

Fabio Ercoli

A Comparison of the Impacts of  
Introduced Signal Crayfish and Native  
Noble Crayfish in Boreal Lake  
Ecosystems



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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella  
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303,  
marraskuun 7. päivänä 2014 kello 12.

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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2014

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JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE 293

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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2014

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Jyväskylä Studies in Biological and Environmental Science

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Department of Biological and Environmental Science, University of Jyväskylä

URN:ISBN:978-951-39-5925-8

ISBN 978-951-39-5925-8 (PDF)

ISBN 978-951-39-5924-1 (nid.)

ISSN 1456-9701

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Jyväskylä University Printing House, Jyväskylä 2014

## ABSTRACT

Ercoli, Fabio

A comparison of the impacts of introduced signal crayfish and native noble crayfish in boreal lake ecosystems

Jyväskylä: University of Jyväskylä, 2014, 34 p.

(Jyväskylä Studies in Biological and Environmental Science

ISSN 1456-9701; 293)

ISBN 978-951-39-5924-1 (nid.)

ISBN 978-951-39-5925-8 (PDF)

Yhteenveto: Vieraslaji täpläravun ja alkuperäisen jokiravun ekologisten vaikutusten vertailu boreaalisissa järvissä

Diss.

The North American signal crayfish (*Pacifastacus leniusculus* Dana) has been widely introduced in Europe where the species outcompetes the native noble crayfish (*Astacus astacus* L.) and threatens native communities. There is still controversy over whether or not the two crayfish species occupy similar ecological roles in lake ecosystems. The aim of this study was to investigate the impacts of signal and noble crayfish on lake littoral communities at the whole-lake scale. The study was conducted in the central part of Finland where 8 lakes containing signal crayfish, 8 lakes containing noble crayfish and 8 lakes without any crayfish were selected. In addition, three different sites (with no-crayfish, with crayfish established, and with crayfish newly introduced) were chosen in the large Lake Päijänne, where the temporal effects of signal crayfish on littoral communities were investigated over 5 years. Stable isotope results indicated that signal crayfish exhibited a wider trophic niche width than noble crayfish at species level, but not at the level of within-lake populations. Moreover, the two species appeared to exploit approximately the same food sources in the same proportions. The results indicate that the two species affected macroinvertebrate abundance, species richness and community composition, similarly in the littoral habitat, but differently in the sublittoral habitats, where the invasive species exhibited stronger negative impacts than the native species. The temporal effects on the littoral macroinvertebrate community appeared fairly stable. However, the presence of signal crayfish was associated with a generally decreased macroinvertebrate species richness as well as snail abundance and richness. Results suggest that impacts of crayfish on lake communities are habitat- and species-specific. The results improve understanding of the potential ecological effects of signal and noble crayfish, and contribute to the scientific basis for their management.

Keywords: Boreal lake ecosystems; invasive signal crayfish; macroinvertebrate communities; native noble crayfish; stable isotopes.

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## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV.

The study plan for the thesis was developed by me, Roger Jones, Heikki Hämäläinen and Timo Ruokonen. The lakes for studies I, II and III were selected by Esa Erkamo and Timo Ruokonen and the sites for study IV were selected by Timo Ruokonen. I was responsible for data collection for studies I, II, and III, and Timo Ruokonen was responsible for data collection for study IV. I carried out most of the laboratory work and wrote the first draft of manuscripts I, II and III. Timo Ruokonen was the responsible author for manuscript IV while I analysed the data and contributed to the first draft of the manuscript. All papers were finalised together with all co-authors.

- I Ercoli F., Ruokonen T.J., Hämäläinen H. & Jones R.I. 2014. Does the introduced signal crayfish occupy an equivalent trophic niche to the lost native noble crayfish in boreal lakes? *Biological Invasions* 16: 2025–2036.
- II Ercoli F., Ruokonen T.J., Erkamo E., Jones R.I. & Hämäläinen H. 2014. Comparing the effects of introduced signal crayfish and native noble crayfish on the littoral invertebrate communities of boreal lakes. *Freshwater Science*. Accepted.
- III Ercoli F., Ruokonen T.J., Koistinen S., Jones R.I. & Hämäläinen H. 2014. The introduced signal crayfish and native noble crayfish have different effects on sublittoral invertebrate communities of boreal lakes. Submitted manuscript.
- IV Ruokonen T.J., Ercoli F. & Hämäläinen H. 2014. Are effects of an invasive crayfish on lake littoral communities consistent in time? Submitted manuscript.

# 1 INTRODUCTION

## 1.1 Freshwater biodiversity

An important issue in ecology during recent decades has been how loss of biodiversity can affect ecosystem processes and functioning (Hopper *et al.* 2005, Cardinale *et al.* 2012). It is widely agreed that biodiversity plays an important role in strengthening the functional efficiency of ecological communities and enhancing the temporal stability of ecosystem processes (Hector *et al.* 2010, Campbell *et al.* 2011, Cardinale *et al.* 2012). However, biodiversity is increasingly threatened by anthropogenic impacts, and freshwater ecosystems are particularly strongly affected (Strayer and Dudgeon 2010), including due to the introduction of non-native species (Lodge *et al.* 1998, Sala *et al.* 2000, Dudgeon *et al.* 2006, Strayer and Dudgeon 2010, Jackson and Grey 2012).

## 1.2 Crayfish and their ecological effects

Introductions of non-native species, either accidental or deliberate, are increasing worldwide, threatening native communities, and altering habitats and functionality of recipient ecosystems (Mack *et al.* 2000, Simberloff *et al.* 2013). However, evaluation of the impacts of invasive species and how they are driving effects on native communities is a challenge for invasion ecologists (Paolucci *et al.* 2013). Although research dealing with effects of species invasions has been increasing, more efforts are needed to explore at what spatial and temporal extents the consequences of invasions will affect ecosystem functioning (Strayer 2012, Ricciardi *et al.* 2013), in order to understand and manage the ecosystems and the invasions (Strayer 2012).

Freshwater crayfish are a well-known example of animals which have been widely translocated from their natural habitats and have become invasive in the recipient ecosystems (Gherardi 2010, Reynolds and Souty-Grosset 2012).

Indeed, after introduction and successful establishment in the new habitat invasive crayfish can pose direct or indirect detrimental effects to native communities and physical habitats (Nyström *et al.* 1999, Usio 2000, Nyström *et al.* 2001, Wilson *et al.* 2004, Ruokonen *et al.* 2014).

Crayfish can affect species richness and abundance of other organisms and hence can have strong effects on the structure of food webs by feeding at several trophic levels (Stenroth and Nyström 2003, Dorn and Wojdak 2004). Nyström *et al.* (1999) suggested that, although crayfish were top consumers, they also had both direct and indirect effects on lower trophic levels. Invertebrate grazers were greatly reduced by crayfish, and indirectly periphyton was positively affected by crayfish. Previous studies reported that invasive crayfish species can also affect littoral benthic fishes (Guan and Wiles 1997, Hirsch and Fischer 2008), although recent findings (Ruokonen *et al.* 2012) have demonstrated the contrary. Moreover, invasive crayfish represent a severe threat to their native counterparts and in the majority of cases outcompete and replace native species (Nyström *et al.* 2001, Stenroth and Nyström 2003, Bubb *et al.* 2006).

