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ORIGINAL PAPER

Does the introduced signal crayfish occupy an equivalent trophic niche to the lost native noble crayfish in boreal lakes?

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Abstract The introduced North-American signal crayfish (*Pacifastacus leniusculus*) has become widespread throughout Europe where it has often replaced the native noble crayfish (*Astacus astacus*). The impact of this replacement on ecosystem processes in boreal lakes is still largely unknown. We compared the trophic niches of these two crayfish species in 16 small to medium sized boreal lakes in southern Finland; eight lakes with noble crayfish and eight lakes where the native crayfish populations had been lost and replaced by signal crayfish. We analysed carbon and nitrogen stable isotopes from samples of the crayfish and their putative food sources, and used stable isotope models to compare trophic niche widths of the two species of crayfish and to quantify the food sources used by them. At species level the signal crayfish exhibited a substantially larger trophic niche than that of the noble crayfish, but within-lake populations of the species did not differ in their niche widths. The isotopic niches of the two species strongly overlapped, and while the estimated proportions of food resources (profundal and littoral macroinvertebrates, terrestrial leaf detritus and macrophytes) used by crayfish varied considerably among individual populations, they did not differ consistently between the species. Our results suggest that, contrary to often expressed concerns, replacement of lost noble crayfish populations by the signal crayfish may not greatly alter the littoral food web structure in boreal lakes.

Keywords Invasive species · Niche width · Stable isotopes · Food sources · Boreal lakes

Introduction

The introduction of alien species is recognized as one of the greatest biological threats to global biodiversity, since they can affect the distribution and abundance of native species as well as ecosystem function (Lodge et al. 1998; Mack et al. 2000; Sala et al. 2000; Hoper et al. 2005; McCarthy et al. 2006). Freshwater ecosystems are considered particularly susceptible to introductions of alien species (Dudgeon et al. 2006; Strayer 2010) which in many cases are able to become established, reach high densities and have a major impact on the whole ecosystem at many ecological levels (Light 2003; McCarthy et al. 2006). The success of any introduced species is related to its adaptability to the new habitat and to how it responds to biological and physical factors such as resource availability

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(Petren and Case 1996; Jefferies 2000), interspecific competition (Mack et al. 2000) and environmental features (Moyle and Light 1996; Hanshew and Tiffany 2012). In many cases, introduced species that have become successfully established have been recognized to show a wide ecological niche (Shea and Chesson 2002). If an introduced species can occupy a wider trophic niche than a native species it replaces, this may not only enable it to be successful but may mean its establishment alters food web structures in the ecosystem.

Freshwater crayfish are often considered keystone species in freshwater ecosystems and hence in food webs (Momot 1995; Nyström et al. 1996, 1999; Usio 2000). Crayfish feed on benthic invertebrates, macrophytes, algae, detritus, and fish carcases and eggs (Whitledge and Rabeni 1996, 1997; Stenroth and Nyström 2003), and are themselves eaten by larger animals (Roel and Orth 1993; Barrientos et al. 2013). Crayfish can thus affect the species richness and abundance of other organisms, and can have strong effects on the structure of food webs by feeding at several trophic levels (Stenroth and Nyström 2003; Dorn and Wojdak 2004). The North-American signal crayfish (*Pacifastacus leniusculus*) is one of the best-documented examples of an introduced species in the world (Holdich et al. 2009), and has become widespread throughout Europe, including Finland. Many studies have shown how signal crayfish can threaten freshwater flora and fauna including native crayfish (Nyström et al. 2001; Stenroth and Nyström 2003; Bubb et al. 2006), showing high adaptability to new habitats (Lewis 2002), wider feeding habits (Ruokonen et al. 2012), faster growth and reproduction (Lodge and Hill 1994) and aggressive behaviour (Ligth 2005; Hudina and Hock 2012). The signal crayfish has spread rapidly into Finnish lakes, where it has been widely introduced since the late 1960s to replace stocks of the native noble crayfish (*Astacus astacus*) lost due to crayfish plague (Smith and Söderhäll 1986; Söderbäck 1995; Holdich et al. 2009), and signal crayfish can now be considered a new component in the ecosystems of many Finnish lakes. Although the two species have been argued to be ecologically equivalent (Kirjavainen and Sipponen 2004), it is currently not clear if the alien species simply replaces the native by occupying the same niche, or if it creates some additional ecological impact on lake ecosystems.

