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Interactions among stream fishes: predator-induced habitat shifts and larval survival

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Summary. Adult largemouth bass alter habitat use by, and abundances of, other fishes in small streams. Experimental manipulations of bass in natural stream pools (Brier Creek, Oklahoma) showed that responses of other fishes to adult bass were highly dependent on prey size, and that both direct and indirect effects of adult bass influence the distribution and abundance of other stream fishes. Experiments measuring the distributional responses of members of natural pool assemblages to adult bass revealed differences among adult sunfishes, "small" fishes (16–80 mm SL), and larval sunfish and minnows. Adult sunfishes (*Lepomis* spp.) did not detectably alter their depth distribution in response to adult bass, but changes in abundance of adult *Lepomis* on the whole-pool scale appeared positively related to changes in the number of bass. Small fishes tended to occupy shallower water when adult bass were present; changes in abundance of small fishes were negatively related to the number of adult bass. Larval minnows and larval *Lepomis* occupied primarily deep, mid-regions of pools, and were found only in pools which contained, or had contained, adult bass. A second set of experiments was motivated by censuses of small prairie-margin streams which revealed co-occurrence of larval fishes (of both minnow and sunfish species) and adult largemouth bass. Experimental manipulation of bass and *Lepomis* larvae on the whole-pool scale showed that adult bass enhanced short-term survival of *Lepomis* larvae. This effect appears to be an indirect result of habitat shifts by small fishes in response to bass; additional experiments indicated that these small fishes are potentially important predators of larvae. The interactions suggested in this study are analogous to those hypothesized for bass and sunfish in lakes by Werner and Hall (1988).

Key words: Predator-prey – Stream – Fishes – Larval fish – Habitat shifts

One frequently observed response to predators in aquatic environments is a change in use of habitat by prey (e.g. Stein and Magnuson 1977; Crowder and Cooper 1982; Sih 1982; Werner et al. 1983; Cooper 1984; Fraser and Emmons 1984; Jones 1984; Power 1984, 1987; Mittelbach 1986; Schlosser 1987). Among lentic fishes, the presence of predators often results in increased use of vegetated or other physically complex habitats by prey (Crowder and Cooper 1982; Savino and Stein 1982; Werner et al. 1983). Observational studies of stream fishes (Schlosser 1982; Power 1984; Mahon and Portt 1985; Moyle and Vondracek 1985; Gorman 1987) suggest that smaller fishes are more common in shallow habitats. Fraser and Emmons (1984), Power et al. (1985) and Schlosser (1987, 1988a, 1988b) provided evidence that, for the juveniles and adults of some prey taxa, this pattern can be caused in part by piscivorous fishes.

Consequences of predator-induced shifts in use of habitat are of considerable interest because they may affect food webs at lower trophic levels. For example, Power and Matthews (1983) and Power et al. (1985) provided evidence that adult largemouth bass *(Micropterus salmoides)* indirectly enhance algal biomass in stream pools by directly altering habitat use by an herbivorous minnow, *Campostoma anomalum.* Bowlby and Roff (1986) suggested that piscivorous trout reduce the density of smaller fishes, thereby enhancing the biomass of stream invertebrates.

Another important aspect of predator/prey relationships is their dependence on the body sizes of both predator and prey. Werner and Gilliam (1984) suggested that size-specific changes in the ability of prey to avoid predators and to harvest resources leads to ontogenetic shifts in habitat or resource use. Werner and Hall (1988) examined habitat shifts by bluegill in lakes on this basis. Specifically, they showed that the size at which juvenile bluegill move from the littoral zone to the pelagic zone (51–83 mm standard length [SL]) can be explained on the basis of differential food resource availability and predation risk from adult largemouth bass in these two hab-

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itats: juveniles move into the more profitable pelagic zone at a larger size when adult bass density (and therefore predation risk) is high.

Both the size-specific nature of predator/prey interactions and the potential for multi-trophic level effects may be important for some fishes early in their life history. Sunfishes are known to change habitats in lakes as larvae in addition to their later movements as juveniles: bluegills hatch in the littoral zone, and later are found in open water, then move back to the littoral zone at 12–25 mm SL (Werner 1967; Storck et al. 1978; Werner and Hall 1988). Werner and Hall (1988) hypothesized that very young fish (< 12 mm SL) are safer in the pelagic zone because the littoral zone normally contains a number of small fishes capable of consuming larvae, while these small fishes are excluded from the pelagic zone by adult bass. Later, these young fish move to the littoral zone because they become more attractive to adult bass as their size increases, and are susceptible to bass predation in open water.

In this paper I examine interactions among stream fishes similar to those between sunfish and bass in lakes described above. I first experimentally document the response of other fishes to the presence of adult bass in stream pools, then examine the hypothesis that adult bass indirectly create safe areas for the larvae of other species by causing habitat shifts by "small fishes" (which will henceforth refer to all fishes 16–80 mm SL), as suggested by Werner and Hall (1988) for sunfishes in lakes. This hypothesis is tested by documenting natural patterns of abundance of adult bass and larvae of other species, testing the ability of small fishes to consume larvae, and experimentally comparing survival of larval fish in stream pools in the presence and absence of adult bass.

