

## Effects of depth and crayfish size on predation risk and foraging profitability of a lotic crayfish

C. A. Flinders<sup>1</sup>

Patrick Center for Environmental Research, Academy of Natural Sciences, 1900 Benjamin Franklin Parkway,  
Philadelphia, Pennsylvania 19103 USA

D. D. Magoulick<sup>2</sup>

US Geological Survey, Arkansas Cooperative Fish and Wildlife Research Unit, Department of Biological  
Sciences, University of Arkansas, Fayetteville, Arkansas 72701 USA

**Abstract.** We conducted field surveys and experiments to determine whether observed distributions of crayfish among habitats were influenced by differential resource availability, foraging profitability, and predation rates and whether these factors differed with crayfish size and habitat depth. We sampled available food resources (detritus and invertebrates) and shelter as rock substrate in deep (>50 cm) and shallow (<30 cm) habitats. We used an enclosure–enclosure experiment to examine the effects of water depth and crayfish size on crayfish biomass and survival, and to determine whether these factors affected silt accrual, algal abundance (chlorophyll *a* [chl *a*]), and detritus and invertebrate biomass (g ash-free dry mass) differently from enclosures without crayfish. We conducted tethering experiments to assess predation on small (13–17 mm carapace length [CL]) and large (23–30 mm CL) *Orconectes marchandi* and to determine whether predation rates differed with water depth. Invertebrate biomass was significantly greater in shallow water than in deep water, whereas detritus biomass did not differ significantly between depths. Cobble was significantly more abundant in shallow than in deep water. Depth and crayfish size had a significant interactive effect on change in size of enclosed crayfish when CL was used as a measure of size but not when biomass was used as a measure of size. CL of small crayfish increased significantly more in enclosures in shallow than in deep water, but CL of large crayfish changed very little at either depth. Silt, chl *a*, and detritus biomass were significantly lower on tiles in large- than in small- and no-crayfish enclosures, and invertebrate biomass was significantly lower in large- than in no-crayfish enclosures. Significantly more crayfish were consumed in deep than in shallow water regardless of crayfish size. Our results suggest that predation and resource availability might influence the depth distribution of small and large crayfish. Small crayfish grew faster in shallow habitats where they might have had a fitness advantage caused by high prey availability and reduced predation risk. Size-dependent reduction of silt by crayfish might influence benthic habitats where large crayfish are abundant.

**Key words:** field experiment, *Orconectes marchandi*, growth, resource availability.

Optimal foraging theory predicts that in a patchy environment where the relative abundance of food varies between patches, foragers should occupy patches or habitats where the net rate of energy intake is greatest (MacArthur and Pianka 1966). However, risk of predation often results in selection of habitats

that offer diminished foraging yields but greater protection from predators (Sih 1982, Werner et al. 1983, Holbrook and Schmitt 1988, Pettersson and Brönmark 1993, Turner 1997, McIntosh et al. 2004). Prey must make appropriate decisions between mortality risk and energy gain to maximize fitness when a trade-off exists between resource abundance or quality and prey survival.

Choice of habitat by prey under predation risk can be influenced by prey size (Werner et al. 1983, Schlosser 1987, Utne and Aksnes 1994, Magoulick 2004) and is often complicated by the presence of

<sup>1</sup> Present address: National Council for Air and Stream Improvement, Inc., P.O. Box 1259, Anacortes, Washington 98221 USA. E-mail: cflinders@ncasi.org

<sup>2</sup> To whom correspondence should be addressed. E-mail: danmag@uark.edu

multiple predator types (Power 1987, Scrimgeour et al. 1994). However, if the presence of one predator modifies the behavior of another, predation risk for the prey species might be diminished. For example, in many fish communities, interference between 2 potential predators can drive small fish into shallower habitats. Large fish are susceptible to predation by wading birds and mammals and, therefore, use deep habitats as a predator-avoidance mechanism. Small fish, on the other hand, are less susceptible to terrestrial predators and use shallow areas to avoid predation by large fish (Power 1987, Schlosser 1987).

Similar patterns of size-dependent habitat use have been observed in crayfish communities (Rabeni 1985, Creed 1994, Flinders 2000, DiStefano et al. 2003, Flinders and Magoulick 2003, 2007), and it appears that these patterns also are predation-driven. Crayfish are important prey items to aquatic predators, such as largemouth bass (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*) (Rabeni 1992, Garvey et al. 1994), and terrestrial predators, including wading birds, mink (*Mustela vison*), and raccoon (*Procyon lotor*) (Ruiz-Olmo et al. 2002, Figueroa and Stappung 2003). Englund and Krupa (2000) examined size-dependent predation rates using a tethering experiment and showed that small crayfish (25–30 mm total length [TL]) were readily preyed upon by fish in deep habitats (40–70 cm) and by terrestrial predators in shallow habitats (5–15 cm). In contrast, large crayfish (50–75 mm TL) experienced little mortality caused by fish but were heavily preyed upon by terrestrial predators in shallow habitats. When fish predators were absent, small crayfish were distributed across a depth gradient, whereas large crayfish remained in deep habitats.

Crayfish species seek and actively compete for substrate shelters (Garvey et al. 1994) and are opportunistic omnivores (Huryn and Wallace 1987, Lodge and Lorman 1987, Chambers et al. 1990, Hart 1992, Creed 1994, Lodge et al. 1994, Charlebois and Lamberti 1996). If shelter and food differ with stream depth, then stream depth should influence crayfish habitat selection. In freshwater systems, the trade-off between foraging profitability and reduced predation risk ultimately affects fitness (Peckarsky et al. 1993, Lewis 2001). However, small crayfish using shallow habitats might gain a fitness advantage from simultaneous reduction of predation risk and increased energy gain if prey resources were more abundant in shallow habitats and fish were the main predation risk.

The distribution of crayfish density in the Warm Fork River in the Ozark Mountains is related to stream depth in a size-dependent manner. Small crayfish (<17 mm carapace length [CL]) disproportionately select

shallow habitats relative to their availability, and large crayfish (>23 mm CL) select habitats across a greater range of depths (Flinders 2000, Flinders and Magoulick 2007). The purpose of our present study was to examine the influence of resource availability, foraging profitability, and predation on these size-dependent depth distribution patterns. We conducted field surveys and experiments to answer 4 main questions: 1) Do food (invertebrates and detritus) and shelter (substrate) differ with habitat depth? 2) Is foraging profitability (measured by changes in crayfish mass and CL) affected by water depth and crayfish size? 3) Do rates of predation on crayfish differ with respect to crayfish size and stream depth? 4) Do the effects of crayfish on benthic invertebrate and algal biomass depend on crayfish size and stream depth?

### Study site

We conducted our study in the Warm Fork River in south-central Missouri (lat 36°32'00"N, long 91°32'00"W) in the Salem Plateau physiographic region of the Ozark Plateaus. The geology and soils in this region are Ordovician and diverse, and consist predominantly of medium-textured, rapidly permeable dolomites, cherts, and limestone, which create a karst topography (Adamski et al. 1995). The Warm Fork River drains 684 km<sup>2</sup> in Oregon County, Missouri, before entering the Spring River at the Arkansas–Missouri border. The Warm Fork River is fed by numerous springs and spring seeps. In the headwaters of the watershed, it is a losing stream flowing above and below ground primarily through pastureland and oak–hickory (*Quercus* and *Carya* spp.) forest. At the study site, water is turbid (14–32 NTU) and relatively warm (18–24°C), with a well-defined canopy cover and riparian area (~10 m). The 400-m-long study site has a 35-cm mean depth and a 14-m mean wetted width and flows over coarse gravel (0.1–3 cm), pebble (3–6 cm), cobble (6–24 cm), boulder (≥25 cm), and some bedrock.

