**Master's thesis**

# Impacts of the non-native crayfish (*Pacifastacus leniusculus*) on littoral benthic invertebrate communities in Lake Päijänne

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## ABSTRACT

The introduced North American signal crayfish (*Pacifastacus leniusculus*) is now a permanent resident in many of the large lakes in Finland, but the effects of this large omnivore on lake ecosystems are largely unknown. In general, it is thought that when crayfish abundance increases, species composition of benthic invertebrates may change towards species less vulnerable to predation by crayfish and the snail abundance is expected to decrease. However, indirect impacts of crayfish on benthic communities can also be expected. The impacts of *P. leniusculus* on littoral benthic invertebrate communities in large Lake Päijänne were therefore studied by comparing the benthic invertebrate assemblages of stony shores in lake areas with well established crayfish populations to those in areas without crayfish. The invertebrate community composition differed between the areas, and there was a clear reduction in species richness and abundance and of snail abundance in particular in the presence of signal crayfish. The crayfish sites were dominated by Chironomidae and Oligochaeta and small number of other invertebrate groups. The non-crayfish sites were dominated evenly by Chironomidae and Oligochaeta, Elmidae, Amphipods, Gastropoda and Trichoptera. The results suggest that the signal crayfish will have significant impacts on littoral communities and food webs in large boreal lakes.

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## TIIVISTELMÄ

Suomeen tuotu täplärapu (*Pacifastacus leniusculus*) on jo pysyvä asukas monissa suurissa järvissämme, mutta tämän suurikokoisen omnivorin vaikutukset järviekosysteemeihimme ovat lähes tuntemattomat. Tässä työssä tutkittiin täpläravun vaikutuksia litoraalivyöhykkeen pohjaeläimistöön Päijänteessä. Monissa aikaisemmissa tutkimuksissa on todettu että raputiheyden kasvaessa pohjaeläimistön lajikoostumus voi muuttua niin että vähemmän arkojen saaliseläinten osuus yhteisössä kasvaa. Kotilotiheyksien oletetaan pienenevän ravun läsnä ollessa. Lisäksi ravulla oletetaan olevan epäsuoria vaikutuksia litoraalipohjaeläimistöön. Tutkimus tehtiin vertailemalla kivikkorantojen pohjaeläimistöä alueella jossa on vakiintunut rapukanta, eläimistöön alueella, jossa ei ole rapuja laisinkaan. Pohjaeläimistö erosi alueiden välillä ja havaittiin selvä lajiston köyhtyminen, eläintiheyden väheneminen ja erityisesti kotilomäärien väheneminen täpläravun läsnä ollessa. Ravullisilla alueilla dominoivat surviaissääsken toukat sekä harvasukasmadot, kun taas ravuttomilla alueilla oli tasaisesti surviaissääsken toukkia, harvasukasmatoja, kovakuoriaisia, äyriäisiä sekä kotiloita. Tulokset viittaavat siihen, että täpläravulla on huomattava vaikutus litoraalipohjaeläimistöön ja luultavasti laajemmin ravintoverkkoon suurissa boreaalisissa järvissä.

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# Contents

## 1. INTRODUCTION

Growing global disturbances increase the chance of biological invasions by creating suitable habitats for exotic species (Guo 2003, Correia & Anastacio 2008). Exotic species are a threat to global biodiversity (McCarthy *et al*. 2006) since they affect the distribution and abundance of native species. Freshwater habitats have suffered particularly from changes arising from introductions of non-indigenous species that interfere in aquatic systems at many ecological levels (McCarthy *et al.* 2006). The North-American signal crayfish (*Pacifastacus leniusculus* Dana, 1852) is one widespread example of such introduced species.

Crayfishes are often a central component of freshwater food webs and ecosystems (McCarthy *et al*. 2006). They can have strong effects on species richness of other organisms and hence on the structure of food webs in lakes and ponds by feeding at several trophic levels (Stenroth & Nyström 2003). Crayfish feed on benthic invertebrates (including other crayfish), detritus, macrophytes, algae and fish and are themselves eaten by larger predatory fish (Roell & Orth 2003). Small crayfish are more likely to be carnivorous and also to be consumed themselves by many fish species, whereas large crayfish are more omnivorous and are often big enough to prevent fish predation (Holdich 1988). Crayfish and especially juveniles feed significantly on benthic invertebrates and hence provide a direct link from primary production and detritus-based food webs to fish.

The majority of studies examining the impacts of crayfishes on benthic communities have been small scale experimental manipulations, with variable results, including negative effects on snails and diversified effects on other zoobenthic taxa. The first assessment of non-native crayfish impacts over a longer temporal scale was by Wilson *et al*. (2004), who found negative effects on native crayfishes, fishes, invertebrates and macrophytes. Via "trophic cascades", predators can affect the abundance of species to which they have no direct trophic links (Bernot & Turner, 2001), and the impact of crayfish on snails can have indirect consequences for littoral communities. As snails are important grazers, crayfish may indirectly increase the abundance of micro algae by releasing them from herbivory, causing a "trophic cascade" in the littoral food web (Gherardi & Acquistapace, 2007).

The North-American signal crayfish (*Pacifastacus leniusculus*) was introduced to Finland in the late 1960s-1970s and thereafter it has been spreading rapidly into Finnish lakes. *P. leniusculus* is a carrier of the crayfish plague *Aphanomyces astaci* which is lethal to the native noble crayfish (*Astacus astacus* Linnaeus, 1758). The nonindigenous crayfish in Europe and North America have often eliminated native crayfishes from lakes and streams, and have reduced abundance of aquatic vegetation (which is important fish and macroinvertebrate habitat) and invertebrates (Lodge *et al.* 2000a, 2000b). However, the effects of signal crayfish in boreal aquatic ecosystems, and in large lakes in particular, are not well known.

Signal crayfish are a new component in large lakes ecosystems in Finland, as they succeed well in large lakes, and are now an important commercial fishery. The native noble crayfish, in contrast, has never been abundant in large lakes. In 2005-2006 over 78 000 signal crayfish were stocked into 36 medium to large sized lakes in Finland (Ruokonen *et al*. 2008). The trend in stocking crayfish has slightly decreased from earlier years, but eventually a large number of the Finnish lakes will be occupied by the signal crayfish.

Therefore it is of great importance to conduct wider research on the signal crayfish in lake ecosystems.

The present work is a pilot study for a wider project ("Impacts of invasive signal crayfish (*Pasifastacus leniusculus*) on the littoral communities of large boreal lakes") of Jyväskylä University and the Finnish Game and Fisheries Research Institute. The signal crayfish was introduced in the beginning of 1990s to Padasjoki, south Lake Päijänne. From there it has been spreading north naturally and with human help. The aim of this study was to investigate whether the presence of the non-native crayfish has an impact on the littoral benthic invertebrate communities in Lake Päijänne by comparing the benthic invertebrate assemblages in areas with well established crayfish populations, 'impact sites', to those in areas without crayfish, 'control sites'.

When crayfish abundance increases, species composition of invertebrates may change towards less vulnerable prey species. For example, the relative abundance of mobile predatory invertebrates such as heteropterans, adult beetles and insect grazers may increase at the expense of slow moving invertebrates such as molluscs (Stenroth & Nyström 2003). A study by McCarthy *et al.* (2006) indicated reductions in Chironomidae (Diptera), Ephemerellidae (Ephemeroptera), Coenagrionidae (Odonata) and Hydroptilidae (Trichoptera) in the presence of rusty crayfish *Orconectes rusticus*. The changes in invertebrate composition can lead to other consequences in the ecosystem; for example, the reduction of grazing snails can consequently be reflected in increased biomass of periphyton (Nyström *et al*. 2001).

The basis for this study is the expectation that the nonindigenous crayfish reduces the invertebrate abundance and diversity. The abundance of snails, in particular, is expected to decrease and lead to an increased number of other grazers in the invertebrate community.

The specific hypotheses for the study were:

1. The nonindigenous crayfish will reduce the invertebrate abundance and diversity.
2. The abundance of snails will decrease.
3. The reduction of snails leads to an increased number of some insect grazers.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

Lake Päijänne (Figure 1) is situated in Päijät-Häme, central Finland and is the main lake of the Kymijoki water course. Päijänne is the second largest lake in Finland with a surface area of 1118 $km^2$, mean depth of 16 m and maximum depth 95.3 m. The retention time of the lake is 2.5 years. The Kymijoki river outlet drains into the Gulf of Finland. The water quality of the lake has been classified by the Finnish Environment Institute mainly as good and excellent south from Jämsä. The wastewater load into the lake was greatest in 1960-1985 due to industry and municipal wastewater, since when it has decreased. At the moment the lake water is affected mostly by agriculture, which is abundant in some areas surrounding the lake.

The study areas (Figure 1) are in the southern part of Päijänne, in Padasjoki (P, Padasjoenselkä) and Kuhmoinen (K, Kuhmoistenselkä), and also in Saalahti (S) which is located in Korpilahti in central Päijänne. Five sites representing stony shores were chosen from Padasjoenselkä (P1, P2, P3, P4 and P5) (Appendix 1), where crayfish was introduced

in 1990, and where populations are now abundant. Five similar sites at Kuhmoistenselkä (K1, K2, K3, K4 and K5) (Appendix 1), about 40 km north from Padasjoki, were used as control sites with no crayfish. An additional control site was selected from Saalahti (S3) (Appendix 1) further north where signal crayfish was to be introduced in autumn 2007. The aim was that the study sites should be comparable with regard to habitat structure, like substrate type and slope, which are important in shaping littoral macroinvertebrate communities (Tolonen *et. al* 2001). Some variation between sites appears from differences in habitats of the sample sites (small island, large island, shoreline, cape) and the aspect of the site and the wind exposure on it.

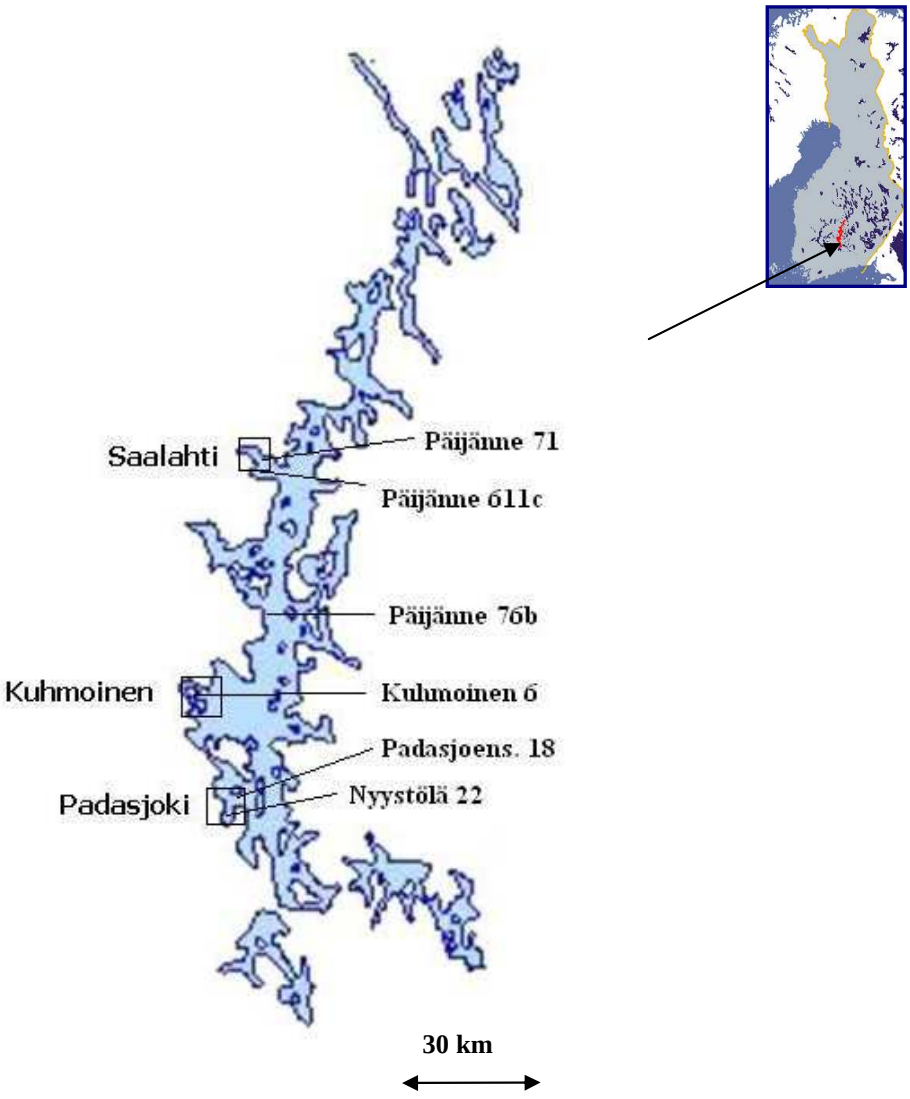


Figure 1. Map of Finland indicating location of Lake Päijänne in red and a map of Lake Päijänne with the three study areas marked by squares; Padasjoki, Kuhmoinen and Saalahti; and the locations of water quality samples reported in Table 2 (Oiva/ Hertta).

