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# EFFECTS OF AN OMNIVOROUS CRAYFISH (*ORCONECTES RUSTICUS*) ON A FRESHWATER LITTORAL FOOD WEB[1]

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*Abstract.* Cascading trophic interactions are important in many freshwater pelagic food webs, but their importance in more complex, omnivore-rich littoral-zone food webs is less well known. We tested the existence of a trophic cascade involving omnivorous crayfish (*Orconectes rusticus*), macroinvertebrates, periphyton, and macrophytes using 9-$m^2$ cages in the littoral zone of Plum Lake, Wisconsin, USA. Treatments in the replicated ($N$ = 4) experiment were crayfish enclosures, crayfish exclosures, and cageless references. During June–September, we measured macrophyte shoot numbers, macroinvertebrate numbers, and periphyton (on plastic strips) chlorophyll *a*, and dry mass (DM). We expected that crayfish foraging would directly reduce abundance and change species composition of macrophytes and macroinvertebrates and would indirectly enhance periphyton abundance by reducing the abundance of grazing snails.

In enclosures, macrophyte and snail (but not nonsnail macroinvertebrate) densities declined significantly throughout the experiment, whereas densities of macrophytes, snails, and nonsnail macroinvertebrates increased in exclosures and cageless references. Some of the reduction in macrophytes resulted from nonconsumptive fragmentation of macrophytes by crayfish. Consistent with the cascading trophic interactions model, periphyton chlorophyll *a* per unit surface area increased in enclosures, but declined in exclosures. Periphyton quality (as indexed by chlorophyll *a*/DM) also increased in enclosures relative to exclosures and cageless references. However, because of large reductions in macrophyte surface area (which periphyton colonizes) in enclosures, total amount of periphyton chlorophyll *a* in enclosures (relative to exclosures) probably declined while periphyton quantity per unit surface area and periphyton quality increased. Thus, the impacts of crayfish omnivory on periphyton, expressed in two conflicting indirect effects, confirm the possibility that omnivory can complicate cascading trophic predictions. Overall, results support the existence of strong trophic interactions in the littoral zone, in which omnivorous crayfish control abundance of macrophytes, snails, and periphyton.

*Key words: benthos; crayfish; littoral zone; macroinvertebrates; macrophytes; omnivory;* Orconectes rusticus; *periphyton; snails; trophic cascade.*

## INTRODUCTION

Biological communities respond to multiple ecological forces, including abiotic factors and food web configurations (Diamond and Case 1986, Menge and Sutherland 1987, Oksanen and Ericson 1987, Bartell et al. 1988). For many communities, however, attention by ecologists to different factors has shifted over time. For example, an older emphasis on the important role played by abiotic factors, especially nutrients, in determining freshwater pelagic community structure and productivity (Wetzel 1983) has given way to a synthetic view that includes the important role of cascading trophic interactions (Carpenter et al. 1991).

A similar, but less conclusive, research trend exists for freshwater littoral communities. An ongoing research tradition emphasizes the importance of abiotic factors in determining abundance and species composition of macrophytes (Spence 1982, Wetzel 1983, Chambers and Kalff 1985, 1987, Anderson and Kalff 1986, Chambers 1987*a*, *b*), periphyton (Stevenson et al. 1985, Cattaneo 1987, Fairchild et al. 1989), and invertebrates (Lodge et al. 1987, Rasmussen 1988). However, a large proportion of more recent work has explored the importance of biotic factors (Sih et al. 1985, Lodge et al. 1988), especially predation by fishes on invertebrates (Hall et al. 1970, Crowder and Cooper 1982, Morin 1984, Post and Cucin 1984, Bendell and

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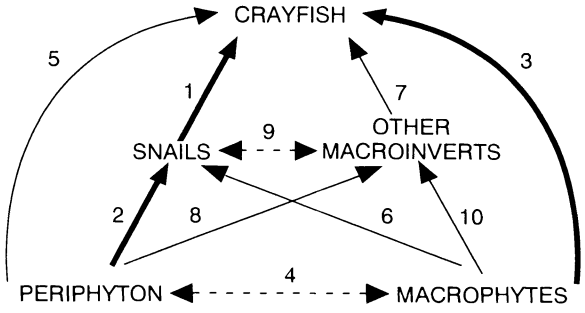


FIG. 1. Simplified food web for the littoral zone of Plum Lake, Wisconsin. —— hypothesized strong interactions (1, 2, 3); —— interactions that are either hypothesized to be weak or whose strength is unknown. – – – indicate competition (9) or competition in one direction (periphyton shading macrophytes) and facilitation in the other (macrophytes provide a surface for periphyton) (4).

McNichol 1987, Mittelbach 1988, Collins 1989, Diehl 1992), competition among macrophyte species (McCreary 1991), and herbivory on periphyton (Lamberti and Moore 1984, Cattaneo and Kalff 1986, Osenberg 1989) and macrophytes (Lodge 1991, Newman 1991). This recent body of work, including discoveries of cascading, indirect effects (Mazumder et al. 1989, Weber and Lodge 1990, Brönmark et al. 1992, Martin et al. 1992), suggests that food web configuration, in addition to abiotic factors, may be a major force in structuring freshwater littoral communities.

Strong (1992) suggests that trophic cascades exist almost exclusively in aquatic communities, and that this pattern exists because these communities are species-poor and based on poorly defended plants (algae). Strong (1992) argues that top-down forces are unlikely to affect producers in more speciose communities. However, even if freshwater pelagic food webs are simple (cf. Sprules and Bowerman 1988, see Polis 1991 for a cautionary analysis of an apparently simple food web), benthic communities in the same lakes are certainly not (Lodge et al. 1988). Benthic communities are more like terrestrial than pelagic communities (Lodge et al. 1988) with regard to habitat structure, spatial heterogeneity, the prominence of vascular plants (in addition to algae), and the prevalence of omnivory. While the arguments of Strong (1992) have intuitive appeal and some empirical support, increasing evidence suggests that even speciose benthic communities may respond strongly to top-down forces (Posey and Hines 1991, Brönmark et al. 1992, Martin et al. 1992, Power 1992*a*). As Power (1992*b*) points out, even tangled trophic webs can respond with chain-like dynamics. In this paper, we test the strength of top-down effects, including indirect effects, by an omnivorous crayfish, *Orconectes rusticus,* on a freshwater food web complicated by multiple omnivorous links and competitive interactions.

Omnivory by *O. rusticus* and some aspects of its impact on littoral communities have been described previously. The diet of *O. rusticus* includes macrophytes, invertebrates, and periphyton (Lorman 1975, 1980), but individuals grow best on a diet of invertebrates or a mixed diet that includes invertebrates (Hill et al. 1993). Preliminary experiments suggest that *O. rusticus* reduces macrophyte abundance (Lodge and Lorman 1987, Lodge 1991). In addition, much work suggests that among invertebrates, snails are particularly vulnerable to predation by *O. rusticus* (Lodge and Lorman 1987, Olsen et al. 1991) and other crayfish (Crowl and Covich 1990, Hanson et al. 1990, Alexander and Covich 1991). This is consistent with the model of Lodge et al. (1987) that argues that snail assemblages in permanent lakes are likely to be structured by predation. In preliminary support of these patterns and predictions, a correlative field study in Trout Lake, Wisconsin suggested crayfish reduced abundance of snails (which often control periphyton abundance [Brönmark 1989]), and indirectly enhanced periphyton abundance (Weber and Lodge 1990). Thus, the potential for strong top-down direct and indirect effects exists, but the extent to which crayfish omnivory could dampen the effects of a trophic cascade in a complex community is unknown.

In about the 1960s, *Orconectes rusticus,* native to the lower midwestern U.S., was introduced into northern Wisconsin, where two ecologically similar, congeneric crayfishes (*O. virilis* and *O. propinquus*) already occurred (Capelli and Magnuson 1983, Lodge et al. 1986, Hill et al. 1993). The impact of *O. rusticus* on the benthic community may be greater than that of its congeners, but all congeners (Seroll and Coler 1975, Chambers et al. 1990, Hanson et al. 1990, Olsen et al. 1991, Hazlett et al. 1992, Hill et al. 1993) and some other crayfish genera (Flint and Goldman 1975, Coffey and Clayton 1988, Feminella and Resh 1989, Matthews and Reynolds 1992) probably have strong negative effects on macrophytes and macroinvertebrates. Our experiment specifically tests the impact of *O. rusticus,* but may more generally suggest the role of crayfishes in benthic communities.

The littoral-zone food web in which we established crayfish enclosures, crayfish exclosures, and cageless reference areas is complex (Fig. 1). Possible outcomes of changing crayfish abundance are many, depending on the relative strength of interactions (sensu Paine 1980). With our experiment, we are able to compare the relative strength of competing direct (omnivorous) and indirect links, as explained below. Based on earlier work (citations above), our prediction (bold arrows in Fig. 1) was that increased crayfish abundance would cause a decrease in snails (arrow 1) and an increase in periphyton (arrow 2). Both the direct effects of crayfish herbivory on macrophytes (arrow 3) and increased competition for light (as a result of a thicker periphyton) would reduce macrophytes (arrow 4; Brönmark 1989, Underwood 1991, Martin et al. 1992). Alternative outcomes are many and include the following.

If the direct, negative effect of crayfish on periphyton (arrow 5, France and Welbourn 1992) exceeds the indirect, positive effect (arrows 1 and 2), periphyton abundance would decline with increased crayfish, and the indirect effect on macrophytes (arrows 5 and 4) would be positive. Macrophytes would also be positively affected if the herbivorous interaction between snails and macrophytes (arrow 6) is strong, as suggested by Sheldon (1987, 1990, cf. Brönmark 1990) (indirect linkage 1, 6 outweighing direct linkage 3). If direct and indirect interactions of crayfish with other macroinvertebrates (arrow 7) and periphyton (arrow 8), respectively, are also strong, they would simply accentuate the positive response of periphyton produced by interactions 1 and 2. If, however, the competitive interaction between snails and other macroinvertebrate algivores (arrow 9; Cuker 1983, Cattaneo and Kalff 1986) is strong, nonsnail algivores would respond positively as crayfish reduce snails, and grazing pressure on periphyton might stay constant. Thus, most of the interactions indicated on Fig. 1 have been demonstrated in experiments, but their relative strength has not been tested and is often a contentious issue among ecologists (e.g., Sheldon 1987, 1990, cf. Brönmark 1990).