Study sites

Brier, Brushy and Buncombe creeks are small, clear streams in south-central Oklahoma with base discharges of approximately 0.03, 0.05 and 0.02 m^3/s, respectively. Brier (33° 70'N, 96° 55'W) and Buncombe (33° 60'N, 96° 47'W) creeks (Marshall County) have predominantly gravel and bedrock substrates and distinct pools are separated by narrow, shallow riffles (maximum depths 2–6 cm, minimum widths often < 1 m). Brushy Creek (34° 17'N, 96° 49'W, Johnston County) contains bedrock and sand substrates and has a less distinct pool-riffle structure. The fish faunas in the study reaches of all three streams are numerically dominated by central stoneroller *(Campostoma anomalum)*, bigeye shiner *(Notropis boops)*, green sunfish *(Lepomis cyanellus)*, longear sunfish *(L. megalotis)*, and largemouth bass.

These streams differ from lakes in several ways that are important to predator/prey interactions among adult bass and other fishes: 1) Pools that adult bass occupy are typically 5–10 m wide and 20–60 m long with maximum depths 1–2 m; 2) Aquatic vegetation is scarce for much of the year, and there is generally little cover for small fishes; 3) Adult bass are not present in all pools, and not able to move among pools during base flow; smaller fishes such as minnows and juvenile sunfishes can move among pools at base flow.

Methods

Habitat use responses to adult bass

The hypothesis that adult bass can positively affect the survival of larval fishes is dependent on the ability of adult bass to affect the use of habitat by smaller fishes. As a first step in testing for habitat shifts by smaller fishes in response to adult bass, I conducted a pilot experiment in May-June 1984 to determine important response variables in adult bass/sunfish interactions in stream pools. In this experiment the distributional response of juvenile sunfish (*Lepomis* spp.) to adult largemouth bass was measured in a Brier Creek pool gridded into 1 m^2 units by placing surveyor's flags or nailing plastic markers at each grid intersection. Water depth, cover and substrate were measured for each quadrat. Twenty observations, each at a minimum of 1 h apart, were made of all juvenile sunfish in the pool when no bass were present (18 May–10 June) and after the bass (185 and 230 mm SL) were added (12–17 June). Twenty additional observations were made during 18–22 June, after the bass were removed. Observations of sunfish species were grouped to facilitate rapid observation of the entire pool. No more than four observations were made on any one day. I determined the number and estimated the size of fish in each 1 m^2 unit from a concealed streambank position, and recorded data on audio tape. Data were taken only on undisturbed fishes, as indicated by behavioral patterns: fishes commonly remained stationary or fed slowly on the benthos when undisturbed, and immediately swam away from a streamside observer when the observer was first detected. The behavior patterns of undisturbed fishes were confirmed by longer-distance observations using binoculars.

Study of the habitat use responses of fishes to adult bass was expanded to include whole stream pool fish assemblages in two experiments conducted in 1986 (29 June–15 July and 18–23 July). In both of these experiments, I manipulated the number of adult bass (225–295 mm SL) in six natural, main-channel pools in Brier Creek, then measured the habitat use and changes in the abundances of all other fishes. These two experiments were designed as single-factor analyses of variance: the first used three levels of bass (0, 1 or 3 bass per pool) with two replicate pools per treatment, and the second two levels of bass (0 or 3) with three replicate pools per treatment. Natural densities of adult bass in Brier Creek were commonly 0–6 fish per pool. All fishes in each of the six pools were censused before and after each experiment (on 28 June, 16 and 25 July) by snorkeling. The pools ranged from 18–38 m in length, 4.6–7.7 m in average width and from 24.5 to 42.1 cm in average depth. Shallow riffles prevented movement among pools by adult bass but not most smaller fishes. All six pools lacked adult bass when these experiments were begun; bass were moved into and among experimental pools after being captured with hand nets by a diver. Pools were undisturbed and no observations made for a minimum of 24 h after bass densities were manipulated.

Because the pilot experiment indicated that juvenile sunfish responded to adult bass mainly by moving to shallower microhabitats, I measured total water column depth of microhabitats occupied by undisturbed fishes in the 1986 experiments. Other often-measured microhabitat variables for stream fishes were not recorded. Water velocity was not measured because it was extremely low and uniform in experimental pools. Substrate was not measured because the pilot experiment indicated that it was not a significant parameter in the response of other fishes to adult bass in this system. I made all habitat measurements while snorkeling, and recorded species (family for larval fish), estimated length (to the nearest 5 mm), and habitat depth on waterproof paper. Depth was measured with a wooden meter stick. Visual estimates of fish length were frequently checked by direct measurement of quiescent fishes with the meter stick, and by reference to inanimate objects which could be measured exactly.