We did field sampling and experiments in a deep pool and adjacent shallow stream-margin habitat during a period of rapid crayfish growth (5 July–21 August 1999). The deep habitat was 50 to 70 cm deep and had a mean current velocity (measured at 0.6 × depth) of  $9.2 \pm 0.56$  (SE) cm/s. The shallow habitat ranged from 15 to 30 cm deep and had a mean velocity of  $4.4 \pm 0.41$  cm/s. Substrate in both habitats was predominantly pebble, gravel, and sand (0.02–0.1 cm) with some cobble. In both habitats, substrate was covered with a fine layer of silt and canopy cover was open. Snorkeling surveys at the study site showed that potential fish predators included shadow bass (*Am-*

*bloplites ariommus*), sunfish (*Lepomis* spp.), and small-mouth bass. Observed terrestrial predators included mink, raccoon, green heron (*Butorides striatus*), and great blue heron (*Ardea herodias*). River otter (*Lontra canadensis*) also might have been present, but were not observed.

Four species of crayfish, *Orconectes marchandi*, *Orconectes ozarkae*, *Orconectes punctimanus*, and *Cambarus hubbsi*, were present at the site, but only *Orconectes* species were common in the habitats studied (Flinders 2000). Density of small crayfish (13–17 mm CL) was greater in shallow stream-margin habitats ( $9.68 \pm 1.36$  ind./m<sup>2</sup>) than in deep pool habitats ( $3.6 \pm 0.56$  ind./m<sup>2</sup>). Density of large crayfish (23–30 mm CL) was  $\sim 2\times$  greater in deep habitats ( $4.78 \pm 0.62$  ind./m<sup>2</sup>) than in shallow habitats ( $2.32 \pm 0.38$  ind./m<sup>2</sup>) at the study site, and reflected patterns seen at other sites in the watershed (Flinders 2000, Flinders and Magoulick 2007). Distribution data were based on daytime measurements, and patterns might differ at night. We used *O. marchandi* in all experiments because of its abundance at the study site and other intensively sampled locations in the watershed, and because of its status as a species of special concern (S1/S2, G2; Taylor et al. 1996, Missouri Natural Heritage Program 2006).

## Methods

### Field methods

**Resource availability.**—On 5 July 1999, we collected 22 Hess samples (0.08 m<sup>2</sup>) at randomly selected locations in shallow (mean depth  $\pm$  SE,  $20.2 \pm 0.9$  cm) and deep ( $57.0 \pm 1.1$  cm) habitats to determine the relative abundances of detritus and invertebrates (food) and substrate size classes (shelter). We collected Hess samples in the same areas from which habitat-selection data were collected (Flinders 2000, Flinders and Magoulick 2007) and within 30 m of tethering and enclosure–enclosure experiments. We set the sampler and measured depth and mean current velocity ( $0.6 \times$  depth) 10 cm in front of the sampler and recorded % cover of sand, gravel, pebble, and cobble within the sampler. We selected alternative sampling locations twice because we encountered large boulders ( $\geq 30$  cm diameter) that did not fit in the Hess sampler. We collected invertebrates and detritus by thoroughly disturbing the substrate within the sampler and regularly sweeping the water and suspended material toward the collecting net (mesh size: 363  $\mu$ m). We placed all contents of the collecting net into a large Whirl-Pak<sup>®</sup> bag (Nasco, Fort Atkinson, Wisconsin) and preserved the sample with 70% ethanol.

**Foraging profitability and benthic response.**—We used an enclosure–enclosure experiment to examine the

effect of water depth (shallow and deep) and crayfish size (large: 23–30 mm CL, small: 13–17 mm CL) on crayfish foraging profitability. We used the same experiment to evaluate the effect of water depth and crayfish size on invertebrate and algal biomass by comparing results from enclosures with crayfish to results from enclosures without crayfish. We expected small crayfish to have faster growth rates and greater molting frequencies than large crayfish. Nevertheless, our decision to use crayfish growth as a response variable was appropriate because adult crayfish grow and molt in summer in Ozark streams, and they require adequate resources to maintain mass (Reynolds 2002). For example, adult *Orconectes neglectus chaenodactylus* in a north-central Arkansas stream molted twice during summer, in addition to the usual molts in spring and fall (Price and Payne 1978). In a Missouri Ozark stream, 5 to 35% of adult *Orconectes peruncus* and 5 to 15% of adult *Orconectes quadruncus* collected in July and August had molted recently (Riggert et al. 1999).

We constructed 54 enclosures of acrylic plastic (40 cm long  $\times$  20 cm wide  $\times$  15 cm high) with polyethylene screen (mesh size: 6 mm) at the upstream and downstream ends. We chose this enclosure area to ensure that replicates fit within the study habitats. We set enclosures in a randomized block design to identify within-habitat spatial variation. Each block consisted of 3 enclosures bound together with wire, and we assigned treatments (single large crayfish, single small crayfish, and no crayfish) randomly to enclosures within blocks using a random number table. We placed 9 replicate enclosures of each treatment in shallow stream-margin habitat (mean depth =  $20.0 \pm 2.54$  cm) and 9 enclosures in deep pool habitat (mean depth =  $60.8 \pm 2.55$  cm) in a staggered configuration to minimize the effects of impeding stream flow on downstream enclosures.

Each enclosure contained 4 unglazed paving tiles (9 cm  $\times$  18 cm  $\times$  0.75 cm) that we had set on the streambed near the experimental site for 30 d before the experiment began to allow organisms to colonize the tiles. We transferred the colonized tiles to the enclosures at the beginning of the experiment. We did not add any other substrate to the enclosures. On days 10 (20 July), 20 (30 July), 30 (10 August), and 40 (21 August), we removed a single paving tile from each enclosure, placed it in a resealable plastic bag, and froze it. Sampling of the tiles was destructive (i.e., material on tile was removed for analysis). Therefore, we replaced sampled tiles with colonized tiles. We sampled tiles from corresponding locations in all enclosures on a given sampling date.

We collected large and small *O. marchandi* from



nearby habitats, measured CL (to the nearest 0.1 mm) and blotted wet mass (to the nearest 0.1 g), and placed individuals in randomly assigned enclosures on 9 July 1999 (day 0) through an opening in the screen. We used only males in the experiment because crayfish have sex-specific feeding and growth rates (Grandjean et al. 1997, Streissl and Hoedl 2002). Crayfish density in enclosures was higher ( $12.5 \text{ ind./m}^2$ ) than ambient densities for our size classes in both shallow (small:  $9.68 \pm 1.36$ , large:  $2.32 \pm 0.38 \text{ ind./m}^2$ ) and deep habitats (small:  $3.6 \pm 0.56 \text{ ind./m}^2$ , large:  $4.78 \pm 0.62 \text{ ind./m}^2$ ), but lower than the overall crayfish density in shallow areas ( $34.5 \pm 6.73 \text{ ind./m}^2$ ). Crayfish can move within a 10- to 60-m<sup>2</sup> area of streambed and can migrate as far as 417 m along a stream reach, but the tendency to stay in one area, often under the same substrate cover, is more typical (Merkle 1969, Bubb et al. 2004). We used a mask and snorkel to examine the enclosed crayfish frequently during the experiment, and crayfish usually were foraging or crouched along the side of the enclosure. At the end of the experiment (day 40; 21 August), we removed crayfish from the enclosures and measured final blotted wet mass and CL before releasing them at the study site.

