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Heidi Dukat
University of Central Arkansas

Daniel D. Magoulick
University of Central Arkansas

Effects of Predation on Two Species of Stream-Dwelling Crayfish (*Orconectes marchandi* and *Cambarus hubbsi*) in Pool and Riffle Macrohabitats

Heidi Dukat and Daniel D. Magoulick
Department of Biology
University of Central Arkansas
Conway, Arkansas 72035
501-450-5930
501-450-5914 FAX

Abstract

Community structure may be governed by many abiotic and biotic factors. Of the biotic factors, predation is often considered to be critical in structuring freshwater stream communities. In the Warm Fork of the Spring River, the crayfish *Cambarus hubbsi* is found mainly in riffles, whereas the crayfish *Orconectes marchandi* is found in high numbers in pools. We hypothesized that predation, mainly by fish, is a factor causing this segregation. Higher predation rates for *C. hubbsi* than *O. marchandi* in the pools and higher predation rates for *O. marchandi* than *C. hubbsi* in the riffles were expected. A transplant tethering experiment was conducted to test whether predation influences habitat selection. Substrate, water depth, and current velocity were also taken into account. In the pool, predation rates were significantly greater on *C. hubbsi* than *O. marchandi*, but predation rates were equal for the two species in the riffle. This suggests that predation is a factor in keeping *C. hubbsi* out of pools, but is not a factor in keeping *O. marchandi* out of riffles. Also, significantly greater predation rates overall were found in the pool than in the riffle. The pool was significantly deeper and had lower substrate diversity than the riffle. These findings suggest that predators are important in affecting crayfish habitat use; differential predation rates occur between habitats and greater predation rates occur in pools than in riffles.

Introduction

Many species in streams show habitat segregation, including crayfish (Bovbjerg, 1970; Jordan et al., 1996), fish (Stauffer et al., 1996), and algae (Traaen and Lindstrom, 1983). There are many hypotheses that attempt to explain why segregation among crayfish occurs. Most hypotheses explaining habitat segregation deal with either biotic factors (competition, behavior or predation), or abiotic factors (habitat complexity, current velocity, substrate). Resource partitioning may lead to species segregation based on Gause's principle (Schoener, 1974). For two species that share both a food source and common predators, it would be expected that competition occurs mainly for habitat locations which provide the highest foraging rates and the lowest predation rates (Schoener, 1974; Bowyer et al., 1998), assuming there are no significant behavioral differences.

Based on studies on rocky intertidal zones, Menge and Sutherland (1976) suggested that predation is a more important factor for determining community structure at high trophic levels with high trophic complexity, whereas competition is more important at low trophic levels with low trophic complexity. Some studies have shown a positive relationship between the presence of predators and crayfish segregation. For example, Jordan et al. (1996) found that the presence of predatory fish influenced habitat selection in populations of the crayfish *Procambarus alleni.* If segregation is due primarily to unequal predatory effects among the competing species, then there is some morphological and/or behavioral adaptation in one species which allows it to outcompete the other (Vance, 1978). For example, certain crayfish morphologies are better suited to high current velocities, indicating that morphology is an important factor in determining the most suitable macrohabitat for a crayfish (Maude and Williams, 1983). Also, some crayfish species use aggression to compete for food and shelter, which may lead to competitive exclusion (Bovbjerg, 1970).

Reice (1983) found that substrate was more influential than predation for habitat choice in macroinvertebrates. In general, more complex habitats would provide more possible niches than less complex habitats (Downes et al., 1998). Jordan et al. (1996) found that crayfish survival rates increased with increased habitat complexity due to lower predation rates in complex habitats. Bovbjerg (1970) found evidence suggesting that abiotic conditions including current velocity, substratum, and oxygen content were factors that contributed to the segregation of two similar crayfish species. These studies suggest that abiotic conditions may be the most important factor in habitat selection and, therefore, should be included when exploring the cause of segregation.