The two experiments conducted in 1986 included 4988 and 2668 measurements of habitat use by individual fishes, respectively. Depth availability was measured in each pool on three dates (before, between and after the two experiments) by taking measurements at points 1 m apart along regularly spaced cross-stream transects (with the initial point on each transect positioned between 10 cm and 1 m from the bank at random; 284–561 measurements were made per pool).

For statistical analyses, *L. cyanellus* and *L. megalotis* were separated into three size classes: 5–15 mm SL, 16–80 mm SL and > 80 mm SL, approximately corresponding to larvae, juveniles and adults, respectively. Larval minnows were separated from larger size classes for analysis, but juvenile and adult minnows were grouped because of their similarity in size.

One-way univariate analyses of variance were performed on species/size classes for which I had data from all pools in the first of the two 1986 experiments or at least 2 replicate pools of both treatments in the second 1986 experiment (i.e., at least 2 replicates of each treatment). The analysis was based on within-pool averages of water depth at points occupied by fish for each species/size class. To determine if habitat availability influenced the response of fishes to adult bass, analysis of covariance was conducted using average pool depth (averaging availability data from the beginning and end of each experiment) as the covariate.

To examine the effect of adult bass on other fishes based on "prey" size across species in the 1986 experiments, fish length was regressed on depth of microhabitat using pool-specific data from each experiment exclusive of benthic fishes [orangethroat darters *(Etheostoma spectabile)* and logperch (*Percina* sp.)] and larvae of all species. Benthic fishes were excluded because their cryptic coloration and use of substrate as cover made them less likely to be affected by the presence of bass than fishes which occupy the water column. Larvae were excluded because their small size made them unlikely to suffer significant predation from adult bass.

Predation on larval fish

The hypothesis that adult bass positively affect the survival of larval fishes is also dependent on the ability of small fishes to prey on larvae. To evaluate the intensity of predation by small fishes on larval fish in the field, I manipulated numbers of larval fish and small fishes in a Brier Creek pool which had been divided longitudinally into two halves. This experiment consisted of three treatments: 1) 25 sunfish larvae (approximately 7 mm SL) released into a pool half in the presence of the natural density of small fishes; 2) natural densities of small fishes added to a pool half containing 25 larvae; and 3) 25 larvae released as above but with small fishes removed (control). (The initial densities of fishes in the unmanipulated pool were used to determine natural densities.) Treatment 2 was used to determine if the predation rates observed in treatment 1 were due to initial disorientation of larvae. Treatments 1 and 3 were conducted twice in each pool half. Treatment 2 was conducted once in each half. Larvae were censused at irregular intervals for at least one day after each manipulation. Six mm mesh plastic screen was used to divide the pool; after colonization by algae, larvae would not pass through the screen. Larval fish used in this experiment were captured from elsewhere in the study reach with an aquarium net. Larvae were released into the pool by slowly submerging the containers used to transport them (17 l buckets); this method provided temporary protection from predation, because larger fish did not enter the buckets. (Larval fish approximately 7 mm SL were used in these and later field experiments because smaller larvae are both more fragile and more difficult to locate.) Densities of small fishes were manipulated by electrofishing and seining. The narrow riffles at the head and tail of this pool were on opposite sides of the screen fence, preventing movement of larvae between pool halves. Drift nets positioned in the upstream and downstream riffles prevented immigration and emigration of larvae during the experiment.

Adult bass/Larval fishes

If adult bass positively affect the survival of larval fishes, one might predict a natural pattern of co-occurrence between bass and larvae. I conducted snorkeling censuses of sunfish and *Notropis* larvae, and adult largemouth bass in Brier (six dates in 1984), Brushy (two dates in 1985) and Buncombe creeks (once in 1986) to determine if such a pattern existed. Because adult bass did not move among pools at base flow and the drift of larvae from pool to pool is very low (B. Harvey, unpub. data), census data were based on the whole-pool scale. I censused fishes in pools while slowly crisscrossing the pools in an upstream direction. Censuses were conducted only when visibility was at least 1.5 m. To test my ability to census larvae, I counted sunfish larvae that had been added to natural Brier Creek pools by a second person. My censusing efficiency averaged 70% in 10 such tests.

To experimentally test the hypothesis that adult bass positively affect the survival of larvae, I manipulated the number of adult largemouth bass in four Brier Creek pools and monitored the short term survival of larvae that were added. The design incorporated two pools nested within each of two pool types, cross-classified with two bass treatments. Both bass treatments (no bass or 2 bass 191–230 mm SL) were conducted twice in each pool through time in a random sequence (Table 1). Replication through time was dictated by the low number of experimental units available. This is not pseudoreplication sensu Hurlbert (1984), because each replicate represents a distinct experimental trial, with separate additions of adult bass and larvae. Pool type was based on pool area and depth: large and shallow (Pool 3: max. depth 54 cm, area 225 m^2; Pool 6: max. depth 60 cm, area 236 m^2), or small and deep (Pool 7: max. depth 90 cm, area 97 m^2; Pool 9: max. depth 86 cm, area 102 m^2).