**Predation risk.**—We conducted tethering experiments from 5 to 7 August 1999 and 17 to 19 August 1999 to assess effects of stream depth and crayfish size on rates of predation on crayfish. In each experiment, we placed 20 small and 20 large crayfish in shallow ( $20.0 \pm 1.0 \text{ cm}$ ) and deep ( $44.2 \pm 0.7 \text{ cm}$ ) habitats. We used only male crayfish because of potential sex-dependent differences in predation risk (Stein 1977, Garvey and Stein 1993). We used acrylamide gel to glue 6-lb-test monofilament fishing line to the dorsal portion of the carapace of each crayfish. We anchored the free end of the tether to a rock and adjusted the monofilament line so that each crayfish could move freely within an area of 30-cm radius around the rock. The tether did not impede crayfish from seeking shelter under available substrates within its range of mobility. In preliminary tests of the tethering technique, no crayfish escaped because of failure of adhesive or by cutting the monofilament. Therefore, we assumed that missing crayfish had been eaten or removed by predators.

We set up the experimental area in each habitat in a checkerboard pattern with grid points 1 m apart. We marked only the outside perimeter of the grid because marking locations of individual crayfish might have attracted predators. We randomly selected crayfish size classes for placement at grid points in each habitat. The number and size of crayfish missing from their tethered locations in each habitat were recorded daily for 2 d during both experiments.

### *Laboratory methods*

**Resource availability.**—We sorted invertebrates and detritus (coarse particulate organic matter [CPOM], >1 mm) collected in Hess samples in a white enamel pan under a magnifying lamp (10 $\times$ ). We placed invertebrates and detritus into separate, preweighed crucibles and dried the samples at 105°C for 24 h. We recorded the dry mass of each sample, combusted the crucibles and samples at 550°C for 3 h, and reweighed each sample to determine ash-free dry mass (AFDM).

**Foraging profitability and benthic response.**—We thawed tiles at 4°C and removed invertebrates with forceps. We rinsed the remaining material with deionized water into large graduated cylinders. We allowed samples to settle in the dark at 4°C for 14 to 16 h and withdrew excess water to leave only a thick slurry of silt. We recorded the total volume of silt and then homogenized the sample by gently stirring the thick slurry with a glass rod. We removed two 1-mL subsamples for analysis of chlorophyll *a* (chl *a*) and to determine dry mass and AFDM. We filtered the remaining silt through a 355- $\mu\text{m}$  sieve to separate any remaining invertebrates. Invertebrate AFDM was determined in the same manner as Hess sample benthic invertebrates. The number of invertebrates in the silt was low for all samples.

We extracted chl *a* from 1 mL of silt in a known volume of acetone in the dark for 24 h at 4°C. We analyzed chl *a* using a Beckman DU 640B spectrophotometer (Beckman Coulter, Fullerton, California). We determined total chl *a* associated with each tile by multiplying the chl *a*/mL silt by the total volume of silt in the sample. We measured AFDM of silt in the second 1-mL subsample in the same manner as described previously for other samples.

### *Statistical analysis*

We used multivariate analysis of variance (MANOVA) to identify differences in invertebrate and detritus biomass and % cover of substrate size classes between habitat depths. Bedrock was rare in both habitats, and we excluded % cover of this substrate size class from the analysis. We transformed biomass data ( $\ln[x + 1]$ ) and % cover of cobble, pebble, gravel, and sand ( $\sqrt{[x + 1]}$ ) before analyses to meet MANOVA assumptions. We used analysis of variance (ANOVA) to examine the significance of individual response variables following a significant MANOVA.

We used a 2-factor MANOVA to analyze the effect of habitat depth and crayfish size on crayfish growth (CL and wet mass). We used  $\sin(x)$  to transform crayfish CL. This transformation is unusual but resulted in the best fit of the data to meet MANOVA assumptions.

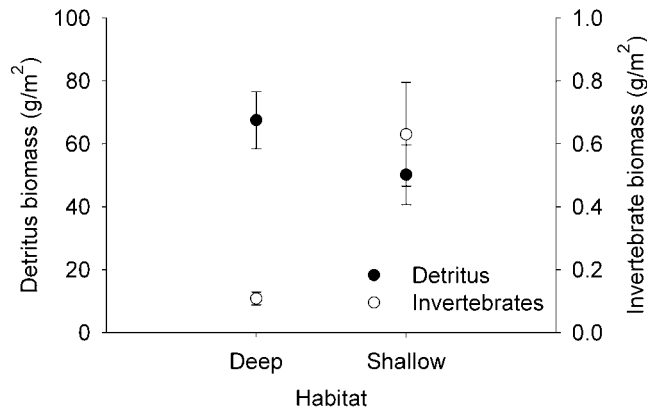


FIG. 1. Mean (+1 SE) biomass of detritus and invertebrates in shallow and deep habitat.

Crayfish wet mass did not require transformation. We used repeated-measures (RM) ANOVA (with randomized blocks) to examine effects of habitat depth, crayfish size, and time period on each benthic response variable (silt dry mass, chl *a* concentration, detritus biomass, and invertebrate biomass) on tiles in enclosures. We transformed all 4 response variables ( $\ln[x + 1]$ ) prior to analyses to meet RM ANOVA assumptions. The block effect was not significant in any multifactor RM ANOVA, so we removed this variable from models in further analyses (Sokal and Rohlf 1995). When significant interactions occurred, we used ANOVA and pairwise comparisons to examine main effects.

We used 2-factor contingency tables and  $\chi^2$  tests to examine the effect of crayfish size and habitat depth on the number of crayfish consumed during each predation-risk experiment. If the main effects were independent, then we examined each main effect with a 1-factor table and  $\chi^2$  test. We used number of crayfish consumed after 1 d as the response variable because most crayfish were consumed within 1 d. With the exception of Bonferroni-corrected pairwise comparisons, we determined significance at  $p < 0.05$  for statistical tests. SYSTAT (version 9.0; SPSS, Chicago, Illinois) was used for all statistical analyses.

## Results

### Resource availability

Food and substrate composition differed significantly between shallow and deep habitats (MANOVA:  $F_{6,34} = 5.86$ ,  $p < 0.001$ ; Fig. 1). Invertebrate biomass was significantly greater in shallow than in deep habitat ( $F = 38.02$ ,  $p < 0.001$ ). In contrast, detritus biomass did not differ significantly between depths ( $F = 3.24$ ,  $p = 0.080$ ). Percent cover of cobble was

significantly greater in shallow than in deep habitat ( $F = 6.37$ ,  $p = 0.016$ ). Percent cover of pebble, gravel, and sand did not differ between habitat depths (Fig. 2).

### Foraging profitability and benthic response

Habitat depth and crayfish size class produced a significant interactive effect on crayfish growth measured as change in CL, but not on crayfish growth measured as change in wet mass (MANOVA:  $F_{2,31} = 4.67$ ,  $p = 0.017$ ; Fig. 3A, B). Small crayfish grew significantly larger (mm CL) in shallow than in deep water ( $F = 13.87$ ,  $p = 0.001$ ; Fig. 3A), whereas growth of large crayfish did not differ significantly between habitats ( $F = 1.44$ ,  $p = 0.29$ ; Fig. 3A). Crayfish wet mass did not change significantly over the 40-d experiment for either size class of crayfish regardless of habitat depth (Fig. 3B).