Previous studies have shown that invasive crayfish often have a more opportunistic feeding behaviour than the native species, showing more adaptability in the new habitat. Beatty (2006) investigated the differences in diet and trophic positions between two crayfish species in an Australian river and found that both species had a predatory trophic and omnivorous functional role during the summer, when there was a high density of prey available. However, during the winter, when the density of prey was low, the invasive crayfish changed its diet to become more omnivorous than the other crayfish species which maintained its predatory character. Moreover, Rudnik and Resh (2005) in a study conducted in the freshwater tributaries to San Francisco Bay found that although the two invasive decapod species there generally played a role of omnivores, they exhibited differences in diet that suggested important differences between the two species in their impacts on the studied ecosystem.

Determining the trophic role of omnivorous crayfishes in the freshwater communities is complicated because they feed on several trophic levels and their trophic position might not always reflect their functional roles, when they have different resource assimilation (Parkyn et al. 2001). Olsson et al. (2009) used a stable isotope approach to compare the trophic niche width of introduced signal crayfish and native noble crayfish in a set of Swedish streams. They concluded that, although signal crayfish had twice the niche width of noble crayfish at the species level, individual populations of the two species had similar niche widths. However, this conclusion may not be applicable to lakes in which greater variability can be found in important environmental conditions such as depth, temperature and oxygen availability. Indeed, Johnston et al. (2011) found that omnivorous crayfish may show different diet and trophic position among different locations and environmental characteristics for the same species. Furthermore, Ruokonen et al. (2012) showed that in the largest Finnish lakes signal crayfish are able to colonise deeper littoral and sub-littoral areas that are not considered a typical habitat for the native noble crayfish. Therefore, to evaluate similarities or differences in the effects of crayfish species, as for ecological patters in general (Belovsky et al. 2004), repeating investigations across different types of ecosystems is necessary. Thus we used a stable isotope approach to study whether the trophic niches of the introduced signal crayfish and the native noble crayfish can also be considered equivalent in small to medium sized boreal lakes. We used the newly introduced stable isotope Bayesian ellipse in R (SIBER) method to quantify trophic niche area (Jackson et al. 2011). In particular, we sought to evaluate for a set of boreal lakes (1) if the invasive signal crayfish displays a wider trophic niche than the noble crayfish at species or population level, and (2) whether the two species differ in their use of food resources.

Methods

Study lakes

We selected 8 lakes in southern Finland still containing noble crayfish and 8 lakes now containing signal crayfish but which had originally contained noble crayfish. The lakes were chosen to have similar size and environmental characteristics (see appendix Table S1 in supporting information). The presence of either of the two species of crayfish was checked for each lake using the Finnish Game and Fisheries Research Institute (FGFRI) crayfish introduction register. No systematic quantitative information on crayfish abundance was available, but all lakes had a well-established and harvestable crayfish population. According to the FGFRI data, the signal crayfish was introduced almost 20 years ago into the Finnish lakes selected for this study, so that the populations are clearly well-established and can be assumed to have "stabilised" within the lake ecosystems. The noble crayfish populations are assumed to have occupied their lakes for a long time. We had originally planned that our study should also include lakes containing both crayfish species, but this proved impossible as the two species effectively never coexist in Finnish lakes because of the susceptibility of noble crayfish to the crayfish plague (Diéguez et al. 2006) carried and transmitted by signal crayfish.

Environmental factors

Littoral community structure may be greatly affected by the environmental factors and habitat type (Tolonen et al. 2001; Johnson and Goedkoop 2002; Nyström et al. 2006). Therefore we selected lakes with similar environmental characteristics (see Table S1), based on lake morphometry (lake area, shoreline), and water quality (pH, colour, nitrogen and phosphorus concentrations at 1 m depth), which were obtained for each lake from the HERTTA database (http://wwwp2.ymparisto.fi/scripts/hearts/welcome.asp) maintained by the Finnish Environment Institute. Water quality values for each lake were calculated as mean values of all available annual measurements during the previous 10 years.

All lake sampling sites were checked for substrate particle size at 0.5 m depth, taking three replicates per site and using a modified Wentworth's scale (Allan 1995). We adopted a visual-method to estimate the percentage of a particle size confined within a metal frame of surface area 0.25 m^2. The mean percentage-weighted particle size was calculated per replicate and the average was then calculated for the site.

The shore slope at each of the three replicate sampling sites was determined by measuring the perpendicular distance from the shoreline at 0.5, 1.0, 2.0, 3.0 and 4.0–5.0 m of water depth using a laser distance measurer. The mean slope of each site, expressed as the angle between the bottom and the water surface, was calculated from the five distance measures. A mean slope value was then calculated from the three sampling site values.

