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AN EXPERIMENTAL TEST OF THE EFFECTS OF PREDATION RISK ON HABITAT USE IN FISH¹

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Abstract. We present an experiment designed to test the hypothesis that fish respond to both relative predation risk and habitat profitability in choosing habitats in which to feed. Identical populations of three size-classes of bluegill sunfish (*Lepomis macrochirus*) were stocked on both sides of a divided pond (29 m in diameter), and eight piscivorous largemouth bass (*Micropterus salmoides*) were introduced to one side. Sizes of both species were chosen such that the small class of bluegills was very vulnerable to the bass, whereas the largest class was invulnerable to bass predation. We then compared mortality, habitat use, and growth of each size-class in the presence and absence of the bass.

Only the small size-class suffered significant mortality from the bass (each bass consumed on average about one small bluegill every 3.8 d); the two larger size-classes exhibited similar mortality rates on both sides of the pond. In the absence of the bass, we found that habitat use of all size-classes was similar and that the pattern of habitat use maximized foraging return rates (Werner et al. 1983). In the presence of the bass the two larger size-classes chose habitats to maximize return rates, but the small size-class obtained a greater fraction of its diet from the vegetation habitat, where foraging return rates were only one-third of those in the more open habitats. The small size-class further exhibited a significant depression in individual growth in the presence of the bass; the growth increment during the experiment was 27% less than that for small bluegills in the absence of the bass. Because of the reduced utilization of more open habitats by the small fish in the presence of bass, resources in these habitats were released to the larger size-classes, which showed greater growth in the presence of the bass than in its absence. We develop methods to predict the additional mortality expected on a cohort due to a reduction in growth rate (because individuals are spending a longer time in vulnerable sizes), and discuss the potential for predation risk to enforce size-class segregation, which leads de facto to resource partitioning.

Key words: foraging efficiency; habitat use; *Lepomis*; Michigan; *Micropterus*; *Osteichthyes*; predation risk; predator avoidance; size-class interactions.

INTRODUCTION

Recently, optimality models have been usefully applied to problems in animal behavior and evolution. In general, the costs and benefits associated with particular behaviors are described and solutions derived which minimize a postulated cost/benefit function. When this approach is used to study the evolution of morphological structures or life histories, serious questions arise concerning genetic constraints and the existence of tradeoffs (e.g., Gould and Lewontin 1979). When applying the approach to the study of behavior, we are often able to measure directly the costs and benefits associated with a tradeoff and simply ask: does the individual organism over the short term have the capabilities to assess changes in its environment and have the flexibility to respond to these changes as the model predicts? A second related question, especially germane when such models are to be tested under relatively uncontrolled field situations, is: are the costs

and constraints conceived by the investigator sufficiently accurate and inclusive to account for the major selective forces that have molded the behavior(s) of interest?

We have experimentally demonstrated that fish have the capability to respond to changes in resource levels in the environment by modifying their selection of food particle size in approximate accordance with optimal foraging models (Werner and Hall 1974, Mittelbach 1981, Werner et al. 1983). We have further demonstrated that fish have the flexibility to shift habitats as relative resource levels in these habitats change and that we can predict these shifts, using the foraging models in small experimental ponds (Werner 1982, Werner et al. 1983). However, testing the predictions of such models under less controlled conditions is more difficult due to additional constraints which might be expected to modify optimal behavior, i.e., the second question above. For example, we have noted that in natural lakes small fish are restricted to weedbeds and do not conform to the predictions of models specifying optimal habitat use from the standpoint of foraging rates (Hall and Werner 1977, Mittelbach 1981). We postulate that predation risk due to piscivorous fish is responsible for this deviation from predicted behavior.

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Often in natural communities a richer habitat, from the standpoint of potential foraging rate, is also one in which a forager experiences higher predation risk. Thus decisions on where to feed presumably involve some weighting of these factors according to their relative impact on fitness, i.e., there is a foraging rate/mortality risk tradeoff. It is therefore important to test whether animals assess predation risk and modify their foraging behavior accordingly, and to build this constraint into our models of optimal habitat use if they do.

A large literature documents the qualitative effects of predators on prey behavior (see Stein [1979] and Curio [1976] for reviews), but surprisingly few studies have quantified this effect, especially in the context of methods which predict the optimal behavior in the predator's absence (but see Milinski and Heller 1978, Caraco et al. 1980, Sih 1980). Clearly such studies are required if a quantitative theory of how animals adaptively balance these two conflicting demands is to be constructed.

In this paper we present an experiment designed to test the hypothesis that fish modify their habitat use under risk of predation and examine the consequences of such changes in behavior on individual growth rate, which is a major component of fitness and population dynamics in fish. Further, the magnitude of the growth depression when predators are present provides some index of the magnitude of the foraging rate/mortality risk tradeoff. In particular, we demonstrate that the presence of the largemouth bass (*Micropterus salmoides*, hereafter simply the bass) causes vulnerable sizes of the bluegill sunfish (*Lepomis macrochirus*) to utilize less profitable but safer habitats. We do this by first measuring resource levels and estimating habitat-specific foraging rates, which are used to predict optimal habitat use successfully in the absence of the bass (i.e., the control situation; see Werner et al. [1983] for details). We then contrast this case with habitat use by the bluegill in an identical environment in the presence of the bass. We further show that the changes in habitat use in the presence of the bass result in a significant decrease in growth rates of the vulnerable bluegill sizes. These results suggest that fish can balance the conflicting demands of foraging and predation risk but that this behavioral response occurs at some significant cost in terms of growth rate. We discuss the implications of these results for optimal foraging theory and the theory of species interactions.

