then be found graphically by increasing the slope of a line through the origin until it meets an option.

When would discrete habitat shifts be predicted? Graphically, mixed habitat use might occur when $\mu(g)$ is a convex function, but use of only one habitat would be expected if $\mu(g)$ is a linear or concave function. This is illustrated in Figure 7. In the original statement of the problem, the concavity of $\mu(g)$ was taken to be a result of growth inefficiencies, i.e. that growth rate is a concave function of foraging rate, at high foraging rates. When growth is strongly food-limited, $\mu(g)$ may be approximately linear. Thus, we might expect discrete habitat shifts during periods in the life history in which growth is strongly food-limited.

Other factors which would favor habitat specialization include a cost (in energy or mortality) of transit between habitats and reduced foraging efficiency, due to short-term learning effects, when two habitats are used. Both of these effects are illustrated in Figure 8. The displacement of g downward for a mixed strategy represents a travel cost, and the "sag" in g represents a foraging rate depression from short-term learning effects, i.e. over some range, the animal's foraging rate in a habitat is an increasing function of the time spent there during that day. Mathematically, μ is no longer a function of

Figure 7. (a) Illustration of habitat specialization when μ is linear in g. The "corners" each represent exclusive use of a habitat. (b) choice of an intermediate growth rate (use of both habitats) when μ is convex.



Figure 8. An example of added complexity in the µ-g plane: the effect of travel costs and short-term learning on mortality and growth. Both factors favor habitat specialization.

(a) Energetic travel costs are depicted as displacing the growth rate downward. Short-term learning effects are represented by a "sag" in the growth rate, depicting a case in which an animal's foraging rate while in a habitat is a function of the time spent there.
(b) The dashed line represents no travel or learning cost. The travel cost "detaches" the line and moves it to the left. The learning cost makes it bend. Both effects make a mixed strategy unlikely.





g, but the graph in the μ -g plane is sufficient.

Having seen that the optimal behavior is the behavior which maximizes survivorship to each size, and that an animal does this by minimizing μ/g (or maximizing g/μ) at each size and age, it is worth noting what the strategy does not do. First, it usually does not maximize the probability of survivorship to each age, $\ell(x)$. For example, if $\partial \mu / \partial s = 0$ and $\partial \mu / \partial g > 0$ for all sizes, an animal would maximize its survivorship (to each age) by not growing at all. Second, it is not the strategy which "projects" the maximal biomass of the cohort into the next day. This strategy can be approximated for small μ and g as maximizing $y = (1-\mu)(s+g)$. Setting $\frac{\partial y}{\partial g} = 0$ yields $\partial \mu / \partial g = (1-\mu)/(s+g)$. This strategy would result in acceptance of a higher marginal risk (higher $\partial \mu / \partial g$) by small animals and lower marginal risk by large animals than the optimal strategy. Third, it is not the same as maximizing the expected gain in cohort biomass during a day. This can be approximated by maximizing $y = (1-\mu)(g)$, and setting $\partial y/\partial g = 0$ yields $\partial \mu/\partial g = (1-\mu)/g$. Since $1-\mu > \mu$ for small μ , this strategy would result in acceptance of a higher marginal risk by all sizes.

Optimal Decisions for Adults

For adults, the condition is Eq. 9. For small values of $e^{-D}b/\lambda_D$, the condition is very close to the condition for juveniles; as $e^{-D}b/\lambda_D$ increases, the condition diverges from that for juveniles.

What is the meaning of the term $e^{-D}b/\lambda_D$? The expression $e^{-D}b$ is the rate of offspring produced by a cohort of age x. It turns out (see below) that λ_D can be interpreted as the negative of the expected number of future offspring produced by the cohort. Thus, the term

 $e^{-D}b/\lambda_D$ is a measure of the ratio of present and future reproduction.

To see that λ_D is the expected number of future offspring produced by a cohort, first recall that $\lambda_D(T) = 0$. From Eq. 7, $\lambda_D(T) = \lambda_D(0) + \int_0^T e^{-D(x)}b(x)dx$. Since this integral is just $R_0 = 1$, $\lambda_D(0) = -1$ (= $-R_0$). Thus $\lambda_D(x)$ begins at -1, is constant for juveniles, and upon onset of reproduction approaches zero as age progresses. At age x, $\lambda_D(x) = \lambda_D(0) + \int_0^X e^{-D(y)} b(y)dy =$ $- \int_0^\infty e^{-D(y)} b(y) dx + \int_0^X e^{-D(y)} b(y)dy$, where y is a dummy variable. Thus,

$$\lambda_{\mathbf{D}}(\mathbf{x}) = - \int_{\mathbf{x}}^{\infty} e^{-\mathbf{D}(\mathbf{y})} \mathbf{b}(\mathbf{y}) d\mathbf{y}$$
(12)

This shows that ${}^{\lambda}D(x)$ is the negative of the cohort's expected reproduction.

Defining R(x) as the cohort's expected future reproduction, R(x) = $-\lambda_D(x)$, so Eq. 9 can be rewritten as

$$\frac{\partial \mu}{\partial g} = \frac{\mu - e^{-D} b/R}{g}$$
(13)

Alternatively, define V(x) as the reproductive value of an animal of age x. Then V(x) = $R(x)/l(x) = R(x)/e^{-D(x)} = -\lambda_D(x)/e^{-D(x)}$, and Eq. 9 can be rewritten as:

$$\frac{\partial \mu}{\partial g} = \frac{\mu - b/V}{g}$$
(14)

Equations 13 and 14 emphasize that the solution for adults is similar to that for juveniles, but the acceptable marginal risk is "discounted" by the ratio of present to future reproduction. A graphical relationship is represented in Figure 9.

For juveniles, the optimal growth rate at each size depends only

Figure 9. Optimal growth rate for adults. The optimal marginal risk $(\partial \mu/\partial g)$ for an adult is less than that for a juvenile with the same $\mu(g)$ for a given size. Starting with the juvenile solution, $\partial \mu/\partial g = \mu/g$, the adult relationship can be viewed as (a) reducing $\partial \mu/\partial g$ until $\partial \mu/\partial g = (\mu-b/V)/g$, or (b) drawing a new function, $(\mu-b/V)/g$, and finding the tangent through the origin, at which $\partial(\mu-b/V)/\partial g = (\mu-b/V)/g$. (a) and (b) are equivalent because $\partial(\mu-b/V)/\partial g = \partial \mu/\partial g$, since the derivative is evaluated with the state and auxiliary variables, and hence b/V, held constant.



upon the growth and mortality rates extant at that size, but for adults, $\lambda_{D}(x)$ (or R(x) or V(x)) must also be determined. The value of $\lambda_{D}(x)$ depends upon the growth, mortality, and birth rates at all other adult sizes. Since much more information is required to depict adults' optimal behavior, quantification of optimal growth rates in experiments will often be more difficult for adults than for juveniles.

Increasing And Declining Populations

In an increasing or declining population, the task is to find the behavior which maximizes r in the equation,

$$1 = \int_{0}^{T} e^{-rx} \ell(x)b(x)dx \qquad (15)$$

This problem is mathematically closely related to the density-dependent case, though conceptually the problems differ. In the density-dependent case, operationally, r was set equal to zero, the strategy which maximized the integral in Eq. 15 was determined, and it was assumed that density-dependent processes must adjust $\ell(x)$ and b(x) so as to make Eq. 15 true (i.e. $R_0 = 1$). In the problem of increasing or declining populations, the strategy which maximizes the integral is found, where the optimal strategy is specified in part by r, and then r is adjusted so as to make Eq. 15 true (see Leon 1976, Goodman 1982).

