OPTIMISTIC GROWTH: COMPETITION AND AN ONTOGENETIC NICHE-SHIFT SELECT FOR RAPID GROWTH IN PUMPKINSEED SUNFISH (*LEPOMIS GIBBOSUS*)

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Abstract.—Intrinsic growth rate is emerging as an important life-history trait that can be modified by natural selection. One factor determining optimal intrinsic growth rates is the pattern of resource availability. Organisms that experience chronically low resource levels tend to have slow intrinsic growth rates. However, this does not necessarily hold if resource levels change as an organism grows. We present a theoretical model showing that rapid growth is favored when resource levels for small size classes are low relative to resource levels for large size classes. We call such a growth strategy "optimistic" because rapid growth is based on an expectation that resources will improve once a minimum size is reached. We provide empirical support for this hypothesis by examining the intrinsic growth rates of pumpkinseed sunfish derived from three populations sympatric with bluegill sunfish (an important competitor with small size classes) to three populations allopatric with bluegill sunfish raised under common conditions. Rapid growth has evolved in the sympatric fish to reach the size refuge from competition as quickly as possible.

Key words.—Interspecific competition, intrinsic growth rate, *Lepomis gibbosus*, ontogenetic niche-shift, pumpkinseed sunfish.

Life-history theory often postulates a trade-off between growth and reproduction (Charnov 1991; Roff 1992: Stearns 1992) but seldom treats intrinsic growth rate during the juvenile stage as a parameter that evolves. Often, juveniles are assumed to grow as fast as possible (e.g., Sibly and Calow 1985; Stearns and Koella 1986; Perrin and Rubin 1990; Hutchings 1993), in which case their growth rates are determined by properties of the environment such as temperature or resource abundance. In some life-history models (e.g., Kozlowski 1992) growth rate over an extended period of time is described as a parameter that evolves, but the trade-off is actually between time allocated to growth versus reproduction during this period, which again assumes that intrinsic growth rate is maximized during the periods that growth is occurring. In the few studies that have modeled growth rate as a parameter that evolves, growth rate–dependent mortality is the only trade-off considered other than reproduction (Case 1978; Sibly et al. 1985).

In contrast to the theoretical literature, empirical studies suggest that growth rate is a parameter that evolves but is rarely, if ever, maximized (Calow 1982). Differences in intrinsic growth rate exist between closely related species (Ricklefs 1984; Werner 1986, 1994; Shine and Charnov 1992) and local populations of the same species (Berven and Gill 1983; Smoker 1986; Conover and Present 1990; Niewiarowski and Roosenburg 1993; Gotthard et al. 1994). Intrinsic growth rate can be increased by artificial selection (Gjerde 1986; Lilja and Marks 1991) and genetic engineering (Zhu 1992). The list of possible trade-offs with growth rate, apart from reproduction, includes developmental rate (Ricklefs et al. 1994), developmental stability (Leamy and Atchley 1985), defense against pathogens (Smoker 1986; Kirpichnikov et al. 1993), starvation resistance (Gotthard et al. 1994), and longevity (Jonsson et al. 1992).

One factor that is known to have a strong effect on the evolution of growth rates is the pattern of resource availability. It is well known that plant species found under chronically poor resource conditions cannot grow fast even when nutrients are provided (Grime 1979; Chapin 1980). This "stress-tolerant" (Grime 1979) or "pessimistic" growth strategy (Iwasa 1991) contrasts with plants that can respond to high nutrients with high growth rate (Iwasa's "optimistic" strategy). Although these patterns are well known in plants (Grime and Hunt 1975; Chapin 1980), they are only beginning to be described in animal species (Winemiller and Rose 1992; Niewiarowski and Roosenburg 1992; Arendt 1997).

Patterns of resource availability become more complicated when organisms shift diet through ontogeny. For example, some species experience chronically poor resource conditions as juveniles but not as adults (Werner 1988). It is likely that natural selection favors a high intrinsic juvenile growth rate in this situation, in contrast to the low intrinsic growth rate of species that experience poor conditions during their entire life cycle. What we call "optimistic" growth is selected, not to exploit pulses of abundant resources in the juvenile stage, but to achieve the adult stage, in which resources are consistently abundant, as quickly as possible.