However crayfish impacts can vary in different habitats and between species. Recent field studies and meta-analyses have shown that crayfish effects can be habitat-specific (Krebs *et al.* 2012, Hansen *et al.* 2013, Ruokonen *et al.* 2014) or species-specific (Haddaway *et al.* 2012, Jackson *et al.* 2014). Furthermore, crayfish impacts might change in the long-term (Strayer *et al.* 2006, Kelly *et al.* 2013), and hence it has been stressed that effects should be investigated at large temporal scales to observe changes that develop in native biota over time. Thus, because the effects can be different at different temporal and spatial scales, it is important that investigations of impacts are designed to allow wider understanding of outcomes at ecologically relevant scales (Sax *et al.* 2005).

Several previous studies have suggested that invasive crayfish can have a large potential impact on macroinvertebrate abundance, species richness and community composition (McCarthy *et al.* 2006, Twardochleb *et al.* 2013), but the evidence has mainly come from small-scale mesocosm experiments or from manipulative laboratory experiments, or from investigations on single crayfish species. Small-scale experiments in created environments tend to reduce the heterogeneity and then homogenize the habitat, thereby excluding many biotic and abiotic interaction effects, which occur under natural condition. This can strongly compromise the relevance of results, and can even produce misleading results (Carpenter 1996) or overestimate the between species interactions (Gurevitch *et al.* 1992), making it difficult to extrapolate results to realistic ecological scales under natural conditions. For instance, Lagrue *et al.* (2014) recently reported that invasive and native crayfish similarly affected the macroinvertebrate community in the studied river, thus apparently playing an equivalent ecological role. However their study was conducted at a small spatial scale in the field and in laboratory experiments, with potential shortcomings and difficulties in applying the results in nature, for example in regard to management. In general, comparisons of invasive

and native crayfish species effects or evaluation of long-term invasive crayfish impacts, under natural conditions and at the whole-lake scale, are scarce. Twardochleb *et al.* (2013) noted from their meta-analysis study how limited and uncertain were the findings on crayfish impacts, due to the lack of direct comparisons between non-native and native crayfish, and they stressed that more studies at larger spatial scales and including multiple crayfish species are strongly needed. Thus there is a clear need for further studies that evaluate impacts under natural conditions and at larger and more relevant spatial and temporal scales.

Stable isotope analyses (SIA) of carbon and nitrogen is a useful tool to study the diets of organisms integrated over time and hence reveal what an animal has eaten, or rather assimilated, over the last days, weeks or months, depending on the size and elemental turnover rate of the animal (Fry 2008). Ideally, the relative contribution of different potential food types to the diet of a consumer can be estimated using mixing models (Phillips and Gregg 2001, 2003). Earlier stable isotope studies have come to a range of conclusions regarding the diets of crayfish. Some authors have suggested detritus as an important food source for crayfish (France 1996, Evans *et al.* 2001), whereas others have suggested that invertebrates are the primary energy source for crayfish (Nyström *et al.* 1999, Hollows *et al.* 2002). However, Olsson *et al.* (2009) showed that SIA can reveal important aspects of crayfish roles in lake trophic structures and can be a powerful tool to test ecological theory and study ecosystem responses to introductions of invasive species.

The North-American signal crayfish (*Pacifastacus leniusculus* Dana) is one introduced species that has become widespread throughout Europe, including Finland (Holdich 2009). Signal crayfish was introduced to Finland in the late 1960s-1970s to compensate for the dramatic decline of populations of native noble crayfish (*Astacus astacus* L.). Thereafter the species has been spreading rapidly into Finnish lakes, where, as elsewhere in Europe, it has often replaced the native noble crayfish by transmitting lethal diseases to the native species and by competitive exclusion (Smith and Söderhäll 1986, Söderbäck 1995). Although the two species display similarities (Kirjavainen and Sipponen 2004) and it has been argued that they can be considered ecologically equivalent at least in some ecosystems (e.g. Lagrue *et al.* 2014), it is still not clear if invasive signal crayfish and noble crayfish really have equivalent ecological effects or whether the introduced species might more strongly affect lake ecosystems.

### 1.3 Aims of the thesis

The main objectives of this thesis were to assess the impact of the introduction of signal crayfish on the communities of boreal lakes and to evaluate whether the ecological impacts of the invasive and native species can really be considered equivalent. The research was mainly conducted in replicate small to medium-sized lakes representing three different ecological situations: lakes

containing non-native crayfish; lakes containing native crayfish; and lakes where no crayfish are present. In addition, three different sites (with established crayfish, with no crayfish, and with crayfish newly introduced) were compared in the large Lake Päijänne.

The first aim was to compare the trophic niche widths of signal and noble crayfish species in boreal lake ecosystems (I). This aim was approached using carbon and nitrogen stable isotope data from the introduced signal crayfish and native noble crayfish, as well as from samples of their potential food items. Using combined carbon and nitrogen isotope analyses was expected to allow evaluation of whether signal crayfish use the same food resources and occupy the same trophic position in the food web as native noble crayfish in the study lakes; i.e. whether the two species effectively occupy an equivalent ecological trophic niche.

The second aim was to investigate the impacts of signal and noble crayfish on the abundance, species richness and taxonomic composition of littoral macroinvertebrate communities (II). Based on previous studies, it was expected that in the presence of crayfish the abundance of macroinvertebrates, and of certain groups like snails in particular, would be reduced.

A recent study has indicated that signal crayfish can forage deeper in lakes (Ruokonen *et al.* 2012) and consequently might negatively affect the sublittoral communities more than native noble crayfish, which is known to be more restricted to shallower littoral habits. Thus the third aim was to compare the effects of signal and noble crayfish on sublittoral macroinvertebrate communities (III). The investigation of macroinvertebrate abundance, species richness, biomass and community composition aimed to reveal whether and how much the two crayfish species differ in their exploitation of this lake habitat.

Finally, the temporal dynamic effects on littoral macroinvertebrate communities of signal crayfish introduced into the large boreal Lake Päijänne were explored (IV). The fourth aim was to study whether the littoral macroinvertebrate community responses vary temporally with varying signal crayfish populations, and if the degree of temporal variation in the littoral community is associated with the presence of crayfish.

## 2 MATERIAL AND METHODS

### 2.1 Study lakes

For I, II and III, 8 lakes containing signal crayfish, 8 lakes with noble crayfish and 8 lakes without any crayfish were selected in the region of south central Finland (Fig. 1). Lakes were chosen to have similar environmental features on the basis of the crayfish introduction register maintained by the Finnish Game and Fisheries Research Institute (FGFRI). However, the impacts of signal and noble crayfish had to be assessed separately because the two species do not co-occur in the same lakes in Finland owing to the fungal disease (*Aphanomyces astacii*) which is carried by the resistant signal crayfish and transmitted to the vulnerable noble crayfish.

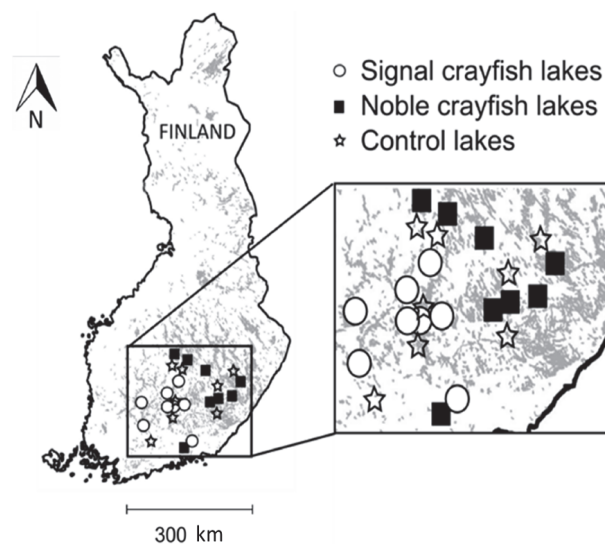


FIGURE 1 Map showing the location of the eight lakes in each category in south central Finland (I, II, III).