Mathematically the problem is to find the growth path, g(x), which maximizes

$$J = o^{\int_{0}^{T} e^{-rx} e^{-D(x)}b(x)dx}$$
(16)

subject to the constraints on the state variables, Eqs. 2 and 3. The problem can be substantially simplified by introducting a new state variable, z(x), defined as z(x) = rx + D(x). Then Eq. 16 can be written as

$$J = \int_{0}^{T} e^{-z(x)} b(x) dx \qquad (17)$$

Noting that $dz/dx = r + \mu$, the Hamiltonian and associated equations are

$$H = e^{-z}b + \lambda_{z}(r+\mu) + \lambda_{g}g$$
(18)

$$\frac{\partial \mathbf{H}}{\partial g} = \lambda_{\mathbf{Z}} \frac{\partial \mu}{\partial g} + \lambda_{\mathbf{S}}$$
(19)

$$\frac{d \lambda_z}{dx} = -\frac{\partial H}{\partial z} = e^{-z}b$$
 (20)

$$\frac{d\lambda_{s}}{dx} = -\frac{\partial H}{\partial s} = -e^{-z}\frac{db}{ds} - \lambda_{z}\frac{\partial \mu}{\partial s}$$
(21)

The introduction of z(x) has allowed the problem to be written in an autonomous form rather than the nonautonomous form in Eq. 16. In fact, as before, the Hamiltonian is constant and equal to zero. Solving Eq. 19 for $\partial \mu / \partial g$ yields $\partial \mu / \partial g = -\frac{\lambda_s}{\lambda_z}$, and solving Eq. 18 for λ_s and substituting into the above expression for $\partial \mu / \partial g$ yields

$$\frac{\partial \mu}{\partial g} = \frac{(\mu + r) + e^{-z} b/\lambda_z}{g}$$
(22)

The behavior of λ_z is analogous to the behavior of λ_D in the equilibrial density-dependent case. For the value of r which results in J = 1, $\lambda_z(0) = -1$, dz/dx = 0 for juveniles, λ_z approaches zero as x becomes large, and λ_z (T) = 0. Also, the reproductive value, V,

equals $-(\lambda_z/e^{-z})$; the term $e^{-z}b/\lambda_z$ in Eq. 22 can be written as b/V. Thus, this "density-independent" case differs from the equilibrial density-dependent case only in that $r \neq 0$ in Eq. 22.

For juveniles, the rule thus becomes "minimize the quantity $(\mu + r)/g$ at each age (size)," where r is the rate of increase of the optimal strategy. When r > 0, the minimization of $(\mu + r)/g$ becomes more nearly equivalent to the maximization of g; i.e. an animal should accept greater mortality risk and decrease its time to maturity (and fecundity at each adult age) relative to the density-dependent, equilibrial case, (r = 0). When r < 0, the opposite is true; the animal should reduce its daily mortality rate with the effect of slowing its growth rate and lengthening its age at maturity. Thus, compared to juveniles in a density-dependent population near equilibrium which maximize fitness by maximizing survivorship to each size, animals in an increasing population should tend towards being "bold" "growth maximizers," and animals in declining populations should tend towards being "timid" "mortality minimizers."

Conclusion

The ways in which animals respond to predators have been of interest to animal behaviorists and ecologists for some time, but the development of a testable predictive basis has lagged behind the recognition of the question's evolutionary and ecological importance. Certainly, the major impediment to the development of such a construct has been that the tradeoff between growth and mortality involve benefits and costs expressed in different units. The simplicity of the central result for juveniles, "minimize μ/g ," is encouraging given the initial complexity of the problem. It is also encouraging that

this simple rule is "central" with respect to temporary disturbances from equilibrium; in increasing populations, natural selection will favor greater risk-taking, and in declining populations, it will favor less. Of course, the particular form of perturbations may influence long-term strategies (e.g. Turelli and Petry, 1980), but the rule appears to be a good starting point for density-dependent size-structured populations near equilibrium.

In addition to quantitative predictions of habitat use, the model suggests some qualitative results which are perhaps not obvious a priori. First, as developed earlier, rather discrete habitat shifts are expected at sizes at which growth is strongly food-limited, but not at which growth is not strongly food-limited in at least one habitat. Second, if "background" mortality rates in two habitats are increased by a constant, an optimizing animal may shift from the safer to the more dangerous habitat. Graphically, this can be seen in Fig. 7(a) by uniformly raising or lowering $\mu(g)$. However, if μ is multiplied by a constant, the solution is unchanged. Third, given the same $\mu(g)$ function for a juvenile and an adult, the adult should adopt a lower marginal risk $(\partial_u/\partial g)$ than juveniles. However, this does not necessarily mean that the adult would, for example, forage for a shorter time, since it must produce offspring ("maintain" the prescribed b (s)). A model incorporating reproductive effort could provide more complete predictions of adult foraging behavior relative to juveniles (see below).

Some previous work provides a basis for describing optimal behavior in populations which are not size-structured. Pulliam, Pyke, and Caraco (1982) have derived and tested a predicted tradeoff between

feeding and scanning for predators by flocking birds, under the goal of minimizing mortality from either predators or starvation. Katz (1974) described annual patterns of foraging rates which would minimize the total time spent foraging during the year, and listed some alternative criteria. Craig, DeAngelis, and Dixon (1979) presented a similar model with the objective of minimizing total time spent handling prey. Pearson (1976) developed a model of optimal prey selection under the objective of maximizing the energy gain per mortality cost during a foraging bout; this criterion maximizes the total energy gained over the lifetime of an animal with no age- or size-dependent properties, and is reminiscent of the minimization of μ/g in juveniles near equilibrium. Hopefully, the present paper, together with the above work, will provide starting points which approximate the tradeoff in many species.

When discussing the problem of habitat selection under mortality risk, a question often raised is whether animals are capable of making the sort of decision suggested by the theory developed here. The question can be divided into two parts. First, can an animal make an appropriate decision, given all necessary information (mortality and growth rates of options)? Second, can an animal obtain the necessary information in the first place?

To answer the first question, experimentation is necessary. Some tests with centrachid fish are in progress. <u>A priori</u>, given that the fish have accurate information on alternatives, I see no strong impediment to the evolution of appropriate behaviors. The behavior of many animals is obviously influenced by "fear" and "hunger," and these motivations must be integrated in some way to effect a behavior. I

would expect natural selection to select for particular integrative processes which maximize fitness. The theory presented here is a beginning in the description of the particular integrative process which does maximize fitness.

The second question, that of obtaining information on which to make decisions, certainly can present major difficulties to animals. To respond facultatively, an animal must assess at least relative mortality risk and foraging rates associated with different options. It does appear that many animals can assess and compare different foraging rates, and behave in such a way as to approach maximization of their foraging rate (e.g. Krebs 1978; Werner, Mittelbach, Gilliam and Hall 1983), but the assessment of mortality risk probably presents a more difficult "sampling" problem. Especially when predators are seldomly encountered, information on mortality risk may be both rare and highly variable. When information is impossible or expensive to gather and process, and/or the benefit of facultative responses is small due to constant conditions, rather inflexible behaviors may evolve. When information can be gained at small cost, and/or conditions change often, evolution of more plastic behavior may occur, as has now been documented for several species.

The bluegill may exhibit both types of behavior at different points in its ontogeny. As outlined earlier, upon hatching from eggs laid in nests in the shallow littoral zone, bluegill fry swim to the limnetic zone of lakes. At about 10-20 mm standard length, they return to the littoral zone. Since visual sensory abilities are limited at these very small sizes, the fry may not assess the presence of predators at all, and the timing may be inflexibly set by natural

selection. However, at larger sizes (ca. 35 mm, one year old fish in the experiment by Werner <u>et al</u>, 1982b), bluegill sunfish are known to assess predation risk and respond facultatively. Direct underwater observations suggest to me that in lakes and ponds with somewhat clear water, fish routinely encounter predators on a daily basis, and likely form some sort of estimate of danger in various habitats. In lakes with less opportunity for visual assessment, habitat selection may be less flexible, and might depend in part upon an evolved affinity for physical structure. The affinity, which might decline with fish size, could be integrated with information on foraging rates to effect a habitat choice.

