

Context-specific behavior: crayfish size influences crayfish–fish interactions

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Abstract. Predator–prey interactions are often studied by examining either predator or prey behavior. This focal species approach ignores complexity that may determine the outcome of encounters. We used a dual species analysis to characterize how crayfish size (prey) influenced behavioral interactions between fish (predators) and crayfish. This interaction is particularly important in structuring energy flow patterns in aquatic communities. Fish and crayfish behavior were quantified after small (<30 mm carapace length) or large (>30 mm carapace length) crayfish (*Orconectes virilis*) were placed in wading pools with shelters and with 1 rock bass (*Ambloplites rupestris*), 2 yellow perch (*Perca flavescens*), 2 darters (*Etheostoma exile*, *E. nigrum*), or no fish (control). Small crayfish spent less time moving, decreased the number of pincer displays, reduced movement (particularly with rock bass), and increased tailflip frequency compared to large crayfish (with fish present). Neither crayfish size nor fish species present affected time crayfish stayed in shelters. Yellow perch approached crayfish more frequently than other fish. Darters interacted with smaller crayfish more frequently than larger crayfish, whereas the opposite was true for rock bass and perch. That both predator and prey behavior were influenced by prey size suggests the intensity and frequency of predator–prey interactions are affected by prey size.

Key words: displays, fish-initiated interactions, refuge use, interspecific encounters, predator behavior, prey size.

Much of the attention on predator–prey interactions has focused on either predator or prey behavior, but not both simultaneously (Stein and Magnuson 1976, Pitcher et al. 1986, Werner and Anholt 1996). Studying ecological interactions using this focal species approach often yields an incomplete picture because the outcome of interactions between predator and prey may well depend on the behavior of both individuals. To produce a more complete understanding of the complexity of interactions between organisms, it is important to study how both organisms affect the behavior of each other during encounters. This complete approach to examining predator–prey behavior is particularly relevant for interactions, e.g., predatory fish and crayfish, where the outcome is influenced by the behavior and morphology of predator and prey (Stein and Magnuson 1976).

Interactions between fish and crayfish influence energy flow patterns and the biological composition of aquatic communities. Crayfish

dominate the standing biomass of benthic invertebrates (Momot 1995). By consuming crayfish, fish predation transfers energy from the benthos to the water column (Rabeni 1992). Removal of crayfish by predators can also have cascading effects on other species because crayfish typically influence the composition of macrophyte, algal, and invertebrate assemblages (Chambers et al. 1990, Creed 1994, Nyström et al. 1996). Interactions among crayfish and fish are important for anglers because prized fish such as largemouth (Rickett 1974), smallmouth (Stein 1977), and rock bass (Rabeni 1992) rely on crayfish as a food resource.

Although bass effects on crayfish ecology have been closely examined, less is known about crayfish interactions with yellow perch and darters (Rahel and Stein 1988). Yellow perch consume crayfish in natural communities (Stein 1977). In addition, smaller non-threatening fish such as sculpins or darters may compete with crayfish for refugia or food resources (Rahel and Stein 1988, McNeely et al. 1990). Thus, the nature of the crayfish interactions with non-predatory fish would benefit from further investigation, particularly when it includes an exami-

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nation of both fish and crayfish behavior during encounters.

Crayfish traits such as chela size (Stein 1976) and body size (Stein and Magnuson 1976, Butler and Stein 1985) influence the outcome of crayfish–fish interactions. Large crayfish size reduces an individual's susceptibility to predatory fish (Stein and Magnuson 1976, DiDonato and Lodge 1993, Mather and Stein 1993). Ecological theory predicts that the behavioral responses of crayfish and fish should reflect this size-dependent nature of their encounters with one another (Werner and Gilliam 1984). This study examines 3 hypotheses regarding adaptive behavioral response of both fish and crayfish during interactions: 1) small crayfish will show more intense antipredator behavior during encounters with fish when compared to large crayfish, 2) fish should initiate encounters with small crayfish more frequently than with large crayfish because small crayfish are their preferred prey, and 3) crayfish should avoid rock bass more than perch or darters because rock bass are more formidable crayfish predators.

