Mechanisms of Impact of an Introduced Crayfish (*Orconectes rusticus*) on Littoral Congeners, Snails, and Macrophytes

T. Mark Olsen and David M. Lodge[1]

Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

Gregory M. Capelli

Department of Biology, College of William and Mary, Williamsburg, VA 23185, USA

and Robert J. Houlihan

Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA

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Since its introduction 30 yr ago, *Orconectes rusticus* has displaced *O. propinquus* and *O. virilis* and reduced macrophytes in several northern Wisconsin lakes. Since 1973, rate of displacement by *O. rusticus* varied among lakes, but relative abundance of *O. rusticus* increased in all nine lakes sampled in 1988 (eight of which were sampled in 1973 or 1975 and 1980). Using long-term field data and laboratory experiments, we explored mechanisms of differential impact of *O. rusticus* (relative to congeners) on benthic community structure. Displacement of *O. propinquus* (but not *O. virilis*) by *O. rusticus* increased mean crayfish size. Congener feeding preference did not differ among morphologically different macrophytes or between different-sized snails; however, weight-specific consumption and destruction rates did. *Orconectes rusticus* consumed more snails than its congeners and sublethally damaged more snails than *O. virilis*. *Orconectes rusticus* consumed more macrophyte biomass than *O. propinquus*; however, *O. rusticus* did not destroy (consumption plus fragmentation) more macrophyte biomass than its congeners. Changes in benthic community structure after displacement of congeners by *O. rusticus* may result from larger size (which probably lowers resource depression in the presence of size-selective fish predators) and greater weight-specific reductions of prey.

Depuis son introduction trente ans passés, *Orconectes rusticus* a déplacé *O. propinquus* et *O. virilis* et a entraîné une baisse de la biomasse de macrophytes dans plusieurs lacs septentrionaux du Wisconsin. Depuis 1973, le taux de déplacement a varié parmi les neuf lacs expérimentaux échantillonnés en 1988 (dont huit ont été échantillonnés en 1973 ou en 1975 et 1980), mais l'abondance relative de *O. rusticus* a augmenté dans tous ces bassins. À l'aide de données recueillies sur le terrain pendant une longe période et de données expérimentales, les auteurs ont étudié des modes d'impact différentiel de *O. rusticus* (par rapport à ses congénères) sur la structure de la communauté benthique. Le déplacement de *O. propinquus*, mais non de *O. virilis*, par *O. rusticus* a entraîné une augmentation de la longueur moyenne des écrevisses. En ce qui concerne l'alimentation des congénères, leur préférence entre des macrophytes morphologiquement différents ou des escargots de différentes tailles n'était pas différente; toutefois, les taux de consommation et de destruction relatifs au poids l'étaient. *Orconectes rusticus* a consommé plus d'escargots que ses congénères et en a blessés un plus grand nombre que *O. virilis*. De plus, elle a consommé une plus grande biomasse de macrophytes (consommation plus fragmentation) que *O. propinquus*, mais la biomasse qu'elle a détruite n'était pas aussi importante que celle détruite par ses congénères. Les modifications de la structure de la communauté benthique après le déplacement des congénères de *O. rusticus* peuvent être le résultat de la plus grande taille des proies (qui amène probablement une baisse de l'abondance des ressources en présence de poissons recherchant certaines tailles de proies) et d'une baisse plus importante du nombre de proies de certains poids.

The recent (circa 1960), probably inadvertent introduction of the crayfish, *Orconectes rusticus*, in northern Wisconsin lakes (Capelli and Magnuson 1983) has affected congeneric crayfish and other benthic fauna and flora. At least in the short term, *O. rusticus* has displaced its congeners (*O. propinquus* and *O. virilis*) (Capelli 1982). In addition, anecdotal evidence suggests that *O. rusticus* has a negative impact (relative to its congeners) on the abundance of submersed macrophytes, associated benthic invertebrates and fish in at least seven northern Wisconsin lakes (Lorman 1975; Magnuson et al. 1975; Lorman 1980; Lodge et al. 1985; Lodge and Lorman 1987). Residents and commercial crayfish trappers on these lakes noticed a decline in submersed macrophyte abundance coincident with an increase in crayfish abundance (Lorman 1975). Soon after *O. rusticus* introduction, macrophytes disappeared from Lake Metonga and walleye recruitment ceased (Lodge

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[1] Author to whom correspondence should be addressed.

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et al. 1985). In Long Lake, visual SCUBA sampling in 1974 indicated that the abundances of submerged macrophytes and *O. rusticus* were inversely related (Magnuson et al. 1975). In in situ cage experiments, *O. rusticus*, at densities not exceeding those found regionally, substantially reduced macrophyte abundance and species richness (Lodge and Lorman 1987).

Mechanisms of differential impact of *O. rusticus* (relative to congeners) on littoral benthic community structure are not well understood but may include higher metabolic rate (Momot 1984), larger individual size, higher population density, and higher population biomass (Lorman 1980; Lodge et al. 1985, 1986). In this study, we document long-term trends in crayfish species displacement and test six potential mechanisms of the apparently greater impact *O. rusticus* has on benthic communities (relative to *O. propinquus* and *O. virilis*).

Because previous studies indicated highly variable among-lake changes in percentage of *O. rusticus* over the short term (Capelli 1982; Capelli and Magnuson 1983) or reversible displacement of *O. virilis* by *O. propinquus* over the long term within one lake (Lodge et al. 1986), we document displacement patterns over a longer time span in several northern Wisconsin lakes. Specifically, we assess current crayfish species composition and abundance in nine lakes, eight of which were previously sampled by Capelli (1982) or Capelli and Magnuson (1983) in 1973 or 1975 and 1980.