The littoral zone extent is strongly influenced by lake shape; indeed, lakes with the same surface area but increasing shore length will have a larger littoral area influencing the habitat characteristics and community composition (Kalff 2003). Consequently the trophic niches of crayfish might be affected by lake shape. We estimated the degree of lake shoreline irregularity as the shoreline development factor (SDF) calculated as (Wetzel 2001):

$$\mathrm{SDF} = \frac{\mathrm{L}}{2\sqrt{\mathrm{A}\pi}}$$

where L is the shoreline length (km) and A is the area of the lake (km^2).

Sampling of crayfish and food resources

Lakes were randomly sampled for crayfish and potential food resources in August 2010 and August 2011 (Table S1). Mean temperature and rainfall data were checked from the Finnish Meteorological Institute database (http://en.ilmatieteenlaitos.fi) and were found to be similar in both sampling years, indicating that data from the 2 years should be comparable with regard to inter-annual variations in weather. At each lake adult signal or noble crayfish (>3 cm carapace length) were caught using cylindrical plastic traps (trademark August and Rapurosvo, slot width 15 mm) baited with dead cyprinids. Traps were placed at 1–4 m depth along the shoreline in the late afternoon and collected the following morning. From 14 to 52 crayfish per lake and altogether a total of 292 signal crayfish and 290 noble crayfish were caught.

From each lake three replicate sample sites were chosen from open stony shore areas. From these sites samples of macroinvertebrates, detritus and macrophytes were collected as putative food items of the two crayfish species. At each site macroinvertebrate samples were taken at 0.5 m depth by hand and using a sweep net (mesh size 0.5 mm), and five replicates from 4 to 5 m depth were taken using an Ekman grab (area 225 cm^2), representing littoral and profundal food sources respectively. Macroinvertebrate samples were sorted soon after sampling using a sieving bucket (mesh size 0.5 mm). At each site leaves of riparian deciduous trees (*Alnus glutinosa*, *Betula pendula*) and undefined soft vegetable material of terrestrial origin were collected along the shoreline sites to represent terrestrial detritus. Submerged and floating material from macrophytes including *Lobelia dortmana*, *Nymphaea alba*, *Nuphar lutea*, *Ceratophyllum demersum*, *Myriophyllum* sp., *Potamogeton natans*, *Potamogeton gramineus* and *Potamogeton perfoliatus*, were collected at each site when they were available. All samples were kept cool and frozen within a few hours of collection.

Stable isotope analysis

As recommended by Stenroth et al. (2006), abdominal muscle tissue was taken from the tail of each signal and noble crayfish for carbon and nitrogen stable isotope analysis. Carapace length and sex were also determined from each individual. Samples of macroinvertebrates, terrestrial leaf detritus and macrophytes were mostly separated to species or genus level for analysis.

Muscle tissue from individual crayfish, macroinvertebrates, detritus and macrophytes were dried for 48 h at 60 °C and ground to a fine homogeneous powder. Around 0.5 mg of animal samples or 1.5 mg from plant and detritus samples was then precisely weighed into tin cups for stable isotope analysis, using a Carlo Erba Flash EA 1112 elemental analyzer connected to a Thermo Finnigan DELTA^{plus} Advantage continuous-flow isotope ratio mass spectrometer (CF-IRMS). The relative difference in isotope ratio between the samples and known standards is expressed as δ (‰) notation according to:

$$\delta X = \left(\left(R_{sample}/R_{standard}\right) - 1\right) \times 1000$$

where X is either ^{13}C or ^{15}N and the corresponding ratio is either $R = {}^{13}C/{}^{12}C$ or $R = {}^{15}N/{}^{14}N$.

The standards used as reference materials were Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen. White muscle tissue of pike (*Esox lucius*) or potato leaves (*Solanum tuberosum*) of known isotopic compositions were run as internal working standards for animal and plant samples respectively after every 6 samples to control for instrument stability. Analytical precision was <0.1 ‰ for $\delta^{13}C$ and <0.2 ‰ for $\delta^{15}N$.

Because $\delta^{13}C$ and $\delta^{15}N$ of basal resources can show considerable variation among lakes, a baseline correction was made for both C and N isotope values to facilitate among-lake comparisons. Cabana and Rasmussen (1996) and Vander Zanden et al. (1999) recommended using long-lived primary consumers, such as snails, for baseline calculations as these show reduced spatial and temporal variations in isotope values compared to primary producers. We were not able to collect snails in every lake; instead we used *Asellus aquaticus* which is another primary consumer feeding on periphyton and detritus (Arakelova 2001; Aberle et al. 2005) to represent the littoral baseline. Non-predatory chironomid larvae were chosen to represent the profundal baseline as they incorporate organic material that sediments from the water column. Following Anderson and Cabana (2007), we calculated the trophic position of crayfish using the formula:

$$T_p = \left(\left(\delta^{15}N_{cray} - \delta^{15}N_{baseline}\right)/3.23\right) + 2$$

where T_p is the trophic position of crayfish, $\delta^{15}N_{cray}$ represents the nitrogen isotope value of crayfish, $\delta^{15}N_{baseline}$ is the isotopic ratio from several individuals of primary consumer (*Asellus* and chironomids), 3.23 is the nitrogen isotope fractionation between trophic levels (Vander Zanden and Rasmussen 2001) and two is the trophic level of the organisms chosen as baseline (in this case *A. aquaticus* and chironomids).