In the model presented in this paper, it has been assumed that $\mu(g,s)$ is time-invariant and that fecundity, b(s), is continuous and a function of size. This has allowed an interpretable analytical solution from which the impact of alternative assumptions can be explored. For example, seasonality of growth rates and/or mortality rates for a given behavior can be summarized by making μ a function of age as well as growth and size. Seasonality in birth rate can similarly be introduced. If particular forms of the seasonality are assumed, specific cases are solvable in principle. One might expect, for example, that animals would accept a higher marginal risk at times immediately preceeding a predictable decline in resource levels if an increased size during the decline confers some benefit; e.g. if the mortality rate in winter is negatively size-dependent, an animal might accept a higher marginal risk in the preceeding summer. Similarly, if resources are expected to increase in the near future, allowing a lower mortality rate for a given growth rate, an animal may "wait out

the storm" by temporarily accepting a low marginal risk (or even shrinking). Reproductive effort questions could also be explored by both making g and b control variables, and compactly describing the relationships between growth, fecundity, size, mortality, and perhaps age in a single function, $\mu(g, b, s, x)$.

Hopefully, the beginning presented here will prove useful in exploring community-level interactions between size-structured populations. The development of optimal foraging theory in the 1970's has provided what appears to be a powerful tool in the prediction of resource utilization by animals unconstrained by mortality risk. If the theory developed here and modifications of it prove useful in predicting habitat use, the essential tools will be available to predict both habitat use and prey utilization within a habitat by species in a community. This would provide a more powerful alternative to exhaustive experimentation and "intuition" in exploring the impacts of species introductions (or removals) and resource changes in a community, and could provide predictions of evolutionary directions in extant or perturbed communities.

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CHAPTER 2

Recruitment of a piscivore through a competitive bottleneck: Competitive effects of bluegill sunfish on juvenile largemouth bass

INTRODUCTION

Fish, as many other animals, usually exhibit dramatic niche shifts during their ontogeny. These shifts usually involve changes in diet and often habitat use, and results in an individual's encountering a series of different competitors and predators as it grows. This complexity renders suspect any blanket classification of a species as being another's predator, prey, or competitor since the interaction may be very age- or size-specific.

In this paper, we investigate a case in which a species, the largemouth bass, competes with at least some size-classes of another species, the bluegill sunfish, early in its life, and then preys upon the same species at larger sizes. Werner (1977) and Keast (1977) have noted that many fish species which eventually become piscivores pass through stages during which they consume mainly zooplankton and/or insects, as commonly do all sizes of species on which the piscivorous individuals prey. This suggests the possibility of a competitive "bottleneck" in which an increase in the density of the "prey" species may decrease the growth and survivorship of small individuals but increase the growth and survivorship of large individuals in the

"piscivorous" population, therefore altering the population's age and size structure. This effect would be enhanced if the "piscivorous" species' morphology rendered it a poor competitor on small invertebrate prey. The possibility of the complete exclusion of bass or other "piscivores" from a community due to a competitive bottleneck is raised, similarly to the size-specific developmental bottlenecks between crustacean competitors described by Neill (1975). While the exclusion of a species is a very dramatic example of a competitive bottleneck, more subtle effects on a species' age and size structure may commonly occur, affecting not only the "predator's" population structure but its impact on other members of the community. The survival of small fish is often thought to strongly influence the strength of a year-class of fish (e.g. Cushing 1974, Kramer and Smith 1962), and reductions in the growth rate of small fish might strongly affect early survival (next section).

The interaction we investigate is between the largemouth bass (<u>Micropterous salmoides</u>) and bluegill sunfish (<u>Lepomis macrochirus</u>), two dominant fish in lakes through much of Eastern North America. There is a huge literature on the life histories and especially diets of both of these species (reviewed in Carlander 1977), but nearly all of the studies deal with a single species or do not provide information on the nature of size-specific interactions (but see notable exceptions below). The bass-bluegill system has usually been viewed as a predator-prey interaction, but at small sizes largemouth bass feed upon invertebrates, as, typically, do all sizes of bluegills. We know of no detailed work on the simultaneous diets of specific sizes of small bass and bluegills other than the work by

Mullan and Applegate (below) and the work reported in this paper. However, single-species studies indicated the potential for extensive overlap in resource use.

Life histories of course vary somewhat between lakes, but the basic pattern is as follows. Largemouth bass spawn at a water temperature of about 16°C and the male tends the nest and fry until the fry reach a length of about 10-25 mm Standard Length (SL, the length from the anterior tip of the mandible to the end of the vertebral column; essentially, the length excluding the caudal fin). The bass usually switch to progressively larger prey as they grow, first consuming small zooplankters (e.g. rotifers, Bosmina, copepod nauplii), then larger zooplankters (e.g. Daphnia, Sida, copepods) initially at 8-12 mm, then sometimes insects or amphipods at initially 10-30 mm, and finally switch to fish prey at 25-90 mm. In Michigan, bass are commonly about 100 mm long at one year of age and are largely piscivorous. Bluegills first spawn at a water temperature of about 20°C, which in Michigan commonly occurs about three or four weeks after the spawning of the bass. Unlike the bass, bluegills commonly continue to spawn for several weeks after the initial activity. Bluegill fry are not tended by the male after leaving the nest and apparently travel to the limnetic regions of lakes and feed upon zooplankton until they reach 8-20 mm SL, at which time they usually return to the littoral zone. They then consume zooplankton, insects, and other invertebrates thereafter, switching habitats on a seasonal and size-specific basis (Mittelbach 1981). In Southwest Michigan, bluegills are commonly about 30 mm SL at age I, 60 mm at age II, and 80 mm at age III.

In addition to the diet similarities noted above, there is some more direct evidence that competition occurs between juvenile largemouth bass and other fish. Applegate and Mullan (1966) and Mullan and Applegate (1968) documented the diets of bass and other fish in two reservoirs and noted that in the newer reservoir bass between 20 mm and 40 mm SL utilized chironomid larvae as a "bridge" between diets of zooplankton and fish. In the older reservoir, the chironomids were essentially absent from the bass diets although bluegills and other centrarchids consumed midges throughout the year. The bass grew faster in the new reservoir. Von Geldern (1971) noted an inverse relation between the density of adult threadfin shad in a California reservoir and the size of largemouth bass year classes; he suggested that competition for food or interference with spawning success may be responsible. Von Geldern and Mitchell (1975) and Fast et al. (1982) showed that the first-year growth rates of largemouth bass decreased dramatically following the introduction of threadfin shad into California reservoirs, and that the growth rates of older bass increased concurrently.

This type of interaction may be common in other fish, although it remains largely uninvestigated. Crossman (1959) and Larkin <u>et al</u>. (1957) reported some effects of the introduction of the redside shiner into Paul Lake, British Columbia, which included a decrease in the growth rate of rainbow trout less than about 120 mm fork length and a probable increase in the growth rate of rainbow trout over about 200 mm. Svardson (1976) noted that species introduced into Scandinavian lakes were more likely to substantially impact resident species if the invader was more planktonic than the resident. One explanation

offered by Svardson is that the invader competed with the young of the resident species. Maly (1976) has suggested that a competitive bottleneck may occur among copepods, and Neill and Peacock (1980) have shown experimentally that an increase in algal productivity increases the recruitment of herbivorous <u>Cyclops nauplii</u> to the carnivorous adult population.

This paper is organized as follows. First, we develop a simple representation of the effect of reduced individual growth rates on the recruitment of small bass to the piscivorous population. Then the potential for competition is assessed by four measures: the relative handling times on invertebrate prey, a survey of habitat use, measurement of growth rates in two lakes with a comparison to maximal growth rates when food is abundant, and documentation of diets in two lakes. Finally, the hypothesis that the growth rate of small bass is a function of the density of bluegills is tested in a pond in which small bass are exposed to a gradient of bluegill densities.

GROWTH RATE AS A KEY PARAMETER

What follows is a simple abstraction of the effect of a reduced growth rate on the survivorship through some size interval, such as the size at commencement of feeding and the size at commencement of piscivory. If the growth and mortality rates are taken to be functions of the animal's size rather than its age, as appears to be the case for fish at least at early ages (e.g. Ricker 1979), a simple expression may be derived relating the survivorship through the size interval following changes in the size-specific growth and mortality rates.