Methods

Animals and collection sites

We examined crayfish (*Orconectes virilis*) encounters with rock bass (*Ambloplites rupestris*), yellow perch (*Perca flavescens*), and darters (*Etheostoma nigrum*, *E. exile*). We chose *O. virilis* because this native species is widely distributed throughout North America (Taylor et al. 1996). We collected *O. virilis* from 4 sites: Fleming Creek (lat 42°16'N, long 83°39'W), Little Sucker Creek (lat 45°44'N, long 84°57'W), Douglas Lake (lat 45°33'N, long 84°40'W), and Burt Lake (lat 45°28'N, long 84°40'W). Both male and female crayfish were included in this study to ensure realistic results. The fish species chosen differ in their reliance on crayfish as food, and co-occur with *O. virilis* in northern Michigan streams and lakes (T. A. Keller, personal observations). Rock bass obtain nearly 70% of their total caloric intake from crayfish, and thus are important predators of crayfish (Rabeni 1992). Yellow perch consume juvenile crayfish (Stein 1977), whereas darters rarely feed on crayfish (Hobbs 1993). Rock bass and yellow perch were collected from Douglas Lake. Darters were collected from Douglas Lake and Big Sucker Creek.

Experimental design and protocol

We examined the behavior of 2 sizes of crayfish with 4 fish treatments in a fully factorial experimental design. Behavior was analyzed from video recordings of crayfish housed in laboratory pools with either 1 rock bass, 2 yellow perch, 2 darters, or no fish.

Pools (1.8 m diameter, 30 cm deep) were arranged in 2 rows of 4 (8 total); hanging plastic tarps visually isolated each pool. We placed the pools indoors at the University of Michigan Biological Station to avoid inclement weather that can damage video equipment. Each pool was illuminated using three 150 W incandescent bulbs placed equidistant around the pool perimeter. In an attempt to mimic the shoreline of natural ponds, the outside edges of the pools were filled with sand to a depth of 15 cm above the bottom. Plastic sheeting was placed over the sand-contoured pools to ensure that the water remained clear for video analysis. An additional layer of sand (5 mm deep) was placed on the plastic liner to provide a seminatural substrate in the pools. Water from Douglas Lake was used to fill the ponds (22 cm deep). One broken clay pot (10 cm × 3 cm) was placed, open end toward the center, on the north, south, east, and west edges of each pool (4 per pool). A floating Styrofoam[®] pad (0.0625 m²), anchored in the deepest portion of each pool, provided habitat for fish. Crayfish also moved under these floats when they moved to deeper portions of the pools. Video recordings (S-VHS) were filmed using a camera suspended 2.5 m above the pools on a moveable track.

Crayfish were given at least 3 d to acclimate to the indoor conditions. All crayfish were fed aquatic macrophytes. We divided the crayfish into 2 size categories: <30 mm and >30 mm carapace length (CL; Table 1). These size classes were chosen because they represent crayfish that are either susceptible or invulnerable to fish predators (Stein 1977).

Rock bass and yellow perch were fed earthworms, whereas darters were fed an ad libitum diet of invertebrates collected from Douglas Lake. Fish were starved at least 8 h before testing. Because of the large size differences between the fish species tested, we used only 1 rock bass in the pools but 2 yellow perch or 2 darters in their respective trials (Table 2). Numbers of fish used were also chosen to reflect the

TABLE 1. Mean carapace lengths (CL), measured from tip of rostrum to end of cephalothorax, of the 2 size classes of *Orconectes virilis* used in the interactions indicated.

Crayfish size	Total <i>n</i> (no. of females)	CL (mm)	SE
Control			
<30 mm	13(10)	18.8	1.33
>30 mm	13(8)	41.2	1.88
Darters			
<30 mm	13(4)	19.1	1.20
>30 mm	11(8)	40.4	1.90
Perch			
<30 mm	12(8)	19.1	1.34
>30 mm	14(7)	44.4	1.69
Rock bass			
<30 mm	12(8)	18.0	1.01
>30 mm	14(10)	41.2	1.67

behavioral patterns of these animals. Rock bass of the size used in this study develop hierarchies (Brown 1983), so we used only 1 rock bass per pool. We decided to minimize aggressive behavior among fish because aggression could alter the nature of fish-crayfish interactions. We used 2 perch and 2 darters because group foraging has been reported in Percidae (Eklöv 1992).

