

# Direct and Indirect Effects of Channel Catfish (*Ictalurus punctatus*) on Native Crayfishes (Cambaridae) in Experimental Tanks

SUSAN B. ADAMS<sup>1</sup>

USDA Forest Service, Southern Research Station, 1000 Front St., Oxford, Mississippi 38655

**ABSTRACT.**—For the incised, sand-bed streams of north-central Mississippi, USA, fish predation is one plausible mechanism to explain both relatively low crayfish densities and differences in stream size occupied by various native crayfishes. I conducted two mesocosm experiments to test effects of a fish predator (channel catfish, *Ictalurus punctatus*) on the survival and size structure of native crayfishes (primarily *Procambarus hayi* and *Orconectes chिकासawae*) in the presence and absence of shelter. I used predominantly the larger species, *P. hayi*, in the first experiment and the smaller species, *O. chिकासawae*, in the second. Experiments lasted 19–21 d, and each consisted of four replicated treatments: crayfish without shelter, crayfish with shelter, crayfish and predator without shelter, crayfish and predator with shelter. In both experiments, catfish significantly reduced crayfish survival. Shelter significantly reduced catfish predation on the smaller, but not the larger, crayfish species. Comparisons between experiments showed that in tanks containing catfish, *P. hayi* had higher survival than *O. chिकासawae*. In both experiments, the mean size of crayfish increased less in the presence than in the absence of catfish, and I argue that the effect is due largely to a reduction in crayfish growth. Channel catfish directly and indirectly influenced crayfish in experimental settings, with the degree of influence varying by crayfish species and presumably related to crayfish size. Thus, fish predation and shelter availability are likely important factors influencing densities of and macrohabitat use by these native crayfishes.

## INTRODUCTION

In the incised, sand-bed streams common in northern Mississippi, USA, habitat is typically uniform, and shelter for fish or crayfish in the form of woody debris, rocks, vegetation or undercut banks is relatively scarce (Shields *et al.*, 1994, 1995). During electrofishing in local streams, I captured crayfish predominantly near cover, even small patches of leaves or debris, and rarely over open sand. Abundant shelter can reduce fish predation rates on crayfish (Garvey *et al.*, 1994), and even gravel and pebble substrates afford more protection from predation than does sand (Stein and Magnuson, 1976). Given choices of substrate and habitat complexity, crayfish tend to avoid open sand substrates, the effect being most pronounced for small crayfish when fish predators are present (Stein and Magnuson, 1976; Hill and Lodge, 1994; Kershner and Lodge, 1995).

Size-selective fish predation within and among crayfish species has been studied extensively in the upper midwestern U.S.A. for a suite of crayfishes including the native *Orconectes virilis* and invaders *O. propinquus* and *O. rusticus*, and appears to facilitate species replacement by the invaders. Fishes selectively prey on small or medium sized crayfish and seem to select crayfish based primarily on chelae size (Stein, 1976; Garvey *et al.*, 1994; Keller and Moore, 2000; Roth and Kitchell, 2005). Crayfish behavior also influences crayfish predation risk and tends to be size-dependent as well (Garvey *et al.*, 1994; Keller and Moore,

<sup>1</sup>Telephone: (662) 234-2744 ext. 267, e-mail: sadams01@fs.fed.us

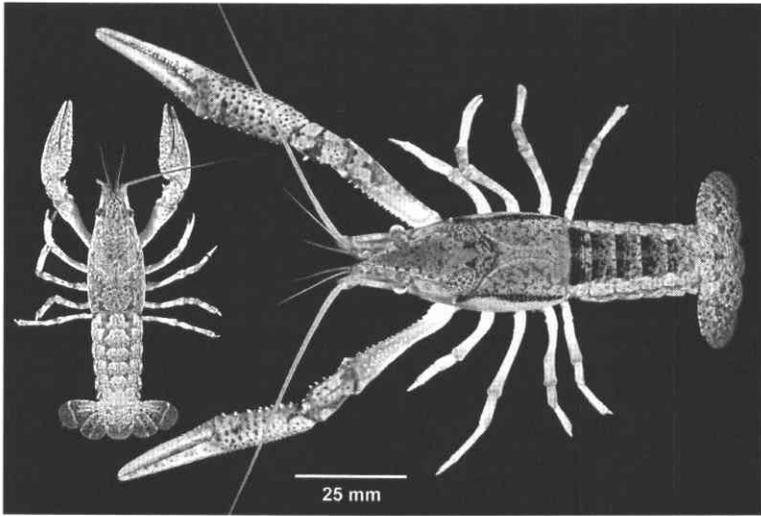


FIG. 1.—Reproductive form males of *Orconectes chickasawae* (left) and *Procamburus hayi* (right) from Mississippi, USA

2000). However, relative predation risk has received little attention as a potential mechanism determining crayfish distributions in assemblages of native, co-evolved species.

