

A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake

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Abstract: Rusty crayfish (*Orconectes rusticus*) were first observed in Trout Lake, Wisconsin, in 1979 and took 19 years to completely disperse around the littoral zone, advancing at an average rate of 0.68 km-year⁻¹. With the invasion of rusty crayfish, we found that fishes that share prey taxa with crayfish declined in numbers over time, but piscivorous fish species did not change in abundance. Snails declined from >10 000 to <5 snails·m⁻² in one of the first invaded areas. Mean abundance of Odonata, Amphipoda, and Trichoptera decreased significantly lake-wide. Resident crayfish species nearly disappeared, although total crayfish abundance, driven by high abundances of rusty crayfish, continued to rise. Submerged macrophyte species richness declined by as much as 80% at some locations. Together these responses demonstrate dramatic long-term changes in the littoral zone biota of Trout Lake. Continued invasions of similar lakes in the region suggest that these impacts are occurring on a region-wide basis with potentially irreversible effects on communities and ecosystems. Only through long-term natural experiments such as this study can researchers ascertain the full extent of invasions and their impacts on community and ecosystem process that respond at spatial and temporal scales not captured in mesocosm studies.

Résumé : Les écrevisses américaines (*Orconectes rusticus*) ont été observées pour la première fois en 1979 dans le lac Trout, Wisconsin, et elles ont mis 19 ans à se disperser autour de l'entière zone littorale du lac, progressant à une vitesse moyenne de 0,68 km·an⁻¹. Après l'invasion de l'écrevisse américaine, les poissons qui partagent les proies de mêmes taxons que l'écrevisse ont subi un déclin de densité dans le temps, alors que les espèces de poissons piscivores n'ont pas changé d'abondance. Les gastéropodes sont passés de >10 000 à <5 individus·m⁻² dans l'une des premières régions à être envahies. Les abondances moyennes des odonates, des amphipodes et des trichoptères ont baissé significativement dans tout le lac. Les espèces d'écrevisses indigènes ont presque disparu, bien que l'abondance totale des écrevisses, à cause des fortes abondances de l'écrevisse américaine, aient continué à augmenter. La richesse en espèces des macrophytes submergées a baissé de jusqu'à 80 % dans certains sites. Dans leur ensemble, ces réactions démontrent l'existence de changements spectaculaires à long terme chez les organismes de la zone littorale du lac Trout. L'invasion se poursuit dans des lacs semblables de la région, ce qui indique que de tels impacts se réalisent à l'échelle de toute la région avec des effets potentiellement irréversibles sur les communautés et les écosystèmes. C'est seulement à l'aide d'expériences en nature à long terme comme la nôtre que les chercheurs peuvent évaluer l'étendue complète des invasions et leur impact sur les mécanismes des communautés et des écosystèmes, car ceux-ci réagissent à des échelles spatiales et temporelles qui ne sont pas perçues dans les études de mésocosmes.

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Introduction

Rusty crayfish (*Orconectes rusticus*), like many crayfish species, are strong interactors in many freshwater systems and, as a consequence, may have disproportionately large effects on invaded systems. For many North American streams

and lakes, invasions of rusty crayfish result in a substantial disturbance through modification of complex trophic interactions and physical habitat (reviewed in Lodge et al. 2000). Crayfish are large and often abundant, comprising important elements of lentic and lotic benthic food webs (Lodge et al. 2000). Most crayfish, including *O. rusticus*, are trophic gen-

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eralists, readily consuming terrestrial leaf litter (France 1996), benthic algae (Luttenton et al. 1998), macrophytes (Lodge and Lorman 1987; Nyström and Strand 1996; Wilson 2002), aquatic invertebrates (Momot 1995; Nyström et al. 1996), fish eggs (Horns and Magnuson 1981), and detritus (Momot 1995). Small crayfish are more likely to be carnivorous and consumed themselves by many species of fish, whereas large crayfish are more omnivorous and often obtain a size and behavioral refuge from all but the largest fishes (Stein and Magnuson 1976; Momot 1995; Whitledge and Rabeni 1997). Crayfish integrate into foods web at many levels and can persist on the substantial energy reserves of the detrital pool (France 1996), making crayfish good candidates for invading aquatic systems (Moyle and Light 1996).

In short-term laboratory, pond, and field studies, researchers have chronicled a myriad of direct and indirect effects of crayfish on subsets of aquatic communities (e.g., Rickett 1974; Lodge et al. 1994; Nyström et al. 1996), but these sometimes complex interactions have not been investigated at larger scales. The lack of long-term studies on crayfish invasions and the complex trophic and behavioral interactions inherent to natural systems make it unclear how crayfish invasions affect lake littoral communities over time spans of multiple generations.

The rusty crayfish is a highly visible invader in northern Wisconsin, spreading from a historical range in the Ohio River drainage over the last 40–50 years (Hobbs et al. 1989). Rusty crayfish may have been introduced by anglers emptying their bait buckets after fishing (Capelli 1982; Hobbs et al. 1989; Ludwig and Leitch 1996), well-intentioned lake users desiring to rid their lake of nuisance weeds (Magnuson et al. 1975), or intentional releases by commercial crayfish harvesters. Capelli and Magnuson (1983) found that human activity and lack of geographic isolation best explained the presence of rusty crayfish in 67 lakes in Vilas County, northern Wisconsin. Once established, rusty crayfish may spread from lake to lake via streams and rivers or through intentional or unintentional movement by humans.

Rusty crayfish were first detected in Trout Lake, Vilas County, Wisconsin, in 1979 (Lodge et al. 1986) near a heavily used boat landing. We suspect that rusty crayfish were introduced to the lake sometime between 1973 and 1979 based on historical trapping data (Lodge et al. 1986). In 1981, researchers with the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) group began a monitoring program designed in part to track changes in lake biota as rusty crayfish spread from a known introduction point around the littoral zone of Trout Lake (Lodge et al. 1986). This presented a unique opportunity to observe temporally and spatially sequential invasions in the same environment, thus avoiding the confounding effects of comparing invasions in multiple systems.

Here we document the invasion of Trout Lake by *O. rusticus* and effects of this invasion on the resident crayfish, fish, macroinvertebrate, and macrophyte communities in the lake. We focused our efforts on changes in species richness, biomass (when available), and abundance.

With increases in rusty crayfish abundance, we expected that (a) the abundance of other crayfish species, as direct competitors, would decrease, (b) crayfish prey species would decrease in abundance and species richness (i.e., snails,

other macroinvertebrates, macrophytes), and (c) fish species (Centrarchidae) that closely interact with rusty crayfish would increase if the species consumed crayfish and decrease if the species competed with crayfish for food or had nests vulnerable to crayfish predation. We investigated two scales of response: (i) at the individual-site level as rusty crayfish arrived and established local populations and (ii) at the whole-lake scale for which we summed species richness and biomass for all sites.

