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Journal of the North American Benthological Society, Vol. 15, No. 4 (Dec., 1996),
551-563.

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Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates

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Abstract. Crayfish are common inhabitants of North American streams and many species are undergoing human-assisted range expansions. We studied the effects of an introduced crayfish (*Orconectes rusticus*) on benthic macroinvertebrates and periphyton in a northern Michigan (USA) stream by 1) conducting a 46-d enclosure-exclosure experiment and 2) sampling benthic communities along a longitudinal gradient in crayfish density. In stream enclosures, crayfish reduced total macroinvertebrate densities by 47-58% and herbivore densities by 55-72% relative to exclosures. Over the course of the experiment, periphyton chlorophyll *a* increased by 48-70% in enclosures compared to an increase of only 8% in exclosures. Periphyton biomass, however, did not vary across treatments. Periphyton primary productivity increased 4-7 times in the presence of crayfish, probably because crayfish reduced grazer densities (indirect effect) and removed non-autotrophic components of the periphyton matrix (direct effect). The longitudinal survey supported experimental results. At sites along a crayfish density gradient occurring over 3 km of stream, periphyton chlorophyll *a* on rocks increased and macroinvertebrate density decreased with increasing crayfish density. These studies show that crayfish directly and indirectly affected the stream benthos, thereby producing responses at more than 1 trophic level. Some responses were consistent with a trophic cascade, but crayfish increased food web connectance by consuming periphyton. Therefore, crayfish can have complex, multi-trophic-level effects on the food webs of invaded streams.

Key words: *Orconectes rusticus*, crayfish, macroinvertebrates, periphyton, food webs, exotic species, stream, enclosure-exclosure, trophic cascade.

Crayfish can dominate the benthic animal biomass of some streams (Momot et al. 1978, Webster and Patten 1979, Huryn and Wallace 1987), but few studies have examined the effects of crayfish on stream benthic communities. Most studies of stream crayfish have focused on their production (Momot 1984), diet (Eggleston 1975, True 1990), breeding periodicity and behavior (Berrill and Arsenault 1982, 1984), or species distribution and life histories (Lippson 1976, Berrill 1978, Payne 1984). Studies of biotic interactions mostly have concentrated on mechanisms of species replacement by a congener or other closely related species (Butler and Stein 1985, Mather 1990).

Studies of the function of crayfish in streams suggest that crayfish can play an important role in organic matter processing and in food web regulation. Huryn and Wallace (1987) reported that feeding and egestion by the crayfish *Cambarus bartoni* accelerated the conversion rate of coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM). Crowl

and Schnell (1990) studied 11 Oklahoma streams and found that abundances of the crayfish *Orconectes virilis* and the snail *Physella virgata* were negatively related, but that crayfish abundance and snail size were positively related, suggesting a snail size refuge from crayfish predation. In Augusta Creek (Michigan, USA), Hart (1992) and Creed (1994) independently demonstrated that grazing by *Orconectes propinquus* on the macroalga *Cladophora glomerata* affected the distribution of the macroalga, its associated microalgae, and small grazers. These studies show that stream crayfish are generalist feeders that potentially can affect the local composition of detritus, algae, and macroinvertebrates.

The rusty crayfish, *Orconectes rusticus* (Girard), has particular potential to exert strong effects on stream benthic communities. This species is native to the lower Midwest (USA), but has invaded many lakes and streams of the upper Midwest, Northeast, and Ontario (Canada) (Berrill 1978). In lakes of one invaded region (northern Wisconsin), *O. rusticus* significantly reduced the abundances of littoral periphyton, macrophytes, and macroinvertebrates (Lorman

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1980, Lodge and Lorman 1987, Lodge et al. 1994). To our knowledge, no previous study has examined the effects of an exotic crayfish on a stream benthic community. We designed our study to determine if *O. rusticus* had detectable effects in a stream that it had invaded. To address this question, we conducted an in-situ enclosure-exclosure experiment and a study of natural benthic communities at stream sites containing different densities of *O. rusticus*.

Study Animal

Orconectes rusticus is native to Missouri, Kentucky, Tennessee, Illinois, Indiana, Ohio, and southern Michigan, where it is found in streams, ponds, and lakes (Lorman 1980, see also review by Hobbs and Jass 1988). Within the last 30 y, however, *O. rusticus* has spread into lakes and streams of Wisconsin (Capelli 1975), northern Michigan (Lippson 1976), southern Ontario (Berrill 1978), and parts of northeastern USA (Lorman 1980, Smith 1981). In these areas, initial introductions of *O. rusticus* were probably from bait buckets of anglers (Capelli and Magnuson 1983). *Orconectes rusticus* has become well established in these regions, often replacing native crayfish species, especially congeners (Berrill 1978, Smith 1981, Capelli 1982).

In northern Wisconsin, rusty crayfish live for up to 4 y (Lorman 1980), with adults ranging in size from 18.5 to 58.0 mm CL (carapace length) (Lorman 1980, A. M. Hill, Northeast Louisiana University, personal communication). On rocky or sandy sediments of invaded lakes, densities of adults typically range from 1 to 15/m² (Lodge et al. 1994). In streams within its native range, *O. rusticus* densities as high as 21 adults/m² have been reported (Momot et al. 1978). We have measured densities of 18–21/m² in invaded northern Wisconsin streams, but average densities of 3–5/m² are more common. Rusty crayfish consume various food resources including detritus (Prins 1968), algae (Eggleston 1975), macrophytes (Prins 1968, Lorman 1980), and macroinvertebrates (Lorman 1975, Hill et al. 1993), and thus this species is considered an omnivore (Lodge et al. 1994). The crayfish uses the chela of its walking legs (pereiopods) to grasp and transfer food items to its mandibles (Holdich and Reeve 1988, Creed 1990, Lodge et al. 1994).