In this paper we present a theoretical model that confirms a pessimistic growth strategy for chronically poor resource levels and an optimistic growth strategy when resource levels shift from low to high with a size-determined niche shift. We test the latter hypothesis by exploiting an interesting ecological relationship between pumpkinseed sunfish (*Lepomis gibbosus*) and bluegill sunfish (*L. macrochirus*). As juveniles, both species are confined by predators to the littoral zone of lakes and compete for similar resources. However, after reaching about 70 mm standard length, predators are no longer an important threat and bluegills shift to a diet dominated by zooplankton while pumpkinseed specialize on snails (Mittelbach 1984). Because zooplankton are a more abundant resource than snails, bluegill are numerically dominant and contribute many more offspring than pumpkinseed to the littoral zone (Mittelbach and Chesson 1987; Osenberg et al. 1988). The presence of bluegill therefore dramatically alters the pattern of resource

availability for the pumpkinseeds. By estimating age-specific growth rates from scales, Osenberg et al (1992) showed that pumpkinseeds are most food limited during the juvenile stage in lakes inhabited by bluegill and most food limited during the adult stage in lakes in which bluegill are absent. We therefore predict that juvenile pumpkinseeds that coexist with bluegill will evolve a high (i.e., optimistic) intrinsic growth rate, despite the fact that their juvenile resources are chronically low, to facilitate passage to the adult stage in which resources are more abundant. We test this prediction with a common-garden experiment comparing pumpkinseed derived from populations where bluegill are present with pumpkinseed from populations where bluegill are absent.

THE MODEL

We know of only three theoretical models that treat juvenile intrinsic growth rate as a trait that evolves. Two of these assume a survival cost to rapid growth (Ricklefs 1969 [modified by Case 1978]; Ricklefs 1984; Sibly et al. 1985), the third assumes a trade-off between growth rate and resource acquisition (Iwasa 1991). However, none of these models incorporates an ontogenetic niche-shift. We developed the following model to examine the effects of resource patterns and mortality on growth rate both with and without an ontogenetic niche-shift.

We divide the juvenile lifecycle into several size classes (i) and use probability of survival to the end of the final juvenile size class as our measure of fitness (analogous to Case 1978). Thus the base survival rate is measured as:

$$w = \prod (P_i)^{t_i} , \quad (1)$$

where w is overall survival: P_i is the probability of surviving one time unit in size class i, including both size dependent and size independent sources of mortality (see below): and t_i is the number of time units spent in size class i. We assume that t_i is determined by environmental conditions (resource level, temperature, salinity, etc.) so that as conditions worsen the amount of time spent in each size class increases. Size classes are selected so that $t_i \geq 1$. Increasing the intrinsic growth rate decreases the amount of time spent in a size class by some proportion (b). However, this comes at a decrease in survival probability by some proportion (a). The modified fitness becomes:

$$w = \prod (aP_i)^{bt_i} , \quad (2)$$

These two factors, a and b, are assumed to be positively correlated. Thus, a faster intrinsic growth rate means an individual benefits by spending less time in a given size class, but pays a cost in decreasing the probability of surviving one time unit in that size class. Because a small b means less time is spent in a given size class, b is an inverse measure of growth rate. Both Case (1978) and Sibly et al. (1985) note that the shape of the trade-off curve between a and b affects how the optimal growth rate changes with environmental conditions. If the relationship is linear or concave-down, there is no intermediate optimum and either a minimum or maximum growth rate will evolve. Only a concave-up trade-off curve results in intermediate values. Our model also produces this effect with one important difference. Concave-up

curves always result in intermediate optimal growth rates in Sibly et al. (1985), but only sometimes in our model. However, this does not qualitatively affect the results described below as long as a and b are positively correlated.

To find the optimal growth rate (the b that maximizes overall survival), we differentiate with respect to b and set the entire equation equal to zero:

$$\frac{1}{w}\frac{\delta w}{\delta b} = \left[b\frac{a'}{a} + \ln(a)\right]\sum t_i + \sum[t_i \ln(P_i)] = 0 , \quad (3)$$

The a' in equation (3) is the derivative of a. This equation equals zero when:

$$\left[b\frac{a'}{a} + \ln(a)\right] = \frac{-\sum[t_i \ln(P_i)]}{\sum t_i} , \quad (4)$$

This configuration is convenient because the left side of equation (4) contains only the intrinsic factors of growth, while the right side contains only the environmental factors. However, we still have four parameters to consider. Rather than try to describe the entire parameter space in detail, we will focus on the parameter values that seem relevant to creating pessimistic growth (i.e., low resource levels throughout life) and optimistic growth (i.e., low resource levels for small size classes, shifting to high resource levels for large classes).

First, we want to know if pessimistic growth emerges under chronically poor resource conditions. Initially, we set survival (P) equal for all size classes, a common assumption of life-history models (Roff 1992; Stearns 1992). In addition, we set resource levels (t) equal for all size classes (Fig. 1A). Each line in Figure 1 represents a set of conditions for which an optimal b can be calculated. If pessimistic growth occurs as a result of chronically poor resource levels throughout life, then the optimal growth rate should decrease (b increases) as t increases for all size classes (i.e., as the y-intercept increases in Fig. 1A). This does not occur, and examination of the right side of equation (4) shows why. If P, t, or both are independent of size, then t_i cancels out of the equation and we are left with growth rate depending entirely on P. Note that as mortality levels increase, $-\Sigma ln(P_i)$ becomes larger and the optimal growth rate will increase (see Appendix). This agrees with the conclusions of both Case (1978) and Sibly et al. (1985).