EXPERIMENTAL DESIGN AND METHODS

The experiment was performed in a circular pond (29 m diameter, 1.8 m deep) at the Kellogg Biological Station. All macrophytes were removed from the pond except for a 3 m wide border of cattails (*Typha* spp.). This manipulation yielded three very discrete habitats: a ring of dense vegetation and an unstructured pond center of open water and bare sediments. The pond

was then divided in half by a 0.6-cm mesh nylon partition, which was suspended from ropes and anchored to the pond bottom.

The experiment was initiated on 15 July 1979 and terminated by draining the pond on 28 September. Each half of the pond was stocked with identical bluegill populations: 500 small (35.5 ± 0.4 mm, average standard length measured from the tip of the snout to the posterior of the vertebral column ± 1 SE), 300 medium (52.9 ± 0.4 mm), and 100 large (73.0 ± 0.8 mm) bluegills. These size-classes and relative proportions were similar to those found in bluegill populations of local lakes (Hall and Werner 1977). One-half of the pond was also stocked with eight bass (198.8 ± 2.9 mm in length). The size of the bass was carefully chosen to set up a gradient in predation risk for the different size-classes of bluegills. Using laboratory data on largemouth bass feeding (Lawrence 1957, Werner 1977) as a guide, we chose a bass size, such that the small bluegills would be extremely vulnerable and the large bluegills would be too large for the bass to catch and swallow. Bass of this size can swallow the medium size-class of bluegills in the laboratory, but it is doubtful that they could very easily capture bluegills of this size in the field. All surviving fish were recovered in September by draining the pond.

At intervals of 1 wk (or more frequently, in July), 10–20 small, 10 medium, and 10 large bluegills were seined and removed from each half of the pond for stomach analyses and determination of growth rates. We replaced the sampled fish with bluegills of identical length from a nearby holding pond. Because we wanted to make comparisons of bluegill growth in the presence and absence of the bass, we were concerned about the potentially confounding effects of reduced bluegill densities in the one pond-half due to predation by the bass. In an attempt to minimize this difference, we assumed that the bass would be eating primarily the small size-class and estimated that initially a bass would consume one small bluegill every 3 d. We further adjusted this estimate as the size of the bluegills and bass increased during the experiment. Thus on the bass side we initially added ≈ 20 small bluegills in addition to the replacements of the fish sampled for stomach analyses. Replacement for bass predation tapered to < 10 individuals per sample date at the end of the season. Over the entire experimental period, we added an additional 144 small bluegills to the pond-half with the bass.

Habitat utilization by the fish was determined by classifying prey in the stomachs according to the habitat from which those prey originated (open water, sediments, vegetation). The vast majority of the prey in all size classes across the season could be unambiguously assigned to one of these habitat types ($> 90\%$ of the diets on average across the season). Further details concerning prey sampling and the generation of predictions of optimal diet and habitat use for the

fish can be found in the companion paper (Werner et al. 1983).

RESULTS

Mortality

Mortality rates were similar for the two larger size-classes of bluegills across treatments. When we recovered populations in the fall, the cumulative mortality of the medium size-class was 10% on both sides, and for the large size-class, 11% in the presence of the bass and 19% in the control half of the pond. No mortality occurred in the bass population.

As explained earlier, we added more small bluegills to the bass side to compensate for expected predation losses. Our estimates of bass feeding rates were appropriate since the numbers of small fish recovered in the fall were similar: 348 on the bass side and 359 on the control side. Thus growth data were not confounded by different bluegill densities on the two sides. From these data we estimated a mortality of 28% for small fish on the control side, which is higher than that experienced by the two larger size-classes. The mortality rate of the small bluegills in the presence of the bass, however, was 59% of the original 500 fish. (Including the 144 fish added during the experiment, 296 fish died on the bass side.) Assuming the same non-bass mortality rate (28%) on each side, we estimate that each bass consumed a small fish every 3.8 d. The small size-class, therefore, did incur significant mortality due to the presence of the bass. In the Discussion and the Appendix we further examine how this increased mortality might be apportioned between the "direct" and "indirect" effects of the presence of the bass.

Habitat use

The design of this experiment was predicated on the assumption that predation risk for the bluegill would be much reduced in the cattails compared to the unstructured water column and bare sediments. Accordingly we chose a pond with very high resource levels in the open water and bare sediments, relative to the vegetation. Only if the more profitable habitats were also more dangerous could we test whether the fish were capable of responding to a predation risk/foraging rate tradeoff.