Effect of habitat depth, crayfish size, and time depended on the response variable examined (Table 1). The time  $\times$  depth  $\times$  crayfish size and time  $\times$  block interaction effects were not significant for any of the response variables examined. However, the time  $\times$  depth interaction effect was significant for silt dry mass, chl *a* concentration, and detritus and invertebrate biomass. Time  $\times$  depth interaction effects were similar for silt dry mass, chl *a* concentration, and detritus biomass—concentrations were higher in the deep than in the shallow habitat (Fig. 4A–C). Silt dry mass, chl *a* concentration, and invertebrate biomass differed among sampling dates in both depths (Fig. 4A, B, D), and detritus biomass (Fig. 4C) differed among sampling dates in deep habitat (Table 1). In the shallow habitat, silt dry mass was significantly greater on day 20 than on days 30 and 40 (RM ANOVA pairwise comparisons:  $p < 0.028$ ; Fig. 4A), and chl *a* concentration was significantly lower on day 40 than on days 20 and 30 (RM ANOVA pairwise comparisons:  $p < 0.03$ ; Fig. 4B). In the deep habitat, silt dry mass was significantly greater on day 20 than on all other sampling dates and significantly lower on day 10 than on days 30 and 40 (RM ANOVA pairwise comparisons:  $p < 0.027$ ; Fig. 4A). Chl *a* concentration was significantly greater on day 20 than on other days (RM ANOVA pairwise comparisons:  $p < 0.0001$ ; Fig. 4B) and detritus biomass was significantly greater on day 20 than on day 10 (RM ANOVA pairwise comparisons:  $p < 0.001$ ; Fig. 4C). Invertebrate biomass was greater and more variable in the shallow than in the deep habitat on day 10 but was lower in the shallow than in the deep habitat during the remainder of the experiment (Fig. 4D). In shallow habitat, invertebrate biomass was significantly lower on day 30 than on all other days (RM ANOVA pairwise

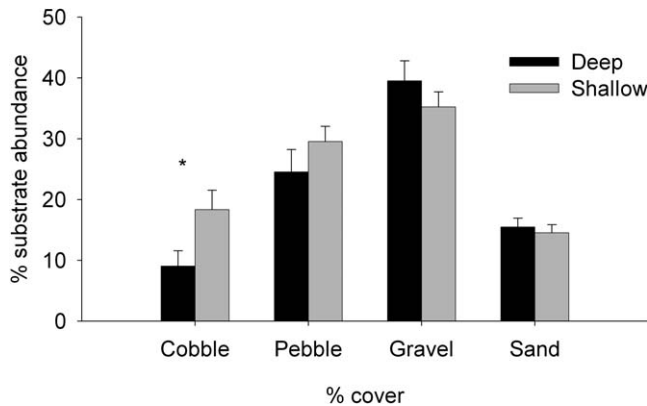


FIG. 2. Mean ( $\pm 1$  SE) % cover of substrate size classes in shallow and deep habitat. \* indicates significant difference between depths within a substrate size class.

comparisons:  $p \leq 0.009$ ). In deep habitat, invertebrate biomass was significantly lower on day 10 than on all other days (RM ANOVA pairwise comparisons:  $p < 0.001$ ).

The time  $\times$  crayfish size interaction effect was significant for silt dry mass, chl *a* concentration, and detritus biomass (Table 1, Fig. 5A–C). Silt dry mass, chl *a* concentration, and detritus biomass were significantly lower in the large-crayfish treatment than in the small- and no-crayfish treatments (RM ANOVA Pillai trace:  $p \leq 0.027$ ), but did not differ between small- and no-crayfish treatments (RM ANOVA Pillai trace:  $p > 0.257$ ). Invertebrate biomass was significantly lower in the large-crayfish treatment than in the no-crayfish treatment (RM ANOVA Pillai trace:  $p = 0.005$ ; Fig. 5D), but did not differ between the small- and no-crayfish treatments (RM ANOVA Pillai trace:  $p = 0.526$ ) or between the small- and large-crayfish treatments (RM ANOVA Pillai trace:  $p = 0.133$ ).

Silt dry mass and chl *a* concentrations varied over time in the no-crayfish and large-crayfish treatments (Fig. 5A, B). In the no-crayfish treatment, silt dry mass and chl *a* concentrations were significantly lower on day 10 than during the remainder of the experiment (RM ANOVA pairwise comparisons:  $p < 0.001$ ). In the large-crayfish treatment, silt dry mass and chl *a* concentrations were greater on day 20 than on other days, and they were lower in the 2<sup>nd</sup> half of the experiment than on day 10 (RM ANOVA pairwise comparisons:  $p < 0.020$ ).

Detritus biomass varied over time in all crayfish treatments (Fig. 5C). In the large-crayfish treatment, detritus biomass differed on day 20 from all other days (RM ANOVA pairwise comparisons:  $p \leq 0.034$ ). In the small-crayfish treatment, detritus biomass was lower on day 10 than on days 20 and 30 (RM ANOVA pairwise comparisons:  $p \leq 0.014$ ). In the no-crayfish

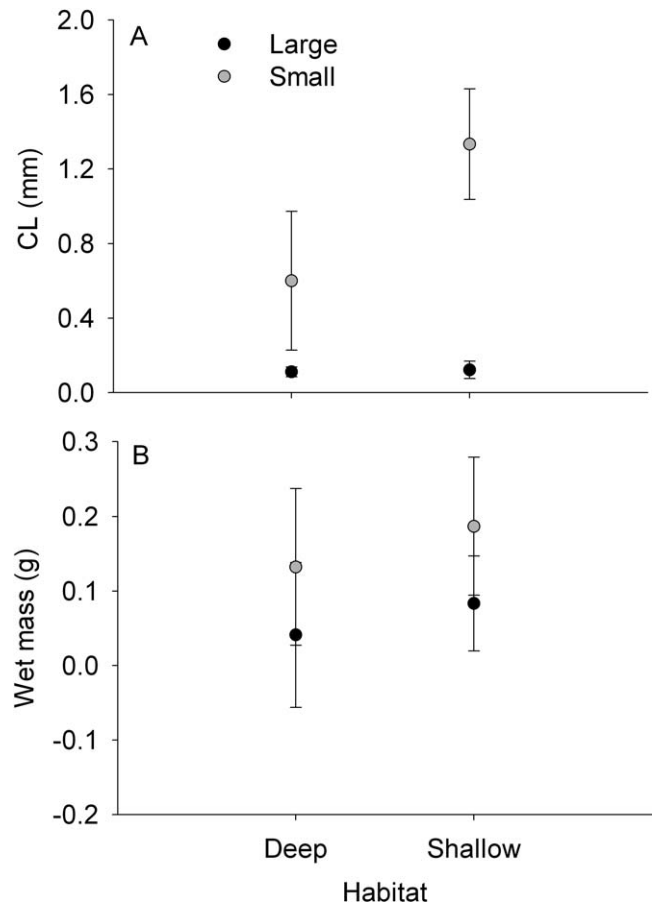


FIG. 3. Mean ( $\pm 1$  SE) change in crayfish carapace length (CL) (A) and wet mass (B) with respect to habitat depth for small and large crayfish.

treatment, detritus biomass was lower on day 10 than on all other days (RM ANOVA pairwise comparisons:  $p \leq 0.014$ ).

Invertebrate biomass varied over time in the large- and small-crayfish treatments (Fig. 5D). In the large-crayfish treatment, invertebrate biomass was greater on day 20 than on all other days (RM ANOVA pairwise comparisons:  $p \leq 0.011$ ), and in the small-crayfish treatment, invertebrate biomass was greater on day 40 than on day 30 (RM ANOVA pairwise comparisons  $p \leq 0.009$ ).

