Direct and Indirect Effects of Fish Predation on the Replacement of a Native Crayfish by an Invading Congener

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In Ohio streams, the crayfish *Orconectes rusticus* is replacing *O. sanborni*, and herein we test how predators influence this replacement. In a field survey, crayfish were scarce when fish were abundant, suggesting that predators can adversely affect these prey. In laboratory experiments, we examined underlying mechanisms for this inverse relationship; specifically, we tested how crayfish species, adult aggression, and habitat heterogeneity influenced the predator–prey interaction. In a laboratory stream, smallmouth bass (*Micropterus dolomieu*) ate similar numbers of equal-sized *O. rusticus* and *O. sanborni*, but when sizes mimicked those in the field (i.e., *O. rusticus* 4 mm > *O. sanborni*), fewer *O. rusticus* were eaten. Fish also reduced juvenile activity and behaviors whereas adult aggression increased the frequency of these risky responses. More affected by adult crayfish, *O. sanborni* should suffer disproportional predation where adults and juveniles interact. Thus, fish predators should increase replacement rates and adult aggression should further accelerate this process. Manifested through crayfish size, both indirect and direct predator effects contribute to the replacement of *O. sanborni* by *O. rusticus*.

Dans les cours d'eau de l'Ohio, l'écrevisse *Orconectes rusticus* remplace *O. sanborni*, et nous avons examiné la façon dont la prédation influe sur ce phénomène. Dans une étude menée sur le terrain, les écrevisses étaient rares quand les poissons étaient abondants, ce qui semble indiquer que les prédateurs peuvent avoir un effet négatif sur la présence des crustacés. Dans les expériences de laboratoire, nous avons examiné les mécanismes qui sous-tendent cette relation inverse; plus précisément, nous avons étudié la façon dont les espèces d'écrevisses, l'agression par les adultes et l'hétérogénéité de l'habitat influent sur l'interaction entre prédateurs et proies. Dans un cours d'eau artificiellement recréé en laboratoire, les achigans à petite bouche (*Micropterus dolomieu*) mangeaient des nombres similaires de *O. rusticus* et de *O. sanborni* de taille égale, mais quand on reproduisait les tailles existant dans la nature (c.-à-d. *O. rusticus* mesurant 4 mm > *O. sanborni*), le nombre de *O. rusticus* consommées était inférieur. Les poissons réduisaient ainsi l'activité des juvéniles et leurs comportements, tandis que l'agression par les adultes augmentait la fréquence de ces réactions à risque. Davantage affectée par l'action des écrevisses adultes, *O. sanborni* doit subir une prédation disproportionnée quand les adultes et les juvéniles sont en interaction. Ainsi, la prédation par les poissons doit accentuer le remplacement d'une espèce par l'autre, et l'agression par les adultes doit accélérer ce processus. Par le biais de la taille des écrevisses, les effets indirects et directs de la prédation contribuent au remplacement de *O. sanborni* par *O. rusticus*.

In central Ohio streams, a crayfish species replacement is occurring and provides a unique opportunity to explore processes that underlie species interactions and extirpations. *Orconectes rusticus* is a large, aggressive crayfish (Capelli 1982; Butler and Stein 1985) that naturally occurs in Indiana, Kentucky, and western Ohio. This invader is becoming increasingly common outside its native range, probably as a result of baitbucket introductions (Capelli 1982), and has been associated with declines of native crayfish in Ontario (Berrill 1978) and Wisconsin (Capelli 1982). Within Ohio, *O. rusticus* has continued to expand its eastern boundary (Turner 1926; Rhoades 1962) and has displaced the native crayfish *O. sanborni* in parts of the Licking River (Butler and Stein 1985). In the replacement of native crayfishes by *O. rusticus*,

the roles of abiotic factors (Rhoades 1944, 1962; Capelli and Magnuson 1983; Flynn and Hobbs 1984), reproductive interference (Tierney and Dunham 1984; Butler and Stein 1985), competition (Capelli and Munjal 1982; Butler and Stein 1985; Lodge et al. 1986), and community interactions (Olsen et al. 1991) have been examined. These crayfish replacements, although frequently documented, are difficult to study, inadequately understood, and appear to be a complex interaction among multiple factors (Lodge et al. 1986; Olsen et al. 1991).

Predation affects community structure in many aquatic systems (Sih et al. 1985), and juvenile crayfish are especially vulnerable to fish predators (Stein and Magnuson 1976; Stein 1977; Rabeni 1992). Elsewhere, we have described how differences in habitat-specific growth and overall mortality contribute to this replacement (Mather and Stein 1993). Here we test if fish predators play a role in the Ohio crayfish species replacement. For example, fish predators may affect crayfish either directly by consuming them or indirectly by causing them to change behavior, alter activity patterns, or shift habitats. If either cray-

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fish species is more vulnerable to direct or indirect predator effects and if these effects result in reductions in survival, fecundity, or growth, then fish predation can contribute to the replacement.

Herein we combine a field survey with laboratory experiments to ask the following specific questions: (1) Do stream fish predators limit the abundance of crayfish? (2) Does a common fish predator, smallmouth bass (*Micropterus dolomieu*), differentially influence vulnerability, activity, behavior, or habitat use of the two crayfishes in a simulated laboratory stream? (3) Does aggression of adult crayfish or habitat heterogeneity modify these responses? (4) Do any of these factors differentially affect either species when crayfish size reflects natural size distributions? (5) Do fish predators contribute to this ongoing replacement?

Methods

Field Survey

To assess the general relationship betwen predator and prey, we sampled fish and crayfish in five allopatric *O. sanborni* sites and six sympatric *O. sanborni/O. rusticus* sites ($N = 11$). These sites, 6–24 m wide ($\bar{X} = 12$ m), 0.5–0.9 m average depth ($\bar{X} = 0.6$ m), 0.7–1.5 m maximum depth ($\bar{X} = 1.0$ m), were located in four second-order streams in two drainages. Limited availability of sympatric sites prevented us, in this field study, from assessing the response of each crayfish species to predation, but supplementing sympatric with allopatric sites, at least, allowed us to examine the effect of fish on both crayfish species combined.