It is generally accepted that complex habitats are safer for prey, but this has not often been quantitatively demonstrated (see, e.g., Huffaker 1958). We know of three sources of direct experimental inference that the cattail habitat should interfere with the bass' predatory efficiency. First, Glass (1971) found in laboratory pools with different densities of vertical wooden dowels that the capture rate of bass preying on guppies (*Poecilia reticulata*) decreased monotonically with an increase in dowel density (0–370 dowels/m²). Second, Savino and Stein (1982) have found that predatory success of bass feeding on bluegills declined with

increasing simulated plant density (0–1000 stems/m²). In small wading pools (2.4–3 m in diameter) containing strands of polypropylene rope, success of the bass declined most sharply between 50 and 250 stems/m². Third, in a similar set of experiments we contrasted the success of bass (100–270 mm) feeding on bluegills (20–75 mm) in open and vegetated habitats (0 and 500 stems/m² polypropylene rope). Preliminary analyses of these data indicate that the small bluegills in the present study (≈ 35 mm), if pursued by a 200-mm bass, would be at least twice as vulnerable in the open habitat. The density of cattails in the pond study reported here averaged 176 stems/m², but individual samples ranged as high as 400 stems/m². Thus we are confident that the small bluegills incurred much less risk in the cattail habitat of the pond.

In the companion paper (Werner et al. 1983) we examined habitat use by the fish in the absence of predation risk from the bass. We generated foraging rates for each size-class of fish in the three habitats (open water, sediments, and vegetation), using an optimal foraging model where costs and benefits were estimated from laboratory feeding experiments. Examining the return rates in the three habitats across the season, we predicted that to maximize return rates, all size-classes should begin feeding in the open water and then shift to feeding from the sediments when the profitabilities of these two habitats crossed in late July. Thus, the more open habitats were indeed the more profitable, as we had anticipated.

In the absence of the bass, the behavior of all three size-classes was in excellent accord with the model predictions (Werner et al. 1983; Fig. 5). The fish consumed >80% plankton initially and between 21 and 25 July switched dramatically to a diet of >80% sediment-dwelling prey. Utilization of sediments remained high for the remainder of the experiment except for the small size-class, which switched back to plankton in late September when profitability of the open-water habitat was again highest for this size-class (Werner et al. 1983).

While the medium and large bluegills exhibited very similar patterns of habitat use in the presence and absence of the bass, the small bluegills behaved very differently. Several lines of evidence demonstrate the effects of the bass on the foraging behavior of small bluegills. Early in the experiment *Daphnia pulex* was extremely abundant (up to 73 individuals/L) and as a consequence the profitability of the open water was 7- to 27-fold greater than that of either the vegetation or the sediments (Werner et al. 1983). All fish fed extensively on *D. pulex*, and this species very quickly disappeared. Reduced utilization of this very profitable resource by the small bluegills in the presence of the bass can be shown by comparing their use with that of the larger size-classes. (Comparisons of the small class across treatments cannot be made due to the large disparity in *D. pulex* abundance which devel-

TABLE 1. Average percent composition (± 1 SE) of the diet by habitat for the three bluegill size-classes (6 August–6 September). Row sums do not add to 100% because a small fraction ($\leq 3\%$) of prey could not be assigned to a specific habitat (see text for details).

		Vegetation	Plankton	Benthos
No predator	Small	9 \pm 2	19 \pm 5	69 \pm 7
	Medium	14 \pm 4	2 \pm 0.5	81 \pm 4
	Large	11 \pm 3	trace	86 \pm 3
Predator	Small	34 \pm 10	17 \pm 5	46 \pm 9
	Medium	9 \pm 3	16 \pm 6	74 \pm 7
	Large	14 \pm 5	6 \pm 4	78 \pm 6

oped on the two sides of the pond; see below.) As *D. pulex* densities declined, its contribution to the diets declined most rapidly in the small size-class. By 30 July the small class had nearly ceased feeding on *D. pulex* (4% of diet), whereas the diet of the large and medium classes still contained 67 and 74% of this species, respectively. Over the first four dates the diet of the large size-class averaged 78% *D. pulex* and that of the small size-class only 53%. This contrasts with the control side where large, medium, and small size-classes averaged 90, 73, and 85% *D. pulex* in the diet, respectively, on those dates when they were feeding on plankton.

The reduced utilization of *D. pulex* on the side with the bass was also clearly reflected in the dynamics of the daphnids. On the control side, *D. pulex* abundances declined from 73 to 1 individual/L in 10 d, and by 25 July no *D. pulex* were found in the fish from this half of the pond. In contrast, on the side with the bass, *D. pulex* remained abundant for >20 d into the experiment and was a major part of the diet of the two larger size-classes through 6 August. Clearly the predation pressure on *D. pulex* in the open water was much reduced on this side, evidently due to the reduced utilization by the small size-class discussed above.

Direct comparisons of habitat use in the presence and absence of the bass are best made when resource levels in the three habitats are similar on the two sides. Following the demise of *D. pulex*, resource levels in each habitat were similar on the two sides for the period 6 August–6 September. Over this period then, we can compare habitat utilization of size-classes in the presence and absence of the bass, unconfounded by large differences in resource levels across treatments. Further, a large fraction of the seasonal growth occurred during this period, and the small size-classes of bluegills began to diverge in size on the two sides (see later).

