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Probable Displacement of Riffle-Dwelling Invertebrates by the Introduced Rusty Crayfish, *Orconectes Rusticus* (Decapoda: Cambaridae) in a North-Central Wisconsin Stream

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PROBABLE DISPLACEMENT OF RIFFLE-DWELLING INVERTEBRATES BY THE INTRODUCED RUSTY CRAYFISH, *ORCONECTES RUSTICUS* (DECAPODA: CAMBARIDAE), IN A NORTH-CENTRAL WISCONSIN STREAM

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ABSTRACT

The rapid northward range expansion of the rusty crayfish, *Orconectes rusticus*, and its negative effects on Wisconsin lakes have been the subjects of intense study throughout the last fifteen years. In this study, we investigated the possible impact of rusty crayfish on the benthic macroinvertebrate community structure of the Prairie River in north-central Wisconsin. Rusty crayfish and other invertebrates were collected during August and September, 1994, from three sections of the Prairie River. Rusty crayfish relative abundance increased significantly from the upper to middle, and middle to lower sections; and correlated negatively with a significant 77% decrease in total density of aquatic invertebrates between sections. Mean density of all important invertebrate families and trophic guilds decreased significantly between the upper and lower sections. Due to the similarity of most environmental conditions between river sections, decrease of invertebrates is attributed to the increased abundance of rusty crayfish and its interactions with the native fauna. Our results suggest that a high abundance of rusty crayfish may negatively impact Wisconsin lotic systems.

The rusty crayfish, *Orconectes rusticus* (Girard), is native to the Ohio River Drainage and was introduced to Wisconsin circa 1960 (Olsen et al. 1991) largely through escaping from angler bait containers (Lodge and Hill 1994). Since then it has greatly increased its range by moving up Wisconsin rivers, expanding its thermal tolerance range, and avoiding Wisconsin predatory fish (Maude and Williams 1983, Mundahl 1989, DiDonato and Lodge 1993, Willman et al. 1994). Rusty crayfish are now found in all of Wisconsin's major drainage basins except the Trempealeau-Black (Hobbs and Jass 1988) and in the littoral zone of many Wisconsin lakes (McBride 1983). The rusty crayfish is considered detrimental to Wisconsin lentic systems as it has altered primary production and decreased habitat by consuming rooted aquatic macrophytes; displaced native congeners with its aggressive behavior, large size, and fast growth; altered benthic productivity by consuming snails and other invertebrates; and lowered recruitment of many fish species by consuming fish eggs and fry (Magnuson et al. 1975, Lorman 1980, Capelli 1982,

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Lodge et al. 1985, Olsen et al. 1991, Hill et al. 1993, Lodge and Hill 1994, Lodge et al. 1994).

When we began this study we found no published literature addressing rusty crayfish effects on lotic systems. However, many observations from both the Wisconsin Department of Natural Resources (WDNR) and Wisconsin residents suggested that substantial decreases in invertebrate densities had occurred in some pristine Wisconsin trout streams following the appearance of rusty crayfish. Fishery managers were concerned that lower macroinvertebrate densities may not sustain trout populations in streams invasible by rusty crayfish. The purpose of this study was to address this concern by determining if rusty crayfish abundance corresponded with density or diversity of aquatic invertebrates in a cold-water stream.

MATERIALS AND METHODS

Study Site. The Prairie River arises in Langlade County, Wisconsin and flows for approximately 69 kilometers, southwest, through a watershed comprised of 70% forested and 30% agricultural lands until its confluence with the Wisconsin River in Lincoln County. The upper Prairie is classified by the WDNR (1980) as a high-grade trout fishery (Class I) with naturally reproducing populations of brook trout, *Salvelinus fontinalis* (Mitchill), rainbow trout, *Oncorhynchus mykiss* (Waulbaun), and brown trout, *Salmo trutta* L. The river downstream of Wisconsin State Highway 17 is classified as a medium-grade trout fishery (Class II) requiring limited stocking to maintain fishable trout populations (Figure 1). This reclassification is attributed to a natural warming of the water due to a decrease in upwelling of cold springwater, and a gradual widening of the river with loss of canopy cover and increase in solar radiation (M. O. Johnson - WDNR Area Fishery Manager, personal communication). According to WDNR officials, rusty crayfish have been