The survivorship of a fish from age x_1 to age x_2 can be described by

$$L(x_1, x_2) = e^{\int x_2} u(x) dx$$
 (1)

where x = age and (x) = instantaneous mortality rate at age x (see e.g. Hassell, 1978, Appendix I). If the mortality rate is explicitly a function of size rather than age, we can rewrite $\mu(x)$ as $\mu[s(x)]$. We can then change the variable of integration from age to size to obtain an expression for survivorship from size s₁ to size s₂. Equation 1 can thus be rewritten as

$$L[x(s_1), x(s_2)] = e^{-\int_{x(s_1)}^{x(s_2)} \mu[s(x)]dx}$$
(2)

Changing the variable of integration yields

$$L(s_1, s_2) = e^{-\int_{s_1}^{s_2} \mu(s)/(ds/dx) ds}$$
(3)

Since ds/dx is the growth rate, g(s), we have

$$L(s_{1}, s_{2}) = e^{-\int_{1}^{s_{2}} \mu(s)/g(s)ds}$$
(4)

VanSickle (1977) has derived this equation by a different method. Intuitively, Eq. 4 represents survivorship across a size interval because $\mu(s)/g(s)$ is the instantaneous probability of death at a particular size, since that probability is the product of $\mu(s)$ (i.e. deaths/time) and the inverse of the growth rate (a measure of the time spent at that size).

Assume some arbitrary "baseline" state at which some values of $\mu(s)$ and g(s) occur (e.g. bass in the absence or a given density of

bluegills). Now assume some change multiplies the growth rate by a factor, c (c < 1 for a growth reduction). Then the new survivorship, L', can be expressed as

$$L' = e^{-\int_{s_{1}}^{s_{2}} \mu(s)/cg(s) ds}$$

$$= e^{-(1/c)\int_{s_{1}}^{s_{2}} \mu(s)/g(s)ds}$$

$$= \left[e^{-\int_{s_{1}}^{s_{2}} \mu(s)/g(s)}\right] 1/c$$
(5)

Since the expression in brackets is just $L(s_1, s_2)$, this yields (omitting the size range for compactness),

$$L' = L^{(1/c)} \tag{6}$$

This equation relates simply the survival through the size interval before and after the reduction in growth rate. For example, if the growth rate is reduced to one third its former level, the new survivorship is just the cube of the former survivorship.

The qualitative message from Eq. 6 is this: at parts of the animal's life history at which survivorship is already low, reductions in the growth rate have a much larger impact on survivorship than at points at which survivorship is initially high. For example, if c =1/3 and L = .90, then L' = .73, a reduction of 19%. However, if L =.01, L' = .000001, a decrease of 99.990%. The effect of the decrease in growth rate is depicted in Figure 1 for various values of c and L. Little is known of the size-specific mortality rates of fish during the first year, but it is clear that the survivorship between first feeding and piscivory lies near the origin in Figure 1 for bass Figure 1. Percent reduction in survivorship through a size (not an age) interval due to a reduction in growth rate. $L(S_1, S_2)$ is the survivorship prior to the reduction in growth rate. c is the value by which the growth is multiplied.



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(Zweiacker et al. 1975) and other fish (Braum 1978).

The impact of an increase in the size-specific mortality rate, $\mu(s)$, can also be assessed by the above method. By a derivation analogous to that shown above, if $\mu(s)$ is multiplied by a factor k, Eq. 6 still applies if k/c is substituted for 1/c, and Fig. 1 also applies if the same substitution is made. Large bluegills and other centrarchids are known to prey upon bass fry (e.g. Mullan and Applegate, 1967; pers. obs.), so an increase in their density may have a substantial "direct" effect on bass survivorship through a size interval in addition to the "indirect" effect through the depression of growth rate.

This representation is of course a vastly simplified representation of the complex biological processes occurring during the early life history of fish. Eipper (1975) reviewed many biotic and physical factors which are thought to affect early survival of bass and other fish, and there clearly are abiotic factors such as wave action which can cause large variation in survival. The deterministic treatment presented above is intended only to provide a starting point from which to assess the impact of decreased growth rates within the context of many other factors thought to affect mortality, and to motivate the investigation of growth rates as a key factor in an idealized deterministic system. The approach is most directly applicable to systems in which density-dependent, biotic processes are strong, but in more stochastic systems it can also provide a starting point for assessing the effect of reduced growth rate on the mean value of survivorship.

METHODS

Handling times were measured for fish feeding on <u>Simocephalus</u> and Coenagrionid damselfly nymphs. These two prey were chosen as representative of littoral zone cladocerans and insect nymphs, respectively. The <u>Simocephalus</u> were cultured in the laboratory and sorted with sieves to select individuals of 1.8-2.2mm length, mean = 2.0mm. The damselflies were collected from ponds at the Kellogg Biological Station. Two sizes were used: 5.0-7.0mm long, excluding the anal gills, and 9.0-11.0mm long. These sizes will be called 6mm and 10mm damselflies, respectively.

Handling times on these prey were measured for bass of lengths of 25, 35, 45, 55, 70, and 138mm SL, and for bluegills of lengths 25, 35, 45, 55, and 80mm SL. The handling times were measured in 200-liter aquaria while a fish foraged for a given prey size among a dense bed of <u>Chara</u>. The handling times were measured with an event recorder and were taken to be the time between the initial attack of a prey to the resumption of searching behavior.

Dry weights of the prey and the fish were calculated from regressions of the form $W = aL^b$, where the length measurement was in mm and the weights in mg or gm. The parameters were: <u>Simocephalus</u> (mg), a = .01737, b = 2.17 (Ivanova and Klakowski 1972); coenagrionids (mg), a = .00124, b = 2.74 (unpublished); bass (gm), a = 0.00000170, b = 3.2157 (regression for bass from Three Lakes and Lawrence Lake); bluegills (gm), a = .00000676, b = 3.043 (Lawrence Lake).

The habitat use of the fish was recorded in Lawrence Lake (described below) on July 25 and 26, 1978. The method was as described in Werner, et al. (1977) and was taken along transect II in
Werner <u>et al</u>. Divers counted all bass and bluegills along a 100m transect and classified the location of each fish on two axes: the "position" and the "microhabitat." The "position" is a measure of the distance from the shore and hence the depth of the water. Position 1 was closest to the shore and was on a shallow (0.5m water depth) bench without vegetation cover. Positions 2 and 3 were in about 1m of water depth on the bench and at its point of contact with the beginning of the sloping bottom, respectively. Positions 4 and 5 were at depths of 2m and 4m, respectively. Except for Position 1, the area was covered with a dense growth of primarily <u>Scirpus subterminalis</u>. The "microhabitat" measurement refers to the position of the fish in or above the vegetation. The fish were recorded as being in the lower vegetation, upper vegetation, or at some height above the vegetation at 0.25m intervals.

Fish were collected for growth and diet studies by seining in Lawrence Lake, Barry County, Michigan, and Three Lakes, Kalamazoo County, Michigan. Lawrence Lake is a mesotrophic lake, 4.9 hectares surface area, and 12.6m maximum depth. Three Lakes refers to a chain of three lakes; we collected fish in the middle lake of the chain. The lake is more productive than Lawrence Lake, is about 10 ha in surface area, and has a maximum depth of 10m. The vegetation along the sampling area on the south side of the lake is predominantly <u>Chara</u>. Fish were collected between 0900 and 1100 h on a weekly basis. The fish were killed with an overdose of tricaine methanesulfonate and preserved in 10% formalin. Stomach contents were identified and prey length measurements taken. Length-weight regressions were used to convert the measured lengths to weights.

The maximal growth rates of bass were estimated by placing bass fry from a holding pond into a fishless pond at the Kellogg Biological Station. Approximately five hundred 15.5 to 19mm bass fry were introduced into a circular pond (29m diameter, 1.8m deep) with abundant zooplankton and insect nymphs. Bass were sampled weekly for growth and resources qualitatively monitored for depletion. Some resource depletion became apparent by July 9, at which time 198 bass were transferred to another pond. The stomachs of the bass were distended throughout the experiment. The length (mm)-weight (gm) power function regression had the parameters, a = .0000007863, b = 3.491.