We use our long-term field studies and laboratory feeding experiments to test six predictions about mechanisms causing *O. rusticus* to have a greater negative impact than its congeners on the abundance of littoral flora and fauna: (1) After establishment of *O. rusticus*, mean carapace length of crayfish populations is greater. Because susceptibility to fish predation is inversely related to crayfish size (Stein 1977), larger crayfish should forage longer and farther from shelter. (2) After establishment of *O. rusticus*, total (i.e. all species pooled) crayfish population density increases. (3) Likewise, after establishment of *O. rusticus*, total population biomass increases. Assuming similar weight-specific feeding rates, a greater biomass of crayfish would consume a greater biomass of macrophytes and associated benthic invertebrates (Lodge and Lorman 1987). (4) On a weight-specific basis, *O. rusticus* consumes or sublethally damages more snails than its congeners. We chose snails from the invertebrate benthos because they are typically the dominant benthic invertebrate in circumneutral northern Wisconsin lakes (Lodge et al. 1987). (5) Greater selectivity by *O. rusticus* for single-stemmed versus highly branched, prostrate macrophytes would more greatly (relative to congeners) reduce macrophyte biomass. Field enclosure experiments indicate that single-stemmed macrophytes are more susceptible to grazing loss from crayfish than are more prostrate, highly branched forms (Lodge and Lorman 1987). (6) On a weight-specific basis, *O. rusticus* consumes or destroys (consumption plus fragmentation) more macrophyte biomass than *O. propinquus* or *O. virilis*.

Materials and Methods

Field Studies

Nine moderately productive drainage lakes (89–344 ha) in Vilas County, Wisconsin, were sampled for crayfish by trapping (as per Capelli 1982) from mid-July to mid-August 1988. Crayfish were sampled with 18–20 cylindrical, wire mesh minnow traps (21 cm diameter, 3.5–4.5 cm entrance holes)

TABLE 1. Regression equations used to convert carapace length (CL, in millimetres) to live crayfish biomass (*B*, in grams).

Species	Regression equation	Source
O. rusticus	$B = (1.38 \times 10^{-4}) CL^{3.28a}$	Lorman 1980
O. propinquus	$B = (3.16 \times 10^{-4}) CL^{3.01c}$	Stein and Murphy 1976[b]
O. virilis	$B = (2.49 \times 10^{-4}) CL^{3.03c}$	Stein and Murphy 1976 Morgan 1987

[a]Equation is for both males and females because differences in biomass between equal carapace length male and female crayfish are nonsignificant (Stein and Murphy 1976).

[b]Reference contained dry biomass to live biomass conversion (live biomass = 3.73 dry biomass) used to modify dry biomass equation of Lorman (1980).

[c]Regression equations based on length to weight data for male crayfish.

baited with 120 ± 5 g of beef liver. Traps were set in the most favorable habitat available (rocky substrate or woody debris) at 2 m depth, 100 m apart, in mid- to late afternoon and were recovered 20–24 h later. Neither deployment nor recovery time significantly affects total catch of traps set for 24 h (Collins et al. 1983; Lodge et al. 1986). During the trapping period, crayfish were intermolt; Form II comprised only 0.4–12% of the catch.

During trap deployment, in all but three lakes, we also deployed 10 square 1.0-m² quadrats, one quadrat in every other space between traps. In Birch, Van Vliet, and South Turtle lakes, one quadrat was deployed in each of the first 10 spaces between traps; quadrats here were representative of 50% of the area sampled by traps. In comparisons of visual counts with trap indices of species composition and abundance in these three lakes, we used only the data from the first 11 traps.

On the morning following deployment, we counted adult crayfish species (≥20 mm carapace length) in each quadrat using SCUBA. Moving diagonally from one corner, we carefully removed rocks and other cover to expose crayfish. Because we thoroughly and systematically searched each quadrat, our visual SCUBA surveys accurately sampled crayfish density. After sampling quadrats, traps were retrieved. For each trap, we counted and sexed each crayfish, determined Form for males, and measured carapace length (± 0.1 mm) of 200 male crayfish in each species (or all males caught if less than 200).

We tested the reliability of traps as indices for species composition using visual count data as the standard. Only numbers of adult males were used to calculate trap indices of species composition because baited traps are highly selective for adult males (males typically comprise greater than 80% of the trap catch (Capelli 1975; this study)) and female and male trap catches change independently during the year (Lodge et al. 1986).

We then used chi-square to compare 1988 trap indices of species composition with those obtained in 1973 (Capelli and Magnuson 1983), 1975, and 1980 (Capelli 1982). For each year, we determined trap indices of crayfish abundance (male crayfish per trap) and tested their reliability using visual survey results as the standard. Because *O. rusticus* was more trapable than its congeners (see below), we corrected all data (including those previously published by Capelli (1982) and Capelli and Magnuson (1983)) for trapping bias. For all lakes but White Sand (where size was not measured), we determined, by species, a size–frequency distribution for males ≥20 mm carapace length caught in traps in 1975, 1980, and 1988. From

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size–frequency distributions, we estimated live crayfish biomass (adult male biomass per trap) based on carapace length to weight regressions (Table 1). Because only total numbers, not catch per trap data, were available for 1973, 1975, and 1980, we tested statistically null hypotheses about change in trap indices of carapace length, abundance, or biomass by determining whether mean values for 1973, 1975, or 1980 fell outside of the 95% confidence range for 1988 data.

We tested whether mean carapace length of crayfish populations increased after establishment of *O. rusticus* (Prediction 1) using estimates, based on trap catches, for 1975, 1980, and 1988. We present only means in this paper, but medians and modes showed the same trends as the means (Olsen 1989). Using trap catches as indices for population abundance, we determined species-specific density and tested if establishment of *O. rusticus* increased total (i.e. all species pooled) crayfish population density (Prediction 2). Likewise, we determined contribution of *O. rusticus* to population biomass and tested whether total population biomass increased after establishment of *O. rusticus* (Prediction 3). Predictions 1–3 were tested in five lakes that were dominated by either *O. propinquus* (Big, Birch, Boulder, and Papoose) or *O. virilis* (Van Vliet) in 1975 but were dominated by *O. rusticus* in 1988. We concluded that the respective prediction was supported if three of the four lakes originally dominated by *O. propinquus* showed the predicted increase in mean carapace length, population density, or population biomass after switching to *O. rusticus* domination.

