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Comparing the effects of introduced signal crayfish and native noble crayfish on the littoral invertebrate assemblages of boreal lakes

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Abstract: The introduced North American signal crayfish *Pacifastacus leniusculus* (Dana) has replaced the native noble crayfish (*Astacus astacus*) in many European freshwaters and can be considered a new component of these ecosystems. The 2 species are apparently similar in many respects, but their ecological equivalence is uncertain and has been little investigated, especially at the whole-lake scale. We compared the effects of the 2 species on the abundance, species richness, and composition of littoral macroinvertebrate assemblages in a set of small- and medium-sized boreal lakes, which included 8 lakes with noble crayfish, 8 lakes with signal crayfish, and 8 lakes without crayfish. We collected semiquantitative littoral macroinvertebrate samples with a kick net from 3 replicate sites in each lake. The abundance of invertebrates did not differ significantly among the 3 lake categories, but lakes with crayfish had lower species richness than lakes without crayfish. Mollusk taxa, in particular, were fewer in lakes with crayfish. Assemblage composition also differed between lakes with and without crayfish. However, macroinvertebrate species richness and composition did not differ between lakes with signal or noble crayfish, indicating that the 2 crayfish species are ecologically equivalent with respect to their effects on shallow, littoral invertebrate assemblages of boreal lakes.

Key words: signal crayfish, noble crayfish, invasive species, native species, impacts, benthic communities, boreal lakes

Freshwater ecosystems worldwide are among the habitats particularly affected by introductions of invasive exotic species, which represent a serious threat to their biodiversity (Dudgeon et al. 2006, Strayer and Dudgeon 2010, Jackson and Grey 2012). Freshwater crayfish have been widely translocated from their native ranges to new habitats all over the world (Holdich et al. 2009, Gherardi 2010). Because they are omnivorous and capable of interacting across multiple trophic levels (Lodge et al. 1994, Geiger et al. 2005), crayfish can be considered particularly influential in foodweb structure (Nyström 2002, Stenroth and Nyström 2003, Reynolds and Souty-Grosset 2012b) and as ecosystem engineers that exert a strong effect on native biota (Nyström et al. 1999, Wilson et al. 2004, McCarthy et al. 2006).

Many investigators have reported that nonnative crayfish can strongly affect littoral macroinvertebrate assemblages, especially snails (Nyström and Perez 1998, Nyström et al. 2001, Correia 2002, Wilson et al. 2004, McCarthy et al. 2006, Gherardi 2007, Ruokonen et al. 2014), reducing abundance and species richness directly by predation

(Nyström et al. 2001, Wilson et al. 2004, McCarthy et al. 2006, Ruokonen et al. 2014) or indirectly via more complex interactions through habitat alteration (Nyström et al. 1999), bioturbation, and consumption of detritus (Usio 2000).

Authors of global meta-analyses (McCarthy et al. 2006, Twardochleb et al. 2013) have found that nonnative crayfish tend to have stronger negative effects than native crayfish on benthic invertebrates and especially snails. However, studies specifically contrasting ecological effects between invasive and native crayfish are few and do not provide conclusive support for differences in ecological roles between them (McCarthy et al. 2006, Twardochleb et al. 2013). In general, studies of the effects of nonnative crayfish species have mainly been small-scale experiments or single crayfish species investigations, reporting effects on specific taxa or ecosystem processes (Lodge et al. 2000, Geiger et al. 2005, Crawford et al. 2006, Gherardi and Acquistapace 2007, Ruokonen et al. 2014). Moreover, only small-scale studies based on experimental manipulations were included in the meta-analyses by McCarthy et al. (2006) and Twar-

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dochleb et al. (2013). A more comprehensive understanding of the effects of invasive crayfish requires complementary research done at different spatial scales (McCarthy et al. 2006, Rosenthal et al. 2006, Hansen et al. 2013). Lodge et al. (1998) found consistent results among a laboratory experiment, small field-cage experiment, and a lake survey. Even though their study suggested that small-scale experiments can provide information relevant to management of invasive crayfish, results of studies done at different spatial scales often are not consistent (Schindler 1998). Hence, in general, direct comparisons of the effects of invasive and native crayfish species and, in particular, studies done in natural conditions at the whole-lake scale are needed. In the absence of comparative studies done at a realistic scale, whether invasive and native crayfish have equivalent roles in and effects on lake ecosystems will remain unclear. However, this information is important for assessing risk associated with invasive species (Leung et al. 2012) and for detecting the effects of native crayfish on littoral assemblages in their natural range. It also is essential to understand the potential ecological effects of native species when transferred to new ecosystems, e.g., the potential threat posed to other protected or endangered native species (Olden et al. 2010).