Quantitative sampling on the Warm Fork of the Spring River found that relative abundances of *Orconectes marchandi*

(Mammoth Spring crayfish) were positively correlated with margins, backwaters, and pools, whereas relative abundances of *Cambarus hubbsi* (Hubbs' crayfish) were positively correlated with riffles and runs (D.D. Magoulick and C.A. Flinders, unpublished data). The presence of predatory fish as well as many other benthivorous animals suggests that predation is a possible explanation for the segregation of these two species. We hypothesized that *C. hubbsi* would be preyed upon more heavily in pools, and *O. marchandi* would be preyed upon more heavily in riffles. A transplant experiment was designed to determine whether predation has an effect on the segregation of these two species.

Materials and Methods

The study site was on the Warm Fork of the Spring River north of the city of Thayer, Oregon County, Missouri, along County Road 19-326. The Warm Fork is in the eastern Ozark Mountains; land use is dominated by agriculture with riparian corridors ranging from several hundred meters to 3 meters or less. The study site had an average width of 12.2 m and an average depth of 30 cm. The riffle used in the study was a heterogeneous mixture of pebble, cobble and boulder. The study pool, directly downstream of the riffle, was composed mainly of sand.

Crayfish were collected from the study site on 28 July 1998 using a kicknet technique (Mather and Stein, 1993). Individuals from the same size class were selected for the experiment with preference given to those with both chela intact. Crayfish were pierced in the abdomen just above the telson, tied with 0.5m of clear monofilament line, and anchored to a rock. The tether did not seem to impede the mobility of the crayfish, and it is unlikely that the crayfish would be able to remove itself from the tether (Heck and Wilson, 1987; Power, 1987; McIvor and Odum, 1988). Transects were placed 1.5m or more apart running perpendicular to the flow of the stream. Crayfish were placed 1.5m or more apart along the transects and at least 0.5m from shore. The species placed at each location was chosen randomly. The carapace length, sex, and species of each crayfish were recorded. Estimations of the percent abundance of each substrate size class and depth from the area of crayfish mobility were recorded at each crayfish location. Ten random readings of the mean and substrate current velocities were taken in each macrohabitat. Twenty crayfish of each species were placed in the riffle between the hours of 09:30 and 14:30, and 19 crayfish of each species were placed in the pool between the hours of 16:00 and 20:00 on 29 July 1998. The next two consecutive mornings the sites were searched to determine which crayfish survived.

To calculate substrate diversity at each crayfish location, the following formula (Simpson's Index) was used. Substrate Diversity = $1 - [\Sigma n_1(n_1-1)/N(N-1)]$ where n_1 = the percent of a substrate at a crayfish location, and N = the total percent of substrates at each crayfish location. Chi square tests were used to determine if significantly more ($P < 0.05$) of either species were consumed in each macrohabitat (Figs. 1 and 2). T-tests were used to determine if the mean values for depth, current velocity, and substrate diversity were significantly different between the riffle and pool macrohabitat (Table 1). SYSTAT version 6.0 was used for all statistical tests (SPSS, Inc., Chicago, IL).

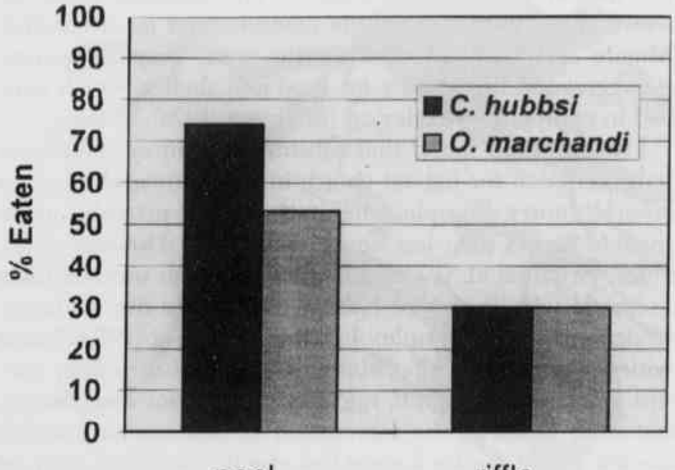

Fig. 1. Percent of *Orconectes marchandi* and *Cambarus hubbsi* consumed on day one in pool and riffle macrohabitats. The experiment began with 20 of each species in the riffle, and 19 of each species in the pool.