We made a carbon correction for basal resources according to Olsson et al. (2009) using the following formula:

$$\delta^{13}C_c = \left(\delta^{13}C_{cray} - \delta^{13}C_{meaninv}\right)/C_{Rinv}$$

where $\delta^{13}C_c$ is the baseline-corrected crayfish carbon isotope value, $\delta^{13}C_{cray}$ is the measured carbon isotope value of crayfish, $\delta^{13}C_{meaninv}$ represents the mean carbon isotope value calculated from invertebrates collected in each lake and C_{Rinv} is the carbon range value ($\delta^{13}C_{max} - \delta^{13}C_{min}$) of the same macroinvertebrates (primary consumers) selected for the baseline in the trophic position calculation.

Mixing models

We used the Bayesian mixing model SIAR-package (Parnell et al. 2010) run in R (R Development Core Team 2012) to produce a four source mixing model in order to provide probability estimates of the proportions of different food sources used by the crayfish. This model is considered superior to previously published mixing models because it is capable of integrating variation in consumer and resource isotope signatures. The model was run separately for each lake using four putative food sources: non-predatory chironomids as profundal source, *A. aquaticus* as littoral source, terrestrial detritus source and submerged-floating macrophytes (according to their availability) in each lake. As recommended by Vander Zanden and Rasmussen (2001), we used fractionation factors in the model of 3.23 ± 0.41 ‰ for $\delta^{15}N$ and 0.47 ± 1.23 ‰ for $\delta^{13}C$ for animals, and 2.4 ± 0.42 ‰ for $\delta^{15}N$ and 0.40 ± 0.28 ‰ for $\delta^{13}C$ for detritus and macrophytes (McCutchan et al. 2003).

Niche width

Depiction of trophic niche width in a $\delta^{15}N$ and $\delta^{13}C$ bi-plot space has been recognized as a useful tool to investigate resource use and compare niche width at population and community level (Layman et al. 2007). However, since the convex hull area, originally proposed by Layman et al. (2007), has been shown to be highly sensitive to sample size (e.g. Syväranta et al. 2013), we adopted the standard ellipse area (SEA) approach to improve the comparability of measures of trophic niche when sample sizes are different (Jackson et al. 2011), as in our study ($n = 14$–52). We estimated niche widths of signal and noble crayfish for each within-lake population and for species (across populations) by calculating the standard ellipse area (SEA_B) using SIBER in a carbon (C_c) and nitrogen (T_P) corrected stable isotope data space. The calculated SEA_B contains ca. 40 % of the data and provides an estimate of niche area that is less sensitive to differences in sample size (Jackson et al. 2011; Syväranta et al. 2013).

Statistical analysis

We compared SEA_B values of populations and species between the two species using an independent-samples *t* test and confidence intervals, respectively. Using independent-samples *t* tests we also compared crayfish length and several environmental variables, which might affect the niche widths of crayfish, between the two crayfish lake categories. Those variables which were not normally distributed were log-transformed. All statistical analyses were conducted in R 2.14.2 (R Development Core Team 2012). The significance level was set at $\alpha = 0.05$.

Results

Environmental and biological influences

The study lakes (see Table S1) varied in their size (area 0.11–5.72 km^2), trophic state (total P 4–89 $\mu g\ l^{-1}$), pH (5.4–7.2) and water colour (10–160 mg Pt l^{-1}). However, the two lake categories (signal crayfish lakes and noble crayfish lakes) did not differ significantly (i.e. all *P* values >0.05) with respect to any of the measured environmental characteristics (Table 1).

