

Timo Ruokonen

Ecological Impacts of Invasive Signal Crayfish in Large Boreal Lakes



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Timo Marjomäki

Department of Biological and Environmental Science, University of Jyväskylä

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Department of Biological and Environmental Science, University of Jyväskylä

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ABSTRACT

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Yhteenveto: Täpläravun ekologiset vaikutukset suurissa boreaalisissa järvissä
Diss.

Freshwaters suffer strongly from anthropogenic disturbances and are among the most endangered ecosystems in the world. Spread of non-native species is a major reason for decreased biodiversity and impaired function of aquatic ecosystems. This thesis investigated impacts of the widely spread North American signal crayfish (*Pacifastacus leniusculus* (Dana)) in large boreal lakes across varying habitats and biotic compartments of the ecosystem. The results showed that signal crayfish has detrimental effects on native macroinvertebrate taxa richness and community composition, but that the impacts are habitat specific, being pronounced only at stony shores. Analysis of stable isotopes revealed that signal crayfish are mostly predators in the studied lakes and share basal food sources with littoral benthic fish. However, regardless of the evident niche overlap, the presence of crayfish had no effect on density, size or diet of the benthic fish. To complete their life cycles, many parasites of fish need invertebrates as intermediate hosts. Hence, signal crayfish, by inducing changes in the benthic invertebrate fauna, might indirectly affect parasites of native fish. In support of this expectation, the study documented lower parasite abundances in perch (*Perca fluviatilis* L.) inhabiting sites with crayfish. The potential of signal crayfish to increase connectivity between littoral, profundal and terrestrial habitats was studied using a stable isotope mixing model and trophic niche estimation. The results suggested that mobile signal crayfish creates a new link between littoral and profundal areas and thereby increases connectivity between these spatially distinct habitats. In summary, the results of this study carried out in a natural setting and at ecologically relevant spatial and temporal scales, showed that signal crayfish can have wider ecological impacts than previously anticipated. These impacts should be taken into consideration in management of the spread of crayfish populations if the biodiversity and valuable natural resources in large lakes are to be maintained.

Keywords: Habitat connectivity; invasive species; native fish; macroinvertebrates; *Pacifastacus leniusculus*; parasites

Timo Ruokonen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address Timo Ruokonen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
timo.j.ruokonen@jyu.fi

Supervisors Dr. Heikki Hämäläinen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Professor Juha Karjalainen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Reviewers Professor Timo Muotka
Department of Biology
P.O. Box 8000
90014 University of Oulu
Finland

Dr. Francesca Gherardi
Dipartimento di Biologia Evoluzionistica 'Leo Pardi'
Università degli Studi di Firenze
Via Romana 17
50125 Firenze
Italy

Opponent Dr. Per Nyström
Ekoll AB
Majgatan 17b
215 65 Malmö
Sweden

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV. I planned the studies with Heikki Hämäläinen (I, II, III), Juha Karjalainen (I, II, III), Katja Pulkkinen (III) and Mikko Kiljunen (IV). I was responsible for the site selection and the data collection for all the studies. I did most of the laboratory work, analysed the data and wrote the first draft of I, II and IV. In III, Katja Pulkkinen was the responsible author, while I did the data analysis and contributed to writing the first manuscript draft. All the papers were finished together with all co-authors.

- I Ruokonen T.J., Karjalainen J. & Hämäläinen H. 2012. Impacts of an invasive crayfish on the littoral macroinvertebrate communities of large boreal lakes are habitat-specific. Submitted manuscript.
- II Ruokonen T.J., Karjalainen J., Kiljunen M., Pursiainen M. & Hämäläinen H. 2012. Do introduced crayfish affect benthic fish in stony littoral habitats of large boreal lakes? *Biological Invasions* 14: 813–825.
- III Pulkkinen K., Ruokonen T.J., Mykrä M., Tambe G., Karjalainen J. & Hämäläinen H. 2012. Indirect effects of invasive crayfish on native fish parasites. Submitted manuscript.
- IV Ruokonen T.J., Kiljunen M., Karjalainen J. & Hämäläinen H. 2012. Invasive crayfish increase habitat connectivity in large boreal lakes. Submitted manuscript.

1 INTRODUCTION

Freshwaters constitute a tiny fraction of the Earth's surface but support high biodiversity and offer valuable natural resources (Dudgeon et al. 2006). Unfortunately, freshwaters suffer severely from anthropogenic disturbances and are among the most endangered ecosystems (Strayer & Dudgeon 2010). Invasion by non-native species is one of the main threats to global biodiversity and the function of ecosystems (Sala et al. 2000). Freshwaters, and lakes in particular, are especially vulnerable to invasions because of extensive release of non-native species strengthened by other anthropogenic impacts (Sala et al. 2000, Dudgeon et al. 2006).

1.1 Invasive crayfish in freshwaters

Numerous freshwater crayfish species have been spread beyond their native range by humans either unintentionally, e.g. with ship ballast waters, or intentionally for aquaculture and to improve the economic value of fisheries (Lodge et al. 2000, Crandall & Buhay 2008). The growing number of non-native crayfish species spread globally via the aquarium trade increases the possibility of releases into natural ecosystems (Holdich et al. 2009). Species originating from North America (e.g. *Orconectes limosus* (Rafinesque), *Pacifastacus leniusculus* (Dana) and *Procambarus clarkii* (Girard)) are the most widely spread non-native crayfish in Europe (Barbaresi & Gherardi 2000, Holdich et al. 2009). Signal crayfish (*Pacifastacus leniusculus* (Dana)) has been introduced to over 20 European countries (Holdich et al. 2009) and spread over a large scale in Sweden and Finland where abundant populations now support commercially and recreationally important fisheries (Ackefors 1999, Kirjavainen & Sipponen 2004).

In Finland, the first signal crayfish introductions were made at the end of the 1960s (Westman 1973). The poor recovery of the native crayfish (*Astacus astacus* L.) populations after repeated crayfish plague outbreaks combined with a growing interest in the management of crayfish stocks prompted massive signal

crayfish introductions at the end of the 1980s (Erkamo et al. 2010). According to Finnish Game and Fisheries Research Institute introduction register nearly 2 million signal crayfish were released into hundreds of lakes and rivers between 1990 and 2006 to compensate for the disappeared native crayfish stocks. As a result, the signal crayfish, with a catch in 2009 estimated to be ca. 4.5 million individuals, has become one of the most economically valuable species in Finnish inland fisheries (Pursiainen et al. 2011).

Several reviews suggest that non-native crayfish can strongly affect native freshwater biota from benthic primary producers to top predators (Nyström 1999, Lodge et al. 2000, Gherardi et al. 2011). Studies conducted in the laboratory, experimental enclosures, wetlands, ponds, lakes and rivers show drastic negative impacts from populations of single species up to the function of whole ecosystems (Dorn & Wojdak 2004, McCarthy et al. 2006). However, invasive species could also facilitate native species (Rodriguez 2006), and non-native crayfish could, for example, provide a new prey source for native predators (Nyström et al. 2006, Tablado et al. 2010).

1.2 Impacts of invasive crayfish on littoral communities

Non-native crayfish can substantially modify lake littoral macroinvertebrate communities by direct and indirect pathways. Crayfish are effective predators of slow moving macroinvertebrates (Nyström et al. 1999, Wilson et al. 2004, McCarthy et al. 2006, Bjurström et al. 2010) and reduction of effective grazers (e.g. snails) could increase periphyton biomass and thereby release resources for other macroinvertebrates (Lodge et al. 1994, Nyström et al. 1999). Alternatively, selective predation could benefit species which are less sensitive to crayfish predation or by affecting relationships between other predators and prey (Nyström et al. 2001). Omnivorous crayfish could also feed on attached algae and detritus (Usio 2000, Gherardi & Lazzara 2006) reducing food resources for other consumers. Crayfish are effective ecosystem engineers (Crooks 2002) and could alter the macroinvertebrate communities by changing the habitat structure (Wilson et al. 2004). Alternatively, crayfish presence could also change the behaviour of the native species leading to increased energy demand and decreased performance (Lewis 2001).

Many freshwater crayfish and benthic fish species prefer similar shallow water stony habitats (Blake & Hart 1993, Guan & Wiles 1997, Fischer 2000a) and use the same food resources such as benthic macroinvertebrates (Welton et al. 1983, Guan & Wiles 1998, Stenroth et al. 2006). Reduced fish population densities and growth rates are often assumed to be related to interspecific competition for habitat and food resources (Griffiths et al. 2004, Carpenter 2005, Light 2005, Hirsch & Fischer 2008). Crayfish can also decrease fish survival via direct predation on eggs, larvae and juveniles (Dorn & Mittelbach 2004). Wilson et al. (2004) found that the decreased density of non-predatory fish in a northern lake was related to macrophyte reduction, food competition and direct predation

caused by invasive rusty crayfish (*Orconectes rusticus* (Girard)). However, the generality of negative impacts of crayfish on native fishes remains in dispute (Stenroth & Nyström 2003, Degerman et al. 2007).