The instantaneous growth rates were calculated for fish from Lawrence Lake, Three Lakes, and the maximal growth experiment. The calculation of the instantaneous rate between day i and day j was calculated from r = [ln (weight at i)-ln(weight at j)]/(days betweensamples). In each case, the growth rate of a fish of the mean lengthin the cohort was calculated. Thus, on each date, the mean length ofthe cohort was calculated. Thus, on each date, the mean length wascalculated, and that value was entered into the growth rate equationtogether with the weight of the mean fish length of the previoussample. This growth rate was then estimated to have applied to a fishof the standard length which was at the midpoint of the two standardlengths used in the calculations.

The bass-bluegill competition experiment was performed in an experimental pond of the same dimensions as the ponds used in the maximum growth experiment. To simulate conditions in local lakes, a ring of cattails was removed from the pond, and the dense growth of

<u>Potamogeton</u> was thinned to approximate densities in local lakes. The pond was then quartered with partitions made of 3mm fish seines, and bluegills of a mean length of 34.3 mm (sd = 2.80) were introduced in a gradient of densities: 300, 500, 1000, and 1500 per quadrant. 250 bass (27.5mm, sd = 2.59) were placed into each quadrant. Samples for growth and diet calculations were taken weekly. Only a cursory treatment of the experiment is given here; a more complete account is in preparation.

RESULTS

HANDLING TIMES

On prey ranging from 2mm <u>Simocephalus</u> to 10mm damselflies, a bass of a given standard length took a greater mean time to handle a prey than did a bluegill of the same length. Figure 2 shows the regressions for both species and the original data for bass. The data points corresponding to a (prey length)/(predator length) < 0.1 are for <u>Simocephalus</u> and represent the mean handling time per prey during a foraging bout; the points corresponding to a length ratio greater than 0.1 refer to damselflies and are handling times on individual prey items.

The regressions of handling time (H) on the ratio of prey length to fish length (PL/FL) were fitted by a nonlinear regression algorithm (program P3R in the EMDP computer programs series). This allowed the regression line to better approximate the mean handling time rather than the mean of the logarithm of handling time, which differed as a result of the large variances in the data. The fitted equations were as follows: bass, $H = 1.68 \exp[6.438(PL/FL)]$, serial correlation coefficient = 0.20, n = 388; bluegills, $H = 0.80 \exp[7.904(PL/FL)]$, Figure 2. Handling times on <u>Simocephalus</u> and damselflies for largemouth bass and bluegills. Data points are the individual values for the bass.

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correlation = 0.16, n = 129. Regressions of handling time on the ratio of prey weight to fish weight (PW/FW) are: bass, H = 1.80exp[178.3(PW/FW)], correlation = 0.38, n = 388; bluegills, H = 0.80exp[516.7(PW/FW)], correlation = 0.26, n = 129, where both the prey weight and the fish weight are expressed as mg dry weight.

The optimal prey weight is taken to be the weight which minimizes the ratio of mean handling time to prey weight for a given fish weight; the variance in handling times is not considered in this calculation, although in a more detailed treatment of foraging rates the variance might alter the optimal value somewhat (Gilliam, unpublished). The regressions of the form H = (a)exp[b(PW/FW)] have the convenient property that the value of PW/FW which minimizes H/PW for a given fish weight occurs at (1/b), or PW = FW/b. Therefore, the above regressions estimate the optimal prey weight for bass to occur at FW/178.3 = 0.0056FW and at 0.0019FW for bluegills.

Figure 3 shows the optimal prey weights for bass and bluegills as a function of their standard lengths, calculated from the above relationships. For present purposes, the utility of the figure is to suggest that a bass of a given length has the same optimal prey weight as a bluegill that is about ten percent longer. This is one way to estimate the potential for the source of the most direct competition from an array of bluegill sizes present.

It should be noted that in Figure 3, the optimal prey weight exceeds the weight of a 10mm damselfly for bass larger than 33mm and bluegills larger than 36mm. Since invertebrate prey of that size are usually rare in lakes, both fish species may in practice be limited largely to invertebrates below the optimal prey size. If this is the Figure 3. Optimal prey weights for bluegills and largemouth bass. Left curve: bass. Right curve: bluegill.





case, the opportunities for segregation of bluegill diets by prey size may be limited for bluegills of about 36mm and above. Thus, Figure 3 suggests that bass of about 33mm and perhaps smaller may compete directly with most sizes of bluegills present in the littoral. It should also be noted that the curves are extrapolated for optimal prey weights above the weight of a 10mm damselfly, 0.68mg. Thus, while the curves are appropriate for the original purpose of suggesting the optimal sizes of invertebrate prey likely to be found in lakes, and hence the fish sizes with similar optimal prey sizes, the curves may not be appropriate for describing the optimal prey sizes of fish above about 35mm.

HABITAT USE

Figure 4 describes the habitat use by young-of-year bass and four size classes of bluegills in Lawrence Lake on the afternoons of July 26 and 27, 1978. The patterns were similar for the two dates and the data are combined. In the microhabitat dimension, the bass were found mainly in the upper half of the vegetation (predominantly <u>Scirpus</u> <u>subterminalis</u> about 0.5mm tall). Young-of-year bluegills (0-25mm size class) were found among and just above the vegetation. The 26-50mm bluegills were distributed similarly to the bass, and larger bluegill classes shifted progressively higher in the water column. Across positions, the bass were distributed across all positions except the unvegetated portion of the shallow bench. The 26-50mm and 51-75mm bluegills showed a similar distribution to the bass. These results are in general agreement with previous surveys (Werner <u>et al</u>. 1977, Hall and Werner 1977). Qualitative observations in 1979 and 1980 yielded the same general pattern. Mittelbach (1981) found that

Figure 4. Habitat use by largemouth bass and bluegills. "Microhabitat" represents location in or above the vegetation. LV = lower vegetation, UV = upper vegetation, 0-.25 = zero to 0.25m above vegetation. "Position" represents distance from shore.



bluegills larger than 75mm did not forage extensively in the littoral zone in July; this is also consistent with the present data.

These results show that there is not extensive habitat segregation betwen bass and 25-75mm bluegills in the littoral zone, and that the 25-50mm (predominantly one-year-old) bluegills utilize essentially the same areas as the bass.

GROWTH RATES

Figure 5 depicts the growth curves for cohorts of bass in Three Lakes, Lawrence Lake, and the "unlimited growth" experiment in ponds. On all dates, the fish in the ponds were substantially larger than in the lakes. The sizes are plotted as lengths since fish length is a more familiar quantity than weight; if the size were expressed as weight, the difference between the lakes and the ponds would appear even larger.

While Figure 5 might suggest a substantial depression of growth rates below their maximum, the data are confounded by a difference in spawning times in the lakes. By expressing the growth rates as a function of the fish size rather than time, specific sizes at which the growth rates are depressed can be identified.

The estimated instantaneous relative growth rates are shown in Figure 6. The growth curves are somewhat irregular, as expected with the estimation of growth rates from mean sizes of bass caught at tabout one-week intervals. However, the data yield useful information on the extent of growth depression at different sizes.

Three growth curves are shown for Lawrence Lake. The curve designated LL80S is a school of bass which we were able to locate regularly early in 1980. After the school's dispersal, we were able Figure 5. Mean largemouth bass lengths in a maximal growth rate experiment (Ponds) and two lakes. 3L1980 = Three Lakes in 1980. LL1980 = Lawrence Lake in 1980.

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Figure 6. Instantaneous relative growth rates (day⁻¹) of largemouth bass in the maximal growth rate experiment (Ponds), Three Lakes (3L1980), a school in Lawrence Lake (LL80S), all bass collected in Lawrence Lake (LL80) and Lawrence Lake in 1979 (LL79). The arrow indicates the point of transferral of the fish from one pond to another.



to identify individuals from the school over the next two weeks since those fish formed a distinct, large size class relative to bass which were spawned later. The calculated instantaneous relative growth fluctuate somewhat, but it appears that the cohort grew at about one-half the rates of the bass in the pond between the lengths of about 22mm and 42mm. The second curve is designated by LL80. It is calculated from the lengths of all fish captured on a date in Lawrence Lake during 1980. At sizes < 28mm, the curve is identical to the LL80S curve. The "dip" at 36mm and peak at 41mm are not judged to reflect real changes in the growth rate since the size-frequency distribution was bimodal and the changes can be attributed to sampling error in the proportion of fish near each mode. The overall trend suggested by LL80 is that growth rates are depressed in Lawrence Lake, and that the depression occurs across all sizes. The third curve, LL79, is constructed from bass collected in 1979. Over the size range collected, growth rates were substantially depressed.