Stable isotope data

Signal and noble crayfish species showed comparable mean (±SD) values of $\delta^{13}C$ (−26.89 ± 1.46 and −25.78 ± 2.03 ‰) and $\delta^{15}N$ (8.83 ± 2.02 and 8.33 ± 1.62 ‰) (Fig. S1). Mean carbon and nitrogen isotope values for the putative food sources did not differ significantly between the two crayfish lake categories (Fig. S1) (*t* test; $df = 14$; littoral $\delta^{13}C$ and

Table 1 Mean values and ranges of biotic and abiotic variables measured for the two lake categories. Environmental characteristics have been compared for differences using *t* tests

Biotic and abiotic variables	Signal crayfish lakes		Noble crayfish lakes		*P* value	*t* test	*df*
	Mean	Range	Mean	Range		*t* value	
Lake size (km^2)	1.34	0.11–4	2.42	0.65–5.72	0.22	1.339	14
Slope (°)	12.42	5.52–21.5	8.27	2.76–15.3	0.09	1.833	14
Shoreline development factor (SDF)	4.65	2.0–16.0	3.84	2.0–6.0	0.53	0.645	14
Stone-size	6.32	5.42–7.61	6.29	5.84–6.82	0.09	0.122	14
P (μ l^{-1})	16	8.0–24.0	21.42	4.0–89.0	0.59	0.546	14
N (mg l^{-1})	593.11	407.0–885.0	473.68	200.0–718.0	0.18	1.409	14
pH	6.49	5.4–7.1	6.8	6.3–7.2	0.16	1.467	14
Shoreline (km)	17	1–79	16	5–37	0.50	0.69	14
Colour (mg Pt l^{-1})	56.77	21.0–160.0	43.99	10.0–115.0	0.58	0.571	14

δ^{15}N, $t = -1.26$, $P = 0.22$, $t = 0.77$, $P = 0.44$; profundal δ^{13}C and δ^{15}N, $t = -1.26$, $P = 0.22$, $t = 1.01$, $P = 0.32$; detritus δ^{13}C and δ^{15}N, $t = 0.51$, $P = 0.61$, $t = 0.78$, $P = 0.44$; macrophytes δ^{13}C and δ^{15}N, $t = -0.80$, $P = 0.43$, $t = 0.71$, $P = 0.48$), although there was appreciable among-lake variation, particularly in δ^{15}N (see SD intervals in Fig. S1). Littoral and profundal macroinvertebrates showed distinct differences in δ^{13}C and δ^{15}N mean values for both lake categories (Fig. S1). Mean values of terrestrial leaf detritus (Fig. S1) differed with respect to both δ^{13}C and δ^{15}N, but in some individual lakes the difference was small. δ^{13}C values for detritus, and to a lesser degree of macrophytes, were often similar to those of littoral macroinvertebrates, but δ^{15}N values were more distinct (Fig. S1).

On average the sampled signal crayfish were significantly longer (difference in mean lengths of 0.6 cm) than the noble crayfish (see Table S2; *t* test; $t = 14.09$; $df = 572$; $P < 0.001$); however, the small difference was not reflected in their trophic ecology as at the species level signal and noble crayfish had comparable mean trophic position (T_P) values, even though signal crayfish showed a greater range of T_P values (Table S2). One lake, Keijärvi, yielded particularly low T_P values for signal crayfish and hence this lake mainly accounted for the wider trophic level range observed in this species. Signal crayfish also showed an overall wider range of $\delta^{13}C_c$ (range -0.22 to 0.66), compared with that obtained for noble crayfish (range 0.05–0.13), mainly due to the wider $\delta^{13}C_c$ values obtained in the lakes Aujärvi, Iso-Tarus and Karikkoselkä (Table S2).

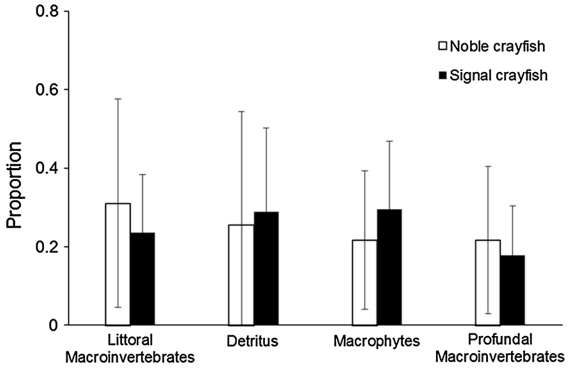

Fig. 1 Overall proportions of food sources (littoral macroinvertebrates, detritus, macrophytes and profundal macroinvertebrates) exploited by signal and noble crayfish according to SIAR modelling of stable isotope data. For each species values are mean ± SD from the eight lakes containing that species

Crayfish diets

Outputs from the SIAR model showed no appreciable or consistent differences between signal and noble crayfish at species level in their use of the putative food sources (littoral macroinvertebrates, profundal macroinvertebrates, terrestrial detritus and macrophytes) (Fig. 1; see Table S3 in Supporting Information). However, there was a suggestion that signal crayfish had consumed a slightly higher proportion of plant material (Fig. 1).