The signal crayfish, *Pacifastacus leniusculus* Dana, has been introduced repeatedly from the Pacific Northwest of North America to Europe, including Finland, since ~1960. Introductions often were deliberate attempts to replace populations of native noble crayfish, *Astacus astacus*, lost during the outbreak of crayfish plague (*Aphanomyces astacii*) (Söderbäck 1995, Holdich et al. 2009). In Finland, signal and noble crayfish often are regarded as being ecologically equivalent (Kirjavainen and Sipponen 2004), even though the results of some earlier (e.g., Nyström et al. 1999) and quite recent (Dunoyer et al. 2014) manipulative studies have suggested that the invasive signal crayfish can have greater

impacts than native noble crayfish on littoral assemblages and ecosystem processes.

We investigated the effects of nonnative signal crayfish and native noble crayfish on benthic macroinvertebrate assemblages under natural conditions at a replicated whole-lake scale in a set of small- and medium-sized boreal lakes. Our main aims were to: 1) investigate the effects of crayfish on littoral macroinvertebrate assemblages, and 2) examine whether the effects of invasive signal and native noble crayfish are equivalent in such lakes. We used 8 replicate lakes in each of 3 categories (with signal crayfish, with noble crayfish, and without crayfish), so our findings should be more robust than, and an important supplement to, those reported from small-scale and short-term experimental manipulations.

METHODS

Study lakes

We identified potential study lakes on the basis of the crayfish introduction register maintained by the Finnish Game and Fisheries Research Institute. We made the final selection of study lakes on the basis of similar abiotic features (Tables 1, S1) and the crayfish species present. We selected 8 lakes with signal crayfish, 8 with noble crayfish, and 8 lakes without crayfish (controls), from south-central Finland (Fig. 1). We had originally planned to include lakes with both crayfish species, but we were unable to find lakes in which the 2 species coexist. Signal and noble crayfish lakes fell into 2 more-or-less distinct regional groups (Fig. 1) that reflected the current distributions of the 2 species in the area, but control lakes were chosen to cover the whole study lake area and, thus, countered any possible geographical differentiation in response variables between lakes with and without crayfish.

The signal crayfish was introduced into the study lakes in the 1990s and is now well established. We assumed that

Table 1. Means and ranges of environmental characteristics for the 3 lake categories, with results of analysis of variance (ANOVA) testing for differences across lake categories.

Biotic and abiotic variables	Signal crayfish lakes		Noble crayfish lakes		Control lakes		ANOVA		
	Mean	Range	Mean	Range	Mean	Range	<i>p</i> -value	<i>F</i> -value	df
Lake size (km ²)	1.34	0.11–4	2.42	0.65–5.72	2.25	0.13–5.51	0.44	0.84	21
Slope (°)	12.42	5.52–21.5	8.27	2.76–15.3	9.45	2.54–18.87	0.23	1.54	21
Shoreline development factor	4.65	2.0–16.0	3.84	2.0–6.0	2.44	0.64–4.16	0.53	2.02	21
Stone size	6.32	5.42–7.61	6.29	5.84–6.82	6.59	5.83–7.19	0.54	0.62	21
Shoreline (km)	17	1–79	16	5–37	17	2–39	0.66	0.41	21
Maximum depth (m)	13.17	4.5–26.59	15.4	2.16–30	12.26	6.26–20	0.66	0.42	21
pH	6.49	5.4–7.1	6.8	6.3–7.2	6.8	6.5–7.5	0.31	1.22	21
P(μg/L)	16	8.0–24.0	21.42	4.0–89.0	9.49	5.0–16.91	0.21	1.65	21
Color (mg Pt/L)	56.77	21.0–160.0	43.99	10.0–115.0	33.58	20.0–61.0	0.54	0.61	21

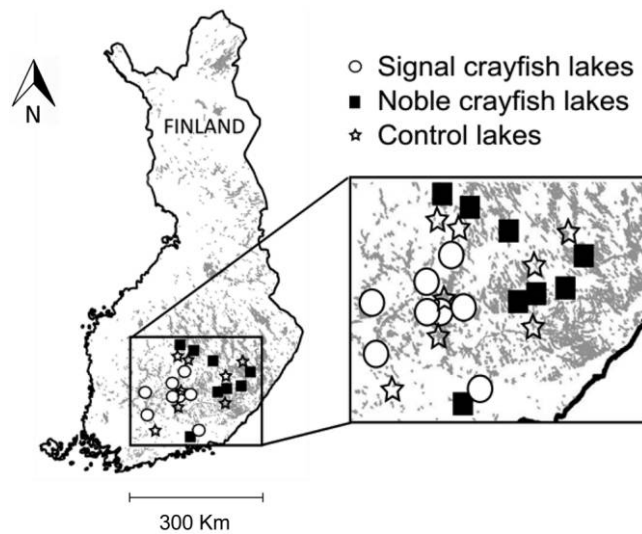


Figure 1. Map showing the locations of the 8 lakes in each category in south-central Finland.