Pool type was included in the design of this experiment because I hypothesized that avoidance of shallow water by adult bass would reduce a positive indirect effect on larvae by reducing the effect of bass on small fishes (i.e. adult bass movement would be restricted to smaller regions of large shallow pools). To increase similarity of pools of the same type (large and shallow vs small and deep), pools 6 and 7 were modified by blocking the downstream end from bank to bank with 6 mm mesh plastic screen; this screen was impassable to all fishes. All pools contained similar unmanipulated assemblages of other species/size classes of fishes.

Differences between pools of the same type in the abundances of fishes other than adult bass and larvae, and in pool morphology, do not make them inappropriate as replicates. Any effects originating from such differences should contribute to experimental error, thereby reducing the power of the analysis. A similar argument applies to changes within pools through time: because bass treatments were randomly assigned through time, any time-related effects are included as experimental error.

Table 1. Chronology of treatments in the experiment measuring the effect of adult bass on the survival of larval sunfish, conducted June/July 1985 in Brier Creek, Oklahoma. Dates are the days on which the censuses of larvae were conducted following the manipulation of larval abundance one day earlier. NB = no adult bass; B = 2 adult bass

Pool 3		Pool 6		Pool 7		Pool 9	
Trmt	Date	Trmt	Date	Trmt	Date	Trmt	Date
B	22 JUN	NB	20 JUN	NB	20 JUN	NB	21 JUN
NB	24 JUN	NB	23 JUN	B	24 JUN	NB	23 JUN
B	29 JUN	B	1 JUL	NB	26 JUN	B	16 JUL
NB	17 JUL	B	19 JUL	B	19 JUL	B	18 JUL

Before each run in a given pool, I removed or added the needed number of bass at least 24 h in advance and removed any naturally occurring larval fish. Drift nets were set at the head and tail of pools to detect any movement of larvae among pools during the experiment. The drift nets were positioned such that they filtered at least 80% (usually >90%) of a given inflow or outflow. I then slowly submerged a 17 l plastic bucket containing 100 sunfish larvae at a depth of approximately 40 cm, near the deepest part of the pool. All runs were initiated between 1500 and 2000 h, and ended when all fishes in a given pool were censused 23–25 h later. Each census required 1–2 h; I used SCUBA to census fishes in small, deep pools because I detected larvae more easily when my line of sight was horizontal or at an upward angle. An appropriate line of sight could be achieved without SCUBA in shallow pools, where censuses were performed by snorkeling. Larvae used in this experiment were captured from unmanipulated pools within the study reach with an aquarium net. Elapsed time from capture of larvae to experimental addition never exceeded 1.5 h; no mortality of larvae occurred during this holding period. Adult bass were moved among pools after being captured with hand nets. Because of limitations set by the number and size of naturally-occurring larvae and by floods, I initiated the 16 23–25 h runs at irregular intervals from 19 June to 18 July 1985. The proportion of larvae surviving during a given run (out of the 100 added) was transformed (arcsine square root) before analysis.

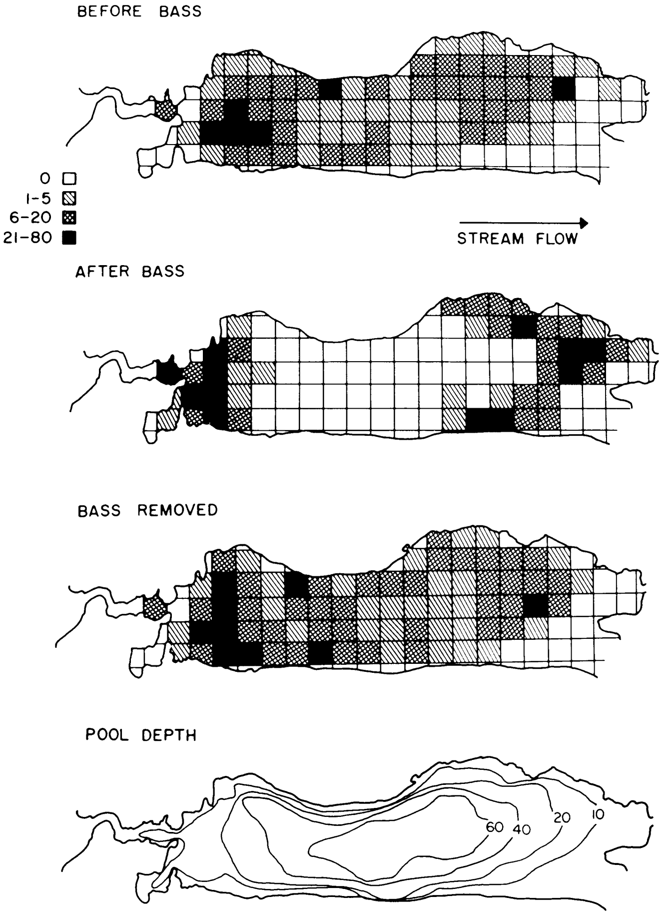

Fig. 1. Within-pool distribution of juvenile *Lepomis* in the presence and absence of bass. Twenty observations of the pool per treatment are summarized. Total numbers of observations of individual fish: before bass = 710, bass added = 759, bass removed = 789. Contour lines *(bottom panel)* indicate depth in cm

Results

Habitat use responses to adult bass

The response of juvenile sunfish in the pilot experiment illustrates the basic response of small fishes to adult bass observed during the later experiments and in nature: they rapidly moved to shallower water when adult largemouth bass were added (Fig. 1). The shift to a shallower distribution by juvenile sunfish was reversed when bass were removed (Fig. 1).