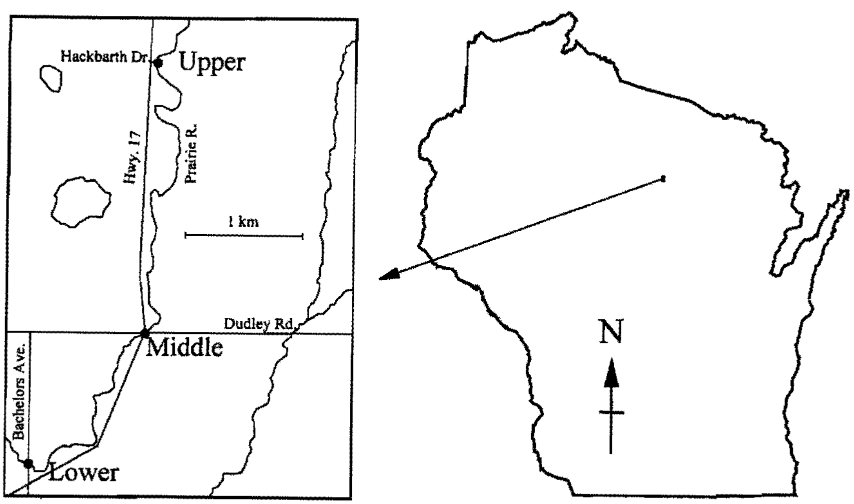

Figure 1. Location of our study sites in Lincoln County, Wisconsin.

abundant in the lower reaches of the Prairie River since the mid 1980s. However, rusty crayfish appeared to not have colonized the upper reaches of the Prairie River, possibly due to lower water temperature. This offered an opportunity to study their interactions with native fauna.

We sampled three sections of the river (Figure 1) based on our previous inspections: the upper section (Hackbarth Drive) appeared to not have been colonized by rusty crayfish, the lower section (Bachelor's Avenue) had a high observed abundance of rusty crayfish, and the middle section (Highway 17) appeared to be intermediate in rusty crayfish abundance. Physical and chemical data were collected from two riffles within each section during July and August, 1994. Fish populations were sampled during the same period by electrofishing and the number of each species caught per section was expressed as a percent of the total catch. Substrate composition was measured by randomly placing a surber sampler in three riffles of each section and determining the relative abundance of each substrate type. Habitat and riparian vegetation were observed in all three sections.

Invertebrate Sampling. Three stream riffles were selected from each section. Three sample points were selected from each riffle and their physical properties measured to assure homogeneity of points. All sample points had mixed substrate (sand, gravel, cobble), water depth of 23.4–31.2 cm, current velocity of 0.69–1.19 m/s, and little macrophyte growth. Benthic invertebrates were collected at each point during August and September, 1994, with a Hess sampler composed of #30 Nitex™ mesh and with an area of 0.058 m^2. The sampler was set into the substrate to the level of impenetrability. Pieces of substrate approximately 3 cm or larger were brushed off into the sampler and then removed from the sampling area. The remaining substrate was then disturbed for about one minute. Dislodged invertebrates were removed from the Hess sampler netting, preserved in 80% isopropyl alcohol, transported to the laboratory, and identified to the lowest taxon possible. The number of invertebrates in each family from each Hess sample was extrapolated to estimate density per square meter. Mean familial and total density (number of individuals per m^2) per riffle were then calculated from these data. Taxa represented by less than twenty individuals were grouped together in density calculations. Epineustonic invertebrates captured were not included in calculations.

The Family Biotic Index (FBI) and percent by count Ephemeroptera, Plecoptera, and Trichoptera (EPT) were used as stream water quality indicators (Hilsenhoff 1988, Plafkin et al. 1989, Wallace et al. 1996). The Shannon Diversity Index was used to assess invertebrate diversity in each section (e.g. DeJong 1975). Taxa were grouped into generic-level trophic guilds based on Merritt and Cummins (1996) to assess trophic guild composition in each section. Invertebrates with an undetermined trophic guild (e.g. nematodes), or in a non-feeding state (pupae), were not included in calculations. Familial and trophic guild compositions between sections were analyzed using Nested ANOVA. This and all other statistical analyses followed Zar (1984) using Statisical Analysis System (SAS) software (SAS Institute 1985).