Between 6 August and 6 September, a distinct pattern of habitat use emerged (Table 1). All three size-classes on the control side and the two larger size-classes on the bass side had switched to feeding from the sediments and exhibited similar diets. The small class on the bass side, however, averaged 36% vege-

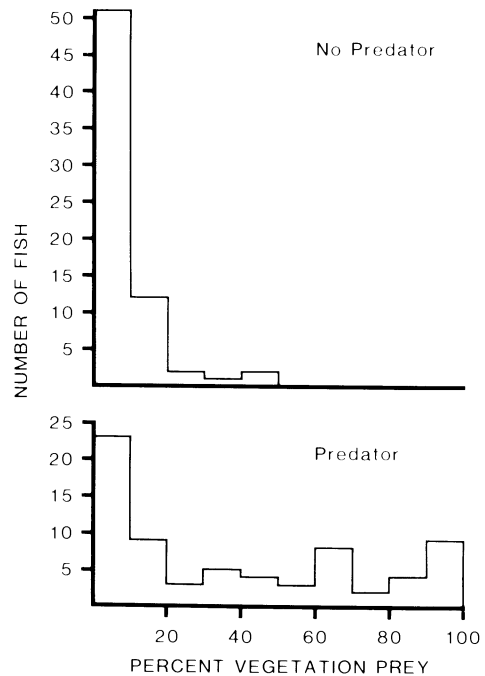


FIG. 1. Number of fish containing different fractions of prey derived from the vegetation. Data are for the small size-class in the presence and absence of largemouth bass. Numbers are for fish from 6 August and 6 September combined. The distributions differ at the $P < .001$ level (Kolmogorov-Smirnov test).

tation-dwelling prey in the diet, as compared to 9–15% for all other fish. This increased use of prey from the vegetation by the small fish was accompanied by a reduced use of prey from the sediments; all other fish were taking at least 70% benthic prey as opposed to 46% in the small class with the bass (Table 1). The increased use of vegetation-dwelling prey is clearly exhibited in Fig. 1, which indicates that use of the vegetation was not uniform among individuals in the population. In the absence of the bass, 93% of the small fish contained <20% prey from the vegetation, and no fish contained >50%. In the presence of the bass, however, 54% of the individuals contained >20% vegetation-dwelling prey. There was no relation between the fraction of vegetation-dwelling prey used and fish size, within the small size-class (regression of percent prey from vegetation against body size over range of 35–55 mm, $r^2 = 0.05$, $n = 70$, $P > .5$).

The small fish on both sides consumed more zooplankton than the large and medium classes (the high value for the medium class on the bass side is due to one anomalous date [Table 1]). The vast majority of the zooplankton eaten during this period was *Ceriodaphnia*, a form found in the vegetation as well as in the open water, and therefore it is possible that the small class in the presence of bass was also obtaining these prey from the vegetation. Thus we conclude that all fish were using habitats in very similar ways, except

TABLE 2. Mean individual dry mass (g) \pm 1 SE for the three bluegill size-classes in the presence and absence of the predator. Final values are for the entire population recovered in the fall. Differences between means between predator and no predator treatments were determined by *t* test.

	Size-class					
	Small		Medium		Large	
	Predator	No predator	Predator	No predator	Predator	No predator
Initial mass (g)	0.28 \pm 0.01 (n = 44)		1.35 \pm 0.03 (n = 27)		3.64 \pm 0.12 (n = 30)	
Final mass (g)	0.90 \pm 0.02 (n = 348)	1.13 \pm 0.02**† (n = 359)	4.45 \pm 0.05 (n = 270)	4.35 \pm 0.05 (n = 270)	9.17 \pm 0.15 (n = 89)	8.64 \pm 0.15** (n = 81)
Increment (g)	0.62	0.85	3.10	3.00	5.53	5.00
Population increment (g)	191.0	269.5	768.8	750.0	392.6	230.0
Difference in population increment (g)	-78.5		18.8		72.6	

** $P < .01$.

**† $P < .005$.

for the small size-class in the presence of the bass, which exhibited increased use of the vegetation.

The expected foraging profitabilities provide a measure of the cost of foraging more in the vegetation (Werner et al. 1983). The predicted return rate for the small class feeding in the vegetation averaged only 32 \pm 6% of that for the sediments from 6 August through 6 September. We show below that, as a consequence, growth was slower in the presence of the bass.

In late August, *Daphnia ambigua* (an open-water species) appeared and increased to \approx 100 individuals/L by late September. Similarly, *Bosmina* and *Ceriodaphnia* increased in late September. These three species are much smaller than adult *D. pulex* (by at least an order of magnitude in mass), and, in general, only the small bluegills utilized these forms to any extent. If we compare the last two dates when the small size-class on both sides was taking predominantly *D. ambigua*, we find that 77% of the diet of the small fish on the control side was plankton, whereas only 52% of the diet of the small fish on the bass side consisted of plankton, although resource levels in the open water and vegetation were similar on both sides of the pond. Thus, the effect of the bass was again to reduce the small bluegills use of the open water, as was the case when the small bluegills were feeding on *D. pulex* early in the experiment.