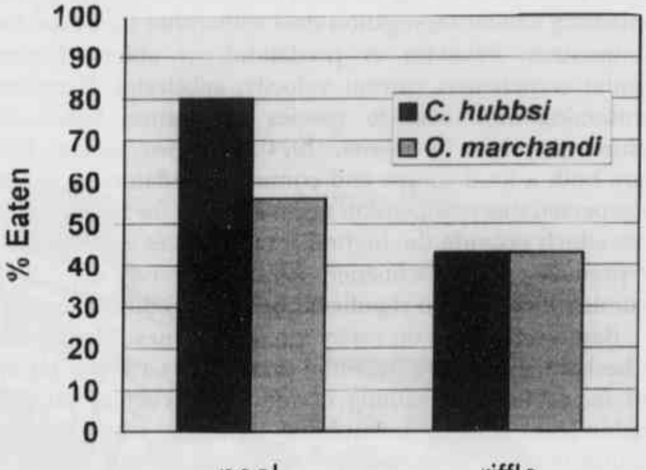

Fig. 2. Percent of *Orconectes marchandi* and *Cambarus hubbsi* consumed on day two in pool and riffle macrohabitats. The experiment began with 20 of each species in the riffle, and 19 of each species in the pool.

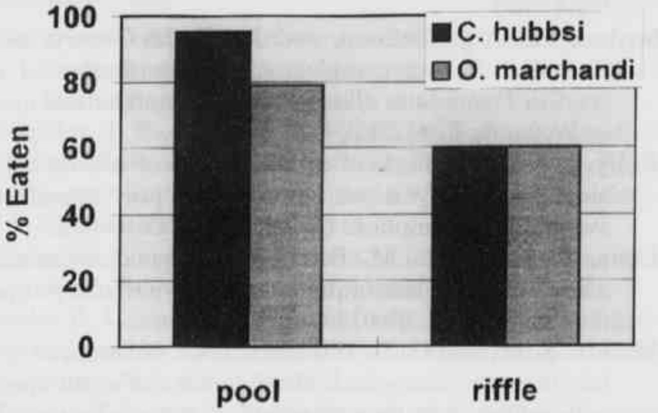

Fig. 3. Total cumulative percents of *Orconectes marchandi* and *Cambarus hubbsi* consumed after two days. The original numbers were 20 of each species in the riffle and 19 of each species in the pool.

Results

Equal numbers of both species were preyed upon in the riffle (Figs. 1, 2 and 3). On the first day and for the total of both days, significantly more *C. hubbsi* were preyed upon in pools than *O. marchandi* (Chi square day one $P = 0.028$, total $P < 0.001$; Figs. 1 and 3). On the second day more *C. hubbsi* were preyed upon in the pool than *O. marchandi*, but the sample size was too small to be significant (Chi square $P > 0.05$; Fig. 2). Also, there were significantly more crayfish preyed upon overall in the pools than in the riffles (Chi square $P < 0.05$; Figs. 1, 2 and 3).

Pools were significantly deeper, with significantly lower current velocity than riffles (Table 1). There was no significant difference in the mean substrate diversity index between pool and riffle (Table 1). However, one crayfish location in the riffle was encompassed entirely of boulder, giving it a substrate diversity of 1.0. If this location is treated as an outside value, then the riffle has significantly greater substrate diversity than the pool ($P < 0.05$).

Table 1. Mean (SE) of depth (cm), current velocity (cm-s^{-1}), and substrate diversity in pool and riffle macrohabitats. T-test probability values are for each habitat variable.