Crayfish Sampling. Crayfish were captured after their molting period using wire-mesh crayfish traps, baited with chicken livers, during August and September, 1994 (Capelli 1982, Sommers and Stechy 1986). In each section, one trap was placed in each riffle where Hess samples were taken, two traps were placed in runs adjacent to the riffles, and one trap was placed in a pool for a total of six traps per section. Traps were set three times for 18–24 h each time, with a 48 h interval between settings. Captured crayfish were identified to species (Capelli 1975), sexed, and measured. Crayfish with total carapace length ≥20mm were considered adults (Hobbs and Jass 1988). No differentiation was made between Form I and Form II males. All individuals were released on site. The total number of juvenile, adult male, and adult female rusty crayfish caught in each section were recorded. Since traps do not accurately quantify total rusty crayfish abundance due to a variety of factors, and are 80–100% selective for adult males, the total number of adult males caught in each section was considered a measure of relative rusty crayfish abundance in each section (Capelli 1975, Capelli 1982, Sommers and Stechy 1986). The number of adult male rusty crayfish caught in each section were compared with Chi-square Goodness of Fit tests.

RESULTS

Orconectes rusticus was the only species of crayfish captured although *O. propinquus* (Girard) and *O. virilis* (Hagen) are both reported from this region (Hobbs and Jass 1988; M. O. Johnson, pers. comm.). Numerous rusty crayfish were captured in our Hess samples when sampling for invertebrates. The number of both total and adult male rusty crayfish caught were significantly different among sections (Chi-square Goodness of Fit, $p < 0.001$ for both) and increased significantly from upper to middle, and middle to lower sections (Pairwise Chi-square Goodness of Fit with Yates Correction, $p < 0.001$ for all pairwise comparisons) (Figure 2). Only juvenile rusty crayfish were found in the upper section and 83% of these had missing or broken appendages. Juvenile rusty crayfish were not found in the other sections.

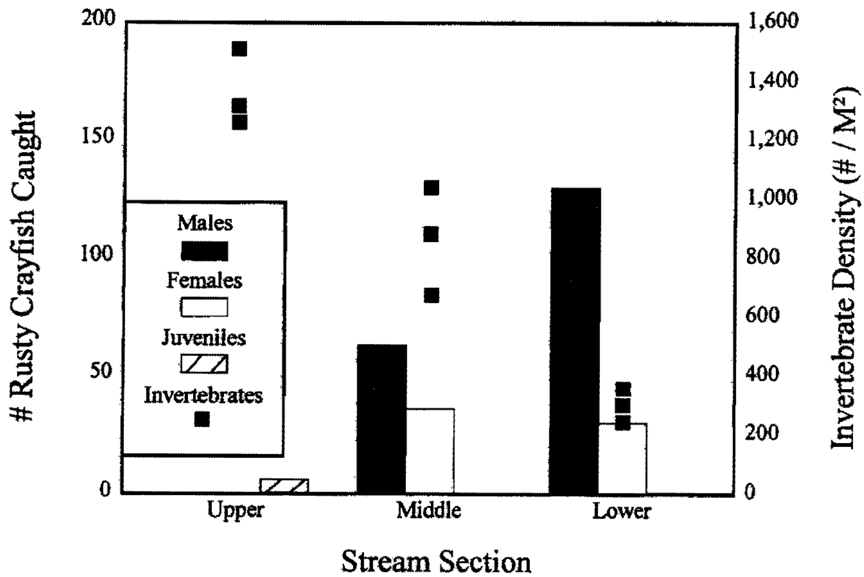

Figure 2. Invertebrate density and the number of rusty crayfish caught in three sections of the Prairie River, Wisconsin, collected during August and September, 1994. Each invertebrate marker represents the mean total density from a riffle.