Table 1. Location, gradient, stone size and maximum effective fetch (Lf) of the sampling sites.

| Site | Coordinates E | Coordinates N | Gradient (°) | Stonesize (scale) | Lf (km) |
|---|---|---|---|---|---|
| P1 | 6804072 | 2573284 | 12.8 | 5.8 | 3.0 |
| P2 | 6805132 | 2573944 | 11.4 | 7.1 | 23.2 |
| P3 | 6806226 | 2571099 | 12.2 | 6.0 | 35.8 |
| P4 | 6805234 | 2571577 | 6.6 | 6.9 | 41.1 |
| P5 | 6804864 | 2572141 | 15.5 | 6.8 | 43.1 |
| K1 | 6824625 | 2568717 | 6.9 | 6.5 | 38.9 |
| K2 | 6821917 | 2568813 | 7.5 | 7.1 | 27.7 |
| K3 | 6824033 | 2566813 | 8.4 | 6.4 | 25.5 |
| K4 | 6822745 | 2567055 | 6.7 | 7.1 | 29.8 |
| K5 | 6824817 | 2566105 | 10.1 | 6.9 | 29.1 |
| S3 | 6869787 | 2575381 | 4.6 | 6.0 | 13.5 |

The habitat variables (measured as described below) inevitably varied slightly among the sites (Table 1). The littoral gradient of the impact sites P1, P2, P3 and P5 were somewhat higher than the ones at the control sites. S3 had the smallest gradient. The calculated average stone size varied from 5.8 to 7.1 and there was no consistent difference between the impact and control areas. Maximum effective fetch (Lf) was smallest at P1 (3.0 km) which is located in a bay (Nyystölänlahti) and at S3 (13 km) that was located behind an island, otherwise the values varied from 23.2 to 43.1 km, again with no systematic difference between the areas.

According to data taken from the Oiva/Hertta database of the Finnish Environment institute, there are no marked differences in water quality among the study areas (Table 2). Representative water samples are from 1-5 km distance from the study areas; one sample (Päijänne 76b) is 18 km away from the nearest sample site and is situated between Kuhmoinen- and Saalahti areas (Figure 1). The sample from ‘Nyystölä 22’ is from year 2003, but the water quality has not altered since then. Saalahti area is a little more eutrophicated than Padasjoenselkä and Kuhmoistenselkä, with slightly higher TN and TP (Table 2)

Table 2. Water quality data taken from the Oiva/Hertta database of the Finnish Environment Institute. ‘Nyystölä 22’ and ‘Padasjoenselkä 18’ are from Padasjoenselkä; ‘Kuhmoinen 6’ is from Kuhmoistenselkä, ‘Päijänne 76b’ is from between Kuhmoinen and Saalahti and ‘Päijänne 71’ and ‘Päijänne 611c’ are from Saalahti area. The values represent data from 1 m depth.

| Name | | Nyystölä 22 | Padasjoens. 18 | Kuhmoinen 6 | Päijänne 76b | Päijänne 71 | Päijänne 611c |
|---|---|---|---|---|---|---|---|
| Date | | 30.9.2003 | 22.8.2007 | 22.8.2007 | 23.8.2007 | 27.8.2007 | 27.8.2007 |
| Coord. grid E 27° | | 6802443-3411315 | 6806709-3409559 | 6826920-3405234 | 6840050-3420055 | 6867135-3423529 | 6866233-3416739 |
| Temp | C° | 11.7 | 19 | 18.9 | 19.4 | 18.2 | 17.9 |
| Transp. | m | 4.5 | 5 | 4 | 3.7 | | 3.1 |
| pH | | 7.1 | 7.5 | 7.4 | 7.4 | 7.3 | 7.3 |
| Turbidity | FNU | 0.7 | 0.4 | | 0.6 | 0.8 | 0.7 |
| Cond. | mS/m | 6.7 | 7 | 7.1 | 7.2 | 7.3 | 7.4 |
| Col. | mg Pt/l | 10 | 15 | 25 | 20 | 25 | 30 |
| CODMn | mg/l | 5 | 5.3 | 6.1 | 6.4 | 6.9 | 7.3 |
| Tot. P | ug/l | 6 | 4 | 8 | 7 | 8 | 8 |
| Tot. N | ug/l | 460 | 440 | 490 | 490 | 500 | 530 |

## 2.2. Crayfish data

All sites were crayfished during summer 2007, 18-19 June in Kuhmoinen, 5-6 July in Saalahti and 21-22 July in Padasjoki (P5 was crayfished 4-5 June), to estimate the crayfish abundance and ensure the absence of crayfish in the control sites. A 125 m long area of the shoreline in the 1-3 m depth zone was crayfished using a line of 25 baited (fresh roach) crayfish traps at 5 m intervals. Catch per trap per night was calculated.

## 2.3. Macroinvertebrate sampling

The benthic invertebrate sampling was done during August 2007 in the middle of each crayfished study area of 125 m using a centrifugal ignition-engine pump. A scuba diver brushed a framed area of 0.5 x 0.5 m of substrate with a dishwasher brush and sucked the material through an inlet hose to the pump in the boat (Figure 2). The sample was led through an outlet hose to a sieving bucket (mesh size 0.5 mm) held on the water surface. The sample was then preserved immediately in 70 % ethanol. Three randomly selected parallel samples were taken from each depth of 0.5 m, 1 m and 2 m. As an exception, because of narrow stony zone, no sample from 2 m depth could be taken from the site S3. In addition five replicate samples were taken from soft bottom by an Ekman-grab at approximately two meters distance from the outer edge of stony substrate (depth ~5 m). Altogether 151 samples were taken for the study.

The invertebrates were sorted from the samples, identified mostly to species or genus level and counted in the laboratory. Chironomidae- and Ceratopogonidae larvae and Oligochaeta were only counted without further identification.

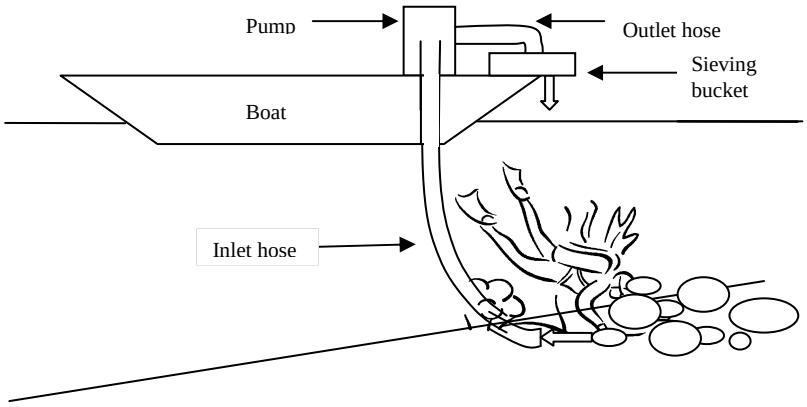


Figure 2. Simplified illustration of the sampling method for benthic invertebrates. The scuba diver sucks the sample by the inlet hose and the sample goes through the pump in the boat and comes out from the outlet hose to a sieving bucket that is held by the water surface.

## 2.4. Environmental variables

### 2.4.1. Shore slope

The depth was measured at 0.5 m, 1 m and 2 m using a scaled stick and the distance to the shoreline from those depths was determined with a laser meter. For each site the shore slope was calculated from the angle between the depth and distance to the shore by calculating the angle between these (Equation 1). A mean value of the slopes from 0.5 m, 1 m and 2 m depths was calculated.

$$gradient(^\circ) = arctan\left(\frac{depth}{distance}\right) \qquad (1)$$

### 2.4.2. Substrate particle size

The substrate particles or the stone size more accurately was estimated from each sampling square during scuba diving. Particle size was calculated by applying modified Wentworth‘s scale: 1=0.007-0.2 cm, 2= 0.21-0.8 cm, 3=0.81-1.6 cm, 4=1.61-3.2 cm, 5=3.21-6.4 cm, 6=6.41-12.8 cm, 7=12.81-25.6 cm, 8=25.61-51.2 cm, 9=51.21-102.4 cm, 10= >102.4 cm (rock). The percentage cover of each size group was estimated at each sampling square and a weighted average size value was calculated using equation 2:

$$\overline{x} = \frac{\sum_{i=1}^{c} MSi * MPi}{\sum_{i=1}^{c} MPi} \qquad (2)$$

where ‘c’ is the number of size classes, ‘i’ is the sample, ‘MSi’ is the size class (1-10) and ‘MPi’ is the percentage cover of the size class. The final value for the substrate particle size presented in Table 1 is the mean value of nine sampling squares at a sampling site.

### 2.4.3. Wind effect

Waves can affect the benthic invertebrate community composition through the currents and the motion of the water. A surface gravity wave appears from the power of the wind and the height of the wave is dependent on the distance that the wind can impact at the lake without hindrance (Kalff 2002). As surface gravity waves have little impact on invertebrates in the deeper zones, the littoral invertebrates are more influenced by the waves (Saari 2007). Wavelength and period are largely determined by the maximum fetch, the longest distance over which the wind can impart its kinetic energy to a lake (Kalff 2002).

Håkanson (1981) presented two methods to calculate the effective fetch of winds: “effective fetch”, which considers the prevailing wind, and the “maximum effective fetch”, which does not consider the wind directions, and the latter was used in this study. The maximum effective fetch is calculated by measuring the baseline (0˚) to the furthest distance that the wind can blow without hindrance (islands and coast). Then 7 measures at 6˚ intervals are taken starting from the baseline and in both directions; altogether 15 distances are measured (0˚, ± 6˚, ±12˚, ± 18˚, ±24˚, ±30˚, ±36˚, ±42˚) and the outcome is the fetch (Figure 3). The bigger the maximum fetch value, the more open and sensitive is the site for winds and waves, and the bigger and stronger will the waves be. Equation 3 was used to calculate the maximum effective fetch.

$$L_f = \frac{\Sigma x_i \cos \gamma_i}{\Sigma \cos \gamma_i} \qquad (3)$$

Where:

$x_i$ = distance at the map from the study site to the nearest obstacle (km)

$\gamma_i$ = 0˚, ± 6˚, ±12˚, ± 18˚, ±24˚, ±30˚, ±36˚, ±42˚

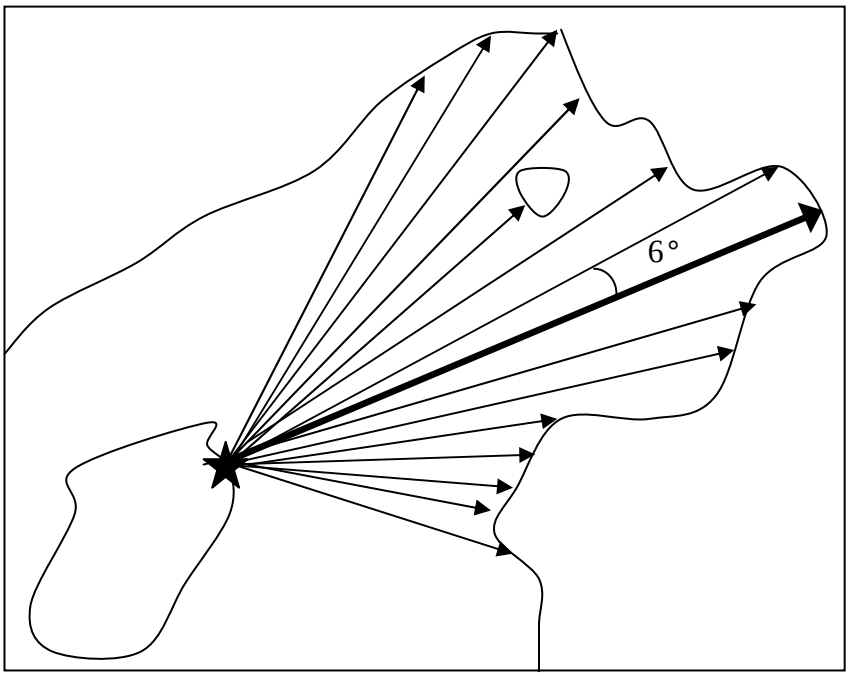


Figure 3. Illustration of the method used to calculate maximum effective fetch on a map. The star represents the sample site at the shore of an island; the thick arrow represents the baseline 0° from where the distances between each 6° angle are measured.

### 2.5. Numerical methods

The invertebrate density (ind $m^{-2}$), density of snails (ind $m^{-2}$) and number of taxa were calculated. The relative contributions of invertebrate groups were calculated for pooled samples (0.5 m, 1 m, 2 m and Ekman-grab sample) per study site and as average percentage values for whole study areas (P, K and S).

The effects of crayfish and depth on invertebrate density, invertebrate taxon richness, snail density and densities of other invertebrate groups or species were tested by two-way analysis of variance (ANOVA) by SPSS program, version 15.0. The effects of crayfish on different taxa and invertebrate groups were also tested by two-way analysis of variance.

The variation in the benthic invertebrate community composition among sites and depths was analyzed by NMS (Non-metric Multidimensional Scaling) ordination. NMS is suitable for data that do not follow a normal distribution, that are discrete or are indefinite in some other ways. NMS is based on distance measures between the observations and tries to find solutions with a minimum stress value, i.e. the maximum rank correlation between the distances in the ordination space and the original calculated distances among samples. The NMS-ordination was conducted using PC-ORD Version 4.0. (McCune & Mefford 1999). Bray-Curtis distance measure and invertebrate density data were used for the ordination of averaged samples of each site and depth.

Indicator species analysis test is used to search for species that are typical of some groups of sites defined *a priori*. Here the test was used to find taxa that are characteristic of sites with or without crayfish. This method uses the abundance and frequencies of species in a group/community. It gives each species an indicator value for each of the groups compared, in this case for two groups; crayfish or no crayfish. The significance of each value is tested by Monte Carlo simulation. The indicator values vary from zero (no indicator value) to one hundred (absolute value). An absolute value means that the species exists in all sites of one group (crayfish or no crayfish) and nowhere else.

## 3. RESULTS

### 3.1. Crayfish abundance

The crayfish sites had an average of 1.2-3.9 crayfish per trap (Table 3). The non-crayfish sites had 0 crayfish per trap.