Habitat variable	Pool Riffle	P
Depth <0.001	47.00 (1.20)	25.20 (1.74)
Velocity <0.001	14.30 (1.09)	54.00 (6.20)
Substrate diversity	0.54(.02)0.59(.02)	0.096

Discussion

Many studies have examined how predators affect different crayfish species in freshwater communities (Stein and Magnuson, 1976; McNeely et al., 1990; Soderback, 1992; Mather and Stein, 1993; Soderback, 1994; Garvey et al., 1994). It has been shown that predators affect certain habits of their prey, for example changing feeding patterns, habitat use or patch use (Lima and Dill, 1989). In the current study, one of the observed predatory affects was that significantly higher numbers were consumed in the pool than in the riffle (Figs. 1, 2 and 3). Higher predation rates in streams have often been associated with pools because of higher concentrations of predators. Power (1987) noted that "pools are habitats for larger species and size classes of stream fish", leading to the suggestion that predators were responsible for the often-noted bigger fish – deeper water pattern found in streams. Furthermore, Todd and Rabeni (1989) found that adult smallmouth bass, which are major predators of crayfish and occur in the Warm Fork of the Spring River, seemed to prefer deeper water (> 0.66m) and current velocities of less than 20cm/s (i.e. pools). Other studies have shown a tendency for piscivorous fish to exclude prey items from deeper water (Mittelbach and Chesson, 1987; Power, 1987; Schlosser, 1988). Therefore, our results confirm that predators can have a strong influence on prey in deeper, more slowly flowing water.

Along with shallower water, there was also a trend toward lower predation rates in areas of higher substrate diversity (Table 1). Prey available for predation decreases with increasing habitat complexity because of an increase in refugia (Kelly, 1996; Mather and Stein, 1993). There can be competition if one refuge is sought by two organisms (Mittelbach and Chesson, 1987). This has been shown between species of crayfish (Soderback, 1994; Garvey et al., 1994) and between a benthic fish and a crayfish (McNeely et al., 1990). This type of exploitative competition is described by Power (1987) when the dominant species was changed by the addition of shelter. Since the lower substrate diversities were associated with the pool at the study site, the lack of habitat complexity could be a contributing factor to the higher predation rates observed in the pool.

Our hypothesis was partially supported because significantly more *C. hubbsi* than *O. marchandi* were preyed upon in pool than in riffle habitat (Figs. 1 and 3). However, the prediction of more *O. marchandi* than *C. hubbsi* being eaten in riffles was not supported. These data suggest that factors other than predation may be responsible for the selection of habitats by *O. marchandi*. Conversely, *Cambarus hubbsi* appears to be strongly affected by predation in pools and may avoid pool habitat due to predation risk. Additional experiments will be required to address the underlying causes of the observed differences in predation rates, such as different behaviors or morphologies.

The selection of riffles and runs by *C. hubbsi* may be related to their strategy of burrowing, as large substrates in riffles and runs provide large pore space for use as shelter and also facilitates movement. Pflieger (1996) found that both *O. marchandi* and *C. hubbsi* prefer boulder, cobble and gravel over sandy areas. However, in a more quantitative study, *O. marchandi* densities were correlated with pebble and sand substrates, whereas *C. hubbsi* densities were correlated with boulder and cobble substrates (D.D. Magoulick and C.A. Flinders, unpublished data). Maude and Williams (1983) found that morphologies of burrowing species help crayfish to burrow, as well as maintain positions in strong currents, so *C. hubbsi* may be better suited to riffles and runs than *O. marchandi* based on morphology. However, Pflieger (1996) noted that *C. hubbsi* was a poor swimmer, which would make them less suited to macrohabitats with fast flow. Further work will be necessary to determine whether crayfish morphology or predation risk is more important in affecting crayfish habitat selection.

Observations from the current study suggest that predation could participate in the segregation of *C. hubbsi* into riffles, but has less influence on the distribution of *O. marchandi*. However, both species were preyed upon more heavily in pools and in areas of lower substrate diversity. In accordance with findings from related studies, this may be due to greater concentrations of predators in pools and a smaller number of refugia in areas of lower substrate diversity.

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