Fish were placed in pools the night prior (after 21:30) to testing to allow the fish to acclimate to the pools. We chose to acclimate fish to pool conditions because fish appeared to take longer than crayfish to return to a less agitated state (i.e., no fast movements, reduced hiding under the float) after introduction (T. A. Keller, personal observations).

To record behavior, we placed crayfish singly into pools containing 1 fish species and filmed for 15 min. Filming began once the crayfish was added to the pool because fish-crayfish interactions occurred immediately after crayfish introduction. Trials were conducted during the morning (08:00–12:00) and evening (20:30–24:30). These times were chosen to maximize activity of both the crayfish and fish. Trials were conducted from 20 September through 5 October 1997.

The assignment of fish treatments and crayfish sizes within the specific pools was randomized between days. Every effort was made to test all treatment combinations (2 crayfish sizes by 4 fish treatments) each morning and after-

noon (16 total). Because of the difficulty involved with capturing the large number of fish needed to run trials, individuals were used more than once and not all treatments were tested during each testing period. Trials were conducted on 10 separate days. Fish were left undisturbed in the same pool for morning and evening sessions to minimize fish handling. All crayfish were used only once.

Behavioral observations

Crayfish movement and habitat use were characterized from the video recordings. We calculated the time spent moving, time stationary, time in refugia, and time under float as percentages. The number of retreats (i.e., crayfish moving away from approaching fish), chela displays, nonresponses, and tailflips after fish approaches were also recorded. Chela displays were defined as instances when a crayfish raised and spread their chelipeds and opened their chelae. These behaviors are considered threat displays for crayfish (Rubenstein and Hazlett 1974). A retreat was recorded whenever a crayfish moved away from a fish within 5 s of an approach. No apparent change in crayfish behavior after a fish approached was recorded as a nonresponse (within 5 s). To determine the total distance crayfish traveled, movement paths were traced onto acetate sheets and measured with a cartographer's wheeled-map measurer (AlvinTM). Measured distances were scaled to actual distances.

Fish-initiated interactions were defined as encounters where fish rapidly approached within a 10 cm radius of the crayfish. Prior observations indicated that fish behaviors could be categorized as lateral or head-forward displays, depending on how the fish was oriented to the crayfish (T. A. Keller, personal observation). Predatory or aggressive approaches were not

TABLE 2. Mean wet mass and number of fish in the pools with crayfish.

Taxa	Total <i>n</i>	Wet mass (g/fish)	SE
Darters	18	1.88 (4) ^a	0.239
Perch	21	33.5 (15)	7.25
Rock bass	10	132 (7)	19.5

^a Number of fish measured.

designated because the observer could not definitively determine the fish's motivational state.

Statistical analyses

We tested the data to determine whether the assumptions of the parametric statistical models were met. We used a Lilliefors' test, combined with calculations of skewness and kurtosis, to examine normality. Homogeneity of variances was tested using Bartlett's test.

A χ^2 contingency test was used to examine interactions between crayfish sex and size or between crayfish size and fish species. Darters were omitted from the analysis of head-forward approaches because there were too few observations.

To examine how crayfish behaved during encounters with fish (i.e., fish approach within 10 cm radius), we used MANOVA with the dependent variables including number of crayfish retreats, chela displays, and nonresponses. Independent variables for this MANOVA included crayfish size, fish species, and an interaction between crayfish size and fish species. This MANOVA was necessary because crayfish in the fishless controls displayed no retreats or chela displays.

A multiple analysis of variance (MANOVA) was used to determine how crayfish size and fish species affected 5 dependent variables associated with crayfish habitat use. This 2nd analysis was necessary because we were comparing crayfish habitat use for crayfish in fish and fishless pools. Thus, all 102 crayfish were included in this analysis. The 4 dependent variables were percentages (time crayfish moved, remained stationary, stayed under the float, and hid in shelters). Percentage data were arcsine-square-root transformed before the analysis because % data deviate from the assumption of normality (Sokal and Rohlf 1995). The 5th dependent variable was a linear measure of the total distance crayfish traversed (while moving forward).