Our field cage experiment does not have the power to discriminate among all possible mechanistic pathways in this highly connected web, because we do not examine the mechanisms directly. Our experimental design allows us, however, to infer the *relative* strength of conflicting interactions on the basis of the direction and strength of responses by different trophic levels. For example, if both snails and periphyton declined (and other macroinvertebrates did not respond) with increasing crayfish, we could conclude that the direct link between crayfish and periphyton (arrow 5) is stronger than the indirect link (arrows 1 and 2). We would therefore reject the trophic cascade model for this littoral zone community.

## Materials and Methods

### *Study site*

In May–September 1987, we studied the effect of a benthic omnivore, *Orconectes rusticus* (Girard), on the abundance of littoral zone macroinvertebrates, macrophytes, and periphyton. Our study site was located along the northwest shore of Plum Lake (Vilas County, Wisconsin, Township 41N Range 8E), a circumneutral, mesotrophic, drainage lake (methyl orange alkalinity 49.5 mg/L, conductivity 90 $\mu$S, surface area 380 ha, maximum depth 15 m) (Black et al. 1963). At the experimental site, the lake bottom was sand with a thin organic covering, with abundant submersed macrophytes. Three congeneric crayfishes, *Orconectes rusticus, O. virilis* (Hagen), and *O. propinquus* (Girard), occur in the lake, but in low abundance at the experimental site (<1 adult crayfish/m$^2$; see *Results*). The fact that crayfish occur in the lake, abundantly at some sites (D. M. Lodge et al., *unpublished data*), indicates that lake-wide physicochemical conditions are suitable for crayfish. The duration of our experiment was too short for demographic responses or colonization by most prey. We therefore chose to conduct the experiment at a site where crayfish abundance was low, in the hope that even prey species that are particularly vulnerable to crayfish would be present initially. Thus, our experiment mimics responses of the benthic community to changes in crayfish abundance that may result from declines in predatory fish abundance or from invasions by *O. rusticus*.

### *Design and installation of the experiment*

During June, we installed an in situ cage experiment that consisted of four replicates of three treatments: crayfish exclosures, crayfish enclosures, and cageless reference areas. Each cage and cageless reference area encompassed 9 m$^2$ (3 × 3 m) at a water depth of 0.95–1.30 m. Each cage was 2 m tall.

The cageless reference treatment differed from caged treatments both in the absence of a cage and the presence of fishes (which we excluded from cages). Although a treatment controlling for cage effects would have been desirable, partial cages would have been unsatisfactory because any such structure in the littoral zone attracts dense concentrations of fish and crayfish. Thus, the comparison of greatest interest is between enclosures and exclosures because it directly tests the effects of crayfish while controlling for any cage artifacts. Because exclosures and cageless reference treatments had similarly low densities of crayfish (both <1 adult crayfish/m$^2$; see *Results*), a comparison between exclosures and cageless references may provide some insight into both cage and fish effects, but these two factors cannot be rigorously separated. Thus, this comparison is of secondary interest.

Cages consisted of wooden frames, covered on all four sides by aluminum window screening (square mesh size = 1 mm). Screening held directly above a LI-COR light sensor reduced light by 30%, but the reduction in light experienced by plants in the cages would have been much less because the tops of the cages were uncovered. Every 1–2 wk, we scrubbed the mesh walls of the cages to reduce fouling and enhance water movement. Cage bottoms and tops were left open, but because tops protruded at least 0.70 m above the water surface, no crayfish escaped. Cage bottoms were buried 15 cm in the sediments and anchored with cinder blocks. Metal flashing (sheeting 15 cm wide) on the cage top (parallel to the water surface) and bottom (perpendicular to the sediment surface) of all cages prevented crayfish escape or entry. Twice-monthly visual inspections confirmed the absence of crayfish burrowing under the cage bottoms.

Each experimental block (one enclosure, one exclosure, one cageless reference, in random placement

within each block) was 15–20 m from other blocks. Within each block, enclosure and exclosure cages were 2–4 m apart. Cageless references were farther (10–12 m) from the cages to prevent artifacts in the cageless references resulting from predation by fish and crayfish attracted to the cages. Cageless references were marked with a metal stake at each corner. The entire experiment spanned ≈140 m of shoreline.

Before establishing the treatments, we used baited traps to remove crayfish from each exclosure and enclosure. Visual SCUBA surveys in each cage confirmed that we had removed all crayfish.

Crayfish for stocking were collected in nearby Trout Lake (Vilas County, Wisconsin Township 41N, Range 7E) during 8–15 June and maintained in outdoor tanks. On 20 June, we added adult male *O. rusticus* to enclosures at the density of 8 animals/m$^2$ (72 crayfish/cage), equivalent to a wet biomass density of 68 g/m$^2$ (as estimated from carapace lengths, CL, in millimetres, using the following regression for male *O. rusticus*: log mass = 0.0435CL − 0.3972; $N = 25$, $r = 0.9717$, $P < 0.001$). Each enclosure received the same size distribution (<25 mm carapace length [6 crayfish], 25–29 mm [37], 30–34 mm [22], and 35–55 mm [7]).

Crayfish densities in enclosure cages (8 individuals/m$^2$) accurately simulated predation and grazing pressures experienced in many northern Wisconsin benthic communities. The size range of crayfish we used includes some 1-yr-old crayfish (<25 mm), but mostly ages 2 and 3 yr (Lorman 1980). In Upper Sugarbush Lake, the Vilas County lake for which the most detailed information exists, summer densities of 1–3 yr old *O. rusticus* were 1–56 individuals/m$^2$, depending on habitat and month (Lorman 1980). In other lakes, mean densities of *O. rusticus* and/or congeners (>20 mm) in sandy to rocky habitats are 1–15 individuals/m$^2$ (Capelli 1975, Stein 1977, Lodge et al. 1987, Olsen et al. 1991). Thus, the density of crayfish in our enclosure cages is well within the range of natural densities of adult crayfishes.

The exclusive use of crayfish >19 mm carapace length and the exclusive use of male crayfish may have introduced countervailing biases into the experiment. Large *O. rusticus* are more herbivorous than small crayfish, but males are more carnivorous than females during most of the year (Lorman 1975). (Comparisons of feeding by male and female *O. virilis* made by Hanson et al. [1990] apply only to females carrying eggs like those used in their experiments.) While natural crayfish populations have a sex ratio near 50:50 (Momot 1986), our inability to catch small crayfish and female crayfish in early summer (see Lodge et al. 1986) dictated our stocking regime.

### *Monitoring crayfish densities*

Crayfish densities in exclosures and enclosures were monitored throughout the experiment. Once per month, a snorkeler counted all visible crayfish in each cage. During the first 3 d after introduction, we replaced 13 dead crayfish in enclosures with crayfish of equal carapace lengths, but did not add any crayfish thereafter. Baited traps were kept in the crayfish exclosures for the entire summer to ensure that cages in this treatment remained free of crayfish. We visually censused adult crayfish within the boundaries of each cageless control on 8 August.

Sixteen days before the introduction of *O. rusticus* and at monthly intervals thereafter, we used SCUBA to sample macrophytes, macroinvertebrates, and periphyton in all cages and cageless controls as described below.

### *Macrophyte sampling*

We used a 1-m$^2$ quadrat (3 × 1/3 m) to census the macrophytes present in each cage and cageless reference. For each sampling, the quadrat was placed across the middle of the cage (in the same position each time); we refer to this as the visual census area. Number of rosettes (for *Vallisneria americana* Michx. and *Sagittaria* sp. [submersed form]) or number of shoots (most other species) of each species of macrophyte in the quadrat was recorded by a SCUBA diver (nomenclature after Fassett 1957). For *Elodea canadensis* Michx., we estimated cover on a scale of 0–5 (where 0 = 0% cover, 1 = 20%, . . . 5 = 100%) because the highly branched growth form made it impossible to count shoot numbers. Because of the different metric used for *Elodea,* results on *Elodea* abundance are presented separately from that for other species, and analysis of relative density of macrophytes excludes *Elodea.* To relate *Elodea* density to that of other species, we measured *Elodea* cover, *Elodea* biomass, and total macrophyte biomass for 10 0.33-m$^2$ quadrat samples in the experimental area on 18 August 1990.

Once per week, we collected all macrophyte fragments floating on the water surface within each cage using a dip net (mesh size 2 × 2 mm). Samples were stored at 5°–10°C until they were dried at 55°C and weighed.

### *Macroinvertebrate sampling*

To estimate macroinvertebrate populations in each cage, we sampled cage walls, sediment, and macrophytes. Macroinvertebrates on cage walls (in exclosures and enclosures) were sampled with a 14.2 cm wide dustpan, covered (except at the leading edge) with a 0.5-mm mesh. We placed the dustpan at the bottom of a screen in a randomly selected spot on each side of the cage ($N = 4$), pressed it tightly against the wall, and moved it steadily upwards to the water's surface. Macroinvertebrates present within the area sampled were caught by the scoop.