Methods

Site description

Trout Lake (46°2'N, 89°40'W; Fig. 1) is a 1608-ha mesotrophic lake located in the Northern Highlands Lake District of Wisconsin within a matrix of forested land and small lakes, rivers, and streams. Its 26-km shoreline consists primarily of sand and cobble substrates, with scattered areas of submerged macrophytes and muck (Wilson 1941). The littoral zone (defined here as ≤5 m deep) occupies approximately 21% of the lake area. Mean depth is 14.6 m; maximum depth is 35.7 m. Physiochemical conditions in Trout Lake have remained similar throughout this study (Bowser et al. 1999; Magnuson et al. 1999).

Sampling methods

Crayfish invasion data

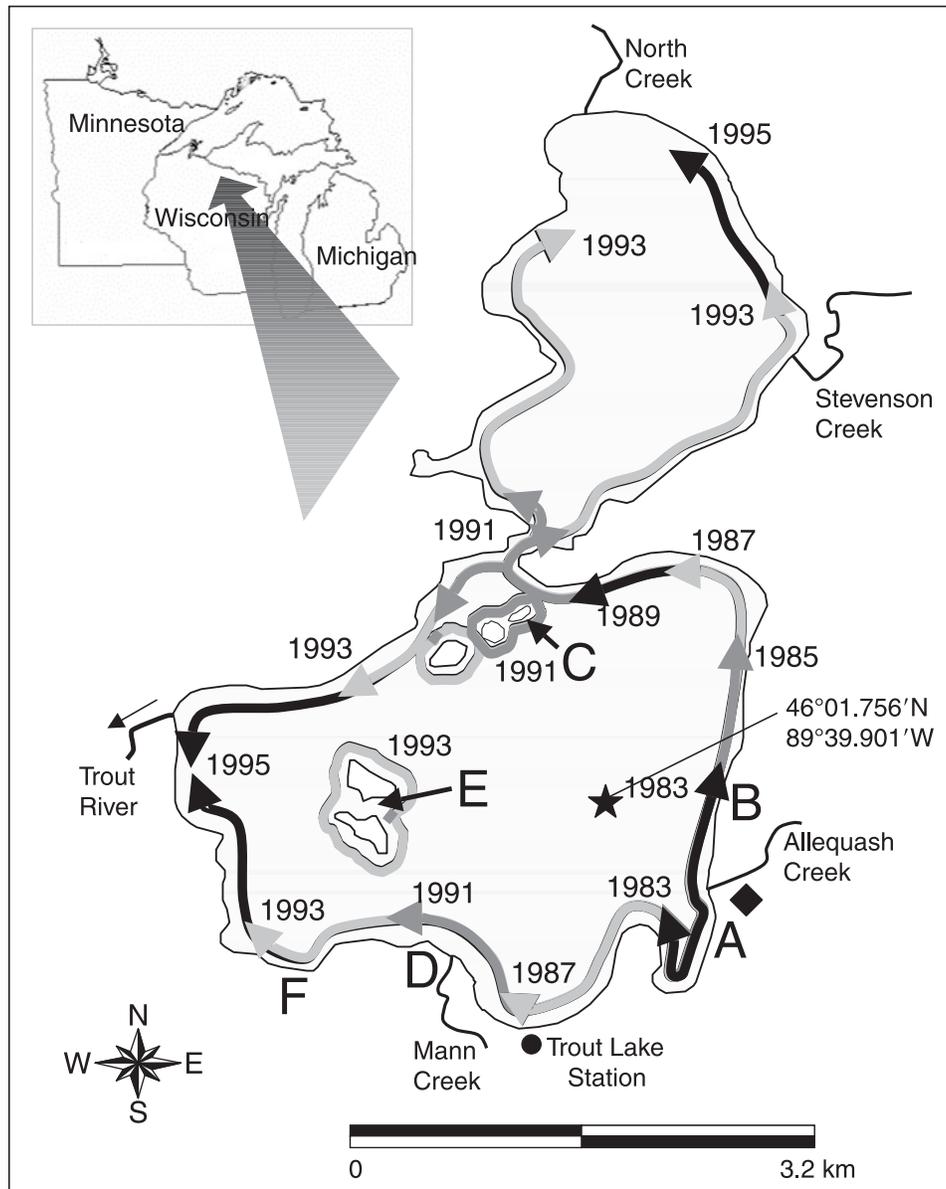
To monitor the dispersal of rusty crayfish around the lake littoral zone, an average of 73 traps (± 0.68 standard error (SE) resulting from loss of traps in the field) were set roughly equidistant ($0.39 \text{ km} \pm 0.014 \text{ SE}$) around the lake shore and islands once annually from 1983 to 1999 by Lodge, Kratz, and associates. In some years (1984, 1985, 1988, 1989), trapping was concentrated around the edges of the invasion front to better characterize crayfish species distributions and consisted of fewer traps (21, 35, 25, and 45 traps, respectively). The invasion front was defined as more than one *O. rusticus* per trap. Distances were calculated as straight lines between traps and therefore represented minimum distances traveled. We assumed that the origin of the rusty crayfish invasion was at the mouth of Allequash Creek (Fig. 1), which was the midpoint in the initial distribution of rusty crayfish in 1983.

To trap crayfish, we used modified minnow traps (entrance holes ~5 cm diameter) baited with $120 \pm 10 \text{ g}$ of beef liver and set for 24 h in 1.5–2 m of water. Crayfish were trapped during the period of late July to late August to minimize the number of molting (and therefore inactive) individuals in the population. Traps select for adult male rusty crayfish over other crayfish species (Olsen et al. 1991) and may underestimate abundances of other crayfish. Olsen et al. (1991) used one-half of the adult rusty crayfish males caught as a conservative estimate of rusty crayfish numbers relative to congeners. Here we present total rusty crayfish per trap to facilitate direct comparisons between the Lodge–Kratz data set and the NTL-LTER data set (discussed below).

NTL-LTER data

The abundance of crayfish, fish, and macroinvertebrates was measured annually at six permanent sampling sites (A–

Fig. 1. Rusty crayfish (*Orconectes rusticus*) invasion of Trout Lake, Vilas County, Wisconsin, in 2-year time blocks. Arrows tracing the shoreline indicate the spatial distribution of *O. rusticus* through time, where the edge of the *O. rusticus* distribution is defined as >1 *O. rusticus*-trap⁻¹. Rusty crayfish reached the Trout River by 1995 and completely surrounded the lake in 1997 (arrow not shown for clarity) when they reached North Creek. North Temperate Lakes Long-Term Ecological Research (NTL-LTER) sampling sites are lettered in the order in which they were invaded. Rusty crayfish were first detected near site A in 1979. The lake's distinct north and south basins are separated by a deep narrow constriction. Four streams enter the lake and the Trout River exits the lake. The lake's deepest point (star) is located at 46°01.756'N, 89°39.901'W. The diamond denotes a heavily used public boat landing.