Table 1. Mean invertebrate density (number per square meter) from three sections of the Prairie River, Wisconsin, during August and September, 1994; p values were calculated using Nested ANOVA.

Invertebrate Family	Upper (U) Mean Density	Change (U–M)	Middle (M) Mean Density	Change (M–L)	Lower (L) Mean Density	Change (U–L)	p
Hydropsychidae	377.4	+12%	423.4	–68%	134.1	–64%	0.043
Chironomidae	369.7	–68%	118.8	–56%	51.7	–86%	0.000
Perlidae	132.2	–83%	23.0	–67%	7.7	–94%	0.000
Elmidae (Larvae)	101.5	+17%	118.8	–79%	24.9	–75%	0.000
Baetidae	97.7	–53%	46.0	–83%	7.8	–92%	0.004
Elmidae (Adults)	80.5	–83%	13.4	–86%	1.9	–98%	0.000
Athericidae	72.8	–34%	47.9	–40%	28.7	–61%	0.023
Heptageniidae	49.8	–69%	15.3	–88%	1.9	–96%	0.003
Others*	91.9	–44%	51.7	–4%	41.1	–42%	
All	1375.5	–37%	865.9	–64%	308.4	–77%	0.000

*The families Aselidae, Brachycentridae, Corydalidae, Gammaridae, Glossosomatidae, Ephemeridae, Hydrophilidae (larvae), Hydropsychidae (pupae), Isonychiidae, Limnephilidae (pupae), Lumbricidae, Psychomyiidae, Tipulidae, and the Phylum Nematoda were represented by less than 20 individuals each and were grouped together in density calculations. The artificiality of this category precludes statistical analysis.

Total macroinvertebrate density decreased by 37% from the upper to middle section and 64% from the middle to lower section, for a total decrease of 77% (Table 1). Mean density of all invertebrate families from which at least 20 individuals were collected decreased significantly between sections (Nested ANOVA); although hydropsychid and elmid larvae decreased only between the middle and lower sections (Table 1). Total invertebrate density correlated negatively with the number of adult male rusty crayfish caught ($r = -0.999985$, $p = 0.0026$, $n = 3$) (Figure 2). Most important genera and identifiable species remained in all three sections (Table 2). Of the 25 taxa that we identified, six were confined to the upper section. Of these taxa, five were represented by only one specimen. Past qualitative stream surveys have also shown a similar generic and specific composition between our sites (WDNR unpublished databases).

Mean density of all trophic guilds except shredders decreased significantly between sections; although filter feeders decreased only between the middle and lower sections (Nested ANOVA) (Figure 3). FBI was constant and neither EPT nor Shannon's Index was positively or negatively correlated between sections (Table 3).

We found no important differences in physical and chemical properties between sections except for temperature which gradually increased downstream (Table 3). Habitat was similar between sections. Riparian vegetation was common with sedges, *Carex* spp., tag alders, *Alnus rugosa* DuRoi, and ferns, *Onoclea* spp., abundant in all three sections. Fish species composition remained similar between sections although salmonids decreased between the upper and lower sections and catostomids increased (Table 4). This concurs with WDNR data for this area of the Prairie River and corresponds to the Prairie River's reclassification from a Class I to a Class II stream (Steuk et al. 1977, WDNR 1980, Carlson and Andrews 1982).

Table 2. List of taxa collected from three sections of the Prairie River, Wisconsin, during August and September, 1994.

