

# Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities

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## SUMMARY

1. Biological invasions are widely recognised as a significant component of human-caused environmental change and a primary threat to native biodiversity. The negative impacts of species invasions are particularly evident for freshwater crayfish faunas.
2. This study provides novel insight into the ecological effects of native and non-native crayfish on zoobenthic communities (with emphasis on the non-native rusty crayfish, *Orconectes rusticus*) across broad scales by combining a meta-analysis of small-scale experimental studies with a long-term observational study conducted over a 24 year period in Sparkling Lake, Wisconsin, U.S.A. (46°00'N, 89°42'W).
3. The meta-analysis summarised quantitatively the results of cage experiments for seven species of crayfish spanning four continents. We found that total zoobenthos densities (primarily Gastropoda and Diptera) were significantly lower in treatments containing crayfish relative to controls; a result that was significant for non-native crayfish but not for crayfish in their native range, perhaps owing to a small sample size. In contrast to other species, rusty crayfish were also negatively associated with Ephemeroptera.
4. Results from the time series analysis comparing temporal trends in rusty crayfish and invertebrate abundances from Sparkling Lake were consistent with the findings from the meta-analysis. Rusty crayfish were negatively correlated with the abundance of total zoobenthos, Diptera, Ephemeroptera and Odonata, as well as families of Trichoptera.
5. By coupling the results from short and long-term research, our study offers greater insight into the nature of crayfish-invertebrate interactions in aquatic systems, revealing consistent effects of invasive crayfish on native fauna. The control and management of invasive species is facilitated by the knowledge that well executed small-scale studies may be extrapolated to understand larger-scale ecological interactions.

*Keywords:* food webs, invasion, macroinvertebrates, *Orconectes rusticus*, rusty crayfish, scaling issues

## Introduction

Invasive species are recognised as an important driver of global environmental change and are ranked as a

leading cause of biodiversity loss in freshwaters (Vitousek *et al.*, 1996; Sala *et al.*, 2000; Hooper *et al.*, 2005; Millennium Ecosystem Assessment, 2005). Recent evidence suggests that non-native species can dramatically alter aquatic food webs, although these complex interactions have proven difficult to untangle (Lodge *et al.*, 1994; Vander Zanden, Casselman & Rasmussen, 1999; Crooks, 2002). Forecasting food web consequences of species invasions is critical for directing invasive species management and prevention efforts (Vander Zanden *et al.*, 2004), and for

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guiding ecosystem restoration efforts (Zavaleta, Hobbs & Mooney, 2001). However, it is increasingly apparent that our understanding of invader impacts is constrained by the difficulty of assessing interactions at ecologically relevant spatial and temporal scales (Lodge *et al.*, 1998). Research conducted at larger scales provides a better understanding of invader impacts and dynamics, although the cost and duration of these studies impose severe practical constraints, both in terms of conducting research and mounting effective and timely management responses to invaders (Parker *et al.*, 1999). Ultimately, a combination of small- and large-scale experiments may enhance our knowledge of non-native species impacts by yielding novel insights that are not revealed through one study type alone (Diamond, 1986).

Crayfishes play a central role in aquatic food webs, constituting a significant component of benthic invertebrate production and providing a direct link from primary production and detrital-based food webs to fish (Momot, 1995; Rabeni, Gossett & McClendon, 1995; Dorn & Mittelbach, 1999; Geiger *et al.*, 2005). Globally, more than 20 crayfish species have been introduced beyond their native range (Hobbs, Jass & Huner, 1989), a number of which have had major impacts on the invaded aquatic ecosystems (Taylor *et al.*, 1996; Lodge *et al.*, 2000). The majority of studies examining the impacts of crayfishes on benthic communities have been small-scale experimental manipulations, and the results have been highly variable, with negative effects on snails (Gastropoda) (Lodge & Lorman, 1987; Lodge *et al.*, 1994; Charlebois & Lamberti, 1996; Perry, Lodge & Lamberti, 1997; but see Stewart, Miner & Lowe, 1998; Perry, Lodge & Lamberti, 2000) and inconsistent effects on other zoobenthic taxa (Lodge *et al.*, 1994; Perry *et al.*, 1997, 2000; but see Charlebois & Lamberti, 1996; Parkyn, Rabeni & Collier, 1997; Stewart *et al.*, 1998; Stelzer & Lamberti, 1999). Short-term experiments may provide mechanistic insight into crayfish-zoobenthos interactions, but the applicability of these results to natural ecosystem settings, where effects unfold over greater spatial and temporal scales, is poorly known (Carpenter, 1996; Lodge *et al.*, 1998). Few comparative field studies (Charlebois & Lamberti, 1996; Houghton, Dimick & Frie, 1998) and even fewer long-term studies have characterised the impacts of crayfish on zoobenthic communities. Wilson *et al.* (2004) was one of the first studies to assess non-native crayfish

impacts over longer temporal scales, and found negative effects on native crayfishes, fishes, invertebrates and macrophytes.