F; see Fig. 1 and Table 1) in the south basin of Trout Lake as part of NTL-LTER research group's annual sampling (1981 to present; data presented are through 1999). The NTL-LTER sampling sites are lettered in order of rusty crayfish invasion. NTL-LTER data are archived at <http://limnosun.limnology.wisc.edu/>.

Crayfish

To compare the change in crayfish abundances with other lake biota, we used the NTL-LTER data (Magnuson and Kratz 1999a) instead of the crayfish invasion data because these six sites correspond spatially and temporally to littoral

zone macrophyte, macroinvertebrate, and fish sampling sites and so best represented site-specific crayfish abundances relative to other biota. Five crayfish traps were set at each LTER site until 1997, when effort was reduced to three crayfish traps per site to reduce operating costs. Traps were set within 10 m of a fyke net at the same time as the annual fish sampling (see Fish below). Crayfish were trapped in the same manner as described above.

Fish

Yearly fish sampling (1981–1999) was conducted by NTL-LTER at the same six sites where crayfish were sam-

Table 1. North Temperate Lakes Long-Term Ecological Research (NTL-LTER) sampling site characteristics.

Site	NTL-LTER site name	Primary substrate	Resident crayfish abundance (± 1 SD)	Year ^a
A*	7	Sand	3.3 (2.3)	1988
B	17	Cobble	9.6 (7.5)	1988
C*	31	Sand-cobble	8.0 (3.7)	1993
D*	56	Sand	1.5 (1.1)	1995
E	67	Sand	5.4 (3.9)	1995
F*	50	Sand-muck	3.1 (1.5)	1996

Note: Sites at which macrophytes were also sampled are indicated with an asterisk (*). Resident crayfish (*Orconectes propinquus* + *O. virilis*) trap catches were averaged over the years before *O. rusticus* reached >9 crayfish-trap⁻¹. SD = standard deviation.

^aYear *O. rusticus* reached >9 crayfish-trap⁻¹.

pled in the south basin of Trout Lake in mid- to late July (Magnuson and Kratz 1999b). For site-specific comparisons, we present only data from the night seines (three per site) and fyke nets (one 24-h set per site). To better characterize annual variation in species abundance in whole-lake catches, we combined all beach seine and fyke net catches, as well as trammel net and electroshocking catches from sites that did not necessarily overlap spatially with the six main sampling sites. Because trapping effort varied slightly from year to year, we calculated abundances as the number of fish caught divided by the number of sets of a gear in the lake for a year (i.e., catch per unit effort, CPUE). We then summed the CPUEs across gear types because fishing gears differ in their proficiency for catching different species and size classes of fish and thus may not be directly comparable (Weaver and Magnuson 1993).

We removed young-of-the-year (YOY) centrarchids from the analysis because their abundance can depend strongly on fluctuations in spring and summer temperature during spawning (Casselman 2002). Young-of-the-year were removed from the analysis by visually inspecting the size distribution and choosing a length that distinguished the YOY from juveniles (1+-year-olds) and adults for as many years as possible. Length criteria (millimetres total length) were similar to published size-at-age records (Becker 1983): smallmouth bass (*Micropterus dolomieu*) ≤ 80 , largemouth bass (*Micropterus salmoides*) ≤ 80 , rock bass (*Ambloplites rupestris*) ≤ 65 , pumpkinseed (*Lepomis gibbosus*) ≤ 75 , bluegill (*Lepomis macrochirus*) ≤ 75 . Only a subsample of the fish caught in the field were measured, so that at times, individual fishes of a given length represented many unmeasured, but counted, fish of that length class. We thus adjusted the data for (i) changes in sampling effort over time (CPUE) and (ii) additional unmeasured fish of a given size class.

Macroinvertebrates

Invertebrates were sampled by NTL-LTER using modified Hester–Dendy artificial substrate samplers set in mid-August and pulled in mid-September of each year at each of the six main sampling sites (1981 or 1982 to 1999). The Hester–Dendy samplers consisted of a 7.26 cm \times 7.26 cm \times 10.2 cm high sandwich of interspersed components (six wide-meshed squares, four narrow-meshed squares, two tempered hard-

board squares, and one plastic scrubber puff) to provide a variety of interstitial structure and substrate for macroinvertebrates. Three Hester–Dendy samplers were set at a depth of 1 m at each site; however, not all samplers were recovered in all years. Macroinvertebrates were identified to order.

Because the Hester–Dendy macroinvertebrate data were highly variable over time, we compared the mean abundance of macroinvertebrates in years of low rusty crayfish abundance and years of high rusty crayfish abundance. We defined low (≤ 9 crayfish-trap⁻¹) and high (>9 crayfish-trap⁻¹) rusty crayfish abundances based on the rapid increase in rusty crayfish abundance after ~ 9 crayfish-trap⁻¹ were observed at most sites (see Fig. 2). We felt that this was an ecologically significant breakpoint, because at abundances of >9 crayfish-trap⁻¹, rusty crayfish were from two to six times more abundant than average abundances of resident crayfish before the rusty crayfish invasion (Table 1).

Snails

Because snails were not well sampled by the NTL-LTER Hester–Dendy samplers, we relied on core sampling conducted under the auspices of other projects (e.g., Lodge et al. 1987, 1994) to characterize changes in snail abundance. Snails were sampled on five occasions in the southeast bay of the South Basin. For the years 1995–2000, sediments were cored using a polyvinyl chloride pipe (inside diameter 15.22 cm) with a leading metal edge. The corer was pushed 5 cm into the sediments, and then sediments were contained by a metal plate slipped into a slot at the bottom of the corer. In 1984, samples were collected using a smaller corer (inside diameter 6.25 cm) (for details, see Lodge et al. 1994).

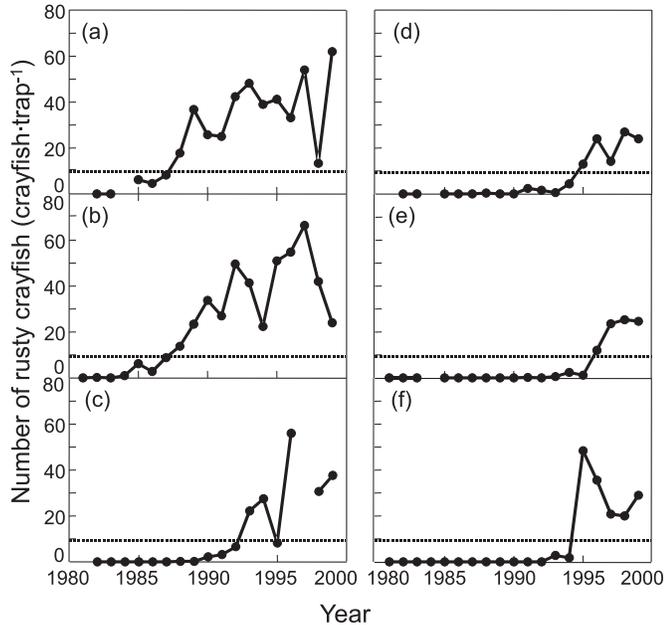
Macrophytes

Macrophytes at four of the six sites (sites A, C, D, and F) were assessed annually in mid-August (1982–1999) for species presence and biomass (Kratz 1999). Species presence in 0.25-m² quadrats was assessed by SCUBA divers at 1- or 2-m intervals along a permanent transect located along the substrate from 0.5 to 5 m in depth. Five above-sediment biomass samples (0.25 m² each) were taken adjacent to the permanent transects at depths of 1.5, 2.5, and 4 m for a total of 15 biomass samples per site. Biomass samples were separated by species, dried at least 24 h at 60 °C, and weighed.