Study Site

The Middle Branch of the Ontonagon River is in Michigan's Upper Peninsula (46°N, 89°W). From its origin as a lake outflow, the stream flows northward, and joins other branches to form the Ontonagon River, which empties into Lake Superior. Approximately 36 km downstream of its origin, the stream has been impounded to allow diversion of some water for electric power generation. This impoundment contains *O. rusticus* and may have been the original source of *O. rusticus* to the downstream area. A hypolimnetic release from the reservoir maintains stream discharge at 1.13 m³/s from June to August and 0.85 m³/s from September to May (Stone and Webster Michigan, Inc. 1987). A high waterfall (Bond Falls) formed by a basalt outcrop, 0.5 km downstream of the impoundment, forms a natural barrier to upstream movement of animals. The site of our enclosure-exclosure experiment was about 3 km downstream of the falls. Longitudinal survey sites were distributed from 0.1 km below the falls to 3 km downstream.

The channel substratum is composed of cobble-on-sand punctuated by bedrock and boulders. Wetted and active channel widths average 17 and 27 m, respectively. The stream is shallow (0.25 m deep on average), has a low gradient (0.4%), and is moderately shaded by riparian vegetation including birch (*Betula* spp.), speckled alder (*Alnus rugosa*), maple (*Acer* spp.), poplar (*Populus* spp.), and eastern hemlock (*Tsuga canadensis*). Within the study area, the cool-water fish assemblage is composed primarily of brook trout (*Salvelinus fontinalis*), blacknose dace (*Rhinichthys atratulus*), longnose dace (*R. cataractae*), mottled sculpin (*Cottus bairdi*), and slimy sculpin (*C. cognatus*). Rusty crayfish are abundant at the base of Bond Falls, but decline gradually in density with distance downstream. A congeneric native crayfish, *Orconectes virilis*, also is present in the stream, but only where densities of *O. rusticus* are very low (<0.1/m²). During extensive snorkeling surveys, no *O. virilis* were observed within our 3-km study reach.

Methods

Enclosure-exclosure experiment

An enclosure-exclosure experiment was conducted from July to August 1992 within a deep

riffle (average depth = 22 cm) that was nearly devoid of *O. rusticus* (0.18 ± 0.05 *O. rusticus*/m²; $\bar{x} \pm 1$ SE of 2 sampling dates, see below). The experimental site coincided with 1 of the stream reaches (LS4) used in the longitudinal survey described below. We constructed 15 experimental enclosures from 0.2-m² clear plastic containers (50 cm long \times 40 cm wide \times 20 cm high) by replacing the upstream and downstream ends with flexible plastic screening (8 \times 14-mm mesh) to allow water to pass through. The screens reduced current velocity within the enclosures by 60% (from 0.48 to 0.19 m/s), but the large mesh did not prevent colonization by algae or movement of most invertebrates and small fish. Small crayfish probably also had access through the mesh, but none were observed in the enclosures. An earlier study comparing substrata within the enclosures with substrata placed on the streambed showed that the enclosures had no significant effect on periphyton and macroinvertebrate colonization rates (Charlebois 1994). Each enclosure had 1 cm of sand, on which were placed 28 (4 rows of 7) egg-shaped, artificial substrata. The artificial substrata were made of rough, unglazed ceramic that mimicked natural rocks, and were used as the primary sampling unit because of their uniformity in surface area and reproducibility across treatments (Lamberti and Resh 1985). Each substratum had a surface area of 130 cm². A screen cover (8 \times 14 mm mesh) was attached to the top of each enclosure with removable metal clips; the mesh reduced irradiance by 20%.

The enclosures were placed within a relatively unshaded stream reach in a randomized block design (3 treatments \times 5 blocks), and were allowed to colonize with algae and macroinvertebrates for 22 d before crayfish were added. Adult *O. rusticus* were collected from upstream and added to the enclosures on 24 July (designated day 0) in densities of 0/m² (ZERO crayfish, or enclosure), 5/m² (LOW; 1 crayfish per enclosure), or 10/m² (HIGH; 2 crayfish per enclosure). These densities were within the range of *O. rusticus* densities found within endemic and invaded areas. Each treatment was replicated 5 times. Crayfish collected for the experiment were of similar size (CL = 23–25 mm) and mass (4.12 ± 0.20 g wet weight). Only males were used in the experiment because some enclosures contained only 1 crayfish, and

we were concerned about sex-specific feeding differences (e.g., Hanson et al. 1990).

On day 0 (after the 22-d colonization period, but just before crayfish were added) and on day 46 of the experimental period (10 August), the enclosures were sampled for macroinvertebrates, periphyton chlorophyll *a*, and periphyton biomass. Two substrata per enclosure were removed at random and pooled for each measurement. When sampling macroinvertebrates, we placed a 50- μ m-mesh net directly downstream of each substratum to collect any dislodged or escaping organisms. Substrata removed on day 0 were replaced with similarly colonized substrata, which were not resampled on day 46. Substrata sampled for periphyton were placed in opaque containers, and either frozen (chlorophyll *a*) or refrigerated (biomass) at 4°C for <24 h and then analyzed. Macroinvertebrates were preserved with 90% ethanol. At the end of the experiment, crayfish were retrieved from the enclosures and frozen for later analysis of stomach contents.