In this study, we examine the impacts of crayfish on zoobenthic communities, with an emphasis on the widespread non-native species, rusty crayfish [*Orconectes rusticus* (Girard)]. We use a meta-analysis to systematically synthesise crayfish impacts on zoobenthos from short-term experimental studies, and couple this with a long-term (24 year) time series of rusty crayfish and zoobenthos abundances from a north temperate lake in Wisconsin, U.S.A. By combining multiple modes of inference to assess impacts of non-native crayfish, we seek to gain new insights into the dynamic relationship between introduced crayfishes and the native aquatic communities they invade. Understanding how small-scale experimental studies relate to natural ecosystems is essential for the management of invasive species and highlights the need for multi-scale investigations in invasion biology.

## Methods

### *Invasion history of rusty crayfish, O. rusticus (Girard)*

The rusty crayfish is a prolific invader in North America, and over the last 40–50 years has spread from its historical range in the Ohio River drainage, to waters throughout much of Illinois, Michigan, Wisconsin, Minnesota and parts of New England, Ontario and the Laurentian Great Lakes (Hobbs *et al.*, 1989; Lodge *et al.*, 2000). The invasion dynamics and impacts of rusty crayfish have been most intensively studied in lakes and streams of Wisconsin and the Upper Peninsula of Michigan. In Wisconsin, long-term occurrence records show that rusty crayfish have increased from 7% of all crayfish records collected during the first 20 years of their invasion (1965–1984) to 36% of all records during the most recent 20 years (Olden *et al.*, in press). Rusty crayfish were first reported in Sparkling Lake in 1973 and by 1980 had significantly reduced populations of their native congeners (Capelli, 1982). Once established, rusty crayfish can have substantial impacts on invaded freshwater ecosystems by feeding on organisms from all trophic levels, including benthic algae, macrophytes, invertebrates, snails, native congeners and fish (e.g. Lodge, Beckel &

Magnuson, 1985; Lodge & Lorman, 1987; Olsen *et al.*, 1991; Wilson *et al.*, 2004).

*Meta-analysis of the effects of rusty crayfish on benthic invertebrate assemblages*

We examined the effects of rusty crayfish (and other crayfish species) on benthic invertebrate densities by conducting a fixed-effect model meta-analysis using cage experiments that excluded crayfish as the control and maintained a given density of crayfish as the treatment. Data were obtained from the primary literature (via keyword searches and examining references within) or by direct communication with the authors, and consisted of the mean and standard deviations of zoobenthos densities or abundances by order. Because of differences in methodological approaches, a specific set of criterion was designed for our analyses. First, we selected the highest density crayfish treatment when multiple levels were examined (similar conclusions were obtained using the lowest density treatment data but resulted in a smaller sample size). Second, we used the last sampling date when several sampling occasions were reported, and third, because the majority of studies used only male crayfish, we used only the male treatment when sexes were tested as separate treatments. Following Gurevitch & Hedges (2001), the effect size  $d$  was calculated as:

$$d = \frac{\bar{X}_E - \bar{X}_C}{SD_{\text{pooled}}} J \quad (1)$$

where  $\bar{X}_E$  and  $\bar{X}_C$  are the means of the experimental and control groups, respectively, and  $SD_{\text{pooled}}$  is the pooled standard deviation of the control and experimental groups and is calculated as:

$$SD_{\text{pooled}} = \sqrt{\frac{(n_E - 1)(SD_E)^2 + (n_C - 1)(SD_C)^2}{n_E + n_C - 2}} \quad (2)$$

where  $SD_E$  and  $SD_C$  are the standard deviations of the experimental and control groups, respectively, and  $n$  is the sample size. In the expression  $d$ ,  $J$  corrects for bias because of different sample sizes by weighting each study as follows:

$$J = 1 - \frac{3}{4(n_C + n_E - 2) - 1} \quad (3)$$

The effect size  $d$  can be viewed as the difference between the effects of crayfish on zoobenthic abundance in normal versus elevated densities, measured in units of standard deviation. A negative  $d$  signifies a negative effect of crayfish on zoobenthos abundance or density. We calculated 95% confidence intervals of the weighted mean effect size for each invertebrate order following Gurevitch & Hedges (2001). Separate analyses were conducted to compare crayfish effects on total zoobenthos density and individual zoobenthic orders (Table 1). We also conducted analyses