In headwater streams of the Little Tallahatchie River drainage, Mississippi, five species of native crayfishes are common (*Cambarus striatus*, *Orconectes chickasawae*, *Procamburus hayi*, *P. ouachitae* and *P. vioscai*), but abundances are fairly low (e.g.,  $0.09\text{ m}^{-2}$  in perennial, fish-bearing stream reaches, Adams and Warren, 2005). *Procamburus hayi* is common in lakes and ponds (Payne, 1972) and reaches its highest stream abundances in deep, slow-flowing stream sites close to lakes. *Procamburus hayi* is one of the larger local species (post-orbital carapace length [POL] up to 37 mm) and is characterized by very long chelae (pincers), especially on mature males (Fig. 1). The smallest of the local species, *O. chickasawae* (POL up to 26.5 mm), is common in a variety of small-stream habitats, even in intermittent streams, and its densities are inversely correlated with stream size. The chelae of adult *O. chickasawae* are much smaller than those of *P. hayi* (Fig. 1).

A shortage of shelter may contribute to the low crayfish densities in sand-bed streams in northern Mississippi, U.S.A. Also, if fish prey preferentially on certain crayfish species, then predation pressure in conjunction with limited shelter may contribute to the differences in stream sizes used by some native crayfish species. I conducted two experiments to examine whether shelter availability affects channel catfish predation on crayfish (primarily *P. hayi* and *O. chickasawae*) and whether catfish influence crayfish size structure. Comparisons between experiments provided insights into the relative direct and indirect effects of channel catfish on the two species.

I used channel catfish (*Ictalurus punctatus*) as the predator for the experiments because it is a common, native fish that sometimes forages extensively on crayfish (Flotemersch and Jackson, 2003). To ensure that channel catfish would be appropriate predators under the experimental conditions, I conducted a brief pilot study. I placed six *Orconectes chickasawae* crayfish and one channel catfish in each of two outdoor tanks (without gravel substrate),

one with shelter and one without. In tanks without and with shelter, all crayfish were eaten by the first and third mornings, respectively.

The objectives of the two main experiments were to test: (1) whether shelter for crayfish reduced channel catfish predation rates on crayfish, (2) whether shelter influenced crayfish cannibalism, (3) whether catfish influenced crayfish size structure and (4) whether catfish had a greater influence on the survival and size structure of *Orconectes chिकासawae* compared to *Procambarus hayi*.

#### METHODS

I conducted two experiments in outdoor tanks. Both experiments included four treatments: (1) crayfish with no shelter, (2) crayfish with shelter, (3) crayfish and catfish with no shelter and (4) crayfish and catfish with shelter. The experiments were designed with four tanks per treatment, although variations in sample size occurred. Treatments were randomly assigned to tanks for experiment 1 and kept essentially the same for experiment 2 (Table 1).

The plastic tanks were oval-shaped (137 cm wide by 158 cm long) with a mean water depth of 48 cm and volume of 946 liters and were arranged outdoors in two rows under a shade-cloth canopy within a fenced enclosure. My observations and the lack of unexplained mortality in the no-catfish tanks indicated that predation on crayfish by birds or other wild predators did not occur. Water recirculated from crayfish tanks into two large storage tanks and then flowed through three tanks containing physical and biological filters before re-entering crayfish tanks. Each crayfish tank had a layer of pea gravel (average median axis = 7.7 mm, SD = 1.6 mm) approximately 20 mm thick.

Crayfish shelter consisted of bricks tied together so that the holes formed tubes. Two sizes of brick were used to accommodate large and small crayfish. The smaller bricks had two rows of five round holes (20-mm diameter) and were tied in pairs, creating 115-mm-long tubes. The larger bricks had one row of four oval holes (40 mm wide  $\times$  25 mm tall) and were tied in bundles of three, creating 205-mm-long tubes. Shelter availability was consistent between experiments, with each tank in shelter treatments containing two sets of each size brick for a total of 20 small and 8 large holes. Catfish shelter was provided in all shelter treatment tanks, even those lacking fish, by a PVC tube (155 mm diameter, 400 mm long). Crayfish often hid between a brick and the tank wall, and smaller individuals sometimes burrowed under bricks or PVC tubes.

Crayfish and catfish were collected from local streams. Catfish were held 1–2 d prior to experiment 1 and 27–36 d prior to experiment 2. The same catfish were used in both experiments. Most crayfish were held for 2–14 d before experiments, but some had been in outdoor tanks for about 3 mo.

I fed catfish feed (6-mm-diameter pellets) to both crayfish and catfish 5 to 7 days per week both before and during experiments, adding more pellets to tanks with catfish than to those with only crayfish. Pellets were scattered over the water during daylight and sank to the bottom within about 20 min. During other studies, crayfish in laboratory aquaria and outdoor tanks thrived on the pellets, presented in the same manner, for more than one year. In addition, tanks were colonized by a variety of small aquatic invertebrates.