Table 3. Crayfish abundance results from the impact sites P1-P5. Note the different date of the trapping for P5.

| Site | Date | Total catch (number of ind.) | Catch per Unit Effort (ind. trap-1 night -1) |
|---|---|---|---|
| P1 | 21.-22.7.07 | 98 | 3.9 |
| P2 | 21.-22.7.07 | 77 | 3.1 |
| P3 | 21.-22.7.07 | 70 | 2.8 |
| P4 | 21.-22.7.07 | 80 | 3.2 |
| P5 | 4.-5.6.07 | 29 | 1.2 |

### 3.2. Macroinvertebrate fauna

Altogether 22399 individuals and 80 taxa were identified from the samples (Appendix 2). The most common taxa were Chironomidae, Oligochaeta, the amphipod *Asellus aquaticus*, the riffle beetle *Oulimnius tuberculatus*, the caddis fly larvae *Athripsodes cinereus*, *Polycentropus flavomaculatus*, *Hydroptila* spp., *Ecnomus tenellus*, and *Oecetis* spp., larvae of the mayflies *Caenis horaria* and *Centroptilum luteolum*, the snails *Bithynia*, *Gyraulus* and *Radix* and *Pisidium* mussels.

#### 3.2.1. Invertebrate density

The total invertebrate density varied from 239 to 2000 ind $m^{-2}$ at impact sites, with an average of 904 ind $m^{-2}$. At control sites the invertebrate density varied between 313 and 3515 ind $m^{-2}$, averaging 1302 ind $m^{-2}$. The deepest zone sampled by Ekman-grab had the highest density of invertebrates, 1528 at impact sites and 2380 at control sites on average (Figures 4 and 5). The effect of crayfish on total invertebrate density was highly significant ($F = 6.36$, $p = 0.016$) and the effect of depth was also significant ($F = 15.0$, $p < 0.001$), whereas there was no interaction ($p = 0.323$).

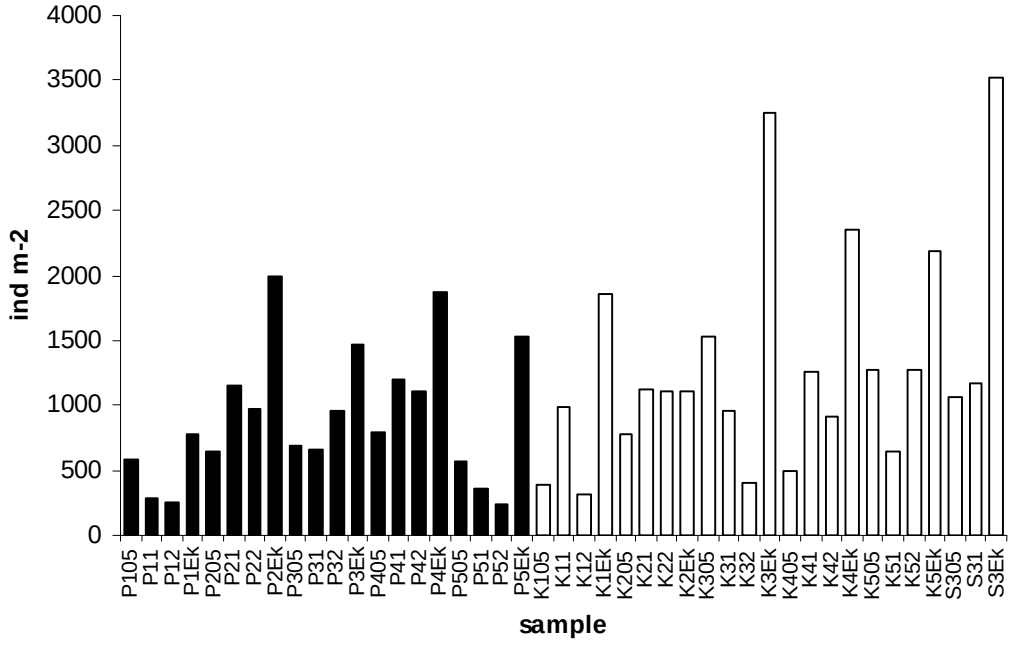


Figure 4. Mean density of invertebrate individuals per sample. Black columns on the left show the crayfish areas (P = Padasjoki) and white columns on the right show the control areas (K = Kuhmoinen and S = Saalahti). For each column, the first number is the site code, and the latter one indicates the depth (05 = 0.5m, 1=1m, 2 = 2m, Ek = deepest soft bottom).

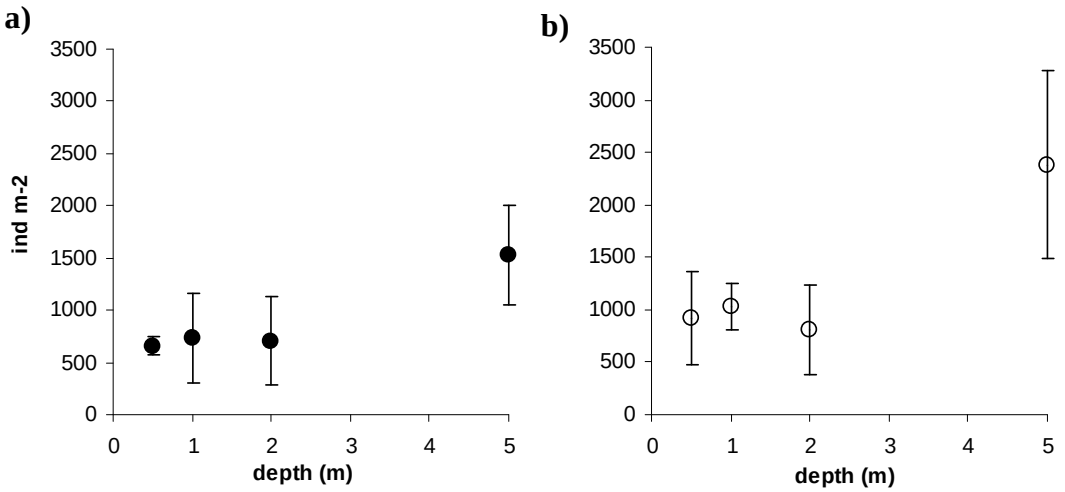


Figure 5. Mean density of invertebrates at each depth in areas with crayfish (a) and without crayfish (b), whiskers show standard deviation.

### 3.2.2. Snail density

The data suggest a strong negative correlation between the presence of crayfish and snail (Gastropoda) abundance (Figure 6). The average abundance of snails was 7 ind $m^{-2}$ at crayfish areas and 54 ind $m^{-2}$ at control sites. The effect of crayfish on snail density was significant ($F = 19.9$, $p < 0{,}001$), depth was not significant ($F = 1.8$, $p = 0.175$) and there were no interaction ($F = 1.4$, $p = 0.247$). Most snails were found at the depth of 0.5 m at crayfish sites and at the depth 1 m at control sites (Figure 7).

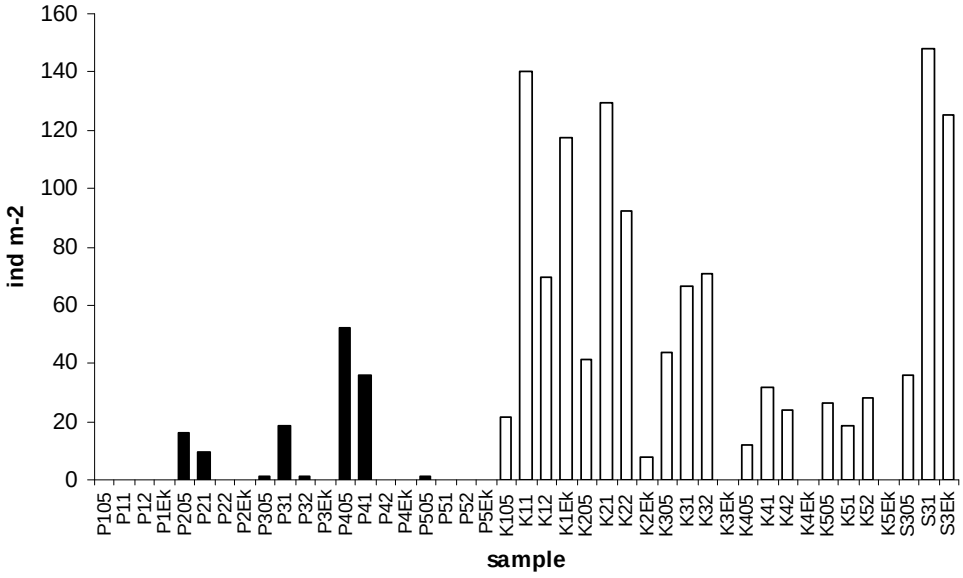


Figure 6. Mean density of Gastropoda per sample. Black columns on the left show the crayfish areas (P = Padasjoki) and white columns on the right show the control areas (K = Kuhmoinen and S = Saalahti). For each column, the first number is the site code, and the latter one indicates the depth (05 = 0.5m, 1=1m, 2 = 2m, Ek = deepest soft bottom).

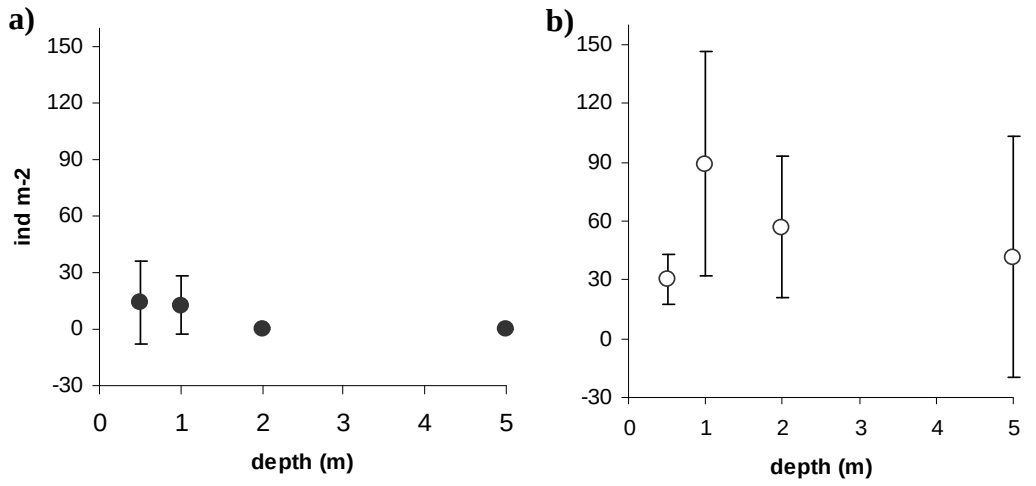


Figure 7. Mean density of snails at each depth in areas with crayfish (a) and without crayfish (b), whiskers show standard deviation.

### 3.2.3. Taxon richness

The mean number of taxa per sample (Figure 8) mirrors the invertebrate densities of the samples. The trend for the mean number of taxa without snail taxa (Figure 9) is similar as with all taxa. Crayfish showed an effect on species richness ($F = 54.8$, $p < 0.001$) as did depth ($F = 14.6$, $p < 0.001$), whereas there was no interaction ($p = 0.36$). The taxa at the impact sites decrease with depth, whereas the control sites have peaks at 1 and 2 m depths (Figure 10).

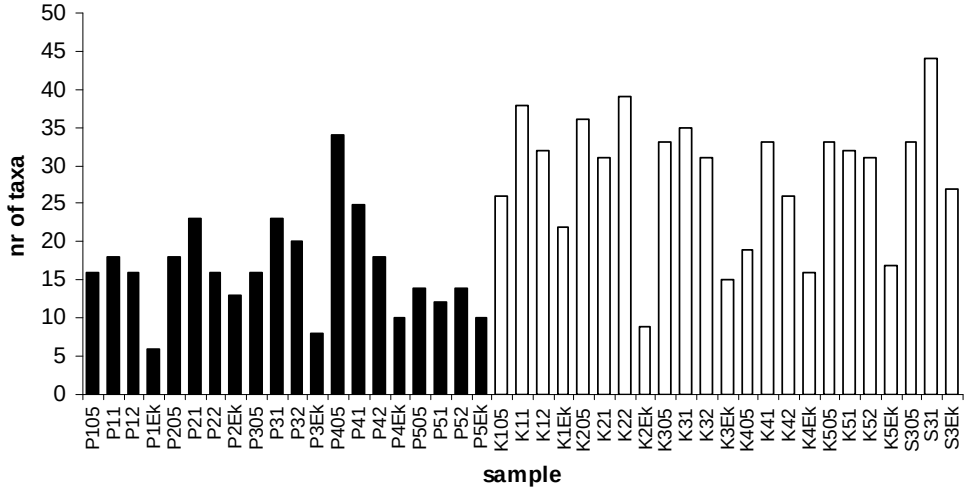


Figure 8. Mean number of taxa per sample. Black columns on the left show the crayfish areas (P = Padasjoki) and white columns on the right show the control areas (K = Kuhmoinen and S = Saalahti). For each column, the first number is the site code, and the latter one indicates the depth (05 = 0.5m, 1=1m, 2 = 2m, Ek = deepest soft bottom).

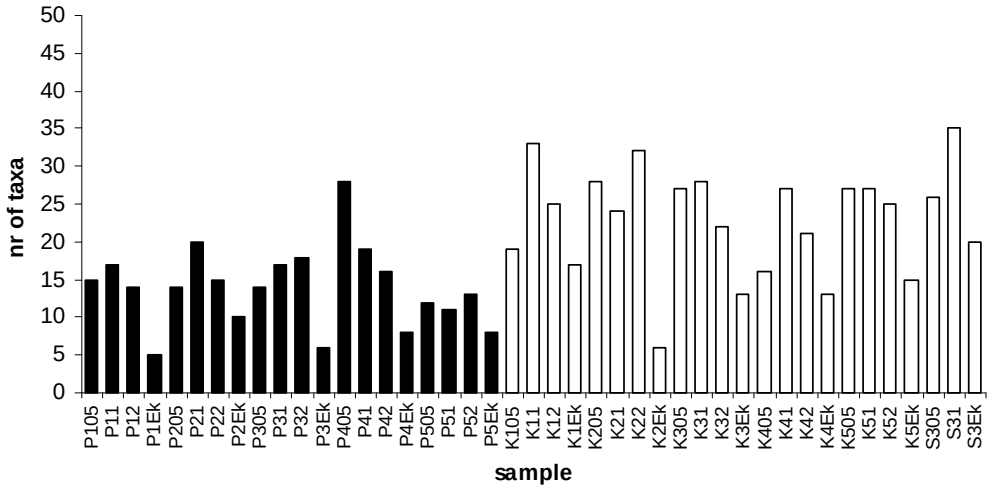


Figure 9. Mean number of taxa per sample, excluding the taxa of snails. Black columns on the left show the crayfish areas (P = Padasjoki) and white columns on the right show the control areas (K = Kuhmoinen and S = Saalahti). For each column, the first number is the site code, and the latter one indicates the depth (05 = 0.5m, 1=1m, 2 = 2m, Ek = deepest soft bottom).