What does it take to get pessimistic growth rate? Both resource level and survival rate must depend on size. For many animals, survival rate increases with size (Nakaoka [1994]; amphibians reviewed by Werner [1986]; fish reviewed by Sogard [1997]). Survival also increase with size for pumpkinseed sunfish (Hoyle and Keast 1988; Mittelbach and Chesson 1987; Werner and Hall 1988), which is important because we ultimately want to relate this model to the pumpkinseed system. In addition, as animals grow they begin to include larger items in their diet while maintaining smaller items (Wilson 1975). This means that more resources are available to a large individual than to a small individual, even if there is not a niche shift (Fig. 1B). When both survival and resources are positively correlated with size, the right-hand side of equation (4) decreases as resource levels decrease for all size classes (see Appendix). This means that the optimal growth rate decreases as resources decrease, that
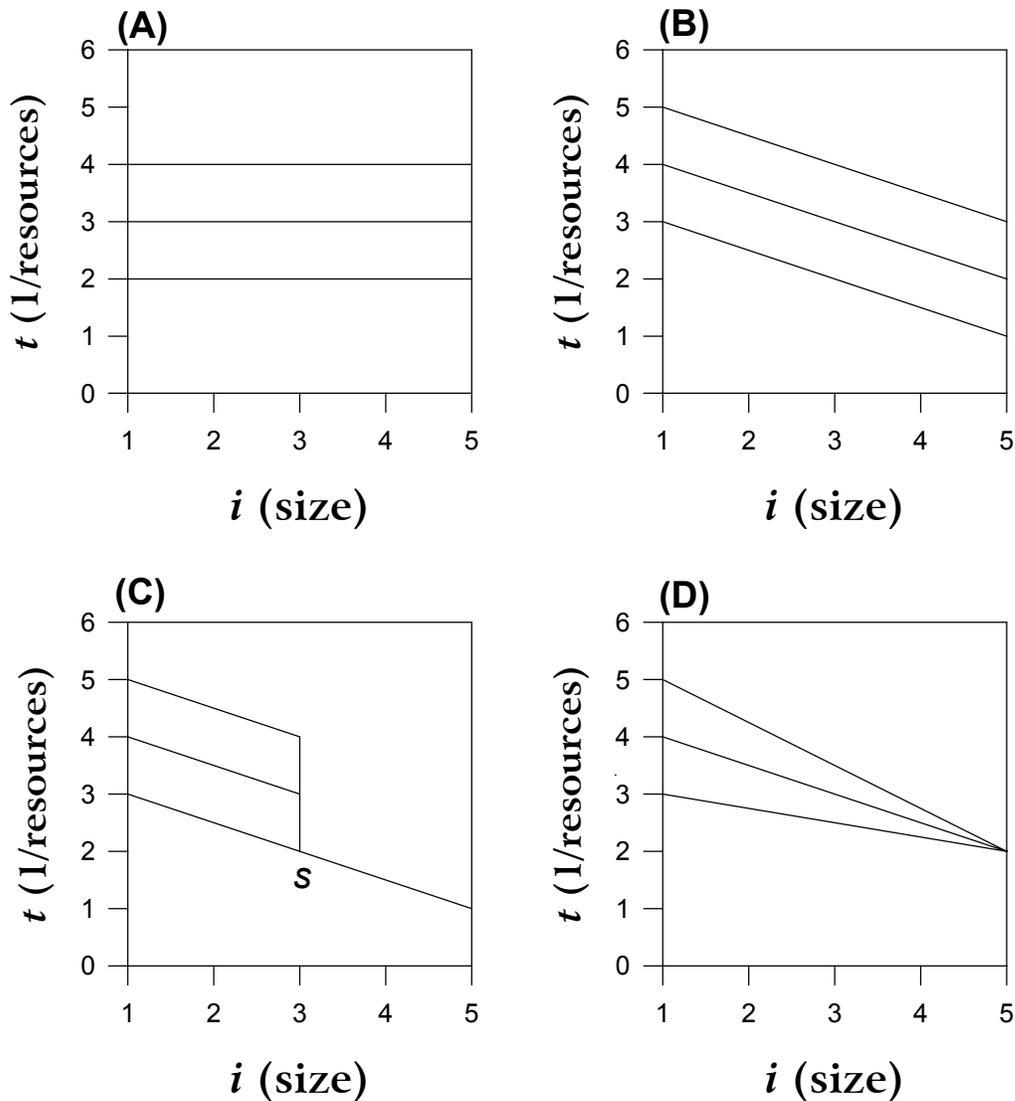
(A)

(B)

(C)

(D)