Taxon	Stream Section	Taxon	Stream Section
Lumbriculidae		Trichoptera	
Lubricidae		Brachycentridae	
Lumbricus sp.	U, M, L	*Brachycentrus numerosus* (Say)	U
Ephemeroptera		*Brachycentrus occidentalis* Banks	U
Baetidae		Glossosomatidae	
Baetis spp.	U, M, L	*Glossosoma* sp.	U
Heptageniidae		Hydropsychidae	
Stenonema sp.	U, M, L	*Ceratopsyche* spp.	U, M, L
Ephemeridae		*Cheumatopsyche* spp.	U, M, L
Ephemera simulans Walker	U, L	Limnephilidae	
Isonychiidae		*Pycnopsyche* sp.	U
Isonychia sp.	U, M	Psychomyiidae	
Plecoptera		*Psychomyia flavida* Hagen	U
Perlidae		Diptera	
Acroneuria sp.	U, M, L	Athericidae	
Agnetina capitata (Picket)	U, M	*Atherix variagata* Walker	U, M, L
Paragnetina media (Walker)	U, M, L	Chironomidae	U, M, L
Megaloptera		Tipulidae	
Corydalidae		*Antocha* sp.	U, M, L
Nigronia serricornis (Say)	U, L	*Tipula* sp.	U, M, L
Coleoptera		Amphipoda	
Elmidae		Gammaridae	
Optioservis spp.	U, M, L	*Gammarus pseudolimnaeus*	
Stenelmis spp.	U, M, L	Bousfield	U, M, L
Hydrophilidae	U	Asellidae	
Tropisternus sp.	U	*Asellus intermedius* (Morgan)	U, M, L
		Nematoda	U, M, L

DISCUSSION

It appears, due to the strong negative correlation between them, that the decrease in benthic invertebrate density was brought about by the increasing abundance of rusty crayfish. This assumes that the prevalence of rusty crayfish was the only difference between our study sites that would cause this invertebrate decrease. The three sections were separated by 4 km of virtually contiguous forest and were without major tributaries between them. We believe no significant source of organic input occured throughout the sampling area as indicated by our FBI and EPT values. Sampled riffles exhibited similar physical characteristics. Habitat, substrate, chemical, and fish population data were similar between sections.

The warming of the river due to decreased spring-water upwelling and increased solar radiation to the lower reaches of the Prairie River account for its reclassification from a Class I to a Class II trout stream and may explain the increase of catostomids as well. Based on the stream continuum concept (Cummins 1977, Vannote et al. 1980), these are natural, gradual morphological changes in the lotic continuum and cannot explain the dramatic decrease in aquatic invertebrate density that we have documented. Taxa replacement may occur in the lower reaches of a stream as temperature and primary production increase, and allochthonus input decreases. However, most impor-

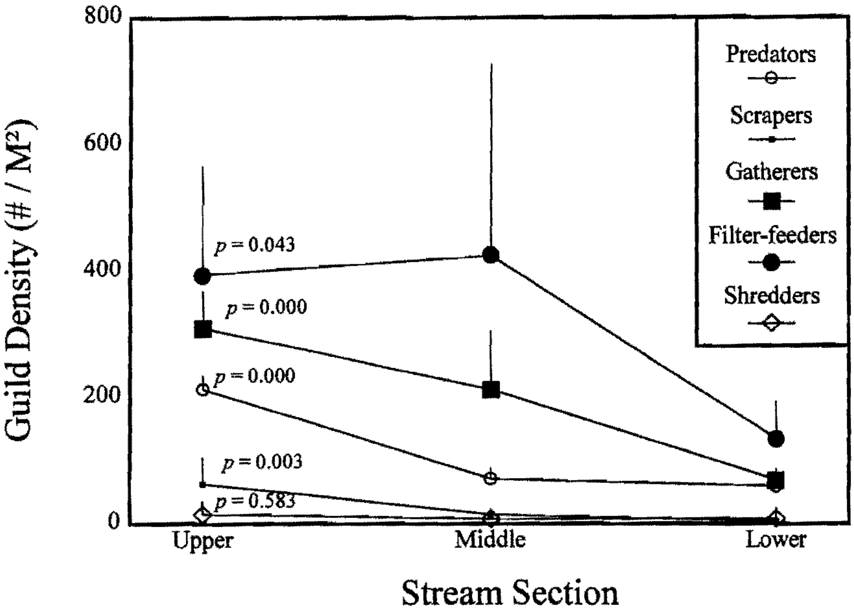

Figure 3. Mean and upper CI of invertebrate trophic guild densities in three sections of the Prairie River, Wisconsin, collected during August and September, 1994; p values for each guild calculated using Nested ANOVA

tant genera and species remained in all of our sections. This suggests that the observed temperature increase was not important enough to stimulate notable taxa replacement over the short distance between our sites.