On days 44–46, additional substrata from each treatment were selected at random for estimates of periphyton net primary productivity (NPP). NPP was estimated by oxygen evolution (Orion Model 840 dissolved oxygen meter) within 2.2-L, recirculating, cylindrical, Plexiglas® chambers (10 cm diameter \times 30 cm long). Three replicate incubations were conducted in the stream for each treatment from approximately 1000 to 1300 h at a minimum irradiance of 250 μ mol quanta m⁻² s⁻¹.

Longitudinal survey

During June–July 1992, we sampled 4 stream reaches (designated LS1–LS4), with LS1 located 0.1 km downstream of Bond Falls and LS2–LS4 located at successive downstream sites separated by 0.4 to 1.6 km (Table 1). All sites were deep riffles that had distinctly different *O. rusticus* densities, but similar physical and chemical conditions (Table 1). Crayfish densities at each site were estimated twice (28 June and 23–28 July 1992) by snorkeling and counting all *O. rusticus* (male and female adults) within 4 replicate 0.5-m-wide belt transects aligned perpendicular to stream flow. This method of estimating crayfish densities was the most effective of those tested (e.g., trapping, seining, electrofishing, quadrat sampling) in this system (Charlebois 1994). Av-

TABLE 1. Descriptive parameters for longitudinal survey sites (LS1-LS4) within the Middle Branch of the Ontonagon River (measurements made 23-28 July 1992). Lake outlet site included for comparison of nutrients and suspended matter with downstream sites. NS = not sampled.

Site	Crayfish (no./m ²)	Distance from outlet (m)	Canopy (% cover)	Q (m ³ /s)	Water temp. (°C)	Susp. AFDM (mg/L)	Susp. chl. <i>a</i> (µg/L)	TDS (mg/L)	Cond. (µS/ cm)	NO ₃ ⁻ (mg/L)	PO ₄ ⁻³ (mg/L)	Ca ⁺⁺ (mg/ L)
Outlet	NS	5	0	1.22	NS	2.3	2.2	NS	NS	0.22	0.03	NS
LS1	3.10	658	47	1.28	18.8	2.2	2.1	67.5	134	0.26	0.01	43
LS2	1.80	1075	30	1.35	20.6	2.5	2.6	60.0	116	0.26	0.03	42
LS3	0.93	2628	27	1.74	22.0	2.1	2.1	58.7	117	0.24	0.00	41
LS4	0.18	3931	22	1.45	21.0	2.5	2.2	60.0	120	0.22	0.01	42

erage *O. rusticus* densities at the 4 sites ranged from 0.2 to 3.1 crayfish/m² (Table 1); no other crayfish species were found at these sites. In late July of 1992 and 1993, we measured various physical, chemical, and biological variables at each site (Table 1).

During 23-28 July 1992, 15 rocks were chosen haphazardly from a 10-m reach of each site for analysis of periphyton chlorophyll *a* ($n = 5$), periphyton biomass ($n = 5$), and macroinvertebrate abundance and taxa richness ($n = 5$). Samples were treated as in the enclosure-exclosure experiment. Periphyton productivity was measured by removing an additional 9 rocks from each site and estimating NPP as for the enclosure-exclosure experiment (3 rocks/chamber; $n = 3$ replicate incubations/site).

Laboratory analyses

Macroinvertebrates.—In the laboratory, macroinvertebrates from each substratum were sorted under a dissecting microscope, identified to the lowest practical taxonomic level (generally genus), and counted. Invertebrates were assigned to a trophic level (detritivore, herbivore, or carnivore) based on their principal food source as given in Merritt and Cummins (1984). Most chironomid larvae were early instars and were not identified further; chironomids were excluded from trophic classification because of the broad range of diets within the family (Berg 1995).

Periphyton.—For biomass determination, periphyton was removed from a substratum with a toothbrush, transferred to water, and filtered onto a Whatman GF/F filter (pore size = 0.45 µm). The filter was dried at 60°C for 24 h,

weighed to the nearest 0.1 mg, combusted at 500°C for 24 h, and then reweighed to determine ash-free dry mass. For chlorophyll *a* analysis, the whole substratum (artificial or natural) was frozen, placed in a known volume of acetone, and extracted in the dark for 24 h at 4°C. The extract was then analyzed with a spectrophotometer (Perkin-Elmer Lambda 6) for chlorophyll *a* using the trichromatic method (APHA 1985). Rock surface area was determined by wrapping each rock with aluminum foil (Lamberti et al. 1991). Exposed surface area of each substratum was calculated as 50% of the total surface area.

Crayfish stomach contents.—At the end of the enclosure-exclosure experiment, crayfish were frozen at -4°C. Each crayfish stomach subsequently was excised and contents were examined under both a dissecting and a compound microscope for the presence of detritus, algae, and macroinvertebrates. Each of these food types was classified as either present or absent within each stomach. Because of problems associated with dissecting stomachs from crayfish, only 6 of the 15 crayfish stomachs were sufficiently intact to identify contents. Stomachs of crayfish from both the LOW and HIGH treatments, however, were examined.

Data analyses

For the enclosure-exclosure experiment, MANOVA (randomized block design) was used to examine total macroinvertebrate density, herbivore density, and macroinvertebrate taxa richness on day 46, and percent change (from beginning to end of the experiment) in periphyton chlorophyll *a* and biomass. We did not analyze

macroinvertebrate percent change because macroinvertebrate colonization of the enclosures was incomplete at the beginning of the experiment (Charlebois 1994). Each significant response variable from the MANOVA was then analyzed with a protected ANOVA (Scheiner 1993) and Tukey's HSD test to reveal specific differences among treatments. Periphyton NPP on day 46 was analyzed separately with ANOVA and Tukey's test because there were fewer replicates of NPP than of the other variables. When Bartlett's test for homogeneity of variances detected unequal variances among treatments, data were logarithmically transformed. Means and standard errors presented in the text and figures are non-transformed. All analyses were done with SYSTAT (version 5.03, SYSTAT, Inc., Evanston, Illinois).