The data for Three Lakes shows a substantially different pattern from that of Lawrence Lake. At lengths up to about 33mm, the bass grew at approximately maximal rates. At sizes > 35mm, growth rates were somewhat depressed. In Three Lakes, therefore, neither internor intraspecific density-dependent growth appeared to occur at sizes less than about 33mm.

The growth data therefore suggest a possibility for a competitive bottleneck affecting bass in Lawrence Lake, but provides evidence against such an effect in Three Lakes for small sizes, though the effect might occur at larger sizes.

DIETS IN LAWRENCE LAKE AND THREE LAKES

A summary of the diets of young-of-year bass in Lawrence Lake are shown in Table 1 for each sampling date. As they grew, the fish switched from a diet of copepods and Bosmina to a diet of littoral cladocerans (<u>Sida</u>, <u>Latona</u>, <u>Simocephalus</u>) and insects and finally to fish (centrarchid fry). The transition is depicted in Figure 7, in which the diets of the cohort are plotted against the mean length of the fish in the cohort on a date. The cladocerans act as a "bridge" between small copepods and fish prey for bass between about 20mm and 30mm.

The diets of bass in Three Lakes were somewhat similar to those in Lawrence Lake, as shown in Table 2. However, in Three Lakes, Baetid mayfly nymphs formed the transition between the copepod and fish diets. This is seen in Figure 8. Unlike Lawrence Lake, the mayfly nymphs continued to contribute substantially to the diet after the cohort reached 30mm in mean length.

In both lakes, the shifts in taxonomic categories coincided with a shift to progressively larger prey. In Figure 9, the mean prey weight in the stomach of each fish collected in Lawrence Lake is plotted as a function of the individual's length. The dots represent bass without fish prey; the x's represent bass with at least one fish prey. The mean prey size is clearly strongly related to the size of the fish, and over the summer the mean prey size spanned nearly five orders of magnitude. Figure 10 shows the same relationship for Three Lakes.

The presence of the mayfly nymphs in the bass in Three Lakes resulted in a smoother progression to larger prey than did the

Table 1. Diets of young-of-year largemouth bass in Lawrence Lake, 1980, expressed as percent dry weight of total diet. To be included in the table, an item must have comprised at least five percent of the diet on at least one date. Values rounded to the nearest percent, and values less than 2 percent omitted. Prey categories are, in order, copepods: Cyclopoida, Calanoida; cladocerans: <u>Bosmina, Sida, Latona,</u> Simocephalus; Chironomid larvae; Baetidae; centrarchid fry.

Date	<u>n</u>	<u>mean SL</u>	<u>Cycl</u>	Cala	Bosm	<u>Sida</u>	Lato	Simo	<u>Chir</u>	Baet	Cent
6-16	8	13.9	45	40	7						
6-23	9	16.2	15	63	16						
6-30	12	23.8	6			43	15	6	10	13	
7-8	10	31.1	19			11	3		2	2	61
7-14	12	27.1				5			4	4	81
7-21	10	31.6		3		7			2		86
7-28	10	35.7		3		4				3	85
8-4	10	36.0								4	95
8-12	8	45.9									99
8-26	9	51.7									99
9-26	10	65.1									99

Figure 7. Diets of largemouth bass in Lawrence Lake.

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Table 2. Diets of young-of-year largemouth bass in Three Lakes, 1980. Description as in Table 1. Acro = <u>Acroperus</u> (a littoral cladoceran), Cypr = Cyprinid fish.

Date	<u>n</u>	mean SL	<u>Cycl</u>	<u>Sida</u>	<u>Simo</u>	Acro	Baet	Cypr	Cent
6-24	5	13.9	99						
7-1	11	13.4	38	20	17	8			16
7-10	8	24.3		4			54		39
7-15	22	29.3					19	6	72
7-23	13	37.2					4		95
7-30	10	36.9					27	13	58
8-6	10	41.7					33	17	48
8-13	10	50.7							99
8-27	10	59.7							99
9-26	8	68.9							99

Figure 8. Diets of largemouth bass in Three Lakes.



Figure 9. Mean dry weight of prey in the stomachs of individual largemouth bass in Lawrence Lake. The X's represent bass with at least one fish prey. The E's represent fish with empty stomachs.



Figure 10. Mean dry weight of prey in the stomachs of individual largemouth bass in Three Lakes. Symbols as in Figure 9.

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cladocerans in Lawrence Lake, as can be seen in a comparison of Figure 9 and Figure 10. Inspecting the mean prey weights of 20 to 30mm bass in Lawrence Lake, it is seen that the weights fall mainly between 0.01 and 0.05mg. These bass were feeding mainly on Sida and other cladocerans. The two bass in that size range with mean prey weights of 0.1 to 0.2mg had Baetid nymphs in their stomachs, along with littoral cladocerans. In Three Lakes, the mean prey sizes in the stomachs of 20 to 30mm bass was shifted up by an order of magnitude relative to Lawrence Lake. These mean weights reflect a diet of Baetid nymphs, and the mean prey weights of 20 to 30mm bass in Three Lakes is close to the optimal prey weight of 0.4mg calculated from the laboratory experiments. It appears that the presence of Baetids in the diet of Three Lakes bass may be a major contributor to the difference in growth rates between the Lawrence and Three Lakes fish.

The bluegill diets were substantially different from the bass in both lakes, though this could not be anticipated from the handling time data and the habitat use patterns, both of which suggested substantial potential for diet overlap. Table 3 shows the diets of 25mm to 60mm bluegills in Lawrence Lake. Throughout the sampling period, the diets consisted largely of chironomid larvae. However, a substantial part of the diet consisted of <u>Sida</u> and some <u>Latona</u>. Thus, in Lawrence Lake, it appears that direct competition between bass and bluegills occurs for the littoral cladoceran and chironomid larvae resources. The low level of Baetids in the Lawrence Lake bass cannot be attributed to their depletion by bluegills based on the diets of the bluegills, since Baetids were hardly consumed over the sampling period.

Diets o weight	of 25-60mm bluegill sunfish in Lawrence Lake, 1980, expressed as percent dry of the total diet on a date. Criteria for inclusion as for Table 1, except
tids	also included. Values rounded to the nearest percent, and values l
cent	omitted. Ophr = <u>Ophryoxus</u> (a littoral cladoceran), Caen = Caenidae (may
ph),	Coen = Coenagrionidae, Tric = Trichoptera, Amph = Amphipoda, Acar = Acari
N	Gastropods.

Date	۲	Chir	Sida	Ophr	Simo	Lato	Cyc1	Cala	Caen	Baet	Coen	Tric	Amph	Acar	Gast
6–30	20	54	21	٢		3	2		2				7	e	
7-8	2	35	52	4	2	e						2			2
7-14	10	22	30	6		4						2			2
7-21	10	71	12	2			2		2		2		2	2	e
7–28	7	34	35			4	2			4	2			11	c
8-4	10	31	12						9			29	œ	S	2
8-12	10	72	2			7		°,					2	11	
8–26	10	56	5				9	4			5		11	9	
9-26	20	26					13	31			2		9		

Habitat surveys (Werner <u>et al</u>. 1977 and unpublished data) indicate that the density of 25 to 60mm bluegills is at least ten times the density of young-of-year largemouth bass in Lawrence Lake. Absolute consumption rates are not known for the fish, but even if the 25 to 60mm bluegills had only the same consumption rate (mg/day) per fish as the 25mm bass, the total demand on the <u>Sida</u> population by the bluegills would exceed the demand by the bass, given that <u>Sida</u> formed 12-52% of the bluegills' diets in July. This suggests that if the density of <u>Sida</u> was depressed by foraging, the primary source of the depression was from the bluegill population, and the levels of <u>Sida</u> largely set by the bluegills rather than the bass. Phoenix (1976) found that fish can strongly depress population levels of littoral zone cladocerans.