noble crayfish populations have occupied their lakes for much longer (Järvi 1910), but the picture is confused because in Finland the noble crayfish has been extensively stocked in lakes in its historic range that lacked crayfish and in lakes well beyond its natural range. Quantitative data on crayfish abundance were not available for all lakes and not for the study years, but previously collected catch per unit effort (CPUE) data suggest that the 2 crayfish species had similar abundances in our studied lakes (Table S1). All lakes containing crayfish had a harvestable population during the study years, and qualitative samples of crayfish were caught for other purposes (Ercoli et al. 2014).

Lake environmental characteristics

Environmental features and habitat type greatly affect littoral macroinvertebrate assemblage composition, and effects of the crayfish species on the invertebrate assemblages could be masked by differences in environmental features among lake categories. Therefore, we selected lakes that were as similar as possible in their key environmental characteristics. We obtained water-quality (pH, color, and P concentration at 1 m depth) and lake morphometry (lake area, shoreline length) data for each lake from the HERTTA database (<http://www.p2.ymparisto.fi/scripts/hearts/welcome.asp>) maintained by the Finnish Environment Institute. Values of water-quality variables were calculated as means of annual measurements registered during the previous 10 y for each lake.

We sampled macroinvertebrates from 3 replicate sampling sites at 0.5 m depth in each lake (see below). For each replicate, we visually estimated the % cover of each mineral particle size (modified Wentworth's scale; Allan 1995) within a 0.25-m² quadrat. We calculated the mean percentage-weighted particle size per replicate, used those values to

calculate a site mean, and used the site means to calculate the mean for each lake.

We estimated the shore slope at each of the 3 replicate sampling sites by measuring the perpendicular distance from the shoreline at 0.5, 1.0, 2.0, 3.0, and 4.0 to 5.0 m of water depth with a laser distance measurer (400LH; Opti-Logic Corp., Tullahoma, Tennessee). We calculated the mean slope of each site, expressed as the angle between the bottom and the water surface, from the 5 distance measures and used the values from the 3 sites to calculate a mean slope value for the lake.

Lakes with the same surface area but increasing shore length will have a larger littoral area, which will influence habitat characteristics and assemblage composition (Kalf 2003). Thus, macroinvertebrate assemblage structure and crayfish feeding might be affected by lake shape. We estimated the degree of lake shoreline irregularity as the shoreline development factor (Sdf) calculated as:

$$\text{Sdf} = \frac{L}{2\sqrt{A\pi}} \quad (\text{Eq. 1})$$

where L is the shoreline length (km) and A is the area of the lake (km²) (Wetzel 2001).

Macroinvertebrate sampling

We collected macroinvertebrate samples in August 2010 or 2011. We sampled at 3 replicate sites chosen at each lake from open stony shore areas at 0.5 to 1 m depth. We selected stony shores because they are the preferred habitat for and, therefore, could be most strongly affected by the 2 crayfish species (Ruokonen et al. 2014). At each site we moved along a 1-m stretch of bottom (parallel to the shoreline) for 30 s while kicking the substrate and capturing the detached and suspended material by sweeping with a kick net (Johnson and Goedkoop 2002), after which samples were immediately preserved in 70% ethanol. In the laboratory, samples were sorted, identified to the lowest feasible taxonomic level (mostly to species or genus), and counted.

Statistical analysis

We tested for differences in each environmental variable among lake categories with 1-way analysis of variance (ANOVA) to evaluate if the 3 groups of lakes represented comparable samples from the same parent lake population.

We calculated mean macroinvertebrate abundance for each lake from the mean number of animals/sample and taxon richness as the total number of taxa sampled from each lake. We also calculated the Shannon diversity index (McCune and Grace 2002) to quantify species diversity among the 3 lake categories by taking into account both the richness and the relative abundance of macroinvertebrate taxa. We then tested abundance and diversity

metrics for differences among the 3 lake categories with 1-way ANOVA and Tukey's Honestly Significant Difference (HSD) post hoc pairwise comparisons. We also compared abundance and richness separately for the main taxonomic groups. The normality assumption was violated for some groups, so we used nonparametric Kruskal–Wallis tests and pairwise Bonferroni-corrected Mann–Whitney *U*-tests for this analysis.