Fig. 1. Relationship between t_i (inverse of resource availability) and body size. Conditions for growth (total level of resources available in the environment) decrease as t increases. Each line represents a set of environmental conditions for which a single optimal growth rate can be calculated. (A) Ability of organism to garner resources is unrelated to size. In this case, altering resource availability has no effect on the optimal growth rate. (B) Ability of organism to garner resources is positively correlated with size. Here, pessimistic growth is selected as resources decline (see Fig. 2). (C) Resource availability with a niche shift; s is the size after which the niche shift occurs (in this case $i = 3$). Here, resources decline for the small-size niche only. (D) Resource availability without an abrupt niche shift, but ability to garner resources increases with size. A decrease in resources effects the smaller size classes more than the larger size classes. In both (C) and (D), optimistic growthis favored as resources decline (see Fig. 3).

is, pessimistic growth is selected (Fig. 2). These assumptions are also present in Iwasa's (1991) model, where a plant's ability to garner resources is positively correlated with size. Survival rate is not included in Iwasa's model, but fecundity does increase with size and appears to function in a similar manner as survival does in our model.

Second, we want to know if optimistic growth is favored when resources improve after an ontogenetic niche-shift. Instead of decreasing resource levels for all size classes, this time we decrease resources only for the smaller size classes (Fig. 1C). As before, survival rate must increase as size increases or else resource level has no effect on the optimal growth rate. In contrast to pessimistic growth, resource level does not have to depend on size because the niche shift takes

care of this. Now as we increase t for small i the optimal growth rate increases (Fig. 3A), the opposite of what happened when t increased for all size classes. When the niche shift (represented by the s in Fig. 1C) occurs in the lifecycle is important for the optimal growth rate. As the niche shift (s) occurs later in the lifecycle, the relationship between size and resources begins to converge on the conditions selecting for pessimistic growth (compare Fig. 1B,C). The optimal growth rate is fastest if the niche shift occurs early in the lifecycle, diminishing as the shift comes later and later (Fig. 3B). Note also that a niche shift need not be abrupt as we have modeled it here. As long as resources improve as the organism gets larger, decreasing resources for smaller size classes will select for rapid growth (Fig. 1D).
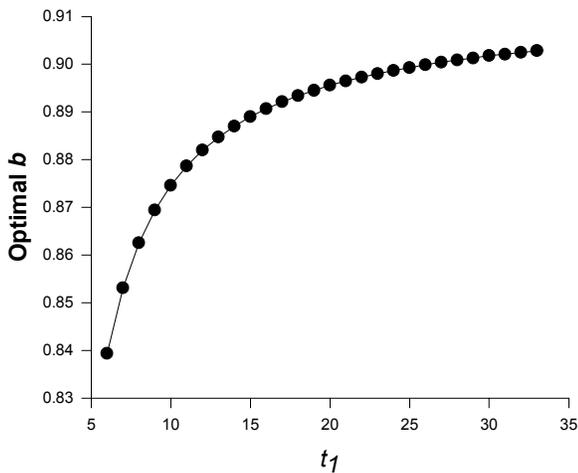
Fig. 2. Selection for pessimistic growth. As resources decrease (i.e., time spent in each size class increase), the optimal b increases. This means that the optimal growth rate decreases as conditions for growth worsen. Five size classes were used in this simulation. Parameter values are $t_1 = 6$, $t_2 = 5$, $t_3 = 4$, $t_4 = 3$, $t_5 = 2$, and $a = 1 - e^{-4.5b}$. The x-axis indicates values for t_1 only, with t increasing similarly for all size classes.

In summary, chronically poor resources throughout life selects for slow growth rate, "pessimistic" because the organism will probably not experience a change in conditions. However, this only occurs if the ability to acquire resources increase with size and either survival (our model) or fecundity (Iwasa 1991) is positively correlated with size. In contrast, if resources improve after a certain size is reached, then rapid growth evolves to hasten passage through the low resource stage. This is "optimistic" because rapid growth evolves despite low resource conditions, since the organism will probably experience improved conditions later. As with "pessimistic" growth, survival must be positively correlated with size. However, resource level does not have to depend on size to get "optimistic" growth, only on the niche shift. This suggest that "optmistic" growth may be a more general phenomenon than is "pessimistic" growth. If survival is negatively correlated with size (e.g., Sogard 1997) the results are reversed for both strategies. In addition, it is possible that resource levels may decrease for the large size niche, but not the small size niche (Werner 1986), which also reverses our predictions about optimal growth rate. These assumptions must be taken into account for each system. As stated above, "pessimistic" growth is well known in plants and is becoming apparent in animals. What is missing is empirical support for "optmistic" growth based on ontogenetic changes in resource abundance.