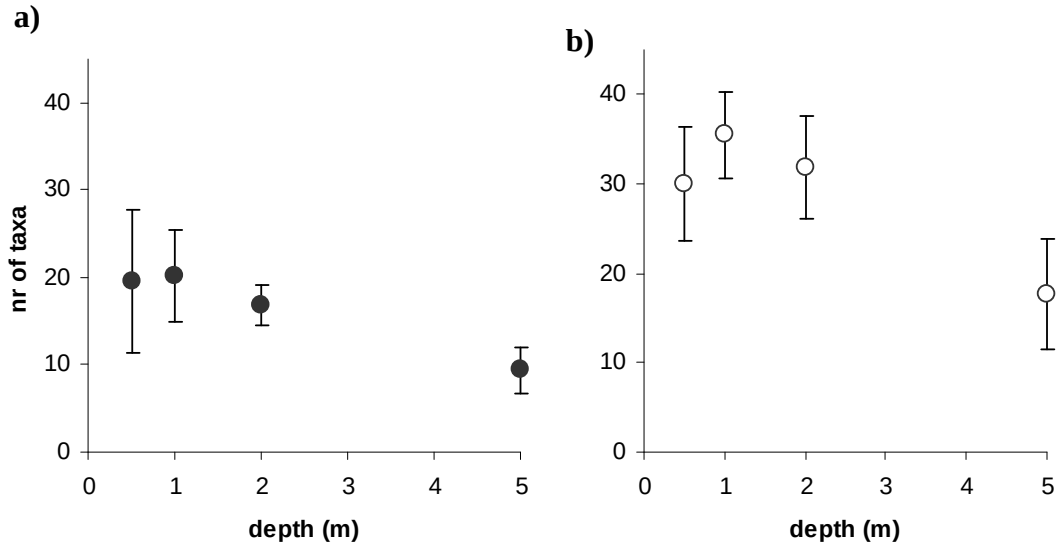


Figure 10. Mean number of taxa at each depth in areas with crayfish (a) and without crayfish (b), whiskers show standard deviation.

### 3.2.4. Relative contributions of invertebrate groups

Densities of invertebrate groups (Figure 11) show the evident difference of invertebrate composition between the areas. It seems the impact sites (P) were dominated by Chironomidae, Oligochaeta and Ephemeroptera, while the control sites (K and S) were dominated by Chironomidae, Oligochaeta, Elmidae, Amphipods, Gastropoda and Trichoptera and Ephemeroptera.

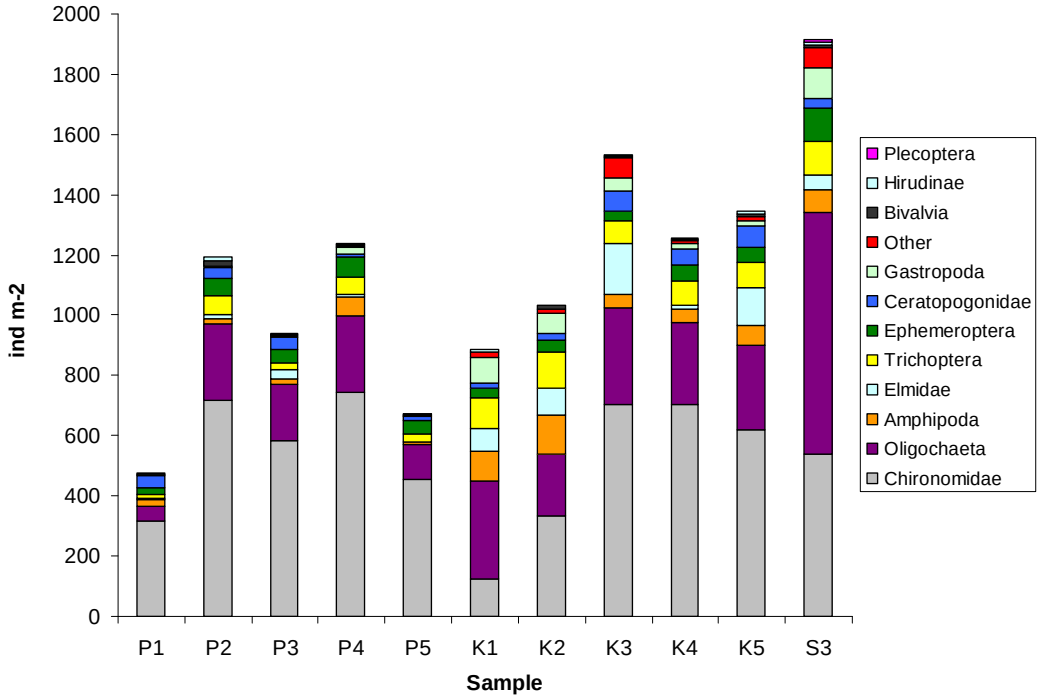


Figure 11. Absolute densities of invertebrate groups at all sampling sites. P symbols represent the impact sites, K and S symbols the control sites, the number stands for the code of the site.

The contribution of Chironomidae was 58-71 %, (average 63 %) in the impact area (Padasjoki), 13-50 % (average 31 %) in the first control area (Kuhmoinen) and 31 % in the other control area (Saalahti) (Figure 12). The second largest group of invertebrates was the Oligochaeta that varied from 7-22 % at all sites. The distribution of Oligochaeta was on average 14 % at Padasjoki, 19 % at Kuhmoinen and 29 % at Saalahti. Elmidae varied from 1-4 % at Padasjoki-sites with an average of less than 2 %. At Kuhmoinen the group was on average 12 % at and 4 % at Saalahti. Gastropoda had an average of 1 % at Padasjoki, 6 % at Kuhmoinen and 7 % at Saalahti. Trichoptera were on average 5 % at Padasjoki, 11 % at Kuhmoinen and 9 % at Saalahti of the total invertebrate amounts.

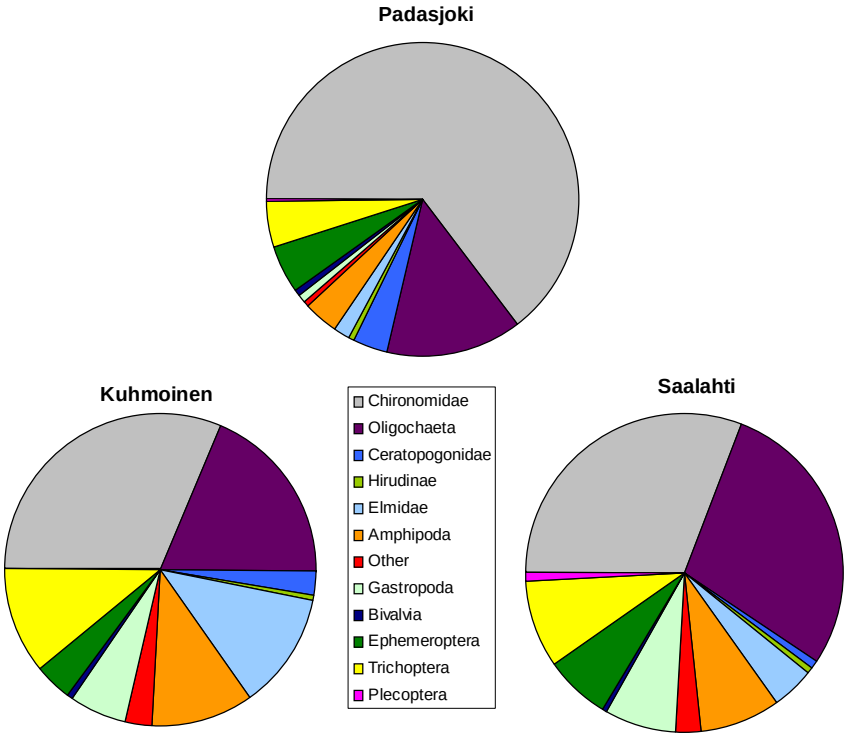


Figure 12. Relative contribution (%) of invertebrate groups at the impact area (Padasjoki) and the control areas (Kuhmoinen and Saalahti).

### 3.3. NMS-ordination

The NMS analysis of the invertebrate densities gave a two-dimensional solution (stress = 10.82417, instability = 0.00001). In the ordination graph (Figure 13) the samples from crayfish and non-crayfish areas are fairly distinctively clustered into separate groups. None of the observed environmental variables correlated strongly with the ordination axes. Sampling depth (axis 1 r = 0.408; axis 2 r = 0.634) and stone size (axis 1 r = -0.475; axis 2 r = -0.615) showed the strongest correlation, but there are no clear groups for different depths except for the deepest zone sampled by Ekman -grab.

Examples of the variation of some taxa chosen based on the interest of certain species and the Indicator Species Analysis in section 3.4. in the NMS ordination space are presented in figures 14 and 15. The Chironomidae distribution (Figure 14a) shows a clustered group of Ekman-grab samples for both impact and control sites and the other depths are slightly in separate areas of the graph. In two-way analysis of variance (ANOVA) the Chironomidae did not differ between the areas ($p = 0.493$), except that when the Ekman-grab samples were excluded, the Chironomidae was more abundant at the impact areas than at the control areas ($p = 0.039$). The *Asellus aquaticus* (Figure 14b) ($p = 0.004$), *Oulimnius tuberculatus* (Figure 15a) ($p = 0.004$) and *Radix* (Figure 15b) ($p = 0.001$) results show similar variation in the samples between impact and control sites; the control sites are separated from the impact sites and are more abundant. The Ephemeropteran *Centroptilum luteolum* (Figure 15c) differed between the areas ($p = 0.001$), but was more abundant at the impact sites. *Caenis horaria* (Figure 15d) also differed between the areas ($p = 0.006$), but was more abundant at the control sites. The *Oecetis* spp. (Figure 15e) and *Hydroptila* spp. (Figure 15f) were both affected by the crayfish ($p = 0.014$ and $p < 0.001$) and the graphs show clearly the higher abundance of the taxon at the control sites.

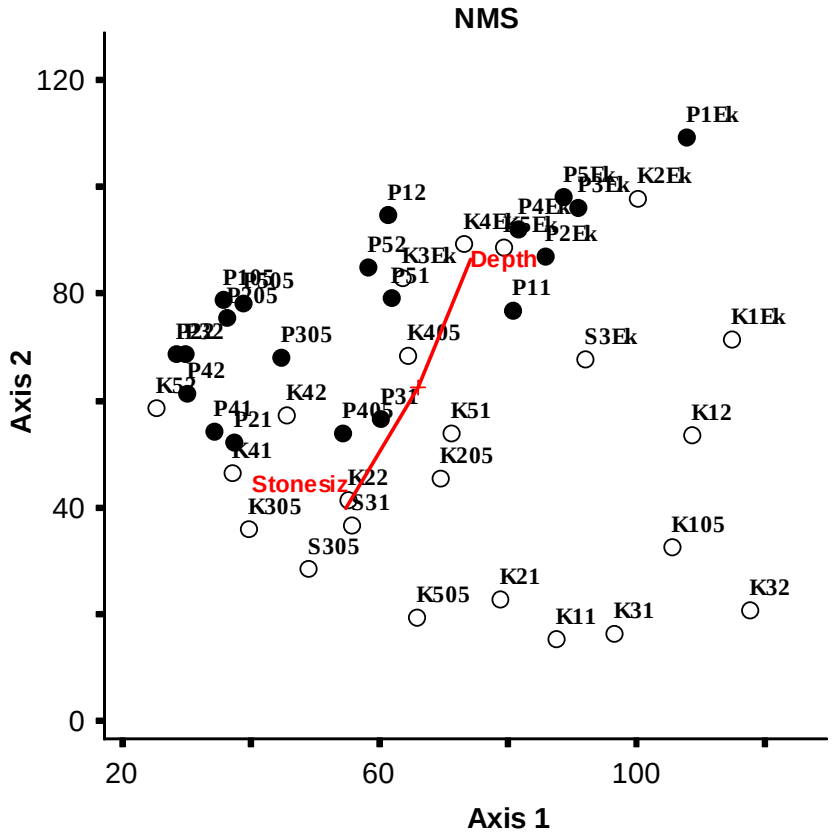


Figure 13. NMS-ordination plot showing the variation of benthic invertebrate community composition among study sites and the depth vector representing the direction of increasing depth and stone size vector representing the direction of increasing stone size. Each dot depicts a combined sample from each depth zone of each site. Black dots represent samples from the area with crayfish, white dots represent non-crayfish samples. The letters (P, K and S) stand for the study areas Padasjoki, Kuhmoinen and Saalahti, the first number is the site code, the second number is the depth.