**Table 1** Description of the published studies included in the meta-analyses

Species	$n$	Cage area (m <sup>2</sup> )	Density (number m <sup>-2</sup> )	Days	Habitat	Locality	Reference
<i>Orconectes rusticus</i>	4	0.2	30.0	30	Stream	United States	Charlebois, 1994*
<i>Orconectes rusticus</i>	5	0.2	10.0	46	Stream	United States	Charlebois & Lamberti, 1996*
<i>Orconectes rusticus</i>	5	3.0	10.0	32	Lake	United States	Lodge & Lorman, 1987 <sup>†</sup>
<i>Orconectes rusticus</i>	8	0.2	20.0	28	Stream	United States	Perry <i>et al.</i> , 1997 <sup>†</sup>
<i>Orconectes rusticus</i>	7	0.2	20.0	105	Stream	United States	Perry <i>et al.</i> , 2000* <sup>†</sup>
<i>Orconectes rusticus</i>	5	0.2	20.8	28	Lake	United States	Stewart <i>et al.</i> , 1998* <sup>†</sup>
<i>Orconectes propinquus</i> <sup>‡</sup>	5	0.2	5.0	42	Stream	United States	Stelzer & Lamberti, 1999* <sup>†</sup>
<i>Orconectes virilis</i>	3	4.7	1.7	34	Pool <sup>§</sup>	Canada	Hanson, Chambers & Prepas, 1990* <sup>†</sup>
<i>Pacifastacus leniusculus</i>	5	1.3	0.8	7	Pool <sup>§</sup>	Sweden	Nyström & Perez, 1998 <sup>†</sup>
<i>Pacifastacus leniusculus</i>	5	4.5	6.0	60	Pool <sup>§</sup>	Sweden	Nyström, Bronmark & Graneli, 1999 <sup>†</sup>
<i>Pacifastacus leniusculus</i>	5	6.0	12.0	63	Pond	Sweden	Nyström <i>et al.</i> , 2001 <sup>†</sup>
<i>Paranephrops phanifrons</i> <sup>‡</sup>	4	0.5	19.0	217	Stream	New Zealand	Parkyn <i>et al.</i> , 1997* <sup>†</sup>
<i>Paranephrops zealandicus</i> <sup>‡</sup>	4	0.4	5.0	44	Stream <sup>§</sup>	New Zealand	Usio & Townsend, 2002 <sup>†</sup>
<i>Procambarus clarkii</i>	12	0.2	4.8	5	Reservoir	Kenya	Hofkin <i>et al.</i> , 1991 <sup>†</sup>

\*Indicates total invertebrate data were available.

<sup>†</sup>Indicates invertebrate order data were available.

<sup>‡</sup>Indicates species are native to the study area.

<sup>§</sup>Indicates the experiment was conducted in an artificial stream.

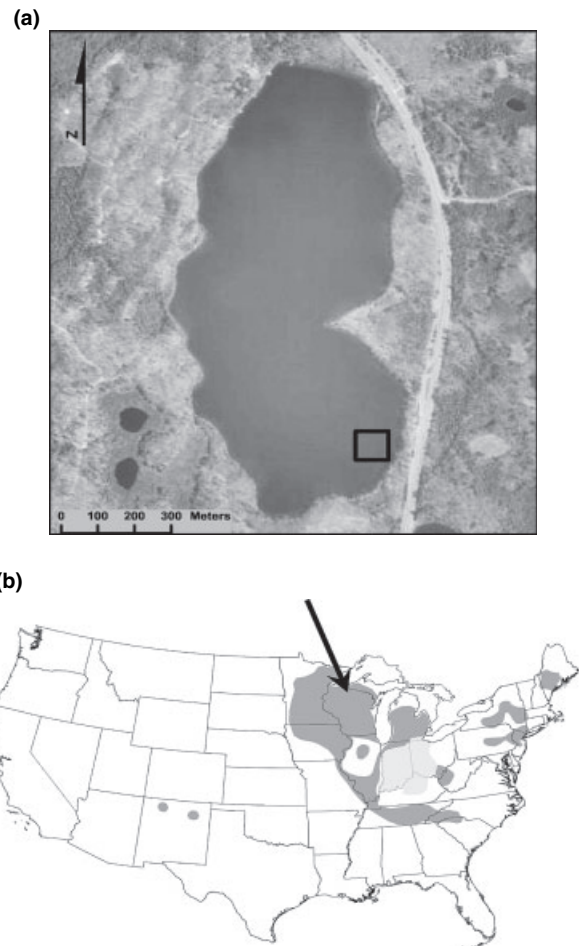
to compare the effects of native versus non-native crayfish and rusty versus non-rusty crayfish. For the most part, these studies were conducted in field cages ( $n = 10$  of 14) in the non-native range of the crayfish species ( $n = 11$  of 14). Several meta-analyses have revealed correlations between the effect size and artefacts of the experiment, such as mesh size (Cooper, Walde & Peckarsky, 1990), study duration and cage area (Wooster, 1994). We used linear regression to test whether crayfish density or study duration were related to effect size.

#### *Long-term study in Sparkling Lake, Wisconsin (U.S.A.)*

Sparkling Lake is a mesotrophic seepage lake (area = 0.64 km<sup>2</sup>, maximum depth = 20.0 m, shoreline perimeter = 4.3 km) located in Vilas County, Wisconsin, U.S.A. (46°00'N, 89°42'W). Sparkling lake is one of 11 lakes included in the North Temperate Lakes – Long-Term Ecological Research (NTL-LTER) programme and lies in the Northern Highlands Lake District and the Northern Highlands-American Legion State Forest. The lake bottom is composed mostly of sand and muck with interspersed cobble, coarse woody habitat and few macrophyte beds.