Laboratory Experiments

Collection and holding of experimental organisms

We collected adult male crayfish with traps as described previously. For tests of crayfish consumption on the hydrobiid snail *Amnicola*, crayfish and snails were housed separately at the University of Notre Dame Environmental Research Center (UNDERC), Land O' Lakes, Wisconsin, in aerated aquaria and exposed to natural summer photoperiod and daily fluctuations in ambient air temperature (water temperature 17–26°C). To eliminate potential intersex variability within the congeners, only males were used. For tests of sublethal damage of *Helisoma* by crayfish and consumption and fragmentation of macrophytes, crayfish, snails, and macrophytes were housed separately in 150-L fiberglass flow-through aerated aquaria (well water temperature 12–15°C) exposed to a 16 h light : 8 h dark photoperiod. Crayfish were fed Purina Fish Chow; snails were fed commercial flake fish food. All experiments were conducted during June–September.

Consumption and damage of snails: testing Prediction 4

We used *Amnicola* spp. as prey to test if *O. rusticus* has a greater weight-specific feeding rate than *O. propinquus* or *O. virilis*. In each replicate of this experiment, three male congeners (± 1 g and of the same Form) were put separately in 45-L aquaria. Crayfish (range of carapace length 31–36 mm) were not used more than once. Aerated water depth was 3.0 cm to keep snails within reach of crayfish. During the first six replicates, water temperature fluctuated with daily ambient air temperature (water temperature 17–26°C). In the remaining replicates (7–16), water temperature was 17.5–18.5°C.

Crayfish were fed 100 *Amnicola*; crayfish were then starved for 24 h and subsequently allowed to feed on 250 *Amnicola* (shell length 2.2–5.3 mm) for 24 h. Snails remaining were counted. We checked crayfish before and after the experiment

TABLE 2. Equations used in Experiment C to compute corrected consumption (CC) (consumed macrophyte biomass (grams) corrected for change in macrophyte biomass in control macrophytes).

Equation (1) $\Delta CB = CB_f \div CB_i$

Equation (2) $CC = ((\Delta CB)(EB_i)) - EB_f$

ΔCB = change in live macrophyte biomass in the control (no crayfish) chamber
CB_f = final live macrophyte biomass in control chamber
EB_f = final live macrophyte biomass in experimental chamber
CB_i = initial live macrophyte biomass in control chamber
EB_i = initial live macrophyte biomass in experimental chamber

for signs of molting. If crayfish molted within 4 d of the experiment, data were not used. We used two morphologically similar, but different-sized *Helisoma* congeners (*Helisoma campanulatum* (Say), 6–9 mm diameter; *H. trivolvis* (Say), 10–13 mm diameter) to determine if *O. rusticus* (range of carapace length 31–39 mm) sublethally damaged more snails than its congeners. We used the same protocol as above except that we added a barrier at the air–water interface to prevent *Helisoma* spp. from crawling beyond reach of crayfish. After the feeding trial, we counted the number of snails with damaged shells yet alive.

Consumption and destruction of macrophytes: testing Predictions 5 and 6

We used four macrophyte species, two prostrate and highly branched (*Ceratophyllum demersum* (L.) and *Elodea canadensis* (Michx.)), one rosulate (*Isoetes* spp.), and one single-stemmed (*Potamogeton richardsonii* (Benn)), to test Prediction 5 that *O. rusticus* prefers (relative to congeners) single-stemmed macrophytes and Prediction 6 that *O. rusticus* consumes or destroys (consumption plus fragmentation) more macrophyte biomass than *O. propinquus* or *O. virilis*. We used crayfish (range of carapace length 31–40 mm) and macrophytes within 3 wk of collection.

Each 38-L aquarium was divided with Plexiglas into control (no crayfish) and experimental (one crayfish) halves and had a perforated Plexiglas false floor. Macrophyte species were randomly assigned to perforations. Crayfish shelters were provided in both halves of the tanks. Intermolt male congeners (± 1 g) were starved for 24 h in the experimental chamber and removed. Aerated water level was deep enough at 5.0 cm to cover macrophyte shoots but shallow enough to ensure that no macrophyte tissue was inaccessible to crayfish; temperature was 16–17°C. Macrophytes were spun to constant weight and seven shoots (≤ 5.0 cm) of each species (4 ± 0.4 g per macrophyte species) were secured to the floor holes with paper clips.

Crayfish were then replaced, allowed to feed for 6 d, and then removed. Attached and detached macrophyte shoots were spun and weighed by species (nearest 0.01 g). Weight change in experimental macrophytes was corrected for mean weight change in control macrophytes (Table 2). In most cases, control macrophytes grew slightly.

For all crayfish, the total macrophyte biomass eaten per crayfish (pooled over all macrophyte species) was less than maximum stomach capacity (based on regression of maximum stomach capacity (grams dry weight) on carapace length for *O. rusticus* (Butler 1983)). Weight-specific differences in congener stomach capacity were assumed to be negligible. Because crayfish did not satiate during the experiment, this suggests that crayfish choice among macrophytes remained independent dur-
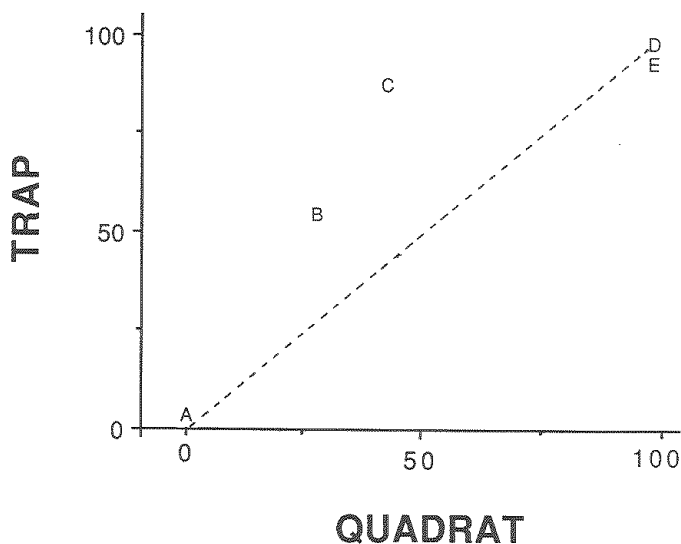
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FIG. 1. Relationship between percent *O. rusticus* determined by visual sampling of quadrats and by trapping. Points represent the mean for quadrat (*N* = 9–10) and trap catches (*N* = 18–20) in each of nine lakes: White Sand (A), South Turtle (B), Boulder (C), Birch, Island, and Papoose (D), and Big, Clear, and Van Vliet (E). Broken line indicates perfect correlation between trap and quadrat catches.