Growth

The presence of the predator clearly caused a shift in the habitat use of the small size-class; the question now is whether this habitat shift had any effect on growth of the surviving fish. In the absence of the bass, the three size-classes each grew markedly, but at very different rates (Table 2). Larger size-classes exhibited progressively higher growth rates. However, in the presence of the bass, the small fish exhibited a significant depression in growth, whereas the medium

and large classes grew larger than in the absence of the bass (Table 2). The average growth increment of small fish was 27% less when with the bass, while those of the medium and large fish were 3 and 11% more than when no bass were present. These differences are highly significant for the small and large classes (Table 2). Examination of the size-frequency distributions of the small class on the two sides indicated no evidence of selective predation within this class. The distributions were very similar in shape, but smaller fish were recovered on the predator side, indicating a growth response. The bass increased in length from 198.8 \pm 2.9 to 228 \pm 3.8 mm during the experiment.

Thus, the presence of the bass significantly depressed growth rates of the small fish in accord with their increased use of the poorer habitat (vegetation). Further, because the small fish spent more time in the less profitable vegetation, this apparently released resources for the larger fish in the sediments and open water. The large class especially benefited from this release in resources (Table 2). Indeed, there was nearly equal compensation by the larger classes for the total production lost to the small class in the bass' presence. A crude estimate of total fish production (number surviving \times growth increment) on the two sides only differed by 13 g or \approx 1% of the production of either side (Table 2).

The resource samples also indicated the effect of the predator. We have already noted that *D. pulex* lasted nearly 2 wk longer in the predator's presence. Though not as dramatic, the effect was also apparent in the sediment habitat. *Chironomus* densities were always higher in the predator's presence after July, when the fish began feeding on this species (with the exception of two dates when they were equal). Though these differences were not large, the trend to higher midge densities in the predator's presence was very consis-

tent, apparently due to reduced foraging pressure by the small fish. In both the open water and the sediments prey densities prior to the introduction of fish were actually slightly higher in the pond-half without the bass. Clearly, the presence of the bass had striking effects on the distribution of resources among size-classes of the bluegill.

DISCUSSION

The commonly observed fact that habitats vary temporally and spatially in foraging profitability and predation risk suggests that many animals need to balance gains and risks in their decisions on where and when to forage. Can animals assess these gains and risks, and are these factors weighted or balanced in such a way that tends to maximize fitness? This is an especially complex and critical question in the context of species that exhibit strong ontogenetic niche shifts due to the fact that relative foraging abilities and risks to predators change markedly with body size over the life history. Thus, decisions on where and when to forage must be made not only in the face of changing resource and predator dynamics, but also as these relations change with increases in body size.

We have demonstrated that the bluegill is able to assess changes in both foraging profitability and predation risk. In the companion paper (Werner et al. 1983) we showed that temporal habitat shifts by all size-classes occurred when foraging rates in another habitat became greater than those of the habitat currently used. In this paper, we further demonstrated that small, vulnerable size-classes of the bluegill showed a marked shift in foraging behavior in the presence of the bass. These data provide experimental support for the hypothesis of Hall and Werner (1977) and Mittelbach (1981) that small bluegills in natural lakes are confined to weedbeds because of a behavioral response to the greater predation risk in more open habitats. The quantitative predictions of habitat profitabilities also indicate that the small bluegills were evaluating this risk in the face of threefold greater foraging rates in the more open habitats. Whether this response also maximizes fitness remains to be tested.

The response of the small bluegills was not of an all or none nature, i.e., they did not use the unstructured or vegetated habitats exclusively on any given day. This must in part be due to the proximity of these habitats in the ponds; the small fish could feed in the open water or sediments and yet be only a matter of a metre or two from the vegetation refuge. In natural lakes the spatial separation of these habitats is usually much greater and consequently precludes this possibility. Mittelbach (1981) found that small bluegills in a natural lake did not feed on the very profitable offshore plankton prey at all except on one date when zooplankton were found within several metres of the shore. Thus the effect of the presence of the bass may be expected to be even stronger and more sharply de-

fined in natural lakes where large areas of open habitats intervene between those in which the fish feed. Of course, decreased foraging rates due to the presence of a predator may be generated not only by shifts in habitat use, but also by the necessity of greater wariness, or escape responses, which can decrease feeding rates in a particular habitat (Milinski and Heller 1978, Caraco et al. 1980). It is not known how the fish evaluate predation risk, but laboratory studies indicate that bluegills seemingly pay little attention to bass in a tank, until the bass shows subtle inclinations to begin to feed (R. Stein and J. O'Brien, *personal communication*).

The question also arises as to why the small fish exhibit such individual variation in their use of the vegetation in the presence of the predator (Fig. 1). We do not know if certain fish consistently spend more time in the vegetation than do others, i.e., if individuals tend to be risk averse or risk prone, or if this variation simply represents short-term (days, weeks) changes in habitat use by all individuals. This is an important problem, as these two hypotheses lead to very different ideas concerning individual behavior and fitness. We would expect that if risk-prone individuals existed, they would incur higher mortality rates but would also grow faster because of their use of the richer habitats. Thus, there should be a relation between size and habitat use. We noted earlier that there was no relation between body size among the small fish (ranging from ≈ 35 to 55 mm in length) and the fraction of their diet that came from the vegetation. The question of this individual variation in behavior deserves more detailed study.