As part of the NTL-LTER programme, benthic invertebrates were sampled with Hester-Dendy artificial substrate samplers set in mid-August and pulled in mid-September of each year from 1981 to 2004. One of the five LTER zoobenthos sampling sites in Sparkling Lake was selected for analysis because of its small within-year variability of crayfish trap rates and its proximity to adequate crayfish and invertebrate habitat (Fig. 1). Three samplers were set at 1 m depth, but not all samplers were recovered in all years. Zoobenthos samples were preserved in 95% ethanol and were later identified to family. Because of the passive nature of Hester-Dendy samplers, catch rates represent both the abundance of animals in the environment and their movement rates into and onto the sampler (Turner & Trexler, 1997). Because we do not distinguish these sources of variability, invertebrate abundance should be interpreted as a measure of relative abundance. Oligochaeta and Gastropoda abundances were excluded from the time series analysis because they were not accurately represented using this sampling protocol.

Bi-monthly measurements of water temperature and chlorophyll *a* data were averaged from each



**Fig. 1** (a) Sparkling Lake, Wisconsin, U.S.A. (46°00'N, 89°42'W) of the North Temperate Lakes – Long-Term Ecological Research programme and the site location (square) where rusty crayfish and benthic macroinvertebrates were sampled annually from 1981 to 2000. (b) Native (light grey) and non-native (dark grey) distributions of rusty crayfish in the United States (source: <http://nas.er.usgs.gov/>).

meter depth within the epilimnion and then across sampling dates in August and September of each year (NTL-LTER). Crayfish abundances were measured annually using three or five cylindrical traps baited with beef liver. Catch per unit effort (CPUE), a good indicator of relative abundance (Capelli, 1975; Olsen *et al.*, 1991), was calculated for rusty crayfish by dividing the total number of captured individuals by the total number of traps set. Littoral fish abundances were approximated from LTER fish sampling (conducted annually in August) using the sum of beach seine (3.2 mm mesh) CPUE and fyke net (7 mm mesh) CPUE from a site adjacent to the

invertebrate sampling site (NTL-LTER). Littoral fish species were categorised as those that consume crayfish (*Ambloplites rupestris*, *Micropterus dolomieu* and *M. salmoides*) and those that do not (Becker, 1983).

### Statistical analyses

Time series analysis was used to quantify temporal relationships between rusty crayfish abundance and zoobenthos abundance (for both families and orders). This analysis did not include the last 2 years of LTER sampling, 2003 and 2004, because a whole-lake experimental removal of rusty crayfish began in Sparkling Lake in mid-2001. Autocorrelation functions were calculated for each time series with lags up to 5 years (25% of the time series length), and statistically significant correlations were taken as evidence for serial interdependence within the time series (Chatfield, 1996). Serial autocorrelation (time lag of 1 year) was observed for rusty crayfish and eight invertebrate families and was subsequently removed using a first-differencing technique (autocorrelation functions were then calculated for the prewhitened time series to ensure that the degree of autocorrelation was minimal). Partial cross-correlation analysis was used to quantify lagged correlations between rusty crayfish and zoobenthos abundance after controlling for the effects of water temperature, chlorophyll *a* concentration (a surrogate of pelagic zone productivity), and the abundance of crayfish-consuming and other littoral-zone fishes. This analysis was restricted to time lags of  $k = \pm 1$  year to correct for the fact that repeated cross correlation computations between a pair of time series can increase the probability of erroneously identifying a significant time lagged relationship (see Olden & Neff, 2001). All data were  $\log_e$  transformed to meet the assumption of homoscedasticity and the analysis was conducted using SPSS (v.11).

## Results

### Meta-analysis of short-term crayfish effects

Seven species of crayfish spanning four continents were represented among the fourteen experimental studies included in this meta-analysis (Table 1). Total zoobenthos densities were significantly lower in

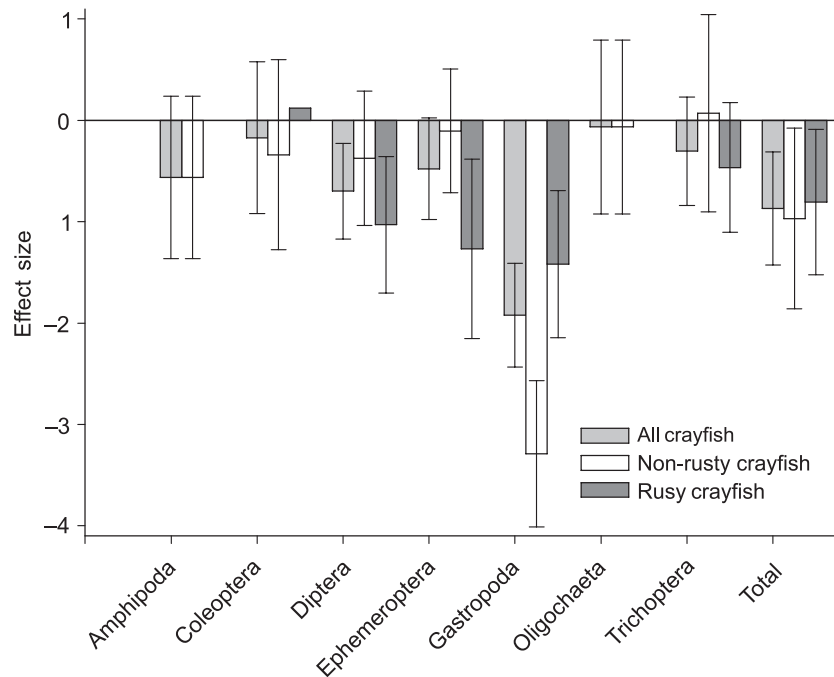
treatments containing crayfish relative to enclosures with a mean effect size of  $-0.8696$  ( $t = -3.05$ , d.f. = 6,  $P = 0.011$ ). The significant negative effect of crayfish on total invertebrate abundance appears to be driven by declines in abundance of a few taxonomic orders. Gastropoda and Diptera abundances were significantly lower in the presence of crayfish than in their absence (Fig. 2). Similarly, abundance of Amphipoda, Coleoptera, Ephemeroptera, Oligochaeta and Trichoptera were also reduced in crayfish treatments, although results for these taxa were not significant (note sample sizes in Fig. 2 caption). Comparisons across orders show that crayfish had the greatest negative impacts on the abundance of Gastropoda, followed by Diptera, Amphipoda and Ephemeroptera.