Because MANOVAs incorporate multiple dependent variables simultaneously, we used univariate ANOVAs to subsequently determine which dependent variables were most affected by fish and crayfish size treatments. ANOVAs were corrected for the number of comparisons using a Bonferroni method (Sokal and Rohlf 1995). For variables showing statistically significant size or fish species effects in the univariate

TABLE 3. MANOVAs of fish species and crayfish size effects on crayfish behavior and habitat use

Source of variation	Wilk's λ	<i>p</i>
Behavior^a		
Crayfish size	0.779	0.009
Fish species	0.890	0.047
Size \times Species	0.747	0.003
Habitat use^b		
Crayfish size	0.809	0.002
Fish species	0.755	0.039
Size \times Species	0.732	0.017

^a Dependent variables included retreat, chela displays, and nonresponses. Fishless controls were omitted from this analysis because the analysis focused on crayfish behavior after encounters with fish ($n = 76$)

^b Dependent variables included forward distance traveled, % time moving, % time stationary, % time under float, and % time in shelters ($n = 102$)

ANOVAs, we used pair-wise post hoc comparisons to determine where differences existed (Tukey-hsd corrected). Unadjusted *p*-values are shown in the text and figures.

We tested whether the number of crayfish that tailflipped was equal between small versus large crayfish using the binomial expansion (there were too few observations of tailflips in some groups to use χ^2 ; Sokal and Rohlf 1995). We set equal probabilities associated with tailflips for small and large crayfish ($p = q = 0.5$). If the binomial probability was low ($p < 0.05$), then the assumption that small and large crayfish were equally likely to tailflip can be rejected.

Results

Crayfish behavior

Crayfish size, fish species, and crayfish size by fish species interaction influenced crayfish behavior after fish approached (Table 3). Small crayfish displayed their chelae less frequently when approached by fish than did large crayfish (Fig. 1). This pattern of size-specific chela displays was similar among fish species (Table 4). Size did not alter a crayfish's propensity to retreat or not respond to fish approaches (Fig. 2A and 2B, Table 4). Most retreats and nonresponses by crayfish, particularly large crayfish, were observed with yellow perch (Fig. 2A and 2B).

The number of crayfish that tailflipped was

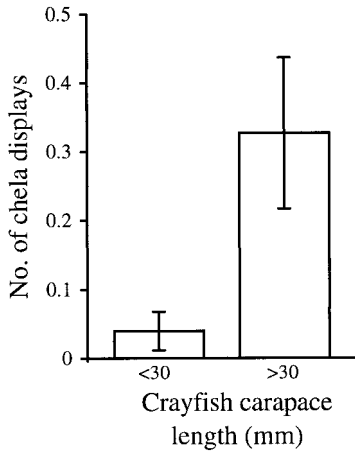


FIG. 1. Mean (± 1 SE) number of chela displays by small (<30 mm) and large crayfish (>30 mm) during 15 min encounters with darters, yellow perch, and rock bass combined.

also influenced by crayfish size and fish presence. Approximately 13.7% of crayfish tailflipped, and 87.5% of these were small (binomial $p = 0.006$). We only observed tailflips in pools with fish.

Crayfish size, fish species, and the crayfish size \times fish species interaction affected crayfish habitat use (Table 3). The % of time that crayfish spent moving and the distance they traveled differed between size classes (ANOVA $p \leq 0.005$ for both). Large crayfish spent on average 30%

TABLE 4. Univariate ANOVA table of fish species, crayfish size, and fish species \times crayfish size interaction effects on crayfish behavior during fish encounters. Fishless controls were omitted from these analyses ($n = 76$). Bolded p -values are statistically significant after Bonferroni adjustment.

Source of variation	df	F	p
Fish species			
Chela displays	2	0.677	0.511
Retreat behavior	2	3.63	0.031
Nonresponse	2	5.70	0.0051
Crayfish size			
Chela displays	1	6.79	0.0112
Retreat behavior	1	0.266	0.607
Nonresponse	1	4.02	0.0489
Species \times Size			
Chela displays	2	2.30	0.108
Retreat behavior	2	4.64	0.0128
Nonresponse	2	6.61	0.0023