We sampled the sediment to a depth of 5 cm with a cylindrical PVC benthic core sampler (height = 29 cm, inside diameter = 15.22 cm, sample area = 182 cm$^2$). A metal plate was inserted into a slot at the

bottom of the corer and the sample, including any macrophytes, was transferred to a plastic bag above the water. Four cores were obtained from each cage on each of four monthly sampling dates. Locations of the cores were determined using a stratified random design. Each cage was considered to be a 4 × 4 grid containing 16 cells of 0.56 $m^2$ area. Because crayfish used the cage edges for shelter, sampling was stratified to account for any center-to-edge effects. Each month, three cores were taken from among the 12 perimeter grid cells and one from one of the four central grid cells. Each cell was sampled only once during the study. Exact location of each core within the grid cell was chosen by tossing a small, orange-painted rock.

To determine the number of macroinvertebrates present on macrophytes (exclusive of sediments), we also removed randomly selected (using a toss of the marker rock) individual macrophyte shoots. Based on the visual census data, ≤20% of the total population in each cage of each macrophyte species was removed over the entire experiment, with 1–3 shoots/species being sampled in each cage on each date. Samples were never taken from the 1-$m^2$ visual census area. Shoots were removed by carefully placing a polyethylene bag over the shoot and cutting the base of the stem. At the surface, we drained excess water out of the bag through a 0.5-mm mesh screen.

Cage-wall, core samples, and macrophyte-removal samples were washed through plastic sieves (mesh size 0.5 mm). All macroinvertebrates retained were preserved in 95% ethanol. Macroinvertebrates were later identified and counted at the species level for snails (with nomenclature after Burch 1982), order level for insects, and class to suborder level for other taxa. Each macrophyte shoot in the shoot-removal and core samples was identified to species and its leaf number counted (rosulate species) or shoot length (the sum of the length of all branches) measured (other species). All floating macrophyte fragments (see *Macrophyte sampling,* above) were examined visually for macroinvertebrates; because no snails and very few other macroinvertebrates were ever found, we did not include these in our population estimates for macroinvertebrates.

Because macrophyte densities declined quickly in enclosures (see *Results*), core samples in enclosures rarely contained macrophytes, while those in exclosures often contained macrophytes. To estimate macroinvertebrate abundances in just the sediments, we therefore corrected (reduced) macroinvertebrate totals from all core samples based on the macrophyte removal sampling results for each sampling date, as follows. The mean number of macroinvertebrates per centimetre of shoot (or number of snails per rosette for *Vallisneria* and *Sagittaria*) on each species of macrophyte in the macrophyte-removal samples was determined. Based on the species, number, and size of the macrophytes in each core sample, the appropriate number of macroinvertebrates for each species was subtracted from the number sampled by the corer. The corrected core results therefore allowed us to estimate the number of macroinvertebrates on sediments only, while the macrophyte removal results allowed us to estimate the number of macroinvertebrates on macrophytes only. For analysis, we thus generated an estimate of number of macroinvertebrates per cage by adding numbers of macroinvertebrates on cage walls, sediments, and macrophytes.

To estimate changes in grazing pressure on periphyton, we used Strayer (1985) and Thorp and Covich (1991) to classify as algivorous any invertebrate group that includes species that are algivorous at any stage of their aquatic life.

### *Periphyton sampling*

Eighteen days before crayfish were stocked, 12 green polyethylene strips (3 cm wide, 65 cm long forestry flagging) were placed in each cage and cageless reference to allow colonization by periphyton. The lower end of each strip was anchored, while the top end was buoyed by a small piece of styrofoam. Strips were destructively sampled three times for periphyton biomass and chlorophyll *a*. In a parallel study, Brönmark et al. (1992) used exactly the same kinds of cages and flagging in an experiment with pumpkinseed sunfish and compared periphyton biomass on strips to that on natural *Potamogeton robbinsii*. Snails and other macroinvertebrates colonized strips readily, and periphyton biomass on strips was very strongly correlated to biomass on natural macrophyte (slope = 1.01, $r = 0.85$, $P < 0.001$) (Brönmark et al. 1992), supporting our assumption that strips closely mimic macrophytes with respect to periphyton biomass.

For each cage on each sampling date, periphyton was scraped with a razor blade from the entire length (both sides) of four randomly selected strips. Periphyton from each strip was homogenized by rapid shaking in 100 mL of filtered lake water. One volumetric subsample was filtered (Fisher G4 glass fiber, 1.2 μm nominal pore retention) for chlorophyll *a*. Chlorophyll *a,* corrected for pheopigments, was determined fluorometrically after extraction of filters (24 h in dark refrigerator) in 99% methanol (Strickland and Parsons 1968, Holm-Hansen and Riemann 1978). A second subsample for determination of dry mass (DM, 60°C) was filtered onto a preweighed glass fiber filter.

### *Statistical analysis*

Because we sampled the same experimental units repeatedly over time, the most appropriate analysis was a repeated-measures ANOVA (Hand and Taylor 1987). Within the repeated measures analysis, we used the "contrast" option in SAS (SAS Institute 1990) to make the comparisons of interest on macrophyte and macroinvertebrate responses. The contrast of primary interest tested the crayfish effect with a comparison of enclosures and exclosures (EN vs. EX) and with the

interaction of this main effect with time [$T$·(EN vs. EX)]. The contrast of secondary interest tested the statistically inseparable cage and fish effects with a comparison of exclosures and cageless references (EX vs. CR) and with the interaction of this main effect with time [$T$·(EX vs. CR)]. Because these two contrasts are non-orthogonal, we took the conservative approach of making a Bonferroni adjustment of critical alpha for two nonindependent comparisons, as suggested by Maxwell and Delaney (1990). Thus, we used a critical alpha of 0.025 instead of 0.05, whereas the true critical alpha lies somewhere between 0.05 and 0.025 (Maxwell and Delaney 1990). When transformations were necessary to normalize residuals, the rankit method (Sokal and Rohlf 1981:122–124) was used to choose the best transformation. All $P$ values reported are for Pillai's Trace, the most conservative of the available adjustments for the $F$ statistic in repeated measures ANOVA.

The repeated measures ANOVA routine in SAS eliminates any replicate from the analysis that is missing a datum for one or more time periods. Because a few periphyton samples were lost, we could not apply repeated measures ANOVA to the periphyton data. Therefore, we used a one-way ANOVA and Tukey's test to compare treatments on the last sampling date.

## Results

### *Crayfish densities*

Exhaustive trapping at the end of the experiment revealed that mortality reduced crayfish in enclosure cages to a final density of 4.8–6.1 crayfish/m$^2$ from the original 8 individuals/m$^2$. Observations of dead crayfish and monthly visual counts suggested that mortality was relatively constant during the experimental period, and was related to molting. Over the summer, only four crayfish were caught in exclosure cages (all male *O. propinquus*), to give a mean density of 0.1 adult crayfish/m$^2$ (range 0.0–0.2 individuals/m$^2$). In August, we counted 0.9 adult crayfish/m$^2$ (range 0.1–2.2 individuals/m$^2$) in cageless references. In cageless references, 70% of crayfish sampled were *O. propinquus* and 30% *O. virilis*. Although no *O. rusticus* were ever sampled in cageless references, we did see a few at the experimental site.

Because of the low densities of crayfish (<1 adult/m$^2$) in both exclosures and cageless references, we expected responses of snails, macrophytes, and periphyton in cageless references to be similar to those in exclosures. Any differences between responses in cageless references and exclosures would have to be attributed to the small differences in crayfish density (possible if responses are strongly nonlinear), cage effects, or fish effects.

### *Macrophytes*

In May, when cages were installed, few macrophyte shoots from the previous year (predominantly *Potamogeton robbinsii* Oakes) were present. By the first macrophyte census on 3 June, most species had begun new growth from winter resting stages. In exclosures and cageless references, total shoot number increased through August and remained at similar levels through September, when plants were beginning to senesce (Fig. 2A). In significant contrast to exclosures, enclosure shoot number declined throughout the summer (Fig. 2A). In September, total shoot density in enclosures was 10% that in exclosures. Results for *Elodea* cover were similar to those of all other macrophytes (Fig. 2B). Exclosures and cageless references did not differ, but in enclosures, *Elodea* was significantly reduced relative to exclosures (Fig. 2B).

Whereas we cannot incorporate *Elodea* density estimates into total macrophyte density estimates (because of the different units used; Fig. 2A, B), the one-time mid-August cover and biomass sampling allowed us to calibrate the abundance of *Elodea* relative to other species. Mean total macrophyte dry biomass was 174 g/m$^2$ (range = 108–231 g/m$^2$). The percentage of total macrophyte biomass consisting of *Elodea* was well predicted by *Elodea* cover estimates (% biomass = 0.6235[% cover] − 12.78, $r^2 = 0.8666$, $P < 0.001$). This relationship suggests that *Elodea* was a small component of total biomass in all treatments at all times, ranging from <1 to 8% at the beginning of the experiment. Peak percentage *Elodea* biomass (in exclosures in July) was ≈15%. Thus, ≥85% of total macrophyte biomass is accounted for in the analysis of changes in species relative abundance.

Whereas few macrophyte fragments floated in exclosures, biomass of floating fragments in enclosures was high at the first two sampling dates (Fig. 3). Cumulative floating biomass of all species combined was significantly higher in enclosures, but leveled off as fewer and fewer plants remained to be clipped by crayfish (Fig. 3). For single-stemmed species, most fragments were large proportions of shoots, and for rosulate species, fragments were large proportions of leaves. This suggests that these fragments result from crayfish clipping a plant or leaf near the substrate and then releasing or losing grasp of it. We clearly underestimated floating biomass, because some species (*Elodea*) often did not float, and shoots of all species eventually sank, often after a shorter interval than our weekly sampling.