In the longitudinal survey, we analyzed each macroinvertebrate or periphyton parameter with ANOVA followed by Tukey's test to compare the 4 sites. To reduce our procedure-wise error rate, the α -level for each ANOVA was adjusted using the sequential Bonferroni procedure (Rice 1990, Scheiner 1993). Multiple univariate ANOVAs were used rather than a MANOVA because estimates of macroinvertebrates, periphyton chlorophyll *a*, and periphyton biomass were obtained from separate sampling units.

Similarity in macroinvertebrate taxonomic composition among longitudinal sites was determined by calculating the SIMI metric for pooled samples (McIntire and Moore 1977). SIMI values range from 0 to 1.0, with 0 indicating that the samples have no taxa in common, and 1.0 indicating that the samples are identical in taxonomic composition and relative abundance.

Results

Enclosure-exclosure experiment

Benthic macroinvertebrates within the enclosures were affected negatively by the presence of crayfish. At the end of the experiment, total invertebrate density and herbivore density were significantly lower ($p < 0.01$) in the enclosures than in the exclosures (Fig. 1A,B). The number of invertebrate taxa in the HIGH treatment was significantly lower ($p < 0.01$) than in the ZERO treatment (Fig. 1C). Of the prevalent taxa (those

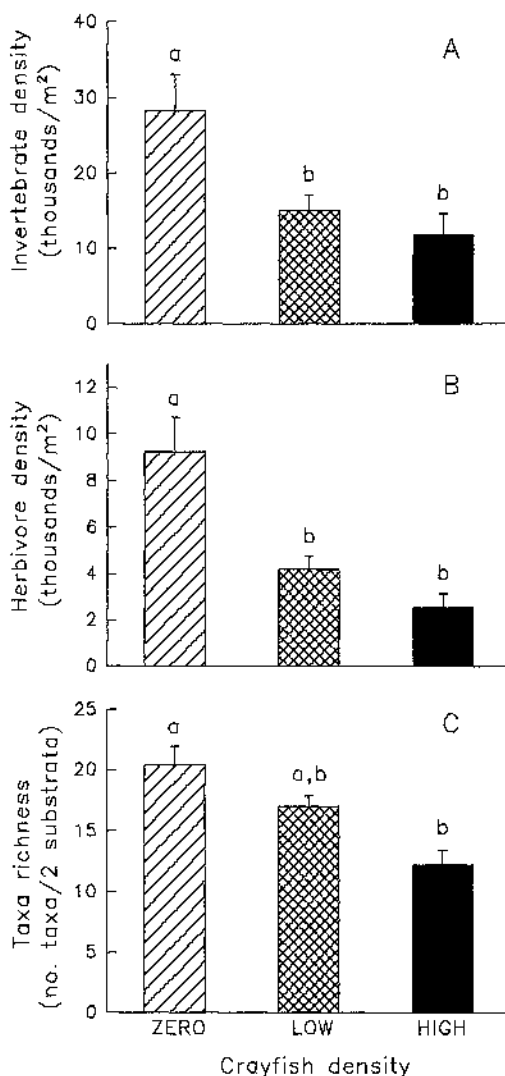


FIG. 1. Macroinvertebrate response to crayfish treatments in the enclosure-exclosure experiment ($\bar{x} \pm 1$ SE): (A) macroinvertebrate density ($F_{1,8} = 15.7$, $p < 0.01$), (B) herbivore density ($F_{1,8} = 14.9$, $p < 0.01$), and (C) taxa richness ($F_{1,8} = 11.0$, $p < 0.01$). ZERO = 0 crayfish/m²; LOW = 5 crayfish/m²; HIGH = 10 crayfish/m². Different lower-case letters over bars denote significantly different means ($p < 0.05$), as determined by Tukey's test.

accounting for more than 1% of the total macroinvertebrate assemblage), all but larvae of the caddisfly family Hydroptilidae (mostly *Leucotrichia* spp.) were less abundant in the enclosures than in the exclosures (Fig. 2).

Periphyton, in general, responded positively

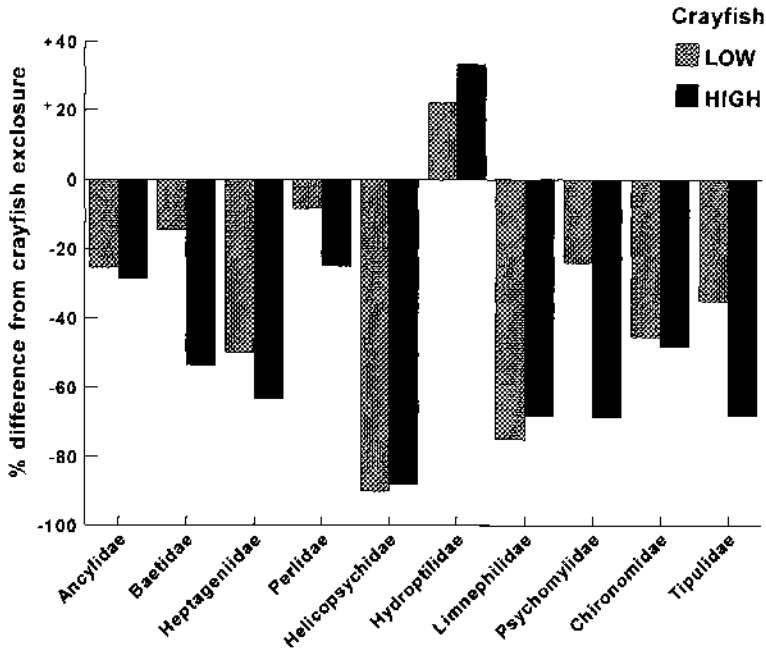


FIG. 2. Relative responses of prevalent macroinvertebrate taxa from the LOW and HIGH crayfish treatments of the enclosure-exclosure experiment. Data presented are percent differences from the crayfish enclosure (ZERO crayfish treatment).