In the 1986 experiments, fishes in Brier Creek pools responded to adult bass on a size-specific basis in terms of both change in abundance and use of habitat. The abundance of small fishes decreased, while that of fishes >80 mm SL increased, when bass were added to a pool (Fig. 2). Movement by schools of *C. anomalum* and *N. boops* out of pools containing bass and into pools lacking bass strongly influenced the overall relationship for small fishes. Change in abundance of larvae was positively related to the presence of bass: abundance of larvae increased only in pools where bass were added.

Fishes also responded size-specifically to bass in terms of the depth of microhabitats occupied (Fig. 3). Adult sunfishes did not detectably alter their habitat use in the presence of bass, but small fishes (16–80 mm SL) generally occupied shallower water when bass were present. Analysis of covariance of depth of microhabitats occupied by individual species/size classes with number of bass as the main effect (and mean pool depth as the covariate) generally yielded the same results of analysis of variance both quantitatively and qualitatively.

Summarizing across taxa (with benthic fishes and larvae excluded), depth of habitat occupied was significantly (all P's < 0.001) related to fish length in all six pools in both experiments, regardless of the presence or absence of bass (Fig. 4). However, the presence of bass strengthened the depth/fish size relationship for the assemblage (one-way ANOVA of r^2 values for each pool with number of adult bass as treatments: $P = 0.001$). These regression lines also indicate that adult bass forced small fishes into shallow water.

Predation on larval fish

Larvae were readily consumed by small fishes when they were experimentally combined in stream pools. In particular, I observed pursuit of larvae by juvenile bass and juvenile *Lepomis* during this experiment. Survival of larvae in pools with juvenile fishes was extremely low; larvae were found (3 of the 25 individuals added) after 24 h in only one of six trials in which larvae and older fishes were in contact (treatments 1 and 2). When older fish were absent (treatment 3, 4 trials), 15–21 larvae (60–84%) were recovered after 24 h. The results of this experiment are corroborated by feeding rate measurements on juvenile bass (up to 12 larvae/min) under natural conditions (unpublished data), and the fact that minnows and juvenile sunfishes held in aquaria readily consume larvae.

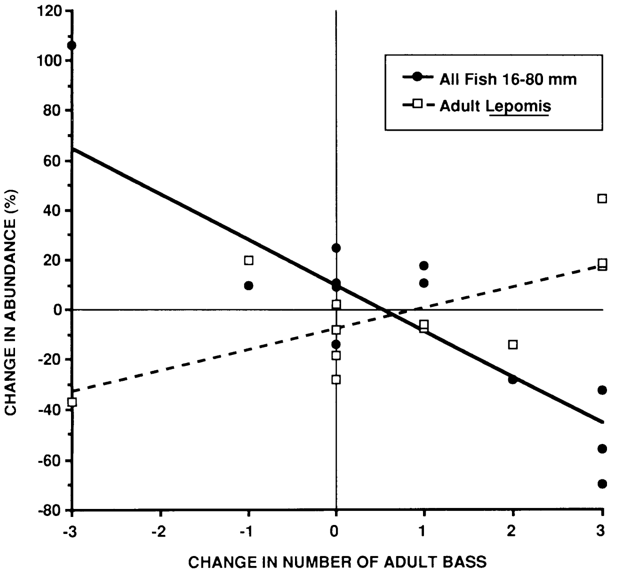

Fig. 2. Change in abundance of fishes versus change in number of adult bass. Experimental manipulations determined the change in adult bass. Because all six pools used in these experiments initially lacked bass, the first experiment yielded two changes each of 0, 1 and 3 bass. The second experiment yielded two changes of 0, and one each of -3, -1, $+2$ and $+3$ bass. For fishes 16–80 mm SL, % change$=-18.39$ (change in bass) $+9.51$ ($r^2=0.69$, $P=0.0015$). For adult Lepomis, % change$=8.4$ (change in bass) -7.47 ($r^2=0.44$, $P=0.0188$). The point at $x=-3$ for 16–80 mm fish is the change in abundance in Pool 9 in the second experiment, which was not included in the regression analysis due to lack of independence from the datum from Pool 10 in the first experiment

Adult bass/Larval fishes

Adult bass and larval *Lepomis* and *Notropis* co-occurred in pools in all three streams censused (Table 2). The censuses suggested that co-occurrence could not be explained by shared habitat preferences: the pattern remained significant in Brier Creek even though the distribution of adult bass among pools changed as a result of movement during floods. Similarly, pool-to-pool variation in reproductive activity of *Lepomis* and *Notropis* may contribute to, but cannot adequately explain the pattern of co-occurrence. *Lepomis* data from all three streams include only those pools in which *Lepomis* nests with eggs were observed. *Notropis* adults are not more abundant in Brier Creek pools with adult bass, suggesting that reproductive activity would not be greater where adult bass are present. In contrast to adult bass/larval fish co-occurrence, the density of small fishes is generally greater in pools without adult bass (W. Matthews and B. Harvey, unpublished data).