1.3 Invasive species and parasites

The importance and role of parasites in invasions of non-native animals is increasingly recognized (Prenter et al. 2004, Perkins et al. 2008). Invasive species can act as vectors in parasite spread and introduce novel diseases and parasites to natives (Crowl et al. 2008). For example, transmission of crayfish plague (*Aphanomyces astaci*) from North American signal crayfish to native European crayfish species has been highly detrimental to native crayfish stocks (Edgerton et al. 2004). Invasive species could also modify the native host-parasite dynamics by diluting parasite effects by acquiring part of the parasite load (Thieltges et al. 2009). In turn, if invaders are preferred hosts of native parasites, they can even amplify the negative effects by spillback of parasites to native hosts (Kelly et al. 2009). Alternatively, invasive species could interfere with native parasite-host transmission by modifying abiotic or biotic interactions within the ecosystem (Thieltges et al. 2009). Several aquatic parasites have complex life cycles with one or more species-specific intermediate hosts (Karvonen et al. 2003, Faltynkova et al. 2009). Transmission between hosts is a critical stage in parasite life-cycles, and if any of the hosts is influenced, either positively or negatively, it will affect the overall parasite performance. For example, crayfish are effective predators of aquatic snails (McCarthy et al. 2006), which are important intermediate hosts of many fish parasites. Invasive crayfish might thereby affect native parasites and hence have indirect impacts more far-reaching than previously anticipated.

1.4 Habitat connectivity in lakes: role of invasive crayfish?

Littoral and pelagic habitats in lakes are spatially distinct and have traditionally been treated as having discrete food webs. However, recently it has been better appreciated that these habitats and food webs are often integrated by movements of matter and energy across habitat boundaries (Vander Zanden & Vadeboncoeur 2002, Vanni 2002). Among other impacts, invasive species have been shown to change ecosystem processes and energy dynamics in lakes (Vander Zanden et al. 1999, Eby et al. 2006). Crayfish typically inhabit littoral areas in lakes (Abrahamsson & Goldman 1970, Lodge & Hill 1994), but as biotic interactions reach also across habitat boundaries (Holomuzki et al. 2010), broader scale direct and indirect impacts related to crayfish invasion are probable.

Mobile animals transfer organic matter and energy across habitats in freshwater ecosystems (Covich et al. 1999, Schindler & Scheuerell 2002). For instance, cross-habitat foraging of mobile predators is an important pathway of

energy transfer and one of the main factors connecting spatially distinct habitats in lakes (Vander Zanden & Vadeboncoeur 2002, Dolson et al. 2009). Signal crayfish use a wide range of littoral and profundal habitats in large lakes (Abrahamsson & Goldman 1970, Flint 1977) and in general crayfish can travel tens to hundreds of meters in 24 hours (Byron & Wilson 2001, Bubb et al. 2004). Therefore, non-native signal crayfish appear to represent a potential new link between spatially distinct littoral and profundal habitats in large boreal lakes. Animals can also be important links in energy transfer between aquatic and terrestrial environments (Nakano & Murakami 2001, Vander Zanden & Gratton 2011). As the omnivorous crayfish are known to utilize a wide range of food sources, including allochthonous detritus (Stenroth et al. 2006), they could also increase connectivity between terrestrial and aquatic environments (Usio 2000).

The use of stable isotopes as intrinsic biochemical markers is considered an effective technique for providing information about feeding by animals because their tissues reflect the isotope values of their food (Rubenstein & Hobson 2004). When there are clear distinctions in isotope values among food sources in different habitats, this information can be used to track movements (e.g. Hobson et al. 2003) and energy pathways across habitats (Peterson & Fry 1987, Vander Zanden et al. 2006). In lakes, three main basal resources (littoral benthic production, pelagic phytoplankton production and terrestrial subsidies) can have distinct $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Syväranta et al. 2006) providing an opportunity to track the movements of crayfish and matter across littoral-profundal gradient and evaluate their potential contribution to habitat connectivity.

1.5 Study aims

Impacts of invasive species are well recognised and during the last 20 years the number of studies reporting new invasions and negative impacts on native biota has extended rapidly (Davis 2009). Although numerous studies have shown the detrimental impacts of invading species on freshwaters, few have included simultaneous examination of several levels of biological organization (Ricciardi & MacIsaac 2011). Furthermore, most of the previous studies on impacts of non-native crayfish on lake littorals have been small-scale experiments in the laboratory, artificial ponds or enclosures. In contrast, investigations of impacts in natural conditions, and especially in large lakes, are still scarce, but crucial, as direct extrapolation of small scale study results to greater spatial scale and more complex environmental settings could be misleading (Lodge et al. 1998, Schindler 1998). The general aim of this thesis was to explore the direct and indirect impacts of non-native signal crayfish on the littoral area of large boreal lakes. To achieve a broader perspective of the impacts at the whole lake ecosystem level, the examination of effects on littoral communities (I, II) were combined with studies on ecosystem effects reflected to other habitats and organisms (III, IV).

The first objective of this thesis was to explore whether signal crayfish change the macroinvertebrate community composition in littoral areas (I). As impacts of invasive species could be influenced by the structure of the invaded ecosystem, different habitat types were investigated. Since periphyton is an important driver of the whole littoral ecosystem and tightly linked with higher trophic levels, the impact of crayfish on periphyton biomass was also studied (I).

The second objective was to investigate whether signal crayfish has negative impacts on littoral fish (II), by comparing community composition and the densities of two common benthic fish species between crayfish and non-crayfish sites. To evaluate whether signal crayfish compete for the same food resources with benthic littoral fish or change fish feeding habits, mixing models and trophic niche estimates based on analyses of stable isotopes of carbon and nitrogen were used.

As biotic relationships in lakes form a complicated network of interactions, the appearance of invasive species might have far reaching indirect ecological effects on the native community members. The third objective was to explore the indirect effects of signal crayfish on perch (*Perca fluviatilis* L.) parasites (III). Crayfish can alter the macroinvertebrate community composition which could interfere with parasite pathways from macroinvertebrate intermediate hosts to the fish main host.

The fourth objective was to widen the scope to the lake ecosystem level and evaluate the potential of signal crayfish to alter energy pathways by increasing habitat connectivity between littoral, profundal and terrestrial areas (IV). That question was approached by using stable isotope analysis of carbon and nitrogen to estimate the contribution of different food sources to the diets of crayfish captured from different habitats. From those data, isotopic feeding niche, crayfish movements and transport of organic matter and energy across the littoral-profundal gradient were inferred.

2 MATERIAL AND METHODS

2.1 Study lakes and site selection

Data for the studies I, II, and III were collected in 2008 from Lake Päijänne (61°31' N, 25° 24' E) and in 2009 from Lake Saimaa (61°15' N, 25° 13' E) (Fig. 1). Päijänne is an oligotrophic lake with a surface area of 1 118 km² with maximum and mean depths of 95 m and 16 m. Saimaa (1 377 km²) is classified as an oligo-mesotrophic in trophic status with 86 m maximum depth and 11 m mean depth.

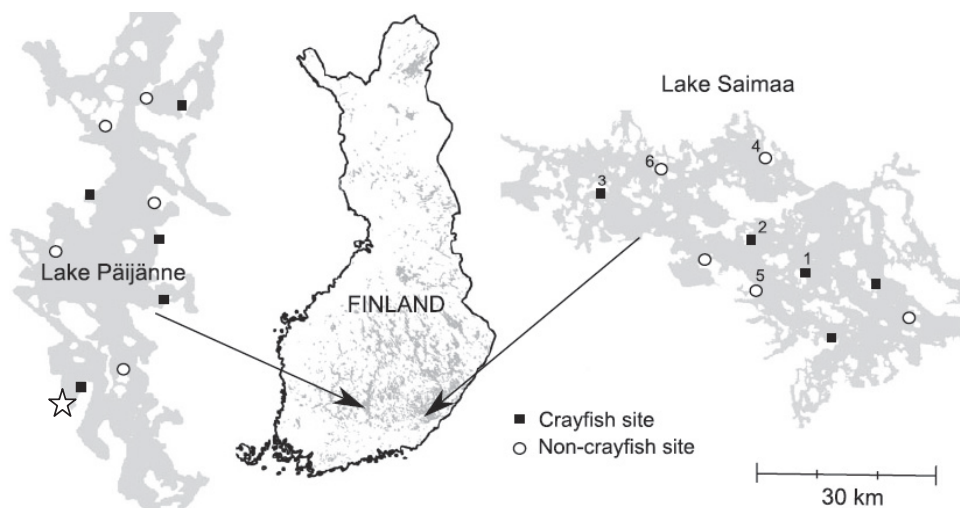


FIGURE 1. Location of study sites (I, II, III) in Lakes Päijänne and Saimaa, Finland. Sites from which stable isotope samples (II) were taken are indicated with numbers from 1 to 6. Location of Nyystölä Bay (IV) is indicated with an asterisk.