To determine crayfish density, we randomly chose three to five locations in each riffle and adjacent pool for quantitative kick seines (total = 6–10 samples in each riffle/pool combination). When crayfish movements were monitored over 24 h, only one crayfish attempted to change habitat (True 1990); thus, for our sampling, we assumed that crayfish remained in either riffle or pool. To sample, one person held the 1.5-m-wide seine while two others quickly and vigorously kicked 1 m upstream of the seine. All rocks were overturned swiftly to dislodge crayfish and the seine was quickly pulled through the 1.5-m² sample area. Crayfish were identified to species, sexed, and measured (nearest millimetre carapace length (CL)). All sites were sampled for crayfish within 10 d in late June 1987. Several survey sites were in the same tributary, but all pool samples were separated by at least 100 m or a riffle, obstacles adequate to ensure that crayfish populations at each site did not overlap.

To determine fish density, we sampled these same pools during 25 June through 5 July 1987. Blocknets were placed between (1) riffle and pool and (2) 35 m into the pool (about 560 m² of pool per site) ensuring that a representative area of both large and small pools was sampled. The area within the two blocknets was electroshocked twice ($\bar{X} = 22.5$ min/pass) with a pulsed DC unit. Upon capture, fish were identified to species, measured, and stomachs of all fish >100 mm total length (TL) were pumped (Seaburg 1957). Because only smallmouth bass and rock bass (*Ambloplites rupestris*) ≥150 mm contained crayfish, we limited our analysis to these larger predators. Riffles were not sampled because fish predators were never observed in these shallow-water habitats. For the same reason, only crayfish densities in pools were used in the analysis that follows.
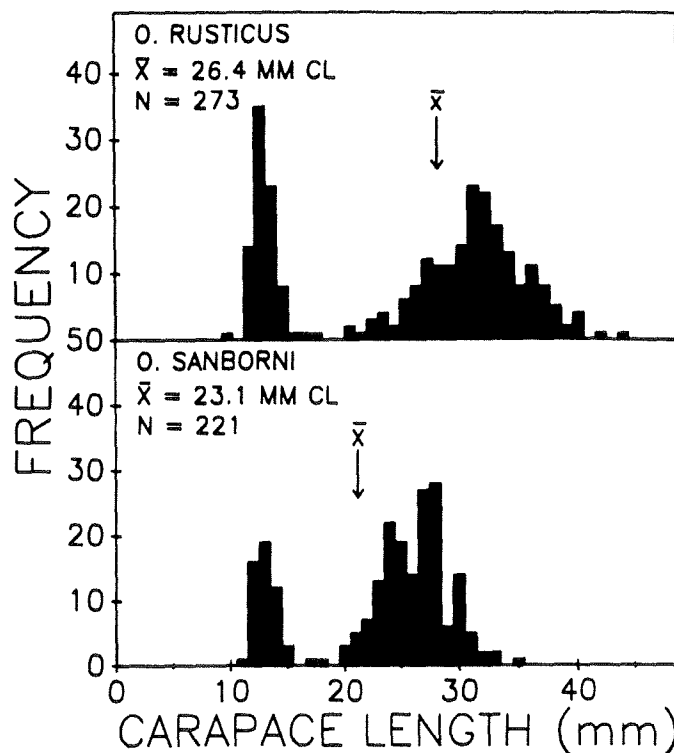

FIG. 1. Size distributions of *O. rusticus* and *O. sanborni* in North Fork Creek, Licking and Knox counties, Ohio, during June through September 1988.

Laboratory Experiments

Once a general relationship between fish and crayfish abundances was established by field sampling, we examined potential mechanisms for this replacement by examining the relative response of each crayfish species to predators in the laboratory. Specifically, in a stream tank, we quantified how fish predators influenced juvenile crayfish survival and behavior and how crayfish species, adult aggression, and habitat heterogeneity altered this predator–prey interaction. Our stream tank had two identical, independent, 2.6 × 0.9 × 1.5 m channels. Each channel contained a paddlewheel adjusted to generate bottom currents of 30 cm/s upstream to 1 cm/s downstream and included (1) a 0.9 × 0.9 × 0.06 m (deep) upstream riffle and (2) a 0.9 × 0.9 × 0.6 m (deep) downstream pool connected by (3) a 0.9 × 0.8 m transitional area (depth range = 0.06–0.6 m). Substrate was 5-mm dark pebble glued to Plexiglas to preclude crayfish burrowing. To eliminate chemical effects, water (16°C) was changed between experiments. A 14 h light: 10 h dark photoperiod with simulated dawn and dusk allowed us to observe diurnal, nocturnal, and crepuscular interactions in each 21-h experiment.

Treatments

We used a complete randomized 4 × 2 block design with the following treatments: (1) fish ($N = 1$ or none), (2) species (*O. rusticus, O. sanborni*), (3) adults ($N = 6$ *O. rusticus* males (i.e., 26 crayfish per experiment) or no adults (i.e., 20 crayfish per experiment)), and (4) shelters ($N = 10$ pool shelters or none). Fish predation, known to influence crayfish distribution and abundance (Stein and Magnuson 1976; Stein 1977; Rabeni 1992), occurs continuously in the field; to detect predation within a 21-h experiment, we used a higher fish density

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(0.33/m²) in the laboratory than normally observed in the field (see Fig. 2). When testing species in the laboratory, we focused on sympatric interactions because relative performance of each species is critical to understanding the replacement.

Third, we tested the effect of adult crayfish on juveniles because crayfish size affects both inter- and intraspecific interactions (Butler and Stein 1985; Rabeni 1985), and juvenile crayfish probably encounter ubiquitous adult crayfish frequently ($\bar{X}$ = 3/m²). In preliminary experiments, juvenile crayfish responded to adults of both species similarly (ANOVA, $p > 0.05$); consequently, only easily obtained $O.$ $rusticus$ adults were used. To test how large adult crayfish affect the smallmouth bass/juvenile crayfish interaction, six adult males ($\geq$25 mm CL, mostly form II) were used. Our experiments with form II males probably reflected natural levels of aggression but underestimated effects of more aggressive form I males.