The field experiment indicated a direct connection between the presence of adult bass and the survival of larval sunfish (Table 3; $P=0.007$ for the bass effect in the nested ANOVA). The number of larvae surviving in trials with adult bass present ranged 38–83 (average$=63.5$), and in trials without adult bass 0–9 (average$=2.25$). The effect of adult bass was not detectably different in both small, deep pools and large, shallow pools (bass X pool type interaction, $P=0.451$), and pool

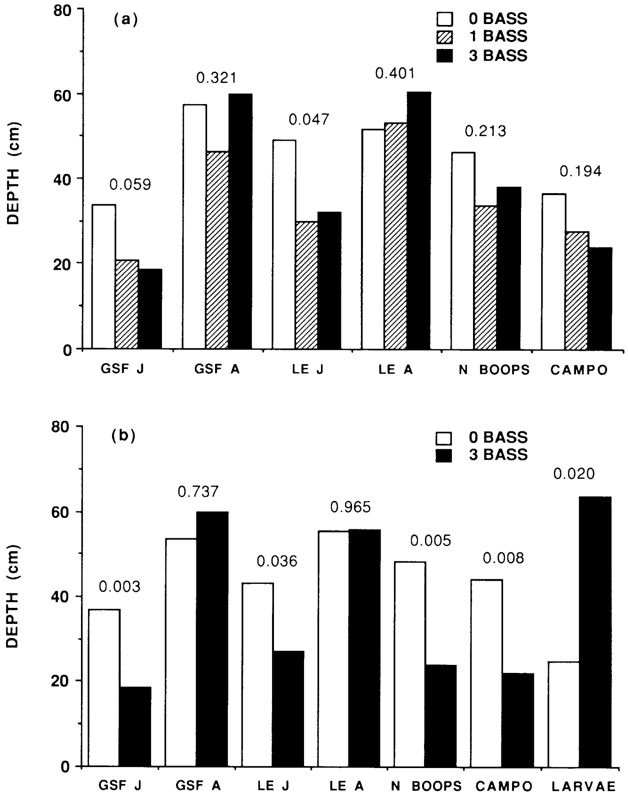

Fig. 3a, b. Means of depth of microhabitat occupied by fishes subject to different bass densities in two experiments **a** first experiment, 3 bass densities, 2 replicates per treatment; **b** second experiment, 2 bass densities, 3 replicates per treatment). Probability of no difference among treatments for each species/size class are above each set of bars. *GSF J*= green sunfish juveniles (16–80 mm SL), *GSF A*= green sunfish adults (> 80 mm SL), *LE J*= longear sunfish juveniles, *LE A*= longear sunfish adults, *N BOOPS*= big-eye shiners, *CAMPO*= central stoneroller, *LARVAE*= sunfish 5–15 mm SL. Treatment means were based on within-pool averages for each group (average within pool sample size per species/size class for the first experiment = 99; for the second experiment = 51)

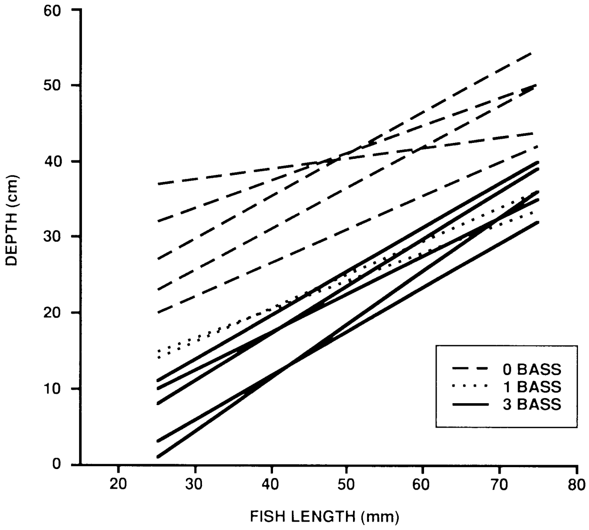

Fig. 4. Regressions of depth utilization versus length for fishes in Brier Creek pools (excluding benthic fishes and larvae) in which bass density was manipulated. Total degrees of freedom for each line range 266–909; $P<0.001$ for all regressions