Furthermore, overall ecosystem productivity as well as invertebrate density often increase in the mid-reaches of a river while we documented significantly decreasing densities for all important taxa and important riffle-dwelling trophic guilds. Invertebrates in the scraping and filter-feeding guilds typically increase in density in the mid-reaches of a river due to increased prevalence of periphyton and CPOM (Cummins 1977, Vannote et al. 1980). The Prairie River filter-feeders (hydropsychid caddisflies) exhibited some increase between our upper and middle sections, and then decreased between the middle and lower sections; scrapers exhibited the largest percent decrease between sections of all trophic guilds (Figure 3).

Quantitative historical invertebrate data for this reach of the Prairie River are lacking, precluding a comparison to the invertebrate assemblage before the appearance of rusty crayfish. However, our study indicates that rusty crayfish may have impacted this particular benthic macroinvertebrate community. It may have done so by preying directly on invertebrates, out-competing them for food, and out-competing them for space. Rusty crayfish are opportunistic omnivores which have been observed as predators, scrapers, collector-gatherers, herbivores, detritivores, and carrion feeders (Magnuson et al. 1975, Olsen et al. 1991, Lodge et al. 1994, Willman et al. 1994)

Table 3. Water physical, chemical, and community metric data collected from two riffles within three sections of the Prairie River, Wisconsin, during July and August, 1994. FBI = Family Biotic Index; EPT = percent by count Ephemeroptera, Plecoptera, and Trichoptera; H′ = Shannon Diversity Index; R/G, S, D, and V = relative percent of rubble/gravel, sand, detritus, and vegetation, respectively, in the substrate of each section.

Section	Temp (°C)	pH	D.O. (ppm)	Alk. (mg/l)	Hard. (mg/l)	K (mho)	FBI	EPT	H′	R/G	S	D	V
Upper	14.8	7.5	10.5	51.0	88.0	0.07	4.1	51%	2.9	83	12	5	1
Upper	15.4	7.5	10.0	85.6	102.7	0.13							
Middle	18.6	8.0	8.9	73.3	110.0	0.17	4.1	60%	2.4	81	11	7	1
Middle	19.2	7.5	9.8	48.7	75.5	0.14							
Lower	21.8	8.6	10.3	85.5	108.3	0.17	4.1	53%	2.7	79	12	6	2
Lower	23.8	8.3	10.1	51.3	102.6	0.15							

Table 4. The number of each fish species caught, expressed as a percent of the total catch, combined from two riffles in each of three sections of the Prairie River, Wisconsin, collected during July and August, 1994.

Species	Upper	Middle	Lower
Catostomous commersoni (Lacepede)	1	5	12
Cottus bairdi Girard	12	13	9
Etheostoma flabellare Rafinesque	–	1	4
Etheostoma nigrum Rafinesque	–	1	–
Hypentelium nigricans (Lesueur)	1	10	16
Ichthyomyzon fossor Reighard and Cummins	–	–	4
Luxilus cornutus Mitchill	–	–	3
Percina caprodes (Rafinesque)	–	1	1
Oncorhyncus mykiss (Waulbaum)	2	1	–
Rhinichthys atratulus (Hermann)	12	17	10
Rhinichthys cataractae (Valenciennes)	6	15	12
Salmo trutta L.	22	12	6
Salvelinus fontinalis (Mitchill)	43	23	19
Semotilus atromaculatus (Mitchill)	–	–	3

which gives them many opportunities to affect aquatic ecosystems. Studies on *Orconectes propinquus* in Michigan streams have shown it to be a keystone consumer and predator; being able to influence abundances of invertebrate taxa through direct predation, spatial competition, and manipulation of benthic habitat through grazing (Paine 1966, Hart 1992, Creed 1994). In the Ontonagon River in northern Michigan, *O. rusticus* decreased macroinvertebrate densities by 47–79% in enclosures while crayfish and macroinvertebrate densities were inversely related in the stream itself (Charlebois 1994). Based on these past studies and our observations, we believe that the rusty crayfish is responsible for the decrease in invertebrate density occurring in the Prairie River.