Of the 12 macrophyte species occurring in the experiment, *Potamogeton robbinsii, Sagittaria, Vallisneria,* and *Najas flexilis* (Willd.) Rostk.&Schmidt were the most common (Fig. 4). Other species were *Ceratophyllum demersum* L., *Chara* (a macroalga referred to as a "macrophyte" in this paper), *Elodea, Megalodonta beckii* (Torr.) Greene, *Myriophyllum exalbescens* Fernald, *Potamogeton amplifolius* Tuckerm., *Potamogeton richardsonii* (Benn.) Rydb., and *Potamogeton zosteriformis* Fernald. Visual inspection of plots (not shown) of individual species abundance over time in

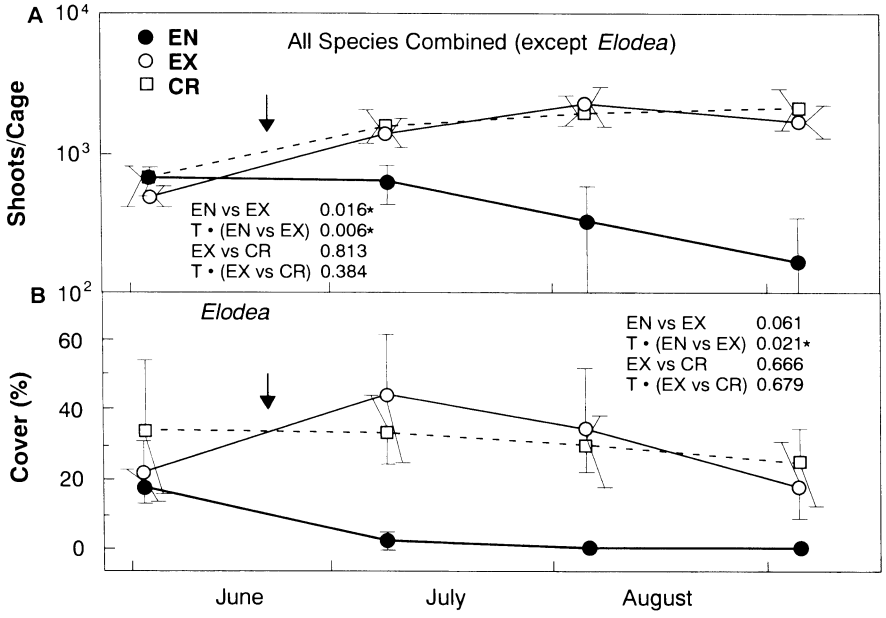


FIG. 2. Abundance (means ± 1 SE) of (A) all macrophyte species (except *Elodea*) combined (shoot number plus rosette number, respectively, for single-stemmed and rosulate species) and (B) *Elodea* (% cover) with time (*T*) in enclosures (EN), exclosures (EX), and cageless references (CR). Arrow indicates the addition of crayfish *Orconectes rusticus* to enclosure cages. *P* values less than the adjusted critical alpha of 0.025 are starred (*). Repeated-measures *F* values corresponding to *P* values on the figure are as follows. For A: EN vs. EX, $F_{1,9} = 8.80$; *T*·(EN vs. EX), $F_{3,7} = 10.53$ ; EX vs. CR, $F_{1,9} = 0.06$; *T*·(EX vs. CR), $F_{3,7} = 1.18$. For B: EN vs. EX, $F_{1,9} = 4.58$; *T*·(EN vs. EX) $F_{3,7} = 6.37$; EX vs. CR, $F_{1,9} = 0.20$; *T*·(EX vs. CR), $F_{3,7} = 0.52$. Repeated-measures ANOVAs were conducted on square-root transformed data. Note log scale on ordinate.

the three treatments showed that densities of all macrophyte species declined in enclosures and increased in exclosures and cageless references. Crayfish also reduced macrophyte species richness. In September, we sampled 3 species in enclosures, and 12 species in both exclosures and cageless references.

Comparison between enclosures and exclosures in macrophyte species composition over time (Fig. 4, Table 1) suggest that any disproportionate effect of crayfish on different species was not strong. Fig. 4 suggests crayfish precluded the occurrence of *Najas,* a late-sprouting species that overwinters exclusively as a seed; but because of high cage-to-cage variation in *Najas* abundance, ANOVA comparison of enclosures and exclosures (Table 1) provides only marginal support for this interpretation (EN vs. EX $P = 0.0519$). The only significant difference between exclosures and cageless references was *Vallisneria* (Table 1), but that difference may largely reflect the initially high abundance of *Vallisneria* in cageless references.

### *Macroinvertebrates*

*Snails.*—Response in total snail abundance was similar to that of macrophyte abundance. Through the summer, snail numbers increased in both exclosures and cageless references, but decreased in the presence of crayfish (Fig. 5). In September, snail density in enclosures was 1% that of exclosures. Thus, crayfish significantly reduced snail numbers (EN vs. EX $P = 0.024$). No significant difference existed between exclosures and cageless references (Fig. 5).

Of the 11 snail species that occurred in the experiment, *Amnicola* sp., *Physella* sp., and *Helisoma anceps*

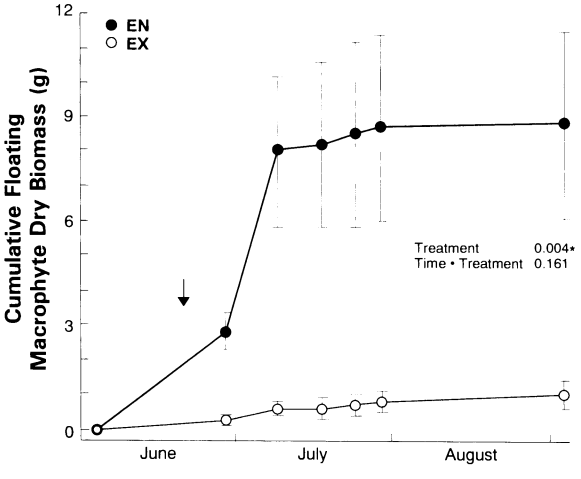


FIG. 3. Macrophyte dry biomass (all species combined) floating in enclosures and exclosures that accumulated over time (means ± 1 SE). Arrow indicates the addition of *O. rusticus* to enclosures. *P* values less than the critical alpha of 0.05 are starred (*). Repeated-measures ANOVA *F* values corresponding to the *P* values on the figure are: Treatment, $F_{1,6} = 21.50$; Time·Treatment, $F_{5,2} = 5.50$. Repeated measures ANOVA was conducted on square-root transformed data.

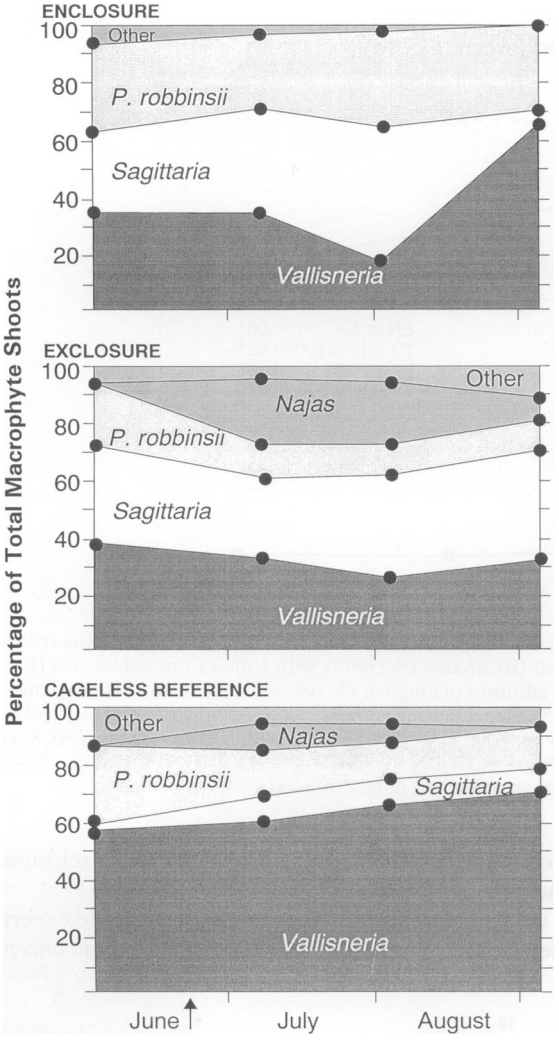


FIG. 4. Relative abundance of macrophyte species over time in enclosures, exclosures, and cageless references. Arrow on bottom abscissa indicates the addition of *Orconectes rusticus* to enclosures. See Table 1 for statistical evaluation.

(Menke) were most abundant (Fig. 6). Other species were *Gyraulus parvus* (Say), *Promenetus exacuous* (Say), *Stagnicola (Lymnaea) emarginata* (Say 1821), *Campeloma decisum* (Say 1816), *Acella haldemani* ('Deshayes' W.G. Binney 1867), *Planorbella campanulata* (Say 1821), *Lymnaea stagnalis* (Linnaeus), and *Valvata tricarinata* (Say 1817). Visual inspection of plots (not shown) of individual species over time in the three treatments suggested that densities of all snail species declined throughout summer in enclosures and increased in exclosures and cageless references. Patterns of relative species abundance suggest *O. rusticus* reduced species richness, especially by eliminating *Physella* and *Helisoma anceps* (Fig. 6). In September, three species, represented by fewer than six specimens each, were sampled in enclosures (*Amnicola, Campeloma decisum,* and *Promenetus exacuous*). In exclosures and cageless references, many more individuals were contained in samples, coming from six species in exclosures (*Amnicola, Physella, Helisoma anceps, Lymnaea stagnalis, Planorbella campanulata,* and *Stagnicola emarginata*) and five in cageless references (*Amnicola, Physella, Helisoma anceps, Planorbella campanulata,* and *Campeloma decisum*).

Species-specific repeated measures ANOVA on relative abundance supported the apparent patterns (Table 1). Both *Helisoma anceps* and *Physella* differed significantly between enclosures and exclosures, whereas no significant differences existed between exclosures and cageless references (Table 1). Data for *Lymnaea stagnalis, Acella haldemani,* and *Valvata tricarinata* were not analyzed because only one specimen of each was sampled during the experiment.

*Nonsnail macroinvertebrates.*—Total numbers of macroinvertebrates other than snails did not respond significantly to *O. rusticus,* as indicated by nonsignificant contrasts between enclosures and exclosures (Fig.