Calculations and statistical analyses

We checked for evidence of temporal autocorrelation using partial autocorrelation plots (SPSS Inc. 2000). Autocorrelations were present in the macrophyte biomass time series (site B only) and the macrophyte species richness time series (sites A, B, and C), as well as rusty crayfish abundance time series at all sites and the whole lake. In all cases, autocorrelation occurred at a lag of 1 year, suggesting that values in these time series can be predicted, to some extent, by the value from the year before. However, because we were interested in how values changed in concert with increasing rusty crayfish abundance rather than predicting future change and because rusty crayfish abundance was highly correlated with time, we did not remove this time trend from the data. The data do not fit all assumptions of traditional parametric statistics; we used the nonparametric

Fig. 2. Rusty crayfish (*Orconectes rusticus*) trap catches over time for each North Temperate Lakes Long-Term Ecological Research sampling site. The dotted line denotes 9 crayfish-trap⁻¹. Each lettered panel corresponds to the same sampling site (sites A–F).



Spearman's rank coefficient (r) to describe correlations between crayfish abundance and other taxa.

Mean abundance of macroinvertebrates from years of low and high rusty crayfish abundance were compared using analysis of variance (ANOVA) to test for effects of site and level of rusty crayfish abundance. Data were $\ln(x + 1)$ transformed to achieve normality. We calculated individual ANOVAs for each macroinvertebrate order that tested the contribution of site and level of rusty crayfish abundance to variation in abundance ($N = 87$). Replicates in this case were the average macroinvertebrate abundance for each year. We assumed sites were independent because it took several years for crayfish to spread between sites and macroinvertebrates are relatively immobile (although adult forms are not).

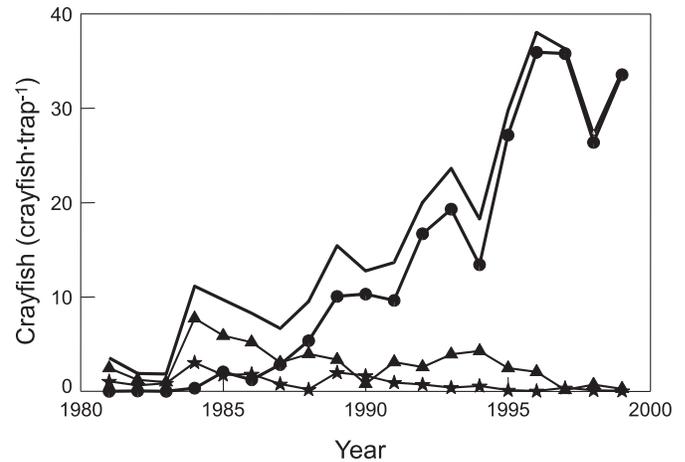
To reduce the possibility of type I errors resulting from multiple comparisons, we used the sequential Dunn–Šidák method to calculate more conservative α values for an experiment-wise $\alpha = 0.05$ (Sokal and Rohlf 1995). Tests are considered significant if p values are less than the Dunn–Šidák associated α value ($D-\dot{S} \alpha$).

Results

Rusty crayfish invasion

By 1983, rusty crayfish were well established in the southeast corner of Trout Lake (Fig. 1). The *O. rusticus* population dispersed along the shores of Trout Lake at an average rate of $0.68 \text{ km}\cdot\text{year}^{-1}$ ($\pm 0.14 \text{ SE}$). By 1990, they had crossed to the opposite shore of Trout Lake at the constriction between the two basins, traveling to depths greater than 12 m. The invasion front continued north along both shores of the North Basin and west along the north shore of the

Fig. 3. Change in whole-lake crayfish trap catches over time. Total crayfish (solid line) is the sum of the abundance of all three species of crayfish. Individual species are *Orconectes rusticus* (●), *O. propinquus* (▲), and *O. virilis* (★).



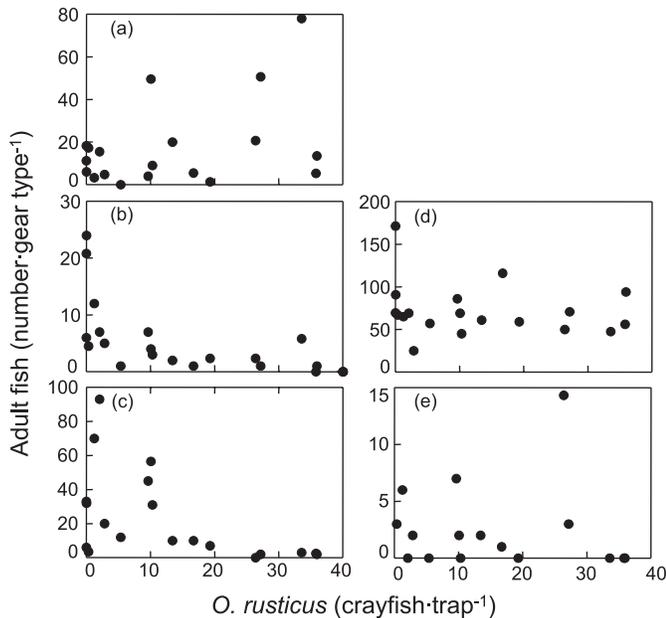
South Basin. Islands were invaded within 2 years after the arrival of *O. rusticus* on the corresponding shoreline. Rusty crayfish reached all sections of the lake by 1997.

The NTL-LTER data and Lodge–Kratz data generally agreed on annual estimates of crayfish abundance. At the six different NTL-LTER sites, Pearson pairwise correlations between the NTL-LTER trap catches and five nearby crayfish invasion traps ranged from 0.42 to 0.90 for *O. rusticus*, 0.11 to 0.94 for *O. propinquus*, and -0.19 to 0.93 for *O. virilis*. At the whole-lake scale, correlations were 0.79 ($p = 0.003$) for *O. rusticus*, 0.67 ($p = 0.05$) for *O. propinquus*, and 0.71 ($p = 0.02$) for *O. virilis*. Lower correlations may be attributable in part to the different spatial extents of the data sets; for any given year, *O. rusticus* could have reached the NTL-LTER sample site but not all of the Lodge–Kratz traps. In particular, this may be true for estimates of *O. propinquus* and *O. virilis* abundances because trapping may underestimate the abundance of these species in the presence of *O. rusticus* (Olsen et al. 1991).