In this study we were able to quantify the effects of predator-restricted habitat use on the growth rates of the fish. The small fish exhibited a 27% reduction in growth over part of one growing season. A growth reduction of this magnitude would certainly have far-reaching effects on the dynamics and population structure of these fish. Fish are indeterminate growers, and it is well recognized that fecundity is a direct function of size (e.g., Bagenal 1978) and that mortality rate is an inverse function of size, at least during the early part of the life history (Ricker 1979). Thus, lower growth rates protract the time spent in vulnerable stages, lower survivorship, and increase the time to reproductive maturity. Where the probability of death per day is a function of size, some of the demographic consequences of increased daily mortality rates and decreased growth rates can be assessed by examining the survivorship of fish through a size- (not age-) interval. Assume that for all sizes in the interval the presence of a predator multiplies the daily mortality rate by a factor c_μ and the growth rate by a factor c_g ($c_g = 1$ indicates no effect). It can then be shown (see Appendix) that the survivorship from size s_1 to size s_2 in the presence of a predator is given by

$$l_p(s_1, s_2) = [l_{np}(s_1, s_2)]^{c_\mu/c_g}, \quad (1)$$

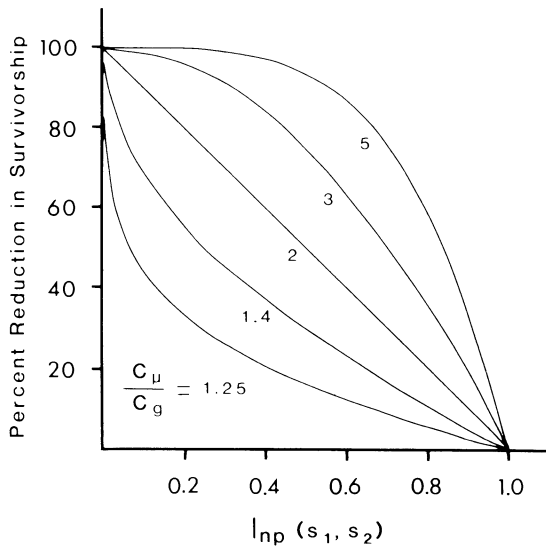


FIG. 2. Percent reduction in survivorship through a size-interval due to the presence of a predator. $l_{np}(s_1, s_2)$ is the survivorship in the absence of the particular predator (or before a predator's density is increased). c_μ is the factor by which the predator's presence (or increase) multiplies the size-specific daily mortality rate. c_g is the factor by which the predator's presence (or increase) multiplies the forager's daily (individual) growth rate.

where $l_p(s_1, s_2)$ = survivorship in the presence of a predator, and $l_{np}(s_1, s_2)$ = survivorship in the absence of the predator. Thus, halving the growth rate (setting $c_g = 1/2$, holding $c_\mu = 1$) has the same effect on survivorship through a size-interval as doubling the daily mortality rate (setting $c_\mu = 2$, holding $c_g = 1$); both result in $c_\mu/c_g = 2$. In both cases the survivorship through the size-interval is squared. The decrease in growth rate has the further consequence of increasing the time required to reach reproductive size. It appears that a predator's "indirect" effect on the prey, inducing a lowered growth rate measured by c_g , might have greater effects on population demography than the "direct" effect of raising daily mortality rates (measured by c_μ).

Fig. 2 illustrates the effect of various values of c_μ/c_g on survivorship through a size-interval. The crucial observation here is that for a given value of c_μ/c_g the impact of the presence of the predator is much stronger if the predator affects a size-interval which already exhibits low survivorship, which is the case for small fish. For example, in the case of $c_\mu/c_g = 2$, a size-interval with $l_{np}(s_1, s_2) = 0.8$ initially will have a new survivorship of $l_p(s_1, s_2) = 0.64$ by application of Eq. 1. This is a reduction of 20%. However, if $l_{np}(s_1, s_2)$ were 0.1, this would yield $l_p(s_1, s_2) = 0.01$, a reduction of 90%. Thus, unless density-dependent processes compensate in other size-intervals (which is likely), the number of fish reaching a given adult size will be

reduced by 20 or by 90%, respectively, for the two cases.

We can also use this approach to derive a crude estimate of the relative effect of the "direct" effect of adding more predators to a system (i.e., raising the probability of death/day) and the "indirect" effect of inducing lowered growth rates (which causes the prey to be in a size-interval longer and therefore accrue greater mortality through the size-interval; see Appendix). In the experiment presented here we partition the effects over the size-interval of 0.28 g (the initial mass of the small size-class of bluegills on both sides) to 0.90 g (the final mass on the predator side). We estimate that over the size-range the total reduction in survivorship in the presence of the bass was 37%. If only the "direct" effect of increased daily mortality rates (c_μ) had occurred, we estimate the reduction in survivorship would have been 23%. If only the "indirect" effect of decreased growth rates (and hence a longer time in the interval) had occurred, we estimate that the reduction would have been 10%. Thus the total reduction of 37% can be partitioned into 23% due to the c_μ alone, 10% due to c_g alone, and an additional 4% when both factors acted concurrently. Our estimates of the value of c_μ/c_g ranged from 2.34 to 3.89.