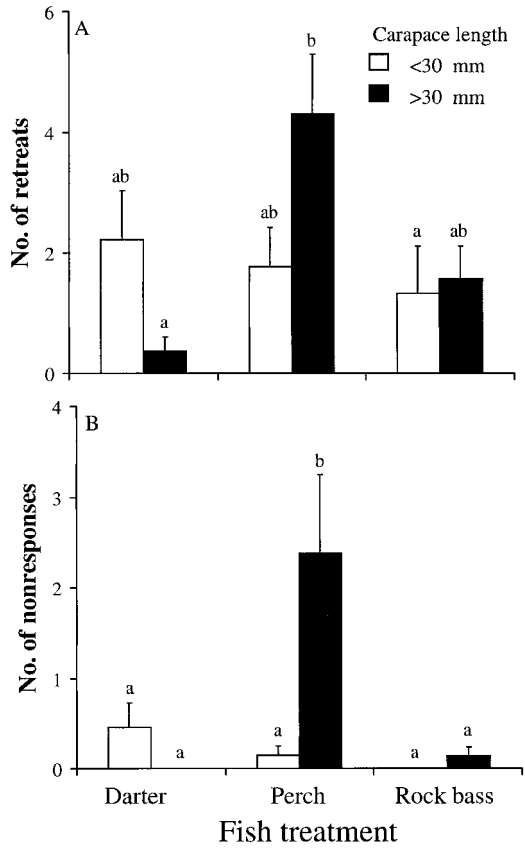


FIG. 2. Mean (± 1 SE) number of crayfish retreats (A) and nonresponses (B) by small (<30 mm) and large crayfish (>30 mm) in darter, yellow perch, and rock bass treatments during 15 min trials. Bars that share letters were not statistically different in multiple pair-wise comparisons ($p > 0.05$).

of their time moving, whereas small crayfish spent only 18% of their time moving (ANOVA $p = 0.003$). Large crayfish moved farther than small crayfish, particularly in the treatments with rock bass (Fig. 3A, Tukey's hsd $p = 0.046$). The forward distance traveled by small crayfish in the rock bass treatments was less than the distances traveled by small crayfish in the fishless controls (Fig. 3A, Tukey's hsd $p = 0.001$). There was a significant crayfish size \times fish species interaction in the % of time crayfish spent stationary outside of shelters (Table 4). In yellow perch treatments, small crayfish were more stationary than large crayfish (Fig. 3B, Tukey's hsd $p = 0.002$). Small crayfish in perch treatments moved less than similar-sized individuals in

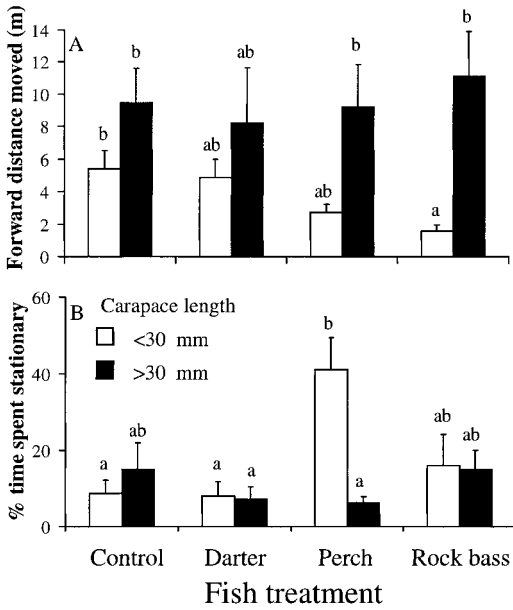


FIG. 3. Mean (+1 SE) forward distance traveled (A) and % time stationary (B) for small (<30 mm) and large crayfish (>30 mm) in different fish treatments during 15 min trials. Bars that share letters were not statistically different in pair-wise comparisons ($p > 0.05$).

darter and fishless treatments (Tukey's hsd $p < 0.004$ for both).

Fish behavior

Fish initiated interactions with 53% of crayfish. Fish approached male and female crayfish of different sizes in a similar manner as indicated by the lack of a statistically significant sex \times size interaction ($\chi^2 p = 0.7$). However, the fish differed in the frequency with which they laterally displayed to crayfish of different sizes ($\chi^2 p = 0.015$, Fig. 4A). Darters directed 80% of their lateral displays to small crayfish (Fig. 4). Head-forward displays by darters were too infrequent to be included in statistical analyses (Fig. 4B). Both rock bass and perch exhibited similar numbers of head-forward displays ($\chi^2 p = 0.9$). Most head-forward displays by perch and rock bass were directed to large crayfish (Fig. 4B).