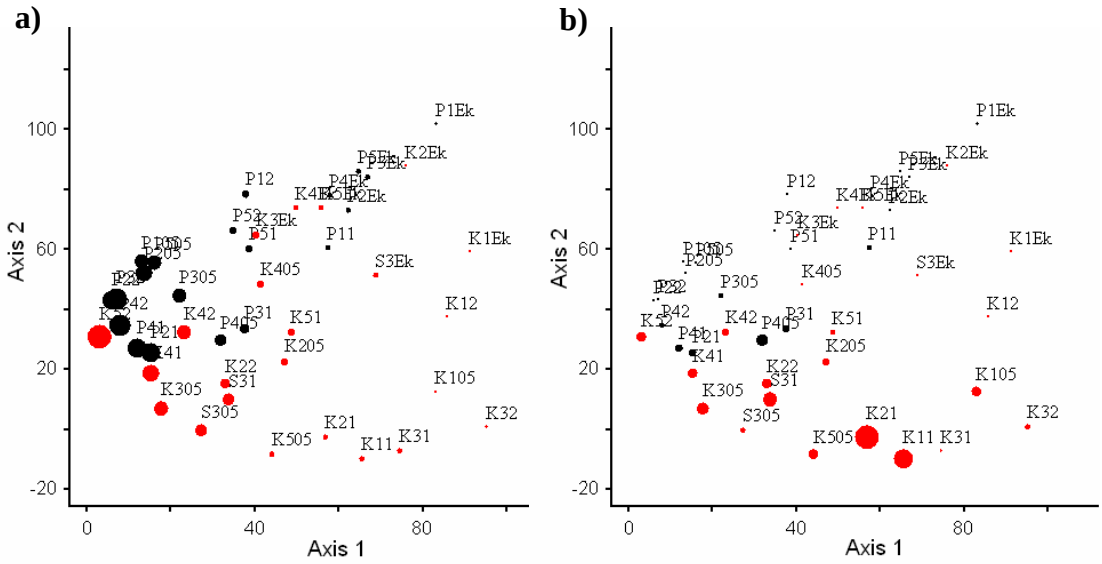


Figure 14. NMS ordination graphs showing the appearance of a) Chironomidae and b) *Asellus aquaticus* among study sites. Each dot depicts a combined sample from each depth zone of each site. Black dots represent samples from the area with crayfish, red dots represent non-crayfish samples.

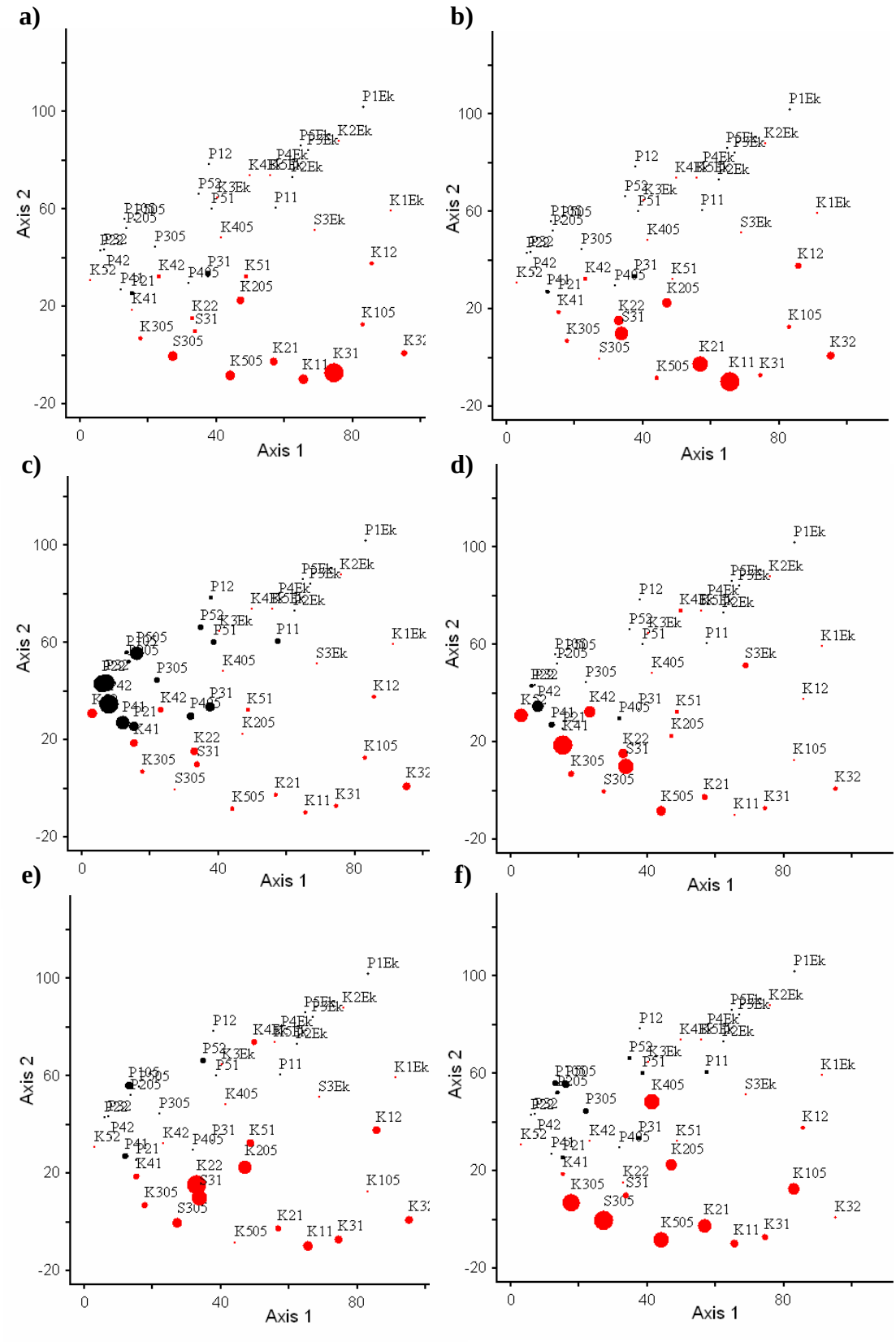


Figure 15. NMS ordination graphs showing the appearance of a) *Oulimnius tuberculatus*, b) *Radix*, c) *Centroptilum luteolum*, d) *Caenis horaria*, e) *Oecetis* spp. and e) *Hydroptila* spp. among study sites. Each dot depicts a combined sample from each depth zone of each site. Black dots represent samples from the area with crayfish, red dots represent non-crayfish samples.

### 3.4. Indicator species analysis

The indicator species analysis was done excluding the Ekman-grab samples since the samples were systematically different in invertebrate composition from those from the shallow areas, and the stony littoral samples were of the main interest in the study. The test gave a significant indicator value for 22 species (Table 4) of the total 79 species. Only two taxa (Chironomidae and *Centroptilum luteolum*) were found as indicators of impact sites, areas with crayfish, whereas 20 indicators were found for control sites, areas with no crayfish (Table 4). The highest indicator values were 95 for *Radix*; 90.5 for water mites (Acarina); 87.4 for *Normandia nitens* and 82.7 for *Oulimnius tuberculatus*. Crustaceans, beetles and snails plus some caddis flies generally had the highest indicator values.

Table 4. Indicator taxa for impact sites (group 1) and control sites (group 0). For each taxon, the indicator value (IV) observed (0-100), and its significance (p = proportion of the random IV > observed IV, Monte-Carlo randomization, N=1000) is presented.

| Taxon | Group | Ind. value | p |
|---|---|---|---|
| DIPTERA | | | |
| Chironomidae | 1 | 61.9 | 0.03 |
| CRUSTACEA | | | |
| *Asellus aquaticus* | 0 | 76.6 | 0.002 |
| *Pallasea quadrispinosa* | 0 | 56.2 | 0.003 |
| COLEOPTERA | | | |
| *Oulimnius tuberculatus* | 0 | 82.7 | 0.002 |
| *Normandia nites* | 0 | 87.4 | 0.001 |
| ARACHNIDA | | | |
| *Acarina* | 0 | 90.5 | 0.001 |
| GASTROPODA | | | |
| *Bathyomphalus contortus* | 0 | 45.7 | 0.008 |
| *Bithynia* | 0 | 78.8 | 0.002 |
| *Gyraulus* | 0 | 67.4 | 0.004 |
| *Radix* | 0 | 95.1 | 0.001 |
| EPHEMEROPTERA | | | |
| *Caenis horaria* | 0 | 65.1 | 0.016 |
| *Centroptilum luteolum* | 1 | 74.4 | 0.001 |
| *Heptagenia fuscogrisea* | 0 | 57.6 | 0.021 |
| TRICHOPTERA | | | |
| *Hydroptila sp.* | 0 | 60.7 | 0.049 |
| *Oxyethira sp.* | 0 | 29.4 | 0.041 |
| *Mystacides sp.* | 0 | 49.1 | 0.036 |
| *Athripsodes cinereus* | 0 | 81.6 | 0.001 |
| *Ceraclea sp.* | 0 | 45.7 | 0.01 |
| *Lepidostoma hirtum* | 0 | 45.9 | 0.032 |
| *Ecnomus tenellus* | 0 | 35.3 | 0.024 |
| *Molanna angustata* | 0 | 75.0 | 0.001 |
| *Tinodes waeneri* | 0 | 62.0 | 0.003 |

# 4. DISCUSSION

## 4.1. Validity in site selection

The 1.2-3.9 crayfish caught per trap at the impact sites can be classified as moderate abundance (Böhling & Rahikainen 1999) (Table 5). However for this time of the summer, when the crayfish have moulted and the catching season is about to start and the crayfish are not that active, the abundance was quite high and verifies the well established crayfish population at the impact sites for the study.

Table 5. A scale by Böhling P. & Rahikainen M. (1999) for estimating the abundance of crayfish.

| Catch per Unit Effort (ind. trap-1 night -1) | Crayfish population |
|---|---|
| >10 | very dense |
| 4-10 | dense |
| 1-4 | moderate |
| 0.1-1 | sparse |
| <0.1 | very sparse |

However an unavoidable feature of the design of this study is that when two or three different areas are compared to each other, those differences that are here interpreted as being a result of the crayfish could theoretically be caused by any other differences between the areas. However, in practice there were no noticeable differences between areas in important environmental variables, such as the water quality and physical characteristics of the sites. In addition the second control area in Saalahti, which was the most different area from the two others, had a similar benthic invertebrate composition as the main control area in Kuhmoinen. This indicates that the basic underlying assumptions of the study are probably reasonable robust. Nevertheless, the problems inherent in the design of this experiment are recognized and kept in mind when drawing conclusions. For a better validity of the study more randomly selected sites and sites from different lakes would be useful. Comparing the impacts of sites with different crayfish abundances would also be an excellent approach.

## 4.2. Invertebrate density and taxon richness

The results show that invertebrate density and taxon richness were both reduced in the presence of crayfish. The invertebrate density was on average 44 % lower at areas with crayfish than without crayfish. Especially Gastropoda, Trichoptera, Elmidae (in Coleoptera) and *Asellus aquaticus* (in Crustaceans) were negatively affected by the presence of crayfish. Similar results have been reported by McCarthy *et al.* (2006) and Wilson *et al.* (2004) who both studied the rusty crayfish *Orconectes rusticus.* McCarthy *et al.* found a negative effect of the crayfish on total invertebrate densities in a cage experiment. Gastropoda and Diptera abundances declined significantly in the presence of rusty crayfish and Amphipoda, Coleoptera, Ephemeroptera, Oligochaeta and Trichoptera were also reduced but not significantly. In the long term study a significant negative relationship between rusty crayfish and total zoobenthos abundance was noticed, as well as the invertebrate orders Diptera, Ephemeroptera and Odonata. Significant negative relationships at the family level included Chironomidae (Diptera), Ephemerellidae (Ephemeroptera), Coenagrionidae (Odonata) and Hydroptilidae (Trichoptera). In the study by Wilson *et al.* (2004), where the invasion by rusty crayfish in a north temperate lake in Canada was examined macroinvertebrate, snail, macrophytes and crayfish species richness

and in some cases abundance, decreased within a few years of the arrival of rusty crayfish. They reported significant reductions in Diptera, Odonata and Amphipoda.

The crayfish had the opposite influence on the chironomids than the other invertebrates in this study. The relative contribution of chironomids in areas with crayfish was higher than with no crayfish, whereas the impact and control areas had on average similar densities of chironomids. Additionally, Chironomidae were an indicator species group for crayfish areas at the depths 0.5-2 m, where also their density was significantly greater than in areas without crayfish. Due to the scope of this project the Chironomidae were not identified. Also information about the biomasses of the midges as opposed to densities of individuals could have been valuable for drawing conclusions. It would have been interesting to study the taxa of Chironomidae to see if some species are more consumed or affected by crayfish than others. For example Nyström *et al.* (1999) and Stenroth & Nyström (2003) suggested that active macroinvertebrate predators and sediment-living prey could be more difficult for crayfish to capture than large slow-moving herbivores. On the other hand, Usio & Townsend (2004) found that higher abundances of Chironomidae larvae were related to the presence of the native New Zealand crayfish *Paranephrops zealandicus*. The crayfish strongly consumed Tanypodinae larvae, which are the most active predators of Chironomidae larvae. In our study there might be some other predator on the chironomids that the crayfish has consumed or omitted and therefore the Chironomidae abundance is high or then the Chironomidae were very small in size and not predated by the crayfish. Olsson & Nyström (2008) stated that crayfish reduces the abundance of chironomids, but in their study this was regarding the presence of juvenile crayfish. This might be associated with the small size of the prey. In the same study adult crayfish reduced biomass of some invertebrate taxa (Coleoptera and Limoniidae), which were too large for juveniles to feed on. This indicates that competition for food is not so strong between juvenile and adult crayfish (Olsson & Nyström 2008). In my study the impacts of juveniles and adult crayfish could not be separated, but it can be assumed that the influence of juveniles is greater at the shallow depths (0.5 and 1 m) than at the depths of 2 m and over (Rajala 2006).

According to the indicator species analysis test the Trichoptera were greatly affected by the crayfish. Nine caddisfly species (*Hydroptila* sp, *Oxyethira* sp., *Mystacides* sp., *Athripsodes cinereus*, *Ceraclea* sp., *Lepidostoma hirtum*, *Ecnomus tenellus*, *Molanna angustata* and *Tinodes waeneri*) were indicators of the control sites. Seven of these species have case-bearing larvae and two are caseless, suggesting that the crayfish feed a lot on case-bearing caddisfly larvae, which are most probably slow moving. The two caseless species *E. tenellus* and *T. waeneri* are both typical species of stony substrates; *E. tenellus* is a predator that feeds by spinning nets on the surface of stones and *T. waeneri* builds galleries and mainly scrapes algae from the stone surface into the galleries (Edington & Hildrew 2005). The two species seem very “positional” and therefore probably easy prey for the crayfish.