At the beginning of each experiment, every tank contained seven crayfish, creating a density of 3.2 crayfish  $m^{-2}$ , higher than we find in local streams but much lower than in some other eastern streams (e.g., Riggert *et al.*, 1999). All individuals were adults or large juveniles expected to mature within several months. Difficulty in obtaining adequate numbers of any one crayfish species dictated that I use a small number of individuals other

TABLE 1.—Numbers of crayfish of each species by tank and treatment in experiments

Treatment	Tank	<i>P. hayi</i>	<i>O. chickasawae</i>	<i>P. vioscai</i>
<i>Experiment 1</i>				
No catfish/shelter	4	6	1	
	8	6		1
	11	7		
	13	6		1
No catfish/no shelter	2	7		
	5	7		
	17	6	1	
	18	7		
Catfish/shelter	16	6		1
	12 <sup>1</sup>	6		1
	14	7		
	15	7		
Catfish/no shelter	1	7		
	3	7		
	6 <sup>1</sup>	7		
	7 <sup>1</sup>	7		
<i>Experiment 2</i>				
No catfish/shelter	1		6	1
	4		6	1
	11	1 <sup>2</sup>	5	1
	13		6	1
No catfish/no shelter	2		6	1
	5		6	1
	17		7	
	18	1	6	
Catfish/shelter	12	1 <sup>2</sup>	5	1
	14		6	1
	15		6	1 <sup>3</sup>
	16		7	
Catfish/no shelter	3		6	1 <sup>2</sup>
	6		6	1
	7	1 <sup>2</sup>	5	1

<sup>1</sup> Catfish jumped out of tank. Experiment started over in tank with new catfish and crayfish as needed (two crayfish in tank 6; one in tank 12)

<sup>2</sup> Individual was larger than any *O. chickasawae* in experiment 2

<sup>3</sup> Only non-*O. chickasawae* individual that survived to end of experiment 2 in a catfish treatment

than the target species in both experiments (*see* below). However, I interpret results in terms of *Procambarus hayi* and *Orconectes chickasawae* because they constituted the vast majority of individuals in the first and second experiments, respectively. Tanks in the catfish treatments each contained one catfish. I measured crayfish post-orbital carapace lengths (POL, carapace measured from the edge posterior to the eye to the posteriomedian margin) with calipers at the beginning and end of each experiment and measured catfish at the beginning of experiments.

During both experiments, I or an assistant typically counted the crayfish remaining in tanks at least five times per week and noted molted exoskeletons. We used a viewing bucket

to observe crayfish and lifted bricks to search for crayfish in the holes. During the latter part of the second experiment, water clarity was reduced across all treatments, so we counted crayfish less frequently but captured them with a hand net each time to prevent double counting. When a crayfish count exceeded the count made on a previous day, I adjusted the earlier count to reflect the crayfish we had overlooked. At the end of each experiment, we drained the tanks and searched thoroughly for crayfish.

Experiment 1 ran for 19 d, from 9 to 28 June 2004. *Procambarus hayi* constituted 93% of individuals in the experiment. Six tanks assigned to three treatments included one individual of another species (Table 1). Average POL of crayfish was 23.0 mm (SD 4.0, range 15–30) at the beginning of the experiment, and all non-*P. hayi* individuals were within the size range of the *P. hayi*. Crayfish lengths did not differ significantly between catfish and no-catfish treatments at the beginning of either experiment (*t*-tests,  $p > 0.17$ ).

Catfish jumped out of four tanks and died early in experiment 1 (Table 1). I considered initial data from those tanks as treatments without catfish. On June 15, I returned the four tanks to their initial states by replacing the catfish and any missing crayfish and began the day count anew for those tanks. Therefore, the results included different numbers of tanks in each treatment for some days, a given day in the experimental duration did not represent the same date for all tanks, and experimental durations varied within treatments. After replacing the four catfish, average total length of catfish was 380 (SD 40) mm.

Experiment 2 ran for 21 d, from 12 July to 2 August 2004. *Orconectes chिकासawae* constituted 80% of the individuals in experiment 2, with the remainder being *Procambarus vioscai* and *P. hayi*. Ten tanks included one individual of another species, and three tanks included two individuals of other species (Table 1). Average crayfish size was 14.3 mm POL (SD 2.5, range 10–26) at the beginning of the experiment, and four non-*O. chिकासawae* individuals were larger than any of the *O. chिकासawae* (Table 1).

*Statistical analyses.*—Within each experiment, I assessed the influence of catfish and shelter on crayfish survival by using the Kruskal-Wallis (K-W) procedure to test for differences in the number of surviving crayfish among treatments. If overall differences were significant, I used Mann-Whitney U-tests (M-W) tests to determine which pairs of treatments had significant differences. I compared survival 4 to 6 days into experiments and again near the end of the experiments, exact days for each experiment being determined by when the most tanks were inspected for crayfish. Significance levels were  $\alpha < 0.05$  and were one-sided for M-W tests. All statistics were conducted with SPSS 14.0 (SPSS, 2005).

In addition, after finding no overall significant differences in survival in experiment 1, I increased the statistical power by pooling data across shelter treatments. I then used the M-W procedure to test for differences in survival between the pooled catfish treatments and the pooled no-catfish treatments.