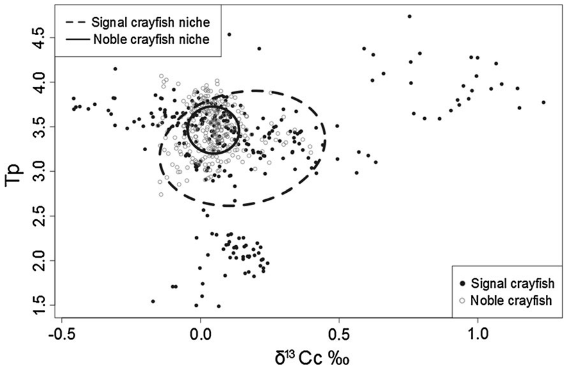

Fig. 2 Niche widths of signal and noble crayfish at the species level (estimated as SIBER model *ellipses*) based on combined data from all 16 lakes

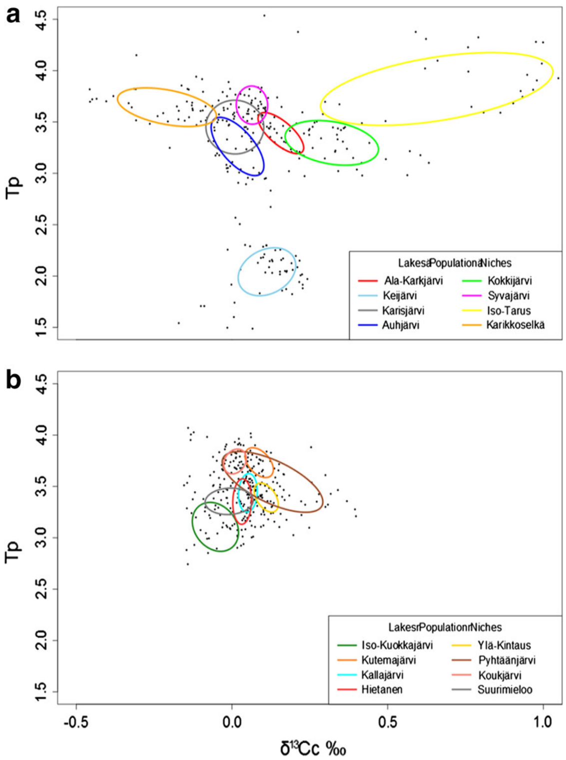

Fig. 3 Biplots of trophic position and baseline-corrected δ^{13}C values for individual crayfish (*black circles*) from all lakes. *Ellipses* represent the *feeding niche areas* for crayfish from individual lakes (estimated as SIBER model *ellipses*) from (**a**) eight signal crayfish populations and (**b**) eight noble crayfish populations

Crayfish niche widths

The combined data from all lakes showed a much wider spread of values of T_P and $\delta^{13}C_c$ for signal crayfish than for noble crayfish (Fig. 2). Consequently the standard ellipse area (SEA_B) for signal crayfish was almost five times that obtained for noble crayfish [0.62 ± 0.7 (95 % CI); 0.10 ± 0.01 (95 % CI)]. However, within individual lakes the spread of T_P and $\delta^{13}C_c$ values was more restricted (Fig. 3), and in fact there were no differences between SEA_B (*t* test; $t = 1.59$; $df = 15$; $P = 0.132$), and hence estimated niche widths, for signal and noble crayfish lake populations (Fig. 4).

Discussion

We compared trophic characteristics of 8 populations of signal crayfish that had been introduced into lakes that previously held noble crayfish and eight populations of native noble crayfish. Since the two lake groups showed no significant differences in the available environmental characteristics, our comparative approach appears sound, and any differences in trophic characteristics between the crayfish species should be attributable to species differences rather than reflecting environmental differences between the lake groups. In fact we found that at species level signal crayfish showed a greater range for both $\delta^{13}C_c$ and T_P, and thus apparently has a wider potential trophic niche than noble crayfish. However, according to the SEA_B results, at the within-lake population level the two species exhibited equivalent trophic niche widths.