According to the FGFRI data, signal crayfish was introduced to the study lakes around 20 years ago and has become well-established and harvestable. The noble crayfish lakes are assumed to be occupied by their natural historical populations, although some populations might also have been mixed with restocked crayfish. Crayfish abundance data were provided by the FGFRI, though mainly from years before the field sampling in this study, to check that crayfish abundances were broadly comparable between the signal and noble crayfish lakes.

Research for study IV was conducted in the second largest Finnish lake Päijänne where one established crayfish site was selected at Padasjoki (61°20' N, 25°21' E), one non-crayfish site at Kuhmoinen (61°31' N, 25°15' E) and one site with newly introduced crayfish at Saalahti (61°55' N, 25°26' E). Signal crayfish was introduced at the Padasjoki crayfish site in 1990, and the population now reproduces naturally and supports important recreational and commercial fisheries in the area. The Saalahti site was inspected for crayfish presence before crayfish introduction started in September 2007, when 800 signal crayfish juveniles (age-group 1+, mean length 38 mm) were released to the study area by the local water owners and similar stocking continued through 2008–2010.

## 2.2 Lake environmental characteristics

Study lakes and sites were selected to have similar characteristics because it is known that the composition of littoral and sublittoral communities can be strongly influenced by biotic and abiotic characteristics (Johnson and Goedkoop 2002, Nyström *et al.* 2006). Thus values for lake morphometry (lake area and shoreline) and water quality (pH, colour, total nitrogen and total phosphorus concentration at 1 m depth, oxygen concentration at 3–5 m depth) were checked from the HERTTA database (<http://www.p2.ymparisto.fi/scripts/hearts/welcome.asp>) maintained by the Finnish Environment Institute. Mean values of water quality parameters were calculated from the annual measurement taken in the 10 years previous to the study field sampling (I, II, III, IV).

Substrate particle size was checked for every sampling site at 0.5 m depth (I, II) where 3 replicate plots were taken using a metallic frame (0.25 m<sup>2</sup>) and the percentage cover of varying particle size categories was estimated using a modified Wentworth' scale (Allan 1995).

Shore slope was calculated at each site (I, II, III, IV) by measuring the distance from the shoreline at 0.5, 1.0, 2.0, 3.0 and 4.0–5.0 m depth. The slope was expressed as the angle between the bottom and the water surface, calculated from the 5 distance measures. A mean slope value was then calculated from the 3 sampling site values.

Lake littoral habitat may also be influenced by the lake shape, so that lakes may have same area but different degree of lake shoreline irregularity; consequently a lake with greater littoral shore may have different habitats



harbouring different communities (Kalff 2002). This lake shape irregularity was calculated (I, II) as the shoreline development factor (*SDF*) according to Wetzel (2001)

$$SDF = L (2\sqrt{A\pi})^{-1}$$

where *L* is the shoreline length (km) and *A* is the area of the lake (km<sup>2</sup>).

### 2.3 Crayfish sampling

At each lake adult signal or noble crayfish for stable isotope analysis (I) were caught by the lake owner using cylindrical plastic traps baited with dead cyprinids.

For studies I, II and III crayfish abundance for the times of field sampling could not be estimated, but catch per unit effort (CPUE) data were provided by the FGFRI. Although these data were mainly from years before the study field sampling, they confirmed broadly comparable abundances of signal and noble crayfish in the study lakes. In order to provide signal crayfish abundance (CPUE) for the sites in Lake Päijänne (IV), crayfish were sampled using 25 cylindrical traps baited with dead cyprinids. Traps were set parallel to the shoreline at 1–3 m depth and 5 m apart during the evening and were collected the following morning.

### 2.4 Macroinvertebrate sampling

Lake stony shores are the preferred habitat of crayfish (Ruokonen *et al.* 2014), so to evaluate crayfish impacts on this zone, littoral samples were all taken on stony and open shore areas where the bottom was characterised by cobbles and boulders.

Macroinvertebrates were sampled in August 2010 or August 2011 (I, II, III), and in the same month from 2007 to 2011 for IV. In the littoral zone samples of macroinvertebrate were taken at 0.5–1 m depth using a sweep net of mesh size 0.5 mm (I, II, III). At each site the sampler moved along a 1 m stretch of bottom (parallel to the shoreline) for 30 s kicking the substrate while capturing the detached and suspended material by sweeping with the net (Johnson and Goedkoop 2002). Five replicate sublittoral macroinvertebrate samples (I, III) were taken at each of the 3 sites at each lake at 4–5 m depth using an Ekman grab (*A* = 0.026 m<sup>2</sup>). At the same littoral sites samples of macroinvertebrates, detritus and macrophytes were also collected as representing potential food resources for signal and noble crayfish (I).

At each of the 3 sample areas in Päijänne 3 random replicate littoral macroinvertebrate samples were taken from 1 m depth (IV), using a system



powered by a water pump operated on a boat (Tolonen *et al.* 2001). A framed area of bottom (0.25 m<sup>2</sup>) was cleaned by a scuba diver sucking up the sample to a sieve of mesh size 0.5 mm (see Ruokonen *et al.* 2014 for a more detailed description).

For stable isotope analysis (I) macroinvertebrate samples were frozen within a few hours of collection. Otherwise (II, III and IV) samples were immediately preserved in 70 % ethanol, and in the laboratory macroinvertebrates were sorted from the samples, identified to the lowest feasible taxon (mostly to species or genus level) (I, II, III, IV), counted for density and species richness (II, III, IV), and wet-weighed for biomass (III) of higher taxa (families or orders). After weighing, head capsules of Chironomidae larvae were mounted on microscope slides in Euparal® and identified to genus (III).

## 2.5 Detritus, macrophyte and periphyton sampling

At each lake from the 3 replicate sites samples were taken of detritus and macrophytes as potential food sources of the two crayfish species (I). At each site leaves of *Alnus glutinosa* and *Betula pendula* together with soft organic matter of terrestrial origin were collected on the shoreline to represent a detritus source, whereas *Lobelia dortmanna*, *Nymphaea alba*, *Nuphar lutea*, *Ceratophyllum demersum*, *Myriophyllum* sp., *Potamogeton natans*, *P. gramineus* and *P. perfoliatus*, were collected as submerged and floating-leaved macrophytes. Samples of periphyton were taken from 1.0 m depth at crayfish and non-crayfish sites in 2008–2010, to calculate biomass (IV). Unfortunately periphyton samples from 2007 and from introduction site were accidentally lost, thus it was not possible to include them in the study. Random subsamples (n = 5) were collected from stone surfaces using a brush sampler (Meriläinen *et al.* 1987). In the laboratory each sample was filtered onto a pre-weighed glass fibre filter (Whatman® GF/C) and oven dried at 60 °C for 24 h. After drying, samples were weighed, and sample biomasses were calculated by subtracting the weight of the filter from the final weight.