The natural distribution of the only Finnish native crayfish species, noble crayfish (*Astacus astacus* L.), was mainly confined to southern rivers and small lakes, and the open water parts of these study lakes were not previously inhabited by crayfish (Järvi 1910). According to Finnish Game and Fisheries Research Institute crayfish introduction register signal crayfish introductions to these lakes started in the 1990s. Despite the intensive introductions and unrecorded transfers within the lakes, the overall distribution of signal crayfish in the study lakes is still patchy (Fig. 1). Finnish inland waters are mostly privately owned and lakes are usually divided into several management units administered by their own shareholder associations (Sipponen 2001). Different shareholder associations have discrete fisheries management policies and strategies on which the introduction of signal crayfish mainly depends. Even though signal crayfish also spread naturally within the lakes, the speed of crayfish dispersal is relatively low (Bubb et al. 2004), and the complex shore structure and the large size of the lakes slow down the complete colonisation.

The present situation thus provided an excellent opportunity to conduct this study in large-scale natural settings. In both lakes, five stony shores and five nearby vegetated shores, both with well-established signal crayfish populations, and five otherwise similar site pairs without crayfish, were selected for the study (Fig. 1). To avoid spatial bias, crayfish and non-crayfish sites were both distributed around the lakes equally in longitudinal and latitudinal directions (Fig. 1).

Data for the study IV were collected in 2009 from Nyystölä Bay of Lake Päijänne (Finland, 61°33' N 25°35' E) (Fig 1). The surface area of Nyystölä Bay is 7 km² with a maximum depth of 30 m. Signal crayfish introductions to the Nyystölä area started in the early 1990s and the crayfish are now abundant all over the bay area supporting a commercially and recreationally important crayfish fishery.

2.2 Data collection and processing

2.2.1 Crayfish and benthic fish abundance

All study sites (I, II, III) were trapped at the end of July to estimate the crayfish abundance (catch per unit effort, CPUE) and to confirm the lack of crayfish at control sites. Since the traps are size-selective (Abrahamsson & Goldman 1970), the method provides an estimate of crayfish abundance (> 30 mm in carapace length). At stony shores, 25 cylindrical traps (mesh size 15 mm) baited with fresh roach (*Rutilus rutilus* L.) were set in transects parallel to the shore line in the 1–3 m depth range at 5 m intervals during the evening and collected the following morning. At vegetated shores 13–15 traps, with equivalent set up as at stony shores, were placed close to the outer edge of the dense macrophyte stands. At the non-crayfish sites, the absence of crayfish was additionally confirmed visually by a scuba diver.

Crayfish abundance at different depths was studied in the Bay of Nyystölä of Lake Päijänne during the collection of crayfish samples (IV) by trapping across the gradient from littoral to profundal areas, divided into 4 depth zones. The depth zone from the shoreline to 3 m represents the productive, well illuminated, littoral habitat with stony bottom. The depth from 3 to 6 m roughly represents the sublittoral transition zone (gravel, some stones) between littoral and deep profundal. The zones from 6 to 9 m and 9 to 20 m both represent soft bottom, deep water, profundal habitat (fine gravel, mud, silt). Traps were set in transects perpendicular to the shore line and extending from the depth of 0.5 m to 15–20 m. Each line consisted of 25 traps at 5 m intervals (total length 125 m) to prevent overlap of effective trapping area (Abrahamsson & Goldman 1970).

Benthic fish community composition and fish density (II) at stony shores were estimated by electrofishing in August using battery-powered backpack electrofishing gear. Electrofishing was conducted along the shore line so that the maximum sampled depth was ca. 80 cm. The sampled area varied from 100 to 250 m². Each captured fish was identified to species, measured for total length and weighed. The total amount of fish caught with the three pass-removal method was used as the minimum population density estimate (individuals 100m² for each species) in the analysis of community composition. To ensure accuracy, population density estimates using the Junge and Libovarsky equation (Bohlin et al. 1989) were calculated for the two most abundant local benthic fish species, bullhead (*Cottus gobio* L.) and stone loach (*Barbatula barbatula* (L.)) (II).

2.2.2 Macroinvertebrate sampling

The macroinvertebrate samples (I) were collected using an ejector pump system operated on a boat. At stony shores, a scuba diver brushed a framed area of 0.25 m² of substrate simultaneously sucking up the loose material to a sieving bucket. At vegetated shores, the sampled area (0.24 m²) was covered with a long net attached to a heavy metal frame (Tolonen et al. 2001). Macrophytes inside the net were first agitated vigorously and then all loose material was sucked to the sieving bucket. At each site, from both habitats, 3 random replicate samples were taken from each depth of 0.5 m, 1 m and 2 m. In addition, 5 replicate soft bottom samples were taken from with an Ekman-grab (0.026 m²) at approximately 2 m distance from the outer edge of the stony substratum at stony shores (depth 3.6–8.5 m). The invertebrates were preserved in 70 % ethanol. In the laboratory, invertebrates were sorted, identified to lowest possible taxon and counted.

2.2.3 Perch collection and parasite examination

Benthic gillnets were used to catch perch for the parasite examination (III). The nets were set during the evening at each site and lifted after 12 h. Fish were collected and immediately frozen in randomly pre-coded plastic bags. In the laboratory, fish were measured, weighed and examined for parasites. The digestive tract, organs (heart, liver, spleen, swim bladder) and left eye were removed, pressed separately between glass plates and examined under a

microscope. During parasite investigation, examiners were unaware of the origin of fish to eliminate subjective bias in the results. Prevalence of infection was calculated as percentage of fish infected within each site and mean abundance as the mean number of parasites per fish within each site. For analyses, parasites were assigned to 4 groups according to their intermediate hosts. Parasites transmitted from snails, mussels, planktonic copepods or isopods (*Asellus aquaticus* L.) each formed one group.

2.2.4 Environmental measurements

Environmental variables are important in structuring lake littoral communities (Fischer 2000b, Tolonen et al. 2001, Nyström et al. 2006). Therefore the factors which are known to be important in shaping communities were measured to control for the environmental variation among sites (I, II, III). Shore slopes were determined by measuring the distance from the shore line to 0.5 m, 1.0 m, 2.0 m and 3.0 m depth from a transect perpendicular to the shore line. Slope for each measure was expressed as the angle between bottom and water surface. An average calculated over these 4 depths was used as the shore slope for each site. The wind-induced disturbance (relative exposure) at each shore was calculated from wind and fetch measurements according to Brodersen (1995). Mean wind values for the open water season (May–November) for 2006–2008 from the nearest observation stations of the Finnish Meteorological Institute were used for the calculations.

At stony shores, substratum particle size at 0.5 m, 1 m and 2 m depth was estimated from 3 replicate plots enclosed with a metallic frame (0.25 m²) using a modified Wentworth's scale (Allan 1995). At vegetated shores, the bottom quality was mostly soft (fine silt/sand or mud) containing a lot of decomposing macrophytes and terrestrial detritus at 0.5 m depth.

Periphyton samples were taken from three depth zones (0.5 m, 1.0 m and 2.0 m) at each stony site. From each depth, one pooled sample (total area of 48.1 cm²) was collected consisting of 5 random subsamples taken from flat stone surfaces using a brush sampler (Meriläinen et al. 1987). In the laboratory, chlorophyll-a (mg m⁻²) was analyzed according to Finnish standard SFS 5772.

2.2.5 Stable isotope analyses (SIA)

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios were analysed using a Carlo Erba Flash EA 1112 elemental analyser connected to a Thermo Finnigan DELTAplusAdvantage continuous-flow isotope ratio mass spectrometer (CF-IRMS) at the Aquatic Sciences laboratory, University of Jyväskylä. The reference materials used were internal standards of known relation to the international standards of Vienna Pee Dee belemnite (for carbon) and atmospheric N₂ (for nitrogen). White muscle tissue of pike (*Esox lucius* L.) and potato leaves (*Solanum tuberosum* L.) with known isotopic compositions were used as internal working standards to ensure the precision of analyses. Two replicate standards were run

after every 6 samples in each sequence. All samples for SIA were freeze-dried to constant weight and powdered for analysis.