to the presence of crayfish. The percent change in periphyton chlorophyll *a* from the beginning to the end of the experiment was significantly greater in the LOW crayfish treatment than in the ZERO treatment ($p < 0.05$); the response in the HIGH treatment was intermediate between the two (Fig. 3A). Percent change in periphyton biomass, however, did not differ significantly among the 3 treatments (Fig. 3B). At the beginning of the experiment, periphyton chlorophyll *a* and biomass (all treatments pooled) were $32.3 \pm 3.05 \text{ mg/m}^2$ and $6.86 \pm 0.67 \text{ g/m}^2$ ($\bar{x} \pm 1 \text{ SE}$), respectively. At the end of the experiment, chlorophyll *a* in the ZERO, LOW, and HIGH treatments respectively was $39.8 \pm 3.57 \text{ mg/m}^2$, $41.6 \pm 5.20 \text{ mg/m}^2$, and $45.5 \pm 5.62 \text{ mg/m}^2$, while periphyton biomass in the same respective treatments was $6.89 \pm 0.35 \text{ g/m}^2$, $7.63 \pm 0.35 \text{ g/m}^2$, and $8.93 \pm 0.88 \text{ g/m}^2$. At the end of the experiment, net primary productivity of periphyton in the HIGH treatment was intermediate between the ZERO and LOW treatments, which were significantly different ($p < 0.01$) (Fig. 3C). Periphyton respiration exceeded production for the ZERO treatment.

All crayfish stomachs contained algae (mostly

diatoms) and detritus at the end of the experiment. Macroinvertebrates were found in one-third of the stomachs, and included intact chironomid larvae (Diptera) and remnants of other benthic insects (Ephemeroptera, Trichoptera, and Diptera).

Longitudinal survey

To determine if our experimental results could be used to predict benthic community structure at different crayfish densities within the stream, we sampled sites along a longitudinal gradient in *O. rusticus* density. In general, invertebrate density increased with increasing distance downstream. Total invertebrate density and herbivore density were significantly lower ($p < 0.01$) at LS1 than at LS3 and LS4 (Fig. 4A,B). At LS2, total invertebrate density and herbivore density were intermediate between LS1-LS3 and LS1-LS4, respectively. Taxa richness tended to increase downstream (Fig. 4C), but the ANOVA was not significant ($p = 0.19$). SIMI analysis indicated that as crayfish densities decreased, similarity between invertebrate assemblages along the gradient also decreased

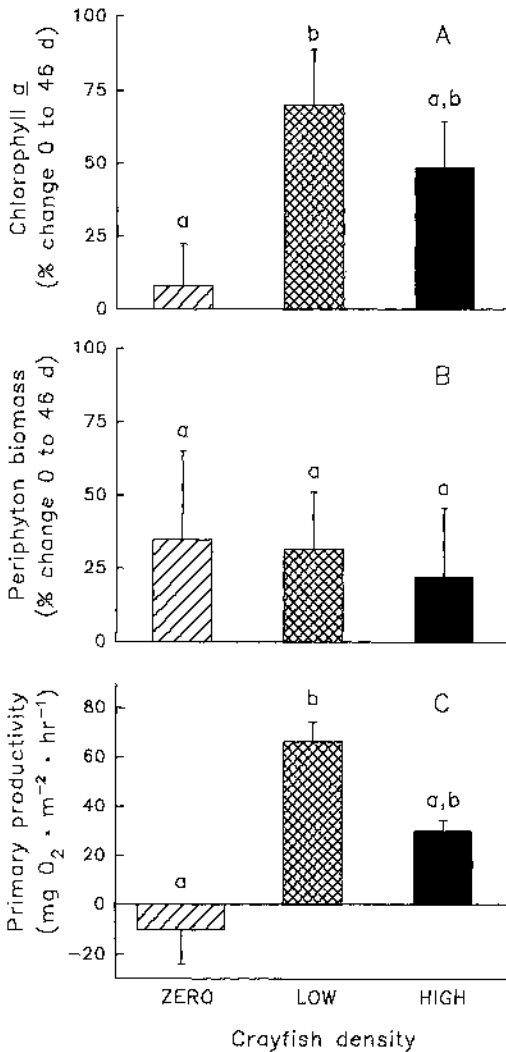


FIG. 3. Periphyton response to crayfish treatments in the enclosure-exclosure experiment as percent change from beginning to end ($\bar{x} \pm 1$ SE) in (A) periphyton chlorophyll *a* ($F_{2,8} = 4.47, p < 0.05$) and (B) periphyton biomass ($F_{2,8} = 0.11, p = 0.90$); and (C) net primary productivity ($F_{2,4} = 18.8, p < 0.01$) at the end of the experiment. ZERO = 0 crayfish/m²; LOW = 5 crayfish/m²; HIGH = 10 crayfish/m². Different lower-case letters over bars denote significantly different means ($p < 0.05$), as determined by Tukey's test.