Finally we quantified how habitat heterogeneity, via shelters, affected crayfish susceptibility to smallmouth bass predation because habitat heterogeneity changes the interaction between predators and prey (Huffaker 1958; Stein 1977; Brusven and Rose 1981; Savino and Stein 1982; Feltmate et al. 1986). We placed 10 single-crayfish shelters (5 × 2.5 × 3 cm pieces of slate supported by a 5-cm screw and sufficiently large to house a single juvenile) in pools. Experimental order within a block was random except that to prevent contamination by chemical cues, smallmouth bass were either present or absent from both channels.

Size Treatments

In the field, size distributions of the two crayfishes overlapped, but $O.$ $rusticus$ was larger than the displaced native $O.$ $sanborni$ (by 3.3 mm CL; Fig. 1). To evaluate the role of size, two sets of experiments testing the variables described above (fish predators, crayfish species, adult crayfish, habitat heterogeneity) were completed. In the first set of experiments ($N = 8$ replicates per treatment), conducted during September through December 1988, we used equal-sized juvenile crayfish ($\bar{X}$ = 15 mm CL). Juvenile crayfish of this size were common, large enough to mark, easy to handle, and readily consumed by experimental fish (250 mm TL). In the second set of experiments ($N = 3$ replicates per treatment), completed during September through December 1989, we used unequal-sized crayfish. To separate the effect of size and species in these unequal-size experiments, we continued to use about 15 mm CL ($\bar{X}$ = 15.5) as the small size; to this we added 4 mm (similar to 3.3 mm, the size difference observed in the field) to generate the larger juvenile size, 19.5 mm. Juveniles of these sizes ($O.$ $rusticus$: $\bar{X}$ = 19.5 mm CL, $O.$ $sanborni$: $\bar{X}$ = 15.5 mm CL, 4-mm size difference) may occur in the field between the end of their first summer (fast growers) and the end of their second summer (slow growers). Although 19.5 mm is not common (Fig. 1), all individuals must grow through this stage. In three quarters of the first experiments and two thirds of the second experiments, naive untested crayfish were used. Only in the last blocks were crayfish reused.

Experimental Animals

Collected from allopatric populations, each crayfish species was held separately in 625-L tanks and fed lettuce, fish, and liver ad libitum. Before experiments, each crayfish was measured and marked (2-mm epoxy paint mark on the carapace) to indicate species. In each experiment, we used 20 juvenile crayfish, 10 each of $O.$ $rusticus$ and $O.$ $sanborni$ (1:1 sex ratio), resulting in a combined density of 7/m², a density within the natural range found in Ohio streams (see Fig. 2). For simplicity, all small crayfish (15–19 mm CL) were termed juvenile. Smallmouth bass were collected from the Olentangy River, Franklin County, Ohio. Fish were maintained in individual 200-L tanks ($\bar{X}$ = 18°C) and fed minnows and crayfish ad libitum. Fish were starved 72–96 h and acclimated to 16°C for 24 h before each experiment. When equal-sized crayfish were used, smallmouth bass were 250–275 mm TL; in the following year when unequal-sized crayfish were used, fish were 320–350 mm TL.

General Protocol

Before experiments, habitats (riffle, transitional area, pool) were separated by screens. One smallmouth bass was placed in the transitional area between riffle and pool the evening before experiments to acclimate. The next morning, 4 h before an experiment, crayfish were divided equally between riffle and pool. Experiments began when screens were raised and fish and crayfish could interact. The following morning, 21 h into experiments, we lowered the screens, recorded final crayfish distribution, drained the tank, and recovered all surviving crayfish. After 1 and 20 h, crayfish activity, habitat choice, and agonistic behaviors were recorded. In the first 16 experiments, fish stomachs were pumped to verify that the number of crayfish eaten was the difference between the number added and the number recovered. For all these experiments, we could account for all crayfish, and consequently, we did not pump stomachs in the remaining experiments.

Response Variables

We measured six responses: number eaten, proportion active, habitat changes, swimming escapes, fights, and final habitat choice. Number eaten and final habitat choice were measured only at experiment's end. Other responses were quantified for 5 min in each habitat during two observation periods, 1 and 20 h (total observation time/experiment = 5 min/habitat × 3 habitats × 2 observation periods = 30 min/experiment). Crayfish responses at 1, 2, 3, and 4 h were similar (ANOVA, $p > 0.05$); hence, the 1-h observation period was chosen to depict early crayfish interactions. Because responses were similar for 1 and 20 h, these data were combined.

Proportion active was estimated by scan sampling each habitat. If a crayfish did not move for 5 s, it was considered inactive. Habitat changes occurred when a crayfish moved between riffle, transitional area, or pool. Fights included both contact and noncontact aggressive interactions, i.e., when a crayfish was located within one body length of and oriented toward another individual. Swimming escapes occurred when crayfish jumped off the bottom and swam or drifted away in response to a threat from another crayfish. To determine habitat choice, riffle and pool crayfish were counted at the end of experiments. Here, riffles were defined as the area from which fish were excluded, i.e., the shallow, fast riffle and the upstream 10 cm of the transitional area between riffle and pool. Functionally defined as the habitat the fish frequented, the pool included the deepest quadrant and the 70 cm of transitional area to which fish had access. Because pool/riffle comparisons were not made within an experiment, the size of these habitats was not standardized.
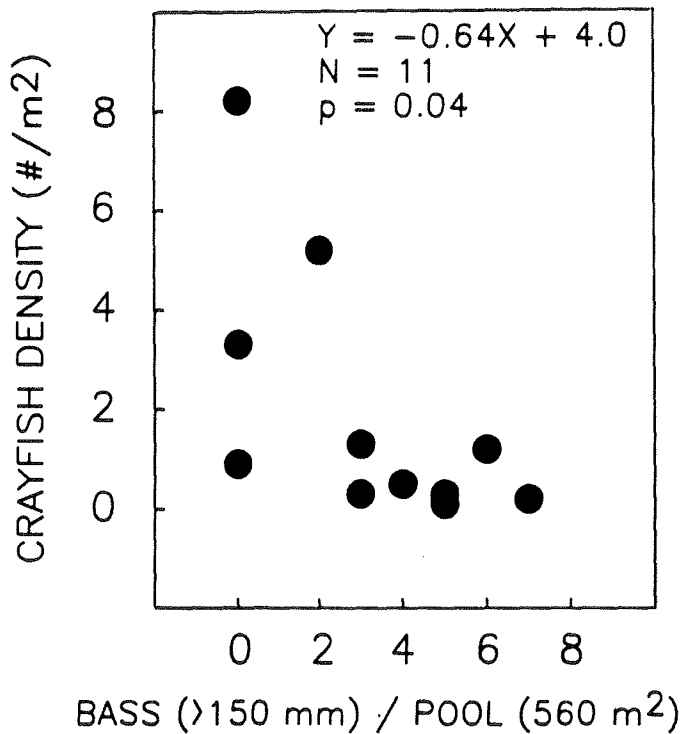
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FIG. 2. Relationship between fish predator density (rock bass and smallmouth bass >150 mm TL·560 m^{-2} pool) and total crayfish density (all crayfish captured in three to five quantitative kick seines per site) in central Ohio streams in June and July 1987.