Orconectes rusticus abundance increased slowly at newly invaded sites but often rapidly at sites behind the invasion front (Fig. 2). A sharp rise in abundance at a site often occurred once *O. rusticus* reached an abundance of 9 crayfish-trap⁻¹. In some cases, abundances reached >60 crayfish-trap⁻¹. Despite the almost complete elimination of *O. propinquus* and *O. virilis* from Trout Lake, total crayfish abundance in the lake continued to increase (Fig. 3). Increases in total crayfish abundance were particularly dramatic at sandy-sediment sites, where total crayfish abundance went from <5 crayfish-trap⁻¹ to 20 or more (see Table 1 for abundances of resident crayfish at these sites). At individual sites, *O. propinquus* and *O. virilis* abundances decreased exponentially with increases in *O. rusticus* abundance: $O. propinquus$ (crayfish-trap⁻¹) = $3.455e^{(-0.026 O. rusticus)}$, $R^2 = 0.40$; $O. virilis$ (crayfish-trap⁻¹) = $1.473e^{(-0.112 O. rusticus)}$, $R^2 = 0.49$.

In addition to our trapping, commercial crayfish harvesting has occurred in the lake since approximately 1990. Most of the commercial trapping effort is concentrated in areas of high rusty crayfish abundance (sites A and B, see Fig. 1) at depths between 2 and 3 m.

Fig. 4. Whole-lake abundance of centrarchid species vs. rusty crayfish (*Orconectes rusticus*) abundance. Young-of-year fishes are excluded. Fish species are (a) smallmouth bass (*Micropterus dolomieu*), (b) pumpkinseed sunfish (*Lepomis gibbosus*), (c) bluegill sunfish (*Lepomis macrochirus*), (d) rock bass (*Ambloplites rupestris*), and (e) largemouth bass (*Micropterus salmoides*).



Fish

At the whole-lake scale, catches of smallmouth bass, rock bass, and largemouth bass were not correlated with increases in *O. rusticus* abundance, but bluegill (*Lepomis macrochirus*; $r = -0.63$, $p = 0.004$, $D\text{-}\check{S} \alpha = 0.009$) and pumpkinseed sunfish (*Lepomis gibbosus*; $r = -0.75$, $p < 0.001$, $D\text{-}\check{S} \alpha = 0.007$) were significantly negatively correlated (Fig. 4). Fish response was highly variable at individual sites.

Macroinvertebrates

Most invertebrate groups decreased in abundance with increases in rusty crayfish abundance. Total whole-lake macroinvertebrate abundance was not significantly correlated with increases in *O. rusticus* abundance ($r = -0.47$, $p = 0.05$, $D\text{-}\check{S} \alpha = 0.01$). Results from ANOVAs for Odonata, Amphipoda, and Trichoptera demonstrated that low abundance (pre-invasion) *O. rusticus* years boasted significantly higher counts of these macroinvertebrates than high abundance (post-invasion) *O. rusticus* years (Table 2; Fig. 5), despite significant site-to-site variation in mean abundance. Interaction terms for Amphipoda and Trichoptera were marginally significant and nonsignificant when sequential Dunn-Šidák corrections to the α value were applied. There was no significant variation for Diptera and Ephemeroptera between high and low rusty crayfish years.

Snails

Snail abundance also decreased with increasing *O. rusticus* abundance (Fig. 6). High snail abundances recorded in 1984 and 1986 were consistent with qualitative

observations (D.M. Lodge, personal observation) of many snails in 1983 and 1985 in the site A area. Snails in this area declined sharply as *O. rusticus* became abundant, and by 2000, almost no snails were observed.

Macrophytes

Macrophyte species richness remained steady throughout the lake until 1996 when *O. rusticus* abundances reached high levels (>9 crayfish-trap⁻¹) at all four macrophyte sites. All sites eventually exhibited losses in macrophyte species richness with increasing *O. rusticus* abundance (Fig. 7), although this pattern was only significant in site A ($r = -0.85$, $p < 0.001$, $D\text{-}\check{S} \alpha = 0.006$) and site C ($r = -0.78$, $p < 0.001$, $D\text{-}\check{S} \alpha = 0.009$). Macrophyte species richness has remained low in recent years at site A (Fig. 8), as well as at site C, despite annual fluctuations in *O. rusticus* abundance. With increasing *O. rusticus* abundance, mean total macrophyte biomass decreased significantly at site C ($r = -0.81$, $p < 0.001$, $D\text{-}\check{S} \alpha = 0.007$) and marginally at site D ($r = -0.60$, $p = 0.015$, $D\text{-}\check{S} \alpha = 0.01$), was variable at site A, and steady at site F (Fig. 9).

Discussion

Rusty crayfish have had a profound effect on their competitors and prey in Trout Lake. Macroinvertebrate, snail, macrophyte, and crayfish species richness and, in some cases, abundance decreased within a few years of rusty crayfish arrival at sampling points around the lake. More sedentary or short-lived species, e.g., snails and some macroinvertebrates, exhibited dramatic whole-lake and site responses to increasing *O. rusticus* abundance, whereas more mobile and (or) long-lived species, e.g., fishes, macrophytes, and crayfish, required several years of exposure to increasing *O. rusticus* abundance before responding at either the local or whole-lake spatial resolution. Changes in taxa apparent at the site level often were masked at the whole-lake level, in part because of the slow *O. rusticus* invasion rate, which resulted in areas of the lake free of rusty crayfish until late in the time series.

Dispersal

The dispersal of rusty crayfish around Trout Lake was relatively slow compared with invasive species with pelagic life stages (e.g., zebra mussels, *Dreissena polymorpha*) and considering the distances that crayfish can move in short time periods. Rusty crayfish completely encircled Trout Lake in a minimum of 16 years (1981–1997), traveling up to 9.8 km from the point of first introduction. Evidence from other area *O. rusticus* introductions suggests that *O. rusticus* invasion rates are highly variable (Olsen et al. 1991). Byron and Wilson (2001) found that *O. rusticus* moved on average 29 m-day⁻¹ (at ~20 °C) between traps in Trout Lake; in the same study, several crayfish traveled up to 200 m in 48 h. Others have reported similar rates of movement for other crayfish species in ponds (15–20 m-day⁻¹, Camougis and Hichar 1959; 62 m-day⁻¹, Momot and Gowing 1972). Using this estimate for Trout Lake during the months of June, July, and August, when *O. rusticus* are most active (Lorman 1980), rusty crayfish could move 2.7 km-year⁻¹ and might have encircled the lake in approximately 3 years. Clearly,

Table 2. Sources of variation in macroinvertebrate abundance ($\ln(x + 1)$ transformed).