Fish samples for SIA (II) were collected from Saimaa at 3 sites with a dense crayfish population and 3 sites without crayfish (Fig. 1) while electrofishing. In the laboratory, weight and total length were measured and a piece of white muscle tissue was dissected from posterior to the dorsal fin for analysis. Crayfish samples were collected by crayfish traps (II, IV), by a scuba diver (II) or by using a pump sampler (II). To study the potential of signal crayfish to increase habitat connectivity (IV), crayfish for the analysis were collected by trapping across the gradient from littoral to profundal areas. In the laboratory, crayfish carapace lengths were measured and, as recommended by Stenroth et al. (2006), a piece of abdominal muscle tissue from each crayfish was dissected for analysis.

The macroinvertebrate samples for SIA (II, IV) were collected from stony littoral using an ejector pump system and a hand net. Additionally, profundal food sources were collected at the open water area (depth ~ 10 m) using an Ekman grab (IV). Pelagic zooplankton, profundal sediment, periphyton, and leaves of deciduous trees (*Betula pendula* Roth., *Alnus glutinosa* (L.)) were collected to represent different food sources and other members of the food web (II, IV).

2.3 Data analyses

2.3.1 Stable isotope mixing models and trophic niche width

The SIAR-package in R (Parnell et al. 2010) was used to create two and three source mixing models to estimate the proportions of different food sources used by littoral benthic fish (II) and crayfish collected from different depths (IV). SIAR utilizes a Bayesian approach, which allows consideration of the variation and uncertainty in isotopic values of consumers and food sources, and which also takes into account the trophic enrichment factors and different assimilation of food sources (Parnell et al. 2010). These model features are especially beneficial in the case of omnivorous crayfish known to utilize food sources with different ratios of carbon and nitrogen.

As no crayfish-specific fractionation corrections were available, commonly used values collected from the literature were used in the SIAR mixing models. For animal tissues correction values of $3.23 \text{ ‰} \pm 0.41$ for $\delta^{15}\text{N}$ and $0.47 \text{ ‰} \pm 1.23$ for $\delta^{13}\text{C}$ were used (Vander Zanden & Rasmussen 2001). As fractionation of plant and algae material is supposed to differ from animal tissue, fractionation values of $2.4 \text{ ‰} \pm 0.42$ for $\delta^{15}\text{N}$ and $0.40 \text{ ‰} \pm 0.28$ for $\delta^{13}\text{C}$ were used for plants and algae (McCutchan et al. 2003).

The variation in stable isotope values is commonly used to measure the width of trophic (feeding) niches and to assess changes or differences in food web structures (Layman et al. 2007b, Olsson et al. 2009). The population level trophic niche widths (total area, TA) of benthic fish and crayfish (II) were

determined from $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values by calculating the convex hull encompassed by the smallest convex polygon containing the individuals from each site in isotopic space (Layman et al. 2007a). Convex hull areas were calculated and visualised using the *adehabitat* package in R.

Isotopic feeding niches for signal crayfish captured from different depths (IV) were determined as standard ellipse areas (SEA) from crayfish location in trophic position and $\delta^{13}\text{C}$ space using the SIBER (Stable Isotope Bayesian Ellipses in R) package (Jackson et al. 2011). Trophic position of each crayfish was estimated using a two-source trophic position model according to (Post 2002).

2.3.2 Statistical analyses

Impacts of crayfish on macroinvertebrate taxa richness (I) and on benthic fish densities and size (II) were tested with two-factor ANOVA. Differences in crayfish stable isotope ratios and trophic position among depth zones were tested using ANCOVA with length of crayfish as covariate (IV). Differences in crayfish length among depth zones and between sexes were tested using 2-factor ANOVA followed by Tukey's pair-wise comparisons (IV). ANOVAs were conducted using R 2.10.0 (R Development Core Team) and with SPSS version 15.0 (SPSS Inc., Chicago, IL, USA).

The impact of crayfish on the macroinvertebrate densities (I) and periphyton biomass (I) were tested with linear mixed effects split-plot models. A generalised linear mixed modelling approach (GLMM) (Zuur et al. 2009) was used to examine the effect of crayfish presence on the prevalence and abundance of perch parasites grouped according to intermediate hosts (III). Models with a binomial error distribution for parasite prevalence and with a Poisson error distribution for parasite abundance were used. Linear mixed effects models and GLMM were conducted R 2.15.0 (R Development Core Team).

The patterns of variation in the macroinvertebrate (I), benthic fish (II), and perch parasite (III) community compositions between crayfish and non-crayfish sites were explored and illustrated by non-metric multidimensional scaling (NMS) ordination. In addition, differences in community composition were tested with Multi-response Permutation Procedures (MRPP), analysis of similarities (ANOSIM) and non-parametric multivariate analysis of variance (perMANOVA) in I, II and III, respectively. The indicator species analysis (ISA; Dufrene & Legendre 1997) was used to distinguish macroinvertebrate taxa which were characteristic of crayfish and non-crayfish sites (I). ANOSIM were performed with the VEGAN-package with R. NMS, MRPP, ISA and perMANOVA were conducted with PC-ORD 5.0 software.

3 RESULTS AND DISCUSSION

3.1 Crayfish abundance and distribution

The mean signal crayfish mean abundance (CPUE) (I, II, III) in Päijänne at stony crayfish shores varied rather much among sites with a range from 1.5 to 8.6 crayfish per trap per night (Fig. 2). In Saimaa the mean CPUE was slightly lower with range from 0.8 to 6.4. The mean crayfish CPUE was lower at vegetated shores, than at stony shores in both lakes (Fig 2).

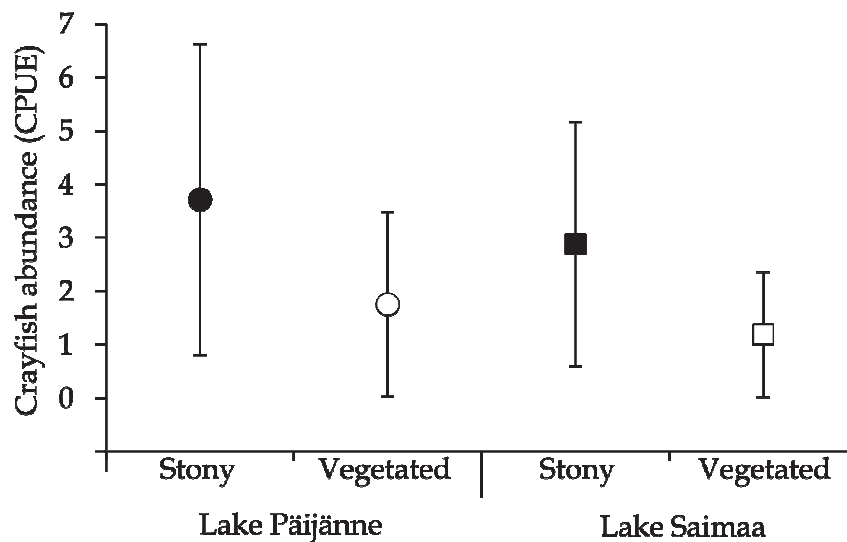


FIGURE 2. Signal crayfish mean abundance (CPUE) (\pm sd, $n=5$) at stony and vegetated shores of the study sites in Lakes Päijänne (2008) and Saimaa (2009).

Signal crayfish CPUEs at the investigated stony shores were moderate to high in terms of crayfish population densities in Finland, reflecting the present general situation in lakes in southern Finland (Erkamo et al. 2010). Previous studies have

shown crayfish (*A. astacus*, *P. leniusculus*, *O. rusticus*) to prefer stony shores (Lodge & Hill 1994, Kirjavainen & Westman 1999, Westman et al. 2002). Hence, the observed crayfish densities at vegetated shores were surprisingly high, and indicate that crayfish can also colonise rather effectively the vegetated areas of large lakes.