(Table 2). For example, invertebrate assemblages at sites LS1 (3.1 crayfish/m²) and LS2 (1.8 crayfish/m²) were very similar (SIMI = 0.910), whereas assemblages at sites LS3 (0.9 crayfish/m²) and LS4 (0.2 crayfish/m²) were different (SIMI = 0.357).

The periphyton abundance measures, chlorophyll *a* and biomass, differed in their relationships with crayfish density. Chlorophyll *a* was significantly greater at LS1 than at LS2-LS4 ($p < 0.01$), whereas periphyton biomass showed no significant difference among the 4 sites ($p = 0.41$) (Fig. 4D,E). Benthic primary productivity (NPP) decreased from LS1 to LS3 (Fig. 4F), but high NPP at LS4 resulted in a nonsignificant ANOVA ($p = 0.13$).

Discussion

Concordance of experimental and descriptive studies

The manipulative experiment, coupled with our longitudinal survey of the benthic community of the Middle Branch of the Ontonagon River, showed that crayfish significantly affected lower trophic levels in this stream. In the experiment, crayfish had a direct negative effect (no involvement of intermediary organisms) on macroinvertebrate density and diversity. Several mechanisms probably were involved in the removal of invertebrates including: 1) consumption by crayfish; 2) increased drift through prey escape and incidental dislodgement by foraging crayfish; and 3) possible inhibition of invertebrate colonization by these large consumers (*sensu* Peckarsky and Dodson 1980). Each of these mechanisms could have different consequences (e.g., direct mortality vs. displacement to downstream areas) for the local macroinvertebrate assemblage. Results of the longitudinal survey, however, support the idea that crayfish reduced the overall density and diversity of macroinvertebrates within this stream.

We believe that periphyton was affected both indirectly (through intermediary organisms) and directly by rusty crayfish. The presence of crayfish increased benthic chlorophyll *a* and primary productivity, but restricted the accumulation of periphyton biomass (Fig. 5). Crayfish likely generated these responses by 1) reducing the abundance of algalivorous invertebrates, which can indirectly increase algal abundance; 2) consuming and dislodging periphyton during feeding or movement (Flint and Goldman 1975, Lodge and Lorman 1987), and 3) fertilizing periphyton with waste products (Flint and Goldman 1975, McCormick 1990). The increase in chlorophyll *a* and primary productivity but lack of increase in periphyton biomass appears

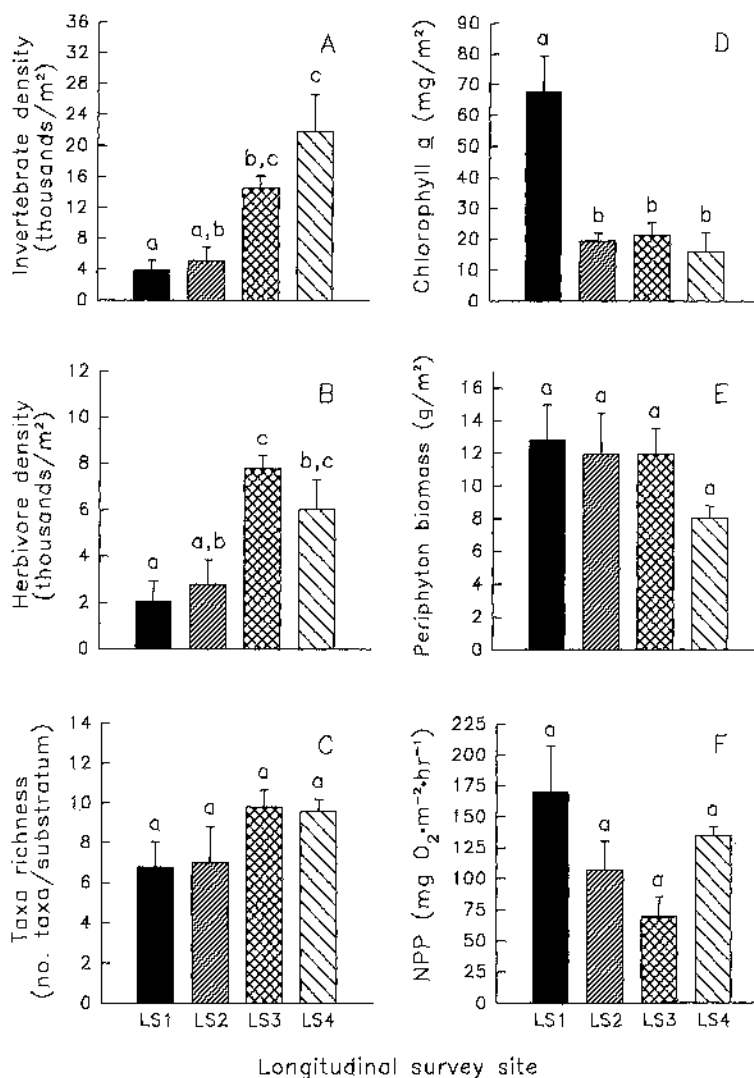


FIG. 4. Macroinvertebrate and periphyton variables ($\bar{x} \pm 1$ SE) at longitudinal survey (LS) sites in the Middle Branch of the Ontonagon River: (A) macroinvertebrate density ($F_{3,16} = 7.3, p < 0.05$), (B) herbivore density ($F_{3,16} = 7.6, p < 0.05$), (C) macroinvertebrate taxa richness ($F_{3,16} = 1.8, p = 0.19$), (D) periphyton chlorophyll *a* ($F_{3,16} = 12.2, p < 0.01$), (E) periphyton biomass ($F_{3,14} = 1.0, p = 0.41$), and (F) net primary productivity (NPP) ($F_{3,6} = 2.9, p = 0.13$). LS1 = 3.1 *O. rusticus*/m²; LS2 = 1.8 *O. rusticus*/m²; LS3 = 0.9 *O. rusticus*/m²; LS4 = 0.2 *O. rusticus*/m².