I compared crayfish survival in the presence of catfish between experiments by using M-W tests on the number of crayfish surviving to day 10. I compared both the catfish/shelter and the catfish/no-shelter treatments across experiments without pooling the data.

To assess channel catfish effects on crayfish size structure, I calculated the change in the mean size of crayfish per tank over the course of each experiment and compared the size changes among treatments using analysis of variance (ANOVA). For experiment 1, presence or absence of catfish and shelter were used as fixed factors in a two-way ANOVA. For experiment 2, I used size change data only from tanks with shelter because all crayfish were eaten in the catfish/no-shelter treatment; therefore, I included only the catfish factor in a one-way ANOVA.

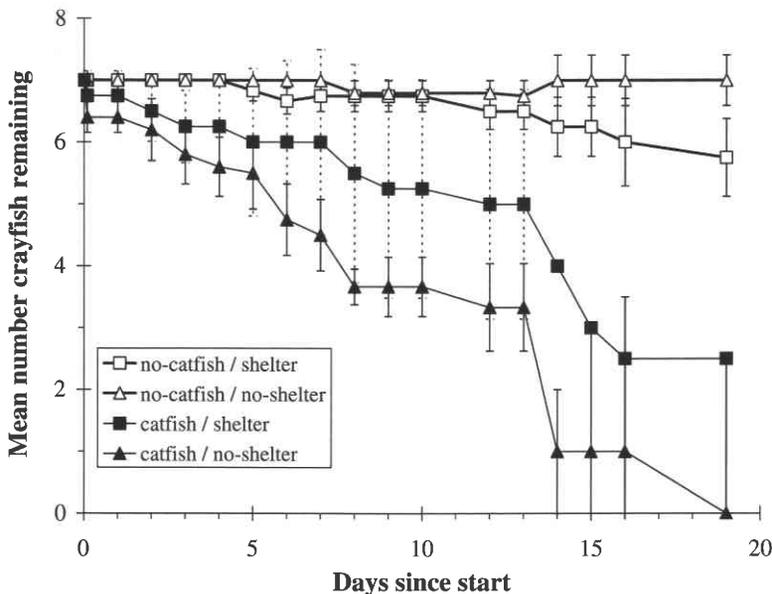


FIG. 2.—Mean ( $\pm 1$  SE) number of crayfish remaining by treatment during experiment 1. When data were pooled by presence or absence of catfish, significantly more crayfish remained in no-catfish than in catfish treatments on days 6 and 12. After day 13, sample sizes were too small for statistical comparison (catfish treatments,  $n < 3$ ). Some lines increase slightly in places due to differences in sample sizes on different days (see Methods). Broken lines on catfish/shelter error bars are to improve clarity

## RESULTS

Channel catfish reduced survival of *Procambarus hayi* overall, but predation in the shelter treatment was highly variable. In experiment 1, crayfish survival did not differ significantly among all treatments on day 6 (K-W test,  $\chi^2 = 4.6$ ,  $df = 3$ ,  $p$ -value = 0.20) (Fig. 2). On day 12, differences in survival were only marginally significant (K-W test,  $\chi^2 = 6.7$ ,  $df = 3$ ,  $p$ -value = 0.08). Variation in survival in the catfish/shelter treatment was high by day 12, with the number of surviving crayfish ranging from 1 to 7. When I increased statistical power by pooling data to compare catfish vs. no-catfish treatments, regardless of shelter, I found that significantly more crayfish had survived in no-catfish than in catfish treatments on both days 6 and 12 (M-W test,  $U \leq 28$ , 1-tailed  $p$ -value  $< 0.03$ ).

In experiment 2, channel catfish reduced survival of *Orconectes chिकासawae* dramatically, and shelter clearly reduced predation. Results of overall (K-W test,  $\chi^2 > 12.1$ ,  $p$ -value  $< 0.01$ ) and pairwise tests among treatments on days 4 and 18 indicated that crayfish survived best in the absence of catfish and that when catfish were present, shelter significantly increased survival (Fig. 3).

Shelter did not influence crayfish survival in the absence of the predator in either experiment (M-W tests,  $U \geq 7$ , 1-sided  $p$ -values  $\geq 0.07$ ). Although Figures 2 and 3 may mislead one to believe that shelter tended to increase cannibalism, in fact, most crayfish deaths in no-catfish/shelter treatments were due to causes other than cannibalism, including crushing by bricks during counting (three crayfish), mortality during an unusual algae bloom in one tank (two crayfish) and unknown causes but crayfish bodies intact (two