When comparing the effect size between rusty crayfish and non-rusty crayfish species we found that both had significant negative effects on total zoobenthos and Gastropoda, consistent with the results from all crayfish (Fig. 2). Rusty crayfish also significantly reduced Diptera and Ephemeroptera, but non-rusty crayfish effects on these taxa were not significant. A lack of significant results may be because of small sample sizes for certain taxa like Amphipoda ( $n = 1$  for rusty crayfish). Across-order comparisons show that rusty crayfish had the greatest negative impacts on the abundance of Gastropoda, followed by Ephemeroptera, Diptera and Trichoptera.

A comparison of impacts by non-native and native crayfishes showed that the effect size of non-native crayfish for total zoobenthos was statistically significant (effect size =  $-0.815$ ,  $SD = 0.113$ ,  $n = 5$ ), whereas the effect size of native crayfish was not (effect size =  $-1.008$ ,  $SD = 0.289$ ,  $n = 2$ ). Importantly, there was a weak relationship between order-level effect size and crayfish experimental density ( $R^2 = 0.112$ ,  $P = 0.04$ ) and study duration ( $R^2 = 0.067$ ,  $P = 0.12$ ), indicating that the meta-analysis results were not biased by experimental design.

### Long-term trends in Sparkling Lake

Zoobenthic taxa corresponded with rusty crayfish abundances over the 24 year time period (Fig. 3). Rusty crayfish catch rates were variable over the course of the study, with a general increase in relative abundance over the study period until the commencement of the removal experiment in 2001.



**Fig. 2** Results from the meta-analysis depicting crayfish effect sizes ( $\pm 95\%$  CI) for total invertebrate and individual order densities. Negative values indicate a negative effect of crayfish on invertebrate density. Confidence intervals that do not intercept zero are statistically significant based on  $\alpha = 0.05$ . Sample sizes ( $n$ ) for 'all crayfish' were as follows: Amphipoda (3), Coleoptera (3), Diptera (7), Ephemeroptera (7), Gastropoda (9), Oligochaeta (3), Trichoptera (5) and total (7).