We used multivariate analyses to compare assemblage composition among lake categories. We grouped macroinvertebrates into higher taxa: Gastropoda, Bivalvia (*Sphaeriidae*), Oligochaeta, Hirudinea, Isopoda (*Asellus aquaticus*), Ephemeroptera, Odonata, Plecoptera, Neuroptera (Sisyridae), Megaloptera (Sialidae), Heteroptera (Corixidae), Coleoptera, Chironomidae, Ceratopogonidae, and Trichoptera. We used this low taxonomic resolution because most lower-level taxa (species and genera) were rare and, therefore, higher taxonomic resolution resulted in greater assemblage variation within and less differentiation among lake categories. We used nonmetric multidimensional scaling (NMDS) ordination on transformed ($\log[\text{mean count} + 1]$) abundance data and the Bray–Curtis distance measure to visually explore whether invertebrate assemblages differed systematically among lake categories. We used the same data to test for differences in assemblages among lake categories with Multi-Response Permutation Procedures (MRPP). Statistical analyses were performed in R (version 2.15.2; R Project for Statistical Computing, Vienna, Austria). For the NMDS we used *metaMDS* and *ordiellipse* functions, which are part of the package *vegan* (Oksanen 2013).

RESULTS

The measured environmental characteristics did not differ among the 3 lake categories (Table 1), indicating that our lakes represented 3 different crayfish treatments but otherwise had equivalent characteristics.

Total invertebrate abundance did not differ significantly among lake categories ($F = 0.341$, $df = 2$, $p = 0.71$; Fig. 2A), but total taxon richness did ($F = 6.723$, $df = 2$, $p = 0.005$; Fig. 2B). Signal ($p = 0.03$) and noble ($p = 0.004$) crayfish lakes had significantly fewer taxa than control lakes, but taxon richness did not differ between signal and noble crayfish lakes ($p = 0.65$) (Fig. 2B). The Shannon diversity index differed among lake categories ($F = 10.18$, $df = 2$, $p = 0.0008$; Fig. 2C). Signal ($p = 0.005$) and noble ($p = 0.001$) crayfish lakes had lower Shannon diversity than control lakes, but Shannon diversity did not differ between signal and noble crayfish lakes ($p = 0.79$).

Most macroinvertebrate taxonomic groups showed comparable abundance and taxon richness among lake categories, but certain groups showed marked and significant differences (Table 2). Gastropoda abundance differed among lake categories (Kruskal–Wallis $\chi^2 = 7.43$, $df = 2$, $p = 0.02$; Fig. 3, Table 2), but post hoc comparisons did not reveal

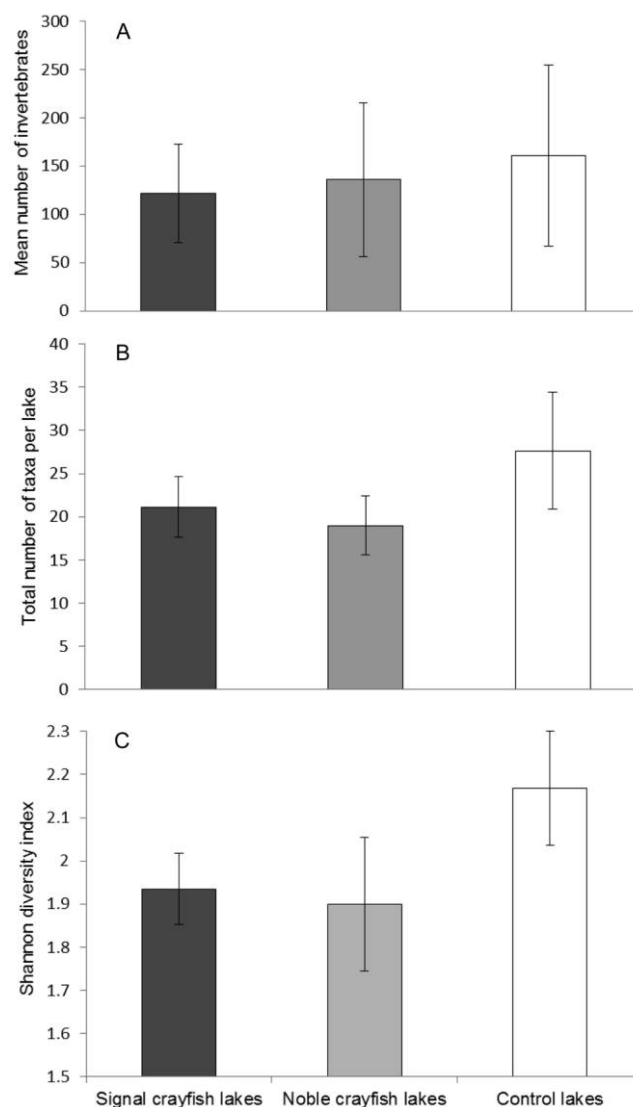


Figure 2. Mean (± 1 SD) abundance (A), taxon richness (B), and Shannon diversity (C) of all macroinvertebrates for signal crayfish, noble crayfish, and control lakes.