## 2.6 Littoral fish sampling

Littoral benthic mean fish population density was calculated using the Junge and Libovarsky equation (Bohlin *et al.* 1989), on the basis of densities of bullhead (*Cottus gobio* L.) and stone loach (*Barbatula barbatula* L.) which were the most abundant littoral benthic fish at the study sites (IV). Battery-powered backpack electrofishing gear (GeOmega FA4, Geomega AS, Sjetnemarka, Norway) with a pulsed (50 Hz) 350 V direct current, and a 3 pass-removal method was used to collect fish. Electrofishing was conducted along the shore

line so that the maximum sampled depth was *ca* 80 cm. The sampled area was *ca* 100 m<sup>2</sup> at each site and year. Captured fish were identified to species and counted.

## 2.7 Stable isotope analysis

Carbon (C) and nitrogen stable isotopes were analysed from samples of the two crayfish species and their putative food sources (I) to compare niche widths of signal and noble crayfish and to quantify resources used by the invasive and native crayfish.

Abdominal muscle tissue was taken individually from the tail of each crayfish species (Stenroth *et al.* 2006). Samples of muscle tissue, macroinvertebrates, terrestrial detritus and macrophytes were then 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.

Stable isotope analyses were made using a Carlo Erba Flash EA 1112 elemental analyzer connected to a Thermo Finnigan DELTAplus Advantage continuous-flow isotope ratio mass spectrometer (CF-IRMS) at the University of Jyväskylä. The relative difference in isotope ratio between the samples and known standards was expressed as  $\delta$  (‰) notation according to:

$$\delta X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) * 1000$$

where  $X$  is either <sup>13</sup>C or <sup>15</sup>N and the corresponding ratio  $R$  is either  $R^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . The standards used as reference materials were Vienna Pee Dee belemnite for C and atmospheric N<sub>2</sub> 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  $\delta^{13}\text{C}$  and < 0.2 ‰ for  $\delta^{15}\text{N}$ .

Because of the variability of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of basal resources among the two lake categories a baseline correction was calculated for C and N stable isotope values to compare between lakes. The primary consumer *Asellus aquaticus* which is known to feed on periphyton and detritus (Arakelova 2001, Aberle *et al.* 2005) was used for a littoral baseline, and non-predatory chironomid larvae, as organisms which are able to incorporate organic matter sedimenting from the water column, were used to represent a profundal baseline.

Trophic position (TP) was calculated using the formula proposed by Anderson and Cabana (2007):

$$TP = ((\delta^{15}N_{\text{cray}} - \delta^{15}N_{\text{baseline}}) 3.23^{-1}) + 2$$

where  $TP$  is the trophic position of crayfish,  $\delta^{15}N_{\text{cray}}$  represents the N isotope value of crayfish,  $\delta^{15}N_{\text{baseline}}$  is the isotopic ratio from several individuals of primary consumer (*Asellus aquaticus* and chironomids), 3.23 is the N isotope fractionation between trophic levels (Vander Zanden and Rasmussen 2001) and 2 is the trophic level of the organisms chosen as baseline (in this case *Asellus aquaticus* and chironomids).

Basal resource correction was made according to Olson *et al.* (2009) using the following formula :

$$\delta^{13}C_c = (\delta^{13}C_{\text{cray}} - \delta^{13}C_{\text{meaninv}}) C_{\text{Rinv}}^{-1}$$

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

## 2.8 Mixing model and niche width

The proportions of different food sources used by the crayfish were estimated using the Bayesian mixing model SIAR-package (Parnell *et al.* 2010) run separately for each lake using non-predatory chironomids as a profundal source, *Asellus aquaticus* as a littoral source, a terrestrial detritus source, and a submerged and floating-leaved macrophyte source (I). As there were no specific fractionation values for crayfish reported in the literature, the fractionation factors used in the model were  $3.23 \pm 0.41$  % for  $\delta^{15}N$  and  $0.47 \pm 1.23$  % for  $\delta^{13}C$  for animal food as recommended by Vander Zanden and Rasmussen (2001), and  $2.4 \pm 0.42$  % for  $\delta^{15}N$  and  $0.40 \pm 0.28$  % for  $\delta^{13}C$  for detritus and macrophyte foods (McCutchan *et al.* 2003).

The standard ellipse area (SEA) approach (Jackson *et al.* 2011) was used to evaluate niche widths of signal and noble crayfish in each within-lake population and at species level, which was considered more appropriate than the convex hull area (Layman *et al.* 2007), due to the differences in sample sizes from each lake. Standard ellipse area ( $SEA_B$ ) was calculated using SIBER from the corrected carbon  $\delta^{13}C_c$  and nitrogen TP stable isotope data.

## 2.9 Statistical analysis

Lake environmental features were tested for differences using *t*-test (I) and one-way ANOVA (II, III). Independent-sample *t*-test was also used to compare  $SE_{AB}$  values of within-lake populations and between signal and noble crayfish species (I), as well as for differences in crayfish individual length (I) between the two species. Differences in the effects on macroinvertebrate abundance, species richness and Shannon diversity index between signal, noble and control lakes were tested using one-way ANOVA (II, III) followed by Tukey *post-hoc* comparisons when differences were statistically significant. Because the normality assumption was violated for some taxonomic groups, non-parametric Kruskal-Wallis and pairwise Bonferroni-corrected Mann-Whitney *U* tests were used for differences in abundance and richness (II).

Two-way ANOVA and linear mixed effects models were performed to evaluate effects of site (established crayfish / no-crayfish / introduction) and time (years) on macroinvertebrate abundance and species richness (IV), as well as on littoral fish density and periphyton biomass respectively. When significant relationships were detected, Tukey *post-hoc* comparisons were performed. Variation in macroinvertebrate community composition among lakes (II, III), sites and years (IV) was visually represented by non-metric multidimensional scaling (NMDS) ordination on transformed [ $\log(\text{mean count} + 1)$ ] density data with the Bray-Curtis distance measure. Differences between lake categories (II, III) and sites (IV) were tested by Multi-Response Permutation Procedures (MRPP) and by blocked MRPP using sampling year as blocking factor respectively.

Indicator species analysis (ISA) (Dufrene and Legendre 1997) was performed (II, III, IV) to evaluate which macroinvertebrate species were distinctive across lake categories (II, III) and sites (IV).

## 3 RESULTS AND DISCUSSION

### 3.1 Stable isotopes and food sources (I)

Stable isotope data (I) indicated that signal crayfish showed a wider trophic niche than noble crayfish at species level, with a standard ellipse area ( $SEA_B$ ) almost 5 times greater than noble crayfish (Fig. 2A,B). However within-lake populations of the two species indicated comparable niche widths, as signal and noble crayfish, albeit with considerable variation, had similar  $SEA_B$ . Furthermore, signal and noble crayfish used the same food resources in similar proportions (I) indicating an equivalent role in the food web structure in the littoral zone of these study lakes. Olsson *et al.* (2009) found the same from their study of a set of Swedish streams, where the two species also exhibited similar niche widths among populations but at species level signal crayfish had a wider trophic niche than noble crayfish.