Source	Sum of squares	df	Mean square	F ratio	P value	Associated α
Ephemeroptera (multiple $R^2 = 0.40$)						
Site	23.94	5	4.79	7.51	<0.001	0.006
<i>O. rusticus</i>	0.85	1	0.85	1.34	0.251	0.025
Site \times <i>O. rusticus</i>	5.06	5	1.01	1.59	0.174	0.013
Error	47.8	75	0.637			
Odonata (multiple $R^2 = 0.52$)						
Site	7.32	5	1.47	7.82	<0.001	0.005
<i>O. rusticus</i>	2.34	1	2.34	12.48	0.001	0.006
Site \times <i>O. rusticus</i>	1.67	5	0.33	1.78	0.127	0.010
Error	14.06	75	0.19			
Trichoptera (multiple $R^2 = 0.71$)						
Site	31.86	5	6.37	17.3	<0.001	0.004
<i>O. rusticus</i>	11.85	1	11.85	32.18	<0.001	0.003
Site \times <i>O. rusticus</i>	4.16	5	0.83	2.26	0.057	0.009
Error	27.63	75	0.37			
Diptera (multiple $R^2 = 0.45$)						
Site	46.16	5	9.23	9.04	<0.001	0.005
<i>O. rusticus</i>	0.31	1	0.31	0.31	0.581	0.050
Site \times <i>O. rusticus</i>	7.66	5	1.53	1.5	0.2	0.017
Error	76.6	75	1.02			
Amphipoda (multiple $R^2 = 0.57$)						
Site	22.95	5	4.59	10.59	<0.001	0.004
<i>O. rusticus</i>	6.71	1	6.71	15.49	<0.001	0.004
Site \times <i>O. rusticus</i>	5.1	5	1.02	2.35	0.049	0.007
Error	32.49	75	0.43			

Note: "*O. rusticus*" is a binary effect representing low (≤ 9 crayfish-trap⁻¹) or high *Orconectes rusticus* abundance. $N = 87$ for each ANOVA; replicates are mean invertebrate abundance by year. P values less than the sequential Dunn-Sidak associated α are considered significant at an experiment-wise $\alpha = 0.05$.

factors other than mobility slowed *O. rusticus* establishment and spread.

Although our data cannot distinguish between factors influencing invasion speed, we suspect that availability of cobble habitat, the presence of predatory fishes, and interactions with conspecifics were critical factors influencing how quickly rusty crayfish spread throughout Trout Lake. The lake's littoral zone is a mosaic of patchy macrophytes and cobble interspersed with substantial stretches of sand (Wilson 1941). In northern Wisconsin lakes, crayfish densities are consistently higher in cobble substrates (Lorman 1980; Kershner and Lodge 1995), where predation risk is low for smaller crayfishes (15- to 18-mm carapace length) relative to sand or macrophyte habitats (Kershner and Lodge 1995). Cobble areas are also nursery habitats for egg-bearing females and YOY crayfish (Lorman 1980). Perry et al. (2001a) found that rusty crayfish marked near the leading edge of the Trout Lake invasion front (in 1995) tended to disperse back to the nearest cobble habitat rather than forward into new, sandy habitat.

The presence of abundant predatory fishes in Trout Lake was likely an additional factor slowing the spread of rusty crayfish. Many larger fish species in Trout Lake are effective predators of small or molting crayfish (reviewed in Dorn and

Mittelbach 1999), and smaller fishes like bluegill and pumpkinseed eat YOY crayfish when available (T.V. Willis, personal observation). In laboratory experiments, the presence of predatory fishes reduced foraging and other activity of *O. rusticus* (Stein and Magnuson 1976; Hill and Lodge 1994), especially over substrates that provided little refuge. However, laboratory experiments have demonstrated that *O. rusticus* generally displaces other *Orconectes* species from preferred refuge (Hill and Lodge 1999), which may increase the rate of predation on crayfish other than rusty crayfish (Capelli and Munjal 1982; DiDonato and Lodge 1993; Garvey et al. 1994) and contribute to the rapid extirpation of native crayfishes. This conspecific-predator interaction may release rusty crayfish from competition with their congeners (*O. propinquus* and *O. virilis*) and over time compensate for the inhibitory effect of predatory fishes. In addition, interbreeding between male *O. propinquus* and female *O. rusticus* is thought to have sped the establishment of rusty crayfish at, and ahead of, the invasion front (Perry et al. 2001a). *Orconectes rusticus* – *O. propinquus* hybrids are fecund and more competitive than either parent species (Perry et al. 2001a) and composed at least 6% of the Trout Lake crayfish population (F_1 hybrids) during the rusty crayfish invasion (Perry et al. 2001b).

Fig. 5. The mean abundance of macroinvertebrate orders ($\ln(x + 1)$ data) for years with low abundances of rusty crayfish (dotted line with triangles) and years with high abundances of crayfish (solid line with circles). High *O. rusticus* abundance was >9 crayfish-trap⁻¹. Error bars represent ± 1 standard error. In a two-way analysis of variance, crayfish abundance (high or low) explained significant variation in (d) odonate, (e) trichopteran, and (a) amphipod abundance. (c) Ephemeropterans and (b) dip- terans varied significantly between sites only.

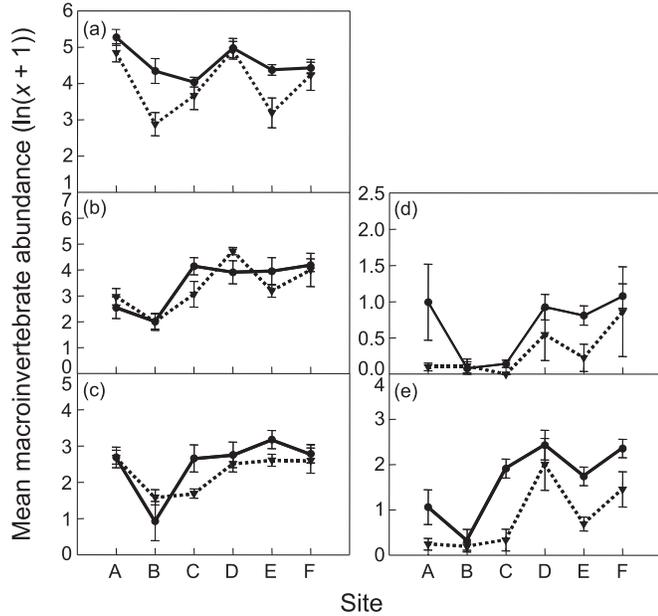
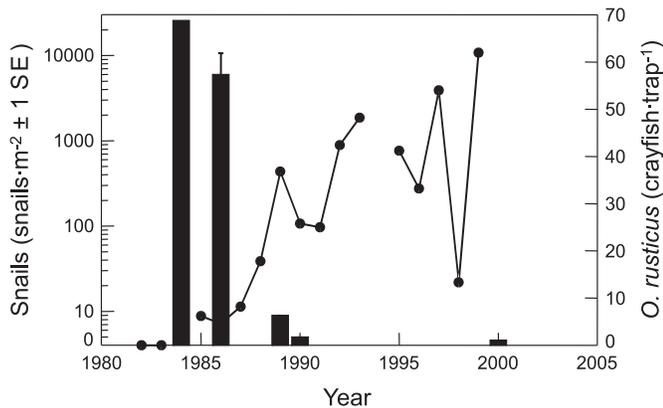