It also appears that the colder water temperatures are keeping rusty crayfish from the upper reaches of the Prairie River. In their native range, rusty crayfish may be exposed to a temperature range of 0–39° C and have subsequently developed the ability to physiologically and behaviorally adjust their thermal tolerance limits to diel and seasonal temperature changes (Layne et al. 1984, Mundahl 1989). However, these adjustments may not compensate fully. Mundahl and Benton (1990) found that post-molting mortality in rusty crayfish increased dramatically when the temperature was held below 20° C, and rusty crayfish did not grow at temperatures below 14° C. They hypothesized that while rusty crayfish can survive cold temperatures during non-molting and non-growing periods, consistently cold temperatures are detrimental to them. In their native range, rusty crayfish typically avoid spring-fed streams with constant 12–14° C temperatures, presumably because these temperatures inhibit molting (Prins 1968).

Water temperatures around 15° C in our upper section of the Prairie River, and 19° in our middle section were recorded; ambient air temperatures during this time were 30–32° C. The upper stream reaches have substantial cold spring-water influence and canopy cover, subsequently lower temperatures, and less suitable habitat than the lower reaches, and would be suboptimal for rusty crayfish molting and survivorship during the majority of the year. Optimal temperature is a limiting resource in many poikilothermic organisms causing intraspecific competition (Magnuson et al. 1979). Immatures of many species, including the rusty crayfish, are often attacked and displaced into thermally suboptimal habitat (Beitinger and Magnuson 1975, Mundahl and Benton 1990). We found exclusively juveniles in the upper section of the Prairie River, most of which appeared injured This suggests that rusty crayfish are on the very edge of their thermal tolerance and adults have displaced juveniles into areas further upstream. The temperature intolerance of the non-native rusty crayfish may be keeping it from the upper reaches of the Prairie River even though the same temperature change does not seem to affect the native invertebrates.

In summary, it appears that a high abundance of rusty crayfish may impact Wisconsin lotic systems. Rusty crayfish presence in a natural stream correlates with a substantial decrease in macroinvertebrate density. Further research will be needed to elucidate the mechanisms of faunal interaction, the possibility of rusty crayfish thermal tolerance and range expansion, and overall rusty crayfish potential for harming Wisconsin trout fisheries.

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LITERATURE CITED

Beitinger, T. L., and J. J. Magnuson. 1975. Influence of social rank and size on thermoselection behavior of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 32: 2133–2136.

Capelli, G. M. 1975. Distribution, life history, and ecology of crayfish in northern Wisconsin with emphasis on *Orconectes propinquus* (Girard). Doctoral Dissertation. University of Wisconsin, Madison, WI.

_____ 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnol. Ocean. 27: 741–745.

Carlson, H., and L. M. Andrews. 1982. Surface water resources of Lincoln County, summary report. Wisconsin Department of Natural Resources, Madison, WI.

Charlebois, P. M. 1994. The effects of the crayfish *Orconectes rusticus* on the macroinvertebrate and algal assemblages in a northern Michigan stream. Masters Thesis. University of Notre Dame. Notre Dame, IN.

Creed, R. P., Jr. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75: 2091–2103.

Cummins, K. 1977. From headwater streams to rivers. Amer. Biol. Teach. May: 305–312.

DeJong, T. M. 1975. A comparison of three diversity indices based on their components of richness and eveness. Oikos 26: 222–227.

DiDonato, G. T., and D. M. Lodge. 1993. Species replacements among orconected crayfishes in Wisconsin lakes: The role of predation by fish. Can. J. Fish. Aquat. Sci. 50: 1484–1488.

Hart, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologica 91: 220–228.

Hill, A. M., D. M. Sinars, and D. M. Lodge. 1993. Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. Oecologia 94: 303–306.

Hilsenhoff, W. L. 1988. Rapid field assessment of organic pollution with a family biotic index. J. N. Amer. Benthol. Soc. 7:65–68.