ing the experiment. Therefore, we use ANOVA to test for differences in selectivity among crayfish congeners.

Results and Discussion

Field Studies

Reliability of trap catches as indices of species composition

Because *O. rusticus* was the only species found in both traps and quadrats in eight of nine lakes sampled, comparison of trap and quadrat catches was based on only one species. Percent *O. rusticus* in traps was well predicted by visual surveys (r^2 = 0.95, $p < 0.001$, N = 9 lakes, 7 df, arcsin $\sqrt{p}$ transform). Because data points for six of nine lakes were clustered (Fig. 1), we also tested significance using df = 2 (as if only four lakes were sampled); with this conservative criterion, p = 0.05. Our data do, however, indicate that *O. rusticus* is overrepresented in trap catches. In the two lakes with intermediate abundance of *O. rusticus* population (89 and 56% of trap catch, respectively, in Boulder and South Turtle; Fig. 1), traps apparently overestimated relative abundance of *O. rusticus* by factors of 2.1 and 2.0, respectively. Therefore, to correct for trapping bias in subsequent analyses, we divided trap catch of *O. rusticus* by 2 in each lake to give corrected trap index of species composition. Given that trapping bias probably declines towards both extremes of percentage composition, our correction is conservative.

In a similar study comparing visual survey and trap estimates of species composition in 13 northern Wisconsin lakes, Capelli and Magnuson (1983) found that trap catches were reliable indices of species composition. Our results suggest, however, that in lakes with *O. rusticus*, trapping may exaggerate actual change in species composition over time (species displacement rate). Factors that may contribute to differential species trapability include aggressive interactions (Capelli 1975;

Capelli and Munjal 1982), abundance of predatory fishes (Collins et al. 1983), and lunar light intensity (Somers and Stechey 1986). Because *O. rusticus* is generally larger than *O. propinquus* and more aggressive than both its congeners (see Lodge et al. 1985), its trapability may be affected less by predators and light level.

Changes in corrected trap indices of species composition

From 1975 to 1980, relative abundance of *O. propinquus* decreased with regard to *O. rusticus*, while that of *O. virilis* decreased with regard to both congeners (Fig. 2A). However, displacement rate of congeners by *O. rusticus* was highly variable among lakes. For instance, rapid displacements occurred in Birch and Papoose lakes with relative abundance of *O. rusticus* increasing from 6 to 92% and 7 to 100%, respectively. But in South Turtle, *O. rusticus* increased from 5 to only 18%. Despite our more conservative analysis, our conclusions regarding 1975–80 changes are little different from Capelli's (1982) analysis of the same period.

From 1980 to 1988, six of eight lakes had increases in relative abundance of *O. rusticus*, although increases were significant in only four lakes ($p < 0.05$, chi-square; Fig. 2A). In the remaining two lakes, relative abundance of *O. rusticus* either remained 100% (Papoose) or did not change (Birch). As during 1975–80, the rate of displacement of congeners by *O. rusticus* was highly variable among lakes. Between 1973 and 1988, *O. rusticus* invaded White Sand Lake (monospecific for *O. virilis* in 1973; Fig. 2A) and in 1988 comprised <2% of the crayfish species total.

Displacement of congeners by *O. rusticus* is generally consistent with Capelli's hypothesis of competitive exclusion (Capelli 1982; Capelli and Munjal 1982; Berrill 1985). However, variable displacement rate among lakes and reversible displacement of *O. virilis* by *O. propinquus* within one lake (Lodge et al. 1986) suggest that additional community structuring forces, including reproductive interference and differential susceptibility to size-selective fish predation (relative to congeners) (Berrill 1978, 1985; Butler and Stein 1985; Lodge et al. 1985), are probably involved (Lodge et al. 1986). Elucidation of the mechanisms underlying this variable displacement rate among lakes warrants further study.

Our results indicate that *O. rusticus* continues to displace its congeners in many northern Wisconsin lakes. Displacements of congeners (*O. deanae*, *O. limosus*, *O. obscurus*, *O. propinquus*, *O. sanbornii*, and *O. virilis*) by *O. rusticus* have been documented for other lentic and lotic habitats in Massachusetts (Smith 1981), New Mexico (Bouchard 1978), Ohio (Turner 1926; Flynn and Hobbs 1984; Jezerinac 1982; Butler and Stein 1985; Jezerinac 1986), and Tennessee (Bouchard 1978). Our data suggest that invasion by *O. rusticus* results in long-term establishment of this crayfish as a dominant species in northern Wisconsin lakes.