The original distribution of the native noble crayfish in Finland was confined mainly to rivers and shallow littoral areas (< 3m) of small lakes (Westman et al. 2002), whereas signal crayfish also inhabit deeper sublittoral and profundal areas (Abrahamsson & Goldman 1970, Erkamo et al. 2010). The crayfish were evenly abundant all over the Nyystölä bay area from shallow littoral area down to 9 m depth, after which catches declined sharply (Fig. 3). Signal crayfish may use a wider range of food and habitat resources than noble crayfish (Olsson et al. 2009), which could explain the wide spatial distribution in the studied area, and also in general in large lakes. Signal crayfish have been observed to move to deep water during autumn to avoid harsh winter conditions (Abrahamsson & Goldman 1970). In addition, female signal crayfish are supposed to migrate to deeper areas during the reproductive season to find better incubation conditions for eggs (Momot & Gowing 1972). In this study, crayfish trapping was conducted in the warm water period, so the wide distribution in the littoral and sublittoral habitats would not have been related to reproductive behaviour and can be assumed to indicate a wide range of possible foraging areas in the studied area and probably in large boreal lakes in general.

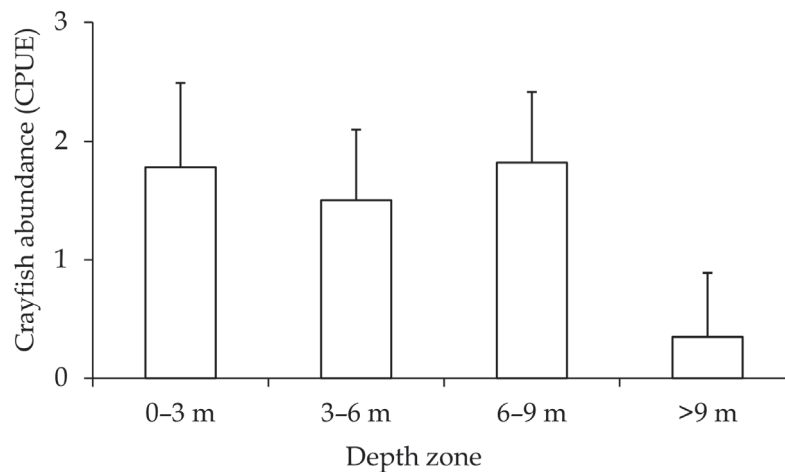


FIGURE 3. Signal crayfish mean abundance (CPUE) (\pm sd) from different depth zones at 5 locations in Nyystölä Bay (2009).

3.2 Impacts on littoral communities

3.2.1 Benthic macroinvertebrates

The examination of different habitats and influence of environmental factors were combined to achieve a more complete picture of the impacts of non-native crayfish on littoral benthic macroinvertebrate communities, from single habitat type to whole-lake scale (I). For both stony and vegetated shores, the mean densities of benthic macroinvertebrates were similar at crayfish and non-crayfish sites in both study lakes and across sampled depths (I). In the deeper sublittoral area, density was also similar between crayfish and non-crayfish sites in both lakes. These results indicate that signal crayfish do not affect the overall macroinvertebrate density in the studied lakes.

In contrast, macroinvertebrate taxa richness was higher at non-crayfish sites than at crayfish sites, while the significant interaction between crayfish status and habitat type indicated that negative crayfish impacts depended on habitat type. On average, stony non-crayfish sites contained 10 (16 %) taxa more than crayfish sites, whereas at vegetated shores taxa numbers were equal (I). In the sublittoral area, taxa richness was similar between crayfish and non-crayfish sites as well as between lakes. Patterns in snail taxa richness were similar to those of all taxa, with non-crayfish sites having more snail taxa than crayfish sites. Snail taxa number was similar at vegetated habitats, but stony non-crayfish sites contained on average 4 (33 %) taxa more than crayfish sites.

Analysis of macroinvertebrate and snail community compositions showed clear and consistent differences between crayfish and non-crayfish stony littoral sites in both study lakes (I). However, at vegetated shores no difference was detected. At stony shores in both lakes indicator species analysis revealed several taxa, mainly snail (Gastropoda), aquatic beetle (Coleoptera) and caddisfly (Trichoptera) species, as significant indicators for non-crayfish sites (I). Typical taxa for stony crayfish shores were only aquatic bugs (Micronectinae sp.) in Saimaa, and mayflies from the family Leptophlebiidae and a caddisfly *Polycentropus flavomaculatus* (Pictet) in Päijänne. For vegetated shores, in line with the absence of compositional differences between the crayfish and non-crayfish sites, there were fewer significant indicator taxa.

Crayfish predation, the strength of which depends for example on the activity of prey and on habitat structure, is supposed to be an important mechanism for negative impacts on benthic communities (Nyström et al. 1999, Kovalenko et al. 2012). The results of the present study also suggest that crayfish predation was a likely reason for the detected differences between crayfish and non-crayfish sites. Snails, which are apparently the most vulnerable group to crayfish predation (Lodge et al. 1994, Nyström et al. 1999), were clearly affected in terms of overall density and taxa richness. The snail assemblages at stony crayfish shores were dominated by hard-shelled, spherical species which are suggested to be less vulnerable to crayfish predation (Alexander & Covich 1991).

Moreover, the finding, that indicators of crayfish presence included taxa which are active swimmers (mayflies, aquatic bugs) (Jansson 1996, Merrit & Cummins 1996) or in other ways capable of co-existing with predators (caddisfly *P. flavomaculatus*) (Edington & Hildrew 2005), supports the importance of direct predation by crayfish. That signal crayfish at stony shores in these lakes predominantly feed on benthic invertebrates (II, IV), also supports the importance of direct feeding as a mechanism behind the detected differences.

In addition to the evident direct predatory impacts, invasive crayfish might change the macroinvertebrate community structure by indirect pathways. For example, crayfish could change the relationships and behaviour of native predators and prey (Nyström et al. 2001). At stony shores, several predator species (*Glossiphonia complanata* (L.), *Helobdella stagnalis* (L.), *Erpobdella octoculata* (L.), *Diura bicaudata* (L.), *Somatochlora metallica* (Vander Linden)) were indicators of crayfish absence indicating negative relationship with presence of crayfish. For example, leeches (Brönmark 1992) and dragonflies (Turner & Chislock 2007) prey on snails, and decreased prey availability could decrease their abundance or change their spatial distribution.

The results clearly indicated that impacts of signal crayfish on benthic macroinvertebrates were habitat-specific in the studied lakes, suggesting that signal crayfish do not strongly affect macroinvertebrate communities at vegetated shores. Habitat complexity is known to affect the predator-prey interactions in aquatic environments (Kovalenko et al. 2012). The sampled vegetated shores were covered with dense stands of hard-stemmed reeds (*Phragmites australis* (Cav.)) and the shelter provided by complex macrophyte structures could be an explanation for the results obtained. Moreover, crayfish abundances were lower in vegetated areas than in stony areas, which could also explain the lack of impacts. Signal crayfish are mobile animals (Bubb et al. 2006) and at least occasionally occur in the sublittoral area (IV), but the results indicated that sublittoral macroinvertebrate communities were not affected by the presence of signal crayfish. The observed macroinvertebrate densities were low and communities were dominated by rather small sized taxa like Oligochaeta and Chironomidae which are mostly living within the bottom substratum. Therefore, their availability for crayfish predation could be limited and predation unprofitable for crayfish (Nyström et al. 2001).

The factors shaping the structure of littoral macroinvertebrate communities form a complicated network of abiotic and biotic interactions (Tolonen et al. 2001, Johnson & Goedkoop 2002, Holomuzki et al. 2010). Hence, the observed differences in benthic macroinvertebrate communities could have been influenced by factors other than crayfish. The macroinvertebrate community composition was related to the shore slope and relative exposure (NMS-ordination) indicating that those environmental factors are influencing the community structure in both stony and vegetated habitats. At stony shores, directions of these environmental correlations were not parallel with the crayfish status and associated compositional difference suggesting that the variation associated with crayfish impact could not be explained by the environmental

variation (I). Moreover the two categories of sites did not consistently differ in the measured environmental characters. In addition, the predation of fish could also shape the structure of macroinvertebrate communities (e.g. Diehl 1992). However, benthic fish density and fish community composition were similar across studied sites (II) and hence fish predation and impacts were assumed to be also similar among the study sites. In fact, the apparent crayfish impacts were parallel within and between studied lakes supporting the contention that introduced signal crayfish has major negative, though habitat-specific, impacts on littoral macroinvertebrate communities in large boreal lakes.

3.2.2 Periphyton

Crayfish could affect the periphyton biomass in several direct and indirect ways. For example, reduction of snail grazers by crayfish predation could increase periphyton biomass via a trophic cascade (Lodge et al. 1994, Nyström et al. 1999). Regardless of lower snail grazer densities at stony crayfish shores (I), the periphyton biomass was similar at crayfish and non-crayfish sites in both study lakes and at all sampled depths (I). Impacts could also be dependent on crayfish density (Weber & Lodge 1990), but no significant effect of crayfish density on periphyton biomass ($p=0.689$) was found (Fig. 4). However, the mean periphyton biomass was higher in Lake Saimaa than in Päijänne ($p<0.001$).