When fish ate crayfish, prey density differed at the beginning and the end of the experiment. Our experiments were not designed to separate behaviors of surviving crayfish from those that were eaten. Examining frequency of behaviors scaled to the initial number of crayfish incorporates all activities that occurred before crayfish were eaten; the alternative, reformulating each response as the proportion of the surviving population, accounts for the density change, but ignores initial behaviors. Because of the importance of prepredation activities, we chose to scale responses to the *initial* number of crayfish.

Statistical Analyses

Six four-way ANOVAs determined how species, fish, adults, and shelters influenced number of juveniles eaten, proportion active, habitat changes, swimming escapes, fights, and proportion in the riffle (SAS Institute, Inc. 1982). Number eaten was evaluated at the $p \le 0.05$ level. The other five nonlethal responses were not independent, and to control experimentwise error, we evaluated each comparison at the $p \le 0.05/5$ (0.05 for 5 responses) or $p \le 0.01$ level (0.01 for each response). In preliminary experiments, juvenile crayfish responded similarly whether (1) all 20 juvenile crayfish were the same species or (2) species were mixed 1:1 *O. sanborni/O. rusticus* (ANOVA, $p > 0.05$). Because juvenile crayfish responded to density and not to species, species was considered a treatment effect. When an analysis of residuals revealed that a transformation was necessary to stabilize variances, proportions and behaviors were arcsin and log transformed, respectively. Only significant trends are discussed below unless explicitly noted otherwise.
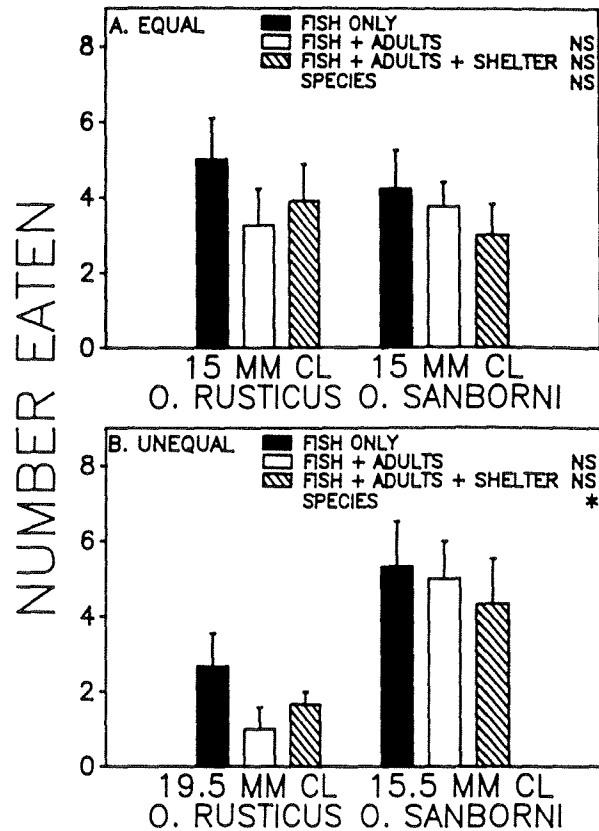

FIG. 3. Number of *O. rusticus* and *O. sanborni* eaten by smallmouth bass. (A) Both crayfish species were of equal size ($N = 8$); (B) crayfish were of unequal size, reflecting a natural size difference ($N = 3$). Data are means ± 1 SE. A three-way ANOVA tested for effects of crayfish species, adult crayfish, and shelters on juvenile crayfish survival. NS, $p > 0.05$; *$p \le 0.05$. Significant SS, F, and df are given in the text.

Results

Direct, Lethal Fish Effects

In the field, fish predators did not occur in equal numbers at all sites. Across 11 sites, fish abundance varied from 0 to 7 fish/560 m^{-2} pool and crayfish density ranged from 0 to 8.3/m^{-2}. As predator abundance increased, total crayfish density declined (Fig. 2).

To determine if smallmouth bass negatively affect crayfish, as the field survey suggests, we quantified predator effects in the laboratory. In the stream tank, fish ate similar numbers of equal-sized *O. rusticus* and *O. sanborni* (Fig. 3A). When crayfish were of unequal-size (*O. rusticus* 4 mm > *O. sanborni*), fewer large *O. rusticus* were eaten than small *O. sanborni* (Fig. 3B: SS = 2.00, F = 4.49, df = 23, p = 0.05).