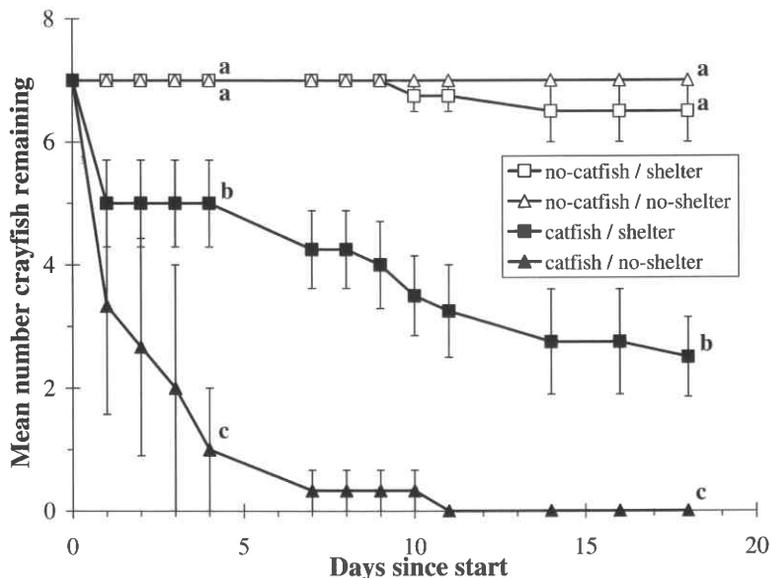


FIG. 3.—Mean ( $\pm 1$  SE) number of crayfish remaining by treatment during experiment 2. Treatments with the same letters are not significantly different from each other in pairwise comparisons (Mann-Whitney U-tests, one-tailed,  $\alpha = 0.05$ ) for days 4 and 18

crayfish). I found only two mortalities in tanks without catfish where the crayfish were missing, and, thus, apparently eaten (as is typically the case when killed by another crayfish).

Crayfish survival in the presence of a predator was highest in experiment 1. After 10 d with a channel catfish, significantly more crayfish remained in experiment 1 than in experiment 2, regardless of the presence or absence of shelter (M-W tests,  $U \leq 2$ , 1-sided p-values  $< 0.04$ , for both catfish treatments). Conversely, without a predator, survival to day 10 was the same between experiments (M-W tests,  $U = 8$ , 1-sided p-values  $> 0.37$ , for both no-catfish treatments). So, *Procambarus hayi* experienced less predation than did *Orconectes chिकासawae*.

Crayfish size structure was influenced by channel catfish in both experiments, but to a greater degree in experiment 2. During experiment 1, mean crayfish size increased significantly less in tanks containing catfish than in those without catfish but did not differ significantly with respect to shelter (Table 2, Fig. 4). In experiment 2, catfish had a highly significant effect on mean crayfish size; mean size increased much less in tanks with, than in those without, catfish (Table 2, Fig. 4). Channel catfish consumed crayfish of the entire size range available in the two experiments (11–29 mm POL), as determined by comparing the initial crayfish sizes with the sizes of those surviving to the end of experiments. Catfish consumed many of the smallest crayfish, especially in experiment 2. Although catfish also consumed the largest crayfish in six of the seven catfish tanks in experiment 2, in experiment 1, they consumed the largest crayfish in only three of the eight catfish tanks.

#### DISCUSSION

Channel catfish reduced survival of crayfish relative to predator-free controls, and shelter reduced predation on the smaller crayfish species, *Orconectes chिकासawae*, relative to no-

TABLE 2.—Analysis-of-variance (ANOVA) of treatment effects on the change in mean crayfish size by tank. Data from all treatments in experiment 1 were analyzed by a two-way ANOVA. For experiment 2, only shelter treatments were included in a one-way ANOVA (*see text*)

Source	df	MS	F	P
<i>Experiment 1</i>				
Catfish	1	8.268	4.945	0.050
Shelter	1	0.395	0.236	0.638
Catfish × shelter	1	0.161	0.096	0.763
Error	10	1.672		
<i>Experiment 2</i>				
Catfish	1	10.163	10.455	0.018
Error	6	0.972		

shelter treatments. In other studies, crayfish increased shelter use in the presence of fish predators (Stein and Magnuson, 1976; Garvey *et al.*, 1994; Hill and Lodge, 1994), and shelter or complex habitat typically increased survival, especially for small crayfish (Garvey *et al.*, 1994; Kershner and Lodge, 1995, but *see* Mather and Stein 1993).

The reduction in predation rate in the presence of shelter suggests that a shortage of cover may contribute to the relatively low overall crayfish densities in north-central Mississippi streams. Adams and Warren (2005) found densities in these streams of 0.09–0.23 crayfish  $m^{-2}$ ; although certainly underestimates, the densities are much lower than densities in many other eastern rivers (*e.g.*, 1.8–10.3  $m^{-2}$  in Missouri, Riggert *et al.*, 1999). Cover and habitat complexity are limited in most of the incised streams, both large (Shields *et al.*, 1994, 1995) and small (Warren *et al.*, 2002).

In comparisons between experiments, the large-bodied *Procambarus hayi* survived better overall than the smaller *Orconectes chिकासawae* in the presence of channel catfish, particularly when cover was lacking. The result suggests that crayfish species-specific size or behavior influenced channel catfish predation and is consistent with numerous studies showing size-selective predation on smaller crayfish in experimental (*e.g.*, Garvey *et al.*, 1994) as well as field settings (Roth and Kitchell, 2005). Presumably, the smallest crayfish were susceptible to predation by catfish at all times, whereas, the largest *P. hayi* were vulnerable primarily around the time of molting.