Reliability of trap catches as indices of crayfish absolute abundance

Trap catches (all species pooled and corrected for twofold greater trapability of *O. rusticus*; see above) were reliable indices of visual survey data (r^2 = 0.71, $p < 0.01$, ANOVA, log–log transform). In another study of five northern Wisconsin lakes, trap catches and visual surveys were significantly correlated (r = 0.97, $p < 0.05$) (Capelli 1975). In a similar study of 19 central Ontario lakes, Collins et al. (1983) found that abundance of predatory fishes affected trapability. Because predatory fish abundance data are unavailable for our study

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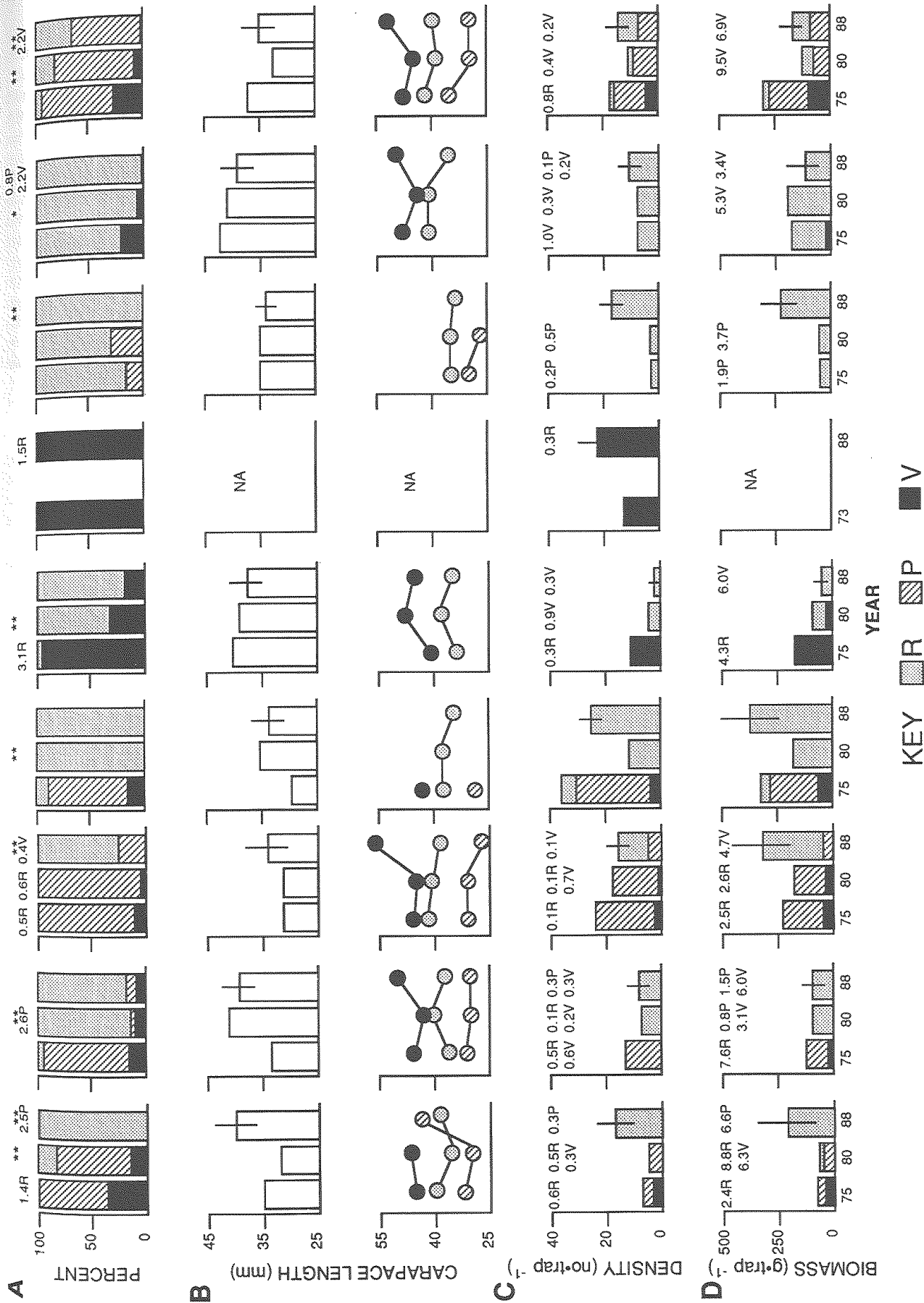*Can. J. Fish. Aquat. Sci., Vol. 48, 1991*

FIG. 2. Changes in corrected trap index of (A) relative abundance, (B) population (top) and species-specific (bottom) mean carapace length, (C) corrected trap index of absolute abundance, and (D) corrected trap index of biomass (live weight) for adult male crayfish in nine northern Wisconsin lakes. Asterisks above the middle bar in Fig. 2A indicate significant changes (*p < 0.05, **p < 0.001, chi-square) from 1975 to 1980. Asterisks above the right bar indicate significant changes from 1980 to 1988. Percents <4% (Fig. 2A) and values <1.4 (Fig. 2C) or <10 (Fig. 2D) are indicated by numbers above the bars. Vertical lines denote 95% confidence intervals (Fig. 2B–2D, all species combined). Confidence intervals could not be calculated for the 1973, 1975, and 1980 data because catches per trap were unavailable. Carapace length data were not available (NA) for White Sand Lake and for the one Clear Lake O. propinquus caught in 1988.

lakes, we restricted ourselves to within-lake comparisons and assumed that major changes in predator density did not occur over the span of our survey.

Because trap catches provided estimates similar to visual surveys in this and previous studies, and only trapping data were available for 1973, 1975, and 1980, we used corrected trap catches as indices of crayfish abundance.

Mean crayfish size, density, and population biomass: testing Predictions 1–3

Our data support the prediction that mean crayfish size increases after establishment of *O. rusticus*. In three of the four lakes where *O. rusticus* replaced *O. propinquus* as the dominant crayfish, trap index of mean crayfish size increased (Big, Birch, and Papoose; Fig. 2B, top). However, in the one lake where *O. rusticus* displaced *O. virilis*, mean crayfish size did not change (Van Vliet; Fig. 2B, top). Because carapace length hierarchy was generally *O. virilis* > *O. rusticus* > *O. propinquus* (Fig. 2B, bottom), Prediction 1 was supported when *O. rusticus* displaced *O. propinquus*, but not *O. virilis*.