Overall signal crayfish  $\delta^{13}C_c$  had a wider range than that of noble crayfish. This was mainly due to the  $\delta^{13}C_c$  range of some lakes where crayfish C signatures indicated wider variation and thus a wider trophic niche. Ruokonen *et al.* (2012) found that individual signal crayfish caught from the littoral in large Lake Pääjärvi had smaller trophic niche than those sampled from the profundal. Lake Iso-Tarus, which had the largest crayfish C signature range of the study lakes (I), registered low values of sublittoral macroinvertebrate abundance and species richness (III), but among the highest in the littoral, whereas signal crayfish lakes with the smallest crayfish carbon signature range, like lakes Ala-Karkijärvi and Syväjärvi, exhibited an opposite pattern. This suggests that where signal crayfish forage more on sublittoral communities they more acutely reduce the sublittoral macroinvertebrate density and species richness, and broaden their own  $\delta^{13}C$  population range.

The equivalent within-lake trophic niche widths exhibited by the two crayfish species, according to SIA (I), were consistent with the findings of II where the two crayfish species were found to affect littoral macroinvertebrate

communities in a similar way (Fig. 2C,E,G). This suggests that the two aspects can be viewed as cause and effect. Nevertheless, although the similarity in the trophic niche widths found between signal and noble crayfish at within-lake population level could be translated to similar effects on littoral macroinvertebrate communities (I), the same could not be said for the wider signal crayfish trophic niche width than that of noble crayfish found at species level. This difference suggests a somewhat wider overall feeding range for signal crayfish, presumably able to exploit some additional resources or habitats than noble crayfish. Ruokonen *et al.* (2012) have reported that signal crayfish can colonise deeper zones in larger Finnish boreal lakes compared with noble crayfish which prefer the shallower littoral zone (Westman *et al.* 2002). The larger signal crayfish trophic niche width found at species level then led to further investigations to explore the effects of the two crayfish species at a larger spatial scale. In particular, the sublittoral habitat was included for the studied lakes, which, although not deep enough to have a true profundal, contained sublittoral macroinvertebrate communities that could be a potential target on which signal crayfish could exert further effects.

### 3.2 Crayfish impacts on macroinvertebrate communities (II, III)

There were no differences in the total littoral macroinvertebrate abundance between signal, noble and control lake categories (Fig. 2C). However, species richness (Fig. 2E) and Shannon diversity index were significantly lower in signal and noble crayfish lakes than in the control lakes (II). The two crayfish species mostly exhibited similar effects on abundance and species richness, as Lagrue *et al.* (2014) found in a recent study conducted in a French stream where invasive signal crayfish and native noble crayfish had similar effects on macroinvertebrate community density and species richness. However, in the Finnish study lakes the two species had different effects on some macroinvertebrate taxonomic groups. For example, signal crayfish had negative effects on snail species richness, as has been widely demonstrated in previous studies (Lodge *et al.* 1994, Dorn and Wojdak 2004, Klose and Cooper 2012, Ruokonen *et al.* 2014), but in the Finnish study lakes signal crayfish effects were stronger than those of noble crayfish. Similar negative effects were obtained from IV, where the presence of signal crayfish substantially reduced the species richness, especially of snail taxa, compared to non-crayfish and crayfish introduction sites, where the value was generally higher.

In contrast, sublittoral macroinvertebrate abundance, species richness and community composition were substantially different between signal and noble crayfish lakes (Fig. 2D,F,H). Indeed all measurements were negatively affected by the presence of signal crayfish, whereas values were comparable between noble crayfish and control lake categories (Fig. 2D,F,H). These greater impacts of the invasive as compared to native species on native macroinvertebrate communities in the sublittoral zone are in line, though from a different habitat,

with recent findings of field studies and meta-analyses (Nyström *et al.* 1999, Dunojer *et al.* 2013, Twardochleb *et al.* 2013). These effects on sublittoral communities might support the view that invasive signal crayfish can exert stronger negative effects than native noble crayfish on the recipient ecosystem. Moreover this might be one crucial explanation for the wider trophic niche width at species level revealed by stable isotope analyses (Fig. 2A).

As reported from previous studies (Hansen *et al.* 2013, Ruokonen *et al.* 2014), the different effects shown by crayfish on macroinvertebrate communities in two different habitats, littoral and sublittoral, suggest that crayfish impacts are habitat-specific. Furthermore, and as demonstrated by previous studies (Dorn 2013, Dunoyer *et al.* 2013, Jackson *et al.* 2014), the results in this thesis indicate that crayfish effects are also species-specific, and hence that they cannot be generalized for every habitat and condition.

Indicator species analysis (ISA) revealed differences in sublittoral macroinvertebrate composition between lake categories where *Tanytarsus* and *Dicrotendipes* (Chironomidae), and *Ephemera vulgata* and *Caenis luctuosa* (Ephemeroptera), were distinctive for noble crayfish and control lake categories, whereas *Ecnomus tenellus* (Trichoptera) was characteristic of control lakes. However, no taxa were distinctive for signal crayfish lakes. Thus, while Chironomidae, Ephemeroptera and Trichoptera were taxa most affected by signal crayfish in the sublittoral habitat (III), Gastropoda, Bivalvia and Odonata were those groups in the littoral habitat whose abundance and species richness were negatively influenced by both signal and noble crayfish (II). This reflects the difference in food availability from the two different habitats, and supports the habitat-specific effects of crayfish species.

### **3.3 Temporal effects of signal crayfish on littoral macroinvertebrate communities (IV)**

This study of crayfish impacts on macroinvertebrate communities in small and medium-sized boreal lakes, although conducted at the whole-lake scale with replicate lakes in each of three crayfish status categories, was based on samples collected at a single point in time. To complement this temporal variation of the effects of signal crayfish and development of these effects over time were also explored using three contrasting sites in large Lake Päijänne (IV). The three study sites were without crayfish, with an established crayfish population, and with an attempt to introduce and establish a new crayfish population. In fact, the attempt to introduce a signal crayfish population at the Saalahti site was not considered successful; the low mean CPUE (0.19) revealed that a population was not established during the follow up period. Sandström *et al.* (2014) highlighted how invasive populations of signal crayfish are inclined to instability. However, temporally consistent differences in macroinvertebrate



community composition were detected between the three sites indicating that crayfish status influenced macroinvertebrate assemblage structure. Presence of an established signal crayfish population negatively affected littoral macroinvertebrate species richness, snail richness and community composition, and the structure of the macroinvertebrate community, compared to introduction and non-crayfish sites in which values did not differ.

These results are consistent with those of a spatial comparative study by Ruokonen *et al.* (2014) from Lake Päijänne, which found that signal crayfish affected macroinvertebrate community composition and strongly reduced species richness, and snail density and richness. Moreover, they found comparable overall macroinvertebrate densities between crayfish and non-crayfish sites in line with results in IV but in contrast with previous studies (Nilsson *et al.* 2012, Twardochleb *et al.* 2013). Although snail richness showed temporal stability between sites, macroinvertebrate and snail densities indicated crayfish status effects through the years studied. The crayfish introduction site revealed a significant difference from the non-crayfish and established crayfish sites, in particular in 2007 and 2009 following the introduction of signal crayfish; contrary to our expectation there was an overall increase in macroinvertebrate and snail density and richness following the crayfish introduction. Thus the significant differences detected across sites and time, for macroinvertebrate species richness were apparently not simply due to the crayfish status of the sites. Nevertheless, at the established crayfish site macroinvertebrate density and species richness generally registered low values over the years but suddenly increased in 2011 following an evident collapse of the signal crayfish population in 2010. As indicated by Hansen *et al.* (2013), macroinvertebrate communities have the ability to respond promptly to a decline in crayfish density, returning close to their original condition.