Indirect, Nonlethal Fish Effects

Without fish, the majority of *O. rusticus* and *O. sanborni* of both sizes were active (Fig. 4A, 4B). When unequal in size, *O. rusticus* was more active than *O. sanborni* (Fig. 4B: SS = 1.08, F = 17.08, df = 47, p = 0.0002). Fish reduced activity for both species and both sizes (Fig. 4A: SS = 1.66, F = 41.06, df = 127, p = 0.0001; Fig. 4B: SS = 2.42, F = 8.33, df = 47, p = 0.0001). When crayfish were of
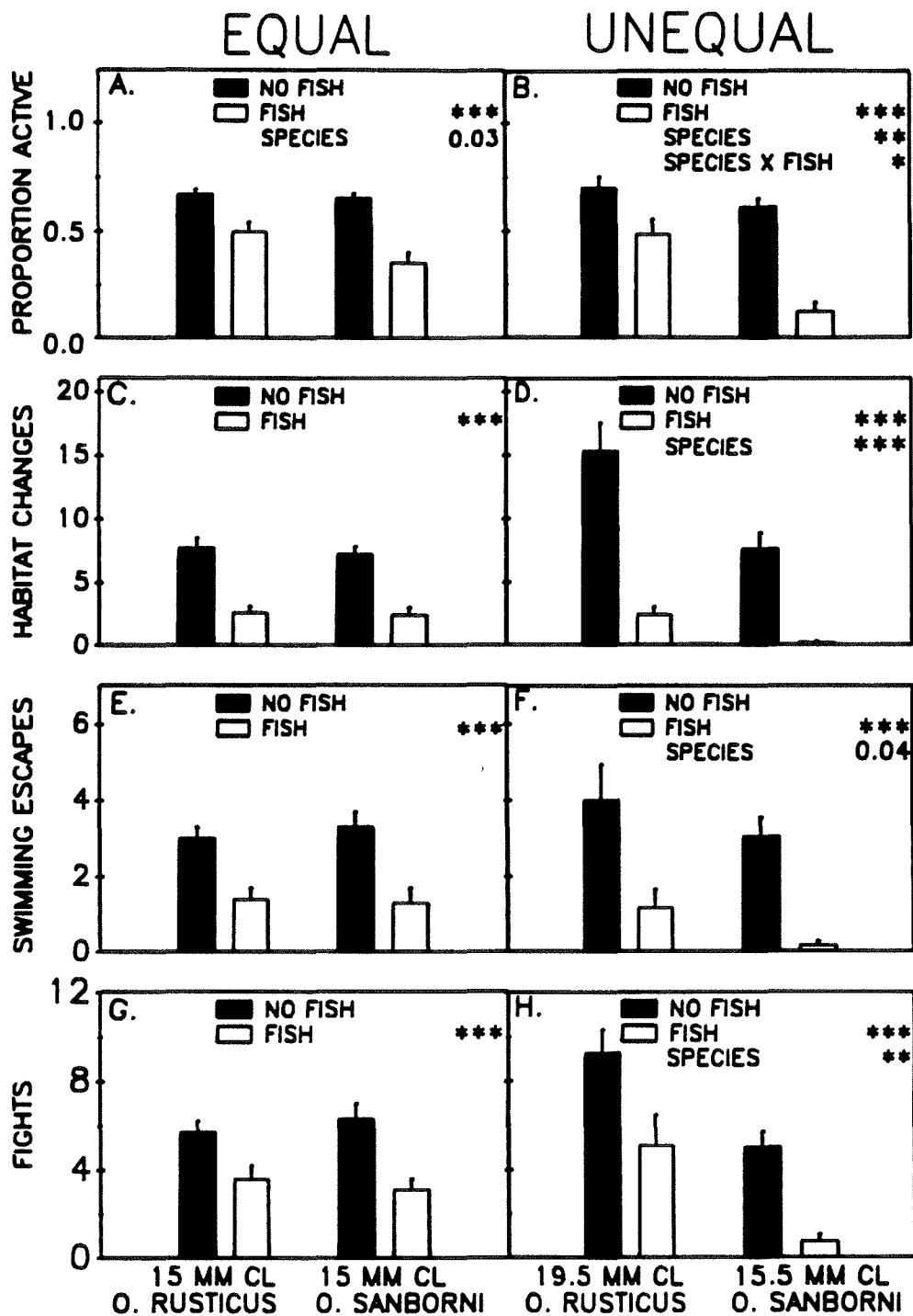
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FIG. 4. Effect of fish on (A and B) proportion active, (C and D) habitat changes, (E and F) swimming escapes, and (G and H) fights of *O. rusticus* and *O. sanborni*. In the left-hand panels, both crayfish species were of equal size (N = 7–9); in the right-hand panels, crayfish were of unequal size, reflecting a natural size difference (N = 3). Data are means ± 1 SE. A four-way ANOVA tested for effects of fish predators, crayfish species, adult crayfish, and shelters on juvenile crayfish activities and behaviors. When necessary to stabilize the variance, data were transformed (proportions, arcsin transformation, other data, log transformation). Because five nonlethal responses were measured, trends were considered significant at the $p \leq 0.05/5$ or $p \leq 0.01$ level. NS, $p > 0.01$; *$p \leq 0.01$; **$p \leq 0.001$; ***$p \leq 0.0001$. Significant SS, F, df are given in the text.

unequal size, fish reduced activity of the small, vulnerable *O. sanborni* more than the large, less-vulnerable *O. rusticus* (Fig. 4B: species × fish, SS = 0.44, F = 6.95, df = 47, p = 0.01).

Without fish, equal-sized *O. rusticus* and *O. sanborni* changed habitats with similar frequency (Fig. 4C). However, when sizes reflected a natural size difference, large *O. rusticus* changed habitats more than twice as often as small *O. sanborni*

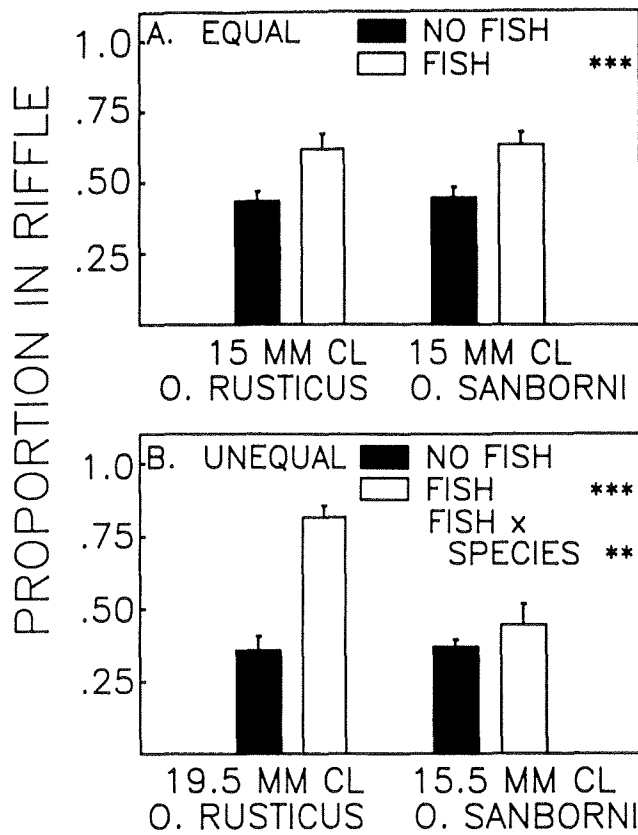*Can. J. Fish. Aquat. Sci., Vol. 50, 1993*