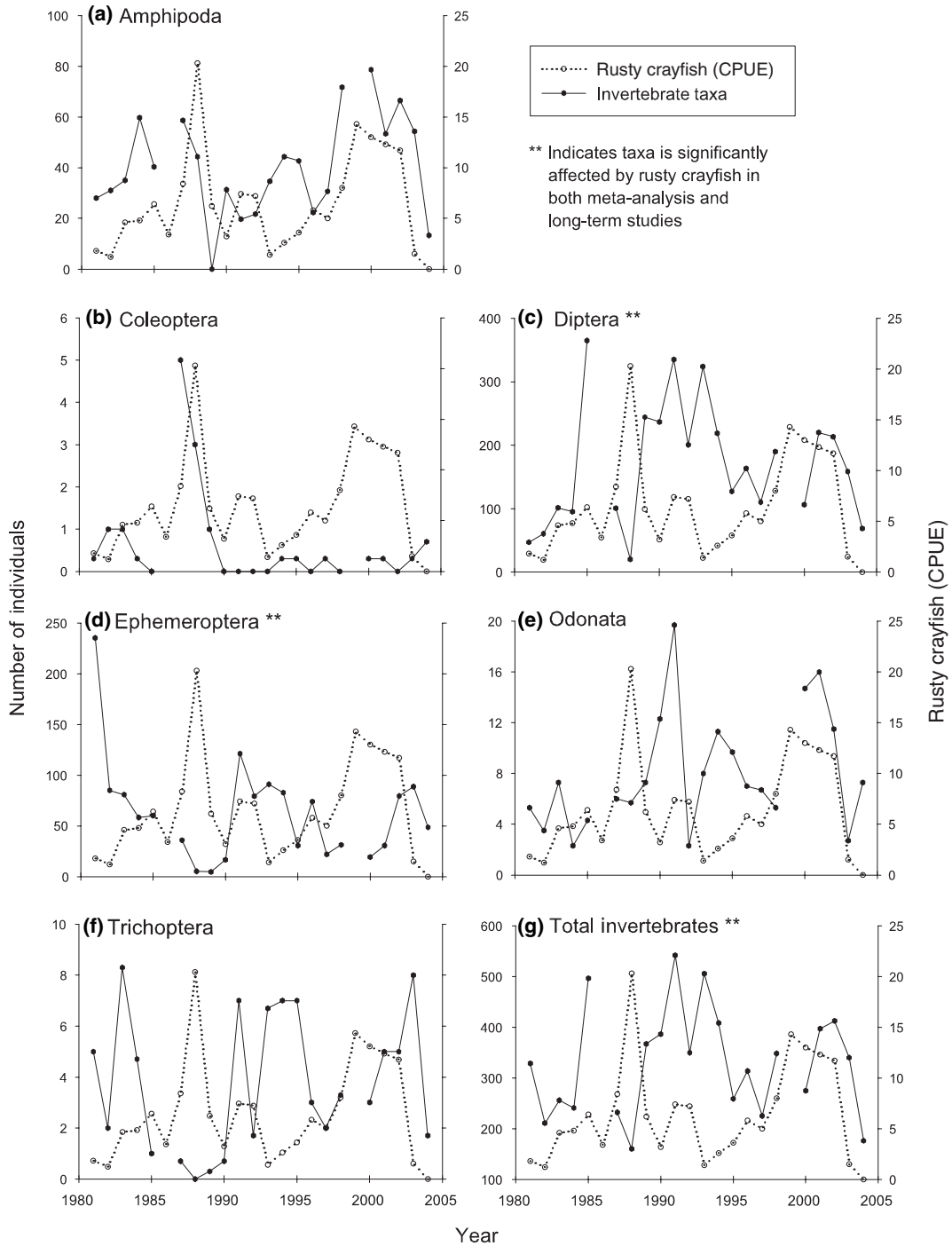
Time series analysis revealed 1-year time lagged relationships between three macroinvertebrate taxa and the covariables. These include Coleoptera/Elmidae with bass and Gomphidae with non-bass littoral fishes. Partial cross-correlation analysis indicated a significant negative relationship between rusty crayfish and total zoobenthos abundance, as well as the invertebrate orders Diptera, Ephemeroptera and Odonata (Fig. 4). Significant negative relationships at the family level included Chironimidae (Diptera), Ephemerellidae (Ephemeroptera), Coenagrionidae (Odonata) and Hydroptilidae (Trichoptera). All non-significant relationships with rusty crayfish were negative except for Amphipoda and Aeshnidae (Odonata). Taxa within the orders Diptera, Ephemeroptera and Trichoptera showed consistent negative relationships with rusty crayfish, whereas taxa relationships within Odonata were much more variable (Fig. 4).

## Discussion

Our study demonstrates that non-native crayfish have a significant, although variable impact on zoobenthic communities of freshwater systems. By using two very different approaches, long-term analysis of crayfish and zoobenthos trends from a single lake and meta-analysis of previous small-scale experimental studies,

we infer effects of crayfish on zoobenthic communities and demonstrate that similar trends are evident across broad scales of analysis. Although our results are derived from two different modes of inference, the negative effects of crayfish on specific components of the zoobenthic fauna were consistent between small- and large-scale approaches. These general patterns correspond with the whole-lake effects of rusty crayfish in Wilson *et al.* (2004). This study compared years with high and low crayfish abundances, and found significant negative effects at a whole-lake scale on Gastropoda, Odonata, Trichoptera and Amphipoda. Ephemeroptera and Diptera also significantly declined at specific sites in years with high abundance of rusty crayfish. The strong concordance of patterns between methodologies demonstrates the utility of using long-term data sets to provide context for the interpretation of meta-analysis results.

In natural ecosystems, the invasion of rusty crayfish is typically accompanied by rapid declines and extirpation of native crayfishes, as well as massive and sustained declines in snail populations (Capelli, 1982; Lodge *et al.*, 1985; Wilson *et al.*, 2004). In agreement with the meta-analysis results, we found that other invertebrate taxa also respond to changing rusty crayfish densities, yet demonstrate much greater resilience in the long-term. Nearly all invertebrate taxa were negatively affected by rusty crayfish within



**Fig. 3** Time series of total insect abundance (g) and order-level abundances (a–f) with respect to rusty crayfish catch per unit effort (CPUE) from 1981 to 2004 in Sparkling Lake. Reported value is the mean of three replicates.

a 1 year lag, but no taxa exhibited sustained declines over the course of the rusty crayfish invasion. Several factors may explain these patterns. Large-bodied invertebrate taxa such as snails and crayfish have

slower generation times and are not as productive as smaller taxa, and are thus less able to respond numerically following population reductions of crayfish. In addition, aquatic insect larvae have a winged