A further consequence of the predator-restricted habitat use of the small fish was the significant compensatory increase in growth of the larger size-classes. Thus, predation risk enforced a degree of intraspecific resource partitioning which exacerbated the differences in growth rates between size-classes (Table 2). This habitat segregation obviously has important consequences to population size-structure and intraspecific competition. Resources in open habitats, which often would be the preferred prey of all size-classes, may become exclusive resources for large fish in the presence of predators. The open-water plankton in particular is likely an important exclusive resource for larger bluegills in natural lakes with extensive limnetic zones. In the absence of predators, bluegills invariably develop "stunted" populations of uniformly small individuals (e.g., Swingle and Smith 1940, Wenger 1972). In such cases foraging demands evidently drive down resource levels (and mean prey size [Hall et al. 1970]), such that intense intraspecific competition prevents sustained growth. The presence of predators, which provides larger fish with exclusive resources, may be a major factor enabling them to continue to grow. Thus predation risk and its effect on habitat use may be an important mechanism mediating intraspecific competition in the field that has been largely overlooked (but see Jackson 1961). We feel that predation risk is most likely the cause of the patterns in size-class segregation noted in the bluegill, rather than an evolutionary response to intraspecific competition (e.g., Keast 1977).

We have noted that predation risk tends to concentrate the young of many species in the vegetation of natural lakes (Hall and Werner 1977, Laughlin and

Werner 1980, Mittelbach 1984). The observation that juvenile diets of several sunfishes are more similar than adult diets (Laughlin and Werner 1980, Mittelbach 1984) is likely the result of this habitat restriction of juveniles. Thus if vegetation is relatively rare and/or resources in it low, risk of predation can create significant competitive bottlenecks for these species at this point in their life histories. Identifying these bottlenecks is obviously central to considerations of niche packing in such systems, but the effects of these sorts of bottlenecks have been virtually unexplored. Our understanding of community structure in fish and other organisms with size-structured populations will be very limited until we systematically explore the consequences of these sorts of interactions.

Our experimental work suggests that competition and predation may interact in subtle but critical ways in fish communities. Shifts in competitive advantages between species due to the presence of a predator may be a great deal more subtle than simply accounting for the differential removal of each species. If bottlenecks of the sort we have hypothesized are important, the mere presence of a predator population could result in extinction of prey that are not even eaten by the predator due largely to the predator's indirect effects of increasing competition in protected habitats. These ideas connote very different mechanisms of "predator-mediated" coexistence than those ordinarily considered. Clearly the effects of a predator on the spatial distribution of its prey and the resultant changes in the strength of interactions within and between prey species may have profound effects that would not be evident from measures of prey removal rates or energy flows.

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APPENDIX

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

$$l(x_1, x_2) = \exp\left[-\int_{x_1}^{x_2} \mu(x) dx\right], \tag{A1}$$

where x = age, and $\mu(x)$ = 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 s_1 to size s_2 . Eq. A1 can thus be rewritten as:

$$l[s(x_1), s(x_2)] = \exp\left\{-\int_{s(x_1)}^{s(x_2)} \mu[s(x)] dx\right\}. \tag{A2}$$

Changing the variable of integration yields:

$$l(s_1, s_2) = \exp\left[-\int_{s_1}^{s_2} \mu(s)/(ds/dx) ds\right]. \tag{A3}$$

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

$$l(s_1, s_2) = \exp\left[-\int_{s_1}^{s_2} \mu(s)/g(s) ds\right]. \tag{A4}$$

Van Sickle (1977) has derived this equation by a different method. Intuitively, Eq. A4 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).

For heuristic purposes, assume that over some size-interval (s_1, s_2) the presence of the bass uniformly multiplies $\mu(s)$ by a factor c_μ and multiplies $g(s)$ by a factor c_g . Then the survivorship through a size-interval in the presence of the predator (l_p) is:

$$\begin{aligned} l_p(s_1, s_2) &= \exp\left\{-\int_{s_1}^{s_2} [c_\mu \cdot \mu(s)]/[c_g \cdot g(s)] ds\right\} \\ &= \exp\left[-(c_\mu/c_g) \int_{s_1}^{s_2} \mu(s)/g(s) ds\right] \\ &= \left\{\exp\left[-\int_{s_1}^{s_2} \mu(s)/g(s) ds\right]\right\}^{(c_\mu/c_g)}. \end{aligned} \tag{A5}$$

Since the expression in the braces is just the survivorship without the predator, $l_{np}(s_1, s_2)$, this yields:

$$l_p(s_1, s_2) = [l_{np}(s_1, s_2)]^{c_\mu/c_g}. \tag{A6}$$

This is Eq. 1. The percent reduction in survivorship is thus (the arguments of l_p and l_{np} are dropped for convenience):

$$\begin{aligned} (100)(l_{np} - l_p)/l_{np} &= (100)(l_{np} - l_{np}^{c_\mu/c_g})/l_{np} \\ &= (100)[1 - l_{np}^{(c_\mu/c_g - 1)}]. \end{aligned} \tag{A7}$$