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FIG. 5. Effect of fish on habitat use by *O. rusticus* and *O. sanborni*. (A) Both crayfish species were of equal size ($N = 8$); (B) crayfish were of unequal size, reflecting a natural size difference ($N = 3$). Data are means ± 1 SE. A four-way ANOVA tested for effects of fish predators, crayfish species, adult crayfish, and shelters on juvenile crayfish habitat use. When necessary to stabilize the variance, data were arcsin transformed. Because five nonlethal responses were measured, trends were considered significant at the $p \leq 0.05/5$ or $p \leq 0.01$ level. *$p \leq 0.01$; **$p \leq 0.001$; ***$p \leq 0.0001$. Significant SS, F, df, and p values are given in the text.

(Fig. 4D: SS = 7.66, $F = 26.68$, df = 47, $p = 0.0001$). With fish, habitat changes declined precipitously for both species and both sizes (Fig. 4C: SS = 786.65, $F = 65.11$, df = 127, $p = 0.0001$; Fig. 4D: SS = 37.41, $F = 130.38$, df = 47, $p = 0.0001$).

Without fish, equal-sized crayfish of both species escaped aggressive threats with a similar swimming response (Fig. 4E). Fish reduced this risky behavior for both crayfish species and sizes (Fig. 4E: SS = 13.70, $F = 38.43$, df = 127, $p = 0.0001$; Fig. 4F: SS = 12.89, $F = 45.24$, df = 47, $p = 0.0001$). Without fish, equal-sized crayfishes fought with similar frequency regardless of species (Fig. 4G). When of unequal size, large *O. rusticus* fought more than small *O. sanborni* (Fig. 4H: SS = 7.36, $F = 17.20$, df = 47, $p = 0.0002$). Fish reduced the number of fights in both species and both sizes (Fig. 4G: SS = 11.76, $F = 25.08$, df = 127, $p = 0.0001$; Fig. 4H: SS = 13.83, $F = 32.32$, df = 47, $p = 0.0001$).

Without fish, equal-sized crayfish did not prefer either habitat (riffles 38%/1 m² versus pools 62%/2 m²; Fig. 5A). With fish, when crayfish were of equal size, both crayfishes increased riffle use and reduced use of dangerous pools (Fig. 5A: SS = 1.05, $F = 18.18$, df = 127, $p = 0.0001$). When crayfish were unequal in size, large, less vulnerable *O. rusticus*

increased their use of riffles (82%) and reduced their use of risky pools (18%; Fig. 5B), but small, more vulnerable *O. sanborni* did not shift habitats in response to fish (fish × species, SS = 00.44, $F = 13.56$, df = 47, $p = 0.0008$). Possibly any movement of these small, vulnerable crayfish triggered a lethal attack.

Adult Effects

Adult crayfish did not alter the number of juvenile crayfish eaten for either species or size (Fig. 3). When crayfish were of equal size, *O. rusticus* activities (proportion active and habitat changes) were uninfluenced by adults (Fig. 6A, 6C); *O. sanborni* activity, however showed a biologically suggestive, albeit nonsignificant, increase when adults were present (Fig. 6A: proportion active, adult × species, SS = 0.23, $F = 5.57$, df = 119, $p = 0.02$; Fig. 6C: habitat changes, SS = 61.44, $F = 5.09$, df = 127, $p = 0.03$). The adult effect on activity was in the opposite direction of the fish effect (Fig. 4A and 4C versus Fig. 6A and 6C: fish × adult, SS = 80.55, $F = 6.68$, df = 127, $p = 0.01$).

When crayfish were the same size, adult crayfish dramatically increased swimming escapes for both species (Fig. 6E: SS = 6.41, $F = 17.97$, df = 127, $p = 0.0001$); *O. sanborni* was again more affected by adults than was the invader *O. rusticus* (Fig. 6E: species × adult, SS = 2.20, $F = 6.17$, df = 127, $p = 0.01$). Adults increased the number of fights for both species when crayfish were of equal size (Fig. 6G: SS = 4.93, $F = 10.51$, df = 127, $p = 0.002$). When crayfish were of unequal-size, adult crayfish had no effect on crayfish activity (Fig. 6B, 6D) or behavior (Fig. 6F, 6H), probably because of low sample size and low power ($N = 3$). Neither adults nor shelters affected habitat use for either size or species of crayfish.

Discussion

Direct, Lethal Fish Effects

Both in the field and in our simulated stream, fish predators directly reduced numbers of both crayfishes. In the field survey, when fish were scarce, many factors affect crayfish abundance, and crayfish densities vary widely across sites. But at the few sites where fish were abundant, crayfish density was consistently low, suggesting that fish predators adversely affect crayfish. Although these high-density sites were limited in number, we believe that they demonstrate an important, real trend.

Similarly, predators influence community structure in many systems (Connell 1975), including lakes (Brooks and Dodson 1965; Hall et al. 1970) and ponds (Crowder and Cooper 1982; Morin 1984a, 1984b). In streams, the role of predation is less clear. Some stream predators reduce prey numbers by consumption (Oberndorfer et al. 1984; Power et al. 1985). Others reduce prey numbers only in certain streams (Wilzbach et al. 1986) or of select taxa (Flecker 1984; Walde and Davies 1984). Still other predators have no effect on prey number (Allan 1982; Reice 1983; Flecker and Allan 1984; Reice and Edwards 1986; Culp 1986).