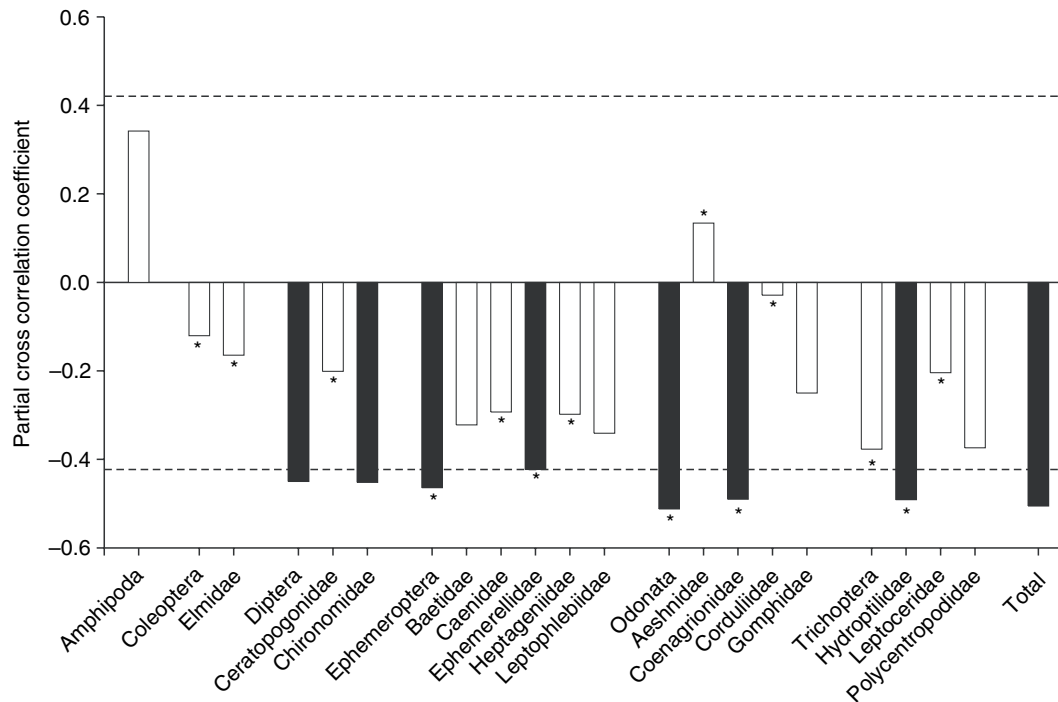


Fig. 4 Partial cross-correlation coefficients for the relationship between rusty crayfish abundance and macroinvertebrate abundance after controlling for the effects of water temperature, chlorophyll *a* concentration and the abundance of bass and other littoral-zone insectivores. Filled bars represent statistically significant relationships ( $P < 0.05$ ). Symbol '\*' represents a significant negative 1-year time lagged relationship. Dashed line represents the significance threshold for partial-cross correlation coefficient.

adult stage and as a consequence, great dispersal ability – thus facilitating quick recovery.

#### *Direct and indirect effects of crayfishes*

Crayfish are highly omnivorous, with a diet that includes zoobenthos, macrophytes, periphyton and detritus. These food web components can be directly affected by the feeding behaviours of crayfish and also indirectly influenced through habitat alteration or resource competition (Momot, 1995). With respect to the results of our study, both mechanisms likely play central roles in zoobenthos declines. Diptera and Ephemeroptera are common prey items of crayfish (Capelli, 1975; Lorman, 1975), and the slow movements and soft bodies of Diptera may make them especially vulnerable to predation (Whitledge & Rabeni, 1997). In addition, through consumption and destruction of macrophytes, crayfish can dramatically alter littoral habitats, leading to declines in macrophyte-associated invertebrate taxa (Olsen *et al.*, 1991; Nyström, Bronmark & Graneli, 1996). In Sparkling Lake, two zoobenthic taxa that commonly reside in

macrophytes, Coenagrionidae (Hilsenhoff, 1995) and Hydroptilidae (Wiggins, 1996), were negatively associated with rusty crayfish, suggesting macrophyte loss may be linked to their decline. Crayfish may also influence detrital substrates through bioturbation and feeding: for example, the crayfish *Paraneohrops zealandicus* greatly increased leaf decomposition rates, which has been linked to decreased detrital quality (Usio, 2000). Reduction in detritus has potential consequences for zoobenthic communities, particularly collector-gatherers and detritivores such as taxa in the orders Ephemeroptera, Trichoptera and Diptera.

Although our analysis only considers the direct impacts of rusty crayfish on zoobenthic taxa, the zoobenthic community itself is a network of predator-prey interactions. For example, crayfish predation upon other zoobenthic predators such as Odonata larvae could reduce their abundance, subsequently allowing an increase in abundance of *their* prey. Likewise, crayfish may compete with Odonata for prey resources. While it is important to consider the prospect of indirect food web effects, negative impacts of rusty crayfish on zoobenthos were ubiquitous



across the community, suggesting that these indirect food web effects are minor relative to the direct predation effects of rusty crayfish. However, because no specific mechanisms were analysed in this paper, the relative importance of direct and indirect effects remains unknown.