METHODS

In June 1995 adult pumpkinseeds were seined from six lakes located in Ontario, Canada, to use as brood stocks. Three lakes also contained bluegill (sympatric populations), and three did not (allopatric populations). These lakes were selected because they come from a restricted geographic region and contain similar fish assemblages (for details about lakes, see Table 1). In addition, the presence or absence of
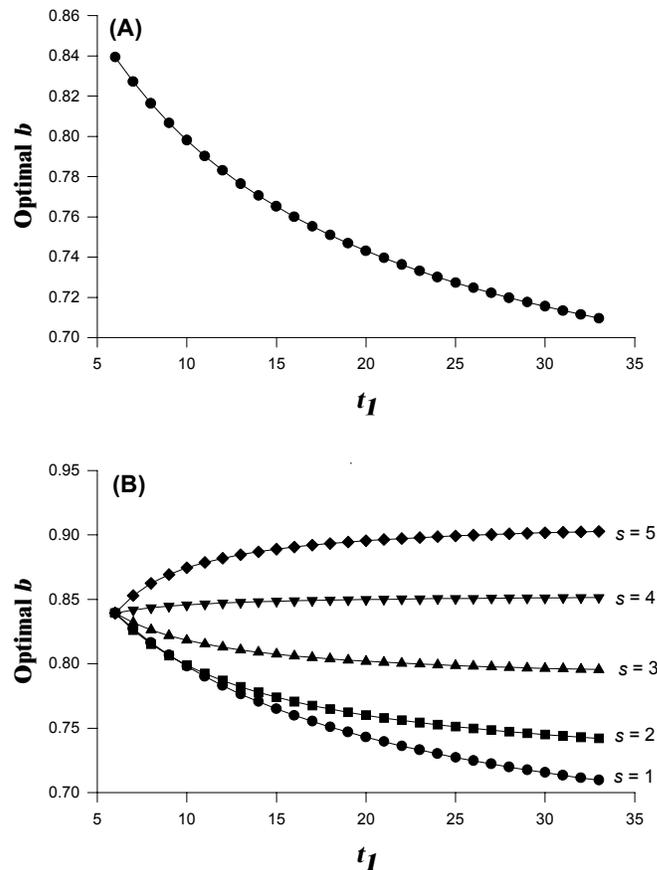

Fig. 3. (A) Selection for optimistic growth. Parameters same as for Figure 2 except that only t_1 and t_2 decrease. Values for t_3, t_4, and t_5 remain constant. As t_1 and t_2 decrease, the optimal b also decreases, thus the optimal growth rate increases as conditions become proportionately worse for the small size classes. (B) Effect of changing switch point, s, between niches. As s comes later in the lifecycle, the optimal growth strategy changes from optimistic to pessimistic growth.

bluegill has been shown to correlate with differences in reproductive traits in these lakes (Fox 1994). The adults were transferred to fishless 30 m × 30 m ponds located at the Cornell University Experimental Pond Facility in Ithaca, New York, one pond for each population. At least 10 males and 10 females were used for each population (except Beloporine Lake, where only three males were captured). Males began to build nests within a few days of being transferred and larval fish appeared soon after. Subsequent to stocking, one pond was accidentally treated with rotenone and this population was replaced the following week with fish from a local lake in which pumpkinseed coexist with bluegill (Quaker Lake, Susquehanna Co., Pennsylvania). Conover and Present (1990) found that growth rate was positively correlated with latitude in Atlantic silverside, suggesting that any geographic effect would result in Quaker Lake fish having the slowest growth rates. Because the geographic effect is opposite to our predicted competition effect, we considered Quaker Lake to be an acceptable substitute for our lost population.

Young-of-year (25-34 mm standard length) were collected

TABLE 1. Description of lakes from which brood stsocks are derived. Quaker Lake is located in northeastern Pennsylvania. Other lakes are located in southeastern Ontario.

Lake	Surface area (ha)	Location	Date stocked	Predators	Bluegill present?
Beloporine	7.2	44°29'N, 77°57'W	16 June	yellow perch, brown bullhead	no
Warrens	34	44°50'N, 76°47'W	16 June	large mouth bass, pickerel, yellow perch	no
Otter	572	44°47'N, 76°20'W	14 June	large mouth bass, small mouth bass, yellow perch, pickerel	no
Black	39.6	44°47'N, 76°46'W	16 June	large mouth bass, small mouth bass, yellow perch, pickerel	yes
Quaker	75	41°58'N, 75°55'W	23 June	large mouth bass, yellow perch, pickerel, brown bullhead	yes
Opinicon	787	44°34'N, 76°20'W	14 June	large mouth bass, yellow perch, northern pike	yes