Signal crayfish appeared to use slightly more plant material than noble crayfish, but since both species are evidently opportunistic omnivores this suggestion of a slight diet difference may simply reflect small difference between our lakes in the availability of the main food types. Thus our findings from lakes are consistent with those reported by Olsson et al. (2009) from Swedish streams, where at species level signal crayfish had a trophic niche almost three times wider than that of noble crayfish, while there were no differences between species in trophic niche width at the population level among streams. Hence it appears that as introduced signal crayfish progressively replace native noble crayfish, within around 20 years from their introduction into boreal freshwaters they are probably in most cases occupying an approximately equivalent trophic niche to that vacated by the lost noble crayfish, rather than becoming established by virtue of wider

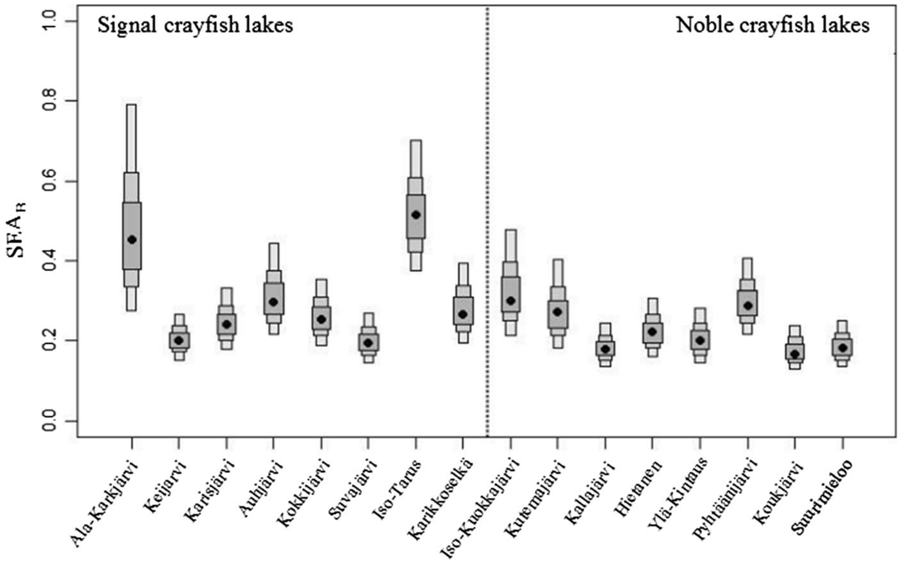

Fig. 4 *Niche areas* of signal and noble crayfish populations. The *black point* in each *box* corresponds to the mean standard *ellipse* area (SEA_B) obtained for each population. *Box areas* represent the 95 % (*light grey*), 75 % (*grey*) and 50 % (*dark grey*) Bayesian credibility confidence intervals

and more versatile feeding. Even though previous studies have shown that crayfish may be mostly considered omnivores, some of them can have greater diet plasticity than others, especially when they are faced with different habitat types or other species (Beatty 2006; Johnston et al. 2011). Our results together with those of Olsson et al. (2009) suggest that signal crayfish with a greater niche width at species level can occupy more variable environments and niche positions than noble crayfish. As our data were collected from only 1 year for each lake, we cannot know whether the crayfish niche widths might be in a state of flux. Jackson et al. (2012) used SIBER to examine trophic niche of alien Louisiana swamp crayfish (*Procambarus clarkii*) in Lake Naivasha, Kenya, and reported evolution of niche dimensions over several years following introduction of competing carp (*Cyprinus carpio*). However, as noble crayfish are native to the Finnish lakes in our study there is no reason to suppose their niche widths might still be evolving, and moreover because signal crayfish were introduced to these lakes approximately at the beginning of the 1990s, their populations are evidently well-established so again there is no reason to suppose their niche widths are unstable.

Our estimates of trophic niche widths were based on the SEA approach proposed by Jackson et al. (2011). As SEA values are known to be influenced by sample size, especially when isotope data are not normally distributed as is frequently the case with ecological material, Syväranta et al. (2013) recommended sample sizes of at least 30 for reliable application of SEA. At the species level we had large and comparable sample sizes (292 signal crayfish and 290 noble crayfish), so our comparisons of species-level trophic niche widths can be considered robust. At within-lake (population) level, only from three lakes did we have <30 crayfish individuals (mean sample size per lake 36, range 14–52), so again our estimates of the realised trophic niche width in the lakes may be considered mostly reliable. The lake Ala-Karkjärvi, from which we were only able to obtain a particularly small sample of 14 crayfish, actually gave the widest credibility confidence intervals for SEA_B (Fig. 4) and it may be that the niche width values from this lake are less reliable.