Patterns in mean size change in the three lakes where there was little change in species composition tend to corroborate that the increase in individual size observed in Big, Birch, and Papoose lakes was linked to the displacement of *O. propinquus* by *O. rusticus*. For example, in lakes dominated by one species from 1975 to 1988 (Island, Clear, and South Turtle), there was no change in individual size of crayfish from 1975 to 1988 (Fig. 2B).

Our results do not support the prediction that crayfish density increases after establishment of *O. rusticus*. In three of four lakes after *O. rusticus* displaced *O. propinquus*, corrected trap indices of crayfish population density (CPD, all species pooled) decreased (Fig. 2C). In one lake (Big Lake), CPD increased after establishment of *O. rusticus* (Fig. 2C). In Van Vliet Lake, where *O. virilis* dominated in 1975, CPD decreased after establishment of *O. rusticus* (Fig. 2C).

However, population biomass did not change after establishment of *O. rusticus*. In only one of the four lakes where *O. rusticus* replaced *O. propinquus* as the dominant crayfish did trap index of crayfish population biomass (CPB, all species pooled) increase (Big; Fig. 2D). In the remaining three lakes that switched from *O. propinquus* to *O. rusticus* domination, CPB did not change (Birch, Boulder, and Papoose; Fig. 2D). In the one lake where *O. rusticus* displaced *O. virilis*, CPB decreased (Van Vliet; Fig. 2D).

In summary, long-term field studies (1973–88) support predictions of increased crayfish size, but not crayfish density or population biomass, when *O. rusticus* displaces *O. propinquus*, but not *O. virilis*. Increase in mean individual crayfish size after *O. rusticus* establishment may result in a greater negative impact on macrophytes and benthic invertebrates when crayfish populations are dominated by *O. rusticus*.

Laboratory Experiments

Consumption and sublethal damage of snails: testing Prediction 4

Congener feeding rates at the two temperature regimes (17–26 and 17.5–18.5°C) did not differ ($p > 0.25$, ANOVA); therefore, only pooled results ($N = 16$) are reported. Results strongly support Prediction 4: weight-specific feeding rate of *O. rusticus* on *Amnicola* was higher than that of *O. propinquus* or *O. virilis* ($p < 0.0001$, ANOVA, Tukey's multiple comparisons; Fig. 3A). For the following reasons, we conclude that
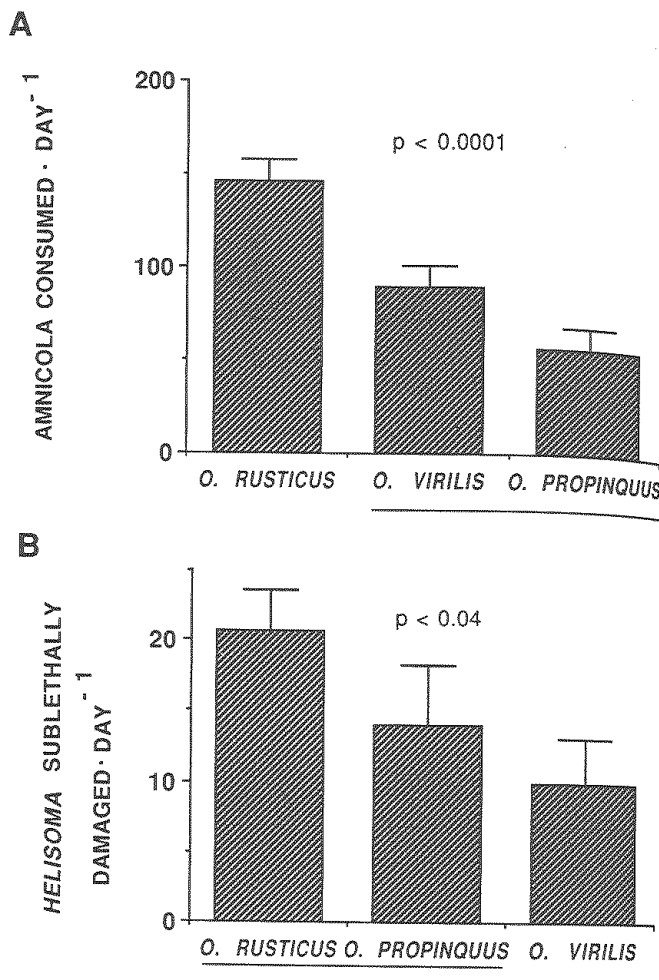

FIG. 3. (A) Consumption of *Amnicola* ($N = 16$) and (B) sublethal damage of *Helisoma* ($N = 8$) by three crayfish congeners during 24-h laboratory experiments. Note the different order of crayfish species on the abscissae. Bars denote one standard error of the mean. Lines connect means that do not differ ($p > 0.05$, ANOVA, Tukey's multiple comparisons).

our results probably accurately reflect the actual hierarchy of congener feeding rates during summer in northern Wisconsin lakes: we conducted experiments with crayfish collected ≤10 d before from northern Wisconsin lakes and exposed them to natural summer photoperiod and temperature. *Amnicola* spp. are among the natural prey of northern Wisconsin crayfish (see Lodge and Lorman 1987) and are abundant in northern Wisconsin lakes.

Because handling time for crayfish on hydrobiid snails was <10 s per snail (pers. obs.), it is improbable that interspecific differences in handling time accounted for the differences in feeding rate among congeners. *Orconectes rusticus* has a higher metabolic rate than *O. virilis* at 17–25°C (Lippson 1976; Momot 1984), which would account for its greater feeding rate relative to *O. virilis*. However, *O. propinquus*, has a higher metabolic rate than *O. rusticus* (Lippson 1976) and this does not support our feeding rate results. However, such comparisons are limited because Lippson (1976) did not report the range of crayfish sizes used and whether his replicates were run using equal-biomass crayfish. Regardless of the mechanism contributing to differences in ingestion rate among *Orconectes* congeners, our experiment strongly suggests that greater weight-specific inges-

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tion rate by *O. rusticus* may result in greater impact on the abundance of aquatic snails in northern Wisconsin lakes.