from the experimental ponds on September 21, 1995, using a seine net, transferred to 76-L aquaria (35–40 fish per tank) and maintained at 18°C with a 14:10 L:D photoperiod. Fish were fed to satiation (i.e., some food remained after fish stopped eating) once a day and allowed to acclimate to laboratory conditions for 22 days (until October 13). For the experiment, 38-L aquaria were divided into quarters with clear plexiglass. Each aquarium held four fish from a given population, one in each compartment, and the sides were covered with paper so that fish in other aquaria were not visible. Fish were chosen for the experiment so that initial lengths (mean 28.7 ± 1.6 mm) did not differ significantly among population or competition type (sympatric vs. allopatric to bluegill) and matched within 2 mm within each aquarium. This design reflects a number of considerations. Fish growth is often influenced by social factors, so intrinsic growth rate is best measured in isolated fish. However, pumpkinseeds are a gregarious species that do not behave normally in isolation. It might seem that pumpkinseeds from ponds with and without bluegill could be housed in the same aquarium to reduce tank effects. We initially tried this and discovered that sympatric pumpkinseeds socially dominated same-sized allopatric pumpkinseeds. The difference in social behavior obscured possible differences in intrinsic growth rates, requiring us to house fish from separate ponds in separate aquaria. The difference in social behavior is interesting in its own right and will be reported elsewhere. Because the plexiglass dividers were not sealed, our design allowed visual and olfactory contact among fish from the same pond without allowing physical contact. This seemed to be the best compromise between complete isolation and complete contact.

All fish were fed a commercial pelleted food (Hikari Cichlid Gold). Sixteen fish from each population were put on a low-food treatment and fed one pellet each twice a day (approximately 1% of the fish's wet weight). Twelve fish from each population received a high-food treatment of three pellets each twice a day (approximately 3% of wet weight). After 40 days one additional daily feeding (a total of three pellets per day for the low-food treatment and nine for the high-food treatment) was added to maintain the 1% and 3% ration levels.

We measured standard length of each fish at days 0, 20, 40, and 60 after transfer to the test aquaria. Lengths were converted to instantaneous growth rate (IGR) for statistical analysis:

$$IGR = \frac{\ln(sl_2) - \ln(sl_1)}{time}, \qquad (5)$$

where sl_2 is length at time 2 and sl_1 is length at time 1. Results were analyzed with a 2×2 factorial analysis of variance with one factor nested (population replicate nested within population type) and crossed by food level. The population level was treated as a random effect. Tank means were used for analysis to avoid sacrificial pseudoreplication (Hurlbert 1984). Because the fish had grown enough between day 20 and day 40 that they were no longer receiving the same proportion of food as during the 0 to 20 day interval, each time interval was analyzed separately.

RESULTS

As predicted by our model, fish derived from stock sympatric with bluegill grew faster than did those from allopatric stock (Fig. 4A,B,C). This effects was statistically significant for all time periods (Table 2). In addition, food level had a highly significant effect (Table 2) with fish growing two to three times faster on the high-food treatment than on the low-food treatment. A significant population effect appeared in the first time interval and was probably entirely due to the poor growth of the Quaker Lake fish on the high-food treatment (Fig. 4A). The fish in this treatment appeared to not have acclimated fully to the experimental conditions at the start of the experiment. This may have happened because initially the Quaker Lake fish were slightly, although not significantly, smaller than fish from the other populations. This effect disappeared over the later intervals (Fig. 4B,C). None of the interaction effects was significant, suggesting that all fish responded to the change in food level in the same way.

DISCUSSION

Workers have been slow to incorporate the evolution of intrinsic growth rates into life-history theory. Case (1978) and Sibly et al. (1985) showed that the optimal growth rate increases as size-specific mortality increases. Iwasa (1991) suggested that chronically low resource levels will select for
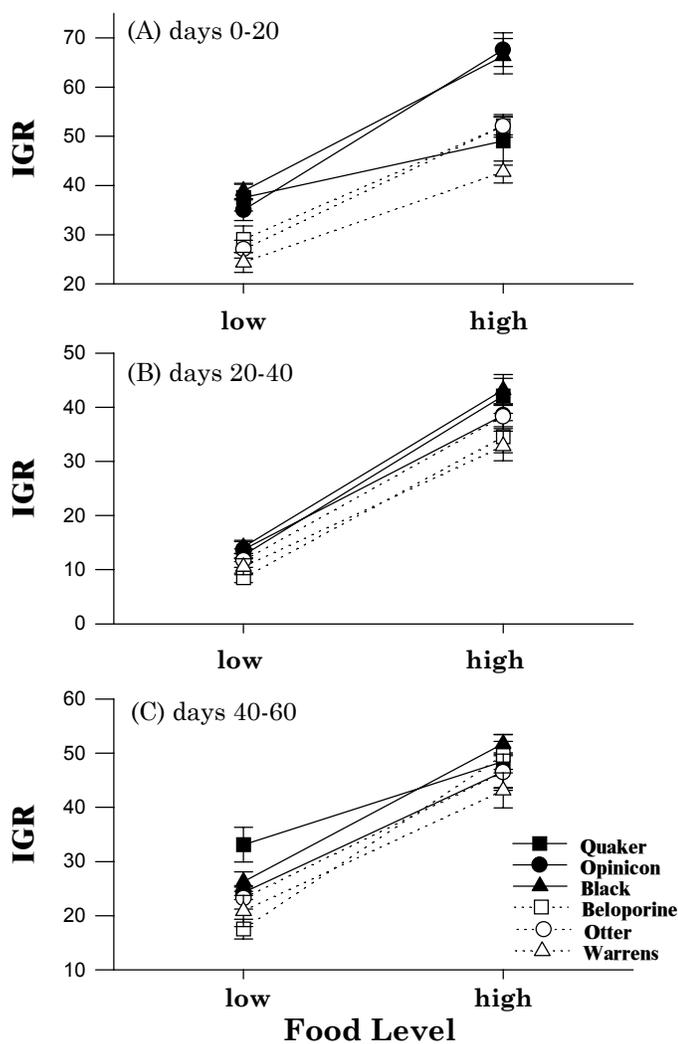
Fig. 4.   Mean instantaneous growth rates (IGR) for pumpkinseed sunfish derived from six different populations raised under low (1% wet weight) and high (3% wet weight) food rations. Solid symbols and solid lines are for populations sympatric with bluegill sunfish, open symbols and dashed lines are for allopatric populations. Error bars represent standard errors. (A) First 20 days of experiment; (B) second 20 days when fish had grown large enough so that rations were no longer 1% and 3% of wet weight; (C) third 20 days after ration levels had been adjusted for growth.