contradictory. Crayfish could elicit this response, however, if their foraging removes loosely attached components of the periphyton matrix (e.g., fine detritus, senescent cells, and metaphytic forms), thereby exposing live algal cells to higher light and nutrient concentrations (Gregory 1983, Lamberti and Resh 1983). The chlorophyll content and primary productivity of the periphyton matrix thus can increase even

though biomass may decline (McIntire 1973, Hunter 1980).

Results of the longitudinal survey were generally consistent with those of the enclosure-exclosure experiment. Invertebrate density and richness were lower, and periphyton chlorophyll *a* was higher at sites where crayfish were abundant than at sites where crayfish were rare. Periphyton primary productivity generally in-

TABLE 2. Results of SIMI analyses comparing macroinvertebrate assemblages at 4 longitudinal survey (LS) sites within the Middle Branch of the Ontonagon River. SIMI ranges between 0 and 1, where 1 denotes complete similarity between 2 sites. Crayfish densities are averages for 1992.

Site (no. crayfish/m ²)	LS1 (3.1)	LS2 (1.8)	LS3 (0.9)	LS4 (0.2)
LS1 (3.1)	—			
LS2 (1.8)	0.910	—		
LS3 (0.9)	0.757	0.804	—	
LS4 (0.2)	0.448	0.494	0.357	—

creased with increasing crayfish density. Therefore, patterns in the natural stream may be due to mechanisms postulated to explain the experimental results.

Factors other than crayfish abundance undoubtedly also contributed to the patterns of invertebrates and periphyton that we observed in the Middle Branch of the Ontonagon River. We examined the possibility that nutrients or sus-

pending matter (seston) from the upstream reservoir became diluted or depleted downstream (Hynes 1970, Morin et al. 1988). However, no chemical or seston gradients were detected (Table 1). In addition, the invertebrate abundance patterns that we observed were contrary to those expected for lake-outlet streams, which typically have their highest invertebrate densities near the outlet because of high seston concentrations (Wotton 1979, Brönmark and Malmqvist 1984, Richardson and Mackay 1991). In our system, the highest invertebrate density was at the site farthest downstream from the outlet, which had the lowest crayfish density. Furthermore, lake outlet effects usually diminish after a relatively short distance (e.g., 0.5 km; Wotton 1979, Vadeboncoeur 1994); our site nearest the reservoir was 0.7 km below the outlet, and thus reservoir effects probably had already diminished. Therefore, although other factors and organisms certainly contribute to community structure, crayfish appear to be strong regulators of the benthos in this system.

An important aspect of the benthic commu-

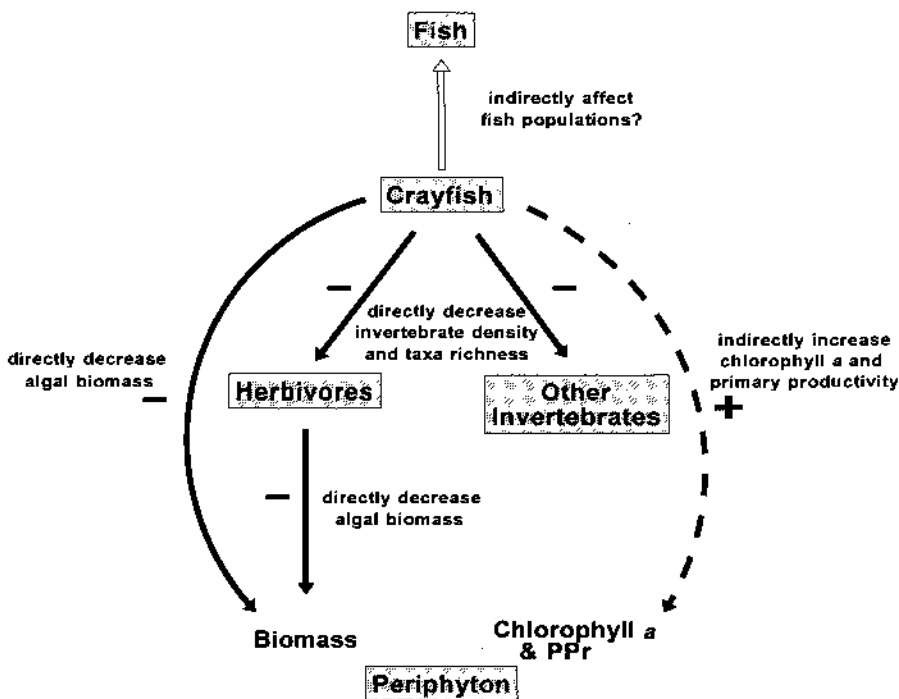


FIG. 5. Generalized summary of direct (solid line) and indirect (broken line) effects of crayfish in the Middle Branch of the Ontonagon River. PPr = primary productivity. Unfilled line represents postulated indirect effect of crayfish on benthivorous fish.

nity structure in the Middle Branch of the Ontonagon River is the mechanism(s) responsible for the crayfish density gradient. Our study did not explicitly address this issue, but the most likely explanation involves the upstream impoundment and the waterfall. The *O. rusticus* that originally colonized the stream may have come from the impoundment. Regulation of streamflow by the impoundment may limit downstream dispersal of crayfish by peak flows. Furthermore, the waterfall is a barrier to upstream movement by crayfish. These features may account for the decrease in crayfish densities with increasing distance downstream of the impoundment.