Likewise, Prediction 4 is supported: *O. rusticus* sublethally damaged more *Helisoma* spp. than *O. virilis* ($p < 0.04$, ANOVA, Tukey's multiple comparisons; Fig. 3B). Sublethal snail damage rate was not confounded by differences in selectivity among crayfish congeners for the two *Helisoma* species (snail species effect, $p = 0.67$; crayfish × snail interaction effect, $p = 0.55$, ANOVA). We used two sizes of *Helisoma* congeners because the experiment was designed originally to test crayfish selection between the two morphologically similar (yet different-sized) snails. High encounter rates in our experiment (relative to those in lakes) may have increased the frequency of sublethal damage. In any case, this sort of sublethal damage of snails by crayfish (i.e. removal of shell whorl on planorbid snails) probably does not lower snail fitness (Stahl and Lodge 1990).

Consumption and destruction of macrophytes: testing Predictions 5 and 6

Crayfish consumed and destroyed macrophytes selectively (macrophyte effect, $p < 0.001$, df = 3 in each case); all three congeners showed the same selectivity among macrophyte species for both consumption (crayfish × macrophyte interaction effect, $p = 0.28$, df = 6) and destruction (crayfish × macrophyte interaction effect, $p = 0.88$, df = 6). Highly branched *Ceratophyllum* and *Elodea* were as susceptible to grazing loss as single-stemmed *P. richardsonii*. *Isoetes* was consumed and destroyed the least, with no difference existing among the other three plant species for either consumption or destruction (Tukey's multiple comparisons) (Fig. 4).

In this and previous experiments, *Orconectes* crayfish graze selectively (Lodge 1991), reducing macrophytes in both the laboratory (Seroll and Coler 1975; Lorman 1980) and the field (Lodge and Lorman 1987). In situ enclosure experiments suggest that macrophyte morphology can affect susceptibility to grazing loss: single-stemmed macrophytes appear more susceptible to destruction than rosulate or highly branched forms (Lodge and Lorman 1987). In contrast with the Lodge and Lorman (1987) field results and Prediction 5, greater impact of *O. rusticus* on macrophyte abundance did not result from greater selectivity by *O. rusticus* for the single-stemmed (*P. richardsonii*) macrophyte species.

Because congener feeding rate on macrophytes was not confounded by macrophyte species selection among crayfish congeners (see above), this experiment also tested Prediction 6. Crayfish congeners differed in the amount of macrophyte biomass consumed (*O. rusticus* > *O. propinquus*; Fig. 4A) and destroyed (consumption plus fragmentation: *O. virilis* > *O. propinquus*; Fig. 4B). Total destruction is probably the most relevant measure of crayfish impact on macrophyte abundance in northern Wisconsin lakes. On a weight-specific basis, *O. virilis* is just as destructive of macrophytes as *O. rusticus*.

General Discussion

Our 1973–88 field data indicate that *O. rusticus* tends to displace congeners and becomes the numerically dominant species. During 1973–88, rate of displacement by *O. rusticus* varied among lakes, but relative abundance of *O. rusticus* increased in all nine lakes studied. Successful establishment of *O. rusticus* in northern Wisconsin lakes probably results from
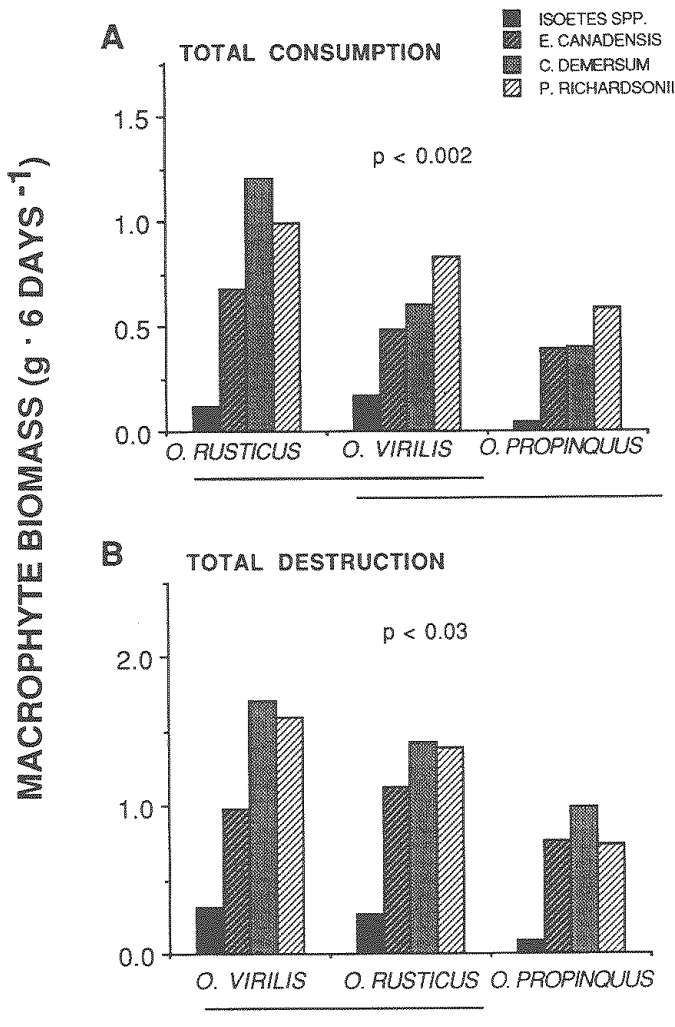