Behavioral differences may have helped large *Procambarus hayi* avoid predation. Male *P. hayi* often displayed their large chelae toward catfish that swam around tanks lacking cover. I never observed *Orconectes chिकासawae* making such aggressive postures toward the fish. During experiment 2, I observed (but could not quantify) an increase in crayfish hiding behavior in the presence of catfish. Most noticeable was that more crayfish took refuge under the PVC tubes in the presence than in the absence of catfish. However, even in several no-catfish/no-shelter tanks, the smallest *O. chिकासawae* buried themselves in the gravel and remained immobile, avoiding detection by us for days and perhaps by other crayfish. This was evidently not an effective strategy for ultimately avoiding catfish predation, as all *O. chिकासawae* in the catfish/no-shelter tanks were eaten. My results are consistent with those of other crayfish predation studies in which small individuals reduced their activity, shifted habitat use, or swam away more often and made chelae displays less often than did large individuals (Stein and Magnuson, 1976; Englund and Krupa, 2000; Keller and Moore, 2000).

Given suitable soil types, crayfish can take refuge in burrows they construct in stream banks, but burrowing tendency varies among species. *Procambarus hayi* adults often occupy

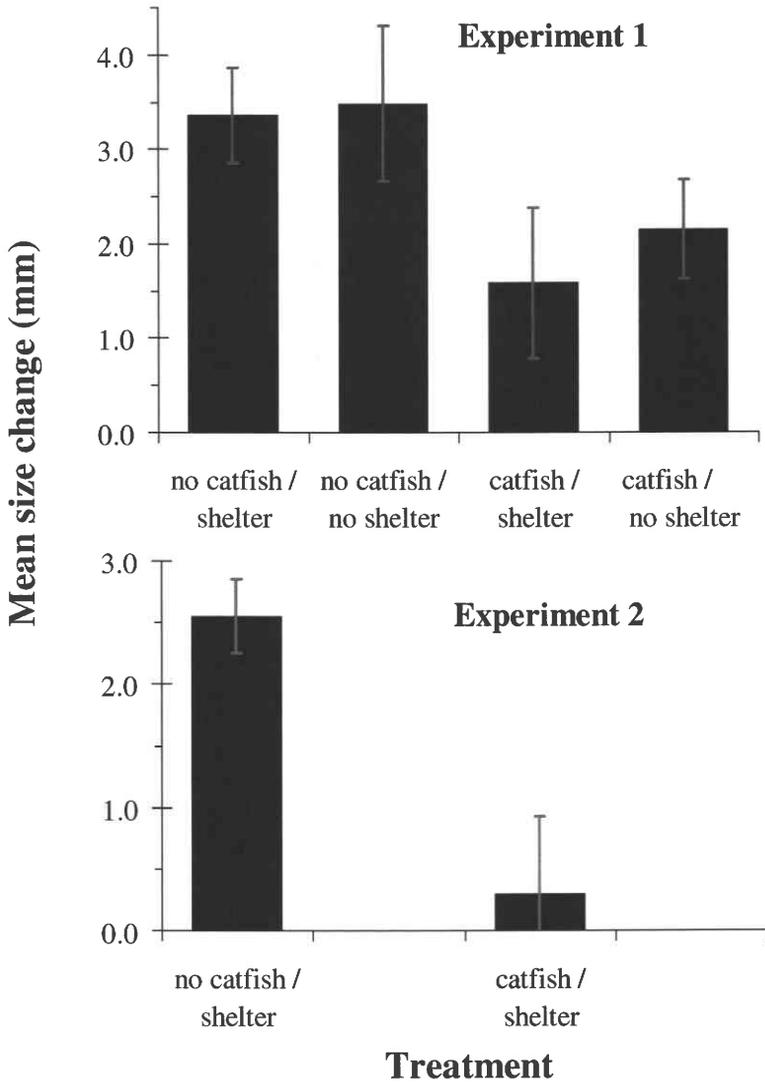


FIG. 4.—Changes (mean  $\pm$  1 SE) in mean crayfish post-orbital lengths by tank. For experiment 2, only treatments with shelter are shown because no crayfish survived in the catfish/no shelter treatments. Durations of experiments 1 and 2 were 19 and 21 days, respectively

burrows from late-spring through summer, but some occur in open water during all months (Payne, 1972). Dramatic decreases in *O. chickasawae* densities in streams from summer to winter suggest that *O. chickasawae* may occupy burrows during winter, but adults are encountered frequently in open water from spring through autumn. The greater tendency of *P. hayi* to burrow during summer months, when fish feed most actively, may also decrease their susceptibility to fish predation relative to *O. chickasawae*.