differences between signal crayfish and control lakes ($p = 0.07$), noble crayfish and control lakes ($p = 0.12$), or signal and noble crayfish lakes ($p = 1.00$). Gastropoda taxon richness differed among lake categories ($\chi^2 = 8.27$, $df = 2$, $p = 0.01$; Fig. 4, Table 2), with significantly fewer snail taxa in signal crayfish than in control lakes ($p = 0.03$), but no difference between noble crayfish and control ($p = 0.15$), or between signal and noble crayfish lakes ($p = 0.88$).

Bivalvia (all were pea clams, *Sphaeriidae*) and Odonata abundances differed among lake categories (Table 2), mainly between noble crayfish and control lakes ($p = 0.008$, $p = 0.01$, respectively; Fig. 3). Odonata taxon richness did not differ among lake categories (Fig. 4, Table 2), whereas Bivalvia taxon richness was significantly lower in signal and noble crayfish lakes than in control lakes (noble vs

Table 2. Mean and standard deviation (SD) for the abundance and species richness of the main taxonomic groups among lake categories. Kruskal–Wallis test was used to test for differences among lake categories. Bold indicates significant results.

Taxon	Signal crayfish lakes		Noble crayfish lakes		Control lakes		Kruskal–Wallis test		
	Mean	SD	Mean	SD	Mean	SD	χ^2	df	<i>p</i> -value
Abundance									
Gastropoda	0.33	0.94	0.15	0.21	5.67	12.33	7.43	2	0.02
Bivalvia	0.31	0.50	0.04	0.11	5.35	4.89	11.50	2	0.003
Oligochaeta	20.19	19.91	10.08	5.93	13.77	4.39	1.32	2	0.51
<i>Asellus aquaticus</i>	16.44	15.97	6.08	5.84	18.48	29.22	1.23	2	0.53
Ephemeroptera	32.46	25.06	61.48	56.89	41.00	39.96	0.45	2	0.79
Odonata	0.67	1.10	0.23	0.27	1.56	1.26	8.91	2	0.01
Coleoptera	7.42	7.39	1.83	2.69	7.50	8.74	2.96	2	0.22
Chironomidae	32.02	9.49	42.98	21.22	38.88	36.88	0.86	2	0.64
Trichoptera	14.42	8.81	9.35	8.69	15.13	10.04	3.18	2	0.20
Species richness									
Gastropoda	0.13	0.35	0.38	0.52	1.38	1.06	8.27	2	0.01
Bivalvia	0.38	0.52	0.13	0.35	1.38	0.74	11.24	2	0.003
Ephemeroptera	4.00	1.31	4.25	1.39	4.63	1.30	0.67	2	0.71
Odonata	0.63	0.74	0.63	0.74	1.25	0.46	4.6	2	0.10
Coleoptera	0.75	1.16	0.13	0.35	1.63	1.92	3.53	2	0.17
Trichoptera	8.00	2.33	6.88	2.59	7.88	2.53	1.36	2	0.50

control lakes: $p = 0.01$, signal vs control lakes: $p = 0.04$; Fig. 4, Table 2). Neither abundance nor taxon richness of Oligochaeta, Isopoda (*Asellus aquaticus*), Ephemeroptera, Coleoptera, Chironomidae, and Trichoptera differed among lake categories (Figs 3, 4, Table 2).

Nonmetric multidimensional scaling (NMDS) ordination suggested a 3-dimensional solution (final stress = 0.15) for the best representation of the lake categories grouped on the basis of their macroinvertebrate assemblages (Fig. 5A–C). Signal and noble crayfish lakes overlapped each other and were clearly separated from the control lakes in the plots of axis 1 vs 2 and axis 1 vs 3 (Fig. 5A, B), indicating a similar macroinvertebrate composition in the 2 crayfish lake categories and differing composition in the control lakes. NMDS axes 2 and 3 did not strongly differentiate among lake categories (Fig. 5C). MRPP showed significant differences in assemblage composition between signal crayfish and control lakes ($A = 0.06$, $p = 0.04$) and between noble crayfish and control lakes ($A = 0.09$, $p = 0.009$), but not between signal and noble crayfish lakes ($A = 0.02$, $p = 0.15$). A permutation test did not reveal any significant correlations between environmental variables and NMDS ordination axes.