In our view, stream communities where predators have little effect differ predictably from those communities where predators reduce prey number. For example, predator effects are probably unimportant in streams where the following conditions occur: (1) the habitat is highly heterogeneous
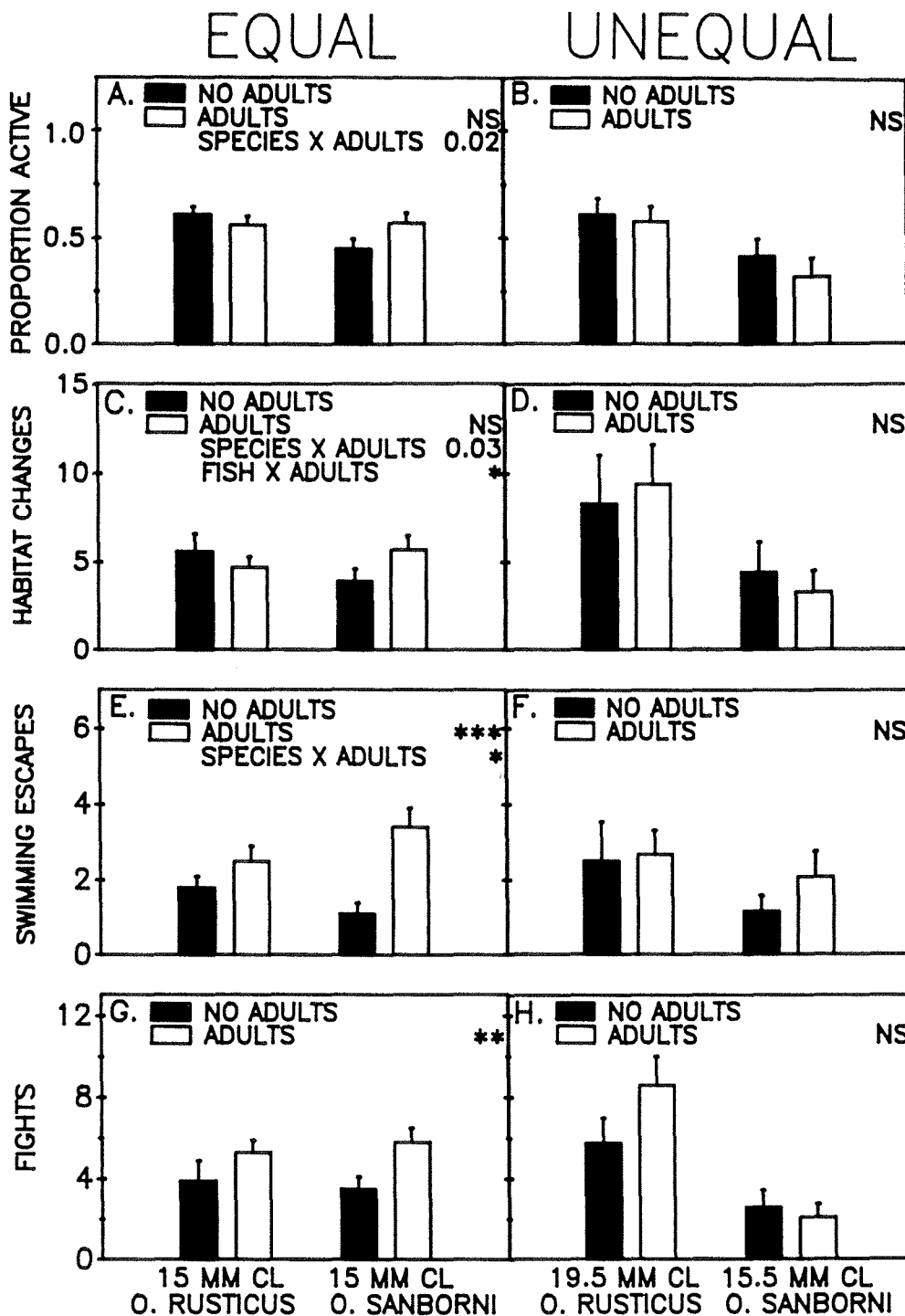
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FIG. 6. Effect of adults on (A and B) proportion active, (C and D) habitat changes, (E and F) swimming escapes, and (G and H) fights by *O. rusticus* and *O. sanborni*. In the left-hand panels, both crayfish species were of equal size ($N = 7-9$); in the right-hand panels, crayfish were of unequal size, reflecting a natural size difference ($N = 3$). Data are means ± 1 SE. A four-way ANOVA tested for effects of fish predators, crayfish species, adult crayfish, and shelters on juvenile crayfish habitat use. When necessary to stabilize the variance, data were arcsin or log transformed. Because five nonlethal responses were measured, trends were considered significant at the $p \leq 0.05/5$ or $p \leq 0.01$ level. $*p \leq 0.01$; $**p \leq 0.001$; $***p \leq 0.0001$. Significant SS, F, df, and p values are given in the text.

(Brusven and Rose 1981; Allan 1982, 1983), (2) abiotic conditions are extreme (Peckarsky 1983, 1985; Walde 1986; Schlosser and Ebel 1989), (3) prey immigration rates are high (Flecker and Allan 1984; Cooper et al. 1990), (4) prey demonstrate strong affinity for specific substrate types (Reice 1983; Flecker and Allan 1984), (5) top predators interact weakly with prey (sensu Paine 1980), (6) invertebrate predation compensates for fish predation (Soluk and Collins 1988a, 1988b, 1988c), or (7) where indirect nonlethal effects are not quantified. In our system, we speculate that these conditions

were absent. For example, in our streams, habitat heterogeneity was limited and large-bodied crayfish were relatively unaffected by abiotic disturbances. Crayfish, as active walkers and swimmers, probably drifted infrequently and were not restricted to specific substrates. Crayfish are strongly preferred by smallmouth bass (Stein 1977; Probst et al. 1984; Rabeni 1992), an efficient predator that can consume a wide range of crayfish sizes, and were probably unaffected by invertebrate predators. For these reasons, we speculate that fish predators numerically reduced crayfish prey in our survey and laboratory stream and also contribute to the replacement of *O. sanborni* by *O. rusticus* in Ohio streams.