The apparent wider species-level trophic niche of signal crayfish reflects the wide scatter of values for trophic position (baseline-corrected $\delta^{15}N$) and corrected $\delta^{13}C$ values for this species (Fig. 3a) whereas values for noble crayfish were more tightly clustered (Fig. 3b), similar to the results of Olsson et al. (2009) from Swedish streams. In our data the wide T_P range for signal crayfish was mainly attributable to the values from Lake Keijärvi, which yielded exceptionally high $\delta^{15}N$ values for macroinvertebrates and macrophytes, although not for detritus (of terrestrial origin). This lake is moderately eutrophic with high concentrations of TN and TP and also high pH. In eutrophic lakes crayfish are reported to feed mainly on invertebrates (Nyström et al. 2006). However in Keijärvi the stable isotope data indicated that crayfish did not feed on *A. aquaticus* that we had selected as the most representative littoral macroinvertebrate source across the lakes; instead crayfish in this lake appeared to feed mostly on detritus and macrophytes. Hence the validity of the baseline correction in this lake is questionable and may have somewhat distorted the apparent trophic position of signal crayfish in the lake. However, the results from this single lake have only limited influence on the trophic niche width of this species based on all our data.

Similarly, the wider $\delta^{13}C_c$ range shown by the invasive species mainly reflects the higher values obtained from lakes Iso-Tarus and Kokkijärvi (Fig. 3a). Niche width tends to increase as the population density increases (Svanbäck and Persson 2004), intensifying intraspecific competition and driving individuals to greater dietary and habitat shift (e.g. Almeida et al. 2013a) rather than specialization. In relation to this, wide littoral zones could enable greater habitat differentiation amongst crayfish individuals and consequent differences in isotope signatures, as well as in diet and trophic level of omnivores within and between populations (Stenroth et al. 2008; Ruokonen et al. 2012). Kokkijärvi and Iso-tarus lakes have clearly lower mean values for shoreline steepness amongst the signal crayfish lakes. Thus these lakes might have provided a more heterogeneous habitat that could offer a better and wider foraging area with a substantial primary production where crayfish could have selected a wider range of food items.

Of course, our results were obtained from a restricted region in southern Finland and from a suite of small to medium sized lakes in which it is likely that all available habitats have been occupied by either the invasive signal crayfish or the native noble crayfish in such a way as to maximise their use of all possible food resources. Although signal crayfish showed evidence of a wider trophic niche width at the species level, in these lakes the realised trophic niche may necessarily be restricted so that any higher adaptability of the introduced species compared to that of noble crayfish might only be seen at a larger spatial scale. For example, Ruokonen et al. (2012) have shown how signal crayfish are able to colonise littoral and sublittoral areas in the largest Finnish lakes that had not been a habitat for the native noble crayfish. However Söderbäck (1995) noted that this signal crayfish habitat preference seemed not to be shown when the two species were in sympatry, with the introduced species instead occupying the same habitats as noble crayfish (Westman et al. 2002).

Thus, our findings suggest that across a wide range of lakes in Finland, and by extension across the boreal region, as noble crayfish populations are lost due to crayfish plague, replacement with introduced signal crayfish is unlikely to directly modify the littoral food webs of these lakes, as the two species exhibit comparable diets and realised trophic niche widths, even though the signal crayfish as a species apparently has a wider potential trophic niche and more plastic habits. These results contrast with the experimental findings by Nyström et al. (1999) that over a 2-month period signal crayfish had stronger impacts than noble crayfish on littoral food webs created artificially in small plastic pools. Thus we argue that small-scale and short-term experiments cannot recreate complex ecosystem-level interactions, and may even generate misleading results (e.g. Carpenter 1996), and that robust evaluation of competitive interactions between invasive and native crayfish species requires ecosystem-scale studies like ours (cf. Almeida et al. 2013b).

Our results with the two crayfish species suggest that the widespread establishment of an introduced species does not necessarily have to lead to major disruption of food web structure, as is often feared. Some introduced species may effectively just take over a niche vacated by a native species, and may actually be viewed as maintaining the integrity of an ecosystem when the native species has been lost for reasons other than competitive replacement by the introduced species. However, we emphasise that our results and conclusions should not be extrapolated to other introduced-native species combinations. Moreover, our findings relate solely to the trophic characteristics of the two species we studied, and do not exclude the possibly differing effects of the two species on e.g. abundance and species composition of natural flora and fauna. It is possible that other aspects of the ecology of the two crayfish species, such as their relations to parasites and pathogens, or reproductive interference between the two species, differ in important ways. Indeed, there is some evidence from Finnish lakes that lakes stocked with signal crayfish tend to yield higher crayfish densities than lakes restocked with noble crayfish (Erkamo et al. 2010) and the potential effect of crayfish density on littoral food web structure and energy flow in these lakes needs to be investigated. Therefore, to preserve native species from any potential negative impact that this invasive species can induce, we emphasise that further stocking of signal crayfish as a commercial compensation for lost noble crayfish should proceed with prudence.

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