Invading crayfish and benthic food webs

The hypothesized role of rusty crayfish in the benthic trophic linkages of the Middle Branch of the Ontonagon River is illustrated in Figure 5. These interactions are consistent with other studies of crayfish in different freshwater habitats. Lodge et al. (1994) observed a decline in snail abundance and an increase in periphyton chlorophyll *a* (attached to plastic strips) within enclosures containing *O. rusticus* in a northern Wisconsin lake. Crayfish, however, also reduced macrophyte surface area (which periphyton colonizes), and thus total periphyton abundance probably declined within crayfish enclosures. Hart (1992) and Creed (1994) demonstrated that a congeneric crayfish (*O. propinquus*) directly reduced the abundance of the macroalga *Cladophora glomerata* in Augusta Creek (Michigan, USA), and thus changed benthic habitat structure from a macroalgal forest to an epilithic microalgal lawn. Because *O. propinquus* reduced *Cladophora* abundance, thereby allowing microalgae and associated macroinvertebrates to proliferate, it served as a "keystone predator" (Hart 1992, Creed 1994). Hart and Creed also showed that certain macroinvertebrates such as microcaddisflies (family Hydroptilidae) were positively affected by crayfish. This is consistent with our findings in which *Leucotrichia* (a microcaddisfly that builds a silken case tightly appressed to the rock surface) was the only taxon to increase in the presence of crayfish. Protection from crayfish afforded by the prostrate case and reduced interspecific competition with other macroinvertebrates may have combined to produce this increase in *Leucotrichia*.

Our results suggest that stream benthic communities will be altered by the invasion or introduction of *O. rusticus*. Results from the experiment showed that *O. rusticus* in moderate densities of 5/m² significantly affected both macroinvertebrates and periphyton. In native and invaded streams, *O. rusticus* can reach a density of 21/m² and a biomass of 30 g/m² (e.g., Momot et al. 1978); at these densities, we would expect even greater effects on macroinvertebrates and periphyton than those observed in our study. Crayfish also may indirectly affect resident fishes (e.g., trout, minnows) that rely on macroinvertebrates or algae for food. Although crayfish are eaten by some fish (e.g., bass), depletion of the benthos by *O. rusticus* may decrease overall food availability, and thus may affect fish growth and recruitment.

We also expect *O. rusticus* to have a greater effect on stream benthic communities than either *O. propinquus* or *O. virilis*, 2 congeners of *O. rusticus* that currently inhabit streams of northern Wisconsin and Michigan. *Orconectes virilis* is the native orconectid crayfish, and *O. propinquus* was introduced about 60 y ago (Capelli and Munjal 1982). *Orconectes rusticus* has a higher per capita feeding rate than the other 2 species (Olsen et al. 1991), and thus likely would consume more benthic organisms than its congeners at similar densities. Also, because *O. rusticus* is larger than *O. propinquus* and more aggressive than *O. virilis*, adult *O. rusticus* are less susceptible to predation by fish (e.g., bass) (Olsen et al. 1991, DiDonato and Lodge 1993, Garvey et al. 1994). However, bass intimidate rusty crayfish thereby reducing crayfish predation on benthic macroinvertebrates (Hill and Lodge 1995). In cool-water streams that lack bass, crayfish may be able to forage with minimal interference from aquatic predators.

Our study also demonstrated that as generalist feeders, rusty crayfish play an important ecological role in the Middle Branch of the Ontonagon River. Large predators (usually carnivorous fish) can initiate linear "trophic cascades" in freshwater communities (e.g., Carpenter et al. 1987, Power 1990). Our results suggest that rusty crayfish triggered only a weak cascade (i.e., moderate increase in chlorophyll *a*; no increase in periphyton biomass) because by consuming periphyton along with macroinvertebrates, crayfish also directly affected primary producers. This increase in food web connect-

ance by crayfish has also been demonstrated in a Wisconsin lake by Lodge et al. 1994 (see above), who found that the food web of the littoral zone was considerably more complex when the omnivory (cf. only carnivory) of crayfish was considered. We conclude that omnivorous rusty crayfish are important consumers within the Middle Branch of the Ontonagon River, and we suspect that crayfish play an important role in structuring other stream benthic communities as well (e.g., Hart 1992, Creed 1994). Furthermore, *O. rusticus* is an invading species whose range is rapidly expanding. Our results indicate that major changes will occur in stream benthic systems upon invasion and establishment of this crayfish.

Acknowledgements

We thank Marty Berg and David Lodge for their valuable advice during various phases of this research. Marty Berg, Terry Ehrman, Kristi Hannam, Eileen Perkins, Dan Maloney, and Marty Sneen kindly assisted with laboratory and field work. Alan Steinman, Ronald Hellenenthal, David Strayer, Antoine Morin, Rosemary Mackay, and 2 anonymous reviewers provided helpful comments on an earlier version of this paper. Allie Kurtie allowed access to the stream experimental site. This research was supported by grants from the National Science Foundation (BSR-8907968), the United States Environmental Protection Agency (CR820290-01-0), and Sigma Xi (Grant-in-Aid-of-Research to PMC). This paper is a contribution from the University of Notre Dame Environmental Research Center.

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Received: 22 February 1996

Accepted: 21 September 1996