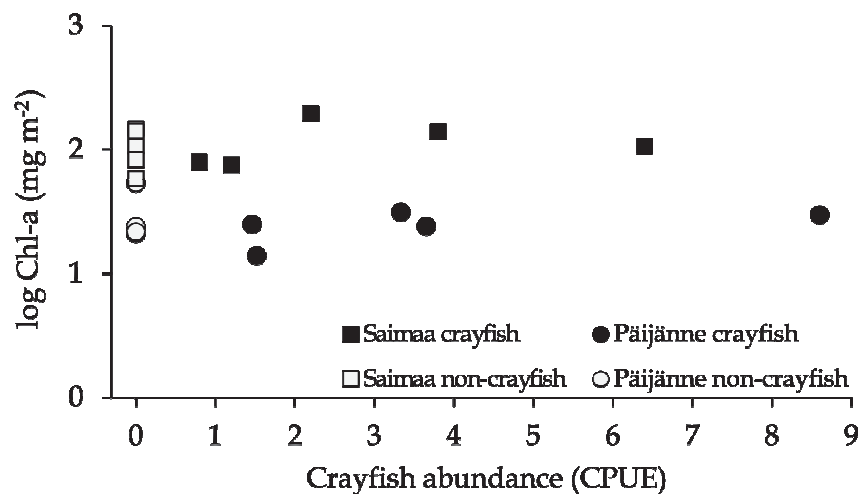


FIGURE 4. Relationship between crayfish abundance (CPUE) and periphyton biomass in Lakes Saimaa and Päijänne.

Thus, it seems that either the presence of signal crayfish does not have an effect on the periphyton biomass or else any impacts are masked by other crayfish-associated changes. One explanation might be that top-down regulation of periphyton by snail grazers in these large lakes is not as important as would be inferred from small-scale studies (Weber & Lodge 1990, Nyström et al. 1999). This view is supported by the rather low natural snail densities in studied lakes

compared with other lakes, where also absolute decrease in snail densities by crayfish has been much greater (Wilson et al. 2004). Alternatively, some other grazer group, such as mobile mayflies, may benefit from the released resources and might replace snails in the top-down regulation chain. However, macroinvertebrate data do not show clear evidence for this grazer replacement theory (I). As omnivores, crayfish could feed directly on periphyton (Gherardi & Lazzara 2006, Phillips et al. 2009), but stable isotope analysis results (II, IV) suggest that crayfish are mostly predators in these study lakes utilizing littoral macroinvertebrates as their main food source.

3.2.3 Benthic fish

In the study lakes, dense signal crayfish populations inhabit the stony shores and evidently change their macroinvertebrate community compositions (I). Increased competition for shelter and food resources between invading crayfish and native fish are potential causes of decline in fish populations and growth (Wilson et al. 2004, Carpenter 2005, Hirsch & Fischer 2008). The most common fish species in stony littoral areas were stone loach, bullhead and Eurasian minnow (*Phoxinus phoxinus* (L.)). Some burbot (*Lota lota* (L.)), ruffe (*Gymnocephalus cernuus* (L.)), Eurasian perch (*Perca fluviatilis* L.), nine spined stickleback (*Pungitius pungitius* (L.)) and roach (*Rutilus rutilus* (L.)) were also caught. On the basis of fish community composition, the study sites were placed in the NMS-ordination space without evident aggregation according to crayfish status and ANOSIM did not show significant differences in community composition either. The mean density, length and weight of the two most common benthic fish, stone loach and bullhead, were similar between crayfish and non-crayfish sites (II).

The appearance of crayfish in the naive environment could potentially lead to food competition, which could be seen as changes in use of basal resources (Vander Zanden et al. 1999) or as changes in trophic niche width (Layman et al. 2007b) of benthic fish. Stable isotope analysis indicated that crayfish do utilize benthic macroinvertebrates as their main food source (II) and therefore potentially compete with benthic fish for food. The signal crayfish clearly changed the macroinvertebrate community structure at stony shores (I), but not necessarily the availability of food resources as the overall invertebrate densities were equal at crayfish and non-crayfish sites (I). Stone loach and bullhead are also known to be flexible with respect to food source use (Hyslop 1982, Welton et al. 1991), so the fish may have shifted to prey on other invertebrates, with similar stable isotope ratios, in the presence of crayfish. In fact, the outputs from the two-source mixing models indicated that the diets of stone loach and bullhead consisted mainly of littoral food sources at all sites regardless of crayfish presence or absence (II). The contribution of pelagic food to diet was slightly higher in bullhead than in stone loach (II), but bullheads also primarily utilized littoral food sources. The trophic niches of stone loach and bullhead measured in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ space were clearly separated from each other at all sites and variation in niche widths was independent of the crayfish status (II). The niche widths of signal crayfish populations were much larger and overlapped with

both fish species (II) at all sites. Several studies have also pointed to the importance of shelter competition (Griffiths et al. 2004, Light 2005, Bubb et al. 2009) and habitat destruction (i.e. loss of macrophytes) (Wilson et al. 2004) as reasons behind decreased fish densities with crayfish occupancy. However, in this study, the sites were stony shores without vegetation and the shallow littoral areas were continuously covered with small to medium size stones providing an apparently ample supply of suitable habitat for benthic fish and crayfish along the lake shores.

3.3 Indirect impacts on fish parasites

Parasite abundances showed clear differences between crayfish and non-crayfish sites. As expected, the abundances of parasites transmitted from snails as well as from isopods were significantly lower at crayfish sites (III). The abundances of parasites transmitted from planktonic copepods and from mussels were similar between crayfish and non-crayfish sites. Fish length had a significant effect on abundance for all parasite groups. In contrast, none of the examined perch parasites showed any effect of crayfish presence on parasite prevalence (III). The results indicated significantly lower prevalence of parasites transmitted from planktonic copepods in Lake Saimaa, and, as with abundance, perch length had a significant effect on prevalence for all parasite groups.

The perch parasite communities in both study lakes showed a response to presence of crayfish (III). The studied sites separated in the NMS-ordination solution according to site crayfish status on the basis of the parasite assemblages found. The visual interpretation was supported by PerMANOVA result, which indicated significant differences between crayfish and non-crayfish sites ($p=0.010$) and between lakes ($p=0.001$).

The results suggest that the parasite-crayfish interaction was mediated indirectly via the changes in the composition, demography or behaviour of benthic invertebrate fauna acting as intermediate hosts for parasites. An impact of signal crayfish on littoral macroinvertebrates in the studied lakes was obvious at stony shores, where snail abundance, taxa richness and community composition were significantly affected, apparently by crayfish predation (I). However, the interaction between the isopod-transmitted parasite *Acanthocephalus lucii* Müller and crayfish impact was not straightforward as no direct impact was evident on the *Asellus aquaticus* abundances. *A. aquaticus* infected with *A. lucii* have been shown to be more susceptible to predation (Seppälä et al. 2008), so selective feeding by crayfish on infected individuals could be one explanation for the observed differences.

Lake littorals are open systems without strict physical boundaries (Strayer & Findlay 2010), and perch could in principle move rather freely across the lakes. However, it has been shown that perch tend to cluster into small patches having limited dispersal between sites (Bergek & Olsson 2009, Bertrand et al. 2011), which might explain the observed consistent effects of crayfish on the local

parasite fauna of perch. These results demonstrate that indirect effects of invasive crayfish on lake ecosystems could extend beyond the most obvious effects of competition with and predation on native species.

3.4 Signal crayfish increase habitat connectivity

Crayfish captured from the different depths showed clear differences in mean $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ values and trophic position (IV). $\delta^{13}\text{C}$ values were significantly higher in crayfish from the littoral and sublittoral areas than in crayfish captured from the profundal area. Crayfish mean $\delta^{15}\text{N}$ values and trophic position increased consistently from the littoral area to the profundal. The three source mixing model outputs indicated that the mean contribution of food sources in crayfish diets at the population level differed between littoral and profundal areas (IV). Crayfish caught from the littoral had mainly used food which originated from the littoral food web, accounting for between 64 % and 83 % of diet. Crayfish from the sublittoral had also relied mostly on littoral food sources (48 %-70 %). The proportion of profundal sources increased progressively with depth and crayfish caught from the two deep water areas had used more profundal food sources (44-65 % and 44-68 %) than littoral sources. The proportion of terrestrial sources was very low in all habitats representing only 0-9 % of the diet.