DISCUSSION

Many studies have been done on the effects of one or more nonnative crayfish on freshwater littoral assemblages at different spatial scales. However, very few investigators

have compared the ecological effects of native and invasive crayfish species in the same region. We addressed long-term effects of signal and noble crayfish on macroinvertebrate assemblages at a whole-lake scale in small- and medium-sized Finnish boreal lakes. We think our study is the most comprehensive comparison to date of the effects of nonnative signal and native noble crayfish in boreal lakes.

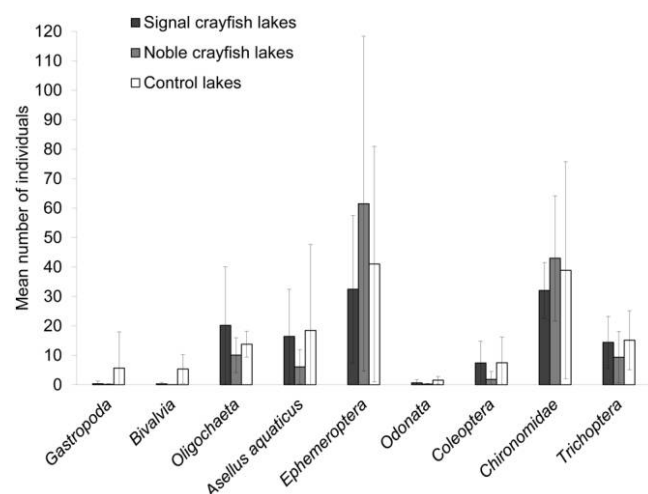


Figure 3. Mean (± 1 SD) abundance of different invertebrate taxonomic groups in signal crayfish, noble crayfish, and control lakes.

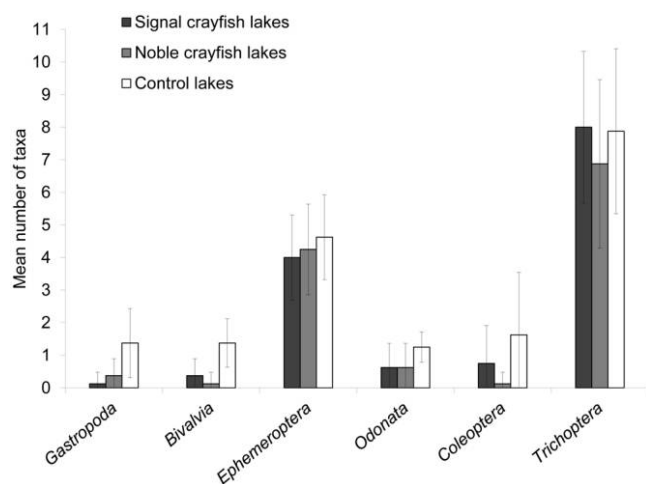


Figure 4. Mean (± 1 SD) taxon richness of different invertebrate taxonomic groups for signal crayfish, noble crayfish, and control lakes.

Overall macroinvertebrate abundance did not appear to differ between crayfish and control lakes. This result is consistent with a study by Ruokonen et al. (2014) who found that macroinvertebrate density was not reduced by invasive signal crayfish in large boreal lakes. However, our results differ from those reported by Nilsson et al. (2012) who found that macroinvertebrate abundance was negatively affected by invasive rusty crayfish (*Orconectes rusticus*) in 10 Wisconsin lakes. This discrepancy might be accounted for by the generally low abundance of crayfish in boreal lakes (CPUE typically $\ll 10$ individuals; Erkamo et al. 2010, Ruokonen et al. 2014, Sandström et al. 2014), including our study lakes (Table S1), compared to the large catches of *O. rusticus* typically reported from North American lakes (Kreps et al. 2012, Nilsson et al. 2012). Signal crayfish were introduced into our study lakes almost 20 y ago, and presumably, noble crayfish have occupied their lakes for a very long time. Thus, populations probably have reached an equilibrium in each lake (Sandström et al. 2014). Hence, crayfish in these lakes do not have an important effect on macroinvertebrate abundance, although lakes with unusually high crayfish densities might be an exception.

However, lakes in both crayfish categories had significantly lower macroinvertebrate taxon richness relative to control lakes, and the Shannon index clearly showed higher diversity in control than in signal or noble crayfish lakes. Many investigators have reported similar results for lakes (Nilsson et al. 2012, Ruokonen et al. 2014) and streams (Stenroth and Nyström 2003, Crawford et al. 2006, Moorhouse et al. 2014). However, taxon richness and taxonomic composition did not differ between signal crayfish and noble crayfish lakes, a result suggesting that the 2 species have an equivalent role as consumers in these lakes. Signal and noble crayfish exploit the same food resources (Nyström and Strand 1996, Nyström et al. 1999) and

have similar trophic niches (Olsson et al. 2009, Ercoli et al. 2014). Signal crayfish consumed more food than noble crayfish, but these results were from short-term experiments in small artificial settings (Nyström 2005, Dunoyer et al.