Table 4 shows the diets of 25 to 60mm bluegills in Three Lakes. These fish also mainly consumed chironomid larvae. They also consumed some littoral cladocerans and Baetids. While there was some overlap with the bass' diets, it was not so large as in Lawrence Lake. Unlike Lawrence Lake, neither the diet information nor the growth rates strongly suggest the operation of a competitive bottleneck.

A QUANTIFICATION OF THE EFFECT OF BLUEGILL

DENSITY ON BASS GROWTH RATES

The prey partitioning between the bass and bluegills was greater than the laboratory experiments and habitat use survey suggested might occur, and it brings into question whether any substantial competition is likely to occur. Therefore, the effect of bluegill density on bass growth was quantified in an experimental pond, as described in the Methods. Here, the main result of the

Table	4.	Diets of	25-60	man blu	lligen	sunfis	h in T	hree L	akes,	1980.	Descr	lption	as fo	r Tabl	e 3, p	lus
		the foll	owing	additi	onal p	rey ca	tegori	es:	ury =	Euryce	rcus (a litt	oral c	ladoce	ran),	Daph =
	•	Daphnia,	Chao	= Chao	borus	(a pla	ktonic	dipte	ran la	rva).						
Date	F	Chir	Sida	Sino	Eury	Cyc1	Cala	Baet	Caen	Coen	Tric	Amph	Acar	Gast	Daph	Chao
6-24	10	61	2	18	5			80				5	15	5		
7-1	11	72	4	4	7			5				S	2	e.		
7-10	10	99			2			S				2	11	2		
7-15	10	51	S	4							4	9	80	9		
7–23	10	34									39	6	6			
7–30	12	33											2		17	23
8-6	10	79							10		e					
8-13	12	99	4			6			9	7		5				
8-27	10	29			2	e.					2				48	٢
9-26	6	48					15		4						37	

experiment is presented; the experiment will be treated more fully elsewhere (Gilliam, Werner, and Hall, in prep.), but is included here because of its direct relevance to the material presented so far.

Figure 11 shows the final mean weights of the bass and bluegills after forty-seven days. The bluegill growth rates were strongly density-dependent. The bass growth rate was not differentially affected by bluegill density across the first two densities, then declined markedly. In the presence of 300 bluegills, surviving bass each gained an average of 1.0gm dry weight; in the presence of 1500 bluegills, they gained an average of 0.25gm. The initial mean length was 27.5mm, and the final mean lengths were 56.3mm at the highest density.

The reduction in growth rate occurred despite a degree of resource partitioning similar to the lakes. At the lowest density, the bluegills' diet consisted of chironomid larvae, 78%; <u>Simocephalus</u>, 7%; and cyclopoid copepods, 5%. No other prey composed more than 3% of the diet. The bass' diets consisted of Baetidae, 35%; <u>Simocephalus</u>, 14%; Ceriodaphnia, 11%; cyclopoid copepods, 10%, calanoid copepods, 10%; and chironomid larvae, 7%. The major source of overlap was on a littoral zone cladoceran (<u>Simocephalus</u>) and chironomids, as in Lawrence Lake. At the highest density, the bluegills' diets consisted of chironomid larvae, 65%; cyclopoid copepods, 8%; <u>Simocephalus</u>, 4%; and gastropods, 4%. The bass' diets were calanoid copepods, 42%; Baetidae, 27%; chironomid larvae, 11%; and <u>Simocephalus</u>, 7%. Again, the main overlap was on <u>Simocephalus</u> and chironomids.

Figure 11. Final mean dry weights of bluegills and largemouth bass, as a function of the density of bluegills in an experimental pond.



CONCLUSION

The results of the pond experiment demonstrate the depression of the bass' growth rates by increased bluegill densities, despite substantial resource partitioning between the species. This increases our confidence in the existence of a competitive effect of bluegills on bass in Lawrence Lake, and contrasts with the apparent absence of a strong depression in Three Lakes. The difference in the bass' growth rates in Lawrence Lake and Three Lakes corresponds with the existence of the Mayfly "bridge" in Three Lakes. The growth rates of fish have previously been found to be closely related to the mean prey size consumed (Paloheimo and Dickie 1966, Martin 1970, Kerr 1971, Wankowski and Thorpe 1979), so a causal relationship is a reasonable hypothesis. It is not known to what extent the paucity of Baetids in the bass' diets in Lawrence Lake is attributable to their depletion by bluegills or other fish, but their absence does appear to contribute to the bass' reduced growth rates and forces competition with the bluegill on the Sida resource.

There is agreement between the expected impact of the bottleneck and the population levels of bluegills and bass in the two lakes. Censuses of the fish populations of Lawrence Lake and Three Lakes by Werner <u>et al</u>. 1977 showed that the density of bluegills was an average of 411 per 100m in the littoral zone of Lawrence Lake, but only 326 in Three Lakes. This coincided with a lower bass density in Lawrence Lake than in Three Lakes, 54 versus 66 per 100m.

The level of resource partitioning between the species was greater than anticipated at the beginning of this investigation. The bluegills' extensive consumption of chironomids is contrasted by the
bass' low utilization. Applegate and Mullen's (1967) report of the bass' use of the chironomids when the resource seemed to be abundant suggests that chironomids can afford high growth rates to the bass. Thus the low levels of chironomids in the bass' diets in Lawrence Lake may signify another source of the bottleneck. Indeed, the chironomids in the diets of the bluegills usually average between 0.1 and 0.5mg dry weight, which is similar to the weights of the Baetids utilized by the bass in Three Lakes. Preliminary laboratory observations have indicated that bass lack an ability to cleanly extract chironomids from tubes in sediments, while bluegills can do so. When feeding on chironomids, bluegills would attack burrowed chironomids by sucking a precise area of the sediments into its mouth, and then expelling the sediments while retaining the chironomid. The bass, which has a larger mouth than the bluegill (see illustrations and descriptions in e.g. Werner 1977), would attempt to grasp the tube or a partially exposed chironomid between the jaws, employing little suction; this behavior was less effective than the bluegill's. The bass also appeared to position itself less precisely than the bluegill; this seems to be related to the more gibbose body shape of the bluegill relative to the fusiform shape of the bass usually associated with efficient and rapid swimming speeeds rather than maneuverability (Alexander 1967).

Although the bass' larger mouth and fusiform body shape may contribute to its poor utilization of chironomids, its morphology clearly confers an advantage in capturing large or elusive prey, such as fish. It is not known to what extent this ability may apply to elusive invertebrates, such as the calanoid copepods consumed in the

pond competition experiment, but elucidation of this question may contribute substantially to our understanding of prey selection by the bass. Timms (personal communication) has found that bass feed at a substantially higher rate on Baetids in aquaria than do bluegills, and that the bass dart at the mayflies and engulf them, while bluegills attempt to maneuver precisely and employ suction, which is often unsuccessful.

The foraging experiments on <u>Simocephalus</u> and damselflies also led to an entirely unanticipated behavior which may ameliorate the competitive effect of the bluegills somewhat. As reported more fully elsewhere (in preparation), when foraging on these prey in <u>Chara</u>, the bass would approach an area of the vegetation, lower the mandible, and then close it rapidly, "blowing" water from its mouth. This would often dislodge prey from the vegetation and resulted in the bass' experiencing about twice the effective encounter rate (prey attacked per second searching but not handling prey), though it also incurred the reported higher handling cost than the bluegill.

It is not known to what extent this behavior is utilized in the lakes by the bass. Even with this behavior, the reduction in the <u>Sida</u> by the greatly numerically dominant bluegills would be expected to contribute to the observed reduction in the bass' growth rates. However, the "included niche" nature of the interaction with bluegills suggests that the bass' contribution to the reduction of <u>Sida</u> levels would not affect the bluegills as much as the bluegills affect the bass. This is because <u>Sida</u> forms most of the diet of the bass using that resource, but the bluegills usually utilize <u>Sida</u> less than or to about the same extent as chironomids.