Discussion

The structure of ecological communities is influenced by the behavioral interactions among

species (Werner 1992). Thus, characterizations of factors that alter species interactions will provide insight into the mechanisms that maintain ecological communities. This study demonstrates the importance of crayfish body size in shaping interactions between both crayfish and fish. Small crayfish rarely displayed their chelae but often tailflipped after fish approached them. Fish had little effect on the movement of large crayfish.

Our results agree with those of Stein and Magnuson (1976) and confirm that crayfish show size-specific behavior during encounters with fish. These findings suggest crayfish recognize their size-specific vulnerability to predators and choose behaviors that reduce their exposure. Because large size provides crayfish with a refuge against predation, the behavior of

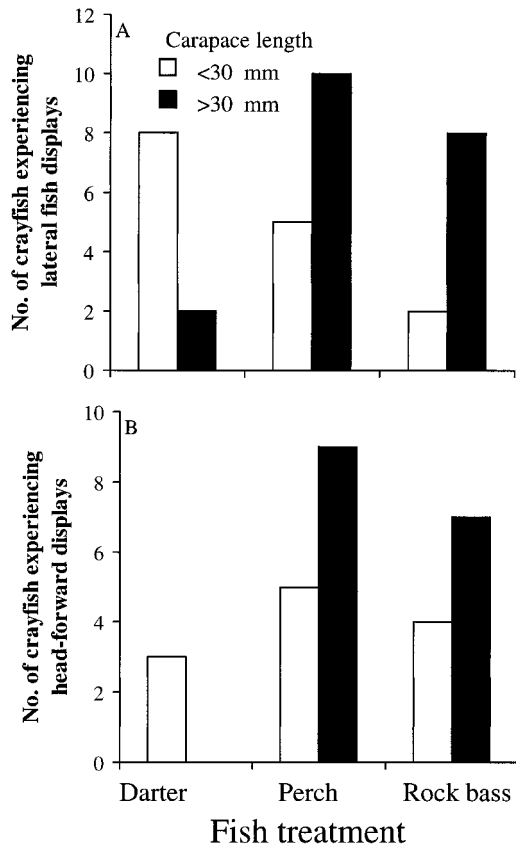


FIG. 4. Number of lateral (A) and head-forward displays (B) that small (<30 mm) and large (>30 mm) crayfish experienced in rock bass, yellow perch, and darter treatments during 15 min trials.

small crayfish should decrease their vulnerability to fish predators (Stein 1977). Organisms that experience size-specific predation risks are predicted to use behavioral strategies that maximize growth while minimizing risk of mortality during periods when they experience risk (Werner and Gilliam 1984).

Prey use information about potential predators to determine predation risk (Eklöv and Diehl 1994). Among behaviors quantified in this study, there is little evidence that crayfish can recognize predatory fish from non-predatory fish species. These results are consistent with those of Blake et al. (1994). Thus, it appears that crayfish may not distinguish between predatory and non-predatory fish species. Crayfish may rely on alternative strategies that do not require predator recognition, such as being nocturnally active when fish are inactive (Mitchell and Hazlett 1996).

Fish behavior was also influenced by crayfish size. Perch and rock bass showed similar behavior. Both species advanced toward large crayfish >60% of the time. Crayfish may compete with fish for access to food resources, and large crayfish may pose a potential physical threat to fish. Fish were expected to approach small crayfish more frequently because small individuals are potential prey for both rock bass and perch (Hobbs 1993). Our results suggest that the antipredator behavior employed by small crayfish conceals their presence from potentially dangerous fish.

Darters, which are not crayfish predators, behaved differently toward crayfish than rock bass or yellow perch. Darters directed their displays laterally and mostly at small crayfish. Large crayfish can capture and consume darters, making encounters with these potential predators risky for darters (Hobbs 1993). Both darters and crayfish use rocks and other debris for refugia. This overlap in resource use could lead to competition, particularly when predators increase the need for the use of refugia (Rahel and Stein 1988). However, darters approached and initiated interactions with crayfish even when refuges were not limited. These results indicate that crayfish and darters also compete for other resources such as invertebrate prey.