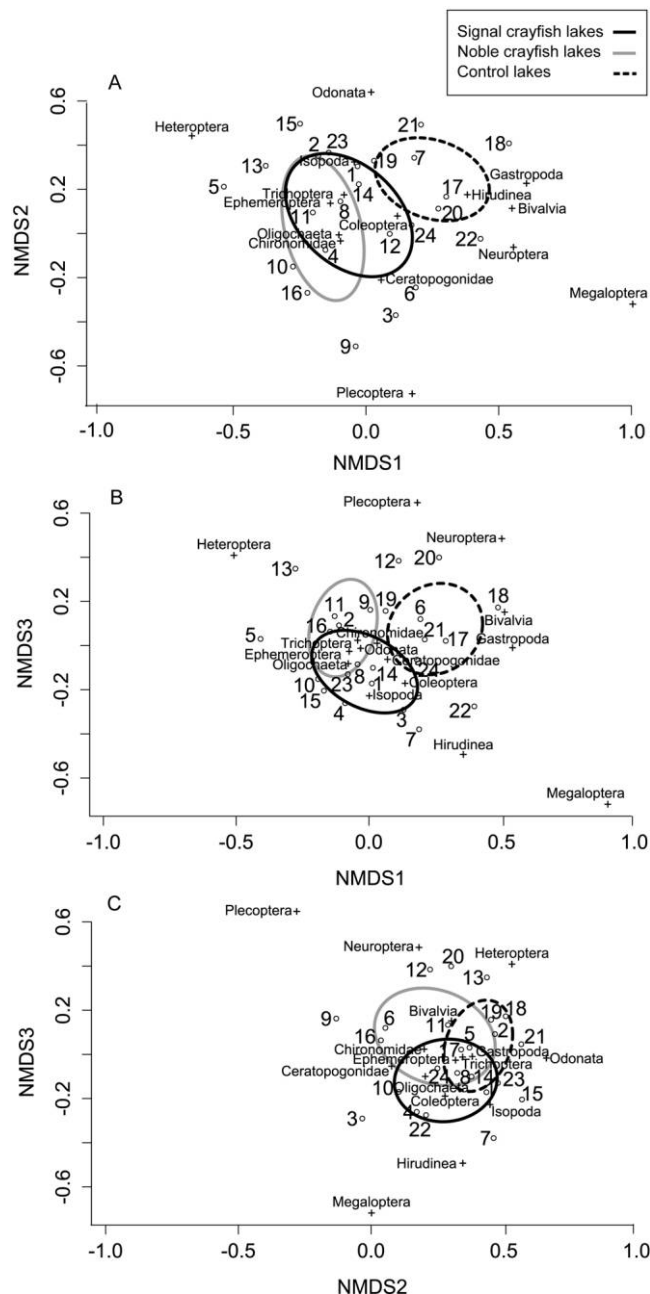


Figure 5. Nonmetric multidimensional scaling (NMDS) ordination plots of the study lakes in 3 dimensions: axis 1 vs 2 (A), axis 1 vs 3 (B), and axis 2 vs 3 (C). Ellipses indicate signal crayfish, noble crayfish, and control lakes with 95% of standard deviations of their weighted averages built on the basis of different macroinvertebrate assemblages. Circles indicate lakes (1–8: signal crayfish lakes, 9–16: noble crayfish lakes, 17–24: control lakes), and crosses represent macroinvertebrate groups. Lakes are numbered according to their order in Table S1.

2014). Thus, our conclusions with regard to the similar effects of the 2 species of crayfish on macroinvertebrate assemblages are broadly in line with previous studies and provide no clear evidence that the signal crayfish is a more active predator than the noble crayfish.