#### Predation risk

The crayfish size  $\times$  habitat depth interaction effect was not significant in either experiment (Table 2). Predation rates on crayfish were significantly greater in deep than in shallow habitats in both experiments regardless of crayfish size (Table 2, Fig. 6A, B). The number of crayfish consumed per day did not differ between crayfish size classes (Table 2, Fig. 6A, B).

TABLE 1. Summary of results from enclosure experiments in the Warm Fork River, Missouri, with crayfish size and depth as main effects and time as the repeated variable in a repeated-measures analysis of variance. Main-effect variables are examined in terms of time. AFDM = ash-free dry mass.

Source	df	Statistic	Response			
			Silt (g dry mass/m <sup>2</sup> )	Chlorophyll <i>a</i> (mg/m <sup>2</sup> )	Detritus biomass (g AFDM/m <sup>2</sup> )	Invertebrate biomass (g AFDM/m <sup>2</sup> )
Time × depth × crayfish size	6, 78	<i>F</i>	1.17	2.16	1.29	0.91
		<i>p</i>	0.330	0.056	0.272	0.495
Time × crayfish size	6, 78	<i>F</i>	5.75	4.41	3.57	2.16
		<i>p</i>	<0.001	0.001	0.004	0.058
Time × depth	3, 38	<i>F</i>	12.38	21.66	8.39	8.18
		<i>p</i>	<0.001	<0.001	<0.001	<0.001
Time × block	24, 120	<i>F</i>	1.22	1.24	1.25	0.70
		<i>p</i>	0.243	0.223	0.218	0.839
Depth						
Shallow	3, 24	<i>F</i>	4.17	3.52	2.92	4.48
		<i>p</i>	0.016	0.030	0.054	0.015
Deep	3, 24	<i>F</i>	110.10	47.65	44.17	32.88
		<i>p</i>	<0.001	<0.001	<0.001	<0.001
Crayfish size						
Large	3, 15	<i>F</i>	9.60	14.34	15.00	7.33
		<i>p</i>	0.001	<0.001	<0.001	0.003
Small	3, 15	<i>F</i>	2.99	2.50	4.84	3.58
		<i>p</i>	0.064	0.099	0.015	0.044
None	3, 15	<i>F</i>	21.55	9.94	16.57	0.75
		<i>p</i>	<0.001	0.001	<0.001	0.546

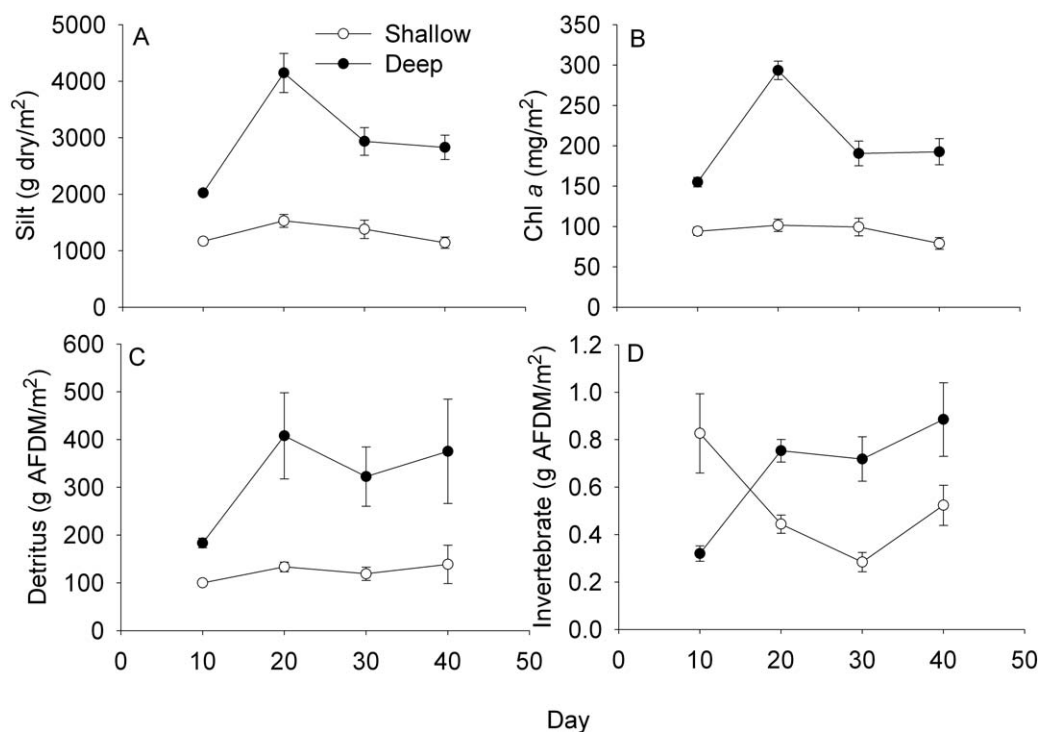


FIG. 4. Mean ( $\pm 1$  SE) silt dry mass (A), chlorophyll *a* (chl *a*) concentration (B), detritus biomass (C), and invertebrate biomass (D) over time with respect to shallow- and deep-water treatments in the enclosure experiment. AFDM = ash-free dry mass.



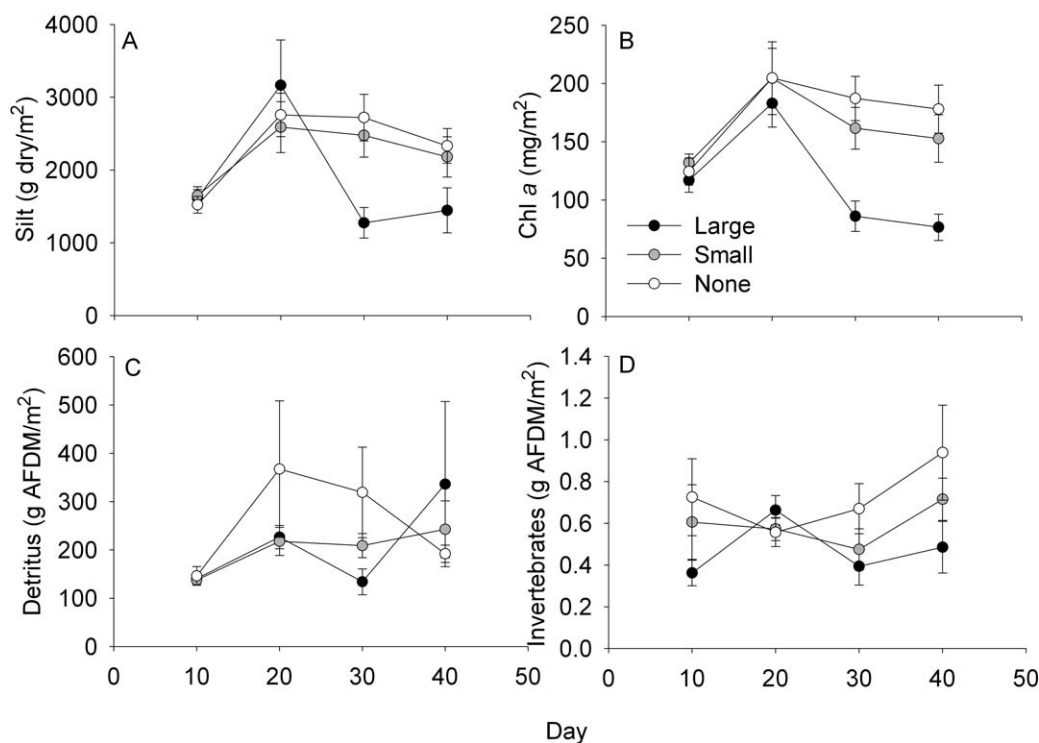


FIG. 5. Mean ( $\pm 1$  SE) silt dry mass (A), chlorophyll *a* (chl *a*) concentration (B), detritus biomass (C), and invertebrate biomass (D) over time with respect to crayfish size treatments in the enclosure experiment. AFDM = ash-free dry mass.