By estimating c_μ and c_g in this experiment, we can somewhat crudely estimate the relative intensities of the predator's "direct" effect (increased daily mortality rates) and its

"indirect" effect (reduced growth rate) on the bluegill's survivorship through a size-interval. Here we consider survivorship over the size-interval from 0.28 g (the initial mass on both pond sides) to 0.90 g (the final mass on the predator side). We take $c_g = 0.729$ (Table 2). By specifying l_p (0.28, 0.90) and l_{np} (0.28, 0.90), c_μ can be calculated from Eq. A6 and the relative effects of c_μ and c_g assessed. Below, we calculate values for l_p (0.28, 0.90) and l_{np} (0.28, 0.90) and then partition the total reduction in survivorship into components due to the direct effect (c_μ), the indirect effect (c_g), and their interaction when both occur simultaneously.

The value of l_p (0.28, 0.90) cannot be calculated exactly because fish were replaced at various times and sizes on the predator side, and we have no data on the shape of $\mu(s)$. However, we can bracket the possible values for l_p (0.28, 0.90) by calculating the survivorship as if all the replacements were added on (1) the first day of the experiment, or (2) the last day of the experiment (equivalently, not added at all). The first calculation yields a survivorship of 348/644 = 0.540 (348 fish recovered from 644 total fish). The second calculation yields 204/500 = 0.408 (348 recovered minus 144 replacements, divided by the 500 original fish). Thus we take l_p (0.28, 0.90) to lie somewhere between the extreme limits of 0.408 and 0.540. The parameter l_{np} (0.28, 0.90) also cannot be calculated exactly since we know only the survivorship to 1.13 g (the final size with no predator); l_{np} (0.28, 1.13) was 359/500 = 0.718. We can bracket the possible values of l_{np} (0.28, 0.90) by performing the calculation as if (1) no fish died after reaching 0.90 g (i.e., the mortality rate was a very strongly declining function of fish size), and (2) the mortality rates were independent of fish size. The first case yields l_{np} (0.28, 0.90) = l_{np} (0.28, 1.13) = 0.718. The second case yields l_{np} (0.28, 0.90) = 0.787. This was calculated by letting μ represent the size-independent daily mortality rate. Then $N_t = N_0 e^{-\mu t}$, where N_t = survivors at time t , N_0 = initial number of fish, t = time. Taking $t = 76$ d (the length of the experiment), $N_{76} = 359$, and $N_0 = 500$ yields $\mu = 0.004359$. The fish reached a mean size of 0.90 g after 55 d; $N_{55} = N_0 e^{-\mu(55)}$, which yields $N_{55} = 393.4$. Thus l_{np} (0.28, 0.90) = 393.4/500 = 0.787.

These survivorship ranges can now be used to estimate the relative impact of c_μ and c_g on survivorship. First, we calculate our "best estimate" of the relative effects by taking the midpoints of the survivorship ranges. Thus, we take l_{np} (0.28, 0.90) = 0.753 and l_p (0.28, 0.90) = 0.474, a reduction in survivorship of 37.1%. Application of Eq. A6 with $c_g = 0.729$ yields $c_\mu = 1.92$. If the predator had not affected the prey's growth rate (take $c_g = 1$), this model would predict survivorship to have been l_p (0.28, 0.90) = $l_{np}^{c_\mu}$ (0.28, 0.90) = (0.753)^{1.92} = 0.580, a reduction of 23.0%. Similarly, if the predator had affected only the growth rate, the model would predict l_p (0.28, 0.90) = l_{np}^{1/c_g} (0.28, 0.90) = (0.753)^{1/(0.729)}} = 0.678, a decrease of 10.0%. Thus, we estimate that the total of 37.1% reduction in survivorship can be partitioned into 23.0% due to the "direct" effect of increased daily mortality rates acting alone, 10.0% due to the "indirect" effect of decreased growth rates acting alone, and the remainder, 4.1%, to their interaction when both factors acted simultaneously.

Finally, there are four combinations of the endpoints of the ranges of l_{np} (0.28, 0.90) and l_p (0.28, 0.90). Taking the highest estimate of l_{np} (0.28, 0.90) and the lowest estimate of l_p (0.28, 0.90) yields l_{np} (0.28, 0.90) = 0.787 and l_p (0.28, 0.90) = 0.408, a reduction of 48.2%. Taking $c_g = 0.729$ and solving Eq. A6 yields $c_\mu = 2.73$. This results in a partitioning of the 48.2% into 33.9, 8.5, and 5.8% attributable to c_μ , c_g , and their interaction, respectively. Taking the lowest estimate of l_{np} (0.28, 0.90) and the highest estimate of l_p (0.28, 0.90) yields l_{np} (0.28, 0.90) = 0.718 and l_p (0.28, 0.90) = 0.540. In this case, $c_\mu = 1.36$, and the total reduction of 24.8% can be partitioned into 11.3, 11.5, and 2.0% attributable to c_μ , c_g , and their interaction. The results of the other two combinations lie within the range of the above combinations.