### 4.3. Snails

The abundance of snails (Gastropoda) was clearly negatively affected by the crayfish in this study, as has been reported by Alexander & Covich (1991), Bernot & Turner (2001), Nyström *et al.* (2001) and Wilson *et al.* (2004). Some snail taxa were indicator species of the presence of crayfish in the study: *Bathyomphalus contortus*, *Bithynia*, *Gyraulus* and *Radix*. Freshwater snails are slow moving and partly therefore easy prey for crayfish. There is some evidence that snail predation is dependent on size, shape of the shell and shell thickness (Alexander & Covich 1991, Renai & Gherardi 2004, Lakowitz T.

*et al.* 2008,). Nyström *et al.* (1998) noted that crayfish preferred the smaller size classes of snails in their experiment. The results suggest that that crayfish can structure the abundance and size distribution of thin-shelled snails, through size-selective predation and reduction of macrophytes.

Depth was not a significant factor in the distribution of snails in the presence of crayfish, but the study suggests some relationship between abundance of snails in different depths and presence or absence of crayfish. In the absence of crayfish the most abundant snail densities were found at 1m depth and least at 0.5 m, whereas in the presence of crayfish most snails were found at 0.5 m and least under the depth of 2 m. This might be explained by the vertical distribution of the crayfish (Rajala 2006) and perhaps predatory avoidance behaviour of the snail. Alexander *et al.* (1991) studied the vulnerability and predator avoidance behaviour of two freshwater snails, *Physella virgata* and *Planorbella trivolvis,* to the crayfish *Procambarus simulans*. In response to crayfish predation, the snails crawled above the waterline for hours and then returned to the water. Freshwater snails have different kinds of predator avoidance mechanisms, for example, they bury themselves to substrates, crawl into vegetation or above the waterline. *P. virgata* appeared to react to chemicals coming from crayfish and from injured individuals of the same species. *P. virgata* were more vulnerable to crayfish than similar sized *P. trivolvis* because the crayfish could not consume large *P. trivolvis* since they could not crush the thicker planspiral shell or manipulate the shell to a position where the mouthparts could crush it or chip the thickened aperture lip. The large *P. trivolvis* seems to rely on its strong shell structure and did not play any avoidance behaviour. Small *P. trivolvis* displayed the most crawl-out responses with most of the surviving snails above the waterline. All sizes of *P. virgata* were equally vulnerable and were equally likely to crawl above the waterline. In a study by Turner *et al*. (1999), snails (*P. virgata*) in the presence of crayfish avoided benthic cover and moved to the water surface, while in the presence of fish the snails moved under cover.

Brönmark (1992) stated that snails would also be affected by leeches, since leeches are predators of newly hatched and juvenile snails and might therefore reduce the snail abundance. In my study the leeches were not significantly affected by the crayfish although I had assumed that they would be easy prey for the crayfish. However there seemed to be slightly more individuals of leeches in the control sitesIn my study it is hard to say whether the leeches reduced the snail abundance or not, but the leeches were more abundant where they did not have to compete for prey with the crayfish and where more prey was available.

### 4.4. Potential changes in the ecosystem

Although this study was limited to the impacts of crayfish on littoral invertebrates, other impacts and changes in the ecosystem could be expected according to the literature. The reduction of grazing snails can appear as increased biomass of periphyton (Nyström *et al*. 2001), which might evidently lead to an increased number of other grazers in the invertebrate community. In my study the number of *Centroptilum luteolum* and *Baetis* sp., which are both mobile grazers; and Chironomidae (many different feeding groups) increased in the presence of crayfish at the 0.5 -2 m depths. Other taxa or groups of invertebrates were not found to be positively affected by the crayfish.

Reduction in detritus has potential consequences for zoobenthic communities (McCarthy *et al*. 2006). Especially collector-gatherers and detrivores, such as taxa in the orders Ephemeroptera, Trichoptera and Diptera are affected by this (McCarthy *et al*. 2006). The zoobenthic community itself is a network of predator-prey interactions. For example,

crayfish predation upon other zoobenthic predators such as Odonata larvae could reduce their abundance, subsequently allowing an increase in abundance of their prey. Likewise, crayfish may compete with Odonata for prey resources (McCarthy *et al.* 2006).

Crayfish graze and destroy macrophytes by clipping and uprooting them, as well as consuming them as food. However the destruction of much more of the plant tissue than the crayfish can eat might sometimes even have a positive effect. For example some plant species that readily root adventitiously (e.g. *Elodea* spp.) or species without roots (e.g. *Ceratophyllum* spp.) may benefit from crayfish fragmentation (Lodge *et al.*, 1994). However, hydrophyte destruction in nutrient rich conditions can in general be followed by a switch from a clear to a turbid state dominated by surface microalgae. This may lead to decreased primary production due to the reduced light penetration. Change in hydrophyte biomass can also have non-trophic effects on the lake community, because of their role as protective cover, substratum or breeding sites for many organisms (Dorn & Wojdak 2004). Besides crayfish directly consuming invertebrates, reductions in invertebrates over a longer period may be caused by loss of macrophytes habitat or competition for prey with the crayfish (Wilson *et al.* 2004).

Non-indigenous crayfish such as *Pacifastacus leniusculus* may be able to cause direct damage through their predatory activity to benthic fish or may outcompete them for access to shelters (Guan & Wiles 1997). In this study burbot (*Lota lota*), stone loach (*Barbatula barbatula*), bullhead (*Cottus gobio*), perch (*Perca fluviatilis*) and the ruffe (*Gymnocephalus cernuus*) that are common littoral species of freshwaters in Finland, could have been affected by the presence of crayfish. Wilson *et al.* (2004) showed the first evidence that rusty crayfish have had long term negative impacts on populations of bluegill and pumpkinseed sunfish, probably due to reductions in their habitats (macrophytes) and competition for invertebrate prey, plus direct predation on their eggs.

## 5. CONCLUSIONS

This study presents preliminary evidence that the presence of signal crayfish can reduce invertebrate density and abundance in large lakes. Snail abundance in particular is negatively impacted by the crayfish and had on average eight times lower abundance in the presence of the crayfish. The impact sites were dominated by Chironomidae and Oligochaeta and small abundances of other invertebrate groups, while the control sites were dominated more evenly by Chironomidae and Oligochaeta, Elmidae, Amphipods, Gastropoda and Trichoptera and Ephemeroptera. At the depths 0.5-2 m, Chironomidae and the mayfly *Centroptilum luteolum* were indicator species for the impact sites, while the control sites had 22 species that indicated the absence of crayfish, mostly species of crustaceans, gastropods and Trichoptera. The presence of signal crayfish increased the amount of some mobile grazers such as the mayflies *Centroptilum luteolum* and *Baetis* sp.

Some important factors were not considered in this study because of its limitations. The study was focused on the taxa and abundance of the invertebrates, which are certainly important, but comparing biomasses of the invertebrate groups between the areas could have brought additional insights to the study. As the impact sites were dominated by Chironomidae and Oligochaeta, the biomasses of the invertebrates were most probably small. In addition the identification of the species would have been important for studying the food web related to the signal crayfish. When considering the snails, it would have been interesting to study the sizes and shapes of the shells to detect prey selection of the crayfish and possible avoidance behaviour of the snails. Evaluating the periphyton coverage would have been beneficial for studying the effect of crayfish and reduced snail abundance.

The results of this study indicate evident impacts of signal crayfish on benthic invertebrate communities of Lake Päijänne and likely large lakes in general, in accordance with results of previous studies. Therefore there is a great need for better management and control on the spreading of the signal crayfish and serious consideration before the signal crayfish is stocked and introduced into more lakes. Further studies on the signal crayfish in large lakes are necessary to detect the dimensions of the impacts of the crayfish on whole food webs. The signal crayfish can be a threat to the biodiversity of the lakes in the future if its spread is not controlled. First of all, spreading the crayfish by any persons other than legal authorities should be strictly banned. At the moment most people are not aware of the threats that the signal crayfish bears, apart from the crayfish plague. The knowledge and care of the public should be increased.

What are the most serious outcomes that can arise of the increasing signal crayfish abundances? In general the crayfish mostly inhabit the littoral zone and this is where fish feed and spawn. Therefore the crayfish may outcompete some fish species by using their habitat and feeding on their prey, eggs and juvenile fish. What happens if the gastropods disappear? The gastropods are important grazers and important food for some fish and bird species, so the absence of snails and increase in periphyton might lead to noticeable changes in the ecosystems. Moreover, gastropods are intermediate hosts for many important fish parasites, so changes in gastropod abundances as a result of crayfish invasion may affect parasite infection intensities. Thus many complex questions remain open related to the impacts of this non-indigenous crayfish species.

## ACKNOWLEDGEMENTS

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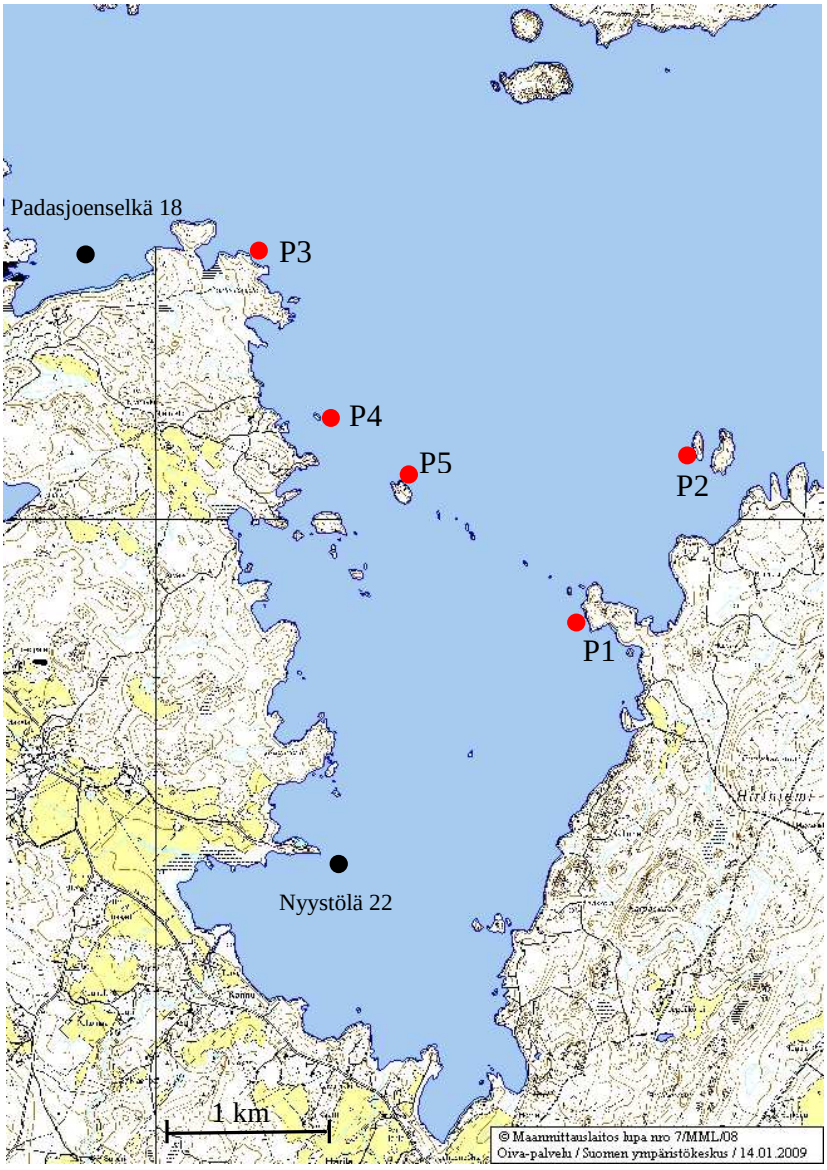
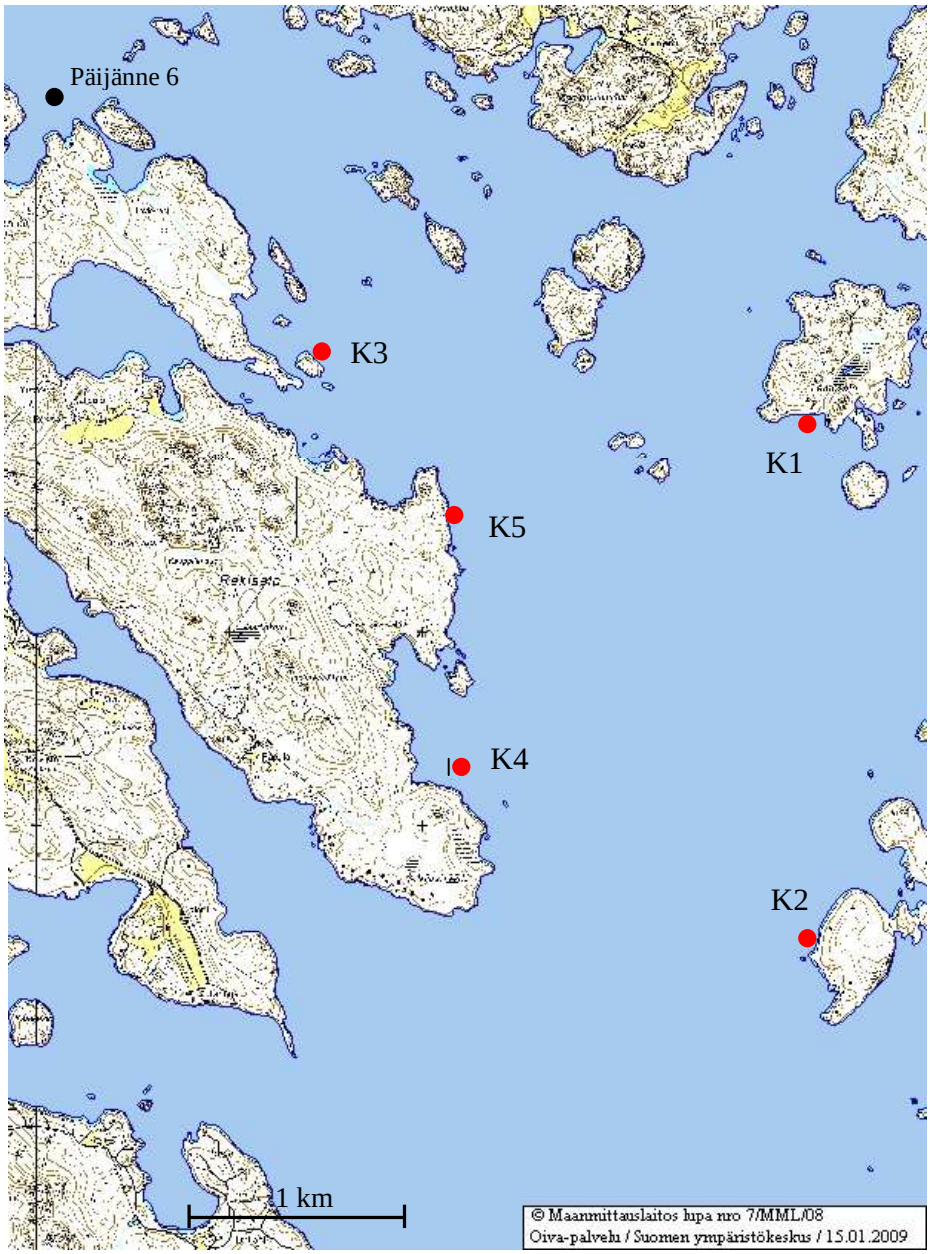
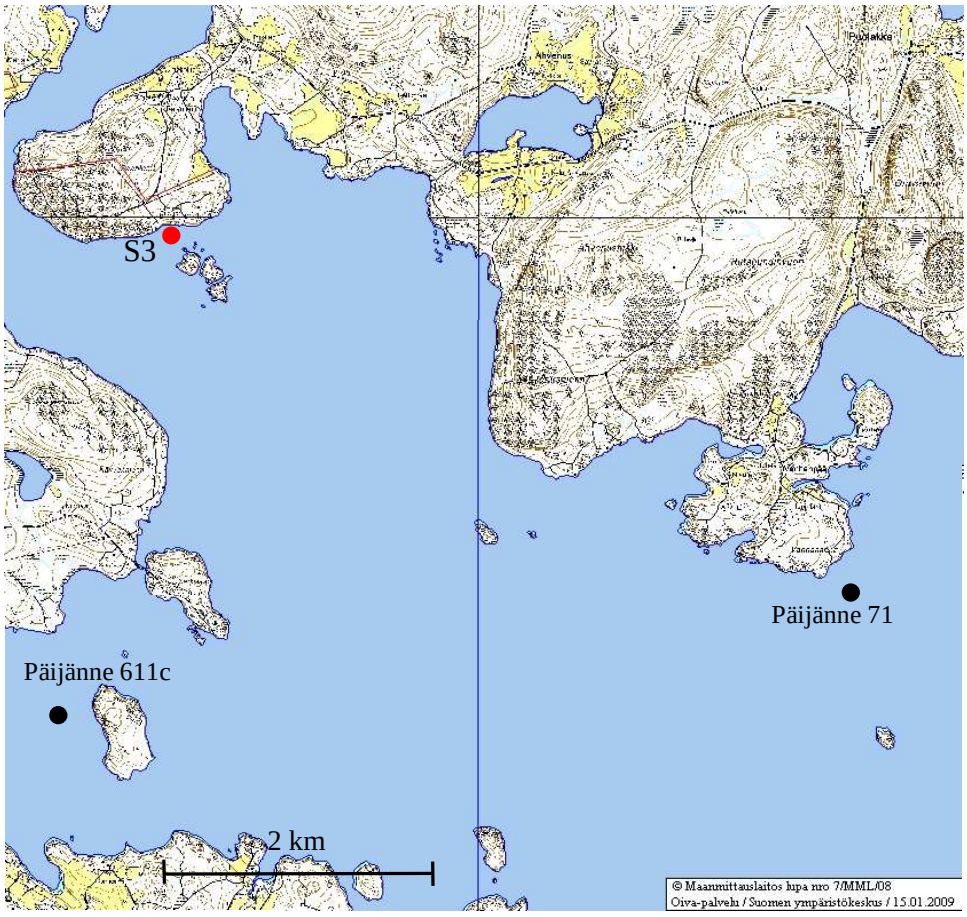
Appendix 1. Map of Padasjoenselkä with sampling sites P1, P2, P3, P4 and P5 and water sample sites Nyystölä 22 and Padasjoenselkä 18.