of time spent in the food-limited stage, that is, optimistic growth occurs. Note that the difference in intrinsic growth rates is the opposite of the difference in realized growth rate due to resource abundance as seen in the field (Osenberg et al. 1992). That is, intrinsic growth rate seems to have evolved to compensate for the low resource levels caused by the presence of bluegill, a pattern known as countergradient variation (Conover and Schultz 1995).

All fish were raised under common conditions, os our results likely reflect a genetic difference in intrinsic juvenile growth rate. However, because the F_1 generation was used we cannot entirely rule out the possibility that maternal effects played a role. The parental generation was collected during the breeding season and maternal condition may have carried over from the field. Wethink it unlikely that such an effect, if it exists, was important in our measurements of growth rate because maternal effects generally disappear when individuals are raised under favorable conditions (Marsh 1986; Hutchings 1991; Parichy and Kaplan 1992). All young experienced nearly four months in the breeding ponds, where conditions for growth are very good, before being brought into the lab.

Rapid growth is often thought to confer a competittive advantage to plant species (Grime 1979). Our study is the first evidence we know of suggesting that rapid growth may help an animal reach a size refuge from competition, although this has been suggested on theoretical grounds for sessile animals (Sebens 1982). Size-mediated comeptitive interactions similar to what occurs in the pumpkinseed-bluegill system appears to be common for teleost fish (e.g., roach and perch, Persson and Greenberg [1990]; perch ans white sucker, Hayes et al. [1992]). Niche-dependent competition is not the only instance in which resource levels change from poor to good. Piscivorous fish often feed on invertebrates until the are large enough to begin feeding on other fish (Hayes and Taylor 1990; Olson 1996). Growth rates are faster after switching to piscivory, sugesting that these fish have gone from a poor resource to a good resource. Olson (1996) describes prepiscivore growth rates for bass from several populations in Michigan. In the field, these populations vary greatly in the rate at which they grow (0.03 to 0.06 g/d) while feeding on invertebrates. From the results presented in this paper, we predict that the bass from slow-growth lakes will have faster intrinsic growth rates (i.e., optimistic growth) than those from fast-growth lakes when the two are raised under common conditions.

Seed and Brown (1978) were perhaps the first to suggest that rapid growth may evolve to allow organisms to reach a size refuge from predation. Reznick (1983) suggested that rapid growth has evolved in some guppy populations for the same reason, although recent evidence suggests the situation is more complicated (Reznick et al. 1996). Predation may play a role in our system if compeition with bluegill forces pumpkinseeds to expose themselves to predation in an effort to obtain food (e.g., Fraser and Gilliam 1987). If so, the fast growth we have found may have evolved to escape the gape limit of predators rather than to escape competition directly. This seems unlikely as there is no difference in how sympatric and allopatric fish react to potential predators in terms of either inspection or feeding tenacity (unpubl. data). In any

a slow growth rate, a phenomenon he called "pessimistic" growth. Our model confirms both of these predictions. In addition, our model shows that there can be selection for rapid growth during periods of low resource levels, provided that resources increase after an ontogenetic niche-shift. We call this "optimistic" growth. Our model also shows that   there must be an advantage to being large, such as improved survival (our model) or fecundity (Iwasa 1991), before resource level has any effect on growth rate. Our empirical results show that juvenile intrinsic growth rate varies among populations of pumpkinseed sunfish as predicted by the model. When competition with bluegill sunfish causes resources to be scarce for juveniles but more abundant for adults, juvenile intrinsic growth rate increases to reduce the amount

TABLE 2. Analysis of variance for differences in growth rate. * $P < 0.05$, ** $P < 0.01$.