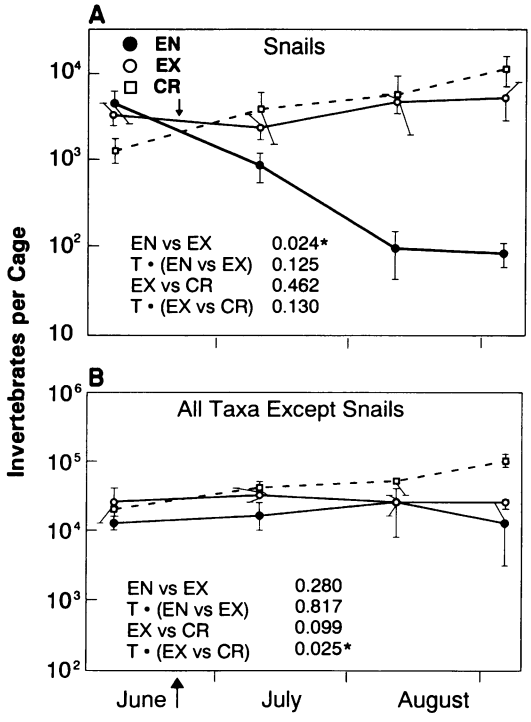


FIG. 5. Numbers of snails (top) and all other macroinvertebrates (bottom) (means ± 1 SE; see *Materials and methods: Macroinvertebrate sampling* for calculation) with time (*T*) in enclosures (EN), exclosures (EX), and cageless references (CR). Arrow below abscissa indicates the addition of *O. rusticus* to enclosures. *P* values less than the adjusted critical alpha of 0.025 are starred (*). Repeated measures ANOVA *F* values corresponding to *P* values on the figure are as follows. For snails (top): EN vs. EX, $F_{1,9} = 7.39$; $T$·(EN vs. EX), $F_{3,7} = 2.71$; EX vs. CR, $F_{1,9} = 0.59$; $T$·(EX vs. CR), $F_{3,7} = 2.65$. For other macroinvertebrates (bottom): EN vs. EX, $F_{1,9} = 1.32$; $T$·(EN vs. EX), $F_{3,7} = 0.31$; EX vs. CR, $F_{1,9} = 3.39$; $T$·(EX vs. CR), $F_{3,7} = 5.91$. Repeated measures ANOVAs were conducted on square-root transformed data. Note log scales on ordinates.

TABLE 1. Repeated measures ANOVA contrasts comparing percentage abundance (arcsine transformed) in experimental treatments and their interactions for the seven most common macrophyte species, the eight most common snail species, and the five most common macroinvertebrate taxa. Significant $P$ values ($<0.025$) are underlined.

| | Enclosure–exclosure | | | | Exclosure–cageless reference | | | |
|---|---|---|---|---|---|---|---|---|
| | EN vs. EX | | $T$·(EN vs. EX) | | EX vs. CR | | $T$·(EX vs. CR) | |
| | $F_{1,9}$ | $P$ | $F_{3,7}$ | $P$ | $F_{1,9}$ | $P$ | $F_{3,7}$ | $P$ |
| Macrophytes | | | | | | | | |
| *Ceratophyllum* | 0.34 | .5751 | 1.51 | .2926 | 0.42 | .5345 | 1.54 | .2877 |
| *Najas* | 5.01 | .0519 | 2.17 | .1800 | 1.85 | .2071 | 1.60 | .2700 |
| *P. amplifolius* | 0.39 | .5502 | 0.32 | .8089 | 1.71 | .2239 | 1.38 | .3245 |
| *P. richardsonii* | 1.30 | .2830 | 1.15 | .3950 | 0.04 | .8446 | 0.67 | .5987 |
| *P. robinsii* | 0.08 | .7814 | 2.11 | .1875 | 0.21 | .6559 | 0.05 | .9850 |
| *Sagittaria* | 0.31 | .5920 | 2.34 | .1601 | 3.03 | .1155 | 0.20 | .8919 |
| *Vallisneria* | 1.42 | .2678 | 2.00 | .2150 | 12.87 | .0071 | 0.18 | .9067 |
| Snails | | | | | | | | |
| *Amnicola* | 0.56 | .4750 | 3.47 | .0794 | 0.07 | .7911 | 2.20 | .1755 |
| *Campeloma* | 0.74 | .4109 | 1.33 | .3379 | 0.86 | .3784 | 1.40 | .3213 |
| *Gyraulus* | 0.21 | .6563 | 1.21 | .3743 | 0.03 | .8687 | 2.64 | .1312 |
| *Helisoma* | 8.20 | .0186 | 3.00 | .1048 | 2.96 | .1196 | 1.31 | .3435 |
| *Stagnicola* | 1.81 | .2114 | 0.28 | .8418 | 0.00 | .9649 | 0.83 | .5167 |
| *Physella* | 25.56 | .0007 | 3.84 | .0648 | 0.07 | .7958 | 1.79 | .2372 |
| *Planorbella* | 1.43 | .2616 | 2.64 | .1306 | 3.19 | .1076 | 1.67 | .2595 |
| *Promenetus* | 1.06 | .3296 | 1.32 | .3431 | 0.09 | .7747 | 1.05 | .4287 |
| Total macroinvertebrates | | | | | | | | |
| Amphipoda | 0.82 | .3888 | 4.44 | .0478 | 1.96 | .1954 | 2.60 | .1341 |
| Diptera | 5.47 | .0441 | 1.24 | .3642 | 1.79 | .2141 | 0.12 | .9426 |
| Isopoda | 0.32 | .5862 | 1.54 | .2862 | 0.43 | .5296 | 4.94 | .0376 |
| Total snails | 3.65 | .0883 | 9.24 | .0079 | 4.40 | .0654 | 1.79 | .2357 |
| Trichoptera | 5.78 | .0397 | 0.93 | .4758 | 0.32 | .5881 | 4.28 | .0517 |

5). In both enclosures and exclosures, numbers remained relatively constant through the summer. In cageless references, numbers of nonsnail macroinvertebrates increased through the summer, producing a marginally significant difference between exclosures and cageless references [$T$·(EX vs. CR) $P = 0.0248$; Fig. 5].

*Macroinvertebrate community composition.*—The macroinvertebrate community (including snails and all other taxa) was dominated numerically by Diptera larvae, snails, isopods, amphipods, and Trichoptera larvae (Fig. 7). Other insects consisted primarily of immature odonates and Ephemeroptera. Other crustaceans consisted primarily of ostracods, cladocerans, and copepods. Remaining macroinvertebrates consisted primarily of oligochaetes, leeches, sphaeriid clams, water mites, and triclad turbellarians.

Because *O. rusticus* reduced snails but affected other macroinvertebrate taxa weakly or not at all, the only significant change in macroinvertebrate community composition in enclosures relative to exclosures was the decline in relative abundance of snails (Fig. 7, Table 1). Relative numbers of Diptera seemed to increase in enclosures as snails declined (Fig. 7), but this interpretation was only weakly supported by repeated measures ANOVA (Table 1, EN vs. EX $P = 0.0441$). Repeated measures ANOVA also suggested weakly that *O. rusticus* affected Trichoptera numbers (Table 1, EN vs. EX $P = 0.0397$), but given the initially low abundance of caddisflies in enclosures (Fig. 7), little meaning can be attached to this apparent difference. Comparing exclosures and cageless reference areas, no significant differences in relative abundance of macroinvertebrates existed (Table 1).

*Numbers of algivores.*—The literature on macroinvertebrate feeding (Strayer 1985, Thorp and Covich 1991) indicated that all macroinvertebrate taxa other than odonates, leeches, clams, mites, and triclads include species that are algivorous on periphyton during at least part of the aquatic life stage. Accordingly, algivorous taxa comprised 93% of the total numbers of nonsnail macroinvertebrates (range = 75–99%, depending on sampling date). Thus, a plot of all nonsnail algivores (not shown) looks exactly like Fig. 5B except with the vertical axis shifted slightly upward. Thus, total nonsnail algivores did not differ between enclosures and exclosures, and the only difference in grazer numbers in enclosures relative to exclosures was the reduction in snail numbers. We therefore expected periphyton to be higher in enclosures (relative to exclosures) because of reduced snail numbers in enclosures. Because the greatest numbers of grazers (snails plus nonsnail grazers) occurred in cageless references (because of higher numbers of nonsnail grazers), we expected cageless references to have the lowest periphyton abundance.