Appendix 1 continues. Map of Kuhmoistenselkä with sampling sites K1, K2, K3, K4 and K5 and water sample site Päijänne 6.



Appendix 1 continues. Map of Saalahti area with sample site S3 and water sample sites Päijänne 611c and Päijänne 71.



# Appendix 2. Average densities (ind $m^{-2}$) of the taxa at each depth in all the sites

| **Sample** | **P1** | | | | **P2** | | | | **P3** | | | | **P4** | | | | **P5** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek |
| **Taxon** | | | | | | | | | | | | | | | | | | | | |
| PLATYHELMINTHES | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| NEMATODA | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| OLIGOCHAETA | 20 | 36 | 11 | 133 | 37 | 236 | 91 | 648 | 97 | 151 | 105 | 398 | 120 | 256 | 148 | 500 | 29 | 68 | 29 | 344 |
| HIRUDINEA | | | | | | | | | | | | | | | | | | | | |
| *Erpobdella octulata* | 1 | 7 | 7 | 0 | 0 | 24 | 0 | 16 | 0 | 11 | 1 | 0 | 0 | 4 | 5 | 0 | 1 | 1 | 0 | 0 |
| *Glossiphonia heteroclita* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Glossiphonia complanta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Helobdella stagnalis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pisciola geometra* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GASTROPODA | | | | | | | | | | | | | | | | | | | | |
| Hydrobidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bathyomphalus contortus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Acroloxus lacustris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bithynia* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 37 | 20 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gyraulus* | 0 | 0 | 0 | 0 | 13 | 8 | 0 | 0 | 1 | 7 | 0 | 0 | 11 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Radix* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Myxas glutinosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Planorbis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Valvata* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lymnea stagnalis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Physa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Armiger* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BIVALVIA | | | | | | | | | | | | | | | | | | | | |
| *Anodonta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pisidium* | 0 | 0 | 5 | 0 | 0 | 1 | 37 | 23 | 0 | 1 | 15 | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 1 | 16 |
| *Sphaerium* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| CRUSTACEA | | | | | | | | | | | | | | | | | | | | |
| *Pallasea quadrispinosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Monoporeia affinis* | 0 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 23 |
| *Asellus aquaticus* | 5 | 53 | 3 | 0 | 3 | 67 | 0 | 0 | 19 | 57 | 4 | 0 | 136 | 69 | 36 | 0 | 5 | 4 | 1 | 0 |
| ARACHNIDA | | | | | | | | | | | | | | | | | | | | |
| Acari | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 3 | 3 | 3 | 0 | 1 | 3 | 3 | 0 |
| ODONATA | | | | | | | | | | | | | | | | | | | | |
| *Corduliidae sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EPHEMEROPTERA | | | | | | | | | | | | | | | | | | | | |
| *Ephemera vulgata* | 0 | 0 | 4 | 55 | 0 | 0 | 1 | 31 | 0 | 0 | 0 | 86 | 0 | 0 | 1 | 47 | 0 | 0 | 0 | 109 |
| *Caenis lactea* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Caenis luctuosa* | 0 | 1 | 7 | 0 | 0 | 15 | 24 | 31 | 0 | 0 | 13 | 0 | 0 | 3 | 15 | 31 | 0 | 0 | 3 | 0 |
| *Caenis horaria* | 0 | 0 | 0 | 0 | 0 | 1 | 9 | 16 | 0 | 1 | 3 | 0 | 7 | 13 | 36 | 16 | 0 | 0 | 0 | 8 |
| *Centroptilum luteolum* | 7 | 8 | 4 | 0 | 5 | 17 | 41 | 0 | 9 | 17 | 39 | 8 | 16 | 28 | 44 | 0 | 28 | 11 | 9 | 0 |
| *Leptophlebia sp.* | 0 | 3 | 0 | 0 | 5 | 3 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Paraleptophlebia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Baetis fuscatus* | 4 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 7 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 12 | 0 | 0 | 0 |
| *Heptagenia dalecarlica* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Heptagenia fuscogrisea* | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cloeon dipterum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

# Appendix 2 continues. Average densities (ind $m^{-2}$) of the taxa at each depth in all the sites

| **Sample** | **P1** | | | | **P2** | | | | **P3** | | | | **P4** | | | | **P5** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek |
| PLECOPTERA | | | | | | | | | | | | | | | | | | | | |
| *Nemoura* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Leuctra fusca* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 7 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Diura bicaudata* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| DIPTERA | | | | | | | | | | | | | | | | | | | | |
| Chironomidae | 444 | 117 | 196 | 508 | 531 | 633 | 680 | 1023 | 448 | 293 | 703 | 883 | 345 | 696 | 737 | 1195 | 439 | 240 | 256 | 961 |
| Ceratopogonidae | 71 | 29 | 4 | 55 | 11 | 0 | 21 | 117 | 53 | 16 | 31 | 47 | 7 | 4 | 9 | 23 | 7 | 1 | 3 | 39 |
| *Brachycera sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| COLEOPTERA | | | | | | | | | | | | | | | | | | | | |
| *Oulimnius tuberculatus* | 7 | 5 | 0 | 8 | 8 | 53 | 4 | 0 | 19 | 75 | 3 | 8 | 19 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Normandia nites* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Elmis aena* | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gyrinidae | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| *Gyrinus sp.* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Dytiscidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Haliplidae sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hydroporinae sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Nebriporus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Platambus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| NEUROPTERA | | | | | | | | | | | | | | | | | | | | |
| Sisyridae sp. | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| HETEROPTERA | | | | | | | | | | | | | | | | | | | | |
| Corixidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| TRICHOPTERA | | | | | | | | | | | | | | | | | | | | |
| *Hydroptila sp.* | 20 | 8 | 3 | 0 | 15 | 5 | 0 | 0 | 17 | 8 | 0 | 0 | 3 | 0 | 0 | 0 | 27 | 13 | 11 | 0 |
| *Oxyethira sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Polycentropus flavomaculatus* | 1 | 5 | 0 | 0 | 7 | 24 | 0 | 8 | 7 | 3 | 0 | 0 | 37 | 15 | 0 | 0 | 8 | 9 | 0 | 8 |
| *Mystacides sp.* | 0 | 1 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Athripsodes cinereus* | 1 | 4 | 3 | 0 | 0 | 11 | 23 | 0 | 0 | 1 | 7 | 0 | 1 | 16 | 43 | 23 | 0 | 1 | 3 | 0 |
| *Ceraclea nigronervosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ceraclea annulicornis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ceraclea albimacula* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidostoma hirtum* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 5 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| *Ecnomus tenellus* | 0 | 3 | 8 | 0 | 1 | 32 | 20 | 70 | 0 | 0 | 19 | 31 | 1 | 25 | 19 | 31 | 0 | 1 | 3 | 0 |
| *Molanna albicans* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Molanna angustata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Molanna submarginalis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Leptoceridae sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 |
| *Cyrnus flavidus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cyrnus trimaculutus* | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 23 |
| *Tinodes waeneri* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Oecetis testacea* | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Oecetis ochracea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Oecetis sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neureclipsis bimaculata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Goera pilosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hydropsyche contubernalis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chaetopteryx villosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Apatania muliebris* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Apatania sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Limnephilidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SUM | 589 | 285 | 256 | 773 | 648 | 1155 | 969 | 2000 | 687 | 663 | 952 | 1461 | 788 | 1193 | 1104 | 1875 | 565 | 353 | 239 | 1531 |