Days 0 to 20

Source	df	Error term	SS	MS	F	P
Competition	1	pop (compt)	1156.74	1156.74	9.678	0.036*
Population (compt)	4	error	478.07	119.52	3.267	0.025*
Food	1	food × pop (compt)	5384.59	5384.59	64.375	0.001**
Food × compt	1	food × pop (compt)	4.50	4.50	0.054	0.828
Food × pop (compt)	4	error	334.57	83.64	2.286	0.084
Error	29		1060.96	36.58		
Total	40		8419.43			

Days 20 to 40

Source	df	Error term	SS	MS	F	P
Competition	1	pop (compt)	216.35	216.35	10.346	0.032*
Population (compt)	4	error	83.65	20.91	1.350	0.275
Food	1	food × pop (compt)	7052.30	7052.30	880.741	0.000**
Food × compt	1	food × pop (compt)	10.11	10.11	1.262	0.324
Food × pop (compt)	4	error	32.03	8.01	0.517	0.724
Error	30		464.81	15.49		
Total	41		7859.24			

Days 40 to 60

Source	df	Error term	SS	MS	F	P
Competition	1	pop (compt)	281.51	281.51	8.348	0.045*
Population (compt)	4	error	134.89	20.91	0.624	0.649
Food	1	food × pop (compt)	5836.30	5836.30	124.050	0.000**
Food × compt	1	food × pop (compt)	32.94	32.94	0.700	0.450
Food × pop (compt)	4	error	118.19	47.05	0.871	0.493
Error	30		1621.24	54.04		
Total	41		8095.08			

case, the root cause of rapid growth is competition, whether acting directly through resource levels or indirectly through predation

Why is juvenile growth rate not always maximized, as assumed by many life-history models? There must be competing demands for energy besides growth and reproduction. Some possibilities include developmental rates (Ricklefs et al. 1994), defense against pathogens (Smoker 1986; Kirpichnikov et al. 1993), and longevity (Jonsson et al. 1992). Because of the benefits of rapid growth for reaching a competition refuge, pumpkinseed from bluegill lakes should show slower development, be more susceptible to disease, and/or have shorter life spans than pumpkinseeds from lakes without bluegill. Costs of rapid growth in pumpkinseed sunfish has been investigated in our lab and will be reported elsewhere.

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APPENDIX

The interaction of P and t is easiest to see if we rearrange the right side of equation (4) as:

$$- \sum \left[\ln \left(P_i^{\,t_i / \Sigma\, t_i} \right) \right]. \tag{A1}$$

We are interested in how this expression behaves as resources become progressively scarce. That is, the change in this sum as t_i goes from a small number to a very large number. When this happens, the exponenent in expression (A1) approaches the value $1/i$. As we reduce resources, each t_i is increased by one unit while the sum of t_is increases by i units. This means that when t_i is small, the exponenet is greater than $1/i$. It shoulde be clear, then, that the entire summation will decrase as t_i increases.

The situation is more complex if there is a niche shift. If resources are decreaseing only in the smaller size classes, the exponent approaches the value $1/s$, where s is the size class after which the niche shift is made. This applies only $s < i$. For $s > i$, the exponent approaches zero. When resources are relatively abundant, survival rates for all size classes contribute to the sum. However, because the exponent for size classes greater than s approaches zero as t grows infinitely large, $ln(P)$ will also go to zero for these size classes and not contribute to the sum. The result is that the sum increases as resources become scarce. If the first niche takes up a large proportion of the lifecycle, then $1/s$ approaches $1/i$. At some point expression (A1) will change from increasing to decreasing as resources become scarce.

How does this effect the optimal b? Solving for b in equation (4) gives:

$$b = \frac{-\,a \left[\ln(\,a\,) + \sum \left[\ln(\,P_i^{\,t_i / \Sigma\, t_i}\,) \right] \right]}{a'}. \tag{A2}$$

If expression (A1) increases, as when mortality increases or t increases for small sizes only, then $ln(a)$ must decrease. The a and a' terms in equation (A2) only effect the magnitude of b, not the direction it changes as t changes. Because a and b are positively correlated, this means that b will also decrease. Conversely, if expression (A1) decreseases, as when t increases for all size classes, then $ln(a)$ increases and b also increases.

Overall, this means that if resources decrease only for size classes less than s, then b will decreases as conditions worsen (optimistic growth is selected). As s increases, b will eventually switch from decreasing to increasing and pessimistic growth will be selected.