Nyström et al. (1999) argued that prey activity would be an important influence on crayfish consumption. Mollusks are slow moving and probably are the taxa most vulnerable to predation by crayfish, which can greatly reduce mollusk population size and species richness (Lodge et al. 1994, Dorn and Wojdak 2004, Klose and Cooper 2012, Ruokonen et al. 2014). We found significantly lower abundance of Sphaeriidae and a tendency for lower abundance of Gastropoda in crayfish lakes than in control lakes. Furthermore, Gastropoda species richness differed between signal crayfish and control lakes but not between noble crayfish and control lakes, a result that might be explained by more selective feeding by signal crayfish. A meta-analysis by Twardochleb et al. (2013) showed consistently negative effects of crayfish on Gastropoda abundance and suggested a tendency for effects of nonnative species to be stronger than that of native species. However, the abundance and species richness of Sphaeriidae and Gastropoda did not differ between signal and noble crayfish lakes, and recent direct experimental comparisons indicate that effects can be either similar or different between species independent of species origin (Nyström et al. 1999, Olden et al. 2009, Haddaway et al. 2012, Dorn 2013, Jackson et al. 2014). Limited data are available on effects of crayfish on small Bivalvia in general (e.g., they were not included in the meta-analysis by Twardochleb et al. 2013), but Klockner and Strayer (2004) found that the invasive species *Orconectes rusticus* and the native crayfish *Orconectes limosus* both fed readily and to the same extent on native bivalves (Sphaeriidae) in a laboratory experiment.

The effects of crayfish on the abundance of macroinvertebrate groups other than snails tend to be weak and variable (McCarthy et al. 2006, Twardochleb et al. 2013). Larger, more mobile invertebrates generally are less susceptible than smaller, less mobile invertebrates to crayfish predation (e.g., Hanson et al. 1990), but burrowing taxa may be concealed and less susceptible to predation by crayfish. Nyström et al. (1999) suggested that sediment-dwelling, infaunal taxa can become dominant in the presence of crayfish. However, the abundance and taxon richness of most groups, including mobile taxa like Ephemeroptera and Coleoptera, less mobile taxa like Trichoptera or Isopoda (*Asellus aquaticus*), and burrowing taxa like Chironomidae and Oligochaeta, did not differ among lake categories. Odonata was the only group apart from Mollusca that was significantly less abundant in crayfish lakes (particularly noble crayfish) than in control lakes. However, crayfish did not affect Odonata taxon richness. Ruokonen

et al. (2014) reported similar findings from larger boreal lakes, but in general, responses of Odonata to crayfish have been variable (McCarthy et al. 2006, Twardochleb et al. 2013). Odonata are mostly sit-and-wait or stalking predators, and their large body size may make them particularly attractive prey for crayfish.

Recent meta-analyses have suggested that nonnative consumers generally have greater effects than native consumers (Paolucci et al. 2013), and that nonnative crayfish potentially have stronger effects than native crayfish on native assemblages (McCarthy et al. 2006, Twardochleb et al. 2013). Ercoli et al. (2014) used a stable-isotope approach to show that signal and noble crayfish in our study lakes had very similar diets and similar within-lake trophic niche widths. They did find some evidence that, across the whole set of lakes, signal crayfish had a somewhat broader trophic niche than noble crayfish. Similar results were obtained in a study of Swedish streams (Olsson et al. 2009). In our study, the similar trophic characteristics of the 2 crayfish species were manifested as equivalent effects on littoral macroinvertebrate abundance and assemblage structure among crayfish lakes. However, different crayfish species can have different effects on macroinvertebrate abundance (e.g., Haddaway et al. 2012, Dunoyer et al. 2014, Jackson et al. 2014), so our results, which pertain to one pair of invasive and native species, should not be generalized.

We showed that signal and noble crayfish have similar effects on littoral macroinvertebrate assemblages in boreal lakes. Nevertheless, we urge caution when considering the introduction of signal crayfish to lakes like those in our study because the 2 species can differ in their effects on other ecosystem components, e.g., leaf-litter decomposition (Dunoyer et al. 2014, Jackson et al. 2014), macrophytes (Hansen et al. 2013), fine sediment dynamics (Harvey et al. 2014), or macroinvertebrates in other habitats than stony littoral zones. Influence of crayfish on invertebrate prey generally is habitat-specific (e.g., Kreps et al. 2012, Hansen et al. 2013, Ruokonen et al. 2014). For instance, Ruokonen et al. (2012) suggested that signal crayfish can exploit prey and have impacts at greater depths than noble crayfish, although this wider foraging range might not be relevant for our smaller, shallower lakes (Table S1).

Our results also show that equal caution should be exercised when considering the domestic introductions of native noble crayfish into lakes currently without crayfish, either with the purpose of creating "Ark sites" (Reynolds and Souty-Grosset 2012a, Rosewarne et al. 2013) for this endangered native crayfish species or for fisheries purposes. Noble crayfish had effects on macroinvertebrate assemblages that were similar to the effects of signal crayfish. Thus, the native crayfish can be considered an introduced "native invader" (Simberloff et al. 2012) in lakes that previously lacked this omnivorous species even if those lakes

lie within the natural range of the species, and particularly if they lie beyond that natural range.

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