Table 2. Results of censuses in Brier, Brushy, and Buncombe creeks, Oklahoma, showing the number of pools with each combination of adult largemouth bass (LMB) and *Lepomis* larvae presence(+)/absence(−), followed by similar data for Brier Creek cyprinid larvae. Probability of independence was determined by Fisher's exact test

LMB	*Lepomis* Larvae	Brier	Brier	Brier	Brier	Brier	Brier	Brushy	Brushy	Buncombe
		19 JUN 1984	24 JUN 1984	30 JUN 1984	02 JUL 1984	10 JUL 1984	18 JUL 1984	01 JUL 1985	07 JUL 1985	21 JUN 1986
+	+	6	7	7	6	6	5	5	7	10
+	−	1	0	0	1	1	2	1	0	0
−	+	0	0	0	0	0	0	0	1	1
−	−	4	4	4	4	4	4	7	5	11
Probability		0.0303	0.0061	0.0061	0.0303	0.0303	0.0909	0.0093	0.0093	<0.0001

LMB	Cyprinid Larvae	Brier	Brier	Brier	Brier	Brier	Brier
		19 JUN 1984	24 JUN 1984	30 JUN 1984	02 JUL 1984	10 JUL 1984	18 JUL 1984
+	+	6	7	6	6	7	5
+	−	1	0	1	1	0	2
−	+	0	1	2	3	1	0
−	−	9	8	7	6	8	9
Probability		0.0018	0.0014	0.0406	0.1091	0.0014	0.0096

Table 3. Number of *Lepomis* larvae surviving after 23–25 h (of 100 added) in Brier Creek pools in which adult largemouth bass abundance was manipulated

Bass Treatment	Pool Type			
	Large, shallow		Small, deep	
	Pool 3	Pool 6	Pool 7	Pool 9
Two Bass	51, 71	83, 38	78, 46	77, 64
No Bass	9, 6	0, 0	0, 0	1, 2

type alone had no effect on the survival of larvae ($P = 0.905$). Like the naturally occurring larvae observed during censuses, and in the experiments which measured changes in habitat use in response to bass, larvae released into pools during this experiment were found almost exclusively in the deep middle regions of pools (where adult bass are most often found). The fact that larvae were concentrated in these deep middle regions may have mitigated the importance of pool-to-pool differences in the areal extent of adult bass effects on the habitat use of small fishes. No larval fish were captured in any of the drift nets at the inflows and outflows of experimental pools, as expected based on the weak connections (narrow, shallow riffles) among pools.

Discussion

Adult largemouth bass had significant direct and indirect effects on habitat use and abundance patterns of other fishes in stream pools; responses of other fishes to bass were largely size-specific. As expected if size is a refuge from predation (Lawrence 1957; Werner et al. 1983), larger fishes (e.g. adult *Lepomis* >80 mm SL) did not alter their depth distribution in response to bass. Indeed, pool-specific abundances of adult *Lepomis* were positively related to change in bass density, but this relationship is based on small changes in numbers (0–7 fish per pool). Pools with bass may be advantageous to adult *Lepomis* for at least two reasons. First, this study suggests that bass improve survival of larval *Lepomis*; this could provide a relative reproductive advantage for *Lepomis* adults in these pools. Spawning success and egg survival of *Lepomis* is also probably higher in pools with bass because of reduced harassment or egg predation by smaller fishes (B. C. Harvey, *personal observation*). Second, as shown by Werner et al. (1983) in ponds, availability of food resources shared by adult *Lepomis* and smaller fishes is likely to be greater for adult *Lepomis* in stream pools that contain bass, because smaller fishes are spatially confined to shallower water by bass, and also less abundant in these pools.

For stream fishes in the size range most susceptible to predation by adult bass, shallow water microhabitats provide reduced predation risk, as do the vegetated regions of lakes and ponds. Adult bass are unlikely to be effective predators in very shallow water both because of physical limits on the depth of water they can occupy, and the predation risks large bass may face from birds and mammals (Power 1984, 1987; Power et al. 1989) in shallow areas. The lack of cover for small fishes in these streams probably enhanced their change in depth distribution in response to adult bass.

Recent studies indicate that small freshwater fishes select habitats based on assessment of both predation risk and foraging rate (Gilliam and Fraser 1987; Werner and Hall 1988; Abrahams and Dill 1989; Gotceitas and Colgan 1990a, 1990b). Brier Creek pools with and without adult bass may be substantially different for juvenile fishes with regard to both parameters. Low density of juvenile fishes in pools with adult bass may lead to greater food resources where predation risk is also higher, relative to pools in which adult bass are absent. Brier Creek pools with and without adult bass may thus offer juvenile fishes alternative strategies with similar fitness (Abrahams and Dill 1989). Future field experiments in which habitat-specific predation risks and foraging rates of stream fishes are measured would be valuable; habitat selection on both among and within pool spatial scales is important.