*Relative impact on snails of predation and macrophyte herbivory.*—We expected that crayfish would consume snails selectively over macrophytes. Thus, we expected the ratio of snails : macrophytes to decline in

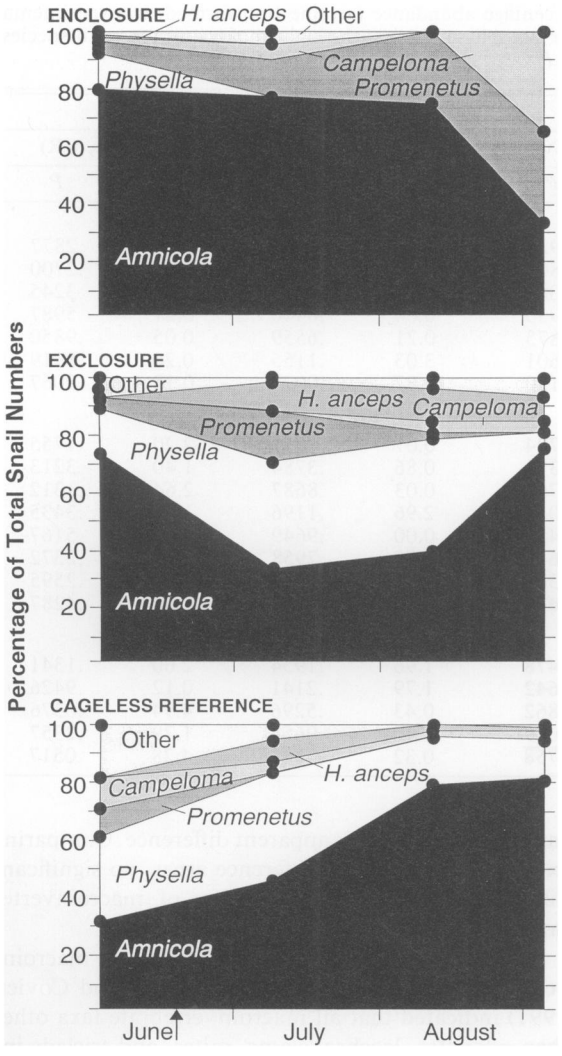


FIG. 6. Relative abundance of snail species over time in enclosures, exclosures, and cageless references. Arrow on bottom abscissa indicates addition of *O. rusticus* to enclosures. See Table 1 for statistical evaluation.

enclosures relative to exclosures and for the ratio in cageless references to be similar to that for exclosures. We tested this prediction separately for snails and all other macroinvertebrates using repeated measures ANOVA contrasts on the number of macroinvertebrates in a cage divided by the number of macrophytes (shoots plus rosettes) in a cage. Natural phenological changes in numbers of both macroinvertebrates and macrophytes would cause this ratio to change over time. Thus, we had no interest in predicting the absolute value of this ratio or the specific direction or magnitude of its temporal trends. Rather, the focus of our analysis was how the ratio in enclosures changed over time relative to changes in the ratio in exclosures.

For the ratio of snails : macrophytes, the relative trends were consistent with expectations but not strongly supported by the statistical analysis (Fig. 8). That is, the ratio of snails to macrophytes in enclosures declined relative to that in exclosures and cageless references, but the enclosure–exclosure contrast was not significant. As expected, the trends for exclosures and cageless references did not differ significantly (Fig. 8). This analysis suggests that *O. rusticus* did not strongly select snails over macrophytes. However, given that a substantial proportion of macrophyte destruction resulted from nonconsumptive fragmentation (see Fig. 3), the snail : macrophyte ratio for enclosures (but not for exclosures and cageless references) is an inflated index of relative consumption of snails and macrophytes, and thus decreases the real difference between enclosures and exclosures. Thus, our analysis underestimates the crayfish impact.

For the ratio of nonsnail macroinvertebrates : macrophytes, relative trends for enclosures and exclosures contradicted our initial expectation that crayfish predation would reduce nonsnail invertebrates as well as snails (Fig. 8). While the enclosure ratio increased, the

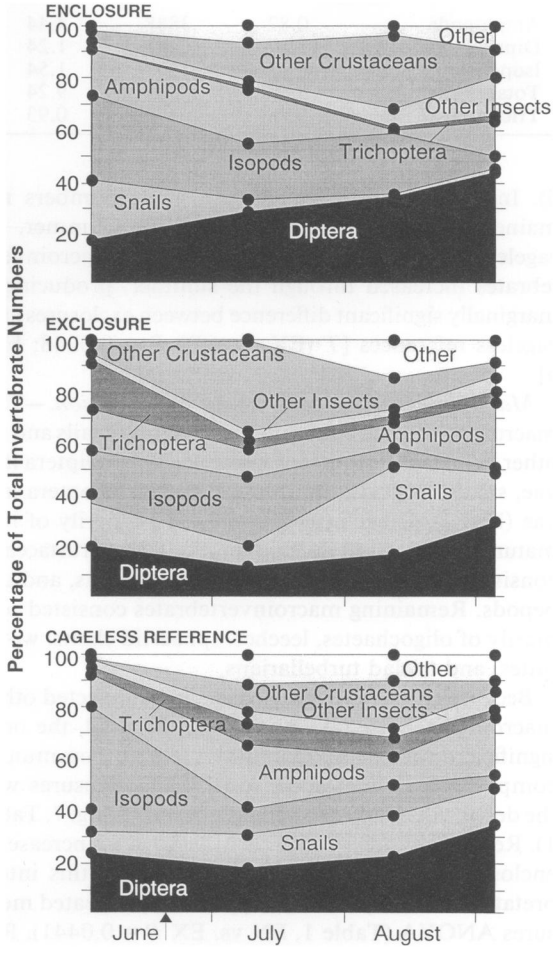


FIG. 7. Relative abundance of all macroinvertebrate taxa over time in enclosures, exclosures, and cageless references. Arrow on bottom abscissa indicates addition of *Orconectes rusticus* to enclosures. See Table 1 for statistical evaluation.

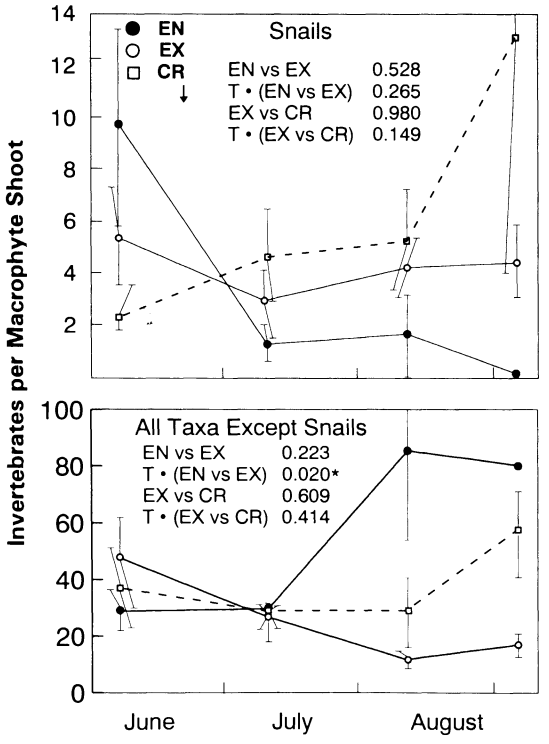


FIG. 8. Numbers of macroinvertebrates per macrophyte (shoots plus rosettes) over time ($T$) in enclosures (EN), exclosures (EX), and cageless references (CR) for snails and for all other macroinvertebrates (means ± 1 SE). Arrow indicates addition of *O. rusticus* to enclosures. $P$ values less than the adjusted critical alpha of 0.025 are starred (*). Repeated measures ANOVA $F$ values corresponding to the $P$ values on the figure are as follows. Snails (top): EN vs. EX, $F_{1,8} = 0.44$; $T$·(EN vs. EX), $F_{2,7} = 1.61$; EX vs. CR, $F_{1,8} = 0.00$; $T$·(EX vs. CR), $F_{2,7} = 2.53$. All other macroinvertebrates (bottom): EN vs. EX, $F_{1,8} = 1.75$; $T$·(EN vs. EX), $F_{2,7} = 7.27$; EX vs. CR, $F_{1,8} = 0.28$; $T$·(EX vs. CR), $F_{2,7} = 1.00$. Repeated-measures ANOVA was conducted on square-root transformed data. Only the first three dates could be used because on the last sampling date, macrophyte number was zero in three of the four enclosure cages.

exclosure ratio declined [$T$·(EN vs. EX) $P = 0.020$]. However, as noted above, the enclosure ratio is inflated and the difference between the enclosure and exclosure ratios is therefore exaggerated. Nevertheless, the pattern is still consistent with the simultaneous lack of effect of *O. rusticus* on nonsnail invertebrates (see Fig. 5) and the strong negative effect on macrophytes (see Fig. 2). Despite the destruction of macrophyte habitat, the nonsnail invertebrates were apparently unaffected. As expected, no significant difference existed between exclosures and cageless references (Fig. 8).

### *Periphyton*

Consistent with the predicted top-down effect, periphyton areal chlorophyll *a* increased in enclosures (as snails were reduced), while it initially increased slightly and later declined in exclosures (Fig. 9A). On the last sampling date, enclosure chlorophyll *a* was three times higher than exclosure chlorophyll *a* (Tukey's $P < 0.05$). However, the pattern of chlorophyll *a* in cageless references contradicted the expectation (based on total grazer abundance) that it would be the lowest of all three treatments. Instead, at the conclusion of the experiment, chlorophyll in cageless references was high and did not differ significantly from that in enclosures (Fig. 9A).

As an index of how *O. rusticus* affected the composition of the periphyton matrix, we also examined the amount of chlorophyll *a* per unit dry mass of periphyton (Fig. 9B). In enclosures, chlorophyll *a*/DM increased throughout the experiment and was 4.5× higher than exclosures at the last sampling date. This suggests that the enclosure periphyton matrix was increasingly dominated by live algae (relative to detritus and other components), whereas in the exclosure matrix, the proportion of live algae declined slightly overall. The chlorophyll *a*/DM ratio in cageless references was similar to that in exclosures throughout the ex-

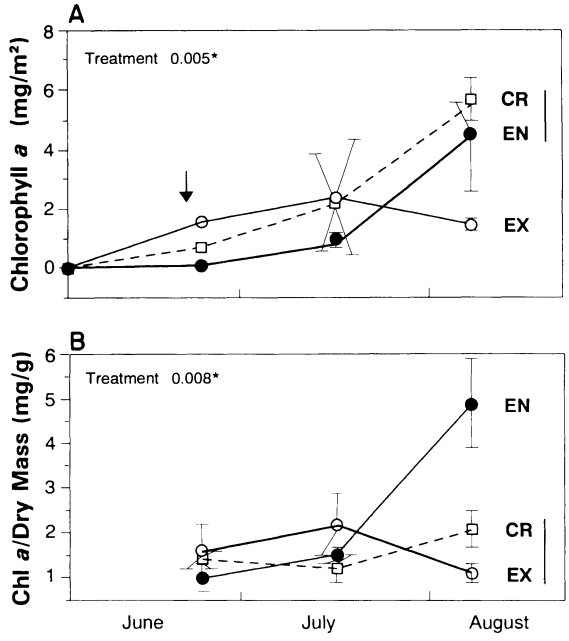


FIG. 9. Areal densities on plastic strips (means ± 1 SE) for periphyton chlorophyll *a* (A) and chlorophyll *a* per unit dry mass (B) with time in enclosures (EN), exclosures (EX), and cageless references (CR). Arrow in top panel indicates the addition of *O. rusticus* to enclosures. Repeated-measures ANOVA could not be used on periphyton data because of missing values (see *Materials and methods: Statistical analysis*). ANOVA $P$ values less than the critical alpha of 0.05 are starred (*). Results of Tukey's tests ($P < 0.05$) comparing treatments on the last sampling date are indicated by the vertical bars on the right side of each panel; treatments that did not differ significantly are connected by a bar. ANOVA $F$ values corresponding to $P$ values on the figure are as follows. Chlorophyll *a* (A): Treatment, $F_{2,7} = 12.29$. Chlorophyll/DM (B): Treatment, $F_{2,7} = 10.27$. ANOVAs and Tukey's tests were conducted on square-root transformed data.

periment and did not differ from that in exclosures at the last sampling date (Fig. 9B).