#### *Comparative effects of native versus non-native crayfish*

By comparing the ecological interactions of species in their native versus non-native range, we are likely to gain a better understanding of the varying success and impacts of invasive species. Unfortunately, few experimental studies have examined the impacts of crayfish in their native range or compared the relative impacts between native and invaded ecosystems. This lack of information precluded us from making a robust comparison, although our results do provide preliminary evidence that the effects of non-native crayfishes on zoobenthos may be greater than the effects of crayfishes in their native range. However, this comparison is limited because of a small sample size for native crayfishes. Evolutionary history plays an important role in this regard where invasive species may have greater impacts in systems without co-evolved prey. For example, the findings of Renai & Gherardi (2004) suggest that greater predatory efficiency of crayfishes in non-native environments may be a result of greater prey naivety.

Previous studies have shown that rusty crayfish have higher growth rates, achieve higher densities, are less vulnerable to predators than their native congeners and outcompete natives for food and shelter (Lodge *et al.*, 1985; Hill, Sinars & Lodge, 1993). However, little is known of their comparative ecological impacts in their native and non-native ranges. The results from such studies would provide further evidence for our observation that non-native crayfish have greater ecological effects on the benthic community than native crayfishes.

#### *Advantages of multi-scale studies*

Species invasions are dynamic processes and thus the scope of invasive species impacts may be difficult to assess (Parker *et al.*, 1999). Coupling the results of analyses at multiple scales to address these issues may help to gain greater insights, although each method is not without its own biases. Meta-analysis is a power-

ful tool for synthesising the results of previous research and allows rigorous statistical comparison of past findings, especially with respect to biological invasions (e.g. Levine, Adler & Yelenik, 2004). Although this statistical approach is effective for synthesis of previous work, the small-scale studies themselves may suffer from experimental artefacts, 'cage-effects' or other problems. In addition, such experiments characterise short-term ecological responses, not the long-term dynamics likely to be manifested over several prey generations.

In contrast, long-term studies can provide important insight into the threats of an invasion and the potential adaptability of the native taxa to the new invader, but may also be confounded by environmental factors that cannot be controlled (Parker *et al.*, 1999). We accounted for this potential bias by factoring out the influence of primary productivity and fish predation before assessing the relationship between rusty crayfish and zoobenthos. Because the disadvantage of one approach is the advantage of another, coupling multiple scales of analyses reveals a method in which interactions at one scale can be translated to another.

Together, short and long-term studies aid in the overall understanding of community relationships. The short-term studies included in the meta-analysis were able to quantify the immediate effects of crayfish on the benthic community, while the long-term experiment offered the capacity to examine dynamic temporal relationships, including the prolonged effects of an aquatic invader. Thus, the pairing of short and long-term results offers a greater understanding of the broader implications and trends in crayfish-invertebrate interactions.

#### *Management implications*

Understanding invader impacts on aquatic ecosystems is an important first step towards the ultimate goal of developing effective approaches for conserving native biodiversity (Vitousek *et al.*, 1996). Our results indicate that potential impacts of non-native crayfish on zoobenthos, an important component of lentic and lotic ecosystems, are evident at multiple scales of analysis and are of great concern, particularly in light of the growing number of non-native crayfishes worldwide (Hobbs *et al.*, 1989).

With regards to our long-term analysis, it is notable that efforts are currently underway to experimentally

reduce rusty crayfish populations in Sparkling Lake with the goal of eliminating this invader. A two-tiered approach was initiated in late summer of 2001 and has continued through summer of 2005 to remove rusty crayfish by intensively trapping and reducing angling bag limits to promote fish predation (Hein, in press). While the prospect for total eradication of rusty crayfish from Sparkling Lake remains unknown, the sharp decline in crayfish CPUE from 2002 to 2004 (Fig. 3) is a direct consequence of these efforts. In response, a number of macrophyte species have increased in abundance (C.L. Hein, personal observation), and patterns of recovery of the zoobenthic community will be examined in the coming years. Our long-term zoobenthos and crayfish data sets provide a valuable backdrop from which to describe not only the ecological impacts of a potent non-native crayfish, but also the reversibility of their impacts on aquatic ecosystems. Indeed, understanding how the control of exotic species influences food web recovery is an emerging research need in restoration ecology (D'Antonio & Meyerson, 2002). The persistence of most zoobenthic taxa in Sparkling Lake in the face of rusty crayfish invasion, albeit at low abundances for some taxa, indicates a high degree of biotic resilience and a high degree of restoration potential.

### Acknowledgments

We are most grateful to two anonymous reviewers for valuable comments, Pieter Johnson and Jim Rusak for providing valuable assistance with invertebrate identification, NTL-LTER for sample collection, P.M. Charlebois, S.M. Parkyn, R.S. Stelzner and N. Usio for providing data from their manuscripts for use in our meta-analysis, Jeff Maxted for assistance with Fig. 1 and the entire Vander Zanden lab for comments on an early version of the manuscript. Funding was provided by North Temperate Lakes Long-Term Ecological Research (NTL-LTER), Wisconsin Department of Natural Resources, a Chase Noland Award for Research in Limnology (JMM) and The Nature Conservancy David H. Smith Postdoctoral Fellowship Programme (JDO).

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(Manuscript accepted 8 October 2005)