In the study of Päijänne, littoral benthic fish density exhibited substantial temporal variation within study sites, but no consistent differences between the three sites of different crayfish status. Contrasting previous studies have reported that invasive crayfish can affect benthic fish density (Wilson *et al.* 2004, Carpenter 2005, Hirsch and Fischer 2008) or do not have any significant influence on littoral fish (Ruokonen *et al.* 2012). Thus effects on littoral benthic fish communities probably can be expected to vary considerably, depending on the density and size structure of the crayfish population, the fish species present, and the littoral habitat structure.

The results for periphyton biomass were similar to those found by Ruokonen *et al.* (2014) in that, although indicating high variation within sites and a mainly similar temporal pattern among years, crayfish and non-crayfish sites showed comparable values. Thus in this study signal crayfish status seemed not to affect periphyton biomass, which was probably governed instead by other factors as suggested by Twardochleb *et al.* (2013).



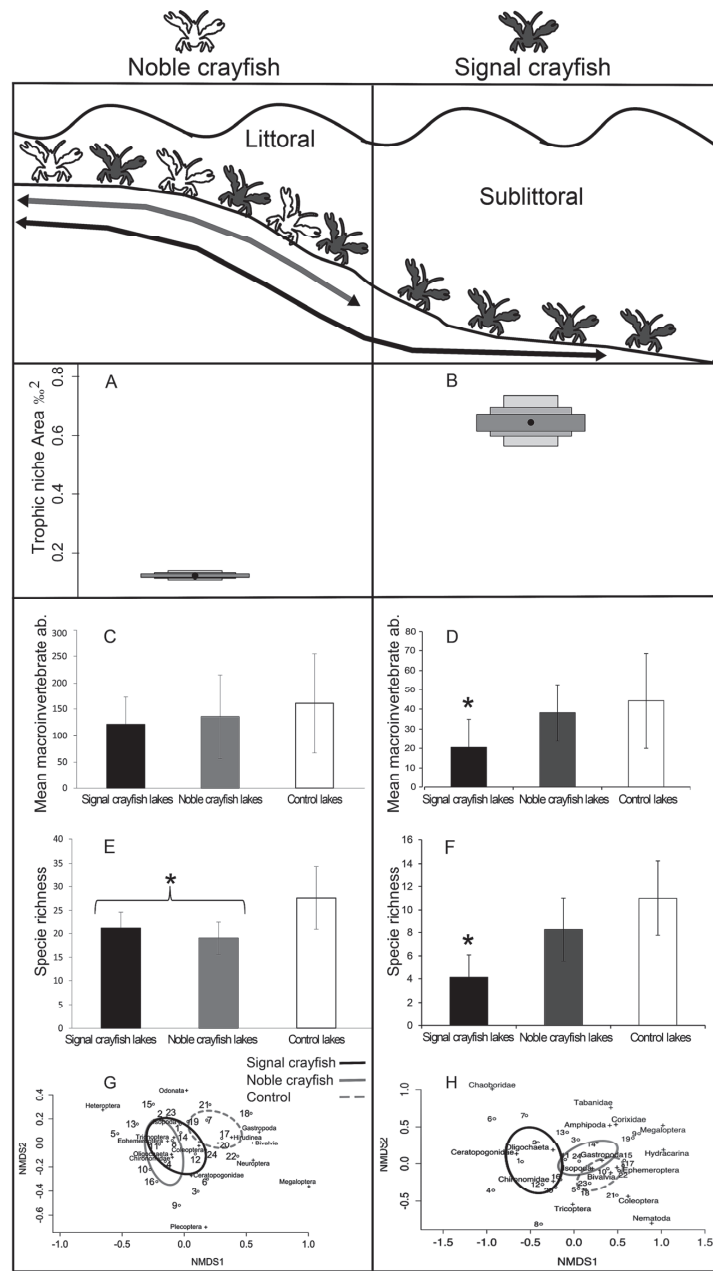


FIGURE 2 Trophic niche areas of noble (A) and signal (B) crayfish. The black point in each box corresponds to the mean standard ellipse area ( $SEA_B$ ) obtained for each species. Box areas represent the 95 % (light grey), 75 % (grey) and 50 % (dark grey) Bayesian credibility confidence intervals. Also shown are macroinvertebrate abundance (C,D), species richness (E,F) and NMDS ordination (G,H) for noble crayfish and signal crayfish in littoral and sublittoral habitat. Asterisks represent significant differences between lake categories for the respective measurements.

## 4 CONCLUSIONS

The introduction of non-native invasive species is recognized as one of the main threats to freshwater biodiversity. Invasive crayfish species are nowadays among the most introduced species worldwide and evaluation of their impacts on native species and ecosystem functioning are needed to understand and improve management of invasive species as well as conservation of native species. Many previous studies have dealt with the impacts of invasive crayfish on native communities, but have mainly been conducted at small spatial and temporal scales. In particular, many studies have involved small-scale, controlled field, mesocosm or laboratory experiments, which can overestimate or underestimate certain impacts, leading to difficulties in extrapolating findings to natural conditions. This has led to recommendations to expand studies of the effects of invasive crayfish to a wider spatial scale at the ecosystem level and if possible incorporating long-term studies. In the light of that this thesis provides one of the few comprehensive studies to date comparing and evaluating the impacts of invasive signal crayfish and native noble crayfish species in boreal lakes at realistic scales. The studies at the whole-lake scale, using 8 replicate lakes in each of 3 categories with different crayfish status, provide results at relevant ecological scales. Even though for practical reasons the results necessarily derive from a single sampling date for each lake, and from a single habitat type (stony shores), I believe these results offer a particularly sound basis for informing strategies for managing crayfish in boreal lakes.

The results showed that signal and noble crayfish had similar impacts on macroinvertebrate abundance, species richness and community composition in the littoral habitat of the study lakes. However, the two species showed different effects in the sublittoral zone, where signal crayfish had stronger negative effects than noble crayfish on the macroinvertebrate community. These effects were clearly shown in the macroinvertebrate community composition where signal crayfish lakes were clearly separated from the noble crayfish and control lake categories. Snail abundance and species richness were evidently affected by crayfish, but in littoral habitat were reduced by both crayfish species,

whereas in the sublittoral signal crayfish exerted stronger negative effects than noble crayfish. Moreover, signal crayfish generally also posed negative effects on macroinvertebrate communities in the littoral of large Lake Päijänne, and especially on snail abundance and richness, as shown by a substantial differentiation between sites (crayfish status), albeit with high variation. However, the long-term monitoring of effects of signal crayfish revealed between-years variation for the sites for macroinvertebrate communities, periphyton biomass and littoral fish density.

For an invasive species to successfully establish in a new ecosystem it must overcome a number of challenges, including finding an environment with suitable abiotic and biotic characteristics, obtaining sufficient resources for its maintenance, growth and reproduction, and avoiding pre-reproductive mortality. Consequently the successful establishment of a stable population of an invasive species largely depends on its traits. Signal crayfish is considered to be one of the most successful invasive crayfish species due to its strong adaptive capability. This is especially well-known in Europe, where the wide spreading of the translocated signal crayfish has long attracted the attention of management policy makers in many countries to monitoring and assessing its potential impacts (Reynolds and Souty-Grosset 2012).