Fig. 6. Change in snail (Gastropoda) abundance over time (1984, 1986, 1989, 1990, 2000) on sandy sediments in the southeast bay of Trout Lake (near site A). Line indicates *Orconectes rusticus* abundance at site A over the same time period. Data from 1984 are from Lodge et al. (1987). Error bars represent ± 1 standard error (SE). A measure of sampling error was not available for 1984.



Biological impacts

In north temperate lakes, rusty crayfish and its native congeners occupy similar ecological niches, although rusty crayfish reach abundances far greater than those of the native species. In Trout Lake, we measured trap catches of rusty crayfish 2–18 times greater than the historical catches

Fig. 7. Macrophyte species richness vs. *Orconectes rusticus* abundance at the four macrophyte sites, calculated as the species richness for post-*O. rusticus* years divided by the mean species richness for pre-*O. rusticus* years: (a) site A, (b) site C, (c) site D, (d) site F. In some years, species richness is greater than one because species richness was still high (and variable) during the early years of *O. rusticus* invasion.

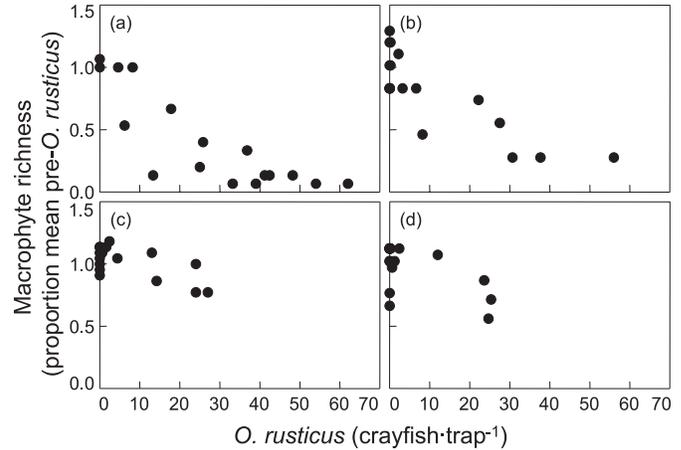
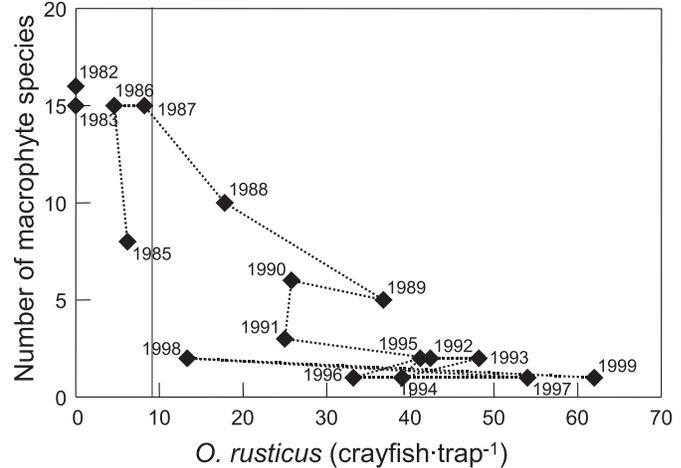
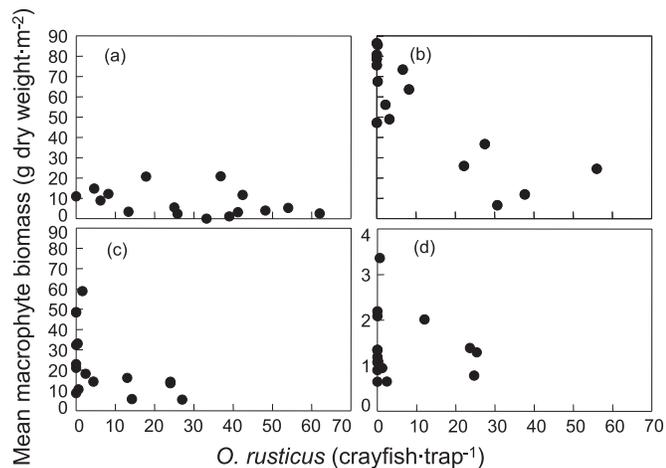


Fig. 8. Time series of macrophyte species richness at site A vs. *Orconectes rusticus* abundance. Notice the variation in crayfish abundances in later years and low variation in macrophyte species richness. The vertical solid line denotes the abundance of *O. rusticus* after which *O. rusticus* abundance increased (often sharply) at all sites.



of native crayfishes, and these catches were sustained in some cases for 10 years or more (e.g., site A). Despite the differential trapability among crayfish species (Olsen et al. 1991), the increase in trap catches suggests a strong increase in total crayfish abundance. Negative impacts were generally observed at rusty crayfish catches >9 crayfish-trap⁻¹, suggesting that above this threshold value, we should expect observable changes in invaded systems. In addition, rusty crayfish consume more macroinvertebrates and macrophytes by weight than the native crayfish species (Olsen et al. 1991), adding to the impact of the sheer numbers of rusty crayfish present in invaded systems.

Fig. 9. Mean total macrophyte biomass (g dry weight·m⁻²) vs. *Orconectes rusticus* abundance for each of the four macrophyte sites: (a) site A, (b) site C, (c) site D, (d) site F. Values for site F are 100 times the labeled value.



The most visible impact of rusty crayfish in Trout Lake was a shift to lower macrophyte abundance and species richness. Negative effects of crayfish on macrophytes are well documented (Lodge and Lorman 1987; Hanson and Chambers 1995; Nyström and Strand 1996). In experimental work, rusty crayfish have reduced macrophyte abundance as a result of nonconsumptive destruction (Lodge et al. 1994). Crayfish may also cause damage while grazing on periphyton or physically uproot seedlings or established plants in the process of digging burrows or foraging. In Trout Lake, loss of macrophyte species was not mirrored by decreases in macrophyte biomass at all sites, suggesting that persistent species were larger or that the loss of more vulnerable species allowed the remaining species to increase in abundance. Because some of the species lost from the lake represent highly complex and valuable habitat for macroinvertebrates, shifts in the macrophyte community to robust, often single-stemmed species likely reduced available refugia for both macroinvertebrates and fishes (e.g., Chick and McIvor 1994). Fluctuations in rusty crayfish abundance (i.e., site A) were not accompanied by recovery of the macrophyte community, suggesting that macrophyte recovery may require substantial and prolonged reductions in rusty crayfish abundance.