## Discussion

### *Littoral zone trophic cascade confirmed*

For all responses, the difference between enclosure and exclosure cages confirmed the existence of a three-level trophic cascade in which *O. rusticus* indirectly increased periphyton abundance on plastic strips by directly reducing the abundance of algivorous snails. This pattern occurred because snails are both the prey group primarily affected by crayfish, and the functionally most important grazer group among the many grazer taxa present in the community. Thus, this food web responded as predicted, with chain-like dynamics, despite its interconnectedness and the omnivory of crayfish (Fig. 1).

In addition to the direct and indirect effects on snails and periphyton, respectively, *O. rusticus* directly reduced macrophyte abundance. The occurrence of floating macrophyte fragments, which is typical of other field and laboratory experiments on crayfish grazing (Lodge and Lorman 1987, Lodge 1991, Olsen et al. 1991), confirm that macrophyte reduction resulted primarily from direct crayfish foraging and not from any indirect links.

With regard to Fig. 1, overall experiment results demonstrated that interactions 1, 2, and 3 were strong, as predicted, whereas interactions 5, 6, 7, and 9 were weak. The lack of responses by periphyton and macrophytes to increases in nonsnail macroinvertebrates in cageless references further suggests that interactions 8 and 10 were weak.

The trophic cascade evoked in our experiment is parallel to those described by Brönmark et al. (1992) and Martin et al. (1992) for sunfish, snails, and periphyton in two northern Wisconsin lakes and a Tennessee lake, respectively. Unlike crayfish, however, sunfish do not consume appreciable quantities of macrophytes. Therefore, crayfish have an additional indirect impact on periphyton that sunfish do not—the reduction of macrophyte surface area available for periphyton colonization. Although algal abundance in the presence of crayfish is higher per unit surface area of strip (and presumably per unit surface area of macrophyte and sediment), there is less colonizable surface remaining. In terms of total periphyton per unit area of lake bottom, then, it remains possible that omnivory by crayfish may complicate substantially the chain-like dynamics discussed above, which were illustrated by periphyton per unit of remaining surface area.

To estimate the net impact of these counteracting forces on periphyton, we calculated the total amount of periphyton chlorophyll *a* in cages (on 9 $m^2$ of sediment plus macrophyte surfaces), exclusive of the scrubbed screen walls. We calculated macrophyte surface area using August macrophyte shoot number (Fig. 2) and an estimate of 0.03 $m^2$ surface area per macrophyte shoot (from Brown and Lodge 1993). Macrophyte surface area per cage was thereby estimated to be 19 and 75 $m^2$ in enclosures and exclosures, respectively. For both sediments and macrophytes, we multiplied by August chlorophyll *a* densities on strips (Fig. 9). From this, enclosures and exclosures were estimated to have 87 ± 38 mg (mean ± 95% CL) and 113 ± 30 mg of chlorophyll *a* per cage, respectively. Although confidence limits overlap broadly, these estimates suggest that in this specific experiment the net effect of crayfish was to reduce total resource abundance for algivores, while at the same time improving the quality of the remaining resource (as indicated by higher chlorophyll *a* densities and higher chlorophyll *a* : dry mass ratios; see Fig. 9). The lack of any enclosure-exclosure difference in numbers of nonsnail invertebrates (which could arise through changes in survivorship) suggests, however, that there was no strong net effect of these changes on algivores.

Extrapolations of the net effect of crayfish on total periphyton abundance in other lakes or streams would depend on crayfish density, density and susceptibility of macrophytes to crayfish grazing, periphyton abundance, and the susceptibility of the algivorous benthos to crayfish predation. For communities like that in our Plum Lake experiment, where crayfish abundance was moderate to high, initial macrophyte density was high, and susceptible algivores (snails) were initially abundant, the net impact on total periphyton abundance is likely to be negative. In many other communities (particularly where background macrophyte abundance is low), the increase in algal biomass per unit of occupied area may more than offset losses of macrophyte surface area, and net impact of crayfish on periphyton would be positive. In our experiment, a three-level trophic cascade clearly occurred with respect to periphyton abundance per unit of colonized area, but perhaps not with respect to total periphyton abundance (i.e., on macrophytes and sediments) per area of lake bottom. Thus, omnivory by *O. rusticus,* feeding on two trophic levels, each of which affects periphyton indirectly (Fig. 1 indirect links 1, 2 and 3, 4), does make generalization of net effects more difficult, as suggested by Strong (1992).

Below, we discuss some details of the impact of *O. rusticus* on macrophytes, macroinvertebrates, and periphyton, as revealed by comparison of enclosures and exclosures. We then consider what the cageless reference treatment may suggest about how experimental results may be extrapolated to natural lakes.

### *Impact on macrophytes and macroinvertebrates*

*Impact on abundance.*—In enclosures, crayfish essentially clear-cut macrophytes, almost eliminated snails, and had no impact on nonsnail macroinvertebrates. For macrophytes, this supports the observations of Lodge and Lorman (1987), who found that

densities of *O. rusticus* as low as 19 g/m$^2$ significantly reduced submersed macrophyte biomass. Other studies also demonstrate the significant, negative impact that several species of crayfish can have on submersed macrophytes (Feminella and Resh 1989, Chambers et al. 1990, Lodge 1991, Hazlett et al. 1992). The floating macrophyte fragments collected from enclosures are consistent with results of laboratory experiments, in which a large proportion (typically >50%) of macrophyte reduction results from nonconsumptive destruction (Lodge 1991, Olsen et al. 1991). This behavior is not uncommon among consumers of freshwater macrophytes (Lodge 1991) and marine macroalgae (e.g., Elner and Vadas 1990).

The negative impact of crayfish on the population of most plant species will be the same whether plant tissue is eaten or fragmented. However, population size and dispersal of species that readily root adventitiously, e.g., *Elodea,* or species that are always rootless, e.g., *Ceratophyllum,* could, in fact, be enhanced by crayfish fragmentation. Cut shoots of most species, however, would join the detrital pool, often after being deposited by wave action on shore or in shallow water. For microbes and detritivores, macrophyte fragments resulting from crayfish feeding could be an important source of high-quality detritus during the growing season when fresh detritus is ordinarily scarce.

For snails, the reduction of abundance through direct predation by crayfish in our experiment is consistent with earlier laboratory and pool experiments with *O. rusticus* (Lodge and Lorman 1987), *O. propinquus* (Olsen et al. 1991) and *O. virilis* (Hanson et al. 1990). In contrast to these other experiments, we stocked realistic densities and sizes of crayfish in a natural prey assemblage typical of many mesotrophic northern Wisconsin lakes. For the direct effects of crayfish on both macrophytes and snails, therefore, the current results are more robust than earlier ones.

For nonsnail macroinvertebrates, no other investigators have tested the impact of *O. rusticus,* but the lack of impact is roughly consistent with the impact of *O. virilis* on macroinvertebrates in laboratory pools (Hanson et al. 1990). *O. virilis* strongly reduced snail numbers, but had only a weak negative effect on some nonsnail macroinvertebrates (Hanson et al. 1990). Most nonsnail macroinvertebrates may move quickly enough to escape tactile-feeding crayfish (e.g., isopods, amphipods, some Diptera), escape recognition by living in cases (e.g., Trichoptera), or avoid contact by living in the sediments (e.g., some Diptera). In very shallow habitats, some snails crawl out of water on emergent tree branches or other vegetation in response to other snails being eaten by crayfish (Alexander and Covich 1991). However, in Plum Lake, as in most lakes, such escapes are impossible, and we did not observe any snails crawling above the waterline on our cage walls.

*Impact on species richness.*—*Orconectes rusticus* reduced species richness of both macrophytes and snails. Mechanisms of species elimination that probably operated in the experiment include selective feeding by crayfish and rarefaction. The results of our experiment do not allow us to rigorously distinguish these two mechanisms.

For macrophytes, results of laboratory selection experiments demonstrate that consumption and fragmentation of macrophytes by *O. rusticus* is species-selective (Lodge 1991). In our field cage experiment, the apparent elimination by crayfish of at least one plant species, *Najas,* may have resulted from selective grazing by crayfish, but probably also resulted from the inability of *Najas* to tolerate even small amounts of biomass removal. *Najas* is the only species in the Plum Lake macrophyte assemblage that is obligately sexual and annual, an unusual reproductive habit among aquatic plants. It overwinters as a small seed, whereas coexisting *Potamogeton* species have underground rhizomes, *Vallisneria* overwinters as a turion, and most other species overwinter in relatively large vegetative forms (Hutchinson 1975:233 ff., Bartley and Spence 1987). Consequently, *Najas* seedlings have a relatively small energy reserve to recover from the removal of even a very small amount of biomass by crayfish. Crayfish might therefore have a disproportionate impact on *Najas,* regardless of any preference for *Najas.*

Because few snail individuals were sampled in enclosures in September, definitive statements about the impact of crayfish on species composition are impossible. Our results are generally consistent with a reduction in species richness of snails that has occurred in Trout Lake, Wisconsin as *O. rusticus* has invaded the lake (Lodge et al. 1986): the only snail species now remaining in areas with high abundance of *O. rusticus* is *Campeloma,* a species with a very thick shell and large adult size (D. M. Lodge and M. W. Kershner, *unpublished data*). Thus, for snails, some of the impact by *O. rusticus,* as for other crayfish (Alexander and Covich 1991), may result from selective feeding by crayfish. The most striking result, however, is that all snail species were very much reduced.