Crayfish feeding niches were consistently different among the habitats. Individuals captured from the littoral had the smallest niche area, and their placement in the trophic position and $\delta^{13}\text{C}$ space indicates that most crayfish there had been mainly utilizing littoral food sources. The variation in $\delta^{13}\text{C}$ values among individuals increased consistently with depth and crayfish caught from deeper water zones had broader feeding niches compared to littoral crayfish (IV). In fact, some crayfish individuals having high $\delta^{13}\text{C}$ values, similar to those of littoral food sources, were found all over the lake bottom, which indicates significant use of littoral food sources also by some of the crayfish trapped from deeper habitats.

The results suggest that invasive signal crayfish create a new link in energy transfer from productive shallow littoral to less productive deep water profundal areas and thereby might even significantly subsidize deep water areas with littoral energy. In contrast, crayfish with carbon signatures overlapping with profundal food source signatures were virtually lacking from the littoral area. These patterns indicate that the prevailing direction of energy transfer by crayfish is from littoral to profundal. Mixing model outputs gave a very low proportion of terrestrial food sources in the crayfish diets at all depths, indicating that signal crayfish were hardly using terrestrial leaf litter during the summer season in the studied area (IV). Hence in large lakes, where total input of terrestrial material is generally low (Gasith & Hasler 1976), signal crayfish presumably do not substantially link terrestrial and aquatic habitats by direct feeding on terrestrial detritus.

The magnitude and significance of energy transfer depends on the abundance of crayfish and on their movement patterns, which cannot be inferred from stable isotope data alone. In addition, results showed that part of the crayfish population uses profundal food sources extensively, suggesting that crayfish live rather permanently in the deep water area or at least predominantly forage there. The spread of large bodied crayfish to profundal habitats introduces a new functional group into deep water areas where physical conditions are relatively stable and natural perturbation is low (Stendera & Johnson 2008), which potentially alters the function of profundal ecosystem in several ways. For example, crayfish can cause mechanical disturbance by walking or burrowing activities which can affect nutrient exchange between sediment and overlying water (Rodriguez et al. 2005). In addition, crayfish can enhance nutrient recycling and translocation via excretion and egestion (Vanni 2002). Therefore, more research is needed for better understanding of the role of invasive crayfish at the whole-lake level.

4 CONCLUSIONS

The results of this thesis showed that introduced, non-native signal crayfish has wide impacts in large boreal lakes, ranging from effects on littoral benthic macroinvertebrates to effects on parasite-fish interactions. Signal crayfish has major negative effects on littoral macroinvertebrate communities in the study lakes, but that impacts are habitat and taxon dependent. The total macroinvertebrate taxa richness and snail taxa richness were significantly reduced as well as community compositions changed in the presence of crayfish at stony shores. However, there were no evident changes in macroinvertebrate communities at vegetated or deeper sublittoral areas, emphasizing that effects of non-native species in lakes should be investigated comprehensively across different habitats and spatial scales.

Regardless of spatial overlap in habitat use and share of the same basal food sources with benthic fish, the results suggest that signal crayfish do not currently have major impacts on littoral fish at the stony littoral shores of the two studied lakes. However, the signal crayfish populations are still in a growth phase and increase in crayfish numbers could intensify the competition for resources. Hence, the possibility of negative impacts on fish in the future cannot be ruled out.

The study, conducted at natural spatial and temporal scales, represents an important addition to the existing knowledge about interactions between invasive species and native parasites, and thereby demonstrates that the effects of invasive crayfish on lake ecosystems could be more far-reaching than generally anticipated. The results suggest that signal crayfish has indirect impact on native fish parasites via changes in the benthic invertebrate fauna acting as intermediate hosts for parasites. Parasites are key components in ecological processes in lakes, so understanding and evaluation of net effects of invading crayfish on native parasite dynamics should be studied further.

Invasive species could also have effects on ecosystem level properties in lakes and change the energy flows and processes. This study presents the first empirical evidence that invasive crayfish can create a new route in energy transfer from littoral to profundal areas and thereby potentially increase

integration between these spatially distinct habitats in large lakes. The results highlight a need for better understanding of the role of crayfish, both native and non-native, in lakes.

The results presented in this thesis, with the wide previous knowledge, should increase awareness of the concrete impacts on native biota, intensify efforts to prevent new crayfish invasions and enhance the established practices for management of non-native crayfish populations. As signal crayfish has been introduced and deliberately spread widely merely for fisheries management purposes in Finland, the future direction of management should focus more on minimizing the negative effects on other ecosystem members while developing ecologically sustainable crayfish fisheries.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Täpläravun ekologiset vaikutukset suurissa boreaalisissa järvissä

Vieraslajien leviäminen on yksi suurimpia uhkia luonnon monimuotoisuuden säilymiselle ja eliöyhteisöjen toiminnalle. Sisävesistöt ovat kärsineet voimakkaasti ihmisperäisistä häiriöistä, jotka yhdessä intensiivisen istutustoiminnan kanssa ovat tehneet niistä erityisen alttiita vieraslajien leviämislle. Useat makeanveden rapulajit ovat levinneet laajasti alkuperäisen levinneisyysalueensa ulkopuolelle, ja niiden on havaittu vaikuttavan haitallisesti alkuperäislajistoon. Pohjois-amerikkalainen täplärapu (*Pacifastacus leniusculus* (Dana)) tuotiin Suomeen 1960-luvun lopulla korvaamaan toistuvista rapurutoista kärsineitä alkuperäisiä jokirapukantoja. Täplärapujen laajamittainen istutustoiminta käynnistettiin 1980-luvun lopulla, ja tähän mennessä lähes kaksi miljoonaa yksilöä on istutettu pääasiassa eteläisen Suomen vesistöihin.

Tässä väitöskirjassa tutkittiin täpläravun vaikutuksia suurten boreaalisten järvien rantavyöhykkeen eliöyhteisöihin. Tutkimus toteutettiin Päijänteellä ja Saimaalla, joihin täplärapuistutukset aloitettiin 1990-luvulla. Täplärapu on uusi eliöyhteisön osakas suurten järvien selkävesillä, sillä alkuperäisen rapulajin, jokiravun (*Astacus astacus* L.), luontainen levinneisyysalue rajoittui pääasiassa pienempiin vesistöihin eteläisessä Suomessa. Suuri osa aiemmista vierasperäisten rapulajien vaikutuksia tutkineista töistä on toteutettu pienen mittakaavan kokeellisissa olosuhteissa, keinotekoisissa lammissa tai jokiympäristössä. Koska vaikutukset voivat riippua ympäröivästä elinympäristöstä, aiempien tutkimusten tulosten suoraviivainen yleistäminen koskemaan suuria järviä voi johtaa vääriin tulkintoihin.

Työn ensimmäisenä tavoitteena oli selvittää, aiheuttaako täpläravun saapuminen aiemmin ravuttomille alueille muutoksia selkärangattomien pohjaeläinten tiheydessä, lajirunsaudessa tai yhteisökoostumuksessa. Useat aiemmat tutkimukset ovat osoittaneet, että vierasperäisten rapujen saalistus vähentää voimakkaasti etenkin hitaasti liikkuvien pohjaeläinten, kuten esimerkiksi kotiloiden ja vesiperhosten, määrää ja lajirunsautta. Vaikutusten voimakkuus voi kuitenkin riippua elinympäristön rakenteesta, joten vaikutusten samankaltaisuutta tutkittiin sekä kivikko- että kasvirannoilla. Lisäksi tutkittiin, onko muilla ympäristötekijöillä, kuten syvyydellä, yhteyttä ravun aiheuttamiin vaikutuksiin. Ennako-odotusten mukaisesti kotilotiheyksien sekä kaikkien pohjaeläinten ja kotiloiden lajirunsauden havaittiin olevan pienempiä ravullisilla kuin ravuttomilla kivikkorannoilla. Lisäksi pohjaeläinyhteisöjen koostumus ravullisilla kivikkorannoilla poikkesi selvästi ravuttomien rantojen yhteisökoostumuksesta. Sen sijaan kasvintojen pohjaeläinten runsauksissa ja yhteisökoostumuksessa ei havaittu merkitsevää eroa ravullisten ja ravuttomien paikkojen välillä. Syvyydellä tai muilla tässä tutkimuksessa mitatuilla ympäristömuuttujilla ei havaittu olevan yhteyttä ravun aiheuttamiin muutoksiin. Tulokset osoittivat selkeästi, että täplärapu muuttaa suurten järvien kivikkorantojen pohjaeläinyhteisöjen rakennetta ja vähentää lajiston monimuotoisuutta. Vastaavia

muutoksia ei havaittu kasvillisuusrannoilla, minkä oletetaan johtuvan kasvillisuuden tarjoamasta suojasta rapujen saalistusta vastaan sekä pienemmästä raputiheydestä kivikkorantoihin verrattuna.