Short-term reductions in macroinvertebrate abundance in the presence of high densities of crayfish have been documented in a variety of experimental and natural settings (Hill and Lodge 1995; Charlebois and Lamberti 1996; Nyström et al. 1996), although reductions in non-gastropod invertebrates are less common (Lodge et al. 1994; Perry et al. 1997). In almost all cases, macroinvertebrate response to crayfish is highly variable. In this study we saw significant reductions in dipterans, odonates, and amphipods and large reductions in dipterans and ephemeropterans at some sites in years with high (>9 crayfish·trap⁻¹) rusty crayfish abundance. Although crayfish directly consume most invertebrates, reductions in numbers over long time periods may have also occurred from loss of macrophyte habitat or, in the case of predatory odonates, for example, competition for prey with rusty crayfish. The use of artificial substrates in this study may have

overestimated the number of macroinvertebrates present at the different sites within the lake, because the samplers represent a more complex substrate than available in some sites (i.e., sand) or sites where macrophytes were lost over time. Rickett (1974) and Nyström et al. (1996) found that sediment-dwelling invertebrates (e.g., many Diptera, especially Chironimidae) dominated invertebrate communities in the presence of crayfish. Although we did see reductions in dipterans at some sites, Hester–Dendy samplers do not quantify sediment-dwelling organisms well and so would not have detected changes in sediment-dwelling dipterans. However, if sediment dwellers are surface grazers or detritivores, we would expect their numbers to decrease in direct competition with crayfish for prey items or reductions in detritus.

Constraints imposed by the limited spatial and temporal extent of field and laboratory experiments have prevented exploration of the impacts of rusty crayfish on long-lived and (or) highly mobile fish species (Dorn and Mittelbach 1999). Our results represent the first evidence that rusty crayfish have had long-term negative impacts on populations of bluegill and pumpkinseed sunfish populations, likely through reductions in habitat (submerged macrophytes), competition for invertebrate prey, and direct predation on eggs. Lake-wide reductions in odonates, trichopterans, amphipods, and snails represent a significant reduction in the availability of macroinvertebrate prey. Snails in particular are preferred prey for both crayfish (Lodge et al. 1998) and pumpkinseed sunfish. Pumpkinseed sunfish are rarely found in lakes containing abundant crayfish (Lodge et al. 1998) and in Trout Lake exhibited the greatest loss in abundance with increases in rusty crayfish numbers. Bluegill and pumpkinseed sunfish may also have experienced increasing frequency of nest predation by rusty crayfish (Dorn 2003). Although larger centrarchids (e.g., smallmouth bass and rock bass) can intimidate or physically remove all but the largest crayfish from their nests, pumpkinseeds (and presumably bluegill) do a poor job of defending their eggs from crayfish, especially at night (J.J. Magnuson, personal communication). In the summer of 1998 and 1999, both bluegill and pumpkinseed were observed nesting within open crayfish enclosures in Trout Lake, but nowhere nearby (Wilson 2002). Rock bass were also seen successfully nesting in heavily vegetated crayfish enclosures in 2001 and 2002 (K.A. Wilson, personal observation). We presume that these fish nested within the enclosures because of low rusty crayfish densities (Dorn 2003). In contrast to decreases in smaller centrarchid species, we detected no significant response in the abundance of adult predatory centrarchids. Before the invasion of rusty crayfish, smallmouth bass and rock bass diets in Trout Lake included 60–100% *O. propinquus* (Stein 1977). In 1990, when rusty crayfish were present only along the eastern shore of the South Basin, Garvey et al. (2003) found that rusty crayfish occurred in fish diets in proportion to their relative abundance in the lake, suggesting that rusty crayfish presently compose a large proportion of fish diets. We would expect that high availability of rusty crayfish as prey should benefit the larger centrarchids; however, competition for invertebrate prey between YOY centrarchids and crayfish, as well as loss of macrophyte habitat, may have counteracted any positive influence of increasing crayfish abundance.

The accumulated change in Trout Lake observed during the invasion of rusty crayfish represents significant changes in the forage base of Trout Lake, with the potential to modify pathways of energy transfer at the whole-lake scale. Decreases in the abundance of macroinvertebrates may disrupt trophic links and energy passage from primary producers and detritus up to higher consumers by forcing juvenile and adult centrarchids to feed on pelagically derived food sources (e.g., zooplankton, pelagic minnows; Vander Zanden et al. 1999). Alternatively, many larger fish species in Trout Lake are effective predators of small or molting crayfish (Rach and Bills 1989; Dorn and Mittelbach 1999; Weidel et al. 2000), and smaller fishes like bluegill and pumpkinseed eat YOY crayfish when available (T.V. Willis, personal observation). Under conditions of high crayfish abundance, centrarchids may switch to a crayfish-dominated diet. Under both scenarios, rusty crayfish invasions have the potential to greatly alter benthic–pelagic linkages in aquatic systems (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). Some authors have gone further to suggest that the loss of benthic prey items may destabilize food webs by removing alternate prey items for pelagic species (Post et al. 2000; Schindler and Scheuerell 2002).

In conclusion, the invasion of Trout Lake by rusty crayfish was a slow process, with over 19 years from first detection in 1979 to eventual dominance throughout the littoral zone. Drastic declines of biota above a threshold of rusty crayfish abundances >9 crayfish-trap⁻¹ suggest that high abundance is a primary reason for the large impacts of rusty crayfish, even in lakes with pre-existing crayfish populations. Sustained high abundances of rusty crayfish in the earliest invaded sites and the persistence of rusty crayfish in other regional lakes (Olsen et al. 1991) suggest that rusty crayfish will remain permanent and abundant residents of Trout Lake. The impacts observed in this study are not unique to Trout Lake; in Vilas County (Wisconsin) alone, rusty crayfish have been documented in over 40 lakes (Perry et al. 2002; Wilson 2002), and many of these lakes exhibit signs of rusty crayfish impacts (Wilson 2002). Potential for further spread is great, for example, approximately 70% of lakes located in the Canadian shield are vulnerable to rusty crayfish invasions based on pH and Ca²⁺ tolerances (although not on geographic isolation) (Vander Zanden et al. 2004), and rusty crayfish continue to spread throughout eastern North America (Lodge et al. 2000). Impacts of rusty crayfish are likely to be compounded by other human-induced stresses to aquatic ecosystems such as reductions in water quality and the loss of macrophytes from recreational boats and clearing in front of cabins (Radomski and Goeman 2001). Through shifts in littoral food web structure and energy flows, rusty crayfish have the potential for impacting recreational fisheries and rare native communities, including extirpation of native crayfish species.

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