Catfish influenced crayfish size structure in both experiments. Crayfish size increases in no-catfish tanks during both experiments indicated that the basic experimental conditions were suitable for crayfish growth. Possible mechanisms by which catfish could have reduced increases in mean crayfish size include: (1) suppression of crayfish growth due to behavioral shifts by crayfish, (2) suppression of crayfish growth by domination of food resources, (3) preferential predation on faster-growing crayfish or (4) size-selective predation on larger crayfish. Size-selective predation on larger individuals is an unlikely mechanism because catfish consumed many of the smallest crayfish and fewer of the largest crayfish. The domination of food resources is also unlikely for two reasons. First, I added more food to catfish than to no-catfish tanks. Second, in comparison to the smaller species, the larger crayfish species should require more food to grow, but in the presence of catfish, the mean size of *Procambarus hayi* increased more than that of *Orconectes chickasawae*.

Catfish did not completely suppress crayfish growth, as demonstrated by the continued molting of crayfish in catfish tanks throughout the experiments. Although crayfish molted in the presence of catfish, behavioral shifts in the presence of catfish (*see below*) may have reduced growth increments or molt frequencies. Smallmouth bass caused reductions in grazing and daily ration of juvenile, and to a degree small adult, but not large adult, *Orconectes propinquus* under experimental conditions (Stein and Magnuson, 1976). The *O. chickasawae* at the beginning of experiment 2 were between the sizes of juveniles and small adults in Stein and Magnuson's (1976) study, and *Procambarus hayi* at the beginning of experiment 1 were the size of the large adults. Growth of signal crayfish (*Pacifastacus leniusculus*) was suppressed even in the presence of a planktivorous fish, suggesting a generalized crayfish response to fish presence (Nyström, 2005). My results are consistent with previous work showing that predatory fish suppress growth of small more than of large crayfish.

Preferential predation on faster-growing crayfish is also likely because faster growth implies more frequent molts. Molting greatly increases crayfish susceptibility to predation, regardless of size (Stein, 1977), so growth itself may increase predation risk, at least under the experimental conditions. Smallmouth bass (*Micropterus dolomieu*) preyed preferentially on recently-molted crayfish in the laboratory (Stein, 1977). In my experiments, catfish ate some, but not all, recently-molted crayfish. All but the smallest crayfish evidently left the brick shelters during molting, thereby completely exposing themselves to predation. In the wild, molting crayfish may find better shelter than that I provided in the experiments, but I have often collected recently-molted individuals during stream sampling. It appears likely that channel catfish influenced crayfish size structure via both indirect suppression of growth and increased predation on crayfish that grew.

Crayfish habitat use can be influenced by predaceous fishes both via direct (*e.g.*, differential predation among habitats) and indirect (*e.g.*, changes in growth rate) effects. Fish predators influence crayfish habitat use at micro (Stein and Magnuson, 1976; Stein, 1977; Hill and Lodge, 1994; Englund and Krupa, 2000), meso- (Kershner and Lodge, 1995; Usio and Townsend, 2000; Magoulick, 2004) and macro scales (Usio and Townsend, 2000; Roth and Kitchell, 2005), with effects generally being more pronounced for smaller crayfish (Stein and Magnuson, 1976; Magoulick, 2004). Crayfish, especially small ones, tend to avoid simple substrates such as sand in favor of more complex substrates (*e.g.*, cobble) that provide refuge from predation, and the pattern is intensified in the presence of predators (Stein and Magnuson, 1976; Hill and Lodge, 1994; Kershner and Lodge, 1995). The lower predation rate in experiment 2 compared to the pilot experiment indicates that the pea gravel substrate in the latter afforded *O. chickasawae* some survival advantage over bare plastic. The presence and use of the brick shelters provided crayfish with further protection

from channel catfish predation, especially for the smaller species. At a meso-habitat scale, field experiments and surveys indicate that densities of crayfish and smallmouth bass in pools are negatively associated (Mather and Stein, 1993; Magoulick, 2004).

Correlative evidence indicates that experimental results on fish predation scale up well to the macrohabitat scale and that predaceous fishes influence crayfish distributions and densities even at scales of small lakes or stream segments. Seiler and Turner (2004) found that crayfish densities were highest in low pH stream segments where predaceous fish were absent, despite low pH being detrimental to crayfish growth. In at least some circumstances, densities of several *Orconectes* species are higher in intermittent or drought-desiccated streams compared to perennial streams (Flinders and Magoulick, 2003; Adams and Warren, 2005). Patterns in all of these systems are consistent with the hypothesis that fish predation is important in structuring assemblages of native crayfishes.

Differential predation by fish is a likely mechanism explaining the reduced density and abundance of *Orconectes chickasawae* in large, compared to small streams in the region. *Procambarus hayi*, on the other hand, are more common in deeper, lower velocity stream habitats where larger fish predators occur more frequently. *Procambarus hayi* has an advantage in body and chelae size, and possibly in burrowing habits, over *O. chickasawae* in avoiding fish predation. Although size- or species-selective fish predation has not been documented as a mechanism determining habitat selection or distributions of sympatric, co-evolved crayfish species, Rabeni (1985) hypothesized that fish predation contributed to habitat partitioning between two native *Orconectes* species in Missouri. Furthermore, any effect of differential predation on the species may be magnified by a shortage of refuges (Garvey *et al.*, 1994; Hill and Lodge, 1994). Differential predation pressure coupled with anthropogenically simplified habitats may strongly influence the distributions and relative abundances of *P. hayi* and *O. chickasawae* in northern Mississippi streams.