Larval sunfish and minnows violated the bigger-deeper pattern of distribution observed for older fishes (Fig. 4), and larval sunfish suffered lower mortality in pools with adult bass. Combined with evidence from this study that adult bass cause habitat shifts by small fishes, and that predation on larvae by small fishes is potentially strong, these facts suggest three mechanisms which may increase the survival of larval centrarchids and cyprinids in the presence of adult bass: 1) predation by bass on small fishes; 2) emigration by small fishes from pools with bass to pools with lower predation risk; and 3) in pools with adult bass, small fishes occupy shallow water areas which creates relatively safe areas for larvae in deep regions. Also, small fishes may be less efficient predators in the presence of adult bass due to a need for vigilance (Magurran et al. 1985; Godin 1986; Prejs 1987). The experiment measuring larval fish survival in the presence and absence of adult bass probably provided a conservative measure of the effect of adult bass because of the short duration of the bass treatments and the prevention of downstream emigration by fences in two pools; i.e., there was less opportunity for bass to affect the densities of fishes on a whole-pool scale relative to most natural conditions.

The ontogenetic pattern of habitat use in stream minnows and sunfish may parallel those lentic species that move offshore as larvae, return to the littoral zone as juveniles, then move back to the pelagic zone when predation risk from adult bass is reduced as a result of their increased size. The evidence from this study that areas where small fishes are concentrated are dangerous for larvae, and that adult bass indirectly reduce the risk for larvae, directly supports the hypothesis of Werner and Hall (1988) for bluegill in lakes. In lakes, small fishes are concentrated in the littoral zone by adult bass; in the streams studied here small fishes are concentrated in pools without adult bass and shallow regions of pools with bass.

While this study suggests an overall positive effect of bass on larval fish survival, it provides no direct evidence against predation on larvae by adult bass. The explanation of enhanced larval fish survival based on the effect of adult bass on smaller predators assumes that this effect is large relative to the negative direct effect of any predation on larvae by adult bass. Under all but the most severe conditions of food limitation, adult bass are probably not significant predators of larvae. Food habit studies of adult piscivorous fishes in lakes indicate that fishes <15 mm SL are rarely included in the diet (e.g. Mills et al. 1987).

The overall impact of bass on the abundance and population structure of prey species is complicated: for sunfishes and some minnows, adult bass appear to have a positive impact on larval survival, but adult bass prey on juveniles, and juvenile bass are important predators of larvae. Larvae of some prey species probably do not interact strongly with bass because of separation in space or time. In Brier Creek, some minnows spawn well before bass (e.g. *Campostoma anomalum*), thereby avoiding predation by young-of-the-year bass. Although *Fundulus* larvae co-occur with juvenile bass in time, they appear not to interact with juvenile or adult bass, because they commonly occupy water <4 cm deep.

This study suggests that large piscivorous fish may strongly affect habitat use by stream fish assemblages. Recall, however, that regressions of water column depth versus fish size were significant in all 12 pool/experiment combinations in the two experiments which measured habitat use, including the 5 treatments without adult bass. In the absence of adult bass, this relationship was strongest for adult and small juvenile fishes, suggesting the importance of avian and mammalian predators to the former (Power 1984, 1987; Power et al. 1989), and piscine predators other than large bass to the latter. Piscivory by green sunfish adults, for example, could be significant for a relatively small size range of fish prey. Experimental treatments without bass are not equivalent to "no predator" treatments for many species/size classes.

The biotic interactions evident in these experiments occur in a stream where flooding is common and droughts are occasional during the reproductive periods of the resident fishes. Minnow and sunfish larvae <10 mm total length (TL) are extremely susceptible to displacement by flooding, but resistance to displacement by flooding increases rapidly with size for individuals larger than 10 mm TL (Harvey 1987). Biotic processes affecting survival of larval fish can operate only within a framework provided by flooding. Evidence from these experiments suggests that reductions in flow can also supersede biotic processes: *C. anomalum* abundance in one pool increased by 70 fish when the area of bordering riffles decreased as discharge declined, even though this pool contained an adult bass. Both abiotic and biotic mechanisms are likely to be involved in regulating stream fish assemblages (Schlosser 1982, 1985; Schlosser and Ebel 1989), and many interactions between the two classes of factors are possible. For example, in Brier Creek, the timing of spring floods appears to strongly influence the year-class strength of bass; these young-of-the-year bass are important predators of larval fish of other species later in the year. Floods may also alter both the distribution of juvenile and adult fishes and the morphology of the stream channel, thereby affecting site-specific predation risk for all fishes. During drought, abiotic and biotic factors may interact to the extent that reductions in habitat forces individuals into closer proximity, thereby intensifying biotic interactions.

Models of habitat selection by stream fishes should include the effects of large piscivores and the recognition that shallow-water areas can serve as spatial refugia from these predators. Because habitat-specific predation risk appears to be very different for larval and juvenile stream fishes, the former should be included as a separate component in conceptual frameworks of biotic interactions among stream fishes. The "ontogenetic niche" concept (Werner and Gilliam 1984) which has been successfully applied to bluegill in lakes (Werner and Hall 1988) appears very appropriate for some stream fishes.

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