Indirect, Nonlethal Fish Effects

Predator-induced habitat shifts and other nonlethal, indirect effects also influence prey survival, growth, and reproduction. In our experiments, smallmouth bass reduced crayfish activity, aggressive behaviors, and pool use. In another survey exploring this replacement, crayfish at sites with fish predators were smaller and less dense than at sites without fish, suggesting that predators also influence crayfish growth and habitat use in the field (Mather and Stein 1993). Similar indirect predator effects have been widely reported. For example, fish predators alter the distribution and activities of other stream prey (Stein and Magnuson 1976; Peckarsky 1980; Fraser and Cerri 1982; Sih 1982; Collins et al. 1983; Cooper 1984; Dill and Fraser 1984; Power 1984; Power et al. 1985; Schlosser 1987). Indirect, nonlethal predator effects or a combination of direct and indirect effects appear to be more common in streams than prey reductions due to direct consumption alone (Peckarsky and Dodson 1980; Petranka 1983; Hildrew et al. 1984; Power et al. 1985; Bowlby and Roff 1986; Feltmate and Williams 1989). Whether this is an inherent quality of stream systems is unclear. For the Ohio replacement, clearly both direct and indirect effects were important.

In our work, juvenile activity was inconsistently related to survival. Whereas increased activity has negative consequences, i.e., attracts predators, increased activity also may have positive consequences, i.e., lead to increased feeding, opportunities to change habitats, and advantages in competitive encounters. When crayfish were small, increased activity probably consistently increased predation risk, but when crayfish were larger and able to repel initial fish attacks, increased activity, habitat changes, fights, and swimming escapes probably provided crayfish with a chance to escape attack. Hence, size plays an important part in determining how increased crayfish activity affects survival.

Among other crayfish, size-related aggression can cause differential feeding (Lorman 1975) and habitat use (Butler and Stein 1985; Rabeni 1985). In our experiments, responses of juveniles to adults were counter to those elicited by fish; thus, the presence of adults could further increase predation risk for juvenile crayfish. Our work with field patterns and individual behavioral responses supports the hypothesis that size-mediated predation contributes to the replacement. Our experiments show that (1) fish prefer small over large crayfish, (2) fish reduce activity and frequency of all behaviors of small crayfish more than large crayfish, and (3) adult crayfish may exacerbate the predator–prey interaction. Thus, through a variety of mechanisms, size affects this replacement. Because the displaced native *O. sanborni* is smaller than the invader, fish predators may differentially reduce both survival and growth of *O. sanborni*.

Shelter Effects

In other systems, habitat heterogeneity modifies interactions between predators and prey by providing refuges (Stein 1977; Brusven and Rose 1981; Savino and Stein 1982; Holomuzki 1989) or by affecting dispersal (Huffaker 1958). Predators can also influence substrate choice (Feltmate et al. 1986); conversely, substrate can alter patterns of selective predation (Peckarsky and Penton 1989). Surprisingly, shelters in our study did not modify juvenile crayfish survival, activity, or behavior. Apparently, crayfish had other behavioral options available; reducing activity, flattening against the substrate, shifting into riffles, and using shelters were all common responses. If shelterless when a fish appeared, these responses appeared to be more appropriate than shelter-seeking. Because *O. rusticus* and *O. sanborni* did not differ in response to shelters, habitat heterogeneity per se probably does not contribute to the replacement. However, if refuges are limited in streams, being small could be especially risky. Because *O. sanborni* is smaller than *O. rusticus*, under conditions of shelter limitation, the native, again, might be disadvantaged.

Species Replacement

Abiotic Factors

No evidence exists that abiotic factors influence replacement rates (Capelli and Magnuson 1983; Flynn and Hobbs 1984). Neither in Wisconsin (Capelli 1982; Capelli and Magnuson 1983) nor in Ohio (Mather 1990) do lakes and streams containing *O. rusticus* appear to differ abiotically from adjacent environments without the invader. Therefore, we believe that abiotic factors are less important than biotic ones.

Species

Species-specific differences in competitive ability exist among orconectid crayfish (Bovbjerg 1970). Equal-sized *O. rusticus* are innately more aggressive than the native crayfish *O. virilis* in northern Wisconsin (Capelli and Munjal 1982). Unlike this Wisconsin replacement, in Ohio, innate species differences are less important than body size (Butler and Stein 1985). Our work further demonstrates that *O. sanborni* and *O. rusticus* differ little except that *O. rusticus* (1) is less susceptible to adult aggression, (2) is larger, and (3) tends to be more active. Because *O. sanborni* is more similar to *O. rusticus* than the displaced Wisconsin species, mechanisms underlying the Ohio replacement are, we think, more subtle. In turn, these similarities may explain why the replacement is occurring relatively slowly in Ohio streams.

Size

For other animals, as size increases, predation risk declines (Werner and Gilliam 1984; Semlitsch and Gibbons 1988). Similarly, big crayfish are eaten less frequently than small crayfish. Crayfish reach an invulnerable size (measured as TL) at about 20% of fish predator length (Stein 1977); in this study, large *O. rusticus* 19.5 mm CL were 15% of predator length and approaching the size refuge. Hence, body size has a critical impact on the outcome of crayfish interactions, especially predator–prey relationships.

Size had at least three other effects. First, without fish, big crayfish shifted habitat, swam, and fought more than small crayfish. Where these activities confer an advantage, large

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crayfish should benefit. Second, as in other size-structured communities (Sih 1982; see Sih 1987 for a more complete review), more vulnerable, small *O. sanborni* reduced activity more in response to the fish threat than the less vulnerable, large *O. rusticus*. If reduced activity reduces long-term growth, then *O. sanborni* should suffer disproportionately. Third, in the equal-size experiments, both species shifted into riffles with fish; however, when of unequal size, only the large juveniles shifted, suggesting that interactions between large and small juveniles prevented riffle use by small *O. sanborni*. Because large nonadults also can affect small juveniles negatively, rapid growth should always be favored for crayfish and larger size should be an advantage to *O. rusticus*.

Relationships among prey species, size, activity, and predation rates are complex. We examined individual behaviors and assumed that these reponses would translate into population-level effects. However, crayfish population dynamics are not well understood and compensatory mechanisms could affect these populations. To test our conclusions, population responses of the two species should be examined explicitly.

Rates of Replacement

Because the exact time of each introduction of *O. rusticus* is unknown, rates of replacement in the field and how fish, adults, and shelters influence these rates are unknown. However, based on data herein, we postulate that fish predators accelerate this crayfish species replacement and that adult crayfish affect the replacement by exacerbating this predator–prey interaction. Thus, both indirect and direct effects of predation, mediated through size, play an important role in the replacement of *O. sanborni* by *O. rusticus* in Ohio streams.

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