*Acknowledgments.*—Creative engineering and persistence by G. McWhirter enabled completion of the experiments. M. Bland and J. Stone generously shared some of their catfishing secrets. K. Anazia (an American Fisheries Society Hutton Scholar), M. Bland, A. Commens, C. Harwell and G. McWhirter assisted in many aspects of the experiments. T. Dell, A. Commens and anonymous reviewers provided helpful suggestions for the analyses and manuscript. Funding was provided by the USDA Forest Service, Southern Research Station.

#### LITERATURE CITED

- ADAMS, S. B. AND M. L. WARREN, JR. 2005. Recolonization by warmwater fishes and crayfishes after severe drought in upper Coastal Plains streams. *Trans. Am. Fish. Soc.*, 134:1173–1192.
- ENGLUND, G. AND J. J. KRUPA. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshwater Biol.*, 43:75–83.
- FLINDERS, C. A. AND D. D. MAGOULICK. 2003. Effects of stream permanence on crayfish community structure. *Am. Midl. Nat.*, 149:134–147.
- FLOTEMERSCH, J. E. AND D. C. JACKSON. 2003. Seasonal foraging by channel catfish on terrestrially burrowing crayfish in a floodplain-river ecosystem. *Ecohydrol. Hydrobiol.*, 3:61–70.
- GARVEY, J. E., R. A. STEIN AND H. M. THOMAS. 1994. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. *Ecology*, 75:532–547.
- HILL, A. M. AND D. M. LODGE. 1994. Diel changes in resource demand: competition and predation in species replacement among crayfishes. *Ecology*, 75:2118–2126.
- KELLER, T. A. AND P. A. MOORE. 2000. Context-specific behavior: crayfish size influences crayfish-fish interactions. *J. N. Am. Benthol. Soc.*, 19:344–351.
- KERSHNER, M. W. AND D. M. LODGE. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *J. N. Am. Benthol. Soc.*, 14:414–422.

- MAGOULICK, D. D. 2004. Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. *Hydrobiologia*, **527**:209–221.
- MATHER, M. E. AND R. A. STEIN. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading congener. *Can. J. Fish. Aquat. Sci.*, **50**:1279–1288.
- NYSTRÖM, P. 2005. Non-lethal predator effects on the performance of a native and an exotic crayfish species. *Freshwater Biol.*, **50**:1938–1949.
- PAYNE, J. F. 1972. The life history of *Procambarus hayi*. *Am. Midl. Nat.*, **87**:25–35.
- RABENI, C. F. 1985. Resource partitioning by stream-dwelling crayfish: the influence of body size. *Am. Midl. Nat.*, **113**:20–29.
- RIGGERT, C. M., R. J. DISTEFANO AND D. B. NOLTIE. 1999. Distributions and selected aspects of the life histories and habitat associations of the crayfishes *Orconectes peruncus* (Creaser, 1931) and *O. quadruncus* (Creaser, 1933) in Missouri. *Am. Midl. Nat.*, **142**:348–362.
- ROTH, B. M. AND J. F. KITCHELL. 2005. The role of size-selective predation in the displacement of *Orconectes* crayfishes following rusty crayfish invasion. *Crustaceana*, **78**:297–310.
- SEILER, S. M. AND A. M. TURNER. 2004. Growth and population size of crayfish in headwater streams: individual- and higher-level consequences of acidification. *Freshwater Biol.*, **49**:870–881.
- SHIELDS, F. D., JR., S. S. KNIGHT AND C. M. COOPER. 1994. Effects of channel incision on base flow stream habitats and fishes. *Environ. Manag.*, **18**:43–57.
- , ——— AND ———. 1995. Use of the index of biotic integrity to assess physical habitat degradation in warmwater streams. *Hydrobiologia*, **312**:191–208.
- SPSS. 2005. SPSS Base 14.0 User's Guide. SPSS Inc., Chicago, IL.
- STEIN, R. A. 1976. Sexual dimorphism in crayfish chelae: functional significance related to reproductive activities. *Can. J. Zool.*, **54**:220–227.
- . 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology*, **58**:1237–1253.
- AND J. J. MAGNUSON. 1976. Behavioral response of crayfish to a fish predator. *Ecology*, **57**:751–761.
- USIO, N. AND C. R. TOWNSEND. 2000. Distributions of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physico-chemistry, predatory fish, and invertebrate prey. *N. Z. J. Mar. Freshwat. Res.*, **34**:557–567.
- WARREN, M. L., JR., W. R. HAAG AND S. B. ADAMS. 2002. Forest linkages to diversity and abundance in lowland stream fish communities, p. 168–182. *In*: M. M. Holland, M. L. Warren Jr. and J. A. Stanturf (eds.). Proceedings of a conference on sustainability of wetlands and water resources: how well can riverine wetlands continue to support society into the 21st century? USDA For. Serv. Gen. Tech. Rept. SRS-50. Asheville, North Carolina.