The results in this thesis highlighted the habitat-specific and species-specific effects of this pair of crayfish species, shining a clearer light not only on the ecological role of the invasive signal crayfish but also on that of the native noble crayfish. I stress caution in making any generalizations when assessing and comparing impacts of single or multiple crayfish species in different habitats or ecosystems. Furthermore, I recommend care in the “Ark-site” approach to conserving threatened native crayfish, as the thesis demonstrated that native noble crayfish affected littoral macroinvertebrate communities similarly to the invasive signal crayfish. Consequently the native species may equally be viewed as a potentially harmful non-indigenous species when plans are being considered to introduce and stock the native species into lakes that historically have not contained crayfish.

Although the results from Lake Päijänne did not reveal any immediate effects of signal crayfish on littoral communities at the introduction site, but constant effects at the established crayfish site, particularly on diversity of invertebrate and snails richness, the combination of space-for-time and long-term study approaches adopted in the thesis for evaluation of impacts of signal crayfish, provided a wider exploration of the invasive species effects. Such approaches offer the chance to assess effective monitoring and action plans, as well as to predict future implications of the impacts for native biota.

The commercial and recreational crayfish fisheries in Finland provide a good example of exploitation of a valued resource, currently utilizing both native noble crayfish and introduced signal crayfish. However, there has been a pressing need to assess whether the two species can really be considered ecologically equivalent or if they act differently on lake communities, and in particular to evaluate whether invasive signal crayfish exert stronger effects than noble crayfish. I believe my thesis contributes to a better understanding of

the potential impacts of invasive signal crayfish on native lake communities and therefore to prevention of deliberate or accidental introductions of this species. However, the comparisons between the two species will be useful not only in the control and management of the invasive signal crayfish, but also for developing a more robust conservation strategy for native noble crayfish.

*Acknowledgements*

This doctoral thesis has been the result of such intense work and fruitful cooperation, it would not have been possible without all people directly or indirectly involved during the last five years of my study. I am most indebted to my supervisors Prof. Roger Jones, Dr Heikki Hämäläinen and Dr Timo Ruokonen for their help and support during my PhD studies. I will never end to thank Roger for the great opportunity he gave me for growing professionally day by day as scientist, and for believing in me. I thank him for introducing me the fascinating world of stable isotopes, and also for his helpfulness and invaluable advises. My deepest gratitude to Heikki who guided me through the research always available when I needed further clarification and help. I am thankful for Heikki for his friendly way he followed me, leaving me do research independently, learning by doing and improving by mistakes. This research would have not been possible without the great support of Timo Ruokonen with whom I shared field work, opinion, new ideas, helpful criticisms and productive coffee-breaks. Timo helped me from the beginning making the start of my research very smooth; I would have been lost without your help. I am also thankful to Professor Juha Karjalainen and Senior Lecturer Jari Haimi, members in my thesis support group (BIOINT), who always encouraged and supported me. I am grateful to Markku Pursiainen and the co-author Esa Erkamo, (FGFRI) to have provided the study area and lakes selection.

A special thanks to the Aquatic Sciences section people for their helpfulness and for making me feel welcome, in particular Tuula, Mikko, Jari, Timo Marjomäki, Jonna, Hannu, Juhani, Katja, Jatta, Jouni and Toni.

My deepest thanks to my roommates Paulina, Jyrki, Sanni and my ex-roommate Antti for making the busy working days very enjoyable and funny, especially during the not easy long winters.

I want to thank master-students involved in my project for their valuable contribute to my research, Kimmo Sivonen with whom I shared long hard-working days in the field, Sofia Koistinen, co-author, and Polain Nzobeuh who both helped me in the never ending macroinvertebrate identification, thank you very much for the great work.

I thank Adriano, for all the pleasant scientific discussions during our breaks. My special thanks to my father Ladino and my mother Anna Maria "*anche se lontani siete sempre in me presenti*".

Finally, my two gorgeous daughters Anja and Enni, sons of my life everywhere I am, and Sonia my wife, vital inspiration and adventures companion, thank you for your incommensurable patience and especially for believing in me.

The study was funded by Finnish Cultural Foundation (2011) and by Maj and Tor Nessling Foundation (2012–2014). I would like also to thank the Biological Interactions Graduate School (BIOINT) for the opportunity to share my research project during such stimulating meeting.

## YHTEENVETO (RÉSUMÉ IN FINNISH)

### Vieraslaji täpläravun ja alkuperäisen jokiravun ekologisten vaikutusten vertailu boreaalisisä järvisä

Luonnon monimuotoisuudella on merkittävä yhteiskunnallinen ja kulttuurillinen arvo, mutta ihminen aiheuttaa sille monia uhkia. Ihmisen tarkoituksellisesti tai tahattomasti uusille alueille levittämät vieraslajit ovat maailmanlaajuisesti yksi suurimmista luonnon monimuotoisuuden vaarantajista. Pohjoisamerikkalainen täpläräpu (*Pacifastacus leniusculus* Dana) on esimerkki ihmisen laajalti Eurooppaan siirtämistä vieraslajeista. Suomeen täpläräpu tuotiin ensi kertaa 1960-luvulla, ja laajamittaiset istutukset aloitettiin 1990-luvun alussa. Vaikka rapuistutuksia on pyritty lupakäytännöin rajaamaan eteläiseen Suomeen, on selvää, että ilman valvonnan tehostamista yhä suurempi osa järvistämme tulee täplärävun asuttamiksi. Täpläräpu on levittämänsä rapuruton sekä syrjäyttävän kilpailun kautta uhka alkuperäisille rapulajeille, Suomessa jokiravulle (*Astacus astacus* L). Osassa istutusvesistöjä ei ole ollut aiemmin lainkaan rapuja, joten näissä täpläräpu on kokonaan uusi ja merkittävä ekosysteemin osakas.

Ravut ovat moniruokaisia, ja ne käyttävät sekä elävää että kuollutta kasvi- ja eläinravintoa kaikilta ravintoketjun tasoilta. Lisäksi ne lukeutuvat itse monien petokalojen saalisvalikoimaan. Ravut voivat säädellä muiden eliölaajien populaatioita suoraan saalistamalla, epäsuorien biologisten vuorovaikutusten välityksellä tai muuttamalla elinympäristön rakennetta. Ravuilla on näin todennäköisesti merkittävä rooli ravintoverkoissa ja siten koko vesiekosysteemeissä, mutta niiden ekologiset vaikutukset tunnetaan vielä verrattain huonosti. Koska alkuperäisten lajien elinympäristön laajentamiseen suojelutarkoituksessa ja toisaalta vieraslajien istutusten lisäämiseen raputalouden kehittämisen kannalta on suuria paineita, on tärkeää tietää, mitä ekologisia vaikutuksia ravuilla on ja miten eri rapulajit tässä suhteessa mahdollisesti poikkeavat toisistaan. Tutkimusten perusteella ravuilla voi olla merkittäviä vaikutuksia elinympäristön rakentamiseen, eliöyhteisöihin ja ekosysteemien energia- ja ainevirtoihin. Arviot vaikutuksista perustuvat pääosin pienen tila- ja aikamittakaavan kokeellisiin tutkimuksiin, eikä niitä voi varauksetta soveltaa luontoon. Siksi on tärkeää tutkia vaikutuksia myös realistista aika- ja tilaulottuutta edustavissa, vaihtelevissa luonnon olosuhteissa. Tämän väitöskirjatutkimuksen päätavoitteena oli kenttä-tutkimusten perusteella selvittää alkuperäisen jokirävun ja vieraan täplärävun asemaa ravintoverkossa sekä erityisesti vaikutuksia boreaalisten järvien pohja-eläinyhteisöihin, ja näin pyrkiä arvioimaan lajien ekologisten vaikutusten rinnastettavuutta.