In conclusion, the size of 1 species in a cross-species encounter can influence the behavior of both participants. Our results indicate that small crayfish respond more strongly to the

presence of fish than do large crayfish. Crayfish behaved similarly when interacting with predatory and non-predatory fish. This result suggests that crayfish avoid interactions with fish altogether, rather than rely on signals (e.g., chemical cues) that would warn them of the status of fish they encounter. This study also demonstrates that fish approaches and interactions with crayfish are influenced by crayfish size and fish species. Because fish approached large crayfish more frequently, fish advances may not represent foraging. Morphological traits like size can alter the behavior of initiators and responders during ecological interactions, so the outcome and importance of ecological interactions will likely depend on the size structure of species composing biological communities.

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Literature Cited

- BLAKE, M., P. NYSTRÖM, AND P. HART. 1994. The effect of weed cover on juvenile signal crayfish (*Pacifastacus leniusculus* Dana) exposed to adult crayfish and non-predatory fish. *Annales Zoologici Fennici* 31:297-306.
- BROWN, J. A. 1983. A comparative study of behavioural ontogeny in four species of centrarchid fish. PhD Thesis, Queen's University, Kingston, Ontario.
- BUTLER, M. J., AND R. A. STEIN. 1985. An analysis of the mechanisms governing species replacement in crayfish. *Oecologia* 66:168-177.
- 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.
- CREED, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. *Ecology* 75:2091-2103.
- DiDONATO, G. T., AND D. M. LODGE. 1993. Species replacements among *Orconectes* crayfishes in Wisconsin lakes: the role of predation by fish. *Can-*

- dian Journal of Fisheries and Aquatic Sciences 50: 1484–1488.
- EKLÖV, P. 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Animal Behaviour* 44:313–326.
- EKLÖV, P., AND S. DIEHL. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. *Oecologia* 98:344–353.
- HOBBS, H. H. 1993. Trophic relationships of North American freshwater crayfishes and shrimps. Milwaukee Public Museum Contributions in Biology and Geology 85:1–110.
- 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. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1279–1288.
- MCNEELY, D. L., B. N. FUTRELL, AND A. SIH. 1990. An experimental study on the effect of crayfish on the predator-prey interaction between bass and sculpin. *Oecologia* 85:69–73.
- MITCHELL, B., AND B. A. HAZLETT. 1996. Predator avoidance strategies of the crayfish *Orconectes virilis*. *Crustaceana* 69:400–412.
- MOMOT, W. T. 1995. Redefining the role of crayfish in aquatic ecosystems. *Reviews in Fisheries Science* 3:33–63.
- NYSTRÖM, P., C. BRÖNMARK, AND W. CRANÉLI. 1996. Patterns in benthic food webs: a role for omnivorous crayfish? *Freshwater Biology* 36:631–646.
- PITCHER, T. J., D. A. GREEN, AND A. E. MAGURRAN. 1986. Dicing with death: predator inspection behaviour in minnow shoals. *Journal of Fish Biology* 28:439–448.
- RABENI, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1714–1721.
- RAHEL, F. J., AND R. A. STEIN. 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia* 75:94–98.
- RICKETT, J. D. 1974. Trophic relationships involving crayfish of the genus *Orconectes* in experimental ponds. *Progressive Fish-Culturist* 36:207–211.
- RUBENSTEIN, D. I., AND B. A. HAZLETT. 1974. Examination of the agonistic behaviour of the crayfish *Orconectes virilis* by character analysis. *Behaviour* 50:193–216.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. 3rd edition. W. H. Freeman and Company, New York.
- STEIN, R. A. 1976. Sexual dimorphism in crayfish chelae: functional significance linked to reproductive activities. *Canadian Journal of Zoology* 54:220–227.
- STEIN, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237–1253.
- STEIN, R. A., AND J. J. MAGNUSON. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57:751–761.
- TAYLOR, C. A., M. L. WARREN, J. F. FITZPATRICK, H. H. HOBBS, R. F. JEZERINAC, W. L. PFLIEGER, AND H. W. ROBINSON. 1996. Conservation status of crayfishes of the United States and Canada. *Fisheries* 21(4):25–38.
- WERNER, E. E. 1992. Individual behavior and higher-order species interactions. *American Naturalist* 140:S5–S32.
- WERNER, E. E., AND B. R. ANHOLT. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. *Ecology* 77:157–169.
- WERNER, E. E., AND J. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.

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