# Appendix 2 continues. Average densities (ind $m^{-2}$) of the taxa at each depth in all the sites

| **Sample** | **K1** | | | | **K2** | | | | **K3** | | | | **K4** | | | | **K5** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek |
| PLATYHELMINTHES | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 8 | 0 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| NEMATODA | 1 | 7 | 0 | 16 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 16 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 8 |
| OLIGOCHAETA | 28 | 85 | 41 | 1156 | 107 | 115 | 193 | 398 | 509 | 117 | 15 | 641 | 80 | 371 | 145 | 484 | 389 | 91 | 64 | 578 |
| HIRUDINEA | | | | | | | | | | | | | | | | | | | | |
| *Erpobdella octulata* | 3 | 5 | 5 | 8 | 0 | 8 | 1 | 0 | 1 | 9 | 4 | 0 | 9 | 1 | 4 | 0 | 3 | 19 | 1 | 0 |
| *Glossiphonia heteroclita* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Glossiphonia complanta* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Helobdella stagnalis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pisciola geometra* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| GASTROPODA | | | | | | | | | | | | | | | | | | | | |
| Hydrobidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bathyomphalus contortus* | 3 | 0 | 3 | 8 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 13 | 0 |
| *Acroloxus lacustris* | 0 | 0 | 4 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bithynia* | 5 | 21 | 25 | 8 | 1 | 39 | 28 | 0 | 9 | 36 | 16 | 0 | 8 | 24 | 12 | 0 | 9 | 7 | 9 | 0 |
| *Gyraulus* | 8 | 28 | 11 | 70 | 3 | 9 | 15 | 0 | 19 | 15 | 4 | 0 | 0 | 0 | 1 | 0 | 4 | 5 | 1 | 0 |
| *Radix* | 5 | 83 | 20 | 31 | 33 | 65 | 36 | 0 | 11 | 13 | 24 | 0 | 4 | 7 | 8 | 0 | 9 | 4 | 3 | 0 |
| *Myxas glutinosa* | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Planorbis* | 0 | 0 | 0 | 0 | 1 | 8 | 0 | 0 | 5 | 0 | 15 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Valvata* | 0 | 0 | 0 | 0 | 0 | 3 | 11 | 8 | 0 | 1 | 5 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 |
| *Lymnea stagnalis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| *Physa* | 0 | 3 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Armiger* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BIVALVIA | | | | | | | | | | | | | | | | | | | | |
| *Anodonta* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pisidium* | 0 | 0 | 0 | 8 | 0 | 0 | 36 | 0 | 0 | 0 | 1 | 16 | 0 | 8 | 1 | 8 | 1 | 0 | 11 | 23 |
| *Sphaerium* | 0 | 0 | 1 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| CRUSTACEA | | | | | | | | | | | | | | | | | | | | |
| *Pallasea quadrispinosa* | 0 | 0 | 4 | 8 | 1 | 0 | 5 | 0 | 0 | 1 | 4 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 7 | 8 |
| *Monoporeia affinis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Asellus aquaticus* | 96 | 267 | 3 | 16 | 59 | 329 | 124 | 0 | 129 | 16 | 32 | 0 | 11 | 119 | 59 | 0 | 95 | 55 | 99 | 8 |
| ARACHNIDA | | | | | | | | | | | | | | | | | | | | |
| Acari | 3 | 4 | 11 | 16 | 13 | 5 | 8 | 0 | 19 | 41 | 47 | 0 | 3 | 12 | 7 | 0 | 3 | 11 | 5 | 0 |
| ODONATA | | | | | | | | | | | | | | | | | | | | |
| *Corduliidae sp.* | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| EPHEMEROPTERA | | | | | | | | | | | | | | | | | | | | |
| *Ephemera vulgata* | 0 | 1 | 0 | 39 | 0 | 0 | 3 | 8 | 0 | 0 | 3 | 39 | 0 | 0 | 0 | 39 | 0 | 1 | 0 | 39 |
| *Caenis lactea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 1 | 3 | 16 |
| *Caenis luctuosa* | 0 | 5 | 0 | 31 | 0 | 0 | 13 | 0 | 0 | 0 | 4 | 0 | 0 | 3 | 0 | 8 | 0 | 1 | 0 | 0 |
| *Caenis horaria* | 0 | 3 | 0 | 8 | 8 | 13 | 28 | 16 | 13 | 5 | 4 | 23 | 0 | 60 | 32 | 39 | 29 | 9 | 37 | 23 |
| *Centroptilum luteolum* | 3 | 3 | 3 | 0 | 1 | 4 | 15 | 0 | 3 | 5 | 16 | 0 | 0 | 15 | 11 | 0 | 5 | 3 | 19 | 0 |
| *Leptophlebia sp.* | 1 | 25 | 0 | 0 | 5 | 1 | 28 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| *Paraleptophlebia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Baetis fuscatus* | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Heptagenia dalecarlica* | 0 | 1 | 0 | 0 | 12 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Heptagenia fuscogrisea* | 4 | 4 | 1 | 0 | 15 | 0 | 0 | 0 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cloeon dipterum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |

# Appendix 2 continues. Average densities (ind $m^{-2}$) of the taxa at each depth in all the sites

| Sample | K1 | | | | K2 | | | | K3 | | | | K4 | | | | K5 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek | 0.5 | 1 | 2 | Ek |
| PLECOPTERA | | | | | | | | | | | | | | | | | | | | |
| *Nemoura* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Leuctra fusca* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Diura bicaudata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| DIPTERA | | | | | | | | | | | | | | | | | | | | |
| Chironomidae | 57 | 87 | 67 | 281 | 241 | 153 | 333 | 617 | 473 | 83 | 41 | 2219 | 245 | 537 | 495 | 1539 | 161 | 212 | 832 | 1273 |
| Ceratopogonidae | 1 | 15 | 3 | 47 | 20 | 4 | 4 | 47 | 15 | 16 | 3 | 234 | 8 | 1 | 32 | 180 | 33 | 63 | 48 | 133 |
| *Brachycera sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| COLEOPTERA | | | | | | | | | | | | | | | | | | | | |
| *Oulimnius tuberculatus* | 59 | 179 | 29 | 8 | 143 | 128 | 51 | 0 | 63 | 409 | 89 | 8 | 0 | 8 | 28 | 0 | 187 | 49 | 1 | 0 |
| *Normandia nites* | 0 | 8 | 1 | 8 | 4 | 5 | 8 | 0 | 4 | 80 | 20 | 0 | 3 | 0 | 3 | 0 | 187 | 49 | 1 | 0 |
| *Elmis aena* | 0 | 0 | 0 | 0 | 4 | 1 | 3 | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 |
| Gyrinidae | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 5 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Gyrinus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 13 | 1 | 0 | 0 |
| Dytiscidae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Haliplidae sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Hydroporinae sp. | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Nebriporus* | 0 | 0 | 0 | 0 | 0 | 4 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 |
| *Platambus sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 3 | 0 | 4 | 0 |
| NEUROPTERA | | | | | | | | | | | | | | | | | | | | |
| Sisyridae sp. | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| HETEROPTERA | | | | | | | | | | | | | | | | | | | | |
| Corixidae | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 108 | 4 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| TRICHOPTERA | | | | | | | | | | | | | | | | | | | | |
| *Hydroptila sp.* | 51 | 33 | 15 | 0 | 47 | 59 | 1 | 0 | 79 | 19 | 0 | 0 | 69 | 11 | 0 | 0 | 69 | 0 | 0 | 0 |
| *Oxyethira sp.* | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 8 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 |
| *Polycentropus flavomaculatus* | 3 | 19 | 8 | 0 | 15 | 7 | 3 | 0 | 9 | 0 | 0 | 0 | 4 | 3 | 0 | 0 | 16 | 0 | 1 | 0 |
| *Mystacides sp.* | 1 | 3 | 0 | 39 | 0 | 4 | 12 | 0 | 1 | 1 | 5 | 0 | 0 | 4 | 3 | 0 | 1 | 3 | 0 | 0 |
| *Athripsodes cinereus* | 37 | 55 | 17 | 31 | 24 | 120 | 76 | 0 | 11 | 41 | 20 | 16 | 15 | 23 | 17 | 0 | 15 | 19 | 48 | 8 |
| *Ceraclea nigronervosa* | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 8 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ceraclea annulicornis* | 7 | 8 | 5 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ceraclea albimacula* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lepidostoma hirtum* | 9 | 16 | 0 | 0 | 1 | 3 | 0 | 0 | 19 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Ecnomus tenellus* | 0 | 0 | 9 | 8 | 0 | 17 | 44 | 0 | 0 | 9 | 12 | 16 | 11 | 13 | 33 | 8 | 1 | 7 | 23 | 31 |
| *Molanna albicans* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 16 | 0 | 0 | 1 | 16 |
| *Molanna angustata* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 8 | 0 | 1 | 13 | 0 |
| *Molanna submarginalis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 8 |
| *Leptoceridae sp.* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cyrnus flavidus* | 0 | 1 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Cyrnus trimaculutus* | 0 | 0 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 1 | 7 | 8 |
| *Tinodes waeneri* | 0 | 1 | 3 | 0 | 0 | 4 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 27 | 5 | 0 | 1 | 13 | 16 | 8 |
| *Oecetis testacea* | 0 | 4 | 3 | 0 | 5 | 1 | 7 | 0 | 1 | 3 | 3 | 0 | 0 | 1 | 0 | 8 | 0 | 3 | 0 | 0 |
| *Oecetis ochracea* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 |
| *Oecetis sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Neureclipsis bimaculata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Goera pilosa* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Hydropsyche contubernalis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chaetopteryx villosa* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Apatania muliebris* | 0 | 1 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Apatania sp.* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| Limnephilidae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SUM | 388 | 991 | 313 | 1851 | 785 | 1131 | 1111 | 1109 | 1523 | 955 | 399 | 3258 | 489 | 1264 | 913 | 2359 | 1268 | 640 | 1279 | 2187 |

## Appendix 2 continues. Average densities (ind $m^{-2}$) of the taxa at each depth in all the sites

| **Sample** | **S3** | | |
|---|---|---|---|
| | 0.5 | 1 | Ek |
| PLATYHELMINTHES | 0 | 1 | 8 |
| NEMATODA | 3 | 15 | 117 |
| OLIGOCHAETA | 389 | 91 | 1914 |
| HIRUDINEA | | | |
| *Erpobdella octulata* | 3 | 8 | 8 |
| *Glossiphonia heteroclita* | 0 | 0 | 0 |
| *Glossiphonia complanta* | 0 | 3 | 0 |
| *Helobdella stagnalis* | 0 | 0 | 8 |
| *Pisciola geometra* | 0 | 0 | 0 |
| GASTROPODA | | | |
| Hydrobidae | 0 | 0 | 0 |
| *Bathyomphalus contortus* | 9 | 16 | 0 |
| *Acroloxus lacustris* | 1 | 1 | 0 |
| *Bithynia* | 1 | 1 | 39 |
| *Gyraulus* | 11 | 23 | 23 |
| *Radix* | 4 | 53 | 23 |
| *Myxas glutinosa* | 0 | 0 | 0 |
| *Planorbis* | 0 | 0 | 0 |
| *Valvata* | 0 | 5 | 31 |
| *Lymnea stagnalis* | 0 | 0 | 0 |
| *Physa* | 0 | 0 | 0 |
| *Armiger* | 9 | 48 | 8 |
| BIVALVIA | | | |
| *Anodonta* | 0 | 0 | 0 |
| *Pisidium* | 3 | 15 | 8 |
| *Sphaerium* | 0 | 0 | 0 |
| CRUSTACEA | | | |
| *Pallasea quadrispinosa* | 0 | 4 | 0 |
| *Monoporeia affinis* | 0 | 0 | 0 |
| *Asellus aquaticus* | 39 | 187 | 8 |
| ARACHNIDA | | | |
| Acari | 8 | 17 | 31 |
| ODONATA | | | |
| *Corduliidae sp.* | 0 | 0 | 0 |
| EPHEMEROPTERA | | | |
| *Ephemera vulgata* | 0 | 1 | 39 |
| *Caenis lactea* | 1 | 1 | 0 |
| *Caenis luctuosa* | 5 | 1 | 31 |
| *Caenis horaria* | 9 | 49 | 102 |
| *Centroptilum luteolum* | 0 | 8 | 0 |
| *Leptophlebia sp.* | 5 | 21 | 0 |
| *Paraleptophlebia* | 0 | 1 | 0 |
| *Baetis fuscatus* | 0 | 0 | 0 |
| *Heptagenia dalecarlica* | 5 | 0 | 0 |
| *Heptagenia fuscogrisea* | 12 | 29 | 16 |
| *Cloeon dipterum* | 0 | 0 | 0 |

| | 0.5 | 1 | Ek |
|---|---|---|---|
| PLECOPTERA | | | |
| *Nemoura* | 4 | 0 | 0 |
| *Leuctra fusca* | 5 | 12 | 0 |
| *Diura bicaudata* | 0 | 1 | 0 |
| DIPTERA | | | |
| Chironomidae | 371 | 347 | 906 |
| Ceratopogonidae | 7 | 0 | 86 |
| *Brachycera sp.* | 0 | 0 | 0 |
| COLEOPTERA | | | |
| *Oulimnius tuberculatus* | 20 | 92 | 8 |
| *Normandia nites* | 0 | 0 | 16 |
| *Elmis aena* | 5 | 4 | 0 |
| Gyrinidae | 0 | 0 | 0 |
| *Gyrinus sp.* | 0 | 0 | 0 |
| Dytiscidae | 0 | 0 | 0 |
| Haliplidae sp. | 0 | 0 | 0 |
| Hydroporinae sp. | 0 | 0 | 0 |
| *Nebriporus* | 0 | 0 | 0 |
| *Platambus sp.* | 0 | 0 | 0 |
| NEUROPTERA | | | |
| Sisyridae sp. | 0 | 0 | 0 |
| HETEROPTERA | | | |
| Corixidae | 0 | 0 | 0 |
| TRICHOPTERA | | | |
| *Hydroptila sp.* | 92 | 17 | 0 |
| *Oxyethira sp.* | 0 | 0 | 0 |
| *Polycentropus flavomaculatus* | 1 | 1 | 0 |
| *Mystacides sp.* | 0 | 3 | 0 |
| *Athripsodes cinereus* | 3 | 28 | 23 |
| *Ceraclea nigronervosa* | 0 | 3 | 0 |
| *Ceraclea annulicornis* | 0 | 4 | 0 |
| *Ceraclea albimacula* | 0 | 0 | 0 |
| *Lepidostoma hirtum* | 15 | 3 | 0 |
| *Ecnomus tenellus* | 0 | 39 | 31 |
| *Molanna albicans* | 0 | 0 | 0 |
| *Molanna angustata* | 0 | 0 | 0 |
| *Molanna submarginalis* | 0 | 0 | 0 |
| *Leptoceridae sp.* | 0 | 0 | 16 |
| *Cyrnus flavidus* | 0 | 0 | 0 |
| *Cyrnus trimaculutus* | 0 | 0 | 0 |
| *Tinodes waeneri* | 1 | 3 | 8 |
| *Oecetis testacea* | 4 | 7 | 0 |
| *Oecetis ochracea* | 0 | 0 | 0 |
| *Oecetis sp.* | 0 | 0 | 0 |
| *Neureclipsis bimaculata* | 0 | 0 | 0 |
| *Goera pilosa* | 0 | 1 | 8 |
| *Hydropsyche contubernalis* | 0 | 0 | 0 |
| *Chaetopteryx villosa* | 0 | 0 | 0 |
| *Apatania muliebris* | 0 | 0 | 0 |
| *Apatania sp.* | 11 | 4 | 0 |
| Limnephilidae | 0 | 0 | 0 |
| SUM | 1057 | 1169 | 3515 |