Tutkimukseen valittiin 24 ympäristöpiirteiltään mahdollisimman samantyyppistä pientä tai keskisuurta etelä- ja keskisuomalaisista järveä, joista kolmasosassa oli jokiräpukanta, kolmasosassa täpläräpukanta ja kolmasosassa ei lainkaan rapuja. Rapulajien käyttämää ravintoa ja ravinnonkäytön laajuutta verrattiin järvien (populaatioiden) sisällä sekä niiden välillä isotooppianalyysillä hiilen ja typen vakaita isotooppeja käyttäen. Rapujen vaikutuksia pohjaeläimistöön run-

sauteen, lajikirjoon sekä lajikoostumukseen tutkittiin molempien lajien suosi-  
milla matalilla kivikkorannoilla. Aiemmista tutkimuksista tiedettiin, että ravut  
voivat saalistamalla vähentää monien selkärangattomien, erityisesti kotiloiden,  
runsautta ja lajimäärää. Aiemmat havainnot viittaavat täplärapujen elävän jär-  
vissä myös syvemmillä ja suojattommilla pohjilla kuin jokiravut. Näin täplä-  
ravun vaikutuksen voi odottaa olevan jokirapua voimakkaampi syvemmillä.  
Tätä hypoteesia testattiin tutkimalla rapujen vaikutusta myös sublitoraalin  
pehmeiden pohjien selkärangatonyhteisöihin. Lisäksi tutkittiin täpläravun eko-  
logisia vaikutuksia ja niiden ajallista vaihtelua seuraamalla Päijänteen kivikko-  
rantojen rapukannan, kalaston, pohjaeläimistön ja päällysläyväbiomassan vuosi-  
en välistä vaihtelua 5 vuoden ajan paikalla, jossa on tiheä rapukanta, ravutto-  
malla vertailupaikalla sekä paikalla, johon rapu istutettiin seurantajakson alus-  
sa.

Isotooppianalyysien perusteella jokirapu ja täplärapu käyttävät järvis-  
sämme varsin samankaltaista ravintoa. Ravinnonkäytön laajuudessa järvien  
sisällä oli lajinsisäistä vaihtelua, mutta lajien välillä ei havaittu eroa. Sen sijaan  
lajin sisäinen (järvien välinen) vaihtelu oli suurempi täpläravulla, mikä viittaa  
siihen, että sen ekolokero on suurempi kuin jokiravun. Tulokset ovat yhtäpitä-  
viä aiemman Ruotsin virtavesissä tehdyn tutkimuksen kanssa.

Rapujen asuttamien järvien kivikkorantojen pohjaeläimistö oli lajistoltaan  
merkittävästi niukempi kuin ravuttomissa vertailujärvissä ja myös lajikoostu-  
mus johdonmukaisesti poikkeava. Esimerkiksi kotiloiden runsaus ja lajimäärä  
oli rapujärvissä vähentynyt. Yhtäpitävästi edeltävän isotooppitutkimuksen  
kanssa molempien rapulajien vaikutus pohjaeläimistöön oli kuitenkin saman-  
lainen.

Sen sijaan asetettua hypoteesia noudatellen täplärapujärvien syvemmän  
vyöhykkeen pehmeiden pohjien pohjaeläimistön runsaus ja lajimäärä olivat  
pienentyneet ja yhteisökoostumus muista järvistä poikkeava. Jokiravulla puo-  
lestaan ei ollut vaikutusta pohjaeläimistöön syvemmillä alueilla.

Päijänteen kivikkorantojen eliöyhteisöissä oli voimakasta vuosien välistä  
vaihtelua, mutta ravullisten ja ravuttomien rantojen erot tai niiden puuttumi-  
nen pysyivät ajallisesti vakaina. Kalastossa ja päällysläyväbiomassassa ei ollut  
eroa rapujen asuttaman ja ravuttoman paikan välillä. Sen sijaan pohjaeläinten  
lajimäärä, erityisesti kotiloiden runsaus ja lajikirjo, olivat rapupaikalla vuodesta  
riippumatta pienempiä kuin ravuttomilla paikoilla. Tulokset ovat yhtäpitäviä  
aiemman pelkästään tilassa tehdyn vertailututkimuksen kanssa. Istutuspaikan  
rapukanta kehittyi hitaasti tutkimusjaksolla, joten rapujen vaikutusten ajallista  
kehittymistäkään ei voitu havaita.

Luonnonmittakaavassa toteutetun tutkimuksen tulokset osoittavat, että  
ravuilla on järvissä merkittävä vaikutus rantavyöhykkeen pohjaeläimistöön ja  
siten oletettavasti myös laajemmin ravintoverkkoihin. Tulokset osoittavat, että  
rapujen vaikutukset ovat osin laji- ja elinympäristöriippuvaisia, eikä niitä voida  
yleistää. Matalilla rannoilla jokiravun vaikutus on yhtä voimakas kuin täplära-  
vun, joten myös jokiravulla voi olla haitalliseksi katsottavia vaikutuksia silloin,  
kun se istutetaan uusiin vesistöihin. Alkuperäisen levinneisyysalueensa ulko-

puolella jokirapu on täpläravun tapaan vieraslaji. Koska täpläravun ekosysteemi-vaikutukset ulottuvat laajemmalle kuin jokiravun, ei täpläravulla voida varauksetta korvata jokirapua ekosysteemin osakkaana edes niissä järvissä, joihin alkuperäistä jokirapua ei toistaiseksi ole onnistuttu palauttamaan. Tutkimuksen tulokset toivat merkittävää uutta tietoa rapujen merkityksestä järviekosysteemeissä, ja niitä voidaan hyödyntää vieraslaji täplärapuun perustuvan raputalouden säätelyssä sekä alkuperäisen jokiravunlajin suojelussa.



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**ORIGINAL PAPERS**

**I**

**DOES THE INTRODUCED SIGNAL CRAYFISH OCCUPY AN  
EQUIVALENT TROPHIC NICHE TO THE LOST NATIVE  
NOBLE CRAYFISH IN BOREAL LAKES?**

by

Fabio Ercoli, Timo J. Ruokonen, Heikki Hämäläinen & Roger I. Jones 2014

Biological Invasions 16: 2025–2036.

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## II

# COMPARING THE EFFECTS OF INTRODUCED SIGNAL CRAYFISH AND NATIVE NOBLE CRAYFISH ON THE LITTORAL INVERTEBRATE ASSEMBLAGES OF BOREAL LAKES

by

Fabio Ercoli, Timo J. Ruokonen, Esa Erkamo, Roger I. Jones & Heikki  
Hämäläinen 2014

Accepted manuscript

### **III**

## **THE INTRODUCED SIGNAL CRAYFISH AND NATIVE NOBLE CRAYFISH HAVE DIFFERENT EFFECTS ON SUBLITTORAL INVERTEBRATE COMMUNITIES OF BOREAL LAKES**

by

Fabio Ercoli, Timo J. Ruokonen, Sofia Koistinen, Roger I. Jones & Heikki  
Hämäläinen 2014

Submitted manuscript



## **IV**

### **ARE EFFECTS OF AN INVASIVE CRAYFISH ON LAKE LITTORAL COMMUNITIES CONSISTENT OVER TIME?**

by

Timo J. Ruokonen, Fabio Ercoli & Heikki Hämäläinen 2014

Submitted manuscript