Vierasperäisten rapujen on havaittu vaikuttavan haitallisesti alkuperäisiin kalalajeihin esimerkiksi kilpailun ja saalistuksen kautta. Täpläravut suosivat erityisesti kivikkorantoja, ja viimeaikaiset tutkimukset ovat osoittaneet selkärangattomien pohjaeläinten olevan tärkeä rapujen ravintokohde. Suurten järvien kivikkorantoja asuttavat myös pohjakalat, kuten kivisimppu ja kivennuoliainen, joten täplärapujen ilmestyminen aiemmin ravuttomille alueille voi johtaa kilpailutilanteeseen tila- ja ravintoresurseista.

Toisen osatyön tavoitteena oli tutkia, vaikuttaako täplärapu kivikkorantojen kalayhteisöjen rakenteeseen ja ilmeneekö ravun läsnäolo pienempinä kalatiheyksinä tai heikentyneenä kasvuna. Lisäksi tutkittiin, hiilen ($\delta^{13}\text{C}$) ja typen ($\delta^{15}\text{N}$) vakaiden isotooppien avulla, muuttaako ravun läsnäolo kivikon pohjakalojen ravinnonkäyttöä. Kalayhteisöjen rakenne ja kivisimppujen sekä kivennuoliaisten tiheys ja yksilöiden keskimääräinen koko olivat samankaltaisia niin ravullisilla kuin ravuttomilla rannoilla. Täpläravun läsnäolo ei myöskään muuttanut havaittavasti pohjakalojen ravinnonkäyttöä selkeästä ravinnonkäytön päällekkäisyydestä huolimatta. Tulosten perusteella arvioitiin, että nykyisillä raputiheyksillä täplärapu ei vaikuta haitallisesti suurten järvien kivikkorantakaloihin.

Loiset ovat olennainen osa kaikkien eliöiden elämää ja siten myös tärkeässä roolissa vierasperäisten lajien leviämisprosesseissa. Kolmannessa osatyössä tutkittiin täpläravun epäsuoria vaikutuksia ahvenen loisintaan. Useilla kaloissa yleisillä loislajeilla on epäsuora elämänkierto, jonka eri vaiheissa loinen siirtyy väli-isännästä toiseen päätyen lopulta pääisäntään, jossa kehittyy sukukypsäksi. Selkärangattomat pohjaeläimet ovat yleisiä kalojen loisten väli-isäntiä, joten muutokset esimerkiksi niiden runsaudessa tai käyttäytymisessä vaikuttavat myös loisten elämänkiertoon. Näin ollen havaitut täpläravun aiheuttamat muutokset pohjaeläinyhteisöissä voivat heijastua myös kalojen loisintaan. Työssä vertailtiin ahvenen eri väli-isäntien kautta siirtyvien loisten yleisyyttä ja määrää sekä loisyhteisöjen rakennetta ravullisten ja ravuttomien alueiden välillä. Kotilo- ja vesisiiravälitteisten loisten määrän havaittiin olevan pienempi ravullisilla alueilla. Sen sijaan eläinplankton- ja simpukkavälitteisten loisten määrissä ei havaittu eroja. Ahventen loisyhteisöjen rakenne oli erilainen ravullisten ja ravuttomien paikkojen välillä, mutta loisten yleisyydessä ei havaittu eroa. Havaittujen tulosten perusteella arvioitiin, että täpläravun aiheuttamat muutokset pohjaeläinyhteisöissä, erityisesti kotilotiheyksissä, ilmenevät pienentyneinä kotilovälitteisten loisten määrinä kaloissa. Vesisiirajien tiheyksissä ei kuitenkaan havaittu selvää muutosta ravullisten ja ravuttomien alueiden välillä, joten rapujen vaikutusmekanismi loisintaan ei ole yhtä suoraviivainen kuin kotilovälitteisten loisten tapauksessa. Loisittujen siirajien on todettu olevan loisittomia siirajia alttiimpia saalistukselle, joten rapujen valikoiva saalistus voi selittää havaitun eron. Osatyön tulokset osoittavat, että vierasperäisillä ravuilla voi olla aiempaa ajateltua laaja-alaisempia vaikutuksia alkuperäislajistoon.

Vieraslajien on havaittu vaikuttavan myös ekosysteemitason toimintoihin. Esimerkiksi kalojen istuttamisen on havaittu muuttavan energiavirtojen kulkua järvissä, ja vaikutukset voivat ulottua jopa maaekosysteemiin saakka. Täplärapujen on havaittu jokiravusta poiketen asuttavan myös järvien syvempiä alueita ja liikkuvan pitkiäkin matkoja lyhyessä ajassa. Täpläravut voivat siten luoda uuden väylän fyysisesti erillisen rantavyöhykkeen ja syvänveden pohja-alueen välille. Neljännessä osatyössä tutkittiin lisäävätkö täpläravut rantavyöhykkeen, syvänveden ja maaekosysteemin välistä yhteyttä. Hiilen ($\delta^{13}\text{C}$) ja typen ($\delta^{15}\text{N}$) vakaita isotooppeja hyväksikäyttäen arvioitiin eri syvyysvyöhykkeistä (0–3 m, 3–6 m, 6–9 m, >9 m) pyydettyjen rapujen käyttämien ravintokohteiden suhteellista osuutta sekä rapujen ravinnonkäyttöön liittyvän ekolokeron laajuutta ja sijoittumista suhteessa saatavilla olevaan ravintoon. Rapujen ravinnonkäytössä havaittiin selkeitä eroja eri syvyysvyöhykkeiden välillä. Rantavyöhykkeestä pyydetty ravut käyttivät pääosin rantavyöhykkeestä peräisin olevaa ravintoa syvänveden ravintokohteiden osuuden lisääntyessä yhdenmukaisesti pyyntisyvyyden kasvaessa. Maalta peräisin olevan lehtikarikkeen osuus rapujen ravinnossa oli vähäinen kaikissa syvyysvyöhykkeissä. Lisäksi havaittiin, että rapuyksilöiden välinen vaihtelu ravinnonkäytössä kasvoi syvyyden kasvaessa, mikä ilmeni suurempina ravinnonkäyttölokeroina. Syvänveden alueelta havaittiin rapuja, jotka olivat käyttäneet pääasiassa rantavyöhykkeestä peräisin olevaa ravintoa, kun taas syvänveden ravintokohteita käyttäneitä rapuja ei rantavyöhykkeestä juuri havaittu. Tulokset osoittavat, että täplärapu luo uuden väylän rantavyöhykkeen ja syvänveden välille ja mahdollisesti lisää rantavyöhykkeestä peräisin olevan energian siirtymistä syvänveden alueille. Sen sijaan pieni maalta peräisin olevan ravinnon osuus täplärapujen ravinnossa kertoo, että täpläravut eivät merkittävästi lisää vesi- ja maaekosysteemin yhteyttä tutkimusalueella. Vaikutusten laajuus ja merkitys riippuvat kuitenkin rapujen tiheydestä ja liikkeistä, joita ei voida tarkasti määrittää käytetyillä menetelmillä. Työn tulokset osoittivat, että täplärapu voi vaikuttaa järvien energiavirtoihin, mutta vaikutusten laajuuden ja seurauksien selvittämiseksi tarvitaan lisätutkimuksia.

Väitöskirjan tulokset osoittivat, että laajalle levitetty täplärapu pienentää suurten järvien alkuperäisluonnon monimuotoisuutta, mutta vaikutukset riippuvat eliöryhmästä ja elinympäristön rakenteesta. Lisäksi täpläravut aiheuttavat aiemmin huomiotta jääneitä epäsuoria muutoksia lajiryhmien välisissä suhteissa ja voivat muuttaa aineksen ja energian kulkua järvissä. Nämä havainnot osoittavat täpläravun vaikutusten ulottuvan järvien ekosysteemeissä laajemmalle kuin aiemmin on oletettu. Täplärapu on istutettu Suomeen turvaamaan raputuotantoa, joten tulevaisuudessa sen aiheuttamat - sekä tässä väitöskirjassa osoitetut että aiemmin havaitut - vaikutukset alkuperäislajistoon ja ekosysteemien toimintaan tulisi ottaa laajemmin huomioon ekologisesti kestävä raputalouden kehittämiseksi.

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