In addition, rarefaction probably played an important role in reducing species richness of both plants and animals in enclosures. Even if crayfish ate prey as encountered, rare species would be eliminated as total abundance declined.

### *Impact on periphyton*

Our expectation that periphyton biomass would increase when snails decreased was informed by earlier experiments and observations (Lamberti et al. 1987, Brönmark 1989, Osenberg 1989, Weber and Lodge 1990, Brönmark et al. 1992, Martin et al. 1992). Snails comprised 10–35% of macroinvertebrate numbers in exclosures (Fig. 7). Because individual snails were on average much larger than individuals of all other macroinvertebrate taxa (D. M. Lodge and M. W. Kershner, *unpublished data*), snails constituted a much higher

percentage of total macroinvertebrate biomass and an even higher percentage of grazer biomass. Because in comparing enclosures and exclosures, snails were the only group of macroinvertebrates that responded to crayfish, we believe that periphyton increases in enclosures were responses to decreases in snail numbers.

On the other hand, our use of a 500-$\mu$m mesh sieve means that we did not sample many smaller invertebrate taxa (Strayer 1985), which probably have higher mass-specific ingestion rates of algae than larger grazers. In at least one experiment (Cattaneo and Kalff 1986), numerical increases in small grazing taxa compensated for reductions in large grazing taxa. Our results showed no evidence of compensatory numerical increases of nonsnail macroinvertebrates, but we cannot rule out increases in micrograzers that we did not sample. Nevertheless, abundant earlier work on similar mixed-algivore assemblages (Brönmark 1989, Osenberg 1989, Brönmark et al. 1992, Martin et al. 1992) support our interpretation that snails were the dominant grazers on periphyton.

*Orconectes rusticus* eats periphyton (Lorman 1975, 1980, Hill et al. 1993), but our results reported here and the Trout Lake patterns of crayfish, snails, and periphyton (Weber and Lodge 1990) suggest strongly that the positive indirect effect that crayfish have on periphyton outweighs the negative direct effect (Fig. 1).

In addition to increasing the amount of live algae (as indexed by chlorophyll *a*), crayfish altered the quality of periphyton, increasing the chlorophyll *a* : dry mass ratio (Fig. 9B). Based on long experience of watching crayfish in laboratory and field situations, we believe that *O. rusticus* directly reduced loosely attached, nonalgal components of periphyton (e.g., flocculent detritus) through nonconsumptive foraging behavior. During ordinary locomotion (walking, climbing, tail-flipping, etc.), crayfish often disturb the surface over which they move. In addition, during night dives, one of us (D. M. Lodge) has observed *O. rusticus* climbing on macrophytes, often temporarily collapsing the macrophyte. In our cages, one of us (J. E. Aloi) saw crayfish crawling on and pulling the plastic strips down to the sediment and observed many small tears in the strips that probably resulted from bites with crayfish mandibles. During foraging, *O. rusticus* constantly picks at the substrate with its walking legs. Our results and ancillary observations thus suggest that *O. rusticus* activity increases sloughing of loosely attached nonalgal material, but does not significantly reduce abundance of living algae, which are more firmly attached.

### *Cageless references*

In our experiment, the only two responses that differed from our expectations occurred in cageless references (relative to exclosures): the marginally significant increase in nonsnail invertebrates (Fig. 5) and the significant increase in periphyton chlorophyll *a* (Fig. 9). Taken together, these two results are doubly puzzling because the first (high invertebrates) should produce a response in the second (periphyton chlorophyll *a*) that is exactly the opposite of that observed. Although the occurrence of both of these two apparently anomalous responses in cageless references (relative to exclosures) may suggest they result from cage artifacts, we do not believe these results are a direct effect of cages.

The most likely effects of cages (in comparison with the cageless treatment) would be reduced light and reduced water movement. For invertebrates, we would not expect reduced light to have a perceptible direct effect. Reduced water movement could reduce importation of broadcast insect eggs, but relative abundance of insects did not increase in cageless references relative to caged treatments (Fig. 7). Thus, we do not think the difference in nonsnail invertebrates results from cage artifacts.

For periphyton chlorophyll *a,* both low light and reduced water movement could bias results in the observed direction, but should also affect macrophytes. However, there was no apparent cage artifact for macrophytes (Fig. 2). Furthermore, periphyton at this depth in Plum Lake were nutrient-limited, not light-limited. In an experiment designed to test factors limiting periphyton growth (and run concurrently with the crayfish experiment reported here), periphyton biomass in small, screen-covered, snail-free cages increased 30% in response to phosphorus addition (J. E. Aloi, *unpublished data*). Finally, in similar field experiments (involving pumpkinseed sunfish instead of crayfish), using cages identical to those in this study in two more productive lakes, no apparent cage effect occurred for periphyton (Brönmark et al. 1992). Thus, for both nonsnail invertebrates and periphyton chlorophyll *a,* we reject cage artifacts per se as explanations for unexpected results.

Obvious potential indirect effects of cages were the exclusion of fishes, many of which are benthivorous fishes that include snails and other invertebrates in their diet. Rank abundance (from most to least) of littoral fish from electroshocking in Plum Lake in summer 1987 was: walleye (*Stizostedion vitreum*), bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieui*), pumpkinseed (*Lepomis gibbosus*), and northern pike (*Esox lucius*) (R. A. Stein et al., *unpublished data*). We observed many fishes, especially the specialist molluscivore pumpkinseed and the polyphagous molluscivore bluegill in the experimental area. However, the similarity of trends in snail abundance in cageless controls and exclosures, and the increase in nonsnail invertebrates in cageless controls relative to exclosures suggest that fish did not strongly affect overall macroinvertebrate numbers in the cageless controls. However, it is possible that visually feeding fish predators (in contrast to tactile-feeding crayfish) preferentially removed snails from the relatively

broad, smooth plastic strips in the cageless references. In our experiment, these strips were more exposed relative to similar strips in Brönmark et al. (1992), because macrophyte density in cageless references in Plum Lake were low relative to those in the two lakes used by Brönmark et al. (1992). Thus, with respect to fish predation (but not periphyton colonization [see *Materials and methods*] or crayfish predation), our strips may have been a poor mimic of natural macrophytes. Unfortunately, we did not census snails or other invertebrates on the strips.

Thus, for nonsnail invertebrates and periphyton chlorophyll *a*, results in cageless references remain largely unexplained, although we are confident in ruling out direct effects of cages. Nevertheless, the primary comparisons of interest in our experiment, between enclosures and exclosures, reflect the overwhelming impact of *O. rusticus* on snails, periphyton, and macrophytes, as discussed under *Impact on macrophytes and macroinvertebrates*.

### *Duration of experiment*

If our experiment had included more than one growing season, some results might have been different. The lack of response of nonsnail invertebrates even after macrophytes were almost eliminated by crayfish may suggest that macrophytes are not a unique or critical habitat for most invertebrates (Brown and Lodge 1993, cf. Lodge 1986). These invertebrates apparently simply took up residence elsewhere in the cage with no detectable increase in mortality. However, any sublethal effects on these originally epiphytic invertebrates might have been expressed in reduced population growth in the subsequent growing season.

Conversely, previous experiments (Cuker 1983, Cattaneo and Kalff 1986) suggest that as snails decline, smaller macroinvertebrates show compensatory numerical increases. For many taxa in our experiment, such responses were largely impossible, except through changes in survivorship, because the experiment included only one growing season.

### *Effects of crayfish on littoral communities*

*O. rusticus* is the latest invader of three *Orconectes* congeners common in northern Wisconsin lakes (Lodge et al. 1986, Olsen et al. 1991). Abundant evidence suggests that it may have a more negative impact on macrophytes and fisheries than *O. virilis* (the only species present in northern Wisconsin in a 1932 survey [Creaser 1932]) and *O. propinquus*. Recent studies suggest that may be true for at least three reasons: (1) higher growth rate and larger adult size of *O. rusticus* than *O. propinquus* (but not *O. virilis*) (Olsen et al. 1991, Hill et al. 1993); (2) higher mass-specific ingestion rate of snails by *O. rusticus* than both congeners (Olsen et al. 1991); (3) lower vulnerability to fish predators by *O. rusticus* than congeners (DiDonato and Lodge 1993). Although *O. rusticus* may have a quantitatively greater impact on littoral zone communities, all three congeners probably have a qualitatively similar impact. For example, *O. virilis* reduces macrophyte abundance in laboratory pools (Chambers et al. 1990), and when the reduction in macrophytes was compared to that of *O. rusticus* in field cages, it was similar (Hazlett et al. 1992). In addition, *O. virilis* reduces abundance of snails and other invertebrates in laboratory pools (Hanson et al. 1990) and apparently competes for food with trout in a Utah reservoir (Hepworth and Duffield 1987). Thus, crayfish of all three species are likely to have important impacts on communities in which they occur. Results of this study and a survey of 21 northern Wisconsin lakes (D. M. Lodge et al., *unpublished data*) strongly suggest that lakes with high densities of crayfish have reduced abundance and species richness of both macrophytes and snails. Such large community impacts probably also have important consequences for nutrient cycling in lakes (Carpenter and Lodge 1986).

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