FIG. 4. (A) Total consumption and (B) total destruction (consumption plus fragmentation) of four macrophyte species by three crayfish congeners during a 6-d laboratory selection experiment. Note the different order of crayfish species on the abscissae of each graph. Lines connect crayfish that do not differ in total consumption or total destruction ($p > 0.05$, N = 9, ANOVA, Tukey's multiple comparisons).

superior size-specific competitive ability (relative to *O. propinquus* and *O. virilis*) (Capelli and Munjal 1982) in combination with lower susceptibility to size-selective fish predation (Stein 1977; Berrill 1978; Capelli 1982; Capelli and Munjal 1982; Capelli and Magnuson 1983; see Lodge et al. 1985; Butler and Stein 1985; Lodge et al. 1986). Our long-term data suggest that invasions by *O. rusticus* do not follow the typical "boom and bust" pattern for introduced species (see Simberloff 1981; Williamson and Brown 1986). Whether other lotic and lentic systems recently invaded by *O. rusticus* will show a similar long-term pattern of differential impact by *O. rusticus* on congeners and littoral benthic community structure awaits further study.

We investigated six mechanisms underlying the greater negative impact of *O. rusticus* (relative to congeners) on the abundance of littoral macrophytes and associated benthic invertebrates in northern Wisconsin lakes. Results were at least partly consistent with Predictions 1, 4, and 6 but contradicted Predictions 2, 3, and 5 (Table 3). Our results suggest that on a per biomass basis, a population of *O. rusticus* would produce a

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TABLE 3. Summary of test results for mechanisms governing the apparently greater impact of *O. rusticus* (*Or*) (relative to *O. propinquus* (*Op*) and *O. virilis* (*Ov*) on benthic community structure. Four lakes served to test mechanisms 1–3 when *Or* displaced *Op* and one lake when *Or* displaced *Ov* (see Fig. 2).

Mechanisms	Re *O. propinquus*	Re *O. virilis*
1. Individual size: $Or > Ov > Op$	$Or > Op$	$Or < Ov$
2. Population density: $Or > Op > Ov$	$Or < Op$	$Or < Ov$
3. Population biomass: $Or > Ov > Op$	$Or < Op$	$Or < Ov$
4. Weight-specific consumption (*C*)	$C: Or > Op$	$Or > Ov$
and sublethal damage (*D*)	$D: Or = Op$	$Or > Ov$
of snails: $Or > Op, Ov$		
5. Weight-specific selection for single-stemmed		
macrophytes: $Or > Op, Ov$	$Or = Op$	$Or = Ov$
6. Weight-specific consumption (*C*)	$C: Or > Op$	$Or = Ov$
and destruction (*D*)	$D: Or = Op$	$Or = Ov$
of macrophytes: $Or > Ov, Op$		

greater impact on the abundance of benthic flora and fauna than an equal population of its congeners. However, the magnitude of impact on the benthic community after establishment of *O. rusticus* may depend on which congener *O. rusticus* displaces. Field data suggest that in three of four lakes that switched from *O. propinquus* to *O. rusticus* domination during 1975–88, crayfish are larger. Larger size would allow *O. rusticus* to forage longer with impunity from size-selective fish predators (see Stein 1977) over a wider range of substrates (being less restricted to protective cobble shelter) (see Lodge et al. 1985). This impact is intensified by the significantly greater weight-specific ingestion rate of *O. rusticus* (on snails and macrophytes) compared with *O. propinquus* shown in our laboratory experiments.

When *O. rusticus* displaced *O. virilis* ($N = 1$ lake), however, crayfish size decreased (Table 3). In laboratory experiments, *O. rusticus* sublethally damaged more snails than *O. virilis*, and *O. rusticus* had a greater weight-specific ingestion rate than *O. virilis* on snails but not macrophytes. Given data from only one lake, and the potentially counteracting mechanisms, it is difficult to predict what impact on littoral benthos a switch from *O. virilis* to *O. rusticus* entails.

Additional laboratory experiments could further clarify mechanisms of differential impact of *O. rusticus* on benthic community structure. For example, feeding separately housed crayfish congeners, snails, and macrophytes simultaneously in controlled laboratory experiments would elucidate the effect alternative resources have on each congener's rate of macrophyte and invertebrate consumption (see Covich 1977). For example, an alternative food (beef liver) significantly reduced consumption and nonconsumptive destruction of the macrophyte *Vallisneria* by *O. rusticus* (Lorman 1980). The presence of snails probably reduces macrophyte consumption by *O. rusticus* in the littoral zone of northern Wisconsin lakes (Lodge and Lorman 1987).

To ensure that our comparative feeding rate experiments were unbiased, we should ideally have collected all crayfish congeners from one lake or from lakes of similar predation risk. However, we could not trap sufficient numbers of all three crayfish congeners from any one lake. In laboratory behavioral studies, for at least 3 wk after collection, *O. propinquus* from a lake with high bass density were generally less active and more shelter-bound than crayfish from a lake without bass (Collins et al. 1983). In our experiments on snail and macrophyte consumption in which this could have been a problem, we used crayfish 1–18 d from date of collection. Our crayfish source

lakes, unlike those of Collins et al. (1983), all contain bass (Black et al. 1963; Olsen 1989); therefore, all our experimental crayfish probably demonstrated some degree of predator-induced resource depression. We could not, however, determine a rank order of predation risk for our crayfish source lakes because predatory fish abundance data are unavailable.

In conclusion, long-term field data from nine northern Wisconsin lakes indicate that invasions by *O. rusticus* tend to result in the displacement of congeners and its long-term dominance; however, displacement rate among lakes is highly variable. Field and laboratory studies support three mechanisms (Table 3) that additively help explain the greater declines in macrophytes and benthic invertebrate abundance in lakes where *O. rusticus* has displaced its congeners: (1) larger size (which probably results in less behavioral inhibition of feeding in the presence of size-selective fish predators), (2) greater weight-specific consumption of snails, and (3) greater weight-specific consumption of macrophytes.

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