### Discussion

Size-dependent habitat selection by crayfish might be driven by predator avoidance behavior, availability or quality of resources (e.g., food or shelter), or a combination of both. Our results suggest that both predation risk and resource availability influenced the use of habitat by small crayfish. Cobble substrates and benthic invertebrate biomass were significantly greater in habitat <30 cm deep than in habitat >50 cm deep, whereas % cover of other substrates and detritus biomass did not differ significantly between depths. We also found that foraging profitability, as measured by crayfish growth, was greater for small crayfish in shallow than in deep habitats. Last, patterns of predation risk showed that crayfish were more

vulnerable to predation in deep than in shallow habitats regardless of crayfish size.

#### Resource availability and foraging profitability

The effects of crayfish on physical (silt accumulation) and biological (chl *a* concentration, invertebrate biomass) benthic structure were dependent on crayfish size in both deep and shallow habitats. Silt dry mass and chl *a* concentrations were lower in enclosures with large crayfish than in enclosures with small or no crayfish, and invertebrate biomass was lower in enclosures with large crayfish than in enclosures with no crayfish. These findings corroborate results of many other studies (e.g., Creed 1994, Usio and Townsend 2004, Helms and Creed 2005), although Charlebois and Lamberti (1996) reported no effect and Stenroth and Nyström (2003) reported a positive effect of crayfish on algal chl *a*. In our study, the reduction of chl *a* and invertebrates by large crayfish probably were consequences of silt reduction and crayfish predation, respectively. We were surprised that silt dry mass, chl *a*, and invertebrate biomass were not affected by the presence of small crayfish in either habitat. However, natural densities of small crayfish in shallow habitats were  $\sim 3\times$  densities in the enclosures, so effects of small crayfish on invertebrates in natural habitats might have been underestimated.

TABLE 2.  $\chi^2$  results for predation experiments examining the effects of habitat depth and crayfish size on number of *Orconectes marchandi* consumed after 1 d of tethering in the Warm Fork River, Missouri.

Source	df	Experiment 1		Experiment 2	
		$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
Depth $\times$ size	1	1.73	0.188	0.88	0.348
Depth	1	6.15	0.013	14.23	<0.001
Size	1	1.72	0.189	1.58	0.209



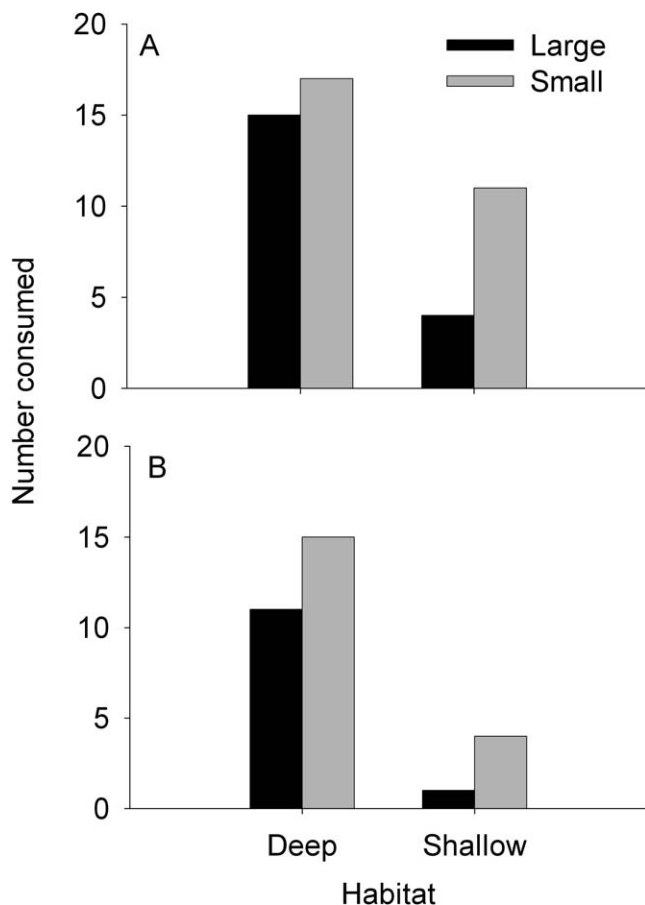


FIG. 6. Number of crayfish consumed after 1 d with respect to habitat depth (shallow and deep) and crayfish size (large and small) in tethering experiments 1 (A) and 2 (B).

Crayfish are omnivores and consume mainly plant detritus in forested streams (Whitledge and Rabeni 1997, Parkyn et al. 2001, Bondar et al. 2005). However, assimilation efficiency and stable-isotope analyses indicate that crayfish, especially small ones, convert a disproportionate amount of animal matter to biomass (Whitledge and Rabeni 1997, Bondar et al. 2005). Similar patterns have been observed in the Spring River watershed, where crayfish consume mainly detritus, but most of the energy incorporated into biomass is derived from aquatic insects and filamentous green algae (DDM and G. Piercey, Memorial University of Newfoundland, unpublished data). Thus, crayfish often rely largely on detritus and biofilms as food sources, even though crayfish growth would be more rapid on a diet of animal protein (Gherardi et al. 2004, Bondar et al. 2005).

Invertebrate biomass did not differ between small- and no-crayfish enclosures, a result that suggests that small crayfish had little effect on invertebrate food resources. Nevertheless, small crayfish grew faster in

enclosures in shallow than in deep habitat. This result, coupled with the greater ambient invertebrate biomass in shallow habitats, suggests that small crayfish might have a selective advantage in shallow habitat because shallow habitat provides more invertebrate food resources.

In contrast, large crayfish did not grow during the 40-d experiment or show any differential benefits from differences in food resources between habitats. Invertebrate biomass was much lower in enclosures with large crayfish than in enclosures with small or no crayfish, a result that suggests large crayfish consumed the invertebrates in the enclosures. Other studies have shown that large crayfish consume more detritus than other food sources, such as invertebrates or algae (Whitledge and Rabeni 1997, Parkyn et al. 2001, but see Bondar et al. 2005), even though greater growth rates are expected when they consume animal matter (Gherardi et al. 2004, Bondar et al. 2005). In our study, fine particulate organic matter (FPOM) was seen in enclosures, but the mesh excluded larger CPOM. Thus, an important component of the typical diet of large crayfish might have been missing from the enclosures. Consumption of invertebrates might have compensated for the absence of other food sources, but the fact that large crayfish did not molt or increase in biomass might indicate that the resource base in enclosures was inadequate to support growth of large crayfish. Alternatively, the duration of the experiment might have been too short for us to observe significant changes.

#### *Resource availability and predation risk*

Crayfish often choose habitat that offers an increased level of complexity (e.g., submerged or emergent vegetation) over simpler habitat regardless of underlying substrate (Hill and Lodge 1994, Jordan et al. 1996, Flinders 2000, Flinders and Magoulick 2007). Some crayfish species actively seek and compete for larger substrates (i.e., pebble and cobble) over fine-grained substrates (e.g., sand) (Hill and Lodge 1994, Bergman and Moore 2003). In our study, more cobble was available in shallow habitat than in deep habitat, and availability of cobble might have contributed to the disproportionate use of shallow areas by small crayfish observed at some sites in our previous work (Flinders and Magoulick 2007). Larger substrates can offer reduced predation risk over small substrates, especially for smaller size classes (Garvey et al. 1994, Kershner and Lodge 1995), and larger substrates support biofilms, macroinvertebrates, and other food sources.