Hobbs, H. H., and J. P. Jass. 1988. The crayfishes and shrimps of Wisconsin (Cambaridae, Paleomonidae). Milwaukee Public Museum publication. pp. 66–79.

Layne, J. R., Claussen, D. L., and M. L. Manis. 1984. Annual, seasonal, and diel variation in heat and cold tolerances of the crayfish *Orconectes rusticus*. Amer. Zool. 24: 92A.

Lodge, D. M., Beckel, A. L., and J. J. Magnuson. 1985. Lake-bottom tyrant. Nat. Hist. 94: 32–37.

Lodge, D. M., and A. M. Hill. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. Nordic. J. Freshw. Res. 69:111–136.

Lodge, D. M., M. W. Kershner, and J. E. Aloi. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food web. Ecology 75:1265–1281.

Lorman, J. G. 1980. Ecology and Life History of the rusty crayfish (*Orconectes rusticus*) in Northern Wisconsin. Doctoral Dissertation. University of Wisconsin, Madison, WI.

Magnuson, J. J., Capelli, G. M., Lorman, J. G., and R. A. Stein. 1975. Consideration of crayfish for macrophyte control. *In*: P. L. Brezonik and J. L. Fox (eds.) The proceeding of a symposium on water quality management through biological control. Rep No. ENV 07-75-1. University of Florida. Gainesville, FL.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19:331–343.

Maude, S. H., and D. D. Williams. 1983. Behavior of crayfish in water currents, hydrodynamics of eight species with reference to their distributional patterns in southern Ontario Canada. Can. J. Fish. Aquat. Sci. 40: 68–77.

McBride, J. 1983. Meet the rusty crayfish. Wisc. Sportsman 12: 42–46.

Merritt, R. W. and K. W. Cummins. 1996. An introduction to the aquatic insects of North America, 3rd. Edition. Kendall/Hunt, Dubuque, IA. 862 pp.

Mundahl, N. D. 1989. Seasonal and diel changes in thermal tolerance of the crayfish *Orconectes rusticus* with evidence for behavioral thermoregulation. J. N. Am. Benthol. Soc. 8: 173–176.

Mundahl, N. D., and M. J. Benton. 1990. Aspects of the thermal ecology of the rusty crayfish (*Orconectes rusticus*) Girard. Oecologia 82: 210–216.

Olsen, T. M., Lodge, D. M., and G. M. Capelli. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Can. J. Fish. Aquat. Sci. 48:1853–1861.

Paine, R. T. 1966. Food web complexity and species diversity. Amer. Nat. 100: 65–75.

Plafkin, J. L., M. Y. Barbour, K. D. Porter, S. K. Gross, and R. M. Hughes. 1989. EPA 444/4-89-001. U. S. Environmental Protection Agency, Washington, D.C.

Prins, R. 1968. Comparative ecology of the crayfishes *Orconectes rusticus* and *Cambarus tenebrosus* in Doe Run, Mead County, Kentucky. Int. Rev. Ges. Hydrobiol. 53: 667–714.

SAS Institute. 1985. SAS user's guide: statistics. SAS Institute, Cary, NC.

Sommers, K. M., and D. P. M. Stechy. 1986. Variable trapability of crayfish associated with bait type, water temperature and lunar phase. Amer. Midl. Nat. 116: 6–44.

Steuk, R., L. M. Andrews, and H. Carlson. 1977. Surface water resources of Langlade County, summary report. Wisconsin Department of Natural Resources, Madison, WI.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130–137.

Wallace, J. B., J. W. Grubaugh, and M. R. Whiles. 1996. Biotic indices and stream ecosystem processes: results from an experimental study. Ecol. Appl. 6:140–151.

Willman, E. J., A. M. Hill, and D. M. Lodge. 1994. Responses of three crayfish congeners (*Orconectes* spp.) to odors of fish carrion and live predatory fish. Amer. Midl. Nat. 132:44–51.

Wisconsin Department of Natural Resources. 1980. Wisconsin trout streams. WDNR Publi. 6-3600 (80).

Zar, J. H. 1984. Biostatistical analysis, 2nd Edition. Prentice-Hall, Englewood Cliffs, NJ. 718 pp.