The reduction of the bass' growth rates in Lawrence Lake and the pond competition experiment occurred despite the absence of large bluegills. Mittelbach (1981) has shown that bluegills larger than about 75mm forage largely on limnetic zooplankton during the summer months. Mittelbach elucidated some of the implications of the presence of limnetic zooplankton in providing a means of resource partitioning between large and small bluegills, and showed that the absence of limnetic resources would be likely to result in greater resource depletion in the littoral zone and stunting of the bluegill population. This often happens in shallow ponds without distinct littoral and limnetic areas. If this occurred, the small bass would also be expected to be impacted by the same processes of resource depletion and greatly reduced growth rates experienced by the bluegills.

The size-specific reductions in growth rates have substantial implications for the size structure of the population of bass and other fish experiencing size-specific interactions. Since depression of a cohort's growth rate at a particular size results in a reduction in survivorship through that size interval, growth rates at subsequent sizes would increase if the growth rates are intraspecifically density-dependent; this would happen whether or not the large sizes prey upon the species causing the growth reduction at a smaller size. Thus a competitive bottleneck would usually act to increase the subsequent survivorship and fecundity of animals surviving the bottleneck. Thus, although the bottleneck acts to reduce the number of fish in the piscivorous population, it may or may not reduce the biomass and production of the piscivores. To this

extent, the effect of a bottleneck is somewhat analogous to problems approached in work on optimal harvesting. The usual goal of harvesting models is to find the amount of imposed mortality (usually on the adult population, unlike the bottleneck) which maximizes production. At low harvest rates, stunted populations of many slowly growing individuals can result; at high harvest rates, low population numbers of fast-growing individuals can result. Thus, the effect of harvesting or a competitive bottleneck changes the demography of the population, but the effects on total biomass and production depend upon the severity of the density-dependent processes occurring.

The presence of a bottleneck is also expected to affect the evolution of an animal's morphology. If the introduction of a competitor severely lowers a species' survivorship through some size interval, the species would be expected to evolve to increase its growth rate through that size range. This could occur either by character convergence (e.g. become a better planktivore) or by character divergence (e.g. become an even better piscivore, and switch to fish at an even smaller size). However, the evolution of morphology at one size carries with it morphological changes at all previous and subsequent sizes, since fish do not extensively rework their morphology ontogenetically, except for a few examples of metamorphosis. The ways in which fish and other animals morphologically balance selective pressures at various points in their ontogeny remains a virtually uninvestigated problem at the intersection between the disciplines of evolutionary ecology and development.

Finally, a graphical model is presented here which is motivated

by the bass-bluegill interaction. The intent of the model is to begin to assess the potential population dynamics and equilibria in a system in which one species preys upon another, but whose young incur increased mortality as the "prey" population increases. This is done by severely abstracting the bass-bluegill and similar systems to obtain a conceptually manageable, simple graphical representation as a beginning from which the impact of the reintroduction of meaningful biological features can be assessed.

The development of the model is presented in the Appendix and the resulting predator-prey phase plane is shown in Figure 12a, where H = prey and P = predator. The model ignores size structure except for the existence of "juvenile" predators whose survivorship is a decreasing function of H and P. It also ignores time lags in the system.

In Figure 12a, the prey zero isocline, denoted by H' = 0, is drawn as in "standard" predator-prey theory (Rosenzweig and MacArthur 1963, Tanner 1975). However, unlike other predator-prey theory, the predator isocline (P' = 0) forms a "dome." Under the dome, the predator population increases; outside it declines.

Figure 12a tells us that there are two alternate stable equilibria to which the populations can move in this abstraction. The equilibrium on the left leg of the dome represents the "standard" predator-prey equilibrium. The other (at H = K, P = 0) represents exclusion of the predator by the prey. Thus, depending upon the initial population densities, the system could behave like a "standard" predator-prey relationship or result in the extinction of the predator. If the prey exist at H = K, the system is

Figure 12. Phase-plane representation of a predator and a prey species, in which the offspring of the predators first compete with the prey. See Appendix for assumptions. H = prey, P = predator. The prey and predator isoclines are represented by H' = 0 and P' = 0, respectively. K = maximal prey density. (a) The predator-prey phase plane (b) The relationship of R_1 to H and the relationship of L to H for three densities of P: 0, P_1 , and P_2 .



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non-invasable by small numbers of predators, but the predator can invade if H is temporarily reduced to a level between the "window" at the base of the dome or if it arrives in initially large numbers and the population trajectories are attracted to the left leg of the dome. In this context, it is interesting to note that much effort has been given to trial-and-error studies of initial stocking densities of bass and bluegill in farm ponds. Implicit in the justification for such studies must be the assumption that alternate stable states exist, or that initial densities strongly affect the population trajectories so as to provide desirable though temporary population structures.

The above model of the bottleneck problem shows that the prey can exclude the predator if it reduces L to a point at which $1/L > R_1$. This necessary condition was clear from initial considerations of the problem, but the questions of stability of the populations in that region, multiple equilibria, and the nature of the stabilities at each equilibria point were not clear. The addition of age and size structure back into the model sets up time lags and hence "inertia" into the trajectories of the populations, but the abstraction provides a starting point from which those complexities can be assessed. As investigations of size-structured population interactions continue, a combination of simplified theory and illuminating, sobering field and laboratory data appears to be essential for substantial progress on this sometimes almost paralyzingly complex problem.

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APPENDIX

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The abstraction results in the isoclines in Figure 12a and was formulated as follows. The "prey" population level is described only by their density, H; no age or size structure is assumed. The "predator" population level is represented by the density, P, of individuals large enough to consume the prey. The rate of change of H is a function of H and P. Following standard predator-prey theory, in Figure 12a the prey zero isocline is drawn as in Rosen zweig and MacArthur (1963) and is labelled as H' = 0. The rate of change of P is a function of H and P. P does not change if $R_0 = 1$, and R_0 is taken to be $L(H,P) \cdot R_1(H)$. L(H,P) is the survivorship of the predator's offspring (hereafter called "juveniles") to predatory size, and is a decreasing function of H due to a bottleneck effect, and also a decreasing function of P due to cannibalism (the feature of cannibalism may be easily removed; see below). $R_1(H)$ is the expected number of juveniles produced by a predator over its lifetime given that it has reached predatory size, and is an increasing function of It is assumed that the predator receives negligible benefit from H. cannibalism and that the prey incur negligible cost from competition with juveniles. Then P is stationary when L $\cdot R_1 = 1$, or $R_1 = 1/L$. In Figure 12b, R is drawn as are the values of 1/L for three levels of P. P is stationary at the intersections of R_1 and 1/L; when R > 1/L, P increases, and when R < 1/L, P decreases.

This allows the construction of the predator isocline. The first two points of the isocline can be drawn as depicted by the dashed lines; at very low P, P increases if H is between the two points just plotted. If H is higher, P decreases because the low survivorship of the juveniles outweighs the high reproduction of the predators. If H is lower, the survivorship of the juveniles is high, but the reproduction of the predators is low since the density of prey is low. The next points on the predator isocline can be plotted at the value P and the value of H at which $1/L(P_1) = R_1$. Similarly, at a predator level of P₂, there is a single point.

The predator isocline thus constructed will be called the "dome." At any point inside the dome, the predator increases; at any point outside, the predator decreases. If cannibalism is not assumed to occur, then L depends only upon H, and the dome does not close at the top; instead, there are two vertical lines positioned at the first two points drawn on the predator isocline.

There are three equilibrium points in Figure 12a (in addition to H = 0, P = 0). The first is the intersection of the left leg of the dome with the prey isocline. The second equilibrium is the intersection of the right leg with the prey isocline. This equilibrium is unstable and is reminiscent of the unstable two-competitor case in Lotka-Volterra competition theory. The third equilibrium is at H = K, P = 0, which represents the exclusion of the prey by the predator. Thus in this mixed predator-prey-competitor system, one equilibrium occurs at which the predator-prey interaction appears to dominate the dynamics of the system, and two equilibria occur at which the competitive effects are salient.

If the prey have little effect on L, the right leg of the dome will intersect the H-axis at H > K and the system will behave essentially as a predator-prey interaction. The dome may also be shifted to the left if the predator has alternative prey. Numerous similar variations are left to the interested reader.