More crayfish were consumed in deep than in shallow habitat regardless of crayfish size. This result

does not fit the hypothesized pattern that small crayfish are at a greater risk of predation in deep water and large crayfish are at greater predation risk in shallow water (Englund and Krupa 2000). One possible reason for this discrepancy might be the type of deep-water predators in the Warm Fork River. Englund and Krupa (2000) worked in a Kentucky stream where the major predatory fishes were green sunfish (*Lepomis cyanellus*) and creek chub (*Semotilus atromaculatus*). These species are capable of consuming small crayfish but not medium or large crayfish (Englund and Krupa 2000). The major fish predators in the Warm Fork River are smallmouth bass, shadow bass, and sunfish. Shadow bass and smallmouth bass are important predators on crayfish in Ozark streams (Rabeni 1992, DiStefano et al. 2003). Smallmouth bass and rock bass (*Ambloplites rupestris*), a close relative of shadow bass, can consume medium-sized crayfish (11–22 mm CL; CL calculated from TL based on Rabeni 1985), and smallmouth bass can consume large crayfish >25 mm CL (Probst et al. 1984). Our large-crayfish size class (23–31 mm CL) was smaller than the large-crayfish size class used by Englund and Krupa (2000) (~24–36 mm CL), so high predation rates on large crayfish in deep water in our study might not be surprising. Moreover, mink were present in Warm Fork River, and they are effective predators of crayfish in deep water (CAF and DDM, personal observation).

#### *Size-specific crayfish distributions*

It is unclear why larger crayfish use deeper habitats in the Warm Fork River. Our assessment of resource availability and quality (Whitledge and Rabeni 1997, Parkyn et al. 2001, Gherardi et al. 2004, Bondar et al. 2005) and high predation rates in deep habitat (pools) suggest that large crayfish should be found predominantly in the shallow habitats where invertebrate biomass is greater, more shelter is available, and risk of predation is lower than in deep habitats (Dill 1987, Lima and Dill 1990). However, in Warm Fork River, only small crayfish are found consistently in shallow habitats, and large crayfish show greater use of deep habitats (Flinders and Magoulick 2007).

Large crayfish were often found in pool habitats in the Warm Fork River, but crayfish density and water depth are negatively related in the Spring River watershed overall (Flinders 2000, Flinders and Magoulick 2003, 2005). Crayfish density is often between 25 and 60 ind./m<sup>2</sup> and can exceed 100 ind./m<sup>2</sup> in shallow margin habitats in Warm Fork River and other sites in the Spring River watershed (Flinders 2000). High crayfish densities in shallow habitats could result in increased competition for resources. Therefore, large

crayfish might risk increased predation in deeper habitats because foraging efficiency is low in shallow habitats. Further research will be required to test this hypothesis.

Density-dependent dispersal is a well-known phenomenon in many species (Fonseca and Hart 1996, Sutherland et al. 2002), but density-dependent dispersal and subsequent effects on crayfish distribution across habitats are not well understood. Bovbjerg (1959) manipulated crayfish density (1, 5, 10, or 20 individuals in an ~20-cm-wide laboratory stream channel) and showed that dispersal rates were positively related to initial density. As individuals dispersed and local density decreased, rates of movement decreased (Bovbjerg 1959). However, dispersal appeared unrelated to crayfish density in a study examining the movements of an invasive crayfish in 2 English rivers with high (~20 ind./m<sup>2</sup>) and low (1–2 ind./m<sup>2</sup>) crayfish density (Bubb et al. 2004).

We examined resource availability, predation risk, and foraging profitability during the period when crayfish growth and predation rates were at their highest, but patterns might differ during nighttime hours or at different sites and streams. Spatial and temporal variation in crayfish habitat selection does occur in the Spring River watershed (Flinders and Magoulick 2007), and it is likely that factors driving habitat selection also vary spatially and temporally. Seasonal changes in food resource quantity and quality and shifts in predation pressure caused by changes in predator behavior could alter the relative importance of these variables in crayfish habitat selection.

Our results suggest that both predator avoidance behavior and the fitness advantage inferred by greater resource availability influenced the use of habitat depths by small crayfish. Factors driving the patterns of habitat selection of large crayfish are less clear because large body size offered no advantage in terms of predation risk in deep habitats. Selection of deeper but lower-quality habitats by large crayfish might be related to crayfish density, but further study is needed to adequately address this hypothesis. Regardless of habitat depth, large crayfish had a greater effect on their immediate surroundings than did small or no crayfish by reducing sediment loads, chl *a* concentration, and invertebrate biomass.

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### Literature Cited

- ADAMSKI, J. C., J. C. PETERSEN, D. A. FREIWALD, AND J. V. DAVIS. 1995. Environmental and hydrologic setting of the Ozark Plateaus study unit, Arkansas, Kansas, Missouri, and Oklahoma. US Geological Survey Water-Resources Investigations Report 94-4022. US Geological Survey, Little Rock, Arkansas.
- BERGMAN, D. A., AND P. A. MOORE. 2003. Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. *Biological Bulletin* 205:26-35.
- BONDAR, C. A., K. BOTTRIELL, K. ZERON, AND J. S. RICHARDSON. 2005. Does trophic position of the omnivorous signal crayfish (*Pacifastacus leniusculus*) in a stream food web vary with life history stage or density? *Canadian Journal of Fisheries and Aquatic Sciences* 62:2632-2639.
- BOVBJERG, R. V. 1959. Density and dispersal in laboratory crayfish populations. *Ecology* 40:504-506.
- BUBB, D. H., T. J. THOM, AND M. C. LUCAS. 2004. Movement and dispersal of the invasive signal crayfish *Pacifastacus leniusculus* in upland rivers. *Freshwater Biology* 49:357-368.
- CHAMBERS, P. A., J. M. HANSON, J. M. BURKE, AND E. E. PREPAS. 1990. The impact of the crayfish *Orconectes virilis* on aquatic macrophytes. *Freshwater Biology* 24:81-91.
- CHARLEBOIS, P. M., AND G. A. LAMBERTI. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* 15:551-563.
- CREED, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. *Ecology* 75:2091-2103.
- DILL, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. *Canadian Journal of Zoology* 65:803-811.
- DIStEFANO, R. J., J. J. DECOSKE, T. M. VANGILDER, AND L. S. BARNES. 2003. Macrohabitat partitioning among three crayfish species in two Missouri streams, U.S.A. *Crustaceana* 76:343-362.
- ENGLUND, G., AND J. J. KRUPA. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. *Freshwater Biology* 43:75-83.
- FIGUEROA, R. A., AND E. S. C. STAPPUNG. 2003. Food of breeding Great White Egrets in an agricultural area of southern Chile. *Waterbirds* 26:370-375.
- FLINDERS, C. A. 2000. The ecology of lotic system crayfish in the Spring River Watershed in northern Arkansas and southern Missouri. MS Thesis, University of Central Arkansas, Conway, Arkansas.
- FLINDERS, C. A., AND D. D. MAGOULICK. 2003. Effects of stream permanence on crayfish community structure. *American Midland Naturalist* 149:134-147.
- FLINDERS, C. A., AND D. D. MAGOULICK. 2005. Distribution, habitat use and life history of stream-dwelling crayfish in the Spring River drainage of Arkansas and Missouri with a focus on the imperiled Mammoth Spring crayfish (*Orconectes marchandi*). *American Midland Naturalist* 154:358-374.
- FLINDERS, C. A., AND D. D. MAGOULICK. 2007. Habitat use and selection within Ozark lotic crayfish assemblages: spatial and temporal variation. *Journal of Crustacean Biology* 27:242-254.
- FONSECA, D. M., AND D. D. HART. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* 75:49-58.
- GARVEY, J. E., AND R. A. STEIN. 1993. Evaluating how chela size influences the invasion potential of an introduced crayfish (*Orconectes rusticus*). *American Midland Naturalist* 129:172-181.
- GARVEY, J. E., R. A. STEIN, AND H. M. THOMAS. 1994. Assessing how predation and intraspecific competition influence a crayfish assemblage. *Ecology* 75:532-547.
- GHERARDI, F., P. ACQUISTAPACE, AND G. SANTINI. 2004. Food selection in freshwater omnivores: a case study of crayfish *Austropotamobius pallipes*. *Archiv für Hydrobiologie* 159:357-376.
- GRANDJEAN, F., D. ROMAIN, C. AVILA-ZARZA, M. BRAMARD, C. SOUTY-GROSSET, AND J. P. MOCQUARD. 1997. Morphometry, sexual dimorphism and size at maturity of the white-clawed crayfish *Austropotamobius pallipes pallipes* (Lereboullet) from a wild French population at Deux-Sevres (Decapoda, Astacidea). *Crustaceana* 70:31-44.
- HART, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. *Oecologia (Berlin)* 91:220-228.
- HELMS, B. S., AND R. P. CREED. 2005. The effects of 2 coexisting crayfish on an Appalachian river community. *Journal of the North American Benthological Society* 24:113-122.
- 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.
- HOLBROOK, S. J., AND R. J. SCHMITT. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* 69:125-134.
- HURYN, A. D., AND J. B. WALLACE. 1987. Production and litter processing by crayfish in an Appalachian mountain stream. *Freshwater Biology* 18:277-286.
- JORDAN, F., C. J. DELEON, AND A. C. MCCREARY. 1996. Predation, habitat complexity, and distribution of the crayfish *Procambarus allenii* within a wetland habitat mosaic. *Wetlands* 16:452-457.
- KERSHNER, M. W., AND D. M. LODGE. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *Journal of the North American Benthological Society* 14:414-422.
- LEWIS, D. B. 2001. Trade-offs between growth and survival: responses of freshwater snails to predaceous crayfish. *Ecology* 82:758-765.



- LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- LODGE, D. M., M. W. KERSHNER, J. E. ALOI, AND A. P. COVICH. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. *Ecology* 75:1265–1281.
- LODGE, D. M., AND J. G. LORMAN. 1987. Reductions in submerged macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Canadian Journal of Fisheries and Aquatic Sciences* 44:591–597.
- MACARTHUR, R. H., AND E. R. PIANKA. 1966. On the optimal use of a patchy environment. *American Naturalist* 100:603–609.
- 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.
- MCINTOSH, A. R., B. L. PECKARSKY, AND B. W. TAYLOR. 2004. Predator-induced resource heterogeneity in a stream food web. *Ecology* 85:2279–2290.
- MERKLE, E. L. 1969. Home range of crayfish *Orconectes juvenalis*. *American Midland Naturalist* 81:228–235.
- MISSOURI NATURAL HERITAGE PROGRAM. 2006. Missouri species and communities of conservation concern checklist. Missouri Department of Conservation, Jefferson City, Missouri. (Available from: <http://mdc.mo.gov/nathis/heritage/>)
- PARKYN, S. M., K. J. COLLIER, AND B. J. HICKS. 2001. New Zealand stream crayfish: functional omnivores but trophic predators? *Freshwater Biology* 46:641–652.
- PECKARSKY, B. L., C. A. COWAN, M. A. PENTON, AND C. ANDERSON. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* 74:1836–1846.
- PETTERSSON, L. B., AND C. BRÖNMARK. 1993. Trading off safety against food: state dependent habitat choice and foraging in crucian carp. *Oecologia (Berlin)* 95:353–357.
- POWER, M. E. 1987. Predator avoidance by grazing stream fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333–351 in W. C. Kerfoot and A. Sih (editors). *Predation: direct and indirect impacts in aquatic communities*. University Press of New England, Dartmouth, New Hampshire.
- PRICE, J. O., AND J. F. PAYNE. 1978. Multiple summer molts in adult *Orconectes neglectus chaenodactylus* Williams. *Freshwater Crayfish* 4:93–104.
- PROBST, W. E., C. F. RABENI, W. G. COVINGTON, AND R. E. MARTENEY. 1984. Resource use by stream-dwelling rock bass and smallmouth bass. *Transactions of the American Fisheries Society* 113:283–294.
- RABENI, C. F. 1985. Resource partitioning by stream-dwelling crayfish: the influence of body size. *American Midland Naturalist* 113:20–29.
- RABENI, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1714–1721.
- REYNOLDS, J. D. 2002. Growth and reproduction. Pages 152–191 in D. M. Holdich (editor). *Biology of freshwater crayfish*. Blackwell Science Publishers, Oxford, UK.
- 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. *American Midland Naturalist* 142:348–362.
- RUIZ-OLMO, J., J. M. OLMO-VIDAL, S. MANAS, AND A. BATET. 2002. The influence of resource seasonality on the breeding patterns of the Eurasian otter (*Lutra lutra*) in Mediterranean habitats. *Canadian Journal of Zoology* 80:2178–2189.
- SCHLOSSER, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 68:651–659.
- SCRIMGEOUR, G. J., J. M. CULP, AND F. J. WRONA. 1994. Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly. *Journal of the North American Benthological Society* 13:368–378.
- SIH, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* 63:786–796.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. 3<sup>rd</sup> edition. W. H. Freeman, New York.
- STEIN, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237–1253.
- STENROTH, P., AND P. NYSTRÖM. 2003. Exotic crayfish in a brown water stream: effects on juvenile trout, invertebrates and algae. *Freshwater Biology* 48:466–475.
- STREISSL, F., AND W. HOEDL. 2002. Growth, morphometrics, size at maturity, sexual dimorphism and condition index of *Austropotamobius torrentium* Schrank. *Hydrobiologia* 477:201–208.
- SUTHERLAND, W. J., J. A. GILL, AND K. NORRIS. 2002. Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences. Pages 134–151 in J. M. Bullock, R. E. Kenward, and R. S. Hails (editors). *Dispersal ecology*. Blackwell Science, Oxford, UK.
- TAYLOR, C. A., M. L. WARREN, J. F. FITZPATRICK, H. H. HOBBS, R. F. JEZERINAC, W. L. PFLEIGER, AND H. ROBINSON. 1996. Conservation and status of crayfishes of the United States and Canada. *Fisheries* 21(4):25–38.
- TURNER, A. M. 1997. Contrasting short-term and long-term effects of predation risk on consumer habitat use and resources. *Behavioral Ecology* 8:120–125.
- USIO, N., AND C. R. TOWNSEND. 2004. Roles of crayfish: consequences of predation and bioturbation for stream invertebrates. *Ecology* 85:807–822.
- UTNE, A. C. W., AND D. L. AKSNES. 1994. An experimental study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult two-spotted goby *Gobiussculus flavescens* (Fabricius). *Journal of Experimental Marine Biology and Ecology* 179:69–79.
- WERNER, E. E., J. F. GILLIAM, D. J. HALL, AND G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- WHITLEDGE, G. W., AND C. F. RABENI. 1997. Energy sources and ecological role of crayfishes in an Ozark stream: insights from stable isotope and gut analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2555–2563.

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